Chapter 11
Larval Supply and Dispersal

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11.1 Introduction

Most marine organisms have planktonic larvae that spend between minutes and months in the water column before settlement. For over 50 years, marine ecologists have recognised that the number of larvae that are produced, disperse and recruit successfully is extremely variable (Thorson 1950). More recently, it has been realised that variation in larval supply can drive the dynamics of marine populations and communities (Underwood and Fairweather 1989). To understand how marine populations and communities vary in time and space, we must first understand how propagule supply and dispersal are influenced. This chapter examines the causes of variability in larval production, survival in the plankton, and scales of dispersal and their consequences for marine organisms living on hard substrata.

11.2 Variability in the Production of Larvae

The enormous variability in production of larvae by any species can come from a variety of sources with two basic elements: (1) variation in fecundity (the production of gametes) and (2) variation in fertilisation success (the production of zygotes).

11.2.1 Variation in Fecundity

Despite the realisation that variation in egg production helps determine larval supply, surprisingly few patterns of variation in fecundity have been identified for marine organisms. This may be because fecundity is often difficult to quantify (Ramirez-Llodra 2002) but the paucity of identifiable patterns may also arise because data are scattered across studies on individual species. Studies of variation in fecundity show that there can be dramatic differences among populations and individuals (Ramirez-Llodra 2002). For example, the number of eggs produced by individual

M. Wahl (ed.), *Marine Hard Bottom Communities*, Ecological Studies 206,
DOI: 10.1007/978-3-540-92704-4_11, © Springer-Verlag Berlin Heidelberg 2009

females within a population of crabs ranged between 10 and 1,443 in the study of Sampedro et al. (1997).

The production of eggs is energetically expensive and, overall, reproductive output is limited by access to resources and the costs of somatic maintenance and/or growth. Accordingly, most factors affecting resource availability influence fecundity in marine organisms (Ramirez-Llodra 2002). Many factors affect fecundity but maternal size, nutritional history and age are major intrinsic factors. Importantly, maternal size and fecundity are not isometrically related—i.e. the ratio of body mass to fecundity increases with size such that larger mothers produce many more offspring per unit of body weight than do smaller mothers. Allometric reproduction has important implications for the relative contributions of small and large individuals to the next generation and, of course, exploitation by fisheries (Birkeland and Dayton 2005). The major extrinsic influences on fecundity seem to be environmental stress, pollution and both inter- and intra-specific competition (Ramirez-Llodra 2002). Overall, fecundity is highly plastic and variation across orders of magnitude should be expected both within and among marine populations.

Like egg quantity, the quality of eggs can also vary. The average within-population coefficient of variation in egg size across 102 species of marine invertebrates is ~9%, yielding a twofold size range across the largest and smallest 5% of eggs (Marshall and Keough 2008). Variation in egg size is important because offspring size can be a good proxy for offspring quality; bigger eggs typically have a better chance of being fertilised, developing in the plankton and recruiting successfully (Marshall and Keough 2008). Although variation in egg quality may be as important to recruitment as variation in their numbers, this is rarely considered.

11.2.2 Variation in Fertilisation

The production and release of eggs is not sufficient to ensure the supply of larvae into a population—these eggs must also be fertilised. In internally fertilising species, fertilisation success is largely assured; so, in this case fecundity is a good estimate of larval production. However, most marine animals reproduce by broadcast spawning, with eggs and sperm shed into the environment and external fertilisation. In such species, fertilisation is not assured, so fecundity and larval production may be decoupled.

Thorson was the first to consider the fertilisation rates of broadcast spawned eggs and concluded that, because many animals aggregate to spawn, the vast majority of eggs are fertilised. This assumption was largely unchallenged until Timothy Pennington examined the fertilisation success of sea urchin eggs in the field in 1985. Pennington found that when eggs were spawned further than 20 cm away from spawning males, less than 15% were successfully fertilised (Pennington 1985). Since this pioneering work, studies on a range of species have shown that fertilisation success is highly variable and rarely 100%. This has led to speculation that the dynamics of broadcast spawning populations are limited by fertilisation rates, though this remains controversial (Levitan and Petersen 1995; Yund 2000).

