Recruitment of Marine Invertebrates: the Role of Active Larval Choices and Early Mortality

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Summary. Spatial variation in the recruitment of sessile marine invertebrates with planktonic larvae may be derived from a number of sources: events within the plankton, choices made by larvae at the time of settlement, and mortality of juvenile organisms after settlement, but before a census by an observer. These sources usually are not distinguished.

A study of the recruitment of four species of sessile invertebrates living on rock walls beneath a kelp canopy showed that both selection of microhabitats by settling larvae and predation by fish may be important. Two microhabitats were of interest; open, flat rock surfaces, and small pits and crevices that act as refuges from fish predators.

The polychaete *Spirorbis eximus* and the cyclostome bryozoan *Tubulipora* spp. showed no preference for refuges, but settled apparently at random on the available substrata. *Tubulipora* was preyed upon heavily by fish, while *Spirorbis* was relatively unaffected. The bryozoans *Celleporaria braneae* and *Scrupocellaria bertholetti* both recruited preferentially into refuges. *Scrupocellaria* were preyed upon, while *Celleporaria* juveniles seemed unaffected. Predation by fish modified the spatial distribution (*Tubulipora*), abundance (*Tubulipora*), or size distribution (*Scrupocellaria*) of the juvenile population, or had relatively little effect (*Celleporaria, Spirorbis*).

All of the above events occur within three weeks of settlement. Since inferences about the effect of larval events on the population dynamics of adult organisms are often based on observations of the patterns of recruitment after one or two months, they are therefore likely to be misleading.

Introduction.

The colonisation of habitats by marine organisms with planktonic larvae involves three phases: development (including dispersal as a planktonic form), testing of a habitat for suitability, and settlement (summarised by Underwood 1979). For sessile invertebrates, the latter phase also includes attachment to the substratum and metamorphosis. The organism is unlikely to be detected immediately, because of small size, cryptic habitat, etc., and there is a fourth "phase"; survival until the organisms is counted by an observer. This phase may last from hours to months (Scheltema 1974), but it is not a true life-history stage, merely a reflection of the limitations of the observer. The number of organisms passing through the fourth phase is termed recruitment, while the number passing to the third phase is termed settlement. Recruitment is a composite of larval and juvenile stages, while settlement involves only larval stages.

It is important to distinguish between settlement and recruitment. Non-random patterns of recruitment, such as differences in the density of recruitment with height on the shore (Underwood 1979) or differences in the density of recruitment with patch size (Jackson 1977; Keough 1982a), or with microhabitat, may have two causes: (1) differential settlement, and (2), different probabilities of early mortality in different parts of an organism's habitat. The first may involve an active response by larvae at the time of settlement that may be an evolved response to patterns of mortality, while the second involves no active choice by larvae.

Failure to distinguish between these two phenomena may lead to misleading inferences in a number of areas. First, explanations for the spatial distributions of adult organisms have frequently neglected the importance of recruitment (Underwood and Denley 1982), and second, many of the studies that have included recruitment in the intertidal zone of rocky shores, have not distinguished between recruitment and settlement. This may have led to an overestimation of the importance of interactions between adult organisms and physical factors in limiting these distributions. The same is true of work on subtidal hard substrata; the terms recruitment and settlement are used interchangeably, when recruitment is actually measured. Patterns of recruitment have then been used to make inferences about larval settling behaviour (e.g. Day and Osman 1982; Dean and Hurd 1980; Jackson 1977; Osman 1977; Schoener and Schoener 1981).

At the community level, it has been suggested for some subtidal systems, species arriving first may be able to resist further invasion by other species, so that the abundance of sessile species in such communities can be explained by measuring the colonising ability of component species (e.g. Dean and Hurd 1980; Sutherland and Karlson 1977). It is often considered that the ability of a species to colonise a habitat can be measured accurately by its recruitment rate (usually over a time period of 1–2 mo.).

In a similar way, many other studies have considered the effect of predation in natural communities (e.g. Day 1977; Day and Osman 1982; Keough and Butler 1979; Osman 1977; Paine 1966; Russ 1980; Sammarco 1980).
Most have used exclusions (cages, fences, etc.) that modify the physical environment, such as light, water flow, sedimentation, in some way. Differences in the abundance of taxa between controls and exclusions may be a result of two (not exclusive) factors; the presence or absence of predators, and larval responses to two different physical regimes. These alternatives have rarely been separated (Choat 1982; Keough 1982b).

The above examples have in common the question of how much the observed pattern of recruitment reflects active choices by larvae, and how much it reflects mortality subsequent to settlement. As a consequence, the implicit assumption of many studies is that settlement can be measured with sufficient accuracy by recruitment, i.e. either there is little mortality during the first few weeks after settlement, or the mortality processes affect all species equally, so that their relative abundances are unchanged.

