

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/226040644>

# Distribution of crustacean diapause: Micro- and macroevolutionary pattern and process

Article in *Hydrobiologia* · March 1996

DOI: 10.1007/BF00016802

---

CITATIONS

135

---

READS

481

2 authors, including:



[Nelson Hairston](#)

Cornell University

170 PUBLICATIONS 13,955 CITATIONS

[SEE PROFILE](#)

## Distribution of crustacean diapause: micro- and macroevolutionary pattern and process

Nelson G. Hairston, Jr. & Carla E. Cáceres

*Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853, USA*

### Abstract

Theoretical predictions for the relationships between duration of dormancy, reproductive life span, and dispersal ability developed for plants in temporally varying environments are applied here to crustaceans. Mathematical models suggest that diapause duration should negatively covary with adult life span, and that both diapause and life span should negatively covary with dispersal ability. A survey of 167 crustacean species from 20 orders and three classes confirms that species with prolonged diapause have short adult life spans and those with long adult lives either have diapause lasting less than a year, or do not diapause at all. Prolonged diapause is more common among small or inland water crustaceans than it is among large or marine species, whereas large or marine species have significantly longer adult life spans on average than do those that are small or from inland waters. A greater fraction of species in the Branchiopoda exhibit prolonged diapause than do members of the Maxillopoda which, in turn, are more likely to exhibit prolonged diapause than are the Malacostraca. A greater fraction of malacostracan species have adult life spans exceeding one year than do species in either the Branchiopoda or the Maxillopoda. Cladistic analysis shows that phylogenetic constraint is likely to be at least in part responsible for the expression of diapause among the Crustacea. We conclude that both natural selection and macroevolutionary pattern have influenced the distribution of diapause among modern crustaceans.

### Introduction

The diapause trait is by no means evenly distributed within the Crustacea, either among species living in different habitats or among higher taxonomic categories. Crustaceans found in inland bodies of water, especially those that dry occasionally, are more likely to possess a diapausing stage than are those living in the open ocean. The Malacostraca, including the decapods, euphausiids, amphipods, isopods, and so on, are markedly depauperate in species exhibiting diapause, whereas the Branchiopoda such as the 'cladocerans', 'conchostracans', anostracans, and notostracans are rich in such species, and the Maxillopoda (e.g., copepods, ostracods) present a mixed picture. Two possible explanations for these uneven ecological and taxonomic distributions of diapause are: (1) the patterns reflect selection pressures exerted on crustacean species by the environments in which they live: diapause is favored in some habitats and not in others, and (2) the patterns are the result of phylogenetic history: the diapause trait is primitive for some groups and not

for others, hence its uneven distribution between broad taxonomic categories.

These two possibilities are not necessarily independent since direction and strength of selection are in part a function of the characters an organism already possesses, and these are in part a function of past selection pressures (which are frequently not statistically independent of current selection pressures).

Here we ask how selection might be expected to act on the expression of diapause, by applying predictions of optimization and ESS (Evolutionarily Stable Strategy) models developed principally to understand plant seed dormancy. We then investigate whether the association between diapause and other life-history traits within the Crustacea conforms with theory. We explore the phylogenetic expression of diapause among crustacean taxa, and end by asking how selection at the microevolutionary scale may have interacted with macroevolutionary pattern to produce the distribution of diapause we observe in nature.

There is a robust theoretical literature concerning how selection might be expected to act on seed dormancy in plants. Duration of dormancy, expressed as the fraction of seeds expected to germinate in each year, has been related both to environmental features and to other plant life history characteristics. Dormancy response to temporal or spatial variation in reproduction and survival has been investigated by Cohen (1966), Ellner (1984), and Philippi (1993), while response to the life history traits, seed dispersal, adult life span, and offspring survival have been explored by Venable & Lawlor (1980), Levin *et al.* (1984), Cohen & Levin (1985) and Rees (1994). Because the environments in which crustaceans live are also variable, and because prolonged diapause is a prominent feature in the life history of many crustacean taxa, much of this plant dormancy theory has potential relevance for understanding the distribution of the diapause trait among the Crustacea.

Although theory has also been developed specifically for understanding animal diapause in both insects (e.g., Levins, 1969; Cohen, 1970; Taylor, 1980) and crustaceans (Hairston & Munns, 1984; De Stasio & Hairston 1992), these efforts have been restricted largely to predicting seasonal diapause timing. The questions we address here concern instead the evolution of diapause duration, and this theory has been the province of plant ecologists and evolutionary biologists (Livdahl's, 1979, paper on insects is an exception). It is our thesis that the prolonged survival of crustacean diapausing eggs is analogous to seed dormancy that lasts over multiple years (or multiple opportunities to germinate or hatch), and thus subject to many of the same analyses.

Our reason for concentrating on prolonged diapause lies in its relevance to fitness in a temporally varying environment. Most, perhaps even all, environments vary in suitability for reproduction and survival between years. Occasional years may be so poor that no new individuals are recruited to the population, and cannot be survived by an annual organism that saves no eggs for hatching in subsequent years. Although the optimal duration of prolonged dormancy is related to the frequency of low recruitment years, note that it is not necessary that recruitment ever reach zero (Ellner, 1985). Cohen (1966) showed that as the variance in the quality of the environment for recruitment increases, the fraction of seeds that germinate (or diapausing eggs that hatch) should decline, although zero germination

or hatching should never occur. Ellner (1985) pointed out that this result depends quantitatively on the probability a seed (egg) has of surviving until the next opportunity to germinate (hatch). The lower the probability, the higher the germination (hatching) fraction. Furthermore, Easterling & Ellner (1994), considering copepod diapausing eggs, have shown that the result also depends on the probability that eggs receive the hatching cue.

In plant ecology, the pool of seeds that do not germinate the year after they are produced is called the 'seed bank'. For crustaceans, the analogous pool of diapausing eggs has been termed the 'dormant propagule pool' (Hairston & De Stasio, 1988) or the 'egg bank' (De Stasio, 1989; Marcus *et al.* 1994). The presence of an egg bank in a population can alter its dynamics by effectively lengthening generation time, which can lead to a slowing of the rate of response to natural selection (Hairston & De Stasio, 1988), maintenance of genetic variation (Ellner & Hairston, 1994), or alterations of the outcome of competition (Ellner, 1984; Shmida & Ellner, 1984; Cáceres, 1994; Hairston *et al.*, 1995a).

Two life-history characters should, in theory, alter expected duration of prolonged diapause in a temporally variable environment: (1) the degree of iteroparity, and (2) dispersal capability. Iteroparity is itself hypothesized to be an adaptation to a temporally varying environment (Murphy, 1968; Stearns, 1976; Roff 1992). Here we take environmental variation between years to be the most important temporal scale, and so by iteroparity we mean reproduction by one individual in more than one year (our argument holds for other temporal scales as well). If occasional recruitment failures are probable, then iteroparity provides reproduction in future favorable years. In fact, iteroparity and prolonged diapause can be seen as alternative mechanisms to solve the same problem of temporal environmental variation. Rees (1993, 1994) has recently explored the tradeoffs between these two traits for plants. His fundamental conclusion is that when offspring survival varies between years, plants with long adult life span should make seeds with a much higher germination probability (shorter or no prolonged diapause) than plants with a short adult life span. There is no reason to have both iteroparity and prolonged diapause. In a review of the literature for 171 plant species, he found that the general trend predicted was in fact observed (Rees, 1993).

Venable & Lawlor (1980) and Levin *et al.* (1984) explored an alternative tradeoff in plant life histories:

that between duration of seed dormancy and dispersal ability. Their proposal is that if an environment varies both temporally and spatially, so that different patches of the environment are of different quality at any given time, an annual organism may avoid unfavorable conditions by either surviving in dormancy or by dispersing (note that prolonged diapause can be thought of as dispersal in time; Templeton & Levin, 1979). The result depends quantitatively on how successful a dispersing organism is at finding a suitable habitat (Levin *et al.*, 1984; Cohen & Levin, 1985), but the general conclusion is that as dispersal ability increases, the duration of dormancy should decrease. Venable & Lawlor (1980) reviewed data for 28 plant species with seed polymorphisms for dispersal near-to and far-from the parent plant. Consistent with theory, they found a repeated pattern of near dispersal being associated with delayed germination and far dispersal with rapid germination. Similarly, Rees (1993) found that species with less seed dormancy are significantly more likely to possess efficient dispersal strategies (defined by seed morphology).

Do crustaceans show similar patterns? To answer this question, we reviewed the literature for 167 species (Appendix 1), taken from 20 orders in 3 classes (Table 1). For our analysis we used a definition of diapause taken from Tauber *et al.* (1986): 'a neurohormonally mediated, dynamic state of low metabolic activity'. Because few crustacean species have been sufficiently studied to know their neurohormonal state at different seasons or life history stages, in practice we used instead the list of associated characteristics that Tauber *et al.* (1986) present: 'reduced morphogenesis, increased resistance to environmental extremes, and altered or reduced behavioral activity', with the added stipulation that 'once diapause has begun, metabolic activity is suppressed even if conditions favorable for development prevail'. For phylogenetic comparisons, we adopted Schram's (1986) systematic terminology for the Crustacea with some modification taken from Brusca & Brusca (1990) and Fryer (1987). For each species, we recorded duration of diapause, duration of adult reproductive life, dispersal ability, habitat, and adult body mass. These data were gathered using the following guidelines.

*1. Duration of diapause and duration of life span.* In general, maximum values are used where only one or two durations were found in the literature to compensate for the fact that long durations are less likely to be discovered in the short-term studies typical of ecological investigations. Where more complete data were

Table 1. The average duration of diapause for the 167 species in 20 crustacean orders reviewed in this paper.