While many factors affect fertilisation success in broadcast spawners, the local concentration of sperm is the most important, as it determines the probability of egg/sperm encounters. The dynamic nature of the marine environment can result in rapid dilution of sperm to ineffective concentrations. Given that the average distance between spawning individuals is often inversely proportional to population density (assuming that aggregation during spawning is not always perfect), fertilisation success is positively related to population density. This relationship between fertilisation success and population density is termed an Allee effect and has interesting implications for the production of larvae.

Benthic marine organisms typically show a negative relationship between population density and fecundity, as increasing intra-specific competition can decrease individual reproductive output. Thus, we expect high-density populations to have lower per capita fecundity than do low-density populations. However, for broadcast spawners, fertilisation success increases with population density, suggesting higher fertilisation success in these high-density populations. Potential trade-offs between fecundity and fertilisation success obscure the relationship between population density and larval production for broadcast spawners. The precise relationship between sperm concentration (and its proxy population density) and fertilisation success varies with local hydrodynamics and the properties of the gametes per se, yielding a highly idiosyncratic relationship. Generally, more work is needed on the effects of population density on larval production.

11.3 Mortality in the Plankton

Most marine larvae are less than a few millimetres long and swim slowly. Their small size and poor swimming ability make these larvae vulnerable to a range of predators and to ocean currents, and the larval planktonic period has long been viewed as the greatest source of mortality for organisms with biphasic lifecycles (Thorson 1950). However, small larval size and the sheer scale of larval dispersal make estimating real rates of mortality in the field enormously challenging. This is important because planktonic mortality not only affects the number of larvae that can recruit into a population but it can also affect how far larvae can disperse (i.e. very high larval mortality rates will result in very few larvae surviving long-distance dispersal).

11.3.1 Estimates of Mortality in the Field

Estimating larval mortality in the field is extremely difficult (see reviews by Rumrill 1990 and Morgan 1995) and direct observations are restricted to large, easily observed ascidian larvae, which show ~70% survival (Stoner 1990). This suggests low mortality but such larvae spend less than 10 min in the plankton, so that daily mortality could be very high. Furthermore, the colonial ascidians studied produce large, conspicuous larvae that are good swimmers and may be chemically defended. Seeing that these are our only direct estimates of field mortality, it is unrealistic to extrapolate to more typical marine larvae.

Most studies examining larval mortality in the sea have used indirect methods or experiments (Morgan 1995; Johnson and Shanks 2003). Intuitively, given the high fecundity of most marine organisms with planktonic larvae, high levels of mortality must occur at some stage. Studies that track individual cohorts of larvae estimate that fewer than 0.01% of larvae survive in the plankton (Rumrill 1990; Morgan 1995). Again, it is difficult to determine how reliable such measures are and, overall, planktonic mortality rates remain one of the greatest ‘black boxes’ in marine ecology.

11.3.2 Sources of Planktonic Mortality

The issues that hamper estimates of mortality also hamper the identification of sources of mortality—but there are exceptions. Thorson (1950) considered planktonic predation as the major source of larval mortality in the plankton and many reviews support this view (Morgan 1995). However, in situ larval ‘corrals’ suggest that mortality through predation is typically less than 1% (Johnson and Shanks 2003). Larvae are also small, poorly protected and vulnerable to environmental stresses such as pollution, salinity changes and UV exposure. For larvae that feed in the plankton, starvation may be important but the evidence for such effects is variable (Olson and Olson 1989). Probably one of the greatest causes of mortality is advection: larvae may be transported away from suitable habitats and never reach a place where metamorphosis is successful. Again, whilst this is probably common, we have limited evidence for it in the field.