Here, we describe the patterns of recruitment for four sessile invertebrate taxa and estimate mortality rates for those taxa during the first three to four weeks after settlement.

The four taxa are Spirobranchus eximius (Polychaeta: Serpulidae), and the bryozoans Tubulipora spp. (T. concinna and T. tuba; Cyclostomata: Tubuliporidae); Scrupocellaria bertholetti (Cheilostomata: Scrupocellariidae), and Celleporaria brumae (Cheilostomata: Celleporidae). Predation by fishes is an important source of mortality of sessile organisms in the study area (Downes & Keough unpubl. obs.), of which the most important fish species are the garibaldi, Hypsypops rubicundus (Pomacanthidae), the rock wrasse, Halichoeres semicinctus (Labridae), and juvenile black surfperch, Embiotica jacksoni (Embioticidae).

The sessile organisms live attached to hard substrata, inter alia vertical rock faces. These rock surfaces are uneven, and often bear small pits and cracks, which may offer protection for settling larvae since they are inaccessible to fish. Our aim was to measure the extent to which such refuges are used by recruits, and to separate the presence of active choice by settling larvae from subsequent mortality to yield observed patterns of recruitment.

There are a number of ways in which larvae may respond to the presence of such refuges, and in the absence of in situ observations of the behaviour of the larvae, inferences about such responses can be made only from the spatial distribution of juveniles, more specifically the proportion of juveniles that occur in refuges, relative to the number on more exposed surfaces. A number of models of larval behaviour can be erected that predict different spatial patterns:

1. **No searching** (Dropped-egg model.) Larvae encounter a substratum, but only test it for suitability, and do not search extensively over the substratum. The predicted pattern: Recruits are distributed in refuges and on exposed surfaces in proportion to the surface areas of substratum in the plane of the substratum surface. In this study, the ratio of cross-sectional surface area of refuges to exposed surfaces was 2:98.

2. **Searching, but no active choice** (Ping-pong ball model). Larvae encounter a substratum, and search over it, but settle at random on any surface that is suitable, i.e. no choice of microhabitats. The predicted pattern: Recruits are distributed in proportion to the total surface area of refuges, compared to exposed surfaces. In this case, the ratio is 8:92.

3. **Searching and active choice of microhabitat.** Larvae encounter the substratum, search over it, and then select microhabitats (refuges) for settlement. The predicted pattern: Recruits are found over it, and then select microhabitats (refuges) for settlement. The predicted pattern: Recruits are found disproportionately in refuges. In this case, the ratio exceeds 8:92.

**Methods**

The study site was characterised by north-east facing vertical rock faces beneath a canopy of Macro cystis pyrifera at Isthmus Reef, approximately 500 m from the Catalina Marine Science Center on Santa Catalina Island in southern California (33°27'N, 118°29'W).

Experimental substrata were 150 mm x 150 mm unglazed clay tiles, chosen for their similarity in colour and texture to natural rock surfaces in the area. They were mounted flush against vertical faces at a depth of about 10 m. Refuges from fish were provided on plate surfaces by drilling small pits, 5 mm in diameter and 5 mm deep, on the exposed face of each tile. Twenty randomly positioned pits were drilled on each tile. Surfaces of the panels are thus termed either “pits”, or “flats”.

Fish were excluded from half of the panels by placing small cages over each experimental panel. The cages were made from 1.5–2 mm diameter plastic-coated wire, with mesh sizes 65 mm x 60 mm. Previous observations suggested that fish avoided these meshes, and we have never observed any fish feeding through the meshes.

Panels were placed at three experimental “sites”, about 3–5 m from each other. The experiment was done twice, in November and December 1981. Both caged and uncaged panels were placed at each site. In November, each combination of treatment and site was replicated once, whilst two replicates were used in December. The experiment thus had three factors, caging, site, and time, and was analysed by analysis of variance.

Spatial patterns of recruits were examined by testing the observed patterns against the predictions made by the three models of larval behaviour by log-likelihood ratio goodness-of-fit test (Bishop et al. 1975).

**Results**

**“Settlement” – Distribution of Recruits in the Absence of Fish**

The distribution of juvenile Tubulipora on caged panels was consistent with the non-searching (dropped-egg) model, while that for Spirobranchus differed from the pattern predicted by this model. The distributions of both Spirobranchus and Tubulipora were in accord with models that do not invoke selection of microhabitats (Table 1).

Scrupocellaria and Celleporaria both showed patterns of recruitment on caged panels that differed from both of the first two models (Table 1), with disproportionately more recruits in the pits. This was especially so for Scrupocellaria, where 88% of recruits were found in the pits.

**Recruitment – Distribution of Recruits in the Presence of Fish**

Again, Tubulipora and Spirobranchus showed patterns of recruitment that were consistent with the null hypothesis of no selection of microhabitats (Table 1), but in this case, the