

Chapter 12

Settlement and Recruitment

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12.1 Introduction

The algae and invertebrates living on marine hard substrata cover an enormous variety of life forms and life histories. However, one common theme displayed in benthic algae and in the majority of benthic invertebrates is a planktonic phase within the lifecycle. Larvae of benthic invertebrates and the propagules of algae must survive a planktonic period before beginning their benthic way of life on hard substrata. The transition from pelagic to benthic habitat, which occurs through larval and propagule settlement, and survival through to recruitment, is one of the most important points in the life history of marine organisms. In this chapter, we review patterns of settlement and recruitment over a variety of scales, and examine biological and physical interactions which occur at settlement before looking at the challenges facing propagules at this critical period and assessing the consequences of this process for the dynamics of adult benthic populations.

12.2 Definitions of Settlement and Recruitment

Planktonic larvae of benthic invertebrates spend a variable period in the pelagic realm, from minutes to months, during which time they mature and at some point attain the competence to metamorphose. Metamorphosis is then usually delayed until a suitable substratum is found. On making contact with a hard bottom, larvae undergo a range of often complex behaviours involving exploration and inspection, followed by either acceptance of the site or rejection and release to enter the water column once again. Once accepted, larvae may permanently attach (in the case of sessile organisms), and metamorphosis generally ensues. This complex process leads to a range of definitions of settlement, generally dependent on whether metamorphosis is included. However, given the wide range of behaviour displayed by marine benthic organisms (for example, some taxa metamorphose before settlement), very specific definitions are probably counterproductive, and settlement is generally taken to mean the termination of the pelagic phase and assumption of

a sedentary life. Hence, settlement, rather than a single act, can be considered a process which generally includes reversible contact with the substratum, exploratory behaviour, orientation and metamorphosis (see Pawlik 1992 for discussion). This definition can also be used in considerations of algal settlement, although behaviour of algal propagules is less complex, and spores and zygotes generally do not have an obligate planktonic period (Santelices 1990). Hence, settlement of algal propagules may occur immediately following release.

The process of recruitment is very ill-defined and is not based on any specific life history stage or process. It reflects a combination of settlement and a post-settlement period of arbitrary length, determined by the length of time before the settler is counted by an observer (Keough and Downes 1982). This length of time varies enormously between studies. For example, in algal populations this period may be unusually long, where settled algal propagules delay or prolong development under unfavourable conditions (Hoffmann and Santelices 1991). Keough and Downes (1982) pointed out the importance of distinguishing between settlement and recruitment over a quarter of a century ago, yet the terms still appear to be used interchangeably. The main reasons for this are the logistical difficulty of measuring true settlement rates, especially where larvae are small and/or settle in cryptic habitats, and the generally arbitrary nature of recruitment definitions. In some taxa, clear developmental stages may be used to differentiate settlement from recruitment. For example, settled cyprids and metamorphosed spat may be used as indicators of settlement and recruitment respectively in intertidal barnacles (e.g. Jenkins et al. 2000). Whilst the terms settlement and recruitment will continue to be somewhat ambiguous because of the nature of the concepts, difficulties in interpretation will be avoided where the time periods following true settlement, or life stages where measurement is made, are defined.

12.3 Patterns of Settlement and Recruitment on Hard Substrata

Observations of settlement and recruitment on hard substrata invariably document huge variability at a wide range of spatial and temporal scales in both invertebrates (e.g. Hunt and Scheibling 1996; Hughes et al. 1999; Jenkins et al. 2000) and algae (e.g. Reed and Foster 1984; Aberg and Pavia 1997). One motivation for making quantitative observations of settlement and recruitment is that, through understanding of the scales at which variability occurs, insight will be gained into the processes controlling larval and propagule settlement and early post-settlement events. At a local scale, recruitment variability can be caused by interactions occurring at settlement or soon thereafter. At larger scales, spatial variability in recruitment may be related to patterns in the regional larval pool (e.g. Barnes 1956) and regional physical transport processes (Hughes et al. 1999). A number of large-scale rocky intertidal studies using hierarchical sampling designs have documented recruitment variability at all scales from regional (100s km) to highly localised (metres; Caffey 1985; Jenkins et al. 2000;

O’Riordan et al. 2004), indicating the difficulty in making generalisations about the influence of particular scales. However, although formal meta-analyses have not been conducted, it is likely that as in adult assemblages (see Frascchetti et al. 2005 for review), variability in recruitment at the scale of metres and less will be important across most, if not all taxa because of the ubiquitous importance of small-scale processes.

