REVIEW

Community structure and organization of tidepools

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ABSTRACT: Although tidepools are conspicuous components of rocky intertidal shores, their biotic communities have not been studied as extensively as those on emergent substrata. We examine processes regulating the structure of tidepool communities for comparison with emergent substrata. The physical environment of tidepools is highly regulated by the tidal cycle, although fluctuations in physical factors are smaller in tidepools, and the organisms remain submerged for the entire tidal cycle. As a result, the upper limits of the distribution of organisms are extended in tidepools and some species either tend to aggregate in pools or avoid them. The vertical zonation of organisms is not as pronounced in tidepools as on emergent substrata. Herbivory has been shown to influence the distribution and abundance of algal species in tidepools, but the effect of predation in regulating community structure has been less well documented. The importance of interspecific competition has been consistently shown in tidepools, particularly among algal species, which usually are the dominant space occupiers. Although the introduction of most species into tidepools depends upon recruitment from the surrounding water, the effects of variation in the supply of new individuals has not been examined. Aspects of the physical regime such as habitat complexity and wave exposure affect the community structure of tidepools, as they do communities on emergent substrata. However, the specific characteristics of tidepools such as pool depth, volume, orientation, shading and flushing rate make individual pools unique, resulting in large spatial variability in tidepool community structure. For this reason, replication in tidepool studies should be carefully selected. Because of their variable characteristics, well-defined boundaries and tidepools of manageable size can serve as experimental mesocosms to test general ecological theories about community organization.

INTRODUCTION

The goal of community ecology is to describe patterns of distribution and abundance of species' assemblages and to understand the processes that give rise to these patterns (Begon et al. 1986, Diamond & Case 1986). These processes include biological interactions, such as herbivory, predation and competition, as well as the effect of the physical environment. Community ecologists must understand how and when these regulatory mechanisms operate in community organization, if they are to develop ecological models of broad scope and validity.

A plethora of literature exists on the establishment and organization of communities that inhabit the emergent substrate of rocky intertidal shores. A number of studies have described the general structure of rocky intertidal communities on temperate shores throughout the world (e.g. Pyefinch 1943, Stephenson & Stephenson 1950, 1952, 1954a, b, Underwood 1980, Moore & Seed 1986, Brattström 1990, Janke 1990). Other studies have reviewed processes of community organization on rocky intertidal shores (e.g. Connell 1972) and provided models of community regulation (e.g. Lubchenco & Gaines 1981, Connell 1983, Connell & Sousa 1983, Hawkins & Hartnoll 1983, Dayton 1984, Sousa 1984a, Underwood & Denley 1984, Vadas 1985, Menge & Farrell 1989).

The biotic communities of tidepools are less well studied than those of the emergent substrata of rocky intertidal environments. The literature on tidepool communities has not been reviewed to date and is scattered among several fields such as rocky intertidal ecology, fish biology and natural history. It has even

been suggested that pools do not 'represent an inter-tidal habitat' since 'organisms in pools are not emersed during low tide' (Underwood 1981). Nonetheless, conditions in tidepools, as on emergent substrata, are highly regulated by the tidal cycle. The degree of fluctuations in physical conditions of tidepools will vary greatly with intertidal height, with lower pools being less variable than higher pools. However, the degree of fluctuation is less than that of the emergent substrata and tidepools are potentially important as refuges from stressful environmental conditions.

This review summarizes tidepool community structure and compares the processes that regulate structure between tidepools and emergent substrata. We identify deficiencies in our understanding of community organization and suggest potential uses of these habitats to evaluate general ecological theories. Because of the scarcity of information on some aspects of community organization in marine tidepools, we also have included pertinent studies on freshwater rockpools. Since both habitats represent environments with some similar conditions (e.g. isolated habitats with well-defined boundaries), the regulating factors of community organization may operate in a similar fashion. For the purposes of this review, tidepools harbour marine communities and are located on rocky intertidal shores. They receive input from the surrounding seawater varying from regular submergence (low to high tidepools) to occasional spray during storms (splash pools). In contrast, rockpools harbour freshwater communities and are located higher on the shore between the rocky intertidal and terrestrial habitats.

TIDEPOOLS

Physical environment

The physical environment of tidepools does not fluctuate as much as that of emergent substrata, and the inhabitants of pools remain submerged for the entire tidal cycle; however, the fluctuations are larger than would be encountered under constant submergence in the subtidal zone. Temperature can vary daily by up to 15 °C, depending upon the height of the pool along the intertidal gradient (and, therefore, the extent of isolation from the tide), wave exposure, the degree of shading and the volume of the pool (Brooker Klugh 1924, Stephenson et al. 1934, Pyefinch 1943, McGregor 1965, Green 1971, Daniel & Boyden 1975, Goss-Custard et al. 1979, Morris & Taylor 1983, Huggett & Griffiths 1986). Daily changes in temperature can often result in thermal stratification of the water column of splash pools (McGregor 1965). Fluctuations in salinity depend upon the height of the pool on the shore (Pyefinch

