CHAPTER THREE

Jellyfish Life Histories: Role of Polyps in Forming and Maintaining Scyphomedusa Populations

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Contents

Abstract

Large population fluctuations of jellyfish occur over a variety of temporal scales, from weekly to seasonal, inter-annual and even decadal, with some regions of the world reported to be experiencing persistent seasonal bloom events. Recent jellyfish research has focussed on understanding the causes and consequences of these population changes, with the vast majority of studies considering the effect of changing environmental variables only on the pelagic medusa. But many of the bloom-forming species are members of the Scyphozoa with complex metagenic life cycles consisting of a sexually reproducing pelagic medusa and asexually reproducing benthic polyp.

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Recruitment success during the juvenile (planula, polyp and ephyrae) stages of the life cycle can have a major effect on the abundance of the adult (medusa) population, but until very recently, little was known about the ecology of the polyp or scyphistoma phase of the scyphozoan life cycle. The aim of this review is to synthesise the current state of knowledge of polyp ecology by examining (1) the recruitment and metamorphosis of planulae larvae into polyps, (2) survival and longevity of polyps, (3) expansion of polyp populations via asexual propagation and (4) strobilation and recruitment of ephyrae (juvenile medusae). Where possible, comparisons are made with the life histories of other bentho-pelagic marine invertebrates so that further inferences can be made. Differences between tropical and temperate species are highlighted and related to climate change, and populations of the same species (in particular *Aurelia aurita*) inhabiting different habitats within its geographic range are compared. The roles that polyps play in ensuring the long-term survival of jellyfish populations as well as in the formation of bloom populations are considered, and recommendations for future research are presented.

Key Words: Jellyfish; Scyphozoa; Polyps; Medusae; Life histories; Asexual reproduction; Strobilation; Settlement; Recruitment; Temperature; Food availability; Nudibranchs

1. Introduction

Large population fluctuations of jellyfish occur over a variety of temporal scales, ranging from weekly, seasonal, inter-annual to decadal. With their high water and low carbon (<3%) contents (Lucas *et al.*, 2011) coupled with relatively short lifespan—typically 6–9 months (Arai, 1997; Lucas *et al.*, 2001), jellyfish have the potential for rapid growth and maturity. When food is plentiful, numbers can increase rapidly in a matter of weeks or months to form episodic or seasonal blooms. Localised dense aggregations can also form behaviourally or as a result of wind-driven or hydrodynamic processes (Graham *et al.*, 2001). Year-to-year variability in abundance and phenology is common (e.g. Kovalev and Piontkovski, 1998). For example, populations of the Common jellyfish, *Aurelia aurita*, in Kiel Bight are characterised by years of low numbers of large medusae alternating with years of high numbers of small medusae (Schneider and Behrends, 1994), while in Southampton Water, the timing of the initial appearance of *A. aurita* ephyrae varies by almost 2 months while maximum abundance has varied from 0 to 30 m^{-3} since 1985 (Lucas *et al.*, 2001; Lucas Cathy, unpublished data). In the longer term, population outbreaks can become more frequent or persistent over multiple-year or even decadal time scales (Kogovšek *et al.*, 2010; Lynam *et al.*, 2010), or they may decline (Brodeur

et al., 2008; see also Condon *et al.*, 2012). Noteworthy examples of blooms include detrimental outbreaks of the Giant jellyfish *Nemopilema nomurai* in southeast Asia (Uye and Ueta, 2004; Kawahara *et al.*, 2006; Uye, 2008), increased frequency of *Pelagia noctiluca* blooms in the Mediterranean and NE Atlantic (Licandro *et al.*, 2010) from the previously reported ~decadal fluctuations (Goy *et al.*, 1989) and the biomass of large jellyfish exceeding that of commercially important fish in the Benguela upwelling (Sparks *et al.*, 2001; Lynam *et al.*, 2006).

Because of the increased interest in jellyfish for both environmental and socio-economic reasons (Condon *et al.*, 2012), recent research has focussed on understanding the causes (and consequences) of population change and bloom events (e.g. CIESM, 2001; Mills, 2001; Parsons and Lalli, 2002; Richardson *et al.*, 2009; Dong *et al.*, 2010). Potential (direct or indirect) causal relationships between mass occurrences and anthropogenic disturbances such as eutrophication (Arai, 2001; Ishii, 2001), overfishing (Lynam *et al.*, 2006; Daskalov *et al.*, 2007; Pauly *et al.*, 2009), translocations (Reusch *et al.*, 2010), habitat modification (Purcell *et al.*, 2007; Lo *et al.*, 2008) as well as hydroclimatic variability (Lynam *et al.*, 2004, 2010; Purcell, 2005; Molinero *et al.*, 2008; Richardson *et al.*, 2009) have received the most attention. Many jellyfish species, particularly those inhabiting coastal and shelf ecosystems, are tolerant of a wide range of environmental conditions of temperature, salinity, food availability, oxygen concentration, pH (Arai, 1997; Lucas, 2001). This physiological flexibility coupled with short generation time makes jellyfish ideally suited to exploit niche openings when more advanced competitors such as fish are at the limits of their physiological tolerances. Nevertheless, in many cases, the causes of population fluctuations and outbreaks are not clear cut, and it would seem that synergistic effects are most likely (Purcell *et al.*, 2007). In the case of the Black Sea, for example, eutrophication and over-fishing coincided with translocation of the hermaphroditic ctenophore *Mnemiopsis leidyi* (reviewed in Arai, 2001), resulting in the population explosion of the introduced ctenophore in the late 1980s.

In spite of these major advances, the vast majority of these studies and syntheses have considered only the effect of (changing) environmental variables on the pelagic (medusa) component of jellyfish community (but see Purcell *et al.*, 2007; Lo *et al.*, 2008; Prieto *et al.*, 2010; Holst, 2012). However, Marcus and Boero (1998) reminded us of the importance of benthic-pelagic coupling in determining the production and biological structure of coastal aquatic systems, highlighting the applicability of this concept to life cycles, specifically to those marine organisms (including cnidarians), which have both benthic and pelagic life stages (Fig. 3.1). Selection occurs at all stages in a life cycle, and recruitment success during the juvenile (planula, polyp, ephyrae) stages can have a major effect on the abundance of the adult (i.e. medusa) population (Schneider and Behrends, 1994; Lucas, 2001; Colin and Kremer, 2002). Marcus and Boero's concept

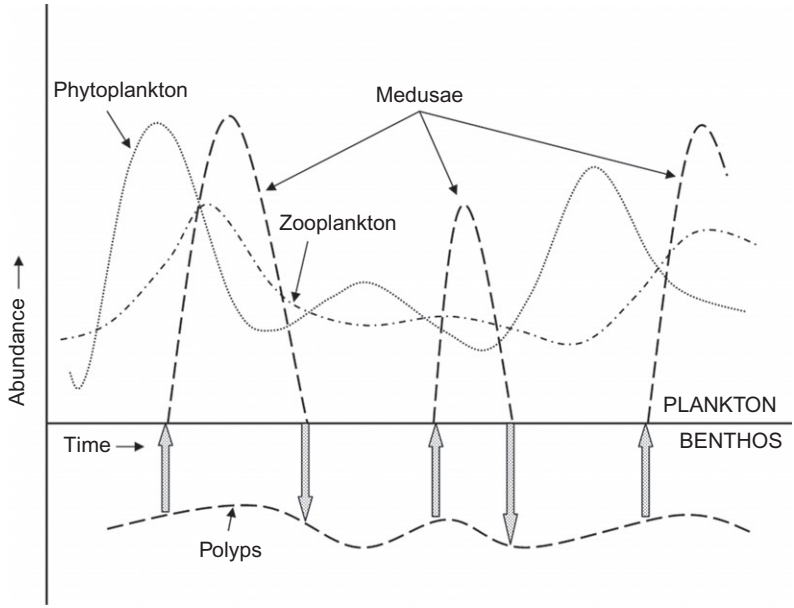

Figure 3.1 Life cycle strategies of scyphozoans with pelagic and benthic life stages. Peaks of abundance in the plankton are regulated by food availability. Exploitation of trophic resources leads to sexual reproduction and larval development, followed by disappearance of adult medusae from the water column. Planulae metamorphose into the polyp benthic stage, which has a continuous presence in the benthos and provides recruits to the next generation of medusae. (Re-drawn from Boero *et al.* (2008), figure 5, with kind permission from Inter-Research Science Center.)

of vertical-supply ecology was developed further by Boero *et al.* (2008). They commented that plankton ecology must seriously regard both the individual-level life cycle and population-level life history patterns (Giangrande *et al.*, 1994) in order to understand the dynamics and blooms of plankton in space and time (Boero *et al.*, 2008), particularly as populations can fluctuate between extremely abundant, rarely found or even absent, followed by mass occurrences again.

From a reproduction point of view, population change can be achieved in two ways: qualitative adjustments to the life cycle or quantitative fluctuations in the life history (see Figs. 3.2 and 3.3; Boero *et al.*, 2008). Gelatinous zooplankton, such as cnidarians, ctenophores and thaliaceans, are able to adopt both strategies, depending on whether they are holoplanktonic (life history) or meroplanktonic, that is, with benthic life stages (life cycle). Within the Cnidaria, many (but not all) of the problematic bloom-forming species are members of the Scyphozoa, most of which have complex metagenic life cycles involving a benthic polyp and a pelagic medusa (Hamner and Dawson, 2009). Understanding the biology and ecology of

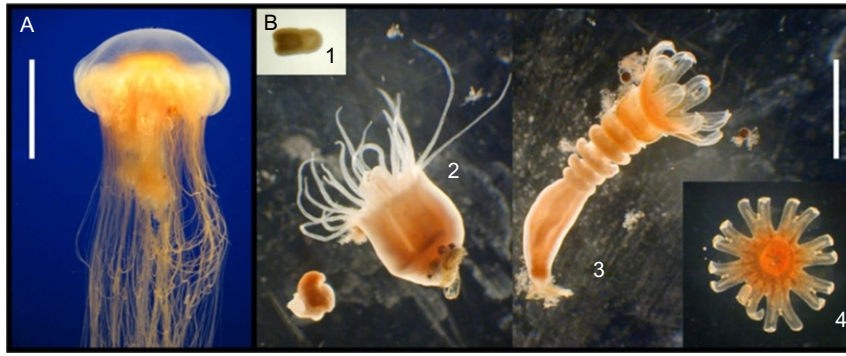

Figure 3.2 General life cycle of jellyfish belonging to the class Scyphozoa. (A) Mature *Cyanea capillata* medusa; scale bar = 5 cm. (B) 1. Planula larva, 2. scyphistoma, 3. strobila, 4. ephyra; scale bar = 2 mm (photos by C. Widmer).

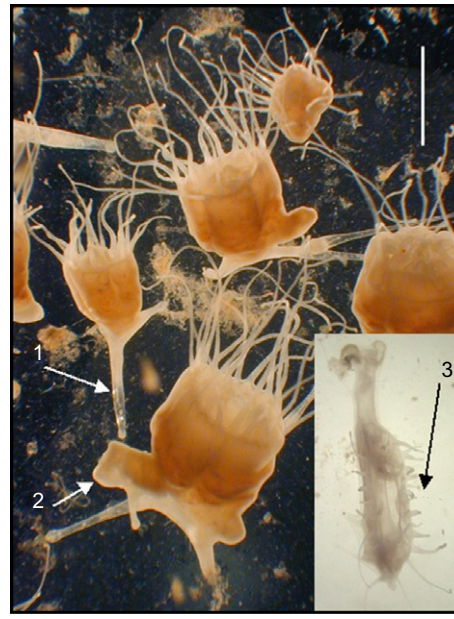

Figure 3.3 Common asexual reproductive modes of *Aurelia aurita* scyphistomae. 1. Stolon, 2. side bud, 3. fission; scale bar = 2 mm (photos by C. Widmer).

benthic polyps, and their potential role in the formation and maintenance of jellyfish outbreaks, whether cyclic or in response to climate change is of paramount importance (see Brewer and Feingold, 1991; Watanabe and

Ishii, 2001; Prieto *et al.*, 2010). In 2001, Mills commented that 'Knowledge about the ecology of both the medusa and the polyp phases of each life cycle is necessary if we are to understand the true causes of these increases and decreases, but in most cases where changes in medusa populations have been recognized, we know nothing about the field ecology of the polyps'. Over the past decade, this knowledge gap has started to be addressed.

This review builds and expands on the paper by Lucas (2001) in which the interplay between the environment and the asexual and sexual phases of the life cycle of common jellyfish, *A. aurita*, was reviewed. We have chosen to focus on the scyphozoans only (rather than scyphozoans and hydrozoans) for a number of reasons. Scyphomedusae are the main protagonists of jellyfish bloom events. We acknowledge that hydrozoans are very widely distributed and that several hydromedusae (e.g. *Aglantha digitale*, *Aequorea aequorea*, *A. vitrina*, *A. victoria*, *Cladonema californicum*, *Clytia hemisphaerica*, *Moerisia lyonsi*, *Obelia* spp., *Phialidium gregarium* and *Sarsia tubulosa*) can be seasonally abundant and consume significant amounts of prey (Matsakis and Conover, 1991; Nicholas and Frid, 1999; Purcell *et al.*, 1999a; Sparks *et al.*, 2001; Costello and Colin, 2002; Hansson *et al.*, 2005). Hydrozoans have been studied extensively for several decades and excellent reviews and monographs on the Hydrozoa have been published by Gili and Hughes (1995), Boero *et al.* (2002), and Bouillon *et al.* (2006). While they share many of the same physiological characteristics as scyphozoans, they are substantially different in many respects, particularly regarding their life cycle. Historically there has been much confusion regarding the nomenclature of the Hydrozoa (Fautin, 2002), as often the medusa and polyp were assigned different genus and species names because the two stages were studied in isolation from each other. Many hydrozoans are holoplanktonic, although the majority of the Anthomedusae and Leptomedusae are meroplanktonic with a life cycle similar to that of the Scyphozoa. But there are many complexities, both in the modes of asexual reproduction (Bouillon, 1994) and morphologies of the life stages (Cornelius, 1992). The hydroids are modular and clonal and are typified by great phenotypic plasticity (Gili and Hughes, 1995). With some exceptions, the scientific history has generated a completely different body of work to that of the scyphozoans, tending to focus on the taxonomy and developmental biology of the hydroid. Thus, the aims of this review are to

(1) synthesise what is currently known of the ecology of scyphozoan polyps;
(2) compare the distribution and life histories of scyphozoans, exploring differences between tropical and temperate species, and populations of the same species inhabiting different habitats within its geographic range;
(3) summarise the role that polyps play in ensuring the long-term survival of jellyfish populations;
(4) summarise the role of polyps in forming bloom populations of jellyfish.

2. Summary of Scyphozoan Life Cycles

The life cycle and developmental biology of the Class Scyphozoa has been comprehensively covered already in the classic texts of Berrill (1949), Russell (1970) and Arai (1997). It is not the intention to cover this again in this review, other than to illustrate the diversity of life cycles in scyphozoan jellyfish and summarise the key points. Illustrations of life cycles of several scyphozoans, including in some cases the duration of each life stage or temporal periodicity, can be found for *Cotylorhiza tuberculata* (Kikinger, 1986), *A. aurita* and *Cyanea capillata* (Gröndahl, 1988a,b), *Cyanea* sp. (Brewer, 1989; Brewer and Feingold, 1991), *Catostylus mosaicus* (Pitt, 2000), *Rhopilema nomadica* (Lotan *et al.*, 1994) and *N. nomurai* (Kawahara *et al.*, 2006).