Propagules of algae generally do not have an obligate planktonic period and, so, may settle immediately following release. Although there are numerous examples of algal propagules being transported over large distances (e.g. Reed et al. 1988), the general pattern, especially in perennial long-lived species, is one of dispersal over short distances of the order of a few metres (Santelices 1990). Aberg and Pavia (1997) investigated the variation in abundance of new recruits of the macroalga *Ascophyllum nodosum* over a range of spatial scales from 100s of kilometres to centimetres. They found variation in recruit abundance at small but not large spatial scales, in agreement with the contention that algal assemblages form more closed populations than is the case for invertebrates with long-lived planktonic larvae. While propagule characteristics suggest limited dispersal, other factors can influence spatial patterns of settlement. For example, variation in environmental conditions such as ice cover over large scales (e.g. Aberg 1992; McCook and Chapman 1997) can affect overall reproductive output and, hence, the supply of propagules and recruitment over large spatial scales.

Temporal variability is another well-characterised feature of benthic invertebrate settlement, with huge differences documented at scales from days (Wethey 1983) to years (Barnes 1956). The barnacle *Semibalanus balanoides* is known to undergo occasional ‘failure’ years in recruitment, when settlement is at least an order of magnitude lower than normal (Barnes 1956; Hawkins and Hartnoll 1982; Jenkins et al. 2000). Such differences between years in pulse recruiters such as *S. balanoides* which recruit within a narrow window are ascribed to mismatches between development of the spring phytoplankton bloom and planktonic larval growth (Barnes 1956).

Integrating spatial and temporal variability, research in Chile has recorded patterns of settlement of intertidal organisms which are spatially synchronised (Lagos et al. 2007). Synchronous settlement implies that processes determining larval arrival to adult habitats and/or post-settlement survival operate simultaneously over a particular spatial scale. Lagos et al. (2007) showed that common invertebrate species with planktonic stages showed recruitment synchrony at spatial scales of less than 30 km along a 120-km stretch of the Chilean coast, whereas those with direct development (and those with planktonic stages but low recruitment levels) showed spatially heterogeneous recruitment dynamics. These results were consistent with mesoscale physical processes affecting delivery of larvae to the shore. In searching for generalities of settlement patterns, consistency among years in the ranking of sites by recruitment density has been recognised at a variety of spatial scales (Kendall et al. 1985; Connolly et al. 2001). Such consistency may reflect the influence of different orientations of coastlines relative to prevailing winds and currents, and the prevalence of large-scale upwelling regimes.

12.4 Behaviour at Settlement

At settlement, pelagic larvae must make contact with a suitable substratum on which to attach. In marine environments, hard substrata are far less common and more patchily distributed than soft sediments. Hence, the specific selection of settlement site is paramount, and invertebrate larvae have developed complex patterns of behaviour and finely tuned discriminatory abilities to ensure that settlement occurs in a habitat which is conducive to survival, growth and, ultimately, reproduction. The behaviour of invertebrate larvae at settlement has perhaps best been characterised in intertidal acorn barnacles. Work by Crisp and co-workers has shown that the exploratory behaviour of the barnacle *S. balanoides*, when seeking a favourable site for settlement, occurs in three consecutive phases—broad exploration, close exploration and inspection. With each advancing stage, the scale of exploration declines until, during ‘inspection’, the larva simply rotates at the scale of its own body size. This phase precedes permanent attachment and metamorphosis (Knight-Jones 1953; Crisp and Meadows 1963).

Larval behaviour is generally characterised as responding to positive cues to stimulate settlement behaviour (see section below). However, rejection of unsuitable substrata by settling invertebrates is an important mechanism in ensuring that settlement occurs in an appropriate environment. For hard bottom invertebrates, the lack of settlement on sedimentary material, for example, is undoubtedly a function of rejection. As well as ensuring settlement, rejection may also be an important driver ensuring aggregated settlement (Berntsson et al. 2004). Although settlers do reject poor-quality habitats, settlement behaviour is anything but uniform and settlers will sometimes colonise what appear to be very poor-quality habitats. Why does this variation occur? Why do some settlers accept one cue over another? Raimondi and Keough (1990) suggested that producing offspring which have uniform settlement behaviour is not necessarily the best strategy for parents to maximise their own fitness. If settlement cues are an imperfect estimator of subsequent habitat quality (either because the cues as such are unreliable or because the habitat changes through time), then producing colonisers which behave identically will mean that, occasionally, all of these will colonise the ‘wrong’ habitat. Raimondi and Keough (1990) speculated that, by avoiding putting all of their offspring into one ‘habitat basket’, parents may minimise the chances of a catastrophic loss of all of their offspring. Theoretical studies support this speculation and, more recently, some studies have shown that mothers produce offspring with intrinsically variable dispersal/settlement behaviour (Krug 2001; Toonen and Pawlik 2001a).

Intrinsic variability is not the only source of variation in settlement behaviour. In recent years, a 50-year-old observation of larval behaviour has been revived and re-examined—the ‘desperate larvae hypothesis’ (Toonen and Pawlik 2001b). In the 1950s, a number of studies found that as larvae age, they begin to accept lower-quality (or, at least, lower-ranked) settlement cues (Knight-Jones 1951, 1953). Recent work suggests that this change in settlement behaviour is typically found only in species with non-feeding larvae, interpreted as larvae becoming ‘more desperate’ to settle as they deplete their nutritional reserves (Botello and Krug 2006; Elkin and Marshall 2007).

