ADVANCES IN MARINE BIOLOGY

Volume 44

A. J. Southward
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Advances in MARINE BIOLOGY

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A Synthesis of Growth Rates in Marine Epipelagic Invertebrate Zooplankton

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We present the most extensive study to date of globally compiled and analysed weight-specific growth rates in marine epi-pelagic invertebrate metazoan zooplankton. Using specified selection criteria, we analyse growth rates from a variety of zooplanktonic taxa, including both holo- and mero-planktonic forms, from over 110 published studies. Nine principal taxonomic groups are considered, the copepods (number of individual data points (n) = 2,528); crustaceans other than copepods (n = 253); cnidarians (n = 77); ctenophores (n = 27); chaetognaths (n = 87); pteropods (n = 8); polychaetes (n = 12); thaliaceans (n = 88); and larvaceans (n = 91). The copepods are further examined by subdividing them into broadcasters or sac-spawning species, and as nauplii (N1–N6), copepodites (C1–C5) and adults (C6).

For each taxonomic group relationships between growth, temperature and body weight are examined using a variety of methods. Weight-specific growth tends to increase with increasing temperature and with decreasing body weight in the crustacean group. Growth does not relate to body weight in the case of chaetognaths and larvaceans, but does increase with temperature. In the cnidarian and ctenophore groups growth does not relate to temperature, but is negatively related to body size. For the thaliaceans growth increases with both increasing body weight and temperature. In the entire broadcasting copepod data set, weight-specific growth increases with increasing temperature and decreasing body weight. In sac-spawners, growth increases with increasing temperature, and increases with decreasing body weight at temperatures below 20°C, but decreases with body weight at temperatures above this.

Comparison between the different taxa shows important differences and similarities. Our extensive synthesis of data generally confirms that larvaceans, pteropods, cnidarians and ctenophores have rates of weight-specific growth that are typically greater than the copepods, chaetognaths and other crustaceans of similar carbon weight. For the cnidarians, ctenophores and larvaceans growth rates are almost always greater than the general relationship describing copepod growth, and are also at the upper limits or beyond the maximum rates for copepods of a similar weight. For the pteropods, growth rates are generally greater than those of copepods, although the data set was limited to a single carnivorous species in a single study (i.e. Clione limacina*). The thaliaceans have the highest growth rates for animals with body weights greater than around 1mg C* ind^{-1}*, with rates of up to 2.1* d^{-1} *for* Pegea bicaudata*. Whilst the larvaceans can achieve rates of 2* d^{-1} *in warm tropical waters (28°C), and as high as* $> 3\ d^{-1}$ *for* < 0.2 *mg C individual*$^{-1}$ *animals of* Oikopleura diocia*. These are possibly the highest rates every recorded in epi-pelagic metazoans. Reasons for the differences between taxonomic groups are discussed in relation to intrinsic and extrinsic factors and limitations.*

The importance of this investigation not only lies in it being the most comprehensive overview of patterns of growth to date, but because the data set highlight the gaps in measurements and current knowledge. We examine the inadequacies in the current data sets, and in the methods being used to measure growth and

production. Most of the data are for animals collected from coastal and estuarine waters, and it is clear that for a fuller understanding there is an urgent need for work in the open ocean, and for investigations outside temperate regions. There is also a need to explore the role of food availability, and how food concentrations in incubations, and under food saturation, relate to those experienced in the natural environment.

1. INTRODUCTION

Pelagic metazoan zooplankton are present throughout the world's oceans and are of fundamental importance to nutrient recycling and regenerated primary production (Banse, 1995), energy and material supply to higher trophic levels, and material flux to the ocean interior. The growth and production of marine metazoan zooplankton have been examined increasingly over the last 30 years, with the main emphasis being on the copepods. However, invertebrates other than copepods can dominate total abundance and biomass of meso- and macro-zooplankton (Alldredge, 1984; Longhurst, 1985) and play a major role in material processing and its subsequent fate (Wiebe *et al.*, 1979; Hopcroft and Roff, 1998a).

Growth is, of course, a key component of the physiology of marine metazoans, and hence in biogeochemical cycling. Yet analysis of growth measurements has lagged other physiological components such as respiration (e.g. Ikeda, 1985; Ikeda *et al.*, 2001), except in marine epi-pelagic copepods, for which a global analysis of *quasi-in situ* weight-specific growth rates has been completed recently (Hirst and Lampitt, 1998). Underlying patterns are emerging, but it is clear that there are important gaps in both our understanding of what controls these rates, and in our ability to predict them accurately.

Compilations of growth in other marine zooplanktonic taxa including crustaceans, chaetognaths, ctenophores, cnidarians, larvaceans and thaliaceans have been undertaken to varying extents in the past (e.g. Banse and Mosher, 1980; Banse, 1982; Alldredge, 1984; Ikeda *et al.*, 1985; Madin and Deibel, 1998). These compilations are not comprehensive as they were either taxonomically restricted, made no attempt to explore the role of temperature and body weight, or are now out of date because new information has been published. In the present investigation we make no effort to include vertebrate groups such as fish and fish larvae, for which growth rates have been analysed elsewhere (e.g. Fuiman, 1983; Kamler, 1992). Our aims are to:

1. Extract and analyse information from the published literature on rates of weight-specific growth of epi-pelagic invertebrate zooplankton, thus providing a framework of measurements.

2. Examine inter- and intra-specific patterns in growth with respect to temperature and body weight (as carbon).
3. Examine the possible causes and implications of these patterns.

2. METHODS

2.1. Data selection

We begin by defining the criteria for copepod data collection, and then move on to the other invertebrates. In selecting data for the copepods, we used an approach similar to that described by Hirst and Lampitt (1998), for animals that were experimentally enclosed to allow growth to be measured. For the other invertebrates we included data from a variety of methods. Given the diversity of taxa, it is not surprising that workers have used many different currently feasible or 'appropriate' methods. We incorporate data from investigations where there was no containment, and growth was measured from natural cohorts. We term this the 'Cohort approach'. We also include data from containment experiments, but separate these into two distinct forms, the 'Natural water approach', and the 'Controlled approach'. These categories of data selection are described in detail below.

2.1.1. *Copepods*

Data on experimentally determined growth rate for copepods were taken from the published literature. Data were selected from studies where populations are contained but where rates are expected to reflect closely those *in situ* (Hirst and Lampitt, 1998). Investigations included in the copepod growth compilation are those where recently caught wild individuals were incubated at near *in situ* temperatures (i.e. within 5°C of their environment) in natural seawater, sometimes pre-screened to remove larger predators and large organisms, over periods of ~1 day. If copepods were incubated for longer than a day, only studies where food was replaced regularly, or incubation volumes were large, were included. Investigations where there was some form of adult female selection on the basis of gonad maturity or reproductive output were excluded, unless this was corrected so that growth rates described all adult females regardless of their reproductive status. When females were selected on the basis of spermatophore attachment, results were included, although this could potentially cause some bias. Studies were also excluded if food was supplemented, or if the incubations were in filtered seawater (e.g. Plourde and Runge, 1993; Bautista *et al.*, 1994; Ohman and Runge, 1994). No selection of studies took place on the basis of the vertical location from which incubation water was taken (e.g. chlorophyll maxima, sea surface or several depths),

only that it was from within close horizontal proximity and collected simultaneously with the copepods. However, we have included the data of Park and Landry (1993), even though water collection and animal collection were separated by 3 km.

The data used for copepods were restricted to collections from the epi-pelagic zone (0–200 m). Deeper collections were excluded, but there were few growth estimates from animals collected below 200 m (although see Hirche, 1991). For inclusion in this synthesis, data on weight-specific growth rates (d^{-1}), temperature of incubation (°C), and either measurements or approximations of the body weights of the growing individuals must have been retrievable from the paper, or communicated personally by an author. In some instances no weights were measured or assumed for adult females in the original study, and in these cases absolute rates were extracted (e.g. eggs $female^{-1}$ d^{-1}). Weight-specific rates were then derived using average egg and/or adult carbon weights for the species (in preference from Kiørboe and Sabatini, 1995), or by using another indirect approach (see Appendix 1 for case by case details). When weights were given as dry or ash-free dry weight they were converted to carbon assuming this to be 40% of dry weight (Omori and Ikeda, 1984; Parsons *et al.*, 1984; Båmstedt, 1986), and ash-free dry weight was assumed to be 89% of dry weight (Båmstedt, 1986). Wherever possible, juvenile body weight was defined as the geometric mean weight during the period for which growth was derived. Weight-specific growth rates derived using dry or nitrogen weights were assumed to be equal to carbon-specific rates, but if carbon-specific rates were included these were used in preference.

The degree of growth and temperature averaging varies between studies. Although some of the data represent averages from more than one location and/or time, the majority were derived from collections at a single location and time. Some measurements represent averages of many individuals, whilst others represent values for individual animals. In some instances this may cause some bias for which we cannot correct. If zero growth values are presented, then these zero values will effectively be excluded using the $\log_{10}$ analysis we undertake here. However, if zero values were used by the original author to derive a population average, which is then not zero, then these will effectively be included.

All data were categorised into adult fecundity or juvenile body weight growth, and further divided into egg-broadcasting or sac-spawning species. In the literature different workers have used different equations to estimate growth, and such differences can result in inter-comparison problems. To standardise the data the juvenile copepod weight-specific growth (g_s d^{-1}) was assumed to be exponential and therefore defined as:

$$g_s = (\ln W_t - \ln W_o) / t \qquad (1)$$

where W_o is the weight of the animal at time zero, W_t is the weight of the animal at time t, and t is the time in days. Adult copepod weight-specific growth (g_R d^{-1})

was assumed to be linear in form, as eggs are shed and not added to the body weight of the female:

$$g_R = W_e / W_a \quad (2)$$

Where W_e is the weight of eggs produced over 24 hours, and W_a is the adult weight (our g_R term here is often referred to as G). The form of equation used is generally standardised within the broadcasters, as given above, but for the sac-spawning species there is some variation. An 'Incubation approach', identical to the broadcasters, has been used on sac-spawners (e.g. Bautista *et al*., 1994; Calbet *et al*., 1996; Saiz *et al*., 1997; Calbet and Agustí, 1999), usually with the incubation of those individuals found to lack eggs upon sorting. We include these results but appreciate that incubating egg-free females may cause some bias. Another method is for eggs and adults to be quantitatively collected using water bottles, filtered out, and then enumerated. Weight-specific growth is then derived from eggs to adult female abundance (E/F), the hatch rate of the eggs (HR d^{-1}), and the weight of the female and the egg (egg W/female W) (e.g. Nielsen and Sabatini, 1996).

$$g_R = (E / F) \times HR \times (\text{egg W} / \text{female W}) \quad (3)$$

Alternatively, growth may be derived in a similar fashion, but from the duration of egg development (D days) (e.g. McKinnon and Klumpp, 1998)

$$g_R = (E / (F \times D)) \times (\text{egg W} / \text{female W}) \quad (4)$$

Both these approaches are known as the 'Egg ratio method' [as originally developed for rotifers by Edmondson (1960, 1968)], and we include results from this approach for the sac-spawners. Sometimes the rate of egg hatching or the time between egg-sac production have been determined on individuals collected at a single temperature and then incubated at a range of temperatures. The resulting equations are then applied to seasonal data of *in situ* temperature and egg-adult abundance data (e.g. Uye and Sano, 1995), or by applying hatching rate vs. temperature relationships derived at one location to the same species at a different time in a different area (e.g. Sabatini and Kiørboe, 1994). We include such data, although appreciate this may not be the best approach as significant biases might be introduced (Andersen and Nielsen, 1997). Using these approaches we are making the assumption that adult body weight is in steady-state, this is an almost universal assumption in this field, but is not always valid (Hirst and McKinnon, 2001).

No results from the Egg ratio method were included for broadcasting species because rapid losses of free eggs have been found to occur in the natural environment (Beckman and Peterson, 1986; Liang *et al.*, 1994; Peterson and Kimmerer, 1994; Liang and Uye, 1996a, b), and this could result in large

underestimates of growth. Patchiness of eggs/adults could also cause severe over or underestimation of rates.

All copepod data, together with detailed notes on derivations, are given in Appendix 1. Species were divided on the basis of whether they represented broadcast- or sac-spawning species, and into the stage categories: N1–N6 nauplii (termed N), C1–C5 copepodites (C), and C6 adult females (A).

All data were divided on the basis of temperature into four 10°C temperature categories, i.e. > –10.0 to ≤ 0.0, > 0.0 to ≤ 10.0, > 10.0 to ≤ 20.0 and > 20.0 to ≤ 30.0°C. Growth rates in each band were adjusted to the mid-temperature i.e. –5, 5, 15, and 25°C, using a Q_{10} value of 3.0, a typical value for individual species of copepods [3.1 and 3.0 for *Eurytemora affinis* and *E. herdmani* respectively (Katona, 1970), *Oithona nana* 2.9 (Haq, 1965); *Oithona similis* 3.1 (Sabatini and Kiørboe, 1994), *Calanus glacialis* 2.9 (Hirche and Bohrer, 1987), *Acartia bifilosa* 2.3 and 1.4 (Koski and Kuosa, 1999)]. In fact our analyses are relatively insensitive to the Q_{10} value chosen, so long as this is within biologically reasonable boundaries. When the data set allowed, least-squares regression analysis (Type I) was completed on $\log_{10}$ weight-specific growth (as the dependent variable) against $\log_{10}$ body weight (as the independent variable). Only when more than one species was included was a regression completed. Regressions were completed for nauplii (N), copepodites (C) and adults (A) at each of the four mid-temperatures (–5, 5, 15 and 25°C) for each of the spawning types: broadcasters (B) and sac-spawners (S), and for all data within each spawning type (i.e. all broadcasters and all sac-spawners).

The influence of temperature on growth in copepods was explored by dividing the data into order of magnitude ranges of body carbon weight (i.e. 0.1–1.0, 1–10, 10–100, 100–1000 and 1000–10000 μg C individual^{-1}). Within each of these ranges we completed linear regressions of $\log_{10}$ weight-specific growth rate against temperature, but only when more than one species was included because our interest was in patterns within each taxon rather than those relating to a particular species.

To examine the roles of temperature and body weight together we undertook backwards stepwise-regression analyses on adult broadcasters (AB), adult sac-spawners (AS), copepodite broadcasters (CB) and sac-spawners (CS), and nauplii broadcasters (NB) and sac-spawners (NS). All broadcasting (AB + CB + NB) and sac-spawning stages (AS + CS + NS) were also examined, as was the entire data set including all stage and spawning types (AB + CB + NB + AS + CS + NS). The dependent variable was $\log_{10}$ weight-specific growth (g d^{-1}) and the independent variables were temperature (T°C) and $\log_{10}$ body weight (BW μg C individual^{-1}), F-to-enter was set at 4.0, and F-to-remove at 3.9. In those cases where neither of the independent variables was removed, multiple linear regressions relating $\log_{10}$ g to both temperature and $\log_{10}$ BW were completed. In those cases

where one of the independent variables was found not to add significantly to the prediction, then a linear regression was completed relating $\log_{10}$ g to the remaining independent variable.

2.1.2. *Other invertebrates*

Weight-specific growth rates of epi-pelagic metazoan zooplankton, other than copepods, were derived from published literature sources. We divided these measurements into three types. Firstly, the 'Cohort approach', where growth was calculated for natural populations from repeated measurements of field populations over intervals that were a small fraction of the total generation time of the animal. We excluded studies where there had been subsequent literature re-evaluation or strong published criticism of the authors' original cohort interpretation. Data from animals incubated *ex situ* were also included, but we divided these in two separate approaches. The first is the 'Natural water approach', defined as those studies where recently captured wild individuals were supplied food from non-concentrated natural seawater containing the prey, and temperature was fixed closely to that *in situ*. The second, the 'Controlled approach' was that in which there was greater investigator manipulation of the studied animals' environment, with one or more of the following occurring: their food environment was created from cultures or at concentrations set by the investigator (which may or may not have been described by the investigators as being representative of natural conditions); the incubation temperature was varied over a large range rather than being chosen to represent closely that in the natural environment at the time of collection; the animals were kept for long periods and the term 'wild-collected individuals' seemed inappropriate. We did not include any results in which individuals were intentionally starved of food as these describe negative growth rates under unnatural conditions that are not investigated here.

All growth rate values were defined as 'body weight increase' (S and g_S in Appendix 2) or 'reproductive output' (R and g_R in Appendix 2). Body weight increase is that where growth is expressed as an increase in body weight of an animal, including exuviae loss when possible. Reproductive output is that where growth is in the form of an output of young through asexual means or through gamete release. In most cases it was clear which form of growth was being measured. For example, with the cohort approach only the body weight growth term is included, although it was not always clear whether there was simultaneous reproductive growth (gamete or young output – our g_R term). We have attempted to define for each measurement whether total growth was being measured, or if only one component was measured and the other unknown. When growth was in the form of an increase in body mass, weight specific growth rates (g_s d^{-1}) were derived as previously given (Equation (1)),

and when given as a production to biomass ratios (P:B), these were converted to g_S as follows:

$$g_S = \ln(P:B+1) \quad (5)$$

When growth was an output of gametes or young (g_R d^{-1}) the total weight-specific growth was derived as given in Equation (2) above. If both body weight and reproductive growth occurred together, we derived a total growth rate (g_T d^{-1}) by the addition of the two terms:

$$g_T = g_S + g_R \quad (6)$$

We made no additions to the growth rates presented by individual authors. For example, if exuviae production was included in the body weight increase it was also included here, whereas if it was not then we made no addition. In larvaceans, house production can be an important contribution to total growth (Alldredge, 1976; Uye and Ichino, 1995; Hopcroft and Roff, 1998a; Tomita *et al*., 1999). However, as the data did not always directly include this (i.e. Paffenhöfer, 1976; Hopcroft *et al*., 1998a), these values may be underestimates. In the analyses of growth patterns that we performed, total growth is included whenever possible. When one of the two components was not known then we have used the single known component (whether somatic growth g_S or the output of young/gametes g_R) to represent total growth (g_T).

Species in an aggregated stage were excluded [e.g. *Thalia democtatica* (Heron and Benham, 1984; Tsuda and Nemoto, 1992)] unless it was possible to derive growth and body weight for the individuals rather than the aggregate as a whole, and in these cases we used individual rather than aggregated weights. We did this so as not to confuse the weight of individuals and their growth with the weight of a colony and its growth (the latter would give a very different and potentially confusing perspective). We included the meroplanktonic stages of benthic organisms and epibenthic organisms (e.g. *Calliopius laeviusculus*) if the species were commonly found in the water column, and not simply as a result of physical suspension from the benthos.

In some instances when using a cohort approach for a natural population, it was difficult to derive the temperature animals experienced over the period for which growth was being measured, accurately. Unless it was possible to ascribe a more specific temperature regime to the growing individuals, we simply derived an arithmetic mean of the maximum and minimum temperature. In the worse case we found differences in water temperature over which animals were migrating to be 13°C [i.e. upper 300 metre water column = 12 to 25°C in the study of Newbury (1978)]. For some animals it was clear that they would migrate below 200 m on a diel basis. In these cases we still included data so long as we had reasons for believing that the animals were spending much of their time, at the point of collection, in surface waters.

The taxonomic groupings into which we divided the invertebrate data were: crustaceans (excluding the copepods, which were analysed separately), chaetognaths, cnidarians, ctenophores, larvaceans, polychaetes, pteropods and thaliaceans. All data for the other invertebrates together with details on derivations are presented in Appendix 2. Data were examined using the same statistical methods and approaches described for the copepods above.

3. RESULTS

3.1. Copepods

In comparison to the data set of Hirst and Lampitt (1998), which included 952 values for the copepods, we have 2528 values with data from a greater diversity of environments (Table 1). Studies ranged from the tropics to the poles, with temperatures from –2.3 to 29.5°C, and body weights from 0.006 to 3,620 μg C individual^{-1}. The vast majority of data came from coastal and estuarine stations, although we also include data from oligotrophic regions and offshore sites (e.g. Calbet and Agustí, 1999). Broadcast-spawning adults dominate the data set (n = 1,597), with smaller contributions from the other groups, and the smallest contribution from nauplii of sac-spawners (n = 48).

Results from analyses of growth versus body weight are presented in Table 2 for each of the 10°C temperature groups (i.e. at the mid-temperatures –5, 5, 15 and 25°C). The data for broadcasters are shown in Figure 1, and for sac-spawners in Figure 2. For the broadcasters, linear regression analysis of $\log_{10}$ g (dependent variable) vs. $\log_{10}$ body weight (independent variable) shows significant negative relationships for the adult females and the copepodites, i.e. growth declined with increasing body weight. In the nauplii there was only sufficient data at 25 and 15°C to complete the regression analysis, and for the former the relationship was negative and significant, whilst the latter was not significant. When all the life stages of the broadcasters are considered together, the relationships were significant and showed a negative slope. The results for the sac-spawners were very different. When all sac-spawning data were considered together, the relationship was significant and positive at 5°C, not significant at 15°C, and significant and negative at 25°C. For adult sac-spawners at 5 and 15°C the relationship was positive and significant, whilst at 25°C it was negative and significant. For copepodite sac-spawners the slope was positive and significant at 15°C but not significant at 25°C, whilst for the nauplii at 15°C the relationship was not significant, but at 25°C the slope was negative and significant. When all data were considered together (i.e. all age classes and spawning types), in each temperature band the slope was found to be negative and significant. At –5, 5 and 15°C this resulted from the dominance of the adult broadcasters in the

Table 1 Summary of the number of species, data points, and ranges in the data compiled in this investigation.

Taxa	No. of data points	No. of species	Temperatue range (°C)		Wt range (µg C ind.$^{-1}$)		g range (d^{-1})		Mean g (d^{-1}) [S.D.]
			Min.	Max.	Min.	Max.	Min.	Max.	
Copepods	2,528	~69	–2.3	29.5	0.006	3,620	0.000	1.620	0.143 [0.209]
AB	1,597	~48	–2.3	29.4	0.440	3,620	0.000	1.620	0.111 [0.172]
CB	180	~14	7.6	28	0.042	72.1	0.003	1.257	0.466 [0.300]
NB	53	7	16.5	28	0.008	0.8	0.200	1.135	0.621 [0.212]
AB + CB + NB	1,830	~52	–2.3	29.4	0.008	3620	0.000	1.620	0.161 [0.231]
AS	576	~13	3	29.5	0.199	119.23	0.000	0.362	0.063 [0.080]
CS	79	~7	6.5	26	0.127	39.179	0.010	0.910	0.205 [0.149]
NS	48	7	6.5	28	0.006	0.480	0.088	0.748	0.339 [0.187]
AS + CS + NS	703	~19	3.0	29.5	0.006	119.23	0.000	0.910	0.098 [0.128]
Crustaceans[1]	253	12	0.5	25.6	2.54	64,172	–0.170	0.369	0.052 [0.062]
Chaetognaths	87	4	1.8	31	0.98	650.2	–0.013	0.410	0.103 [0.125]
Cnidarians	77	6	7.1	28	3.889	114,882	–0.069	0.740	0.157 [0.172]
Ctenophores	27	3	13	31	0.1	24,242	0.069	0.780	0.291 [0.233]
Larvaceans	91	5	13	28	0.012	3.312	0.570	3.312	1.940 [0.705]
Polychaetes	12	~5	—— 22 ——		0.4	1.3	0.150	0.310	0.233 [0.055]
Pteropods	8	1	—— 15 ——		161.3	1,784.6	0.208	0.504	0.370 [0.089]
Thaliaceans	88	7	11	26.5	4.0	34,868.4	0.029	2.201	0.529 [0.629]

[1]Excluding copepods. A = adult (C6 Female) C = copepodite (C1–C5), N = nauplii (N1–N6), B = broadcasting copepods, S = sac-spawning copepods.

Table 2 Linear regression analysis for the Copepoda group of $\log_{10}$ growth versus $\log_{10}$ body weight at each of the four temperature regimes.

Temp. (°C)	Stage	No. data points (No. zero values)	No. species	Weight range (µg C ind.$^{-1}$)	$\log_{10}$[g] vs. $\log_{10}$[BW] Intercept	Slope	r^2	P	$P < 0.05$
–5	AB	92 (12)	4	98.8–3620	–0.980	–0.607	0.0692	<0.02	*
5	AB	647 (77)	~21	2.5–3620	–1.113	–0.213	0.0419	<0.001	*
5	CB	13 (0)	1	1.1–72.1	–	–	–	–	–
5	ALL B	660 (77)	~21	1.1–3620	–1.108	–0.220	0.0455	<0.001	*
5	AS	162 (136)	~6	0.235–116.52	–1.649	+0.255	0.298	<0.001	*
5	CS	20 (0)	1	0.252–3.07	–	–	–	–	–
5	NS	1 (0)	1	0.171	–	–	–	–	–
5	ALL S	183 (136)	~6	0.171–116.52	–1.595	+0.223	0.243	<0.001	*
5	ALL S+B	843 (213)	~27	0.171–3620	–1.391	–0.0236	0.00093	>0.20	NS
15	AB	576 (30)	~29	1.21–219	–1.083	–0.159	0.0289	<0.001	*
15	CB	70 (0)	5	0.24–38.8	–0.532	–0.378	0.539	<0.001	*
15	NB	11 (0)	2	0.12–0.8	–0.512	+0.703	0.045	>0.50	NS
15	ALL B	657 (30)	~29	0.12–219	–0.947	–0.241	0.0744	<0.001	*
15	AS	129 (36)	~6	0.215–81.72	–1.346	+0.106	0.0496	<0.02	*

15	CS	34 (0)	3	0.46–4.419	–0.941	+0.456	0.159	<0.02	*
15	NS	14 (0)	~2	0.12–0.48	–1.031	–0.243	0.0432	>0.20	NS
15	ALL S	177 (36)	~7	0.12–81.72	–1.213	+0.0538	0.00915	>0.20	NS
15	ALL B+S	834 (66)	~36	0.12–219	–1.101	–0.118	0.0288	<0.001	*
25	AB	161 (2)	~20	0.44–160.71	–0.403	–0.646	0.244	<0.001	*
25	CB	97 (0)	~8	0.042–29.394	–0.404	–0.156	0.214	<0.001	*
25	NB	42 (0)	5	0.008–0.107	–0.788	–0.280	0.370	<0.001	*
25	ALL B	300 (2)	~23	0.008–160.71	–0.599	–0.311	0.280	<0.001	*
25	AS	110 (3)	~9	0.199–119.23	–1.059	–0.159	0.0684	<0.01	*
25	CS	25 (0)	~5	0.127–39.179	–0.560	–0.0316	0.00471	>0.50	NS
25	NS	33 (0)	5	0.006–0.364	–0.814	–0.187	0.556	<0.001	*
25	ALL S	168 (3)	~15	0.006–119.23	–0.939	–0.207	0.190	<0.001	*
25	ALL B+S	463 (5)	~38	0.006–160.71	–0.728	–0.246	0.191	<0.001	*

Number of data points does not include those that are zero or negative; these are indicated in brackets. Those with a dash represent groups for which regression analysis was not completed as only one species was contained within the data set. Values marked with an asterisk represent those for which the probability was < 0.05, NS – not significant (i.e. $P > 0.05$). Adult (A); Copepodite (C); Nauplii (N); Broadcaster (B); Sac-spawner (S).

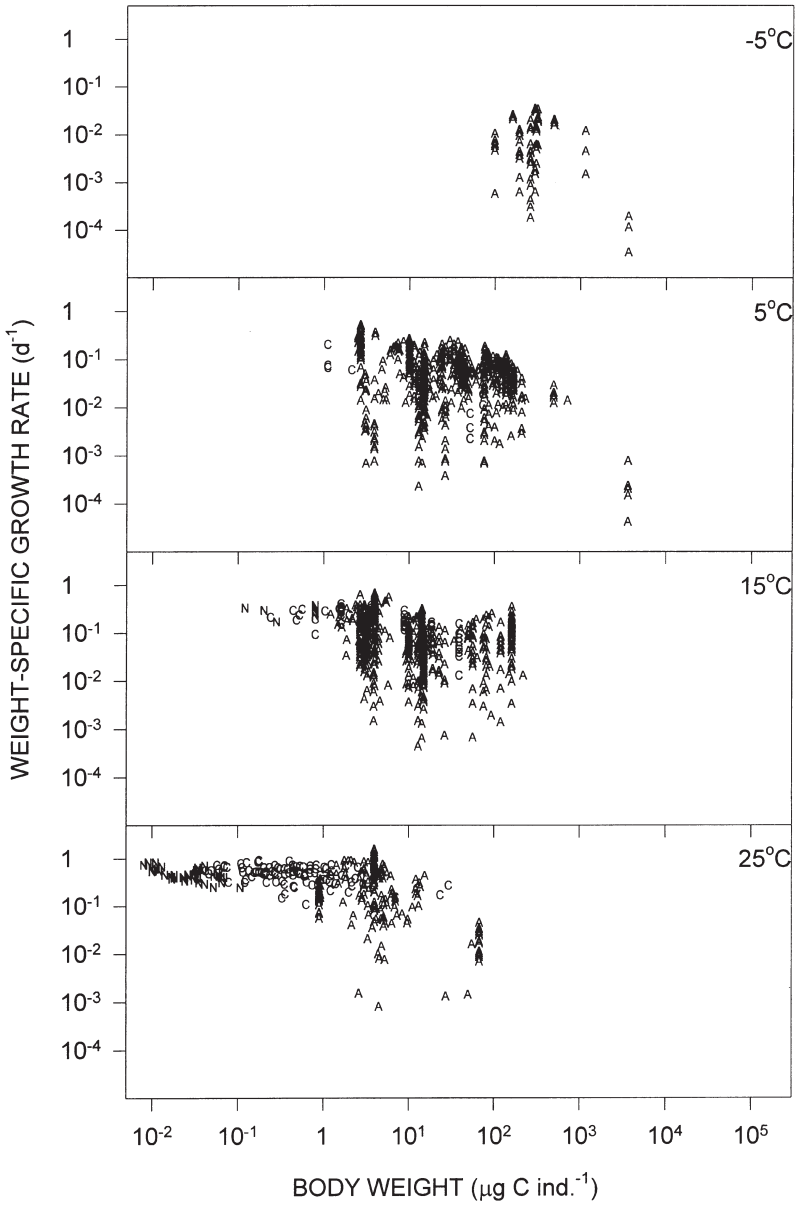

Figure 1 Measured weight-specific growth rates of broadcast-spawning copepods against body weight. Symbols: adult weight-specific fecundity (A), copepodite (C) and nauplii (N) weight-specific somatic growth. Data are divided into four temperature ranges and adjusted to a mid-temperature of each range (i.e. –5, 5, 15 and 25°C) using a Q_{10} of 3.0. See Table 2 for regression analyses results.

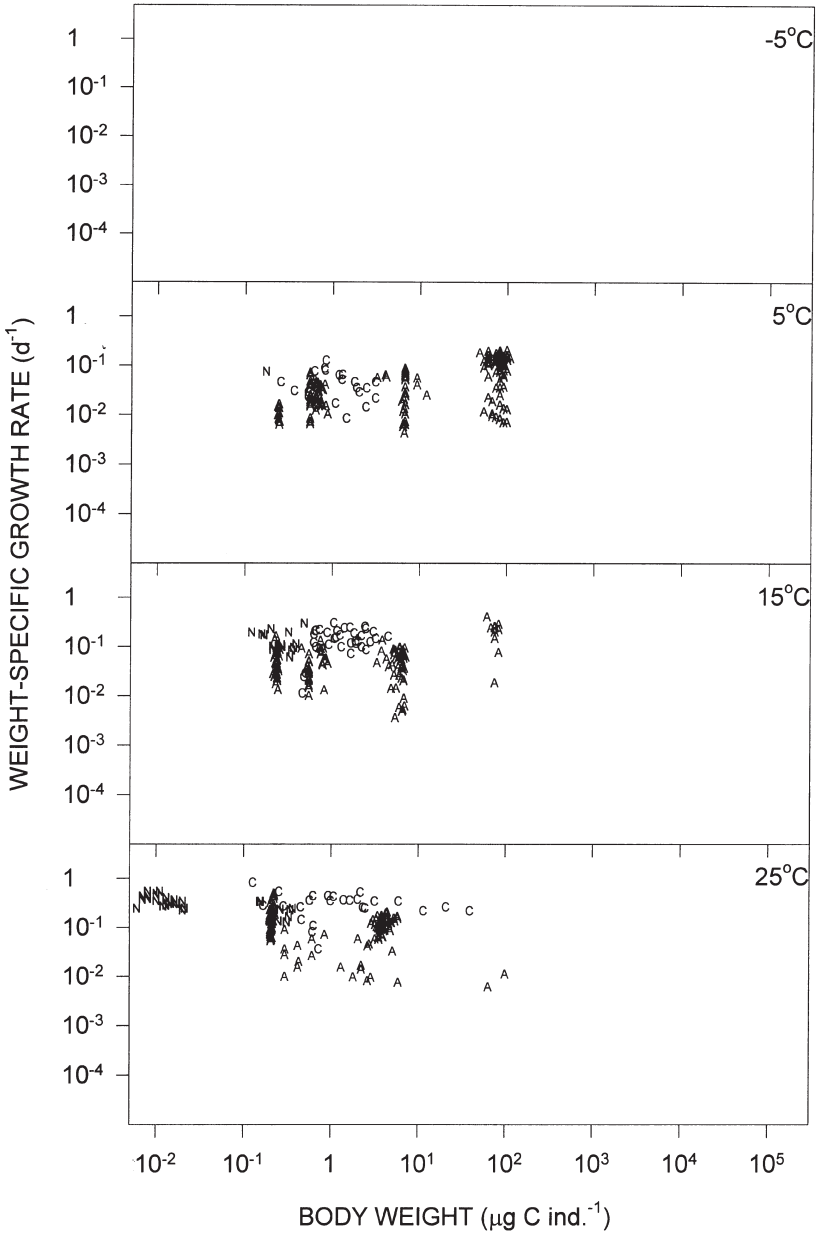

Figure 2 Measured weight-specific growth rates of sac-spawning copepods against body weight. Data are divided into four temperature ranges and adjusted to a mid-temperature of each range (i.e. –5, 5, 15 and 25°C) using a Q_{10} of 3.0. See Table 2 for regression analyses results. Symbols as in Figure 1.

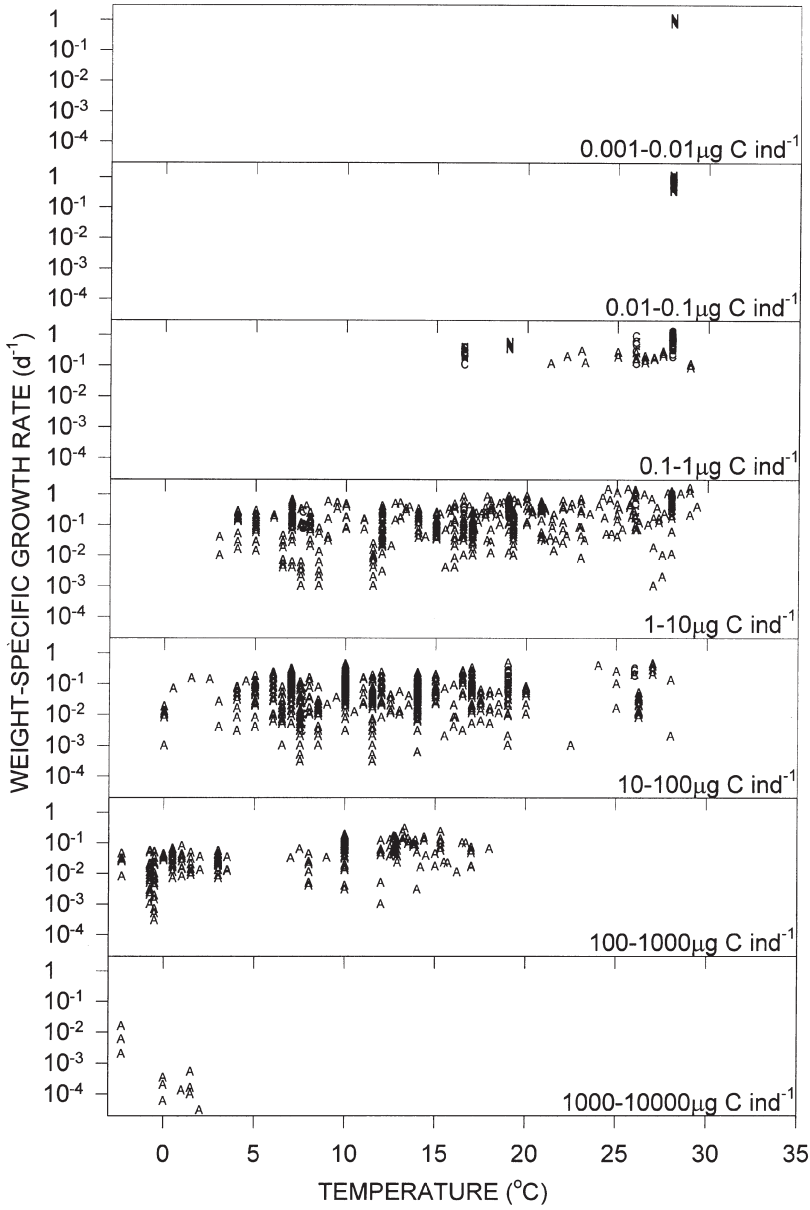

Figure 3 Comparisons for the broadcasting copepods of weight-specific growth as a function of temperature for order of magnitude body weight ranges (0.1–1.0 μg C individual^{-1}, 1–10 μg C individual^{-1}, 10–100 μg C individual^{-1}, 100–1000 μgC individual^{-1}, 1000–10 000 and 10 000–100 000 μgC individual^{-1}). See Table 3 for regression analyses results. Symbols as in Figure 1.

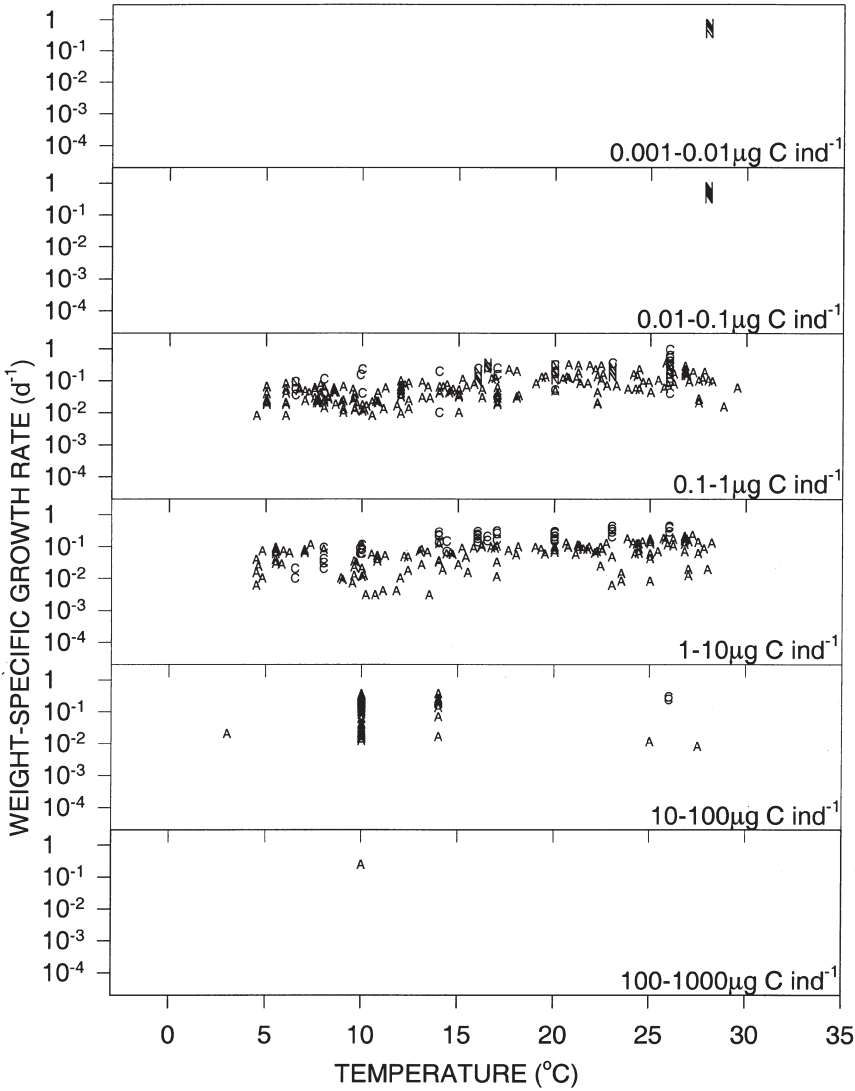

Figure 4 Comparisons for the sac-spawning copepods of weight-specific growth as a function of temperature for order of magnitude body weight ranges (0.1–1.0 µg C individual^{-1}, 1–10 µg C individual^{-1}, 10–100 µg C individual^{-1}, 100–1000 µg C individual^{-1}, 1000–10 000 and 10 000–100 000 µg C individual^{-1}). See Table 3 for regression analyses results. Symbols as in Figure 1.

Table 3 Linear regression analysis between $\log_{10}$ growth and temperature for orders of magnitude ranges in body weight for the copepoda. Those with a dash represent groups for which regression analysis was not completed as only one species was contained within the data set or there was no range in the temperature at which measurements had been made.

Weight (μg C ind^{-1})	Taxon	No. of data points (No. zero or –ve values)	No. of species range (°C)	Temp. (°C)	$\log_{10}$[g] vs. Temp. intercept	Slope	r^2	P	$P < 0.05$	Q_{10}
0.001–0.01	NB	5 (0)	1	28	–	–	–	–	–	–
	NS	10 (0)	2	28	–	–	–	–	–	–
	All B+S	15 (0)	3	28	–	–	–	–	–	–
0.01–0.1	CB	9 (0)	~1	28	–	–	–	–	–	–
	NB	39 (0)	5	28	–	–	–	–	–	–
	All B	48 (0)	~6	28	–	–	–	–	–	–
	NS	16 (0)	4	28	–	–	–	–	–	–
	All B+S	64 (0)	~10	28	–	–	–	–	–	–
0.1–1.0	AB	22 (0)	2	21.3–29	–0.697	–0.00139	1.88×10^{-4}	0.952	NS	0.97
	CB	70 (0)	~12	16.5–28	–1.275	+0.0390	0.363	<0.001	*	2.45
	NB	12 (0)	3	16–28	–0.423	+0.00220	0.00258	0.876	NS	1.05
	All B	104 (0)	~14	16.5–29	–0.978	+0.0242	0.107	<0.001	*	1.75
	AS	181 (0)	~4	4.5–29.5	–1.794	+0.0307	0.346	<0.001	*	2.03
	CS	32 (0)	~6	6.5–26	–1.441	+0.0327	0.287	0.002	*	2.12
	NS	25 (0)	3	6.5–26	–1.030	+0.0138	0.130	0.076	NS	1.37
	All S	238 (0)	~9	4.5–29.5	–1.784	+0.0361	0.357	<0.001	*	2.30

	All B+S	337 (0)	~23	4.5–29.5	−1.938	+0.0521	0.529	<0.001	*	3.32
1.0–10.0	AB	503 (21)	~22	3–29.4	−1.384	+0.0255	0.0746	<0.001	*	1.80
	CB	65 (0)	10	7.6–28	−0.999	+0.0265	0.389	<0.001	*	1.84
	All B	568 (21)	~28	3–29.4	−1.421	+0.0307	0.114	<0.001	*	2.03
	AS	133 (1)	~8	4.5–28.2	−1.721	+0.0240	0.167	<0.001	*	1.74
	CS	44 (0)	4	6.5–26	−1.721	+0.0543	0.703	<0.001	*	3.49
	All S	177 (1)	11	4.5–28.2	−1.664	+0.0279	0.176	<0.001	*	1.90
	All B+S	745 (22)	~39	3–29.4	−1.467	+0.0292	0.113	<0.001	*	1.96
10–100	AB	738 (80)	~26	0–28	−1.311	−0.00257	4.84×10^{-4}	0.551	NS	0.94
	CB	36 (0)	3	7.6–26	−2.178	+0.0637	0.566	<0.001	*	4.34
	All B	774 (80)	~26	0–28	−1.373	+0.00373	0.00110	0.357	NS	1.09
	AS	86 (167)	~3	3–27.5	−0.537	−0.0363	0.0514	0.036	*	0.43
	CS	3 (0)	1	26	–	–	–	–	–	
	All S	89 (167)	~3	3–27.5	−0.831	−0.00773	0.00447	0.534	NS	0.84
	All B+S	863 (247)	~29	0–28	−1.314	+0.00232	4.03×10^{-4}	0.556	NS	1.05
100–1000	AB	269 (20)	~10	−2.3–21.5	−1.967	+0.0601	0.350	<0.001	*	3.99
	AS	1 (7)	~3	10	–	–	–	–	–	–
	All B+S	270 (27)	~13	−2.3–21.5	−1.966	+0.0604	0.351	<0.001	*	4.02
1000–10 000	AB	12 (0)	1	−2.3–2	–	–	–	–	–	–

Number of data points does not include those that are zero or negative, which are indicated in brackets. Values marked with an asterisk represent those for which the probability was <0.05, NS – not significant (i.e. $P > 0.05$).

Table 4 Statistical results of regression (multiple linear and least squares) relating dependent variable weight-specific growth rate [$\log_{10}$ g (d^{-1})] to the independent variables temperature (T, °C) and/or $\log_{10}$ body weight (BW, µg C individual^{-1}). Multiple linear regressions only given in those cases where backwards stepwise-regression analysis demonstrated that both independent variables should be included (F-to-enter = 4.0 and F-to-remove = 3.9). For those data sets in which an independent variable did not statistically significantly add to prediction, results from linear regression using the remaining independent variable [ind. var.] are given.

Taxon	No. of data points (No. zero or –ve values)	No. of species	Backwards-stepwise-regression	Multiple linear regression[1] a	b	c	R^2	*P* ($\log_{10}$ BW; T)	Linear regression[2] a	b	ind. var.	R^2	*P*
Copepods:													
AB	1,476 (121)	~48	both included	+0.0232	–0.285	–1.196	0.220	(<0.001; <0.001)	–	–	–	–	–
CB	180 (0)	~14	both included	+0.0352	–0.233	–1.230	0.700	(<0.001; <0.001)	–	–	–	–	–
NB	53 (0)	7	T removed	–	–	–	–		–0.418	–0.141	$\log_{10}$ BW	0.335	<0.001
All B	1,709 (121)	~52	both included	+0.0271	–0.287	–1.222	0.370	(<0.001; <0.001)	–	–	–	–	–
AS	401 (175)	~13	both included	+0.0223	+0.177	–1.644	0.179	(<0.001; <0.001)	–				
CS	79 (0)	~7	$\log_{10}$ BW removed	–	–	–	–		–1.545	+0.0408	T	0.459	<0.001
NS	48 (0)	7	both included	+0.0138	–0.252	–1.185	0.757	(<0.001; 0.017)	–	–	–	–	–
All S	528 (175)	~19	both included	+0.0324	+0.0657	–1.647	0.199	(0.002; <0.001)	–	–	–	–	–
All B+S	2,232 (296)	~69	both included	+0.0345	–0.128	–1.529	0.297	(<0.001; <0.001)	–	–	–	–	–

[1] $\log_{10}$ g = a[T] + b[$\log_{10}$ BW] + c
[2] $\log_{10}$ g = a + b[ind. var.]

data set. It is clear from Figures 1 and 2 that there is a great degree of scatter in the growth rates at any given temperature and body weight. Much of the scatter probably reflects food quality and/or quantity, and life history status (e.g. proportion going in to diapause, proportion of adult females not producing eggs).

Growth rates versus temperature are presented in Figures 3 and 4 for the broadcasters and sac-spawners respectively. Results from the linear regression analysis are given in Table 3. In all cases where the relationship was found to be significant the slope of the relationship was positive, i.e. growth increased as temperature increased. In seven instances the tested relationship was not significant, viz: for adult and nauplii broadcasters and nauplii sac-spawners of body weight 0.1–1.0 µg C individual^{-1}. However, data were very limited in all these cases. In the body weight range 10–100 µg C individual^{-1}, adult broadcasters and the entire sac-spawning groups showed non-significant relationships.

Table 4 shows the results from the backwards stepwise regression analyses. Except in two cases, copepod $\log_{10}$ growth was found to be dependent upon both $\log_{10}$ body weight and temperature. The exceptions were for broadcaster nauplii where temperature was removed (i.e. growth was temperature independent), and sac-spawning copepodites, for which $\log_{10}$ body weight was removed, (i.e. growth was body-weight independent). Whereas growth declines with increasing body weight for all the broadcasting groups and the nauplii of sac-spawners, it increases for the adult sac-spawner groups, and is not found to add significantly in the case of the copepodites of sac-spawners.

In conclusion, copepod growth appears to be generally temperature-dependent, with growth increasing as temperature increases. With respect to body weight however, patterns are less clear. Growth declined with body weight for all the broadcasting groups, but increased for the adult sac-spawners.

3.2. Other invertebrates

Table 1 summarises the number of species, data points and weight ranges of animals for which data are included. A total of 643 values was found for planktonic invertebrates other than copepods. Crustaceans dominated these data (n = 253) followed by larvaceans (n = 91), thaliaceans (n = 88) and chaetognaths (n = 87). The temperature ranges over which data were included for each of the groups always exceeded 15.5°C, except in the case of polychaetes and pteropods for which growth measurements were at single temperatures. Body weight ranges within each of the groups exceeded two orders of magnitude, with the exception of the polychaetes and pteropods. In many instances body weight ranges exceed 4 orders of magnitude, e.g. for crustaceans, cnidarians, ctenophores and thaliaceans. Table 1 demonstrates the range in growth values for each of the taxonomic groups. Without Q_{10} correction the highest rates within each of the taxonomic groups are 1.620 d^{-1} for the copepod *Acartia tonsa* as adult female egg production

(McManus and Foster, 1998), 0.369 d^{-1} for the crustacean *Panopeus herbstii* (Epifanio *et al*., 1994), 0.410 d^{-1} for the chaetognath *Sagitta hispida* (Reeve and Walter, 1976), 0.740 d^{-1} for the cnidarian *Chrysaora quinquecirrha* (Olesen *et al*., 1996), 0.780 d^{-1} for the ctenophore *Mnemiopsis mccradyi* (Reeve and Baker, 1975), 3.312 d^{-1} for the larvacean *Oikopleura dioica* (Hopcroft *et al*., 1998a), 0.310 d^{-1} for the polychaete *Polydora* spp. (Hansen, 1999), 0.504 d^{-1} for the carnivorous pteropod *Clione limacina* (Conover and Lalli, 1974) and 2.201 d^{-1} for the thaliacean *Pegea bicaudata* [Madin unpublished data – as presented in Madin and Deibel (1998)].

Table 5 describes relationships between $\log_{10}$ weight-specific growth and $\log_{10}$ body weight over each of the 10°C temperature regimes for each of the taxonomic groups (Figure 5). For crustaceans the slope of $\log_{10}$ weight-specific growth vs. $\log_{10}$ body weight was significant and negative at 5 and 15°C, whilst at 25°C the relationship was not significant. For chaetognaths the relationship was significant and negative at 25°C but not significant at 15°C, and for the cnidarians the relationship was significant and negative at 15°C, but significant and positive at 25°C. For ctenophores the relationship was negative and significant at 15°C, whilst for the larvaceans at 25°C the relationship was not significant. There were two instances when the relationship was both significant and had a positive slope, i.e. growth increased with body weight, the polychaetes at 25°C, although the compiled data come from a single study in a single location by Hansen (1999), and the thaliaceans at 15°C. The main reason for this positive slope in the thaliaceans was that the growth rates of the smaller doliolid *Dolioletta gegenbauri* and the salp *Thalia democratica* were much lower than the larger thaliacean salp species: *Cyclosalpa affinis*, *Cyclosalpa backeri*, *Ihlea asymmetrica*, *Pegea bicaudata* and *Pegea confederata*.

In several cases it was not possible to regress $\log_{10}$ growth against temperature because we completed this analysis only when there was more than one species present in the data set, and when there was a range in the temperature at which measurements had been made (Table 6). Data are presented graphically in Figure 6. In eleven cases there was no significant relationship ($P > 0.05$). Relationships were significant and the slope positive in 19 cases, i.e. growth rates increased with increasing temperature. Only in two cases was there a significant negative relationship, for the cnidarians with body weights 1–10 mg C $individual^{-1}$, and the crustaceans with body weights 10–100 mg C $individual^{-1}$.

Table 7 describes the results from the backwards stepwise regression and multiple linear regressions for the other invertebrate groups. In two cases $\log_{10}$ body weight was removed from the analysis as it did not add significantly to the relationship, i.e. for chaetognaths and larvaceans, and in these two cases temperature was significantly and positively related to growth. In the case of ctenophores and cnidarians temperature was found not to add significantly and was removed, possibly a result of insufficient data. In these cases weight-specific growth was negatively related to body weight.

Table 5 Linear regression analysis between $\log_{10}$ growth and $\log_{10}$ body weight over each of the four temperature regimes for each of the taxa. Those with a dash represent groups for which regression analysis was not completed as only one species was contained within the data set.

Temp. (°C)	Taxon	No. data points (No. zero or –ve values)	No. of species	Weight range (µg C ind.$^{-1}$)	$\log_{10}$[g] vs. $\log_{10}$[BW] Intercept	Slope	r^2	P	$P<0.05$
5	Crustaceans[1]	120 (8)	6	2.8–64172	–0.837	–0.313	0.478	<0.001	*
15	Crustaceans[1]	109 (6)	7	2.54–15955	–0.458	–0.336	0.210	<0.001	*
25	Crustaceans[1]	10 (0)	2	3.3–1639.5	–0.663	–0.0725	0.114	>0.20	NS
5	Chaetognaths	43 (0)	1	20.8–650.2	–	–	–	–	–
15	Chaetognaths	11 (1)	2	5.28–70	–2.176	+0.227	0.0208	>0.50	NS
25	Chaetognaths	30 (2)	2	0.98–238.42	–0.322	–0.345	0.184	<0.02	*
5	Cnidarians	10 (0)	1	6.5–646.3	–	–	–	–	–
15	Cnidarians	37 (3)	3	13.4–114882	–0.189	–0.233	0.434	<0.001	*
25	Cnidarians	26 (1)	3	3.889–5934	+0.0723	–0.485	0.672	<0.001	*
15	Ctenophores	12 (0)	2	0.1–10262	–0.331	–0.149	0.435	<0.02	*
25	Ctenophores	15 (0)	1	1.72–24242	–	–	–	–	–
15	Larvaceans	11 (0)	1	0.08–3.77	–	–	–	–	–
25	Larvaceans	80 (0)	5	0.012–0.721	+0.138	–0.0201	0.00445	>0.50	NS
25	Polychaetes	12 (0)	~5	0.4–1.3	–0.486	+0.409	0.514	<0.01	*
15	Pteropods	8 (0)	1	161.3–1784.6	–	–	–	–	–
15	Thaliaceans	57 (0)	4	4–10913.8	–0927	+0.048	0.175	<0.002	*
25	Thaliaceans	31 (0)	4	5.0–34868.4	–0.504	+0.145	0.114	>0.05	NS
5	All groups[1]	173 (8)	8	2.8–64172	–0.870	–0.307	0.437	<0.001	*
15	All groups[1]	245 (10)	20	0.08–114882	–0.674	–0.171	0.114	<0.001	*
25	All groups[1]	204 (3)	~21	0.0125–34868	–0.168	–0.166	0.280	<0.001	*

Number of data points does not include those that are zero or negative; these are indicated in brackets. Values marked with an asterisk represent those for which the probability was < 0.05, NS – not significant (i.e. $P > 0.05$). [1]Excluding copepods.

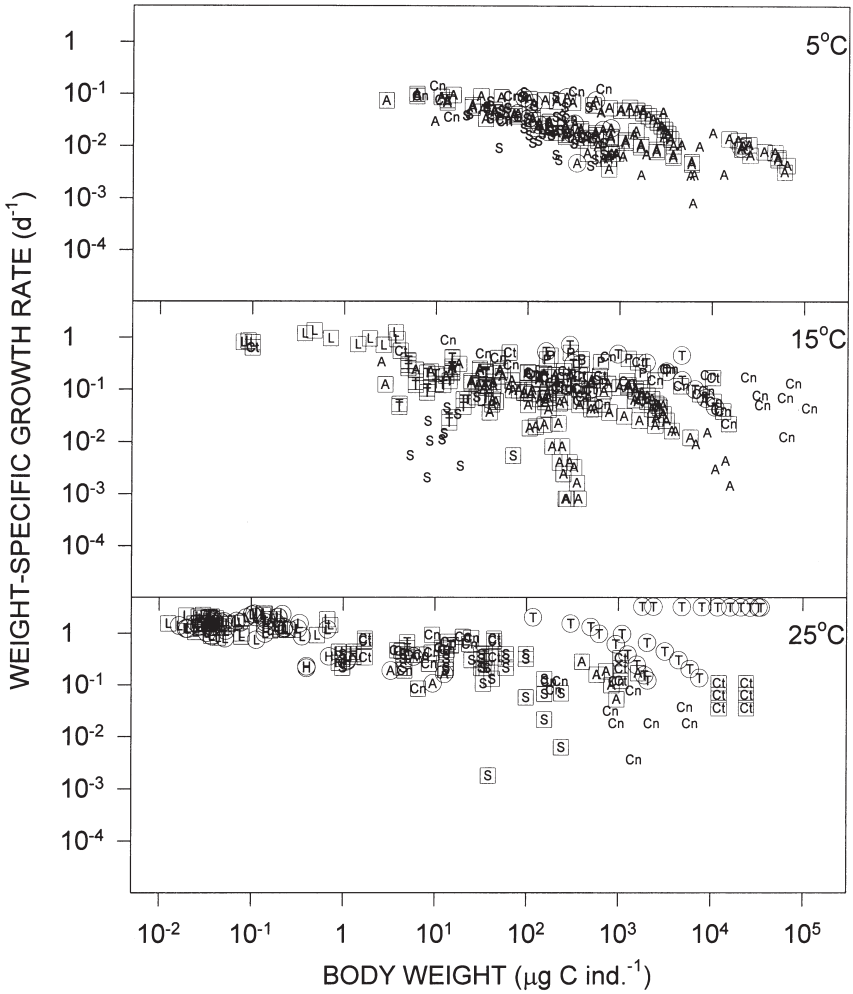

Figure 5 Measured weight-specific growth rates of different pelagic organisms against body weight. Symbols: crustaceans other than copepods (A), chaetognaths (S), cnidarians (Cn), ctenophores (Ct), larvaceans (L), thaliaceans (T), polychaetes (H) and pteropods (P). Data are divided into three temperature ranges and adjusted to a mid-temperature of each range (i.e. 5, 15 and 25°C) using a Q_{10} of 3.0. Taxon symbols within circles are from the 'Natural water approach', those in squares are for the 'Controlled approach' and those in neither are from the 'Cohort approach'. See Table 5 for results of regression analysis.

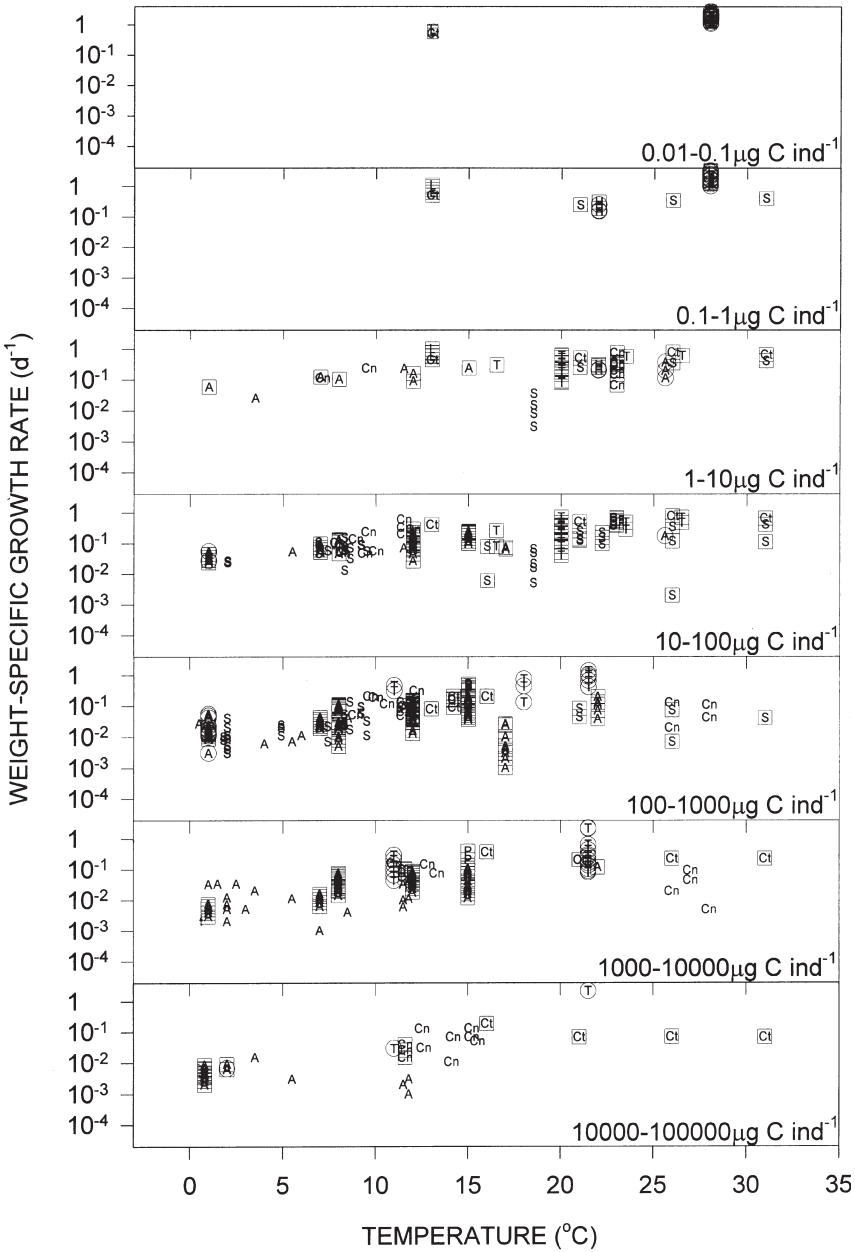

Figure 6 Comparisons for all invertebrates excluding copepods of weight-specific growth as a function of temperature for order of magnitude body weight ranges (0.1–1.0 µg C individual^{-1}, 1–10 µg C individual^{-1}, 10–100 µg C individual^{-1}, 100–1000 µg C individual^{-1}, 1000–10 000 and 10 000–100 000 µg C individual^{-1}). See Table 6 for results of regression analysis. Symbols as in Figure 5.

Table 6 Linear regression analysis between $\log_{10}$ growth and temperature for orders of magnitude ranges in body weight for the different taxa. Those with a dash represent groups for which regression analysis was not completed as only one species was contained within the data set or there was no range in the temperature at which measurements had been made.

Weight (μg C ind^{-1})	Taxon	No. of data points (No. zero or –ve values)	No. of species	Temp. range (°C)	$\log_{10}$[g] vs. Temperature					
					Intercept	Slope	r^2	P	$P < 0.05$	Q_{10}
0.01–0.1	Ctenophores	1 (0)	1	13	–	–	–	–	–	–
	Larvaceans	53 (0)	4	13–28	–0.597	+0.0320	0.502	<0.001	*	2.09
	All groups[1]	54 (0)	5	13–28	–0.649	+0.0339	0.593	<0.001	*	2.18
0.1–1.0	Chaetognaths	3 (0)	1	21–31	–	–	–	–	–	–
	Ctenophores	1 (0)	1	13	–	–	–	–	–	–
	Larvaceans	34 (0)	5	13–28	–0.405	+0.0256	0.445	<0.001	*	1.80
	Polychaetes	5 (0)	~2	22	–	–	–	–	–	–
	All groups[1]	43 (0)	~9	13–31	–0.932	+0.0402	0.268	<0.001	*	2.52
1–10	Crustaceans[1]	11 (0)	4	1–25.6	–1.232	+0.0246	0.450	<0.02	*	1.76
	Chaetognaths	7 (0)	2	18.5–31	–4.334	+0.138	0.628	<0.03	*	23.99
	Cnidarians	11 (0)	2	7.1–23	–0.921	+0.0150	0.0996	>0.20	NS	1.41
	Ctenophores	4 (0)	2	13–31	–0.510	+0.0119	0.670	>0.10	NS	1.32
	Larvaceans	5 (0)	1	13	–	–	–	–	–	–
	Polychaetes	7 (0)	~4	22	–	–	–	–	–	
	Thaliaceans	23 (0)	2	16.5–26.5	–1.655	+0.0522	0.0932	>0.10	NS	3.33
	All groups[1]	68 (0)	~17	1–31	–1.067	+0.0206	0.0678	<0.05	*	1.61
10–100	Crustaceans[1]	46 (0)	9	1–25.6	–1.405	+0.0337	0.394	<0.001	*	2.17
	Chaetognaths	42 (3)	4	2–31	–1.553	+0.0270	0.178	<0.01	*	1.86
	Cnidarians	16 (0)	3	7.9–23.0	–1.306	+0.0457	0.559	<0.001	*	2.86
	Ctenophores	4 (0)	2	13–31	–0.556	+0.0136	0.721	>0.10	NS	1.37

	Thaliaceans	29 (0)	2	16.5–26.5	−1.873	+0.0610	0.134	>0.05	NS	4.07
	All groups[1]	137 (3)	20	1–31	−1.406	+0.0326	0.265	<0.001	*	2.12
100–1000	Crustaceans[1]	102 (6)	11	0.5–22	−1.717	+0.0178	0.0372	>0.05	NS	1.51
	Chaetognaths	32 (0)	2	1.8–31	−1.880	+0.0222	0.181	<0.02	*	1.67
	Cnidarians	23 (0)	5	8.9–28	−0.944	−0.0066	0.0274	>0.20	NS	0.86
	Ctenophores	7 (0)	2	13–16	−2.892	+0.142	0.594	<0.05	*	26.3
	Pteropods	6 (0)	1	15	–	–	–	–	–	–
	Thaliaceans	10 (0)	4	11–21.5	−0.882	+0.0333	0.226	>0.10	NS	2.15
	All groups[1]	180 (6)	25	0.8–31	−1.779	+0.0364	0.163	<0.001	*	2.31
1000–10,000	Crustaceans[1]	68 (7)	7	1–22	−2.196	+0.0587	0.365	<0.001	*	3.86
	Cnidarians	13 (0)	4	11–28	−0.482	−0.0424	0.541	<0.005	*	0.38
	Ctenophores	4 (0)	2	16–31	−0.312	−0.0120	0.456	>0.30	NS	0.76
	Pteropods	2 (0)	1	15	–	–	–	–	–	–
	Thaliaceans	20 (0)	4	11–21.5	−1.498	+0.0505	0.209	<0.05	*	3.20
	All groups[1]	107 (7)	18	1–31	−2.058	+0.0570	0.371	<0.001	*	3.72
10,000–	Crustaceans[1]	18 (1)	4	0.8–11.8	−2.243	−0.0378	0.301	<0.02	*	0.42
100,000	Cnidarians	10 (3)	2	11.6–15.5	−2.601	+0.0923	0.166	>0.20	NS	8.38
	Ctenophores	7 (0)	2	16–31	−0.612	-0.0197	0.461	>0.05	NS	0.64
	Thaliaceans	7 (0)	2	11–21.5	−3.491	+0.178	1.000	<0.001	*	60.26
	All groups[1]	42 (4)	10	0.8–31	−2.411	+0.0750	0.532	<0.001	*	5.62
100,000– 1,000,000	Cnidarians	1 (0)	1	15.8	–					

Number of data points does not include those that are zero or negative; these are indicated in brackets. Values marked with an asterisk represent those for which the probability was <0.05, NS - not significant (i.e. $P > 0.05$). [1] Excluding copepods.

Table 7 Statistical results of regression (multiple linear and least squares) relating dependent variable weight-specific growth rate [$\log_{10}$ g (d^{-1})] to the independent variables temperature (T, °C) and/or $\log_{10}$ body weight (BW, µg C individual^{-1}). Multiple linear regressions only given in those cases where backwards stepwise-regression analysis demonstrated that both independent variables should be included (F-to-enter = 4.0 and F-to-remove = 3.9).

Taxa	No. of data points (No. zero or –ve values)	No. of species	Backwards stepwise-regression	Multiple linear regression[1] a	b	c	R^2	*P* ($\log_{10}$BW; T)	Linear regression[2] a	b	ind. var.	r^2	*P*
Crustaceans[3]	239 (14)	12	both included	+0.0263	−0.327	−0.919	0.447	(<0.001; <0.001)	–	–	–	–	
Chaetognaths	84 (3)	4	$\log_{10}$ BW removed	–	–	–	–	–	−1.851	+0.0367	T	0.323	<0.001
Cnidarians	73 (4)	6	T removed	–	–	–	–	–	–0.423	–0.219	$\log_{10}$ BW	0.380	<0.001
Ctenophores	27 (0)	3	T removed	–	–	–	–	–	–0.176	–0.207	$\log_{10}$ BW	0.642	<0.001
Larvaceans	91 (0)	5	$\log_{10}$ BW removed	–	–	–	–	–	–0.495	+0.0285	T	0.566	<0.001
Polychaetes[4]	12 (0)	~5	no T range	–	–	–	–	–	–0.630	+0.409	$\log_{10}$ BW	0.514	<0.01
Pteropods	8 (0)	1	–	–	–	–	–	–	–	–	–	–	–
Thaliaceans	88 (0)	7	both included	+0.0645	+0.138	−2.070	0.280	(<0.001; <0.001)	–	–	–	–	–

For those data sets in which an independent variable did not statistically significantly add to prediction, results from linear regression using the remaining independent variable [ind. var.] are given.

[1] $\log_{10}$ g = a[T] + b[$\log_{10}$ BW] + c

[2] $\log_{10}$ g = a + b[ind. var.]

[3] Excluding copepods.

[4] In the case of polychaetes temperature was removed as there was no range in this independent variable.

4. DISCUSSION

4.1. Intra-specific scaling

It is important to make the distinction between the patterns of growth for individual species, and for the taxonomic groups as a whole. Organisms do not continue to add weight indefinitely. In many species weight-specific growth is not constant with weight or age, but rather it may initially be approximately constant and then decline for larger (and older) individuals. In some cases this decline may be over-estimated as a result of the omission of reproductive output. However, the pattern is still seen in some species prior to the appearance of recognisable gonads or before the point when reproductive output begins. For example, growth appears to decline with age prior to the appearance of gonads in the hydromedusae *Aeqourea victoria* (Arai, 1980), and growth declines in the scyphomedusae *Aurelia aurita* prior to reproductive output (Lucas and Williams, 1994; Lucas *et al.*, 1997). A reduction in the rate of weight-specific growth with increasing stage/weight and size also occurs in many species of crustacean (Båmstedt and Skjoldal, 1980). This may also be observed in euphausiids (e.g. Ross, 1982; Tanasichuk, 1998a), amphipods (e.g. Dagg, 1976; Ikeda, 1991) and decapods (e.g. Anger *et al.*, 1983). The decline again seems to occur during the pre-reproductive period. In the copepods it has been observed that late pre-reproductive as well as adult copepodite stages often have lower body weight growth than earlier ones (Vidal, 1980; Richardson and Verheye, 1998).

When reproductive maturity and output begins this can, at times, increase total growth [e.g. in the euphausiid data of Ross (1982)]. Generally, however, the reproductive maturation does not stop total growth from declining further with increasing weight/size or age [e.g. see the amphipod data of Dagg (1976)]. There are many possible reasons for this decline, which may be intrinsic to the animal or a consequence of the environment. The decline may relate to a changing ability to consume sufficient food, or that food available for larger animals is more dilute (and growth becomes more food-limited with increasing body weight). Alternatively the nutritional requirements may change as the animal approaches reproductive maturity, and food becomes less suitable (i.e. food biochemical composition). It is also possible that even under ideal food conditions the animal would still be unable to sustain the same growth rates with increasing weight/size and age. Many species demonstrate growth rates that decline more rapidly than the overall relationship for their taxonomic group as a whole. This would tend to suggest that there are intrinsic factors that cause weight-specific growth to reduce with weight/size intra-specifically, and not simply increased food limitation as a consequence of the animals size for example. However, increasing food limitation with stage is certainly a factor for some groups in the natural environment (e.g. copepods – Hirst and Lampitt, 1998). This topic is discussed below.

4.2. Intra-taxon scaling and comparisons

For most of the individual taxonomic groups we have analysed weight-specific growth declines as a function of increasing body weight. This is evident in crustaceans, cnidarians, ctenophores and the broadcasting copepods (Tables 2, 4, 5 and 7). However, for the chaetognaths and larvaceans backward stepwise regression reveals that $\log_{10}$ body weight does not add significantly and is removed, leaving temperature alone as the factor of significant prediction. For thaliaceans, body weight does add significantly to the relationship (see Tables 5 and 7), but in this instance weight-specific growth actually increases with increasing body weight (i.e. the *b* value from the multiple linear regression is positive – see Table 7). These exceptions are consistent in the sense that they are generally found in both the linear regression over fixed temperature regimes and the backward stepwise regression analyses. The results from the backwards stepwise regression for adult sac-spawning copepods also demonstrate increasing growth with increasing body weight, for the copepodites it is invariant and removed, whilst in the nauplii the rate actually declines. The linear regression results, over the 10°C temperature ranges, show that adult and copepodite sac-spawning copepods at temperatures below 20°C have growth rates that increase with increasing body weight (see Table 2). Above 20°C growth rates decline. For the nauplii of sac-spawning species rates consistently decline over the entire temperature range for which we have data.

There are insufficient data for many groups to describe the division between body weight growth and reproductive growth as a function of age and body weight. There are almost no data on reproductive growth in the thaliaceans and larvaceans for example, and little for cnidarians, ctenophores and chaetognaths. In many taxonomic groups there is a suggestion that intra-specific growth declines as a function of increasing body weight. For the thaliaceans and larvaceans groups there is no obvious decline in growth with increasing body weight within the data sets as a whole. Most weight-specific physiological functions have been described as declining with increasing body weight intra-specifically but interestingly, there is an indication that in some salp species weight-specific respiration may be independent of, or increase with, weight on an intra-specific basis (Cetta *et al.*, 1986; see Madin and Deibel, 1998).

It has been suggested that thaliaceans, larvaceans (Heron and Benham, 1984; Hopcroft and Roff, 1995), ctenophores, siphonophores, pteropods and chaetognaths (Alldredge, 1984) may have higher growth rates than copepods and other crustaceans. Our extensive analysis of data generally confirms that larvaceans, thaliaceans, cnidarians and ctenophores have growth rates that are greater than copepods of similar carbon weight, but chaetognaths do not. The other crustaceans typically have rates that fall within the range of those for copepods of a similar weight. Measurements of growth for the chaetognaths also cluster within the envelope for copepods, whilst for the cnidarians, ctenophores and larvaceans

growth rates are almost always greater than the general relationship describing copepod growth, and are also at the upper limits or beyond the maximum rates for copepods of a similar carbon weight. For the pteropods the rates are generally greater than those of copepods, although the data set was limited to a single species, *Clione limacina*, in a single study (i.e. Conover and Lalli, 1974). In addition, *C. limacina* is carnivorous whereas most pteropods are suspension feeders. The thaliaceans have the highest growth rates at body weights greater than 1000 µg C individual^{-1}, with rates of up to 2.1 d^{-1} for *Pegea bicaudata* at body weights of ~2000 to 35,000 µg C individual^{-1} (see Madin and Deibel, 1998). Their rates are not only the highest for taxa of this weight, but are also some of the highest rates in comparison to many animals with much smaller carbon weights. In the thaliacean group, the species with lower carbon weights i.e. *Dolioletta gegenbauri* and *Thalia democratica*, generally appear to have lower growth rates. This is unlike the pattern observed in the other taxonomic groups examined herein.

Figure 7 demonstrates growth rates for each of the taxonomic groups, corrected in all cases to 15°C. Although there are obvious differences between some of the taxa, some appear to have very similar rates at similar body carbon weights. Within the copepods growth appears, generally, not to exceed 0.9 d^{-1} (when corrected to 15°C), except in the case of *Acartia clausi* reaching 1.56 d^{-1}, *Acartia hudsonica* at 0.94 d^{-1}, *Acartia omori* at 0.96 d^{-1} and *Acartia tonsa* at 1.10 d^{-1} (calculated from adult egg production data of Calbet *et al*., (1996), Jónasdóttir *et al.*, (1995), Ayukai, (1988), and McManus and Foster, (1998) respectively). Hence, growth in copepods only exceeds 0.9 d^{-1} for adult *Acartia* at least in the data set we obtained. The copepods, chaetognaths and other crustaceans have broadly similar ranges in their growth rates at given body carbon weight (Figure 7a and b), while the pteropods, cnidarians and ctenophores have higher rates than this first group, but similar rates to one another at similar body carbon weights (Figure 7c). The thaliaceans and larvaceans have the highest rates, with both having maximum weight-specific growth rates corrected to 15°C that exceed 1 d^{-1}; *Oikopleura dioica* reaches 1.36 d^{-1} [calculated from the data of Paffenhöfer (1976)] and *Pegea bicaudata* 1.08 d^{-1} [calculated from the data of Madin unpublished – as presented in Madin and Deibel (1998)].

Inter-taxon comparisons raise the question as to why some groups may have higher rates than others. Hopcroft and Roff, (1995) suggested that copepod and crustacean growth might be limited by their chitinous exoskeleton: moulting and growth are intimately linked, and there are physical limits to how much an animal can swell under a soft new exoskeleton. This argument is not applicable to chaetognaths, and seems less applicable to adult female egg production, as eggs are shed. Yet for both of these groups growth appears to be much lower than in the gelatinous groups. Copepods have daily rations (in carbon terms) of the order 10–100% C d^{-1}, although in smaller nauplii stages this may be as high as 280% C d^{-1} (White and Roman, 1992, as given by Mauchline, 1998). Ctenophores can have higher daily rations than those achieved by copepods (Reeve and Walter,

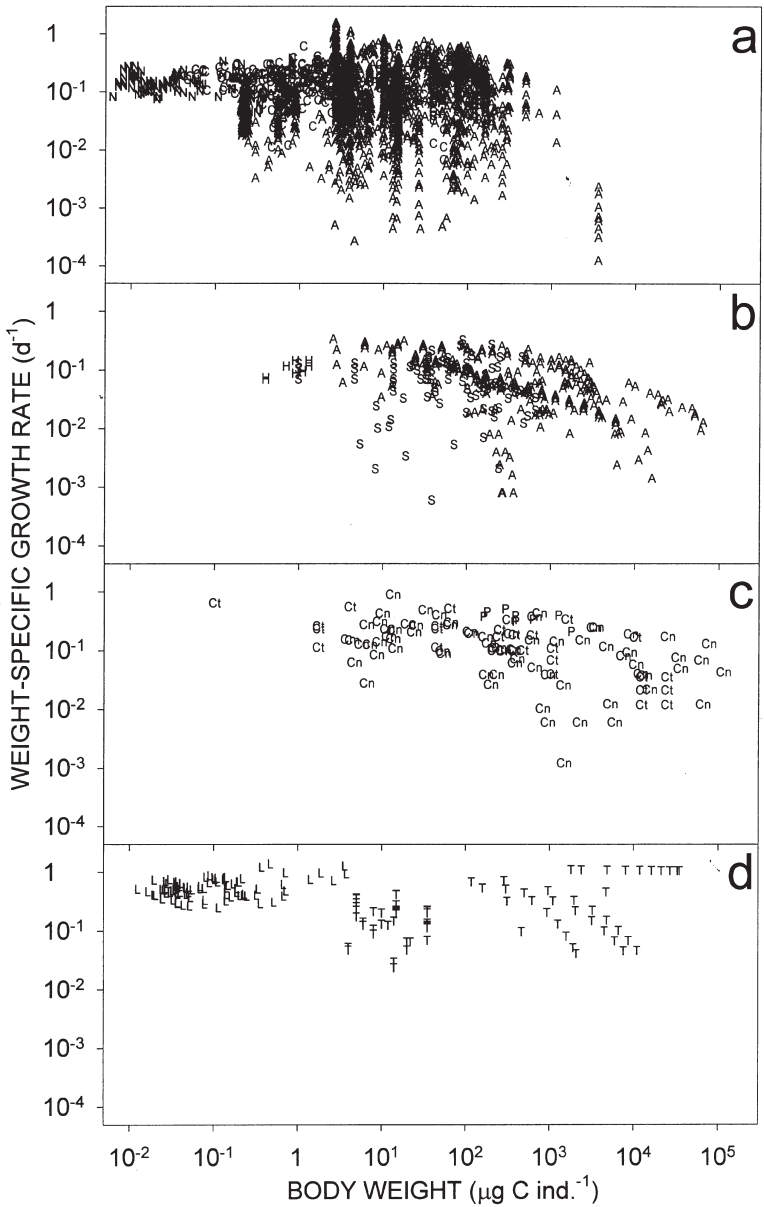

Figure 7 Comparisons of weight-specific growth of marine metazoan zooplankton. All data corrected to 15°C using a Q_{10} of 3.0. **a.** copepods (A adults, C copepodites, and N nauplii) [CW%WW >4%]; **b.** chaetognaths (S), crustaceans other than copepods (A) and polychaetes (H) [CW%WW >4%]; **c.** cnidarians (Cn), ctenophores (Ct), and pteropods (P) [CW%WW >0.3% to <2.4%]; **d.** larvaceans (L) and thaliaceans (T) [CW%WW <0.4%].