Class	Order	Number of species	Average duration of diapause (years)	Standard deviation
Branchiopoda	Anomopoda	18	16.0	20.7
	Anostraca	8	3.9	3.2
	Ctenopoda	1	1.0	0.0
	Haplopoda	1	1.5	0.0
	Notostraca	1	15.0	0.0
	Onychopoda	2	8.8	10.3
	Spinicaudata	6	4.3	1.6
Maxillopoda	Calanoida	34	6.5	13.6
	Cyclopoida	11	0.9	0.7
	Harpacticoida	5	0.6	0.2
	Podocopida	15	3.5	6.2
	Thoracica	3	0.0	0.0
Malacostraca	Amphipoda	3	0.0	0.0
	Anaspidacea	1	0.6	0.0
	Cumacea	1	0.0	0.0
	Decapoda	18	0.04	0.1
	Euphausiacea	9	0.0	0.0
	Isopoda	19	0.04	0.1
	Mysida	8	0.0	0.0
	Stomatopoda	3	0.0	0.0

obtained, we used mean durations or threshold values beyond which survival of dormant stages or adults drops substantially. Where specific durations were not given, we based our judgement on literature discussions, attempting to err on the side of short duration for the sake of being conservative.

*2. Dispersal ability.* The data available for quantifying this trait are scanty. For some species long distance movement of pelagic larvae far from parent populations have been documented (e.g., Rothlisberg & Church, 1994, for *Penaeus*), while for other species dispersal is clearly limited (e.g., some pond-dwelling species). One might suppose that molecular genetic similarities between populations would give an indication of dispersal ability, but these measures are subject not only to dispersal but also assume equilibrium conditions with selectively neutral underlying loci (Endler, 1977; Hedgcock *et al.*, 1982). In general, attempts to establish a close fit between gene flow and dispersal

Table 2. A list of groupings of species from Fig. 1 that have < 1 year diapause duration and < 1 year adult life span. The groupings are explained in the text.

	No. spp.	Dispersal	Notes
1. High dispersal ( $\geq 2.5$ )			
Marine calanoid copepods	14	2.5	Diapause duration > 1 yr.?
Marine ostracods, open water	3	2.5	Diapause not studied
Marine amphipods	3	3	
Marine decapod shrimps	6	2.5	
Marine euphausiids	4	3	
Marine mysids	3	3	
Total	33	Mean 2.7	
2. Misclassified ?			
a. Higher dispersal?			
Inland water cyclopoid copepods	10	1	First to enter new ponds
Inland w. harpacticoid copepods	4	1, 2	Late stage or egg diapause
Marine harpacticoid copepod	1	2	
Marine isopods	8	2	
b. Longer diapause?			
Inland water Branchiopoda	4	2	Diap. duration really unknown
Inland water ostracod	1	2	Diap. dur. conservative estimate
Tide-pool ostracods	4	1	Diap. dur. conservative estimate
Total	32	Mean 1.5	
3. Relict species			
Inland water mysids	5	1	Glacial relicts w/ low dispersal
Inland water calanoid copepod	1	1	<i>Limnocalanus macrurus</i>
Total	6	Mean 1	
4. No plausible explanation			
Inland w. and terrestrial isopods	7	1	
Total	7	Mean 1	
Overall Total	78	Mean 1.9	

in natural populations, including aquatic invertebrates, have failed (Endler, 1977; Burton, 1983). For our purposes, we adopted the following qualitative ranking: 1 – lowest dispersal: pond and lake dwelling species without resistant diapausing eggs. 2 – moderate dis-

persal: pond and lake dwelling species with resistant diapausing eggs. The logic here is that resistant eggs are often depicted in the literature as adaptations for dispersal (Thienemann, 1950; Maguire, 1963) in addition to being a means of surviving seasonally harsh

conditions. We note, however, that Fryer (1972) and Fryer & Frey (1981) emphasized that many littoral 'cladocerans' glue their diapausing eggs to plants or other substrata suggesting that dispersal may be low. Also assigned a score of '2' are the subset of estuarine and near-shore marine species whose larvae are known to spend only a short time in the plankton. 3 – highest dispersal: benthic marine species with long-lived pelagic larvae, pelagic estuarine and marine species. We have also included intermediate scores (1.5 or 2.5) where such scoring seemed appropriate.

3. *Habitat*. This simply indicates whether the species is freshwater, marine (includes estuarine and intertidal), or terrestrial as an adult.

#### *Relationships between diapause, life span, and dispersal*

Diapause duration plotted as a function of adult life span (Fig. 1) shows a striking relationship consistent with Rees' (1994) theory. Crustaceans either have long adult life, or they have prolonged diapause. None of the crustaceans for which we obtained data have both. The result is significantly non-random (Spearman Rank Correlation,  $r_s = -0.73$ ,  $n = 167$ ,  $P < 0.001$ ). The relationship holds as well in a log-log plot, even when the many species with a diapause duration of zero are omitted from the analysis ( $r^2 = 0.23$ ,  $n = 103$ ,  $P \ll 0.0001$ ).

There is a large group of crustaceans, however, that has neither long life nor prolonged diapause (Fig. 1, inset). One explanation for how these species survive environmental variation is that they should have high dispersal ability. Theory suggests that dispersal ability will be higher in groups without prolonged diapause than in those that have this trait (Cohen & Levin, 1985), and we presume that the same is true for species without multi-year iteroparity. Is this the case? Of the 78 species that have both diapause durations and adult life spans of  $\leq 1$  year, we ranked only 33 (Table 2) as having especially high dispersal ability (2.5 or 3). Dispersal scores for this 'corner' group are not significantly greater than those for the remainder of the species that have either diapause duration  $> 1$  year or adult life span  $> 1$  year (Mann-Whitney  $U = 3720$ ,  $P = 0.4$ ). One interpretation of this result is that the theory is flawed. Another is that temporal and spatial variation are not important components of crustacean environments, which can be rejected. A third alternative, however, is that some corner group species are misclassified for one or more of the categories:

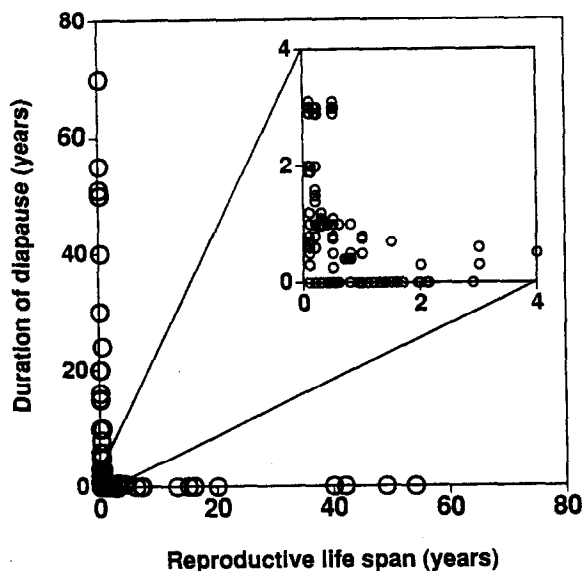


Fig. 1. The relationship between duration of diapause and reproductive life span for 167 crustacean species (see Appendix 1). Inset shows the distribution of data points near the origin.

dispersal, diapause, and life span. For example, our dispersal rankings assume that without a resistant diapausing egg, lake and pond species must have a very weak ability to move between water bodies. Included in this category are the cyclopoid copepods which encyst in a late instar. Yet we know that cyclopoids are among the first species to colonize newly established ponds. Jenkins and Buikema (1994) recently reported that reproductive *Eucyclops agilis* females were found in 12 new ponds dug in an old field within one week after filling from a chlorinated municipal water supply. Two other cyclopoid species were found in many of the ponds within a year of filling. In contrast, no calanoid copepods (many of which make diapausing eggs) were seen during this period. Furthermore, the late copepodid diapause of cyclopoids may be more resistant than is commonly believed: Rylov (1963) recounted an example of encysted cyclopoids surviving in dried mud for 3 years, and more recently Wyngaard *et al.* (1991) reported that several cyclopoid species reappeared in a temporary pond after two or more years of failed reproduction. These latter observations also raise the question of whether the short-term (0.5–0.7 years) diapause duration typically ascribed to cyclopoids is correct.

As with the cyclopoids, harpacticoid copepods also possess a late stage diapause, and it is possible that they are similarly misclassified (Table 2). Other species that

we may have incorrectly placed in the corner are benthic marine isopods which may have greater dispersal than we have credited to them, and a variety of inland water and marine Branchiopoda and Ostracoda that we classified as having diapause durations of  $\leq 1$  year because we had no information to the contrary. Given the diapause durations reported for many of the species in the latter two groups, misclassification is certainly a plausible explanation for their inclusion in the corner group. Altogether there are 32 species in the corner for which we can make a case for misclassification.

There remain 13 species for which we have no plausible rationale for exclusion from the corner. Included in this group are six crustacean species (Table 2) whose natural distribution dates from the last glaciation. The freshwater mysids, and the large copepod *Limnocalanus macrurus*, are all thought to have been stranded in large, deep inland basins as the continental ice sheet receded at the end of the Pleistocene (Segerstrale, 1962; Holmquist, 1972; Williamson, 1991). Recently, Katajisto (1994) has reported finding diapausing eggs of *L. macrurus* in Baltic sediments, though their presence in lakes remains uncertain (Roff, 1972). The mysids at least must have poor dispersal ability since they have recently been successfully introduced into a large number of lakes from which they were previously absent (Lasenby *et al.*, 1986). Given that these six species also have short adult life spans and apparently lack a diapause stage, we conclude that they truly would be vulnerable to short-term recruitment failures. They apparently survive only where they do because the lakes in which they live are relatively constant environments that have existed for a geologically brief period.

In addition to species without prolonged diapause, long reproductive life span or high dispersal, there are some species that have both high dispersal ability and either long adult life (e.g., many marine decapods) or prolonged diapause (e.g., some marine calanoid copepods). Although Venable & Lawlor (1980) predicted that these traits should not be associated, Cohen & Levin (1985) found in models for annual plants that either variation in environmental variability or simultaneous variation in both dispersal success and seed survival would cause dormancy duration and dispersal ability to increase in concert. Presumably the same also applies to dispersal and iteroparity.