For feeding larvae, the situation is more complex: the benefits of delaying metamorphosis, in the absence of appropriate settlement sites, depends strongly on food availability in the plankton (Elkin and Marshall 2007). Overall then, larval age and nutritional state are two of the most important elements of the larval phenotype to affect settlement behaviour.

In situ studies of settlement of the propagules of algae are few in comparison to invertebrates. This is due to the often complex life histories of algae and the very small size of many algal propagules (Schiel and Foster 2006). For example, the flagellated spores of kelps, probably along with fucoids the most important group of macroalgae on hard bottoms in temperate areas, are only approximately 7 μm long. However, fucoid propagules are considerably larger; newly settled embryos and germlings can be identified in the field under low magnification and may be visible to the naked eye after a few weeks or months. Unlike invertebrate larvae, the propagules of algae behave as passive particles at scales greater than a few mm, owing to their immotility or extremely low powers of locomotion. The swimming speeds of propagules (maximum of 80–300 $\mu\text{m s}^{-1}$) may be beneficial at the point of settlement in the slow-moving boundary layer close to the substratum, and potentially aid in selection of microhabitat (Amsler et al. 1992). For example, kelp spores can be positively chemotactic to nutrients and stimulated to settle by these (Amsler and Neushul 1990). Many algal propagules have adhesive properties formed by a high-viscosity mucilage to aid in attachment to settlement surfaces. The ‘stickability’ of propagules varies considerably, both among taxa and over time within a particular species. The extent to which propagules adhere to surfaces will have a considerable effect on settlement success in turbulent habitats, such as the intertidal and shallow subtidal (Vadas et al. 1992).

12.5 Biological and Physical Interactions at Settlement

Whilst some models of hard substratum community structure assume that the level of settlement and recruitment is a direct function of larval supply (e.g. Gaines et al. 1985) and the amount of free space available (Minchinton and Scheibling 1993), a vast range of physical and biological interactions dictate that reality is far more complex. This was elegantly demonstrated by Minchinton (1997), who showed that the level of recruitment of the tubeworm *Galeolaria caespitose* into patches of free space, within beds of the adult, was related not to patch area but to the length of the patch perimeter. These data indicated that recruitment is related to the proximity of conspecifics, rather than availability of space per se.

For sessile species the choice of settlement site is critical, since the exact location at which the benthic stage will spend its entire life is dictated by this one act. Location in relation to adequate food supplies and environmental conditions, and to potential mates, competitors and predators is in all cases dictated by the adequacy of the choice made at settlement. Hence, there is a huge selective pressure to ensure that settlement is dictated by adequate cues.

At the time of settlement, larvae are exposed to a vast range of novel physical and biological cues to which they have not been exposed in the pelagic environment. One very important indicator of the suitability of habitat for the settlement of larvae is the presence of conspecific adults. Numerous laboratory-based studies have demonstrated the importance of cues from conspecifics in promoting settlement of larvae (e.g. Knight-Jones 1953; Crisp and Meadows 1962), potentially leading to gregarious settlement. Field-based work has shown how such cues may have important effects on natural patterns of settlement and recruitment (e.g. Raimondi 1988b; Hills and Thomason 1996). Gregarious settlement among conspecifics carries many advantages but also the potential for enhanced mortality through cannibalism of larvae settling within beds of suspension-feeding adults. Demonstrations of these effects in the field are relatively rare and somewhat equivocal, although Navarrete and Wieters (2000) used field manipulations to show clearly the strong effects of the large intertidal barnacle, *Semibalanus cariosus*, on recruitment of other sessile species.

Another important biological cue is the microbial film, formed predominantly of diatoms and cyanobacteria, which coats all hard substratum surfaces immersed in water. This biofilm provides an interface between the substratum and the water column, and so is the point of first attachment for settling larvae and propagules. Microbial films have been shown to promote settlement in a range of invertebrate larvae (Todd and Keough 1994; Qian et al. 2007), with settlers responding to cues such as age of the film, specific taxa such as diatoms, and film characteristics related to tidal height (Strathmann et al. 1981).

Experimental work on the influence of independent biological cues has taught us much about the discriminatory abilities of invertebrate larvae, and provided insight into understanding natural settlement patterns. However, it is through observations of larval responses to multiple cues that the best progress may now be made. For example, Thompson et al. (1998) showed that while settling barnacle cyprids could discriminate among differently aged microbial films and those from different tidal heights in the laboratory environment, such discrimination was irrelevant under field conditions. Here, the presence of conspecific cues (either live adults or those recently detached) appeared to overrule cues from micro-biota within the film. This work raises interesting questions regarding the applicability of behavioural mechanisms deduced from controlled laboratory experiments on larval settlement behaviour.