1978), while chaetognaths may have lower daily rations than ctenophores, but certainly when young, greater rations than copepods of similar body carbon weight (see Reeve, 1980). Thaliaceans have been reported to have daily rations of between 24 and 200% C d^{-1} [from the Table 5.8 of Madin and Deibel (1998)]. Larvaceans have been reported to have daily rations as high as 980% C d^{-1}, although values of 100–200% C d^{-1} have commonly been found (see Deibel, 1998). It has been observed for the larvacean *Oikopleura dioica*, that although ingestion rate increases with increasing food concentration as would be expected, large individuals ingest more food per unit body mass than small individuals, i.e. weight-specific rates increase with body weight. This has been used to explain why these organisms can maintain exponential growth over their entire life span (King, 1982). We observe this pattern in the data set here, with no decline in growth with increasing body weight for Larvacea (see Tables 5 and 7, and Figure 7). Many weight-specific physiological functions such as filtration rate are inversely related to body weight in most organisms (e.g. copepods). For salps, there are suggestions that the rates remain constant (Andersen, 1985) or increase with increasing weight (Harbison and Gilmer, 1976; Deibel, 1982b; Mullin, 1983). Madin and Deibel, (1998) suggested this might be attributed to the differences in exponents relating filtration and weight to body length, or to the use of muscular rather than ciliary pumping mechanisms, although this pattern of increase was speculative. In some individual species of thaliaceans we find similar growth rates in both small and large individuals (i.e. a lack of scaling intraspecifically), while for the group as a whole we find weight-specific growth increases with increasing body weight (see Tables 5 and 7, and Figure 7). This may indeed lend support to the idea that weight-specific filtration (and ingestion) rates may increase with weight in the thaliaceans.

Alldredge's (1984) review of gelatinous zooplankton includes studies of gross growth efficiency (GGE), but the work compares elementally derived GGE with dry weight-derived GGE values, which gives flawed results (see Hirst and Lucas, 1998). Re-examination of her work only including elementally derived ratios does confirm the idea that GGE may be as high or higher than the values for copepods, which for copepods may centre around 26% (Straile, 1997). The pteropod species included in the data set is also believed to have a very high gross growth efficiency under experimental condition, e.g. in calorific terms 49 to 85% [see Table IV of Conover and Lalli (1974)]. This may in part be because the prey consists of other pteropods and therefore, presumably, having a very similar body composition. We must note that many experiments to determine such efficiencies may not be representative of those *in situ*.

Copepods typically have a carbon content as a percentage of wet weight (C%WW) that ranges between 5 and 8%, but can exceed this (Beers, 1966; Omori, 1969; Båmstedt, 1986). Other crustaceans such as euphausiids, amphipods, mysids and decapods have similar values (Beers, 1966; Omori, 1969). Chaetognaths typically have values of ~5 to 7% (Omori, 1969) although

lower values have been found (Beers, 1966). The pteropod *Clione limacina* included here may be assumed to have a C%WW of ~2.4% (Curl, 1962). In addition, this species is rather unusual in that it is believed to prey exclusively throughout its post-veliger life on two species of thecosomatous pteropod. Cnidarians and ctenophores have much lower C%WW values between ~0.07 and 2.4% (Curl, 1962; Beers, 1966; Larson, 1986), but more typically towards the higher end of this range. For example, the average C%WW from the hydromedusae and scyphomedusae given by Larson, (1986) in his Tables VI and V is 0.461%. The thaliaceans have values that are often lower than the cnidarians, ranging from between 0.3 and 0.4% (Curl, 1962; Larson, 1986). The larvaceans included in our growth compilation are from the genera *Appendicularia*, *Fritillaria* and *Oikopleura*. These have body C%WW of ~10%, although their houses have C%WW of ~0.00007 to 0.00050% (Alldredge, 1976). If one includes the house in the overall C%WW determination the value for *Oikopleura rufescens* is ~0.002% [derived from combining the results presented in Alldredge (1976) with those of Uye and Ichino (1995)]. There is a general relationship between C%WW of taxa and the growth rate. Gelatinous forms generally have higher growth rates at similar temperatures and body carbon weights than the copepods, other crustaceans and chaetognaths, while the thaliaceans and larvaceans appear to have the highest rates, and the lowest C%WW values (see Figure 7). The high water content of the more truly gelatinous organisms allows, through small energetic input, rapid increases in wet biomass, surface area, prey-capture abilities, and predation rates (Larson, 1991). The larvaceans although strictly non-gelatinous effectively occupy, with their house, a total body volume that is more similar to a gelatinous organism. The house is composed of non-living acellular mucous material that is metabolically inert once secreted (although it needs investment for its production and continued replacement). However, because of the effective gelatinous nature of the house, and its weight, they are able to filter volumes considerably in excess of those filtered by organisms of similar body composition that do not have these ‘low biomass content’ structures.

Copepods, other crustaceans and chaetognaths share many similarities. They have similar amounts of carbon per unit of body weight in wet weight terms. They feed either raptorially or by suspension feeding using appendages, and may have fairly similar daily rations on a body weight basis at a given temperature. Cnidarians, ctenophores and pteropods have a lower amount of carbon per unit wet weight. They might have greater daily rations and use a variety of mechanisms to filter water. Thaliaceans are true filter feeders. They pass seawater through a mucous sieve and ingest retained particles (Madin and Deibel, 1998). Copepods and other crustaceans have complex behavioural mechanisms for detecting, entraining, and grasping suspended particles from the water, and may not be regarded strictly as filter feeders. Within the thaliaceans, the doliolids obtain food by ciliary activity, whereas salps have to swim to force water to enter

their mouths. Larvaceans on the other hand have a slightly different mechanism in that they move their tail rhythmically to propel water into their houses, where it is passed through a fine filter. Doliolids appear to be able to filter out small nanoplankton and perhaps even picoplankton with high efficiency (Madin and Deibel, 1998). Experimental work on salps has shown that cells of less than 1.0 μm are caught only with low efficiency, while in most species particles larger than about 3–4 μm are retained with 100% efficiency.

Thaliaceans certainly appear to be among the fastest growing metazoans included in this study. Heron and Benham (1984) stated that for the tunicates "With ten to one hundred times faster feeding rates (Silver, 1971; Harbison and Gilmer, 1976; Deibel, 1980; Alldredge, 1981) and growth rates (Heron, 1972; Wiebe *et al.*, 1979; Deibel, 1982a; King, 1982) than those of slower growing plankton, they must account for a major portion of the cycling of material through the multicellular zooplankton".

Given that adult female copepods have undergone their terminal moult, and most of their growth must be limited to egg production, then the mechanisms that control egg output, including oogenesis, may also set limits to the maximum rate of output and therefore production. Many gelatinous species begin to produce eggs/young at an early age, but also continue to increase their body weight greatly [e.g. ctenophores: see Reeve and Walter (1978); thaliaceans: see Madin and Deibel (1998)]. Although this may aid higher growth rates, it is not the principal reason as to why their growth is higher than in copepods because many of their rates compiled here include only a somatic growth term. Mating success may affect egg production in copepods (Parrish and Wilson, 1978; Uye, 1981). In contrast, with few exceptions (Harbison and Miller, 1986), almost all ctenophores are simultaneous hermaphrodites and capable of self-fertilisation (Reeve and Walter, 1978). Chaetognaths are protandrous hermaphrodites (Hyman, 1959, Alvariño, 1965), while doliolids and salps may produce offspring asexually (Alldredge and Madin, 1982). Many cnidarians are gonochoristic (i.e. they have separate sexes), although some are protandrous hermaphrodites (Arai, 1997). Once again this reproductive mode has implications for the maximum growth rate, although many of the rates included for non-crustacean taxa only represent body weight increases, and not reproductive output, and the differences therefore cannot be attributed simply to these factors. Moulting in crustaceans may act not only as a loss of material from an individual, but feeding may also be suppressed during moulting (Lasker, 1966). Some taxa have substantial losses through the release of mucus or DOC release. In some cnidarians DOC release may be as great as carbon allocated to reproduction and almost half that attributed to body weight increase (Hansson and Norrman, 1995). In the case of larvaceans the turnover of the house as this is renewed can be a large loss term (Clarke and Roff, 1990; Hopcroft and Roff, 1998a; Tomita *et al.*, 1999), yet their growth even excluding this loss is still substantially greater than in many other groups.

Inherent patterns of growth may be related to both the phenomenon of eutely and to the DNA content (Runge and Roff, 2000). Thus, the larvaceans appear to achieve fast and exponential growth because they rapidly replicate cells when they are small, then in later growth as larger animals they may simply expand the size of an existing number of cells. According to McLaren *et al.* (1987, 1988), the copepods may also be eutelic and their growth rates are related to genome size. Thus both groups may achieve almost exponential growth throughout their somatic growth phase, perhaps by limiting the number of body cells. The difference between the faster rates of the larvaceans and the slower rates of the copepods may be related to the production of exoskeleton in the crustaceans (see Hopcroft and Roff, 1995). Is the difference between groups, which can and cannot achieve approximate exponential growth, related to those groups that are eutelic and those that are not?

In conclusion there is probably no single cause as to why some taxa have higher or lower growth rates than others. The daily rations achieved certainly underpin many of the patterns we observe in growth rates, probably more so than patterns in other factors e.g. gross growth efficiency. Methods used in obtaining food, the abundance and size of this prey, and how prey size and abundance changes with predator size are likely to be key for driving patterns in the daily rations, and in turn growth rates and patterns. Gelatinous organisms have long been recognised as standing out from the crustaceans. The larvaceans and thaliaceans have particularly high growth rates, and can attain intra-specific exponential or supra-exponential growth rates against body weight.

4.3. The role of food

In most investigations of zooplankton growth we have little idea of whether the growth measured is in fact resource (food) limited or not. This is because experiments to test for food limitation need to be carried out simultaneously with observations of growth at ambient food concentrations. In the laboratory it typically requires much higher than natural food levels to saturate growth rates. Kiørboe and Sabatini's (1995) compilation of food-saturated rates suggests that nauplii grow slower than copepodites (by 20–40%), and from their data it would appear that in the last copepodite stages before adulthood growth may decline from that in earlier copepodite stages (see also Peterson and Hutchings, 1995). Nauplii develop through stages faster than early copepodites, which in turn develop faster than late copepodites (Kiørboe and Sabatini, 1995). This might be interpreted as an adaptive response, whereby younger stages (especially nauplii) develop faster in order to improve motility or escape performance as quickly as possible so as to minimize cumulative pre-spawning mortality. This faster development rate comes at the cost of reduced somatic growth. An important question is whether growth declines as a function of body weight

because of greater food limitation for organisms with greater carbon mass. Hopcroft and Roff (1998b, 1998c) and Hopcroft *et al.* (1998b) have argued that the patterns of growth rates they observed were indicative of progressively increasing food limitation from nauplii through copepodites to adults in tropical marine copepods. Of course growth might also decline because it is dependent on the ability of animals to ingest and assimilate food, and to balance this against metabolic costs of collection and body maintenance. The relative balance of these factors and how they change with body weight will determine how growth will change with weight.

For most groups there appears to be a general decline of weight-specific growth rate with body weight. However, to what extent is this a product of natural food limitation, and to what extent is it a natural inherent growth pattern? We cannot yet be confident that we know how much of the decline may result from food limitation in the natural environment increasing with the size/weight of the individual. For copepods, the results of Vidal (1980) suggests that even under high food concentrations in the laboratory growth rates could decline with age and body weight. Typically the larger the copepod or crustacean the larger the food particles it exploits (Hansen *et al.*, 1994). Larger animals also exploit larger volumes of their environment, i.e. larger volumes swept clear per unit time for larger animals than smaller animals within species [e.g. in the copepods: Berggreen *et al.* (1998); in the cnidarians: Daan (1986), Olesen (1995); in thaliaceans: Madin and Deibel (1998); in the larvaceans: Deibel (1998)] and between-species (e.g. in the copepods and crustaceans: Peters and Downing (1984); in the larvaceans: see Deibel (1998)]. Larger animals also have lower weight-specific respiration rates (e.g. Ikeda and Mitchell, 1982). Larger animals often prey upon larger prey items. This is not the case for the thaliaceans and larvaceans, which feed on very small particles given their body volume, and for the thaliaceans for their body carbon weight. Smaller food particles are typically more abundant and more constant in concentration, and larger particles are typically more dilute and more variable in concentration (Hopcroft and Roff, 1990, 1998c). How such factors balance out may vary greatly from location to location and from time to time, but this is clearly important. Copepods (copepodites and nauplii) have an optimal prey ESD (equivalent spherical diameter) to predator ESD of ~18 : 1. For meroplankton including polychaete larvae (the only meroplankton we have included herein) this ratio is nearer 50 : 1 (Hansen *et al.*, 1994). As these animals increase in weight/size their optimal prey size typically also increases, but may also decrease in concentration. The predator : prey size ratio for thaliaceans and appendicularian tunicates is many thousands to one. In the larvacans the pharyngeal filter captures particles of the size of colloids up to diatoms, by sieving and by direct interception of particles onto individual filter fibres (Deibel, 1998). Clearly these two groups stand in extreme contrast to the ratios found in the other pelagic invertebrates examined here.

4.4. Errors, gaps, and the future

Methods adopted for the 'Other Invertebrates' have their own benefits and drawbacks, and some are certainly more suitable for some taxonomic groups than others. When studying large active predators it is often very difficult to determine natural feeding condition, particularly as these groups may be able to forage over large distances (greater than those feasible for incubation), and find patches of high prey density and stay within them. Many carnivorous gelatinous species, for example, do not necessarily grow at field rates when prey are supplied at concentrations measured in the field using typical techniques, i.e. when averaged at the scales that biological oceanographers usually make measurements (Reeve and Walter, 1978). Consequently many species have been incubated with much higher prey concentrations or what were deemed food-saturated or maximum ration conditions (e.g. Reeve and Baker, 1975). Investigators incubating zooplankton have often been unable to attain survival or growth characteristics similar to those observed in the field, and the containment dilemma is obviously of continued and great concern (Reeve, 1977). Some of the studies whose results we have included have been criticised by later workers. For example, the slow growth rates for *Pleurobrachia* found by Hirota (1972) have been commented upon by Reeve and Walter (1976). The incubation containers in Hirota's study may have been too small for this tentaculate species (P. Kremer pers. comm.). We have not excluded this study here, and the number of observations included from this study is small ($n = 4$), and hence should not bias our results. Details of methodology problems may become apparent in some taxa only with time and experience.

In all of the other invertebrate data, only growth measurements that were made over a small fraction of the generation time or life span of the animals were included. This was an attempt to reduce the errors that may be associated in measuring growth over large periods of the life history or the entire life span of an organism (Hirst and Sheader, 1997).

Many of the growth measurements for the other zooplankton have been completed under laboratory conditions with controlled, often high, prey concentrations (e.g. Reeve and Baker, 1975). In the case of the results from Ikeda *et al*. (1985) only fastest growth rates during the life-history have been included. While the methodology adopted by Madin [unpublished results – as presented in Madin and Deibel (1998)] was such that only the maximum experimental growth rates were deemed to be representative of natural rates because of problems associated with incubating salps.

The total number of species studied is very limited, and predominantly includes those found in coastal areas. The lack of data with respect to species in the open ocean is of concern, and our analysis can only, therefore, represent a first step at synthesising growth and development of predictive relationships. There is a clear need for improved methods to measure the rates of development and growth of marine zooplankton. Most preferable will be methods that allow rapid

automated measurements of growth with smaller investment on time or effort than is required by current conventional techniques. Unfortunately, development of such methods has been slow, and potential methods have often been used in field applications before being properly evaluated in the laboratory (Runge and Roff, 2000).

Clearly solutions are needed for determining natural growth rates. When natural cohorts occur many of the problems of experimental manipulation and incubation can be directly avoided. However, there are other problems. Many of the cohort measurements we have been able to include only incorporate body weight growth and it may be impossible to incorporate reproductive output of animals under these conditions. Although this is not important for animals prior to reproduction, and some corrections can be made when animals only reproduce at a given stage, many other taxa demonstrate simultaneous reproductive output and body weight growth (negative as well as positive) [e.g. ctenophores (Hirota, 1972), crustaceans (Dagg, 1976) including copepods (Hirst and McKinnon, 2001), chaetognaths (Reeve, 1970)]. Huntley and Lopez (1992) address some of the problems of cohort methods, and point out that populations in nature often do not facilitate the use of such methods, and when they do high temporal resolution sampling is needed in order to avoid great sensitivity to the interpolation techniques. In many groups it has proven impossible to measure growth accurately in the natural environment through the cohort approach. Many animal populations cannot be easily separated into cohorts whose development can be followed through time. *In situ* estimates are also biased by advection and the horizontal and vertical patchiness of populations in the water column (Conover, 1988). Certainly such methods are not always satisfactory, and cohort analyses have been revisited and criticised in many instances (e.g. Russell (1932) vs. Øresland (1986)). There is typically some subjectivity in analysis and interpretation in such methods.

When cohorts cannot be recognised in the natural environment experimental incubation techniques are required, whereby animals must be captured, manipulated and incubated. This raises problems, as many gelatinous forms cannot be easily captured without damage. The feeding, light, chemical and temperature environments an animal occupies over even a 24 hour cycle can vary dramatically, particularly if either the animal or its prey are strong vertical migrators. These factors often go unconsidered by investigators using incubation approaches. Incubation containers are usually very small in comparison to the volume of water that an animal may actively or passively pass through. The use of large mesocosms may alleviate some of the problems associated with incubating animals in smaller volumes in the laboratory because of the more realistic temperature, light, food and turbulence regimes, and less severely restricted movement and migration ambits, and because advection can also be eliminated. Mesocosms are certainly not free from problems, and their use is typically restricted to shallow water sites, and the incubation of local coastal species.

Many epi-pelagic invertebrates are certainly capable of surviving for long periods whilst undergoing negative growth [e.g. cnidarians: see Arai (1997); ctenophores: Reeve and Walter (1978); crustaceans: Hopkins *et al.*, (1984)]. This suggests that such an ability plays an important role in the survival strategy of many groups in the natural environment. Presumably the more seasonal the environment, particularly with respect to food quantity and quality, then the more variable the growth rates may be expected to be, hence the growth rates of copepods at 25°C (see Figures 1 and 2) fall more closely around a linear regression than do the data at 15°C, which in turn is less variable than at 5°C. The estimates of growth at colder temperatures typically come from more seasonal climates, whilst warmer values generally come from (although not exclusively) more tropical and less seasonal environments. Given that shallower waters and upwelling areas may undergo extreme temperature variation compared to offshore non-upwelling regions, then temperature is not simply a function of latitude. Whilst many copepod species in temperate and polar regions undergo some form of diapause or winter resting stage/period, and given that this does not always occur below 200 m (the limit to data exclusion), this may help us to explain why there is greater scatter in growth with decreasing temperature. Some species may even have apparent obligatory negative growth phases as part of their natural life-history, e.g. the cnidarian *Aurelia aurita* (Lucas and Williams, 1994). In the case of *Aurelia aurita*, for which we include two measurements where body weight declines, some although probably not all, will be attributable to gamete release, and therefore negative growth may be over-estimated.

The vast majority of the data come from investigations in, and animals collected from, shallow coastal areas (typically where the total water depth is < 200 m). This has implications for the abundance of food, as concentrations of many of the prey items (phytoplankton, microzooplankton and net zooplankton) are typically much greater in coastal regions than further offshore (Huntley and Boyd, 1984; Hopcroft and Roff, 1998c; Uye *et al.*, 1999), largely as a result of trophic status of the water, the size of the primary producers, and number of trophic links. In terms of growth we are almost certainly over-estimating many growth rates if we assume that coastal rates are equally applicable in more oligotophic regions of similar temperatures. Only once such issues are addressed will we be able to produce a truly global unbiased view of growth rates.

5. SUMMARY

An extensive compilation and analysis is presented of weight-specific growth rates in marine epi-pelagic invertebrate metazoan zooplankton, including both holo- and mero-planktonic forms. Using specific selection criteria we incorporate

growth rates from a variety of zooplanktonic taxa from over 110 published studies. Nine principal taxonomic groups were considered, the copepods (number of individual data points (n) = 2,528); crustaceans other than copepods (n = 253); cnidarians (n = 77); ctenophores (n = 27); chaetognaths (n = 87); pteropods (n = 8); polychaetes (n = 12); thaliaceans (n = 88); and larvaceans (n = 91). Information derived from these sources consists of: body carbon weight (μg C individual^{-1}), temperature at which growth took place (°C), and standardised measures of the total weight-specific growth (g d^{-1}), incorporating when possible the individual components; reproductive output (g_R), and increase in body weight (g_S). Values are divided on the basis of methods used in the original study, into one of three groups:

1. Cohort measurements made on field populations;
2. Artificial incubations of the studied animals and their prey, where both were collected simultaneously (e.g. animals incubated in natural seawater), and;
3. Artificial incubations of the studied animals, where food type or concentration was chosen or manipulated by the investigators.

Because of the relatively larger number of studies on copepods, we included only data in which recently caught wild individuals were incubated in natural seawater-food assemblages, close to natural temperatures, and for short periods of time, of the order of a day. The copepod growth data were analysed with respect to three life-history stages: the nauplii and copepodites (where growth is represented as increase in body weight), and the adults (where growth is represented as reproductive output), and also for two spawning types, the broadcasters (those that release their eggs freely into the water column) and sac-spawners (those that carry eggs attached externally to the female until hatching).

For each taxonomic group the relationships between growth and temperature and body weight was examined separately. To determine whether growth was body weight dependent we divided the data set into four 10°C temperature categories: > –10.0 to ≤ 0.0, > 0.0 to ≤ 10.0, > 10.0 to ≤ 20.0 and > 20.0 to ≤ 30.0°C. Growth rates in each of the categories were then adjusted to the mid-temperature: –5, 5, 15, and 25°C, using a Q_{10} value of 3.0. Least-squares regression-analysis (Type I) of $\log_{10}$ weight-specific growth against $\log_{10}$ body weight was then completed and the results tested for significance. Important differences were observed between the different taxonomic groups and within the copepods. In all cases broadcasting copepods showed a significant relationship ($P < 0.05$) with a negative slope, i.e. weight-specific growth declined with increasing body weight on an inter-specific basis, except for the nauplii of broadcasters at 15°C, in which case the relationship was not significant, but data were very limited (n = 11). For the sac-spawners, weight-specific growth was body weight independent for nauplii at 15°C, for the combined group of nauplii, copepodites and adults at 15°C, and for the copepodites alone at 25°C. All remaining

relationships were significant, but with negative slopes at 25°C, and positive slopes (i.e. weight-specific growth increased with increasing body weight) at both 5 and 15°C. For the other taxonomic groups $\log_{10}$ weight-specific growth vs. $\log_{10}$ body weight had a significant negative relationship for the crustaceans at 5 and 15°C, the chaetognaths at 25°C, the cnidarians at 15°C and 25°C, the ctenophores at 15°C. No significant relationships were found for the crustaceans at 25°C, chaetognaths at 15°C, the larvaceans at 25°C, and the thaliaceans at 25°C. In all cases where significant relationships were found the slope was negative, except for the polychaetes at 25°C and thaliaceans at 15°C when they were positive. In the case of polychaetes the data set was small (n = 12) and came from a single study at a single location.

For each of the groups we examined the relationships between $\log_{10}$ weight-specific growth and temperature. To remove the effects of body weight, animals were divided into order of magnitude groups, the smallest group being 0.001 to 0.01 μg C individual^{-1}, and the largest at 10 to 100 mg C individual^{-1}. Least-square linear-regression analysis (Type I) of $\log_{10}$ weight-specific growth vs. temperature were then completed. For the copepods all significant relationships had a positive slope (17 cases in total), there were seven cases where no significant relationship was found. Adult broadcasters showed non-significant relationships on two occasions, at 0.1–1.0 and 10–100 μg C individual^{-1}. Nauplii of broadcasters at 0.1–1.0 μg C individual^{-1} and all broadcasters at 10–100 μg C individual^{-1} were non-significant. Sac-spawners showed non-significant relationships on two occasions, their nauplii of 0.1–1.0 μg C individual^{-1} and the entire group at 10–100 μg C individual^{-1}. For the other taxonomic groups, in a total of 11 cases there was a non-significant relationship ($P > 0.05$), and in 19 cases there was a significant positive relationship, i.e. weight-specific growth increased with increasing temperature. Only in two instances were there significant relationships with a negative slope, for the cnidarians with body weights 1–10 mg C individual^{-1}, and for crustaceans with body weights 10–100 mg C individual^{-1}.

Backwards stepwise regression analysis tended to confirm the general relationships found using the other approaches. Weight-specific growth increased with increasing temperature and with decreasing body weight in crustaceans and copepods. Body weight did not contribute significantly in the case of chaetognaths and larvaceans and hence was removed, whilst temperature was removed in the case of the cnidarians and ctenophores. For the thaliaceans both temperature and body weight were included, and weight-specific growth increased with increasing body weight and temperature. For the entire broadcasting copepod data set, weight-specific growth increased with increasing temperature and decreasing body weight, whilst for the sac-spawners growth increased with increasing body weight and temperature.

Comparisons between the different taxa showed important differences and similarities. Our extensive synthesis of data generally confirms that larvaceans, pteropods, cnidarians and ctenophores have rates of weight-specific growth

which are typically greater than in the copepods, chaetognaths and other crustaceans of similar carbon weight. Whilst for the cnidarians, ctenophores and larvaceans growth rates are almost always greater than the general relationship describing copepod growth, and at the upper limits or beyond the maximum rates for copepods of a similar weight. For the pteropods growth rates appear greater than those of copepods, although the data set was limited to a single species in a single study (i.e. *Clione limacina*; Conover and Lalli, 1974). This pteropod species is a carnivorous feeder that preys upon other pteropods. The thaliaceans have the highest growth rates for animals with body weights greater than around 1 mg C individual^{-1}, with rates of up to 2.1 d^{-1} for *Pegea bicaudata* at body weights of ~2 to 35 mg C individual^{-1} (from Madin and Deibel, (1998)). Whilst the larvaceans can achieve rates of 2 d^{-1} in warm tropical waters (28°C), and as high as > 3 d^{-1} for < 0.2 μg C individual^{-1} animals of *Oikopleura diocia*. These are possibly the highest rates ever recorded in epi-pelagic metazoans.

The value of this analysis not only lies in its being the most comprehensive overview of patterns of growth to date, but because the data set highlights the gaps in measurements and current knowledge. We examine the inadequacies in the current data sets, and also of the methods being used to measure growth and production. Data are dominated by animals collected from coastal and estuarine waters, and it is clear that for a fuller understanding work is urgently needed on many of the taxonomic groups in the open ocean. The role of food availability must be explored more completely, and how food concentrations available in incubation conditions relate to those experienced in the natural environment.

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APPENDIX 1

Table A1 Weight-specific growth rates (g, d^{-1}) of broadcaster (B) and sac-spawning (S) copepods, divided into nauplii (N) and copepodite (C) somatic growth, and adult fecundity (A). Nauplii growth defined as N1 to N6–C1 moults, copepodite growth defined as studies of moulting from C1 to C5–C6 moults.

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Acartiidae:						
Acartia bifilosa	A	B	16.0	1.87	0.36	54
A. bifilosa	A	B	20.8	1.77	0.57	54
A. bifilosa	A	B	22.4	1.43	0.35	54
A. bifilosa	A	B	24.0	1.24	0.41	54
A. bifilosa	A	B	17.0	1.53	0.27	54
A. bifilosa	A	B	18.3	1.63	0.19	54
A. bifilosa	A	B	14.0	2.16	0.18	54
A. bifilosa	A	B	18.0	2.21	0.25	54
A. bifilosa	A	B	18.5	2.61	0.10	54
A. bifilosa	A	B	21.0	1.82	0.30	54
A. bifilosa	A	B	23.0	1.84	0.29	54
A. bifilosa	A	B	23.0	1.50	0.24	54
A. bifilosa	A	B	18.1	1.21	0.35	54
A. bifilosa	A	B	18.5	1.48	0.22	54
A. bifilosa	A	B	12.7	1.88	0.14	54
Acartia clausi	A	B	22	2.67	0.12	1
A. clausi	A	B	18	2.67	0.36	1
A. clausi	A	B	17	3.06	0.023	2
A. clausi	A	B	17	2.83	0.029	2
A. clausi	A	B	7	2.67	0.620	3
A. clausi	A	B	7	2.67	0.297	3
A. clausi	A	B	7	2.67	0.566	3
A. clausi	A	B	7	2.67	0.485	3
A. clausi	A	B	7	2.67	0.270	3
A. clausi	A	B	7	2.67	0.404	3
A. clausi	A	B	7	2.67	0.485	3
A. clausi	A	B	7	2.67	0.647	3
A. clausi	A	B	7	2.67	0.553	3
A. clausi	A	B	7	2.67	0.553	3
A. clausi	A	B	4	2.67	0.027	4
A. clausi	A	B	5	2.67	0.027	4
A. clausi	A	B	5	2.67	0.014	4
A. clausi	A	B	5	2.67	0.067	4
A. clausi	A	B	5	2.67	0.121	4
A. clausi	A	B	7	2.67	0.135	4
A. clausi	A	B	7	2.67	0.121	4
A. clausi	A	B	7	2.67	0.135	4
A. clausi	A	B	5	2.67	0.148	4
A. clausi	A	B	7	2.67	0.148	4
A. clausi	A	B	7	2.67	0.175	4
A. clausi	A	B	7	2.67	0.202	4

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Acartia clausi	A	B	5	2.67	0.216	4
A. clausi	A	B	7	2.67	0.216	4
A. clausi	A	B	7	2.67	0.256	4
A. clausi	A	B	7	2.67	0.270	4
A. clausi	A	B	5	2.67	0.283	4
A. clausi	A	B	7	2.67	0.300	4
A. clausi	A	B	7	2.67	0.310	4
A. clausi	A	B	7	2.67	0.283	4
A. clausi	A	B	7	2.67	0.270	4
A. clausi	A	B	7	2.67	0.270	4
A. clausi	A	B	7	2.67	0.040	4
A. clausi	A	B	12	2.67	0.067	4
A. clausi	A	B	16	2.67	0.067	4
A. clausi	A	B	16	2.67	0.040	4
A. clausi	A	B	16	2.67	0.067	4
A. clausi	A	B	18	2.67	0.027	4
A. clausi	A	B	18	2.67	0.067	4
A. clausi	A	B	17	2.67	0.027	4
A. clausi	A	B	17	2.67	0.040	4
A. clausi	A	B	17	2.67	0.067	4
A. clausi	A	B	17	2.67	0.081	4
A. clausi	A	B	17	2.67	0.121	4
A. clausi	A	B	17	2.67	0.135	4
A. clausi	A	B	17	2.67	0.148	4
A. clausi	A	B	17	2.67	0.229	4
A. clausi	A	B	15	2.67	0.216	4
A. clausi	A	B	15	2.67	0.094	4
A. clausi	A	B	15	2.67	0.121	4
A. clausi	A	B	17	2.67	0.162	4
A. clausi	A	B	17	2.67	0.162	4
A. clausi	A	B	15	2.67	0.148	4
A. clausi	A	B	15	2.67	0.135	4
A. clausi	A	B	17.7	2.67	0.23	44
A. clausi	A	B	20.3	2.67	0.22	44
A. clausi	A	B	17.1	2.67	0.07	44
A. clausi	A	B	11.5	3.9	0.009	57
A. clausi	A	B	11.5	3.9	0.002	57
A. clausi	A	B	11.5	3.9	0.006	57
A. clausi	A	B	11.5	3.9	0.008	57
A. clausi	A	B	11.5	3.9	0.001	57
A. clausi	A	B	11.5	3.9	0.001	57
A. clausi	A	B	11.5	3.9	0.006	57
A. clausi	A	B	11.5	3.9	0.004	57
A. clausi	A	B	11.5	3.9	0.024	57
A. clausi	A	B	11.5	3.9	0.015	57

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Acartia clausi	A	B	11.5	3.9	0.010	57
A. clausi	A	B	8.5	3.9	0.000	57
A. clausi	A	B	8.5	3.9	0.000	57
A. clausi	A	B	8.5	3.9	0.000	57
A. clausi	A	B	8.5	3.9	0.000	57
A. clausi	A	B	8.5	3.9	0.000	57
A. clausi	A	B	8.5	3.9	0.000	57
A. clausi	A	B	8.5	3.9	0.000	57
A. clausi	A	B	8.5	3.9	0.000	57
A. clausi	A	B	8.5	3.9	0.006	57
A. clausi	A	B	8.5	3.9	0.000	57
A. clausi	A	B	8.5	3.9	0.002	57
A. clausi	A	B	8.5	3.9	0.003	57
A. clausi	A	B	7.5	3.9	0.004	57
A. clausi	A	B	7.5	3.9	0.002	57
A. clausi	A	B	7.5	3.9	0.002	57
A. clausi	A	B	7.5	3.9	0.003	57
A. clausi	A	B	7.5	3.9	0.004	57
A. clausi	A	B	7.5	3.9	0.000	57
A. clausi	A	B	7.5	3.9	0.006	57
A. clausi	A	B	7.5	3.9	0.002	57
A. clausi	A	B	7.5	3.9	0.001	57
A. clausi	A	B	6.5	3.9	0.044	57
A. clausi	A	B	6.5	3.9	0.018	57
Acartia erythraea	A	B	26	4.0	0.089	5
Acartia fossae	A	B	23.2	5.13	0.031	6
A. fossae	A	B	21.3	5.13	0.038	6
A. fossae	A	B	23.0	5.13	0.041	6
A. fossae	A	B	22.9	5.13	0.083	6
A. fossae	A	B	22.2	5.13	0.043	6
Acartia grani	A	B	16.9	4.0	0.20	44
A. grani	A	B	16.0	4.0	0.14	44
A. grani	A	B	18.0	4.0	0.59	44
A. grani	A	B	17.7	4.0	0.35	44
A. grani	A	B	20.3	4.0	0.29	44
A. grani	A	B	25.0	4.0	0.20	44
A. grani	A	B	17.1	4.0	0.08	44
A. grani	A	B	17.8	4.0	0.03	44
A. grani	A	B	16.0	4.0	0.03	44
A. grani	A	B	14.6	4.0	0.00	44
Acartia hudsonica	A	B	4	2.5	0.28	52
A. hudsonica	A	B	4	2.5	0.26	52
A. hudsonica	A	B	4	2.5	0.13	52
A. hudsonica	A	B	4	2.5	0.20	52
A. hudsonica	A	B	4	2.5	0.25	52

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Acartia hudsonica	A	B	4	6.49	0.157	34
A. hudsonica	A	B	4	6.93	0.172	34
A. hudsonica	A	B	4	7.17	0.151	34
A. hudsonica	A	B	4	7.64	0.138	34
A. hudsonica	A	B	4	7.39	0.130	34
A. hudsonica	A	B	4	7.34	0.194	34
A. hudsonica	A	B	4	7.23	0.158	34
A. hudsonica	A	B	4	5.99	0.137	34
A. hudsonica	A	B	8	5.91	0.171	34
A. hudsonica	A	B	8	4.88	0.127	34
A. hudsonica	A	B	8	4.74	0.085	34
A. hudsonica	A	B	8	6.61	0.249	34
A. hudsonica	A	B	12	5.44	0.314	34
A. hudsonica	A	B	12	5.79	0.406	34
A. hudsonica	A	B	12	5.32	0.331	34
A. hudsonica	A	B	16	4.37	0.468	34
A. hudsonica	A	B	16	4.17	0.326	34
Acartia lilljeborgi	A	B	28	3.37	1.123	59
A. lilljeborgi	A	B	28	3.37	0.440	59
A. lilljeborg/ A. spinata	C	B	28	0.214	0.718	58
A. lilljeborg/ A. spinata	C	B	28	0.445	0.745	58
A. lilljeborg/ A. spinata	C	B	28	0.817	0.843	58
A. lilljeborg/ A. spinata	C	B	28	0.312	0.820	58
A. lilljeborg/ A. spinata	C	B	28	0.706	0.820	58
A. lilljeborg/ A. spinata	C	B	28	0.328	0.204	58
A. lilljeborg/ A. spinata	C	B	28	1.211	0.597	58
A. lilljeborg/ A. spinata	C	B	28	0.211	0.684	58
A. lilljeborg/ A. spinata	C	B	28	0.352	0.843	58
A. lilljeborg/ A. spinata	C	B	28	0.584	0.921	58
A. lilljeborg/ A. spinata	N	B	28	0.023	0.558	60
A. lilljeborg/ A. spinata	N	B	28	0.041	0.399	60
A. lilljeborg/ A. spinata	N	B	28	0.035	0.421	60

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Acartia lilljeborg/						
A. spinata	N	B	28	0.018	0.620	60
A. lilljeborg/						
A. spinata	N	B	28	0.034	0.537	60
A. lilljeborg/						
A. spinata	N	B	28	0.017	0.562	60
A. lilljeborg/						
A. spinata	N	B	28	0.033	0.787	60
A. lilljeborg/						
A. spinata	N	B	28	0.014	0.620	60
A. lilljeborg/						
A. spinata	N	B	28	0.014	0.625	60
A. lilljeborg/						
A. spinata	N	B	28	0.034	0.876	60
Acartia longiremis/						
A. tonsa	A	B	3	3.0	0.040	7
A. longiremis	A	B	16.5	4.4	0.13	8
A. longiremis	A	B	16.5	4.4	0.03	8
A. longiremis	A	B	16.5	4.4	0.07	8
A. longiremis	A	B	16.5	4.4	0.05	8
A. longiremis	A	B	16.5	4.4	0.09	8
A. longiremis	A	B	16.5	4.4	0.05	8
A. longiremis	C	B	16.5	0.48	0.22	8
A. longiremis	C	B	16.5	0.80	0.11	8
A. longiremis	A	B	10.0	11.35	0.0541	67
A. longiremis	A	B	10.0	11.35	0.0541	67
A. longiremis	A	B	10.0	12.99	0.0473	67
A. longiremis	A	B	10.0	11.35	0.0541	67
A. longiremis	A	B	10.0	8.50	0.0722	67
A. longiremis	A	B	10.0	11.35	0.0541	67
A. longiremis	A	B	10.0	8.50	0.0722	67
A. longiremis	A	B	10.0	14.77	0.0416	67
A. longiremis	A	B	10.0	11.35	0.0541	67
A. longiremis	A	B	10.0	8.50	0.3994	67
A. longiremis	A	B	10.0	14.77	0.2299	67
A. longiremis	A	B	10.0	11.35	0.2993	67
A. longiremis	A	B	10.0	8.50	0.3994	67
A. longiremis	A	B	10.0	11.35	0.2993	67
A. longiremis	A	B	10.0	11.35	0.1529	67
A. longiremis	A	B	10.0	11.35	0.1529	67
A. longiremis	A	B	10.0	9.86	0.1761	67
A. longiremis	A	B	10.0	12.99	0.1336	67
A. longiremis	A	B	10.0	12.99	0.0981	67
A. longiremis	A	B	10.0	11.35	0.1122	67
A. longiremis	A	B	10.0	11.35	0.1122	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Acartia longiremis	A	B	10.0	11.35	0.1122	67
A. longiremis	A	B	10.0	12.99	0.0981	67
A. longiremis	A	B	10.0	11.35	0.0486	67
A. longiremis	A	B	10.0	11.35	0.1034	67
A. longiremis	A	B	10.0	14.77	0.0795	67
A. longiremis	A	B	10.0	12.99	0.0828	67
A. longiremis	A	B	10.0	12.99	0.0828	67
A. longiremis	A	B	10.0	14.77	0.2262	67
A. longiremis	A	B	10.0	14.77	0.2262	67
A. longiremis	A	B	10.0	12.99	0.0870	67
A. longiremis	A	B	10.0	16.72	0.0514	67
A. longiremis	A	B	10.0	16.72	0.1421	67
A. longiremis	A	B	10.0	16.72	0.1163	67
A. longiremis	A	B	10.0	16.72	0.0415	67
A. longiremis	A	B	10.0	14.77	0.0000	67
A. longiremis	A	B	10.0	9.86	0.0000	67
A. longiremis	A	B	10.0	12.99	0.0599	67
A. longiremis	A	B	10.0	12.99	0.0599	67
A. longiremis	A	B	10.0	14.77	0.0526	67
A. longiremis	A	B	10.0	9.86	0.0789	67
A. longiremis	A	B	10.0	14.77	0.0526	67
A. longiremis	A	B	10.0	14.77	0.0526	67
A. longiremis	A	B	10.0	12.99	0.0599	67
A. longiremis	A	B	10.0	14.77	0.0526	67
A. longiremis	A	B	10.0	11.35	0.0000	67
A. longiremis	A	B	10.0	11.35	0.0000	67
A. longiremis	A	B	10.0	11.35	0.0000	67
A. longiremis	A	B	10.0	11.35	0.0000	67
A. longiremis	A	B	10.0	14.77	0.0000	67
A. longiremis	A	B	10.0	12.99	0.0685	67
A. longiremis	A	B	10.0	11.35	0.0783	67
A. longiremis	A	B	10.0	11.35	0.3341	67
A. longiremis	A	B	10.0	12.99	0.0000	67
A. longiremis	A	B	10.0	11.35	0.1446	67
A. longiremis	A	B	10.0	11.35	0.1446	67
A. longiremis	A	B	10.0	16.72	0.0706	67
A. longiremis	A	B	10.0	12.99	0.0909	67
A. longiremis	A	B	10.0	11.35	0.1086	67
A. longiremis	A	B	10.0	7.28	0.1693	67
A. longiremis	A	B	10.0	12.99	0.0538	67
A. longiremis	A	B	10.0	11.35	0.0616	67
A. longiremis	A	B	10.0	14.77	0.0473	67
A. longiremis	A	B	10.0	14.77	0.0473	67
A. longiremis	A	B	10.0	11.35	0.0616	67
A. longiremis	A	B	10.0	14.77	0.0473	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Acartia longiremis	A	B	10.0	8.50	0.0000	67
A. longiremis	A	B	10.0	11.35	0.0000	67
A. longiremis	A	B	10.0	8.50	0.0000	67
A. longiremis	A	B	10.0	12.99	0.2021	67
A. longiremis	A	B	10.0	11.35	0.0235	67
A. longiremis	A	B	10.0	11.35	0.0235	67
A. longiremis	A	B	10.0	9.86	0.4682	67
A. longiremis	A	B	10.0	14.77	0.0000	67
A. longiremis	A	B	10.0	12.99	0.0000	67
A. longiremis	A	B	10.0	11.35	0.0000	67
A. longiremis	A	B	10.0	11.35	0.0290	67
A. longiremis	A	B	14.0	11.35	0.0100	67
A. longiremis	A	B	14.0	12.99	0.0088	67
A. longiremis	A	B	14.0	11.35	0.0100	67
A. longiremis	A	B	14.0	11.35	0.0100	67
A. longiremis	A	B	14.0	14.77	0.0000	67
A. longiremis	A	B	14.0	11.35	0.0000	67
A. longiremis	A	B	14.0	14.77	0.0000	67
A. longiremis	A	B	14.0	11.35	0.0068	67
A. longiremis	A	B	14.0	12.99	0.0059	67
A. longiremis	A	B	14.0	14.77	0.0517	67
A. longiremis	A	B	14.0	12.99	0.0588	67
A. longiremis	A	B	14.0	11.35	0.0494	67
A. longiremis	A	B	14.0	11.35	0.0494	67
A. longiremis	A	B	14.0	16.72	0.0335	67
A. longiremis	A	B	14.0	12.99	0.0400	67
A. longiremis	A	B	14.0	9.86	0.0527	67
A. longiremis	A	B	14.0	16.72	0.0504	67
A. longiremis	A	B	14.0	16.72	0.0504	67
A. longiremis	A	B	14.0	12.99	0.0777	67
A. longiremis	A	B	14.0	9.86	0.1023	67
A. longiremis	A	B	14.0	11.35	0.0889	67
A. longiremis	A	B	14.0	14.77	0.0683	67
A. longiremis	A	B	14.0	11.35	0.1639	67
A. longiremis	A	B	14.0	16.72	0.1113	67
A. longiremis	A	B	14.0	11.35	0.0518	67
A. longiremis	A	B	14.0	12.99	0.0453	67
A. longiremis	A	B	14.0	11.35	0.0518	67
A. longiremis	A	B	14.0	12.99	0.0000	67
A. longiremis	A	B	14.0	11.35	0.0000	67
A. longiremis	A	B	14.0	14.77	0.0000	67
A. longiremis	A	B	14.0	12.99	0.0000	67
A. longiremis	A	B	14.0	12.99	0.0000	67
A. longiremis	A	B	14.0	12.99	0.0000	67
A. longiremis	A	B	14.0	12.99	0.0000	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Acartia negligens	A	B	23.0	3.35	0.081	69
Acartia omori	A	B	7.8	2.67	0.402	9
A. omori	A	B	9.5	2.67	0.334	9
A. omori	A	B	9.5	2.67	0.524	9
A. omori	A	B	13.0	2.67	0.507	9
A. omori	A	B	12.7	2.67	0.487	9
A. omori	A	B	19.5	2.67	0.491	9
A. omori	A	B	19.5	2.67	0.522	9
Acartia pacifica	A	B	22	4.0	0.066	5
Acartia tonsa	A	B	28	1.98	1.234	59
A. tonsa	A	B	19	2.37	0.6	10
A. tonsa	A	B	23	1.77	0.5	10
A. tonsa	A	B	28	1.43	1.0	10
A. tonsa	A	B	26	2.13	1.0	10
A. tonsa	A	B	19	2.46	0.55	10
A. tonsa	A	B	14	2.46	0.25	10
A. tonsa	A	B	17.3	4.0	0.12	11
A. tonsa	A	B	16.4	4.0	0.04	11
A. tonsa	A	B	14.4	4.0	0.04	11
A. tonsa	A	B	15.8	4.0	0.10	11
A. tonsa	A	B	17.7	4.0	0.23	11
A. tonsa	A	B	18.0	4.0	0.29	11
A. tonsa	A	B	20.2	4.0	0.35	11
A. tonsa	A	B	21.4	4.0	0.08	11
A. tonsa	A	B	21.5	4.0	0.21	11
A. tonsa	A	B	21.4	4.0	0.13	11
A. tonsa	A	B	20.1	3.98	0.295	12
A. tonsa	A	B	26.2	3.98	0.116	12
A. tonsa	A	B	20.8	4.20	0.033	13
A. tonsa	A	B	20.8	5.00	0.322	13
A. tonsa	A	B	20.8	4.40	0.314	13
A. tonsa	A	B	20.8	4.40	0.240	13
A. tonsa	A	B	20.8	4.60	0.240	13
A. tonsa	A	B	20.8	5.60	0.296	13
A. tonsa	A	B	20.8	5.00	0.239	13
A. tonsa	A	B	20.8	3.40	0.041	13
A. tonsa	A	B	20.8	3.40	0.135	13
A. tonsa	A	B	20.8	4.80	0.355	13
A. tonsa	A	B	20.8	5.00	0.239	13
A. tonsa	A	B	20.8	4.00	0.276	13
A. tonsa	A	B	20.8	6.20	0.267	13
A. tonsa	A	B	20.8	4.20	0.055	13
A. tonsa	A	B	20.8	5.20	0.425	13
A. tonsa	A	B	20.8	5.00	0.469	13
A. tonsa	A	B	22.5	3.98	0.47	45

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Acartia tonsa	A	B	21.0	3.98	0.03	45
A. tonsa	A	B	24.6	3.98	0.64	50
A. tonsa	A	B	25.1	3.98	0.33	50
A. tonsa	A	B	25.9	3.98	0.30	50
A. tonsa	A	B	25.7	3.98	0.45	50
A. tonsa	A	B	25.7	3.98	0.38	50
A. tonsa	A	B	13.3	3.98	0.27	50
A. tonsa	A	B	13.3	3.98	0.34	50
A. tonsa	A	B	17.2	3.98	0.24	50
A. tonsa	A	B	17.7	3.98	0.18	50
A. tonsa	A	B	17.8	3.98	0.82	50
A. tonsa	A	B	16.5	3.98	0.80	50
A. tonsa	A	B	13.0	3.98	0.16	50
A. tonsa	A	B	15.7	3.98	0.32	50
A. tonsa	A	B	15.2	3.98	0.22	50
A. tonsa	A	B	25.6	3.98	1.48	50
A. tonsa	A	B	27.8	3.98	1.06	50
A. tonsa	A	B	25.9	3.98	0.81	50
A. tonsa	A	B	9	3.98	0.57	50
A. tonsa	A	B	13	3.98	0.50	50
A. tonsa	A	B	25	3.98	0.46	50
A. tonsa	A	B	26.5	3.98	0.98	50
A. tonsa	A	B	28	3.98	1.21	50
A. tonsa	A	B	29	3.98	1.62	50
A. tonsa	A	B	28.5	3.98	1.04	50
A. tonsa	A	B	26	3.98	1.36	50
A. tonsa	A	B	24.5	3.98	1.47	50
A. tonsa	A	B	20	3.98	0.58	50
A. tonsa	A	B	13.5	3.98	0.38	50
A. tonsa	A	B	12	3.98	0.05	50
A. tonsa	A	B	18.5	3.98	0.49	50
A. tonsa	A	B	9.5	3.98	0.51	50
A. tonsa	A	B	14	3.98	0.32	50
A. tonsa	A	B	23	3.98	0.69	50
A. tonsa	A	B	26	3.98	0.95	50
A. tonsa	A	B	28	3.98	0.98	50
A. tonsa	A	B	29	3.98	1.12	50
A. tonsa	A	B	29	3.98	1.14	50
A. tonsa	A	B	26	3.98	1.20	50
A. tonsa	A	B	25	3.98	1.13	50
A. tonsa	A	B	20	3.98	0.86	50
A. tonsa	A	B	16.5	3.98	0.53	50
A. tonsa	A	B	17.5	3.98	0.23	50
A. tonsa	A	B	19	3.98	0.86	50
A. tonsa	A	B	16.8	3.0	0.39	53

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Acartia tonsa	A	B	23.5	3.0	0.22	53
A. tonsa	A	B	26.9	3.0	0.69	53
A. tonsa	A	B	27.6	3.0	0.23	53
A. tonsa	A	B	17.1	3.0	0.21	53
A. tonsa	A	B	18.7	3.0	0.53	53
A. tonsa	A	B	19.3	3.0	0.63	53
A. tonsa	A	B	20.0	3.0	0.64	53
A. tonsa	A	B	27.2	3.0	0.35	53
A. tonsa	A	B	29.4	3.0	0.40	53
A. tonsa	A	B	26.0	3.0	0.67	53
A. tonsa	A	B	24.2	3.0	0.77	53
A. tonsa	A	B	15.8	3.0	0.24	53
A. tonsa	A	B	19.0	3.98	0.012	55
A. tonsa	A	B	19.0	3.98	0.358	55
A. tonsa	A	B	19.0	3.98	0.462	55
A. tonsa	A	B	19.0	3.98	0.613	55
A. tonsa	A	B	19.0	3.98	0.058	55
A. tonsa	A	B	19.0	3.98	0.104	55
A. tonsa	A	B	19.0	3.98	0.116	55
A. tonsa	A	B	19.0	3.98	0.647	55
A. tonsa	A	B	19.0	3.98	0.462	55
A. tonsa	A	B	19.0	3.98	0.532	55
A. tonsa	A	B	19.0	3.98	0.578	55
A. tonsa	A	B	19.0	3.98	0.451	55
A. tonsa	A	B	19.0	3.98	0.578	55
A. tonsa	A	B	19.0	3.98	0.370	55
A. tonsa	A	B	19.0	3.98	0.613	55
A. tonsa	A	B	15.0	3.98	0.104	55
A. tonsa	A	B	15.0	3.98	0.046	55
A. tonsa	A	B	15.0	3.98	0.035	55
Acartia tumida	A	B	6	24.0	0.006	51
A. tumida	A	B	6	24.0	0.010	51
A. tumida	A	B	6	24.0	0.009	51
A. tumida	A	B	6	24.0	0.053	51
A. tumida	A	B	6	24.0	0.029	51
A. tumida	A	B	6	24.0	0.027	51
A. tumida	A	B	6	24.0	0.109	51
A. tumida	A	B	6	24.0	0.147	51
A. tumida	A	B	6	24.0	0.147	51
A. tumida	A	B	6	24.0	0.080	51
A. tumida	A	B	6	24.0	0.160	51
A. tumida	A	B	6	24.0	0.229	51
A. tumida	A	B	6	24.0	0.072	51
A. tumida	A	B	6	24.0	0.037	51
A. tumida	A	B	6	24.0	0.053	51

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Acartia tumida	A	B	6	24.0	0.083	51
Acartia sp.	A	B	7.5	2.67	0.324	14
Acartia sp.	A	B	9.0	2.67	0.153	14
Acartia spp.	A	B	12	2.67	0.030	25
Acartia spp.	A	B	12	2.67	0.187	25
Acartia spp.	A	B	12	2.67	0.143	25
Acartia spp.	A	B	12	2.67	0.276	25
Acartia spp.	A	B	12	2.67	0.020	25
Acartia spp.	A	B	27.5	2.62	0.002	69
Acartia spp.	A	B	23.0	4.43	0.008	69
Acartia spp.	A	B	22.0	3.79	0.025	69
Acartia spp.	A	B	21.5	3.34	0.014	69
Calanidae:						
Calanoides acutus	A	B	3.5	228.0	0.013	15
C. acutus	A	B	0.5	135.0	0.036	16
C. acutus	A	B	0.5	135.0	0.039	16
C. acutus	A	B	0.5	135.0	0.030	16
C. acutus	A	B	0.5	135.0	0.062	16
C. acutus	A	B	0.5	135.0	0.066	16
C. acutus	A	B	0.5	135.0	0.007	16
C. acutus	A	B	0.5	135.0	0.011	16
C. acutus	A	B	0.5	135.0	0.016	16
C. acutus	A	B	0.5	135.0	0.018	16
C. acutus	A	B	0.5	135.0	0.036	16
C. acutus	A	B	0.5	135.0	0.046	16
C. acutus	A	B	0.5	135.0	0.030	16
C. acutus	A	B	0.5	135.0	0.041	16
C. acutus	A	B	0.5	135.0	0.039	16
C. acutus	A	B	0.5	135.0	0.039	16
C. acutus	A	B	0.5	135.0	0.064	16
C. acutus	A	B	0.5	135.0	0.036	16
C. acutus	A	B	0.5	135.0	0.027	16
C. acutus	A	B	0.5	135.0	0.052	16
C. acutus	A	B	0.5	135.0	0.053	16
C. acutus	A	B	0.5	135.0	0.021	16
C. acutus	A	B	1	135.0	0.014	35
C. acutus	A	B	1	135.0	0.025	35
C .acutus	A	B	1	135.0	0.032	35
C. acutus	A	B	1	135.0	0.037	35
C. acutus	A	B	1	135.0	0.043	35
C. acutus	A	B	1	135	0.080	35
Calanoides carinatus	A	B	17	49.2	0.096	66
Calanus agulhensis	A	B	17	81.0	0.056	66
C. agulhensis	A	B	19	80.8	0.03	17
C. agulhensis	A	B	19	80.8	0.03	17

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Calanus agulhensis	A	B	19	80.8	0.02	17
C. agulhensis	A	B	19	80.8	0.02	17
C. agulhensis	A	B	19	80.8	0.02	17
C. agulhensis	A	B	19	80.8	0.01	17
C. agulhensis	A	B	19	80.8	0.04	17
C. agulhensis	A	B	19	80.8	0.02	17
C. agulhensis	A	B	19	80.8	0.04	17
C. agulhensis	A	B	19	80.8	0.04	17
C. agulhensis	A	B	19	80.8	0.03	17
C. agulhensis	A	B	19	80.8	0.02	17
C. agulhensis	C	B	19	1.6	0.42	17
C. agulhensis	C	B	19	3.6	0.26	17
C. agulhensis	C	B	19	3.6	0.43	17
C. agulhensis	C	B	19	8.8	0.23	17
C. agulhensis	C	B	19	8.8	0.21	17
C. agulhensis	C	B	19	18.4	0.07	17
C. agulhensis	C	B	19	18.4	0.10	17
C. agulhensis	C	B	19	38.8	0.05	17
C. agulhensis	C	B	19	38.8	0.06	17
C. agulhensis	C	B	19	1.6	0.24	17
C. agulhensis	C	B	19	1.6	0.63	17
C. agulhensis	C	B	19	3.6	0.34	17
C. agulhensis	C	B	19	3.6	0.33	17
C. agulhensis	C	B	19	8.8	0.29	17
C. agulhensis	C	B	19	8.8	0.26	17
C. agulhensis	C	B	19	18.4	0.13	17
C. agulhensis	C	B	19	18.4	0.10	17
C. agulhensis	C	B	19	38.8	0.07	17
C. agulhensis	C	B	19	38.8	0.02	17
C. agulhensis	N	B	19	0.8	0.42	17
C. agulhensis	N	B	19	0.8	0.45	17
C. agulhensis	C	B	19	1.6	0.55	17
C. agulhensis	C	B	19	1.6	0.54	17
C. agulhensis	C	B	19	3.6	0.51	17
C. agulhensis	C	B	19	3.6	0.58	17
C. agulhensis	C	B	19	8.8	0.46	17
C. agulhensis	C	B	19	8.8	0.28	17
C. agulhensis	C	B	19	18.4	0.22	17
C. agulhensis	C	B	19	18.4	0.16	17
C. agulhensis	C	B	19	38.8	0.07	17
C. agulhensis	C	B	19	38.8	0.08	17
C. agulhensis	N	B	19	0.8	0.49	17
C. agulhensis	N	B	19	0.8	0.58	17
C. agulhensis	C	B	19	1.6	0.45	17
C. agulhensis	C	B	19	1.6	0.45	17

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Calanus agulhensis	C	B	19	3.6	0.33	17
C. agulhensis	C	B	19	3.6	0.39	17
C. agulhensis	C	B	19	8.8	0.37	17
C. agulhensis	C	B	19	8.8	0.22	17
C. agulhensis	C	B	19	18.4	0.17	17
C. agulhensis	C	B	19	18.4	0.22	17
C. agulhensis	C	B	19	38.8	0.10	17
C. agulhensis	C	B	19	38.8	0.08	17
C. agulhensis	N	B	19	0.8	0.35	17
C. agulhensis	N	B	19	0.8	0.51	17
C. agulhensis	C	B	19	1.6	0.37	17
C. agulhensis	C	B	19	1.6	0.52	17
C. agulhensis	C	B	19	3.6	0.26	17
C. agulhensis	C	B	19	3.6	0.40	17
C. agulhensis	C	B	19	8.8	0.18	17
C. agulhensis	C	B	19	8.8	0.23	17
C. agulhensis	C	B	19	18.4	0.26	17
C. agulhensis	C	B	19	18.4	0.23	17
C. agulhensis	C	B	19	38.8	0.24	17
C. agulhensis	C	B	19	38.8	0.12	17
C. agulhensis	N	B	19	0.8	0.54	17
C. agulhensis	N	B	19	0.8	0.56	17
C. agulhensis	C	B	19	1.6	0.50	17
C. agulhensis	C	B	19	1.6	0.47	17
C. agulhensis	C	B	19	3.6	0.46	17
C. agulhensis	C	B	19	3.6	0.45	17
C. agulhensis	C	B	19	8.8	0.21	17
C. agulhensis	C	B	19	8.8	0.27	17
C. agulhensis	C	B	19	18.4	0.21	17
C. agulhensis	C	B	19	18.4	0.13	17
C. agulhensis	C	B	19	38.8	0.10	17
C. agulhensis	C	B	19	38.8	0.15	17
C. agulhensis	A	B	11	81.0	0.150	43
C. agulhensis	A	B	14	81.0	0.027	43
Calanus chilensis	A	B	14	56.1	0.111	55
C. chilensis	A	B	14	56.1	0.000	55
C. chilensis	A	B	14	56.1	0.000	55
C. chilensis	A	B	14	56.1	0.047	55
C. chilensis	A	B	14	56.1	0.006	55
C. chilensis	A	B	14	56.1	0.076	55
C. chilensis	A	B	14	56.1	0.006	55
C. chilensis	A	B	14	56.1	0.147	55
C. chilensis	A	B	14	56.1	0.117	55
C. chilensis	A	B	14	56.1	0.070	55
C. chilensis	A	B	14	56.1	0.070	55

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Calanus chilensis	A	B	14	56.1	0.026	55
C. chilensis	A	B	14	56.1	0.000	55
C. chilensis	A	B	14	56.1	0.000	55
C. chilensis	A	B	14	56.1	0.003	55
C. chilensis	A	B	14	56.1	0.026	55
C. chilensis	A	B	14	56.1	0.117	55
C. chilensis	A	B	14	56.1	0.021	55
C. chilensis	A	B	14	56.1	0.000	55
C. chilensis	A	B	14	56.1	0.003	55
C. chilensis	A	B	14	56.1	0.018	55
C. chilensis	A	B	14	56.1	0.035	55
Calanus finmarchicus	C	B	7.6	1.1	0.27	62
C. finmarchicus	C	B	7.6	1.1	0.10	62
C. finmarchicus	C	B	7.6	1.1	0.09	62
C. finmarchicus	C	B	7.6	22.8	0.04	62
C. finmarchicus	C	B	7.6	22.8	0.07	62
C. finmarchicus	C	B	7.6	22.8	0.05	62
C. finmarchicus	C	B	7.6	22.8	0.05	62
C. finmarchicus	C	B	7.6	72.1	0.08	62
C. finmarchicus	C	B	7.6	72.1	0.015	62
C. finmarchicus	C	B	7.6	72.1	0.025	62
C. finmarchicus	C	B	7.6	51.1	0.005	62
C. finmarchicus	C	B	7.6	51.1	0.003	62
C. finmarchicus	C	B	7.6	51.1	0.01	62
C. finmarchicus	A	B	3	95	0.026	7
C. finmarchicus	A	B	16.5	50	0.17	8
C. finmarchicus	A	B	16.5	50	0.13	8
C. finmarchicus	A	B	16.5	50	0.05	8
C. finmarchicus	A	B	16.5	50	0.13	8
C. finmarchicus	A	B	16.5	50	0.09	8
C. finmarchicus	A	B	16.5	50	0.11	8
C. finmarchicus	A	B	0	160	0.040	18
C. finmarchicus	A	B	0	160	0.036	18
C. finmarchicus	A	B	0	160	0.044	18
C. finmarchicus	A	B	1	160	0.015	18
C. finmarchicus	A	B	1.5	160	0.009	18
C. finmarchicus	A	B	1.5	160	0.048	18
C. finmarchicus	A	B	1.5	160	0.030	18
C. finmarchicus	A	B	2.0	160	0.035	18
C. finmarchicus	A	B	7.5	119.5	0.063	14
C. finmarchicus	A	B	9.0	119.5	0.033	14
C. finmarchicus	A	B	18	119.5	0.064	4
C. finmarchicus	A	B	17	119.5	0.047	4
C. finmarchicus	A	B	17	119.5	0.057	4
C. finmarchicus	A	B	17	119.5	0.070	4

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Calanus finmarchicus	A	B	15	119.5	0.044	4
C. finmarchicus	A	B	15	119.5	0.017	4
C. finmarchicus	A	B	12	119.5	0.005	25
C. finmarchicus	A	B	12	119.5	0.000	25
C. finmarchicus	A	B	12	119.5	0.059	25
C. finmarchicus	A	B	12	119.5	0.001	25
C. finmarchicus	A	B	7	119.5	0.000	25
C. finmarchicus	A	B	7	119.5	0.032	25
C. finmarchicus	A	B	7	119.5	0.032	25
C. finmarchicus	A	B	12	119.5	0.062	25
C. finmarchicus	A	B	12	119.5	0.121	25
C. finmarchicus	A	B	12	119.5	0.050	25
C. finmarchicus	A	B	7	83.6	0.077	36
C. finmarchicus	A	B	7	83.6	0.129	36
C. finmarchicus	A	B	7	83.6	0.110	36
C. finmarchicus	A	B	7	83.6	0.062	36
C. finmarchicus	A	B	7	83.6	0.110	36
C. finmarchicus	A	B	7	83.6	0.100	36
C. finmarchicus	A	B	7	83.6	0.110	36
C. finmarchicus	A	B	7	83.6	0.110	36
C. finmarchicus	A	B	7	84.9	0.009	36
C. finmarchicus	A	B	7	84.9	0.000	36
C. finmarchicus	A	B	7	84.9	0.014	36
C. finmarchicus	A	B	7	84.9	0.005	36
C. finmarchicus	A	B	7	84.9	0.009	36
C. finmarchicus	A	B	7	75.9	0.232	36
C. finmarchicus	A	B	7	75.9	0.200	36
C. finmarchicus	A	B	7	75.9	0.163	36
C. finmarchicus	A	B	7	75.9	0.148	36
C. finmarchicus	A	B	7	75.9	0.111	36
C. finmarchicus	A	B	7	75.9	0.153	36
C. finmarchicus	A	B	7	75.9	0.126	36
C. finmarchicus	A	B	3	164.29	0.045	38
C. finmarchicus	A	B	3	164.29	0.031	38
C. finmarchicus	A	B	3	164.29	0.013	38
C. finmarchicus	A	B	3	164.29	0.028	38
C. finmarchicus	A	B	3	164.29	0.018	38
C. finmarchicus	A	B	3	164.29	0.007	38
C. finmarchicus	A	B	3	164.29	0.007	38
C. finmarchicus	A	B	3	164.29	0.040	38
C. finmarchicus	A	B	3	164.29	0.025	38
C. finmarchicus	A	B	3	164.29	0.019	38
C. finmarchicus	A	B	3	164.29	0.043	38
C. finmarchicus	A	B	3	164.29	0.024	38
C. finmarchicus	A	B	3	164.29	0.021	38

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Calanus finmarchicus	A	B	3	164.29	0.024	38
C. finmarchicus	A	B	3	164.29	0.009	38
C. finmarchicus	A	B	3	164.29	0.021	38
C. finmarchicus	A	B	3	164.29	0.055	38
C. finmarchicus	A	B	3	164.29	0.034	38
C. finmarchicus	A	B	3	164.29	0.031	38
C. finmarchicus	A	B	3	164.29	0.025	38
C. finmarchicus	A	B	3	164.29	0.018	38
C. finmarchicus	A	B	3	164.29	0.030	38
C. finmarchicus	A	B	3	164.29	0.030	38
C. finmarchicus	A	B	3	164.29	0.030	38
C. finmarchicus	A	B	3	164.29	0.022	38
C. finmarchicus	A	B	–0.75	191	0.000	41
C. finmarchicus	A	B	–0.75	191	0.001	41
C. finmarchicus	A	B	–0.75	191	0.005	41
C. finmarchicus	A	B	–0.75	191	0.005	41
C. finmarchicus	A	B	–0.75	191	0.006	41
C. finmarchicus	A	B	–0.75	191	0.002	41
C. finmarchicus	A	B	–0.75	191	0.018	41
C. finmarchicus	A	B	–0.75	191	0.015	41
C. finmarchicus	A	B	–0.75	191	0.020	41
C. finmarchicus	A	B	–0.75	191	0.007	41
C. finmarchicus	A	B	–0.75	191	0.011	41
C. finmarchicus	A	B	–0.75	191	0.005	41
C. finmarchicus	A	B	–0.75	191	0.001	41
C. finmarchicus	A	B	–0.75	191	0.002	41
C. finmarchicus	A	B	–0.75	191	0.005	41
C. finmarchicus	A	B	–0.75	191	0.000	41
C. finmarchicus	A	B	–0.75	191	0.000	41
C. finmarchicus	A	B	–0.75	191	0.000	41
C. finmarchicus	A	B	–0.75	191	0.000	41
C. finmarchicus	A	B	–0.75	191	0.000	41
C. finmarchicus	A	B	–0.75	191	0.000	41
C. finmarchicus	A	B	–0.75	191	0.000	41
Calanus glacialis	A	B	–0.75	291	0.0490	41
C. glacialis	A	B	–0.75	291	0.0210	41
C. glacialis	A	B	–0.75	291	0.0550	41
C. glacialis	A	B	–0.75	291	0.0090	41
C. glacialis	A	B	–0.75	291	0.0010	41
C. glacialis	A	B	–0.75	291	0.0010	41
C. glacialis	A	B	–0.75	291	0.0030	41
C. glacialis	A	B	–0.75	291	0.0000	41
C. glacialis	A	B	–0.75	291	0.0024	41
C. glacialis	A	B	–0.75	291	0.0029	41

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Calanus glacialis	A	B	–0.5	301	0.052	19
C. glacialis	A	B	–0.5	301	0.022	19
C. glacialis	A	B	–0.5	301	0.049	19
C. glacialis	A	B	–0.5	301	0.010	19
C. glacialis	A	B	–0.5	301	0.008	19
C. glacialis	A	B	–0.5	301	0.023	19
C. glacialis	A	B	–0.5	301	0.021	19
C. glacialis	A	B	–0.5	301	0.004	19
C. glacialis	A	B	–0.5	301	0.004	19
C. glacialis	A	B	–0.5	301	0.004	19
C. glacialis	A	B	–0.5	301	0.004	19
C. glacialis	A	B	–0.5	301	0.004	19
C. glacialis	A	B	–0.5	301	0.004	19
C. glacialis	A	B	–0.5	301	0.004	19
C. glacialis	A	B	–0.5	301	0.004	19
C. glacialis	A	B	–0.5	301	0.004	19
C. glacialis	A	B	–0.5	301	0.010	19
C. glacialis	A	B	–0.5	301	0.019	19
C. glacialis	A	B	–0.5	301	0.004	19
C. glacialis	A	B	–0.5	301	0.004	19
C. glacialis	A	B	–0.5	301	0.004	19
C. glacialis	A	B	–2.3	313.8	0.008	20
C. glacialis	A	B	–2.3	313.8	0.025	20
C. glacialis	A	B	–2.3	313.8	0.027	20
C. glacialis	A	B	–2.3	313.8	0.028	20
C. glacialis	A	B	–2.3	313.8	0.031	20
C. glacialis	A	B	–2.3	313.8	0.045	20
C. glacialis	A	B	0	490	0.035	18
C. glacialis	A	B	0	490	0.031	18
C. glacialis	A	B	0	490	0.027	18
C. glacialis	A	B	1	490	0.008	18
C. glacialis	A	B	1.5	490	0.011	18
C. glacialis	A	B	1.5	490	0.020	18
C. glacialis	A	B	1.5	490	0.014	18
C. glacialis	A	B	2	490	0.013	18
C. glacialis	A	B	–0.5	258	0.0014	39
C. glacialis	A	B	–0.5	258	0.0003	39
C. glacialis	A	B	–0.5	258	0.0005	39
C. glacialis	A	B	–0.5	258	0.0005	39
C. glacialis	A	B	–0.5	258	0.0007	39
C. glacialis	A	B	–0.5	258	0.0003	39
C. glacialis	A	B	–0.5	258	0.0005	39
C. glacialis	A	B	–0.5	258	0.0005	39
C. glacialis	A	B	–0.5	258	0.0014	39
C. glacialis	A	B	–0.5	258	0.0014	39

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Calanus glacialis	A	B	–0.5	258	0.0007	39
C. glacialis	A	B	–0.5	258	0.0051	39
C. glacialis	A	B	–0.5	258	0.0039	39
C. glacialis	A	B	–0.5	258	0.0048	39
C. glacialis	A	B	–0.5	258	0.0051	39
C. glacialis	A	B	–0.5	258	0.0019	39
C. glacialis	A	B	–0.5	258	0.0068	39
C. glacialis	A	B	–0.5	258	0.0019	39
C. glacialis	A	B	–0.5	258	0.0072	39
C. glacialis	A	B	–0.5	258	0.0324	39
C. glacialis	A	B	–0.5	258	0.0225	39
C. glacialis	A	B	–0.5	258	0.0102	39
C. glacialis	A	B	–0.5	258	0.0205	39
Calanus helgolandicus	A	B	7.5	71.10	0.040	14
C. helgolandicus	A	B	11.5	75.4	0.006	57
C. helgolandicus	A	B	11.5	75.4	0.002	57
C. helgolandicus	A	B	11.5	75.4	0.031	57
C. helgolandicus	A	B	11.5	75.4	0.004	57
C. helgolandicus	A	B	11.5	75.4	0.034	57
C. helgolandicus	A	B	11.5	75.4	0.000	57
C. helgolandicus	A	B	11.5	75.4	0.048	57
C. helgolandicus	A	B	11.5	75.4	0.053	57
C. helgolandicus	A	B	11.5	75.4	0.064	57
C. helgolandicus	A	B	11.5	75.4	0.132	57
C. helgolandicus	A	B	8.5	75.4	0.000	57
C. helgolandicus	A	B	8.5	75.4	0.000	57
C. helgolandicus	A	B	8.5	75.4	0.001	57
C. helgolandicus	A	B	8.5	75.4	0.000	57
C. helgolandicus	A	B	8.5	75.4	0.003	57
C. helgolandicus	A	B	8.5	75.4	0.000	57
C. helgolandicus	A	B	8.5	75.4	0.004	57
C. helgolandicus	A	B	8.5	75.4	0.000	57
C. helgolandicus	A	B	8.5	75.4	0.028	57
C. helgolandicus	A	B	8.5	75.4	0.000	57
C. helgolandicus	A	B	7.5	75.4	0.001	57
C. helgolandicus	A	B	7.5	75.4	0.012	57
C. helgolandicus	A	B	7.5	75.4	0.000	57
C. helgolandicus	A	B	7.5	75.4	0.004	57
C. helgolandicus	A	B	7.5	75.4	0.062	57
C. helgolandicus	A	B	7.5	75.4	0.008	57
C. helgolandicus	A	B	7.5	75.4	0.073	57
C. helgolandicus	A	B	7.5	75.4	0.034	57
C. helgolandicus	A	B	7.5	75.4	0.004	57
C. helgolandicus	A	B	7.5	75.4	0.040	57

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Calanus helgolandicus	A	B	6.5	75.4	0.028	57
C. helgolandicus	A	B	6.5	75.4	0.020	57
C. helgolandicus	A	B	6.5	75.4	0.029	57
C. helgolandicus	A	B	6.5	75.4	0.011	57
C. helgolandicus	A	B	6.5	75.4	0.006	57
C. helgolandicus	A	B	6.5	75.4	0.046	57
C. helgolandicus	A	B	6.5	75.4	0.051	57
C. helgolandicus	A	B	6.5	75.4	0.075	57
Calanus hyperboreus	A	B	–2.3	1135.8	0.002	20
C. hyperboreus	A	B	–2.3	1135.8	0.006	20
C. hyperboreus	A	B	–2.3	1135.8	0.016	20
C. hyperboreus	A	B	–2.3	1135.8	0.016	20
C. hyperboreus	A	B	0	3620	0.00034	18
C. hyperboreus	A	B	0	3620	0.00020	18
C. hyperboreus	A	B	0	3620	0.00006	18
C. hyperboreus	A	B	1	3620	0.00013	18
C. hyperboreus	A	B	1.5	3620	0.00016	18
C. hyperboreus	A	B	1.5	3620	0.00053	18
C. hyperboreus	A	B	1.5	3620	0.00010	18
C. hyperboreus	A	B	2	3620	0.00003	18
Calanus marshallae	A	B	10.0	94.73	0.049	67
C. marshallae	A	B	10.0	94.73	0.049	67
C. marshallae	A	B	10.0	60.05	0.059	67
C. marshallae	A	B	10.0	104.11	0.034	67
C. marshallae	A	B	10.0	94.73	0.078	67
C. marshallae	A	B	10.0	90.28	0.132	67
C. marshallae	A	B	10.0	104.11	0.059	67
C. marshallae	A	B	10.0	109.05	0.180	67
C. marshallae	A	B	10.0	70.32	0.105	67
C. marshallae	A	B	10.0	119.46	0.062	67
C. marshallae	A	B	10.0	155.16	0.004	67
C. marshallae	A	B	10.0	114.17	0.124	67
C. marshallae	A	B	10.0	119.46	0.084	67
C. marshallae	A	B	10.0	119.46	0.090	67
C. marshallae	A	B	10.0	90.28	0.119	67
C. marshallae	A	B	10.0	114.17	0.148	67
C. marshallae	A	B	10.0	119.46	0.152	67
C. marshallae	A	B	10.0	124.94	0.146	67
C. marshallae	A	B	10.0	109.05	0.167	67
C. marshallae	A	B	10.0	119.46	0.111	67
C. marshallae	A	B	10.0	114.17	0.117	67
C. marshallae	A	B	10.0	99.34	0.007	67
C. marshallae	A	B	10.0	124.94	0.095	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Calanus marshallae	A	B	10.0	168.65	0.071	67
C. marshallae	A	B	10.0	94.73	0.100	67
C. marshallae	A	B	10.0	119.46	0.079	67
C. marshallae	A	B	10.0	104.11	0.064	67
C. marshallae	A	B	10.0	104.11	0.064	67
C. marshallae	A	B	10.0	183.00	0.098	67
C. marshallae	A	B	10.0	114.17	0.158	67
C. marshallae	A	B	10.0	119.46	0.080	67
C. marshallae	A	B	10.0	161.8	0.031	67
C. marshallae	A	B	10.0	136.44	0.036	67
C. marshallae	A	B	10.0	104.11	0.047	67
C. marshallae	A	B	10.0	109.05	0.020	67
C. marshallae	A	B	10.0	142.48	0.015	67
C. marshallae	A	B	10.0	124.94	0.018	67
C. marshallae	A	B	10.0	99.34	0.143	67
C. marshallae	A	B	10.0	85.99	0.165	67
C. marshallae	A	B	10.0	104.11	0.092	67
C. marshallae	A	B	10.0	148.72	0.065	67
C. marshallae	A	B	10.0	155.16	0.062	67
C. marshallae	A	B	10.0	104.11	0.000	67
C. marshallae	A	B	10.0	104.11	0.186	67
C. marshallae	A	B	10.0	155.16	0.140	67
C. marshallae	A	B	10.0	114.17	0.003	67
C. marshallae	A	B	10.0	104.11	0.013	67
C. marshallae	A	B	10.0	94.73	0.198	67
C. marshallae	A	B	10.0	99.34	0.003	67
C. marshallae	A	B	10.0	136.44	0.000	67
C. marshallae	A	B	10.0	109.05	0.135	67
C. marshallae	A	B	10.0	85.99	0.000	67
C. marshallae	A	B	10.0	104.11	0.123	67
C. marshallae	A	B	10.0	85.99	0.186	67
C. marshallae	A	B	10.0	148.72	0.107	67
C. marshallae	A	B	10.0	104.11	0.059	67
C. marshallae	A	B	10.0	90.28	0.068	67
C. marshallae	A	B	10.0	104.11	0.126	67
C. marshallae	A	B	10.0	90.28	0.122	67
C. marshallae	A	B	10.0	104.11	0.183	67
C. marshallae	A	B	10.0	104.11	0.183	67
C. marshallae	A	B	10.0	104.11	0.000	67
C. marshallae	A	B	10.0	99.34	0.000	67
C. marshallae	A	B	12.0	104.11	0.000	67
Calanus pacificus	A	B	10.0	79.85	0.099	67
C. pacificus	A	B	10.0	79.85	0.154	67
C. pacificus	A	B	10.0	70.24	0.132	67
C. pacificus	A	B	10.0	73.36	0.084	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Calanus pacificus	A	B	10.0	64.24	0.096	67
C. pacificus	A	B	10.0	79.85	0.248	67
C. pacificus	A	B	10.0	83.22	0.238	67
C. pacificus	A	B	10.0	93.83	0.000	67
C. pacificus	A	B	10.0	93.83	0.114	67
C. pacificus	A	B	10.0	105.22	0.111	67
C. pacificus	A	B	14.0	79.85	0.000	67
C. pacificus	A	B	14.0	93.83	0.228	67
C. pacificus	A	B	14.0	79.85	0.067	67
C. pacificus	A	B	14.0	79.85	0.132	67
C. pacificus	A	B	14.0	86.67	0.121	67
C. pacificus	A	B	14.0	61.36	0.172	67
C. pacificus	A	B	14.0	86.67	0.189	67
Calanus simillimus	A	B	3.5	207.2	0.034	15
C. simillimus	A	B	8.0	207.2	0.005	68
C. simillimus	A	B	8.0	207.2	0.011	68
C. simillimus	A	B	8.0	207.2	0.004	68
C. simillimus	A	B	8.0	207.2	0.020	68
C. simillimus	A	B	8.0	207.2	0.044	68
C. simillimus	A	B	8.0	207.2	0.023	68
C. simillimus	A	B	8.0	207.2	0.024	68
C. simillimus	A	B	8.0	207.2	0.020	68
C. simillimus	A	B	13.5	92.46	0.000	69
Calanus tenuicornis	A	B	17	33.83	0.084	2
Calanus spp.	A	B	10.5	88.5	0.012	69
Calanus spp.	A	B	15.5	92.46	0.002	69
Calanus spp.	A	B	25.0	55.34	0.016	69
Calanus spp.	A	B	22.5	27.32	0.001	69
Calanus spp.	A	B	21.5	160.71	0.000	69
Nannocalanus minor	A	B	17	14.0	0.321	66
Neocalanus tonsus	A	B	17	219	0.016	66
Undinula vulgaris	A	B	26.25	67.7	0.030	21
U. vulgaris	A	B	26.25	67.7	0.039	21
U. vulgaris	A	B	26.25	67.7	0.021	21
U. vulgaris	A	B	26.25	67.7	0.010	21
U. vulgaris	A	B	26.25	67.7	0.008	21
U. vulgaris	A	B	26.25	67.7	0.012	21
U. vulgaris	A	B	26.25	67.7	0.028	21
U. vulgaris	A	B	26.25	67.7	0.000	21
U. vulgaris	A	B	26.25	67.7	0.013	21
U. vulgaris	A	B	26.25	67.7	0.038	21
U. vulgaris	A	B	26.25	67.7	0.051	21
U. vulgaris	A	B	26.25	67.7	0.019	21
U. vulgaris	A	B	26.25	67.7	0.011	21
U. vulgaris	A	B	26.25	67.7	0.034	21