The life cycle of the majority of members of the class Scyphozoa is metagenic, involving a sexually reproducing medusa (Fig. 3.2A) and an asexually reproducing benthic polyp or scyphistoma (Fig. 3.2B) (Arai, 1997; Widmer, 2008). Fertilized eggs develop into tiny free-swimming planula larvae (Fig. 3.2B, 1) that typically settle on the undersides of shaded surfaces (Holst and Jarms, 2007). Following settlement, the planulae metamorphose into scyphistomae (Fig. 3.2B, 2) capable of feeding as soon as they develop tentacles and a mouth (Widmer, 2006). In response to environmental triggers, scyphistomae metamorphose into strobilae by a process of transverse fission (Fig. 3.2B, 3), and this generates and releases free-swimming ephyrae (Fig. 3.2B, 4) that go on to develop into medusae. Strobilation may be monodisc (one ephyra) or polydisc (several ephyrae). After the last ephyra is released, the strobila returns once more into a scyphistoma. The perennial polyps also produce new ones by budding them from their bases, by fission and by stolon budding (Fig. 3.3) (Arai, 1997). Stolons are temporary pseudopod-like extensions that sometimes extend from the bases of scyphistomae and attach to the nearby substrate. From these stolons, new buds are also formed (Adler and Jarms, 2009). Many species also produce protective chitin-covered podocysts that protect against adverse conditions and from which new scyphistomae emerge (Fig. 3.4).

Not all members of the class Scyphozoa have life histories with benthic stages and are thus holoplanktonic. Medusae lacking polyps are often observed living in environments where proximity to benthic substrates suitable for scyphistoma habitat is limited, for example, the open ocean or the deep sea. Three out of five families within the order Coronatae are exclusively deep-sea species. *Periphylla periphylla*, for example, lacks not only benthic life history stages but also the planula and ephyra stages. Medusae produce and release large yolky eggs (Lucas and Reed, 2010) that pass through a series of stages and develop directly into juvenile medusae

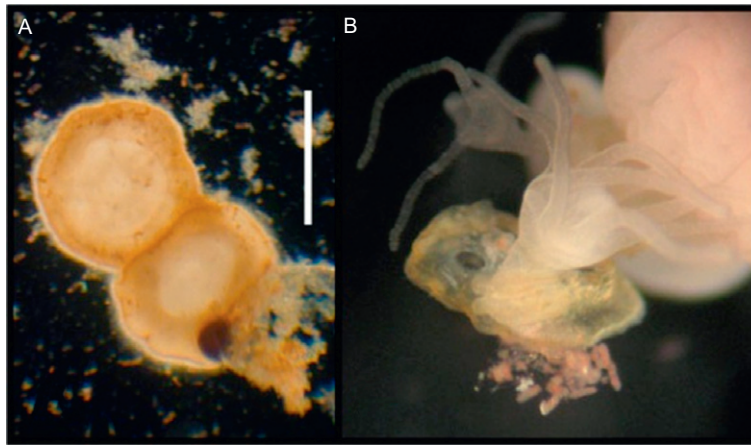

Figure 3.4 Podocysts of scyphozoans. (A) Two podocysts of *Chrysaora fuscescens*. (B) A scyphistoma that has recently excysted from the podocyst; scale bar = 1 mm (photos by C. Widmer).

(Jarms *et al.*, 1999, 2002). The Mauve Stinger, *P. noctiluca*, is a surface cruising semaeostome jellyfish (Zavodnick, 1987) with planula larvae that develop directly into ephyrae and go on to develop into mature medusae (Rottini Sandrini and Avian, 1983).

In most scyphozoans with metagenic life cycles, longevity of medusae is ~4–8 months, although Yasuda (1971) and Miyake *et al.* (1997) report that individuals of *A. aurita* live for >1 year in Japanese waters, and in aquaria medusae may live up to 2–4 years (Raskoff *et al.*, 2003). Polyps are longer-lived, and laboratory studies have shown that they may persist for several years (Spangenberg, 1965a; Gong, 2001).

3. The Ecology of Polyps

In contrast to the majority of scyphozoans with their alternation between the asexually reproducing benthic polyp and sexually reproducing pelagic medusa, the great majority of benthic invertebrates inhabiting the seabed are sexually reproducing adults producing planktonic larvae. Many of these include biofouling organisms in the higher invertebrate taxa, in particular, the barnacles, bivalves, polychaetes and ascidians. As a result, there is a substantial and much-cited literature that has considered the role of life histories and recruitment in regulating of abundance, distribution and community dynamics of these higher taxa, particularly those inhabiting the

rocky intertidal (Underwood and Denley, 1984; Gaines and Roughgarden, 1985). Three processes control the establishment of sessile populations: (1) the number of recruits, (2) the growth rate of settled individuals, and (3) the rate at which animals multiply (Keen, 1987). Much of the literature has focused on adult reproductive strategies (Olive, 1995; McEdward, 1997), the effects that environmental factors such as hydrodynamics, the presence of conspecifics and biofilms, temperature and food have on larval recruitment, settlement and post-settlement success (Gaines and Roughgarden, 1985; Toonen and Pawlik, 1994; Hadfield and Strathmann, 1996; Connelly *et al.*, 2001; Whalan *et al.*, 2008; Menge *et al.*, 2009), and the role that recruitment plays in determining abundance and distribution of the adult population, that is, supply-side ecology (Lewin, 1986; Underwood and Keough, 2001; Menge *et al.*, 2009).

We are nowhere near this level of understanding for jellyfish, principally because the benthic polyps have not been identified for the vast majority of species on account of their small size and cryptic nature. Nevertheless, with the increasing number of jellyfish scientists working in the field of polyp ecology, more wild populations are being discovered and studied, resulting in more published descriptions of the life histories of natural populations, often accompanied by observations and experiments of laboratory cultures. In reviewing and synthesizing what we currently know about the ecology of polyps, this section is divided into four parts: (1) recruitment and settlement of planula larvae, (2) survival and longevity of polyps, (3) asexual propagation and (4) strobilation and recruitment of ephyrae.

3.1. Recruitment and settlement of planula larvae

The timing, periodicity and level of recruitment of jellyfish planula larvae to the seabed depend on sexual reproduction of medusae. Sexual reproduction may be synchronous, semi-synchronous or continuous (for reviews of *Aurelia* spp., see Dawson and Martin, 2001; Lucas, 2001), and as with many marine invertebrates, this is likely to be driven primarily by differences in the temperature and productivity cycles. Continuous or semi-continuous breeding can be found in tropical and sub-tropical habitats, for example, *Mastigias papua* and *A. aurita* in Palau (Hamner *et al.*, 1982; Dawson and Martin, 2001) and *Cassiopea xamachana* in the Caribbean and Australia (Fitt and Costley, 1998), where seasonality is less pronounced. Dense populations inhabiting temperate closed and semi-enclosed lakes and lagoons are also characterised by prolonged or semi-continuous breeding (Lucas, 1996; Pitt and Kingsford, 2000; Malej *et al.*, 2007), most likely caused by relaxed selection for synchronized strobilation and fertilization when large numbers of individuals are confined in a small area (Dawson and Martin, 2001). In temperate coastal and shelf ecosystems, the majority of jellyfish populations consist of single cohorts growing and maturing

synchronously, with sexually mature females with planula larvae present for between 1 and 5 months, often over the summer period (e.g. Cargo and Schultz, 1966; Gröndahl, 1988a; Brewer, 1989; Lucas, 2001; but see Albert, 2005 for *Aurelia labiata* inhabiting Roscoe Bay on the north Pacific coast of Canada). These are broad generalisations, however, and the phasing of the life cycle with season is influenced by where a species is distributed within its geographical (temperature) range and whether the jellyfish is a 'cold water' or 'warm water' species. For example, the timing of sexual or asexual reproduction of *A. aurita* in northern Europe (Lucas, 2001) and *A. labiata* in the eastern Pacific (Purcell, 2007) changes with latitude, suggesting local adaptation, while the life histories of the cold-water species, *C. capillata*, is seasonally opposite to that of *Chrysaora quinquecirrha* in Chesapeake Bay (Cargo and Schultz, 1967).

Evidence suggests that while longevity and sexual maturation is neither size nor age-dependent, females typically become 'ripe' at the upper end of the size range of the population (Lucas and Lawes, 1998), with food and temperature affecting size and subsequent fecundity (Ishii and Båmstedt, 1998; Lucas and Lawes, 1998). Although the number of planula larvae produced at a particular size may be influenced by food availability (Lucas and Lawes, 1998; Lucas, 2001), in general, fecundity increases with increasing body size or weight (Schneider, 1988; Lucas, 1996). Ishii and Takagi (2003) estimated a daily planula production rate of 58,300 in a 420 g *A. aurita* medusa in Tokyo Bay, which, when multiplied by the duration of planula production over days or weeks, and the number of individuals in the population, provides an indication of total reproductive output. Variation in reproductive output not only manifests itself in terms of fecundity but also in terms of organic content of the gametes produced (Olive, 1985). Populations of *A. aurita* living in food-rich environments have been shown to produce large numbers of small planula larvae with low organic content (0.28 μg C), while those in food-poor environments produce fewer numbers of large, C-rich (0.68 μg C) larvae (Schneider, 1988; Lucas, 1996; Lucas and Lawes, 1998), which is also repeated in winter versus summer-produced planula larvae in Japanese waters (Kakinuma, 1975).

Cnidarian larvae are lecithotrophic, and following release into the water column, settlement occurs rapidly, often within 1–10 (typically ≤ 4) days (Calder, 1982; Pitt, 2000; Kawahara *et al.*, 2006; Holst and Jarms, 2007) (Table 3.1). The larger planula larvae of coronates such as *Linuche unguiculata* and *Nausithoe eumedusoides* remain in the plankton for 3–4 weeks (Da Silveira and Morandini, 1998). Time spent in the water column poses major risks for pelagic larvae in the form of predation, offshore transport away from suitable substrata and exposure to extreme environmental conditions, so there is likely to be selection to reduce the time that larvae spend in the plankton. Uthicke *et al.* (2009) consider lecithotrophic larvae to be a 'lower-risk' strategy than planktotrophic larvae in echinoderms, as they are independent

Table 3.1 Summary of the literature on the release, settlement and metamorphosis of planula larvae of scyphozoan jellyfish

	Timing of planula release	Planula size length *L*/width *W* (μm)	Settlement (days)	Factors affecting settlement and metamorphosis	Source
Rhizostomeae					
Cassiopea andromeda	nd	200*L*	<1	Require bacteria *Vibrio* sp.; metamorphose in 2 days	Neumann (1979)
Cassiopea spp.	nd	nd	nd	Biofilm indicates degrading leaves, increases wettability	Müller and Leitz (2002)
Cassiopea xamachana	All year	nd	2	Requires peptide	Fitt and Costley (1998)
Cassiopea xamachana	nd	nd	3	Requires water soluble peptide; no effect of gregariousness	Fleck and Fitt (1999)
Catostylus mosaicus	Dec–Jul	100–130*L*/60–130*W*	4–5	Substrate 'conditioned' for 10 days; gregarious settlement	Pitt (2000)
Cephea cephea	nd	130–230*L*	>14	nd	Sugiura (1966)
Cotylorhiza tuberculata	Collected late Sep–Oct	nd	15 (30 °C), >30 (20 °C)	% settling decreases from 30 to 4 °C; salinity has little effect (except at 20)	Prieto *et al.* (2010)
Lychnorhiza lucerna	Collected Mar	95–207*L*/39–54*W*	1–4	Metamorphose within 24 h	Schiariti *et al.* (2008)
Mastigias papua	nd	120–140*L*	nd	nd	Sugiura (1963, 1965)
Nemopilema nomurai	Oct–Dec	170*L*/130*W*	4–8	nd	Kawahara *et al.* (2006)
Phyllorhiza punctata	Collected Feb	300–500*L*	2–3	25 °C	Rippingdale and Kelly (1995)

(*continued*)

Table 3.1 (*continued*)

	Timing of planula release	Planula size length *L*/width *W* (μm)	Settlement (days)	Factors affecting settlement and metamorphosis	Source
Rhizostoma octopus	nd	110–150*L*/80–90*W*	1–5	Allowed bacterial biofilm to develop; metamorphose immediately	Holst and Jarms (2007), Holst *et al.* (2007)
Rhopilema esculenta	nd	95–150*L*/60–90*W*	3–4	Cultivated at 12–33 °C	Chen and Ding (1983)
Rhopilema verrilli	nd	165–310*L*/75–100*W*	3–10	Cultivated at 10–12–20 °C	Calder (1973)
Stomolophus meleagris	Collected Jul	120–390*L*/30–130*W*	2–5	Cultivated at 27 °C	Calder (1982)
Semaeostomeae					
Aurelia aurita	nd	nd	2	Allowed bacterial biofilm to develop; metamorphose immediately	Holst and Jarms (2007)
Aurelia aurita	Collected Jun	nd	nd	No effect of substrate roughness	Brewer (1978)
Aurelia aurita	Collected Sep	220–375*L*/85–125*W*	nd	Presence of 10 days polyps in high numbers decreases settlement	Gröndahl (1988b)
Aurelia aurita	Collected Jul and Aug	nd	1	Presence of 4 days polyps increases settlement	Gröndahl (1989)
Aurelia aurita	nd	nd	nd	Aggregated settlement due to hydrodynamics not gregariousness	Keen (1987)

Aurelia aurita	Aug onwards	150–200*L* (winter); 200–300*L* (summer)	3–5	nd	Kakinuma (1975)
Aurelia aurita	nd	nd	nd	Settled quicker at low oxygen	Ishii *et al.* (2008)
Chrysaora hysoscella	nd	nd	2	Allowed bacterial biofilm to develop; metamorphose immediately	Holst and Jarms (2007)
Chrysaora hysoscella	nd	100–500*L*	nd	Tested chemical ions to induce metamorphosis	Siefker *et al.* (2000)
Chrysaora hysoscella	Collected Jul and Aug	nd	nd	Settle at salinity 32–20, reduced/no settlement at salinity 15/10	Holst and Jarms (2010)
Chrysaora lactea	nd	140–200*L*/60–90*W*	nd	nd	Morandini *et al.* (2004)
Cyanea capillata	nd	nd	nd	Gregarious settlement with low no. conspecifics; inhibited at dense conspecifics, high flow	Dolmer and Svane (1993)
Cyanea capillata	nd	nd	2	Allowed bacterial biofilm to develop; metamorphose immediately	Holst and Jarms (2007)
Cyanea capillata	Collected May–Jun	185*L*	Short	Inspects surface; weak response to light	Brewer (1976)
Cyanea capillata	Jul–Dec	175–200*L*/100–110*W*	nd	Predation by 10 days *Aurelia* polyps decreases settlement	Gröndahl (1988b)
Cyanea capillata	nd	nd	nd	As light intensity increases more polyps settle on dark side	Svane and Dolmer (1995)

(*continued*)

Table 3.1 (*continued*)

	Timing of planula release	Planula size length *L*/width *W* (μm)	Settlement (days)	Factors affecting settlement and metamorphosis	Source
Cyanea capillata	Collected Jul and Aug	nd	nd	Reduced settlement (20–40%) at salinity 32–20; disintegrate at salinity 7	Holst and Jarms (2010)
Cyanea lamarckii	nd	nd	4	Allowed bacterial biofilm to develop	Holst and Jarms (2007)
Cyanea lamarckii	nd	200–300*L*	nd	nd	Siefker *et al.* (2000)
Cyanea lamarckii	nd	nd	nd	Reduced settlement (80%) at salinity 32–20; disintegrate at salinity 7	Holst and Jarms (2010)
Cyanea sp.	nd	nd	nd	Bacterial biofilm reduces wettability; prefers hydrophobic surfaces	Brewer (1984)
Cyanea sp.	nd	nd	nd	Settle as planulocysts	Brewer (1989)

of planktonic food supply, have lower mortality in the plankton due to their shorter development time and contain maternal provisioning for the early juvenile. While the organic content of the lecithotrophic larvae is expected to increase survivorship and successful metamorphosis into a polyp upon settlement, development and planktonic larval duration (PLD) are strongly influenced by temperature (Reitzel *et al.*, 2004; Byrne *et al.*, 2011, and references therein). Increased temperature may be detrimental to larval development if it increases above the thermal tolerance of the species in a given location, while an inverse relationship between temperature and PLD is well documented for many marine invertebrate larvae (Gillooly *et al.*, 2002; O'Connor *et al.*, 2007). This reduction in PLD with increased temperature may buffer the negative effects on development (Byrne *et al.*, 2011), as well as reduce the predatory and transport risks mentioned above.