1943) and may range between 5 and 25 practical salinity units (psu) (Lami 1931, Pyefinch 1943, Green 1971, Morris & Taylor 1983). Brooker Klugh (1924) and Daniel & Boyden (1975) found little variability in salinity over a period of at least 1 tidal cycle; however, Brooker Klugh (1924) measured salinity only in 2 tidepools and Daniel & Boyden (1975) monitored salinity for only 9 h after tidal input. Salinity stratification will arise seasonally because of freezing in the winter (Naylor & Slinn 1958, Ganning 1971), evaporation in the summer and rainfall (Morris & Taylor 1983). Salinity stratification also may occur due to runoff into the pools (Green 1971). Daily fluctuations in oxygen saturation, alkalinity and pH have been recorded, which are due to biological processes in tidepools (Pyefinch 1943, McGregor 1965, Ganning 1971, Green 1971, Daniel & Boyden 1975, Morris & Taylor 1983). Huggett & Griffiths (1986) recorded higher oxygen values in the daytime (when photosynthesis is occurring) and lower values at night. Daniel & Boyden (1975) observed vertical oxygen stratification in the water column in the daytime but no stratification at night. Daily fluctuations in pO_2 and pCO_2 can vary with season (Morris & Taylor 1983), height of the pool along the intertidal gradient (Daniel & Boyden 1975) or pool depth (Goss-Custard et al. 1979). The amplitude of daily fluctuations of temperature, salinity and pH also varies seasonally (Ganning 1971).

The physical environment of the tidepool fluctuates vertically, horizontally, diurnally and seasonally, although not as much as the adjacent emergent rock surfaces. The fluctuations, in turn, will vary with the volume, surface area and depth of the pool, as well as its height on the shore, degree of shading, drainage pattern (which depends upon the aspect) and exposure to waves and splash. It is virtually impossible for 2 natural tidepools to be similar in all these characteristics: individual tidepools are unique in their physical regime.

Community structure

Studies on species assemblages in tidepools have been mostly descriptive, and many have examined only 1 or 2 pools on a shore or recorded only presence or absence of the flora and fauna (e.g. Brooker Klugh 1924, Pyefinch 1943, Naylor & Slinn 1958, Ganning & Wulff 1969, Ganning 1971, Aleem 1973, Femino & Mathieson 1980, Preston & Moore 1988, Brattström 1990). The types of organisms recorded have varied from marine diatoms (Metaxas & Lewis 1992) to vascular plants and bryophytes (Haeggström & Skytén 1987), and from invertebrates (Ganning 1971) to fish (Green 1971).

The biological assemblages that inhabit tidepools are generally similar to those described for emergent substrata. Differences between the 2 types of habitats may arise because of smaller fluctuations in physical conditions and/or more intense biological interactions in the pools. Several taxa are more abundant in pools than on emergent substrata. These include algae [e.g. the genera *Ceramium*, *Spongomorpha*, *Corallina* and *Rhizoclonium* in Maine, USA (Johnson & Skutch 1928), *Prionitis* in Washington, USA (Dethier 1982) and *Fucus distichus* in Nova Scotia, Canada (Chapman & Johnson 1990)] and gastropods [e.g. the genus *Cellana* in New South Wales, Australia (Underwood 1976) and *Littorina littorea* in Massachusetts, USA (Lubchenco 1982)]. Other species are absent or occur in lower densities in pools than on the emergent rock [e.g. some fucoids such as *F. vesiculosus* and *Ascophyllum nodosum* (Lubchenco 1982) and barnacles in New England, USA (Singletary & Shadlou 1983)]. The physically imposed upper limits of the distribution of some organisms are extended in tidepools compared to emergent substrata. For example, macroalgae such as fucoids, *Scytosiphon*, *Spongomorpha* and *Ulva* occur at higher intertidal levels in tidepools than on the emergent rock surfaces, on the northeast coast of North America (Johnson & Skutch 1928, Femino & Mathieson 1980, Chapman & Johnson 1990). Similar observations have been made for mussels, chitons, limpets and sea urchins in tidepools in British Columbia, Canada (Green 1971) and for the surfgrass *Phyllospadix scouleri* in Washington (Dethier 1984). Tidepools also provide an extra habitat dimension for their occupants, the water column. Phytoplankton, zooplankton and fish can be encountered in pools at all times, as opposed to only at high tide for emergent substrata. In particular, pools may provide refuge for fish of varying sizes (Thompson & Lehner 1976, Moring 1990).

A number of studies have documented the zonation of tidepool biota along the intertidal gradient. Droop (1953) classified 9 types of pools in Finland, based on their position along the intertidal gradient: intertidal seawater pools, permanent rockpools in the normal splash zone, stagnant brackish pools, seaweed pools, ephemeral rain pools, permanent rain pools, moss pools, rock sphagneta and marsh. He examined the phytoplankton communities of these pools and concluded that the lowest abundances of flagellated and nonmotile, planktonic microalgae were in the intertidal and splash pools. In British Columbia, Metaxas & Lewis (1992) found that centric diatom abundance decreased in pools higher up on the shore while pennate diatoms tended to increase.

Macroalgae in tidepools also show zonation along the intertidal gradient, with some green algae (e.g. *Enteromorpha*, *Cladophora* and *Chaetomorpha*) usu-ally dominating higher on the shore while other green algae (e.g. *Spongomorpha*), brown algae (*Fucus*, *Laminaria* and *Scytosiphon*) and corallines (*Lithothamnion* and *Corallina*) are most abundant lower on the shore (Fraser 1936, Green 1971, Daniel & Boyden 1975, Goss-Custard et al. 1979, Femino & Mathieson 1980, Dethier 1982, 1984, Sze 1982, Wolfe & Harlin 1988a, Kooistra et al. 1989). Gustavsson (1972) used macroalgal zonation to classify tidepools in the littoral fringe and splash zone of the Swedish coast. With increasing distance from the water line, the pools were dominated by *Fucus*, *Chondrus*, *Enteromorpha* and cyanobacteria, respectively.