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Undinula vulgaris	A	B	26.25	67.7	0.008	21
U. vulgaris	A	B	26.25	67.7	0.010	21
U. vulgaris	C	B	26	1.643	0.49	22
U. vulgaris	C	B	26	3.834	0.28	22
U. vulgaris	C	B	26	6.999	0.17	22
U. vulgaris	C	B	26	12.573	0.26	22
U. vulgaris	C	B	26	23.514	0.19	22
U. vulgaris	C	B	26	29.394	0.30	22
Candaciidae:						
Candacia spp.	A	B	28.0	49.95	0.002	69
Centropagidae:						
Centropages abdominalis	A	B	10.0	33.07	0.2475	67
C. abdominalis	A	B	10.0	26.53	0.3085	67
C. abdominalis	A	B	10.0	40.59	0.1927	67
C. abdominalis	A	B	10.0	40.59	0.1927	67
Centropages abdominalis	A	B	10.0	36.70	0.2044	67
C. abdominalis	A	B	10.0	33.07	0.2268	67
C. abdominalis	A	B	10.0	33.07	0.2268	67
C abdominalis	A	B	10.0	33.07	0.2268	67
C. abdominalis	A	B	10.0	33.07	0.2268	67
C. abdominalis	A	B	10.0	40.59	0.1001	67
C. abdominalis	A	B	10.0	44.74	0.0908	67
C. abdominalis	A	B	10.0	40.59	0.1001	67
C. abdominalis	A	B	10.0	40.59	0.1001	67
C. abdominalis	A	B	10.0	40.59	0.1001	67
C. abdominalis	A	B	10.0	44.74	0.1001	67
C. abdominalis	A	B	10.0	44.74	0.1001	67
C. abdominalis	A	B	10.0	40.59	0.1104	67
C. abdominalis	A	B	10.0	33.07	0.1355	67
C. abdominalis	A	B	10.0	29.68	0.1509	67
C. abdominalis	A	B	10.0	20.92	0.2142	67
C. abdominalis	A	B	10.0	44.74	0.1001	67
C. abdominalis	A	B	10.0	33.07	0.1355	67
C. abdominalis	A	B	10.0	29.68	0.1509	67
C. abdominalis	A	B	10.0	33.07	0.1355	67
C. abdominalis	A	B	10.0	36.70	0.1221	67
C. abdominalis	A	B	10.0	44.74	0.1001	67
C. abdominalis	A	B	10.0	33.07	0.1355	67
C. abdominalis	A	B	10.0	36.70	0.1221	67
C. abdominalis	A	B	10.0	40.59	0.1104	67
C. abdominalis	A	B	10.0	33.07	0.1181	67
C. abdominalis	A	B	10.0	33.07	0.0843	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Centropages abdominalis	A	B	10.0	40.59	0.1167	67
C. abdominalis	A	B	10.0	33.07	0.3539	67
C. abdominalis	A	B	10.0	26.53	0.2278	67
C. abdominalis	A	B	10.0	23.62	0.2909	67
C. abdominalis	A	B	10.0	36.70	0.1465	67
C. abdominalis	A	B	10.0	23.62	0.1597	67
C. abdominalis	A	B	10.0	29.68	0.2588	67
C. abdominalis	A	B	10.0	36.70	0.1275	67
C. abdominalis	A	B	10.0	36.70	0.1557	67
C. abdominalis	A	B	10.0	26.53	0.2243	67
C. abdominalis	A	B	10.0	40.59	0.2986	67
C. abdominalis	A	B	10.0	40.59	0.1317	67
C. abdominalis	A	B	10.0	40.59	0.1628	67
C. abdominalis	A	B	10.0	36.70	0.1074	67
C. abdominalis	A	B	10.0	36.70	0.3992	67
C. abdominalis	A	B	10.0	40.59	0.3007	67
C. abdominalis	A	B	10.0	36.70	0.1740	67
C. abdominalis	A	B	10.0	23.62	0.0000	67
C. abdominalis	A	B	10.0	40.59	0.3021	67
C. abdominalis	A	B	10.0	40.59	0.0000	67
Centropages abdominalis	A	B	10.0	36.70	0.0889	67
C. abdominalis	A	B	10.0	40.59	0.0902	67
C. abdominalis	A	B	10.0	40.59	0.2454	67
C. abdominalis	A	B	10.0	40.59	0.2385	67
C. abdominalis	A	B	10.0	44.74	0.1317	67
C. abdominalis	A	B	10.0	33.07	0.2964	67
C. abdominalis	A	B	10.0	40.59	0.0833	67
C. abdominalis	A	B	10.0	44.74	0.0755	67
C. abdominalis	A	B	10.0	44.74	0.1202	67
C. abdominalis	A	B	10.0	29.68	0.1811	67
C. abdominalis	A	B	10.0	44.74	0.2826	67
C. abdominalis	A	B	10.0	29.68	0.4259	67
C. abdominalis	A	B	10.0	44.74	0.0775	67
C. abdominalis	A	B	10.0	44.74	0.0775	67
C. abdominalis	A	B	10.0	40.59	0.0855	67
C. abdominalis	A	B	10.0	26.53	0.2366	67
C. abdominalis	A	B	10.0	29.68	0.2115	67
C. abdominalis	A	B	10.0	29.68	0.2115	67
C. abdominalis	A	B	10.0	44.74	0.1403	67
C. abdominalis	A	B	10.0	40.59	0.0498	67
C. abdominalis	A	B	10.0	44.74	0.0451	67
C. abdominalis	A	B	10.0	49.16	0.0411	67
C. abdominalis	A	B	10.0	33.07	0.2487	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Centropages abdominalis	A	B	10.0	44.74	0.1838	67
C. abdominalis	A	B	10.0	44.74	0.1838	67
C. abdominalis	A	B	10.0	49.16	0.0387	67
C. abdominalis	A	B	10.0	49.16	0.0387	67
C. abdominalis	A	B	10.0	49.16	0.0387	67
C. abdominalis	A	B	10.0	40.59	0.0654	67
C. abdominalis	A	B	10.0	33.07	0.0803	67
C. abdominalis	A	B	10.0	49.16	0.0540	67
C. abdominalis	A	B	10.0	58.86	0.0811	67
C. abdominalis	A	B	10.0	29.68	0.1609	67
C. abdominalis	A	B	10.0	23.62	0.2022	67
C. abdominalis	A	B	10.0	40.59	0.1176	67
C. abdominalis	A	B	10.0	53.87	0.0966	67
C. abdominalis	A	B	10.0	44.74	0.0523	67
C. abdominalis	A	B	10.0	40.59	0.0576	67
C. abdominalis	A	B	10.0	49.16	0.1255	67
C. abdominalis	A	B	10.0	44.74	0.1379	67
C. abdominalis	A	B	10.0	40.59	0.1520	67
C. abdominalis	A	B	10.0	40.59	0.1811	67
C. abdominalis	A	B	10.0	64.15	0.1146	67
C. abdominalis	A	B	10.0	40.59	0.1122	67
C. abdominalis	A	B	10.0	44.74	0.1018	67
C. abdominalis	A	B	10.0	53.87	0.0845	67
C. abdominalis	A	B	10.0	44.74	0.0000	67
C. abdominalis	A	B	10.0	40.59	0.0000	67
C. abdominalis	A	B	10.0	44.74	0.0000	67
C. abdominalis	A	B	10.0	44.74	0.1007	67
C. abdominalis	A	B	10.0	44.74	0.1007	67
C. abdominalis	A	B	10.0	49.16	0.0916	67
C. abdominalis	A	B	10.0	44.74	0.0405	67
C. abdominalis	A	B	10.0	40.59	0.0446	67
C. abdominalis	A	B	10.0	49.16	0.0368	67
C. abdominalis	A	B	10.0	36.70	0.1254	67
C. abdominalis	A	B	10.0	53.87	0.0855	67
C. abdominalis	A	B	10.0	36.70	0.1254	67
C. abdominalis	A	B	10.0	53.87	0.1151	67
C. abdominalis	A	B	10.0	49.16	0.1261	67
C. abdominalis	A	B	10.0	40.59	0.1528	67
C. abdominalis	A	B	10.0	44.74	0.1887	67
C. abdominalis	A	B	10.0	44.74	0.1887	67
C. abdominalis	A	B	10.0	44.74	0.1887	67
C. abdominalis	A	B	10.0	49.16	0.1718	67
C. abdominalis	A	B	10.0	49.16	0.0265	67
C. abdominalis	A	B	10.0	36.70	0.0355	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Centropages abdominalis	A	B	10.0	49.16	0.0262	67
C. abdominalis	A	B	10.0	44.74	0.0609	67
C. abdominalis	A	B	10.0	40.59	0.0671	67
C. abdominalis	A	B	10.0	36.70	0.0743	67
C. abdominalis	A	B	10.0	40.59	0.1479	67
C. abdominalis	A	B	10.0	40.59	0.2557	67
C. abdominalis	A	B	10.0	33.07	0.0000	67
C. abdominalis	A	B	10.0	40.59	0.0000	67
C. abdominalis	A	B	10.0	16.16	0.0000	67
C. abdominalis	A	B	10.0	49.16	0.0383	67
C. abdominalis	A	B	10.0	40.59	0.0464	67
C. abdominalis	A	B	10.0	26.53	0.0000	67
C. abdominalis	A	B	10.0	33.07	0.0000	67
C. abdominalis	A	B	10.0	29.68	0.0000	67
C. abdominalis	A	B	10.0	49.16	0.0789	67
C. abdominalis	A	B	10.0	36.70	0.1057	67
C. abdominalis	A	B	14.0	36.70	0.0000	67
C. abdominalis	A	B	14.0	36.70	0.0000	67
C. abdominalis	A	B	14.0	53.87	0.0808	67
C. abdominalis	A	B	14.0	40.59	0.1073	67
C. abdominalis	A	B	14.0	36.70	0.0000	67
C. abdominalis	A	B	14.0	36.70	0.0000	67
Centropages brachiatus	A	B	11	10.0	0.141	43
C. brachiatus	A	B	14	10.0	0.068	43
C. brachiatus	A	B	17	10.0	0.251	66
C. brachiatus	A	B	15.5	4.59	0.004	69
Centropages hamatus	A	B	3	7.7	0.040	7
C. hamatus	A	B	7.5	10.00	0.112	14
C. hamatus	A	B	4	10.00	0.052	4
C. hamatus	A	B	4	10.00	0.016	4
C. hamatus	A	B	5	10.00	0.028	4
C. hamatus	A	B	5	10.00	0.056	4
C. hamatus	A	B	5	10.00	0.080	4
C. hamatus	A	B	5	10.00	0.096	4
C. hamatus	A	B	5	10.00	0.092	4
C. hamatus	A	B	5	10.00	0.180	4
C. hamatus	A	B	7	10.00	0.096	4
C. hamatus	A	B	7	10.00	0.068	4
C. hamatus	A	B	7	10.00	0.076	4
C. hamatus	A	B	7	10.00	0.104	4
C. hamatus	A	B	7	10.00	0.120	4
C. hamatus	A	B	7	10.00	0.136	4

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Centropages hamatus	A	B	7	10.00	0.160	4
C. hamatus	A	B	7	10.00	0.160	4
C. hamatus	A	B	7	10.00	0.180	4
C. hamatus	A	B	7	10.00	0.232	4
C. hamatus	A	B	7	10.00	0.256	4
C. hamatus	A	B	7	10.00	0.236	4
C. hamatus	A	B	7	10.00	0.272	4
C. hamatus	A	B	7	10.00	0.304	4
C. hamatus	A	B	7	10.00	0.216	4
C. hamatus	A	B	12	10.00	0.024	4
C. hamatus	A	B	16	10.00	0.020	4
C. hamatus	A	B	16	10.00	0.008	4
C. hamatus	A	B	16	10.00	0.004	4
C. hamatus	A	B	18	10.00	0.012	4
C. hamatus	A	B	18	10.00	0.012	4
C. hamatus	A	B	17	10.00	0.016	4
C. hamatus	A	B	17	10.00	0.016	4
C. hamatus	A	B	17	10.00	0.052	4
C. hamatus	A	B	17	10.00	0.060	4
C. hamatus	A	B	17	10.00	0.064	4
C. hamatus	A	B	17	10.00	0.064	4
C. hamatus	A	B	17	10.00	0.084	4
C. hamatus	A	B	17	10.00	0.116	4
C. hamatus	A	B	17	10.00	0.068	4
C. hamatus	A	B	17	10.00	0.072	4
C. hamatus	A	B	17	10.00	0.064	4
C. hamatus	A	B	15	10.00	0.120	4
C. hamatus	A	B	15	10.00	0.084	4
C. hamatus	A	B	15	10.00	0.052	4
C. hamatus	A	B	15	10.00	0.036	4
C. hamatus	A	B	15	10.00	0.044	4
C. hamatus	A	B	15	10.00	0.060	4
C. hamatus	A	B	15	10.00	0.064	4
C. hamatus	A	B	15	10.00	0.064	4
C. hamatus	A	B	12	10.00	0.072	4
C. hamatus	A	B	12	10.00	0.044	4
C. hamatus	A	B	8	10.00	0.116	4
C. hamatus	A	B	8	10.00	0.152	4
C. hamatus	A	B	12	10.00	0.094	25
C. hamatus	A	B	7	10.00	0.068	25
C. hamatus	A	B	12	10.00	0.152	25
C. hamatus	A	B	12	10.00	0.105	25
C. hamatus	A	B	6	10.00	0.168	63
C. hamatus	A	B	6	10.00	0.204	63

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Centropages hamatus	A	B	6	10.00	0.200	63
C. hamatus	A	B	7.5	10.00	0.092	63
C. hamatus	A	B	8	10.00	0.072	63
C. hamatus	A	B	8.5	10.00	0.076	63
C. hamatus	A	B	12.5	10.00	0.020	63
C. hamatus	A	B	15.5	10.00	0.068	63
Centropages typicus	A	B	20	14.28	0.02	1
C. typicus	A	B	20	14.28	0.07	1
C. typicus	A	B	20	14.28	0.06	1
C. typicus	A	B	20	14.28	0.05	1
C. typicus	A	B	20	14.28	0.02	1
C. typicus	A	B	17	14.28	0.05	1
C. typicus	A	B	13	14.28	0.01	1
C. typicus	A	B	20	14.28	0.01	1
C. typicus	A	B	17	5.72	0.01	2
C. typicus	A	B	17	6.00	0.098	2
C. typicus	A	B	16.5	12.3	0.26	8
C. typicus	A	B	16.5	12.3	0.15	8
C. typicus	A	B	16.5	12.3	0.22	8
C. typicus	A	B	16.5	12.3	0.25	8
C. typicus	A	B	16.5	12.3	0.25	8
C. typicus	A	B	16.5	12.3	0.24	8
C. typicus	C	B	16.5	0.52	0.28	8
C. typicus	C	B	16.5	1.04	0.34	8
C. typicus	C	B	16.5	2.00	0.28	8
C. typicus	A	B	17	14.28	0.081	4
C. typicus	A	B	17	14.28	0.083	4
C. typicus	A	B	17	14.28	0.090	4
C. typicus	A	B	17	14.28	0.099	4
C. typicus	A	B	17	14.28	0.101	4
C. typicus	A	B	17	14.28	0.112	4
C. typicus	A	B	17	14.28	0.130	4
C. typicus	A	B	17	14.28	0.148	4
C. typicus	A	B	17	14.28	0.150	4
C. typicus	A	B	17	14.28	0.202	4
C. typicus	A	B	15	14.28	0.065	4
C. typicus	A	B	15	14.28	0.069	4
C. typicus	A	B	15	14.28	0.063	4
C. typicus	A	B	15	14.28	0.130	4
C. typicus	A	B	15	14.28	0.170	4
C. typicus	A	B	15	14.28	0.197	4
C. typicus	A	B	12	14.28	0.112	4
C. typicus	A	B	8	14.28	0.016	4

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Centropages typicus	A	B	15	9.96	0.033	23
C. typicus	A	B	15	10.84	0.025	23
C. typicus	A	B	15	16.72	0.055	23
C. typicus	A	B	15	13.72	0.022	23
C. typicus	A	B	10	14.72	0.024	23
C. typicus	A	B	10	16.28	0.011	23
C. typicus	A	B	10	20.32	0.030	23
C. typicus	A	B	10	17.32	0.038	23
C. typicus	A	B	10	18.80	0.027	23
C. typicus	A	B	15	9.28	0.037	23
C. typicus	A	B	12	14.28	0.043	25
C. typicus	A	B	12	14.28	0.106	25
C. typicus	A	B	7	14.28	0.000	25
C. typicus	A	B	12	14.28	0.231	25
C. typicus	A	B	12	14.28	0.074	25
C. typicus	A	B	12	14.28	0.169	25
C. typicus	A	B	19	14.28	0.047	42
C. typicus	A	B	19	14.28	0.009	42
C. typicus	A	B	19	14.28	0.001	42
C. typicus	A	B	19	14.28	0.002	42
C. typicus	A	B	19	14.28	0.001	42
C. typicus	A	B	11.5	14.1	0.144	57
C. typicus	A	B	11.5	14.1	0.018	57
C. typicus	A	B	11.5	14.1	0.041	57
C. typicus	A	B	11.5	14.1	0.186	57
C. typicus	A	B	11.5	14.1	0.007	57
C. typicus	A	B	11.5	14.1	0.045	57
C. typicus	A	B	11.5	14.1	0.116	57
C. typicus	A	B	11.5	14.1	0.075	57
C. typicus	A	B	11.5	14.1	0.054	57
C. typicus	A	B	11.5	14.1	0.003	57
C. typicus	A	B	8.5	14.1	0.000	57
C. typicus	A	B	8.5	14.1	0.011	57
C. typicus	A	B	8.5	14.1	0.022	57
C. typicus	A	B	8.5	14.1	0.001	57
C. typicus	A	B	8.5	14.1	0.018	57
C. typicus	A	B	8.5	14.1	0.011	57
C. typicus	A	B	7.5	14.1	0.000	57
C. typicus	A	B	7.5	14.1	0.029	57
C. typicus	A	B	7.5	14.1	0.023	57
C. typicus	A	B	7.5	14.1	0.039	57
C. typicus	A	B	7.5	14.1	0.005	57
C. typicus	A	B	7.5	14.1	0.003	57
C. typicus	A	B	7.5	14.1	0.006	57

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Centropages velificatus	A	B	28	6.38	0.059	59
C. velificatus	A	B	28	6.38	0.306	59
C. verificatus	C	B	28	0.442	0.62	24
C. verificatus	C	B	28	1.012	0.50	24
C. verificatus	C	B	28	2.150	0.44	24
C. verificatus	C	B	28	3.901	0.38	24
C. velificatus	C	B	28	0.832	1.000	58
C. velificatus	C	B	28	0.704	0.702	58
C. velificatus	C	B	28	0.277	0.647	58
C. velificatus	C	B	28	0.612	0.669	58
C. velificatus	C	B	28	1.251	0.758	58
C. velificatus	C	B	28	2.374	0.525	58
C. velificatus	C	B	28	4.564	0.603	58
C. velificatus	N	B	28	0.031	0.636	60
C. velificatus	N	B	28	0.107	0.336	60
C. velificatus	N	B	28	0.064	0.554	60
C. velificatus	N	B	28	0.069	0.555	60
C. velificatus	N	B	28	0.032	0.682	60
Corycaeidae:						
Corycaeus amazonicus/ C. subulatus	N	S	28	0.013	0.447	60
C. amazonicus/ C. subulatus	N	S	28	0.020	0.468	60
C. amazonicus/ C. subulatus	N	S	28	0.021	0.338	60
C. *amazonicus/ C. subulatus*	N	S	28	0.012	0.371	60
Eucalanidae:						
Eucalanus californicus	A	B	12.9	161	0.117	56
E. californicus	A	B	12.9	161	0.036	56
E. californicus	A	B	13.5	161	0.139	56
E. californicus	A	B	13.5	161	0.094	56
E. californicus	A	B	12.8	161	0.070	56
E. californicus	A	B	12.8	161	0.157	56
E. californicus	A	B	12.8	161	0.094	56
E. californicus	A	B	12.8	161	0.045	56
E. californicus	A	B	12.8	161	0.099	56
E. californicus	A	B	13.3	161	0.297	56
E. californicus	A	B	13.3	161	0.142	56
E. californicus	A	B	13.2	161	0.121	56
E. californicus	A	B	13.2	161	0.130	56
E. californicus	A	B	13.2	161	0.121	56
E. californicus	A	B	13.2	161	0.225	56

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Eucalanus californicus	A	B	13.2	161	0.130	56
E. californicus	A	B	14.4	161	0.117	56
E. californicus	A	B	14.4	161	0.152	56
E. californicus	A	B	14.4	161	0.124	56
E. californicus	A	B	14.5	161	0.038	56
E. californicus	A	B	13.9	161	0.121	56
E. californicus	A	B	13.9	161	0.088	56
E. californicus	A	B	14.2	161	0.016	56
E. californicus	A	B	15.5	161	0.023	56
E. californicus	A	B	14.0	161	0.049	56
E. californicus	A	B	14.0	161	0.003	56
E. californicus	A	B	12.8	161	0.067	56
E. californicus	A	B	12.8	161	0.045	56
E. californicus	A	B	12.5	161	0.036	56
E. californicus	A	B	12.5	161	0.070	56
E. californicus	A	B	12.5	161	0.125	56
E. californicus	A	B	12.7	161	0.163	56
E. californicus	A	B	12.7	161	0.139	56
E. californicus	A	B	12.7	161	0.067	56
E. californicus	A	B	12.7	161	0.053	56
E. californicus	A	B	12.7	161	0.042	56
E. californicus	A	B	12.7	161	0.121	56
E. californicus	A	B	13.8	161	0.075	56
E. californicus	A	B	13.8	161	0.089	56
E. californicus	A	B	13.8	161	0.099	56
E. californicus	A	B	15.3	161	0.233	56
E. californicus	A	B	15.3	161	0.113	56
E. californicus	A	B	15.3	161	0.074	56
E. californicus	A	B	15.3	161	0.056	56
E. californicus	A	B	15.3	161	0.105	56
E. californicus	A	B	16.7	161	0.097	56
E. californicus	A	B	16.5	161	0.099	56
E. californicus	A	B	15.7	161	0.022	56
E. californicus	A	B	15.9	161	0.000	56
E. californicus	A	B	15.8	161	0.000	56
E. californicus	A	B	16.2	161	0.011	56
E. californicus	A	B	12.9	161	0.000	56
E. californicus	A	B	12.9	161	0.085	56
E. californicus	A	B	12.9	161	0.023	56
E. californicus	A	B	12.9	161	0.056	56
E. californicus	A	B	12.9	161	0.039	56
E. californicus	A	B	13.6	161	0.111	56
E. californicus	A	B	12.0	161	0.05	67
E. californicus	A	B	12.0	161	0.04	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Rhincalanus gigas	A	B	3.5	706.0	0.012	15
Rhincalanus nasutus	A	B	17	150	0.017	66
Euchaetidae:						
Euchaeta marina	C	S	26	3.159	0.38	22
E. marina	C	S	26	5.965	0.38	22
E. marina	C	S	26	11.501	0.24	22
E. marina	C	S	26	20.883	0.29	22
E. marina	C	S	26	39.179	0.24	22
Euchaeta spp.	A	S	27.5	64.64	0.000	69
Euchaeta spp.	A	S	27.5	63.80	0.008	69
Euchaeta spp.	A	S	25.0	99.30	0.011	69
Euchaeta spp.	A	S	22.5	119.23	0.000	69
Macrosetellidae:						
Macrosetella spp.	A	S	23.5	2.24	0.014	69
Macrosetella spp.	A	S	28.0	2.24	0.019	69
Macrosetella spp.	A	S	27.0	1.80	0.012	69
Metridiidae:						
Metridia gerlachei	A	B	0	98.8	0.008	37
M. gerlachei	A	B	0	98.8	0.010	37
M. gerlachei	A	B	0	98.8	0.018	37
M. gerlachei	A	B	0	98.8	0.013	37
M. gerlachei	A	B	0	98.8	0.011	37
M. gerlachei	A	B	0	98.8	0.000	37
M. gerlachei	A	B	0	98.8	0.001	37
M. gerlachei	A	B	0	98.8	0.000	37
Metridia lucens	A	B	11.5	26.2	0.007	57
M. lucens	A	B	11.5	26.2	0.015	57
M. lucens	A	B	11.5	26.2	0.006	57
M. lucens	A	B	11.5	26.2	0.0005	57
M. lucens	A	B	8.5	26.2	0.000	57
M. lucens	A	B	8.5	26.2	0.000	57
M. lucens	A	B	8.5	26.2	0.003	57
M. lucens	A	B	8.5	26.2	0.000	57
M. lucens	A	B	8.5	26.2	0.000	57
M. lucens	A	B	8.5	26.2	0.012	57
M. lucens	A	B	8.5	26.2	0.000	57
M. lucens	A	B	8.5	26.2	0.002	57
M. lucens	A	B	7.5	26.2	0.001	57
M. lucens	A	B	7.5	26.2	0.000	57
M. lucens	A	B	7.5	26.2	0.001	57
M. lucens	A	B	7.5	26.2	0.0005	57

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Metridia lucens	A	B	7.5	26.2	0.014	57
M. lucens	A	B	6.5	26.2	0.001	57
M. lucens	A	B	6.5	26.2	0.010	57
M. lucens	A	B	6.5	26.2	0.016	57
M. lucens	A	B	6.5	26.2	0.010	57
M. lucens	A	B	6.5	26.2	0.010	57
M. lucens	A	B	6.5	26.2	0.005	57
M. lucens	A	B	6.5	26.2	0.012	57
Oithonidae:						
Oithona aruensis	A	S	24.9	0.297	0.088	64
O. aruensis	A	S	22.2	0.297	0.020	64
O. aruensis	A	S	29.5	0.297	0.058	64
O. aruensis	A	S	28.8	0.297	0.015	64
Oithona davisae	A	S	18.1	0.221	0.034	65
O. davisae	A	S	18.0	0.222	0.191	65
O. davisae	A	S	17.6	0.229	0.217	65
O. davisae	A	S	15.8	0.226	0.076	65
O. davisae	A	S	16.2	0.223	0.029	65
O. davisae	A	S	15.4	0.219	0.062	65
O. davisae	A	S	14.6	0.226	0.044	65
O. davisae	A	S	14.5	0.229	0.041	65
O. davisae	A	S	14.2	0.228	0.061	65
O. davisae	A	S	14.0	0.230	0.042	65
O. davisae	A	S	14.0	0.230	0.040	65
O. davisae	A	S	13.1	0.232	0.029	65
O. davisae	A	S	12.4	0.232	0.023	65
O. davisae	A	S	12.4	0.230	0.013	65
O. davisae	A	S	11.8	0.237	0.016	65
O. davisae	A	S	11.1	0.237	0.013	65
O. davisae	A	S	10.7	0.234	0.022	65
O. davisae	A	S	10.2	0.236	0.016	65
O. davisae	A	S	10.0	0.235	0.017	65
O. davisae	A	S	9.5	0.235	0.024	65
O. davisae	A	S	9.0	0.238	0.013	65
O. davisae	A	S	10.0	0.243	0.011	65
O. davisae	A	S	10.1	0.237	0.012	65
O. davisae	A	S	9.6	0.241	0.013	65
O. davisae	A	S	9.7	0.241	0.018	65
O. davisae	A	S	8.9	0.241	0.021	65
O. davisae	A	S	9.6	0.241	0.027	65
O. davisae	A	S	9.6	0.246	0.012	65
O. davisae	A	S	10.5	0.243	0.008	65
O. davisae	A	S	10.8	0.246	0.020	65
O. davisae	A	S	10.8	0.244	0.022	65
O. davisae	A	S	10.8	0.248	0.040	65

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Oithona davisae	A	S	11.2	0.252	0.057	65
O. davisae	A	S	12.4	0.245	0.081	65
O. davisae	A	S	12.2	0.243	0.071	65
O. davisae	A	S	13.1	0.239	0.085	65
O. davisae	A	S	14.4	0.240	0.072	65
O. davisae	A	S	13.4	0.238	0.062	65
O. davisae	A	S	15.2	0.243	0.107	65
O. davisae	A	S	14.7	0.237	0.052	65
O. davisae	A	S	16.2	0.235	0.052	65
O. davisae	A	S	16.7	0.236	0.111	65
O. davisae	A	S	16.9	0.233	0.116	65
O. davisae	A	S	19.0	0.234	0.080	65
O. davisae	A	S	19.5	0.231	0.129	65
O. davisae	A	S	19.3	0.231	0.123	65
O. davisae	A	S	20.7	0.229	0.117	65
O. davisae	A	S	20.4	0.231	0.110	65
O. davisae	A	S	21.2	0.225	0.299	65
O. davisae	A	S	21.8	0.221	0.294	65
O. davisae	A	S	20.7	0.223	0.310	65
O. davisae	A	S	22.4	0.220	0.100	65
O. davisae	A	S	21.2	0.223	0.171	65
O. davisae	A	S	22.4	0.222	0.290	65
O. davisae	A	S	22.1	0.221	0.214	65
O. davisae	A	S	22.2	0.218	0.130	65
O. davisae	A	S	22.5	0.218	0.152	65
O. davisae	A	S	24.1	0.215	0.152	65
O. davisae	A	S	24.3	0.215	0.135	65
O. davisae	A	S	24.4	0.215	0.217	65
O. davisae	A	S	25.4	0.213	0.100	65
O. davisae	A	S	26.9	0.209	0.144	65
O. davisae	A	S	26.8	0.210	0.145	65
O. davisae	A	S	25.8	0.205	0.351	65
O. davisae	A	S	26.8	0.202	0.277	65
O. davisae	A	S	26.2	0.199	0.162	65
O. davisae	A	S	26.8	0.199	0.188	65
O. davisae	A	S	27.2	0.201	0.177	65
O. davisae	A	S	26.8	0.203	0.160	65
O. davisae	A	S	26.8	0.201	0.215	65
O. davisae	A	S	27.5	0.203	0.095	65
O. davisae	A	S	27.7	0.203	0.108	65
O. davisae	A	S	27.8	0.205	0.180	65
O. davisae	A	S	28.2	0.205	0.091	65
O. davisae	A	S	27.0	0.205	0.089	65
O. davisae	A	S	26.2	0.206	0.078	65
O. davisae	A	S	25.9	0.206	0.072	65

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Oithona davisae	A	S	25.7	0.205	0.057	65
O. davisae	A	S	24.4	0.206	0.053	65
O. davisae	A	S	24.6	0.203	0.086	65
O. davisae	A	S	24.2	0.206	0.053	65
O. davisae	A	S	24.4	0.208	0.052	65
O. davisae	A	S	23.8	0.212	0.053	65
O. davisae	A	S	23.2	0.209	0.068	65
O. davisae	A	S	22.7	0.211	0.069	65
O. davisae	A	S	21.7	0.212	0.082	65
O. davisae	A	S	21.1	0.212	0.116	65
O. davisae	A	S	21.3	0.212	0.082	65
O. davisae	A	S	20.6	0.214	0.126	65
O. davisae	A	S	20.0	0.215	0.048	65
Oithona nana / *O. simplex*	N	S	28	0.020	0.310	60
O. nana / *O. simplex*	N	S	28	0.007	0.513	60
O. nana / *O. simplex*	N	S	28	0.013	0.553	60
O. nana / *O. simplex*	N	S	28	0.017	0.425	60
O. nana / *O. simplex*	N	S	28	0.010	0.626	60
O. nana / *O. simplex*	N	S	28	0.006	0.339	60
O. nana / *O. simplex*	N	S	28	0.007	0.596	60
O. nana / *O. simplex*	N	S	28	0.011	0.748	60
O. nana / *O. simplex*	N	S	28	0.008	0.745	60
O. nana / *O. simplex*	N	S	28	0.010	0.672	60
O. nana / *O. simplex*	N	S	28	0.007	0.568	60
O. nana / *O. simplex*	N	S	28	0.014	0.432	60
O. nana / *O. simplex*	N	S	28	0.016	0.416	60
O. nana / *O. simplex*	N	S	28	0.013	0.388	60
O. nana / *O. simplex*	N	S	28	0.010	0.482	60
O. nana / *O. simplex*	N	S	28	0.016	0.501	60
O. nana / *O. simplex*	N	S	28	0.008	0.530	60
O. nana / *O. simplex*	N	S	28	0.014	0.459	60
O. nana / *O. simplex*	N	S	28	0.008	0.605	60
Oithona plumifera	A	S	28	0.85	0.098	59
Oithona plumifera	C	S	26	0.167	0.30	22
O. plumifera	C	S	26	0.285	0.30	22
O. plumifera	C	S	26	0.460	0.16	22
O. plumifera	C	S	26	0.614	0.09	22
O. plumifera	C	S	26	0.721	0.04	22
Oithona similis	A	S	4.5	0.55	0.008	46
O. similis	A	S	5	0.55	0.023	46
O. similis	A	S	5	0.55	0.018	46
O. similis	A	S	5	0.55	0.038	46
O. similis	A	S	5	0.55	0.025	46
O. similis	A	S	5	0.55	0.020	46

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Oithona similis	A	S	5	0.55	0.065	46
O. similis	A	S	5	0.55	0.063	46
O. similis	A	S	6	0.55	0.020	46
O. similis	A	S	6	0.55	0.018	46
O. similis	A	S	6	0.55	0.080	46
O. similis	A	S	6	0.55	0.008	46
O. similis	A	S	6	0.55	0.040	46
O. similis	A	S	6	0.55	0.008	46
O. similis	A	S	6	0.55	0.053	46
O. similis	A	S	15	0.55	0.050	46
O. similis	A	S	15	0.55	0.035	46
O. similis	A	S	17	0.55	0.038	46
O. similis	A	S	17	0.55	0.018	46
O. similis	A	S	18	0.55	0.030	46
O. similis	A	S	18	0.55	0.028	46
O. similis	A	S	17	0.55	0.038	46
O. similis	A	S	17	0.55	0.060	46
O. similis	A	S	17	0.55	0.020	46
O. similis	A	S	17	0.55	0.035	46
O. similis	A	S	17	0.55	0.028	46
O. similis	A	S	15	0.55	0.030	46
O. similis	A	S	15	0.55	0.033	46
O. similis	A	S	15	0.55	0.050	46
O. similis	A	S	15	0.55	0.010	46
O. similis	A	S	15	0.55	0.035	46
O. similis	A	S	14	0.55	0.063	46
O. similis	A	S	9	0.55	0.010	46
O. similis	A	S	9	0.55	0.065	46
O. similis	A	S	9	0.55	0.023	46
Oithona sp.	A	S	22.2	0.61	0.019	64
Oithona sp.	A	S	22.2	0.61	0.042	64
Oithona spp.	A	S	12	0.752	0.053	25
Oithona spp.	A	S	9.6	0.643	0.038	25
Oithona spp.	A	S	12	0.746	0.05	25
Oithona spp.	A	S	9.5	0.765	0.052	25
Oithona spp.	A	S	12	0.720	0.067	25
Oithona spp.	A	S	8.2	0.651	0.026	25
Oithona spp.	A	S	8.2	0.648	0.029	25
Oithona spp.	A	S	12	0.752	0.065	25
Oithona spp.	A	S	7.7	0.685	0.02	25
Oithona spp.	A	S	7.7	0.621	0.025	25
Oithona spp.	A	S	12	0.855	0.041	25
Oithona spp.	A	S	8.5	0.734	0.048	25
Oithona spp.	A	S	7.6	0.827	0.02	25
Oithona spp.	A	S	6.7	0.714	0.048	25

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Oithona spp.	A	S	12	0.743	0.095	25
Oithona spp.	A	S	8.6	0.671	0.043	25
Oithona spp.	A	S	8.5	0.668	0.043	25
Oithona spp.	A	S	12	0.789	0.03	25
Oithona spp.	A	S	7.8	0.618	0.071	25
Oithona spp.	A	S	7.6	0.654	0.024	25
Oithona spp.	A	S	7.5	0.640	0.059	25
Oithona spp.	A	S	9.0	0.729	0.024	25
Oithona spp.	A	S	7.0	0.731	0.023	25
Oithona spp.	A	S	12.0	0.789	0.03	25
Oithona spp.	A	S	8.6	0.634	0.018	25
Oithona spp.	A	S	7.8	0.685	0.04	25
Oithona spp.	A	S	6.7	0.668	0.054	25
Oithona spp.	A	S	12.0	0.824	0.04	25
Oithona spp.	A	S	8.0	0.808	0.057	25
Oithona spp.	A	S	12	0.824	0.0093	25
Oithona spp.	A	S	8.0	0.651	0.055	25
Oithona spp.	A	S	8.0	0.656	0.055	25
Oithona spp.	A	S	12.0	0.898	0.032	25
Oithona spp.	A	S	8.0	0.868	0.014	25
Oithona spp.	A	S	8.0	0.752	0.021	25
Oithona spp.	A	S	12.0	0.795	0.066	25
Oithona spp.	A	S	8.5	0.720	0.057	25
Oithona spp.	A	S	7.5	0.705	0.028	25
Oithona spp.	A	S	7.5	0.634	0.049	25
Oithona spp.	A	S	12.0	0.777	0.031	25
Oithona spp.	A	S	8.0	0.673	0.025	25
Oithona spp.	A	S	7.2	0.645	0.040	25
Oithona spp.	A	S	7.0	0.720	0.046	25
Oithona spp.	A	S	10.5	0.51	0.021	69
Oithona spp.	A	S	12.0	0.45	0.066	69
Oithona spp.	A	S	13.5	0.51	0.028	69
Oithona spp.	A	S	27.0	1.31	0.019	69
Oithona spp.	A	S	27.5	0.43	0.026	69
Oithona spp.	A	S	27.5	0.42	0.020	69
Oithona spp.	A	S	25.0	0.42	0.042	69
Oithona spp.	A	S	23.0	2.05	0.046	69
Paracalanidae:						
Acrocalanus gibber	A	B	26.7	4.74	0.10	26
A. gibber	A	B	27.3	7.03	0.16	26
A. gibber	A	B	28.0	7.03	0.21	26
A. gibber	A	B	26.1	7.33	0.07	26
A. gibber	A	B	24.7	9.85	0.05	26
A. gibber	A	B	21.6	9.67	0.03	26
A. gibber	A	B	24.3	6.47	0.17	26

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Acrocalanus gibber	A	B	25.8	4.85	0.18	26
A. gibber	A	B	26.0	6.33	0.18	26
A. gibber	A	B	28.0	5.31	0.06	26
A. gibber	A	B	25.3	8.44	0.07	26
A. gibber	A	B	27.0	5.0	0.16	27
A. gibber	A	B	29.0	5.4	0.21	27
A. gibber	A	B	26.2	5.6	0.12	27
A. gibber	A	B	27.3	6.9	0.12	27
A. gibber	A	B	24.4	4.8	0.05	27
Acrocalanus gracilis	A	B	27	12.15	0.28	26
A. gracilis	A	B	27	13.36	0.38	26
A. gracilis	A	B	24	15.47	0.39	26
A. gracilis	A	B	26	12.33	0.20	26
A. gracilis	A	B	27	12.86	0.20	26
A. gracilis	A	B	27	12.27	0.45	26
A. gracilis	A	B	28	11.10	0.13	26
A. gracilis	A	B	25	13.70	0.25	26
A. gracilis	A	B	25	13.15	0.10	26
Acrocalanus spp.	A	B	28.0	4.56	0.011	69
Acrocalanus spp.	A	B	27.0	4.84	0.018	69
Acrocalanus spp.	A	B	27.0	4.50	0.001	69
Acrocalanus spp.	A	B	27.5	5.25	0.010	69
Bestiolina similis	A	B	26.0	0.90	0.175	28
B. similis	A	B	26.0	0.90	0.140	28
B. similis	A	B	26.0	0.90	0.263	28
B. similis	A	B	25.0	0.90	0.188	28
B. similis	A	B	25.0	0.90	0.273	28
B. similis	A	B	26.5	0.90	0.158	28
B. similis	A	B	26.5	0.90	0.123	28
B. similis	A	B	26.5	0.90	0.200	28
B. similis	A	B	29.0	0.90	0.085	28
B. similis	A	B	29.0	0.90	0.107	28
B. similis	A	B	29.0	0.90	0.112	28
B. similis	A	B	27.5	0.90	0.243	28
B. similis	A	B	27.5	0.90	0.282	28
B. similis	A	B	27.5	0.90	0.207	28
B. similis	A	B	27.0	0.90	0.180	28
B. similis	A	B	27.0	0.90	0.173	28
B. similis	A	B	27.0	0.90	0.157	28
Paracalanus aculeatus	A	B	28	1.71	0.167	59
P. aculeatus	C	B	28	0.146	0.58	24
P. aculeatus	C	B	28	0.355	0.65	24
P. aculeatus	C	B	28	0.742	0.38	24
P. aculeatus	C	B	28	1.212	0.29	24
P. aculeatus	C	B	28	0.177	1.257	58

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Paracalanus aculeatus	C	B	28	0.534	0.948	58
P. aculeatus	C	B	28	0.191	0.702	58
P. aculeatus	C	B	28	0.236	0.889	58
P. aculeatus	C	B	28	1.077	0.849	58
P. aculeatus	C	B	28	0.437	0.995	58
P. aculeatus	C	B	28	1.101	0.497	58
P. aculeatus	C	B	28	0.515	0.673	58
P. aculeatus	C	B	28	0.358	0.248	58
P. aculeatus	C	B	28	0.601	0.593	58
P. aculeatus	C	B	28	0.115	0.725	58
P. aculeatus	C	B	28	0.177	0.719	58
P. aculeatus	C	B	28	0.384	0.832	58
P. aculeatus	C	B	28	0.203	0.883	58
P. aculeatus	C	B	28	0.272	0.990	58
Paracalanus aculeatus / *Parvocalanus crassirostris*	N	B	28	0.011	0.830	60
P. aculeatus / *P. crassirostris*	N	B	28	0.010	0.738	60
P. aculeatus / *P. crassirostris*	N	B	28	0.011	1.124	60
P. aculeatus / *P. crassirostris*	N	B	28	0.010	0.816	60
P. aculeatus / *P. crassirostris*	N	B	28	0.010	0.838	60
P. aculeatus / *P. crassirostris*	N	B	28	0.011	1.135	60
P. aculeatus / *P. crassirostris*	N	B	28	0.024	0.463	60
P. aculeatus / *P. crassirostris*	N	B	28	0.024	0.508	60
P. aculeatus / *P. crassirostris*	N	B	28	0.009	1.130	60
P. aculeatus / *P. crassirostris*	N	B	28	0.008	1.003	60
P. aculeatus / *P. crassirostris*	N	B	28	0.013	0.929	60
P. aculeatus / *P. crassirostris*	N	B	28	0.012	0.769	60
Paracalanus parvus	A	B	16.5	3.3	0.04	8
P. parvus	A	B	16.5	3.3	0.23	8
P. parvus	A	B	16.5	3.3	0.07	8
P. parvus	A	B	16.5	3.3	0.16	8
P. parvus	A	B	16.5	3.3	0.09	8
P. parvus	A	B	16.5	3.3	0.11	8

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Paracalanus parvus	C	B	16.5	0.24	0.25	8
P. parvus	C	B	16.5	0.44	0.35	8
P. parvus	C	B	16.5	0.8	0.23	8
P. parvus	C	B	16.5	1.52	0.38	8
P. parvus	C	B	16.5	2.68	0.10	8
P. parvus	A	B	20	3.00	0.10	1
P. parvus	A	B	20	3.00	0.12	1
P. parvus	A	B	17	1.85	0.042	2
P. parvus	A	B	17	1.86	0.090	2
P. parvus	A	B	17	3.00	0.044	4
P. parvus	A	B	17	3.00	0.051	4
P. parvus	A	B	17	3.00	0.059	4
P. parvus	A	B	17	3.00	0.059	4
P. parvus	A	B	17	3.00	0.066	4
P. parvus	A	B	17	3.00	0.073	4
P. parvus	A	B	17	3.00	0.073	4
P. parvus	A	B	17	3.00	0.081	4
P. parvus	A	B	17	3.00	0.088	4
P. parvus	A	B	17	3.00	0.081	4
P. parvus	A	B	15	3.00	0.154	4
P. parvus	A	B	15	3.00	0.117	4
P. parvus	A	B	15	3.00	0.081	4
P. parvus	A	B	15	3.00	0.081	4
P. parvus	A	B	15	3.00	0.110	4
P. parvus	A	B	15	3.00	0.059	4
P. parvus	A	B	15	3.00	0.059	4
P. parvus	A	B	15	3.00	0.073	4
P. parvus	A	B	12	3.00	0.037	4
P. parvus	A	B	12	3.00	0.022	4
P. parvus	A	B	8	3.00	0.059	4
P. parvus	A	B	12	3.00	0.043	25
P. parvus	A	B	12	3.00	0.019	25
P. parvus	A	B	12	3.00	0.049	25
P. parvus	A	B	12	3.00	0.031	25
P. parvus	A	B	12	3.00	0.038	25
P. parvus	A	B	7	3.00	0.027	25
P. parvus	A	B	7	3.00	0.004	25
P. parvus	A	B	7	3.00	0.006	25
P. parvus	A	B	12	3.00	0.048	25
P. parvus	A	B	12	3.00	0.075	25
P. parvus	A	B	12	3.00	0.150	25
P. parvus	A	B	12	3.00	0.095	25
P. parvus	A	B	12	3.00	0.188	25
P. parvus	A	B	12	3.00	0.234	25
P. parvus	A	B	12	3.00	0.011	25

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Paracalanus parvus	A	B	12	3.00	0.020	25
P. parvus	A	B	12	3.00	0.003	25
P. parvus	A	B	11	3.6	0.152	43
P. parvus	A	B	14	3.6	0.037	43
P. parvus	A	B	8.5	3.1	0.000	57
P. parvus	A	B	8.5	3.1	0.000	57
P. parvus	A	B	8.5	3.1	0.001	57
P. parvus	A	B	8.5	3.1	0.000	57
P. parvus	A	B	8.5	3.1	0.000	57
P. parvus	A	B	8.5	3.1	0.013	57
P. parvus	A	B	8.5	3.1	0.000	57
P. parvus	A	B	8.5	3.1	0.051	57
P. parvus	A	B	6.5	3.1	0.004	57
P. parvus	A	B	6.5	3.1	0.005	57
P. parvus	A	B	6.5	3.1	0.000	57
P. parvus	A	B	6.5	3.1	0.000	57
P. parvus	A	B	6.5	3.1	0.005	57
P. parvus	A	B	6.5	3.1	0.026	57
P. parvus	A	B	6.5	3.1	0.007	57
P. parvus	A	B	6.5	3.1	0.027	57
P. parvus	A	B	10.0	19.05	0.0646	67
P. parvus	A	B	10.0	19.05	0.0646	67
P. parvus	A	B	10.0	30.71	0.0401	67
P. parvus	A	B	10.0	30.71	0.0000	67
P. parvus	A	B	10.0	19.05	0.0000	67
P. parvus	A	B	10.0	15.92	0.0957	67
P. parvus	A	B	10.0	22.54	0.0676	67
P. parvus	A	B	10.0	22.54	0.1594	67
P. parvus	A	B	10.0	30.71	0.0782	67
P. parvus	A	B	10.0	22.54	0.1066	67
P. parvus	A	B	10.0	26.43	0.0110	67
P. parvus	A	B	10.0	30.71	0.0215	67
P. parvus	A	B	10.0	26.43	0.2211	67
P. parvus	A	B	10.0	40.57	0.1440	67
P. parvus	A	B	10.0	13.14	0.2387	67
P. parvus	A	B	10.0	19.05	0.1647	67
P. parvus	A	B	10.0	22.54	0.1391	67
P. parvus	A	B	10.0	19.05	0.1045	67
P. parvus	A	B	10.0	35.42	0.0562	67
P. parvus	A	B	10.0	22.54	0.1887	67
P. parvus	A	B	10.0	26.43	0.0420	67
P. parvus	A	B	10.0	43.17	0.0240	67
P. parvus	A	B	10.0	26.43	0.0420	67
P. parvus	A	B	10.0	22.54	0.0000	67
P. parvus	A	B	10.0	26.43	0.0000	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Paracalanus parvus	A	B	10.0	40.57	0.0168	67
P. parvus	A	B	14.0	26.43	0.0565	67
P. parvus	A	B	14.0	26.43	0.0565	67
P. parvus	A	B	14.0	22.54	0.0145	67
P. parvus	A	B	14.0	15.92	0.1017	67
P. parvus	A	B	14.0	19.05	0.0850	67
P. parvus	A	B	14.0	22.54	0.0718	67
P. parvus	A	B	14.0	19.05	0.0307	67
P. parvus	A	B	14.0	22.54	0.0259	67
P. parvus	A	B	14.0	26.43	0.0998	67
P. parvus	A	B	14.0	22.54	0.1170	67
P. parvus	A	B	14.0	19.05	0.0524	67
P. parvus	A	B	14.0	19.05	0.0524	67
P. parvus	A	B	14.0	19.05	0.0627	67
P. parvus	A	B	14.0	22.54	0.0530	67
P. parvus	A	B	14.0	19.05	0.0627	67
P. parvus	A	B	14.0	19.05	0.0139	67
P. parvus	A	B	14.0	22.54	0.0118	67
P. parvus	A	B	14.0	19.05	0.0139	67
P. parvus	A	B	14.0	22.54	0.0330	67
P. parvus	A	B	14.0	15.92	0.0467	67
P. parvus	A	B	14.0	15.92	0.0467	67
P. parvus	A	B	14.0	22.54	0.0330	67
P. parvus	A	B	14.0	22.54	0.0330	67
P. parvus	A	B	14.0	19.05	0.0390	67
P. parvus	A	B	14.0	19.05	0.0160	67
P. parvus	A	B	14.0	22.54	0.0135	67
Paracalanus sp.	A	B	19.25	3.25	0.01	29
Paracalanus sp.	A	B	19.25	3.25	0.02	29
Paracalanus sp.	A	B	19.25	3.25	0.03	29
Paracalanus sp.	A	B	19.25	3.25	0.05	29
Paracalanus sp.	A	B	19.25	3.25	0.02	29
Paracalanus sp.	A	B	19.25	3.25	0.04	29
Paracalanus sp.	A	B	19.25	3.25	0.09	29
Paracalanus sp.	A	B	19.25	3.25	0.04	29
Paracalanus sp.	A	B	19.25	3.25	0.04	29
Paracalanus sp.	A	B	19.25	3.25	0.06	29
Paracalanus sp.	A	B	19.25	3.25	0.07	29
Paracalanus sp.	A	B	19.25	3.25	0.07	29
Paracalanus sp.	A	B	19.25	3.25	0.07	29
Paracalanus sp.	A	B	19.25	3.25	0.06	29
Paracalanus sp.	A	B	19.25	3.25	0.08	29
Paracalanus sp.	A	B	19.25	3.25	0.09	29
Paracalanus sp.	A	B	19.25	3.25	0.09	29
Paracalanus sp.	A	B	19.25	3.25	0.10	29

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Paracalanus sp.	A	B	19.25	3.25	0.13	29
Paracalanus sp.	A	B	19.25	3.25	0.14	29
Paracalanus sp.	A	B	19.25	3.25	0.18	29
Paracalanus sp.	A	B	19.25	3.25	0.18	29
Paracalanus sp.	A	B	19.25	3.25	0.17	29
Paracalanus sp.	A	B	19.25	3.25	0.18	29
Paracalanus sp.	A	B	19.25	3.25	0.20	29
Paracalanus sp.	A	B	19.25	3.25	0.24	29
Paracalanus sp.	A	B	19.25	3.25	0.29	29
Paracalanus sp.	A	B	19.25	3.25	0.28	29
Paracalanus sp.	A	B	19.25	3.25	0.24	29
Paracalanus sp.	A	B	19.25	3.25	0.22	29
Paracalanus sp.	C	B	28	0.075	0.914	30
Paracalanus sp.	C	B	28	0.173	1.173	30
Paracalanus sp.	C	B	28	0.332	0.464	30
Paracalanus sp.	C	B	28	0.540	0.665	30
Paracalanus sp.	C	B	28	0.867	0.388	30
Paracalanus sp.	A	B	9	4.33	0.03	40
Paracalanus sp.	A	B	8	4.95	0.02	40
Paracalanus sp.	A	B	8	5.33	0.02	40
Paracalanus sp.	A	B	8	5.14	0.03	40
Paracalanus sp.	A	B	9	5.24	0.04	40
Paracalanus sp.	A	B	11	5.24	0.07	40
Paracalanus sp.	A	B	12	4.59	0.09	40
Paracalanus sp.	A	B	13	3.77	0.17	40
Paracalanus sp.	A	B	14	3.92	0.16	40
Paracalanus sp.	A	B	22	2.79	0.37	40
Paracalanus sp.	A	B	22	2.32	0.59	40
Paracalanus sp.	A	B	25	2.15	0.04	40
Paracalanus sp.	A	B	26	2.26	0.07	40
Paracalanus sp.	A	B	26	2.85	0.17	40
Paracalanus sp.	A	B	25	2.85	0.13	40
Paracalanus sp.	A	B	22	3.25	0.32	40
Paracalanus sp.	A	B	21	2.85	0.34	40
Paracalanus sp.	A	B	20	3.11	0.35	40
Paracalanus sp.	A	B	17	2.98	0.28	40
Paracalanus sp.	A	B	16	3.32	0.12	40
Paracalanus sp.	A	B	15	4.50	0.26	40
Paracalanus sp.	A	B	14	3.54	0.21	40
Paracalanus sp.	A	B	14	3.18	0.13	40
Parvocalanus crassirostris	A	B	23.2	0.93	0.123	6
P. crassirostris	A	B	21.3	0.93	0.116	6
P. crassirostris	A	B	23.0	0.93	0.300	6
P. crassirostris	A	B	22.2	0.93	0.198	6

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Parvocalanus crassirostris	A	B	28	0.44	0.932	59
P. crassirostris	C	B	28	0.069	0.915	58
P. crassirostris	C	B	28	0.157	0.713	58
P. crassirostris	C	B	28	0.201	0.660	58
P. crassirostris	C	B	28	0.165	0.723	58
P. crassirostris	C	B	28	0.109	1.082	58
P. crassirostris	C	B	28	0.280	0.446	58
P. crassirostris	C	B	28	0.057	1.000	58
P. crassirostris	C	B	28	0.070	0.975	58
P. crassirostris	C	B	28	0.046	0.670	58
P. crassirostris	C	B	28	0.121	0.439	58
P. crassirostris	C	B	28	0.078	0.441	58
P. crassirostris	C	B	28	0.217	0.434	58
P. crassirostris	C	B	28	0.124	0.496	58
P. crassirostris	C	B	28	0.049	0.772	58
P. crassirostris	C	B	28	0.042	0.774	58
P. crassirostris	C	B	28	0.135	0.774	58
P. crassirostris	C	B	28	0.060	0.831	58
P. crassirostris	C	B	28	0.112	0.888	58
Pontellidae:						
Epilabidocera longipedata	A	B	14.0	63.19	0.027	67
E. longipedata	A	B	14.0	53.81	0.032	67
E. longipedata	A	B	14.0	49.47	0.000	67
E. longipedata	A	B	14.0	47.38	0.000	67
Pseudocalanidae:						
Clausocalanus sp.	A	S	17	6.74	0.011	2
Clausocalanus sp.	A	S	17	6.00	0.032	2
Clausocalanus spp.	A	S	12.0	4.81	0.010	69
Clausocalanus spp.	A	S	13.0	5.11	0.070	69
Clausocalanus spp.	A	S	13.5	5.34	0.003	69
Clausocalanus spp.	A	S	15.0	5.23	0.026	69
Clausocalanus spp.	A	S	15.5	5.49	0.015	69
Clausocalanus spp.	A	S	23.0	5.94	0.006	69
Clausocalanus spp.	A	S	23.5	2.89	0.008	69
Clausocalanus spp.	A	S	25.0	2.65	0.041	69
Clausocalanus spp.	A	S	25.0	2.63	0.008	69
Clausocalanus spp.	A	S	27.5	2.06	0.000	69
Clausocalanus spp.	A	S	27.5	2.75	0.059	69
Clausocalanus spp.	A	S	25.0	2.91	0.119	69
Clausocalanus spp.	A	S	25.0	3.20	0.057	69
Clausocalanus spp.	A	S	25.0	3.45	0.170	69
Clausocalanus spp.	A	S	25.0	3.06	0.140	69

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Clausocalanus spp.	A	S	22.5	3.53	0.073	69
Clausocalanus spp.	A	S	21.5	3.92	0.082	69
Pseudocalanus mimus	A	S	10.0	66.95	0.234	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	81.72	0.236	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	53.87	0.154	67
P. mimus	A	S	10.0	60.21	0.101	67
P. mimus	A	S	10.0	60.21	0.183	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	89.75	0.234	67
P. mimus	A	S	10.0	89.75	0.172	67
P. mimus	A	S	10.0	53.87	0.000	67
P. mimus	A	S	10.0	60.21	0.338	67
P. mimus	A	S	10.0	60.21	0.208	67
P. mimus	A	S	10.0	81.72	0.061	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	89.75	0.100	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	81.72	0.220	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Pseudocalanus mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	74.12	0.124	67
P. mimus	A	S	10.0	53.87	0.210	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	86.35	0.000	67
P. mimus	A	S	10.0	66.95	0.016	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	66.95	0.032	67
P. mimus	A	S	10.0	81.72	0.330	67
P. mimus	A	S	10.0	60.21	0.275	67
P. mimus	A	S	10.0	81.72	0.127	67
P. mimus	A	S	10.0	89.75	0.023	67
P. mimus	A	S	10.0	89.75	0.239	67
P. mimus	A	S	10.0	47.94	0.314	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	60.21	0.339	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	53.87	0.020	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	74.12	0.218	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	81.72	0.084	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	53.87	0.000	67
P. mimus	A	S	10.0	81.72	0.225	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	98.22	0.222	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	81.72	0.014	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	74.12	0.220	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Pseudocalanus mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	74.12	0.015	67
P. mimus	A	S	10.0	74.12	0.231	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	81.72	0.014	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	116.52	0.000	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	74.12	0.266	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	60.21	0.240	67
P. mimus	A	S	10.0	81.72	0.322	67
P. mimus	A	S	10.0	81.72	0.200	67
P. mimus	A	S	10.0	81.72	0.185	67
P. mimus	A	S	10.0	81.72	0.141	67
P. mimus	A	S	10.0	74.12	0.186	67
P. mimus	A	S	10.0	89.75	0.249	67
P. mimus	A	S	10.0	89.75	0.062	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	107.14	0.240	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	81.72	0.341	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	74.12	0.185	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	74.12	0.302	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	98.22	0.000	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Pseudocalanus mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	89.75	0.187	67
P. mimus	A	S	10.0	98.22	0.353	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	89.75	0.204	67
P. mimus	A	S	10.0	98.22	0.022	67
P. mimus	A	S	10.0	98.22	0.275	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	89.75	0.012	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	81.72	0.224	67
P. mimus	A	S	10.0	81.72	0.290	67
P. mimus	A	S	10.0	116.52	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	81.72	0.027	67
P. mimus	A	S	10.0	89.75	0.261	67
P. mimus	A	S	10.0	74.12	0.060	67
P. mimus	A	S	10.0	89.75	0.137	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	107.14	0.000	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	107.14	0.000	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	66.95	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	81.72	0.170	67
P. mimus	A	S	10.0	81.72	0.042	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Pseudocalanus mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	89.75	0.192	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	89.75	0.102	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	66.95	0.018	67
P. mimus	A	S	10.0	89.75	0.107	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	89.75	0.266	67
P. mimus	A	S	10.0	98.22	0.134	67
P. mimus	A	S	10.0	81.72	0.176	67
P. mimus	A	S	10.0	81.72	0.293	67
P. mimus	A	S	10.0	60.21	0.038	67
P. mimus	A	S	10.0	60.21	0.173	67
P. mimus	A	S	10.0	74.12	0.000	67
P. mimus	A	S	10.0	98.22	0.012	67
P. mimus	A	S	10.0	74.12	0.193	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	107.14	0.000	67
P. mimus	A	S	10.0	107.14	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	60.21	0.000	67
P. mimus	A	S	10.0	98.22	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	98.22	0.252	67
P. mimus	A	S	10.0	89.75	0.000	67
P. mimus	A	S	10.0	81.72	0.000	67
P. mimus	A	S	14.0	74.12	0.130	67
P. mimus	A	S	14.0	74.12	0.000	67
P. mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	74.12	0.232	67
P. mimus	A	S	14.0	74.12	0.000	67
P. mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	74.12	0.000	67
P. mimus	A	S	14.0	81.72	0.000	67

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Pseudocalanus mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	81.72	0.068	67
P. mimus	A	S	14.0	74.12	0.000	67
P. mimus	A	S	14.0	74.12	0.000	67
P. mimus	A	S	14.0	74.12	0.000	67
P. mimus	A	S	14.0	81.72	0.000	67
P. mimus	A	S	14.0	74.12	0.000	67
P. mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	74.12	0.016	67
P. mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	81.72	0.000	67
P. mimus	A	S	14.0	81.72	0.198	67
P. mimus	A	S	14.0	81.72	0.000	67
P. mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	81.72	0.000	67
P. mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	81.72	0.000	67
P. mimus	A	S	14.0	60.21	0.000	67
P. mimus	A	S	14.0	81.72	0.256	67
P. mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	74.12	0.218	67
P. mimus	A	S	14.0	74.12	0.218	67
P. mimus	A	S	14.0	74.12	0.000	67
P. mimus	A	S	14.0	74.12	0.000	67
P. mimus	A	S	14.0	74.12	0.000	67
P. mimus	A	S	14.0	81.72	0.000	67
P. mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	74.12	0.000	67
P. mimus	A	S	14.0	60.21	0.362	67
P. mimus	A	S	14.0	74.12	0.000	67
P. mimus	A	S	14.0	60.21	0.000	67
P. mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	66.95	0.216	67
P. mimus	A	S	14.0	74.12	0.177	67
P. mimus	A	S	14.0	60.21	0.000	67
P. mimus	A	S	14.0	66.95	0.000	67
P. mimus	A	S	14.0	74.12	0.000	67
Pseudocalanus sp.	A	S	3	11.8	0.020	7
Pseudocalanus sp.	N	S	16.5	0.12	0.23	8
Pseudocalanus sp.	N	S	16.5	0.20	0.27	8
Pseudocalanus sp.	N	S	16.5	0.32	0.23	8
Pseudocalanus sp.	N	S	16.5	0.48	0.35	8
Pseudocalanus sp.	C	S	16.5	0.72	0.26	8

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Pseudocalanus sp.	C	S	16.5	1.24	0.20	8
Pseudocalanus sp.	C	S	16.5	2.00	0.15	8
Pseudocalanus spp.	A	S	4.8	6.7	0.071	70
Pseudocalanus spp.	A	S	4.8	6.7	0.010	70
Pseudocalanus spp.	A	S	5.5	6.7	0.038	70
Pseudocalanus spp.	A	S	5.5	6.7	0.084	70
Pseudocalanus spp.	A	S	5.5	6.7	0.029	70
Pseudocalanus spp.	A	S	5.5	6.7	0.071	70
Pseudocalanus spp.	A	S	5.5	9.2	0.058	70
Pseudocalanus spp.	A	S	5.8	6.7	0.027	70
Pseudocalanus spp.	A	S	5.9	6.7	0.071	70
Pseudocalanus spp.	A	S	6.2	6.7	0.061	70
Pseudocalanus spp.	A	S	7.0	3.2	0.070	70
Pseudocalanus spp.	A	S	7.0	6.7	0.077	70
Pseudocalanus spp.	A	S	4.5	6.7	0.006	70
Pseudocalanus spp.	A	S	4.5	6.7	0.015	70
Pseudocalanus spp.	A	S	4.6	6.7	0.023	70
Pseudocalanus spp.	A	S	4.5	9.2	0.038	70
Pseudocalanus spp.	A	S	5.5	6.7	0.092	70
Pseudocalanus spp.	A	S	7.0	6.7	0.063	70
Pseudocalanus spp.	A	S	7.0	6.7	0.075	70
Pseudocalanus spp.	A	S	7.3	6.7	0.111	70
Pseudodiaptomidae:						
Pseudodiaptomus hessei	N	S	16	0.166	0.190	31
P. hessei	N	S	16	0.211	0.096	31
P. hessei	N	S	16	0.266	0.110	31
P. hessei	N	S	16	0.345	0.093	31
P. hessei	N	S	16	0.386	0.125	31
P. hessei	C	S	16	0.640	0.233	31
P. hessei	C	S	16	1.147	0.231	31
P. hessei	C	S	16	1.797	0.211	31
P. hessei	C	S	16	2.387	0.286	31
P. hessei	C	S	16	2.751	0.139	31
P. hessei	C	S	16	4.419	0.179	31
P. hessei	N	S	20	0.157	0.309	31
P. hessei	N	S	20	0.209	0.174	31
P. hessei	N	S	20	0.264	0.186	31
P. hessei	N	S	20	0.329	0.104	31
P. hessei	N	S	20	0.364	0.164	31
P. hessei	C	S	20	0.624	0.308	31
P. hessei	C	S	20	1.073	0.254	31
P. hessei	C	S	20	1.644	0.203	31
P. hessei	C	S	20	2.173	0.287	31
P. hessei	C	S	20	2.467	0.149	31

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Pseudodiaptomus hessei	N	S	23	0.157	0.267	31
P. hessei	N	S	23	0.209	0.135	31
P. hessei	N	S	23	0.264	0.184	31
P. hessei	N	S	23	0.329	0.131	31
P. hessei	N	S	23	0.364	0.194	31
P. hessei	C	S	23	0.624	0.350	31
P. hessei	C	S	23	1.073	0.340	31
P. hessei	C	S	23	1.644	0.285	31
P. hessei	C	S	23	2.173	0.419	31
P. hessei	C	S	23	2.467	0.199	31
P. hessei	N	S	26	0.153	0.372	31
P. hessei	N	S	26	0.207	0.214	31
P. hessei	N	S	26	0.250	0.148	31
P. hessei	N	S	26	0.311	0.143	31
P. hessei	N	S	26	0.342	0.251	31
P. hessei	C	S	26	0.569	0.395	31
P. hessei	C	S	26	0.987	0.388	31
P. hessei	C	S	26	1.388	0.404	31
P. hessei	C	S	26	2.011	0.414	31
P. hessei	C	S	26	2.322	0.283	31
Pseudodiaptomus marinus	A	S	18.1	5.20	0.095	61
P. marinus	A	S	18.0	5.80	0.053	61
P. marinus	A	S	17.6	5.77	0.073	61
P. marinus	A	S	15.8	5.26	0.088	61
P. marinus	A	S	16.2	5.37	0.095	61
P. marinus	A	S	15.4	4.95	0.044	61
P. marinus	A	S	14.6	5.58	0.061	61
P. marinus	A	S	14.2	6.69	0.018	61
P. marinus	A	S	14.0	6.79	0.032	61
P. marinus	A	S	14.0	6.40	0.035	61
P. marinus	A	S	13.1	6.59	0.026	61
P. marinus	A	S	12.4	6.40	0.017	61
P. marinus	A	S	11.8	5.98	0.004	61
P. marinus	A	S	11.1	6.87	0.004	61
P. marinus	A	S	10.7	6.45	0.003	61
P. marinus	A	S	10.2	6.55	0.003	61
P. marinus	A	S	10.0	6.70	0.011	61
P. marinus	A	S	9.5	6.60	0.007	61
P. marinus	A	S	9.0	6.38	0.009	61
P. marinus	A	S	10.0	6.38	0.020	61
P. marinus	A	S	10.1	6.73	0.012	61
P. marinus	A	S	9.6	6.71	0.012	61
P. marinus	A	S	9.7	6.18	0.031	61

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Pseudodiaptomus marinus	A	S	8.9	6.41	0.010	61
P. marinus	A	S	9.6	6.52	0.022	61
P. marinus	A	S	9.6	6.49	0.034	61
P. marinus	A	S	10.5	6.02	0.055	61
P. marinus	A	S	10.8	6.28	0.034	61
P. marinus	A	S	10.8	6.64	0.050	61
P. marinus	A	S	10.8	6.33	0.043	61
P. marinus	A	S	11.2	6.30	0.050	61
P. marinus	A	S	12.4	6.04	0.045	61
P. marinus	A	S	12.2	6.62	0.047	61
P. marinus	A	S	13.1	6.00	0.078	61
P. marinus	A	S	14.4	7.00	0.057	61
P. marinus	A	S	13.4	6.42	0.065	61
P. marinus	A	S	15.2	6.51	0.086	61
P. marinus	A	S	14.7	6.67	0.055	61
P. marinus	A	S	16.2	6.87	0.105	61
P. marinus	A	S	16.7	6.74	0.089	61
P. marinus	A	S	16.9	6.59	0.088	61
P. marinus	A	S	19.0	6.64	0.091	61
P. marinus	A	S	19.5	6.34	0.057	61
P. marinus	A	S	19.3	6.16	0.079	61
P. marinus	A	S	20.7	5.86	0.093	61
P. marinus	A	S	21.2	5.83	0.108	61
P. marinus	A	S	21.8	5.42	0.094	61
P. marinus	A	S	20.7	5.33	0.095	61
P. marinus	A	S	22.4	5.12	0.024	61
P. marinus	A	S	21.2	4.84	0.083	61
P. marinus	A	S	22.4	4.94	0.093	61
P. marinus	A	S	22.1	4.81	0.061	61
P. marinus	A	S	22.2	4.73	0.069	61
P. marinus	A	S	24.1	4.42	0.125	61
P. marinus	A	S	24.3	4.17	0.117	61
P. marinus	A	S	24.4	4.04	0.084	61
P. marinus	A	S	25.4	3.89	0.067	61
P. marinus	A	S	26.9	3.89	0.170	61
P. marinus	A	S	26.8	3.73	0.150	61
P. marinus	A	S	25.8	3.87	0.161	61
P. marinus	A	S	26.8	3.87	0.203	61
P. marinus	A	S	26.2	3.85	0.102	61
P. marinus	A	S	26.8	3.60	0.116	61
P. marinus	A	S	27.2	3.85	0.218	61
P. marinus	A	S	26.8	3.55	0.068	61
P. marinus	A	S	26.8	3.77	0.173	61
P. marinus	A	S	27.5	3.39	0.134	61

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Pseudodiaptomus marinus	A	S	27.8	3.52	0.083	61
P. marinus	A	S	28.2	3.66	0.124	61
P. marinus	A	S	27.0	3.24	0.138	61
P. marinus	A	S	26.2	3.32	0.164	61
P. marinus	A	S	25.9	3.80	0.110	61
P. marinus	A	S	25.7	3.91	0.174	61
P. marinus	A	S	24.4	3.67	0.119	61
P. marinus	A	S	24.6	3.79	0.138	61
P. marinus	A	S	24.2	3.95	0.058	61
P. marinus	A	S	24.4	3.89	0.062	61
P. marinus	A	S	23.8	4.33	0.171	61
P. marinus	A	S	22.7	4.39	0.122	61
P. marinus	A	S	21.7	4.59	0.081	61
P. marinus	A	S	21.1	4.20	0.056	61
P. marinus	A	S	21.3	4.30	0.103	61
P. marinus	A	S	20.6	4.45	0.125	61
P. marinus	A	S	20.0	4.27	0.095	61
P. marinus	A	S	20.0	4.52	0.066	61
Temoridae:						
Eurytemora affinis	A	S	8	4.1	0.08	32
E. affinis	A	S	10	4.0	0.11	32
E. affinis	A	S	14	3.8	0.12	32
E. affinis	A	S	17	3.7	0.10	32
E. affinis	A	S	20	3.3	0.08	32
E. affinis	C	S	8	0.52	0.04	32
E. affinis	C	S	8	0.81	0.11	32
E. affinis	C	S	8	1.28	0.09	32
E. affinis	C	S	8	1.98	0.04	32
E. affinis	C	S	8	2.37	0.02	32
E. affinis	C	S	8	3.07	0.03	32
E. affinis	C	S	10	0.52	0.04	32
E. affinis	C	S	10	0.83	0.22	32
E. affinis	C	S	10	1.17	0.11	32
E. affinis	C	S	10	1.76	0.08	32
E. affinis	C	S	10	2.41	0.06	32
E. affinis	C	S	10	3.06	0.08	32
E. affinis	C	S	14	0.46	0.01	32
E. affinis	C	S	14	0.66	0.19	32
E. affinis	C	S	14	1.05	0.27	32
E. affinis	C	S	14	1.61	0.22	32
E. affinis	C	S	14	2.45	0.21	32
E. affinis	C	S	14	3.17	0.13	32
E. affinis	C	S	17	0.48	0.03	32
E. affinis	C	S	17	0.62	0.15	32

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Eurytemora affinis	C	S	17	0.88	0.24	32
E. affinis	C	S	17	1.39	0.30	32
E. affinis	C	S	17	1.87	0.16	32
E. affinis	C	S	17	2.99	0.25	32
E. affinis	C	S	20	0.50	0.05	32
E. affinis	C	S	20	0.65	0.17	32
E. affinis	C	S	20	0.92	0.19	32
E. affinis	C	S	20	1.28	0.17	32
E. affinis	C	S	20	1.88	0.20	32
E. affinis	C	S	20	2.19	0.17	32
E. affinis	C	S	9.9	0.798	0.150	33
E. affinis	C	S	9.9	1.261	0.088	33
E. affinis	C	S	9.9	1.852	0.060	33
E. affinis	C	S	14.4	1.118	0.144	33
E. affinis	C	S	14.4	1.641	0.067	33
E. affinis	N	S	6.5	0.171	0.088	33
E. affinis	C	S	6.5	0.252	0.054	33
E. affinis	C	S	6.5	0.360	0.036	33
E. affinis	C	S	6.5	0.612	0.090	33
E. affinis	C	S	6.5	1.065	0.020	33
E. affinis	C	S	6.5	1.422	0.010	33
Temora longicornis	A	B	3	9.0	0.010	7
T. longicornis	N	B	16.5	0.12	0.39	8
T. longicornis	N	B	16.5	0.20	0.35	8
T. longicornis	N	B	16.5	0.28	0.20	8
T. longicornis	C	B	16.5	0.56	0.37	8
T. longicornis	A	B	16.5	9.4	0.03	8
T. longicornis	A	B	16.5	9.4	0.01	8
T. longicornis	A	B	16.5	9.4	0.01	8
T. longicornis	A	B	16.5	9.4	0.03	8
T. longicornis	A	B	16.5	9.4	0.05	8
T. longicornis	A	B	16.5	9.4	0.03	8
Temora longicornis	A	B	7.5	14.95	0.029	14
T. longicornis	A	B	9.0	14.95	0.021	14
T. longicornis	A	B	7.0	14.95	0.013	3
T longicornis	A	B	7.0	14.95	0.045	3
T. longicornis	A	B	7.0	14.95	0.102	3
T. longicornis	A	B	7.0	14.95	0.043	3
T. longicornis	A	B	7.0	14.95	0.027	3
T. longicornis	A	B	7.0	14.95	0.029	3
T. longicornis	A	B	7.0	14.95	0.037	3
T. longicornis	A	B	7.0	14.95	0.080	3
T. longicornis	A	B	7.0	14.95	0.078	3
T. longicornis	A	B	7.0	14.95	0.072	3
T. longicornis	A	B	4	14.95	0.008	4

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Temora longicornis	A	B	4	14.95	0.003	4
T. longicornis	A	B	5	14.95	0.008	4
T. longicornis	A	B	5	14.95	0.021	4
T. longicornis	A	B	5	14.95	0.019	4
T. longicornis	A	B	5	14.95	0.019	4
T. longicornis	A	B	5	14.95	0.043	4
T. longicornis	A	B	5	14.95	0.048	4
T. longicornis	A	B	5	14.95	0.062	4
T. longicornis	A	B	5	14.95	0.104	4
T. longicornis	A	B	5	14.95	0.115	4
T. longicornis	A	B	5	14.95	0.112	4
T. longicornis	A	B	5	14.95	0.059	4
T. longicornis	A	B	5	14.95	0.126	4
T. longicornis	A	B	7	14.95	0.075	4
T. longicornis	A	B	7	14.95	0.075	4
T. longicornis	A	B	7	14.95	0.080	4
T. longicornis	A	B	7	14.95	0.083	4
T. longicornis	A	B	7	14.95	0.045	4
T. longicornis	A	B	7	14.95	0.051	4
T. longicornis	A	B	18	14.95	0.005	4
T. longicornis	A	B	17	14.95	0.011	4
T. longicornis	A	B	17	14.95	0.005	4
T. longicornis	A	B	17	14.95	0.019	4
T. longicornis	A	B	17	14.95	0.035	4
T. longicornis	A	B	17	14.95	0.043	4
T. longicornis	A	B	12	14.95	0.027	4
T. longicornis	A	B	12	14.95	0.008	4
T. longicornis	A	B	8	14.95	0.032	4
T. longicornis	A	B	12	14.95	0.050	25
T. longicornis	A	B	12	14.95	0.072	25
T. longicornis	A	B	12	14.95	0.053	25
T. longicornis	A	B	7	14.95	0.050	25
T. longicornis	A	B	12	14.95	0.048	25
T. longicornis	A	B	12	14.95	0.045	25
T. longicornis	A	B	12	14.95	0.047	25
T. longicornis	A	B	12	14.95	0.022	25
T. longicornis	A	B	12	14.95	0.051	25
T. longicornis	A	B	12	14.95	0.049	25
T. longicornis	A	B	12	14.95	0.078	25
T. longicornis	A	B	12	14.95	0.020	25
T. longicornis	A	B	0.5	14.95	0.07	47
T. longicornis	A	B	1.5	14.95	0.15	47
T. longicornis	A	B	2.5	14.95	0.14	47
T. longicornis	A	B	4.5	14.95	0.12	47
T. longicornis	A	B	5.0	14.95	0.08	47

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (μg C ind^{-1})	g (d^{-1})	Source
Temora longicornis	A	B	6.0	14.95	0.08	47
T. longicornis	A	B	7.5	14.95	0.01	47
T. longicornis	A	B	8.0	14.95	0.01	47
T. longicornis	A	B	10.0	14.95	0.06	47
T. longicornis	A	B	11.5	14.95	0.03	47
T. longicornis	A	B	11.5	14.95	0.06	47
T. longicornis	A	B	12.5	14.95	0.03	47
T. longicornis	A	B	13.5	14.95	0.02	47
T. longicornis	A	B	16.0	14.95	0.09	47
T. longicornis	A	B	17.0	14.95	0.05	47
T. longicornis	A	B	16.1	14.95	0.008	48
T. longicornis	A	B	16.5	14.95	0.003	48
T. longicornis	A	B	17.0	14.95	0.013	48
T. longicornis	A	B	17.5	14.95	0.006	48
T. longicornis	A	B	3	14.95	0.004	49
T. longicornis	A	B	5	14.95	0.004	49
T. longicornis	A	B	5	14.95	0.023	49
T. longicornis	A	B	7	14.95	0.020	49
T. longicornis	A	B	7.5	14.95	0.024	49
T. longicornis	A	B	11	14.95	0.043	49
T. longicornis	A	B	12.5	14.95	0.043	49
T. longicornis	A	B	14	14.95	0.043	49
T. longicornis	A	B	14	14.95	0.009	49
T. longicornis	A	B	14	14.95	0.027	49
T. longicornis	A	B	18.5	14.95	0.011	49
T. longicornis	A	B	18	14.95	0.056	49
T. longicornis	A	B	18	14.95	0.040	49
T. longicornis	A	B	16.5	14.95	0.039	49
T. longicornis	A	B	6.5	14.95	0.016	49
T. longicornis	A	B	7.5	14.95	0.032	49
T. longicornis	A	B	8	14.95	0.035	49
T. longicornis	A	B	10	14.95	0.037	49
T. longicornis	A	B	10	14.95	0.032	49
T. longicornis	A	B	13	14.95	0.054	49
T. longicornis	A	B	13.5	14.95	0.040	49
T. longicornis	A	B	18.5	14.95	0.051	49
T. longicornis	A	B	18	14.95	0.040	49
T. longicornis	A	B	17.5	14.95	0.019	49
T. longicornis	A	B	17.5	14.95	0.013	49
T. longicornis	A	B	17	14.95	0.019	49
T. longicornis	A	B	17	14.95	0.019	49
T. longicornis	A	B	19	14.95	0.019	49
T. longicornis	A	B	18	14.95	0.016	49
T. longicornis	A	B	17.5	14.95	0.062	49
T. longicornis	A	B	17.5	14.95	0.029	49

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Temora longicornis	A	B	17.5	14.95	0.043	49
T. longicornis	A	B	14	14.95	0.040	49
T. longicornis	A	B	12.5	14.95	0.013	49
T. longicornis	A	B	8.0	14.95	0.011	49
T. longicornis	A	B	9.5	14.95	0.035	49
T. longicornis	A	B	12.5	14.95	0.040	49
T. longicornis	A	B	11.0	14.95	0.024	49
T. longicornis	A	B	11.0	14.95	0.067	49
T. longicornis	A	B	11.0	14.95	0.021	49
T. longicornis	A	B	14.0	14.95	0.054	49
T. longicornis	A	B	17.5	14.95	0.024	49
T. longicornis	A	B	17.0	14.95	0.021	49
T. longicornis	A	B	18.5	14.95	0.021	49
T. longicornis	A	B	17.5	14.95	0.045	49
T. longicornis	A	B	17.5	14.95	0.027	49
T. longicornis	A	B	17.5	14.95	0.048	49
T. longicornis	A	B	13.0	14.95	0.013	49
T. longicornis	A	B	12.5	14.95	0.011	49
T. longicornis	A	B	4	14.95	0.08	52
T. longicornis	A	B	4	14.95	0.07	52
T. longicornis	A	B	4	14.95	0.03	52
T. longicornis	A	B	4	14.95	0.04	52
T. longicornis	A	B	4	14.95	0.03	52
T. longicornis	A	B	11.5	12.9	0.023	57
T. longicornis	A	B	11.5	12.9	0.001	57
T. longicornis	A	B	11.5	12.9	0.006	57
T. longicornis	A	B	11.5	12.9	0.038	57
T. longicornis	A	B	11.5	12.9	0.0003	57
T. longicornis	A	B	11.5	12.9	0.002	57
T. longicornis	A	B	11.5	12.9	0.018	57
T. longicornis	A	B	11.5	12.9	0.028	57
T. longicornis	A	B	11.5	12.9	0.025	57
T. longicornis	A	B	11.5	12.9	0.029	57
T. longicornis	A	B	8.5	12.9	0.000	57
T. longicornis	A	B	8.5	12.9	0.000	57
T. longicornis	A	B	8.5	12.9	0.000	57
T. longicornis	A	B	8.5	12.9	0.000	57
T. longicornis	A	B	8.5	12.9	0.000	57
T. longicornis	A	B	8.5	12.9	0.009	57
T. longicornis	A	B	8.5	12.9	0.000	57
T. longicornis	A	B	8.5	12.9	0.016	57
T. longicornis	A	B	8.5	12.9	0.000	57
T. longicornis	A	B	8.5	12.9	0.014	57
T. longicornis	A	B	8.5	12.9	0.004	57
T. longicornis	A	B	8.5	12.9	0.029	57

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Temora longicornis	A	B	7.5	12.9	0.001	57
T. longicornis	A	B	7.5	12.9	0.002	57
T. longicornis	A	B	7.5	12.9	0.002	57
T. longicornis	A	B	7.5	12.9	0.030	57
T. longicornis	A	B	7.5	12.9	0.004	57
T. longicornis	A	B	7.5	12.9	0.009	57
T. longicornis	A	B	7.5	12.9	0.002	57
T. longicornis	A	B	7.5	12.9	0.0003	57
T. longicornis	A	B	7.5	12.9	0.004	57
T. longicornis	A	B	6.5	12.9	0.007	57
T. longicornis	A	B	6.5	12.9	0.006	57
T. longicornis	A	B	6.5	12.9	0.016	57
Temora stylifera	A	B	20	12.60	0.08	1
T. stylifera	A	B	20	12.60	0.04	1
T. stylifera	A	B	28	18.43	0.017	59
Temora turbinata	A	B	28	2.74	0.281	59
T. turbinata	C	B	28	0.352	0.40	24
T. turbinata	C	B	28	0.637	0.44	24
T. turbinata	C	B	28	1.181	0.45	24
T. turbinata	C	B	28	1.987	0.27	24
T. turbinata	C	B	28	2.941	0.40	24
T. turbinata	C	B	28	1.025	0.907	58
T. turbinata	C	B	28	2.540	0.907	58
T. turbinata	C	B	28	0.798	0.695	58
T. turbinata	C	B	28	0.403	1.229	58
T. turbinata	C	B	28	1.242	1.020	58
T. turbinata	C	B	28	0.705	0.961	58
T. turbinata	C	B	28	1.838	0.957	58
T. turbinata	C	B	28	0.459	0.343	58
T. turbinata	C	B	28	0.619	0.599	58
T. turbinata	C	B	28	0.398	0.695	58
T. turbinata	C	B	28	0.272	0.705	58
T. turbinata	C	B	28	0.296	0.876	58
T. turbinata	C	B	28	0.483	0.916	58
T. turbinata	C	B	28	0.238	0.624	58
T. turbinata	C	B	28	0.489	0.745	58
T. turbinata	C	B	28	0.896	0.454	58
T. turbinata	C	B	28	1.389	0.408	58
T. turbinata	C	B	28	2.164	0.362	58
T. turbinata	N	B	28	0.035	0.815	60
T. turbinata	N	B	28	0.017	0.513	60
T. turbinata	N	B	28	0.041	0.968	60
T. turbinata	N	B	28	0.018	0.576	60
T. turbinata	N	B	28	0.018	0.537	60
T. turbinata	N	B	28	0.039	0.765	60

(*Continued*)

Table A1 (Continued)

Family: Species	Growth type	Spawning type	Temperature (°C)	Body weight (µg C ind^{-1})	g (d^{-1})	Source
Temora turbinata	N	B	28	0.065	0.428	60
T. turbinata	N	B	28	0.031	0.490	60
T. turbinata	N	B	28	0.031	0.506	60
T. turbinata	N	B	28	0.026	0.632	60
T. turbinata	N	B	28	0.026	0.601	60
T. turbinata	N	B	28	0.053	0.592	60
T. turbinata	N	B	28	0.052	0.344	60
T. turbinata	N	B	28	0.060	0.599	60
T. turbinata	N	B	28	0.057	0.670	60
Mixed goups:						
Paracalanus / Clausocalanus spp.	C	B+S	26	0.127	0.91	22
Paracalanus / Clausocalanus spp.	C	B+S	26	0.254	0.60	22
Paracalanus / Clausocalanus spp.	C	B+S	26	0.449	0.29	22
Paracalanus / Clausocalanus spp.	C	B+S	26	0.631	0.12	22
Paracalanus / Clausocalanus spp.	C	B+S	26	0.927	0.49	22

Sources

1. Saiz *et al.* (1997)†# – egg production rates and temperatures from their Table II. Values for *Oithona* sp. not used because only females without eggs initially incubated (see text of original study), *Clausocalanus* sp. not included as no appropriate weights could be found.
2. Calbet *et al*. (1996)# – weight-specific growth from their Table VI, and adult weights derived from Tables V and VI.
3. Kiørboe *et al*. (1990)†# – egg production rates from their Figure 9, and approximate temperature from Figure 2.
4. Kiørboe and Nielsen (1994)†# – egg production rates from their Figures 4 and 5. Monthly average temperatures estimated from their Figure 4.
5. Checkley *et al*. (1992) – values taken from text for Inland Sea of Japan study, equations to derive female growth not given.
6. McKinnon and Ayukai (1996)# – data taken from the bottle incubation results in their Table 1.
7. Kiørboe *et al*. (1985)# – data taken from their Table I.
8. Peterson *et al*. (1991)# – adult values taken from their Tables IV and VI, juvenile values *pers. comm*. from W. T. Peterson.
9. Ayukai (1988)# – temperatures from their Table 1, and egg production from Table 2. Adult and egg weights taken as mean values for *Acartia clausi*†.

