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Original article

Evaluating the importance of predation on subtidal benthic assemblages in sandy habitats around rocky reefs

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Abstract

It was proposed that predation could explain differences in the structure of the benthic macrofaunal assemblages in subtidal sandy sediments close to compared with those far from rocky reefs. This hypothesis was tested using experimental exclusion cages and partial cages at two sites at two distances at two different rocky reefs. Undisturbed uncaged assemblages of macrofauna close to the rocky reefs were generally different from those in the partial cages and full cages. However, caging artifacts could not be detected and there were no strong correlations between the macrofauna and the proportions of different grain size and organic content. The structure of the macrofaunal assemblages close to the rocky reefs was, nevertheless, different from those far from the reefs and the sediments were finer far from than close to the rocky reefs. The results indicated that factors other than predation or grain size caused the differences in the macrofauna. For the spatial and temporal scales used in this study, it was clear that, although predation maybe intense, on its own it cannot explain the differences in the structure of the assemblages close and far from rocky reefs. The importance of adequate replication on caging experiments is discussed and it is suggested that alternative ways need to be found to test predictions about the influence of predation on soft sediment benthic assemblages.

Keywords: Benthos; Predation; Caging experiment; Soft sediments; Rocky reef; Subtidal

1. Introduction

Natural and artificial subtidal rocky reefs provide habitats for diverse assemblages of marine organisms. Many studies have focussed on recruitment, productivity, and behaviour of assemblages of fish and benthic animals in these systems (Wenner et al., 1983; Bohnsack and Sutherland, 1985; Parrish, 1989).

There is general agreement that artificial or natural rocky reefs influence the structure of benthic macrofaunal assemblages inhabiting nearby soft-sediments (Davis et al., 1982; Ambrose and Anderson, 1990; Posey and Ambrose Jr., 1994; Barros et al., 2001). The above studies suggested that modifications of these assemblages might be caused by changes in the intensity of movement of water, direction of currents, rates of erosion or sedimentation, organic content of sediments, and in numbers or types of predators.

It is well known that rocky reefs attract fish (e.g., Bohnsack and Sutherland, 1985). Many reef-associated fish and crustaceans forage extensively over adjacent sandy substrata (Ogden and Buckman, 1973; Alongi, 1989; Frazer et al., 1991), implying that soft-sediment assemblages can subsidise populations of these fishes associated with rocky reefs (Lindquist et al., 1994). Nevertheless, few studies have tested whether reef-associated predators really do alter the adjacent biological environment by eating infauna.

Predation is recognised as an important process in ecological systems (e.g., Wilson, 1991). It involves transfer of energy between species, influencing the structure of assemblages. It can be affected by changes in habitat (e.g., Thrush, 1999) and has been suggested as a major factor affecting benthic populations in soft-sediments (Wenner et al., 1983). It has been argued that the effects of predation may be most drastic in physically controlled environments, because the prey organisms must give adaptative priority to the physical regime, rather than to refinement of biological interactions (Sanders,

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1968). Alternatively, it has been suggested that predation intensity is more important in benign than in harsh soft-sediment habitats (Peterson, 1991). Such debate is extensively discussed in ecological studies, particularly in intertidal rocky shores (e.g., Connell, 1972; Menge and Sutherland, 1976; Menge, 1978; Underwood and Denley, 1984). Nevertheless, there is no doubt that predation at environments subject to different levels of harshness with their different consequences on populations of preys is an important issue in ecology (e.g., Sih et al., 1985).

Field experiments involving manipulations of densities of predators are an important tool for studying the role of predation in natural assemblages (Englund and Olsson, 1996; Englund, 1997). Among the most common manipulations in marine ecology are caging experiments. They have been done in many different habitats, such as salt marshes (e.g., Kneib, 1988; Sarda et al., 1998), intertidal flats (e.g., Quammen, 1984; Raffaelli and Milne, 1987; Raffaelli et al., 1989; Fernandes et al., 1999; Richards et al., 1999; Thrush, 1999), seagrass beds (e.g., Fishman and Orth, 1996; Macia, 2000; Spitzer et al., 2000; Hindell et al., 2002), kelp beds (e.g., Kennelly, 1991; Sala, 1997), coastal lagoons (e.g., Irlandi and Mehlich, 1996; McArthur, 1998), mangroves (e.g., Schrijvers et al., 1998), coral reefs (e.g., Russ, 1987; Connell, 1997), artificial structures (e.g., Connell, 2001) and on subtidal mud-bottoms (e.g., Hines et al., 1990). There have been, however, few studies on subtidal sandy bottoms, possibly due to logistical difficulties involved in the construction and maintenance of the cages in such an exposed habitat. Furthermore, destruction of cages by wave-action, fishing gear and/or boat anchors is a major problem in such experiments (e.g., Arntz, 1977; Virnstein, 1978; Hulberg and Oliver, 1980; VanBlaricom, 1982; Posey and Ambrose Jr., 1994).

