Diversity, recruitment and competition on island shores at south-polar localities compared with lower latitudes: encrusting community examples

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Abstract
Comparisons of temperate and tropical shores have yielded considerable debate as to whether the former really are less benign, diverse and structured by different ecological processes. Studies of comparable boulder communities have shown high within region variability. Equivalent polar assemblages, from island shores compared here, show much reduced within region variability and considerably reduced numbers of phyla and species encrusting boulders. The rate of colonisation (compared from settlement panel studies) was an order of magnitude higher in warmer water, but did vary with isolation (near vs offshore islands). Comparison of the most ubiquitous taxon, the bryozoans, between polar and non polar sites shows a decrease in the proportion of inter-specific competition, indeterminate competitor (species) pairs and incidence of tied outcomes in competition. These three parameters all increased with depth at the localities studied, whilst no obvious influence of isolation was found.

Introduction
In the last few decades, the investigation of latitudinal trends into south-polar waters has changed from being largely theoretical to practical. Hypothesised lower growth rates, greater longevity, reduced basal metabolic rates and lowered tempo of reproduction, with respect to warm water (non-polar) ecological equivalents, have all been found to be generally true (Pearse et al., 1991). Certain exceptions have been found. Growth rates of a couple of south-polar sponges and ascidians are as fast or faster than typical low-latitude representatives of the same taxa (Dayton et al., 1974; Rauschert, 1991). Thorson’s rule (Mileikovsky, 1971), concerning the polar predominance of a suite of reproductive and larval characters, has proved true for only few taxa (Stanwell-Smith et al., 1999 and refs therein). The duration of phytoplankton abundance is greater than previously believed, thus explaining the findings of near year round activity of polar suspension feeders (Barnes & Clarke, 1995). Antarctic fauna have long been considered very stenothermal and tests on some organisms support this (e.g. Peck, 1989) but others experience and tolerate regular fluctuations of both temperature and salinity (Barnes et al., 1996). There has been considerable debate as to the reason for a general latitudinal cline in species diversity, most recently whether it is explained by area (Rosenweig, 1995; Rhode, 1997). What appears certain is that the pattern in the sea differs in the northern and southern hemispheres as many Antarctic localities are highly species rich (Clarke, 1992; Brey et al., 1994). Of the sessile encrusting fauna, some can be relatively species rich in south-polar waters (e.g. polychaetes and bryozoans) whilst others are much more speciesose in warmer waters (e.g. cnidarians, barnacles and bivalves). A preliminary study by Barnes & Arnold (1999) of encrusting boulder fauna on three polar island shores, suggested that south-polar assemblage diversity, growth, mortality and tempo of reproduction may increase with latitude – all the converse of typical patterns.

Boulder communities have proved an important testing ground for many ecological ideas, particularly those centred on the influences of disturbance. Boulders are characterised by being discrete (unlike sediment samples), portable (unlike solid rock surfaces) and with a relative lack of variability. Of course, as with any comparison of different sites, no two boulder fields are identical, but problems of variance in spatial heterogeneity can be minimised by selection of substrata which are similar in size, wear (round-
ness) and smoothness. Of key significance to the ecologist is that (within a region) disturbance is the single most important factor determining faunal assemblage (Sousa, 1979; McGuiness, 1987). Typically, disturbances create space by lethal or sublethal destruction of colonists, thus high frequencies reduce diversity. At intermediate levels, however, disturbance may prevent superior competitors from monopolising resources (Connell, 1978; Huston, 1979).

Comparisons of temperate and tropical shores have yielded considerable debate as to whether the former really are less benign, diverse and structured by different ecological processes (Pianka, 1966; Moore, 1972; Menge & Lubchenco, 1981; McGuiness, 1990). The findings of high levels of variability within regions, and differing results dependent on spatial scale examined, suggest that, overall, we do not have the data to conclude that there are significant differences. The wide geographical range of boulder community and artificial simulation studies have, however, rarely included polar regions until recently (Barnes et al., 1996; Barnes & Clarke, 1998; Barnes & Arnold, 1999). The present study, using boulder substrata, conveys advantages in comparing a similar habitat, over similar areas, using similar sampling design and over a number of sites.

There have been few studies comparing fouling/encrusting taxa across latitudinal or isolation gradients with similar sampling methodology and more than one site at each latitude. Schoener et al. (1978) and Barnes (1996) found that colonisation of artificial panels was much faster at low latitudes, at least in the early stages of community development. In addition, species diversity was much higher at warm water sites, although exceptions have been found to both these trends – probably due to local conditions (Schoener & Schoener, 1981). Long & Rucker (1970) and Hughes & Jackson (1992) compared near and offshore sites, and Holmes et al. (1997) compared two sites at each of two latitudes. The present study sought to examine how phyletic richness, species richness and the bryozoan (the most abundant taxon) species richness at Antarctic and Subantarctic localities compared with other island study sites around the world, with a consideration of isolation and depth. In addition, this study investigated whether rates of colonisation vary significantly: (1) between broad latitudinal regions, and (2) with isolation by comparing the data from four polar, nine temperate and eight tropical studies. Finally, this study aimed at answering a number of questions concerning competition: are there relationships between latitude, depth or isolation and the incidence of inter- vs intraspecific competition of the outcomes of interspecific competition? If there are relationships, are they simple and do they have an obvious biological interpretation? Quinn (1982) considered that the differences he observed between competition in his temperate study and those in tropical studies were due to differing taxa and more specifically that a major taxon, the bryozoans, added intransitivity to assemblage interactions. Here, interactions were studied and extracted from the literature involving a single taxon, the bryozoans, common to all studies.

Materials and methods

Study and literature sites

Intertidal and shallow subtidal zone encrusting species in boulder communities were compared between sites on islands. Particular reference is made to bryozoans as the one taxon present (and abundant) at all locations and studies. Boulder faunas examined during this study included southern hemisphere localities of polar, subpolar, temperate and tropical latitudes (Table 1). Various components of boulder fauna competition were investigated and calculated by drawing up or interpreting existing contact matrices. A contact matrix is a table in which various types of pair-wise interactions between different competitor identities can be displayed. Such a matrix (Table 2) can represent a subset or all competitors and is typically organised such that for each competitor pairing the number of meetings, wins, losses and ties are apparent. A matrix of meetings or interactions can thus be established for the suite of competitors at each site. From each matrix (site), the proportions of inter- and intra-specific encounters, the proportions of tied outcomes, indeterminate species pairs and competitive loops in inter-specific encounters were calculated. Standoffs, redirected growth on meeting or overgrowth by both competitors, were recorded as tied outcomes (Russ, 1982; McKinney, 1992). Overall indeterminate species pairs refers to encounters by competitors such that neither competitor won all encounters, so even if each encounter produced a decided outcome one species won some encounters, the second species, others. At three locations, the above data were also recorded for a variety of depths; 0 and 6 m (South Georgia), 0, 6, 12 and 25 m (Adelaide Is., Antarctica) and 0, 6,