10. Ambler (1985)[#] – data taken from Figure 5b, and temperatures from Table 1, only 'Natural Plankton' experiments included.
11. Kleppel (1992)# – temperatures from their Figure 1, and growth rates from Table 2. The adult weight assumed in paper given as pers. comm. from G. S. Kleppel.
12. Stearns *et al*. (1989)[†#] – egg production and temperatures taken from their Table 3.
13. Durbin *et al*. (1983)[†#]- adult body dry weights and egg production rates and from their Figures 3b and d respectively, mean temperature given in text.
14. Tiselius (1988)[†#] – egg production rates from their Table 3, and surface incubation temperatures from Figure 2.
15. Ward and Shreeve (1995)[#] – mean adult and egg weights taken from their Table 4, egg production rates taken as mean values in Table 2.
16. Lopez *et al*. (1993)[#] – growth rates from their Table 4 (but calculated for all females not just those spawning), temperature and egga and adult weights from text.
17. Hutchings *et al*. (1995)[#] – growth data taken from their Figure 12, average temperature and body weights pers. comm. from H. M. Verheye.
18. Nielsen and Hansen (1995)[#] – temperatures estimated from their Figure 2, and egg production rates from Table 4, egg weights pers. comm. from T. G. Nielsen.
19. Hirche and Bohrer (1987)[#] – growth data extracted from their Figure 1 and 2, those values quoted as <2.5 eggs female^{-1} d^{-1} are given here as 2.5 eggs female^{-1} d^{-1}. Egg and adult weights as given in text. The fact that animals were incubated in natural sea water confirmed as pers. comm. from H.-J. Hirche.
20. Smith (1990)[#] – data taken as means from their Figure 3, egg, adult weight and incubation temperature from text.
21. Park and Landry (1993)[#] – egg production rates from their Table 1, egg and adult weight and temperature from text.
22. Webber and Roff (1995a) – growth rates taken from their Table 7. Juvenile body weights derived from Table 2. Temperature taken as mean given in Webber and Roff (1995b). Adult growth rates not included because these rates do not represent *in situ* population rates.
23. Smith and Lane (1987)[#] – data taken from their Table 5.
24. Chisholm and Roff (1990b) – Finite weight-specific growth rates (G) were converted to instantaneous weight-specific rates (g) using the equation $g = \ln (G + 1)$. Copepod body weights derived from the length-weight and mean lengths given in Table 1 and 3 of Chisholm and Roff (1990a), the data being from a tropical region in which mean prosome lengths in most cases showed no significant seasonal change.
25. Nielsen and Sabatini (1996) – for *Oithona* spp.[#] weight-specific growth rates and temperatures from their Table 2. Weight of the growing individuals were derived from the cephalothorax lengths given using the equation of Sabatini and Kiørboe (1994); for Calanoids weight-specific growth rates from Table 3, and adult weights taken from Kiørboe and Sabatini (1995).
26. McKinnon and Thorrold (1993)[#] – weight-specific growth and prosome lengths from their Table VI for *Acrocalanus gracilis*, and Figures 12 and 13 for *Acrocalanus gibber*, temperatures taken from Figure 3. For *Acrocalanus gracilis* prosome lengths (P) were converted to body carbon weights (CW) by constructing an equation of the form $CW = a P^b$, with the equation being fixed by the two derived points (i.e. for prosome length 920 µm the CW=7.17 µg C; and for a prosome length of 1032 µm the CW=9.0 µg C).
27. McKinnon (1996)[#] – weight-specific growth values taken as mid-point values from their Table 4, temperatures from Table 1, and female carbon weights from Figure 1

28. Kimmerer (1984)[#] – egg production and temperature from their Table 2, adult and egg weights taken from associated publication (Kimmerer, 1980). *Acrocalanus inermis* is now known as *Bestiolina similis.*
29. Uye *et al*. (1992)[†#] – egg production rates from their Figure 6. Egg and adult weights taken as mean values for *Paracalanus* spp.
30. Newbury and Bartholomew (1976)[*] – only copepodite growth rates calculated as nauplii body weights derived indirectly.
31. Jerling and Wooldridge (1991) – growth estimated from development times (their Table 2) using the equation $g = 1/D \times [\ln (W_{max} / W_{min})]$, where D is the development time (days); W_{max} is the maximum weight of the stage (μg C); W_{min} is the minimum weight of the stage (μg C). These weight are calculated as the geometric means between consecutive stages. Body weights estimated from body lengths at the nearest appropriate temperature (their Table 1) using their length-weight equations. Acknowledgement that incubations were all within 5ºC of the temperature at which individuals were collected pers. comm. from H. L. Jerling.
32. Escaravage and Soetaert (1995) and Escaravage and Soetaert (1993)[#] – original data supplied pers. comm. from K.Soetaert.
33. Burkill and Kendall (1982)[*] – values for growth derived from their Table 4, temperatures from Table 2.
34. Durbin *et al*. (1992)[#] – egg production rates, adult weights and incubation temperatures taken from their Table 2, egg weights taken as *Acartia clausi hudsonica* value given in Appendix 1 of Kiørboe and Sabatini (1995).
35. Huntley and Escritor (1991)[#] – egg production rates taken from their Figure 14, egg and adult weights taken as those used by Lopez *et al*. (1993), i.e. 0.24 and 135 μg C respectively.
36. Runge (1985)[#] – egg production rates from his Tables 1, 2 and 3. Female size estimated from mean prosome lengths, using the length:DW equation presented in Cohen and Lough (1981) [sourced to Schwartz, MS 1977], egg weight taken from Appendix 1 of Kiørboe and Sabatini (1995).
37. Calbet and Irigoien (1997)[#] -egg production rates from their Table 1, egg and adult weights taken as averages from Table 3, with adult and egg weights being 98.8 μg C individual^{-1} and 0.29 μg C individual^{-1} respectively.
38. Cabal *et al*. (1997)[#] – egg production rates taken from their Table 4 for FSCREEN experiments only, temperature and body weights from text.
39. Tourangeau and Runge (1991)[†#] – egg production rates taken from their Figure 1C, temperature of incubation from text.
40. Uye and Shibuno (1992)[#] – weight-specific egg production rates, temperature and adult prosome lengths taken from their Figure 9. Prosome lengths converted to body weight using equation given in text. This species was found to be similar to *Paracalanus quasimodo.*
41. Hirche *et al*. (1991)[#] – weight-specific fecundity measures from their Figure 8. Adult weight measurements, incubation temperatures and the fact that incubations in natural sea water supplied pers. comm. from H.-J. Hirche. Adult weights were 424 and 648 μg AFDW individual^{-1} for *Calanus finmarchicus* and *Calanus glacialis* respectively.
42. Guerrero *et al*. (1997)[†#] – egg prduction rate from their Figure 1B.
43. Peterson *et al*. (1990)[#] – data for inshore and mid-shelf stations as given in their Table IV included here, adult weights from Table V and temperatures estimated from Figure 2. Although described as *Calanus australis* we assume this species is the re-described form *Calanus agulhensis* (see Peterson and Hutchings, 1995).
44. Rodríguez *et al*. (1995)[#] – egg production rates and temperatures from their Figures 3 and 5. Egg weight of *Acartia grani* taken as that estimated by Kiørboe and Sabatini

(1995), while adult weight estimated from mean prosome length of 1.1mm (see Rodríguez and Jiménez 1990) using the July equation of *Acartia bifilosa* given by Irigoien and Castel (1995) after correction (see Hirst 1996), these two species having very similar body dimensions. Egg and adult weight of *Acartia clausi* taken as means from Kiørboe and Sabatini (1995).

45. Cervetto *et al*. (1993)[†#] – temperature estimated from their Figure 2, egg production rate from text.
46. Sabatini and Kiørboe (1994)[#] – weight-specific growth rates taken from their Figure 9 and appropriate temperatures from Figure 8a, adult body weights calculated from their length:weight equation assuming a mean length of 465 µm. 47 Peterson and Kimmerer (1994)[†#] – egg production rates from their Table 1, temperature taken from Figure 1.
48. Daan (1987)[†#] – egg production rates and incubation temperatures for *Temora longicornis* taken from their Table 3.
49. Van Rijswijk *et al.* (1989)[†#] – temperature and egg production rates from their Figure 2.
50. McManus and Foster (1998)[†#] – egg production rates and temperatures from their Table I and Figure 2.
51. Hassett *et al.* (1993)[#] – egg production rates from their Table 4, egg diameter given in text as 100 µm, carbon weight estimated as 0.064 µgC by using the equation of Uye and Sano (1995) where; $C_E = 5.32\times10^{-8} \times E_D^{3.04}$, C_E is the egg carbon content (µg) and E_D is the egg diameter (µm). Female adult weight assumed to be 24.0 µgC individual^{-1}. Determined from the mean total length (L) of 2.4mm using the total length to dry weight equation given by Hirota (1981) where $\log_{10}$ BW = 0.8810 + 2.3579 $\log_{10}$ L, where BW is body dry weight (µg), and assuming carbon to be 40%DW (Båmstedt 1986). Although there was selection of mature females in this study, as the authors state that 'generally only a small percentage of females had light-colored ovaries [i.e. were not reproductively mature]', the investigation was included.
52. Jónasdóttir *et al*. (1995)[†#] – egg production rates from their Figure 3.
53. White and Roman (1992)[#] – data from their Table 4, adult weight average of 3.0 µgC female^{-1} pers. comm. from M. Roman.
54. Uriarte *et al*. (1998)[#] – all appropriate data supplied as pers. comm. from F. Villate
55. Peterson and Bellantoni (1987)[#] – egg production data from their Figure 10 for *Calanus chilensis*, adult weight derived from mean dry weight of 140.3 µg (Escribano and Rodriguez 1995) assuming carbon to be 40%DW (Båmstedt 1986) and an egg weight of 0.329 µgC (pers. comm. from R. Escribano, derived from egg diameter). *Acartia tonsa* egg production rates from their Figure 6, egg and adult weights taken from Kiørboe and Sabatini (1995). Growth data for *Temora longicornis* extracted separately from the paper Peterson and Kimmerer (1994) and detailed separately in this appendix.
56. Smith and Lane (1991)[#] – data for incubations of adult females and temperature of incubation (average of maximum and minimum values used here) supplied as pers. comm. from S. L. Smith. Egg weight taken as 0.63 µgDW (as given in text), and adult weight taken as 403 µgDW (mid-value for range of weights of those females within their Table 2).
57. Hay *et al*. (1991)[#] – egg production data from their Table 5, temperatures estimated from their Figure 1. Adult weights taken as means from their Table 2a. Egg weights from Appendix 1 of Kiørboe and Sabatini (1995) except for *Metridia lucens* in which egg weight calculated from diameter [as given in Kiørboe and Sabatini (1994)] using the equation of Uye and Sano (1995).
58. Hopcroft *et al*. (1998) – geometric mean body weights and weight-specific growth values supplied as pers. comm. from R. R. Hopcroft, data previously given in Webber and Roff (1995a) and Chisholm and Roff (1990b) not included as this already given.

59. Hopcroft and Roff (1998a)[#] – growth rates calculated on the basis of all incubations rather than just the actively reproducing females, data to accommodate changes supplied as pers. comm. from R. R. Hopcroft.
60. Hopcroft and Roff (1998b) – geometric mean body weights and weight-specific growth values supplied as pers. comm. from R. R. Hopcroft.
61. Liang and Uye (1997)[#] – temperature, carbon content of adult females and specific egg production rates of all females (rather than just those breeding) supplied as pers. comm. from S.-I. Uye.
62. Diel and Klein Bretler (1986) – growth taken from their Figure 4. Body weights derived using their length-weight equation and applying the lengths of copepods direct from the sea given in their Table 2, for CVs using those from the closest date.
63. Tang *et al*. (1998)[#†] – only *Centropages* data included as *Temora* females selected on the basis of ovary development. Temperature from their Figure 1A and egg production rates from Figure 2A.
64. McKinnon and Klumpp (1998)[#] – only sac-spawners data included as egg-ratio method employed, weight-specifice egg production rates and temperatures taken from their Table 2, *Oithona* sp. 2 not included as egg development times were not directly measured for this species. Body weights of adults taken from their Table 3.
65. Uye and Sano (1995)[#] – body weights, growth and temperature data supplied as pers. comm. from S.-I. Uye.
66. Richardson and Verheye (1998)[#] – mean growth rates of females from their Table II, adult and egg weights for *Calanus agulhensis* and *Centropages brachiatus* from Peterson *et al*. (1990), for *Rhincalanus nasutus* as given in Huntley and Lopez (1992), *Nannocalanus minor* and *Calanoides carinatus* as in Richardson and Verheye (1999), and *Neocalanus tonsus* taken as spring values from Ohman (1987) with egg diameter converted to carbon assuming 0.14×10^{-6} µgC μm^{-3} (Kiørboe and Sabatini 1995). Mean growth rates for juveniles from their Table V, body weights from their Table I, and mean temperature taken as 16ºC.
67. Gómez-Gutiérrez and Peterson (1999)[#] – weight-specific growth rates presented in their Figure 6 supplied as a pers. comm. from J. Gómez-Gutiérrez, dry weights converted to carbon using their converison of C=45%DW, data for *Epilabidocera longipedata* also supplied. Data for *Eucalanus californicus* from their Table III, adult weights derived from Smith and Lane (1991) (403 µgDW, mid-value for range of weights of those females in their Table 2.
68. Miralto *et al*. (1998)[#] – egg production rates taken from their Figure 3, adult and egg weights taken as means from Table 4 of Ward and Shreeve (1995).
69. Calbet and Agustí (1999)[#] – temperature, body weight and weight-specific growth rates supplied as a pers. comm. from A. Calbet.
70. Paul *et al*. (1990)[#] – Adult weight derived from prosome lengths using the length-weight regression of McLaren (1969), DW (µg) = $11.9\ PL^{3.64}$, PL is prosome length in mm, and carbon was assumed to be 40% of dry weight. For the period prior to 7th May 1987 a length of 1.1mm was assumed. Egg weights taken as the mean for all *Pseudocalanus* species in Kiørboe and Sabatini (1995), i.e. 0.140 µgC.

[*]Growth rates re-calculated using the equation $g_i = MR_i \times [\ln (W_{i+1} / W_i)]$, where W_i is the weight of the i^{th} development stage, and MR_i is the proportion of individuals within a stage moulting per 24 hours (i.e. is equal to the inverse of the development time).
[#]Weight-specific egg production rate calculated using the equation $g = (W_e / W_a)$, where W_e is the weight of the eggs produced over 24 hours, and W_a is adult female body weight.
[†]Egg and / or adult weights taken as appropriate species-specific means from Appendix 1 of Kiørboe and Sabatini (1995).

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APPENDIX 2

Table A2 Weight-specific growth rates (g d^{-1}) of epi-pelagic metazoans other than copepods. Growth rates divided on the basis of whether they represent somatic growth (g_S, i.e. body weight change, be this increase in somatic or gametic tissues within the organism itself), gametic output (g_R, i.e. actual reproductive output). If both terms are measured or can be deduced then the total is also given (g_T). If one is measured and the other term unknown then we do not derive a value for the total. In the column headed Approach, C = Cohort Approach; N = Natural Approach; and E = Controlled Approach (see text for details). In the column headed Growth types, S = somatic growth measured; R = reproductive output. If total growth was assessed this is indicated by superscript T in the growth column.

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (µg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
Chaetognatha:								
Pterosagitta draco	C	S^T	18.5	5.28	0.008	0	0.008	20
P. draco	C	S^T	18.5	8.56	0.015	0	0.015	20
P. draco	C	S^T	18.5	12.28	0.021	0	0.021	20
P. draco	C	S^T	18.5	18.60	0.005	0	0.005	20
P. draco	C	S^T	18.5	27.40	–0.006	0	–0.006	20
P. draco	C	S^T	18.5	8.24	0.036	0	0.036	20
P. draco	C	S^T	18.5	11.72	0.016	0	0.016	20
P. draco	C	S^T	18.5	8.10	0.003	0	0.003	20
P. draco	C	S^T	18.5	13.16	0.065	0	0.065	20
P. draco	C	S^T	18.5	17.28	0.049	0	0.049	20
Sagitta crassa	E	$S+R^T$	22.2	25.1	0.051	0.168	0.219	26
S. crassa	E	$S+R^T$	22.2	33.9	0.048	0.106	0.154	26
S. crassa	E	$S+R^T$	22.2	41.6	0.032	0.063	0.095	26
Sagitta elegans	C	S	4.9	127.7	0.024	–	–	14
S. elegans	C	S	4.9	218.2	0.020	–	–	14
S. elegans	C	S	4.9	308.5	0.011	–	–	14
S. elegans	C	S	1.8	377.0	0.010	–	–	14
S. elegans	C	S	1.8	495.3	0.010	–	–	14
S. elegans	C	S	1.8	648.8	0.008	–	–	14
S. elegans	C	S	2.0	37.6	0.024	–	–	14
S. elegans	C	S	2.0	75.2	0.026	–	–	14
S. elegans	C	S	2.0	126.8	0.009	–	–	14
S. elegans	C	S	2.0	162.5	0.020	–	–	14
S. elegans	C	S	2.0	244.9	0.040	–	–	14
S. elegans	C	S	2.0	446.7	0.040	–	–	14
S. elegans	C	S	2.0	650.2	0.005	–	–	14
S. elegans	C	S	7.4	55.7	0.057	–	–	14
S. elegans	C	S	7.4	139.3	0.022	–	–	14
S. elegans	C	S	7.4	221.1	0.007	–	–	14
S. elegans	C	S	8.3	22.3	0.058	–	–	14
S. elegans	C	S	8.3	45.9	0.063	–	–	14
S. elegans	C	S	8.3	100.1	0.023	–	–	14
S. elegans	C	S	8.3	192.8	0.028	–	–	14
S. elegans	C	S	8.3	267.2	0.025	–	–	14

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (μg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
S. elegans	C	S	9.5	94.1	0.055	–	–	14
S. elegans	C	S	9.5	164.7	0.032	–	–	14
S. elegans	C	S	9.5	196.4	0.011	–	–	14
S. elegans	C	S	9.2	34.6	0.090	–	–	14
S. elegans	C	S	9.2	58.4	0.085	–	–	14
Sagitta elegans	C	S	9.2	114.2	0.093	–	–	14
S. elegans	C	S	9.2	196.1	0.057	–	–	14
S. elegans	C	S	8.6	49.8	0.070	–	–	14
S. elegans	C	S	8.6	88.1	0.032	–	–	14
S. elegans	C	S	8.6	109.7	0.017	–	–	14
S. elegans	C	S	8.6	195.0	0.134	–	–	14
S. elegans	C	S	8.3	34.6	0.075	–	–	14
S. elegans	C	S	8.3	47.1	0.013	–	–	14
S. elegans	C	S	8.3	87.6	0.153	–	–	14
S. elegans	C	S	8.3	230.4	0.054	–	–	14
S. elegans	C	S	6.9	20.8	0.047	–	–	14
S. elegans	C	S	6.9	37.6	0.088	–	–	14
S. elegans	C	S	6.9	82.8	0.107	–	–	14
S. elegans	C	S	6.9	175.0	0.020	–	–	14
S. elegans	C	S	2.0	428.6	0.011	–	–	14
S. elegans	C	S	2.0	470.6	0.003	–	–	14
S. elegans	C	S	2.0	526.2	0.004	–	–	14
Sagitta hispida	E	S	21	0.98	0.25	–	–	7
S. hispida	E	S	21	4.53	0.25	–	–	7
S. hispida	E	S	21	13.25	0.25	–	–	7
S. hispida	E	S	21	31.97	0.25	–	–	7
S. hispida	E	S	21	59.27	0.25	–	–	7
S. hispida	E	S	21	97.88	0.25	–	–	7
S. hispida	E	S	21	156.70	0.083	–	–	7
S. hispida	E	S	21	238.42	0.044	–	–	7
S. hispida	E	S	26	0.98	0.35	–	–	7
S. hispida	E	S	26	4.53	0.35	–	–	7
S. hispida	E	S	26	13.25	0.35	–	–	7
S. hispida	E	S	26	31.97	0.35	–	–	7
S. hispida	E	S	26	59.27	0.35	–	–	7
S. hispida	E	S	26	97.88	0.35	–	–	7
S. hispida	E	S	26	156.70	0.074	–	–	7
S. hispida	E	S	26	238.42	0.007	–	–	7
S. hispida	E	S	31	0.98	0.41	–	–	7
S. hispida	E	S	31	4.53	0.41	–	–	7
S. hispida	E	S	31	13.25	0.41	–	–	7
S. hispida	E	S	31	31.97	0.41	–	–	7
S. hispida	E	S	31	59.27	0.41	–	–	7
S. hispida	E	S	31	97.88	0.11	–	–	7
S. hispida	E	S	31	156.70	0.041	–	–	7

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (μg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
S. hispida	E	S^T	16	27.8	0.079	0	0.079	24
S. hispida	E	$S+R^T$	16	70.0	–0.036	0.042	0.006	24
S. hispida	E	S^T	21	13.0	0.123	0	0.123	24
S. hispida	E	S^T	21	36.8	0.135	0	0.135	24
S. hispida	E	$S+R^T$	21	92.0	–0.039	0.026	–0.013	24
Sagitta hispida	E	S^T	26	38.1	0.002	0	0.002	24
S. hispida	E	S^T	26	33.5	0.118	0	0.118	24
S. hispida	E	$S+R^T$	26	74.4	–0.052	0.052	0.007	24
Cnidaria:								
Aequorea victoria	E	S^T	11.6	606.7	0.103	0	0.103	22
A. victoria	E	S^T	11.6	1198.2	0.098	0	0.098	22
A. victoria	E	S^T	11.6	2427.4	0.103	0	0.103	22
A. victoria	E	S^T	11.6	4637.2	0.080	0	0.080	22
A. victoria	E	S^T	11.6	7431.4	0.056	0	0.056	22
A. victoria	E	S	11.6	10557.6	0.040	–	–	22
A. victoria	E	S	11.6	13294.2	0.026	–	–	22
A. victoria	E	S	11.6	15309.4	0.015	–	–	22
Aurelia aurita	C	S^T	9.6	10.0	0.235	0	0.235	3
A. aurita	C	S^T	10.6	339.1	0.118	0	0.228	3
A. aurita	C	S^T	12.8	9102	0.149	0	0.249	3
A. aurita	C	S^T	15.2	62395	0.070	0	0.070	3
A. aurita	C	S	15.8	114882	0.047	–	–	3
A. aurita	C	S^T	9.4	53.8	0.048	0	0.048	3
A. aurita	C	S^T	10.0	327.0	0.192	0	0.192	3
A. aurita	C	S^T	11.0	3531	0.159	0	0.159	3
A. aurita	C	S^T	12.6	11955	0.031	0	0.031	3
A. aurita	C	S^T	14.2	33384	0.070	0	0.070	3
A. aurita	C	S	15.4	53152	–0.069	–	–	3
A. aurita	C	S^T	7.9	11.4	0.105	0	0.105	3
A. aurita	C	S^T	10.0	52.0	0.056	0	0.056	3
A. aurita	C	S^T	12.2	747.6	0.314	0	0.314	3
A. aurita	C	S^T	13.3	8760	0.077	0	0.077	3
A. aurita	C	S	15.5	35491	0.052	–	–	3
A. aurita	C	S^T	7.1	6.5	0.115	0	0.115	3
A. aurita	C	S^T	8.2	14.3	0.051	0	0.051	3
A. aurita	C	S^T	8.9	63.8	0.139	0	0.139	3
A. aurita	C	S^T	8.9	273.1	0.052	0	0.052	3
A. aurita	C	S^T	9.7	646.3	0.209	0	0.209	3
A. aurita	C	S^T	11.0	3302	0.158	0	0.258	3
A. aurita	C	S^T	12.5	24876	0.130	0	0.130	3
A. aurita	C	S	14.1	65537	0.011	–	–	3
A. aurita	C	S	14.7	61796	–0.046	–	–	3
A. aurita	C	S	15.2	76581	0.132	–	–	3
A. aurita	C	S	16.3	92329	–0.029	–	–	3

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (μg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
Chrysaora quinquecirrha	E	S	23	9.238	0.335	0	0.335	38
C. quinquecirrha	E	S	23	3.889	0.371	0	0.371	38
C. quinquecirrha	E	S	23	4.335	0.357	0	0.357	38
C. quinquecirrha	E	S	23	5.645	0.304	0	0.304	38
Chrysaora quinquecirrha	E	S	23	4.655	0.151	0	0.151	38
C. quinquecirrha	E	S	23	24.883	0.643	0	0.643	38
C. quinquecirrha	E	S	23	23.742	0.493	0	0.493	38
C. quinquecirrha	E	S	23	13.450	0.380	0	0.380	38
C. quinquecirrha	E	S	23	8.612	0.203	0	0.203	38
C. quinquecirrha	E	S	23	6.562	0.067	0	0.067	38
C. quinquecirrha	E	S	23	6.562	–0.067	0	–0.067	38
C. quinquecirrha	E	S	23	9.320	0.740	0	0.740	38
C. quinquecirrha	E	S	23	20.113	0.675	0	0.675	38
C. quinquecirrha	E	S	23	13.916	0.540	0	0.540	38
C. quinquecirrha	E	S	23	11.920	0.413	0	0.413	38
C. quinquecirrha	E	S	23	7.047	0.303	0	0.303	38
Linuche unguiculata		C	S	26	173.0	0.13	–	19
L. unguiculata	C	S	26	231.8	0.13	–	–	19
L. unguiculata	C	S	26	948.1	0.13	–	–	19
L. unguiculata	C	S	26	948.1	0.02	–	–	19
L. unguiculata	C	S	26	2289.0	0.02	–	–	19
L. unguiculata	C	S	26	5934.0	0.02	–	–	19
Phyllorhiza punctata	C	S	27	1446.3	0.096	–	–	16
P. punctata	C	S	27	5232.9	0.046	–	–	16
P. punctata	C	S	28	197.6	0.110	–	–	16
P. punctata	C	S	28	820.7	0.043	–	–	16
P. punctata	C	S	28	1479.9	0.005	–	–	16
Sarsia tubulosa	E	S^T	12	47.4	0.288	–	0	37
S. tubulosa	E	S^T	12	110.0	0.150	–	0	37
S. tubulosa	E	S^T	12	169.4	0.122	–	0	37
S. tubulosa	E	S^T	12	222.6	0.079	–	0	37
S. tubulosa	E	S^T	12	245.5	0.079	–	0	37
S. tubulosa	E	S	12	364.6	0.075	–	–	37
S. tubulosa	E	S	12	379.7	0.044	–	–	37
S. tubulosa	E	S	12	652.4	0.037	–	–	37
S. tubulosa	C	S^T	11.5	13.4	0.603	–	0	37
S. tubulosa	C	S^T	11.5	32.7	0.332	–	0	37
S. tubulosa	C	S^T	11.5	65.4	0.203	–	0	37
S. tubulosa	C	S^T	11.5	115.2	0.133	–	0	37
S. tubulosa	C	S^T	11.5	185.9	0.091	–	0	37
S. tubulosa	C	S^T	11.5	281.4	0.067	–	0	37
S. tubulosa	C	S	11.5	405.6	0.049	–	–	37

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (µg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
Crustacea:								
Calliopius laeviusculus	E	S^T	8	15	0.131	0	0.131	12
C. laeviusculus	E	S^T	8	30	0.125	0	0.125	12
Calliopius laeviusculus	E	S^T	8	50	0.119	0	0.119	12
C. laeviusculus	E	S^T	8	100	0.111	0	0.111	12
C. laeviusculus	E	S^T	8	150	0.105	0	0.105	12
C. laeviusculus	E	S^T	8	200	0.101	0	0.101	12
C. laeviusculus	E	S^T	8	300	0.095	0	0.095	12
C. laeviusculus	E	S^T	8	500	0.085	0	0.085	12
C. laeviusculus	E	S^T	8	750	0.075	0	0.075	12
C. laeviusculus	E	S^T	8	1000	0.067	0	0.067	12
C. laeviusculus	E	$S+R^T$	8	1250	0.060	0.016	0.076	12
C. laeviusculus	E	$S+R^T$	8	1500	0.054	0.013	0.067	12
C. laeviusculus	E	$S+R^T$	8	1750	0.048	0.012	0.060	12
C. laeviusculus	E	$S+R^T$	8	2000	0.042	0.011	0.053	12
C. laeviusculus	E	$S+R^T$	8	2250	0.036	0.010	0.046	12
C. laeviusculus	E	$S+R^T$	8	2500	0.031	0.009	0.040	12
C. laeviusculus	E	$S+R^T$	8	2750	0.026	0.008	0.034	12
C. laeviusculus	E	$S+R^T$	8	3000	0.021	0.008	0.029	12
C. laeviusculus	E	$S+R^T$	8	3250	0.016	0.008	0.024	12
C. laeviusculus	E	$S+R^T$	8	3500	0.012	0.007	0.019	12
C. laeviusculus	E	$S+R^T$	8	3750	0.007	0.007	0.014	12
C. laeviusculus	E	S^T	12	15	0.193	0	0.193	12
C. laeviusculus	E	S^T	12	30	0.180	0	0.180	12
C. laeviusculus	E	S^T	12	50	0.171	0	0.171	12
C. laeviusculus	E	S^T	12	100	0.154	0	0.154	12
C. laeviusculus	E	S^T	12	150	0.145	0	0.145	12
C. laeviusculus	E	S^T	12	200	0.137	0	0.137	12
C. laeviusculus	E	S^T	12	300	0.125	0	0.125	12
C. laeviusculus	E	S^T	12	500	0.108	0	0.108	12
C. laeviusculus	E	S^T	12	750	0.092	0	0.092	12
C. laeviusculus	E	S^T	12	1000	0.079	0	0.079	12
C. laeviusculus	E	$S+R^T$	12	1250	0.068	0.019	0.087	12
C. laeviusculus	E	$S+R^T$	12	1500	0.058	0.016	0.074	12
C. laeviusculus	E	$S+R^T$	12	1750	0.049	0.015	0.064	12
C. laeviusculus	E	$S+R^T$	12	2000	0.041	0.014	0.055	12
C. laeviusculus	E	$S+R^T$	12	2250	0.034	0.013	0.047	12
C. laeviusculus	E	$S+R^T$	12	2500	0.026	0.012	0.038	12
C. laeviusculus	E	$S+R^T$	12	2750	0.020	0.012	0.032	12
C. laeviusculus	E	$S+R^T$	12	3000	0.013	0.011	0.024	12
C. laeviusculus	E	$S+R^T$	12	3250	0.007	0.011	0.018	12
C. laeviusculus	E	S^T	15	15	0.247	0	0.247	12
C. laeviusculus	E	S^T	15	30	0.231	0	0.231	12

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (μg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
C. laeviusculus	E	S^T	15	50	0.222	0	0.222	12
C. laeviusculus	E	S^T	15	100	0.207	0	0.207	12
C. laeviusculus	E	S^T	15	150	0.197	0	0.197	12
C. laeviusculus	E	S^T	15	200	0.188	0	0.188	12
Calliopius laeviusculus	E	S^T	15	300	0.174	0	0.174	12
C. laeviusculus	E	S^T	15	500	0.152	0	0.152	12
C. laeviusculus	E	S^T	15	750	0.129	0	0.129	12
C. laeviusculus	E	S^T	15	1000	0.109	0	0.109	12
C. laeviusculus	E	$S+R^T$	15	1250	0.090	0.021	0.111	12
C. laeviusculus	E	$S+R^T$	15	1500	0.074	0.019	0.093	12
C. laeviusculus	E	$S+R^T$	15	1750	0.057	0.018	0.075	12
C. laeviusculus	E	$S+R^T$	15	2000	0.042	0.016	0.058	12
C. laeviusculus	E	$S+R^T$	15	2250	0.027	0.015	0.042	12
C. laeviusculus	E	$S+R^T$	15	2500	0.013	0.015	0.028	12
Euphausia pacifica	E	S^T	8	2.8	0.103	0	0.103	4
E. pacifica	E	S^T	8	11.1	0.120	0	0.120	4
E. pacifica	E	S^T	8	33.9	0.046	0	0.046	4
E. pacifica	E	S^T	8	124.3	0.030	0	0.030	4
E. pacifica	E	S^T	8	198.6	0.025	0	0.025	4
E. pacifica	E	S^T	8	417.2	0.020	0	0.020	4
E. pacifica	E	S^T	8	565.9	0.018	0	0.018	4
E. pacifica	E	$S+R^T$	8	1469.9	0.013	0.014	0.027	4
E. pacifica	E	$S+R^T$	8	2954.3	0.011	0.010	0.021	4
E. pacifica	E	S^T	12	2.8	0.089	0	0.089	4
E. pacifica	E	S^T	12	8.8	0.157	0	0.157	4
E. pacifica	E	S^T	12	33.2	0.076	0	0.076	4
E. pacifica	E	S^T	12	136.9	0.047	0	0.047	4
E. pacifica	E	S^T	12	225.3	0.039	0	0.039	4
E. pacifica	E	S^T	12	491.7	0.030	0	0.030	4
E. pacifica	E	$S+R^T$	12	675.7	0.027	0.040	0.067	4
E. pacifica	E	$S+R^T$	12	1462.7	0.021	0.024	0.045	4
E. pacifica	E	$S+R^T$	12	2654.5	0.017	0.018	0.035	4
E. pacifica	C	S	11.5	2.54	0.228	–	–	31
E. pacifica	C	S	11.5	62.54	0.071	–	–	31
E. pacifica	C	S	11.5	491.14	0.091	–	–	31
E. pacifica	C	S	11.5	2992.76	0.033	–	–	31
E. pacifica	C	S	11.5	6772.26	0.006	–	–	31
E. pacifica	C	S	11.5	9021.82	0.010	–	–	31
E. pacifica	C	S	11.5	11037.82	0.002	–	–	31
Euphausia superba	E	S	8	251.0	0.023	–	–	9
E. superba	E	S	8	252.0	0.021	–	–	9
E. superba	E	S	8	363.7	0.018	–	–	9

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (µg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
E. superba	E	S	8	795.6	0.010	–	–	9
E. superba	E	S	8	438.1	0.010	–	–	9
E. superba	E	S	8	656.3	0.008	–	–	9
E. superba	E	S	8	891.4	0.010	–	–	9
Euphausia superba	E	S	8	734.7	0.008	–	–	9
E. superba	E	S	8	751.4	0.005	–	–	9
E. superba	E	S	0.8	14953	0.0086	–	–	10
E. superba	E	S	0.8	24542	0.0067	–	–	10
E. superba	E	S	0.8	51107	0.0035	–	–	10
E. superba	E	S	0.8	51107	0.0038	–	–	10
E. superba	E	S	0.8	25411	0.0042	–	–	10
E. superba	E	S	0.8	64172	0.0027	–	–	10
E. superba	E	S	0.8	21357	0.0064	–	–	10
E. superba	E	S	0.8	36057	0.0049	–	–	10
E. superba	E	S	0.8	47303	0.0047	–	–	10
E. superba	E	S	0.8	60285	0.0020	–	–	10
E. superba	N	S^T	1	88.2	0.054	0	0.054	25
E. superba	N	S^T	1	112.6	0.042	0	0.042	25
E. superba	N	S^T	1	259.1	0.055	0	0.055	25
E. superba	N	S^T	1	297.4	0.011	0	0.011	25
E. superba	N	S^T	1	536.3	0.048	0	0.048	25
E. superba	N	S^T	1	645.1	0.013	0	0.013	25
E. superba	N	S^T	1	785.4	0.014	0	0.014	25
E. superba	N	S^T	1	76.0	0.027	0	0.027	25
E. superba	N	S^T	1	100.8	0.022	0	0.022	25
E. superba	N	S^T	1	131.5	0.016	0	0.016	25
E. superba	N	S^T	1	160.9	0.012	0	0.012	25
E. superba	N	S^T	1	316.7	0.017	0	0.017	25
E. superba	N	S^T	1	338.1	0.003	0	0.003	25
E. superba	N	S^T	2	20166	0.0066	0	0.0066	34
E. superba	E	S^T	2	18730	0.0092	0	0.0092	34
E. superba	E	S^T	2	20589	0.0063	0	0.0063	34
Homarus americanus	E	S^T	22	402.9	0.200	0	0.200	29
H. americanus	E	S^T	22	581.8	0.112	0	0.112	29
H. americanus	E	S^T	22	734.4	0.131	0	0.131	29
H. americanus	E	S^T	22	841.9	0.071	0	0.071	29
H. americanus	E	S^T	22	956.5	0.038	0	0.038	29
H. americanus	E	S^T	22	1639.5	0.121	0	0.121	29
Hyas araneus	E	S^T	12	41.9	0.100	0	0.100	28
H. araneus	E	S^T	12	91.8	0.062	0	0.062	28
H. araneus	E	S^T	12	165.5	0.062	0	0.062	28
H. araneus	E	S^T	12	217.1	0.016	0	0.016	28
H. araneus	E	S^T	12	224.7	–0.006	0	–0.006	28

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (μg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
H. coarctatus	E	S^T	12	17.8	0.223	0	0.223	27
H. coarctatus	E	S^T	12	24.4	0.094	0	0.094	27
H. coarctatus	E	S^T	12	29.2	0.086	0	0.086	27
H. coarctatus	E	S^T	12	34.6	0.085	0	0.085	27
Hyas coarctatus	E	S^T	12	38.7	0.026	0	0.026	27
H. coarctatus	E	S^T	12	41.5	0.045	0	0.045	27
H. coarctatus	E	S^T	12	53.2	0.128	0	0.128	27
H. coarctatus	E	S^T	12	67.2	0.106	0	0.106	27
H. coarctatus	E	S^T	12	80.1	0.069	0	0.069	27
H. coarctatus	E	S^T	12	91.4	0.063	0	0.063	27
H. coarctatus	E	S^T	12	101.0	0.036	0	0.036	27
H. coarctatus	E	S^T	12	106.0	0.013	0	0.013	27
H. coarctatus	E	S^T	12	112.0	0.070	0	0.070	27
H. coarctatus	E	S^T	12	134.2	0.110	0	0.110	27
H. coarctatus	E	S^T	12	149.7	–0.001	0	–0.001	27
H. coarctatus	E	S^T	12	155.8	0.041	0	0.041	27
H. coarctatus	E	S^T	12	155.6	–0.042	0	–0.042	27
H. coarctatus	E	S^T	12	156.7	0.049	0	0.049	27
H. coarctatus	E	S^T	12	169.4	0.029	0	0.029	27
H. coarctatus	E	S^T	12	171.4	–0.017	0	–0.017	27
H. coarctatus	E	S^T	12	142.2	–0.170	0	–0.170	27
H. coarctatus	E	S^T	12	134.6	0.115	0	0.115	27
H. coarctatus	E	S^T	12	135.5	–0.108	0	–0.108	27
Metamysidopsis elongata	E	S^T	17	45.1	0.072	0	0.072	33
M. elongata	E	S	17	152.8	0.026	–	–	33
M. elongata	E	S	17	239.6	0.010	–	–	33
M. elongata	E	S	17	289.2	0.005	–	–	33
M. elongata	E	S	17	323.9	0.004	–	–	33
M. elongata	E	S	17	349.5	0.002	–	–	33
M. elongata	E	S	17	363.4	0.001	–	–	33
M. elongata	E	S	17	41.1	0.064	–	–	33
M. elongata	E	S	17	123.4	0.024	–	–	33
M. elongata	E	S	17	187.2	0.010	–	–	33
M. elongata	E	S	17	225.0	0.005	–	–	33
M. elongata	E	S	17	248.2	0.003	–	–	33
M. elongata	E	S	17	262.2	0.001	–	–	33
M. elongata	E	S	17	269.1	0.001	–	–	33
Panopeus herbstii	N	S^T	25.6	3.3	0.198	0	0.198	1
P. herbstii	N	S^T	25.6	5.9	0.369	0	0.369	1
P. herbstii	N	S^T	25.6	9.5	0.112	0	0.112	1
P. herbstii	N	S^T	25.6	12.7	0.171	0	0.171	1
Themisto japonica	C	S^T	1.0	6.04	0.0581	0	0.0581	35

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (μg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
T. japonica	C	S^T	1.0	12.87	0.0442	0	0.0442	35
T. japonica	C	S^T	1.0	24.28	0.0353	0	0.0353	35
T. japonica	C	S^T	1.0	42.24	0.0287	0	0.0287	35
T. japonica	C	S^T	1.0	69.38	0.0239	0	0.0239	35
Themisto japonica	C	S^T	1.0	109.38	0.0200	0	0.0200	35
T. japonica	C	S^T	1.0	167.24	0.0170	0	0.0170	35
T. japonica	C	S^T	1.0	250.06	0.0144	0	0.0144	35
T. japonica	C	S	1.0	368.02	0.0123	–	–	35
T. japonica	C	S	1.0	536.34	0.0105	–	–	35
T. japonica	C	S	1.0	778.04	0.0089	–	–	35
T. japonica	C	S	1.0	1129.48	0.0075	–	–	35
T. japonica	C	S	1.0	1650.84	0.0062	–	–	35
T. japonica	C	S	1.0	2448.38	0.0050	–	–	35
T. japonica	C	S	1.0	3724.38	0.0039	–	–	35
T. japonica	C	S	1.0	5909.00	0.0029	–	–	35
T. japonica	C	S^T	7.0	6.04	0.1237	0	0.1237	35
T. japonica	C	S^T	7.0	12.87	0.0942	0	0.0942	35
T. japonica	C	S^T	7.0	24.28	0.0752	0	0.0752	35
T. japonica	C	S^T	7.0	42.24	0.0611	0	0.0611	35
T. japonica	C	S^T	7.0	69.38	0.0508	0	0.0508	35
T. japonica	C	S^T	7.0	109.38	0.0426	0	0.0426	35
T. japonica	C	S^T	7.0	167.24	0.0361	0	0.0361	35
T. japonica	C	S^T	7.0	250.06	0.0307	0	0.0307	35
T. japonica	C	S	7.0	368.02	0.0262	–	–	35
T. japonica	C	S	7.0	536.34	0.0223	–	–	35
T. japonica	C	S	7.0	778.04	0.0189	–	–	35
T. japonica	C	S	7.0	1129.48	0.0159	–	–	35
T. japonica	C	S	7.0	1650.84	0.0132	–	–	35
T. japonica	C	S	7.0	2448.38	0.0107	–	–	35
T. japonica	C	S	7.0	3724.38	0.0084	–	–	35
T. japonica	C	S	7.0	5909.00	0.0062	–	–	35
T. japonica	C	S^T	15.0	6.04	0.2368	0	0.2368	35
T. japonica	C	S^T	15.0	12.87	0.1802	0	0.1802	35
T. japonica	C	S^T	15.0	24.28	0.1437	0	0.1437	35
T. japonica	C	S^T	15.0	42.24	0.1168	0	0.1168	35
T. japonica	C	S^T	15.0	69.38	0.0971	0	0.0971	35
T. japonica	C	S^T	15.0	109.38	0.0816	0	0.0816	35
T. japonica	C	S^T	15.0	167.24	0.0691	0	0.0691	35
T. japonica	C	S^T	15.0	250.06	0.0587	0	0.0587	35
T. japonica	C	S	15.0	368.02	0.0500	–	–	35
T. japonica	C	S	15.0	536.34	0.0426	–	–	35
T. japonica	C	S	15.0	778.04	0.0361	–	–	35
T. japonica	C	S	15.0	1129.48	0.0304	–	–	35
T. japonica	C	S	15.0	1650.84	0.0252	–	–	35

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (μg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
T. japonica	C	S	15.0	2448.38	0.0205	–	–	35
T. japonica	C	S	15.0	3724.38	0.0160	–	–	35
Themisto japonica	C	S	15.0	5909.00	0.0118	–	–	35
Thysanoessa inermis	C	S^T	3.5	9.5	0.025	0	0.025	30
T. inermis	C	S^T	5.5	31.3	0.053	0	0.053	30
T. inermis	C	S^T	8.5	130.0	0.040	0	0.040	30
T. inermis	C	S^T	7	339.5	0.023	0	0.023	30
T. inermis	C	S^T	6	565.0	0.011	0	0.011	30
T. inermis	C	S^T	5.5	745.1	0.007	0	0.007	30
T. inermis	C	S^T	4	908.4	0.006	0	0.006	30
T. inermis	C	S^T	3	1070.7	0.005	0	0.005	30
T. inermis	C	S	2	1388.4	0.012	0	0.012	30
T. inermis	C	S	3	1641.8	–0.001	–	–	30
T. inermis	C	S	2	1683.1	0.002	–	–	30
T. inermis	C	S	2	1899.6	0.005	–	–	30
T. inermis	C	S	3.5	2816.4	0.020	–	–	30
T. inermis	C	S	5.5	4570.3	0.011	–	–	30
T. inermis	C	S	8.5	5751.8	0.004	–	–	30
T. inermis	C	S	7	6131.2	0.001	–	–	30
T. inermis	C	S	6	6179.3	0.000	–	–	30
T. inermis	C	S	5.5	6179.3	0.000	–	–	30
T. inermis	C	S	4	6179.3	0.000	–	–	30
T. inermis	C	S	3	6179.3	0.000	–	–	30
T. inermis	C	S	1	6179.3	0.000	–	–	30
T. inermis	C	S	3	6179.3	0.000	–	–	30
T. inermis	C	S	2	6324.5	0.002	–	–	30
T. inermis	C	S	2	7178.6	0.007	–	–	30
T. inermis	C	S	3.5	10011.5	0.015	–	–	30
T. inermis	C	S	5.5	13279.1	0.003	–	–	30
T. inermis	C	S	8.5	14087.1	0.000	–	–	30
Thysanoessa raschi	C	S	0.5	608	0.0267	–	–	17
T. raschi	C	S	1.0	1011	0.0319	–	–	17
T. raschi	C	S	1.5	1739	0.0337	–	–	17
T. raschi	C	S	2.5	2883	0.0339	–	–	17
Thysanoessa spinifera	C	S	11.8	310.1	0.066	–		32
T. spinifera	C	S	11.8	1591.1	0.041	–		32
T. spinifera	C	S	11.8	4067.4	0.011	–		32
T. spinifera	C	S	11.8	8409.3	0.043	–		32
T. spinifera	C	S	11.8	14262.0	0.003	–		32
T. spinifera	C	S	11.8	15955.2	0.001	–		32

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (µg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
Ctenophora:								
Bolionopsis infundibulum	E	S	16	369.1	0.205	–	–	23
B. infundibulum	E	S	16	1577.2	0.376	–	–	23
Bolionopsis infundibulum	E	S	16	10262.8	0.186	–	–	23
Mnemiopsis mccradyi	E	S	21	1.72	0.50	–	–	7
M. mccradyi	E	S	21	44.21	0.50	–	–	7
M. mccradyi	E	S	21	1055	0.21	–	–	7
M. mccradyi	E	S	21	12208	0.069	–	–	7
M. mccradyi	E	S	21	24242	0.069	–	–	7
M. mccradyi	E	S	26	1.72	0.78	–	–	7
M. mccradyi	E	S	26	44.21	0.78	–	–	7
M. mccradyi	E	S	26	1055	0.23	–	–	7
M. mccradyi	E	S	26	12208	0.071	–	–	7
M. mccradyi	E	S	26	24242	0.071	–	–	7
M. mccradyi	E	S	31	1.72	0.65	–	–	7
M. mccradyi	E	S	31	44.21	0.65	–	–	7
M. mccradyi	E	S	31	1055	0.23	–	–	7
M. mccradyi	E	S	31	12208	0.069	–	–	7
M. mccradyi	E	S	31	24242	0.069	–	–	7
Pleurobrachia bachei	E	S	13	0.1	0.51	–	–	8
P. bachei	E	S	13	4.1	0.44	–	–	8
P. bachei	E	S	13	63	0.41	–	–	8
P. bachei	E	S	13	209	0.08	–	–	8
P. bachei	E	S	13	364	0.08	–	–	8
P. bachei	E	S	14.2	239.4	0.156	–	–	13
P. bachei	E	S	14.2	248.2	0.204	–	–	13
P. bachei	E	S	14.2	469.0	0.092	–	–	13
P. bachei	E	S	14.2	608.5	0.166	–	–	13
Larvacea:								
Appendicularia sicula	N	S	28	0.113	1.018	–	–	18
A. sicula	N	S	28	0.052	1.081	–	–	18
A. sicula	N	S	28	0.033	2.004	–	–	18
A. sicula	N	S	28	0.035	2.127	–	–	18
Appendicularia sicula	E	S	28	0.055	2.061	–	–	18
A. sicula	N	S	28	0.033	2.004	–	–	18
A. sicula	E	S	28	0.037	2.860	–	–	18
A. sicula	E	S	28	0.035	2.127	–	–	18
A. sicula	N	S	28	0.017	1.913	–	–	18

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (µg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
A. sicula	E	S	28	0.030	1.876	–	–	18
A. sicula	E	S	28	0.039	1.862	–	–	18
A. sicula	N	S	28	0.035	2.127	–	–	18
A. sicula	E	S	28	0.012	2.127	–	–	18
Appendicularia sicula	N	S	28	0.027	1.825	–	–	18
A. sicula	E	S	28	0.039	2.355	–	–	18
A. sicula	E	S	28	0.041	2.649	–	–	18
A. sicula	E	S	28	0.036	2.396	–	–	18
A. sicula	N	S	28	0.039	2.355	–	–	18
A. sicula	E	S	28	0.035	2.758	–	–	18
A. sicula	N	S	28	0.111	2.803	–	–	18
A. sicula	N	S	28	0.037	2.243	–	–	18
A. sicula	E	S	28	0.035	2.758	–	–	18
A. sicula	E	S	28	0.047	2.197	–	–	18
A. sicula	N	S	28	0.027	1.825	–	–	18
A. sicula	E	S	28	0.050	1.851	–	–	18
A. sicula	E	S	28	0.047	1.740	–	–	18
A. sicula	E	S	28	0.028	2.643	–	–	18
A. sicula	E	S	28	0.020	3.022	–	–	18
A. sicula	N	S	28	0.053	1.521	–	–	18
A. sicula	E	S	28	0.025	1.444	–	–	18
A. sicula	E	S	28	0.030	3.093	–	–	18
A. sicula	N	S	28	0.020	1.660	–	–	18
A. sicula	E	S	28	0.078	1.367	–	–	18
A. sicula	E	S	28	0.037	1.236	–	–	18
A. sicula	N	S	28	0.037	1.199	–	–	18
A. sicula	E	S	28	0.078	1.180	–	–	18
A. sicula	E	S	28	0.027	2.874	–	–	18
A. sicula	E	S	28	0.037	1.740	–	–	18
Oikopleura dioica	E	S	13	0.09	0.69	–	–	5
O. dioica	E	S	13	0.71	0.77	–	–	5
O. dioica	E	S	13	3.60	1.00	–	–	5
O. dioica	E	S	13	0.08	0.65	–	–	5
O. dioica	E	S	13	0.47	1.09	–	–	5
O. dioica	E	S	13	1.89	0.76	–	–	5
O. dioica	E	S	13	3.77	0.74	–	–	5
O. dioica	E	S	13	0.10	0.64	–	–	5
O. dioica	E	S	13	0.37	0.96	–	–	5
O. dioica	E	S	13	1.41	0.59	–	–	5
O. dioica	E	S	13	2.66	0.57	–	–	5
O. dioica	N	S	28	0.219	3.180	–	–	18
O. dioica	N	S	28	0.109	3.240	–	–	18
O. dioica	N	S	28	0.088	2.733	–	–	18

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (μg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
O. dioica	E	S	28	0.134	3.069	–	–	18
O. dioica	E	S	28	0.137	3.261	–	–	18
O. dioica	N	S	28	0.102	3.112	–	–	18
O. dioica	E	S	28	0.140	3.312	–	–	18
Oikopleura dioica	N	S	28	0.051	2.289	–	–	18
O. dioica	N	S	28	0.077	2.187	–	–	18
O. dioica	N	S	28	0.033	1.387	–	–	18
O. dioica	N	S	28	0.147	2.440	–	–	18
O. dioica	N	S	28	0.069	2.345	–	–	18
O. dioica	N	S	28	0.142	2.208	–	–	18
Oikopleura longicauda	N	S	28	0.141	1.331	–	–	18
O. longicauda	E	S	28	0.672	2.548	–	–	18
O. longicauda	E	S	28	0.515	1.262	–	–	18
O. longicauda	N	S	28	0.678	1.611	–	–	18
O. longicauda	N	S	28	0.357	1.190	–	–	18
O. longicauda	N	S	28	0.196	2.815	–	–	18
O. longicauda	N	S	28	0.322	1.664	–	–	18
O. longicauda	N	S	28	0.142	1.712	–	–	18
O. longicauda	E	S	28	0.721	1.977	–	–	18
O. longicauda	E	S	28	0.170	2.591	–	–	18
O. longicauda	N	S	28	0.199	2.781	–	–	18
O. longicauda	N	S	28	0.336	2.113	–	–	18
Fritillaria borealis sargassi	E	S	28	0.043	1.131	–	–	18
F. borealis sargassi	N	S	28	0.188	2.148	–	–	18
F. borealis sargassi	E	S	28	0.161	1.552	–	–	18
F. borealis sargassi	E	S	28	0.024	2.093	–	–	18
F. borealis sargassi	E	S	28	0.206	1.641	–	–	18
F. borealis sargassi	E	S	28	0.187	1.856	–	–	18
F. borealis sargassi	N	S	28	0.230	1.740	–	–	18
F. borealis sargassi	E	S	28	0.245	1.617	–	–	18
*Fritillaria haplostom*ai	N	S	28	0.226	1.640	–	–	18
F. haplostomai	E	S	28	0.068	2.165	–	–	18
F. haplostomai	N	S	28	0.037	1.828	–	–	18
F. haplostomai	E	S	28	0.037	2.550	–	–	18

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (μg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
F. haplostomai	N	S	28	0.026	2.081	–	–	18
F. haplostomai	N	S	28	0.046	2.277	–	–	18
F. haplostomai	N	S	28	0.020	1.684	–	–	18
F. haplostomai	E	S	28	0.247	1.594	–	–	18
Fritillaria haplostomai	E	S	28	0.027	2.167	–	–	18
Polychaeta:								
Polydora spp.	N	ST	22	1.1	0.21	0	0.21	21
Polydora spp.	N	S^T	22	0.7	0.25	0	0.25	21
Polydora spp.	E	S^T	22	1.3	0.31	0	0.31	21
Polydora spp.	E	S^T	22	1.3	0.28	0	0.28	21
Spio/ Microspio spp.	N	S^T	22	1.1	0.20	0	0.20	21
Spio/ Microspio spp.	N	S^T	22	1.1	0.20	0	0.20	21
Spio/ Microspio spp.	E	S^T	22	1.3	0.25	0	0.25	21
Spio/ Microspio spp.	E	S^T	22	1.3	0.28	0	0.28	21
Nereis (*Neanthes*) *succinea*	N	S^T	22	0.4	0.15	0	0.15	21
Nereis (*Neanthes*) *succinea*	N	S^T	22	0.4	0.16	0	0.16	21
Nereis (*Neanthes*) *succinea*	E	S^T	22	0.9	0.31	0	0.31	21
Nereis (*Neanthes*) *succinea*	E	S^T	22	0.9	0.19	0	0.19	21
Pteropoda:								
Clione limacina	E	S^T	15	625.1	0.339	0	0.339	11
C. limacina	E	S^T	15	291.8	0.504	0	0.504	11
C. limacina	E	S^T	15	176.3	0.448	0	0.448	11
C. limacina	E	S^T	15	1252.4	0.392	0	0.392	11
C. limacina	E	S^T	15	1784.6	0.208	0	0.208	11
C. limacina	E	S^T	15	383.5	0.382	0	0.382	11
C. limacina	E	S^T	15	386.4	0.310	0	0.310	11
C. limacina	E	S^T	15	161.3	0.375	0	0.375	11
Thaliacea:								
Cyclosalpa affinis (solitary)	N	S	21.5	500.5	0.885	–	–	15
C. affinis (solitary)	N	S	21.5	1099.0	0.647	–	–	15
C. affinis (solitary)	N	S	21.5	2052.1	0.438	–	–	15
C. affinis (solitary)	N	S	21.5	3195.9	0.296	–	–	15
C. affinis (solitary)	N	S	21.5	4506.5	0.200	–	–	15

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (µg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
C. affinis (solitary)	N	S	21.5	5967.3	0.135	–	–	15
C. affinis (solitary)	N	S	21.5	7566.2	0.091	–	–	15
Cyclosalpa bakeri (solitary)	N	S+R^T	11	4720	0.090	0.200	0.290	2
Cyclosalpa bakeri (solitary+ aggregated)	N	S	11	286.8	0.454	–	–	2
C. bakeri (solitary+ aggregated)	N	S	11	964.7	0.307	–	–	2
C. bakeri (solitary+ aggregated)	N	S	11	1961.2	0.208	–	–	2
C. bakeri (solitary+ aggregated)	N	S	11	3244.7	0.140	–	–	2
C. bakeri (solitary+ aggregated)	N	S	11	4794.8	0.095	–	–	2
C. bakeri (solitary+ aggregated)	N	S	11	6596.8	0.064	–	–	2
C. bakeri (solitary+ aggregated)	N	S	11	8639.6	0.043	–	–	2
C. bakeri (solitary+ aggregated)	N	S	11	10913.8	0.029	–	–	2
Ihlea asymmetrica (solitary)	N	S	18	158.8	0.732	–	–	15
I. asymmetrica (solitary)	N	S	18	313.2	0.432	–	–	15
I. asymmetrica (solitary)	N	S	18	466.1	0.132	–	–	15
Pegea bicaudata (solitary)	N	S	21.5	1812.4	2.201	–	–	15
P. bicaudata (solitary)	N	S	21.5	2404.7	2.193	–	–	15
P. bicaudata (solitary)	N	S	21.5	4869.3	2.171	–	–	15
P. bicaudata (solitary)	N	S	21.5	8032.6	2.156	–	–	15
P. bicaudata (solitary)	N	S	21.5	11843.5	2.144	–	–	15
P. bicaudata (solitary)	N	S	21.5	16265.0	2.134	–	–	15
P. bicaudata (solitary)	N	S	21.5	21268.7	2.126	–	–	15
P. bicaudata (solitary)	N	S	21.5	26831.7	2.119	–	–	15
P. bicaudata (solitary)	N	S	21.5	32934.7	2.113	–	–	15

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (μg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
P. bicaudata (solitary)	N	S	21.5	34868.4	2.111	–	–	15
Pegea confoederata (solitary)	N	S	21.5	117.6	1.357	–	–	15
Pegea confoederata (solitary)	N	S	21.5	302.2	1.030	–	–	15
P. confoederata (solitary)	N	S	21.5	617.0	0.650	–	–	15
P. confoederata (solitary)	N	S	21.5	936.9	0.410	–	–	15
P. confoederata (solitary)	N	S	21.5	1260.0	0.259	–	–	15
P. confoederata (solitary)	N	S	21.5	1585.6	0.163	–	–	15
P. confoederata (solitary)	N	S	21.5	1913.1	0.103	–	–	15
P. confoederata (solitary)	N	S	21.5	2077.5	0.082	–	–	15
Thalia democratica (aggregated)	E	S^T	20.0	8.0	0.36	0	0.36	6
T. democratica (aggregated)	E	S^T	20.0	8.0	0.15	0	0.15	6
T. democratica (aggregated)	E	S^T	20.0	10.0	0.34	0	0.34	6
T. democratica (aggregated)	E	S^T	20.0	12.0	0.21	0	0.21	6
T. democratica (aggregated)	E	S^T	20.0	14.0	0.05	0	0.05	6
T. democratica (aggregated)	E	S^T	20.0	14.0	0.04	0	0.04	6
T. democratica (aggregated)	E	S^T	20.0	14.0	0.04	0	0.04	6
T. democratica (aggregated)	E	S^T	20.0	4.0	0.09	0	0.09	6
T. democratica (aggregated)	E	S^T	20.0	4.0	0.08	0	0.08	6
T. democratica (aggregated)	E	S^T	20.0	6.0	0.24	0	0.24	6
T. democratica (aggregated)	E	S^T	20.0	6.0	0.21	0	0.21	6
T. democratica (aggregated)	E	S^T	20.0	8.0	0.18	0	0.18	6
T. democratica (aggregated)	E	S^T	20.0	10.0	0.22	0	0.22	6

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (μg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
T. democratica (aggregated)	E	S^T	20.0	12.0	0.21	0	0.21	6
T. democratica (aggregated)	E	S^T	20.0	14.0	0.25	0	0.25	6
Thalia democratica (aggregated)	E	S^T	20.0	20.0	0.08	0	0.08	6
T. democratica (aggregated)	E	S^T	20.0	22.0	0.11	0	0.11	6
Dolioletta gegenbauri (solitary)	E	S^T	20.0	4.0	0.09	0	0.09	6
D. gegenbauri (solitary)	E	S^T	20.0	4.0	0.08	0	0.08	6
D. gegenbauri (soitary)	E	S^T	20.0	6.0	0.24	0	0.24	6
D. gegenbauri (solitary)	E	S^T	20.0	6.0	0.21	0	0.21	6
D. gegenbauri (solitary)	E	S^T	20.0	8.0	0.18	0	0.18	6
D. gegenbauri (solitary)	E	S^T	20.0	10.0	0.22	0	0.22	6
D. gegenbauri (solitary)	E	S^T	20.0	12.0	0.21	0	0.21	6
D. gegenbauri (solitary)	E	S^T	20.0	14.0	0.25	0	0.25	6
D. gegenbauri (solitary)	E	S^T	20.0	20.0	0.08	0	0.08	6
D. gegenbauri (solitary)	E	S^T	20.0	22.0	0.11	0	0.11	6
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	5.0	0.60	0	0.60	36
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	5.0	0.51	0	0.51	36
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	5.0	0.62	0	0.62	36
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	5.0	0.51	0	0.51	36
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	15.0	0.47	0	0.47	36
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	15.0	0.70	0	0.70	36
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	15.0	0.71	0	0.71	36
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	15.0	0.36	0	0.36	36

(*Continued*)

Table A2 (Continued)

Taxa: Species	Approach	Growth types	Temp. (°C)	Body weight (μg C ind^{-1})	Weight-specific growth g_S (d^{-1})	g_R	g_T	Source
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	35.0	0.20	0	0.20	36
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	35.0	0.38	0	0.38	36
Dolioletta gegenbauri (solitary)	E	$S^{T?}$	20.0	35.0	0.37	0	0.37	36
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	35.0	0.21	0	0.21	36
D. gegenbauri (solitary)	E	$S^{T?}$	16.5	5.0	0.30	0	0.30	36
D. gegenbauri (solitary)	E	$S^{T?}$	16.5	15.0	0.26	0	0.26	36
D. gegenbauri (solitary)	E	$S^{T?}$	16.5	35.0	0.08	0	0.08	36
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	5.0	0.51	0	0.51	36
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	15.0	0.70	0	0.70	36
D. gegenbauri (solitary)	E	$S^{T?}$	20.0	35.0	0.34	0	0.34	36
D. gegenbauri (solitary)	E	$S^{T?}$	23.5	5.0	0.56	0	0.56	36
D. gegenbauri (solitary)	E	$S^{T?}$	23.5	15.0	0.48	0	0.48	36
D. gegenbauri (solitary)	E	$S^{T?}$	23.5	35.0	0.28	0	0.28	36
D. gegenbauri (solitary)	E	$S^{T?}$	26.5	5.0	0.60	0	0.60	36
D. gegenbauri (solitary)	E	$S^{T?}$	26.5	15.0	0.69	0	0.69	36
D. gegenbauri (solitary)	E	$S^{T?}$	26.5	35.0	0.47	0	0.47	36

Sources

1. Epifanio *et al*. (1994) -weight-specific growth derived from their Table 2 for *in situ* incubation only. Carbon weight derived assuming it to be 38.1% of DW (Schneider 1989).
2. Madin and Purcell (1992) – data derived from their growth rate equation, and accompanying body weights from their length:CW equation. We also include the values for growth and reproductive growth for the solitary individual presented in their Table 4.
3. Lucas and Williams (1994), Lucas et al. (1997) – data for the Cracknore site during 1990, 1991, 1993 and 1994 used herein, data supplied pers. comm. C. H. Lucas.
4. Ross (1982) – data taken from Table 2 (carbon values). Growth calculated from both weight increase and moult as g = ln (P:B + 1).

5. Paffenhöfer (1976) – data from his Table II, carbon weight derived assuming it to be 45% of AFDW (see Uye and Ichino 1995). Food was supplied as algal cultures.
6. Deibel (1982) – data from his Table II, body weights taken as arithmetic means of each of the ranges. Although the *Thalia democratica* were of an aggregated form, body weights are for individuals (D. Deibel pers. comm.). Although reproductive output was not measured we assumed this to be zero as the original author believed this to be mimal in comparison to body weight increase.
7. Reeve and Baker (1975) – data from their Table 1. *Mnemiopsis* carbon weight derived assuming it to be 8.72% of AFDW (as determined in their study). *Sagitta* carbon weight derived assuming it to be 44.9% of AFDW (as determined in their study).
8. Reeve and Walter (1976) – P:B ratios calculated from their Table 2, converted to the daily weight-specific growth (g) using the equation g = ln (P:B + 1).
9. Lasker (1966) – growth determined from the changes in body weight (including molts) as given in their Table II, carbon weight derived assuming it to represent 42% of DW (as given in text). Temperature taken as approximate mean from their Figure 3.
10. Ikeda *et al.* (1985) – body lengths and weight-specific growth as given in their Figure 3 supplied pers. comm. by T. Ikeda. Body carbon weight taken as 42%DW [as given in Lasker (1966)].
11. Conover and Lalli (1974) – weight-specific growth rates from their Table IV (calorific rates used here). Body weights derived assuming carbon to be 28.7% of DW (Schneider 1989). We assume that body weight growth represents total growth because of omission of any reproductive output term in their laboratory-based budget-balancing approach.
12. Dagg (1976) –body weight growth derived from the addition of body mass increase and molt production from Table 6(a), daily P:B ratios converted to weight-specific growth (g) using the equation g = ln (P:B + 1).
13. Hirota (1972) – growth rates derived from DW increases given in Table III. Carbon weights derived assuming these to represent 4% of DW [approximate mid-point in range of *Pleurobrachia bachei* compositions, see Hirst (1996)].
14. Sameoto (1971) – temperature data from Table 3, growth rates determined from body weights over time as presented in Figure 5, supplied directly as a pers. comm. from D. Sameoto. Carbon weight assumed to be 39.4% of DW (as given in the original study).
15. Madin [unpublished results – as presented in Madin and Deibel (1998)] – data for growth derived from their Table 5.7, temperatures from Table 5.6, and length:carbon weight equations from Table 5.3. Growth calculated within the size range limits given in Table 5.6, growth calculated for the smallest and largest sizes, and each whole 10 mm steps between. *Pegea socia* and *Salpa maxima* not included here because no solitary length-weight equations available.
16. García (1990) – body weights and weight-specific growth rates taken from Table 1 and 2 respectively. Temperature taken from the companion paper García and López (1989) their Figure 2A. Carbon weight calculated by assuming this to be 47.3% of AFDW [mean whole body scyphomedusae value from Larson's (1986) Table III].
17. Vidal and Smith (1986) – growth and body weights taken from their Table 7, carbon weights derived assuming this to be 40.7% of DW [value for the congeneric *Thysanoessa longipes* from Ikeda (1974)]. Temperatures taken as approximate means from Station 12, their Figure 3a.
18. Hopcroft *et al.* (1998) – growth rates and geometric mean AFDWs supplied as pers. comm. from R. R. Hopcroft. Carbon weight derived assuming it represents 46% of DW (Uye 1982) and ash is 10% of DW (as assumed in their original calculations, R. Hopcroft pers. comm.). Incubations with nutrients added defined as controlled approach, those without defined here as natural sea water approach.