With regard to jellyfish, there are very few studies that have examined the effect of environmental stressors on the survivorship of planula larvae in scyphozoans. Schneider and Weisse (1985) estimated the maximal survival period of planula larvae in *A. aurita* to be up to 1 week based on measurements of C:N:P, respiration and excretion. Because of the high metabolic demand of swimming, which cannot be replenished via ingestion, Ishii *et al.* (2008) found that hypoxic conditions were detrimental to the survival of larvae of *A. aurita*. Planula settlement, measured as the percentage of planula settling against time, was enhanced at low dissolved oxygen (DO). Because the respiration rate of newly settled sedentary polyps is lower than the free-swimming planulae, this was considered by the authors to be an adaptive behaviour for overcoming hypoxic conditions during the planula phase. Experiments examining the effects of different temperatures (4–30 °C) and salinities (20–53) on planula settlement of the rhizostome *C. tuberculata* in the hypersaline Mar Menor lagoon in the NW Mediterranean found that the planulae were very resilient to a wide range of environmental conditions (Prieto *et al.*, 2010); the main effect being that the time taken for larvae to settle and metamorphose was longer at colder temperatures. Tolerance to a wide range of salinities was also observed by Holst and Jarms (2010). Reducing salinity from 32 to 10 resulted in less swimming and damage to the planula larvae of *Cyanea lamarckii*, *C. capillata* and *A. aurita*. A further reduction to 7 resulted in larval disintegration in the two *Cyanea* species, while those of *A. aurita* eventually died at a salinity of 5, highlighting its extreme euryhalinity.

The main purpose of pelagic larvae is to exploit ecological niche openings and promote genetic exchange between populations via dispersal. Finding and selecting an appropriate benthic habitat is essential for the continued success of the population, so settlement onto a suitable substrate and subsequent metamorphosis of many marine larvae, including those of cnidarians, is not a random process. The processes of selecting and settling onto a suitable substrate and metamorphosing into a polyp are driven by

external cues, and the larvae of several species (e.g. *A. aurita*, *Chrysaora hysoscella*, *Cyanea* spp., *Rhizostoma octopus*) have been shown to undergo geopositive and geonegative swimming behaviour in search of a suitable substrate (Cargo, 1979; Holst and Jarms, 2007). The sensory capacity of cnidarian planula larvae is limited to mechanoreceptive and chemoreceptive cells, which although allows larvae to explore the immediate microenvironment of the substrate, does not enable them to identify a suitable habitat from a distance (see review of Müller and Leitz, 2002). Both Brewer (1976) and Pitt (2000) observed the larvae of *C. capillata* and *C. mosaicus*, respectively, swimming slowly across the substrate surface, 'inspecting' it prior to settlement; if the substrate was not suitable, larvae would swim away. Similarly, Hartwick (1991b) observed that the planula larvae of the cubozoan *Carybdea sivickisi* were able to temporarily attach to substrates for a few minutes before eventually attaching permanently after 4 days.

In scyphozoan jellyfish, external factors that have been found to affect settlement and metamorphosis include physical cues such as boundary layer properties, gravity, light/shade and the physical nature (e.g. roughness) of the substratum (Cargo, 1979; Brewer, 1984; Keen, 1987; Svane and Dolmer, 1995), chemical cues such inorganic ions, and peptides released by bacterial biofilms and bacterial-decay of mangrove litter (Fitt and Costley, 1998; Fleck and Fitt, 1999; Siefker *et al.*, 2000; Hofmann and Crow, 2002; Müller and Leitz, 2002; and references therein), and biological cues such as the presence of conspecifics, competitors and predators (Gröndahl, 1988b, 1989; Dolmer and Svane, 1993). One of these factors alone is not usually sufficient to induce settling and metamorphosis; instead a hierarchy of key stimuli are required for successful recruitment onto the seabed (Gröndahl, 1989; Müller and Leitz, 2002).

Broadly speaking, the presence of biofilms appears to be an essential requirement for settlement and successful metamorphosis into a polyp, and in most reported laboratory experiments, settling plates are pre-conditioned by soaking in seawater for at least 24 h prior to the start of experiments. It is not entirely clear why biofilms are important for marine larval settlement, but it is suggested that biofilms may indicate the permanence of the substrate in the sea, and/or increase the strength of attachment (Hadfield, 2011) due to the increased hydrophobicity of the film-covered surface (Brewer, 1984; Müller and Leitz, 2002). The rhizostome jellyfish *Rhizophora mangle* and the widely distributed semi-sessile zooxanthellate upside-down jellyfish, *Cassiopea* spp., are found in shallow tropical coastal waters typically associated with sheltered mangrove lagoons. It may be that the diverse biofilms present on degrading mangrove leaves that polyps naturally prefer to colonize (Fleck and Fitt, 1999; Hofmann and Crow, 2002) indicate the presence of their preferred substrate and habitat.

Gregarious settlement is common in many benthic invertebrates such as barnacles, mussels, polychaetes, ascidians, and the benefits and costs of this

behaviour have been summarised by Müller and Leitz (2002). The jellyfish literature on gregarious settlement is rather mixed (e.g. Keen, 1987; Hartwick, 1991a; Dolmer and Svane, 1993; Fleck and Fitt, 1999) with several authors finding no conclusive evidence that it occurs. In scyphozoans, gregariousness has been demonstrated if the conspecific polyps are present in relatively low densities (Dolmer and Svane, 1993) and/or if the polyps are relatively small (Gröndahl, 1989). In a series of experiments using *A. aurita* polyps, Gröndahl (1988a,b, 1989) found that older, larger (10 days, 0.62 mm) polyps decreased settlement of larvae of both *A. aurita* and *C. capillata* because of reduced space and predation caused by the polyps, while the presence of younger and smaller (4 days, 0.28 mm) polyps enhanced settlement and metamorphosis of planulae. This is possibly due to chemicals released by the polyps, which may indicate the suitability of the substrate (viz., biofilms). The findings of Gröndahl (1989) are in contrast to those of Keen (1987), who suggested that reduced shear stress and increased benthic boundary layer were more important in determining the settling pattern of planulae. Gröndahl (1989) suggests that the contrasting hydrodynamic regimes of the two study sites (tidally dominated, shallow Eel Pond versus the virtually non-tidal, deeper Gullmarfjord) may explain these differences.

Both natural and artificial substrates are readily settled upon by planula larvae (Table 3.2). Studies of the natural habitat of jellyfish polyps are still relatively scarce, but polyps of common bloom-forming scyphozoans such as *Aurelia* spp., *Cyanea* spp., and *Chrysaora* spp. have been found on a wide range of natural substrates including live mussel and oyster shells, hard ascidians, polychaete and amphipod tubes, barnacles, rocks and stones, brown macroalgae, as well as man-made structures such as cement walls, pylon legs and polystyrene floats (Gröndahl, 1988a,b; Miyake *et al.*, 1997, 2002, 2004; Östman, 1997; Purcell *et al.*, 2009; Ishii and Katsukoshi, 2010). Species such as the upside-down jellyfish, *C. xamachana*, are more specific, being found mainly on degrading mangrove leaves (Fitt and Costley, 1998) that characterise their preferred habitat. Similarly, *C. quinquecirrha* polyps inhabiting Chesapeake Bay are primarily found on oyster shells (Cargo and Schultz, 1966), as well as some man-made structures (Condon Robert, personal communication). A number of studies have explored whether there is selectivity for different substrate types, both artificial and natural (Brewer, 1984; Fleck and Fitt, 1999; Pitt, 2000; Holst and Jarms, 2007; Hoover and Purcell, 2009). Holst and Jarms (2007) found that the planulae of several species common in European waters displayed a preference for artificial substrates (machined wood, polyethylene, glass and concrete) over shells. Significant differences in substrate preference were determined in the different jellyfish species, the authors suggesting that there was species-specific preference for different bacterial films that might grow on each substrate type. Hoover and Purcell (2009) considered that surface texture and chemical treatment were important determinants in artificial

Table 3.2 Summary of the literature on natural and artificial substrata colonised by scyphozoan polyps *in situ* and used as settling plates in laboratory and field experiments

Species	Location	Natural or artificial substrata and structures	Source
Rhizostomeae			
Cassiopea andromeda	Key Largo, Florida	Empty *Artemia* eggs capsules in lab	Neumann (1979)
Cassiopea xamachana	Southern Florida	Dark red mangrove leaves	Fitt and Costley (1998)
Cassiopea xamachana	Southern Florida	Settled on red, green mangrove leaves, seagrass, alga, gastropod, bivalve, stone; 67% prefer black degrading leaves	Fleck and Fitt (1999)
Catostylus mosaicus	Botany Bay, Australia	Wood, sandstone, empty bivalve, seagrass (fewest and died), glass slides (most)	Pitt (2000)
Cotylorhiza tuberculata	Mar Menor, Mediterranean	Glass slides (lab experiments)	Prieto *et al.* (2010)
Cotylorhiza tuberculata	Lefkada, Ionian Sea, Greece	Glass debris	Kikinger (1992)
Lychnorhiza lucerna	Rio de la Plata, Argentina	Settled on styrene, glass, empty bivalve shells; not on stones; many at air–water interface	Schiariti *et al.* (2008)
Nemopilema nomurai	Oki Island, Japan	Settled on styrene; not many on shells, glass, ceramics; many at air–water interface	Kawahara *et al.* (2006)
Phyllorhiza punctata	Swan-Canning estuary, Australia	Acetate sheet (lab experiments)	Rippingdale and Kelly (1995)
Rhizostoma octopus	Helgoland, German Bight North Sea	~75% of total settle equally on glass, PET, wood, shell, concrete; ~24% settle at air–water interface	Holst and Jarms (2007)
Rhizostoma pulmo	Badalona, Spain	Undersides of concrete columns	Fuentes *et al.* (2011)

Semaeostomeae			
Aurelia aurita	Gullmar fjord, Sweden	*Laminaria saccharina, L. digitata, Fucus serratus, Mytilus edulis*, stones	Östman (1997)
Aurelia aurita	Helgoland, German Bight North Sea	~8% of total settle on glass, PET (45%), wood, shell (25%), concrete; <6% of total on bottom, 85% at air–water interface	Holst and Jarms (2007)
Aurelia aurita	Connecticut, USA	Plastic coverslips smooth and rough (sandpapered or grooves); no effect of roughness	Brewer (1978)
Aurelia aurita	Gullmar fjord, Sweden	Ceramic settling plates; naturally seen on algae, barnacles, polychaete tubes, ascidians, hydroids	Gröndahl (1988a)
Aurelia aurita	Gullmar fjord, Sweden	*Laminaria saccharina* and rock walls; glass slides and ceramic settling plates (*in situ* experiment)	Gröndahl (1988b)
Aurelia aurita	Gullmar fjord, Sweden	*Laminaria saccharina* (*in situ*); petri dishes (lab experiments); glass slides (*in situ* experiments)	Gröndahl (1989)
Aurelia aurita	Woods Hole, USA	Unglazed ceramic tiles (horizontal under pontoons) as settling plates	Keen (1987)
Aurelia aurita	Tokyo Bay, Japan	Acrylic tiles as settling plates	Watanabe and Ishii (2001), Ishii *et al.* (2008)
Aurelia aurita	Tokyo Bay, Japan	Pylon legs at 4–5 m depth	Ishii and Katsukoshi (2010)
Aurelia aurita	Gullmar fjord, Sweden	Ceramic settling plates at 5–25 m depth; natural rocks and shells, *Laminaria, Fucus*	Hernroth and Gröndahl (1983, 1985b)
Aurelia aurita	Gullmar fjord, Sweden	Ceramic settling plates at 5 and 10 m depth; barnacles, polychaete tubes, ascidians, hydroids at 5 m depth	Hernroth and Gröndahl (1985a)
Aurelia aurita	Kagoshima Bay, Japan	Under polystyrene floating piers on ascidians (hard *Styela*), mussels (live only), amphipod tubes, brown weed	Miyake *et al.* (1997, 2002)
Aurelia aurita	Yamaguchi, Japan	Undersides of floating piers, on cigarette packet	Miyake *et al.* (2002)
Aurelia aurita	Tapong Bay, Taiwan	Oyster cultures	Lo *et al.* (2008)

(*continued*)

Table 3.2 (*continued*)

Species	Location	Natural or artificial substrata and structures	Source
Aurelia aurita	Tasmania	Cement breakwater—found on bare substrate and biofouling organisms; black acrylic settling plates	Willcox *et al.* (2008)
Aurelia aurita	Helgoland, North Sea	Watch glass, polythene plates (lab experiments)	Holst and Jarms (2010)
Aurelia labiata	Washington State, USA	Polystyrene, chemically treated wood, vulcanised runner, HDPE, LDPE; Undersides of pontoons covered	Hoover and Purcell (2009)
Aurelia labiata	Washington State, USA	Covered polystyrene floating docks	Purcell *et al.* (2009)
Chrysaora hysoscella	Helgoland, German Bight North Sea	~72% of total settle on glass, PET, wood, shell, concrete; 11% of total on bottom, 5.6% on wall	Holst and Jarms (2007)
Chrysaora lactea	Southeast Brazil	Plastic or glass (lab experiments)	Morandini *et al.* (2004)
Chrysaora quinquecirrha	Chesapeake Bay, USA	Oyster shells	Cargo and Schultz (1967), Calder (1974), Purcell *et al.* (1999b), Condon *et al.* (2001)
Cyanea capillata	Gullmar fjord, Sweden	*Laminaria saccharina, L. digitata, Fucus serratus, Mytilus edulis*, stones	Östman (1997)
Cyanea capillata	Gullmar fjord, Sweden	Ceramic settling plates at 5, 10, 25 m depth	Gröndahl and Hernroth (1987), Gröndahl (1988a)
Cyanea capillata	Gullmar fjord, Sweden	Petri dish, half painted black (lab experiments)	Svane and Dolmer (1995)

Cyanea capillata	Helgoland, German Bight North Sea	~46% of total settle on glass, PET, wood, shell, concrete (15–25% ea); 31% settle on bottom, 17% at air–water interface, 4% on wall	Holst and Jarms (2007)
Cyanea capillata	Connecticut, USA	Coverslips smooth and rough (preferred), effect of shading not significant	Brewer (1976)
Cyanea capillata	Helgoland, North Sea	Watch glass or polyethylene plates—petri dishes (lab experiments)	Holst and Jarms (2010)
Cyanea lamarckii	Helgoland, German Bight North Sea	~74% of total settle on glass, PET (70%), wood, shell, concrete; 25.5% at air–water interface	Holst and Jarms (2007)
Cyanea lamarckii	Gullmar fjord, Sweden	Ceramic settling plates at 5, 10, 25 m depth	Gröndahl (1988a)
Cyanea lamarckii	Helgoland, North Sea	Watch glass or polyethylene plates—petri dishes (lab experiments)	Holst and Jarms (2010)
Cyanea sp.	Niantic River estuary, Connecticut, USA	Glass coverslip, plastic coverslip (95% prefer) rough and smooth; prefer inorganic hydrophobic surfaces	Brewer (1984)
Cyanea sp.	Chesapeake Bay, USA	Oyster shells (natural)	Cargo and Schultz (1967)
Cyanea sp.	Niantic River estuary, Connecticut, USA	Roughened PVC (*in situ* settling plates)	Colin and Kremer (2002)

substrate selection. Many studies have reported a preference for roughened surfaces and concavities—rugophilic behaviour (e.g. Brewer, 1976, 1984; Hartwick, 1991a; Willcox *et al.*, 2007).