11.3.3 Phenotypic Degradation of Larvae in the Field

Larvae are not inert particles but living organisms that experience a range of conditions. The dramatic changes associated with metamorphosis encourage viewing the larval and adult stage as separate; however, their phenotypes are strongly linked. Consequently, events in the larval stage can affect performance in the adult stage (i.e. adult phenotype), and are termed ‘carry-over’ or ‘latent’ effects (Pechenik 2006). This link between life-history stages has some important consequences for understanding planktonic mortality. If larval experience degrades the larval phenotype so that they cannot survive as adults, then these larvae are effectively the ‘swimming dead’ (Pechenik 1990): although alive, they cannot contribute to recruitment. Many experiences can degrade larval phenotype, including pollution, metamorphic delay, increased swimming activity and poor nutrition (reviewed in Pechenik 2006). This could be an important driver of recruitment success because it becomes apparent only in larvae that have survived all other causes of mortality and would otherwise have recruited into the population. Unfortunately, the incidence of phenotypic degradation in the field is unknown, as most studies that manipulate larval phenotype are done in the laboratory.

11.4 Scales of Dispersal and Larval Supply

It is difficult to overestimate the importance of understanding larval supply, due to its influence on both gene flow and community structure. In evolutionary terms, scales of larval dispersal may be implicated in speciation rates, species longevity and geographic ranges (Jeffery and Emlet 2003). Ecologically, larval supply affects the degree to which communities or populations are shaped by competition for space (Gaines and Roughgarden 1985), spatial distribution patterns and how we define metapopulations (Ellien et al. 2000). Consequently, understanding larval supply has profound importance for the design of marine reserves (e.g. Stobutzki 2001; Jessopp and McAllen 2007), particularly where distinct source and sink populations exist (Bode et al. 2006).

Larval supply is affected by multiple factors operating at different spatial and temporal scales, and Pineda (1994) offers an extremely useful model of the hierarchical nature of the control of larval supply. Essentially, this scales down from the control of rates of larval arrival at a site (determined by the size of the larval pool and their physical transport) to small-scale factors including substratum availability, micro-hydrodynamics and behaviour. The advantage of this model is that it incorporates issues of large-scale dispersal occurring over scales of 10–100s km and differential nearshore delivery to places separated by 100s m (e.g. Porri et al. 2006). Importantly, large-scale offshore processes affect greater numbers of larvae and, so, have a disproportionally important influence on population fluctuations (Pineda 2000), while small-scale factors can operate only on the pool of larvae provided by offshore processes. This finds clear expression in the suggestion by Abrams et al. (1996) that large-scale oceanography affects material subsidies to coastal ecosystems, including propagule supply, and thereby dramatically affects the pace of community dynamics and the intensity of species interactions.

It is well known that different zooplankton, including larvae, occur in different water masses (Wing et al. 1998) and that larvae tend to accumulate at fronts (Roughgarden et al. 1991). Many physical processes affect offshore transport, including factors that influence cross-shelf transport, such as upwelling (e.g. Mace and Morgan 2006), surface slicks (Shanks 1986) and internal tidal bores (Pineda 1991), as well as longshore transport mechanisms such as wind-driven surface currents (Barkai and McQuaid 1988).

Coastal topography may have indirect and very powerful effects on larval dispersal and supply through its interaction with nearshore oceanography (Gaylord and Gaines 2000; Roughan et al. 2005; Webster et al. 2007). Bay and open coast sites differ in settlement rates, because of the interaction of topography with wind and tides (Gaines and Bertness 1992), they support different larval assemblages

(Jessopp and McAllen 2007) and, in South Africa, they support mussel populations that differ not only in their densities (unpublished data) but also in their genetic structure (Nicastro et al. 2008). The importance of zones of retention, where larval exchange with adjacent waters is reduced by patterns of water flow, is increasingly recognised (Largier 2004).

Given the small physical size of most larvae, it is tempting to assume that they essentially function as passive particles transported entirely through hydrological processes and, indeed, there is support for this (e.g. Barkai and McQuaid 1988; Griffin et al. 2008). However, growing evidence suggests that larval behaviour can influence dispersal, so that models based on passive transport define potential, not necessarily actual dispersal (Roberts 1997).