The vertical zonation of macroalgae within tidepools was examined in detail by Kooistra et al. (1989) in Brittany, France. Using multivariate statistics, they found that macroalgal samples from similar depths in pools grouped together, and that they could allocate algal species to deeper or shallower parts of tidepools in the lower or higher regions of the shore (e.g. *Phymatolithon polymorphum* in the deeper parts of low- and mid-intertidal zone pools, *Cladophora rupestris* only in the deeper parts of mid pools and canopy-forming species such as *Laminaria* just below the rims of low pools). Kooistra et al. (1989) also observed clear borders between particular species (e.g. between *Corallina elongata* and *P. polymorphum*), although the depth of the borders varied between pools.

Many species of benthic invertebrates and fish also show zonation along the intertidal gradient. The periwinkle *Littorina rudis* is mainly found in high pools whereas *L. littorea*, whelks, mussels, sea urchins and limpets are found in low pools (Fraser 1936, Ganning 1971, Daniel & Boyden 1975, Goss-Custard et al. 1979, Femino & Mathieson 1980). Sze (1982) found that the abundance of *L. littorea* increased from low to high pools. However, this discrepancy is probably due to the lower intertidal height of the pools examined in his study compared to others. Huggett & Griffiths (1986) found that pools lower on the shore on Cape Peninsula, South Africa, were dominated by sponges and bivalves while those higher on the shore were dominated by algae and snails. Zonation has also been observed for various meiofaunal groups: flatworms, rotifers, oligochaetes, cladocerans, cyclopoid copepods, ostracods, barnacles, amphipods, isopods and chironomid larvae (Fraser 1936, Ganning 1971, Dethier 1980). Fish zonation in tidepools has been documented extensively but the results are not quantitative (Green 1971, Nakamura 1976, Gibson 1982, Bennett & Griffiths 1984, Mgaya 1992). Bennett & Griffiths (1984) detected a decrease in the number of fish species with increasing height above low water which they attributed to intolerance to extreme physical conditions.

Biomass and number of algal and invertebrate species decrease in tidepools with increasing height above low water (Femino & Mathieson 1980, Huggett & Griffiths 1986, Wolfe & Harlin 1988b, Kooistra et al. 1989). Gustavsson (1972) and Lawrence & McClintock (1987) reached similar conclusions, although the former study only examined high tidepools and splash pools and the latter study only examined 3 mid-zone pools.

Factors affecting community organization

Herbivory

Numerous experimental manipulations have shown that grazers (mainly littorinids and limpets) limit the distribution and abundance of marine algae on the emergent substrata of rocky intertidal shores (e.g. Dayton 1971, Lubchenco & Menge 1978, Raffaelli 1979, Underwood 1980, Underwood & Jernakoff 1981, 1984, Jernakoff 1983, Lubchenco 1983, Petraitis 1983, 1987, Hill & Hawkins 1991, but see Chapman 1989). Herbivory has similar effects in tidepools. Paine & Vadas (1969) showed that removal of sea urchins resulted in increased macroalgal abundance and diversity in shallow tidepools in Washington. In Massachusetts, Lubchenco (1978) observed the effect of herbivory in 2 mid-zone pools; in one, littorinid snails were absent and the dominant alga was *Enteromorpha* sp., and in the other, snails were present and the dominant alga was *Chondrus crispus*. Lubchenco (1978) added snails to the first pool and observed a decrease in the cover of the dominant *Enteromorpha* sp. On the other hand, when she removed snails from the second pool she observed a decrease in cover of the dominant *Chondrus crispus* (Lubchenco 1978). The cover of *Fucus vesiculosis* and ephemerals increased in a number of tidepools in the mid-intertidal zone of a protected and a semi-exposed rocky shore in Maine and Massachussetts, when littorinids were excluded (Lubchenco 1982). Negative correlations have also been detected between littorinid abundance and cover of green and red macroalgae but not fucoids, and between littorinid abundance and macroalgal species diversity, in tidepools in Rhode Island, USA (Wolfe & Harlin 1988a). In tidepools located near the littoral fringe of an exposed rocky shore in Nova Scotia, Chapman (1990) and Chapman & Johnson (1990) found that grazers (mostly littorinids) have a negative effect on the abundance of *Fucus* spp. sporelings, juveniles of *F. distichus*, *F. spiralis* and *F. vesiculosus* and adults of *F. vesiculosus* and *F. evanescens* (but not *F. distichus*), a positive effect on the abundance of ephemeral algae and no effect on the cover of the red algal crust *Hilden-*

brandia rubra. Dethier (1982) suggested that *Littorina* spp. have a negative effect on the green alga *Collinsiella tuberculata*, on diatoms and possibly on the red alga *Rhodomela larix* but have no effect on articulated corallines or the green alga *Cladophora* sp., in tidepools in Washington. In New South Wales, Underwood & Jernakoff (1984) showed that cover of nonencrusting algae increased in the absence of grazers (mostly limpets) and Arrontes & Underwood (1991) showed that the starfish *Patiriella exigua* reduced the cover of *Ulva* spp., in shallow, artificial tidepools.