The potential role of man-made structures in providing new habitats for polyps, thus enhancing abundance and expanding the range of jellyfish populations has been considered by several authors (Miyake *et al.*, 2002; Holst and Jarms, 2007; Purcell *et al.*, 2007; Lo *et al.*, 2008; Hoover and Purcell, 2009; Duarte *et al.*, 2012). The consensus is that the proliferation of man-made structures may be partially responsible for the increase in jellyfish populations and bloom events (Duarte *et al.*, 2012). Regardless of substrate type, planula larvae have a significant (~82–100%) preference for the undersides of substrates (Brewer, 1976; Fleck and Fitt, 1999; Miyake *et al.*, 2002; Holst and Jarms, 2007; Willcox *et al.*, 2008), typical of many man-made structures (e.g. pontoons). Thus, problems associated with siltation and overcrowding from other biofouling organisms are reduced (Cargo and Schultz, 1966), while expulsion of faecal material is made easier (Holst and Jarms, 2007); so polyp survivorship increases.

3.2. Survivorship of polyps

The distribution and abundance of polyp recruits to a habitat depend on the supply of and settlement success of planula larvae (see above), as well as factors affecting growth and mortality, that is, survivorship. The majority of scyphozoan planula larvae settle and metamorphose directly into polyps. In most rhizostomes and semaeostomes, the initial development of a four-tentacled scyphistoma can take as little as 24 h (Holst and Jarms, 2007; Schiariti *et al.*, 2008). Overall size and the number of tentacles increase until full development is attained within 2–5 weeks of settlement (Lotan *et al.*, 1992; Pitt, 2000; Kawahara *et al.*, 2006; Schiariti *et al.*, 2008), the duration being temperature-sensitive (Prieto *et al.*, 2010). *C. lamarckii*, in general, and *Cyanea* sp. from the lower Chesapeake Bay and Niantic River, typically form planulocysts prior to the formation a polyp (Cargo and Schultz, 1967; Widersten, 1968; Brewer, 1976; Colin and Kremer, 2002; Holst and Jarms, 2007, 2010) which can occur up to 6 months later (Gröndahl, 1988a). However, in the Baltic and off the Swedish coast at least, the larvae of *C. capillata* appear to develop directly into polyps (Gröndahl, 1988a; Holst and Jarms, 2007, 2010). While encystment appears to be part of the normal ontogenetic development of *C. lamarckii*, Hargitt and Hargitt (1910) suggest that encystment in *C. capillata* is facultative. It is suggested that planulocysts provide protection against temperature extremes, competitors or predators, although Holst and Jarms (2010) question whether this is a successful strategy against post-settlement mortality, as there is high mortality resulting from overgrowth by epibiota (Brewer and Feingold, 1991; Holst and Jarms, 2007).

Only a handful of studies have examined the natural feeding ecology of polyps. The vast majority of laboratory experiments use 1–2 day old *Artemia* nauplii as food, although some have used rotifers (Schiariti *et al.*, 2008; Prieto *et al.*, 2010), or copepodites and mixed zooplankton (Rippingdale and Kelly, 1995; Purcell *et al.*, 1999b). Polyps have voracious appetites (Rippingdale and Kelly, 1995; Schiariti *et al.*, 2008), but they can also survive for months without food at low temperatures or salinities (Kakinuma, 1975; Holst and Jarms, 2010). Polyps of *Phylorhiza punctata* polyps shrink if unfed, but re-grow once food becomes available again (Rippingdale and Kelly, 1995), highlighting similar nutritional flexibility to that observed in all medusae. When food is scarce, larger polyps of *A. aurita* may feed on smaller ones nearby (Kakinuma, 1975). Of the few studies that report the natural diets of scyphozoan polyps, there appears to be low selectivity, as a great variety of zooplankton prey are consumed: copepods, mollusc and fish larvae and planulae, including some prey items larger than themselves (Gröndahl, 1988b, 1989; Tsikon-Lukanina *et al.*, 1995; Östman, 1997).

Several rhizostome species are zooxanthellate, containing the genus *Symbiodinium*. In polyps, these symbionts may or may not be an essential requirement for strobilation (discussed later). Planula larvae and newly settled polyps are aposymbiotic and acquire low numbers of cells by ingesting either algal-containing tissue (Sugiura, 1969; Kikinger, 1992) or motile zooxanthellae (Sugiura, 1969). However, other than the critical role of zooxanthellae in strobilation for some species, the importance of autotrophy for polyp growth and survival appears to be less important than heterotrophic ingestion. Several authors have successfully cultured polyps in zooxanthellae-free conditions (including a lack or light and/or nutrients) for several years (e.g. Sugiura, 1965, 1969; Kikinger, 1992; Prieto *et al.*, 2010). In *C. tuberculata*, a lack of heterotrophic feeding was not compensated by the photosynthetic activity of zooxanthellae (Prieto *et al.*, 2010). Nevertheless, the relative rates of autotrophy and heterotrophy in polyps have not been explored in any detail and elemental budgets are completely lacking. In zooxanthellate medusae, elemental budgets have been constructed for *C. xamachana* (Verde and McCloskey, 1998), *L. unguiculata* (Kremer, 2005) and *M. papua* (McCloskey *et al.*, 1994). These indicate that while carbon (C) produced by the zooxanthellae can exceed the C demands of the medusa, the medusa still ingests zooplankton, and if unfed, may shrink. Thus, while heterotrophy may contribute $<10\%$ of C relative to photosynthesis (Kremer, 2005), ingested prey may provide an invaluable source of N (reviewed by Pitt *et al.*, 2009).

Unlike the majority of scyphomedusae, which are considered to be annuals with life spans <1 year, scyphozoan polyps are perennials and are able to live for several years, particularly in laboratory cultures (e.g. Sugiura, 1969; Spangenberg, 1965a; Gong, 2001). This means that, in temperate

coastal waters, they may be exposed to wide-ranging and fluctuating biotic and abiotic environmental variables that affect their survival and longevity. These include intra- and inter-specific competition for space and food, availability of food, predation by nudibranchs, and the effects of temperature, salinity, hypoxia, pH, pollution, light and siltation.

Early post-settlement mortality is widespread among marine invertebrates (e.g. Gosselin and Qian, 1997; Hunt and Scheibling, 1997; Vermeij and Sandin, 2008). Small juvenile benthic forms are at their most susceptible to the effects of predation, sedimentation and over-crowding, and post-settlement mortality is typified by great temporal (weekly, inter-annual) and habitat-scale spatial variability. Although specific studies on early post-settlement mortality are virtually absent for jellyfish (but see Gröndahl, 1988b), inferences can be made from settlement experiments. Newly settled polyps of *A. aurita* on clean settling plates in Horsea Lake 'disappeared' 1 month later, just as other biofouling organisms were beginning to establish (Lucas Cathy, personal observation), with similar findings for *A. aurita* in Tokyo Bay (Watanabe and Ishii, 2001). Colin and Kremer (2002) found that, following initial settlement of *Cyanea* sp. larvae on settling plates, planulocysts had disappeared after 2–3 weeks, coincident with high abundances of newly recruited barnacles and ascidians. Gröndahl (1988b) estimated that the mortality rate within 10 days of settlement was between 4.5% and 28%.

The effects of inter- and intra-specific competition for space and food are at its greatest in the early post-settlement phase when the small developing polyps are at their most vulnerable. Nevertheless, competition for space can occur throughout the benthic phase of the life cycle and this may limit colony growth and therefore polyp density within a particular site (Willcox *et al.*, 2008). Many substrates inhabited by scyphistomae are also home to other encrusting and sessile epibiota such as mussels, barnacles, polychaetes, hydroids, sponges, ascidians and small macroalgae, and these are likely to be competitively superior to the small scyphozoan polyps (Hartwick, 1991a). Because mortality of newly settled polyps can be high, Colin and Kremer (2002) posed the question 'under what conditions can newly settled planulae survive?' Their answer was to seek refuge, either spatially or temporally. If planulae settle and establish before other benthic recruits, they may stand a greater chance of survival. The greater roughness of natural substrata (compared with artificial settling plates used in most experiments) may provide micro-spatial refugia against overcrowding and predation (Colin and Kremer, 2002). In the hypereutrophic Tokyo bay, *Aurelia* polyps, which are tolerant of low levels of dissolved oxygen (Ishii *et al.*, 2008), are free to colonise the bottom hypoxic waters as these are too stressful for most sessile benthic organisms in the region, in particular, the mussel *Mytilus galloprovincialis* (Ishii *et al.*, 2008; Ishii and Katsukoshi, 2010).

While processes controlling the supply of larvae and their subsequent settlement onto preferred substrates have been considered for many benthic

marine invertebrates, research on ascidians and other epifauna indicate that post-settlement predation can significantly affect population abundance (Osman and Whitlach, 2004; and references therein). Quantitative and even descriptive accounts of predation on cnidarian polyps are scarce, which has led to a patchy understanding of the role of predation in controlling polyp abundance. The main predators of jellyfish polyps are aeolid nudibranchs, with *Coryphella verrucosa* (Hernroth and Gröndahl, 1985a,b; Östman, 1997), *Facelina bostoniensis* (Thiel, 1962), *Cratena pilata* (Cargo and Schultz, 1967), *Dondice paraguensis* (Brandon and Cutress, 1985) and *Tenellia adspersa* (Lucas Cathy, personal observation) all found to consume scyphozoan polyps. Other predators include non-selective feeders such as caprellid amphipods, pycnogonids and decapods (Oakes and Haven, 1971), as well as conspecific polyps themselves if food is scarce (Kakinuma, 1975). Nudibranchs are mostly dietary specialists—some are highly stenophagous feeding on only 1 or 2 prey items, with sponges, bryozoans and cnidarians the most common prey groups. Aeolid nudibranchs are considered to be opportunists, characterised by rapid growth, short life span and consumption of transient prey populations (Hernroth and Gröndahl, 1985b). This is borne out by the very close coupling reported between the presence and abundance of predator and prey species. For example, in the Gullmar fjord, massive strobilation by *A. aurita* in October was followed by the virtual disappearance of polyps in November. This was shown to be caused by dense populations (up to 931 m^{-2}) of *C. verrucosa* that consumed up to 200 polyps day^{-1} (Hernroth and Gröndahl, 1985a,b). Subsequently, there was heavy mortality of nudibranchs coincident with the disappearance of their prey. Although this nudibranch-polyp relationship has been described for other jellyfish populations in the Kattegat, southern Baltic (Kiel) and Chesapeake Bay, the relative importance of predation in controlling polyp abundance in other populations, seasonally and from year to year is unknown. In Gullmar fjord, 99% of the polyps are predated upon in the late autumn, but enough survive overwinter to continue the population the following spring.

Regarding the effects of abiotic environmental variables on polyp survivorship, temperature, salinity, hypoxia, light and pH have all been examined, with temperature receiving by far the most attention. The only study that has reported the effect of pH is that of Winans and Purcell (2010). Polyps of *A. labiata* were found to be quite tolerant to low pH over the combined pH (7.2, 7.5, 7.9) and temperatures (9 °C, 15 °C) tested, with 100% survival after 122 days. While light levels have been shown to affect strobilation in several jellyfish species and will be discussed later, light does not appear to affect polyp survivorship directly, even in zooxanthellate species (Sugiura, 1969; Prieto *et al.*, 2010). This is because the polyps of these species are generally aposymbiotic, with only some species requiring the presence of *Symbiodinium* for strobilation. Nevertheless, Fleck and Fitt (1999) speculated that one reason

for the preference for polyps of *Cassiopea* sp. to inhabit the undersides of mangrove leaves was to provide protection against UVL (although this was not tested). Similarly, in Ocean Village marina in Southampton Water, UK, *A. aurita* polyps are only found on the undersides of pontoons situated under an overhanging building where the light levels (μmol m^{-2} s^{-1}) are only 2–18% of light levels elsewhere in the marina (Lucas Cathy, unpublished data) suggested that light may indirectly affect polyp distribution as the shadier areas have very little filamentous macroalgae growth on the pontoons, thus reducing competition for space and allowing a free flow of plankton-containing water past the polyps' tentacles.

Salinity appears to have minimal effect on polyp survivorship of those species examined (Holst and Jarms, 2010) and is in line with the experiments carried out on planula larvae tolerances (e.g. Holst and Jarms, 2010; Prieto *et al.*, 2010). The neritic tropical cubozoan *Chironex fleckeri* feeds and reproduces in salinities >20 and can survive periods of exposure to low (>5) and high (42) salinities (Hartwick, 1991a). In Chesapeake Bay, *Chrysaora quinqecirrha* polyps thrive in salinities 10–25, with encystment only occurring when salinities are <7 (Cargo and King, 1990). This tolerance range is thought to define the geographical range of this species within the region (Cargo and Schultz, 1966). In both Chesapeake Bay (CB) and Tokyo Bay (TB), periods of low dissolved oxygen (DO) occur during parts of the year as a result of density stratification and microbial activity (CB) and eutrophication (TB). Nevertheless, polyps of *C. quinquecirrha* and *A. aurita* are found in the bottom hypoxic waters of Chesapeake Bay (Condon *et al.*, 2001) and Tokyo Bay (Watanabe and Ishii, 2001; Ishii *et al.*, 2008), respectively. Condon *et al.* (2001) found that polyps of *C. quinquecirrha* were able to survive and asexually reproduce, even during prolonged (24 days) exposure to hypoxic conditions (i.e. <2 mg O_2 l^{-1}) as low as 0.5 mg O_2 l^{-1}. This high tolerance provides the scyphistomae of these species a competitive advantage over other biofouling organisms that would otherwise occupy their space.