Physical factors associated with the water column, such as light, temperature, salinity, hydrostatic pressure and flow, influence larval behaviour prior to settlement and will undoubtedly influence settlement patterns. One excellent example is the work of Larsson and Jonsson (2006), who showed that cyprid larvae of *Balanus improvisus* actively rejected high-flow environments which were suboptimal for suspension feeding in the early post-settlement phase. This finding suggests that larval choice can be adaptively connected to a specific part of the lifecycle—in this case, the very critical period in the early post-settlement phase. Physical characteristics of the substratum are important determinants of settlement. In the case of invertebrate larvae, settlers may make an active choice dependent on micro-topography (Berntsson et al. 2000), surface contour (Wethey 1986) and rock type (Raimondi 1988a). These factors may interact; the mineral composition of the substrate determines its hardness

and resistance to weathering and can, therefore, influence surface topography and heterogeneity over considerable spatial scales (Herbert and Hawkins 2006).

12.6 Early Post-Settlement Survival

The period immediately following settlement is an extremely important time in the life history of benthic organisms. This transition from a pelagic to benthic form is associated with a high degree of mortality in both invertebrates and algae. Settlers are generally extremely small, have to cope with a dramatic change in morphology as they metamorphose and, for intertidal organisms, must withstand exposure to air within a few hours of settlement. In a review of juvenile mortality of benthic marine invertebrates, Gosselin and Qian (1997) showed that high levels of mortality soon after settlement were common across a range of taxa, with 20 of 30 studies reporting levels of over 90% mortality during the juvenile period. Examples of high mortality include loss of over 90% of settlers of the ascidian *Diplosoma similis* (Stoner 1990) over a 16-day period and a 50–80% reduction in the urchin *Strongylocentrotus purpuratus* over 24 days (Rowley 1990). In a fouling community, Osman et al. (1992) showed that two species of tiny gastropods, *Mitrella lunata* and *Anachis avara*, are able to prey selectively on newly settled colonial ascidians and eliminate almost all individuals. In algae, post-settlement survival is equally low, if not lower. For example, Schiel (1988) showed that only 5% of *Sargassum sinclairii* settlers survived to a visible size, Dudgeon and Petratis (2005) that survival of furoid embryos to juvenile stages was only between 0.3–3.8% over 400 days, and Wright et al. (2004) that only 2 of 5,395 embryos of *Fucus gardneri* survived to become visible recruits. While survival rates for these furoid algae are low, they are likely to be orders of magnitude lower for the microscopic stages of kelp (Schiel and Foster 2006).

Early post-settlement stages of algae and invertebrates are generally at risk from the same sources of physical and biological mortality, presumably since both are vulnerable to abiotic and biotic environmental stresses not experienced in the pelagic realm. Much of the work on early post-settlement mortality has taken place in the rocky intertidal where physical stresses are particularly limiting factors. Stress associated with emersion during low-water periods increases along a unidirectional stress gradient as height on the shore increases. Evidence suggests that desiccation is a major source of mortality in the early stages of a variety of intertidal species, including patellid limpets (Branch 1975), barnacles (Denley and Underwood 1979) and littorinids (Behrens 1972). Strong wave action can lead to enormous losses of newly attached invertebrate and algal settlers, which have not developed sufficient strength of attachment. Some algae, such as those of the large canopy-forming species *Ascophyllum nodosum*, suffer from dislodgement under even very moderate wave conditions (Vadas et al. 1990). Artificially settled zygotes, when exposed to less than ten low-energy waves, suffered between 85 and 99% mortality. Biological sources of mortality include grazing (Hawkins and Hartnoll 1983), whiplash from canopy-forming algae (Jenkins et al. 1999) and ‘bulldozing’ by grazers (Miller 1989).

Grazing accounts for a high level of early post-settlement mortality in algae. A vast range of grazer types (e.g. molluscs, echinoids, fish, amphipods) have been shown to limit algal recruitment. Microphagous grazers such as patellid limpets, many littorinids and sea urchins, which feed upon the microalgal film growing on hard substrata, have an important role in limiting algal development through consumption of algal propagules (reviewed by Hawkins and Hartnoll 1983). This was first dramatically demonstrated by Jones (1948) in the Isle of Man; a large-scale removal experiment showed that exposed rocky shores were relatively devoid of macroalgae because of the grazing activities of patellid limpets, rather than through physical effects of wave action. Molluscan grazers can also cause mortality in vulnerable settled invertebrate larvae through physical dislodgement or 'bulldozing' (e.g. Miller 1989). Whiplash effects of large-canopy macroalgae are well documented. In the intertidal and shallow subtidal, water movement causes the fronds of macroalgae to scour across the substratum, leading to high mortality in both invertebrate larvae (e.g. Jenkins et al. 1999) and macroalgal propagules (e.g. Santelices and Ojeda 1984).