In a study examining the effects of grazing on bacteria and phytoplankton, Stenton-Dozey & Brown (1992) found that suspended food particles ranging from 1 to 15 µm (presumably bacteria and microalgae) decreased over a tidal cycle in a tidepool in South Africa. They attributed this decrease in particle density in the field to filter feeding by the clam *Venerupis corrugatus* (Stenton-Dozey & Brown 1992). In freshwater rockpools in the Baltic Islands in Finland, Ranta et al. (1987) showed that the size structure of phytoplankton communities was altered depending upon the initial density of the cladoceran *Daphnia* spp. in the pools. The authors, however, only examined 3 rockpools, each located on a different island, and their results varied between rockpools (Ranta et al. 1987).

Predation

On the emergent substrata of rocky shores, predators such as starfish and whelks limit the abundance of barnacles and mussels (Paine 1966, 1984, Connell 1970, Dayton 1971, Menge 1976, Janke 1990) and regulate the overall diversity of species (Paine 1966, 1984, Lubchenco & Menge 1978). Fewer studies have demonstrated the importance of predation in regulating tidepool communities. Fairweather (1987) found that whelks introduced into shallow (1 to 4 cm deep) tidepools in New South Wales reduced the abundance of barnacles, tubeworms and limpets. Lubchenco (1978) suggested that littorinid populations in tidepools in Massachusetts may be controlled by predation by the green crab *Carcinus maenas*. In Washington, Dethier (1980) showed that fish, and to a lesser extent sea anemones, can reduce the abundance of the harpacticoid copepod *Tigriopus californicus* in tidepools in the high zone of rocky shores. She suggested that these copepods are restricted in their distribution to high pools because physical conditions there limit the survival of their predators (Dethier 1980). In Island Bay, New Zealand, Coull & Wells (1983) observed high meiofaunal mortality due to fish predation in tidepools in the absence of *Corallina officinalis* which acts as a refuge.

In a detailed study of the effect of predation on rock-pool biota in the Baltic Islands, Ranta et al. (1987) observed a shift in zooplankton species dominance and size structure, and a decrease in species richness and evenness, after the introduction of predatory fish to the pools. Ranta & Nuutinen (1984) showed that different fish species in these rockpools had different food preferences and thus had different impacts on the resident community. In another study of freshwater rockpools in Sweden, Pajunen & Salmi (1991) showed that chironomid larvae increased in numbers in the absence of predatory corixids.

Competition

Competition for space on the emergent substrata of rocky shores has been shown to be an important determinant of zonation and abundance of the dominant space occupiers such as barnacles, mussels and macroalgae, resulting in competitive hierarchies which vary with intertidal height (e.g. Connell 1961, Dayton 1971, Menge 1976, Grant 1977, Lubchenco & Menge 1978, Schonbeck & Norton 1980, Hawkins & Hartnoll 1985, but see Lively & Raimondi 1987, McCook & Chapman 1991). Interspecific competition also may be important in regulating tidepool community structure, but the evidence is sparse. Lubchenco (1982) and Chapman (1990) have documented decreases in fucoid canopy cover due to competition with ephemeral algae and *Chondrus crispus* in tidepools in Massachusetts and Nova Scotia, respectively. Chapman & Johnson (1990) suggested that the absence of a canopy of *Ascophyllum nodosum* can enhance recruitment by *Fucus spiralis* in tidepools in Nova Scotia. Cecchi & Cinelli (1992) found that canopy removal in *Cystoseira* spp.-dominated tidepools on the west coast of Italy had no effect on either encrusting or articulated corallines (e.g. *Corallina* spp.) or on coarsely branched algae (e.g. *Gelidium pulchellum*), but enhanced the abundance of delicately branched (e.g. *Ceramium, Cladophora* spp.) and thickly branched (e.g. *Padina pavonica*) algal species. Competitive dominance, as indicated by overgrowth, has been shown for the alga *Halichondria panicea* and for thick coralline crusts in tidepools in Brittany (Kooistra et al. 1989). Arrontes & Underwood (1991) reported a negative correlation between the abundance of the starfish *Patiriella exigua* and the limpet *Cellana tramoserica* in natural, small tidepools in New South Wales, although they did not detect an effect of competition in experimental manipulations of the densities of competitors.

In rockpools, Ranta (1982) and Hanski & Ranta (1983) showed that competitive hierarchies involving 3 species of *Daphnia* can lead to competitive exclusion.

This system was successfully modelled by Bengtsson (1989).

Recruitment

A number of studies have shown that settlement and recruitment are important factors in determining adult density of sessile invertebrates and algae on the emergent substrata of rocky shores (e.g. Connell 1985, Gaines & Roughgarden 1985, Roughgarden et al. 1985, Reed et al. 1988, Menge 1991, Minchinton & Scheibling 1991). Recruitment is potentially an important factor in the organization of tidepool communities, although no studies have addressed this directly. The variability in the response of the tidepool community to grazer removal (Paine & Vadas 1969) and in recovery from disturbance (Dethier 1984) have been partially attributed to differences in seasonal availability and 'vagaries of recruitment' of algal spores and invertebrate larvae from the surrounding sea-water. Singletary & Shadlou (1983) concluded that although barnacles settle in pools in Rhode Island, heavy post-settlement mortality prevents their establishment. Chapman & Johnson (1990) suggested that differential recruitment success in high tidepools can lead to competitive displacement between *Fucus evanescens* and *F. vesiculosus*.