The effects of temperature on polyp survivorship have been carried out on a variety of species including the rhizostomes *C. tuberculata* (Prieto *et al.*, 2010), *C. xamachana* (Fitt and Costley, 1998) and *R. nomadica* (Lotan *et al.*, 1994) and the semaeostomes *A. aurita* (Willcox *et al.*, 2007; Liu *et al.*, 2009; Purcell *et al.*, 2012) and *C. quinquecirrha* (Cargo and Schultz, 1967). While one can conclude that the polyps of the most widespread genera such as *Aurelia*, *Cyanea* and *Chrysaora* are highly tolerant of a wide range of environmental conditions, temperature appears to have the greatest effect on polyp survival, particularly for those species living at the edges of their geographical range, tropical species that are exposed to only moderate temperature fluctuations under 'normal' circumstances, and when there are exceptional weather/climate events (Fitt and Costley, 1998; Liu *et al.*, 2009). For example, most species of temperate jellyfish (e.g. *A. aurita*,

C. capillata, *C. quinquecirrha*, *Stomolophus meleagris*) have polyps that survive through the cold winter months. However, in the Mar Menor lagoon (western Mediterranean), an extreme cold event in January 2005, when temperatures were close to freezing for several days, was thought to be responsible for a massive reduction in the polyp population in the lagoon (Prieto *et al.*, 2010). Similar observations have been reported for *A. aurita* in Tasmania (Willcox *et al.*, 2008) and for *R. nomadica* in the eastern Mediterranean (Lotan *et al.*, 1994). In contrast to temperate species, polyps of the tropical jellyfish *C. xamachana* in southern Florida are present only during the spring and summer months (Fitt and Costley, 1998). In laboratory experiments, tentacles were found to contract below 20 °C, so that the polyps could not feed properly. At 15 °C, the polyps died within 5 days. The authors conclude that 'unlike temperate-zone species of scyphozoans, which usually over-winter in the polyp or podocyst form when medusae disappear, this tropical jellyfish has cold-sensitive scyphistomae and more temperature-tolerant medusae'. Nevertheless, this genus displays a certain degree of robustness. Very high numbers of tropical species *C. xamachana* and *Cassiopea andromeda* are found in the Florida Keys and Caribbean (Neumann, 1979; Fitt and Costley, 1998), the Red Sea (Gohar and Eisawy, 1960a,b; Niggl and Wild, 2010), and there have been invasions into Hawaiian and Mediterranean waters (Holland *et al.*, 2004; Çevik *et al.*, 2006; Özgür and Öztürk, 2008).

Although thermal tolerance limits are likely be species-specific, populations of the same species (or genus as in the case of *A. aurita* and *A. labiata*) inhabiting different parts of their geographical range also have different responses to temperature (Connelly *et al.*, 2001; Purcell, 2007) (Table 3.3). *A. aurita* is found throughout northern Europe and SE Asia in regions that can be described as cold-temperate to sub-tropical, while the closely related species *A. labiata* is found in the northeastern Pacific (Dawson and Jacobs, 2001). Thus, different populations will experience narrow or wide seasonal temperature ranges, as well as different minima and maxima (Lucas *et al.*, 2001; Purcell, 2007; Liu *et al.*, 2009; Purcell *et al.*, 2012). In comparing the thermal tolerances of tropical *A. aurita* from Taiwan and temperate *A. labiata* from the NE Pacific (Purcell, 2007), Liu *et al.* (2009) estimated that the thermal maxima (i.e. when polyps died) of these two closely related species were 30 and 20 °C, respectively. Similarly, *A. aurita* polyps from the Mediterranean died at 28 °C in experiments carried out by Purcell *et al.* (2012). However, evidence suggests that *A. aurita* in Taiwan together with other species inhabiting tropical waters (e.g. *Mastigias* sp.) may be living near the upper thermal limits for scyphozoans. Temperature increases of only 1–2 °C above those found *in situ* cause polyp mortality (Dawson *et al.*, 2001; Liu *et al.*, 2009), while *A. labiata* living in waters 7–15 °C are still able to survive and strobilate in temperatures 3 °C above those encountered *in situ* (Purcell, 2007).

Table 3.3 Summary of the literature describing the population dynamics of medusae and polyps of *Aurelia* species across their geographical range

Species	Location	Latitude/ longitude	Temperature range (°C)	Ephyrae month (temp)	Ripe females month (temp)	Budding month (temp)	Podocysts month (temp)	Strobilation month (temp)	Source
Aurelia aurita	Tvarminne, Finland	60° 27′N, 22° 02′E	−0.3–16	May–Aug (5–6 °C)	nd	nd	nd	nd	Palmén (1954)
Aurelia aurita	Gullmar fjord, Sweden	58° 19′N, 11° 32′E	−1.4–16	Nov–Dec, Feb–Apr (8–2 °C, 1–4 °C)	May/Jun–Sep/ Oct	Apr–Aug	Nov–Mar	Oct–Nov, Feb–Mar	Gröndahl (1988a), Hernroth and Gröndahl (1983, 1985a)
Aurelia aurita	Isefjord, Denmark	55° 45′N, 11° 50′E	0–17	Feb 1959 (3–4 °C), Mar–Apr 1963 (5 °C)	Jun–Oct	nd	nd	nd	Rasmussen (1973)
Aurelia aurita	Kertinge Nor, Denmark	55° 35′N, 10° 23′E	2–22	Feb–Apr (3.5–6.4 °C)	nd	nd	nd	nd	Olesen *et al.* (1994)
Aurelia aurita	Kiel Bight, W. Baltic Sea	54° 21′N, 10° 10′E	1–18/20	Dec–Mar, May–Jun (5 °C)	Jul and Aug	Spring and summer	nd	Late Dec–end Mar, May/ Jun, Oct (6–2 °C, 10–14 °C)	Thiel (1962), Möller (1980), Schneider and Behrends (1994)
Aurelia aurita	Wadden Sea, Holland	52° 58′N, 04° 46′E	nd	nd	nd	nd	nd	nd	van der Veer and Oorthuysen (1985)
Aurelia aurita	Horsea Lake, UK	50° 52′N, 01° 06′W	5.8–22	Dec (9.4 °C)	May–Jun (17.8 °C), Jul/Aug–Dec (23.1–7.6 °C)	Spring and summer	nd	nd	Lucas (1996), Lucas C (unpublished data)
Aurelia aurita	Southampton Water, UK	50° 54′N, 01° 25′W	2.6/7.9–20	Jan–Mar (2.6–8.7 °C)	May–Jun (15.1 ± 1.3 °C)	Feb–Oct (greatest at 12 °C, least at >18 °C)	High temperature (20 °C)	Feb–Mar (6 °C)	Lucas and Williams (1994), Lucas C (unpublished data)

Aurelia aurita	NW Mediterranean	~41° 24′N, ~2° 9′E	12–28	~Apr–May?	nd	nd	nd	~Jan–Feb? (13–14 °C)	Purcell *et al.* (2012)
Aurelia aurita	Elefsis Bay, Greece	38° 02′N, 23° 33′E	10.1–24.3	Jan–Feb, Apr–May (10.1–12.1 °C)	nd	nd	nd	nd	Papathanassiou *et al.* (1987), Panayotidis *et al.* (1988)
Aurelia aurita (sp. 1)	Urazoko Bay, Japan	35° 45′N, 136° 1′E	7–29	Jan–Jun (8–22 °C)	Dec–Jul	nd	nd	Direct development planula to ephyra	Yasuda (1969, 1971, 1975)
Aurelia aurita (sp. 1)	Tokyo Bay, Japan	35° 40′N, 139° 40′E	9.4–29.8	Mar–May, Jun	Year-round	Jul–Sep (summer–autumn)	nd	Oct, Dec–Mar/Apr (~18–10 °C)	Omori *et al.* (1995), Toyokawa *et al.* (2000), Watanabe and Ishii (2001), Ishii and Katsukoshi (2010)
Aurelia aurita (sp. 1)	Honjo District, Lake Nakaumi, Japan	35° 28′N, 133° 12′E	5–30	Dec–Apr (winter–spring)	nd	Increase from 18 to 28 °C	>26 °C, low food	Decr from 10 to 14 °C	Han and Uye (2010)
Aurelia aurita (sp. 1)	Inland Sea of Japan	34° N, 132° E	9.3–29.6	Jan and Feb	nd	nd	nd	nd	Uye and Shimauchi (2005)
Aurelia aurita (sp. 1)	Kagoshima Bay, Japan	31° 25′N 130° 37′E	14–30	Late Nov–mid Mar	Feb/Mar–Sep	nd	nd	Dec–Mar (16/17 to 14/15 °C)	Miyake *et al.* (1997, 2002)
Aurelia aurita (sp. 1)	Tapong Bay, Taiwan	22° 27′N, 120° 26′E	19–32	nd	nd	Greatest at 20 °C	nd	Greatest at 25 °C (thermal max 30 °C)	Liu *et al.* (2009)

(*continued*)

Table 3.3 (*continued*)

Species	Location	Latitude/ longitude	Temperature range (°C)	Ephyrae month (temp)	Ripe females month (temp)	Budding month (temp)	Podocysts month (temp)	Strobilation month (temp)	Source
Aurelia (sp. 4)	Jellyfish Lake, Palau	07° 09′N, 134° 22′E	30–33	Year-round, more in Sep	Year-round	nd	nd	Year-round? more in Sep	Hamner *et al.* (1982), Martin (1999), Dawson and Martin (2001)
Aurelia aurita (sp. 7)	Derwent estuary, Tasmania, Australia	42° 52′S, 147° 19′E	7.7–20.4	nd	nd	Spring and summer	nd	Sep and Oct	Willcox *et al.* (2008)
Aurelia aurita (sp. 7)	Kettering, Tasmania, Australia	42° 53′S, 147° 19′E	7.7–20.4	nd	nd	Spring and summer (greatest at 16 °C, least at 10 °C)	nd	Aug–Oct (10.5–12 °C)	Willcox *et al.* (2007, 2008)
Aurelia labiata	Roscoe Bay, Vancouver, Canada	50° 10′N, 124° 46′W	6–20	Jun (~15 °C)	Oct/Nov–Jan/ Mar	nd	nd	nd	Albert (2005)
Aurelia labiata	Whidbey Bay, Washington, USA	48° 24′N, 122° 38′W	5–17	nd	nd	Summer?	nd	Jan/Feb to Mar/Apr (~5–7 °C)	Purcell *et al.* (2009)
Aurelia labiata	Puget Sound, Washington, USA	47° 49′N, 122° 26′W	7–15	nd	nd	Greatest at 7 and 10 °C	nd	Greatest at 10 and 15 °C, but occurs at 7 °C *in situ*	Purcell (2007)
Aurelia labiata	Monterey Bay, California, USA	36° 35′N, 121° 54′W	<8–28	Feb–Apr	Feb–May (medusae year-round)	nd	nd	Feb–Apr	Galigher (1925), Widmer (2005)

Scyphozoan jellyfish produce a number of different types of chitin-covered cysts. They may be formed by encystment of the whole polyp, by pedal discs of the polyp (podocysts), by portions of free stolons contacting the substrate or by settling planulae (planulocysts) as described above. According to Arai (2009), the stoloniferous cysts observed in *C. mosaicus* (Pitt, 2000) may be equivalent to podocysts, but this is unclear. The excellent summary of the present knowledge of podocyst formation and excystment by members of the Semaeostomeae and Rhizostomeae (suborder Dactyliophorae) produced by Arai (2009), and references therein, also considered the potential role of this type of asexual reproduction to the production of some medusae blooms. It is not the intention to repeat the contents of that review, other than to provide a brief summary of the ecology of podocyst production and excystment. Podocysts are thought to serve three purposes: (1) increase the number of polyps, (2) aid survival through short-term periods of low food availability and (3) protect against predation from nudibranchs. While Jiang *et al.* (1993) consider that adverse conditions are not necessary for the formation of podocysts and are a normal form of asexual reproduction they acknowledge that podocysts are able to resist adverse conditions. In contrast, Thien *et al.* (2012) found that cysts were only formed following starvation and considered podosysts to be an important mechanism for surviving periods of adverse conditions and predator attacks. They reported cysts surviving for periods of >3 years on rich organic reserves. Podocysts of both *C. quinquecirrha* and *A. aurita* have been shown to be resistant to predation by the nudibranchs *C. verrucosa* and *Cratena* sp. (Cargo and Schultz, 1967; Hernroth and Gröndahl, 1985b).

The number of podocysts produced by a single polyps can be considerable, with *C. quinquecirrha* reported to form 52 podocysts and 6 polyps in <3 months (Cargo and Schultz, 1966) and *Chrysaora fuscescens* producing 53 podocysts and 51 polyps in 8 months (Widmer, 2008), thus providing a mechanism of increasing the population. Environmental factors that affect the rate of podocyst production include temperature, salinity and food availability (e.g. Guo, 1990; Brewer and Feingold, 1991; Jiang *et al.*, 1993; Lu *et al.*, 1997; Holst *et al.*, 2007; Thien *et al.*, 2012). Findings are mixed, but this may reflect species- or site-specific differences. Although podocysts are often considered to be useful for surviving periods of low food, their production actually increases at higher food levels (Littleford, 1939; Guo, 1990; Morandini *et al.*, 2004). This relationship may increase their survival period, but until the study of Thien *et al.* (2012), where *A. aurita* cysts survived for 3.2 years, the long-term viability of podocysts without food was unknown. Regarding temperature effects, *C. quinquecirrha* polyps encysted at both warmer (up to 34–36 °C) and colder (2–4 °C) temperatures in laboratory experiments, although at 34 and 36 °C the cysts did not turn back into polyps, indicating that the cysts were unable to survive these extreme high temperatures (Cargo and Schultz, 1967). In Chesapeake Bay,

C. quinquecirrha formed podocysts in early August. These excysted, then strobilated in the spring as temperatures rose (Cargo and Schultz, 1967; Cargo and Rabenold, 1980). In the Gullmar fjord, podocysts are formed following strobilation—in the winter for *A. aurita* and in the summer or autumn for *C. capillata* (Gröndahl, 1988a). In Chesapeake Bay and the Niantic River, encystment in *Cyanea* sp. occurs during warming periods and excystment during cooling periods (Brewer and Feingold, 1991).

3.3. Asexual propagation

Reflecting the relative paucity of *in situ* studies of polyp populations, there are relatively few quantitative data on natural abundances or asexual reproductive behaviour, particularly over seasonal timescales. Most of the published data are for the ubiquitous *A. aurita*, and many of these are derived from *in situ* settling plates (Hernroth and Gröndahl, 1983; Gröndahl and Hernroth, 1987; Gröndahl, 1988a; Watanabe and Ishii, 2001; Miyake *et al.*, 2002; Hoover and Purcell, 2009), with rather fewer on natural substrata (Östman, 1997; Willcox *et al.*, 2008; Purcell *et al.*, 2009; Ishii and Katsukoshi, 2010). Published abundances vary greatly. Although several studies report polyp abundances in the order of < 10 cm^{-2}, they can be as low as 0.0005 cm^{-2} in the hypoxic bottom waters of Tokyo Bay (Ishii and Katsukoshi, 2010) or as high as 88 cm^{-2} in a man-made canal in Kagoshima Bay (Miyake *et al.*, 2002). Quantitative abundance is typically recorded as no. m^{-2} or no. cm^{-2}, but densities can display a high degree of small-scale variability, making the scaling up of abundances to no. m^{-2} questionable, particularly if polyps are located on shells (Miyake *et al.*, 2002). In Southampton Water, for example, within a 0.5 m^2 population of mussels attached to the underside of a marina pontoon, fewer than 50% of mussels have polyps, and of those, absolute numbers range from $\sim$10 to 200 per shell (Lucas Cathy, unpublished data). Miyake *et al.* (2002) examined the spatial distribution of polyps within quadrats, noting whether polyps were randomly or uniformly distributed or whether they were aggregated into large or small clumps. Unit colony sizes were 9.4–18.8 mm^2, with larger colonies 150–300 mm^2 in size formed by aggregation of the unit colonies. Average densities were 7.3–17.6 m^{-2} on *Mytilus* shells, with densest aggregations 88 m^{-2}.

