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Early development of subtidal macrofaunal assemblages: relationships to period and timing of colonization

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Abstract

Colonization and successional development of very diverse subtidal assemblages on rocky surfaces are not clearly understood. Artificial units of habitat (AUHs) made of nylon pot-scourers were used to test predictions from various models of succession. An experiment was designed in an attempt to unconfound the period of deployment (equals age of succession) from the time-period during which AUHs were deployed. AUHs were deployed in two sites, 100 m apart, for 1 month, starting at 0, 1, 2 and 3 months, for 2 months, starting 0 and 2 months and for 4 months from 0 month. Ninety-nine taxa were recorded in the AUHs. Successional change was not due to nett accumulation of taxa, nor simply to longer-term AUHs sampling successive different periods of time. Assemblages developing over the same period were different, but only a small amount of the variability was seasonal. Assemblages converged as period of deployment increased. There was less change from one to two months than from two to four months in the development of assemblages, but some of this was due to seasonal difference between the first and last two months. There were no differences between sites in any of the analyses of structure of assemblages. Few individual taxa showed consistent patterns of changing abundance with length of deployment. Different types of organisms showed markedly different patterns of arrival. The increase in number of species of gastropods was much smaller than the corresponding increase in number of taxa of polychaetes. Succession in these assemblages is complex and variable, but shows some repeated patterns. Fitting these to models of succession is only partially successful and new models are needed for very diverse assemblages.

Keywords: Artificial habitat; Colonization; Macrofauna; Subtidal; Succession

1. Introduction

Assemblages of many types of invertebrates are found in marine, shallow-water habitats, such as in sediments (Morrisey et al., 1992a; Warwick, 1988), amongst foliose algae (e.g. Dean and Connell, 1987; Edgar and Klumpp, 2003), in mussel-beds (Suchanek, 1985; Lohse, 1993) and kelp holdfasts (e.g. Moore, 1971, 1973; Smith, 1996). They are diverse, consisting of species from many Phyla. Despite being common throughout the coastal regions of the world and in many types of habitat, the processes structuring complex infaunal assemblages or those in complex patchy habitats are not yet well understood. These assemblages are, however, often extremely patchy at small spatial scales and they vary in structure over short time-scales

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(e.g. Morrisey et al., 1992a; Thrush et al., 1994). The consequence is that assemblages are changing in composition as a result of ecological processes of recruitment and in response to disturbances (Thrush and Dayton, 2002).

Some of the major models about processes leading to temporal changes in assemblages, i.e. succession, were contrasted in a review by Connell and Slatyer (1977). In principle, processes of colonization (i.e. the arrivals of species in a patch of new habitat) are from early-colonizing species, with certain features of life-history and having particular ecological influences after they arrived, to late-colonizing species. The latter have different trends of dispersal or life-history. Different processes of succession would occur according to the types of and interactions between "early" and "late" species in any particular habitat. Note that, in all discussions of succession, observations can only be made on species that stay in the habitat long enough to be observed. Thus, analysing successional change is the analysis of nett changes, i.e. arrivals minus departures (or colonization minus extinction).

This review has been expanded and updated to consider establishment of an assemblage after a disturbance that only partially removes the previous inhabitants (Platt and Connell, 2003). This type of disturbance is probably more common than disturbances that remove everything and can result in numerous types of change in surviving assemblages. As a result of that analysis, it is clear that "directional change" in assemblages, i.e. succession leading predictably from domination by "early" species to domination by "late" species is not the only possible turn of events.

Apart from the magnitude of response to any disturbance that triggers recolonization (Thrush and Dayton, 2002) and possibly succession, in sedimentary habitats, at least, there are important effects of the size of the area to be colonized (Platt and Connell, 2003) and therefore the distance from a source of colonists (e.g. Hall, 1994). As pointed out by Whitlatch et al. (1998), small patches of habitat are likely to be colonized by larval dispersal and by drifting of adults. Larger patches are more likely to be colonized only by larvae. Thus, larger patches will take longer to develop climactic assemblages. They will also probably be colonized earlier by different species, i.e. those with dispersive stages of life-history (Levin, 1984). There are numerous other influences, including for marine assemblages, dependence on which species happen to colonize first (Sutherland and Karlson, 1977; Dean and Hurd, 1980) and the indirect effects of consumers, which influence the outcome of interactions for space (Russ, 1980; Hixon and Brostoff, 1996). The processes leading to a recognizable structure (the types and relative abundances of species) in an assemblage are therefore complex and interactive.

Turfing and other mat-like habitats are widespread in inter- and subtidal habitats. They contain numerous invertebrates, in association with the habitats themselves or with the sediment they trap. They are colonized within a few months (Dean and Connell, 1987; Myers and Southgate, 1980; Kelaher, 2005). There have, however, been very few studies of patterns or processes of colonization of these habitats in relation to temporal succession or spatial variation.

One of the problems encountered in unravelling development of assemblages in complex coastal habitats is the great variability in time and space routinely encountered (e.g. Myers and Southgate, 1980; Morrisey et al., 1992a,b; Kelaher, 2005). Obviously, some of this is due to variations in supply-side processes — the timing and numbers of organisms available to recruit vary considerably from time to time and place to place (e.g. Underwood and Fairweather, 1989). At the same time, there are variations in space and time in the suitability or "acceptability" of habitat (Singer, 2000) to potential colonists. Thus, the history and, in particular, history of disturbances and previous development of assemblages in pieces of habitat can vary spatially and temporally (Sutherland, 1980; Sousa, 1979a,b). These interact to make it difficult to discern patterns by sampling and description of succession. Experiments are necessary (Connell and Slatyer, 1977).

Some of the studies of related assemblages (e.g. Dean and Connell, 1987; Kelaher, 2005) used defaunated patches of habitat, with uncertain artefactual consequences for the subsequent recolonization. Others, such as Rule and Smith (2005), in contrast, used pot-scourers to examine colonization by subtidal fauna over various spatial scales and concluded that small-scale variation (scales of metres) was uncommon, but variation at larger scales (10s of m to km) was widespread. This is inconsistent with the variability at small scales shown by Kelaher (2005), but his studies were intertidal and in a different climatic region of south-eastern Australia.

The processes of colonization and succession – if indeed there is actually a proper succession in such volatile assemblages – are not clearly understood. In fact, the patterns of successional change are not yet well-documented. In the present paper, experiments were done to determine patterns (and, eventually, to be able to understand the processes involved) in colonization of mobile fauna in complex habitats in subtidal areas. Artificial units of habitat (AUHs; namely, pot-scourers;