Physical factors

On emergent substrata, the upper limits of species distributions are mostly determined by tolerance to long periods of desiccation (Lewis 1954, Connell 1961, Paine 1974, Schonbeck & Norton 1978, Denley & Underwood 1979) or freezing (Wethey 1985, Dudgeon et al. 1989). Similarly, the abundance of tidepool algae has been correlated with pool elevation (which determines the length of emergence and extent of temperature fluctuations), topography and shading by surrounding rocks (Johnson & Skutch 1928). The number of species present is also correlated with tidepool depth and volume. Several studies have shown that deeper pools may support more plant and invertebrate species (Droop 1953, Pajunen 1977, Ranta 1982, Fairweather & Underwood 1991). Other studies have shown that fish biomass, species number and abundance may show significant correlations with pool area, depth or volume (Marsh et al. 1978, Bennett & Griffiths 1984, Mgaya 1992, but see Richkus 1978).

A number of studies have shown that topographic heterogeneity of emergent substrata can provide refuge from herbivory (Lubchenco 1983, Menge et al. 1985, but see Jernakoff 1985), predation (McGuinness

& Underwood 1986) and desiccation (Menge et al. 1985, Fairweather 1988, Gosselin & Bourget 1989). In contrast, Lubchenco (1982) and Chapman (1990) found that substrate heterogeneity is apparently unimportant in the development of a fucoid canopy in tidepools. Increased biogenic structure, due to the presence of coralline algae (presumably a refuge from predators), has been shown to increase abundance of harpacticoid copepods, but not amphipods or polychaetes, in tidepools (Coull & Wells 1983).

As on emergent substrata (Menge 1976, 1978, 1983, Lubchenco & Menge 1978, Underwood & Jernakoff 1981), algal cover and the abundance of littorinids and fish in tidepools are correlated with wave exposure. Sze (1982) showed that some algae such as *Enteromorpha*, *Spongomorpha* and *Scytosiphon* are more abundant in tidepools on exposed shores where littorinids are absent, whereas fucoids are more abundant in pools on protected shores. Dethier (1984) also found that the cover of the dominant algal species varied between pools of different wave exposures. For example, the green alga *Collinsiella tuberculata* and the red alga *Rhodomela larix* were found in pools higher on the shore in more exposed habitats (Dethier 1982). Some of the variability in macroalgal species composition observed by Wolfe & Harlin (1988a, b) among pools in Rhode Island can also be attributed to differences in wave exposure. Grossman (1982) found that the abundance of fish in tidepools decreases with increased wave action, possibly because few species can adapt to higher turbulence in exposed pools (Gibson 1982). Green (1971) and Bennett & Griffiths (1984) also found that the vertical distribution of cottid fish was related to the degree of wave exposure in tidepools, with fewer fish found in lower pools on more exposed shores. Some species, however, showed increased abundance at higher exposure levels.

Physical disturbance

On emergent substrata, physical disturbance can greatly affect species composition and richness, depending upon the magnitude and frequency of the disturbance (Sousa 1979a, b, 1984b, Farrell 1989, but see McGuinness 1987a, b). However, there is little information on the effect of disturbance in organizing the communities of tidepools. In tidepools in Washington, Dethier (1984) used an operational definition of disturbance as the destruction of biomass over a period of less than 6 mo which she subjectively categorized as severe, moderate or minimal (affecting most, some or 1 or 2 species of a pool, respectively). Freezing and heat stress were types of physical disturbances for the surfgrass *Phyllospadix scouleri*; bashing by logs and rocks were types of disturbance for mussels, anemones and *Cladophora* spp. More disturbances were recorded in low than high zone pools and the frequency of disturbance was the same in wave-exposed as in more protected sites. The rate of recovery from disturbance varied with species and depended upon the magnitude of the disturbance. In the Aland archipelago in Finland, Ostman & Rönnberg (1991) showed that physical disturbance by ferryboat wash induced an increase in *Enteromorpha intestinalis* cover in tidepools, although the magnitude of the effect varied among pools and among months. Changes in fish abundance have been associated with changes in the topography of tidepools through the movement of boulders by waves (Richkus 1978). Thompson & Lehner (1976) found that short-term disturbances, such as winterkills due to severe drops in temperature, changed the species composition of fish communities in 2 tidepools in the Gulf of California.

Variability in tidepools

The ubiquitous zonation of organisms along the intertidal gradient is perhaps the most striking characteristic of communities of the emergent substrata of rocky intertidal shores (Stephenson & Stephenson 1950, 1952, 1954a, b, Dayton 1971, Lubchenco & Menge 1978, Underwood 1981, Janke 1990). In tidepools, however, the relationship between the distribution of organisms and their height on the shore is less clear. Marked spatial variability in species abundance has been recorded among pools that are at similar heights and close to each other on the shore. For example, on Cape Peninsula, Stephenson et al. (1934) studied 3 pools at the same height on the shore and within 150 m of each other. One was characterized by large plant abundance, another by large animal abundance and the third by intermediate abundances of both plants and animals. Similarly, Pyefinch (1943) found considerable variability in species composition between paired pools at the same height, in both the mid and the high zone, in North Wales, UK. Dethier (1982) measured 95 % confidence intervals nearly equal to the mean percentage cover of the green alga *Collinsiella tuberculata* and the red alga *Rhodomela larix* in pools at the same intertidal height. Lawrence & McClintock (1987) found that macrofloral and macrofaunal species abundance on the island of Kerguelen, in the southern Indian Ocean, varied markedly between 3 pools of similar size, intertidal height (within a maximum distance of 50 cm) and wave exposure. Wolfe & Harlin (1988a, b) detected differences of up to 60 % in average percentage cover of dominant