Published reports of changes in the percentage cover or numerical abundance of natural populations of polyps over the course of a 'season' or year are extremely rare, but the general trend for *Aurelia* spp. at least is for decreasing abundance/coverage in the autumn and winter and increasing abundance in the spring and summer coinciding with higher temperature and food (Willcox *et al.*, 2008; Ishii and Katsukoshi, 2010). Although quantitative data are not available, it should be noted that in the tropical species *C. xamachana*, scyphistomae are found through the mid-late summer

but are completely absent during the winter and early spring months between late November and early June (Fitt and Costley, 1998).

Temporal (and spatial) changes in abundance (or percentage cover) of polyps are regulated by the balance between colony growth resulting from recruitment of newly settled planula larvae and asexual propagation (Fig. 3.5), and mortality caused by predation, inter- and intra-specific competition for space and food and physiological stress, all of which are affected by density-dependent factors and environmental conditions (Watanabe and Ishii, 2001; Colin and Kremer, 2002; Fischer and Hofmann, 2004; Willcox *et al.*, 2008). Numerical expansion via asexual reproduction takes place in a number of ways: strobilation of ephyrae, budding of new polyps from the base of the parent, longitudinal fission, stolon budding, motile buds, pedal laceration and production of podocysts from which new scyphistomae emerge (Berrill, 1949; Kakinuma, 1975; Arai, 1997; and see Table 3.1, Pitt, 2000, for rhizostomes). Only a handful of studies have documented all types of asexual propagation of new polyps (e.g. Kakinuma, 1975; Han and Uye, 2010), with the majority of studies on both semaeostomes and rhizosomes focusing on the formation of podocysts and new polyp buds.

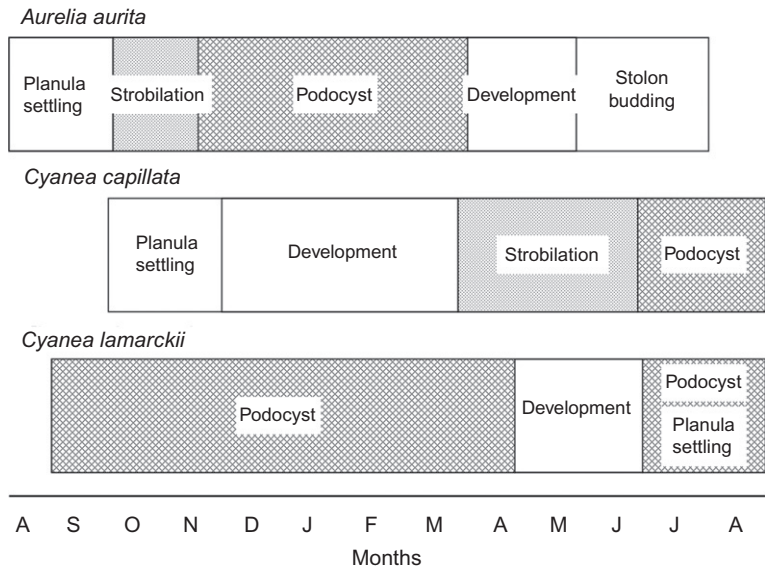

Figure 3.5 Seasonal development of polyps of the scyphozoans *Aurelia aurita*, *Cyanea capillata* and *Cyanea lamarckii* from the Gullmar fjord, showing the timing of of planula settlement, podocyst formation, asexual development, and strobilation. (Re-drawn from Gröndahl (1988a), figure 5, with kind permission from Springer Science and Business Media.)

Rates of asexual reproduction are influenced by environmental parameters such as temperature and food availability. Experiments on *A. aurita* reveal that numerical growth rates generally increase with water temperature (Chiba, 1969; Keen, 1991; Miyake *et al.*, 2002; Willcox *et al.*, 2007), an observation borne out in positive correlations between water temperature and polyp densities of field populations (Willcox *et al.*, 2008). Purcell (2007) and Winans and Purcell (2010), however, report the greatest budding rates in *A. labiata* maintained at lower temperatures (29.2 buds polyp^{-1} after 122 days at 9 °C), with lower rates of budding at temperatures >15 °C. This apparently conflicting trend most likely reflects differences in the thermal tolerances and *in situ* water temperatures experienced by the different study populations of *A. aurita* and *A. labiata*.

Willcox *et al.* (2008) also found a significant correlation between rainfall (as a proxy for salinity) and *in situ* polyp density, but this relationship between budding and salinity has not been confirmed in laboratory experiments (Watanabe and Ishii, 2001; Willcox *et al.*, 2007). Willcox *et al.* (2008) concluded that the perceived effect of rainfall may in fact reflect its effect on other variables such as nutrient input and food availability. Rates of budding are positively correlated with food availability (Hernroth and Gröndahl, 1985b; Keen and Gong, 1989), both independently and in its interaction with temperature (Fig. 3.6). Han and Uye (2010) recorded the maximum number of *A. aurita* buds (40.3 over a 35-day experiment) at high food and temperature (13.3 μg C d^{-1}; 26 °C) and the lowest number of buds (3.0) produced at 1.7 μg C d^{-1} and 18 °C, with numbers increasing linearly over the duration of the experiment. It is suggested that the amount of food available directly affects the allocation of energy to different reproductive strategies. When there is high food availability, both budding and stolonation increase; with less food, energy allocation shifts from budding to the production of ephyrae (Gong, 2001) (Fig. 3.7). This partitioning of energy has also been observed in *Aurelia* medusae (Lucas and Lawes, 1998; Lucas, 2001): when food is abundant, somatic growth increases; when food is limiting, medusae switch to reproductive growth. In addition to abiotic variables, the presence of conspecifics and other epibiota may affect the rate of budding and colony growth (Willcox *et al.*, 2008), as dense aggregations of polyps have been found to inhibit budding (Chiba, 1969).

3.4. Strobilation and recruitment of ephyrae

Strobilation is the process of transverse fission by which polyps produce new medusae in the Scyphozoa (Arai, 1997), as well as in some Hydrozoa and Anthozoa (Fautin, 2002). The developmental sequence of strobilation has been described in some detail in *A. aurita* (Spangenberg, 1965b; Kakinuma, 1975; Kroiher *et al.*, 2000), the upside-down jellyfish *Cassiopea* spp. (Hofmann *et al.*, 1978) as well as other semaeostomes (Kakinuma, 1967;

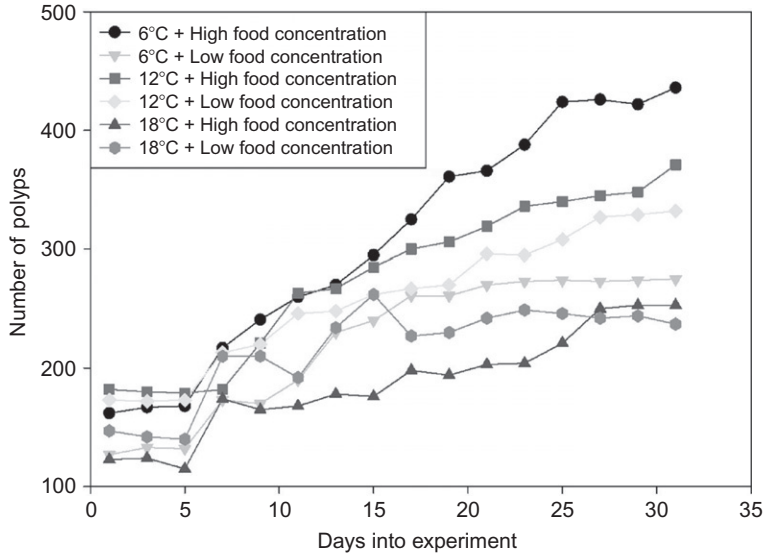

Figure 3.6 Laboratory experiments examing the effects of temperature (6, 12, 18 °C) and food availability (high, low) on the number of *Aurelia aurita* polyps (as a result of asexual budding) over a 32-day period. Polyps were fed daily 1-day *Artemia* nauplii in polyp:*Artemia* ratios of 2:1 (low) or 1:3 (high). A two-way ANOVA of the data indicate a significant interaction between temperature and food concentration on budding ($F=6.475$, $P=0.02$) (Lucas, unpublished data).

Calder, 1974) and rhizostomes (Sugiura, 1966; Calder, 1973, 1982). Briefly, two processes take place: segmentation of discs and metamorphosis of polyp structures into a developing ephyra (see Fig. 3.1, Kroiher *et al.*, 2000). One (monodisc) or many (polydisc) ephyrae can be produced per polyp. In the laboratory, strobilation can be induced in scyphistomae that are less than 2–3 weeks post-settlement (Calder, 1982; Pitt, 2000), but in nature, the majority of scyphozoans strobilate a number of months after the planula larvae have settled and metamorphosed into polyps. The following section will consider the timing and initiation of strobilation, followed by the rate of strobila development and total numbers and quality of ephyrae produced.

In reviewing natural cycles of strobilation in the wild (as indicated by the presence of strobilating polyps or newly released ephyrae in the water column), timing and frequency vary from species to species, from location to location and from year to year (Lucas, 2001; Purcell *et al.*, 2009). For example, in Chesapeake Bay, the onset of strobilation in *C. quinquecirrha* occurs suddenly in mid-spring and continues, to a lesser degree, in pulses throughout the summer and into the early autumn (Cargo and Schultz, 1966; Calder, 1974; Cargo and Rabenold, 1980). *Cyanea* sp. is seasonally opposite, strobilation occurring in the late autumn and winter (Cargo and

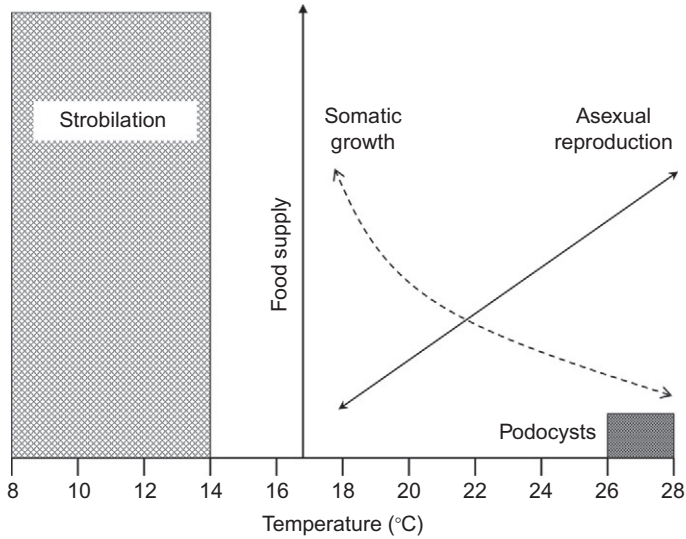

Figure 3.7 Schematic representation of asexual budding and somatic growth of polyps of *Aurelia aurita* from Lake Nakaumi, Japan, in relation to temperature and food supply. Strobilation was induced at temperatures below 14 °C, while podocyst formation occurred only under low food supply and high temperature combinations. Food supply scale is arbitrary. (Re-drawn from Han and Uye (2010), figure 6, with kind permission from the Plankton Society of Japan.)

Schultz, 1967). In the Gullmar fjord, *C. capillata* strobilates in the spring (Gröndahl and Hernroth, 1987; Gröndahl, 1988a). In the common jellyfish, *Aurelia* spp., strobilation occurs in the late winter and early spring throughout much of northern Europe (Lucas, 2001), many parts of Japan (Watanabe and Ishii, 2001; Miyake *et al.*, 2002; Uye and Shimauchi, 2005; Han and Uye, 2010), southern Australia (Willcox *et al.*, 2008), as well as along the temperate NE Pacific (Purcell *et al.*, 2009).

Because a large number of populations of *Aurelia* spp. have been studied throughout the world, we can see that site-specific strobilation patterns exist, and this may reflect ecological adaptation to local conditions across the geographic range and/or the presence of cryptic species (Dawson and Martin, 2001; Dawson *et al.*, 2005). Discrete autumn and spring periods of strobilation in *A. aurita* have been observed in the Gullmar fjord, Sweden (Hernroth and Gröndahl, 1983; Gröndahl, 1988a), with similar observations for the Black Sea (Lebedeva and Shushkina, 1991) and Isefjord, Denmark (Rasmussen, 1973). In the Kiel Bight (54°19.7′N 10°09.5′E), strobilation occurs over a prolonged period of time (Thiel, 1962; Möller, 1980), whereas in the geographically close Kertinge Nor (55°27.0′N 10°34.0′E), ephyrae are present only in February and March (Olesen *et al.*, 1994).

Tropical marine lakes are characterised by pulsed strobilation throughout the year, possibly associated with changing weather patterns (Dawson and Martin, 2001). Similarly, protracted strobilation periods also occur in enclosed temperate lakes (Lucas, 1996, 2001) most likely due to relaxed selection for synchronised breeding (Dawson and Martin, 2001). Multiple (2–5) strobilation events per polyp per season have also been observed in *C. quinquecirrha* (Calder, 1974; Cargo and Rabenold, 1980), *R. nomadica* (Lotan *et al.*, 1994) and *C. mosaicus* (Pitt and Kingsford, 2003). The question is, what causes these inter-population differences in the timing and frequency of strobilation, even in species that are geographically close together? It is well established that environmental cues control or synchronize the reproductive cycle of many marine invertebrates. Of these, photoperiod and temperature have been shown to moderate reproduction in groups such as polychaetes, echinoderms and corals, either individually or in combination (Olive, 1995; Olive *et al.*, 1997; Lawrence and Soame, 2004). Although strobilation in jellyfish is controlled by endogenous factors, the initiation and rate of ephyra production have also been shown to be influenced by chemical and physical environmental factors such as iodine, polypeptides, changing temperature, salinity, levels of irradiance and nutrition (Spangenberg, 1968), as well as the presence of *Symbiodinium* in zooxanthellate species. The relative significance of each factor in affecting strobilation is likely to vary between species; Berrill (1949) considered that natural induction of strobilation may require the 'correct' sequence of environmental factors at critical periods. As illustrated by the *in situ* observations, even within a given species, populations from different locations within their geographic range may respond differently to the same factor.

Most investigations indicate that a period of 'nutritive preparation' is required prior to strobilation (e.g. Thiel, 1962), which may explain why cultured polyps, which are likely to be well-fed, are able to develop from newly settled planula to strobilating polyp in such a short space of time. In several zooxanthellate species of jellyfish (e.g. *Cassiopea* spp., *M. papua*), strobilation can only be initiated once the polyp has acquired *Symbiodinium* cells (Sugiura, 1965; Fitt and Costley, 1998), although this is not a universal requirement in all jellyfish species containing zooxanthellae (Sugiura, 1969; Hofmann and Kremer, 1981). Pitt (2000) found that starved polyps of *C. mosaicus* did not strobilate, but when fed daily, monodisc strobilae were produced in 4 days, while Chen *et al.* (1985) found that polyps of *Rhopilema esculenta* only strobilated when well fed. Although it makes sense for polyps to build up storage products prior to strobilation (feeding tentacles are lost during the metamorphic process and the separation of ephyrae from the polyp is likely to be energetically costly to the polyp) (Thiel, 1962), short periods of starvation have also been suggested as a trigger for strobilation (Arai, 1997; Ishii and Watanabe, 2003; Purcell, 2007).