Rather than focusing on sources of mortality, another approach to understanding patterns of post-settlement survival is the determination of the conditions under which survival of new settlers is favoured. For example, complex micro-topography may not only enhance settlement but also provide developing propagules and larvae with refugia from grazers (Lubchenco 1983), physical stress and algal whiplash (Jenkins et al. 1999). Canopy algae, whilst negatively affecting settlement through scouring, can have positive effects on larval recruitment through mitigation of environmental extremes. The balance between positive and negative effects may be determined by the level of environmental stress experienced (Leonard 1999, 2000).

12.7 Consequences of Variation in Settlement and Recruitment

In open marine systems, the decoupling of local reproduction and input of new recruits has led to a long history of debate regarding the importance of variation in settlement relative to post-settlement density-dependent processes in determining adult density (see Caley et al. 1996 for review). One argument, termed the recruitment limitation hypothesis (*sensu* Doherty 1981), states that larval supply is insufficient for the total population size to reach a carrying capacity, and increases in recruitment will lead to increases in adult population size (e.g. Connell 1985; Menge 1991). Hence, there is a direct relationship between the level of supply/settlement and adult abundance, meaning that spatial and temporal variation in settlement has a strong influence on the density and distribution of benthic juveniles and adults. The implication here is that planktonic processes preceding settlement into the benthic habitat play a role in determining adult population structure. Alternatively, settlement may simply provide the input of new individuals, whose numbers are modified through strong post-settlement density-dependent interactions. Here, the input of larvae and, hence, patterns of settlement have little or no bearing on adult density.

A strong body of evidence suggests populations can be 'recruit limited' at low recruit densities, whereas at high recruit densities, density-dependent post-settlement processes predominate and recruitment variability has little impact on adult abundance. Under this recruit-adult hypothesis (sensu Menge 2000), the relative importance of recruitment declines with increasing density of recruits (Connell 1985; Roughgarden et al. 1985; Sutherland 1990; Menge 2000). However, recent work on the intertidal barnacle *S. balanoides* has shown that recruitment may be a useful predictor of adult density across all recruit densities, from very low to very high (Jenkins et al. 2008). In that study, the relationship between recruitment and adult density switched from positive, at low levels, to negative at high levels, owing to strong over-compensatory density-dependent mortality. Clearly, differences in the level of recruitment from place to place and time to time can be a strong determinant of adult density patterns but the strength of this relationship depends on context and varies with species and their lifecycles, and can be strongly modified by post-recruitment processes (Menge 2000; Penin et al. 2007). Evidently, recruitment limitation and density-dependent interactions are not mutually exclusive but, instead, act jointly to determine the densities of marine benthic populations and assemblages (Chesson 1998; Caselle 1999; McQuaid and Lindsay 2007).

Much of the research on the relationship between recruitment intensity and adult population structure has been carried out in the rocky intertidal on unitary sessile organisms, whereas less information is available for mobile and colonial organisms. In mobile taxa, post-settlement movement can relieve overcrowding due to high settlement intensity (Wahle and Incze 1997). Furthermore, the relationship between recruitment and adult abundance has been rarely explored at the community level. However, work on the Pacific coast of North America has shown how consistent large-scale differences in recruitment intensity can lead to differences in the strength of inter-specific interactions (Connolly et al. 2001). In Oregon and Washington, where recruitment is high, experimental determination of community organisation has emphasised the role of benthic processes such as competition and predation, in contrast to studies in central California where variations in larval supply and settlement have been stressed.

In our discussions of recruitment thus far, the focus has been on the *number* of propagules which reach and settle into a habitat. However, as implied by the desperate larva hypothesis described above, not all settling larvae are of the same quality. Compared to younger larvae, older larvae may be more likely to settle in poorer-quality habitats and, therefore, may have a lower chance of survival overall. In other words, older larvae with fewer nutritional reserves are of lower quality than younger larvae with more nutritional reserves. The dramatic changes in tissue, habitat and trophic mode associated with metamorphosis suggest that any differences among larvae before metamorphosis will be nullified after metamorphosis. However, in the 1980s Jan Pechenik and others found that events during the larval phase (for example, extended periods of swimming) affected performance in the adult stage (Pechenik and Eyster 1988). This link between larval experience and adult performance has been demonstrated in a range of organisms, and a range of larval experiences appear to affect post-metamorphic performance including pollution, salinity stress and the length of

the larval period (Pechenik 2006). For example, Marshall et al. (2003) showed that ascidian larvae which were forced to swim for 3 h had lower post-metamorphic growth rates than larvae which were allowed to settle immediately. In addition to larval experience, larval size has also been shown to affect post-metamorphic performance, and a range of studies now suggest that bigger settlers have higher chances of surviving and growing than do smaller settlers (e.g. Marshall et al. 2006). These effects are not limited to species with non-feeding larvae, since larval nutrition in planktotrophs can also affect post-metamorphic performance (Phillips 2002).

12.8 Summary

The processes occurring immediately before, during and after the settlement of benthic invertebrate larvae and macroalgal propagules are fundamental to determining the distribution, abundance and dynamics of adult populations on marine hard substrata. Complex behavioural mechanisms, especially in invertebrate larvae, and the interaction with a range of physical and biological factors determine where settlement occurs and at what intensity. High levels of mortality immediately after settlement may modify these patterns. In this way, settlement and recruitment set the scene for the complexity of adult interactions which follow.