algal groups and up to 30% in species diversity between pools of similar heights, volumes and exposures. Arrontes & Underwood (1991) detected statistically significant pool effects on algal abundance, demonstrating large among-pool compared to within-pool variability. Wilson et al. (1992) attributed the variability in species composition among 15 tidepools in New Zealand within a maximum vertical distance of 25 cm to random processes. Green (1971) found that the vertical zonation of cottid fish varied horizontally along the shore. Beckley (1985) recorded variability in fish abundance in 3 pools in East Cape, South Africa, in the lower balanoid zone within 100 m of each other. An apparent zonation in fish abundance in tidepools of different intertidal zones in British Columbia was not detected statistically by Mgaya (1992), because of high interpool variability within zones. Pajunen (1990) recorded variation in corixid abundance of up to 100% of the mean in freshwater rockpools in the Tvärminne area, Finland, and attributed variability in species dominance among rockpools to differences in pool size.

Some studies have also shown considerable variability among tidepools at the same height in response to experimental manipulation. For example, Paine & Vadas (1969) showed that sea urchin removal resulted in initial differences in species composition between tidepools in the low zone in Washington, although these differences gradually diminished within 2 yr. In contrast, Dethier (1984) found that species compositions in tidepools from which the dominant species, the surfgrass *Phyllospadix scouleri*, was removed were initially similar but became largely variable after 2 to 4 yr.

It has been argued that differences in wave exposure can result in variability among tidepool communities at the same intertidal height. Sze (1980) characterized the macroalgal communities in tidepools in the high intertidal zone, along a gradient of wave exposures in Maine. He found that at the least exposed site, pools were dominated either by cyanobacteria, *Hildenbrandia rubra* or *Enteromorpha intestinalis*, whereas there was no distinct pattern of dominance at the most exposed site (unless dominated exclusively by cyanobacteria). Bennett & Griffiths (1984) observed differences in fish zonation between sites on different South African coasts which they attributed partly to differences in wave exposure.

The structure of tidepool communities may exhibit large temporal variability, mostly related to season. Microalgal abundance varies seasonally with a maximum in spring and minimum in summer (Aleem 1950, Dethier 1982). Macroalgae in tidepools also vary seasonally (Underwood & Jernakoff 1984) but this variability may be more species-specific than in the microalgae. Femino & Mathieson (1980) found *Ulva*

lactuca in tidepools throughout the year but *Spongomorpha* spp. were only present in the spring and *Fucus distichus* was absent in late summer. Dethier (1982) observed seasonality in cover of *Collinsiela tuberculata* and *Rhodomela larix* which she attributed to seasonality in wave action and herbivory by littorinids. Wolfe & Harlin (1988a, b) found that the different macroalgal species in tidepools peaked at different times of the year but there was also seasonal variation in species diversity and richness. Fish that are either permanent inhabitants or transient species in pools show seasonal changes in abundance that usually are inversely related to temperature (Thompson & Lehner 1976, Grossman 1982, Yoshiyama et al. 1986, Moring 1990).

Synthesis and perspectives for future research

A number of similarities and differences exist in community organization between tidepools and emergent substrata of rocky shores. Biologically, the 2 habitats are similar since many of the same species are common to both. However, certain differences in the physical regime can result in differences in species composition between the 2 habitats. On one hand, the amplitude of the fluctuations in the physical regime tends to be smaller in some tidepools, particularly those located lower on the shore, making them more benign habitats. As a result, the vertical range of many intertidal organisms is extended in tidepools. Tidepools may be an important refuge from the extreme environmental fluctuations of the rocky intertidal habitat, although this has not as yet been quantitatively demonstrated. However, grazing and predation may be more intense in tidepools where both food and favourable foraging conditions (due to continuous submergence) are provided for extended periods. In addition, tidepools that are high on the shore and infrequently flushed can become stagnant, resulting in harsh conditions because of lack of nutrients and food, and pronounced deleterious changes in physical parameters such as pH, salinity and temperature. Low tolerance of a large number of species to harsh conditions in high tidepools can probably account for the observed decrease in species diversity with increasing intertidal height.

The variability in community structure between pools is larger than that on emergent substrata, with pools at the same height on the same shore showing large variability in species composition and abundance. Despite the large variability, some general patterns of species' distribution in tidepools along the intertidal gradient have emerged. Most studies have shown that the dominant space occupiers in lower tide-

pools are fucoid and coralline algae and mussels, whereas higher pools are dominated by green algae. However, a number of physical factors interact to determine the tidepool environment and this may be what sets different pools apart, rather than intertidal height per se. It is difficult to even define the intertidal height of pools, since tidepools at the same absolute height might have very different periodicities of flushing and emergence. Differences in community structure among studies arise because of differences in the determination of intertidal height of the pools. These factors should be carefully considered when replicate tidepools are selected for study or when comparisons are made between studies in different areas.