Initiation of strobilation using chemical compounds containing iodine, such as potassium iodide, iodotyrosines or thyroxine, was discovered in laboratory experiments using *A. aurita*, *C. quinquecirrha* and *Rhizostoma pulmo* in the late 1960s and early 1970s (Spangenberg, 1967, 1971; Silverstone *et al.*, 1977). Black and Webb (1973) found that up to 95% of experimental polyps underwent strobilation within 3 weeks of iodine addition, at concentrations approximating natural Yorke River water, compared with only 2% strobilation among a control population lacking iodine. Neck-inducing factor (NIF) is a large polypeptide that is released into the water column by one polyp and which induces neck formation (i.e. transverse groove below the tentacles) in neighbouring polyps (Loeb, 1974a,b). Studies examining the role of chemicals cues in strobilation are in the minority, however, with the individual and interactive effects of light, salinity, nutrition and, in particular, temperature receiving greatest attention.

Temperature clearly plays a significant role in the timing (initiation) of strobilation, as indicated by the seasonal appearance in ephyrae in the majority of species inhabiting temperate locations. Differences in absolute temperature may define the physiological boundaries of different species (thus the temperature range through which strobilation occurs will be species-specific) or different populations of species within their latitudinal range, as well as the rate and frequency of strobilation, in terms of individual development time, proportion of the polyp population strobilating, and number of ephyrae produced per polyp (see Holst, 2012). However, it may be that this is less important than the magnitude of temperature change in inducing strobilation in individual polyps of most species (Purcell *et al.*, 1999b; Kroiher *et al.*, 2000; Kawahara *et al.*, 2006; Purcell, 2007; Holst and Jarms, 2010; Prieto *et al.*, 2010; Winans and Purcell, 2010). In contrast, some of the rhizostomes appear not to require a change in temperature to induce strobilation, for example, *R. nomadica* (Lotan *et al.*, 1992), *S meleagris* (Calder, 1982) and *C. mosaicus* (Pitt, 2000).

Regarding the most studied temperate populations of the semaeostomes *A. aurita* and *A. labiata*, *C. capillata* and *C. quinquecirrha*, one can broadly state that the main periods of strobilation in the field are late winter–early spring for *A. aurita* and *A. labiata*, mid-late spring for *C. quinquecirrha*, coincident with increasing temperatures, and autumn for *C. capillata* when temperatures decline—although there are of course exceptions which will be discussed below. Nevertheless, these generalised field observations are confirmed in laboratory experiments (Table 3.4). Strobilation in *A. aurita* and *C. quinquecirrha* can be induced by a period of warming by $\sim$5 °C following a period of cooling (Loeb, 1972), while strobilation in the cold-water species of *Cyanea* is stimulated by a reduction in temperature (Brewer and Feingold, 1991). Onset of strobilation coincident with warming temperatures is also noted for the rhizostomes *C. andromeda*, *Cephea cephea*,

Table 3.4 Summary of the literature on laboratory experiments examining the effect of environmental variables (in particular temperature) on the timing and rate of strobilation

Species	Number of discs	Strobilation duration (days)	Temperature	Food availability (including zooxanthellae)	Other triggers and interactive effects	Source
Rhizostomeae						
Cassiopea andromeda	Monodisc	nd	nd	Significantly supported but not triggered by zooxanthellae	nd	Hofmann and Kremer (1981)
Cassiopea xamachana	Monodisc	nd	>20 °C	Acquire *Symbiodinium*	nd	Fitt and Costley (1998)
Catostylus mosaicus	1 (76%), 2 (24%), 3, 4, 5 (rare)	4	Constant 21 °C	No strobilation if not fed daily	nd	Pitt (2000)
Cephea cephea	Monodisc	3–5 at 29–30 °C	Increase 20–29 °C	Zooxanthellae not essential but strobilate 2–3× more if present	nd	Sugiura (1969)
Cotylorhiza tuberculata	Monodisc	nd	No strobilation <19 °C; increase 17.5–23 °C = greatest strobilation	nd	nd	Prieto *et al.* (2010)
Cotylorhiza tuberculata	Monodisc at 21 °C	6.8 days at 21 °C	14–28 °C	nd	nd	Purcell *et al.* (2012)

(*continued*)

Table 3.4 (*continued*)

Species	Number of discs	Strobilation duration (days)	Temperature	Food availability (including zooxanthellae)	Other triggers and interactive effects	Source
Lychnorhiza lucerna	3 every 5–7 days	nd	Constant or pre-cooling	nd	nd	Schiariti *et al.* (2008)
Mastigias papua	Monodisc	12–18 at 20 °C, 6–7 at 24 °C, 3–4 at 27 °C	20–22 °C; may require 1 °C drop for 1 month then increase	Zooxanthellae required	Temperature and zooxanthellae	Suguira (1965)
Nemopilema nomurai	3–7	nd	Change from 18 to 13 or 9–18 = no strobilation; 18–13–23 = strobilation	nd	nd	Kawahara *et al.* (2006)
Phyllorhiza punctata	1	nd	nd	nd	Increase in temperature and photoperiod?	Rippingdale and Kelly (1993)
Rhizostoma octopus	1–5	24 ± 4 days at 10 °C	Change from 10 to 5 °C, 5–10 °C or 10–15 °C	nd	nd	Holst *et al.* (2007)
Rhizostoma pulmo	13.5 at 14 °C, 6.8 at 21 °C, 8.5 at 28 °C	85.5 at 14 °C, 15.0 at 21 °C, 9.8 at 28 °C	14–28 °C. Cold increased survival, duration to strobilation	nd	nd	Purcell *et al.* (2012)
Rhopilema esculanta	up to 17	Up to 14	Increase from 10–18 to 27 °C	nd	nd	Chen and Ding (1983)
Rhopilema nomadica	5–6	6–8 at 18 °C, 4 –6 at 22 °C	14–16 °C minimal, 18–22 °C peak, 24–26 °C decrease	nd	Salinity:	Lotan *et al.* (1992, 1994)
Rhopilema verilli	Usually 1, but can have 3	7 at 20 °C	Increase from 10–12 to 20 °C	nd	nd	Cargo (1971), Calder (1973)
Stomolophus meleagris	1–3, typically 2	3–5	Constant 25 °C	nd	nd	Calder (1982)

Semaeostomeae						
Aurelia aurita	4 (small polyp), 18 (large polyp)	1 month post-settlement	Decrease to 14–18 °C	nd	nd	Kakinuma (1975)
Aurelia aurita	nd	nd	15 °C from week 12	nd	nd	Chiba (1969)
Aurelia aurita	Usually 1, but can have up to 6	2 months post-settlement	nd	nd	Undersides 98.4% strobilate; topsides < 50% strobilate	Watanabe and Ishii (2001)
Aurelia aurita	7.1 ± 1.8	38–43 days after temperature decrease	Decrease	nd	No strobilation at < 2.0 ml O_2/L. Strobilation at 2.0–4.5 ml O_2/L	Ishii *et al.* (2008)
Aurelia aurita	Polydisc (autumn), monodisc (spring)	nd	nd	Polydisc strobilation with more food	nd	Hernroth and Gröndahl (1983)
Aurelia aurita	Polydisc	Max 8 (decrease at higher temperatures)	Proportion of polyps and time to strobilate greatest/fastest at 25 °C > 30 °C > 20 °C	nd	Temperature/light interactive; no strobilation in dark at lowest temperature	Liu *et al.* (2009)
Aurelia aurita	Small polyps = few ephyrae; large polyps = many ephyrae	20–18 °C = 31 days; 20–15 °C = 16 days; 20–12 °C = 17 days	Greater (24%) proportion of polyps strobilate after biggest reduction, 20–12 °C	nd	Requires iodine	Kroiher *et al.* (2000)
Aurelia aurita	Avg 2–9 (fewest at salinity 12, most at salinity 36, 28)	nd	nd	nd	Salinity: > 50% strobilate at 20, 26, 32; 11.6% strobilate at 12	Holst and Jarms (2010)

(*continued*)

Table 3.4 (*continued*)

Species	Number of discs	Strobilation duration (days)	Temperature	Food availability (including zooxanthellae)	Other triggers and interactive effects	Source
Aurelia aurita	Max = 7 at 15–10–15 °C; few at constant 15 °C	Increases with increasing number of ephyrae produced per polyp	15 °C constant; 15–10–15 °C; 15–5–15 °C. Greater % of polyps strobilated following decrease in temperature	nd	Increased age of polyp (1 or 2 years post-settlement) increases % strobilating polyps and no. of ephyrae produced	Holst (2012)
Aurelia aurita	nd	nd	Increase from 12 to 22 °C	nd	nd	Magnum *et al.* (1972)
Aurelia aurita	13.8	18 days	Only strobilation at 14 °C (tested 14, 21, 28 °C)	nd	nd	Purcell *et al.* (2012)
Aurelia labiata	0 (7 °C salinity 34)–41.7 (15 °C salinity 34)	>80 days at 7 °C, 40 days at 15 °C	At higher temperatures: greater % strobilating, more strobilation cycles	nd	Greatest strobilation in TS combinations: 10 °C-27, 10 °C-34, 15 °C-20, 27, 34	Purcell (2007)
Aurelia labiata	1.2 at pH 7.9/7 °C; 20.5 at pH 7.9/15 °C	12.3 at pH 7.9/7 °C; 34.4 at pH 7.9/15 °C	16% polyps strobilated at 9 °C, 100% polyps strobilated at 15 °C; 1–3 × each	nd	Temperature/pH interaction–no effect of pH at 15 °C	Winans and Purcell (2010)
Chrysaora hysoscella	Max = 6 at 15–10–15 °C; fewest (3) at 15–5–15 °C and constant 5 °C	Increases with increasing number of ephyrae produced per polyp. Greater at 10 °C than at 15 °C	15 °C constant; 15–10–15 °C; 15–5–15 °C.	nd	nd	Holst (2012)

Chrysaora hysoscella	4–6	nd	nd	nd	nd	Morandini *et al.* (2004)
Chrysaora lactea	2–4	10 at 22 °C	nd	nd	nd	Morandini *et al.* (2004)
Chrysaora melanaster	20–30	nd	nd	nd	nd	Morandini *et al.* (2004)
Chrysaora quinquecirrha	3–9 (usually 5)	nd	Increase from 20 to 22 °C	nd	Reduce salinity	Cargo and Schultz (1966, 1967)
Chrysaora quinquecirrha	3–11	Strobilate 2–3 × at 8 days intervals	Increase to 20–21 °C from winter low	nd	nd	Cargo and Rabenold (1980)
Chrysaora quinquecirrha	1–13 (high food), fewer ephyrae at 15 °C	Fastest at 25 > 15 > 10 °C	Strobilate at higher temperature tested	Food increases number of strobilae	Greatest ephyrae production at salinity 20, few at 25 and 30, none at 5	Purcell *et al.* (1999)
Chrysaora quinquecirrha	5.5 ± 0.4 air saturated DO; < 1 at 0.5 mg O_2/L	nd	nd	nd	16.7% strobilate at low DO, 51.2% strobilate at high DO	Condon *et al.* (2001)
Chrysaora quinquecirrha	nd	nd	Increase from 12 to 22 °C	nd	nd	Magnum *et al.* (1972)
Chrysaora quinquecirrha	nd	9–>30 in dark; 4–12 in 24 h light	> 18 °C	nd	Inhibited in dark; rapid strobilation in 24 h light	Loeb (1973)
Cyanea capillata	Avg 4–5 (fewest at salinity 12 and 36)	nd	nd	nd	Salinity (12–32) has little effect on numbers strobilating	Holst and Jarms (2010)

(*continued*)

Table 3.4 (*continued*)

Species	Number of discs	Strobilation duration (days)	Temperature	Food availability (including zooxanthellae)	Other triggers and interactive effects	Source
Cyanea capillata	Max = 8 in 2nd year polyp at 15–10–15 °C	Increases with increasing number of ephyrae produced per polyp. Greater at 5 °C than at 10 °C	15 °C constant; 15–10–15 °C; 15–5–15 °C No strobilation at 15 °C % polyps strobilating greatest in 15-5-15 °C than 15-10-15 °C and constant 15 °C		Increased age of polyp (1 or 2 years post-settlement) increases % strobilating polyps and no. of ephyrae produced	Holst (2012)
Cyanea lamarckii	Max = 4 at 15–5–15 °C, 10 at 15–10–15 °C, 12 at constant 15 °C	Increases with increasing number of ephyrae produced per polyp. 5 °C > 10 °C > 15 °C	15 °C constant; 15–10–15 °C; 15–5–15 °C.		nd	Holst (2012)
Cyanea lamarckii	Avg 3–8 (fewest at 12, most at 28 and 36)	nd	nd	nd	Salinity: >50% strobilate at 20%, 26%, 32%, 16% strobilate at 12	Holst and Jarms (2010)
Cyanea sp.	1–2	nd	Decrease to 15 °C	nd	nd	Cargo and Schultz (1967)

C. tuberculata, *M. papua*, *N. nomurai*, *R. esculenta* and *R. nomadica* (Sugiura, 1965, 1966; Rahat and Adar, 1980; Chen and Ding, 1983; Lotan *et al.*, 1994; Kawahara *et al.*, 2006; Prieto *et al.*, 2010), with tropical species requiring warmer temperatures.

Considerable between-site and inter-annual variability in the timing of strobilation has been observed in well-studied species such as *A. aurita* and *A. labiata* (Lucas, 2001; Purcell *et al.*, 2009). Year-to-year differences in (minimum) winter temperature appear loosely correlated with timing of ephyra release, with ephyra production occurring later following cold winters (Palmén, 1954; Rasmussen, 1973; Lucas, 2001). Purcell *et al.* (1999b) also observed that each 5 °C reduction in temperature delayed ephyra production by *C. quinquecirrha* by 1 week. The very cold temperatures associated with winter ice cover in high latitudes may cause strobilation to temporarily cease, so that ephyra production does not occur until the late spring. In the Gullmar fjord, which experiences winter ice cover, peak *A. aurita* ephyra production takes place in the autumn as temperatures decrease, while a secondary peak in strobilation occurring in the spring as temperatures increase. Holst (2012) studied the effects of climate warming on the four species found in the German Bight by comparing strobilation (i.e. strobilation period, percentage of polyps strobilating, number of ephyrae produced) at 10 °C against the current winter minimum temperature of 5 °C. Colder winter temperatures promoted strobilation in the cold-water species *C. capillata* but inhibited strobilation in the more temperate species *A. aurita* and reduced ephyra production in *C. lamarckii* and *C. hysoscella*. Holst suggested that climate warming would benefit *A. aurita*, but not *C. capillata*, while the distributions of *C. lamarckii* and *C. hysoscella* could possibly expand northwards.

Unusually cold winters may be more detrimental to recruitment success in warm water jellyfish species such as *R. nomadica* and *C. tuberculata* that typically experience more stable seasonal temperature regimes, as a large portion of the polyps do not survive through to strobilation when temperatures increase again (Lotan *et al.*, 1994; Prieto *et al.*, 2010).