References

- Aberg P (1992) Size based demography of the seaweed *Ascophyllum nodosum* in stochastic environments. *Ecology* 73:1488–1501
- Aberg P, Pavia H (1997) Temporal and multiple scale variation in juvenile and adult abundance of the brown alga *Ascophyllum nodosum*. *Mar Ecol Prog Ser* 158:111–119
- Amsler CD, Neushul M (1990) Nutrient stimulation of spore settlement in the kelps *Pterygophora californica* and *Macrocystis pyrifera*. *Mar Biol* 107:297–304
- Amsler CD, Reed DC, Neushul M (1992) The microclimate inhabited by macroalgal propagules. *Br Phycol J* 27:253–270
- Barnes H (1956) *Balanus balanoides* (L.) in the Firth of Clyde: the development and annual variation in the larval population and the causative factors. *J Anim Ecol* 25:72–84
- Behrens S (1972) The role of wave impact and desiccation on the distribution of *Littorina sitkana* Philippi. *Veliger* 15:129–132
- Berntsson KM, Jonsson PR, Lejhall M, Gatenholm P (2000) Analysis of behavioural rejection of micro-textured surfaces and implications for recruitment by the barnacle *Balanus improvisus*. *J Exp Mar Biol Ecol* 251:59–83
- Berntsson KM, Jonsson PR, Larsson AI, Holdt S (2004) Rejection of unsuitable substrata as a potential driver of aggregated settlement in the barnacle *Balanus improvisus*. *Mar Ecol Prog Ser* 275:199–210
- Botello G, Krug PJ (2006) Desperate larvae revisited: age, energy and experience affect sensitivity to settlement cues in larvae of the gastropod *Alderia* sp. *Mar Ecol Prog Ser* 312:149–159
- Branch G (1975) Ecology of *Patella* species from the Cape Peninsula, South Africa. IV. Desiccation. *Mar Biol* 32:179–188

- Caffey HM (1985) Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecol Monogr* 55:313–332
- Caley M, Carr M, Hixon M, Hughes T, Jones G, Menge B (1996) Recruitment and the local dynamics of open marine populations. *Annu Rev Ecol Syst* 27:477–500
- Caselle J (1999) Early post-settlement mortality in a coral reef fish and its effect on local population size. *Ecol Monogr* 69:177–194
- Chesson P (1998) Recruitment limitation: a theoretical perspective. *Aust J Ecol* 23:234–240
- Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J Exp Mar Biol Ecol* 93:11–43
- Connolly SR, Menge BA, Roughgarden J (2001) A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology* 82:1799–1813
- Crisp DJ, Meadows PS (1962) The chemical basis of gregariousness in cirripedes. *Proc R Soc B* 156:500–520
- Crisp DJ, Meadows PS (1963) Adsorbed layers: the stimulus to settlement in barnacles. *Proc R Soc B* 158:364–387
- Denley EJ, Underwood AJ (1979) Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. *J Exp Mar Biol Ecol* 36:269–293
- Doherty P (1981) Coral reef fishes: recruitment limited assemblages? In: *Proc Int Coral Reef Symp* 4:465–470
- Dudgeon S, Petraitis PS (2005) First year demography of the foundation species, *Ascophyllum nodosum*, and its community implications. *Oikos* 109:405–415
- Elkin C, Marshall DJ (2007) Desperate larvae: influence of deferred costs and habitat requirements on habitat selection. *Mar Ecol Prog Ser* 335:143–153
- Fraschetti S, Terlizzi A, Benedetti-Cecchi L (2005) Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Mar Ecol Prog Ser* 296:13–29
- Gaines S, Brown S, Roughgarden J (1985) Spatial variation in larval concentration as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67:267–272
- Gosselin LA, Qian P (1997) Juvenile mortality in benthic marine invertebrates. *Mar Ecol Prog Ser* 146:265–282
- Hawkins SJ, Hartnoll RG (1982) Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977–1981). *J Exp Mar Biol Ecol* 62:271–283
- Hawkins SJ, Hartnoll RG (1983) Grazing of intertidal algae by marine invertebrates. *Oceanogr Mar Biol Annu Rev* 21:195–282
- Herbert RJH, Hawkins SJ (2006) Effect of rock type on the recruitment and early mortality of the barnacle *Chthamalus montagui*. *J Exp Mar Biol Ecol* 334:96–108
- Hills JM, Thomason JC (1996) A multi-scale analysis of settlement density and pattern dynamics of the barnacle *Semibalanus balanoides*. *Mar Ecol Prog Ser* 138:103–115
- Hoffmann AJ, Santelices B (1991) Banks of algal microscopic forms: hypotheses on their functioning and comparisons with seed banks. *Mar Ecol Prog Ser* 79:1–2
- Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397:59–63
- Hunt HL, Scheibling RE (1996) Physical and biological factors influencing mussel (*Mytilus trossulus*, *M. edulis*) settlement on a wave-exposed rocky shore. *Mar Ecol Prog Ser* 142:1–3
- Jenkins SR, Norton TA, Hawkins SJ (1999) Settlement and post-settlement interactions between *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) and three species of furoid canopy algae. *J Exp Mar Biol Ecol* 236:49–67
- Jenkins SR, Aberg P, Cervin G, Coleman RA, Delany J, Della Santina P, Hawkins SJ, LaCroix E, Myers AA, Lindegarh M, Power AM, Roberts MF, Hartnoll RG (2000) Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *J Exp Mar Biol Ecol* 243:209–225
- Jenkins SR, Murua J, Burrows MT (2008) Temporal changes in the strength of density-dependent mortality and growth in intertidal barnacles. *J Anim Ecol* 77:573–584