The amount of information available on community organization of tidepools is much more limited than that for emergent substrata of rocky shores. The information on tidepools is highly descriptive and measurements between pools are at times poorly replicated. However, some generalizations can be made. Although several studies have examined herbivory as a regulating factor of tidepool community organization, its effect has varied among studies for some taxa. All studies, despite their limitations, have suggested that grazers have a negative effect on fucoid abundance and most studies have invoked a negative grazer effect on the abundance of green algae. The positive effect of grazers on ephemeral algae noted by Chapman (1989) and Chapman & Johnson (1990) was for pools near the littoral fringe on an exposed shore, where grazer activity may have been reduced relative to lower pools or wave-protected areas. Therefore, although it can be suggested that herbivory is a potentially important regulating factor in tidepool communities, the evidence is either correlative (Wolfe & Harlin 1988a) or based on studies with low replication (Lubchenco 1978) and sometimes yields inconsistent results (e.g. Chapman 1989). In a few studies it has been suggested that predation limits species abundance in tidepools, although as yet there is little direct evidence of this effect. Therefore, unless further studies are conducted, the importance of predation in the regulation of tidepool communities will remain unknown. The importance of competition in organizing tidepool communities has been consistently demonstrated for macroalgae but further studies are necessary to determine the importance of competition among tidepool fauna. Studies of competition probably have been biased towards macroalgae because of the low abundance of animals in pools. For example, the percentage cover of mussels in tidepools may vary between 10 and 30 % (Dethier 1984) whereas on emergent substrata mussels form continuous mats (e.g. Dayton 1971, Paine & Levin 1981). Recruitment also has not been sufficiently well studied to evaluate its impor-

tance in regulating community structure and dynamics in tidepools, and further studies are required. Some studies have suggested correlations between species abundance and physical factors such as pool topography, substrate heterogeneity, pool elevation and exposure to waves, although experimental manipulations have not been conducted to examine causal mechanisms for the observed correlations. The importance of physical disturbance has been addressed in 4 studies. However, in the most detailed study (Dethier 1984) disturbance was defined as its most dramatic end result (i.e. destruction of biomass) which limits interpretation of the importance of the frequency and magnitude of specific agents of disturbance in regulating tidepool communities. The other 3 studies strongly suggest that disturbance is important but their conclusions are largely inferential or based on low replication.

It can be argued that tidepools represent an intermediate habitat type between the subtidal and the emergent substrata of the rocky intertidal habitats. Because of this, caution is advised when applying models that are developed for either subtidal or intertidal systems to the tidepool habitat. Menge & Sutherland (1976, 1987) proposed a model of rocky intertidal community organization that predicted that the relative importance of physical factors, competition and predation in community regulation varied with environmental conditions and the magnitude of recruitment. Menge & Farrell (1989) concluded that this model may not apply to subtidal systems because it was developed for habitats with large environmental fluctuations which are not present in the subtidal. Similar arguments could be raised about the applicability of the Menge-Sutherland model to tidepool communities. In any event, more information on the community organization of tidepools is required before the applicability of any model can be properly evaluated.

Individual tidepools may be unique habitats of the rocky intertidal environment which support distinct communities, depending upon their physical setting. Tidepools may be particularly useful systems in which to test ecological models and theories because they have well-defined boundaries, they can be easily manipulated and they are of manageable size. For species that can actively migrate between pools, pools have been considered as harbouring metapopulations (Bengtsson 1989). For assemblages where active migration is not possible (e.g. macroalgae, sessile invertebrates), the theory of island biogeography (MacArthur & Wilson 1967) can be tested, with the open ocean acting as the 'mainland' and the individual pools as 'islands'. Rockpools and tidepools also can be used as model systems for examining founder effects (Sale 1977, 1979, Sale & Douglas 1984). For example, initial densities of grazers can control the final struc-

ture of the phytoplankton community (Ranta et al. 1987). The intermediate disturbance hypothesis, relating the magnitude and frequency of disturbance to species diversity (Connell & Sousa 1983, Sousa 1984a), may be assessed for pools at different heights along the intertidal gradient. In order for such theories to be tested, however, the mechanisms that regulate the organization of the pools must be better known.

LITERATURE CITED

Aleem, A. A. (1950). Distribution and ecology of British marine littoral diatoms. Ecology 38: 75–106

Aleem, A. A. (1973). Contribution to the study of littoral diatoms on the west coast of Sweden. Bot. Mar. 16: 193–200

Arrontes, J., Underwood, A. J. (1991). Experimental studies on some aspects of the feeding ecology of the intertidal starfish *Patiriella exigua.* J. exp. mar. Biol. Ecol. 148: 255–269

Beckley, L. E. (1985). Tide-pool fishes: recolonization after experimental elimination. J. exp. mar. Biol. Ecol. 85: 287–295

Begon, M., Harper, J. L., Townsend, C. R. (1986). Ecology: individuals, populations, and communities. Sinauer Associates Inc., Boston

Bengtsson, J. (1989). Interspecific competition increases local extinction rate in a metapopulation system. Nature 340: 713–715

Bennett, B. A., Griffiths, C. L. (1984). Factors affecting the distribution, abundance and diversity of rock-pool fishes on the Cape Peninsula, South Africa. S. Afr. J. Zool. 19: 97–104