### Covariates of diapause and life span

A number of interesting associations are apparent, even when we include all of the crustaceans classified as having both short diapause duration and short reproductive life span in our analysis. These relate the form of temporal bet-hedging (diapause or iteroparity) to the body sizes, habitats and phylogenetic affinities of the crustaceans surveyed.

**Body size** – Animals with long adult lives are relatively large, whereas those with prolonged diapause are small. The relationship between body weight and reproductive life span (Fig. 2) is highly significant ( $r^2 = 0.53$ ,  $P < 0.0001$ ,  $n = 145$ ) with a slope on a log-log plot [ $\log(\text{reproductive life span}) = -0.33 + 0.17 \log(\text{mg body weight})$ ] very similar to that reported by others for a variety of animals (e.g., Blueweiss *et al.*, 1978; Peters, 1983). If we take a life span of greater than one year to represent a minimal level of multi-year bet-hedging, then the data in Fig. 2 show that it is principally crustaceans greater than 10 mg adult body weight that achieve this. The relationship between adult life span and body weight is presumably driven at least in part by the fact that it takes longer to reach a large than a small size, though some relatively large animals are semelparous (e.g., octopods and some salmonid fishes). The largest crustacean in our survey with a life span of  $< 1$  year is the pelagic shrimp *Acetes japonicus* with an adult body weight of just 26 g.

The relationship between duration of diapause and body weight (Fig. 3) is also highly significant (Spearman Rank  $r_s = -0.61$ ,  $n = 145$ ,  $P < 0.001$ ), with smaller crustaceans more likely to exhibit prolonged diapause. The nonparametric relationship is principally the result of animals larger than 10 mg having no diapause (with the exception of notostracans). Thus, crustaceans larger than 10 mg tend to have long adult lives, whereas those smaller than 10 mg frequently have a prolonged diapause.

We can think of no *a priori* physiological reason why a large or a long-lived animal should not be able to produce diapausing eggs. A negative correlation has been noted, however, for marine invertebrates between body size and brood care, in which small animals invest more resources per offspring than do large-bodied animals (Strathmann & Strathmann, 1982). The correspondence we observe between small body size and presence of diapause may, then, be an extension of this correlation since it costs more to make diapausing eggs than it does to make eggs that hatch immediately. All of the hypotheses advanced by Strathmann &

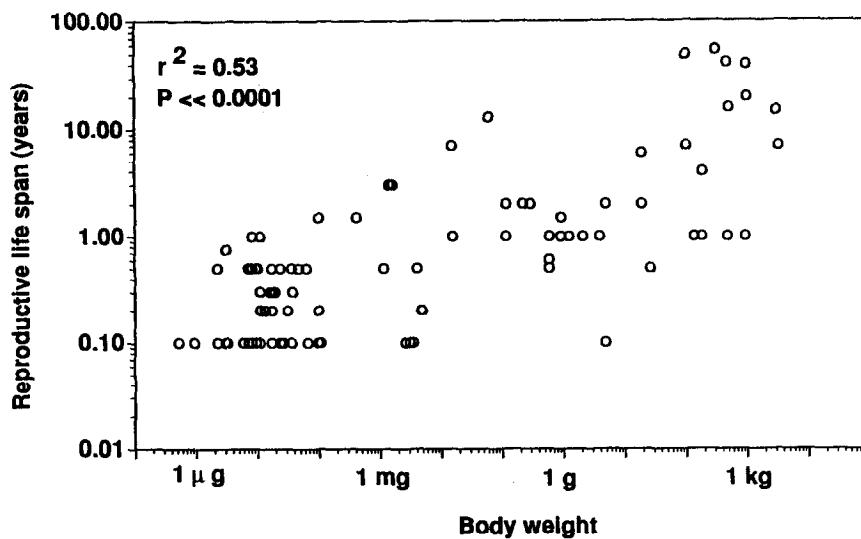


Fig. 2. The relationship between reproductive life span and body weight for 145 crustacean species. Regression equation given in text.

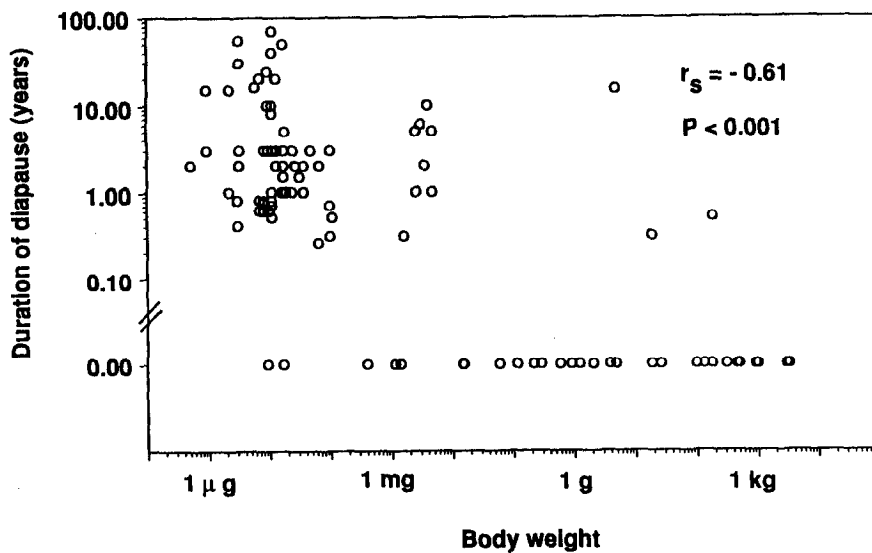


Fig. 3. The relationship between duration of diapause and body weight for 145 crustacean species. Results of nonparametric Spearman Rank correlation are shown.

Strathmann (1982) to explain the brooding-allometry relationship they observed rely upon the greater ability of large animals with numerous offspring to sample a varying environment through spatial dispersal. If it is true, however, that large animals tend also to be iteroparous, then temporal sampling of a variable environment must also be considered. It is also true that diapause at later stages in a large animal might be difficult due to the requirement of protecting such a large mass from attack by predators, microbes, and physi-

cal processes. Body size itself may be constrained by the environment in several ways. If it takes longer for a large animal to reach reproductive size than a small one, large crustaceans in highly seasonal environments (i.e., with 'catastrophic' periods that can only be survived in diapause) may simply be unable to survive. It does appear to be true that only small crustaceans live in highly seasonal environments, with the exception of species in which individuals can migrate away from the harsh conditions or can find microhabitats that are



not uninhabitable (e.g., crayfish and the other crustaceans that survive drought in burrows that descend to the water table, Wiggins *et al.*, 1980).

**Habitat** – Crustaceans living in inland waters are significantly more likely to have a diapause stage that can survive longer than one year than are those living in marine environments (Fig. 4;  $X^2 = 40.9$ ,  $n = 160$ ,  $P < 0.0001$ ). At the same time, marine crustaceans are more likely than those in inland waters to have a reproductive life span that exceeds one year ( $X^2 = 12.5$ ,  $n = 160$ ,  $P < 0.0005$ ). Although exceptions exist, the general trends in Fig. 1 are that the species lying along the axis of 'reproductive life span' are typically marine and large bodied, while those lying along the axis of 'duration of diapause' are typically relatively small and inland water taxa.

**Phylogeny** – In the introduction we asserted that the diapause trait is not evenly distributed among crustacean taxa. For the species we reviewed, significantly more members of the Branchiopoda have a diapause exceeding one year than do members of the Maxillopoda (Fig. 5;  $X^2 = 25.3$ ,  $n = 105$ ,  $P < 0.0001$ ) which in turn show a higher incidence of prolonged diapause than do the Malacostraca ( $X^2 = 29.6$ ,  $n = 130$ ,  $P < 0.0001$ ). In direct contrast, species within the Malacostraca are more likely to have a long adult life span than are members of either the Maxillopoda or the Branchiopoda ( $X^2 = 20.6$ ,  $n = 130$ ,  $P < 0.0001$  and  $X^2 = 18.9$ ,  $n = 99$ ,  $P < 0.0002$  respectively). Life spans of Maxillopoda and Branchiopoda do not differ significantly ( $X^2 = 2.3$ ,  $n = 105$ ,  $P = 0.13$ ).

## Discussion

There are two alternative interpretations for our principal result that duration of diapause is negatively associated with reproductive life span: one is microevolutionary, the other macroevolutionary. From an adaptationist perspective, Fig. 1 may be taken as support for the hypothesis that animals with long adult life have not responded to selection for producing a long-lived diapausing stage as Rees' (1994) theoretical result suggests. Similarly, animals with prolonged diapause apparently have not responded to selection for long adult life.

An alternative, macroevolutionary, interpretation is that phylogenetic constraint contributes to the pattern we observe. If the ancestors of some taxa did not evolve diapause, their descendants may also lack the trait whatever the selection pressures may have been.

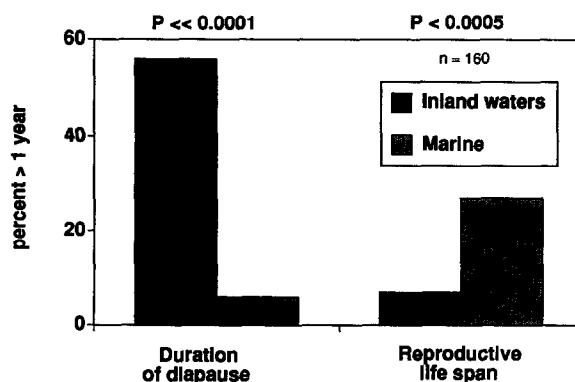


Fig. 4. Percentages of crustacean species from inland aquatic and marine habitats that have either diapause durations or reproductive life spans exceeding one year. P-values are for  $X^2$  tests (see text).