Caging often causes effects other than the exclusion of predators (e.g., reductions in water-flow and/or light, changes in sediment characteristics; Dayton and Oliver, 1980; Gray, 1981; Kennelly, 1983; Underwood and Denley, 1984; Dayton, 1994; Olafsson et al., 1994). These are known as caging artifacts and many studies have neglected such effects. The usual way that these effects have been examined is by including a partial cage treatment in experiments, where predators can enter cages, but part of the structure of the cage is present. Alternatively, Kennelly (1983, 1991) proposed a different approach to test for caging artefacts (also used by Russ, 1987).

Previous work in subtidal soft-sediments around Sydney, Australia, has shown that the structure of the macrofaunal benthic assemblages inhabiting sediments near (within 1 m) reefs were frequently more variable than those living away from (> 5 m) rocky reefs (Barros et al., 2001). This previous study also found differences in the spatial variability, diversity, and in the abundance of specific taxa. In the above experiment, it was observed that different animals (e.g., goatfish, flathead, stingrays, and crabs) disturbed the sediment to eat buried macrofauna, particularly close to rocky reefs. It was proposed that predation is an important process shaping the structure of the benthic macrofaunal assemblages in sandy bottoms close and far from rocky reefs. The hypotheses were: (H1) predators (fishes and large crustaceans) associated with rocky reefs forage over nearby soft sediments, influencing the structure of macrofaunal assemblages close to rocky reefs; (H2) alternatively, predation on soft bottoms far from rocky reefs is an important process that influences the structure of the macrofaunal assemblages inhabiting sediments far from rocky reefs (for example, by predators eating macrofauna during the night) and (H3) a combination of the above two predictions, predation is an important process close to and far from the reef, although it differs between these two habitats (e.g., different predators eating different prey in each habitat).

2. Material and methods

2.1. The study sites

The above hypotheses were tested adjacent to two shallow rocky reefs in Botany Bay, New South Wales, Australia. These rocky reefs, one natural (Yarra) and one artificial (Breakwall), were about 500 m apart. Two sites, approximately 20 m apart, were haphazardly established perpendicular to each reef in depths of 3.5 to 4.0 m at low tide. Along each site, two distances were selected, close to the reef (within 2 m from the reef) and far from the reef (about 10–13 m from the reef). The rationale for these distances was that previous studies indicated that the structure of these assemblages were different at these distances from rocky reef (Barros et al., 2001).

2.2. The experimental treatments

Three pilot studies were done to test if the material used to construct cages were resistant to waves, if the cages were efficient at excluding predators and for edge effects (Barros, 2002). Some types of cages did not adequately excluded predators, others were washed away by waves. Therefore, the following procedure was the most adequate in terms of excluding predators, resistance to wave-action, and logistics (i.e., could be constructed efficiently). These pilot studies also showed that the sample size and number of cores were appropriate to detect differences in the structure of the macrofauna.

At each distance at each site, six cages were constructed. Two of these cages were complete cages and four were partial cages, used to test for caging artifacts (two only with sides, allowing access through the roof, and two only with roof, hereafter called top, allowing access through the sides). Furthermore, there was the uncaged treatment (undisturbed sandy bottom). Each cage was made of plastic oyster mesh (17 mm aperture), which was 40 × 40 cm and 25 cm high. To attach these cages to the sandy bottom, iron star pickets 135 cm high were driven into the sand and each corner of each cage was attached to the pickets using plastic cable ties. To avoid gap forming between the cages and the bottom (previously