19. Kremer *et al.* (1990) – growth rates as demonstrated in their Figure 9, body DW derived from displacement volume using the equation given in their study, and converted to carbon assuming this to be 12.9% of DW [mean whole body scyphomedusae value from Larson's (1986) Table III].
20. Newbury (1978) – data from their Table 3. Temperature taken as mean of range for upper 300 metes e.g. 12 to 25ºC. Body weights converted from nitrogen to carbon assuming C:N ratio (by weight) of 4 (Ikeda 1974). We assume that body weight growth represents total growth as text describes that 'P.draco… matures at about 6 mm, a size range from 3.5 to 5.5 mm... was examined for the growth rate determinations'.
21. Hansen (1999) – growth rates from his Table 2 approximated mean body weight during growth period derived from Fig. 8.
22. Arai (1980) – changes in length taken from her Figure 1, converted to AFDW using the equation they present, and then to carbon assuming this to be 30.3% of AFDW [mean whole body hydromedusae value from Larson's (1986) Table II]. We assume that total growth is represented by body weight growth alone until the point where gonads appear.
23. Greve (1970) – changes in length (aboral axes L, µm) derived from the average values of their Figure 8, these were converted to wet weight (WW, g) using the equation of Persad (1997) for the congeneric *Bolionopsis vitrea*, where log WW = -12.405 + 3.04 log L. Carbon body weights derived from wet weights assuming that carbon is 0.32% of WW [derived from Curl's (1962) value for *Mnemiopsis*].
24. Reeve (1970) – growth rates and body weights derived from DW values given in their Table 3. Carbon weights calculated assuming these to represent 33.6% of DW (Schneider, 1989).
25. Huntley and Brinton (1987) – data on growth and body weight from their Table, body carbon weight derived asssuming this to be 42%DW [as given in Lasker (1966)].
26. Nagasawa (1984) – data taken from their Table I. Body lengths (L, mm) converted to DW (DW, mg) using the equation $DW = 0.197\ L^{3.01}$ (as given in original study) and to carbon assuming this to represent 41.4% of DW (Uye, 1982). Egg weight given as 0.30 µgDW this was converted to carbon assuming same ratio as in other stages.
27. Jacobi and Anger (1985) – carbon weights and growth rates from their Tables 1, 2 and 3.
28. Anger et al. (1983) – carbon weights and growth rates from their Table 1.
29. Logan and Epifano (1978) – data from their Table 6. Carbon derived assuming this to be 40% of DW.
30. Astthorsson (1990) – changes in body size taken from curve fitted on their Figure 10. Total lengths converted back to carapace lengths using the equations in Table 1, juveniles before the first February shown and adult females after this point. Lengths converted to DW using the equation of Matthews and Hestad (1977), carbon weight derived assuming this to represent 40% of DW. Mean water column temperatures estimated from their Figure 2a.
31. Tanasichuck (1998a) – temperature and increase in body length and length wet weight equation supplied as pers. comm. from R. W. Tanasichuck, body length increases as presented in his Figure 11 as a growth trajectory of a natural cohort. Carbon weights derived assuming this to be 42% of DW (approximate mean as given in Iguchi and Ikeda (1998)), and DW to be 20% of WW (R. W. Tanasichuck, pers. comm.).
32. Tanasichuck (1998b) – temperature and increase in body length and length wet weight equation supplied as pers. comm. from R. W. Tanasichuck, body length increases as presented in his Figure 11 as a growth trajectory of a natural cohort. Carbon weights derived assuming this to be 40.7% of DW [value for the congeneric *Thysanoessa longipes* from Ikeda (1974)], and DW to be 20% of WW (R. W. Tanasichuck, pers. comm.).

33. Clutter and Theilacker (1971) – temperature taken as mid-point of range given in text, growth rates taken from their Figure 8 for both females and males. Carbon weights derived assuming these to be 36.8% of DW (as given in their study). Age at sexual maturity (see their Figures 4 and 5) used to define whether body weight increase represented total growth or not.
34. Buchholz (1991) – weight-specific growth derived from rates of increase in length given for experiments I, III and IV. Body DW (DW, g) derived from length (L, mm) using the equation $DW = 0.000001 \times L^{3.16}$ [the 'all' category equation given in Table II of Morris *et al.* (1988)]. Carbon weight derived assuming this to represent 42%DW [as given in Lasker (1966)].
35. Ikeda (1991) [derived originally in the study: Ikeda (1990)] – weight-specific growth rates at each temperature derived from Table 3 of Ikeda (1991). Carbon derived from dry weight using the mean value of 36.93% (Table 2 in the same paper). Body weight changes assumed to represent total growth up to moult number 10 as from moult number 11 adult males may have reproductive output (Table 4).
36. Gibson and Paffenhöfer (2000) – weight-specific growth rates from their Figures 4 and 7.
37. Daan (1986) – laboratory weight-specific growth rates from their Table 1. *In situ* growth rates derived from Table 3, temperature pers. comm. from R. Daan. Size at maturity assumed to occur at 400 $\mu gC\ individual^{-1}$, as described in their text.
38. Olesen *et al.* (1996) – data from their Table 6.

APPENDIX 2 REFERENCES

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Biology of Early Life Stages in Cephalopod Molluscs

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Recent literature on embryonic and post-embryonic development, biology and behavioural ecology of juvenile cephalopods is reviewed. Emphasis is placed on biological processes. Life-history patterns and phylogenetic systematics, which are important for a proper understanding of the evolutionary history of the cephalopods, are only briefly touched upon.

Egg sizes in cephalopods range from less than 1 mm to about 30 mm in diameter, so the hatchlings emerging from the largest eggs are bigger than the adults of pygmy squid, the smallest known cephalopods. Developmental durations from spawning to hatching range from a few days (for very small eggs developing at high temperatures) to one or possibly several years (for very large eggs developing at low temperatures). Such important differences notwithstanding, the morphogenetic processes are very similar in all cephalopod embryos, the major variant being the size of the so-called outer yolk sac, which may be rudimentary in extremely small embryos.

Several questions concerning the timing of hatching in relation to the developmental stage attained, especially in terms of yolk absorption, need clarification. These questions concern the elimination of the transient closure of the mouth, the final differentiation of digestive gland cells, and the removal of the tranquilliser effect of the perivitelline fluid necessary for the onset of the hatching behaviour.

Cephalopod hatchlings are active predators. They refine their behavioural repertoires by learning from individual experience in dealing with prey and would-be predators. There is no truly larval phase, and the ecologically defined term paralarva should be used with caution.

Given the considerable resource potential of cephalopods, investigations into dispersal and recruitment are of particular interest to fishery biology, but they are also important for ecological biogeography. The related studies of feeding and growth involve field sampling and tentative age determination of caught specimens, in combination with laboratory studies to test food quality, measure feeding rates, and validation of periodicities in accretional growth structures (e.g. "daily rings" in statoliths).

1. INTRODUCTION

The early life stages of an animal are of interest, either as components of the life cycle of a given species, or as models for generalized ontogenetic patterns and processes. In applied research, developmental data are useful regarding a commercially important resource, something that many aquatic animals indeed are. The significance of developmental analyses is most obvious, however, in fundamental research dealing with so diverse domains as embryology, genetics, behavioural ecology, and evolutionary biology.

These various domains can be combined in a comprehensive biological investigation of marine organisms. Cephalopods are an exclusively marine class of the

phylum Mollusca. Given their zoological singularity and their notable resource potential, interest to science ranges from applications in aquaculture (Hanlon, 1990; Nabhitabhata, 1996, 1997; Nabhitabhata and Nilaphat, 1999) through fishery biology and ecology (Piatkowski, 1998; Rodhouse *et al*., 2001; Boyle and Rodhouse, in prep.), to theoretical issues in population biology and evolutionary ecology (Boyle and Boletzky, 1996; Rodhouse, 1998). For the traditional field of evolutionary morphology cephalopods offer very instructive models, as they demonstrate extreme structural, sensory and motor adaptations that in many ways appear "fish-like" (Packard, 1972; O'Dor and Webber, 1986). Along with their distinction from other invertebrates, cephalopods are also marked by some severe physiological constraints. Although certain species can survive at relatively low salinities (Paulij *et al*., 1990a), even the most tolerant ones have a limited capacity of osmoregulation, which prevents them from withstanding salinities lower than 16 (Hendrix *et al*., 1981), in spite of their elaborate system of excretory organs (Budelmann *et al*., 1997).

The aim of this review is to survey recent literature on early cephalopod life stages that was not yet covered in three complementary reviews dealing, respectively, with embryonic development (Boletzky, 1989a), laboratory culture (Boletzky, 1989b), and egg encapsulation (Boletzky, 1998). This inventory can only glance cursorily at morphologies and structural details of receptors and effectors in their functional context. It attempts to summarize biological aspects of embryonic and post-embryonic development, and to approach the integration of patterns and processes that make up the early phase of individual life in cephalopods. Special attention is given to the continuation of some essentially embryonic processes reaching beyond the event of hatching, as well as to the flexibility of the physiological mechanisms involved in hatching, and to the early establishment of elaborate behavioural patterns.

Study of early life stages of cephalopods demands the same thorough understanding of early life history traits as Hunter (1981) described for larval and juvenile fish: "parental factors of time and place of spawning, pattern of spawn ditribution, egg size and yolk reserves and such larval characters as feeding behavior, prey selection patterns, swimming and searching behavior, metabolism, growth rate, and time to the onset of schooling. These traits are interrelated and consequently form distinct life history strategies".

2. TAXONOMY AND SYSTEMATICS

Statements made about an entire group of organisms carry the risk of excessive generalizations or oversimplification. A fair illustration lies in the question: what is a squid? It could be a member of the class Cephalopoda as suggested by many popular texts, or a representative of the superorder Decabrachia or of the order Teuthida (Figure 1). In this review, the vernacular name squid is used for members of the three

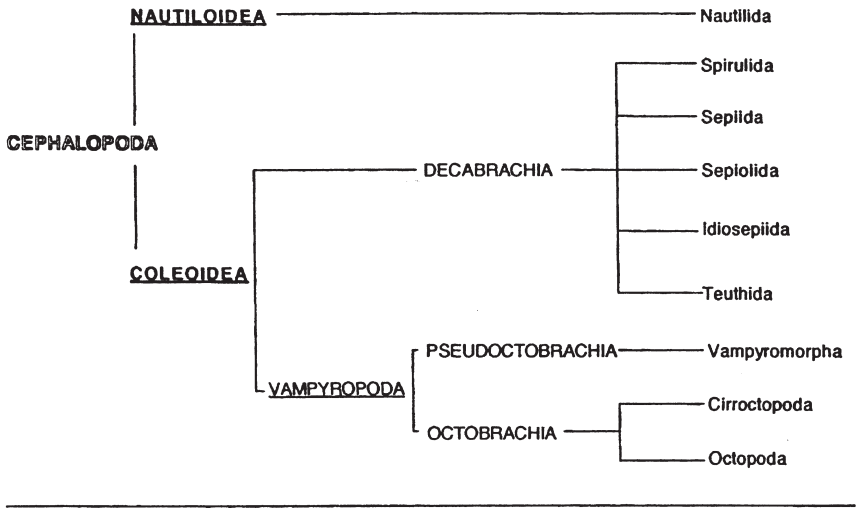

Figure 1 An outline of the classification of living cephalopods, showing likely monophyletic groups, from orders to subclasses. Modified from Boletzky (1999a).

decabrachian orders Teuthida (the neritic [myopsid] squids and various pelagic [oegopsid] squids), Sepiolida (the "bobtail squids") and Idiosepiida (the pygmy squids). It must be noted that idiosepiids are often called pygmy cuttlefish (Yamamoto, 1988). The two remaining decabrachian orders are the Spirulida and the Sepiida, and of these only the sepiids should be called cuttlefish. In the superorder Octobrachia, a finless octopus is a member of the order Octopoda, whereas a finned octopus is a member of the order Cirroctopoda. The so-called vampire squid of the monotypic order Vampyromorpha is the only extant representative of the Pseudoctobrachia, sister taxon of the Octobrachia. All the taxa so far mentioned represent the subclass Coleoidea (dibranchiate or endocochleate cephalopods). The only living ectocochleate or tetrabranchiate cephalopods, the well-known chambered nautilus (genera *Nautilus* and *Allonautilus*), represent the subclass Nautiloidea.

The outline of a phylogenetic system of living cephalopods given in Figure 1 is a compromise elaborated from earlier surveys, that attempted to conserve traditional group names wherever possible in using them for likely monophyletic taxa (Boletzky, 1999a). When viewing early life stages, one may have to distinguish, for example, between octobrachian and octopodan features, remembering that the latter here means the same as incirrate (octopodan) in earlier literature.

Figure 1 could be refined to a true cladogram by integration of fossil groups, such as the belemnoid squids within the coleoid cephalopods (Boletzky, 2001a). By omitting fossil groups in Figure 1, the important question of sister group relationships within the subclass Coleoidea is avoided. It is noteworthy that the

morphogenetic pattern of arm crown development observed in living Decabrachia and Vampyropoda leaves only two possibilities for a sister group relationship: either the Decabrachia and Belemnoida, or the Belemnoida and Vampyropoda, are sister groups (Boletzky, 1999b). In contrast to what Figure 1 seems to intimate, a scheme that links Decabrachia and Vampyropoda as sister groups is untenable (Budelmann *et al.*, 1997).

For the practical purpose of this review, the taxonomic compromise given in Figure 1 must suffice. It considers 9 orders of living cephalopods: Nautilida Agassiz, 1848; Spirulida Stolley, 1919; Sepiida Keferstein, 1866; Sepiolida Grimpe, 1921; Idiosepiida Grimpe, 1921; Teuthida Naef, 1916; Vampyromorpha Pickford, 1939; Cirroctopoda Young, 1989; Octopoda Leach, 1818. Most important for a discussion of ontogenetic features is a solid base for the assumption that Decabrachia and Vampyropoda are two monophyletic groups (Boletzky, 1993a).

3. EMBRYOGENESIS AND THE MICROENVIRONMENT OF THE EMBRYO

The embryonic development of cephalopods is characterized by the yolkiness of the eggs, which measure from nearly 1 mm to about 30 mm in diameter. The corresponding duration of embryogenesis ranges from a few days in small decabrachian eggs developing at high temperatures (O'Dor and Dawe, 1998) to more than one year in large octobrachian eggs developing at low temperatures (Voight and Grehan, 2000). The longer the duration of embryogenesis, the higher the need for protection to counteract embryonic mortality.

3.1. Protective envelopes or capsules

Following the great comparative study by Naef (1928), cephalopod eggs and embryos were always recognized as potentially interesting model systems for developmental biology. How serviceable they really are depends on how easily they can be freed from their capsules or gelatinous envelopes that impede microscopic observation and invasive experimentation (Marthy *et al*., 1990). Obviously the biological role of these "obstructive" covers is to protect the embryos against microbial attack and predation, and to provide a physical and chemical buffer between the immediate microenvironment of the embryo and the surrounding milieu.

3.1.1. *Oviducal and nidamental jellies*

With the exception of the Octopoda, where the females actively protect their embryos covered only by a chorion (see definition below), female cephalopods

protect their developing embryos with some gelatinous material, which is secreted by the oviducal glands and by special nidamental glands. These jellies enwrap the chorion of each egg, often also unite a few, several, or very numerous eggs in one collective wrapping (Boletzky, 1998). Whereas most decabrachian cephalopods abandon their eggs thus protected, the females of some oegopsid squids of the family Gonatidae carry their egg masses until the young hatch (Seibel *et al*., 2000).

The gelatinous envelopes undergo structural modifications throughout the time of embryo development. In the individually laid *Nautilus* eggs, the outer layer of the nidamental jelly rapidly hardens and then forms a tough capsule (with a peculiar folded sleeve). It surrounds the chorion rather tightly but leaves sufficient space for the developing embryo to move freely (Arnold and Carlson, 1991). Hard egg capsules also exist in some representatives of the decabrachian order Sepiolida (family Sepiolidae, subfamily Rossiinae) and in the octobrachian order Cirroctopoda (Boletzky, 1998). Once the animals have hatched, individual capsules and collective envelopes decay, generally after weeks or months of progressive degradation (Billings *et al*., 2000).

Size, structure and consistency of egg capsules or envelopes vary considerably, not only between greater systematic groups, but often also at lower taxonomic levels, apparently in relation to the respective ecology of the species. Decabrachian egg capsules often harbour stable populations of bacteria, which are provided by the accessory nidamental glands of the spawning female (Cronin and Seymour, 2000). The biological role of these bacteria is unknown. In cuttlefish, the egg capsules release a pheromonal peptide acting on sexually mature females as a specific spawning stimulator (Zatylny *et al*., 2000).

3.1.2. *Chorion*

The immediate microenvironment of the developing embryo is defined by the chorion micro-structure which determines its functioning as a filter. The chorion membrane is derived from an extracellular matrix secreted by the follicular syncytium of the ovary (Boyle and Chevis, 1992). The chorion thus forms the chronologically primary envelope of the ovum. Following fertilization by a spermatozoon, which passed the micropyle of the chorion and triggered a reaction leading to the formation of the so-called vitelline membrane (the developmentally primary envelope inhibiting polyspermy), the ovum turns into a zygote.

The developing embryo itself apparently releases substances containing large molecules that cannot leave the chorion, while water enters from the outside through this membrane. Starting from the first perivitelline space formed at fertilization, the perivitelline fluid bathing the embryo takes up water and approaches the osmolarity of the surrounding sea water as far as extensibility of the chorion membrane permits. In oegopsid squids of the teuthid family

Ommastrephidae, Ikeda and Shimazaki (1995) found that only the oviducal gland jelly surrounding the chorion is necessary for the formation of the first perivitelline space at fertilization; apparently the nidamental gland jelly, which surrounds the oviducal jelly, does not induce this chorion swelling.

3.1.3. *The octopodan chorion and its relation to brooding*

The Octopoda are characterized by eggs that have only a chorion as an envelope (Budelmann *et al*., 1997). The females provide active protection for these rather fragile eggs until the young hatch. This behavioural complex is functionally related to a modification of the last stage of oogenesis. During final ovarian egg maturation, the chorion becomes drawn out into a stalk-like appendage (Budelmann *et al*., 1997). Apart from a unique instance of ovovivipary (*Ocythoë*), the octopod eggs are released from the ovary through the oviducts, and the chorion stalks generally attach the eggs to a substratum, or to other egg stalks which then form the axis of a festoon-like egg string (Norman, 2000). In several benthic octopus species the females carry their egg strings or clusters in the arms, like the females of pelagic octopus. Depending on the species, the chorion stalk either is full or hollow (Boletzky *et al*., 2001). Medium to large eggs have relatively short stalks and are laid singly or in small clusters on a solid substrate (Wood *et al*., 1998; Voight and Grehan, 2000). Under normal brooding conditions, a female octopus remains in constant physical contact with her eggs, cleaning the chorion surfaces with the arm suckers and flushing the eggs with water jets from her funnel. Parra *et al*. (2000) measured the oxygen consumption of the embryos of *Octopus vulgaris* shortly before hatching and calculated that the consumption of a medium-size egg mass containing 300,000 eggs is twice that of a brooding female weighing 2 kg. When eggs are laid singly or in small clusters, they cover a large surface inside the den occupied by the female (Boletzky *et al*., 2001).

3.2. Early embryonic stages

3.2.1. *Staging systems*

For descriptions of embryonic development and especially for comparisons between the embryogeneses of different species, a staging system is indispensable. The most widely used scheme of embryonic stages in cephalopods was defined by Naef (1928). More recent systems subdivide the blastula stage I of Naef into a series of polar body and cleavage stages. A system thus defined was first proposed by Arnold (1965) and was subsequently adapted for several other species. The problem of overall stage homology between species was addressed by Naef (1928)

who emphasized the inevitably approximative nature of embryonic stage comparisons, positing that true homology is conceivable only between morphogenetic stages of organs or organ complexes, rather than between whole embryos of different species. Several recent descriptions take account of this variation of characters and character states for embryonic stage comparisons (Baeg *et al*., 1992; Watanabe *et al*., 1996; Guerra *et al*., 2001; Shigeno *et al*., 2001a, c).

3.2.2. *Ambient temperature and rate of embryonic development*

From the outset of embryogenesis, ambient temperature sets the pace of developmental progress and thus influences the duration of embryogenesis (Laptikhovsky, 1991). Within the species-specific range of temperature adaptation, development is faster at higher than at lower temperatures. At the lower and higher limits of this temperature niche, the incidence of embryo deformities increases substantially (Gowland *et al*., 2002).

In *Nautilus macromphalus*, embryonic development takes nearly one year at temperatures higher than 22°C (Uchiyama and Tanabe, 1999). When comparing different Decabrachia, egg size appears negatively correlated with developmental rate for a given temperature ("the bigger the egg, the slower its development"). These data cannot be extrapolated for the Octobrachia, which overall have a much slower development (Boletzky, 1994). In the Octopoda, egg care by the mother animal (i.e. duration of embryonic development plus the time difference between beginning and end of spawning) may last several months even under temperate conditions (Caverivière *et al.*, 1999). It may be close to one year in cold water (Kubodera, 1991) and longer than one year in species producing very large eggs at low temperatures, e.g. *Bathypolypus arcticus* (Wood *et al*., 1998). Egg care probably lasts several years in *Graneledone* spp. (Voight and Grehan, 2000).

3.2.3. *Descriptive embryology based on natural egg masses*

Yamamoto (1988) described normal embryonic development, as a basis for a specific staging system, in the pygmy squid *Idiosepius pygmaeus paradoxus*, and some reviews have summarized data from earlier literature (Boletzky *et al*., 1989; Arnold, 1990; Fioroni, 1990). Since slight variations in cleavage patterns have not been found to correlate with variations in subsequent stages of development, embryological studies often set out from more advanced stages of blastulation (Marthy *et al*., 1990; Fagundez *et al*., 1992; Blackburn *et al*., 1998; Warnke, 1999; Guerra *et al*., 2001) or from the epibolic gastrulation, during which distinct ectoderm and mesendoderm layers are established (Marthy and Dale, 1989). The cells forming the midgut rudiment (the actual endoderm) are derived from the central part of the mesendoderm, and the periphery of the remaining mesoderm

provides a migrating cell population from which the transient musculature of the outer yolk sac is formed (Segmüller and Marthy, 1989).

3.2.4. *Artificial fertilization*

Eggs collected from the ovary of a mature female cephalopod and fertilized artificially permit the study of embryonic development from the earliest stages onward. In studying ooplasm segregation and the role of microtubules and microfilaments in polar body and cleavage furrow formation, Crawford (2000, 2001) used artificially fertilized eggs of an inshore squid, *Loligo pealei*, a species that also readily spawns in aquaria. Artificial fertilization has been especially important in developmental analysis of pelagic squids that are not easily kept alive in an aquarium until spawning occurs (Sakurai *et al*., 1995). Blastulation stages were thus described from the ommastrephid squids *Todarodes pacificus* and *Illex argentinus* by Watanabe *et al*. (1996) and by Sakai *et al*. (1998), respectively.

3.2.5. *The phylotypic phase of development*

A common feature of cephalopod embryogenesis is that gastrulation imperceptibly grades into organogenesis (Boletzky *et al*., 1989). One of the earliest manifestations of individual organ rudiments within a common anlage is the subdivision of the early pedal complex into several pairs of arm rudiments, which subsequently form individual extensions (considered dorsal in morphological, posterior in physiological orientation). The earliest of these extensions provide the funnel tube rudiments (Naef, 1928; Yamamoto, 1988; Marquis, 1989).

For a proper understanding of ensuing organogenetic events, it is indeed important to realize that each of the early arm buds sooner or later forms a superficial extension that grows out towards the mantle complex. The funnel tube ridges arising from the posterior (or ventral) arm buds are the first to become distinct. After that, some time elapses before the extensions forming the secondary head cover, including the primary lid and buccal mass roof, are differentiated. From an evolutionary perspective, this transitional phase of late gastrulation and early organogenesis can be viewed as the phylotypic stage (Slack *et al*., 1993) that characterizes cephalopods, or – in more cautious terms – the phylotypic phase of cephalopod development (Figure 2). The study of the role of *HOX* genes in cephalopod development is now providing detailed information on the peculiar modification of the molluscan body plan in this class (Callaerts *et al*., 2002).

In *Nautilus* embryos, the limited number of initial arm rudiments suggests a roughly ten-armed primitive stage in nautiloids. These early arms are not easily identified among the numerous tentacles which develop subsequently (Boletzky, 1989c; Budelmann *et al*., 1997). In contrast, definitive arm identities are recognizable in most coleoid embryos already at late gastrula stages. Exceptions are the

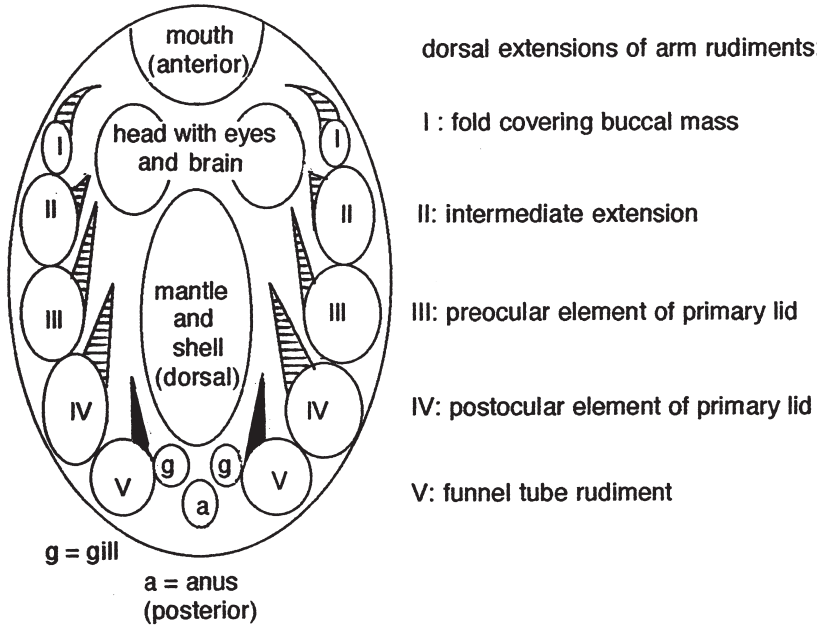

Figure 2. A schematic representation of the phylotypic stage of cephalopods, corresponding to an advanced gastrula stage, in apical (morphologically dorsal) view. The ventral foot derivatives are five pairs of arm rudiments (I–V), each one with a dorsal extension (marked black for V, hatched for IV–I).

pygmy squid and some oegopsid squids where certain arm pair rudiments are retarded and grow out after hatching (Watanabe *et al*., 1998) or during later post-hatching development (Shigeno *et al*., 2001c). It is noteworthy that the rudiments of the future tentacles (the fourth pair in the decabrachian series of 5 pairs of arm rudiments) are always among the well developed rudiments, except in the pygmy squid. In *Idiosepius* the early post-gastrular pattern of the arm crown is very similar to that of myopsid or sepiolid squids (Yamamoto, 1988; Nabhitabhata, 1998), but the rudiments of the fourth pair are soon arrested and remain so throughout embryonic development (Boletzky, 1996b).

3.3. Organogenesis and histological differentiation of the body surface

3.3.1. *Cephalic organs (brain, eyes, extra-ocular photoreceptors, statocysts, stomodaeum)*

The central nervous system (Shigeno *et al*., 2001b, e) and the eyes (Wentworth and Muntz, 1992; Tomarev *et al*., 1997) are formed from ectodermal anlagen.

The ganglia making up the central nervous system and several peripheral ganglia, such as the stellate ganglia (Burbach *et al*., 2001), are formed by cells proliferating from the ectoderm into the underlying mesodermal layer (Marquis, 1989). In contrast, the eyes are formed from a pair of ectodermic invaginations (Meinertzhagen, 1990). In *Nautilus*, the eye vesicles resulting from this process of invagination remain open to the outside through a pore (Tanabe *et al*., 1991). The corresponding pore of the ocular chamber in coleoid embryos is rapidly closed, and the cells involved in this definitive closure of the optic vesicle form the crystalline lens. West *et al*. (1995) described this process using both light and scanning electron microscopy.

Other cephalic organs are formed from ectodermic invaginations much like the eyes. Paired statocysts arise on the posterior/ventral side of the head. They subsequently form the statoliths (Morris, 1991, 1993) which grow at different rates depending on the ambient temperature (Villanueva, 2000b). The statocysts remain in communication with the body surface through the ducts of Kölliker (Stelzner *et al*., 1997). Moreover, there are two sets of small, completely closed vesicular invaginations, at least some of which are extra-ocular photoreceptors (Sundermann, 1990). The largest invagination in the cephalic complex establishes the stomodaeum, from which the buccal mass and the anterior part of the oesophagus are formed. At the end of the invaginating process, the mouth is covered by a membrane that apparently remains intact until hatching (Budelmann *et al*., 1997). It is not yet clear, however, whether a complete closure is achieved, or whether a remaining pore is closed by a sphincter, similar to what occurs in the myopsid eye cover, forming the cornea (Naef, 1928).

3.3.2. *Funnel/mantle complex, arm buds and the secondary head cover (primary lid and buccal mass roof)*

The paired ridges originally extending from the fifth arm pair (see Section 3.2.5.), which make up the funnel tube anlage, grow in height and finally fuse together to form a hollow structure. This rudimentary funnel tube in its turn fuses with the collar pouch, which is derived from the muscular sheath of the visceral mass. In parallel with this morphogenetic process uniting elements of different organogenetic origins, the growth of the originally flat mantle rudiment over the visceral organs results in a bell shaped mantle (Fioroni, 1990). This extension conditions the formation and progressive deepening of the mantle cavity that accomodates the renal and anal papillae and the gills (Shigeno *et al.*, 2001a, d). The anal opening appears only at a late embryonic stage, but once formed it permits fluid uptake by a peristaltic pumping action of the intestine (Boletzky, unpubl. obs.). This fluid uptake may be important for the subsequent functioning of the digestive duct, the anterior end of which is still closed by the transient buccal membrane (see Section 3.3.1.).

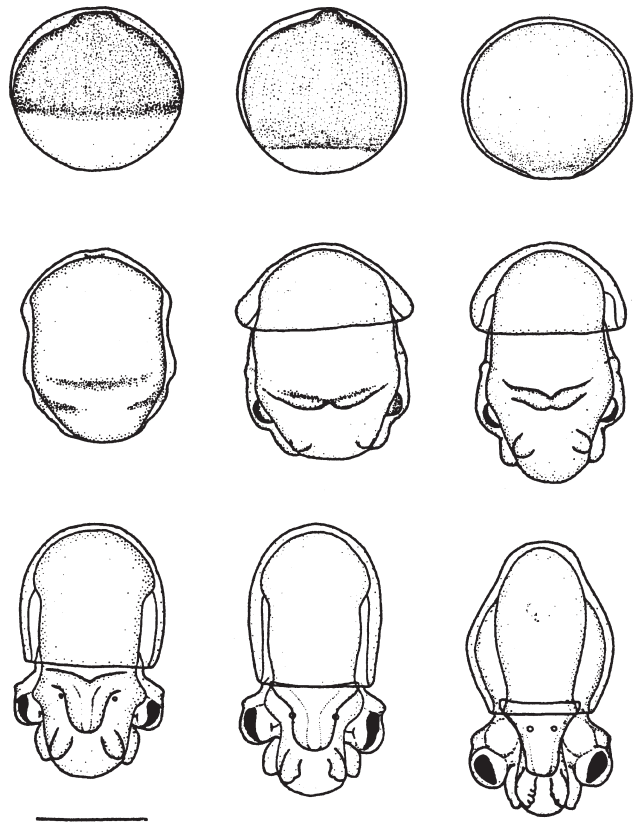

Figure 3 A series of embryonic stages of the ommastrephid squid *Todarodes pacificus* seen from the ventral (morphologically posterior) side, with formation of the funnel tube from paired ridges (NB: arm V is retarded, allowing IV [tentacle] to subsequently fuse, forming the so-called proboscis). Upper 3 embryos: stages 13, 14 and 15 after Arnold (1965), middle 3: 17, 19 and 20, lower 3: 22, 23 and 24. Scale bar 0.5 mm. From Watanabe *et al*. (1996).

The growth processes shaping the mantle and fins (except in the finless Octopoda) and the funnel complex are characterized by essentially laminar spreading, which differs from the invaginations mentioned earlier. A similar laminar growth marks the paired integumental folds extending from the arm buds that cover the head (Figure 3). The edges of this secondary integument of the cephalic organs grow (from arm I) over the buccal mass dorsally (Sundermann, 1990), and they surround the eyes laterally to form the so-called primary lid (Watanabe *et al*., 1998). This latter, circular fold is derived from the integumental extensions of arms 2 and 3 in Octobrachia, arms III and IV (= tentacles) in Decabrachia. When III or IV are retarded in embryogenesis (as in ommastrephids and idiosepiids,

respectively), the neighboring arms II (ommastrephids) or V (idiosepiids) provide the corresponding components of the primary lid. Eventually a true cornea forms from primary lid tissue lying in front of the lens, in the embryos of myopsid, sepiolid, and idiosepiid squids (Yamamoto, 1988) and of octopods (Marquis, 1989).

3.3.3. *Shell*

The sequestration of the shell field in the center of the mantle rudiment of coleoid embryos forms a process generally viewed as an invagination. When comparing this process of shell field submergence with the development of the corresponding area in the mantle rudiment of a *Nautilus* embryo, it seems more appropriate to view it as an initially flat shell complex, which either remains at the mantle surface (*Nautilus*: Landman *et al*., 1989; Arnold *et al*., 1990; Tanabe *et al*., 1991; Arnold, 1992; Mutvei *et al*., 1993; Tanabe and Uchiyama, 1997), or becomes covered by an integumental fold (coleoid embryos: Fioroni, 1990). There is no primordial shell gland invagination comparable to that found in gastropods (Naef, 1928).

An interesting detail of *Nautilus* shell development is the high structural variability of the apical end of the siphuncular tube, the so-called caecum (Mutvei and Dogushaeva, 1997). It is significant that the coleoid shell field is sequestered before secretion of shell matrix begins (in other words, there is no recapitulation of a 'Nautilus' stage). The closed shell sac is a slit-like space with a roughly circular outline, into which the first lamella of organic shell matrix is secreted. Subsequently the cells forming the so-called periostracal groove add secretory products to the margin of this "protoconch"-like lamella (Hopkins and Boletzky, 1994).

An organic matrix is thus provided for the formation of calcified chambered shells (Spirulida, Sepiida) or of uncalcified shell remnants in various squids (Sepiolida, Idiosepiida, Teuthida) and in the Vampyropoda. The different vampyropodan shell forms can be viewed as a morphocline reflecting an evolutionary developmental truncation. This transformation started from a fully developed gladius (Vampyromorpha), continued in suppressing its anterior part (Cirroctopoda), and terminated in splitting the transverse shell rudiment in two (Octopoda). During the embryogenesis of octopods, this splitting coincides with the disappearance of the fin rudiments, which were recognizable in early organogenesis (Naef, 1928).

3.3.4. *Integument*

The integument of coleoid embryos comprises areas of functional specialization on the arm suckers (Schmidtberg, 1997, 1999), in the paired olfactory pits that lie on the ventrolateral side of the head (Lenz, 1997; Wildenburg, 1997), in special

epidermal lines present on the head and arms (Lenz *et al*., 1995), and on the posterior surface of the mantle. Portions of the sucker surfaces, the entire olfactory organs and the epidermal lines forming a "lateral line system" analog bear immotile cilia, which act as sensory structures during late embryonic stages and from hatching onward (Budelmann *et al*., 1997). In contrast, some structures of the mantle surface are very closely related to hatching and have only a transient function. The hatching gland, comprising enzyme-producing cells and complementary attachment cells (Arnold and Singley, 1989; Paulij *et al*., 1991a, c), has a clearly limited function and apparently plays no role before or after hatching (Matsuno and Ouji, 1988; Paulij and Denucé, 1990; Paulij *et al*., 1991b). The bands of short motile cilia that lie close to the hatching gland in most decabrachian embryos (Scharenberg, 1997), and the terminal spine of sepiolid embryos (Boletzky, 1991), function as auxiliary hatching equipments, as do the tufts of Kölliker in octopus embryos (Lenz, 1997). For these tufts, however, a post-hatching function is very likely (Budelmann *et al*., 1997), whereas no such function is known for the specialized ciliary bands or for the terminal spine.

The integument plays a major role during late embryonic development in facilitating oxygen uptake by the body tissues, as the gills become functional only at late embryonic stages (Eno, 1994) or at early post-hatching stages (Watanabe *et al*., 1996; Shigeno *et al*., 2001b).

The developing coloration of the integument has no recognizable function during embryonic development. Chromatophores take on their definitive functions relating to visual effects only at hatching (Messenger, 2001). The generally species-specific patterns of chromatophore distribution are unlikely to have a functional significance (e.g. in visual recognition of conspecifics). However, they provide an interesting model system for intercalary pattern formation (Packard, 1985) and a welcome research tool for (1) assessment of developmental conditions (Gowland *et al*., 2002) and (2) species identification in hatchlings and early juveniles (Young *et al*., 1989; Kubodera, 1991; Warnke, 1999).

3.4. Storage, redistribution and absorption of yolk

3.4.1. *Egg size and the formation of an outer yolk sac*

The early processes of blastulation and the onset of gastrulation appear virtually uninfluenced by the actual size of the yolk mass. In contrast, the further course of gastrulation is strongly marked by the volume of the yolk mass relative to the size of the early gastrula. The peripheral part (the so-called blastopore lip) grows over the uncleaved yolk and forms the cellular envelope of the prospective outer yolk sac (Boletzky 1989c, 1993b). A peculiar feature appears in the very small embryos of certain pelagic squids, e.g. the ommastrephids *Todarodes pacificus* (Watanabe *et al*., 1996) and *Illex argentinus* (Sakai *et al*., 1998). In these forms

gastrulation leads to a nearly total enclosure of the yolk mass in the embryo proper, the outer yolk sac being rudimentary from the outset of post-gastrular development (Figure 3). This special feature of some oegopsid squid embryos was discussed by Naef (1928) who recognized that it is not an obligate correlate of small egg size. Indeed, the embryos of the pygmy squid *Idiosepius* are equally small, but they develop a sizable outer yolk sac (Yamamoto, 1988).

The epibolic growth of the gastrula marks a critical phase prone to malformations. A tendency to enclose the yolk mass incompletely is observed in large octopus embryos (Boletzky, 1997a). Such an aberrant development demonstrates a morphogenetic independence of the embryo proper relative to the transient outer yolk sac. The latter is histologically "mature" and maintains an intensive muscular activity long before any definitive organ is formed. In functional terms, the the outer yolk sac envelope serves as a transient "gill and heart" enclosing a reserve of nutrients. The provisional function of this respiratory surface is enhanced by the dense ciliature covering the entire yolk sac surface (Boletzky *et al*., 1989). The continuous activity of these kinocilia keeps the perivitelline fluid in circulation and thus supports oxygen diffusion to, and oxygen uptake by, the embryo.

3.4.2. *Inner yolk sac*

Under normal developmental conditions, the cap- or bell-shaped anlage of the embryonic body (i.e. the part comprising all the prospective organ areas) undergoes a progressive overall contraction, as soon as the outer yolk sac envelope is completed (Budelmann *et al*., 1997). This contraction results in an increasingly compact arrangement of the different organs, which thus take up their definitive positions in the developing animal. The immediate effect of this overall contraction is a partial extrusion of yolk into the outer sac (Tanabe *et al*., 1991). When the basic processes of organogenesis and the progressive contraction of the embryo cap have come to an end, by stage XV of Naef (1928), the small inner yolk sac begins to increase in size, due to a slow transfer of yolk from the outer sac (Fioroni and Boletzky, 1990; Boletzky, 2002). The pace of this transfer, which finally inverts the respective volumes of the two yolk compartments (outer and inner yolk sac), seems influenced by the temperature at which the embryo develops (Bouchaud and Daguzan, 1990; Bouchaud and Galois, 1990). An actual pressure balance is maintained only within the range of temperature adaptation of the species (Sakurai *et al*., 1996). Outside that range some profound, potentially lethal, malformations are inevitable (Gowland *et al*., 2002).

The inner yolk sac takes on a typical shape that varies between larger taxonomic groups such as octopods or cuttlefish (Boletzky, 2001b). Depending on how far this inner part of the so-called yolk organ is subdivided into lobular niches, its storage capacity at late embryonic stages varies more or less markedly (Figure 4). The volume of yolk remaining in the inner sac at hatching is one of

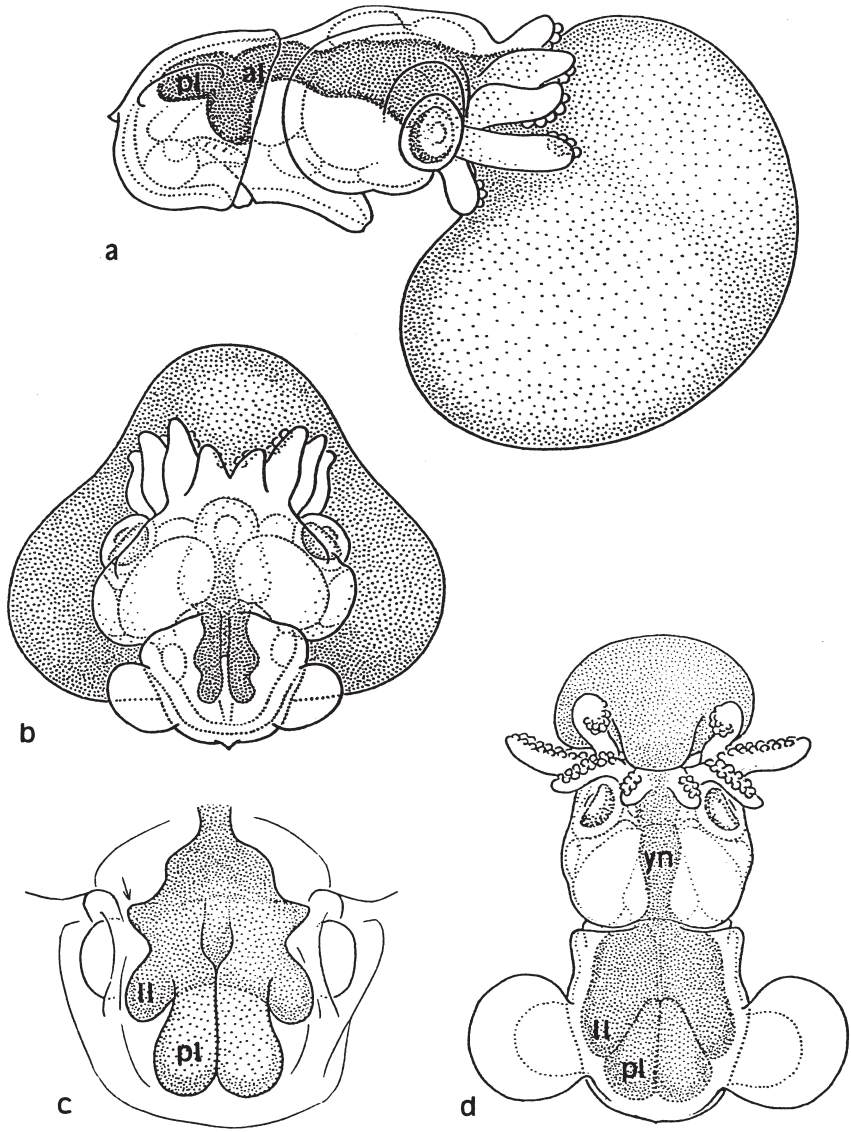

Figure 4 Advanced embryonic stages of *Sepiola* sp. showing the progressive enlargement and subdivision of the inner yolk sac. (a) stage XIV of Naef (1928) in lateral view. (b) same in antero-dorsal view at lower magnification. (c) visceral complex of stage XV; the lateral extensions (arrow) are transient. (d) stage XIX at lower magnification. al = anterior lobe of inner yolk sac, pl = posterior lobe of inner yolk sac, ll = lateral lobe of inner yolk sac, yn = yolk neck. From Boletzky (2002).

the major factors influencing the initial feeding conditions of the hatchling (Balch *et al*., 1985; O'Dor *et al*., 1986).

The enzymatic activity of the yolk syncytium continually breaks down yolk components, which are organized in simple membrane-bound ampullae (forming the artifactual "yolk platelets" described from histological preparations). The retrieved nutrients are taken up by the embryonic blood lacuna of the outer yolk sac and by the vessels and sinuses that surround the inner yolk sac (Budelmann *et al*., 1997). The respiration of both the yolk absorbing syncytium and the rapidly growing organ tissues is reflected by an overall oxygen consumption that increases exponentially as the embryo grows (Cronin and Seymour, 2000).

4. TRANSITION FROM EMBRYO TO YOUNG

The early life stage between the embryo and juvenile is somewhat casually called *the hatching stage*. Certainly the emphasis should be more on transition than on stage, to take full account of this critical phase in terms of a perinatal biology (Boletzky, 1989a).

4.1. The phase of hatching competence

The widely noted flexibility of hatching conditions suggests the existence of a phase of hatching competence rather than a morphologically and/or physiologically well-defined hatching stage (Boletzky, 1994). This flexibility is suspected to offer a means of optimising post-hatching survival.

The following sections do not deal with *Nautilus*, in which hatching differs from coleoid hatching, due to the absence of a distinct hatching gland and the presence of a peculiar capsule structure, which apparently cause a two-step emergence of the hatchling (Okubo *et al*., 1995).

4.1.1. *Hatching gland*

The coleoid hatching gland becomes functional quite early in development; indeed embryos are able to hatch long before the outer yolk sac has disappeared (due to yolk absorption and concomitant yolk transfer to the inner sac). Ultrastructural analyses of the hatching gland illustrate this early attainment of a fully functional state of (1) the cells that provide the enzyme for local capsule digestion, (2) the cells that attach the gland to the chorion, and (3) the accompanying ciliary cells that propel the hatchling through the opening produced by the hatching enzyme (Matsuno and Ouji, 1988; Arnold and Singley, 1989; Paulij *et al*., 1991b, c).

4.1.2. *Yolk reserves*

Premature hatching entails a loss of nutrient reserves that would normally be used for further growth and tissue differentiation, since viable premature young drop the outer yolk sac soon after hatching. Exceptions are known only in some octopods where hatchlings are able to eat a remaining outer yolk sac (Fioroni and Boletzky, 1990). Premature hatching can only be advantageous if the embryonic microenvironment is degrading due to noxious effects of extreme temperature changes, oxygen depletion or chemical pollution (Paulij *et al*., 1990c). Such an emergency hatching has a cost, namely sub-optimal starting conditions for the young animal (O'Dor *et al*., 1986).

4.1.3. *Tranquilliser effect of the perivitelline fluid*

Premature hatching tends to be naturally impeded by a tranquilliser effect of the perivitelline fluid bathing the animal (Marthy *et al*., 1976). It is unknown how the tranquilliser effect of the perivitelline fluid is finally overcome when a hatchling is beyond any risk of losing yolk (Ikeda *et al*., 1999). The observation that hatching mostly occurs after dark (Paulij *et al*., 1990b) provides no satisfactory answer unless one can explain why hatching is not delayed another 24 hours or more – the ultimate limit being total depletion of the yolk reserve. With the exception of a few octopus species producing large benthic hatchlings devoid of an inner yolk reserve, this limit is never reached before hatching, not even at the lowest temperatures tolerated by the embryos (Boletzky, 1994).

Watanabe *et al*. (1996) studied the embryonic development of an ommastrephid squid under laboratory conditions in artificially fertilized eggs embedded in semi-artificial jelly and compared it to development under nearly natural conditions in egg masses spawned in an aquarium. These authors found that embryos developing under artificial conditions hatched at an earlier stage, suggesting that the quality of the jelly surrounding the chorion plays some role in controlling the onset of hatching. But there may also be differences between species, since the hatchlings obtained from artificially fertilized eggs of *Illex argentinus* and described as "hatching stage 30" by Sakai *et al*. (1998) were very similar to the "post-hatching stage 30" of *Todarodes pacificus* described Watanabe *et al*. (1996).

4.2. From yolk absorption to food ingestion

Hatching allows the young animal to start an active mode of foraging (Villanueva, 1994) without shutting down the embryonic nutrient supply from the inner yolk sac. Thus, the early post-hatching phase is marked by the coexistence of two nutritive systems: (1) an embryonic energy source in the form of yolk, (2) a post-embryonic energy supply by captured food that is rapidly digested (Vecchione

and Hand, 1989; Boucaud-Camou and Roper, 1995, 1998; Hernandez-Garcia *et al*., 2000).

This condition raises a nomenclatural problem when comparisons are made with other marine invertebrates. Following traditional terminology, cephalopod hatchlings adopting a midwater habitat can be considered both lecithotrophic and planktotrophic, likewise almost all the benthic cephalopod hatchlings are both lecithotrophic and plankto- or benthotrophic. In an ecological classification using two-state characters with paired antonyms like "feeding/non-feeding", cephalopod hatchlings likewise appear as both "feeding" and "non-feeding" (Poulin *et al*., 2001). Although the embryonic food source available at hatching is relatively short-lived, the fully developed (i.e. non-premature) hatchlings still have sufficient yolk reserves allowing them to practice and improve their hunting behaviour without each attack on a prey animal being successful. The remaining yolk also allows them to cover parts of the high energy loss caused by the active movements involved in attack and flight. Only prematurely hatched animals carrying an exceedingly large inner yolk sac seem to get lesser dynamic lift from active swimming.

Although the yolk reserves of normally hatched animals do not impede functioning of the digestive organs once the first prey is ingested, the physiological conditions under which digestion can begin have not been defined (Boucaud-Camou *et al*., 1985; Vecchione and Hand, 1989).

An alternative means of subsistence would seem useful only with the low energy consumption of young benthic animals, but Vecchione and Hand (1989) found indications that dissolved organic material may be absorbed by planktonic squid hatchlings. Evidence that amino acids are taken up by the integument was obtained from advanced juvenile cuttlefish *Sepia officinalis* (de Eguileor *et al*., 2000). On the other hand, Navarro and Villanueva (2000) concluded from the results of their rearing experiments that planktonic octopus and squid hatchlings as well as benthic cuttlefish hatchlings need prey rich in polyunsaturated fatty acids, phospholipids and cholesterol, with a moderate content of neutral lipids. The positive effect of polyunsaturated fatty acids on juvenile growth of cuttlefish was also demonstrated by Koueta *et al*. (2002). Semmens and Moltschaniwskyj (2000) considered the relatively high lipid concentration in muscles of juveniles to be related to a higher need of storing energy reserves during early life. The likely importance of a rich lipid supply during the post-hatching phase was emphasized also by Segawa and Hanlon (1988) and by Piatkowski and Hagen (1994).

4.3. The bodily outfit of cephalopod hatchlings

4.3.1. *Cephalic organs*

The central nervous system in cephalopod hatchlings is very large compared to the rest of the body (Figure 5), and the smaller their absolute size the larger the

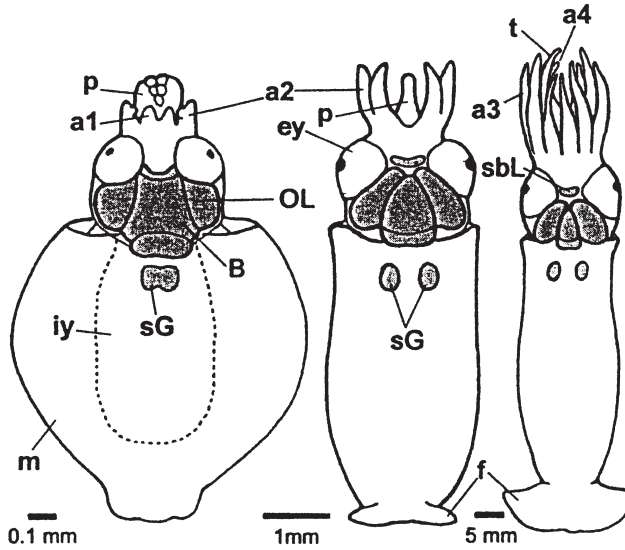

Figure 5 Dorsal (morphologically anterior) view of a hatchling (paralarva 1, left), a post-hatching stage (paralarva 3, middle) and a juvenile after separation of the tentacles (right) of *Todarodes pacificus*. Note the size of the central nervous system and stellate ganglia (in grey). a1 = first arm, a2 = second arm, a3 = third arm, a4 = fourth arm when tentacles (t) are not counted as arms, B = brain, ey = eye, f = fin, iy = inner yolk sac, OL = optic lobe, p = proboscis (fused tentacles), sbL = superior buccal lobe, sG = stellate ganglion. From Shigeno *et al*. (2001c).

relative size of the nervous system (Nixon and Mangold, 1996, 1998; Shigeno *et al*., 2001b, e). The brain and the large eyes and optic lobes are supported by cartilaginous structures (Mause *et al*., 1997). The relatively large size of the eyes of cephalopod hatchlings suggests a perfect adaptation to the very low light levels of deeper water layers and/or during the night (Denton, 1990; Young, 1991). Polarized vision is known to exist in squid hatchlings (Shashar *et al*., 1998) and can be considered as likely in octopod and cuttlefish hatchlings (Shashar and Cronin, 1996; Shashar *et al*., 1996). Probably some cephalic extraocular photoreceptors are present in the hatchlings of most or all decabrachian cephalopods (Sundermann, 1990). In octopod hatchlings, similar structures are associated with the stellate ganglia (Budelmann *et al*., 1997).

The hatchlings always have well developed statocysts holding statoliths that provide the necessary information on linear and angular acceleration (Williamson, 1995; Budelmann, 1996). This information is essential for orientation in space, especially during prey capture (Bülow and Fioroni, 1989). Malformation of statoliths causes erratic swimming movements that makes food capture extremely difficult or impossible (Fermin *et al*., 1985; Hanlon *et al*., 1989; Martins, 1997). On the other hand, Arkhipkin and Golub (2000) observed an aberrant statolith structure

in an individual ommastrephid squid, suggesting that an accidental displacement of the statolith during early life and a subsequent re-attachment to the macula occurred, as later juvenile and adult structures were normal. This observation seems to demonstrate that individuals may successfully forage in spite of a grossly disturbed statocyst organ, but it also draws attention to the question whether ommastrephid hatchlings have a different mode of foraging (see Section 5.).

The buccal mass, a complex of cephalic organs (beaks, radula, salivary glands, muscular systems) is fully developed. It will be considered below in close relation with other parts of the digestive system (see Section 4.3.2.) and in relation to the prehensile organs which capture and subdue prey (see Section 4.3.3.).

4.3.2. *Digestive tract*

The buccal mass, including the radula and the horny beaks, is fully differentiated by the time of hatching (Nixon, 1988). The strong buccal musculature enables the beaks to bite into prey items and to ingest the pieces severed from a prey by the radula. In the hatchlings of teuthid squids, the cutting edge of the lower beak is denticulated (Young *et al*., 1985), whereas both upper and lower beaks are denticulated in idiosepiid and small octopod hatchlings.

Except for final differentiation of the digestive gland cells in cuttlefish (Boucaud-Camou *et al*., 1985) and some squid (Vecchione and Hand, 1989), the alimentary canal seems ready to function as soon as the first prey items are ingested. The inner yolk sac is integrated with the venous system of the digestive gland and continues to release nutrients into the blood stream once predatory activity and digestion of captured food have started (Boletzky, 2002). The onset of food ingestion of course supposes a degeneration or rupture of the embryonic membrane closing the mouth (see Section 3.3.1.).

4.3.3. *Prehensile organs: arms and tentacles*

Embryonic development does not produce identical arm crown morphologies in different cephalopod species. A relation seems to exist between embryo size and arm crown development. Hatchlings developed from large eggs generally have fully developed arms, which may be very long in the benthic "crawl-away" young of some octopodids (Laptikhovsky, 2001). Conversely, the smaller the egg (hence also the embryo and hatchling) the shorter and more rudimentary the arms at hatching. Even in the smallest hatchlings, however, the short arms and tentacles have a few powerful suckers allowing the young animal to seize and manipulate live prey that may be of a size close to its own (Harman and Young, 1985; Haas, 1989; Schmidtberg, 1997, 1999). In several oegopsid squid families, the young animals have fully functional tentacles, which only subsequently degenerate (Young *et al*., 1998).

A peculiar modification of tentacle development occurs during late embryonic development of ommastrephid squids, leading to the so-called rhynchoteuthion hatchling with fused tentacle shafts (Figure 5), the tentacle clubs forming a sucker bearing frontage (Naef, 1928).

Cephalopod suckers cover a remarkable range of soft and hard modules that vary among groups. From hatching onward, suckers of all types undergo continuous modifications related to growth. The "horny rings" of decabrachian suckers become enlarged by the marginal growth of the pentagonal or hexagonal plates composing them (Figure 6). The soft adhesive structures of *Nautilus* are different in shape but suggest that the serial arrangement of the transverse crests differentiated on their cirri still reflects a type of structure from which the coleoid suckers are derived (Budelmann *et al*., 1997).

4.3.4. *Mantle and shell*

The mantle and fins are the main locomotory effectors of cephalopods, except in *Nautilus*. The muscular mantle is especially important in very small hatchlings where the muscular fins have a rather limited function in swimming, or where no fins exist (Octopoda). Thompson and Kier (2001a, b) described the muscular system and the high efficiency of mantle contraction and superinflation in squid hatchlings. Whereas the undulating fins of cuttlefish and sepiolid hatchlings already have clearly locomotory functions, the fins of hatchling teuthid squid mainly achieve active stabilization in rapid forward swimming, especially during prey capture (see Section 5.)

Wherever they exist, shells or shell remnants provide an insertion point for mantle muscles and for funnel and head retractor muscles, and often provide an abutment for the fin bases. Where chambered shells are present in the adults (*Nautilus*, *Spirula*, sepiid cuttlefish), the hatchlings have two (*Spirula*) or several functional gas chambers (Fioroni, 1990; Landman *et al*., 1994, 2001), enabling the young individuals to maintain near-neutral buoyancy. Although a shell sac rudiment is always formed during early organogenesis, a shell is not necessarily formed subsequently. Cephalopods lacking a shell or shell remnant as adults lack it already at hatching.

4.4. Post-hatching growth, morphological changes, and the use of growth records in age determination

The body size at hatching may vary within each species, depending on the actual egg size, on past developmental temperature (Bouchaud and Daguzan, 1990; Gowland *et al*., 2002), and on individual hatching conditions (premature, mature, overmature). Therefore, the *post mortem* reconstruction of past life-history events requires an

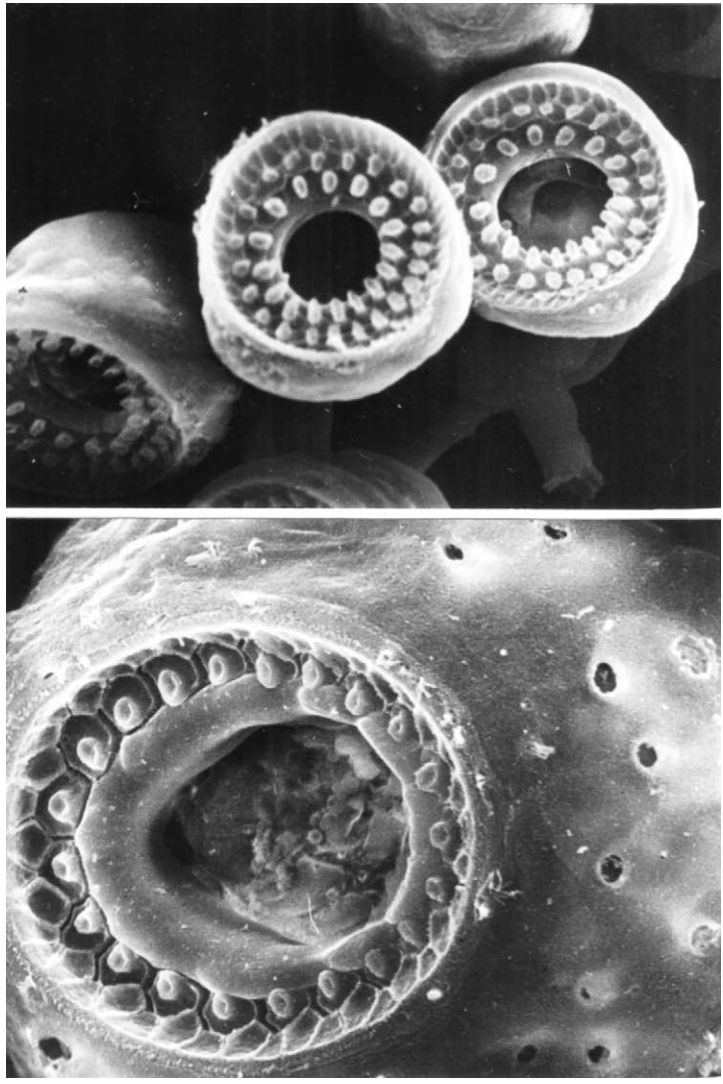

Figure 6 Sucker structures in juvenile *Sepiola affinis*. Above: tentacular club suckers in an individual measuring 4 mm in dorsal mantle length (SEM, enlarged 600×). Below: a sucker from the right ventral arm of an individual measuring 3 mm in dorsal mantle length (SEM, enlarged 1000×). Courtesy of Elisabeth Mauris.

identification of some growth "records" recognizable in each individual. Such records exist in the form of periodic growth structures, including the concentric rings in the rostrum (Raya and Hernandez-Gonzalez, 1998) and lateral walls of the horny beaks (Hernandez-Lopez *et al*., 2001). The most widely used among these readable

structures are the statoliths (Natsukari *et al*., 1988; Jackson *et al*., 1991; Jackson and Choat, 1992; Natsukari and Komine, 1992; Villanueva, 2000a). Their analysis can be combined with the study of uncalcified shell remnants (squid gladii: Arkhipkin and Bizikov, 1991; Jackson *et al*., 1993; Arkhipkin and Perez, 1998; Perez and O'Dor, 2000) and of calcified shells in which distinct septal lamellae exist (sepiid cuttlebones: Ré and Narciso, 1994; Bettencourt and Guerra, 1999, 2001).

The mode of statolith growth is characterized by essentially concentric accretion and is related to the fact that each of the two statoliths, except where attached to the macula of the statocyst wall, is entirely surrounded by the endolymph of the statocyst. From this fluid calcium carbonate is precipitated on an initial nucleus and subsequently on the statolith surface, the rate probably depending on cyclic changes of pH in the statocyst fluid (Morris, 1991). Conversely, absence of clear growth lines may be a sign of less distinct, or lacking, cycles of physiological change, or of different biochemical composition of the statocyst endolymph, as observed in the cuttlefish *Sepia officinalis* (Bettencourt and Guerra, 2000).

Hatchlings inevitably experience some physiological and behavioural stress due to the thorough change of living conditions when leaving the sheltered microenvironment of the egg capsule. In general this stress leaves a check mark in the growth lines, especially in statoliths (Arkhipkin and Seibel, 1999). The septal crowding in sepiid hatchling cuttlebones and the so-called nepionic constriction in the shell of ectocochleate hatchlings can also be viewed as stress marks (Oba *et al*., 1992; Okubo *et al*., 1995). It is unknown whether embryonic growth is actually arrested, perhaps for hours or days, before post-hatching growth begins. Although the exact duration of such a growth deceleration or arrest cannot be deduced from a check mark, these marks generally provide a satisfactory trace representing the onset of post-hatching growth, whenever backcalculations of the hatching date for estimations of age are attempted *post mortem* (Alford and Jackson, 1993; Brodziak and Macy, 1996; Butler *et al*., 1999). Such backcalculations are complementary to size distribution analysis (Dawe and Beck, 1985) and ultimately also permit estimation of hatching sites in the sea if the direction and speed of ocean currents are known (Brunetti and Ivanovic, 1992; Bower, 1996; Bower *et al*., 1999a, b).

A major problem with back calculations is an uncertainty about the time relation of recognizable growth lines (Bigelow and Landgraf, 1993; Gonzalez *et al*., 2000). Clarification can be expected only from studies of cephalopods that can be reared from hatching (Bigelow, 1992), or that can be marked after capture, using chemical markers like strontium, and released to be recaptured later (Rodhouse and Hatfield, 1990). Fluorescent stains like tetracycline or alizarin are often used for such records, in an aquarium or after release and recapture, providing a reliable validation of growth lines as daily marks (Jackson, 1989, 1990; Dimmlich and Hoedt, 1998; Fuentes *et al*., 2000). Precise data of body and statolith growth obtained through rearing studies are now recognized as an essential prerequisite of growth models (Jackson, 1998).

Hard structures undergo more or less profound changes in overall shape during post-embryonic growth. The form changes observed in statoliths during their increase in size are species-specific (Pineda *et al*., 1998). To some extent they also correspond to the progressively altered fluid dynamics inside the growing statocysts (Arkhipkin, 1996; Arkhipkin and Bizikov, 1997; Thomas and Moltschaniwskyj, 1998). Post-embryonic check marks reflect drastic changes of living conditions related to depth and other environmental parameters (Arkhipkin and Bjorke, 2000), possibly also to change of foraging mode (Laptikhovsky et al., 1993), and ultimately to reproductive activity (Arkhipkin *et al*., 1999, 2000). Modifications in the relative concentrations of calcium and strontium in different parts may reflect migratory events (Durholtz *et al*., 1997; Yatsu *et al*., 1998). Sr concentrations are negatively related to temperature, whereas Fe and Zn concentrations are positively related to temperature (Ikeda *et al*., 1996).

In contrast to its profound modification during embryonic development (Landman *et al*., 1989; Fioroni, 1990), the shape of the shell appears rather constant immediately after hatching, major changes occurring only later with an elongation of the mantle (Moltschaniwskyj, 1995). The shape of the so-called gladius in squids may remain very similar in the hatchlings, juveniles and adults of different species (Sanchez *et al*., 1996).

The beak form changes most drastically in small-sized hatchlings, due to a massive thickening and/or elongation of the biting edges, with formation of a pointed rostrum in the upper beak (Nixon, 1988). Where denticles exist on the biting edge at hatching, they become abraded and disappear during post-hatching growth (Harman and Young, 1985). An exception is the pygmy squid *Idiosepius*, in which the denticulation persists in both the upper and the lower beak (Adam, 1986).

In parallel with these changes, which are functionally related to the developing food spectrum of the animals, the prehensile organs used for prey capture undergo strong modifications. Positive allometric growth of arms and tentacles may start very early during post-hatching development (Moltschaniwskyj, 1995; Rodhouse and Piatkowski, 1995), along with an ultrastructural modification in the tentacular shaft musculature (Kier, 1996). Special embryonic features like partial arrest of arm development and fusion of tentacle shafts in ommastrephids (producing the six-armed rhynchoteuthion form) or temporary arrest of tentacle development in idiosepiids (resulting in an eight-armed form) are progressively eliminated by compensatory growth and differentiation during the early post-embryonic phase, including separation of fused tentacles in rhynchoteuthions (Forch, 1986; Brunetti, 1990). Such profound changes are sometimes considered as a metamorphosis (Dunning, 1985) (see Section 4.5.).

The most important environmental factor influencing post-hatching growth is food availability (Koueta *et al*., 2000; Moltschaniwskyj and Jackson, 2000; Semmens and Moltschaniwskyj, 2000; Jackson and Moltschaniwskyj, 2001; Koueta and Boucaud-Camou, 2001). If fed *ad libitum*, squid hatchlings may ingest prey weighing up to 72% their own body weight per day (Segawa, 1990).

An almost equally important factor is ambient temperature (Forsythe and Hanlon, 1989; Segawa, 1995; Moltschaniwskyj and Martinez, 1998; Martinez *et al*., 2000; Forsythe *et al*., 2001). There are also indications of phase-specific temperature sensitivity in squid growth (Hatfield *et al*., 2001). These data permit an interpretation of variability in growth rates and adult sizes (Rocha and Guerra, 1999). The observation that the food ingestion rate achieved during the first weeks following hatching affects the *subsequent* growth process is particularly significant, as it provides a predictive factor in culture work (Koueta and Boucaud-Camou, 1999).

From recent studies, Jackson and O'Dor (2001) conclude that fast growth in cephalopods is due to a combination of (1) efficient digestion, (2) the ability to sustain continued growth by a combination of both an increase in muscle fibre size and a continual recruitment of new muscle fibres (Pecl and Moltschaniwskyj, 1997), (3) efficient use of oxygen and (4) low levels of antioxidative defense (Zielinski and Pörtner, 2000).

4.5. Paralarval specializations: an ecological view

The earlier literature dealing with post-hatching stages of cephalopods described very small hatchlings (those appearing dissimilar to adults) as larvae, generally with the implicit assumption of a subsequent metamorphosis. Larger hatchlings (those already looking similar to adults, having developed from bigger eggs) were generally referred to as early juveniles or newly-hatched young (Naef, 1928; for contrasting terminology see Nomura *et al*., 1997). In a more restrictive view of morphogenetic analysis, post-gastrular features observed prior to hatching were sometimes emphasized as larval in the older literature. In modern publications on marine invertebrate larvae, onset of metamorphosis is generally viewed as the end of larval life, and for want of a profound metamorphosis, cephalopods are rarely mentioned (Young and Eckelbarger, 1994; Young *et al*., 2001).

Earlier discussions about the terminology used for cephalopods were summarized by Young and Harman (1988). These authors proposed the new term paralarva for a certain category of young cephalopods, defining it as a cephalopod of the first post-hatching growth stage that is pelagic in near-surface waters during the day and that has a distinctively different mode of life from that of older conspecific individuals (Young and Harman, 1988). They observed that in general, morphological discontinuities in a developmental series accompany habitat changes and therefore specified: "The definition requires a morphological change only when habitat changes are not obvious (e.g. species that occupy near-surface waters as older individuals such as *Argonauta* spp. or *Thysanoteuthis rhombus*) and requires a habitat change only when morphological changes are not obvious (e.g. the vertically migrating *Pterygioteuthis* spp.)". In teuthid squids, for example, the hatchlings of only 3 among 51 species listed would not qualify as paralarvae, three more are marked as questionable in this respect.

Young and Harman (1988) did not substitute the term paralarva for the term larva. They emphasized that paralarva is based at least partially on ecological criteria and therefore does not compete with the developmental terms larva or juvenile. Technically, a young cephalopod can therefore be both a larva and a paralarva, or a juvenile and a paralarva. Indeed, both larva and paralarva sometimes describe the same stages (Haimovici *et al*., 1998). However, the term paralarva is more often used as if it had replaced the term larva, especially when alluding to quasi-larval features, such as mode of life or body proportions. Thus Hanlon and Messenger (1996) discussed paralarval feeding as being substantially different from the adult behaviour. In the sepiolid squid *Euprymna scolopes*, Hanlon *et al*. (1997) mentioned diurnal paralarval swimming activity, observing that "even the youngest hatchlings spent a large proportion of their day buried in the sand substrate". This application of paralarval indeed corresponds to larval as used in a rather loose sense (Hanlon *et al*., 1985; Rowell and Trites, 1985; Sanchez and Moli, 1985; Stephen, 1985; Young and Harman, 1987; Nesis and Nikitina, 1991; O'Shea and Kubodera, 1996; Sweeney *et al*., 1992; Haimovici *et al*., 1995; Rocha *et al*., 1999; Nesis, 1999).

Likewise, the term juvenile is used for both paralarval and subsequent stages (Guerra *et al*., 1985; Rodhouse and Clarke, 1985; Hatfield and Rodhouse, 1994; Moltschaniwskyj and Doherty, 1994, 1995; Chen *et al*., 1996), or only for post-[para]larval stages of squids (Vecchione and Gaston, 1985; Nigmatullin *et al*., 1995; Uozumi and Forch, 1995; Salcedo-Vargas and Guerrero-Kommritz, 2001), or for planktonic juveniles of *Octopus vulgaris* (Takeda, 1990), and for post-[para]larval, benthic young octopuses not yet qualifying as subadult (Mather, 1992; Mather and Mather, 1994).

To avoid unnecessary confusion, it seems advisable to first address the question whether a special term is really needed when talking about newly-hatched cephalopods. Indeed, terms like hatchling, young animal, or early-life phase often suffice (Rodhouse and Clarke, 1986). Only in an explicit ecological context, use of the term paralarva seems appropriate (Goldman and McGowan, 1991; Vecchione, 1991b, 1998; Saito and Kubodera, 1993; Ueyanagi and Nonaka, 1993; Vecchione and Lipinski, 1995), provided the specific conditions correspond to the definition given by Young and Harman (1988). Indeed, such specifications are easily forgotten. Thus Young and Vecchione (1999) described a paralarva of *Vampyroteuthis infernalis*, although a paralarval stage was originally considered unlikely for the Vampyromorpha. Vecchione and Young (1998) described a paralarva in a new taxon in which the adult form is unknown.

Sometimes the term paralarvae is used collectively for different paralarval stages (Vecchione *et al*., 1992; Piatkowski *et al*., 1993), or successive paralarval stages are defined (Shigeno *et al*., 2001c). Subsequent stages consequently may be called post-paralarval (Bigelow, 1992). Distinctions between paralarval (Tsuchiya *et al*., 1991) and post-paralarval or juvenile stages (Tsuchiya and Mori, 1998) gain in precision when morphological changes are distinct, such as

separation of the rhynchoteuthion tentacles in young ommastrephids (Vidal, 1994), or the transformation of certain suckers into hooks in onychoteuthid (Young and Harman, 1987) and gonatid squids (Falcon *et al*., 2000).

Whatever the descriptive terms chosen, hatchlings exhibit the general body plan of the animal and thus are easily recognized as young cephalopods. They are essentially baby cephalopods (as in colloquial Japanese), no matter how small or large, how different from the adult, or how similar to the adult – as indeed are young sepiid cuttlefish and sepiolid squids, or the crawl-away young of octopuses that produce large eggs (Boletzky, 1997a).

Among the generalizations that can be made about early post-hatching stages is the absence of intrinsic photophores (containing photogenic cells) in the hatchlings of those species that have such light organs at advanced juvenile and adult stages (Sweeney *et al*., 1992). One of the earliest differentiations of likely intrinsic photophores in the arm crown was reported by Loffler and Vecchione (1993). These photophores are totally different from the bacterial light organs (see Section 4.6.).

4.6. Light organs harbouring symbiotic luminescent bacteria

In contrast to the variously positioned intrinsic photophores (see Section 4.5), which appear only during juvenile development, the bacterial light organs occurring in several loliginid and sepiolid squids are always associated with the ventral surface of the ink sac. They are differentiated as a series of paired invaginations and are formed during advanced embryonic stages (Montgomery and McFall-Ngai, 1993), remaining sterile until hatching (McFall-Ngai and Ruby, 1991, 1998). The luminescence produced is entirely due to light-producing bacteria (*Vibrio* spp.), which are taken up by the newly hatched animals from the surrounding sea water and are kept in the crypts of the light organ (Nishiguchi *et al*., 1998; Ruby and McFall-Ngai, 1999; Nishiguchi, 2000; Nyholm *et al*., 2000; Visick *et al*., 2000). The free surface of the organ is covered by a muscle-derived lens tissue (Montgomery and McFall-Ngai, 1992). The intensity of light emission is controlled by muscular expansion and retraction of ink sac diverticula. This adjustable luminescence is supposed to be used as a ventral counterillumination in camouflage directed against predators.

When first taken up, the bacteria trigger (1) an apoptotic reaction of the ciliated cells surrounding the ducts leading into the light organ, through which the bacteria entered the organ (Foster and McFall-Ngai, 1998; Foster *et al*., 2000), and (2) modifications in the epithelium lining the crypts (Montgomery and McFall-Ngai, 1994, 1995; Doino and McFall-Ngai, 1995; Lamarcq and McFall-Ngai, 1998; Lemus and McFall-Ngai, 2000). Once the ciliary cells have disappeared due to apoptosis, the bacterial population established in the crypts becomes independent of the surrounding medium, and no recruitment of new

bacteria occurs. Once in 24 hours the bacterial population undergoes a massive reduction by venting, and subsequently grows to its previous level from the small fraction (about 5–10%) that remains after each extrusion of bacteria. This venting occurs at the end of the nocturnal activity phase, so that the bacterial population regenerates when the host animal is at rest during the day (McFall-Ngai, 2000).

McFall-Ngai (1994) and Montgomery and McFall-Ngai (1998) studied post-hatching development in experimental animals that were not allowed to acquire luminescent bacteria. In these aposymbiotic individuals, the fine morphological changes that would arise under normal conditions were not observed, but the gross morphological changes of the organ did occur in the presence of the remaining rudiments of the ciliated fields, which normally are eliminated after contact with bacteria (see also Claes and Dunlap, 2000; Nishiguchi, 2000).

Comparisons between different luminescent species and genera within the subfamily Sepiolinae reveal significant variation within the general pattern of light organ development and bacterial infection. Thus the light organs of two Mediterranean species of *Sepiola* contain mixed populations of *Vibrio logei* and *V. fischeri*, whereas species of the Pacific genus *Euprymna* contain only *Vibrio fischeri* (Fidopiastis *et al*., 1998). Differences between *Sepiola robusta* and *Euprymna scolopes* exist in the extent of light organ development during embryogenesis (Figure 7). They are probably related to the differences in egg size and the resulting body size of the hatchlings (Foster *et al*., 2002).

5. POST-HATCHING BEHAVIOUR

In the study of animal behaviour, the first question to address is what the animal does under given circumstances. Once this is known, one can raise the question of the function or biological role of a behaviour, i.e. why the animal behaves the way it does. The question of a function or biological role involves the historical background at two levels, (1) individual experience, and (2) past adaptations of the species through evolutionary change. In a newly hatched animal, there is little or no individual experience, so most of the behaviour is defined by naturally selected, genetically determined patterns. This raises the questions of compromise and cooption, as no behavioural expression can be considered in isolation. For example, feeding behaviour cannot be functionally decoupled from defensive behaviour, since efficient predators would prove unfit if they were unable to avoid other predators at the very moment of attack. Certain stereotyped behaviours, such as turning dark when attacking a prey, may serve such a dual function (Boletzky, 1987). Given the complexity of these behaviour patterns and their reticular interdependence, the following subdivisions are only tentative.

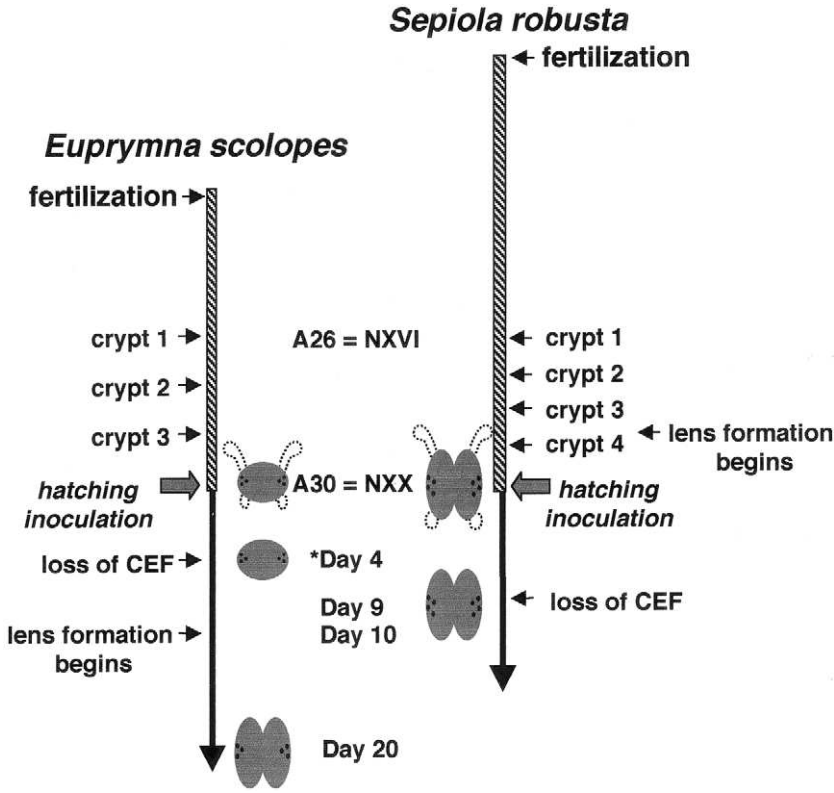

Figure 7 Overview of the light organ development of *Sepiola robusta* compared to *Euprymna scolopes*. Both species begin light organ development at similar stages (Arnold stage 26 = Naef stage XVI). These similarities include the formation of deeply invaginated, paired crypt spaces in succession on the surface of the light organ. *E. scolopes* hatches after formation of the third crypt, whereas *S. robusta* forms a fourth crypt and starts lens formation before hatching. Upon hatching, the light organs of both species undergo a series of morphological changes in response to symbiosis-competent bacteria. The ciliated epithelial field (CEF) on the surface of the light organ is lost through a process of cell death and regression (this takes 4 days in *E. scolopes*, 9 days in *S. robusta*). From Foster *et al*. (2002).

5.1. Learning

A newly hatched animal able to cope with the conditions of life in the sea gains individual experience from successful foraging and by escaping from potential predators. That such experience can mark the behavioural repertoire in very small individuals was demonstrated by Chen *et al*. (1996) who showed that loliginid squid hatchlings having fed on easy prey (brine shrimp) were unable later to capture difficult prey (copepods), whereas individuals that learned to deal with

copepods from hatching onward continually improved their attack behaviour. Over time, the latter squids increased the incidence of head-on attacks on copepods, which appeared to be more successful than attacks from the posterior end of the copepod. The corresponding circling behaviour during positioning and the reorientation in front of a moving copepod became increasingly elaborate. In the semi-schematic line drawings made from sequential video frames, Chen *et al.* (1996) unfortunately omitted the subterminal fins of the young squids. In fact, the undulating movements of these fins are essential for stabilizing the elongate squid body during positioning and for the attack of a prey item (Boletzky, 1987).