- Jones NS (1948) Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. Proc Trans Lpool Biol Soc 56:60–77
- Kendall MA, Bowman RS, Williamson P, Lewis JR (1985) Annual variation in the recruitment of *Semibalanus balanoides* on the North Yorkshire coast. J Mar Biol Assoc UK 65:1009–1030
- Keough MJ, Downes BJ (1982) Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia 54:348–352
- Knight-Jones EW (1951) Gregariousness and some other aspects of settling behaviour of *Spirobis*. J Mar Biol Assoc UK 30:201–222
- Knight-Jones EW (1953) Laboratory experiments on gregariousness during settling in *Balanus balanoides* and other barnacles. J Exp Biol 30:584–598
- Krug P (2001) Bet-hedging dispersal strategy of a specialist marine herbivore: a settlement dimorphism among sibling larvae of *Alderia modesta*. Mar Ecol Prog Ser 213:177–192
- Lagos NA, Tapia FJ, Navarrete SA, Castilla JC (2007) Spatial synchrony in the recruitment of intertidal invertebrates along the coast of central Chile. Mar Ecol Prog Ser 350:29–39
- Larsson AI, Jonsson PR (2006) Barnacle larvae actively select flow environments supporting post-settlement growth and survival. Ecology 87:1960–1966
- Leonard GH (1999) Positive and negative effects of intertidal algal canopies on recruitment and survival of barnacles. Mar Ecol Prog Ser 178:241–249
- Leonard GH (2000) Latitudinal variation in species interactions: a test in the New England rocky intertidal zone. Ecology 81:1015–1030
- Lubchenco J (1983) *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64:1116–1123
- Marshall D, Pechenik J, Keough M (2003) Larval activity levels and delayed metamorphosis affect post-larval performance in the colonial, ascidian *Diplosoma listerianum*. Mar Ecol Prog Ser 246:153–162
- Marshall DJ, Cook CN, Emler RB (2006) Offspring size effects mediate competitive interactions in a colonial marine invertebrate. Ecology 87:214–225
- McCook LJ, Chapman ARO (1997) Patterns and variations in natural succession following massive ice-scour of a rocky intertidal seashore. J Exp Mar Biol Ecol 214:121–147
- McQuaid CD, Lindsay TL (2007) Wave exposure effects on population structure and recruitment in the mussel *Perna perna* suggest regulation primarily through availability of recruits and food, not space. Mar Biol 151:2123–2131
- Menge BA (1991) Relative importance of recruitment and other causes of variation in rocky intertidal community structure. J Exp Mar Biol Ecol 146:69–100
- Menge BA (2000) Recruitment vs. postrecruitment processes as determinants of barnacle population abundance. Ecol Monogr 70:265–288
- Miller KM (1989) The role of spatial and size refuges in the interaction between juvenile barnacles and grazing limpets. J Exp Mar Biol Ecol 134:157–174
- Minchinton TE (1997) Life on the edge: conspecific attraction and recruitment of populations to disturbed habitats. Oecologia 111:45–52
- Minchinton TE, Scheibling RE (1993) Free space availability and larval substratum selection as determinants of barnacle population structure in a developing rocky intertidal community. Mar Ecol Prog Ser 95:233–244
- Navarrete SA, Wieters EA (2000) Variation in barnacle recruitment over small scales: larval predation by adults and maintenance of community pattern. J Exp Mar Biol Ecol 253:131–148
- O’Riordan RM, Arenas F, Arrontes J, Castro JJ, Cruz T, Delany J, Martinez B, Fernandez C, Hawkins SJ, McGrath D, Myers AA, Oliveros J, Pannacciulli FG, Power AM, Relini G, Rico JM, Silva T (2004) Spatial variation in the recruitment of the intertidal barnacles *Chthamalus montagu* southward and *Chthamalus stellatus* (Poli) (Crustacea: Cirripedia) over an European scale. J Exp Mar Biol Ecol 304:243–264
- Osman RW, Whitlatch RB, Malatesta RJ (1992) Potential role of micropredators in determining recruitment into a marine community. Mar Ecol Prog Ser 83:35–43
- Pawlik JR (1992) Chemical ecology of the settlement of benthic marine invertebrates. Oceanogr Mar Biol Annu Rev 30:273–335