If these same taxa tend to have long adult life spans, then fortuitous associations may appear that have little directly to do with adaptation. When we illustrate the presence or absence of diapause on Schram's (1986) cladogram for the crustacean orders, several striking phylogenetic patterns emerge (Fig. 6). The first is the observation that distinct types of diapause occur in the different groups, supporting independent evolution of diapause in different major taxa. Diapausing eggs are limited to the Branchiopoda, and to some of the Maxillopoda (i.e., some ostracods, some calanoid copepods, and one harpacticoid species). Analysis of the structure of Branchiopod egg coats suggests that production of diapausing eggs in this group is a primitive trait (Fryer, 1994; personal communication). Its phylogenetic relationship to the diapausing eggs in the Maxillopoda is, however, less certain. Two possibilities exist: either diapause is primitive for the Branchiopoda and Maxillopoda and there has been selection against diapause in more derived members of the Maxillopoda, or diapause has evolved independently in these two groups.

Late-instar, encysted diapause is limited to the cyclopoid and harpacticoid copepods. The late instar non-encysted diapause of some marine calanoids is almost certainly an independent phenomenon. With the exception of short-duration (i.e., <1 year), overwintering, 'reproductive diapause' in a few members of the Malacostraca (Hickman, 1937; Tandini-Vitagliano *et al.*, 1982; Alekseev, 1989), none of the other groups exhibit the diapause trait. Clearly this is a nonrandom pattern (cf. Fig. 5). Although there are short-lived members of the Malacostraca, they have not evolved prolonged diapause even though some of them (e.g.,

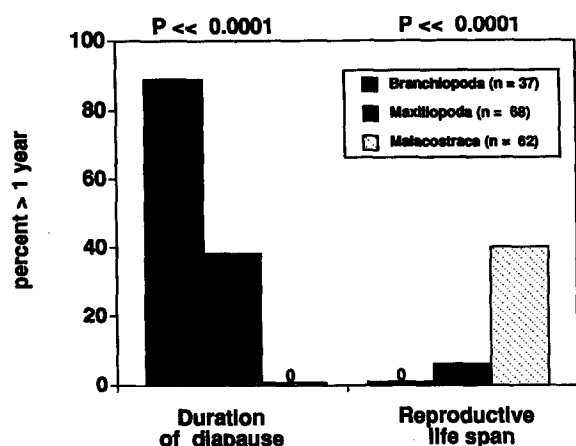


Fig. 5. Percentages of crustacean species from each of the three classes represented in our survey that have either diapause durations or reproductive life spans exceeding one year. P-values are for comparisons of all three classes at once (diapause duration  $\chi^2 = 81.1$ ,  $n = 167$ ,  $P < 0.0001$ ; adult life span  $\chi^2 = 34.6$ ,  $n = 167$ ,  $P < 0.0001$ ). See text for pairwise comparisons.

amphipods and isopods) may occasionally occur in the same temporally variable habitats where diapausing-egg producing Branchiopoda thrive (Wiggins *et al.*, 1980). It is still possible that taxa like amphipods have evolved (or already possessed) high dispersal capability as an alternative to diapause, but as pointed out earlier, we were unable to obtain a convincing assessment of dispersal for many species.

The fact that the harpacticoid and cyclopoid copepods express a very different type of diapause from the other groups, and must represent at least one independent evolutionary event (cladistic analyses typically place harpacticoids and cyclopoids more closely together than either is to the calanoids; Huys & Boxshall, 1991), suggests that the Maxillopoda have evolved diapause independently of the Branchiopoda. As suggested earlier, it may be that possessing either long adult life or prolonged diapause reduces selection for the alternative life history pattern (e.g., long-lived crustaceans do not diapause in part because there is no selection pressure to do so). Finally, it may be that the association between habitat and diapause or habitat and life span facilitates the invasion of a particular habitat. Lindley (1992) has proposed that calanoid copepods of the superfamily Centropagoidea are preadapted to invade freshwater by their ability to produce diapausing eggs in near-shore marine habitats. He ascribed diapause in nearshore environments to adaptation to avoid abrasion and predation on eggs at the sea bottom, and proposed that the diapausing egg coat facil-

itated invasion of freshwater by serving as a protection against osmotic stress. His interpretation has the problem that the egg coat does not protect nauplii newly hatching into fresh water from osmotic stress. An alternative interpretation is that the ability to produce diapausing eggs facilitates survival in highly variable lake and pond environments. Certainly the diaptomids (many, perhaps all, of which produce diapausing eggs, Hairston & Van Brunt, 1994) have experienced enormous diversification in inland waters. Although we do not attempt here to categorize the temporal (especially interannual) or spatial variability of habitats, most freshwater lakes and ponds are generally considered to be more variable than most marine environments.

## Conclusions

Three more or less distinct crustacean groups fall out of our analysis that are both largely consistent with expected patterns of adaptation and with underlying phylogeny. (1) Species with prolonged diapause tend to be small and tend to be found in inland waters. If the variability of inland water habitats is such that bad years for recruitment are also often bad for adult survival, then temporal bet-hedging is best accomplished by rapidly-maturing, small species capable of diapause. Taxa with these characteristics will be the ones likely to invade and proliferate in such inland habitats. Selection for long adult life span is weak or nonexistent, and species possessing this trait are not likely to be successful invaders. (2) Species with long adult life spans tend to be large and tend to be found in marine habitats. Where temporal variability in recruitment is not accompanied by equal or greater variability in adult mortality, iteroparity is a viable bet-hedging strategy. Taxa with these characteristics will be the ones likely to populate marine habitats. (3) A third group of species has small body size and neither long adult life nor prolonged diapause. These animals are difficult to categorize based on the information we have available. They may have high dispersal ability to cope with environmental variation, they may reside in habitats that are relatively invariant, or they may be doomed to a high likelihood of local extinction. It seems likely that this final group must be subject to the most intense selection for some means of spatial or temporal bet-hedging. They may represent the species for which we would most expect novel exceptions to the underlying phylogenetic patterns to appear. It is

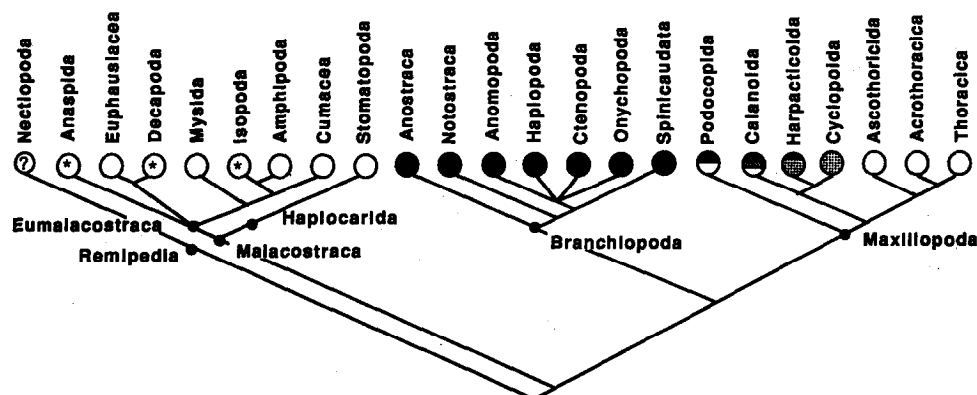


Fig. 6. A cladogram for crustacean orders (some classes and subclasses also shown) based on morphological characters (Schram, 1986) with diapause trait expression represented by the symbols: Open – no diapause; Open with asterisk – most species have no diapause; a few exhibit short duration reproductive diapause; Open with question mark – presence or absence of diapause unknown; Black – diapausing eggs produced; Shaded – late instar diapause. Mixed symbols represent orders in which species express a variety of diapause traits as depicted by the solid symbols. Some taxonomic categories have been modified according to Brusca & Brusca (1990) and Fryer (1987). The orders Leptostraca and Brachypoda, which Schram (1986) included in the clade 'Phyllopoda', have been omitted here because their affinity with the Branchiopoda is controversial, and because we were unable to obtain any information about diapause expression in either of these minor orders.

tempting to speculate that this is what the diversity of diapause patterns in the Maxillopoda represents.

### Acknowledgments

We thank A. Bohonak, F. Ferrari, R. Harrison, C. Holtmeier, and C. Kearns for useful discussions. L. Yampolsky, A. Kondrashov, and H. Schwanninger helped with translations, and V. R. Alekseev, G. Fryer, C. D. Harvell, A. R. McCune, Y. I. Starobogatov and A. Ghilarov provided constructive criticism of the manuscript. This research was funded by U.S. National Science Foundation grants DEB-9118894 to NGH and S. Ellner, and DEB-9410966 to CEC. Carla Cáceres was supported by an NSF Predoctoral Fellowship.