Recent experimental work using the predatory response of the large hatchlings of cuttlefish demonstrated the interplay of short-term and long-term memory in the learning processes building up the individual experience of young animals (Dickel *et al*., 1997, 2000; Agin *et al*., 1998). These processes in particular enable the growing individuals to cope with the variable environmental parameters, including scarcity or abundance of available prey, and high or low density of predators and/or competitors (Blanc and Daguzan, 1999, 2000).

5.2. Feeding

Predators having polarization vision can easily detect transparent prey. Shashar *et al*. (1998) examined predation on live zooplankton by loliginid squid hatchlings using lateral illumination with either linearly polarized or depolarised light, and found that squid hatchlings attacked planktonic prey under polarized illumination at a much greater distance than under depolarised illumination. The advanced juveniles and adults of the species studied (*Loligo pealei*) remain sensitive to polarization, as do cuttlefish (Shashar *et al*., 1996) and octopus (Shashar and Cronin, 1996). These observations suggest that polarized vision may be a widespread ability of young cephalopods, used during prey capture when ambient light levels are very low (Fleisher and Case, 1995), but possibly also in communication among individuals.

The ability to catch fast-moving prey depends, to a large extent, on the stage of development of the prehensile organs, especially of the ejectable tentacles in the decabrachian hatchlings. Whereas sepiolid squid and cuttlefish have fully differentiated tentacles at hatching, the tentacles of hatchling loliginid squid are barely longer than the other arms. Their subsequent growth and functional maturation are characterized by the differentiation of fast-contracting cross-striated muscle cells in the tentacular shaft, which contrast with the obliquely striated muscle cells of the other arms (Kier, 1996). Using high-speed videoscopy, Kier observed the corresponding modification of predatory behaviour in young *Sepioteuthis lessoniana* and noted that very young individuals rapidly swim forward and capture the prey with the arms, whereas older individuals (having developed the fast-contracting muscle cells in the tentacle shaft) swim forward to a much lesser extent but very rapidly extend the tentacles to seize the prey (Figure 8).

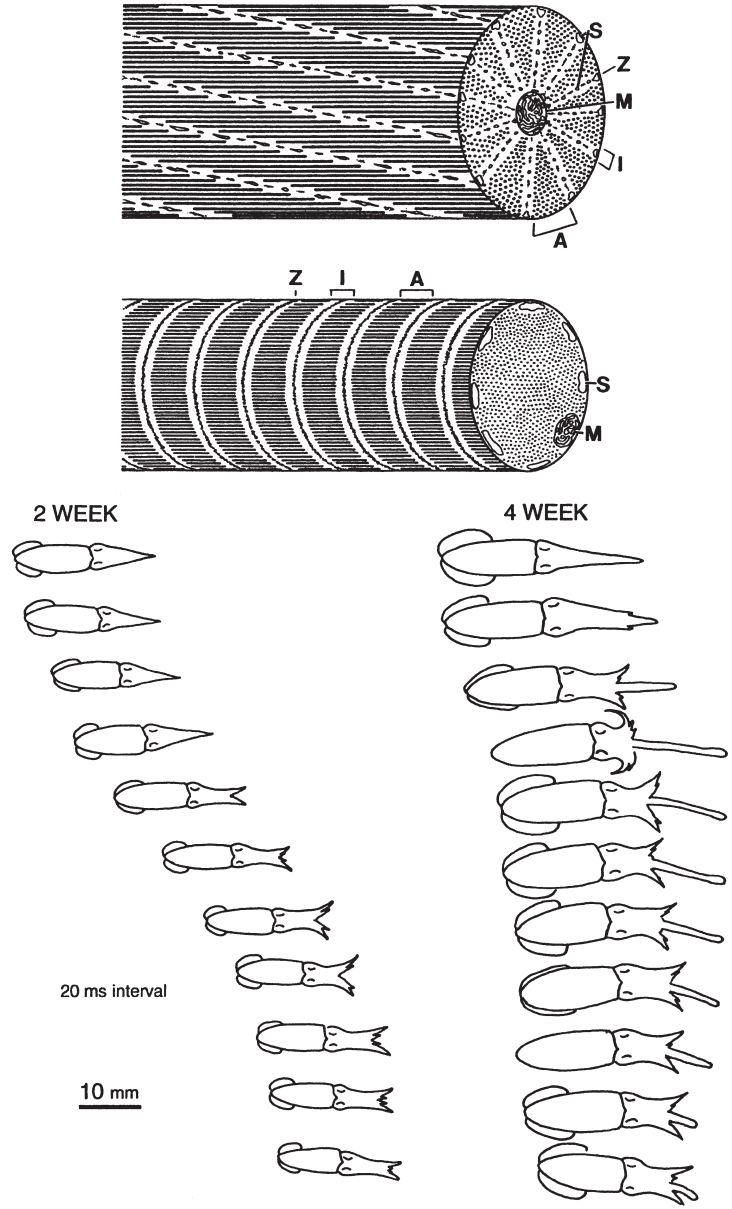

Figure 8 *Above:* schematic diagram of an obliquely-striated (top) and a cross-striated muscle fiber from squid. A cross-section of an obliquely striated muscle cell shows an analogous sequence of bands to those seen in a longitudinal section of the cross-striated fiber. The A band (A), I band (I), Z elements (Z), sarcoplasmic reticulum (S), and mitochondria (M) are labelled for each fiber type. Thin filaments not shown. *Below:* Tracings from video sequences of prey capture in 2-week-old and in 4-week-old *Sepioteuthis lessoniana*. The sequence runs from top to bottom with an interval of 20 ms between frames (see Section 5. 2. for further explanations). From Kier (1996).

The frequently observed absence of recognizable stomach contents in young squid probably reflects their abilities to remove exoskeletons of relatively large crustaceans prior to ingestion (Vecchione, 1991a; Kasugai, 2001).

The feeding behaviour related to the peculiar morphological specialization of fused tentacles in ommastrephid squids is not yet fully understood. The similarity of digestive enzyme systems with hatchlings of other groups would seem to suggest a similar feeding regime (Boucaud-Camou and Roper, 1995, 1998). However, using the transparent whole-mount method described by Vecchione (1991a), Vidal and Haimovici (1998) analysed gut contents to identify the food ingested by the rhynchoteuthion paralarvae of *Illex argentinus*. They found copepod fragments only in the larger individuals, whereas micro-organisms embedded in mucus were observed in both the smallest (early post-hatching) and the larger specimens. These authors therefore concluded that mucus with adhering microscopic organisms may well be ingested as food, as was envisaged by O'Dor *et al*. (1985) who considered suspension-feeding a conceivable intermediary mode of nutrition in rhynchoteuthions. In the course of their analysis, Vidal and Haimovici (1999) found protistan and metazoan parasites in the digestive tracts of the early post-hatching stages of *Illex argentinus* and of two unidentified species, so the origin of these parasites is an additional question relating to the feeding mode.

5.3. Defence

Pelagic young cephalopods are continually exposed to predators and apparently need some special forms of camouflage, e.g. mimicry of unpalatable organisms (Arkhipkin and Bizikov, 1996). Much more elaborate forms of crypsis achieved by colour patterns and body postures exist in most of the species that live on the bottom throughout their life (Hanlon and Messenger, 1988, 1996; Chiao and Hanlon, 2001). Certain substrata, especially sand, are clearly preferred by young cuttlefish (Nabhitabhata and Nilaphat, 2000). When buried in sand, animals are invisible and may remain totally quiescent (Boletzky, 1996a). When settled on a soft substrate, or when attached to a hard substratum, young cuttlefish mimic the appearance of the respective ground and remain alert (Boletzky and Roeleveld, 2000). In spite of well developed "bottom behaviour", all the benthic young are also good swimmers and have the same capacity as the adults to move in the water column, e.g. when pursuing prey or when escaping from a predator. During such excursions into the open water, camouflage by ventral counter illumination can play its role, so that a would-be predator situated below a luminescent squid is unable to spot its potential prey (see Section 4.6.). When frightened, young cephalopods escape by jet-propelled backward swimming (see Section 5.4.),

often combined with ink ejection, much like larger juveniles and adults (Boletzky, 1997b).

Interspecific interactions can be more subtle than in simple predator/prey relationships. For example young octopuses seem to build up complex behaviour patterns involving quasi mutualism with certain fish species (Mather, 1992).

5.4. Swimming

In all the nektonic or macro-planktonic cephalopod species, the hatchlings live in the plankton, and their swimming behaviour is generally considered truly planktonic. In terms of their individual behaviour, however, these hatchlings and the early juveniles appear micro-nektonic rather than planktonic. They can give up their planktonic "rest swimming" (hovering) at any instant and start active forward or backward swimming. When they attack prey they always go through the sequence of action patterns typical for the adults, including rapid "chasing" during the positioning phase (Hanlon and Messenger, 1996).

Studying escape-jet locomotion in post-hatching *Sepioteuthis lessoniana*, Thompson and Kier (2001b) found that (1) the mantle cavity of a hatchling holds a larger volume of water relative to its body size than the mantle cavity of a larger individual, (2) a larger proportion of this volume is ejected from a hatchling, and (3) the maximum rate of mantle contraction during an escape jet is highest in a newly hatched squid. These observations are significant for understanding the biophysical conditions of planktonic and micro-nektonic life in a viscous environment that is characterized by different, size-dependent ranges of Reynolds numbers (Mann and Lazier, 1991). At the ultrastructural level, the ontogenetic changes in escape-jet locomotion are related to (1) a strong modification in the circular mantle muscles, where the ratio of superficial, mitochondria-rich fibers and central, mitochondria-poor fibres changes from an initial 1:1 to about 1:6 at the end of the second month post-hatching (Preuss *et al*., 1997), and (2) changes in the organization of collagen fibers in the mantle muscle, leading to ontogenetic changes in the kinematics of mantle movement and in the elastic energy stored during jet locomotion (Thompson and Kier, 2001a).

5.5. Life style

It is not yet clear whether newly-hatched sepiolids of the subfamilies Sepiolinae and Rossiinae always show higher swimming activity than the benthic adults (Summers and Colvin, 1989; Hanlon and Messenger, 1996; Yau and Boyle, 1996). Conversely, the question of "how benthic" these sepiolids are as adults

remains unanswered (Bello and Biagi, 1995). This question is interesting with regard to the third sepiolid subfamily, the Heteroteuthinae, in which all the species seem to be holopelagic (Orsi-Relini, 1995). However, in spite of the frequent and apparently extended midwater excursions of young and adult animals in the Sepiolinae and the Rossiinae, these two subfamilies can be viewed as having an essentially "holobenthic" life cycle, since individuals apparently spend some time buried in sandy substrata during the photophase of each 24 h period (Boletzky, 1996a).

The only radical departures from a "holobenthic" life cycle in bottom-dwelling species are (1) the pygmy squids, since the hatchlings live continually in the plankton before settling, and (2) a considerable number of "merobenthic" species among the bottom-dwelling Octopodidae, the only family in the order Octopoda that has benthic adults. In the merobenthic species, the hatchlings are characterized by short arms (Figure 9), their behaviour is similar to the behaviour of young squids, and they use their rather globular mantle/funnel complex very efficiently for jet propulsion (Tateno, 1993). The subsequent life style switching in the merobenthic octopodids is correlated with a particular size relation between the hatchling and the adult, hence also between egg size and adult size (Boletzky, 1997a). Only octopodids producing eggs smaller than 8–10% of adult mantle length are merobenthic, the newly-hatched animals living in the plankton for some time (Villanueva, 1995; Boletzky *et al*., 2001b). When these animals have grown to a size at which the arms attain a length similar to the length of the mantle, they switch to bottom life by progressively making contact with the substratum (Villanueva *et al*., 1995, 1996). In contrast, octopodid species producing eggs larger than about 10–12% of adult mantle length are holobenthic, as the crawl-away young adopt the benthic mode of life from hatching (Forsythe, 1984). For discussions about the evolutionary origin of bottom life in the Octopodidae, it is significant that no case of inverse switching (from a juvenile bottom life to an adult pelagic life) has ever been observed.

5.6. Social behaviour

Social interactions are unknown in newly hatched cephalopods. Schooling in loliginid squids begins only several weeks after hatching and then remains the dominant social behaviour throughout juvenile and adult life (Hanlon, 1989). In contrast, the oegopsid squid *Gonatus onyx* forms schools only during a limited phase of juvenile life (Hunt and Seibel, 2000). The cuttlefish *Sepia officinalis* shows no truly gregarious behaviour (Boal, 1996), but differences in feeding rates were observed between group-reared and single individuals, suggesting some group effect (Warnke, 1994). The higher feeding and growth rates noted in group reared cuttlefish could be due to mutual visual stimulation among individuals

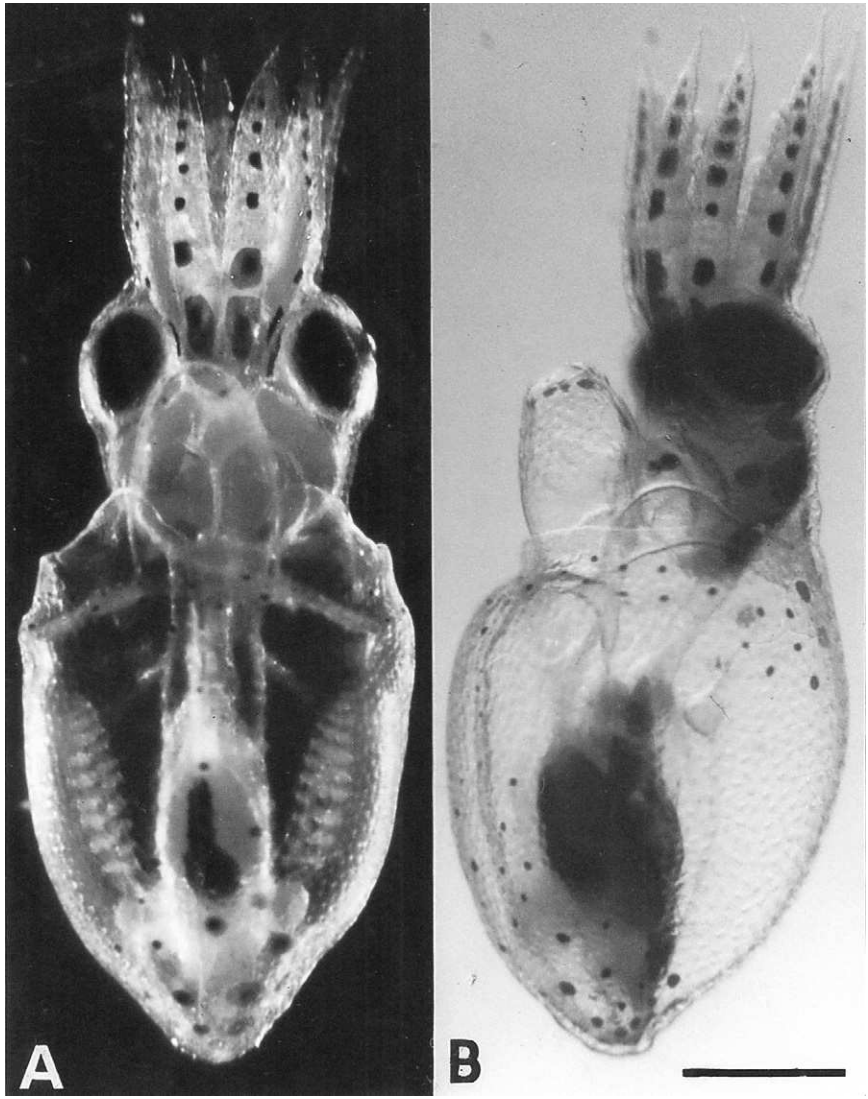

Figure 9 Two newly hatched *Octopus macropus*, under light ethanol anaesthesia. A: ventral (morphologically posterior) aspect. B: lateral aspect. Scale bar: 1 mm. From Boletzky *et al*. (2001).

(perhaps inter-individual begrudging), and/or to distance chemoreception as demonstrated by Boal and Golden (1999)

Advanced juveniles and adults apparently have elaborate means to develop social interaction with their conspecifics (Boal and Marsh, 1998). Apart from agonistic behaviour, for example in a well-established feeding hierarchy

(Warnke, 1994), such contacts imply also mechanisms of social spacing (Mather and Mather, 1994). Even schooling squids, which show the highest degree of sociability, maintain a minimal space between individuals, probably under the control of their lateral line analogue (Budelmann and Bleckmann, 1988).

6. DISPERSAL AND RECRUITMENT

Independently of their specific behaviour, all cephalopod hatchlings are likely to undergo some passive dispersal due to water movements. Moreover, many cephalopod hatchlings migrate actively in the water column and/or along the sea bottom. The horizontal distances covered during post-hatching dispersal range from perhaps less than one kilometre in small bottom-dwelling species that have no distinct planktonic phase (e.g. sepiolid squids of the subfamily Sepiolinae) to probably hundreds of kilometres in pelagic species, especially teuthid squids and octopods (Boyle and Boletzky, 1996).

Dispersal is an essential ingredient of recruitment. Given the lack of a clear-cut metamorphosis in cephalopods, it is a matter of agreement how the term recruitment is perceived. For fisheries, a useful criterion may be the minimal size of individuals turning up in the catches, which is generally related to the mesh size of the nets used. This provides an approximation of recruitment to the exploitable stock that may suffice for the top-down view of stock assessment. It is of only limited significance in the bottom-up view of work dealing with biological processes. Here the main concern is in population biology, where recruitment designates "the appearance of the young in a given population per unit of time" (Baretta-Bekker *et al*., 1992). This definition does not address the variable probabilities for "the young" to attain the stage of reproduction. Boyle and Pierce (1994) already noted that independently of whether one single, or two distinct, recruitment pulses appear in different populations of the squid *Loligo forbesi*, juvenile pre-recruits are present almost everywhere throughout the calendar year (Lum-Kong *et al*., 1992).

The practical interest of understanding cephalopod recruitment for fishery biology has provided support to studies on the basic biology of exploited cephalopod species, as demonstrated in recent years by major research programmes and joint publications (Clarke, 1996; Rodhouse *et al*., 1998). Large data sets are now provided by a combination of results from commercial fishing (Agnew *et al*., 2000), very often including fish as target species (Ueno *et al*., 1990; Rodhouse *et al*., 2001), and of complementary sampling done as part of oceanographic research (Yamaguchi and Okutani, 1990; Rodhouse *et al*., 1992; Piatkowski *et al*., 1993; Filippova and Pakhomov, 1994; Waluda *et al*., 2001). Such joint efforts are funded by international organizations such as the European Commission (Boyle

and Pierce, 1994) and supported by interdisciplinary programs like "Ocean Sciences in Relation to Living Resources" (Bakun and Csirke, 1998).

Cephalopod populations are not homogeneous, nor are they likely to be (continually or seasonally) replenished by quantitatively predictable recruitment or undergo only negligible fluctuation if undisturbed by fishing pressure. To some extent, the combined effects of length and strength of reproductive activity, and of life span, on lifetime fecundity may balance population size and structure, but they cannot totally counter balance environmental effects (O'Dor, 1995). In the case of commercially exploited species, the effects of fishery pressure are superimposed on the natural fluctuations (Dawe and Warren, 1993). Observed fluctuations in stock size of local or regional populations, such as those noted for *Todarodes pacificus*, also demonstrate the limits of long-term stability of migration patterns and related changes in the reproductive schedules, with a likely impact on population turnover (Nakata, 1993). Even long-term surveys that offer highly predictive models on the correlation between stock size and environmental temperature (Agnew *et al*., 2000) do not yet reveal the underlying recruitment dynamics. In approaching these basic mechanisms, the genetic heterogeneity and the complex population structures observed (Katugin, 1993; Brierley *et al*., 1995) raise questions that should be addressed in terms of metapopulation biology (Hanski, 1998; Pannell and Charlesworth, 2000).

Juvenile mortality rates appear as the most conspicuous unknown quantity of cephalopod recruitment. Since large samples of juveniles are rarely taken (Vecchione, 1999), it is difficult to assess how many individuals survive in the small size classes of a given cohort. Mortality curves obtained under laboratory culture conditions are of no use unless the actual causes of juvenile mortality are known. Starvation due to inadequate food and disease are likely to reflect artificial rather than natural mortality factors, and predation is rarely permitted in culture work.

It is likely that very young individuals are readily lost from the marginal parts of a natural population, since hatchlings appear to have little or no social cohesiveness (see Section 5.6.). But there is no means to quantify such effects, as the presence of young individuals outside their normal range of distribution provides no evidence for their actual loss. Indeed, massive or repeated displacement of individuals (provided they subsequently mate) may lead to the establishment of new local populations. *Octopus* cf. *aegina/kagoshimensis*, a possible lessepsian migrant established in the eastern Mediterranean, is a case in point (Salman *et al*., 1999).

7. DISCUSSION AND CONCLUSIONS

Cephalopods are studied for various purely scientific and commercial reasons. Past efforts to make the results of such different approaches and interests

converge on a comprehensive cephalopod biology have undoubtedly borne fruit. Twenty-five years after publication of "The Biology of Cephalopods" (Nixon and Messenger, 1977), the list of cephalopod meetings and related publications aiming at an interdisciplinary coverage, with a focus on biological integration, is long and grows longer every year. It is fortunate that the early life stages of cephalopods are regularly viewed as integral parts of life cycles. To consider them here separately is not meant to suggest anything biologically unique about early stages compared to other life stages. Of course a biological species is characterized by *all* the stages of its life cycle, which form the "machinery for transgenerational integration" (Rollo, 1995).

What deserves a special focus is the *link* between the successive life cycles that form the generational sequence carrying on a biological species. This link is the entrance-gate for genetic change (by recombination and mutation) and therefore is of particular interest to anyone addressing the problem of evolutionary change (Boletzky, 1989c, 2001). For example, the increase or decrease of ovum size is one of the changes that may have conditioned developmental modifications in the offspring (Boletzky, 1997a). Such an evolutionary view is adopted by Shigeno *et al*. (2001c) in reflecting on conserved topological patterns and heterochronies in embryonic development. These authors explicitly follow the instructive thread of developmental morphology, an essential ingredient of the "systematic morphology" approach commended by Naef (1928).

The unity of type expressed in cephalopod embryogenesis is obvious, and its difference from the patterns of other molluscan embryogeneses is impressive. Any attempt to link the peculiar morphogenotype of cephalopods to the spiralian type of other molluscs depends on a combination of approaches aimed to improve the necessary hypotheses about derivation. A new approach is offered by developmental genetics (Callaerts *et al*., 2002). These studies provide information on the genotype that conditions the establishment of embryonic patterns and organisation at the phenotype level. An evolutionary interpretation of observed morphogenetic patterns is supported by the postulate of a phylotypic stage in embryonic development (Slack *et al*., 1993). As the phylotypic stage of a given clade or taxon necessarily integrates some shifting developmental states into a condensed, diagrammatic stage, the term phylotypic phase may be more appropriate. Indeed, a comparison of the phylotypic stage of cephalopods, as given in Figure 2, with the embryonic stages figured by Naef (1928) reveals an integration of developmental stages IX (funnel tube rudiment) to XII (fold covering buccal mass) into one diagram. In order to link this special scheme to the general molluscan scheme of spiral cleavage, a stepwise regress in the opposite direction of developmental time is necessary. It reveals the initial form of a cephalopod embryo in the epibolic gastrula, which progressively encloses the uncleaved yolk mass. This gastrula in its turn is derived from a discoidal blastula that was produced by the superficial cleavage of the animal pole of the zygote. Thus, the morphogenetic expression of a teuthotypic phase is derivable from a special

non-spiral cleavage, which occurred under the genetic competence of *maternal* expression. The latter is the ultimate outcome of an ontogenetically *terminal* modification of the ancestral genotype (Boletzky, 1989c). From this point of view, it appears significant that some vital implements of offspring protection are produced under maternal control, namely egg capsules and related behaviours counteracting embryonic mortality (Boletzky, 2001).

Most of the recent studies of embryonic development provide new data furthering knowledge in both evolutionary developmental biology and fishery biology. Unsolved questions within both these areas of research are related to the transition between embryonic and post-embryonic development. The final opening of the mouth, the final differentiation of essential digestive gland cells, and the ostensible suppression of the tranquillising effect of the perivitelline fluid are among the most intriguing questions that need to be answered. Are these functionally related processes genetically coordinated, or do they form an epigenetic cascade with hatching being induced by the suppression of the tranquilliser effect, disappearance of the buccal membrane being induced by the first prey capture, and final digestive gland cell differentiation being induced by the ingestion of the first meal?

This complex of questions is of some importance if one wishes to redefine larval features and paralarval adaptations. Twenty years after the arrival of the term paralarva, the ecological perspective that was originally highlighted by this term is far from being unanimously perceived. Among the reasons for the lack of a true consensus could be the multifarious concepts that tend to be obscured, rather than exposed, by the term larva (from which paralarva is derived). Such concepts should be displayed, discussed, and if necessary discarded. Morphological and physiological features, and any relationship between them, should be utilized fully in an orderly system of descriptors. Examples include (1) the rudimentary state of the gills and (2) the related dominant respiratory function of the integument in very small hatchlings. Together the two form one noteworthy feature that may or may not be important in the context of ecological adaptation, and this ecological issue calls to mind the pervasive principle of scaling (Schmidt-Nielsen, 1984; Lucas, 1993).

The greatest gaps in our knowledge of early juvenile life relate to cephalopods of the deep sea, in both the pelagic and the demersal and benthic zones. Certainly the small size of the early life stages of these animals is a major limiting factor for observations from manned and unmanned submersibles. As a consequence, we do not know how the hatchlings and juveniles living in deep water cope with extremely low light levels or total darkness, how much bioluminescence from other organisms is perceived, or what chemical and physical signals are received from the surrounding environment and possibly used for orientation in space.

But even inshore cephalopods are often poorly known as far as their post-hatching behaviour is concerned. A striking example are the pygmy squid species of the genus *Idiosepius.* That the hatchlings live in the plankton for some time is virtually all that can be said about their behaviour (Tsuchiya *et al*., 1991).

Two questions are particularly intriguing. How and when do the young pygmy squid integrate their tentacles, which grow out during the post-hatching phase (Yamamoto, 1988), into the motor actions of prey capture? How and when do the juveniles first show the peculiar dorsal attachment response (Kasugai, 2001), on which life style switching depends?

A general lack of data on the causes of juvenile mortality and on the resulting mortality rates hampers most studies of recruitment dynamics. How the surviving individuals fare in the oceans is not yet understood in sufficient detail. The problem of quantifying the dispersal distances is not unique to early juvenile cephalopods; a recent symposium report noted: "The immense difficulty of measuring dispersal, especially long-distance dispersal (LDD), was mentioned by nearly all speakers." (Nathan, 2001). For potential solutions, three methodological groups were emphasized: (1) movement-redistribution methods and direct tracking of individuals in particular; (2) genetic analyses; and (3) mathematical models (Nathan, 2001). For LDD of cephalopod hatchlings, analyses of the variation in genetic markers such as microsatellites and ribosomal DNA would seem the most promising.

Nathan (2001) also comments on "the disproportionate importance of rare LDD events. Such events determine the rate of invasion, …and range expansions, maintain metapopulation structures, enable gene flow between distant locations, and are likely to be crucially important in the face of climate changes… LDD promotes Allee effects, such as difficulties in finding a mate". These questions certainly concern all cephalopod studies relating to ecology and biogeography.

In conclusion, the sheer number of recent papers dealing with early life stages of cephalopods demonstrates the topicality of this field. On the other hand, the numerous questions still unanswered indicate a continued need for further investigations to be carried out both on research vessels and in land-based laboratories. Some of the most promising techniques are relatively easy and generally inexpensive. Artificial fertilization of eggs taken from fresh specimens and small-scale aquarium cultures of hatchlings remain the major tools for future studies of the early life stages of many oceanic and deep-water species. For many open questions, like those regarding the feeding behaviour of rhynchoteuthions, the only prospect of improving our knowledge of post-hatching behaviour lies in aquarium culture studies. Recent success, e.g. in using enriched *Artemia* sp. nauplii in combination with other prey (Vidal *et al*., 2002), certainly opens new avenues for improving cephalopod culture techniques.

8. DEDICATION

This article is dedicated to the memory of Dr. Anna M. Bidder (1903–2001), a kind and generous mentor of countless biology students and academic colleagues, an unerring guide in cephalopod studies and in scientific endeavour at large.

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Movements of Marine Fish and Decapod Crustaceans: Process, Theory and Application

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Many marine species have a multi-phase ontogeny, with each phase usually associated with a spatially and temporally discrete set of movements. For many fish and decapod crustaceans that live inshore, a tri-phasic life cycle is widespread, involving: (1) the movement of planktonic eggs and larvae to nursery areas; (2) a range of routine shelter and foraging movements that maintain a home range; and (3) spawning migrations away from the home range to close the life cycle. Additional complexity is found in migrations that are not for the purpose of spawning and movements that result in a relocation of the home range of an individual that cannot be defined as an ontogenetic shift. Tracking and tagging studies confirm that life cycle movements occur across a wide range of spatial and temporal scales. This dynamic multi-scale complexity presents a significant problem in selecting appropriate scales for studying highly mobile marine animals. We address this problem by first comprehensively reviewing the movement patterns of fish and decapod crustaceans that use inshore areas and present a synthesis of life cycle strategies, together with five categories of movement. We then examine the scale-related limitations of traditional approaches to studies of animal–environment relationships. We demonstrate that studies of marine animals have rarely been undertaken at scales appropriate to the way animals use their environment and argue that future studies must incorporate animal movement into the design of sampling strategies. A major limitation of many studies is that they have focused on: (1) a single scale for animals that respond to their environment at multiple scales or (2) a single habitat type for animals that use multiple habitat types.

We develop a hierarchical conceptual framework that deals with the problem of scale and environmental heterogeneity and we offer a new definition of 'habitat' from an organism-based perspective. To demonstrate that the conceptual framework can be applied, we explore the range of tools that are currently available for both measuring animal movement patterns and for mapping and quantifying marine environments at multiple scales. The application of a hierarchical approach, together with the coordinated integration of spatial technologies offers an unprecedented opportunity for researchers to tackle a range of animal-environment questions for highly mobile marine animals. Without scale-explicit information on animal movements many marine conservation and resource management strategies are less likely to achieve their primary objectives.

1. INTRODUCTION

Understanding animal movement patterns in time and space is fundamental to the study of animal ecology and to the design of effective conservation and resource management strategies. Animal movement is an important ecological process that determines the spatial, demographic and genetic structure of

populations (McCauley, 1995; Hanski and Gilpin, 1997; Wiens, 2000) and links levels within trophic and nutrient hierarchies through the transport of material (including biomass) (e.g. Deegan, 1993; Kneib, 1997b; Marguillier *et al*., 1997; Laffaille *et al*., 1998). Movement paths of individuals and populations reflect both ecological and evolutionary responses to environmental heterogeneity (Southwood, 1977; Levin *et al*., 1984; Cohen and Levin, 1991). For some species, movements between habitat types, such as coral reefs and adjacent seagrasses and mangroves are thought to be critical to the maintenance of populations in an area (Parrish, 1989; Eggleston *et al*., 1998; Acosta, 1999; Nagelkerken *et al*., 2001). Highly mobile species, such as many fish and decapod crustaceans, exhibit complex and sometimes predictable movement patterns (e.g. home range activity and movements associated with ontogenetic shifts, spawning migrations and planktonic eggs and larvae). These patterns cover temporal scales ranging from a few minutes to many years and spatial scales from several centimetres to trans-oceanic movements spanning hundreds of kilometres (Quinn and Brodeur, 1991). The complex nature of movements, however, presents both a conceptual and operational problem in selecting appropriate scales in ecological studies (Wiens, 1976; Addicott *et al*., 1987; Wiens and Milne, 1989; Kotliar and Wiens, 1990; Levin, 1992).

Despite the growing realisation that inferences about ecological phenomena are scale-dependent, ecological scale has rarely been incorporated explicitly into conceptual models or experimental design (Meentemeyer, 1989; Milne, 1991; Levin, 1992; Gardner, 1998). Instead, scales of observation are often selected for their methodological convenience, rather than for their ecological suitability (Meentemeyer, 1989; Haslett, 1990; Petersen and Hastings, 2001). As a result, many studies are undertaken at scales very different from those that are most relevant to the ecological phenomena under study and in many instances, the scales are markedly finer than the routine daily movements of an animal. Unfortunately, this practice constrains and in some cases confounds meaningful inference in ecology. The key question is: How do we identify the appropriate temporal and spatial scales at which to study animal–environment relationships?

The problem of scale selection is by no means a new problem in ecology (reviewed by Schneider, 2001). In terrestrial ecology, it is now widely acknowledged that animals respond to environmental heterogeneity at different scales and in different ways. The variability in response, is in part, a consequence of the way animals move through their environment (Johnson *et al*., 1992). For instance, highly mobile animals are likely to respond to spatial and temporal heterogeneity at broader scales than sessile animals. Although some marine studies have addressed issues of scale, particularly for foraging studies of broad-ranging marine vertebrates (e.g. Russell *et al*., 1992; Boyd, 1996), scale selection has often been overlooked in studies of marine fish and decapod crustaceans. Consideration of animal movement patterns, however, may provide a focal point

for the development of a suitable approach to scaling a functionally meaningful environment (Addicott *et al*., 1987; Wiens and Milne; 1989).

Our overall objective is to develop a scale-explicit conceptual and operational framework that can be applied in the study of animal ecology. The paper is divided into four broad sections. First, we examine a range of life-history strategies and movement patterns of fish and decapod crustaceans that use shallow-water inshore areas, for some or all of their life cycle. Our goal here is to focus explicitly on the scales of movement and to show that: (a) different activity during the life cycle can occupy very different domains in time and space and (b) the scales of animal movement differ widely between species and even between individuals of the same species.

Second, we present a critique of the traditional approach to studies of animal-environment relationships by identifying a number of scale-related limitations. We argue that animal movement has crucial implications for the design of sampling strategies. We focus on examples from studies of free-ranging animals and do not include enclosed experimental studies (e.g. mesocosms), although some of the same scale-related limitations apply (see Petersen and Hastings, 2001). Third, we develop a hierarchical conceptual framework that explicitly incorporates animal movement in scale selection. To facilitate this, a shift in perspective is necessary, away from the traditional anthropocentric view of the 'habitat', with its arbitrary and convenient scales of observation, towards an 'organism-based perspective'. To set the context for this approach we examine the development and application of concepts related to animal-environment relationships including the concept of habitat. Fourth, we present and evaluate a variety of existing techniques that can be integrated through Geographical Information Systems to track animal trajectories and map the environment at multiple spatial scales. These 'tracking and mapping' techniques acquire spatially explicit data that are appropriate for the application of the conceptual framework.

Finally, we discuss the importance of understanding movement patterns to the advancement of our ecological knowledge of marine animals and for improving marine conservation and resource management strategies. We argue that by not considering animal movements, basic ecological studies will have no meaningful spatial and temporal context. Furthermore, without information on animal trajectories throughout their life cycle, many marine resource strategies are less likely to achieve their primary objectives.

2. LIFE CYCLE MOVEMENT PATTERNS IN TIME AND SPACE

Marine fish and decapod crustaceans exhibit a wide range of movements, often covering distances and time scales of several orders of magnitude within a single life cycle. The life cycle movements can be categorised into five broad

types: (1) Movement of eggs and larvae; (2) Home range movement (including tidal and diel movements); (3) Ontogenetic shift; (4) Relocation of home range and (5) Migrations: non-spawning and spawning. Generally, routine movements occupy the smallest domains in time and space and rare movements often occur over greater distances (Meentemeyer, 1989). For instance, home range movements such as foraging activity usually occur at finer spatio-temporal scales than do migrations for spawning. Eggs and larvae can be spatially displaced over large distances owing to hydrographic processes, although throughout most of their life cycle marine fish and decapod crustaceans exhibit active movement (such as swimming, buoyancy control or walking). Movements within a life cycle often occur with predictable sequence and duration, for instance, within daily, tidal, lunar or seasonal cycles.

2.1. Life cycles

Many marine species have evolved a multi-phase ontogeny, in which each phase of life is characterised by changes in morphology, physiology and behaviour (Thorson, 1950; Balon, 1984; Hines, 1986; Fuiman, 1997). These life cycle changes are usually associated with temporally and spatially discrete phases of movement and resource use (Harden-Jones, 1968; Roughgarden *et al*., 1988; Wootton, 1990; Eckman, 1996). In the life histories of fish and decapod crustaceans, a wide variety of strategies and tactics has evolved, often exhibiting high phenotypic plasticity in response to complex abiotic and biotic patterns and processes, including human activity (Johannes, 1978; Morgan and Christy, 1994; Rochet, 2000). The strategies determine and constrain the pattern and purpose of movements in both time and space (e.g. offshore spawning migrations and the subsequent use of inshore nursery areas). Such movements and resource use patterns have been observed and documented for many years and have probably always been an important process for human coastal populations. Over 2000 years ago Aristotle (approx. 340–350 BC) documented the seasonal inshore–offshore movements of several fish species, the locations and scheduling of their spawning and use of nursery areas. Furthermore, he detailed a wide range of reproductive strategies for cartilaginous and teleost fishes. He wrote “Fishes deposit their eggs close in to shore…for the water close in to shore is warm and is better supplied with food than the outer sea and serves as a protection to the spawn against the voracity of the larger fish. The chalcis, however, spawns in deep water in dense shoals” and “the mullet goes up from the sea to marshes and rivers; the eels, on the contrary, make their way down from the marshes and rivers to the sea” (*Historia Animalium* VI, translated by D’Arcy Wentworth Thompson). More recently, extensive studies of estuarine fish have resulted in the recognition of a number of life cycle categories (Day *et al*., 1981; Potter *et al.,* 1990). For instance, Whitfield (1999) proposed and described seven life cycle categories

for fish using coastal areas of South Africa and Dall *et al*. (1990) described four strategies for penaeid prawns.

Many individuals of anadromous and catadromous species such as salmon (*Oncorhynchus* spp.) and eel (*Anguilla* spp.) may undertake offshore–inshore migrations over hundreds of kilometres (spanning several years), with each individual releasing several thousand eggs at spawning (Healey and Groot, 1987; McCleave and Kleckner, 1987). Amphidromous species regularly migrate between the sea and fresh water but not directly for breeding, as in anadromous and catadromous species. Other animals appear to have a critical dependence on shallow inshore areas (primarily in the early-life stages) and are thought to benefit in terms of rapid growth and enhanced predator avoidance (Boesch and Turner, 1984; Rozas and Odum, 1988; Sogard, 1992; Gibson, 1994; Perkins-Visser *et al*., 1996; Rooker and Holt, 1997). In contrast, some animals use inshore areas only occasionally, this often occurring when conditions fluctuate in their favour (termed 'stragglers' by Potter *et al*., 1990 and Whitfield, 1999). Potter *et al*. (1990) estimated at least 70 % of species recorded in estuaries of south-western Australia and temperate southern Africa were 'marine stragglers'. Furthermore, some life cycles will directly link terrestrial and aquatic environments, such as through the spawning activities of semi-terrestrial crabs, which have evolved to live on land but spawn in the sea, thus ensuring the broad-scale distribution of their progeny. In the Caribbean, the grapsid crab (*Sesarma angustipes*) can live in coastal marine, terrestrial and freshwater environments but the larval stages all retain a critical dependence on sea water (Anger *et al*., 1990). In contrast to the 'broadcast spawners', some site-attached animals such as the damselfish (*Acanthochromis polyacanthus*) are non-migratory and have a non-dispersive larval stage. They exhibit intensive biparental care of a small clutch of several hundred relatively large eggs (Kavanagh, 2000), which enhances survival and ensures retention of juveniles to areas of high quality resources.

In inshore coastal areas, a tri-phasic life-history strategy seems to be the most widespread for many highly mobile species of fish and decapod crustaceans (Fairweather, 1991; Whitfield, 1999). Deegan (1993) stated "estuarine fish faunas around the world are dominated in numbers and biomass by species which move into the estuary as larvae, accumulate biomass, and then move offshore after attaining a large proportion of their adult size". There are several features common to animals with tri-phasic life cycles (Figure 1). Typically, three key phases of ontogeny, movement and resource use occur: (1) the planktonic movement of eggs and larvae; (2) juvenile use of shallow water areas; and (3) an increase in the home range related to both animal body size and ontogenetic shifts in resource use. Some animals undertake a movement offshore that coincides with the onset of maturity and for some individuals and populations a distinct seasonal migration may also occur. For example, populations of pipefish (*Syngnathus fuscus*) that spawn inshore make extensive offshore seasonal

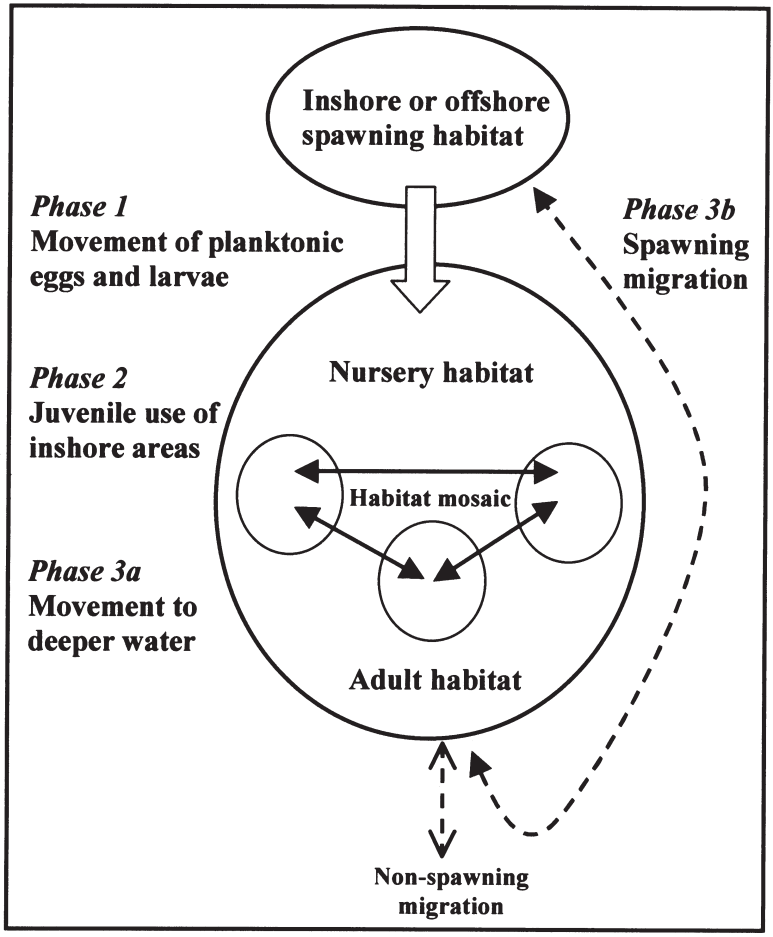

Figure 1 Generalised model of a tri-phasic life cycle showing discrete phases of development and movement. Plasticity in tactics will occur in response to environmental fluctuations and the duration at any developmental phase will vary between species, individuals and geographic location.

migrations to make temporary use of warmer waters (Lazzari and Able, 1990). Life cycle closure may also necessitate a spawning migration to deep offshore waters (Dall *et al*., 1990; Hill, 1994) or to inshore waters where tidal currents will distribute progeny (Campbell, 1990; Campbell and Able, 1998).

Based on the general tri-phasic life cycle model presented in Figure 1, at least two important features relating to scale and resource use are apparent. First, the life cycle can potentially extend over a range of spatial and temporal scales, with the maximum time and movement defined by the life-history characteristics of

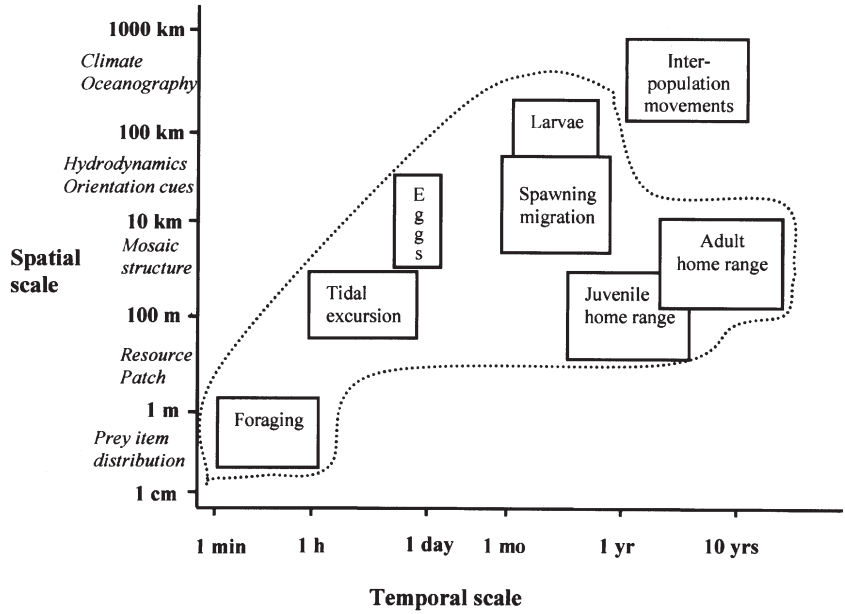

Figure 2 Estimates of space use in time for the life phases of an individual *Acanthopagrus australis* (Sparidae) from Moreton Bay, south-east Queensland, Australia. Scale domains have been estimated using information from tagging studies (Pollock, 1982; Pollock *et al*., 1983). The *x*-axis displays the temporal scope (maximum relative to minimum duration of a life phase and movement pattern). The *y*-axis displays the spatial scope (maximum relative to minimum extent of space use). The environmental patterns and processes that interact to maintain populations in Moreton Bay are aligned on the spatial scale. Scope diagrams such as this can be useful in matching scales between research programs and natural phenomena (Schneider, 1994) and are a useful tool in the scaling procedure undertaken while planning a study. Broken line: scale domain for the whole life cycle.

the species. Second, an animal often requires different resources at different life stages and therefore, the composition and spatial arrangement of those resources will be critical for achieving life cycle closure. For example, yellowfin bream (*Acanthopagrus australis*) is a tri-phasic and estuarine-dependent fish, endemic to eastern Australia (Figure 2). The following is specific to the life cycle of this species in Moreton Bay, southeast Queensland.

Phase 1: Female yellowfin bream produce between 300 000 and 3 million eggs in a single spawning that takes place at entrances to the bay. Several weeks later on a full moon, planktonic larvae move inshore at night to settle in seagrasses.

Phase 2: Post-settlement juveniles use multiple inshore habitat types (e.g. seagrasses and mangroves) through regular tidal excursions from shallow subtidal to upper intertidal areas, which function as ‘nurseries’.

Phase 3: Sub-adults and adults make more use of deeper water than young juveniles through a broader home range. In early spring, some mature adults undertake a spawning migration to specific sites near surf bars at the oceanic entrances to the bay.

2.2. Movements of eggs and larvae

Movement and retention of eggs and larvae of many fish and decapod crustaceans is generally thought to occur through a combination of hydrodynamic processes (e.g. tidal flows, surface and subsurface currents and circulation) and active larval behaviour through horizontal and vertical movements (e.g. swimming, buuyancy control) (for fish see Boehlert and Mundy, 1988; Sponaugle and Cowen, 1997; Leis and Carson-Ewart, 1997; 1998; Forward *et al*., 1999; Epifanio and Garvine, 2001 and for crustaceans see Phillips, 1981; Sulkin, 1990; Young, 1995; Forward *et al*., 1997; Epifanio and Garvine, 2001). Interaction with water motion occurs at a range of scales, from near-substratum flow, which may influence the settlement process (centimetres-metres) (Butman, 1987; Breitburg *et al*., 1995) to Langmuir circulation and Ekman transport, tidal currents, internal waves, fronts, eddies and upwelling (100s metres–100s kilometres) (Phillips, 1981; Kingsford, *et al*., 1991; Shanks, 1995; Werner *et al*., 1997). Even broader-scale (100s kilometres–1000s kilometres) oceanic circulation patterns (e.g. equatorial gyres) are known to influence the distribution of those species with an extensive planktonic duration (Scheltema, 1986) (Figure 3).

Many of these broad-scale physical hydrodynamics are cyclical and animals have evolved behavioural interactions such as the scheduling of spawning to coincide with lunar phases, seasonal winds and tidal currents (Norcross and Shaw, 1984; Morgan and Christy, 1994; Botsford *et al*., 2001), or to place the juvenile ‘growing season’ in the warmer, more productive months of the year (Conover, 1992). For example, in Chesapeake Bay, USA, hatching of blue crab larvae (*Callinectes sapidus*) mainly coincides with night-time ebb tides, which distribute progeny offshore in spring and summer when planktonic food resources for larvae are most abundant (Hines *et al*., 1995). Clearly, this spatio-temporal scheduling of life histories is critical to the maintenance of populations.

For many tri-phasic species, the scales at which eggs and larvae interact with the environment are largely constrained by the distance required for them to reach nursery areas and their duration as a passive, rather than an active component of the plankton. The egg stage is usually just a few days long and has no ability to control its movement, so that individuals can be carried long distances before they begin to influence their movement actively. However, the time spent as eggs and planktonic larvae varies considerably between species. For example, in a variety of fish associated with coral reefs, the planktonic duration can last from a few

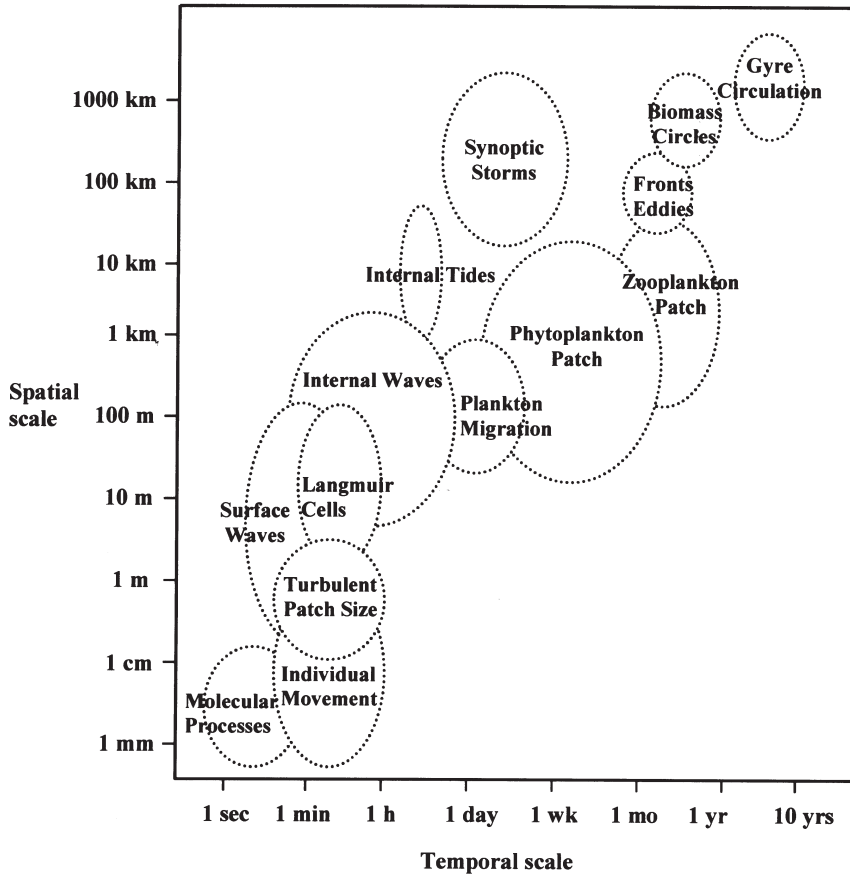

Figure 3 Time-space diagram showing some of the important temporal and spatial scales for physical and biological patterns and processes that are relevant to the movement of planktonic animals in marine ecosystems (adapted from Dickey, 1990).

days to more than three months (Victor, 1991; Lindeman *et al*., 2000). Victor (1986) recorded planktonic larval duration (PLDs) for 100 species of wrasse (Labridae) and found that PLDs varied widely between and within species, from 17 to 103 days. Some species may have an even more extensive planktonic phase, with active behaviour exhibited only late in the larval phase. For example, after hatching on the edge of the continental shelf off Western Australia, phyllosoma larvae of the western rock lobster (*Panulirus cygnus*) spend almost a year offshore and are driven great distances by wind-induced water movements into the southeastern Indian Ocean. Some larvae have been found more than 1000 km offshore although little is known of their subsequent survival. During this time, the larvae undergo significant development and return shoreward using diurnal

vertical migrations to interact with seasonal geostrophic inflows. Metamorphosis to a free-swimming phase occurs at the continental shelf-break and closer to shore, the Leeuwin Current assists in their transport to coastal reefs of Western Australia, were they settle (Phillips, 1981; Phillips and Pearce, 1997). In addition to the western rock lobster, species such as the Atlantic menhaden, *Brevoortia tyrannus* (Quinlan *et al*., 1999) and the blue crab, *Callinectes sapidus* (Olmi and Orth, 1995) offer some fascinatingly complex examples of the multi-scale interaction between physical oceanographic features, animal behaviour and life-history evolution.

Hydrological connectivity is a key determinant of population distributions of herring (*Clupea harengus*) in the North Sea (Figure 4). Herring larvae move to more southerly nursery areas facilitated by oceanic inflow and wind-driven currents, and juveniles and adults use the Norwegian Current to move north to spawning grounds (Harden-Jones, 1968; Steele, 1991). This requires an individual animal to travel at least 3500 km (straight-line distance) in order to close the life cycle. Symonds and Rogers (1995) postulated that the population distributions of adult and juvenile sole (*Solea solea*) in the Irish Sea and Bristol Channel, UK, are determined by the spatial relationship between the spawning and nursery areas and suitable hydrographic conditions, which link the two. Studies on fish associated with coral reefs have suggested that in some regions converging currents and eddies facilitate larval retention to areas beneficial to both larval and post-settlement growth and survival (Jones *et al*., 1999; Swearer *et al*., 1999). However, the importance of water motion in determining distribution varies between species and geographic location (Gaylord and Gaines, 2000).

2.3. Home range movements

Most animals do not roam randomly. Instead, they exhibit site-fidelity and establish areas where they undertake routine activities such as feeding, resting and defending (Elton, 1927; Burt, 1943; Stamps, 1995; Powell, 2000). Much of the understanding of home range use has come from terrestrial studies, which provide great insight into the way animals respond to their environment. Few studies have attempted to study home range movement patterns of marine animals. For instance, Hooge *et al.* (1999) reviewed the scientific literature from the BIOSIS bibliographic database (1994–1999), revealing that of 374 articles investigating movement in fish and crabs, only 48 had examined home range patterns. The majority of these studies have examined the movements of fish in shallow inshore areas that are typically highly structured, such as rocky shores, kelp forests, coral reefs and seagrass beds. The interaction between animals and benthic structure in these heterogeneous environments influences home range size, shape and use patterns. For example, in the southern Caribbean Sea,

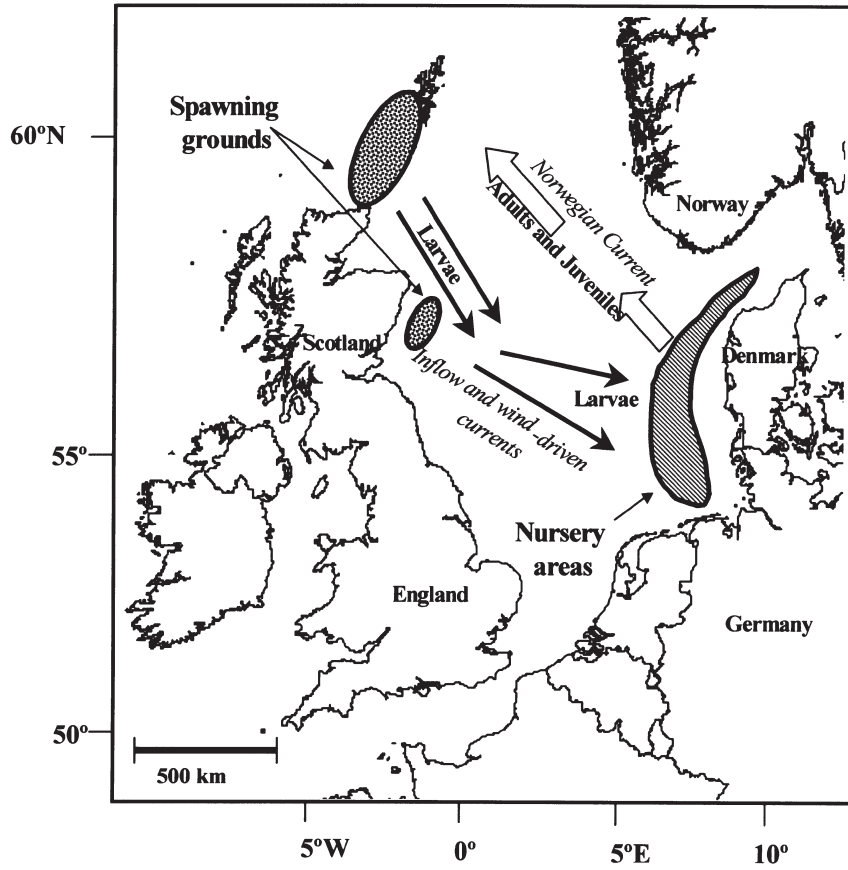

Figure 4 Schematic presentation of the movements within the herring (*Clupea harengus*) life cycle in the North Sea. The larvae move south to nursery areas with wind-driven currents, and juveniles and adults move north to spawning grounds with the Norwegian Current. Movement patterns adapted from Steele (1991). Coastline adapted from a map of the world produced by Environmental Systems Research Institute (ESRI) Inc.

Nemtzov (1997) experimentally manipulated benthic structure by planting artificial seagrasses in close proximity to the territory of green razorfish (*Xyrichtys splendens*). The results showed that individual females increased their home range territory substantially in order to include patches of the artificial seagrasses. Studies by Zeller (1997) on the activity patterns of coral trout (*Plectropomus leopardus*) living in the Great Barrier Reef, Australia, showed that home range contours generally followed the shape of a patch reef. Furthermore, individuals had a preference for a small number of locations within a larger home range area. Similarly, Reese (1989) observed that foraging butterflyfish had highly predictable paths within their home range where they routinely visit,

inspect and feed on certain coral heads. For some animals, a core area within the home range can be identified and within this core area, an individual may move between specific sites for feeding and resting on a daily basis. The home range, therefore, may consist of one or more activity spaces joined by relatively narrow and highly directional movement paths. Covering more than one habitat type with routine, daily movements is thought to be advantageous for many species since this creates an opportunity to use different resources in different patches (Kozakiewicz, 1995).

Some ecological properties of an organism are a function of body size (McNab, 1963; Calder, 1983; Holling, 1992). For land mammals (McNab, 1963; Reiss, 1988; McLoughlin and Ferguson, 2000) and freshwater fish (Minns, 1995) studies have found that home range scaled allometrically with body size. Many authors have found a similar relationship for some marine fish (Sale, 1978; Fitch and Shapiro, 1990; Kramer and Chapman, 1999; Overholtzer and Motta, 1999; Meyer *et al*., 2000; Shepherd and Clarkson, 2001) but not for others (Zeller, 1997). For example, Kramer and Chapman (1999) regressed body size (23–502 cm) and home range length (0.4–4.6 km) for 29 species of fish using coral reefs, to reveal that body size is strongly correlated with home range length ($r^2 = 0.73$). In contrast, Morrissey and Gruber (1993) reviewed 74 published studies that examined the home range sizes of a broader range of fish and did not find any correlation. The likelihood of finding a positive correlation may depend on the selection of species for the analysis. For instance, many of the fish included by Kramer and Chapman (1999) were relatively small species (almost all ≤ 30 cm fork length) and known to be highly territorial, with larger species more able to defend larger home ranges. Further generality requires that analyses include both temperate and tropical species as well as species from a broader range of distinct functional groups. To our knowledge no attempt has been made to examine such scaling relationships for decapod crustaceans, in part due to the dearth of studies that have estimated their home range size.

Some examples of studies that have estimated home range size for marine fish and crabs with various body sizes are provided in Table 1. The minimum home range size was < 1 m^2 for damselfish (body size 2.5–5.5 cm) ranging to a maximum of 93 km^2 for adult lemon sharks (body size 1.5–2.3 m). These data are presented to demonstrate that home range size varies widely between species and between individuals of different sizes and ages. It is important to realise, however, that home range size estimation is also influenced by the methods of data collection and analysis, thereby confounding most comparative analyses.

For marine animals, variability in home range use can be more complex than a simple scaling relationship with body size. For example, ultrasonic telemetry of the cunner (*Tautogolabrus adspersus*) in Newfoundland revealed seasonal differences in home range and even differences between the times of day, with broader space-use patterns in the afternoon than in the morning (Bradbury *et al*.,

Table 1 Home range sizes for marine animals of different species, life stage and body size. The examples are listed in descending order of home range size, which generally increases with body size. However, correlation between body size and home range size is confounded by differences in home range shape, space-time use patterns, sampling strategy and measurement technique.

Species	Home range (km^2)	Life stage/ body length (cm)	Measurement time (frequency and duration)	Technique	Source
Dascyllus aruanus Damselfish (Australia)	< 0.001	Juvenile/ Adult 2.5–5.5	Daily for 12 weeks	Mark and resight	Sale (1971)
Scarus spp. Parrotfish (Florida)	0.018–0.036	Juvenile 4–10	1 hour per fish	Visual sighting using SCUBA	Overholtzer and Motta (1999)
Tautogolabrus adspersus Wrasse (Canada)	0.3–2.3	Adult 19.4–25	2–32 days per fish	External ultrasonic	Bradbury *et al*. (1995)
Maia squinado Spider crab (NW Spain)	0.5–3.7 horizontal distance	Juvenile/ Adult 9–17.1	19.8–141.8 days 0.4–11 d intervals	External ultrasonic	González-Gurriarán and Freire (1994)
Negaprion brevirostris Lemon shark (Caribbean)	Juvenile 0.23–1.26 Adult 9–93	Juvenile 46.8–100.6 Adult 150–230	<10 h continuous day/night	External and internal ultrasonic	Morrissey and Gruber (1993); Gruber *et al*. (1988)
Mulloides flavolineatus Goatfish (Hawaii)	Day 1.2–3.2 Night 5.2–11.6	Adult 28.4–31.8	24–48 h continuous 2–16 days	Internal ultrasonic	Holland *et al*. (1993)
Plectropomus leopardus Grouper (Australia)	Fringing reef 10.4 Patch reef 18.7	Adult 37.6–67.5	3–4 records per day	Internal ultrasonic	Zeller (1997)
Parupeneus porphyreus Goatfish (Hawaii)	14.97–35.16	Juvenile/ Adult 20.5–25.7	42–92 h continuous 3–14 days	Internal and external ultrasonic	Meyer *et al*. (2000)
Kyphosus sectatrix Chub (Caribbean)	14.97–52.54	Adult 26–45	5–51 days	Internal ultrasonic	Eristhee and Oxenford (2001)

1995). In the same region, Clark and Green (1990) tracked Atlantic cod (*Gadus morhua*), revealing broader home ranges during summer. These summer home ranges had distinct diel movements from deep to shallow water and nocturnal feeding activity. In contrast, autumn home ranges were smaller and confined to shallow waters (< 20 m), with daytime feeding and resting at night. Differences in home range use between males and females have also been found in some species (Bradbury *et al*., 1995). For several shark species, males and females have been found to segregate into single sex aggregations and this behaviour is an important factor in the structuring of populations in time and space (Klimley, 1987; Sims *et al*., 2001).

For terrestrial animals, McLoughlin and Ferguson (2000) suggested that a hierarchical pattern of ecological and physiological factors including body size, seasonal food availability, predation and even climate change might determine home range size. It is not clear exactly which factors control home range use for marine animals, but it is likely to be a result of a combination of life-history characteristics, body size, resource requirements, composition and spatial arrangement of resources, as well as inter- and intra specific-interactions. Consequently, home range size, shape and temporal-use patterns vary widely among animals. This variation makes attempts at boundary delineation difficult (Powell, 2000). For marine fish, Kramer and Chapman (1999) hypothesised that a more 'generalist' species (i.e. able to use multiple patches or habitat types) will have a larger home range than a more 'specialist' species. They also proposed the development of an index, based on easily measured morphological, physiological and behavioural traits. The index would provide estimates of mobility and therefore scale, without the direct measurement of movement patterns. For instance, traits associated with low mobility would include relatively small body size, non-schooling behaviour, critical dependence on a particular resource and morphological features associated with a more site-attached mode of locomotion (i.e. non-continuous swimming) (Kramer and Chapman, 1999). However, the calculation and verification of such an index would require extensive data collection on movement patterns using techniques such as those listed in Table 1.

Daily tidal fluctuations in water level and changes in light intensity also significantly influence home range movements. These movement patterns are particularly important considerations in the selection of spatial and temporal scales for studies of animals using inshore areas and therefore warrant further study.

2.3.1. *Tidal excursions*

In tidally dominated waters many fish and crustaceans move with the ebb and flow of the tide on routine excursions between intertidal and subtidal areas. For these animals, the neighbourhood or home range extent will be determined by

interacting factors related to the cost-benefit of an excursion, including life-cycle strategy, body size, shore profile, tidal range and amplitude (water depth change), predation pressure, food availability and the composition and spatial arrangement of resources (e.g. patchy and continuous vegetated areas). In most areas, the overall patterns of distribution are continually changing as individual species move into and out of shallow water at a variety of time scales. For temperate fish, Kuipers (1973), van der Veer and Bergman (1986), Kneib (1987), and Rangeley and Kramer (1995) have recorded higher densities in shallow subtidal waters at low tide than at high tide in both the subtidal and intertidal. This suggests a large influx of fish moving inshore and dispersing over intertidal areas with the flooding tide. Wirjoatmodjo and Pitcher (1984) in Northern Ireland and Szedlmayer and Able (1993) in New Jersey, USA, tracked flounder using ultrasonic telemetry. The authors demonstrated that these fish follow the tide and that frequency, direction, distance, speed and duration of movement were all significantly linked to tidal dynamics.

Many penaeid prawns also have strong tidally-based patterns of behaviour and can be sensitive to small changes in pressure owing to changes in water level (Dall *et al*., 1990; Kneib and Wagner, 1994; Kneib, 2000). For instance, in Kuwait, Bishop and Khan (1991) observed that in the absence of aquatic vegetation, juvenile penaeid prawns (*Metapenaeus affinis*) moved with the edge of the advancing and receding tide. In Moreton Bay, Queensland, some species of toadfish (Tetraodontidae) will use the very edge of the advancing water, moving in and out of the intertidal in only a few centimetres of water (pers. obs). This movement pattern would maintain an animal's position in the shallowest water, thereby gaining refuge from aquatic predators and limiting energy expenditure. Regular tidal excursions may benefit growth in some species (Weisberg and Lotrich, 1982; Peterson and Turner, 1994; Irlandi and Crawford, 1997). Studies have shown a tidal periodicity in feeding, as evidenced by fuller guts on ebbing tides than on flooding tides (for fish see Kuipers, 1973; Rountree and Able, 1992; and for crustaceans see Ryer, 1987).

Another example of tidally synchronous movements was observed for fish assemblages using an inner reef flat in Madagascar (Vivien, 1973). Two distinct species assemblages were recognised, a numerically dominant "permanent stock" composed mainly of smaller omnivorous fish, whose feeding behaviour appeared unaltered by the tides and a "temporary stock", composed mainly of larger carnivores and herbivores that moved with the flooding tide to feed in shallower water. This study showed that fish response to fluctuating water levels was highly variable, even within a relatively small area (Figure 5). On a flooding tide, some fish moved more than a kilometre from open water to the inner reef flat to feed, whilst others moved a few hundred metres from reef to seagrasses or remained within a particular zone and instead moved vertically into the water column. Although home ranges were not estimated, of importance here is that Vivien (1973) recognised the significance of tidal excursions to the

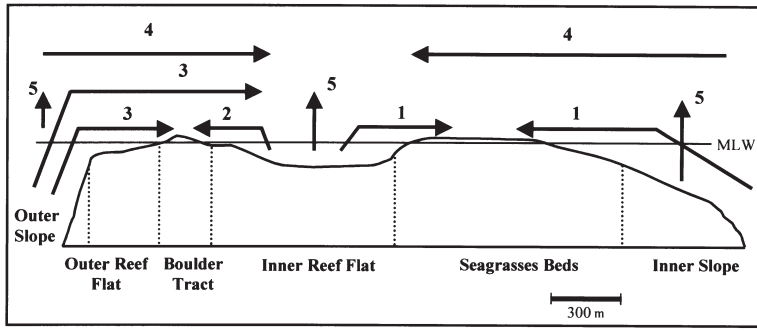

Figure 5 Tidal movements for assemblages of fish on the fringing reef of Tulear, Madagascar. Fish are grouped according to the type of movement between distinct reef zones that were observed during a rising tide. **1** and **2**: movement from the inner reef flat to feed in seagrasses and on the rubble bank; **3**: movement from the outer slopes to feed in shallower water in the inner reef; **4**: movement of pelagic fish from deeper waters to feed on the inner reef; **5**: movement up into water column. Modified from Williams (1991). Originally from Vivien (1973) and redrawn and translated from the French by Williams (1991).

dynamics of assemblage structure. This type of basic movement data is rare, with few studies explicitly stating the scales of movement and even fewer estimating species-specific scales of movement for multi-species assemblages.

From studies in Georgia, USA, Kneib and Wagner (1994) demonstrated that for fish and decapod crustaceans using saltmarshes, a life-history specific relationship with tidal marsh utilisation existed, where distance travelled by resident species was less than that travelled by transient species. Kneib (1997b) proposed that resident species moved in with the tidal front earlier in the tidal cycle than transient species and were the last to leave with the receding tide. However, it is likely that the details of this pattern vary between species and functional groups and from region to region. In some inshore areas of Moreton Bay, Queensland, large-bodied transient species such as mullet (*Mugil cephalus*) are capable of early entry with the flooding tide and of leaving surprisingly late on the ebb. The timing of 'turn–around' of an animal and movement back to subtidal waters will vary and for some, will be related to the need to avoid stranding. Cues for scheduling may include pressure, temperature, direction of water flow and oxygen concentration, as well as biological features such as body size, morphology and physiology. For instance, some crabs and fish have evolved pressure sensors such as specialised hair cells and swim bladders that respond to slight changes (nanometre scale) in hydrostatic pressure enabling them to synchronise their behaviour to tidal cycles (Fraser and Macdonald, 1994; Fraser and Shelmerdine, 2002). Enright (1970) argued that environmental cues alone would not be reliable enough to facilitate a timely turn–around, and in his 'ebbtide theory' proposed that an internal rhythm was necessary to ensure survival.

Not all animals move inshore with a rising tide (Gibson *et al*., 1996) and an inshore assemblage may be composed of animals with varying dependencies on periodically available intertidal resources. Janssen and Kuipers (1980) sampled common shrimp (*Crangon crangon*) in the Wadden Sea, Netherlands, at a range of water depths and found that only 5% of the population made extensive tidal excursions. Although almost all animals found in the intertidal are there as a result of tidal excursions at some stage, some species (and life stages) may be adapted to remain in intertidal areas whether inundated or not, through burial or an ability to survive in residual bodies of water (Gibson, 1982). Many small-bodied animals use residual water trapped in topographically complex areas such as rock pools, pits excavated by feeding stingrays, ponds, creeks, waterlogged areas or human induced modifications to substratum such as baitdug pits, drainage channels and even trampled mud (Gibson, 1982; Kneib, 1997a,b; pers. obs.). It is not clear whether these animals actively select pools or are stranded, or indeed whether they experience enhanced growth and survival. Shallow pools appear to be poor quality since they are exposed to predation from shore birds and some fish and crustaceans and have higher abiotic variability than water in the moving tidal front. For example, on sandflats, mangroves and seagrasses in Moreton Bay, Queensland, high densities of early juveniles (<20 mm TL) of transient schooling species including whiting (*Sillago* spp.), crescent perch (*Terapon jarbua*), mullet (*Mugil cephalus*) and small decapod crustaceans were often observed in stingray pits. In the summer months, these pits frequently experienced low salinity (after heavy rainfall) and attained relatively high temperatures (37°C) (unpub. data). However, early life stages of some species are known to have broad tolerance ranges and the animals in most pits appeared to survive at least until the next flood tide. Experiments by Kneib (1987) suggest that juvenile killifish (*Fundulus heteroclitus*) are adapted to remain in residual water to avoid predation by adults in subtidal waters.

2.3.2. *Diel movements*

In numerous extractive sampling studies and visual censuses, differences in space-use patterns between day and night have been reported as evidence of diel movements (extractive sampling, e.g. Robblee and Zieman, 1984; Sogard *et al*., 1989; Vance and Staples, 1992; Rountree and Able, 1993, 1997; and visual census, e.g. Rooker and Dennis, 1991; Nagelkerken *et al*., 2000a). Evidence of diel movements has also been found for some species through observations of a behavioural response to light in laboratory conditions (e.g. Vance, 1992; Borg *et al*., 1997). Telemetric studies have also shown that many fish move cyclically between the day and night sections of a home range. For instance, using ultrasonic telemetry Holland *et al*. (1996) revealed that blue trevally (*Caranx melampygus*) in Hawaii exhibited predictable movements between spatially

distinct daytime and night-time areas. For some species, the daily 'migrations' are movements from daytime refuges to nocturnal foraging grounds, although for other species the schedule is the opposite. Meyer *et al*. (2000) tracked five goatfish (*Parupeneus porphyreus*) using acoustic transmitters and revealed a distinct diel pattern of movement. The largest individual (257 mm) was tracked continuously for 48 hours travelling distances of up to 500 m from daytime resting areas to night-time foraging areas, where it ranged over as much as 10 000 m^2 for up to nine hours. Klimley (1993) tracked individual scalloped hammerhead sharks (*Sphyrna lewini*) in the Gulf of California to reveal that individuals undertook highly directional movements (along the same paths) between nocturnal feeding areas and daytime schooling areas.

Using simultaneous ultrasonic telemetry of 28 juvenile cod (*Gadus morhua*) off Newfoundland, Cote *et al*. (1998) observed that some individuals travelled several hundred metres to shallow inshore areas at night and spent daylight hours in deeper water (Figure 6). The nocturnal feeding regime is exemplified by juvenile grunts (*Haemulon flavolineatum*) in the Caribbean Sea, which move along highly predictable pathways from daytime refuge in aggregations over coral reefs to individual foraging behaviour in adjacent patches of sand, seagrasses and macroalgae at night (Helfman *et al*., 1982; Nagelkerken *et al*., 2000a). In Hawaii, Holland *et al*. (1993) tracked goatfish (*Mulloides flavolineatus*) and found that they used a consistent route between fixed schooling locations during the day and individual feeding grounds during the night. Brown surgeonfish (*Acanthurus nigrofuscus*) in the northern Red Sea also follow distinct pathways inshore every morning, from nocturnal shelter to daytime feeding sites, with distances ranging from 10 m to over 1 km (Mazeroll and Montgomery, 1998). These authors observed an emergence of *A. nigrofuscus* just before sunrise, with aggregations forming before departure, which they suggest is the use of an internal clock rather than a response to light. In contrast, Zeller (1997) reported high site fidelity throughout day and night for rockcod (*Plectropomus leopardus*) in the Great Barrier Reef, Australia. A diel cycle of emergence and movement is also common in burrowing decapod crustaceans (Vance and Staples, 1992), with most species burrowing during the day and emerging at night (Vance, 1992). Some species of penaeid prawns show peaks in activity following a 'bimodal crepuscular pattern', with a peak after dusk and before dawn (Dall *et al*. 1990).

2.4. Ontogenetic shifts

Ontogenetic changes in morphology and physiology allow life stages to respond individually to the different selection pressures they experience in their environment (Ebenman, 1992). Effective exploitation of widely differing resources often requires different movement patterns within the life of an individual. The most commonly reported ontogenetic changes in movement patterns are

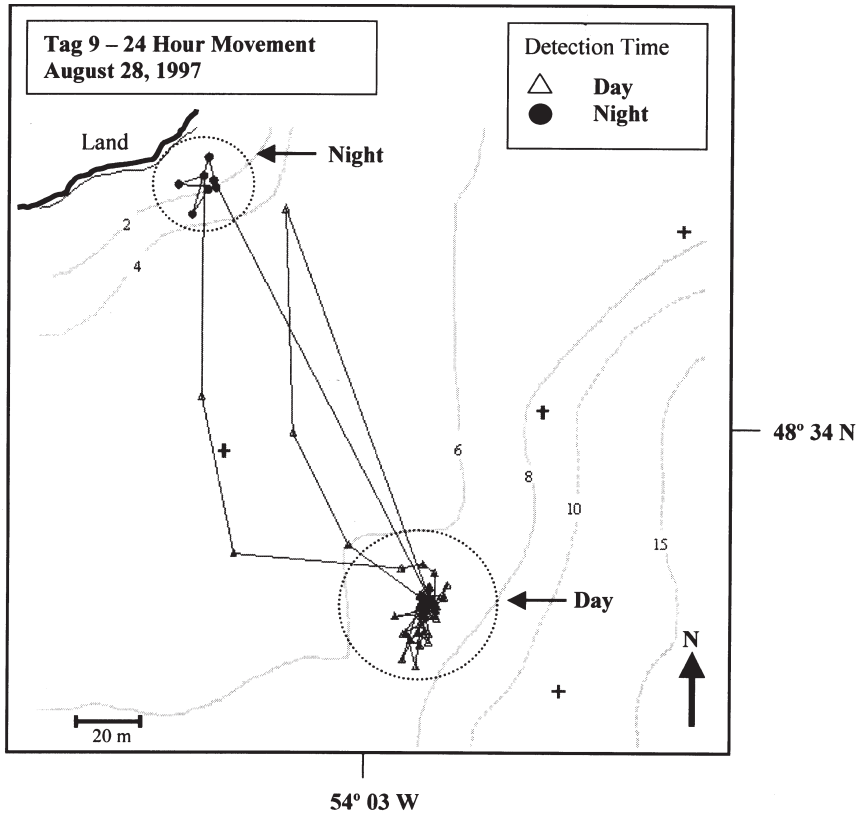

Figure 6 Temporal trace of an individual Atlantic cod (*Gadus morhua*) for a 24-hour period in the summer (Aug. 28th, 1997) off Newfoundland (Cote *et al*., 1998). The data indicate a pattern of relatively limited movements in deeper water during the day followed by distinct linear movements to shallower inshore water at dusk. Numbers along contours indicate depth in metres. Reproduced with permission of David Cote, Parks Canada, Newfoundland, Canada.

associated with refuge function, predation pressure, physiological requirements and diet, all of which are usually associated with increasing body size (Werner and Gilliam, 1984; Dahlgren and Eggleston, 2000). For many species, significant shifts in space-use patterns are reported to occur within the first few weeks and months after settlement, when movement patterns are often represented by a strong size-depth relationship (Ruiz *et al*., 1993; Gibson *et al*., 1996, 2002). For example, after settlement, plaice (*Pleuronecles platessa*) in the North Sea concentrate in shallow waters (< 1 m deep) and show a positive relationship between body length and water depth (Gibson *et al*., 2002). Macpherson and Duarte (1991) observed a significant positive size-depth relationship for most of 75 coastal demersal fish from the Mediterranean and southeast Atlantic. In the same region, Macpherson (1998) observed that juveniles of three species of sparid fish exhibited initial high site

fidelity to shallow water areas and, after several months, a subsequent size-dependent movement to deeper water. Harmelin-Vivien (1989) and Chabanet and Letourneur (1995) observed a differential distribution of size-class cohorts for many fish species around coral reefs. In North Carolina, USA, size-selective offshore movement of brown shrimp (*Penaeus aztecus*) from inshore nurseries has been surmised from catch data showing changes in the length frequency distributions (Wicker *et al*., 1988). Furthermore, extensive studies of nekton using saltmarshes in Georgia, USA, by Kneib (1997b, 2000) resulted in the development of a conceptual model that represented size depth patterns of utilisation for a range of life-cycle strategies (e.g. resident and transient species) (Figure 7).