Some larvae can postpone settlement if conditions are not ideal (Seed and Suchanek 1992), and this carries direct (predation) and indirect costs (depletion of energetic resources). The desperate larva hypothesis (Knight-Jones 1951) predicts that larval discrimination with regard to settlement cues will decrease as their energy stores are diminished, so that they will accept a wider range of cues. For species with non-feeding larvae, dispersal potential can effectively be manipulated through larval size, which is assumed to correlate with energy stores, and influences readiness to settle and responsiveness to settlement cues; essentially, smaller or hungrier larvae become desperate more quickly (Botello and Krug 2006). However, models suggest that, because they can feed, the settlement behaviour of planktotrophic larvae should be strongly affected by the quality of potential settlement sites and local food availability; essentially, given enough food in the water column, they are less likely to become desperate (Elkin and Marshall 2007).

To what degree (if at all) can we regard planktonic larvae as the passive particles that many models (e.g. Man et al. 1995) assume these organisms to be? Clearly, this will differ among taxa, and will depend on larval behaviour (e.g. Shanks 1995), swimming abilities and duration (Stobutzki and Bellwood 1997). For many taxa, larval duration in turn depends on sea temperature, with implications for potential survival and dispersal, so that temperature effects can help to explain differences in recruitment among years (O’Connor et al. 2007).

Unfortunately, the situation is made even more complex by the fact that behaviour can differ within a single taxon. For example:

- Different larval stages of the same species may differ in their behaviour (Gallager et al. 1996) and position in the water column (Tapia and Pineda 2007).
- Conspecific larvae from different populations can show different vertical migration behaviour (Manuel and O’Dor 1997).

There is no doubt that larval dispersal occurs across a wide range of spatial scales (Shanks et al. 2003) that differ among taxa within the same community. Algae generally disperse over relatively small distances and fish over much larger distances; invertebrates, including many taxa, unsurprisingly show a wide range of dispersal scales (Shanks et al. 2003). Scales of connectivity are important in understanding whether reproductive output is correlated with recruitment, i.e. how closed are populations? Early work highlighted the ability of larvae to disperse over large distances (e.g. Scheltema and Williams 1983), so that populations were perceived as being extremely open (Scheltema 1971). Later work has tended to emphasise that dispersal is often less than anticipated (e.g. Barkai and McQuaid 1988) and there is considerable evidence for self-recruitment that exists across life-history types and geographic regions. Thus, marine populations may be much less open than was previously believed (Sponaugle et al. 2002), though there is extreme variability in the dispersal ranges observed in marine propagules (Kinlan and Gaines 2003) and there may be a bias in the reporting of results (Levin 2006).

Sponaugle et al. (2002) suggest that any departure from unidirectional flow that is uniform across depths will offer the possibility of larval retention. They make a useful separation here between physical retention, which operates on all passive particles and requires no behaviour of the larvae, and biophysical retention, which operates through the interaction of physical effects and larval behaviour. Much of the recent evidence emphasising the importance of self-recruitment comes from fish. Jones et al. (2005) marked individual larvae in a population of clown fish using tetracycline and found remarkably little dispersal, despite a 9–12 day larval period. Older fish larvae have considerable swimming potential and behavioural plasticity but the relative importance of behaviour and oceanography in their dispersal remains controversial (e.g. Colin 2003; Taylor and Helleberg 2003). Even for simpler invertebrate larvae, there is evidence that behaviour can have significant effects on dispersal distances (e.g. Shanks and Brink 2005), as well as on patterns of settlement (Bierne et al. 2003).

Even where self-recruitment is important, populations still depend to some degree on allochthonous inputs of propagules and this too can vary (Cowan et al. 2000). Models of the English Channel suggest that wind forcing increases the role of advection and strongly influences larval dispersal (Ellien et al. 2000), so that interannual variation in wind forcing leads to variability in settlement rates, and in the degree to which populations receive “external” or “local” larvae (Barnay et al. 2004).

There is evidence that large-scale oceanographic features and events can have cross-taxon effects (Gaylord and Gaines 2000) but, because dispersal scales can reflect the interaction of behaviour and hydrodynamics, these are likely to be governed by different taxon-specific combinations of factors. Mace and Morgan (2006) found that the crab *Cancer magister* in Bodega Bay settled mainly during relaxation conditions, while *C. antennarius/productus* settled during upwelling conditions, indicating that there may be different taxon-specific delivery mechanisms even for related taxa in the same small area.