### References

- Aiken, D. E., 1969. Ovarian maturation and egg laying in the crayfish *Orconectes virilis*: Influence of temperature and photoperiod. *Can. J. Zool.* 47: 931–935.
- Alekseev, V., 1989. Influence of diapause upon level of oxygen consumption in *Astacus* (Decapoda). State Research Institute for Lake and River Fisheries, Research Reports. 300: 80–90. (In Russian).
- Andrew, T. E. & A. Herzig, 1984. The respiration rate of the resting eggs of *Leptodora kindti* and *Bythotrephes longimanus* Leydig 1860 (Crustacea, Cladocera) at environmentally encountered temperatures. *Oecologia* 64: 241–244.
- Angell, R. W. & J. W. Hancock, 1989. Response of eggs of *Heterocypris incongruens* (Ostracoda) to experimental stress. *J. crustacean Biol.* 9: 381–386.
- Arashkevich, E. G., A. V. Drits & A. G. Timonin, 1994. Diapause in the life cycle of the copepod *Calanoides carinatus*. International Symposium: Diapause in Crustacea, Abstracts p. 7.
- Ban, S., 1992. Seasonal distribution, abundance and viability of diapause eggs of *Eurytemora affinis* (Copepoda: Calanoida) in the sediment of Lake Ohnuma, Hokkaido. *Bull. Plankton Soc. Japan* 39: 41–48.
- Blueweiss, L., H. Fox, V. Kudzma, D. Nakashima, P. Peters & S. Sams, 1978. Relationships between body size and some life history parameters. *Oecologia* 37: 257–272.
- Borowsky, B., 1980. Reproductive patterns of three intertidal salt-marsh gammaridean amphipods. *Mar. Biol.* 55: 327–334.
- Borutzky, E.W., 1929. Zur Frage über den Ruhezustand bei Copepoda-Harpacticoida. Dauereier bei *Canthocamptus arcticus* Lilljeborg. *Zool. Anz.* 83: 225–233.
- Brendonck, L., D. M. Centeno & G. Persoone, 1993. Fecundity and resting egg characteristics of some subtropical fairy shrimp and clam shrimp species (Crustacea: Branchiopoda) reared under laboratory conditions. *Arch. f. Hydrobiol.* 126: 445–459.
- Brusca, R. C. & G. J. Brusca, 1991. *Invertebrates*. Sinauer, Sunderland. 922 pp.
- Burton, R. S., 1983. Protein polymorphisms and genetic differentiation of marine invertebrate populations. *Mar. Biol. Lett.* 4: 193–206.
- Cáceres, C. E., 1994. Egg bank dynamics and daphnid species diversity. *Bull. Ecol. Soc. Amer./Suppl.* 75: 30.
- Carefoot, T. H., 1973. Studies on the growth, reproduction, and life cycle of the supralittoral isopod *Ligia pallasii*. *Mar. Biol.* 18: 302–311.
- Carvalho, G. R. & H. G. Wolf, 1989. Resting eggs of lake-*Daphnia* I. Distribution, abundance and hatching of eggs collected from various depths in lake sediments. *Freshwat. Biol.* 22: 459–470.
- Castro, M., 1992. A methodology for obtaining information on the age structure and growth rates of the Norway Lobster, *Nephrops norvegicus* (L.) (Decapoda, Nephropoidea). *Crustaceana* 63: 29–43.
- Champeau, A., 1970. Etude de la vie latente chez les Calanoïdes (Copépodes) caractéristiques des eaux temporaires de Basse-Provence. *Ann. Fac. Sci. Marseille* 44: 155–189.

- Cohen, A. C. & J. G. Morin, 1990. Patterns of reproduction in ostracods: A review. *J. crustacean Biol.* 10: 184–211.
- Cohen, D., 1966. Optimizing reproduction in a randomly varying environment. *J. theor. Biol.* 12: 119–129.
- Cohen, D., 1970. A theoretical model for the optimal timing of diapause. *Am. Nat.* 104: 389–400.
- Cohen, D. & S. A. Levin, 1985. The interaction between dispersal and dormancy strategies in varying and heterogeneous environments. In: E. Teramoto and M. Yamaguti (eds), *Mathematical topics in population biology, morphogenesis and neurosciences*, Proceedings. Springer-Verlag, Heidelberg: 110–122.
- Cooper, R. A. & J. R. Uzzmann, 1977. Ecology of juvenile and adult clawed lobsters. In: B. F. Phillips & J. S. Cobb (eds), *Workshop on lobster and rock lobster ecology and physiology*: 187–208.
- Cukerzis, J., 1970. *La biologie de l'écrevisse* (Translation to French 1984). Institut Nationale de la Recherche Agronomique, Paris, 313 pp.
- Daly, K. L. & D. M. Damkaer, 1986. Population dynamics and distribution of *Neomysis mercedis* and *Alienacanthomysis macropsis* (Crustacea: Mysidacea) in relation to the parasitic copepod *Hansenulus trebax* in the Columbia River estuary. *J. crustacean Biol.* 6: 840–857.
- Dana, G. L., 1984. *Artemia* in temporary alkaline ponds near Fallon, Nevada with a comparison of its life history strategies in temporary and permanent habitats. In: S. Jain & P. Moyle (eds), *Vernal pools and intermittent streams*. Institute of Ecology Publication No. 28, University of California, Davis: 115–125.
- Delorme, L., 1991. Ostracoda. In: J. H. Thorp and A. P. Covich (eds) *Ecology and classification of North American freshwater invertebrates*. Academic, San Diego: 691–722.
- De Stasio, B. T., Jr., 1989. The seed bank of a freshwater crustacean: Copepodology for the plant ecologist. *Ecology* 70: 1377–1389.
- De Stasio, B. T., Jr., 1990. The role of dormancy and emergence patterns in the dynamics of a freshwater zooplankton community. *Limnol. Oceanogr.* 35: 1079–1090.
- De Stasio, B. T., Jr. & N. G. Hairston, Jr., 1992. Environmental variability and the persistence of multiple emergence strategies. *Bull. math. Biol.* 54: 313–334.
- Dugan, J. E., A. M. Wenner & D. M. Hubbard, 1991. Geographic variation in the reproductive biology of the sand crab *Emerita analoga* (Stimpson) on the California coast. *J. exp. Mar. Biol. Ecol.* 150: 63–81.
- Easterling, M. R. & S. Ellner, 1994. Hatching strategies in a random environment: A structured model. *Bull. Ecol. Soc. Amer./Suppl.* 75: 59.
- Edmondson, W. T., 1955. The seasonal life history of *Daphnia* in an arctic lake. *Ecology* 36: 439–455.
- Elgmork, K., 1955. A resting stage without encystment in the annual cycle of the freshwater copepod *Cyclops strenuus strenuus*. *Ecology* 36: 739–743.
- Elgmork, K., G. Halvorsen, J. A. Eie & A. Langeland, 1990. Coexistence with similar life cycles in two species of freshwater copepods (Crustacea). *Hydrobiologia* 208: 187–200.
- Ellner, S., 1984. Asymptotic behavior of some stochastic difference equation population models. *J. math. Biol.* 19: 169–200.
- Ellner, S., 1985. ESS germination strategies in randomly varying environments I. Logistic-type models. *Theor. Pop. Biol.* 28: 50–79.
- Ellner, S. & N. G. Hairston, Jr., 1994. Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *Am. Nat.* 143: 403–417.
- Endler, J. A., 1977. *Geographic variation, speciation, and clines*. Princeton Univ. Press, Princeton, NJ., 246 pp.
- Farmer, A. S., 1973. Age and growth in *Nephrops norvegicus* (Decapoda: Nephropidae). *Mar. Biol.* 23: 315–329.
- Fryer, G., 1972. Observations on the ephippia of certain macrothricid cladocerans. *Zool. J. Linn. Soc.* 51: 79–86.
- Fryer, G., 1987. A new classification of the branchiopod Crustacea. *Zool. J. Linn. Soc.* 91: 357–383.
- Fryer, G. & D. G. Frey, 1981. Two-egged ephippia in the chydorid Cladocera. *Freshwat. Biol.* 11: 391–394.
- Fryer, G., 1994. Diapause, a potent force in the evolution of freshwater crustaceans. *International Symposium: Diapause in Crustacea. Abstracts*, p. 11.
- Grice, G. D. & N. H. Marcus, 1981. Dormant eggs of marine copepods. *Oceanogr. Mar. Biol. annu. Rev.* 19: 125–140.
- Hairston, N. G., Jr. & B. T. De Stasio, Jr., 1988. Rate of evolution slowed by a dormant propagule pool. *Nature* 336: 239–242.
- Hairston, N. G., Jr. & W. R. Munns, Jr., 1984. The timing of copepod diapause as an evolutionary stable strategy. *Am. Nat.* 123: 733–751.
- Hairston, N. G., Jr. & R. A. Van Brunt, 1994. Diapause dynamics of two diatomid copepod species in a large lake. *Hydrobiologia* 292/293 (Dev. Hydrobiol. 102): 209–218.
- Hairston, N. G., Jr., S. Ellner & C. M. Kearns, 1995a. Overlapping generations: the storage effect and the maintenance of biotic diversity. In: O. E. Rhodes, R. K. Chesser & M. H. Smith (eds), *Population dynamics in ecological space and time*. Univ. Chicago Press, Chicago (in press).
- Hairston, N. G., Jr., R. A. Van Brunt, C. M. Kearns & D. R. Engstrom, 1995b. Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology* 1706–1711.
- Hartland-Rowe, R. C. B., 1972. The limnology of temporary waters and the ecology of Euphyllipoda. In: R. B. Clark and R. J. Wootton (eds), *Essays in hydrobiology*. University of Exeter, Exeter: 15–32.
- Hedgecock, D., M. L. Tracey & K. Nelson, 1982. Genetics. In: L. G. Abele (ed.), *The biology of crustacea*, Vol. 2. Academic, New York: 283–403.
- Hickman, V. V., 1937. The embryology of the syncarid crustacean, *Anaspides tasmaniae*. *Pap. & Proc. r. Soc. Tasm.* 1936: 1–35.
- Hildrew, A. G., 1985. A quantitative study of the life history of a fairy shrimp (Branchiopoda: Anostraca) in relation to the temporary nature of its habitat, a Kenyan rainpool. *J. anim. Ecol.* 54: 99–110.
- Hines, A. H., 1979. The comparative reproductive ecology of three species of intertidal barnacles. In: S. E. Stancik (ed.), *Reproductive ecology of marine invertebrates*. University of South Carolina Press, Columbia, SC: 213–234.
- Holmquist, C., 1972. Das Zooplankton der Binnengewässer V. Mysi-dacea. *Binnengewässer* 26: 247–256.
- Huys, R. & G. A. Boxshall, 1991. *Copepod evolution*. The Ray Society, London, 468 pp.
- Jenkins, D. G. & A. L. Buikema, in prep. Structure and function of zooplankton communities in twelve new experimental ponds.
- Johannsson, O., 1992. Life history and productivity of *Mysis relicta* in Lake Ontario. *J. Great Lakes Res.* 18: 154–168.
- Juchault, P., W. Jasse & J.-P. Mocquard, 1982. Déterminisme de la reproduction saisonnière de femelles d'*Armadillidium vulgare* Latr. (Crustacé, Isopoda, Oniscoida). VI. Mise en évidence d'une photopériode critique permettant l'entrée en reproduction; modalités du maintien en reproduction. *Ann. Sci. Nat. Zool.* 4: 203–210.
- Katajisto, T., 1996. Copepod eggs survive a decade in the sediments of the Baltic Sea. *Hydrobiologia* 320 (Dev. Hydrobiol. 114): 153–159.