Few studies have actually tracked animals for long enough periods to capture directly ontogenetic shifts in space-use and almost all evidence that supports movement is largely indirect, based on spatio-temporal changes in the distribution and abundance of animals (Beck *et al*., 2001). However, some direct evidence has been provided through telemetric and tagging studies. For example, using ultrasonic telemetry, Hines *et al*. (1995) showed an ontogenetic change in movement pattern of juvenile blue crabs (*Callinectes sapidus*) in Chesapeake Bay. After settlement to seagrasses, the crabs moved between 50–250 km into shallower, brackish water sub-estuaries in order to evade predators, feed and grow. After one

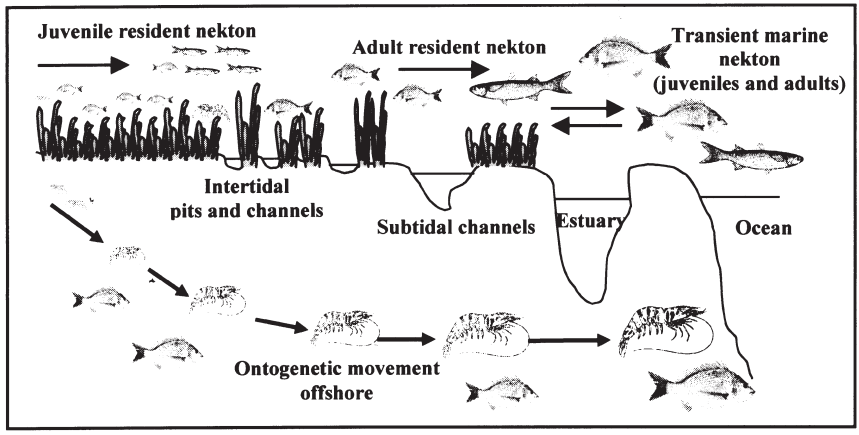

Figure 7 A model of spatial patterns in nekton use of intertidal saltmarsh and adjacent estuarine waters by different life stages of resident and transient species. This is redrawn from Kneib's conceptual model of a trophic relay concept (Kneib, 2000) that represents the inshore-offshore transport of production. The youngest individuals of both resident and transient species use the vegetated intertidal for food and refuge, with some species even remaining on the marsh surface at low tide. As they outgrow refugia, the home range broadens to include deeper water. In subtidal areas at low tide adult resident species become prey for larger juveniles of transient species. This trophic interaction forms another link in the 'trophic relay' (*sensu* Kneib, 2000) that transports intertidal productivity offshore. Animals depicted are intended to be schematic.

year, the crabs moved further into deeper water. In the Tamar Estuary in England, extensive mark–recapture studies for newly-arrived juvenile Dover sole (*Solea solea*) suggest an initial up-estuary movement as far as 22.7 km from the estuary mouth, followed by a later down-estuary movement forced by a seasonal decrease in salinity (Coggan and Dando, 1988).

Some ontogenetic shifts are related to size-specific changes in food types. The most typical changes are from planktonic to benthic feeding, which may also be accompanied by a change in movement patterns. McCormick and Makey (1997) observed a shift in diet and home range size in the goatfish (*Parupeneus multifasciatus*) at Lizard Island, Australia. These animals exhibited a shift from plankton feeding in the water column to the broader roaming movements that are associated with benthic foraging. Furthermore, after settlement McCormick and Makey (1997) observed a rapid increase in home range size from a strongly site-attached home range of 3 m^2 at four days post-settlement to a mean home range of 60 m^2 at seven days and 245 m^2 at two months. In some cases, dietary shifts are attributed to the morphological changes in feeding apparatus. Stoner and Livingston (1984) detailed how the estuarine pinfish (*Lagodon rhomboides*) shifted from zooplanktivore to epibenthic invertivore to omnivore, finally becoming herbivorous. Although, no concomitant change to movement patterns was reported.

The functional attributes of the environment of an animal can either change or diminish with a progressively larger body size. Eggleston (1995) found Nassau grouper (*Epinephelus striatus*) in the Bahamas settle and remain in and around macroalgal clumps for 3–5 months before outgrowing their shelter and moving out to patch reefs. Lipcius *et al*. (1998) found similar shifts in Caribbean spiny lobster (*Panulirus argus*), describing a movement away from areas with ample food but limited shelter, to a high quality refuge in coral reefs. Acosta (1999) also examined the distribution of spiny lobster in the Caribbean Sea and concluded that a range of interlinked habitat types was necessary to meet the changing resource requirements that occurred throughout the complex life cycle. In fact, many fish and decapod crustaceans, shift through a 'critical chain' of habitat types whilst using heterogeneous inshore areas (Acosta and Butler, 1997; Nagelkerken *et al*., 2000b; Nagelkerken and van der Velde, 2002).

Clearly, the composition and spatial arrangement of component habitat types (including their proximities to one another) across a range of scales, is important in meeting the requirements of ontogenetic change. However, it is important to note that some animals show no evidence of ontogenetic shift and juveniles are found in the same areas and using the same resources as adults (Harmelin-Vivien, 1989; Green, 1996).

2.5. Relocations of home range

Relocation of a home range is a change in the location of the home range that is not recognised as an ontogenetic shift or a migration. The factors that initiate

relocation are unlike those that initiate an ontogenetic shift, as they are not necessarily related to life-cycle changes during the morphological and physiological development of an animal. Furthermore, the relocation movement process is unlike a migratory trajectory since it relies largely on routine sensory responses during searching behaviour and will likely be multi-directional. Kramer and Chapman (1999) described relocating behaviour as a highly adaptive response to the changing environment when the net benefits of moving are greater than the net benefits of not moving. Most fish and decapod crustaceans have a highly-tuned sensory ability and great mobility throughout most of the life cycle, which provide an enhanced ability to relocate in response to unfavourable conditions (Sogard, 1994). Several processes can create situations where animals may seek an alternative home range location. For instance, planktonic stages arriving in areas with sub-optimal conditions for growth and survival may settle and redistribute or on not receiving the necessary cues, will delay transition to the benthos and keep moving. However, it is debatable whether a home range would have been established at this early stage. Nevertheless, this type of movement is an important consideration and rarely reported.

Bell and Westoby (1986a, b, c) proposed a "settle-and-stay" hypothesis to explain distribution patterns of animals in seagrasses in New South Wales, Australia. Their model proposed that competent larvae settle into the first seagrass bed they encounter (regardless of quality), then redistribute to suitable microsites within that bed. This model implies site-attachment and largely underestimates the mobility of many marine animals. Several studies suggest that a settle-and-move behaviour is more common for fish. For example, large numbers of fish (of a variety of age classes) moved even over broad expanses of sand to utilize small patches of artificial seagrass (Sogard, 1989) and concrete patch reefs (Walsh, 1985). In addition, Frederick (1997) observed fish that had recently settled on coral reefs move as far as 100 m over open sand. Robertson (1988) has argued that relocation between patches by highly mobile animals is a common phenomena and a major source of the variability reported in studies of fish associated with coral reefs. Furthermore, tagging studies of adults of exploited species have revealed that some animals will move several hundred kilometres, for example, from one bay or estuary to another (Pollock, 1982). The reasons for these types of relocation are usually not known and little information is available on the frequency of such broad-scale inter-population movements.

More well known are examples of relocations resulting from deleterious change to the environment. For instance, a severe storm may increase or decrease availability of shelter and food resources or a pollution event may change water and substratum quality, which may initiate a movement to seek a more suitable location. After severe storms, Stouder (1987) found changes in the distribution of temperate reef fish off Santa Barbara, California, USA. The study area was composed of a complex mosaic of substratum types, which exhibited spatially variable susceptibilities to the storms, thus resulting in patchiness.

In response, some resident fish shifted their home range to include less disturbed patches and some non-resident fish abandoned the reef entirely. Direct human activity such as physical manipulations to the benthos from dredging can also result in some resident animals abandoning or temporarily avoiding an area and opportunistic species moving in to use the disturbed area (Jennings and Kaiser, 1998). Lenihan *et al*. (2001) found that eutrophication, density stratification and oyster dredging combined to deplete dissolved oxygen in bottom waters in the Neuse River estuary, North Carolina, USA. In response, some fishes (termed 'refugees' by Lenihan *et al*., 2001) abandoned the area and moved to nearby oyster reefs in well-oxygenated waters, where they accumulated in high densities, which resulted in a rapid depletion of prey populations. Changes in animal density and assemblage composition, therefore, can also result in changes to the availability of resources and the dynamics of competition, which may evoke a relocation response. Density-dependent relocations in response to localised increases in fish numbers and biomass have been observed as net movements away from some marine reserves and are thought to result in a phenomenon known as the 'spillover' effect (Russ and Alcala, 1996).

It is not always clear when movement of an animal is a response to suboptimal environmental conditions or to an ontogenetic shift. For example, Lirman (1994) found that juvenile damselfish (*Stegastes planifrons*) living around coral reefs in Honduras avoided the dominant adults of the same species by moving to less favourable areas of the reef to hold territories, before moving back to the main reef as sub-adults to increase their chances of finding a mate. Lirman (1994) described these movements and resource use patterns as ontogenetic shifts. However, if the juveniles are displaced by conspecifics or other species (as observed here) it may be appropriate to consider these movements as home range relocations, rather than ontogenetic shifts. Alternatively, changing body size and the onset of sexual maturity may drive some of the space-use patterns observed for damselfish and warrant the description of an ontogenetic shift. The changes that result in a relocation of a home range are numerous and diverse and cannot be adequately covered here. Further examples can be found in Sogard (1994) and Kramer and Chapman (1999).

2.6. Migrations: non-spawning and spawning

Many marine animals exhibit highly directed and often broad-scale migrations, which are usually quite different from those movements within a home range. Migratory movements can be associated with both changing external environmental conditions (e.g. associated with seasonal variations in temperature, rainfall, productivity and hydrodynamic features) and internal conditions, such as reproductive maturity. Migrations are characterised by the temporary suppression of responses to normal environmental stimuli (e.g. food resources)

and high directionality, with animals often following well-defined routes that usually extend beyond the home range (Dingle, 1995). For example, Herrnkind and McLean (1971) investigated movement patterns of the spiny lobster (*Panulirus argus*) in the Caribbean Sea. In an extraordinary synchronised mass migration, the lobsters were observed walking in single file over 10 km, with deviations generally less than 10°. In the scientific literature, migration is often used to describe diel movements and tidal excursions, however, we consider these to be routine movements within the home range. The definition of migratory behaviour as a highly directional movement may also be applied to the movement of some planktonic larvae and post-larvae. However, for present purposes we confine the term to describe animal movements to spawning areas outside their home range and for seasonal movements to alternative home ranges that cannot be defined as relocations. Furthermore, migrations are usually return journeys, although this depends on the life-history characteristics of the animal.

2.6.1. *Non-spawning migration*

A non-spawning migration is a highly directional movement to a temporary alternative home range, typically associated with seasonal changes in abiotic environmental factors, such as temperature or salinity changes. For example, by examining the spatial and temporal distribution of the northern pipefish (*Syngnathus fuscus*) in the North-Western Atlantic Ocean, Lazzari and Able (1990) found that the pipefish undertook an extensive seasonal inshore–offshore migration. During winter, the fish moved to warmer continental shelf waters, an estimated 20 km offshore and from spring through to late autumn returned to estuaries. The authors reported that winter inshore temperatures were as much as 10°C colder than offshore waters. This seasonal use of warmer waters is exhibited by many other fish and decapod crustaceans in temperate latitudes. Another example of this type of migration is shown by the Atlantic silverside (*Menidia menidia*). Conover and Murawski (1982) reported a mass offshore winter migration to warmer inner continental shelf waters. At other times of the year they are found in salt marshes, estuaries and embayments in the western Atlantic Ocean and are known to spawn on daytime high tides in saltmarshes (Middaugh and Takita, 1983). Blue crabs (*Callinectes sapidus*) in Chesapeake Bay, USA, and spider crabs (*Maia squinado*) in northwest Spain have also been observed to move in response to seasonal cycles in temperature and food availability (Hines *et al*., 1995).

Some species, however, undertake seasonal migrations that are strategically placed en route to spawning areas (for fish see, Pihl and Ulmestrand, 1993; Koutsikopoulos *et al*., 1995; and for crustaceans, Hines *et al*., 1995). For instance, multiple recapture data from tagged ovigerous lobsters (*Homarus americanus*), off eastern Canada showed a range of movements, from a few kilometres to 322 km (although most were less than 30 km). Many lobsters moved to deeper

water during winter, returning inshore in summer for egg hatching (Campbell, 1986, 1990). This seasonal shallow to deep migration takes place to meet the physiological requirements (i.e. higher temperature) of molting, mating and egg extrusion (Campbell, 1986). Blue crabs are also known to exhibit an over-wintering or hibernation phase in deeper water, which is thought to be associated with an ontogenetic transition from juvenile to sexually mature adults (Hines *et al*., 1995). Although they may have other functions, these seasonal movements may be better categorised as pre-spawning migrations, rather than seasonal migrations.

2.6.2. *Spawning migration*

Some individuals may remain within a well-defined area for most of their routine activities and may even mate and spawn within the home range (Robertson, 1983; Fitch and Shapiro, 1990; Shpigel and Fishelson, 1991). Others may move to discrete spawning areas (Shapiro, 1987; Aguilar-Perera and Aguilar-Dávila, 1996), which are usually at specific locations and in specific seasons or phases within lunar and tidal oscillations. The distance of a spawning migration is largely constrained by the frequency of spawning and the size and locomotory ability of the animal (Roff, 1988). In Chesapeake Bay, USA, inseminated female blue crabs migrated 150–200 kilometres down-estuary to deep water in the mouth of the bay to over-winter and to brood their eggs during the following spring and summer. Males, on the other hand, over-winter in the main estuary and do not migrate (Schaffner and Diaz, 1988). In Queensland, Australia, mud crabs (*Scylla serrata*) spend most of their lives in mangrove-lined inshore areas, although ovigerous females have been caught as far as 95 km offshore (mean 30 km), before the onset of the monsoon wet season (October–November) (Hill, 1994). The intolerance of larvae to low salinity (*S. serrata* zoea cannot tolerate salinities below 20), combined with a strategy for broader scale distribution of progeny, necessitates this extensive offshore spawning and is common to most species of portunid crab (Norse, 1977; Hill, 1994).

From observations of fish assemblages using mosaics of habitat types in Palau, Micronesia, Johannes (1978) reported that individual fish move a range of distances from their normal home range to their spawning site (Figure 8). The majority of species in the Palau study moved seaward of their home range and spawned on the outer reef slope. However, high within-species and between-species variation is evident. In the Caribbean Sea, for instance, some bluehead wrasse (*Thalassoma bifasciatum*) will travel more than 1.5 km along specific pathways to join large (>10 000 fish) mating aggregations (Warner, 1995), whilst others spawn within the home range (Fitch and Shapiro, 1990). At specific times of the year, some groupers will migrate large distances to form aggregations that can last from days to weeks. For example, Bolden (2000) tagged 11 adult Nassau grouper (*Epinephelus striatus*) with visual markers and

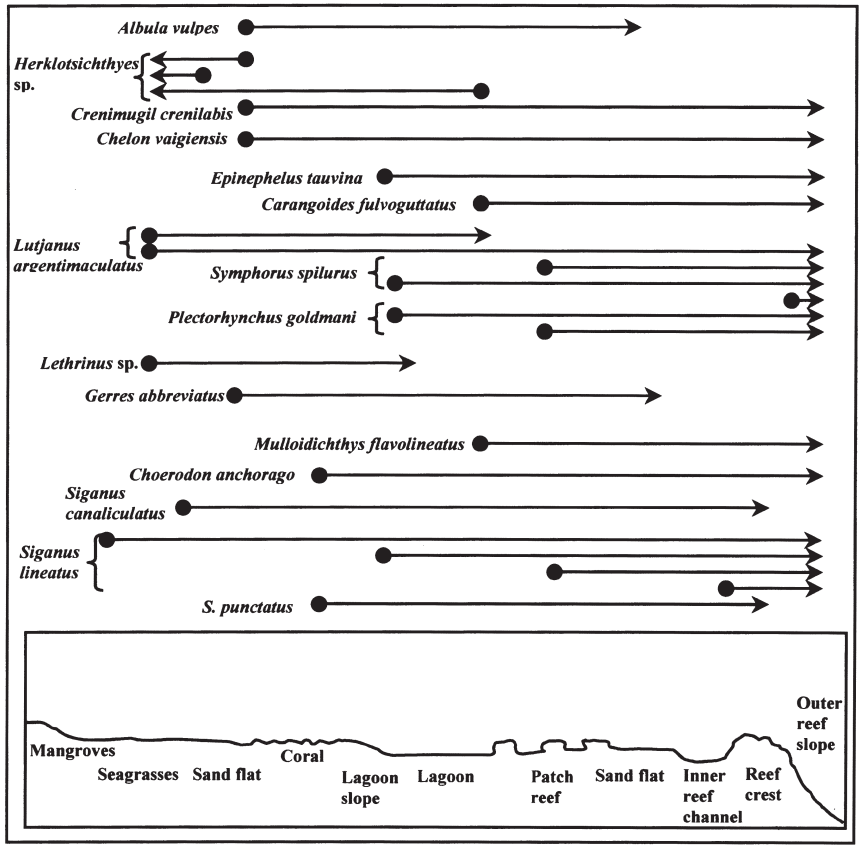

Figure 8 Spawning migrations of fish in Palau, Micronesia, from data collected through underwater observations by Johannes (1978). Arrows show the movement from usual habitat (•) to spawning sites (→). Actual distances travelled were not provided by Johannes (1978). Almost all species undertake a seaward spawning migration, with more than half of all species moving to the outer reef to spawn.

ultrasonic transmitters and tracked them for three weeks, reporting one grouper travelling 220 km to a spawning aggregation. In the Red Sea, Mazeroll and Montgomery (1998) tagged and observed brown surgeonfish (*Acanthurus nigrofuscus*) and found that they exhibited simultaneous evening spawning migrations to either one of two mass spawning sites up to 1 km away. Individuals were then observed returning in long lines along specific pathways to nocturnal shelter. Mazeroll and Montgomery (1998) suggested that fish used landmarks on the reef for navigation and proposed that individuals learn routes to spawning sites before active reproduction begins. Socially transmitted learning of routes has also been found in other marine fish (Helfman and Schultz, 1984).

The factors determining the scheduling of spawning can be complex and usually relate to one or more cues over a range of temporal scales. These can include the stage of the tide, time of day, lunar period and season. In Japan, Yabuta (1997) observed the Indo-Pacific butterflyfish (*Chaetodon trifasciatus*) spawning in the vicinity of offshore tidal currents at dusk at either a full or new moon. Monogamous pairs travelled to specific spawning sites, established a small temporary territory in which to spawn and rest for the night, and then returned to their normal home range the next day.

3. CRITIQUE OF TRADITIONAL APPROACHES IN MARINE ANIMAL ECOLOGY

The above sections provide a wide range of specific examples of animal movements, some of which demonstrate that individuals and species operate over a range of scales in time and space. It is clear, however, that although movement patterns are diverse, they can be usefully categorised according to life cycle strategies and the type of activity or behaviour associated with a particular movement. We now discuss both the theoretical and applied aspects of incorporating animal movements in ecological studies, which have crucial implications for scale selection and the design of sampling strategies. This section reviews and critically examines some of the traditional approaches to field studies of marine animal–environment relationships in relation to scale selection. The examples used here reflect the primary focal area of one of the authors (SJP), which is the utilisation of shallow water inshore areas by marine nekton.

The fundamental questions in any study of animal–environment relationships are: At what scale(s) to measure? How to measure? What to measure? Conventionally, nekton in shallow inshore areas have been sampled using a range of techniques, including both active and passive fishing gears such as trawls, seine nets, drop traps etc. (Rozas and Minello, 1997; Millar and Fryer, 1999) and remote sensing techniques, such as underwater visual census (Samoilys and Carlos, 2000). In attempts to link animals to their environment, relationships have been examined by quantifying variables, including sediment grain size, leaf length or percentage live coral cover using benthic cores, quadrats and transect lines. However, rarely have these studies been undertaken at the scales most appropriate to the way that animals use and respond to their environment. This mismatch has occurred because many studies have not explicitly considered the spatio-temporal patterns of animal movement. Instead many studies have collected data at finer scales than even the home range of the target animals. In addition, environmental data have been collected as point samples without spatial and temporal coordinates and without a spatial context with regard to the surrounding environment. As a result, any correlation with the environment can only represent a relatively small spatio-temporal

segment of the animal–environment relationship. Furthermore, few authors have reported the specific scales at which their observations are made or have considered the existence of a scale bias in their methodology. This has serious implications for attempts to undertake comparisons among different studies, particularly between studies of species with distinctly different life histories (Addicott *et al*., 1987).

The key limitations of traditional approaches to the study of animal–enviroment relationships are related to:

1. The assumption that animals respond to their environment at a single temporal and spatial scale.
2. The focus on a single 'habitat type' for animals that use a mosaic of habitat types.
3. Mismatching scales in the design of sampling strategies.

3.1. Single scale

We now know that animals are influenced by patterns and processes occurring at a range of scales of space, time and organisational complexity (Haury *et al*., 1978; Hatcher *et al*., 1987; Steele, 1988, 1989; Barry and Dayton, 1991; Holling, 1992; Levin, 1992; Marquet *et al*., 1993). Furthermore, marine animals are likely to respond to and be constrained by the composition and spatial arrangement of resources in a hierarchical way, as has been suggested for many terrestrial animals (Senft *et al*., 1987; Schaefer and Messier, 1995; McAlpine *et al*., 1999; Rolstad *et al*., 2000). A single scale approach cannot incorporate important patterns and processes at scales above and below the focal scale and therefore this approach is limited in ecology. In addition, working at one scale is particularly inappropriate for studies of multi-species assemblages since species vary in their response to the environment due to functional differences related to dietary requirements, habitat specialisation, and body size (Pearson, 1993; Lee *et al*., 2002).

3.2. Single habitat type

Until recently, many studies have focused their research questions on single 'habitat types' or 'biotopes'. These classes of structure are distinguished from one another by a set of common characteristics. For example, a mangrove habitat type is defined by plant species (and its specific location in relation to water level) and is therefore distinguishable from seagrasses. This type of classification process is widespread, particularly in resource management where this approach has allowed simplification of a complex spatial pattern. In ecology, a problem occurs when a single habitat type is selected to represent the scale of a study regardless of how the animal(s) under investigation use their environment. The misleading tendency that has sometimes followed this approach is that

investigators (and subsequent users of the results) have assigned animals to a habitat type (e.g. 'salt marsh fish community'), without information on the actual importance or dependence on other neighbouring habitat types. This error has occurred in studies that have focused on fish and crustaceans that use upper intertidal habitat types through tidal excursions (e.g. saltmarsh, mangroves, rocky shore etc.). For many animals, the upper intertidal is only a small part of the home range and may only be accessible for short periods at high tide. The importance of these areas to the animals is often not known and the arbitrary assignment of a single habitat type descriptor is misleading. Clearly, these animals are not saltmarsh or mangrove fish communities but are a product of a mosaic of adjacent subtidal and intertidal patterns and processes, which combine to maintain a population in a particular area. Very few animal assemblages can be appropriately assigned to a particular habitat type since very few spatially discrete environments exist, with perhaps the exception of lakes and ponds that are discrete for at least some of their inhabitants. In most other aquatic environments, communities intergrade, interact and exist within more complex spatial delimitations.

In summary, measuring attributes in a single habitat type for multi-habitat species will confound any meaningful conclusions on correlates and provide misleading information for resource management strategies. As argued by Roughgarden *et al*. (1988), "studies at only one of the habitats tell no more than half the story". Therefore, if information on animal movement is not available, the assumption of single habitat use should be considered carefully or rejected entirely. If an assumption is to be made, then a multi-habitat type assumption may be more suitable, thus allowing for the consideration of broader-scale movement and potential linkages between component habitat types. This argument is also important in relation to the limitations of some traditional sampling strategies.

3.3. Mismatched scale in sampling strategies

As we have already highlighted, sampling strategies and the selection of techniques and equipment for data capture are often designed without *a priori* information on the scales relevant to the dynamic spatial distribution of animals. For example, Epifanio *et al*. (1989) sampled the spatial distribution of crab zoea at weekly intervals and found that this was insufficient to resolve the details of zoeal transport. Subsequent analyses of wind vector and surface current patterns indicated that the distance a parcel of surface water would have travelled during any week was greater than the radius of the study area. Scale mismatching also commonly occurs in studies that aim to investigate environmental correlates for fishes found using coral reefs. Most surveys of coral reef fish and associated benthic structure have involved daytime counts along line transects (e.g. 50 or

100 m long and 5 or 10 m wide) or stationary counts within a known area and time frame (Samoilys and Carlos, 2000). The methods of visual census have received extensive evaluation but critiques have focused primarily on fish movement as it relates to the accuracy and precision of the technique. This is usually defined as bias introduced by fish swimming speed (and body size), their direction of travel and their position in the water column (Thresher and Gunn, 1986; Watson *et al*., 1995). The appropriateness of the scale of sample unit area or scheduling of the survey with respect to the spatial and temporal patterns of fish movement are generally not discussed. The key problem is that many of the fish that use coral reefs have broader-scale movements than previously assumed. During a visual census, fish are recorded as they pass through the field of vision of an observer and it is assumed that the underlying substratum (if significantly correlated) has some relevance to the fish. However, the abundance and species richness recorded may in fact be a function of other attributes such as the proximity of suitable night resting areas or food resources in some other part of their home range possibly some distance outside the study area. Equally, animals can be affected by changes occurring in a portion of a home range that is not included in the survey area and will therefore be undetected. To ameliorate this problem, sampling strategies and techniques should be carefully evaluated with regard to variability in temporal activity patterns and the spatial scale of animal movements.

Scale mismatching can also occur when attempting to examine animal use of tidally dominated inshore areas. For instance, when sampling fish undergoing tidal excursions, sampling should be spatially distributed over a range of depths, taking into account the changing phase of the tide (Gibson *et al*., 1996; Rozas and Minello, 1997). Combinations of techniques may be necessary to achieve this and care must be taken with regard to their suitability for comparative purposes. Only a few studies have attempted to compare two or more inshore habitat types, but these have often been done at the same stage of the tide and have generated non-comparable data sets because of inappropriate sampling strategies.

3.3.1. *Case study*

An example of how an anthropocentric perspective of habitat can disadvantage research is exemplified by the studies of Morton (1990) and Laegdsgaard and Johnson (1995), who sought to evaluate the importance of several adjacent intertidal habitat types in Moreton Bay, Queensland. They sampled fish in mangroves, adjacent seagrasses and unvegetated mudflats using a combination of semi-quantitative and non-quantitative sampling methods at spring high tide. Comparatively higher yields from mangroves led the authors to attribute greater importance to this habitat type. Morton (1990) reported one of the

highest 'standing crops' ever recorded in mangroves and considered those animals part of mangrove productivity. Laegdsgaard and Johnson (1995) also concluded that mangroves offered a more important nursery function than adjacent seagrasses and mudflats. In these studies, comparisons between habitat types should not have been made for at least three reasons, all relating to animal behaviour. First, there are inherent differences in gear selectivity and catch efficiency between block nets used in the mangroves and seine nets used in adjacent habitat types. Second, all samples were collected at peak high tide when many animals (particularly juveniles of larger tri-phasic species) had moved into the shallowest waters (i.e. upper intertidal and mangroves). At this phase of the tide, adjacent deeper waters are utilised less by those species. Third, mangroves at these sites are only available (inundated) to most nekton for approximately 8–10 hours in any 24-hour period. Furthermore, one of us (SJP) examined sites used in these studies and found that extensive areas of intertidal and subtidal seagrasses surrounded mangrove areas in both studies. It is likely, therefore, that both intertidal and adjacent subtidal vegetated areas provided a complementary range of resources during tidal excursions and throughout home ranges. Despite these limitations, results from such studies have still contributed information that has influenced decision-making in resource management. To address this problem, future comparative studies should compare a range of habitat types at scales appropriate to the way that animals use them (i.e. mosaics of mangrove with adjacent seagrasses, *vs.* mosaics of mangroves without seagrasses etc.) (Parrish, 1989). Stratified sampling designs are also needed that incorporate the animal response to fluctuations in water level. If different sampling techniques are employed for comparative evaluations, then comparisons must be made within strata (habitat type) at different locations and not between strata. For example, Nagelkerken *et al*. (2001) studied fish use pattern around Curaçao in the Caribbean Sea. In order to compare the effect of the surrounding mosaics on patch type use, they sampled assemblages of fish using seagrasses and mudflats within different mosaic structures. Seine nets were used to sample fish that used seagrasses with and without adjacent mangroves, and fish that used mudflats with and without adjacent mangroves and seagrasses.

4. THEORETICAL CONSTRUCTS OF THE ANIMAL–ENVIRONMENT LINKAGE

In this section, we examine the historical development of fundamental concepts in animal ecology and their application. We begin by examining the definitions of traditional concepts of habitat and niche. Then we develop a scale-explicit conceptual model that defines an alternative hierarchical organism-based

perspective of the animal–environment interrelationship. This conceptual framework then drives the formulation of an operational approach presented in Section 5.

4.1. Habitat and niche

The concept of habitat is one of the oldest and most fundamental concepts in ecology, yet its meaning is often taken for granted. Yapp (1922) noted that the usage of habitat often "varies according to the concept in the mind of the individual". In the English language, habitat has been broadly defined as "a living or dwelling place of an organism" equivalent to the Greek *Oikos*. However, there are many perspectives and definitions of habitat in use, most of which have originated in plant ecology. Most commonly, definitions have been elaborations of the basic definition, often with reference to interacting biotic and abiotic processes. Corsi *et al*. (2000) reviewed the term habitat and found that definitions ranged from "the place where a species lives", which they considered a Cartesian space-related concept, to "the environment in which it lives". Morrison (1992) considered both Cartesian and non-Cartesian aspects by defining habitat as "the area that has specific environmental conditions that allow the survival of a species". This definition is somewhat similar to the "ecological niche concept", which has often been used interchangeably with habitat and therefore requires brief mention. Hutchinson (1957) defined niche as a "multidimensional hypervolume" (an abstract graph) representing the set of all conditions needed to ensure the successful survival and reproduction of a species. There are many different interpretations (see review by Kolasa and Waltho, 1998) but overall, the ecological niche remains something that cannot be seen or directly measured and therefore is as difficult to scale to the real world as the previously discussed concepts of habitat. Further ambiguity was also introduced with the term 'habitat type'. Habitat type refers to a unit of land usually described by a dominant vegetation community. The term has received wide use, particularly in resource management, where habitat mapping requires the creation of discrete and homogeneous units (Corsi *et al*. 2000).

In a synthesis of definitions, Rejmanek and Jenik (1975) presented a complex of three interrelated aspects of an 'organism–environment linkage' based on the original definitions of habitat and niche (Figure 9). In their synthesis, the response of an organism to its environment lies at the heart of the concept of habitat and niche. The habitat is referred to as the 'operational environment' (Spomer, 1973) a subset of environmental factors that interact directly with the organism (MacMahon *et al*., 1981). In their model, the organism and habitat are parts of a system linked with feedback (Southwood, 1977). While useful in its emphasis on functional interactions between the environment and organism activity, it still does not integrate scale. The 'organism–environment linkage'

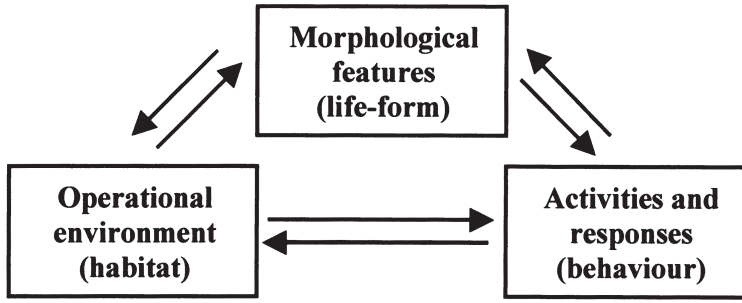

Figure 9 Rejmánek and Jenik's (1975) synthesis of three interrelated aspects of the organism–environment link that are most frequently the basis for the various concepts of habitat and niche. This synthesis offered a more holistic concept of the organism–environment relationship.

concept is closely allied to that of the 'ecotope' (Whittaker *et al*., 1973), which views niche and habitat as complementary terms for different sets of attributes that combine to represent the species' relation to the environment. Whittaker *et al*. (1973), however, did make note of the complication presented by highly mobile animals and while not explicit about movement in their definition, they suggest that an ecotope may include "population movement between two different habitats occupied at different times".

Overall, most of the definitions that have been used appear inappropriate and overly simplistic for their application to the study of highly mobile animals with complex life cycles. Instead, concepts and definitions are required that acknowledge animal behaviour and at least two important dimensions: space and time. More appropriately, Baker (1978) defined habitat specifically as, "the area that provides the resource requirements for a discrete phase of an animal's life". Resource refers to both consumables (e.g. food) and non-consumables (e.g. settlement substratum, refuge etc.) (Wiens, 1984). In terms of movement, Southwood (1981) added that habitat is also, "the area traversed by the animal's trivial movements, that is, those within its sensory range where it forages" (and hides, rests or defends territory). Temporal phases of space-use are emphasised within these concepts, thus making them more appropriate for application to highly mobile animals with multiple phases of development (e.g. eggs, larvae, post-larvae, juvenile, adult).

4.2. Home range and ecological neighbourhood

With the emphasis on movement patterns, Aebischer *et al.* (1993) offered an appropriately broad organism-scaled perspective of habitat use, whereby "an animal's movements determine a trajectory through space and time and its use of

habitat is the proportion of the trajectory contained within each home range". The home range of Aebischer *et al.* (1993) is the "area within which an animal's trajectory is located during a given period". As discussed earlier, home range estimation techniques are well developed in ecology and have been used in behavioural studies of juvenile and adult marine animals. The concept of home range, however, has not generally been applied to include the infrequent and often broad-scale migratory movements of animals or the movement of planktonic life stages for which the total area used over time may not reach an asymptote (Figure 10).

The advantages of considering the home range of an animal is that it does allow, at least initially, for habitat to be operationally defined and scaled using measurements or estimations of an animal's daily movement pattern. The appropriate scales of habitat used are then determined from the observer's interpretation of the

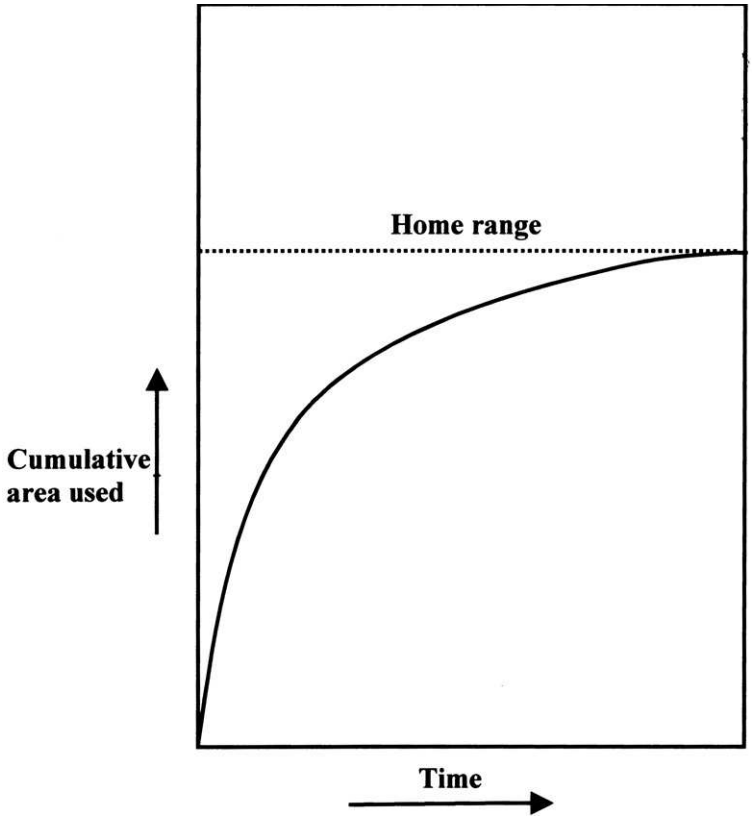

Figure 10 Animal movements will describe a home range if cumulative area used ceases to increase with greater time (i.e. an asymptotic value is approached) (adapted from McLoughlin and Ferguson, 2000).

animal's movements over time. In order to encompass more fully the life cycle dynamics, the concept of home range may be considered as, *the area typically used over some specified period of time or ontogenetic phase* (e.g. planktonic period or benthic nursery period) *or activity* (e.g. foraging, tidal excursion, spawning migration). Activity-based or functional descriptors of habitat are widespread in ecology and resource management. For instance, a species may have 'settlement', 'nursery', 'adult' and 'spawning' habitat all of which form 'essential habitat'. With the emphasis on function or process (Figure 11), the concept is somewhat similar to that of a spatial ambit, applied for scaling the activity spaces of pelagic nekton (Haury *et al*., 1978) and the better-known process-oriented concept of the ecological neighbourhood (Southwood, 1977; Antonovics and Levin, 1980; Addicott *et al*., 1987).

The ecological neighbourhood of an organism is "the region within which that organism is active or has some influence during an appropriate period of time" (Addicott *et al*., 1987). For a given ecological process, there will be an appropriate time scale over which to measure neighbourhood size. Addicott *et al*.

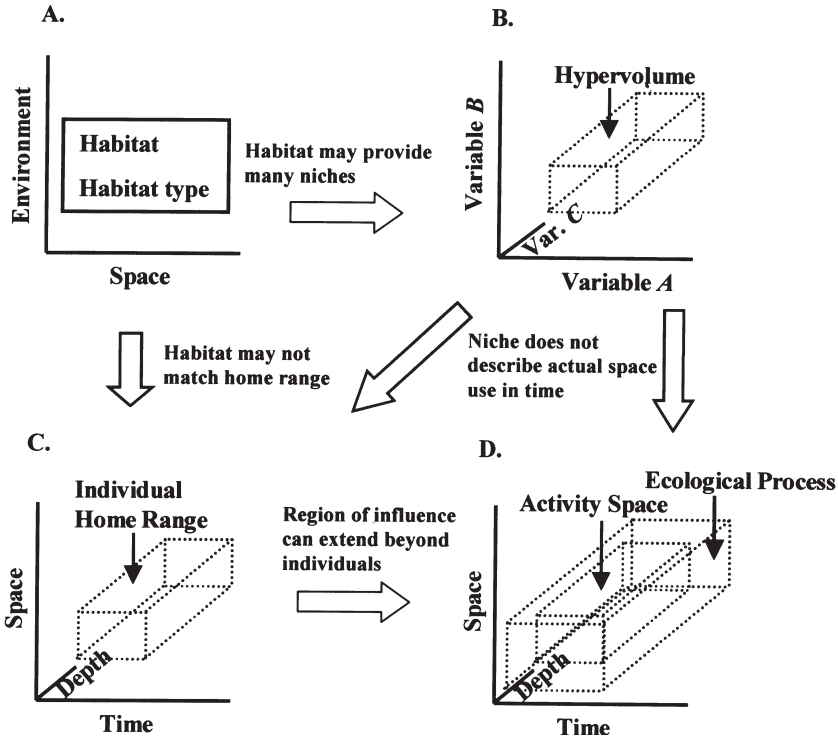

Figure 11 Relationships between four key concepts in animal ecology. (A) habitat and habitat type; (B) ecological niche; (C) home range and (D) ecological neighbourhood.

(1987) also proposed that for relatively mobile organisms, the movement of individuals would usually define the neighbourhood. From this perspective, there can be more than one ecological neighbourhood for an individual, hence a life cycle could be perceived as a multi-movement process and therefore a multi-neighbourhood event. For instance, for a foraging portunid crab, moving between patches of seagrasses, the scale of the foraging neighbourhood would be defined by the period of foraging and the spatial extent of foraging movements. For the planktonic zoea and megalopa life stages of crabs, the study of the neighbourhood may include measures of physical hydrodynamics and the spatio-temporal structure of its chemical aquatic 'landscape' during its planktonic phase from the spawning site to settlement substratum. The process of transition to a benthic phase would be another process-defined neighbourhood, with post-settlement home ranges and adult spawning migrations being others. It may be meaningful to compartmentalise ontogeny, together with associated movements within a characteristic spatio-temporal domain (for example see Figure 2). Applying this reductionist approach to lifetime use of habitat by an animal would also make fieldwork more logistically feasible, whilst maintaining an organism-based perspective. Alternatively, for a more holistic approach, one would need to couple separate neighbourhoods or consider the whole life cycle (Roughgarden *et al*., 1988; Eckman, 1996) as a single spatio-temporal domain. The life-cycle neighbourhood would then be scaled using the spatial and temporal dimensions appropriate to the total trajectory of movement throughout the life cycle. Whatever the spatio-temporal unit may be, the important aspect of an organism-based approach is that the movement process is the scaling mechanism, thus allowing us to describe the relative scales, specific to organisms and their life stages. The value of this approach is that it encourages us to evaluate ecological structure in the context of ecological function.

Generally, these concepts are based on the activities of individuals. However, assemblages may also exhibit predictable activity, for instance, in tidally synchronous movements where even multi-species behaviour is entrained enough to allow a meaningful scale generalisation to be made. Nevertheless, while useful for its placement of the organism at the centre of the scaling process, ecological neighbourhoods alone are limited in their application in ecology since the neighbourhood itself is influenced by broader and finer scale processes.

4.3. Spatial hierarchy

One of the most significant contributions that hierarchy theory has made in ecology has been to enhance the awareness of scale and facilitate operational measures of scale (Wu and Loucks, 1995). It allows one to focus on an event at a particular scale, while recognising that there are other scales relevant to that event (Urban *et al*., 1987). Furthermore, hierarchy theory emphasises the need

to distinguish between the spatio-temporal scale of a structure and the more arbitrary 'type' or 'category' of a structure (Allen, 1998). Spatial and temporal scaling is not an easy concept to grasp, but one way to conceptualise multi-scale pattern in the environment is by framing it within a nested (triadic) hierarchy (Allen and Starr, 1982) (Figure 12). Spatial hierarchies of structure (Kotliar and Wiens, 1990) have been described for several inshore habitat types such as coral reefs (Hatcher, 1997), saltmarshes (Kneib, 1994), seagrass systems (Robbins and Bell, 1994) and mussel beds (Kostylev and Erlandsson, 2001). For instance, Robbins and Bell (1994) described seagrasses as a hierarchy of nested structures, ranging from the individual shoot composed of multiple leaves (millimetres), to clumps (centimetres-metres) arranged in patches (1–100 metres), emerging as meadows (kilometres) surrounded by a coastal mosaic of component habitat types.

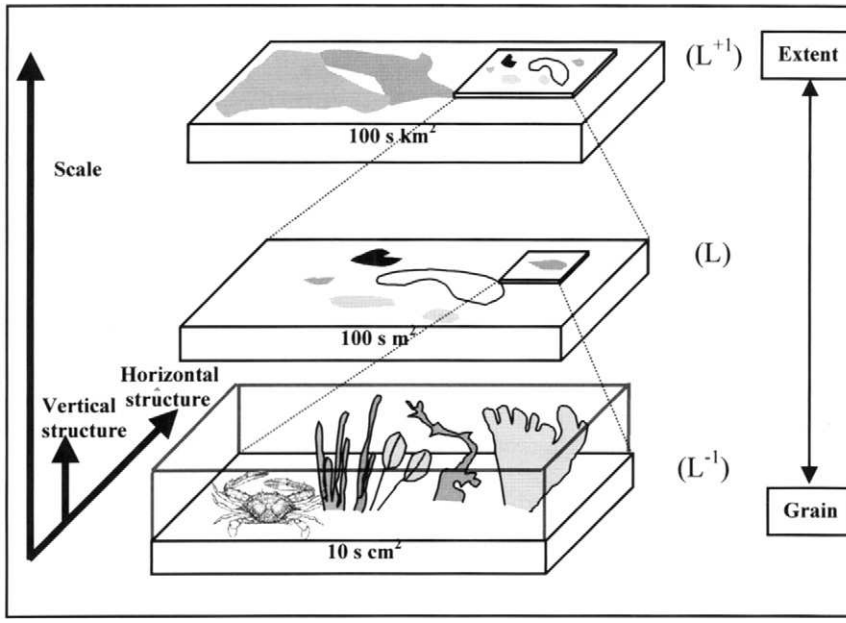

Figure 12 Scaling functional habitat structure in the context of a nested spatial hierarchy. Lower levels, $L^{(-1)}$, occupy less space and are characterised by processes operating at faster rates and finer time scales. Higher levels, $L^{(+1)}$, are of broader temporal and spatial scales (King, 1997). Spatial hierarchies can be used as interpretive tools to develop models of habitat structure at multiple scales (left-hand axis), contextualise relevant processes and to examine related pattern in the responses of animals (right-hand axis showing scale-dependent grain and extent). Vertical structure may include water depth and for aquatic vegetation, features such as canopy height. Horizontal structure may include shoot density and various measures of spatial pattern, such as the size and shape of a patch and its proximity to other patches or the diversity of patch types in a mosaic.

For an example of how this might be relevant to defining the environment for highly mobile animals, consider an assemblage of juvenile fish using a tidally dominated inshore area. In order to evade predators in deeper water and to forage amongst intertidal seagrasses or mangroves, the animals move back and forth with the flooding and ebbing tide through a mosaic of patches from the subtidal at low tide to the intertidal at high tide. A conceptual framework can be constructed with the home range or ecological neighbourhood as the focal level (L) and intermediate in the hierarchy. The focal level is the level at which the phenomenon or process under study characteristically operates (Wu and Loucks, 1995) and is a functional part of a higher and lower level. At any single level, the consequences and significance can only be understood at a higher level(s) and the mechanistic explanation must be investigated at a lower level(s) (O'Neill *et al*., 1986). The finer scale $L^{(-1)}$ components of the mosaic may consist of structure such as seagrass leaf length, epiphyte biomass and patch size and these may explain some of the fish distribution patterns found at high tide. For instance, some animals may have a preference for relatively large patches of long seagrasses. This relationship, however, may not adequately explain the patterns at the broader scale of the home range, which may also include unvegetated subtidal areas where animals spend considerable time at low tide, possibly exposed to a very different environment. At the extent of the home range, distributions may also be influenced by the spatial arrangement of patches of seagrasses and the relative proximity of seagrasses to complementary resources in adjacent mangroves and coral reefs. Lower level explanations may be further lost at the $L^{(+1)}$ level, which would include the environment surrounding the home range, i.e. where animal distributions and abundance respond to a suite of physico-chemical constraints such as a gradient in wave action, salinity, temperature, turbidity etc. These higher-level factors can be treated as constants when viewed from the focal level, though they may be quite variable at broader-scales (Urban *et al*., 1987). At the L and $L^{(+1)}$ levels, the composition and spatial arrangement of components, such as habitat types, may emerge as a significant determinant of animal distribution and abundance.

In this way, the intermediate level of the hierarchy is defined by the spatial activity patterns of the animal(s) within relevant time periods, thus anchoring the hierarchy to an ecologically meaningful scale in time and space. The hierarchical approach presented here can be considered as 'middle out', in contrast to the conventional 'top-down' or 'bottom-up' approaches that tend to be polarised either towards reductionism or holism (Wu and Loucks, 1995). Clearly, though there is no single correct scale or level for observations and ultimately, the appropriate scales will depend on the questions asked, the organisms studied and the time period considered (Wiens, 1989). Studies conducted over several scales, however, will integrate scale-dependent relationships into a more ecologically meaningful investigation of animal–habitat relationships.

Furthermore, a hierarchical model allows the relative scales of animal response to be built into the model, so that $L^{(-1)}$ corresponds to the grain (finest scale of response) and $L^{(+1)}$ to the ecological extent (broadest scale of response) (Kotliar and Wiens, 1990; Kolasa and Waltho, 1998). The lower threshold of heterogeneity is the level of resolution at which an animal no longer responds to structure, while extent is the coarsest scale of heterogeneity to which an animal responds. Response is a broad term that can mean physiological, behavioural or morphological reaction of an individual to the environment. It may be species or life-stage specific (Levin, 1992) and will emerge in patterns of populations and metapopulations (Hanski, 1998). Within a multi-species assemblage the animal response to multi-scale spatial pattern will be diverse owing to the range of behaviours, morphology and physiology. For example, a crab megalopa may respond to relatively fine-scale patchiness that may be unimportant to an older megalopa or a megalopa of another species (Eggleston *et al*., 1998). Likewise, heterogeneity important to the crab may be insignificant to a cod or a shark. However, some generality may be found, since groups of species may respond similarly. Such patterns may emerge within and between functional groups, such as trophic generalists vs. specialists, species with broad geographical distributions vs. narrow ranging species or large vs. relatively small body sizes. For example, Kolasa *et al*. (1996) found a positive relationship between ecological range, abundance and spatial distribution for a total of 42 species of invertebrates inhabiting 49 rock pools in Jamaica. Discontinuities were interpreted as forming groupings of species within three levels; narrow range specialists, intermediate range species and broad range generalists. The framework of hierarchical response may be a useful interpretive tool if there is a relationship between the hierarchical structure of the environment and the responses of species to that structure (Kotliar and Wiens, 1990; Kolasa and Waltho, 1998).

The conceptual basis for this hierarchical and organism-based approach is derived from landscape ecology, which explicitly focuses on scale and the linkages between structure, function and change (Forman and Godron, 1986; Turner, 1989; Wiens, 1995). Researchers that practice landscape ecology recognise that ecological patterns and processes operate at a range of scales in time and space and that many organisms respond to this hierarchically. This organism-based perspective means that ‘habitat’ and the relevant patterns and processes in the surrounding environment are defined and scaled by the activities and responses of the organisms of interest (Wiens, 1976; Harris, 1980; Addicott *et al*., 1987; Morris, 1987; Wiens and Milne, 1989; Kotliar and Wiens, 1990; Pearson *et al*., 1996; McAlpine *et al*., 1999).

In landscape ecology, the underlying assumption is that the environment is a mosaic of interacting components and the composition and arrangement of these components (in both time and space) determine how a system operates (Wiens, 1995). Valuable early contributions to the conceptualisation of ecological systems as “dynamic mosaics of patches” took place in benthic and pelagic

marine environments (e.g. Levin and Paine, 1974; Steele, 1978; Paine and Levin, 1981; Sousa, 1984; 1985). It is in terrestrial environments, however, that the quantification of landscape pattern and the study of the effect of pattern on ecological processes have made significant advances in understanding animal movement and persistence, the effects of disturbance, the importance of broad-scale environmental change and the design of resource management strategies (Turner, 1989; Saunders *et al*., 1991; Hobbs, 1994; Forman, 1995; Farina, 1998). Landscape ecology principles and tools are applicable throughout ecology and recent reviews have outlined the usefulness of a landscape ecology approach for the marine environment (Kneib, 1994; Robbins and Bell, 1994; Bell *et al*., 1997; Irlandi and Crawford, 1997; Eggleston, 1999). These reviews have rekindled interest in spatial pattern in the marine environment, with a number of researchers now applying and further developing concepts and analytical tools that have been used successfully in terrestrial landscape ecology.

With these concepts in mind, we propose that the living space for all animals, whether terrestrial or aquatic, can be considered to occur within a mosaic structure characterised by multi-dimensional heterogeneity of abiotic and biotic features. We present a definition of habitat that is both holistic and organism-centered; whereby *the habitat (or environment) of an animal is the interacting biotic and abiotic patterns and processes that an animal responds to in the course of its life-cycle trajectory*.

Operationally, the identification of habitat requires at least an estimate of the actual movement patterns. In addition, the traditional 'habitat types' (e.g. seagrasses, mangroves, coral reefs) are considered in the context of the amount of time that an animal uses that habitat type as well as its functional importance to the ecology of the animal.

5. APPLICATION AND TOOLS

This section presents an operational framework for studies of animal–environment relationships that is based on the conceptual framework outlined above. We first explain the logical sequence of the procedures that are necessary to ensure appropriately scaled studies. Then we examine a range of techniques that can be used to measure movement patterns for marine animals, followed by a range of techniques for quantifying and mapping environmental variability at multiple spatial scales.

5.1. Operational framework

The first step in any research strategy is to define the research questions (Figure 13). The second step involves the development of a scale-explicit

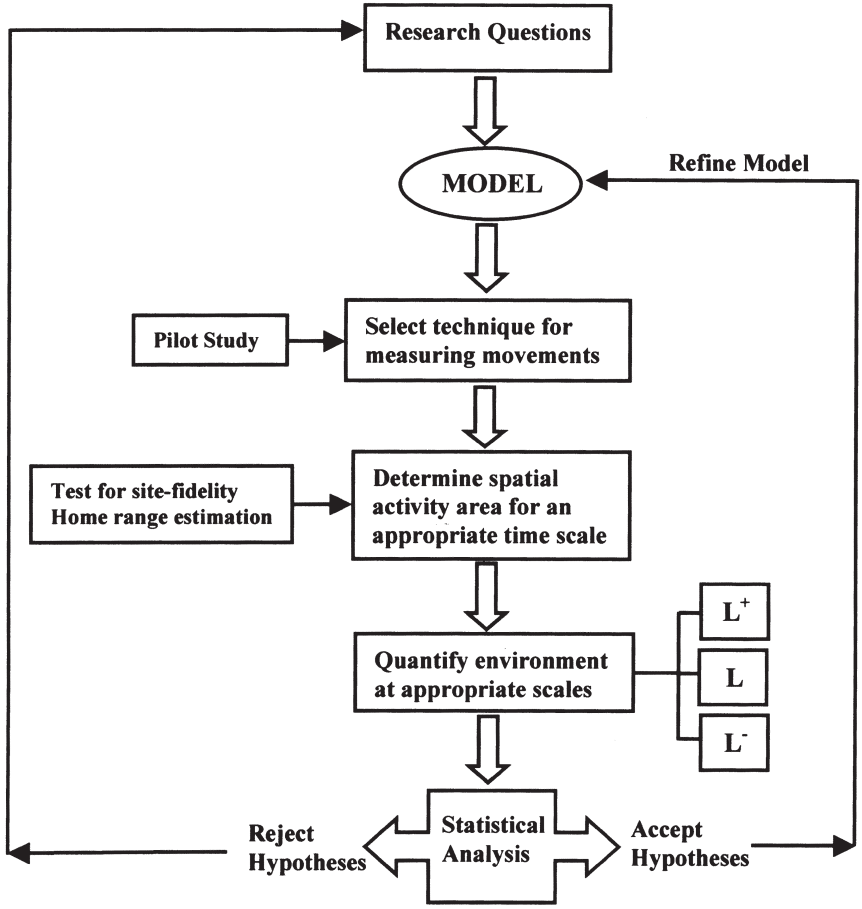

Figure 13 Operational framework showing a logical sequence of components in an experimental procedure for examining animal–environment relations at multiple spatial scales. The model is constructed to make predictions about ecological relations that are then presented as hypotheses. This component involves the development of a conceptual framework that considers temporal and spatial scale. To determine operationally appropriate scales for focal animals, field studies are usually required that involve tracking or fixed-point sampling to collect data on movement patterns. Environmental variables are then quantified at multiple scales including the activity area (L), within the activity area (L^{-1}) and beyond the activity area (L^{+1}). The procedure culminates in the testing of hypotheses that lead to refinement of the model or more observations and experiments.

conceptual framework that will define the approach and generate testable hypotheses. Next, it is necessary to select the appropriate scales at which to investigate the research questions. In studies of highly mobile animals, the movement patterns provide the mechanism for the initial identification of

meaningful scales and an appropriate technique must be selected for quantifying movements at time scales relevant to the research questions. Construction of space–time diagrams (Schneider, 1994, 2001) may prove useful in the early stages of planning for scale selection (see Figures 2 and 3 for examples). The scale selected will then contribute to the rationale for determining the relevant environmental variables and the techniques suitable for their quantification. The data generated through multi-scale animal–environment studies are likely to be in a range of formats (i.e. point measures, map trajectories, aerial photographs, multi-spectral satellite data etc.), with data on movement and multi-scale environmental attributes all needing to be temporally and spatially referenced. This not only provides context but it also provides mappable data that facilitate spatial and temporal statistical analyses.

5.2. Measuring animal movement

Quantification of animal movement in time and space is an essential first step of any attempt at scaling the environment from the perspective of an organism. There are many techniques available (both low- and high-technology) for directly and indirectly measuring and estimating movements (Table 2). It is useful, therefore to separate them into two main approaches: (1) tracking techniques; and (2) fixed-point sampling. Tracking techniques include telemetry or complex Lagrangian computer models, which provide high spatial and temporal resolution data (relative to other techniques) on the individual trajectories of free-ranging animals or virtual animals in computer simulations. In this approach, the individual is the unit of study and raw data usually consist of a series of x–y coordinates collected in the field or predicted over time. Observation above and below the water surface, where an observer follows and records the direction and geographic position of an individual, is also considered a tracking technique. Fixed-point techniques are a "multiple snap-shot" approach involving discrete measurements taken from a set of specific predetermined points in time and space, including extractive sampling, mark and recapture/resight, chemical signatures (such as the microchemistry of otoliths), still photography and fixed position underwater video. Techniques from the two categories have been applied to both planktonic (Levin, 1990) and post-planktonic stages of fish and decapod crustaceans.

5.2.1. *Eggs and larvae*

Mapping the trajectory of eggs and larvae presents a particularly difficult problem because of their small size, relatively long planktonic duration and complex behaviour (Levin, 1990; DiBacco and Levin, 2000). Scheltema (1986) remarked that "although it is quite impossible to follow individual larvae over

long distances at sea, one can nonetheless, from knowing the location of its capture, gain an insight about the probable origin, as well as the route a larva may have taken". In attempts to collect information on movement pathways many early studies used traditional zooplankton capture techniques (e.g. towed nets; settlement collectors) to examine larval distributions. However, even when used intensively these capture techniques have provided only minimal information about larval trajectories (Levin, 1990) and require that scientists infer potential trajectories from physical oceanographic data (DiBacco and Levin, 2000). Attempts have been made at tagging eggs and larvae using chemical markers but advection and mixing, as well as heavy mortality experienced by most larvae often make the recovery impractical, limiting the application of such methods (Levin *et al*., 1993). More recently, Jones *et al*. (1999) demonstrated the utility of chemical marking in a mark-recapture experiment that showed that some juveniles return to their natal reef (Lizard Island, Great Barrier Reef, Australia). The authors marked the otoliths of an estimated 10 million developing embryos laid (on artificial surfaces used as nesting sites) by the damselfish, *Pomacentrus amboinensis*, by immersing them *in situ* into a tetracycline solution. Subsequent sampling of juveniles in the same location revealed that 15 of 5 000 individuals examined were marked.

Larvae with calcified body parts have also been examined for naturally incorporated trace-elements (see also Section 5.2.2.). DiBacco and Levin (2000) applied trace-elemental fingerprinting to stage I zoeae of the striped shore crab, *Pachygrapsus crassipes* to examine the tidally driven movements of the larvae into and out of San Diego Bay, California, USA. Swearer *et al*. (1999) used similar techniques on the bluehead wrasse (*Thalassoma bifasciatum*) in the Caribbean Sea to show that, in some areas, a significant proportion of newly-settled individuals have been locally spawned and retained as planktonic larvae in nearshore waters. While these fixed-point techniques provide invaluable information on the origins of individuals and coarse resolution data on movements that contribute to the understanding of local and regional population dynamics, they provide no direct coordinate data with which to reconstruct a trajectory in time and space.

One of the first attempts to track successfully a patch of plankton in the open water was carried out by Cushing and Tungate (1963). Their team coordinated two ships in a relay of nine cruises in an attempt to continuously track a patch of copepods (*Calanus finmarchicus*) for 66 days over 140 km off the north-east coast of England. The study was designed to examine changes in patch composition and structure and demonstrated that it was possible to follow planktonic animals if the patch is large enough, observations are near-continuous and weather conditions are not severe. In a series of studies undertaken in the mid 1980s (Heath and MacLachlan, 1987; Heath *et al*., 1989; Heath and Rankine, 1988), patches of herring (*Clupea harengus*) larvae were tracked for periods of 2 to 13 days after leaving spawning grounds in the north-west of Scotland. These studies were designed to examine feeding, growth and mortality and showed that

some of the difficulties in tracking free-living larvae at sea could be overcome with the use of drifting marker buoys. Broad-scale sampling was first carried out to identify, measure and map a patch of newly hatched herring. Following this initial survey, a satellite-tracked parachute drogue buoy was deployed in the centre of the patch and on successive days samples were collected around the buoy. Natunewicz and Epifanio (2001) and Natunewicz *et al*. (2001) used a similar technique to follow patches of newly hatched blue crab (*Callinectes sapidus*) larvae for up to 11 days near the mouth of Delaware Bay, USA.

Other techniques have included visual tracking of individual larvae underwater, although such studies have usually focused on large invertebrate larvae with short (several metres) dispersal distances (Levin, 1990). Studies that have visually tracked and recorded the trajectories of individual larval fish are rare. Leis and Carson-Ewart (1997) followed (using SCUBA) individual larvae of coral reef fish on the Great Barrier Reef and recorded their direction, depth and speed every 30 seconds. The authors found that there were inherent difficulties in visually tracking underwater since human observers have limited mobility in water compared to larval fish, with fish swimming speeds ranging from ~2 to 65 cms^{-1} and occasional rapid bursts of acceleration (Leis and Carson-Ewart, 1997). Underwater visual tracking is also limited to studies of animals that inhabit calm, clear and warm waters. It may not be feasible for tracking animals in rough, turbid or cold waters, with trajectories of hundreds of kilometres or where their position in the water column varies in depth, from the surface to several hundred meters below. Furthermore, it is not known whether the pursuit of a larval fish alters its behaviour (i.e. swimming speed and direction).

Because of the difficulties in tracking live larvae at sea, most studies have addressed the mechanisms underlying their transport (Werner *et al*., 2001). Technological developments in biotelemetry, global positioning systems, computer modelling and remote sensing have rapidly increased the feasibility of accurately predicting trajectories in the marine environment. Werner *et al*. (1993) applied a 3-D circulation model to explore the influences of a range of physical and biological processes on the distribution and passive transport of cod and haddock larvae spawned on Georges Bank. Simulations demonstrated that a range of conditions (physical forcing, spawning location and position in the water column) determined whether larvae were retained in an area or advected away to neighbouring regions. Quinlan *et al*. (1999) also used a passive transport approach to develop a physical model that suggested the importance of seasonal changes in circulation and temperature on the life-history strategy and population dynamics of Atlantic menhaden (*Brevoortia tyrannus*) along the Atlantic coast of North America. Simulations led to the formulation of testable hypotheses on the function of alongshore transport and the location of spawning sites in relation to nursery areas.

The integration of remote sensing technology, together with complex hydrodynamic modelling can be especially useful where broad scale oceanographic patterns and processes are important (e.g. chlorophyll *a*, surface

temperature, sea-surface height, surface roughness, ice) (Roughgarden *et al*., 1988). Polovina *et al*. (1999) modelled the trajectory of larvae of the spiny lobster (*Panulirus marginatus*) in the Hawaiian Islands using data from space-borne satellites. The authors used time series data of sea surface height (TOPEX-POSEIDON satellite altimetry) to estimate geostrophic current and to run a simulation model of the transport of lobster larvae released from selected banks. Individual larvae were tracked for a series of time steps starting from a given location by iteratively applying advective displacements (due to water flow) and additional random displacements caused by diffusion. Simulations released 5000 larvae in pulses throughout the spawning season and tracked their spatial distributions for a year, after which they would (in real life) metamorphose into free-swimming pueruli.

Although hydrodynamics can explain distributions without provision for larval behaviour (Reiss *et al*., 2000), lack of consideration of behaviour (and morphology) that may enable larvae to move differently from the motion of the surrounding water will limit their application. Models assuming passive transport are limited by the absence of any behavioural responses (e.g. vertical behaviour) and complex biological interactions, including any feedback mechanisms that may be experienced by the animals (e.g. predation and starvation and density-dependence). Modern computer modelling, however, provides a tool for the integration of biological and physical processes occurring at multiple scales (e.g. larval behaviour and broad-scale circulation). Spatially explicit individual-based models (IBMs) (Judson, 1994) have been developed to incorporate the trajectories of individual animals that experience and respond to complex horizontal and vertical patterns in time and space (reviewed by Werner *et al*., 2001).

The inclusion of spatial history is crucial for many marine species since different life stages may occupy substantially different physical environments. Hinckley *et al*. (1996) developed a spatially explicit biophysical model for walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. The model combined a three-dimensional hydrodynamic model (physical) with a probabilistic life-stage model (biological) for young fish. The physical model reproduced broad-scale circulation features and spatial distributions of important physical factors such as temperature and salinity. The biological model was divided into three life stages: egg, yolk-sac larvae and feeding larval stage. Each interaction of an individual with the abiotic factors was modelled and the unique trajectory mapped through time and space, as well as its growth and survival. Similarly complex IBMs that recognise heterogeneity in biological entities have been developed for north-eastern Atlantic populations of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) (Heath and Gallego, 1997). Incze and Naimie (2000) provide another example of the utility of coupling biological and physical models in order to compute the predicted near-surface trajectories of larval and postlarval lobsters (*Homarus americanus*) in the Gulf of Maine, USA. The authors used an IBM that coupled a model of physical advection with a

biological model of temperature-dependent development to reveal that 'numerical lobster' larvae exhibit high temporal and spatial variability in the distances travelled (19 – 280 km) between hatching and settlement. This was attributed to a combination of spatial and temporal differences in hydrographic features, sea breezes and water temperature effects on development.

However sophisticated the software, these modelling techniques require actual tracking in order to validate predictions. In the absence of tracking real animals, ground-truthing can be achieved by incorporating the use of instruments such as fixed depth drifters and drogues, which can track actual patches of eggs and larvae while describing their environment and transmitting their positions via satellite. One of the principal attractions of drifters and drogues is that broad geographical areas can be sampled. Recently, investigators have modified drifters to mimic the behavioural response of an animal to the environment. Wolcott and Wolcott (1996) developed a 'larval mimic' for the study of the transport of decapod larvae. Their drifter senses water pressure changes, diel and tidal cycles, temperature, light, contact with the substratum, salinity and vertical velocity through the water. It is programmed to compare environmental measurements with its programmed behavioural pattern and to respond accordingly by altering its buoyancy. The machine stores depth profiles and transmits an acoustic signal for tracking. De Robertis and Ohman (1999) used an autonomous vertically-migrating drifter (VMD) to mimic diel vertical migrations in zooplankton. Their mimic used radio telemetry of GPS positions and allowed two-way communication for data telemetry and instrument reprogramming. Whilst even these mimics may be too simplistic for tracking some animals, they are the first step in a new generation of organism-based tracking devices.

5.2.2. Juveniles and adults

For larger individuals, such as post-planktonic juveniles and adults, telemetry is a powerful tool for an ecologist because of its potential for providing unbiased data on how a free-ranging animal utilises space in time. Telemetric tracking techniques commonly utilise five technologies: acoustic, radio, electromagnetic, data storage tags (archival) and satellite-based geolocation (e.g. Argos), some of which can be used most effectively in conjunction with one another (e.g. radio acoustic positioning and telemetry [Solomon and Potter, 1988; O'Dor *et al*., 1998] or ultrasonic telemetry and data storage tags [Stone and Kraus, 1998; Freire and González-Gurriarán, 1998]) (Table 2). Receivers can be hand-held or ship-, water-, air- and shore-based. Transmitters can be fixed externally, lodged internally within the gut or surgically implanted in a body cavity or intramuscularly. Manufacturers of tracking technology are continually pushing the limits, with respect to the size of tags, their longevity and the accuracy of mapped trajectories. Some of the tags and transmitters

that are now being used are as small as 8×19 mm and weigh 2.39 g in air. In all telemetry studies, transmitter size is an important consideration and smaller transmitters are less likely to adversely affect the behaviour and health of an animal. The information gained from tracking assumes that the movements of an animal are unaffected by the transmitter. However, some transmitters (and other tags) have been found to influence mortality and behaviour (Jepson *et al*., 2002). For example, predation trials with tagged and untagged juvenile Chinook salmon (*Oncorhynchus tshawytscha*) revealed a reduced swimming speed and higher susceptibility to predation for fish with surgically implanted transmitters (Adams *et al*., 1998). However, individual animals are likely to respond differently to the tag itself and the tagging procedure and therefore whenever possible it is necessary that devices be experimentally evaluated in a pilot study before being deployed for tracking (Murray and Fuller, 2000).

Most studies using transmitters have been autecological (on single species) and based on only a few individuals. However, engineers have now developed multi-channel telemetry techniques, which involve digital encoding to allow simultaneous tracking of large numbers of animals (Wolcott, 1995; Cote *et al*., 1998; Smith *et al*., 2000). Position data typically are collected but it is also possible to telemeter information on physiological variables such as heart rate, body temperature and respiration rate, as well as environmental variables such as salinity, light, depth and temperature (Klimley, 1993; González-Gurriarán and Freire, 1994; Wolcott, 1995). The majority of studies on marine fish and decapod crustaceans use acoustics, such as ultrasonic telemetry (see examples in Table 1), which can provide fine resolution data with automated, continuous position fixing. The advantages and disadvantages of using acoustic telemetry methods in studies of both fish and decapod crustaceans have been reviewed by Wolcott (1995); Freire and González-Gurriarán (1998); Zeller (1999) and Smith *et al*., (2000) (and Table 2).

Continuous tracking of animals over very long distances has also limited the application of conventional ultrasonic telemetry. For instance, González-Gurriarán and Friere (1994) lost detailed tracking information (using ultrasonic telemetry) when spider crabs (*Maja squinado*) migrated to deeper and colder offshore waters. The application of multidirectional hydrophone arrays that can be towed by ship coupled with independent acoustic receivers may improve data capture for animals undertaking movements over several kilometres (Block *et al*., 1997). Alternatively, fixed position automated 'listening stations' can be deployed on moorings (Klimley *et al*., 1998; Arendt *et al*., 2001). Klimley and Holloway (1999) attached an acoustic receiver, with a detection range of 1.10 km, to a concrete mooring to log positions of tagged yellowfin tuna (*Thunnus albacares*). Righton *et al*. (2001) monitored the movement activity of North Sea cod (*Gadus morhua*) during the summer months (June to August) using a listening station with a 500 m detection range. This study combined data from individually coded acoustic tags together with Data Storage Tags (DST) attached to

cod in the North Sea and in the Irish Sea revealing that seasonal patterns of activity (possibly foraging movements) differ between individuals in different geographical regions. However, acoustic techniques may be limited when tracking burrowing animals or animals over rocky substratum, as sound transmission is adversely affected by attenuation and reflection (Smith *et al*., 2000).

Electromagnetic telemetry has been used to study cryptic, crevice dwelling decapod crustaceans, such as lobsters, in topographically complex environments, which are not amenable to ultrasonic telemetry (Phillips *et al*., 1984; Jernakoff, 1987; Smith *et al*., 1998, 2000). The system uses low frequency signals that can be detected through seawater, rock and sediment via a grid of aerials set out on the seabed (Smith *et al*., 2000) but is limited to site-attached individuals by a relatively short (a few metres) range of detection.

Flat-bed Passive Integrated Transponder (PIT) technology may also be appropriate for site-attached animals. The technique involves inserting a PIT tag into the body cavity of an animal and setting up an antenna or series of antennae to create a local energy field (400 kHz). When the transponder enters the field, it is energised to retransmit (40–50 kHz) an ID code that is then decoded and recorded. This technique has been used mainly for small freshwater fish (<11 cm standard length) (Armstrong, *et al*., 1997; Greenberg and Giller, 2000) but also offers some potential for monitoring the movements of site-attached epibenthic marine animals. The main factor limiting the application of the PIT system is the range at which tags can be detected, since with current techniques, the tag is only detected when fish pass within 15–20 cm of the antenna thereby limiting its application for continuous monitoring.

For exploited species, where recapture is likely, DSTs or archival tags have been used for mapping movement patterns. DSTs allow us to reconstruct the tracks of individual animals for longer periods than would usually be feasible with acoustic tags. For example, tags engineered by CEFAS (Centre for Environment, Fisheries and Aquaculture Science, UK) and Lotek Marine Technologies Inc. are capable of storing over 500 000 data samples for periods of up to 25 years (Metcalfe and Arnold, 1997; Turner *et al*., 2002). The continuous monitoring of environmental variables, such as depth, light, salinity and temperature make it possible to reconstruct the tracks of animals, estimating the time, place and directionality of movements (Friere and González-Gurriarán, 1998). Welch and Eveson (1999) reviewed the techniques used for geopositioning based on variations in light and Gunn and Block (2001) discuss the limitations with regard to geolocating free-ranging fish.

Using DSTs Metcalfe and Arnold (1997) revealed that some mature female plaice (*Pleuronectes platessa*) visited more than one spawning area within a single spawning season and that rates of movement were often as much as ten times faster than those estimated using conventional mark-recapture experiments. Arnold and Holford (1995) combined information from DSTs from several fish species with interpolated tidal stream vectors to predict rates and scales of movement of demersal fish in the North Sea and English Channel.

An example of a data set retrieved from a DST attached to a female plaice (*Pleuronectes platessa*) is shown in Figure 14.

Some DSTs have been designed to transmit information via satellite using the Argos system. The Argos system provides world-wide position fixes of a mobile UHF transmitter via an orbiting satellite (Taillade, 1992). Transmission of data via satellite, however, requires that the transmitter be positioned above the surface of the water. Traditionally, this has limited the use of Argos to air-breathing marine animals such as mammals and turtles (Marsh and Rathbun, 1990; Priede and French, 1991; Plotkin, 1998; Gillespie, 2001) and some surface-dwelling fish (Priede, 1984). However, the necessity for understanding the movements of fast swimming and deep diving (> 1000 m) pelagic fish that are being exploited by fisheries has resulted in the invention of 'pop-off' transmitter tags that are programmed to detach from the animal and float to the surface to transmit position and archived data (Priede and French, 1991; Gunn and Block, 2001). Together with implanted DSTs these have been used successfully for studies of bluefin tuna (*Thunnus thynnus*) (Block *et al*., 1998, 2001) and swordfish (*Xiphias gladius*) (Sedberry and Loefer, 2001). For example, data were retrieved from 95% (Block *et al*., 1998) and 90% (Block *et al*., 2001) of tags detached from bluefin tuna.

DSTs have also been used in conjunction with integrated video and audio systems to simultaneously examine animal–environment linkages by examining the interaction between space use patterns and animal behaviour such as locomotor effort, social interactions and hunting behaviour (Marshall, 1998 and Heithaus *et al*., 2001 for tiger sharks; Davis *et al*., 1999 and 2001 for seals). So far, such systems have only been applied to large vertebrates such as sharks, cetaceans and pinnipeds but in the future, micro-cameras with smaller batteries and longer life will no doubt provide new insights into the behavioral and physiological interactions of small-bodied animals with their environment.

Extractive sampling techniques using combinations of conventional fishing gears could also be used to examine spatial and temporal patterns of distribution. For instance, to estimate the spatial extent of tidal migrations it would be necessary to sample repetitively at various distances (depths) from the shore at all stages of the tide. Another fixed-point technique, mark–recapture, has been used extensively to map movements. Such studies provide information on the locations of release and recovery from which movement patterns can be inferred (Hilborn, 1990). Generally, however, the probability of recapture is low and multiple recapture extremely rare and largely a function of both animal movement and the catch or search effort of the investigator (Whitehead, 2001). Nevertheless, it is this form of data that provides most of our current knowledge of movement in marine animals. Hastein *et al*. (2001) have reviewed innovative methods for marking fish and crustaceans. Mark–resight can also be used, whereby an observer records the position of a marked animal underwater (Zeller and Russ, 1998) or uses *in situ* video recordings. For example, Burrows *et al*.

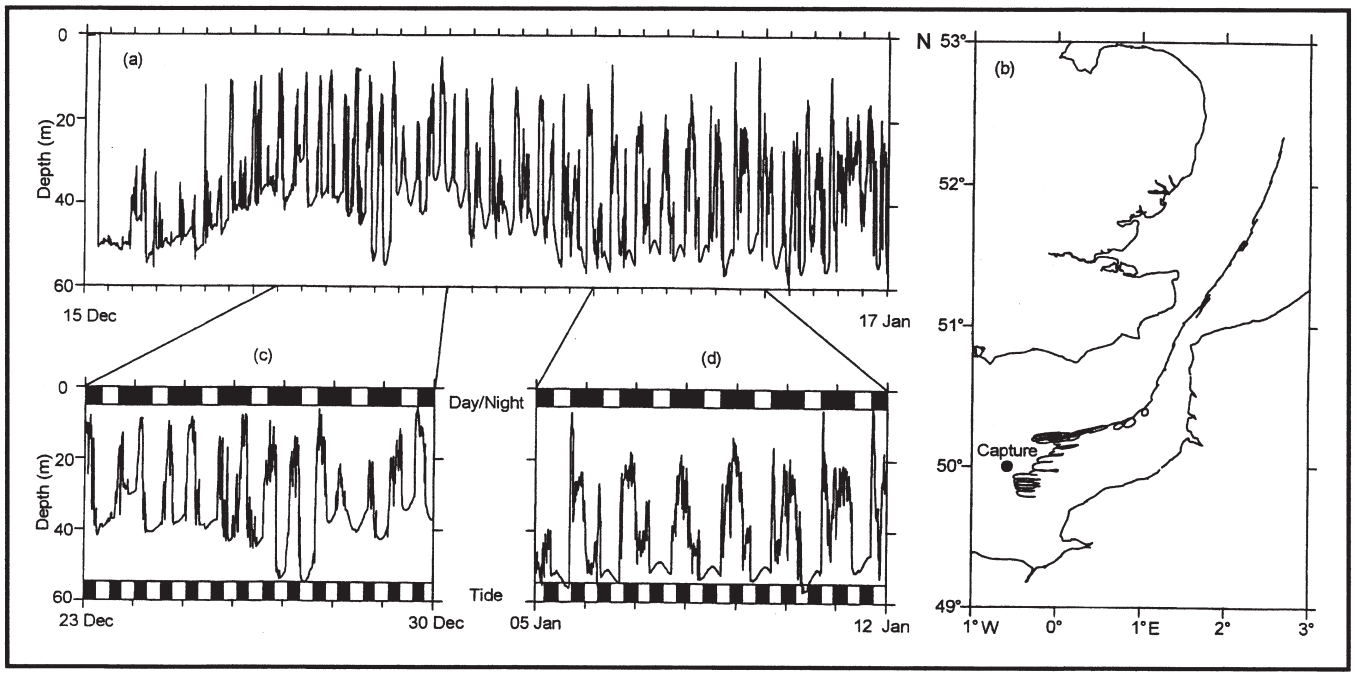

Figure 14 Continuous information on the vertical movement patterns and reconstructed track of a female plaice (*Pleuronectes platessa*) tagged with a CEFAS data storage tag in the North Sea from 15 December 1993 to 17 January 1994. Plaice use the tidal stream to facilitate movements. The DST depth record shows a plaice moving up into mid water on a flowing tide, returning to the seabed when the tide turns (Arnold, 2001). Fish were geolocated using information on geographic variability in the tidal range and times of high and low tide incorporated into a computer simulation model of the tidal streams. Data reproduced by permission of CEFAS, Lowestoft. © Crown copyright.

Table 2 Techniques used to examine animal movement patterns in the marine environment. Techniques are grouped as tracking techniques and fixed-point sampling techniques.