- Pechenik J (2006) Larval experience and latent effects—metamorphosis is not a new beginning. *Integr Comp Biol* 46:323–333
- Pechenik J, Eyster L (1988) Influence of delayed metamorphosis on growth and metabolism of young *Crepidula fornicata* (Gastropoda) juveniles. *Biol Bull* 176:14–24
- Penin L, Adjeroud M, Pratchett MS, Hughes TP (2007) Spatial distribution of juvenile and adult corals around Moorea (French Polynesia): implications for population regulation. *Bull Mar Sci* 80:379–389
- Phillips NE (2002) Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. *Ecology* 83:2562–2574
- Qian PY, Lau SCK, Dahms HU, Dobretsov S, Harder T (2007) Marine biofilms as mediators of colonization by marine macroorganisms: implications for antifouling and aquaculture. *Mar Biotechnol* 9:399–410
- Raimondi PT (1988a) Rock type affects settlement, recruitment, and zonation of the barnacle *Chthamalus anisopoma* Pilsbury. *J Exp Mar Biol Ecol* 123:253–267
- Raimondi PT (1988b) Settlement cues and determination of the vertical limit of an intertidal barnacle. *Ecology* 69:400–407
- Raimondi P, Keough M (1990) Behavioural variability in marine larvae. *Aust J Ecol* 15:427–437
- Reed DC, Foster MS (1984) The effect of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65:937–948
- Reed DC, Laur DR, Ebeling AW (1988) Variation in algal dispersal and recruitment, the importance of episodic events. *Ecol Monogr* 58:321–335
- Roughgarden J, Isawa Y, Baxter C (1985) Demographic theory for an open marine population with space limited recruitment. *Ecology* 66:54–67
- Rowley RJ (1990) Newly settled sea-urchins in a kelp bed and urchin barren ground—a comparison of growth and mortality. *Mar Ecol Prog Ser* 62:229–240
- Santelices B (1990) Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanogr Mar Biol Annu Rev* 28:177–276
- Santelices B, Ojeda F (1984) Recruitment, growth and survival of *Lessonia nigrescens* (Phaeophyta) at various tidal levels in exposed habitats of central Chile. *Mar Ecol Prog Ser* 19:73–82
- Schiel DR (1988) Algal interactions on shallow subtidal reefs in northern New Zealand: a review. *N Z J Mar Freshw Res* 22:481–489
- Schiel DR, Foster MS (2006) The population biology of large brown seaweeds: ecological consequences of multiphase life histories in dynamic coastal environments. *Annu Rev Ecol Evol S* 37:343–372
- Stoner DS (1990) Recruitment of a tropical colonial ascidian—relative importance of pre-settlement vs post-settlement processes. *Ecology* 71:1682–1690
- Strathmann RR, Branscomb ES, Vedder K (1981) Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. *Oecologia* 48:13–18
- Sutherland JP (1990) Recruitment regulates demographic variation in a tropical intertidal barnacle. *Ecology* 71:955–972
- Thompson R, Norton T, Hawkins S (1998) The influence of epilithic microbial films on the settlement of *Semibalanus balanoides* cyprids—a comparison between laboratory and field experiments. *Hydrobiologia* 376:203–216
- Todd CD, Keough MJ (1994) Larval settlement in hard substratum epifaunal assemblages: a manipulative field study of the effects of substratum filming and the presence of incumbents. *J Exp Mar Biol Ecol* 181:159–187
- Toonen R, Pawlik J (2001a) Foundations of gregariousness: a dispersal polymorphism among the planktonic larvae of a marine invertebrate. *Evolution* 55:2439–2454
- Toonen R, Pawlik J (2001b) Settlement of the gregarious tube worm *Hydroides dianthus* (Polychaeta: Serpulidae). II. Testing the desperate larva hypothesis. *Mar Ecol Prog Ser* 224:115–131
- Vadas RL, Wright WA, Miller SL (1990) Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. *Mar Ecol Prog Ser* 61:263–272
- Vadas RL, Johnson S, Norton TA (1992) Recruitment and mortality of early post-settlement stages of benthic algae. *Br Phycol J* 27:331–351

- Wahle RA, Incze LS (1997) Pre- and post-settlement processes in recruitment of the American lobster. *J Exp Mar Biol Ecol* 217:179–207
- Wethey DS (1983) Spatial pattern in barnacle settlement—daily changes during the settlement season. *Am Zool* 23:1021–1021
- Wethey DS (1986) Ranking of settlement cues by barnacle larvae: influence of surface contour. *Bull Mar Sci* 39:393–400
- Wright JT, Williams SL, Dethier MN (2004) No zone is always greener: variation in the performance of *Fucus gardneri* embryos, juveniles and adults across tidal zone and season. *Mar Biol* 145:1061–1073