- Khmeleva, N. M. & V. M. Baichorov, 1987. Comparative estimate of reproductive cycles in two relict, ecologically different mysid species. *Polsk. Arch. Hydrobiol.* 34: 321–329.
- Korpelainen, H., 1986. The effect of diapause on the genetic structure of *Daphnia magna* populations. *Z. zool. Syst. Evolut. -forsch.* 24: 291–299.
- Kulikov, A. S., 1980. On the ecology of two gammarid and one mysid species from the cryopelagic biocenose of the central arctic basin. *Biol. Cent. Ark. Bass:* 111–118. (In Russian).
- Lampert, W. & I. Krause, 1976. Zur Biologie der Cladocere *Holopedium gibberum* Zaddach im Windgfallweiher (Schwarzwald). *Arch. f. Hydrobiol./Suppl.* 48: 262–286.
- Lasenby, D. C., T. G. Northcote & M. Fürst, 1986. Theory, practice, and effects of *Mysis relicta* introductions to North American and Scandinavian lakes. *Can. J. Fish. aquat. Sci.* 43: 1277–1284.
- Levin, S. A., D. Cohen & A. Hastings, 1984. Dispersal strategies in patchy environments. *Theor. Pop. Biol.* 26: 165–191.
- Levins, R., 1969. Dormancy as an adaptive strategy. *Symp. Soc. exp. Biol.* 23: 1–10.
- Lindley, J. A., 1992. Resistant eggs of the Centropagoidea (Copepoda: Calanoida): A possible preadaptation to colonization of inland waters. *J. crustacean Biol.* 12: 368–371.
- Livdahl, T. P., 1979. Environmental uncertainty and selection for life cycle delays in opportunistic species. *Am. Nat.* 113: 835–842.
- Maguire, B., Jr., 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. *Ecol. Monogr.* 33: 161–185.
- Maier, G., 1989. Variable life cycles in the freshwater copepod *Cyclops vicinus* (Uljanin 1875): Support for the predator avoidance hypothesis? *Arch. f. Hydrobiol.* 45: 203–219.
- Marcus, N. H., R. Lutz, W. Burnett & P. Cable, 1994. Age, viability, and vertical distribution of zooplankton resting eggs from an anoxic basin: Evidence of an egg bank. *Limnol. Oceanogr.* 39: 154–158.
- Mattox, N. T. & J. T. Verlardo, 1950. Effect of temperature on the development of the eggs of a conchostracan phyllopod, *Caenotheriella gynecia*. *Ecology* 31: 497–506.
- Mauchline, J. & L. R. Fisher, 1969. The biology of euphausiids. *Adv. Mar. Biol.* 7: 1–454.
- McCaughran, D. A. & G. C. Powell, 1977. Growth model for Alaska king crab (*Paralithodes camtschatica*) J. Fish. Res. Bd. Can. 34: 989–995.
- Miller, C. B. & K. S. Tande, 1993. Stage duration estimation for *Calanus* populations: a modeling study. *Mar. Ecol. Prog. Ser.* 102: 15–34.
- Moghaby, A. el., 1977. A study of diapause of zooplankton in a tropical river – The Blue Nile. *Freshwat. Biol.* 7: 207–212.
- Momot, W. T., 1986. Production and exploitation of the crayfish, *Orconectes virilis*, in northern climates. *Can. Special Pub. Fish. aquat. Sci.* 92: 154–167.
- Momot, W. T., 1992. Further range extensions of the crayfish, *Orconectes virilis*, in the Lake Superior Basin of northwestern Ontario. *Can. Field-Nat.* 106: 397–399.
- Moritz, C., 1987. A note on the hatching and viability of *Ceriodaphnia ephippia* collected from lake sediment. *Hydrobiologia* 145 (Dev. Hydrobiol. 35): 309–314.
- Moritz, C., 1988. Die Verteilung der Ephippien von *Bosmina longirostris* und *Ceriodaphnia pulchella* im Sediment des Piburger Sees (Ötztal, Tirol). *Ber. nat.-med. Verein Innsbruck* 75: 91–107.
- Murphy, G. I., 1968. Pattern in life history and the environment. *Am. Nat.* 102: 391–403.
- Naess, T. & J. P. Nilssen, 1991. Diapausing fertilized adults: a new pattern of copepod life cycle. *Oecologia* 86: 368–371.
- Ng, P. K. L., 1988. The freshwater crabs of peninsular Malaysia and Singapore. S. Lee Press, Kent Ridge, Singapore, 156 pp.
- Omori, M., 1971. The biology of pelagic shrimps in the ocean. *Adv. Mar. Biol.* 12: 233–324.
- Otto, R. S., 1986. Management and assessment of Eastern Bering Sea king crab stocks. *Can. Special Pub. Fish. aquat. Sci.* 92: 83–106.
- Payne, J. F. & J. O. Price, 1983. Studies of the life history and ecology of *Orconectes palmeri palmeri* (Faxon). In: C. R. Goldman (ed.), *Freshwater crayfish* V. AVI Publishing Company, Westport, Connecticut: 183–191.
- Pearce, A. F. & B. F. Phillips, 1994. Oceanic processes, Puerulus settlement and recruitment of the Western Rock Lobster, *Panulirus cygnus*. In: P. W. Sammarco & M. L. Heron (eds), *The bio-physics of marine larval dispersal*. Amer. Geophys. Union, Washington, D.C.: 279–303.
- Peters, R. H., 1983. The ecological implications of body size. Cambridge University Press, Cambridge, UK, 329 pp.
- Philippi, T., 1993. Bet-hedging germination of desert annuals: beyond the first year. *Am. Nat.* 142: 474–487.
- Reaka, M. L., 1979. The evolutionary ecology of life history patterns in stomatopod crustacea. In: S. E. Stancik (ed.), *Reproductive ecology of marine invertebrates*. University of South Carolina Press, Columbia, SC: 235–260.
- Rees, M., 1993. Trade-offs among dispersal strategies in British plants. *Nature* 366: 150–152.
- Rees, M., 1994. Delayed germination of seeds: A look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *Am. Nat.* 144: 43–64.
- Roff, D. A., 1992. The evolution of life histories. Chapman & Hall, New York, 535 pp.
- Roff, J. C., 1972. Aspects of the reproductive biology of the planktonic copepod *Limnocalanus macrurus* Sars, 1863. *Crustaceana* 22: 155–160.
- Rothlisberg, P. C. & J. A. Church, 1994. Processes controlling the larval dispersal and postlarval recruitment of penaeid prawns. In: P. W. Sammarco & M. L. Heron (eds), *The bio-physics of marine larval dispersal*. Amer. Geophys. Union, Washington, DC: 235–252.
- Rylov, V. M., 1963. Freshwater cyclopoida. In: E. N. Pavlovskii & A. A. Shtakel'berg (eds), *Fauna of the USSR*, Vol 3. Translated from Russian by the Israel Program for Scientific Translations, Jerusalem, 314 pp.
- Sarvala, J., 1979a. Benthic resting periods of pelagic cyclopoids in an oligotrophic lake. *Holarct. Ecol.* 2: 88–100.
- Sarvala, J., 1979b. A parthenogenetic life cycle in a population of *Canthocamptus staphylinus* (Copepoda, Harpacticoida). *Hydrobiologia* 62: 113–129.
- Sazhina, L. I., 1987. Reproduction, growth and production of marine copepoda. Institute of Biology of South Seas, Ukrainian Academy of Science, 155 pp.
- Schmitt, W. L., 1965. Crustaceans. Univ. of Michigan Press, Ann Arbor, 204 pp.
- Schram, F. R., 1986. Crustacea. Oxford, New York, 606 pp.
- Segerstrale, S. G., 1962. The immigration and prehistory of the glacial relicts of Eurasia and North America. A survey and discussion of modern views. *Int. Revue ges. Hydrobiol.* 47: 1–25.
- Shmida, A. & S. Ellner, 1984. Coexistence of plant species with similar niches. *Vegetatio* 58: 29–55.
- Stearns, S. C., 1976. Life-history tactics: a review of the ideas. *Quart. Rev. Biol.* 51: 3–47.
- Strathmann, R. R. & M. F. Strathmann, 1982. The relationship between adult size and brooding in marine invertebrates. *Am. Nat.* 119: 91–101.