Technique	Advantages	Disadvantages	Life stage(s) studied	References
Tracking techniques				
Acoustic	Multi-channel allows multiple individuals to be tracked simultaneously.	Sound can be attenuated and reflected by rocky substratum. Limited to shorter range than radio telemetry.	Juvenile Adult	Wolcott (1995) Freire and Gonzalez-Gurriaran (1998)
Radio	Tracks over broad-scales even global coverage via satellite.	Transmitter large, short battery life. Signal transmitted from the surface.	Juvenile Adult	Gillespie (2001)
Electromagnetic	Signals detected through water, sediment or rock.	Shorter range than acoustic telemetry.	Juvenile Adult	Smith *et al*. (2000)
Passive integrated transponder (PIT)	Small size. Useful for mapping of movements for site-attached animals	Requires animal to pass close (15-20 cm) to aerial.	Juvenile	Armstrong *et al*. (1997)
Data Storage Tags (DSTs)	Continuous environmental data for track reconstruction.	Size of tag Retrieval may be difficult Geolocation requires auxiliary data	Juvenile Adult	Metcalfe and Arnold (1997)
Pop-off satellite archival transmitters (PSATs)	Retrieval of archival data from broad-ranging and deep diving animals.	Track reconstruction requires auxiliary data.	Juvenile Adults	Block *et al*. (1997)

Optical tracking (eye, video, photography)	Continuous tracking of a wide range of animals.	Usually requires a motorized platform. Difficult to follow deep diving animals.	Larvae Juvenile Adult	Leis and Carson-Ewart (1997) Sims and Quayle (1998)
Lagrangian computer simulations	Non-invasive and tracks many individuals over broad-scales.	Complex and needs field data to parameterise and validate.	Eggs Larvae	Hood *et al*. (1999)
Fixed-point samples				
Mark/recapture	Marking is low cost, large numbers can be marked.	Intensive sampling required to recapture. Low recapture rate.	All life stages	Levin (1990) Hilborn (1990)
Capture device for study of distributions	Devices are low cost, low maintenance and widely available.	Intensive sampling required to build trajectory, particularly if no a *priori* information are available. Highly selective.	All life stages	Levin (1990) Rozas and Minello (1997)
Fixed position optical sampling (eye, video, photography)	Permanent visual record, non-destructive remote sensing approach.	Coarse taxonomic resolution, limited field of view and focal length.	All life stages	Samoilys and Carlos (2000) Burrows *et al*. (1994)
Elemental fingerprinting	Low cost, non-invasive	Interpretation requires extensive reference data. Trajectory difficult to determine for multi-habitat users. Requires mass-spectrometer.	All life stages	Gillanders and Kingsford (2000) Fry *et al*. (1999)

(1994) used a series of underwater video cameras fixed to the intertidal and subtidal substratum surface to record patterns of tidal movements for fish. Cameras were placed in the centre of a radiating array of nets designed to guide moving animals past the camera, with time-lapse video recordings (3.43 and 2.67 frames per second) made over sixteen 24-h periods.

The microchemical analyses of body parts, such as fish otoliths, which incorporate chemicals from the surrounding environment ("elemental fingerprints") have been used to estimate movement patterns for marine animals (Campana *et al*., 1995 for fish; DiBacco and Levin, 2000 for crustaceans). Thorrold *et al*. (1997) and Gillanders and Kingsford (1996, 2000) suggested that these permanent records of environmental conditions experienced by highly mobile animals could be used to determine the offshore–inshore movement of larvae and specific nursery areas for adult populations. Quinlan *et al*. (1999) suggested that a cohort could be 'tracked' as it arrived at estuaries, using information from both otolith microchemistry and birth-date distributions. Thorrold *et al*. (2001) compared geochemical signatures in whole otoliths of juvenile weakfish (*Cynoscion regalis*) with otolith cores of reproductively mature adult weakfish to reveal that many adults were returning to their natal estuary to spawn.

Secor and Piccoli (1996) used levels of strontium (which are higher in sea water than fresh water) in otoliths to investigate the distances of up-estuary and down-estuary movement during the growth of striped bass (*Morone saxatilis*). Another potentially useful technology involves measurement of stable isotopes (Fry, 1983; Hobson, 1999) acquired from the diet. The range of isotope values (^{13}C, ^{15}N) for animals varies depending on the source of nutrients (e.g. seagrasses and mangroves). Therefore, animals moving between isotopically distinct foodwebs can carry with them information on the location of previous feeding. For example, Fry *et al*. (1999) used isotope signatures to show that seagrass meadows were the main contributor to the diet of pink shrimp (*Farfantepenaeus duorarum*) that moved to join offshore populations in Florida. The difficulty in stable isotope studies comes from variability introduced from animals that have consumed a diet having a range of isotope values. Together with extensive environmental reference data, tissue assay techniques hold great potential for investigating the origins and broad-scale movement patterns, particularly for animals too small for telemetry and unsuitable for mark–recapture experiments.

Clearly, fixed-point techniques cannot easily provide detail of movements that may occur between measurements and therefore the resulting estimate of a trajectory is heavily dependent upon sufficient samples to piece together a movement pattern. Some telemetry techniques can also suffer this limitation, whereby trajectories are largely dependent on the time interval between readings (Swihart and Slade, 1985; Spencer *et al*., 1990). Therefore in all movement studies, a time component must be explicitly stated, for instance, the frequency of observations and the duration of the study (e.g. second, hour, day, season etc.).

This is important in relation to the scaling of habitat use, since individuals do not use their spatial domains evenly and will likely have a core area or several core areas where they spend a significant proportion of time.

In summary, the choice of technique ultimately depends on the animal concerned and the objectives of the study. In some instances quantifying movement patterns for marine animals may require combinations of both tracking and fixed-point techniques and the application of a range of statistical techniques. Telemetry provides detailed tracking of a few larger individuals, whereas chemical markers can generate information on the likely extent of movements for many individuals of a range of sizes. Alternatively, low-technology extractive sampling (e.g. beam trawling or drop-netting) may be the only option available. It is important to appreciate that the spatial and temporal resolution and extent of the data will determine the resulting model of animal movements.

5.3. Analysis of animal movement data

Establishing linkages between animals and their environment at appropriate scales requires that movement patterns such as pathways and home range size be quantified. Telemetry and tracking studies of free-ranging animals typically generate empirical data in the form of a time series of x, y or x, y, z coordinates. Analysis of coordinate data is a rapidly growing area of biostatistics (Powell, 2000) and spatial statistics (Legendre and Fortin 1989; Fortin 1999). There are numerous techniques available to analyse tracking (and fixed-point) geolocational data in order to estimate movement and home range size, shape and structure. Movement patterns for individual animals can be characterised by simple measures such as length, direction, duration, speed and turning angle, each of which reveals something different about movement behaviour (Turchin *et al*., 1991; Wiens *et al*., 1993). Techniques such as re-normalisation (Wiens *et al*., 1993) can also be applied to the data to obtain independence among successive observations (e.g. aggregating a pathway by renormalisation). For home range estimation, frequently-used statistical models include utilisation distributions (Ford and Krumme, 1979), the Fourier transform method, the minimum convex polygon, the harmonic mean and the adaptive kernel method (reviewed by Powell, 2000). These statistical techniques each have specific sensitivities regarding sample size, and the distribution and independence of data. One of the first steps in operationally defining a home range is to test for site fidelity, which can be performed using a robust Monte Carlo random walk test (Spencer *et al*., 1990).

Much software for home range estimation is in the public domain and available via the World Wide Web for both Macintosh and MS-DOS operating systems. Calhome™, Wildtrack™, Home Range™ and Antelope™ are just a few programs widely used for home range estimation. Antelope™ (University of

California, San Diego) for instance, performs spatial statistics on data generated by mapping a group of individuals or from tracking an individual over time. Hooge and Eichenlaub (1997) have created an Animal Movement Analyst Extension (AMAE) to ArcView® GIS for the statistical analysis and modelling of animal movements. This software permits the user to conduct a wide range of spatial analyses and hypothesis testing on movement data taken from both observation and telemetric-tracking data. The program offers more than 50 functions including several to examine habitat selection (e.g. compositional analysis and availability analysis). Compositional analysis (Aebischer *et al*., 1993) uses the utilisation distribution of the animal to determine resoure use, with the habitat types within the home range expressed as a proportion of the total range area. The technique also compares habitat use with the availability of habitat. Four widely-used functions in the preliminary analyses of movement data have been demonstrated on data from a sonic-tracking study of Pacific halibut (*Hippoglossus stenolepis*) in Glacier Bay, Alaska (Hooge *et al*., 1999) (Figure 15). For overviews of the advantages and disadvantages of the many home range estimation techniques, refer to Boulanger and White (1990), Harris *et al.* (1990), Larkin and Halkin (1994), Hooge *et al*. (1999) and Powell (2000).

Moorcroft *et al*. (1999) argued that while the majority of traditional statistical models provided useful information, they are purely descriptive, with no mechanistic basis. Instead, they advocate a mechanistic home range model that uses partial differential equations to form simple behavioural rules, which have been derived from field observations of animal behaviour. Such models can be used to evaluate hypotheses for the factors underlying animal home range patterns and to obtain predictions on the changes to home range patterns following perturbations. Application to marine animals, however, may be more challenging since for many species, insufficient details are available on predictable behaviour with which to parameterise models. Nevertheless, mechanistic models would complement traditional statistical models of home range use. Using several methods may overcome the biases in any one method, allow cross-validation of model results, and enable comparisons with other studies.

In contrast to most statistical models, fractal analysis is relatively insensitive to sample size, measurement error and to measurement scale (Loehle, 1990). The fractal dimension (D) has increasingly been applied to studies of movement including home range movements (e.g. Dicke and Burrough, 1988; Wiens and Milne, 1989; Crist *et al*., 1992). Loehle (1990) calculated D for both the path taken by an animal (measure of tortuosity) and for the pattern of the patches used by the animal. The technique involved building a 3-D surface of spatial activity over a mapped area and calculating the fractal dimension of the surface at multiple scales. Mouillet and Viale (2001) calculated D for trajectories of satellite-tracked fin whale in the north-western Mediterranean Sea and revealed relatively linear paths (D = 1.03). Long straight movements by whales were explained in relation to the movement between aggregated patches of

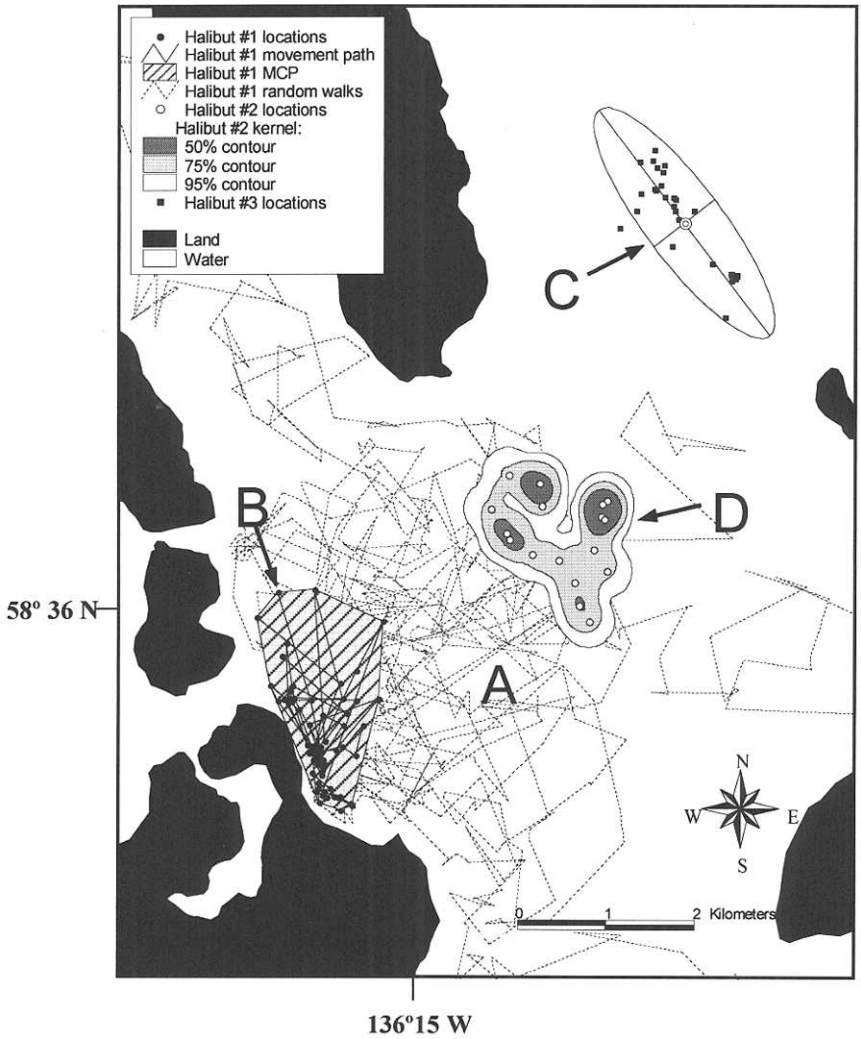

Figure 15 Analyses of acoustic telemetry data from three Pacific halibut in Glacier Bay, Alaska using the Movement Analyst Extension to ArcView® GIS. (A) A test for site-fidelity and the existence of a home range using a Monte Carlo random walk test with land as a constraining polygon for ten random walks. The values of the actual movement path are then compared to the ranked values of the random walks to determine significance. (B) Minimum convex polygon (MCP) home range shown enclosing the actual movement path of the animal tested in (A). Areas can be clipped out of the polygon by ArcView® to more accurately represent the areas used. (C) Jennrich-Turner 95% home range with the major and minor axes of the data shown. (D) Fixed kernel home range with the smoothing factor calculated via least-squares cross validation, showing the 50%, 75% and 95% utilization distribution contours. Data reproduced with permission of Philip Hooge, USGS, Glacier Bay Field Station, Alaska, USA.

zooplankton prey providing information on the way these whales perceive and use their environment. The authors hypothesised that trajectories composed of linear segments correspond to low prey densities (searching) and segments with relatively tight loops correspond to higher prey densities (feeding). With this perspective, it is likely that uni-directional movements such as migrations will exhibit low *D*, while multi-directional movements such as foraging will exhibit highly tortuous movements or high *D* values. If *D* is scale-independent then its use may facilitate ecologically meaningful extrapolations across spatial scales and provide insights into pattern–process relationships when linked to a multi-scale analysis (Crist *et al*., 1992). Turchin (1996) argues that if scale-independence cannot be demonstrated an alternative random-walk model should be used in place of fractal analyses with which to examine animal movement. The correlated random walk model is a theoretical model used to evaluate movement pathways. The model produces pathways in a series of discrete time steps with a net directional bias. It is compared with observations so that correspondence indicates random movement, overpredicted displacement indicates preference for a region and underpredicted displacement indicates avoidance of a region. Deviations from correlated random walk model assumptions may reveal specific behaviour such as changes in turn direction to move along a straightened path or positive correlation in sequential turn direction in area restricted movements (Kareiva and Shigesada, 1983; Bergman *et al*., 2000).

In addition to its great utility in the calculation of and visualisation of home range estimators (Hooge *et al*., 1999) and other statistical models that can be applied to movement data, GIS provides a powerful tool for linking animal movement models with models of environmental heterogeneity. Tischendorf (1997) describes the development of an hierarchical grid-based spatial data model coupled with an object-orientated model of individual movements, which combine to permit simulation experiments to investigate the effects of spatial patterning in the environment on animal movements over a wide range of spatial and temporal scales. Furthermore, species-specific responses to patch attributes such as edge permeability can be assigned to pattern-orientated models, which then act as a template over which movement responses can be simulated. For example, if the foraging movements of a crab are known to be inhibited by a specific gap size between patches of seagrasses, then that spatial information can be programmed into the model.

5.4. Quantifying environmental data at multiple spatial scales

Examining animal–environment linkages for small and highly mobile animals that use a spatially heterogeneous environment requires spatially intensive quantitative environmental data, with both fine resolution and broad extent. It is unlikely that any single technique currently available would be capable of

discriminating structural features at the range of scales that are likely to be important to many fish and decapod crustaceans. Typically, techniques that provide fine scale measures are limited in their spatial coverage by time demands, whilst remote sensing devices, able to record pattern at broad spatial extents (i.e., aerial and space-borne sensors) have fixed limits of spectral sensitivity, spatial resolution and descriptive resolution (Green *et al*., 1996). To address this problem, a range of techniques is needed, each with a unique ability to discriminate pattern. Each technique has advantages and limitations defined by their design, but are complementary when used in an integrated approach.

5.4.1. *Mapping*

A selection of commonly used techniques is reviewed here, with particular emphasis on techniques applicable for benthic mapping. Measures can be ground-based or remote, such as water-, air- and space-borne sensors. Ground-based measurements are usually point samples delineated with cores, quadrats and transect and are well known to most ecologists. Continuous spatial data (i.e. maps), however, are needed to represent the environmental template (*sensu* Southwood, 1977) over which an animal operates. Underwater videography used in conjunction with Global Positioning System (GPS) data can provide continuous geo-referenced images covering broader areas than could be achieved using point sampling, whilst retaining the ability to identify positively substratum composition (albeit not necessarily with high taxonomic resolution). Underwater videography of benthic structure is an increasingly commonly used tool in marine science and is one of the few techniques that can effectively map subtidal substratum in waters with variable depth, turbidity and substratum composition. The camera can either be hand-held, attached to a mobile platform such as a manta-tow board (Carleton and Done, 1995), a benthic sled (Bergstedt and Anderson, 1990), a remotely-operated submersible (Anderson, 1994), or at the surface attached to a boat (Norris *et al*., 1997; Riegl *et al*., 2001). However, video usually requires human visual interpretation and therefore bias can be introduced through variability in water depth and turbidity and in the ability of an observer to discriminate structure (i.e., vegetated from unvegetated).

Acoustic techniques such as sonar are not limited by variable light and such techniques have been shown to provide accurate sediment and vegetation mapping information for marine environments that are not suitable for optical sensors (Bernhardt *et al*., 1998; Lee Long *et al*., 1998; Pasqualini *et al*., 2000). High resolution multibeam sonar and digital sidescan sonar survey techniques are rapidly developing to provide high resolution (<1 metre) images through a range of water depths (Armstrong *et al*., 1998; McRea *et al*., 1999). Interpretation of sonograms usually requires extensive ground-truthing but when coupled with diver

observations, the method can provide accurate maps over broader areas in shorter time than diver surveys or videography alone. However, even water-based videography and acoustic surveys may not easily map the environment at the spatial scales relevant to many marine nekton using shallow inshore areas. Higher altitude sensors are therefore required. Elevated platforms such as balloons, aeroplanes, helicopters, spacecraft and satellites have been used extensively for the mounting of still and video cameras and multispectral and hyperspectral scanners. The applications of air and space-borne remote sensing techniques for acquiring data on marine systems have been extensively reviewed elsewhere (Green, *et al*., 1996, 2000; Mumby *et al*., 1998, 1999; Santos, 2000; Hedley and Mumby, 2002; Mumby and Edwards, 2002). Most animal–environment studies of fish and decapod crustaceans will require a combination of integrated remote sensing techniques. For example (although not specifically for mapping animal environments), Pasquatini *et al*. (1998) mapped seagrasses around Corsica by combining aerial photography for the waters less than 20 m deep with sidescan sonar for waters 20–50 m deep. Our own studies in Moreton Bay, Australia, have used a GIS to integrate geo-referenced samples from multiple scales, ranging from fine-scale point samples for water quality and substratum structure to videographic transects, aerial photographs and Landsat Thematic Mapper data. These data represented environmental variability at multiple scales (including the extent of the home range) to which animals in our study area were likely to respond. An example of a framework for an integrated approach to collecting, classifying and mapping environmental data at multiple spatial scales is shown in Figure 16.

5.4.2. *Delineating functionally-meaningful pattern*

The discrimination of spatial themes or classes can be achieved objectively using various clustering and ordination algorithms (e.g., Sheppard *et al*. 1995; Mumby and Harbourne, 1999; Green *et al*. 2000). The aim of any classification is to simplify heterogeneity by subsuming it within a representative entity that carries a class name or descriptor. Typically, in the production of a thematic or categorical map, an artificial line network supersedes information about fine-scale structure and all accurate quantitative information about within-map unit variation is lost (Burrough and McDonnell, 1998). However, in animal ecology the resulting classification is integrated into a digital map from which to quantify spatial pattern and therefore the map must represent classes that are meaningful to the animal(s) of interest. Otherwise, the output from spatial pattern statistics will be difficult to interpret. The recognition of meaningful structure for any animal requires that a functional interaction be established (Kolasa and Rollo, 1991; McCoy and Bell, 1991; Cale and Hobbs, 1994), which means that *a priori* information on finer-scale relationships must be established through carefully designed mensurative or manipulative experiments.

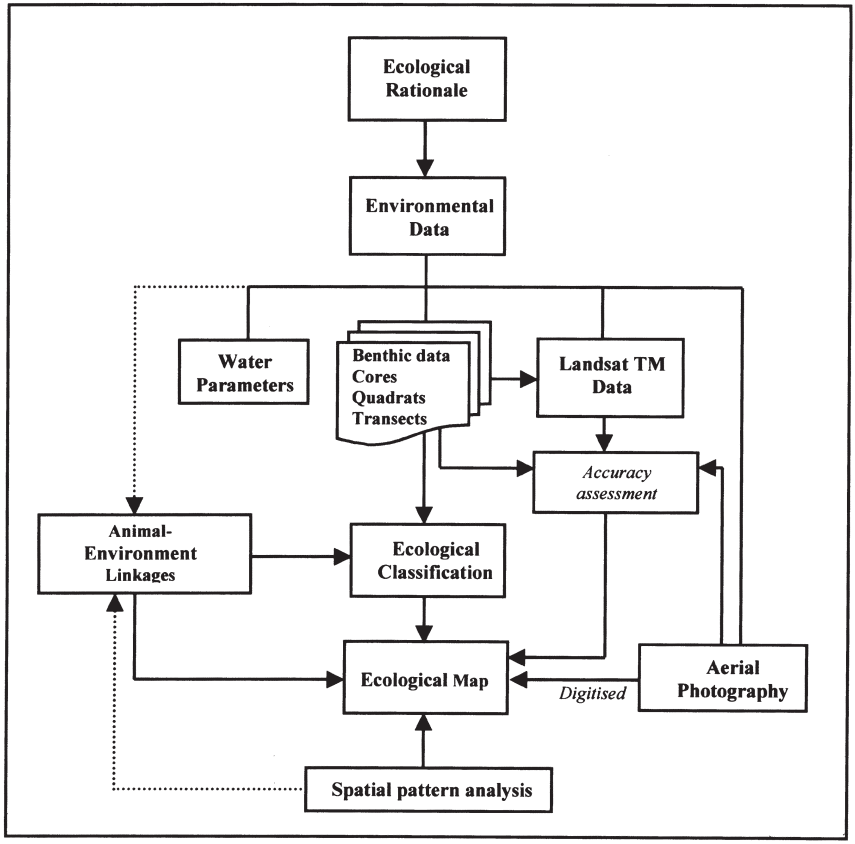

Figure 16 Overview of the structure and flow of information in an integrated multi-scale approach to collecting, classifying and mapping benthic structure. The rationale provides a conceptual framework with which to approach the quantification and analysis of environmental data. The high resolution data (cores, quadrats, transects) provide information for the examination of fine scale linkages and for the composition of the broader scale patterns distinguished through aerial photography and Landsat TM data. Information from all scales contributes to the ecological map, which is a digital thematic map based on the integration of pattern that was digitised directly from the aerial photography, with themes derived from the ecological classification.

The selection of an appropriate minimum mapping unit (MMU) is also an important consideration, since this constrains the lower limits of resolution (Li and Reynolds, 1994; McGarigal and McComb, 1995; Gustafson, 1998) and influences the behaviour of spatial pattern metrics (Saura, 2002). Furthermore, delineating boundaries requires careful consideration, since the production of a categorical map using statistical clustering algorithms typically results in an

abrupt division between groupings. The representation of classes with sharp edges, however, is not necessarily unrealistic since in tidally-dominated inshore areas, gradients in environmental conditions are often characterised by abrupt discontinuity in the distribution of benthic plants and animals. This well recognised pattern of intertidal 'zonation' (Stephenson and Stephenson, 1949; Lewis, 1964; Ranwell, 1972) is a consequence of the responses of benthic plants and animals to variation in the environment (e.g. water depth, immersion/emmersion times, grazing etc.). Burrough (1986) and Fortin and Drapeau, (1995) advocated using statistics to detect boundaries by identifying the location where the measured variables (biotic/abiotic) show the highest shifts (or maximum rate of change). Furthermore, to validate functional meaningfulness to the proposed biophysical boundaries (from the point of view of the animals of interest), the animal response – in terms of the spatial distribution of abundance, mass or species diversity or the trajectory of an individual – could be examined for concomitant discontinuities. Therefore, at every stage in the mapping process, decisions must be made about scale and about which structures and which attributes are meaningful. The challenge for the mapping process is to incorporate functionally meaningful structure at a range of spatial scales, whilst also selecting an appropriate level of simplification that retains sufficient detail to address the problem.

5.4.3. *Quantifying spatial pattern*

Since a suite of complementary and integrated spatial technologies is required to analyse and display data in animal–environment studies, a Geographical Information System (GIS) would be an invaluable tool. Free standing and GIS-integrated spatial pattern analysis programs such as FRAGSTATS®ARC and Patch Analyst, can be used to quantify and model spatial pattern. For studies in terrestrial systems, an extensive set of indices or metrics has been developed and applied to measure the composition and spatial pattern of mosaic structure (e.g. O'Neill *et al*., 1988; Turner, 1989; Gustafson *et al*., 1994; McGarigal and Marks, 1994; McGarigal and McComb, 1995; Haines-Young and Chopping, 1996; Gustafson, 1998; Hargis *et al*., 1998). Mosaic composition encompasses the variety and abundance of patch types, without being spatially explicit and includes the proportion of each class (patch type), as well as richness, evenness and diversity indices. The spatial pattern (physical distribution of patches) is measured by shape, area, amount of edge, patch isolation and contagion. The metrics developed to measure the various aspects of structure are interrelated by their dependency on the same underlying measures of patch area, edge length and inter-patch distance (Riitters *et al*., 1995; Hargis *et al*., 1998). As a result, some partial or complete redundancy occurs (Riitters *et al*., 1995; Haines-Young and Chopping, 1996; Cain *et al*., 1997).

Using Factor Analyses (a principal components analysis based on correlation coefficients between pairs of metrics), Riitters *et al.* (1995) found that six factors explained 87% of the variation among 26 metrics. In animal ecology, however, the process must also ensure that the chosen metrics capture all dimensions of spatial pattern relevant to an animal. For exploratory studies of the influence of mosaic pattern on animals, a suite of metrics is typically used (26 metrics by McGarigal and McComb (1995) for bird assemblages; 17 metrics by McAlpine *et al*. (1999) for kangaroos and eight metrics by Hansen *et al*. (2001) for caribou). For marine systems, however, this type of approach remains largely theoretical (Robbins and Bell, 1994), with few attempts to quantify spatial pattern (Garrabou *et al*., 1998 for rocky shores; Robbins and Bell, 2000 for seagrasses; Teixidó *et al*., 2002, for Antarctic benthic communities).

In addition, exploratory studies undertaken on a wide range of highly mobile animals including hoverflies (Haslett, 1994), birds (Pearson, 1993; McGarigal and McComb, 1995), kangaroos (McAlpine *et al*., 1999) and Florida panther (Kerkhoff *et al*., 2000) have recognised that investigation of a species response to spatial pattern must take place at multiple scales. These previous studies have quantified mosaic structure within a range of spatial extents, delineated around an observation area for a particular species or group of species. For example, from studies of wintering bird populations in Georgia (USA), Pearson (1993) showed a species-specific response to pattern measured at different distances (five concentric bands of 100 m) from a sample transect. In the Alps of southern Germany, Haslett (1994) quantified mosaic complexity by computing fractal dimensions within circles of 300 m radius that were estimated to have incorporated hoverfly home ranges. In Queensland, Australia, McAlpine *et al*. (1999) quantified mosaic structure for kangaroos at a number of radial extents from 5 to 15 km surrounding each 10 km line transect. In Florida, USA, Kerkhoff *et al*. (2000) quantified forest cover at multiple scales using fractal dimensions and assessed the association with known panther locations (telemetry) via conditional mapping. In Moreton Bay, Queensland, benthic mosaic structure was quantified at radial extents of 100 and 300 m around beam trawl and buoyant pop-net samples of marine nekton (Pittman, Ph.D. thesis) (Figure 17).

Although few studies have examined the effect of spatial pattern on nekton, studies that link detailed movement patterns with detailed benthic mapping using spatial statistics are now emerging. Cote *et al*. (1998) investigated the spatial and temporal animal–environment linkages for juvenile cod in Newfoundland through the continuous and simultaneous tracking of a number of fish ($n = 28$). This was coupled to high-resolution mapping of bathymetry, substratum structure, currents and tides as well as spatial and temporal variation in temperature and salinity. Benthic mapping was accomplished using an acoustic seabed mapping system, together with baseline mapping undertaken by scuba divers carrying transmitters and tracing out the various environments within the study area. Fish position was associated with mapped environmental

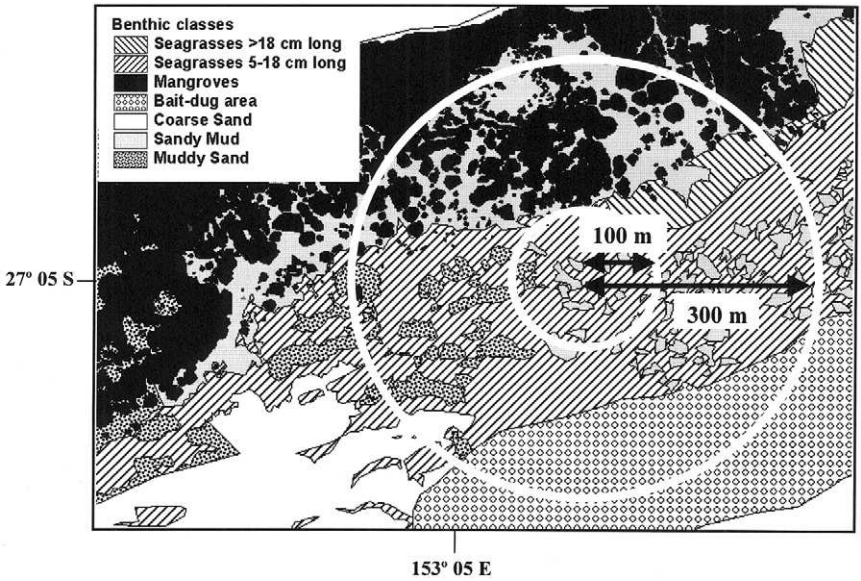

Figure 17 An example of mosaic patterns delineated at two spatial extents (100 and 300 m radii) around a beam trawl sample of 50 m length in Moreton Bay, Australia. Spatial extents were selected to explore the influence of spatial scale (the estimated home range and within the home range scale) on relations between mosaic structure and a number of attributes of the nekton assemblage (e.g., diversity, taxonomic distinctness, live mass, species composition, abundance, etc.). Benthic classes were determined using cluster analysis based on core samples. Boundaries were delineated using a combination of Landsat TM data, aerial photography, underwater videography and ground surveys as well as overlaying animal distributions to examine correlation between proposed biophysical boundaries and those meaningful to the animals of interest. Delineated circles were then clipped out and spatial pattern analysed using FRAGSTATS software (McGarigal and Marks, 1994).

features in a GIS using a point/polygon routine to link features to each fish position. Such an approach would reduce the bias associated with an arbitrary choice of scale and would also facilitate multi-scale spatial pattern analyses of benthic structure.

6. IMPLICATIONS FOR CONSERVATION AND RESOURCE MANAGEMENT

Animal movement is a mechanistic element of many ecological processes and therefore, understanding animal movement patterns throughout their life cycle is

fundamental to the effective design of conservation and resource management strategies (Acosta, 1999; Warner *et al*., 2000). For heavily exploited species, this information is crucial if populations are to be maintained or enhanced (Dugan and Davies, 1993; Zeller and Russ, 1998; Willis *et al*., 2001). The size, shape and geographical placement of management strategies such as reserves or marine parks must be driven by information on animal movement and the locations of key activities that allow a population to persist in an area. Furthermore, management strategies are unlikely to be effective without knowing how the component parts are connected (Wolanski *et al*., 1997). When establishing a reserve the objectives are usually to protect a region of high diversity or specific resource requirements for a threatened species or commercially valuable species (Tuck and Possingham, 2000). However, most reserve designs and site selection procedures have involved little scientific justification (Allinson *et al*., 1998) and rarely do plans for marine reserves incorporate specific movement patterns for key species for scaling reserve area and determining its shape and placement (Botsford *et al*., 2001). Modelling approaches for examining the structure and function of fishery reserves have also tended to assume high site fidelity or limited movements of animals in relation to reserve area (e.g. Sladek Nowlis and Roberts, 1999). This is largely a result of the fact that research has focused primarily on a few relatively site-attached individuals and because trajectories for most species are unknown or only poorly understood.

Where biological information has been used, it is traditionally based on knowledge of the requirements for single life stages (St Mary *et al*., 2000). However, strategies that are designed to consider only single segments of the life-cycle trajectory (e.g. adult or larvae; reproduction or settlement) are likely to be less effective than strategies that consider whole life cycle processes, particularly for exploited populations (Sladek Nowlis and Roberts, 1999). For instance, it may be counterproductive to manage only for locations of high larval retention or known settlement substratum that have no available resources in adjacent areas to support subsequent ontogenetic shifts (Acosta, 1999). Following extensive observations of spiny lobster distributions in the Caribbean Sea, Acosta (1999) recommended that the limited goals of marine reserves "must be expanded to the protection of all important habitats that will support an intact life history". The author also stated, "Shelter, foraging grounds, or movement corridors for exploited species must be quantified and incorporated into the design of protected areas". If a reserve is geographically placed in order to optimise survival for a particular species that uses inshore areas as a "nursery", but distant spawning grounds where mature adults aggregate are heavily exploited (or *vice versa*), then abrupt changes can be expected in overall abundance, regardless of the efforts put into the management strategy. The spatial and temporal domains of larval trajectories, ontogenetic shifts, home ranges, home range relocations and spawning and non-spawning migrations all have implications for reserve design. Essentially, when the home range of an animal is broader than the scale of the refuge, an animal will not receive full protection (Kramer and Chapman, 1999).

Research has shown that some species have evolved life-cycle movements that operate at scales of 10s to 100s km. In contrast, most management strategies operate at much finer-scales. In most parts of the world, matching such broad-scale movements with a single reserve is unlikely to occur. Instead, a system of marine reserves is required that covers locations of essential activities and includes pathways that link these locations. Sladek Nowlis and Roberts (1999) have argued that fish movement across boundaries will decrease the predicted yield from reserves. Consequently, reserves must be designed large enough or in large enough units to contain populations, particularly during the phase of their life in which they are most vulnerable to fishing. Furthermore, scales of movement patterns differ between species and between individuals of the same species. For example, several tagging studies of exploited species have shown both long-term site-fidelity by some individuals and extensive distances travelled by others (Attwood and Bennet, 1994; Beentjes and Francis, 1999). An acoustic telemetry study by Eristhee and Oxenford (2001) on space use of Bermuda chub (*Kyphosus sectatrix*) within a marine reserve, revealed that several individuals spent more than 60% of the their time outside the reserve boundaries. The implications of this variability are that one reserve design will be unlikely to function optimally for all species or all individuals (Allison *et al*., 1998; Sladek Nowlis and Roberts, 1999). Designing optimal strategies for multi-species assemblages is a significant problem that requires substantially more information on movement patterns than is currently available. However, in addition to tracking and tagging studies, it may be possible to use general models of movement parameterised by biological characteristics, such as life-history strategy or allometric scaling relationships or combinations of characteristics, to estimate relevant scales for reserve design (Kramer and Chapman, 1999).

Understanding movement also allows the opportunity to evaluate reserve function (Hixon *et al*. 2001). Reserve function can be examined directly through quantifying movement into and out of reserves, as well as the animal movement response to boundary placement that often occurs along physical discontinuities. For the management of exploited species, the main aim of a refuge or a no-take reserve is that animal biomass will increase within the protected area and eventually high density forces relocation, resulting in "spillover" into surrounding waters where they are fished (Russ and Alcala, 1996; McClanahan and Mangi, 2000). For some reserves, the contribution a relocating individual makes to nearby fisheries will be a function of its mobility and resource requirements. Indirect evidence of the spillover phenomenon can be found through observed changes in abundance and anecdotal reports from fishers. However, direct and more detailed evidence requires the application of tracking and tagging techniques (see Section 5.2 this paper and see Cole *et al*., 2000; Chapman and Kramer, 2000). Computer simulation combined with tracking techniques also provide an unprecedented ability to examine connectivity within networks of

marine reserves and to predict the spatial and temporal dynamics of source and sink areas (Arnold and Holford, 1995; Roberts, 1997; Botsford *et al*., 2001).

As argued here, the management of resources based on a purely anthropocentric perspective may not be sufficient to achieve goals related to effective ecological function. With current spatial technologies and rapid advances in tracking technologies, it is not unrealistic for movement patterns to be quantified and incorporated into management strategies. This information may encourage decision makers to look beyond evaluations of single habitat types and observation at arbitrary scales. For example, for fisheries based on tri-phasic species, the question should not be whether mangroves are more important than adjacent seagrasses, but how mosaics of habitat type, both inshore and offshore, combine to influence populations.

In addition to guiding scale selection in resource management evaluations and reserve design, analysis of movement data (particularly from advanced telemetry), can begin to answer some of the most challenging problems in marine ecology. Often observations of considerable temporal variability are reported to occur seasonally and on a lunar cycle, yet we rarely are able to sample widely enough to know where animals have gone. For instance, it should now be possible to track many species all year therefore allowing the identification of overwintering areas and spawning grounds as well as the trajectories linking these areas of essential activity. With the development of smaller transmitters, it will also be possible to directly quantify the patterns of movement between inshore nurseries and offshore adult populations. Furthermore, little is known of the movement response to changing environmental conditions and we speculate that the application of tracking techniques will provide great insights here. For instance, the dynamics of the response of highly mobile animals to a disturbance have important implications for impact assessment, since species-specific mobility may significantly influence the rate of recolonisation and therefore evaluations of the magnitude of the impact (Breitburg and Loher, 1994).

7. CONCLUSIONS

Differences in the scales of animal movement are the result of the evolutionary and ecological interaction with complex patterns and processes in the environment. Knowledge of the actual distances travelled as well as the directions of movement and movement pathways, is particularly useful in animal ecology, conservation and resource management. Using animal activity patterns to select appropriate scales with which to anchor our observations in time and space will improve sampling design, particularly in comparative studies. The application of a hierarchical approach, together with the coordinated integration of spatial

technologies offers an unprecedented opportunity for researchers to tackle a range of animal–environment related questions for highly mobile marine animals. Technological advances in tracking devices now allow us to fill in the gaps in the movements of animals with increasingly broad extent and fine resolution. This information complements existing studies and forms the basis of studies that aim to determine habitat suitability.

Overexploitation of marine animals is a global problem (Jackson *et al*. 2001) with no foreseeable solution in the near future. Nevertheless, it is clear that some management strategies are constrained by a lack of fundamental data on the scales relevant to the way animals use their environment throughout the life cycle. For exploited populations, it appears likely that maintenance of long-term sustainability will in part depend on understanding the relationship between animal movement patterns and management strategies, such as reserve design, size and placement. The use of computer-based spatial technologies such as GIS and advances in complementary technologies such as mathematical modelling and telemetry will facilitate the implementation of ecological information into planning strategies. Life-cycle trajectories and multi-scale environmental maps must become essential modules in the decision making process for ecologically meaningful resource management strategies. A concomitant shift in perspective toward a multi-scale organism-based approach to resource management will advance any attempts to understand both animal ecology and ensure a diverse and productive marine environment through ecological information-based management strategies.

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Culture of Harpacticoid Copepods: Potential as Live Feed for Rearing Marine Fish

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Copepods are useful as food for marine fish cultivation, in terms of both nutrition and ease of culture. Harpacticoid copepods are favoured over calanoids, since harpacticoids, as a result of their benthic habitat, can be reared at much higher densities. However, their benthic nature also makes mass culture difficult, since large surface areas must be provided. Within Harpacticoida, Tisbe *spp. seem most useful, having high overall fecundity, and positive phototaxis of the nauplii.*

Harpacticoids can synthesise de novo *several nutritionally important essential fatty acids (EFA), making them desirable as food for rearing marine fish. However, a diet rich in EFAs (e.g. animal derived feed) improves the productivity of copepod cultures, suggesting that the synthesis of EFA is rate-limiting for their reproduction. The nature of the substratum is also important in maintaining a good population, since harpacticoid biomass is more dependent on surface area than volume of a culture. Heterogeneous substrates can support large cultures because of their high surface area, but efficient cleaning methods are necessary. Frequent harvesting of populations will maintain good water quality and an overall low density of sexually mature copepods, raising naupliar productivity overall. Over-harvesting will naturally deplete the population.*

Harpacticoids are generally tolerant of environmental fluctuations but they do have temperature and salinity optima, and these will be species- and strain-dependent. Harpacticoid copepods are better food for fish larvae than Artemia, *because of their ability to synthesise EFAs. The nauplii of harpacticoids are energetically poor but appear to have an appetite–stimulatory effect. Uneaten nauplii grow within the fish rearing tanks and graze on the walls, building up their own nutritional value and maintaining tank hygiene.*

1. INTRODUCTION

Intensive culture of copepods is important in the rearing of marine fish. In this review the findings of previous reports on the suitability of cultured copepods as food for marine fish larvae are discussed in terms of nutritional quality and ease of cultivation. The different techniques used in copepod culture (e.g. diet, rate of harvest) are summarised. The suitability of different species for intensive culture of live feed is considered on the basis of their life history.

Cultivation of most marine fish species depends on the provision of live prey during the larval stage (Howell, 1979; Watanabe *et al.*, 1983; Leger *et al.*, 1986). The success of mass culture techniques for rotifers and *Artemia* has resulted in their widespread use as food for fish larvae. Both organisms provide a wide size range suitable for most marine fish larvae, but they are inherently nutritionally inadequate, having low levels of essential fatty acids such as docosahexaneoic

acid (22:6n-3, DHA), eicosapentaneoic acid (20:5n-3, EPA) and arachidonic acid (20:4n-6, ARA) that are required for normal development in several marine species (Sargent *et al.*, 1997, 1999). Both the absolute levels of these fatty acids and the dietary ratios between them are known to be important in maintaining larval viability. Although enrichment regimes to improve the nutritional value of rotifers and *Artemia* are well established, the rearing success of species such as Atlantic halibut (*Hippoglossus hippoglossus*) has had limited success owing to dietary problems.

There is considerable evidence that copepods are superior food organisms for fish and crustaceans in intensive systems (Watanabe *et al.*, 1983; Sun and Fleeger, 1995; Støttrup and Norsker, 1997). Among the order Copepoda, the subclasses Calanoida and Harpacticoida have been most studied in this respect. For example, when offered a mixture of prey items simultaneously, turbot larvae (*Scophthalmus maximus*) selectively ingested harpacticoid nauplii (Van der Meeren, 1991). Furthermore, copepods are known to have greater digestability (Schipp *et al.*, 1999) and a relatively high weight specific caloric content (Kahan *et al.*, 1982; Sun and Fleeger, 1995). They are also more nutritionally valuable than some strains of *Artemia*. Specifically, harpacticoids are rich in essential fatty acids, most notably 22:6n-3 and 20:5n-3 (Leger *et al.*, 1986; Norsker and Støttrup, 1994; Nanton and Castell, 1998a), which are vital for marine larval development (McEvoy *et al*., 1998; Shields *et al*., 1999). In addition, the growth stages of both calanoids and harpacticoids, from first nauplius to adult, provide a broad spectrum of prey sizes (80 to >900 μm in length and 3–5 μg in dry weight). This makes them suitable prey for a similarly broad range of developing fish sizes (Gee, 1989; Sun and Fleeger, 1995; Schipp *et al*., 1999). For example, the calanoid *Acartia* has been sucessfully fed to red snapper (*Lutjanus argentimaculatus*) for which rotifers are too large (Schipp *et al*., 1999). Conversely, Kahan *et al*. (1982) suggest that *Artemia* may be too large for larvae with especially small gapes. In addition to their nutritional and physical superiority as live feed, copepods are also highly suitable for culture because of their eurythermal and euryhaline characteristics. This gives them tolerance to wide environmental fluctuations (Miliou and Moraitou-Apostolopoulou, 1991a; Carli *et al*., 1995).

Although copepods in general make good prey items for fish larvae, it is important to consider certain *inter*-species characteristics if they are to be intensively cultured in sufficiently large numbers. The life-histories of calanoids and harpacticoids are fundamentally different. The majority of calanoid copepods are entirely planktonic, so their cultivation environments are homogenous and relatively easy to operate on different scales (Støttrup and Norsker, 1997). However, calanoid production is limited by difficulties in maintaining broodstock at high densities. Overcrowding decreases fecundity in the calanoid *Centropages typicus* (Miralto *et al*., 1996), and cannibalism of nauplii by adults can also occur (Ohno *et al*., 1990). Conversely, most

harpacticoids are benthic or epibenthic but sometimes enter near-bottom waters. They often serve as preferred prey for wild marine fish larvae (Sun and Fleeger, 1995). Since they are benthic, their population growth rate depends on the area of solid substratum but they can be produced in volumetrically much denser cultures than calanoids. However, such rearing environments are not homogenous and are correspondingly harder to scale-up and manage (Støttrup and Norsker, 1997). The two contrasting life histories in culture are emphasised in two separate studies. A large volume culture of the calanoid *Acartia tonsa* achieved a maximum density of 530 eggs l^{-1} (Støttrup *et al.*, 1986), whereas a small volume culture of the harpacticoid *Tisbe holothuriae* achieved 100,000 nauplii l^{-1} (Støttrup and Norsker, 1997). Nevertheless, a recent study on the intensive cultivation of the calanoid *Gladioferens imparipes* showed production rates comparable to harpacticoid culture (Payne and Rippingale, 2001), as a result of the unusual behaviour of this calanoid. Like harpacticoids, late copepodid and adult stages of *G. imparipes* hold onto surfaces (Rippingale, 1994). However, unlike harpacticoids, they continue to feed in the water column whilst still attached to the substratum, reducing the energy invested in swimming. Therefore, intensive cultivation of this particular calanoid may be enhanced by increasing substratum area (Payne and Rippingale, 2001).

Paffenhöfer and Harris (1979) have reviewed the techniques and problems of the laboratory culture of copepods, as applied to the study of plankton food webs. When we come to mass cultivation, the desirable characteristics of copepods are high reproductive potential, short turnover time (from egg to egg) and fast individual and population growth rates. Other requirements are a diet flexible enough to allow good growth on a variety of food sources and a tolerance of a wide range of environmental factors such as temperature and salinity (Sun and Fleeger, 1995). Although *Acartia* species (Calanoida) have been cultured successfully for many generations in the laboratory (Støttrup *et al.*, 1986) and in large outdoor tanks (Ohno *et al.*, 1990), the low culture densities make calanoids unsuitable for intensive mass cultivation. Furthermore, the large volumes necessary for pelagic calanoid production preclude precise control over food and water quality, resulting in variable copepod production (Ohno and Okamura, 1988). Harpacticoid species are therefore the preferred organisms for the development of intensive copepod culture (Støttrup and Norsker, 1997). Several harpacticoid species have been studied in this respect, under a variety of regimes. This review analyses the different species and rearing techniques used, with regard to life history (reproductive potential, turnover time). The influence of different diets and substratum are summarised, as are the relative merits of batch *versus* continuous culture and the effects of the rearing environment. Optimal harvesting techniques are also discussed. Finally, the general suitability of harpacticoid copepods as a diet for marine fish larvae is reviewed.

2. HARPACTICOID LIFE HISTORIES

2.1. The merits of candidates for harpacticoid culture based on life history

After stocking trays with 40,000 adult *Tisbe holothuriae* (predominantly ovigerous females; Plate 1), Støttrup and Norsker (1997) harvested a daily average yield of 300,000 nauplii per tray (see below for details of the cultivation system), or 125 nauplii $cm^{-2}\,d^{-1}$. This relatively high production is a result of the high reproductive capacity and short life cycle of *Tisbe*. For example, Miliou and Moraitou-Apostolopoupou (1991a, b) reported reproductive characteristics for *Tisbe* of 6.14 d for larval development, 1.40 d for egg sac maturation, up to 76 offspring per female, a longevity of as little as 14.67 d and inter-generation time was on average 8.11 d. Gaudy and Guerin (1982) reported similar findings.

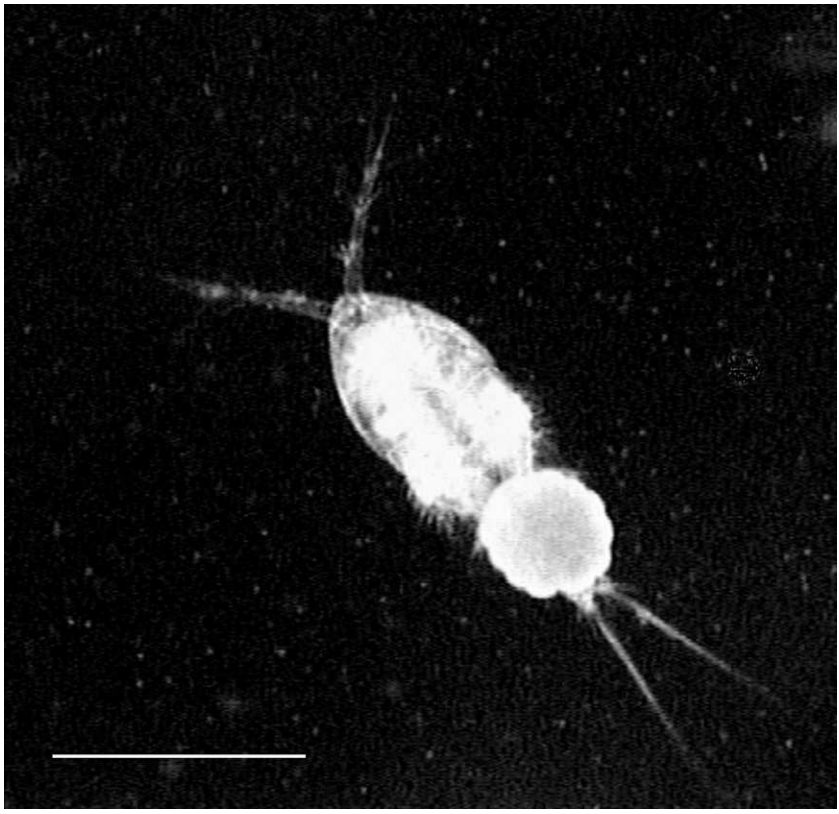

Plate 1 A gravid female *Tisbe holothuriae* with egg sacs (scale bar = 500 μm).

However, species of *Tigriopus* are considered by some to be more suitable for mass culture. Lee and Hu (1981) reported that female *Tigriopus japonicus* can produce up to 204 nauplii in two weeks, and Harris (1973) reported a total production of 301 eggs per female. Therefore *Tigriopus* is more fecund than *Tisbe*. However, generation time for *Tigriopus* is longer than for *Tisbe* (*ca*. 14 d) (Takano, 1971; Carli *et al*., 1995). Although more fecund, the longer generation time of *Tigriopus* means that *Tisbe* can achieve greater maximum yields in mass culture (Miliou & Moraitou-Apostolopoupou, 1991b). Additionally, within the genus *Tisbe*, *T. holothuriae* has higher values of intrinsic rate of natural increase (r_m) than other *Tisbe* species (r_m is the replacement rate of ovigerous females by their female progeny over time).

2.2. Broodstock regulation of naupliar production

There is experimental evidence that *Tigriopus* spp. show maternal hatching inhibition at high population densities (Kahan *et al.*, 1988), and there is also evidence of sex ratio regulation in *Tisbe*. Zhang and Uhlig (1993) discuss possible causes of sex ratio regulation: crowding may cause changes in sex ratio, with low female percentages occurring at high stocking densities. Their result agrees with an earlier study (Uhlig, 1984), and a study on *Tisbe clodiensis* by Fava and Ringoli (1977). However, Hoppenheit (1976) found the opposite situation in exploited populations. Egami (1951) demonstrated that sex ratio modification occurred in the fifth nauplii stage, but differential mortality thereafter between the sexes was unknown. Fava and Crotti (1979) hypothesised that copepods may respond to a complex chemical produced as a response to overcrowding, but Zhang and Uhlig (1993) found no evidence for this. As an alternative hypothesis, Brand (1985) suggested that crowding may change the behaviour of copepods, and perhaps their development. Nevertheless, Zhang and Uhlig (1993) stressed the need for further studies on the selective mortality of specific larval stages and sexes, to understand how sex ratio is regulated.

Early egg sacs produced by females tend to be substantially larger and with more nauplii hatched than later egg sacs. In a study on *Tisbe furcata*, Abu-Rezq *et al.* (1997) found that (although females only produced two pairs of egg sacs in total) up to 32 nauplii could hatch from the first egg sac, compared to a maximum of 19 from the second. The low number of egg sacs produced was because females were kept without males in this study. However, Johnson and Olson (1948) and Lee and Yan (1994) reported similar findings for *T. furcata* and *T. carolinensis* respectively: the first egg sac produced was twice as large as the last two or three produced.

Sexual dimorphism is apparent in many harpacticoid species. For example, male *T. carolinensis* are only 50 to 60% of the female length (Lee *et al.*, 1985). This may influence the choice of food particle size offered to a culture of

harpacticoids. Since males are smaller, with smaller feeding appendages, they may benefit from small food particles. Dimorphism will reduce intraspecific competition for food, but may also account for differential sex mortality under particular dietary regimes (Lee *et al*., 1985).

2.3. Behaviour

In addition to favourable reproductive characteristics, *Tisbe* also demonstrates changes in behaviour that make it suitable as prey for marine fish larvae. Although harpacticoids are benthic, *Tisbe* nauplii will collect in the upper water layers of first-feeding tanks after *ca.* 17 h post-introduction. Prior to this they exhibit benthic behaviour and are found predominantly on the tank walls. This change in behaviour makes them available to foraging fish larvae (Støttrup and Norsker, 1997). Furthermore, *Tisbe* nauplii exhibit positive phototaxis, making them relatively easy to harvest from the upper water layers of a culture. Adult and copepodite *Tisbe* exhibit more benthic behaviour, and are negatively phototactic (Støttrup and Norsker, 1997).

However, the negative phototaxism of adults and copepodites has also been used as a harvesting tool in a third genus, *Amphiascoides*. Sun and Fleeger (1995) collected older stages by harvesting from the dark end of a rearing tank. They also reported harvests of 70 copepods cm^{-2} d^{-1} from their culture system. This harvest included all stages of the life cycle, but no effort was made to maximise yield, so many more could probably have been collected. However, the initial population was much larger than the starting population reported by Støttrup and Norsker (1997): four million compared to 40,000. Despite longer generation times than *Tisbe*, this population of *Amphiascoides* produced a consistently good harvest. This may be, in part, a result of the larger initial population, which was also allowed to grow for one month unharvested.

3. THE EFFECTS OF DIET ON HARPACTICOID NUTRITIONAL QUALITY AND POPULATION GROWTH

3.1. Essential food types for copepod culture

Harpacticoids are widely distributed in coastal waters and particularly abundant in the near-shore benthic marine environment (Hicks, 1980). In their natural habitat, they feed on algae and settled organic particles (Coull and Wells, 1983). Harpacticoids can survive on diverse and nutritionally poor diets, a useful quality in such a variable environment as the near-shore benthos (Weiss *et al*., 1996).

In culture, a combination of different algae has been shown to be a better diet than monoxenic algal cultures, presumably because of the mix of vitamins, minerals and trace elements that are vital for the survival, growth and reproduction of animals (Lee *et al*., 1985). A range of food sizes may reduce differential sex mortality. However, copepod diet (in culture) is not necessarily limited to algae. Carli *et al.* (1995) compared *Tigriopus fulvus* culture performance between an algal diet (*Monochrysis lutheri*, 70,000 cells ml^{-1}) and a yeast diet (*Saccharomyces cerevisiae,* 0.1 mg ml^{-1}). Yeast-fed copepods had a lower daily production of nauplii than those fed on algae, but naupliar production was spread over a longer time period. Algae-fed copepods also exhibited lower survival and a higher incidence of infertile females. The authors concluded that both diets were beneficial: algal food provided a high daily naupliar production, but yeast-fed copepods had higher overall production over a longer period of time. Therefore diet can have a big influence on the reproduction and life history of harpacticoids.

3.2. The effects of diet on productivity

It must be stressed that copepod productivity is directly correlated with several life-history parameters: survival, sex ratio, the number of egg sacs per female, the number of offspring per female and the development rate. Furthermore, different diets may favourably affect different parameters. For example, Miliou and Moraitou-Apostolopoulou (1991b) tested the influence of diet on several life-history parameters. They reported that the seaweed *Ulva* increased the developmental rate of nauplii and copepodids, also increasing the survival of nauplii, whereas the artificial compound feed Fryfood® (Waterlife) increased offspring production and increased the survival of copepodids.

Generally, the suitability of different diets depends on their digestibility and how they fulfil the nutritional requirements of the species. The free amino acid content does not seem to be very important, since the diet richest in amino acids tested by Miliou and Moraitou-Apostolopoulou (1991b) was also the least nutritious. However, total protein content does seem to be important. Lee *et al.* (1985) found that the algal diet with the highest protein content sustained the best copepod reproductive performance in *Tisbe carolinensis*. Similarly, Guidi (1984) found survival and naupliar development rate related to the protein content of the diet. Copepod tissue protein can vary between 24 and 82% dry weight (Båmstedt, 1986). The lowest values tend to occur in high-latitude and deep-water low-latitude species. Female *T. holothuriae* (a mid-latitude species) have a very high protein content (72%; Miliou *et al*., 1992), but has a low lipid (10%) and hence energy content (Miliou *et al*., 1992). However, the nauplii are initially lipid-rich, having received lipid reserves from the mother, and small fish larvae tend to prefer the small naupliar stages for first-feeding (Kahan *et al.*, 1982).

3.3. The importance of fatty acids

As already noted, marine fish larvae have a nutritional requirement for live food with high concentrations of the long chain n–3 essential fatty acids such as eicosapentaenoic acid (EPA; 20:5n–3) and docosahexaenoic acid (DHA; 22:6n–3) (Watanabe, 1982). Arachidonic acid (10:4n–6; ARA) is also considered to be essential for marine fish, but is less important (Castell *et al*., 1994). Marine fish require these fatty acids in their diet since they lack the desaturase enzymes necessary to convert short chain fatty acids into their long chain EFA end-products (Tocher *et al.*, 1989). These three EFAs play a role in maintaining the structural and functional integrity of cell membranes, and a more specific role as precursors of eicosanoids (a group of highly biologically active paracrine hormones). Rod cell outer segment membranes and the membranes of synaptic junctions are especially rich in DHA in fish. The eicosanoids are highly active C20 compounds. They are produced in responses to stress, such as cardiovascular functions including blood clotting and the inflammatory response. Of EPA and ARA, the major precursor of eicosanoids is ARA, with EPA competitively inhibiting the formation of eicosanoids from AA. Similarly, eicosanoids formed from EPA also interfere with the actions of eicosanoids formed from AA. Therefore, stress responses governed by eicosanoid functions are modulated by the ratio of ARA : EPA. High levels of EPA relative to ARA will reduce eicosanoid actions (Sargent *et al*., 1999). Halibut larvae fed a mixture of calanoid copepods (largely *Centropages hamatus* and *Eurytemora* spp.) show higher survival and improved pigmentation than larvae fed on enriched *Artemia* nauplii. This is related to the higher percentage levels and ratios of DHA, EPA and AA found in the copepod diet (Sargent *et al*., 1999).

Harpacticoid copepods can produce significant amounts of EPA and DHA when fed diets deficient in these EFA. *Tisbe* spp. contain the desaturase and elongase enzymes necessary to convert 18-carbon fatty acids into longer chain DHA and EPA (Nanton and Castell, 1998a). Furthermore, copepods have a high proportion of DHA in their polar membrane lipids, as opposed to their neutral lipids (cf. *Artemia*). Polar lipids are involved in the formation of lipid emulsions that facilitate lipid digestion. The increased amounts of DHA in the polar lipid fraction therefore increases the digestibility of DHA in marine fish larvae fed copepods (Nanton and Castell, 1999). Although copepods are capable of *de novo* fatty acid synthesis, it ceases in the presence of a substantial input of dietary fatty acids. However, the fatty acid content of food will influence copepod productivity, namely improving copepodid survival and egg number (Miliou and Moraitou-Apostolopoulou, 1991b). Therefore animal-derived feeds have proved to be more efficient than compound vegetarian feeds (e.g. soya and yeast), and Guérin and Gaudy (1977) have shown that *Tisbe holothuriae* has a higher productivity and lipid content when fed on animal-derived compound artificial diets. *Tisbe* species are attractive live food organisms for marine fish culture since

their high desaturase activity ensures the production of large quantities of favourable fatty acids (such as DHA) even if the EFA composition of their diet is poor (Nanton and Castell, 1999). Since fatty acid synthesis ceases under a large input of dietary fatty acids, the fatty acid distribution in copepods largely reflects that of their diet (Norsker and Støttrup, 1994). Synthesis of EFAs may be rate-limiting for reproduction, so the dietary supply of fatty acids would enhance naupliar production (see above). Furthermore, diets rich in animal-derived fatty acids increase the carbon content, C : N ratio, and the energy content of *T. holothuriae* (Miliou, 1996). Despite improved productivity under such regimes, final body size remains almost constant. It is hypothesised that harpacticoids, since they are not normally subjected to periodic variation in food supply, can utilise excess energy for reproduction at the expense of storage. This will keep final body size constant (Miliou, 1996).

3.4. The physical factors of diet

Suitability of diet does not depend on chemical composition alone. The seaweed *Ulva*, as well as improving developmental rate, increases the substratum available to *Tisbe*, and an increase in the surface to volume ratio in rearing tanks can result in an increase in production (Miliou and Moraitou-Apostolopoulou, 1991b). Furthermore, live seaweed can supply oxygen and absorb toxic compounds (Harlin, 1978). As mentioned earlier, a range of particle sizes is necessary to match the changing size of copepod mouthparts during development. The success of a diet will also depend on whether it allows bacteria to proliferate. Harpacticoids can assimilate bacteria, and bacteria will also serve as food for microzooplankton on which the copepods feed (Rieper, 1978; Miliou and Moraitou-Apostolopoulou, 1991b). Finally, the optimum diet should be cheap and simple, such as an easily available animal-derived compound diet, used in conjunction with algae (rich in fatty acids) or a seaweed to increase surface area (Guérin and Gaudy, 1977; Miliou and Moraitou-Apostolopoulou, 1991b).

4. THE EFFECTS OF DIFFERENT SUBSTRATA ON HARPACTICOID POPULATIONS

Choosing a suitable substratum is essential for good productivity in a copepod culture. Since harpacticoids are benthic, it is important to have a large surface area to volume ratio. Støttrup and Norsker (1997) investigated two different methods for achieving this. One method employed large, shallow trays, to which fresh seawater and algae (*Rhodomonas baltica*) were added daily, after removing *Tisbe* nauplii through a mesh. This is a batch culture method, and is

rather labour-intensive. Therefore Støttrup and Norsker (1997) designed a continuous culture system, to compare efficiency and productivity with batch culture. The continuous culture system consisted of a closed bioreactor continuously supplied with algae. Positively phototactic nauplii were harvested from the upper water layers. In order to provide a large surface area, the bioreactor was filled with polypropylene balls. All the balls developed a thin biofilm. By calculating the surface areas of both systems, the authors deduced that productivity in the bioreactor was only 32 mg m^{-2} d^{-1}, compared with 100 mg m^{-2} d^{-1} in the tray system. The authors suggested that the relatively poor productivity was a result of insufficient capacity of the algal dosing system. The addition of more food did improve productivity in the continuous system (Støttrup, unpublished data).

The preference for sand or mud substrata of a particular size, texture and faunal composition is the main factor that precludes the easy cultivation of harpacticoids (Hockin, 1981; Chandler, 1986). Although *Tisbe* spp. are semi-planktonic, a substratum providing a large surface area will be important for the adults. Chandler (1986) experimented with mud and sand substrata and found that cleaned and sorted mud was superior because all the sediment particles were less than 0.125 mm. Adult and late-stage copepodites are usually larger than 0.125 mm, allowing them to be easily separated in a sieve. Care must be taken to prevent excessive bacterial films overgrowing the substratum, entrapping and killing the copepods. Chandler (1986) prevented fouling by not feeding cultures until accumulated food on the substratum disappeared.

Although most studies attempting large-scale harpacticoid production have eliminated the use of natural substrata, and use glass or plastic surfaces, Sun and Fleeger (1995) used limestone cobbles in a system that produced in excess of one million indivivduals (5 g dry weight biomass) of *Amphiascoides atopus* per day. They covered a surface area of 2 m^2 with cobbles (1 cm in diameter) to 2 cm in depth. Air lifts were used to increase gas exchange. These authors attributed the large daily harvests to the large surface area available for growth, and to the biofilms and bacteria coating the limestone cobbles. The system only ran for 17 weeks, and the authors stressed the need to devise a low-maintenance method to clean the culture and prevent the build-up of faeces and decomposing algae. Kahan *et al.* (1982) used a novel technique, bypassing the use of trays or natural substratum. They employed floating net-bottomed trays with an appropriate pore size, allowing *Tisbe* nauplii to pass directly into the fish tank. This system allowed close observation and control of conditions, particularly of excessive bacterial growth. The total number of nauplii produced per tray (200 cm^2) per day was 132,000, with a density of 10 nauplii per ml for the whole tank volume. The floating trays also removed the need to harvest copepods and then offer them to fish larvae (See Table 1 for the efficacy of different rearing systems standardised for unit area).

Table 1 Rearing systems, food types and subsequent naupliar productivity.

Species	Rearing system	Food type	Temp. (°C), Salinity (ppt)	Productivity	Reference
T. holothuriae	Floating mesh baskets with running water	*Mytilus* powder, lettuce leaves & Ulva	27, 40	660 nauplii cm^{-2} d^{-1}	Kahan *et al*. (1982)
T. holothuriae	Static glass bowls	*Dunaliella tertiolecta*, *Skeletonema costatum*, *Mytilus edulis*	20, 28	150 nauplii cm^{-2} d^{-1}	Zhang and Uhlig (1993)
	Plexiglas cylinders with running water			830 nauplii cm^{-2} d^{-1}	
A. atopus	Recirculating culture tanks with limestone cobbles	*Chaetoceras mulleri* & TetraMarin fish flakes	24, 32	12.5 copepods cm^{-2} d^{-1}	Sun and Fleeger (1995)
T. holothuriae	Static trays	*Rhodomonas baltica*	18, N/A	125 nauplii cm^{-2} d^{-1}	Støttrup and Norsker (1997)
	Closed bioreactor with polypropylene balls			13 nauplii cm^{-2} d^{-1}	

5. THE EFFECTS OF HARVESTING

Harvesting, or the regular exploitation of copepod cultures will affect the biomass and the production of the population. Therefore a good knowledge of the conditions of exploitation is required to guarantee the maintenance of a good yield. Using *Tisbe holothuriae*, Gaudy and Guerin (1982) maintained populations for 70 days and found that mean production was highest in the most frequently harvested culture (weekly exploitation, with 50% of the tank volume being removed). The frequent harvesting increased the ovigerous rate in the population (the percentage of females with egg sacs), demonstrated by the high production. Citing a paper by Alessio (1974), where a population of *Tisbe furcata* were exploited daily at 40% with no decrease in yield, Gaudy and Guerin (1982) suggested that the maximum yield of their own cultures was probably not reached. However, they cautioned that too rapid a harvest frequency will decrease the yield, citing a study on *Acartia tonsa* (Heinle, 1970). This study reported that a harvesting frequency of four days was too rapid to maintain the population level. By also varying the amount of water removed at harvest, Gaudy and Guerin (1982) hypothesised that the increase in production was a result of improvement in water quality and the decrease in density brought about by the harvest. Crowding can lower naupliar production and survival (Zhang and Uhlig, 1993). Sun and Fleeger (1995) also reported no population decline, even with a high level of exploitation (more than one million individuals per day).

These studies complement earlier work by Hoppenheit (1975, 1976). He reported low naupliar mortality at high exploitation rates, attributable to the subsequent low densities. He also proposed that sex ratio was influenced by high exploitation rates or low densities: a surplus of males was found at an exploitation rate of 90%, while more females were found at an exploitation rate of 10%. However, the paucity of explicit studies on the effect of exploitation rates on standing biomass demonstrates that this important factor has been relatively neglected.

6. ENVIRONMENTAL EFFECTS ON HARPACTICOID QUALITY AND GROWTH

6.1. Effects of density

It has already been stated that the density of a population can affect population growth by modulating survival, development and fecundity. This is an important observation, especially since the mass culture of *Tisbe* spp. is related to the

available substratum area, rather than the available water volume (Zhang and Uhlig, 1993). Female fecundity is influenced by both the density of breeding females and nauplii. It has been suggested that complex chemical compounds may be produced by the animals as a result of crowding, allowing them to perceive and respond to different crowding levels (Zhang and Uhlig, 1993). A study on the harpacticoid *Tigriopus japonicus* demonstrated maternal inhibition of hatching at high population densities (Kahan *et al.*, 1988). This was mediated by a physical connection between the mother and mature embryos: proximity of a mother to her detached egg-sac did not prevent hatching. Electron microscopy observations led Kahan *et al.* (1988) to postulate that hatching was inhibited by the mother through an 'umbilical cord' during overcrowded conditions. Such a hatching mechanism may be useful for harpacticoids in tide-pool habitats: hatching inhibition could delay the hatching of nauplii into a crowded environment until the next tide distributed nauplii to less crowded habitats (Kahan *et al*., 1988).

Alternatively, it has also been hypothesised that crowding may change the behaviour of copepods and their development (Brand, 1985). Since fecundity decreases with increasing density, Zhang and Uhlig (1993) suggested a density of 40 female *Tisbe holothuriae* per cm^2 to achieve maximum daily yield of nauplii.

6.2 Effects of salinity

In addition to biotic environmental factors, abiotic factors will also affect the population dynamics of harpacticoids. Harpacticoids are very tolerant to environmental fluctuations, but establishing the most favourable conditions for mass culture is paramount. Using a Greek strain of *Tisbe holothuriae*, Miliou and Moraitou-Apostolopoulou (1991a) found an optimum salinity of 38 for offspring productivity. The decreased fecundity beyond 38 suggested inhibition of an enzymatic mechanism at salinities different from those to which the strain is genetically acclimated. Furthermore, in extreme salinities (20 and 48), the strain tested was not able to survive. Inter-population tolerance differences are therefore of considerable importance, both for their ecology and for mass culture. Generally *Tisbe* has limited euryhalinity and can only reach its maximum development in culture within a narrow range of salinity (Miliou and Moraitou-Apostolopoulou, 1991a). Moreover, sub- and supranormal salinities will cause a decrease in total body length. Extreme salinities require extensive adjustments in osmoregulation and will affect structural properties of aquatic invertebrates (Miliou, 1996). Estuarine harpacticoids, such as *Amphiascoides subdebilis*, are able to survive over a wider range of salinities, but will still show a preferred optimal salinity for fecundity and longevity (Ingole, 1994). Salinity appears to affect mainly longevity and the number of offspring per egg sac.

Temperature appears to have a more pronounced effect (Miliou and Moraitou-Apostolopoulou, 1991a).

6.3. Effects of temperature

Developmental rates are dependent on temperature in addition to food concentration (Peterson, 2001). Miliou and Moraitou-Apostolopoulou (1991a) stated an optimal culture temperature of 19ºC for their strain of *Tisbe holothuriae*. Lower temperatures caused longer development and maturation, but also an increase in the number of offspring per egg sac. Higher temperatures caused an acceleration of development and maturation but a reduction in the number of offspring per egg sac. In both cases the number of egg sacs and offspring decreased. Therefore temperature had a more pronounced effect than salinity. There is a well-documented inverse relationship between temperature and zooplankton body size (McLaren, 1965; Corkett and McLaren, 1978). Fecundity increases with increasing body length (McLaren, 1965). The increase in total body length of *Tisbe holothuriae* at low temperatures is associated with an increase in number of eggs per egg sac (Miliou and Moraitou-Apostolopoulou, 1991a). The two factors of temperature and salinity act on populations independently, as there was no significant interaction between the two variables (Miliou, 1996).

In addition to affecting population variables, temperature can also have a marked effect on the nutritional quality of copepods. Nutritionally important long-chain EFAs, such as DHA, EPA and ARA are incorporated into cell membranes, where they help maintain membrane fluidity. Nanton and Castell (1999) hypothesised that in response to lower temperatures, copepods would increase the amounts of long-chain EFA to maintain a standard membrane fluidity (homeoviscous adaptation; Sinensky, 1974), since they can synthesise fatty acids *de novo*. Using two genera of harpacticoid, *Amonardia* and *Tisbe*, the authors found higher levels of DHA, EPA and ARA at 6ºC compared with 15ºC. However, DHA and EPA were also high at 20ºC. This may have been a result of selective oxidative catabolization of neutral lipids, rather than phospholipids, raising the relative amounts of DHA and EPA accordingly. Although satisfying the hypothesis of homeoviscous adaptation, the high levels of DHA and EPA (and high DHA : EPA ratio) at the higher temperature precludes the need to raise EFA levels by lowering the water temperature (Nanton and Castell, 1999).

6.4. Effects of turbulence

Harpacticoids such as *Tisbe* are semi-planktonic, so it is worth noting the effects of turbulence on copepod productivity. The first limiting step for feeding and

reproduction is the initial encounter of prey or mate. Under turbulence, the contact rates are higher than predicted when only densities and relative velocities of predator and prey are considered (Saiz *et al.*, 1992; Alcaraz, 1997). It can also indirectly increase food intake by changing the patchiness of algal food (Kiørboe, 1993). Although food intake rates can be increased by turbulence, it can also decrease the number of eggs laid per female. This is because of an increase in metabolic rate caused by the turbulent conditions (up to 115%; Alcaraz, 1997), and a concomitant decrease in the energy allocated to egg production (Saiz and Alcaraz, 1992). Food concentration also plays a role, in addition to turbulence, in modifying the energetic balance between gains and losses. For low food concentrations, turbulence increases the energy gains of copepods, while energetic costs are much higher at high food concentrations (Marrasé *et al.*, 1990). Although this work was carried out on calanoid copepods, it will apply to zooplankton in general.

Working on *Acartia grani*, Alcaraz (1997) observed a reduction in the development time for the different instars under turbulent conditions. Life span was also shortened, and both effects may be a result of higher metabolic costs. A lower proportion of males was also observed under turbulent conditions (Alcaraz *et al.*, 1988). Although feeding is increased, turbulence tends to reduce overall biomass owing to the decrease in size and fecundity. Therefore the turbulence characteristics of a culture can be a significant factor in the productivity of copepod populations.

7. HARPACTICOIDS AS PREY FOR MARINE FISH LARVAE

In a study comparing wild copepods with enriched *Artemia*, McEvoy *et al.*, (1998) found much greater proportions of polar lipid in the copepods (66% compared with 36% in the enriched *Artemia*). This was reflected by significantly higher proportions of polar lipid in the copepod-fed fish. It has been suggested that polar lipids are more readily digested by larvae and may facilitate the digestion of other lipids in the digestive tract of larval fish (Koven *et al.*, 1993). Furthermore, halibut larvae fed copepods were heavier from 30 days after first-feeding than their *Artemia*-fed conspecifics (McEvoy *et al.*, 1998).

Harpacticoids such as *Tisbe* have great potential as live food, since they contain large amounts of EFAs and have consistently high DHA:EPA ratios even when fed on EFA-poor food such as yeast. Furthermore, newly hatched nauplii are 90 μm long and reach 2 mm as adult females, so they could potentially replace both rotifers and *Artemia* throughout the first-feeding stage of marine fish (Nanton and Castell, 1998a). However, a potential drawback is their benthic nature. *Tisbe* tends to stay near the sides and the bottom of the tank, rather than swimming freely where the larval fish can feed upon them (Nanton and Castell, 1998a). Nevertheless, a later study by the same authors demonstrated improved

growth in haddock larvae (*Melanogrammus aeglefinus*) fed on *Tisbe* at 19 days post-hatching, compared with those fed rotifers (Nanton and Castell, 1998b). Furthermore, Støttrup and Norsker (1997) demonstrated that, despite their benthic nature, *Tisbe* nauplii were available to fish larvae. Nauplii were present in the water column from ten hours post-introduction, and successful first-feeding of turbot larvae could be established with *Tisbe* nauplii alone. *Tisbe* nauplii are half the size of rotifers, and have a caloric content of 0.00147 J per individual, compared with 0.0036 J for rotifers. Despite this, the introduction of *Tisbe* nauplii seemed to have an appetite-stimulatory effect, and fish co-fed with *Tisbe* and rotifers grew better than those fed rotifers alone (Støttrup and Norsker, 1997). A study using larval Dover sole (*Solea solea*) showed similar results. Including *Tisbe* in the dietary regime resulted in improved appetite and growth rate compared to sole reared on *Artemia* alone (Heath and Moore, 1997). Furthermore, pigmentation is improved in both halibut and sole larvae, possibly as a result of the high levels of DHA present in copepod diets (Heath and Moore, 1997; McEvoy *et al*., 1998).

As well as providing a superior diet, harpacticoid nauplii that are not eaten would be able to find nourishment in fish-rearing tanks by feeding on detritus, the biofilm and bacteria, maintaining their nutritional value as well as keeping the tank clean. These are both important factors in the successful rearing of marine larvae (Norsker and Støttrup, 1994).

8. CONCLUSIONS

Comparing harpacticoid life histories, *Tisbe* spp. seem more suitable for mass culture because of their short generation time and high rate of natural increase. Although *Tigriopus* spp. are generally more fecund, their longer generation time makes them less suitable for mass culture. Although benthic, *Tisbe* nauplii will exhibit positive phototaxis, enabling easy harvesting and increasing availability to foraging fish larvae. In terms of suitable diet for mass harpacticoid culture, the importance of a large size range of food particles must be stressed, since sexual dimorphism occurs, as does changing mouthpart size during copepod development. Of several diets tested, animal-derived compound feed seems best. Although harpacticoids can biosynthesise nutritionally important essential fatty acids, their productivity is rate-limited by this biosynthesis, so cultures fed with EFA-rich diets usually show enhanced productivity. However, seaweed diets, as well as providing food, also provide a large area of substratum. This is an important point, as harpacticoid productivity is related more to surface area than volume, and seaweed will supply oxygen and absorb toxins. Although most cultures have been raised using glass or plastic surfaces, good results can be obtained using more natural substrata, such as limestone cobbles. This technique provides a large surface area for copepod

growth and for biofilm and bacteria deposition. However, effective methods of cleaning are still to be developed.

Harvesting will also affect productivity, by affecting the standing density of the culture. Frequent harvesting (with the addition of fresh seawater to replace that removed by the harvest) maintains a low standing density and high water quality, with subsequent high naupliar productivity. However, too frequent a harvest will eventually reduce the yield, by lowering the population level. A density of 40 female *Tisbe holothuriae* per cm^2 has been suggested to achieve a maximum yield of nauplii. Although *Tisbe* are tolerant of environmental fluctuations, an optimal salinitiy and temperature of 38 ppt and 19°C respectively have been suggested for *Tisbe* cultures, although there will be inter-strain differences in performance. Temperature will also increase the amounts of EFA in copepods, with high amounts at low temperatures. However, there seems to be no need to lower temperature to increase EFA levels, as high levels of EFA are also present at higher temperatures owing to selective oxidative catabolization of neutral lipids. Turbulence will also affect productivity in contrasting ways. Although it can increase feeding rates, turbulence can also increase metabolic expenses, lowering productivity and life span in copepod cultures. Harpacticoids seem suitable as a diet for marine fish larvae because of their relatively high levels of essential fatty acids, even when fed on an EFA-poor diet. The nauplii are available to fish larvae in the water column, although the adults are benthic. Furthermore, although small in comparison to rotifers, *Tisbe* nauplii appear to have an appetite-stimulatory effect on fish larvae when co-fed with rotifers. Uneaten harpacticoids will also graze on rearing tank walls, maintaining their own nutritional value and tank hygiene.

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