For the most part, the timing of strobilation in the field coincides with increased light (as increased photoperiod and/or light intensity) (Rippingdale and Kelly, 1995), as well as temperature (Purcell *et al.*, 2009). The role of light in initiating strobilation has not received a great deal of attention and is difficult to tease out from the effect of the seasonal temperature cycle. Some of the early literature appears rather contradictory. For example, Custance (1964) stated that 6 h day^{-1} light inhibited strobilation in *A. aurita*, whereas Loeb (1973) found that the onset of strobilation in *C. quinquecirrha* was delayed in the absence of light. More recent laboratory experiments have shown that light does positively influence the time taken by polyps to strobilate (Purcell, 2007; Liu *et al.*, 2009). In *A. labiata*, for example, photoperiod and its interaction with light intensity are

significant factors in strobilation (Purcell, 2007); polyps that receive the most light (12 h at highest intensity) strobilate more quickly and strobilate more times than polyps in lower light, although it is suggested that photoperiod is more important than light intensity and total amount of light received. Taken individually, light is probably less important than temperature in affecting the timing of strobilation in *Aurelia* polyps, but it has an additive effect with temperature (Liu *et al.*, 2009) and possibly other environmental variables such as food availability and salinity. Purcell *et al.* (2009) suggest that 'warm temperatures, nutrient delivery from run-off, and high sunlight enhance plankton production, providing abundant food for the polyps and new jellyfish, and those environmental cues synchronize jellyfish and plankton production'. Salinity and food availability have also been shown to be important in regulating the timing of strobilation in *C. quinquecirrha* (Purcell *et al.*, 1999b), although reduced or no strobilation in low food conditions may reflect a polyp's inability to reproduce due to poor nutritive condition rather than food being a trigger for strobilation in the strictest sense.

Environmental factors not only influence the seasonal periodicity of ephyra production but also the rate of development during the strobilation process, the numbers of ephyrae produced and frequency of strobilation cycles per polyp, as well as the percentage of the polyp population strobilating. It has already been shown that light positively influences the rate of strobilation, both in isolation (Purcell, 2007) and in combination with temperature (Liu *et al.*, 2009). Indeed, temperature has a significant effect on almost all aspects of the strobilation process, as highlighted by the study of Purcell (2007) on *A. labiata*. More ephyrae were produced at higher temperatures as a result of a greater percentage of polyps strobilating, more rapid development of strobilae, more ephyrae produced and more strobilation cycles per polyp.

Almost universally, the time it takes for polyps to develop strobilae decreases with increasing temperature (Lotan *et al.*, 1994; Purcell *et al.*, 1999b; Liu *et al.*, 2009), although each species has its own physiological optimum temperature range above and below which strobilation declines or even stops (Lotan *et al.*, 1994; Kawahara *et al.*, 2006; Holst *et al.*, 2007; Liu *et al.*, 2009). Once strobilation has been initiated, new ephyrae can be produced in as little as 1 week (Calder, 1973, 1982; Loeb, 1973; Lotan *et al.*, 1992; Pitt, 2000; Schiariti *et al.*, 2008) or it can take between 2 and 6 weeks (Sugiura, 1969; Loeb, 1973; Kroiher, 2000; Holst *et al.*, 2007; Ishii *et al.*, 2008). Differences in the amount of time it takes to strobilate may reflect species-specific differences, or as Pitt (2000) suggests, it may reflect artefacts of laboratory conditions. Laboratory experiments also reveal that the percentage of the polyp population strobilating also increases in 'optimal' conditions of temperature, salinity and oxygen for each species (Condon *et al.*, 2001; Liu *et al.*, 2009; Holst and Jarms, 2010; Winans and Purcell, 2010). For example, in testing the effects of salinity (12, 20, 28, 36)

on asexual reproduction of the scyphozoans *A. aurita*, *C. capillata* and *C. lamarckii*, Holst and Jarms (2010) reported that while >50% of *A. aurita* strobilated at salinities ≥20, only 11.6% strobilated in salinity 12, with a similar trend observed for *C. lamarckii*. In comparison, >90% of *C. capillata* polyps strobilated in all salinities tested, with no significant differences among salinities. In field populations, the proportion of polyps strobilating is also highly variable, with large between-site and between-year differences (Purcell *et al.*, 2009). In Southampton Water, UK, fewer than 10% of *A. aurita* polyps strobilated in early spring 2010 (Lucas Cathy, unpublished data). Willcox *et al.* (2008) reported between 30% (2004) and 82% (2003) strobilation in Kettering, Australia, and almost undetectable strobilation in Hobart, Australia, while Purcell *et al.* (2009) reported between 40% and 86% strobilation among years in Cornet Bay, USA. The disparity between sites and years most likely reflect small-scale differences in abiotic (e.g. temperature, salinity, light) and biotic (e.g. polyp size and nutritional condition, polyp density, inter-specific competition within and around the polyp colony) conditions experienced by individual polyps.

The numbers of ephyrae produced per polyp during each strobilation cycle can be described as either monodisc (one ephyra) or polydisc (several ephyrae). Many of the rhizostomes produce only one ephyra, while those that have polydisc strobilation typically produce no more than 6 ephyrae per polyp, and are more likely to produce only 1 or 2, for example, *C. mosaicus* (Pitt, 2000), *Rhopilema verrilli* (Calder, 1973), *S. meleagris* (Calder, 1982) and *C. andromeda* (Neumann *et al.*, 1980; Hofmann and Honegger, 1990). However, the low output per strobilation cycle is countered by multiple strobilation events over periods <2 months (e.g. Sugiura, 1963; Hofmann and Kremer, 1981; Calder, 1982; Lotan *et al.*, 1992), so that total output becomes higher. *Lychnorhiza lucerna* polyps are able to produce 50–60 ephyrae over a 4-month period (Schiariti *et al.*, 2008). Semaeostome polyps are typically polydisc and the numbers of ephyrae produced can be as high as 30 (Spangenberg, 1968; Morandini *et al.*, 2004) in *A. aurita* and *Chrysaora melanaster*, respectively. Far more experiments have been carried out on the effects of polyp size, temperature, food availability, salinity and oxygen on the numbers and frequency of ephyrae produced in the semaeostomes, particularly *Aurelia* and *Chrysaora* species. Fewer ephyrae are produced by smaller and younger polyps than by larger polyps (Kakinuma, 1975; Kroiher *et al.*, 2000; Willcox *et al.*, 2007; Holst, 2012) and there is a general trend, both in the field and in the lab, of more ephyrae produced per polyp when there is higher food availability and warmer temperatures (Hernroth and Gröndahl, 1983; Purcell *et al.*, 1999b; Willcox *et al.*, 2008). In the Gullmar fjord, Hernroth and Gröndahl (1983, 1985a) reported that strobilating polyps of *A. aurita* were polydisc in autumn (greater zooplankton, higher temperature) and monodisc in winter/spring. Factors such as polyp size, temperature and food affect the metabolic rate and nutritional condition of

the polyp; larger, more well-fed polyps produce more ephyrae. However, physiological tolerances to environmental factors such as salinity and oxygen also have a bearing on the numbers of ephyrae produced. More discs are produced by *A. aurita* and *C. lamarckii* in higher (28, 36) than lower (12) salinities, whereas low (12) and high (36) salinities result in fewer discs in *C. capillata* (Holst and Jarms, 2010), and unsurprisingly, fewer ephyrae are produced at low dissolved oxygen concentrations (Condon *et al.*, 2001).

4. The Role of Polyps in Ensuring the Long-Term Survival of Jellyfish Populations

The life cycle of scyphozoans living in more temperate-zone climates may be broken during the colder winter months. The medusa stage of most temperate scyphozoan species disappear during colder seasons, including *C. quinquecirrha* (Calder, 1974), *S. meleagris* (Calder, 1982), *C. capillata* (Brewer and Feingold, 1991), and the ubiquitous *A. aurita* (Lucas, 2001). Medusae of the most common rhizostomes in the Mediterranean, *C. tuberculata*, disappear from coastal pelagic habitats during the colder months (Kikinger, 1992). In all the aforementioned species, it is the polyp that survives to repopulate the next spring. In contrast, scyphozoans living in more tropical habitats may experience less seasonal variation typically resulting in pulsed strobilation and multiple size classes throughout the year (Dawson and Martin, 2001). It has also been found in the upside-down jellyfish, *C. xamachana*, inhabiting the Florida Keys, that it is the scyphistoma stage of the life cycle and not the medusa that disappear during the winter months (Fitt and Costley, 1998). The physiological tolerance of the polyp stage to cold stress appears to surpass that of the medusa stage in the former more temperate species, while the opposite holds true for the more tropical species of *Cassiopea* spp., perhaps defining a physiological basis limiting its latitudinal distribution.

Polyps play a crucial role in ensuring the long-term survival of jellyfish populations during unfavourable conditions and 'lean' years caused by conditions associated with climate variability, anthropogenic disturbance, predation and competition for space and resources. Four features are responsible for this: a lifespan of several years, wide physiological tolerance, the formation chitin-covered podocysts, and the ability to asexually propagate in a variety of ways which results in a large population base consisting of thousands of polyps (Hoover and Purcell, 2009) (Table 3.5).

Compared with the medusa phase of the life cycle, the polyp is relatively long-lived and each individual has the ability to asexually reproduce multiple times and on a perennial basis. Adverse conditions coincident with the

Table 3.5 Summary of the characteristics of polyps that enable the long-term survival of jellyfish populations

(1) Tolerance of a wide range of environmental conditions (e.g. temperature, salinity, pH, DO).
(2) Wide ranging diet.
(3) Several species inhabit a wide range of benthic substrata, including man-made structures.
(4) Formation of chitin-covered podocysts ensures survival during extreme environmental conditions and provides protection against predation by nudibranchs.
(5) Live for several year (apart from some tropical species; e.g. *Cassiopea* spp.)
(6) Reproduce over several years.
(7) Asexual propagation results in a large population base of thousands or millions of polyps, some of which are likely to survive even high mortality events.

short-lived annual medusa could result in a dramatic reduction in numbers from which the medusa population itself would not recover. The polyps of many species have been shown to be very resilient. Some species such as *A. aurita* and *C. quinquecirrha* are very tolerant of a wide range of environmental conditions (e.g. low and high temperatures, hypoxia, reduced pH, wide range of salinities) (Condon *et al.*, 2001; Holst and Jarms, 2010; Ishii and Katsukoshi, 2010), and this is reflected in their widespread distribution and regular occurrence from year to year. Podocysts aid survival through short-term periods of low food availability and adverse environmental conditions and protect against predation from nudibranchs (Arai, 2009; Thien *et al.*, 2012). They are also formed during periods of extreme (high and low) temperature (Cargo and Schultz, 1967; Gröndahl, 1988a) when species are reaching their physiological limits. Even if a polyp population experiences high mortality, the shear magnitude of polyps present in some populations would mean that a sufficient number survive and ensure the continued success of the population.

5. The Role of Polyps in Forming Bloom Populations

Success of the next generation can be viewed in terms of successful release of ephyrae and subsequent recruitment into a new (sexually) breeding population. The direct link between polyp strobilation and ephyra survival depends on timing of strobilation and release, food availability in

the water column, and abiotic factors (e.g. temperature, oxygen, salinity) that lead to lethal or sub-lethal effects. In the field, exponential growth of young *A. aurita* medusae is often coincident with a rapid increase in temperature and subsequent increase in plankton productivity (Gröndahl and Hernroth, 1987; Lucas and Williams, 1994). These observations are supported by laboratory investigations on the same species. Båmstedt *et al.* (1999) showed that ephyra feeding and growth was strongly influenced by temperature, with those ephyrae raised at 18 °C exhibiting almost twofold greater diameter and fivefold greater biomass than those raised at 6 °C, thus enhancing the chance of successful recruitment of large numbers of healthy ephyrae into the pelagic population.

It is clear that the metagenic life cycle of scyphozoan jellyfish provides a mechanism for rapid expansion of jellyfish medusae numbers (Table 3.6). In Cornet Bay marina, USA, for example, Hoover and Purcell (2009) observed that polyps of *A. labiata* covered almost the entire underside of one of the marina's covered pontoons. This high abundance coupled with the ability of each polyp to produce multiple ephyrae (either through polydisc strobilation and/or multiple strobilation cycles) means that very large numbers of juvenile medusae can be produced in only a few weeks, particularly in warmer temperatures (Purcell *et al.*, 1999b). Lotan *et al.* (1992) estimated that one settled polyp of *R. nomadica* could give rise to >100 ephyrae within a 2-month period and considered that the enormous number of planulae produced, the rapid formation of podocysts, and the repeated polydisc strobilation may have accounted for the population explosion of *R. nomadica* in the east Mediterranean in the early 1990s.

Many of the bloom-forming jellyfish species inhabit coastal and estuarine environments and are eurythermal and euryhaline in nature. Coupled with their flexible life histories (e.g. Lucas, 2001), the apparent tolerance of a wide range of DO, pH, food as well as temperature and salinity conditions by all stages of the bentho-pelagic life cycle of some species means that these jellyfish

Table 3.6 Summary of the characteristics of polyps that contribute towards the formation of jellyfish bloom populations

Under appropriate conditions of temperature and food, the potential to produce very large numbers of ephyrae in a few weeks due to:
(1) Very high numerical density.
(2) Ability of polyps to strobilate 1–2 months post-settlement.
(3) Rapid reproductive development from trigger to strobilae (< 1 week).
(4) Ability of each polyp to produce several ephyrae per strobilation cycle (up to 20–30).
(5) Ability of each polyp to undergo several (2–3 ×) strobilation cycles.

also have great potential for rapid colonisation and expansion into new habitats via natural distribution changes and man-induced translocations.

6. Recommendations for Future Research

The study of polyp ecology is an emerging topic in jellyfish research, and although our knowledge has increased considerably over the past ~10 years, it still lags far behind that of medusa ecology. Research into the bentho-pelagic life histories of other marine biofouling invertebrates is considerably more advanced than for scyphozoans and we can learn from principals concerning the role of life histories and recruitment in regulating abundance, distribution and community dynamics established from those studies. In order to further understand the role that the asexually reproducing perennial polyp has in the formation and maintenance of jellyfish populations, we recommend the following research priorities:

(1) Long-term quantitative monitoring of bloom-forming scyphozoan populations, describing *both* the benthic and pelagic life histories against a background of biotic and abiotic variables. Data generated from these studies will allow the field to move into hypothesis-testing experimentation regarding the role of metagenic life histories in regulating medusa distribution and abundance.

(2) Develop a greater understanding of the role of ecological interactions (e.g. inter- and intra-specific competition, predation, food availability) in polyp population dynamics, specifically in planula recruitment and polyp survivorship. At present, we cannot definitively explain the causes of natural cycles of polyp abundance, other than to indicate periods of recruitment and predation at the seabed. The interaction between scyphozoan polyps and other epifauna is virtually unknown.

(3) Using a combination of molecular, physiological and ecological methodologies, examine the effects of environmental variables on aspects of polyp function; for example metabolism, growth, reproduction, and how this affects survivorship. By understanding the bioenergetics of species and their response to changing conditions at the molecular and physiological level, we may be able predict how future climate regimes will affect the distribution, phenology and abundance of tropical and temperate species and species at the extremes of their latitudinal range.

(4) Provide empirical evidence on the role of podocysts in ensuring the long-term survival of polyp populations during unfavourable conditions (high/low temperature, low food and predation).

(5) Explore the paradigm that some jellyfish species might expand their distribution and abundance through colonisation of man-made structures in the coastal marine environment.

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