- Swain, R. & C. I. Reid, 1983. Observations on the life history and ecology of *Anaspides tasmaniae* (Thomson) (Syncarida: Anaspididae). *J. crustacean Biol.* 3: 163–172.
- Tadini-Vitagliano, G., F. Valentino & L. Migliore, 1982. Is the mechanism present in *Asellus aquaticus* (L.) an evolutionary stage towards an endogenous calendar? *Z. zool. Syst. Evolut. -forsch.* 20: 144–155.
- Taylor, B. E. & D. L. Mahoney, 1990. Zooplankton in Rainbow Bay, a Carolina Bay pond: population dynamics in a temporary habitat. *Freshwat. Biol.* 24: 597–612.
- Taylor, B. E., G. A. Wyngaard & D. L. Mahoney, 1990. Hatching of *Diaptomus stagnalis* eggs from a temporary pond after a prolonged dry period. *Arch. f. Hydrobiol.* 117: 271–278.
- Taylor, F., 1980. Optimal switching to diapause in relation to the onset of winter. *Theor. Pop. Biol.* 18: 125–133.
- Templeton, A. R. & D. A. Levin, 1979. Evolutionary consequences of seed pools. *Am. Nat.* 114: 232–249.
- Theisen, B. F., 1966. The life history of seven species of ostracodes from a Danish brackish-water locality. *Meddelelser fra Danmarks Fiskeri – og Havundersøgelser*, n.s. 4: 215–270.
- Thienemann, A., 1950. Verbreitungsgeschichte der Süßwassertierwelt Europas. *Die Binnengewässer* 18: 1–809.
- Toda, H., M. Takahashi & S. Ichimura, 1982. Abundance and life history of *Neomysis intermedia* Czerniawsky in Lake Kasumigaura. *Hydrobiologia* 93 (Dev. Hydrobiol. 10): 31–39.
- Venable, D. L. & L. Lawlor, 1980. Delayed germination and dispersal in desert annuals: Escape in space and time. *Oecologia* 46: 272–282.
- Watson, N. H. F. & B. N. Smallman, 1971. The role of photoperiod and temperature on the induction and termination of an arrested development in two species of freshwater cyclopoid copepods. *Can. J. Zool.* 49: 855–862.
- Weaver, C. R., 1943. Observation on the life cycle of the fairy shrimp *Eubranchipus vernalis*. *Ecology* 24: 500–502.
- Weslawski, J. M., 1989. Occurrence and life cycle of *Mysis oculata* (Crustacea) from Spitsbergen. *Pol. Arch. Hydrobiol.* 36: 207–215.
- Westin, L. & R. Gydemo, 1986. Influence of light and temperature on reproduction and moulting frequency of the crayfish, *Astacus astacus* L. *Aquaculture* 52: 43–50.
- Wiggins, G. B., R. J. Mackay & I. M. Smith, 1980. Evolutionary and ecological strategies of animals in annual temporary pools. *Arch. f. Hydrobiol./Suppl.* 58: 97–206.
- Williams-Howze, J. & B. C. Coull, 1992. Are temperature and photoperiod necessary cues for encystment in the marine benthic harpacticoid copepod *Heteropsyllus nunni* Coull? *Biol. Bull.* 182: 109–116.
- Williamson, C. E., 1991. Copepoda. In: J. H. Thorp and A. P. Covich (eds), *Ecology and classification of North American freshwater invertebrates*. Academic, San Diego: 787–822.
- Wolcott, T. G., 1988. Ecology. In: W. W. Burggren & B. R. McMahon (eds), *Biology of the land crabs*. Cambridge University Press, Cambridge: 55–96.
- Wyngaard, G. A., 1988. Geographical variation in dormancy in a copepod: evidence from population crosses. *Hydrobiologia* 167/168 (Dev. Hydrobiol. 47): 367–374.
- Wyngaard, G. A., B. E. Taylor & D. L. Mahoney, 1991. Emergence and dynamics of cyclopoid copepods in an unpredictable environment. *Freshwat. Biol.* 25: 219–232.

*Appendix 1.* List of the crustacean species used in this paper and their associated reproductive life spans, relative dispersal abilities, diapause durations, and habitats (see text for explanations). References are numbered and listed in the footnote.

Class Order Species	Reproductive life span (years)	Relative Dispersal	Duration of diapause (years)	Habitat	References
<b>Branchiopoda</b>					
Anomopoda					
Bosmina longirostris	0.1	2	15	Inland waters	1
Ceriodaphnia pulchella	0.1	2	15	Inland waters	1,2
Ceriodaphnia quadrangula	0.1	2	2	Inland waters	3
Ceriodaphnia reticulata	0.1	2	3	Inland waters	4
Chydorus sphaericus	0.1	2	2	Inland waters	3
Daphnia cucullata	0.1	2	50	Inland waters	5
Daphnia galeata	0.1	2	50	Inland waters	5,6
Daphnia laevis	0.1	2	2	Inland waters	7,8
Daphnia magna	0.1	2	2	Inland waters	9
Daphnia middendorffiana	0.1	2	2	Inland waters	3
Daphnia pulicaria	0.1	2	50	Inland waters	6
Daphnia pulex	0.1	2	2	Inland waters	10
Daphnia retrocurva	0.1	2	30	Inland waters	6
Eubosmina longispina	0.1	2	3	Inland waters	4
Macrothrix sp.	0.1	2	55	Inland waters	11,12
Scapholeberis sp.	0.1	2	2	Inland waters	7,8
Simocephalus exspinosus	0.1	2	2	Inland waters	7,8
Simocephalus serrulatus	0.1	2	2	Inland waters	7,8
Anostraca					
Artemia monica	0.2	2	1	Inland waters	13
Artemia salina	0.5	2	10	Inland waters	13
Branchinecta coloradensis	0.1	2	2	Inland waters	3
Eubranchipus vernalis	0.8	2	1	Inland waters	14
Streptocephalus probocideus	0.2	2	5	Inland waters	15
Streptocephalus seali	0.1	2	6	Inland waters	16
Streptocephalus sudanicus	0.2	2	5	Inland waters	14
Streptocephalus vitreus	0.2	2	1.5	Inland waters	17
Ctenopoda					
Holopedium gibberum	0.1	2	1	Inland waters	18
Haplopoda					
Leptodora kindti	0.2	2	1.5	Inland waters	19
Notostraca					
Triops longicaudatus	0.1	2	15	Inland waters	16,20
Onychopoda					
Bythotrephes longimanus	0.2	2	1.5	Inland waters	19
Podon polyphemoides	0.1	2.5	16	Marine	21

## Appendix I. Continued.

Class Order Species	Reproductive life span (years)	Relative Dispersal	Duration of diapause (years)	Habitat	References
<b>Spinicaudata</b>					
Caenestheriella australis	0.2	2	5	Inland waters	15
Caenestheriella gynecia	0.2	2	5	Inland waters	22
Eocyzicus klunzingeri	0.1	2	5	Inland waters	15
Eulimnadia africana	0.1	2	5	Inland waters	15
Leptestheria aegyptiaca	0.1	2	5	Inland waters	15
Limnadia stanleyana	0.1	2	1	Inland waters	16
<b>Maxillopoda</b>					
<b>Calanoida</b>					
Acartia bifilosa	0.2	2.5	8	Marine	75
Acartia californiensis	0.3	2.5	1	Marine	23
Acartia erythraea	0.3	2.5	1	Marine	23
Acartia hudsonica	0.2	2.5	10	Marine	21
Acartia tonsa	0.3	2.5	1	Marine	23
Aglaodiaptomus spatulocrenatus	0.2	2	3	Inland waters	24
Aglaodiaptomus stagnalis	0.2	2	3	Inland waters	7
Arctodiaptomus wierzejskii	0.2	2	3	Inland waters	25
Calanoides carinatus	0.1	3	0.3	Marine	76
Calanopia thompsoni	0.3	2.5	1	Marine	23
Calanus finmarchicus	1.5	3	0.7	Marine	26
Centropages abdominalis	0.3	2.5	1	Marine	23
Centropages hamatus	0.3	2.5	1	Marine	23
Centropages ponticus	0.3	2.5	1	Marine	23,27
Centropages yamadai	0.3	2.5	1	Marine	23
Diaptomus castor	0.2	2	3	Inland waters	25
Diaptomus cyaneus	0.2	2	3	Inland waters	25
Epilabidocera longipedata	0.3	2.5	1	Marine	23
Epischura nordenskilodi	0.2	2	3	Inland waters	24
Eudiaptomus vulgaris	0.2	2	3	Inland waters	25
Eurytemora affinis	0.2	2	40	Inland waters	21,28,75
Hemidiaptomus ingens	0.2	2	3	Inland waters	25
Labidocera aestiva	0.3	2.5	1	Marine	23
Labidocera bipinnata	0.3	2.5	1	Marine	23
Leptodiaptomus coloradensis	0.2	2	2	Inland waters	3
Leptodiaptomus minutus	0.1	2	20	Inland waters	29
Limnocalanus macrurus	0.5	1	0.25	Inland waters	30
Mixodiaptomus kupelwieseri	0.2	2	3	Inland waters	25
Mixodiaptomus laciniatus	0.2	2	3	Inland waters	25
Onychodiaptomus sanguineus	0.2	2	70	Inland waters	31
Pontella maedi	0.3	2.5	1	Marine	23
Pontella mediterranea	0.3	2.5	1	Marine	23
Skistodiaptomus oregonensis	0.2	2	20	Inland waters	29
Tortanus forcipatus	0.3	2.5	5	Marine	21