Scales of larval dispersal depend on local conditions and hydrodynamics, phylogenetic constraint in terms of behaviour and potential propagule longevity, as well as on possible taxon-specific delivery shaped by the interaction of behaviour and oceanography. Dispersal scale may also differ among conspecific individuals, and a useful approach is to identify dispersal kernels, which describe the possibility of individual propagules dispersing over a given distance before settlement (Kinlan and Gaines 2003). Ultimately, the best method for studying larval dispersal depends on the question asked. In terms of connectivity and the structure of metapopulations, genetic approaches are suitable. In terms of population dynamics, an understanding of the interactions between behaviour and oceanography is required.

11.5 Genetic Consequences of Variation in Larval Production and Dispersal

Molecular genetic approaches are often used to understand gene flow and, indirectly, estimate larval dispersal/connectivity within marine metapopulations. The basic premise is that, assuming selective neutrality of molecular markers, genetic differences among populations suggest that larval exchange among these is limited (Hedgecock 1986). Early studies indicated that organisms with a short or no larval stage showed genetic differentiation on relatively small scales, while those with long-lived larvae showed differentiation across broader scales (Hedgecock 1986). The advent of polymerase chain reaction techniques led to an explosion of studies over the last 10 years using more variable and, thus, statistically more powerful markers, which have uncovered genetic discontinuities over spatial scales smaller than expected (Sotka et al. 2004; Temby et al. 2007). New simulation frameworks for predicting/analysing larval dispersal and gene flow in coastal marine populations (Sotka and Palumbi 2006) are also an exciting prospect, particularly because such models can potentially be adapted to account for realistic oceanographic patterns and large variances in larval output, quality and dispersal among populations.

Given the many processes influencing reproductive and larval success, reproductive skews in marine populations could be larger than previously thought. Large skews in reproductive success imply that the effective genetic sizes of populations may be orders of magnitude smaller than suggested by adult numbers, so that populations may function genetically as though much smaller (Hedrick 2005). Concern about the conservation consequences of small genetic population sizes in marine species (i.e. accelerated genetic drift, inbreeding, etc.) has generally been disregarded, presumably because marine populations are typically numerically enormous, but this lack of attention may be unwarranted (Waples 2002). Understanding reproductive skews is necessary to determine whether they are large or consistent enough to influence the effective size of populations, enabling us to interpret differences among populations that are related to their effective genetic size (N_e) and migration rates for each generation (m). The latter is usually the parameter of interest, because it relates to larval exchange, but it cannot be determined without knowing N_e.

Although data are scarce, initial molecular studies suggest that effective population sizes in sessile marine invertebrate populations are surprising low. Work on two species of oysters indicates that their effective population size may be many orders of magnitude less than their numerical size (Hedgecock et al. 2007). Other studies also show temporal differences in the genetic structure of recruits (Moberg and Burton 2000; Lee and Boulding 2007), a genetic pattern called "chaotic genetic patchiness" by Johnson and Black (1984). Similarly, Veliz et al. (2006) recently found evidence of kin relationships among barnacles with a relatively long planktonic period. These patterns are consistent with larval production by a limited subset of potential parents in a population at different times—i.e. very large skews in reproductive success among individual spawners. What affects effective population size, however, is large skews in the lifetime reproductive success of individuals.

Thus, longer temporal studies across time/multiple reproductive events are needed to understand whether these putative skews are consistent among individuals or change from one spawning event to the next.

11.6 Conclusions

Variation in the number of larvae produced in a population arises because some individuals produce/release fewer propagules in the first place, because gametes do not fertilise, or because the larvae die or are not transported to a suitable place. Transport is influenced by hydrodynamics interacting with larval behaviour. Even when delivered to appropriate habitats, larvae may count as ‘living dead’ because they are physiologically compromised or are reproductively isolated as foreign immigrants. Consequently, larval supply can and does vary enormously, with critical consequences for the ecology and evolution of marine species. Determining which processes are the primary drivers in the variation in larval production and dispersal is a key quest in marine ecology.

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