## Appendix 1. Continued.

Class Order Species	Reproductive life span (years)	Relative Dispersal	Duration of diapause (years)	Habitat	References
<b>Cyclopoida</b>					
<i>Acanthocyclops vernalis</i>	0.1	1	3	Inland waters	32,33
<i>Cyclops kolensis</i>	0.1	1	0.8	Inland waters	34
<i>Cyclops scutifer</i>	1	1	0.75	Inland waters	35
<i>Cyclops strenuus</i>	1	1	0.5	Inland waters	36
<i>Cyclops strenuus strenuus</i>	1	1	0.8	Inland waters	37
<i>Cyclops vicinus</i>	0.1	1	0.7	Inland waters	38
<i>Diacyclops navus</i>	0.1	1	0.6	Inland waters	39
<i>Diacyclops thomasi</i>	0.1	1	0.6	Inland waters	40
<i>Mesocyclops edax</i>	0.5	1	0.6	Inland waters	41
<i>Mesocyclops leuckarti</i>	0.5	1	0.75	Inland waters	34,35
<i>Thermocyclops oithonoides</i>	0.2	1	0.8	Inland waters	34
<b>Harpacticoida</b>					
<i>Canthocamptus arcticus</i>	0.1	2	0.8	Inland waters	77
<i>Canthocamptus staphylinoides</i>	0.7	1	0.4	Inland waters	42
<i>Canthocamptus staphylinus</i>	0.7	1	0.4	Inland waters	42
<i>Canthocamptus microstaphylinus</i>	0.7	1	0.4	Inland waters	42
<i>Heteropsyllus nunni</i>	0.5	2	0.8	Marine	43
<b>Podocopida</b>					
<i>Candona decora</i>	0.5	2	0	Inland waters	44,45
<i>Cypricercus reticulatus</i>	0.1	2	10	Inland waters	45,46
<i>Cypridopsis aculeata</i>	0.5	2.5	1	Marine	44,45
<i>Cyprinotus carobineusis</i>	0.5	2	3	Inland waters	44,45
<i>Cyprois marginata</i>	0.5	2	3	Inland waters	44,45
<i>Cypris</i> sp.	0.5	2	24	Inland waters	44
<i>Cytherura gibba</i>	0.5	1	0	Marine	44,47
<i>Cytherois arenicola</i>	0.5	1	0	Marine	44,47
<i>Cytherois fischeri</i>	0.5	1	0	Marine	44,47
<i>Elofsonia baltica</i>	0.5	1	1	Marine	44,47
<i>Eucypris fuscata</i>	0.5	2	3	Inland waters	44,45
<i>Herpetocypris reptans</i>	0.5	2	3	Inland waters	44,45
<i>Heterocypris incongurens</i>	0.5	2.5	1	Marine	44,45
<i>Heterocypris salinus</i>	0.5	2.5	1	Marine	44,45
<i>Notodromas monacha</i>	0.5	2	3	Inland waters	44,45
<b>Thoracica</b>					
<i>Balanus glandula</i>	7	3	0	Marine	48
<i>Chthamalus fiscus</i>	3	3	0	Marine	48
<i>Tetraclita squamosa</i>	13	3	0	Marine	48
<b>Malacostraca</b>					
<b>Amphipoda</b>					

## Appendix 1. Continued.

Class Order Species	Reproductive life span (years)	Relative Dispersal	Duration of diapause (years)	Habitat	References
<i>Gammarus mucronatus</i>	0.5	2.5	0	Marine	49
<i>Gammarus palustris</i>	0.5	2.5	0	Marine	49
<i>Melita nitida</i>	0.5	2.5	0	Marine	49
Anaspidacea					
<i>Anaspides tasmaniae</i>	3	1.5	0.6	Inland waters	83,84
Cumacea					
<i>Diastylis goodsiri</i>	7	1	0	Inland waters	50
Decapoda					
<i>Acanthephyra pelagica</i>	1	2.5	0	Marine	62
<i>Acanthephyra quadrispinosa</i>	1	2.5	0	Marine	62
<i>Acetes japonicus</i>	0.5	2.5	0	Marine	62
<i>Astacus astacus</i>	4	1.5	0.5	Inland waters	51,78,79
<i>Cardisoma guanhumi</i>	16	1.5	0	Terrestrial	52,53
<i>Emerita analoga</i>	2	3	0	Marine	54
<i>Homarus americanus</i>	40	2.5	0	Marine	55
<i>Lucifer chacei</i>	1	2.5	0	Marine	62
<i>Nephrops norvegicus</i>	7	3	0	Marine	56,57
<i>Orconectes palmeri</i>	2	1.5	0	Inland waters	58
<i>Orconectes rusticus</i>	6	2.5	0	Inland waters	59
<i>Orconectes virilis</i>	2	1.5	0.3	Inland waters	59,80
<i>Panaeus merguensis</i>	1	3	0	Marine	63
<i>Penulirus cygnus</i>	20	3	0	Marine	60
<i>Paralithodes camtschatica</i>	15	2.5	0	Marine	61
<i>Paralithodes platypus</i>	7	2.5	0	Marine	61
<i>Sergestes similis</i>	1	2.5	0	Marine	62
<i>Sergia lucens</i>	1	2.5	0	Marine	62
Euphausiacea					
<i>Euphausia pacifica</i>	1	3	0	Marine	64
<i>Euphausia superba</i>	1	3	0	Marine	64
<i>Euphausia triacantha</i>	2	3	0	Marine	64
<i>Meganocyttiphanes norvegica</i>	2	3	0	Marine	64
<i>Thysanoessa longicaudata</i>	2	3	0	Marine	64
<i>Thysanoessa longipes</i>	2	3	0	Marine	64
<i>Thysanoessa raschii</i>	2	3	0	Marine	64
<i>Thysanoessa spineffera</i>	1	3	0	Marine	64
<i>Thysaropoda acutifrons</i>	1	3	0	Marine	64
Isopoda					
<i>Armadillidium vulgare</i>	3	1	0.3	Terrestrial	65,81
<i>Asellus aquaticus</i>	0.8	1	0.5	Inland waters	65,82
<i>Asellus intermedius</i>	0.8	1	0	Inland waters	65

## Appendix I. Continued.

Class Order Species	Reproductive life span (years)	Relative Dispersal	Duration of diapause (years)	Habitat	References
<i>Asellus meridianus</i>	0.8	1	0	Inland waters	65
<i>Asellus tomalensis</i>	0.1	1	0	Inland waters	65
<i>Cylisticus convexus</i>	1	1	0	Terrestrial	65
<i>Dynamene bidentata</i>	0.1	2	0	Marine	65
<i>Idotes emarginata</i>	0.3	2	0	Marine	65
<i>Jaera albifrons</i>	0.5	2	0	Marine	65
<i>Jaera forsmani</i>	0.5	2	0	Marine	65
<i>Jaera ishiosetosa</i>	0.5	2	0	Marine	65
<i>Jaera praeisuta</i>	0.5	2	0	Marine	65
<i>Ligia oceanica</i>	1.5	2	0	Marine	65
<i>Ligia pallasii</i>	1	2	0	Marine	65
<i>Ligidium japonica</i>	1	1	0	Terrestrial	65
<i>Mancasellus macrourus</i>	0.5	1	0	Inland waters	65
<i>Oniscus asellus</i>	1.5	1	0	Terrestrial	65
<i>Porcellio scaber</i>	1.5	1	0	Terrestrial	65
<i>Triconiscus pusillus</i>	2	1	0	Terrestrial	65
<b>Mysida</b>					
<i>Alienacanthomysis macropsis</i>	0.5	1	0	Inland waters	66
<i>Gnathophausia ingens</i>	1	3	0	Marine	50
<i>Mysis oculata</i>	0.5	3	0	Marine	67
<i>Mysis polaris</i>	0.5	3	0	Marine	68
<i>Mysis relicta</i>	1	1	0	Inland waters	69,70
<i>Neomysis intermedia</i>	0.5	1	0	Inland waters	71
<i>Neomysis mercedes</i>	0.5	1	0	Inland waters	66
<i>Paramysis lacustris</i>	0.6	1	0	Inland waters	70
<b>Stomatopoda</b>					
<i>Gonodactylus chiragra</i>	54	2	0	Marine	72
<i>Gonodactylus falcatus</i>	42	2	0	Marine	72
<i>Gonodactylus graphurus</i>	49	2	0	Marine	72

\*1: Moritz, 1988. 2: Moritz, 1987. 3: A. J. Bohonak, pers. comm. 4: De Stasio, 1990. 5: Carvalho & Wolf, 1989. 6: C. E. Cáceres, unpublished data. 7: Taylor *et al.*, 1990. 8: Taylor & Mahoney, 1990. 9: Korpelainen, 1986. 10: Edmondson, 1955. 11: Moghraby, 1977. 12: Fryer, 1972. 13: Dana, 1984. 14: Weaver, 1943. 15: Brendonck *et al.*, 1993. 16: Hartland-Rowe, 1972. 17: Hildrew, 1985. 18: Lampert & Krause, 1976. 19: Andrew & Herzig, 1984. 20: Schmitt, 1965. 21: Marcus *et al.*, 1994. 22: Mattox & Verlardo, 1950. 23: Grice and Marcus, 1981. 24: N. G. Hairston, Jr., unpublished data. 25: Champeau, 1970. 26: Miller and Tande, 1993. 27: Sazhina, 1987. 28: Ban, 1992. 29: Hairston and Van Brunt, 1994. 30: Roff, 1972. 31: Hairston *et al.*, 1995b. 32: Wyngaard *et al.*, 1991. 33: Rylov, 1963. 34: Sarvala, 1979a. 35: Elgmork *et al.*, 1990. 36: Naess & Nilssen, 1991. 37: Elgmork, 1955. 38: Maier, 1989. 39: Watson & Smallman, 1971. 40: A. M. Hansen, unpublished data. 41: Wyngaard, 1988. 42: Sarvala, 1979b. 43: Williams-Howze & Coull, 1992. 44: Cohen & Morin, 1990. 45: Angell & Hancock, 1989. 46: Delorme, 1991. 47: Theisen, 1966. 48: Hines, 1979. 49: Borowsky, 1980. 50: Schram, 1986. 51: Cukerzis, 1970. 52: Wolcott, 1988. 53: Ng, 1988. 54: Dugan *et al.*, 1991. 55: Cooper & Uzmam, 1977. 56: Farmer, 1973. 57: Castro, 1992. 58: Payne & Price, 1983. 59: Momot, 1986. 60: Pearce & Phillips, 1994. 61: Otto, 1986. 62: Omori, 1971. 63: Rothlisberg & Church, 1994. 64: Mauchline and Fisher, 1969. 65: Carefoot, 1973. 66: Daly & Damkaer, 1986. 67: Weslawski, 1989. 68: Kulikov, 1980. 69: Johannsson, 1992. 70: Khmeleva & Baichorov, 1987. 71: Toda *et al.*, 1982. 72: Reaka, 1979. 73: McCaughan & Powell, 1977. 74: Momot, 1992. 75: Katajisto, 1995. 76: Arashkevich *et al.*, 1994. 77: Borutzky, 1929. 78: Westin & Gydemo, 1986. 79: Alekseev, 1989. 80: Aiken, 1969. 81: Juchault *et al.*, 1982. 82: Tandini-Vitagliano *et al.*, 1982. 83: Swain & Reid, 1983. 84: Hickman, 1937.