Brattström, H. (1990). Intertidal ecology of the northernmost part of the Chilean Archipelago. Report no. 50 of the Lund University Chile expedition 1948–49. Sarsia 75: 107–160

Brooker Klugh, A. (1924). Factors controlling the biota of tidepools. Ecology 5: 192–196

Cecchi, L. B., Cinelli, F. (1992). Canopy removal experiments in *Cystoseira*-dominated rockpools from the western coast of the Mediterranean (Ligurian Sea). J. exp. mar. Biol. Ecol. 155: 69–83

Chapman, A. R. O. (1989). Abundance of *Fucus spiralis* and ephemeral seaweeds in a high eulittoral zone: effects of grazers, canopy and substratum type. Mar. Biol. 102: 565–572

Chapman, A. R. O. (1990). Effects of grazing, canopy cover and substratum type on the abundances of common species of seaweeds inhabiting littoral fringe tide pools. Bot. Mar. 33: 319–326

Chapman, A. R. O., Johnson, C. R. (1990). Disturbance and organization of macroalgal assemblages in the Northwest Atlantic. Hydrobiologia 192: 77–121

Connell, J. H. (1961). The influence of interspecific competi-

tion and other factors on the distribution of the barnacle *Chthamalus stellatus.* Ecology 42: 710–723

Connell, J. H. (1970). A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais.* Ecol. Monogr. 40: 49–78

Connell, J. H. (1972). Community interactions on marine rocky intertidal shores. A. Rev. Ecol. Syst. 3: 169–192

Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat. 122: 661–696

Connell, J. H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J. exp. mar. Biol. Ecol. 93: 11–45

Connell, J. H., Sousa, W. P. (1983). On the evidence needed to judge ecological stability or persistence. Am. Nat. 121: 789–824

Coull, B. C., Wells, J. B. J. (1983). Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. Ecology 64: 1599–1609

Daniel, M. J., Boyden, C. R. (1975). Diurnal variations in physico-chemical conditions within intertidal rockpools. Fld Stud. 4: 161–176

Dayton, P. K. (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351–389

Dayton, P. K. (1984). Processes structuring some marine communities: are they general? In: Strong, D. R. Jr, Simberloff, D., Abele, L. G., Thistle, A. B. (eds.) Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, p. 181–197

Denley, E. J., Underwood, A. J. (1979). Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. J. exp. mar. Biol. Ecol. 36: 269–293

Dethier, M. N. (1980). Tidepools as refuges: predation and the limits of the harpacticoid copepod *Tigriopus californicus* (Baker). J. exp. mar. Biol. Ecol. 42: 99–111

Dethier, M. N. (1982). Pattern and process in tidepool algae: factors influencing seasonality and distribution. Bot. Mar. 25: 55–66

Dethier, M. N. (1984). Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. Ecol. Monogr. 54: 99–118

Diamond, J., Case, T. J. (1986). Community ecology. Harper & Row, New York

Droop, M. R. (1953). On the ecology of flagellates from some brackish and freshwater rockpools of Finland. Acta bot. fenn. 51: 1–52

Dudgeon, S. R., Davison, I. R., Vadas, R. L. (1989). Effect of freezing on photosynthesis of intertidal macroalgae: relative tolerance of *Chondrus crispus* and *Mastocarpus stellatus* (Rhodophyta). Mar. Biol. 101: 107–114

Fairweather, P. G. (1987). Experiments on the interaction between predation and the availability of different prey on rocky seashores. J. exp. mar. Biol. Ecol. 114: 261–273

Fairweather, P. G. (1988). Correlations of predatory whelks with intertidal prey at several scales of time and space. Mar. Ecol. Prog. Ser. 45: 237–243

Fairweather, P. G., Underwood, A. J. (1991). Experimental removals of a rocky intertidal predator: variations within two habitats in the effects on prey. J. exp. mar. Biol. Ecol. 154: 29–75

Farrell, T. M. (1989). Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. J. exp. mar. Biol. Ecol. 128: 57–73

Femino, R. J., Mathieson, A. C. (1980). Investigations of New England marine algae. IV The ecology and seasonal succession of tide pool algae at Bald Head Cliff, York, Maine, USA. Bot. Mar. 23: 319–332

Fraser, J. H. (1936). The distribution of rock pool copepoda according to tidal level. J. anim. Ecol. 5: 1936

Gaines, S., Roughgarden, J. (1985). Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc. natl Acad. Sci. U.S.A. 82: 3707–3711

Ganning, B. (1971). Studies of chemical, physical and biological conditions in Swedish rockpool ecosystems. Ophelia 9: 51–105

Ganning, B., Wulff, F. (1969). The effects of bird droppings on chemical and biological dynamics in brackish water rockpools. Oikos 20: 274–286

Gibson, R. N. (1982). Recent studies on the biology of intertidal fishes. Oceanogr. mar. Biol. A. Rev. 20: 363–414

Goss-Custard, S., Jones, J., Kitching, J. A., Norton, T. A. (1979). Tidepools of Carrigathorna and Barloge Creek. Phil. Trans. R. Soc. B 287: 1–44

Gosselin, L. A., Bourget, E. (1989). The performance of an intertidal predator Thais lapillus, in relation to structural heterogeneity. J. anim. Ecol. 58: 287–303

Grant, W. S. (1977). High intertidal community organization on a rocky headland in Maine, USA. Mar. Biol. 44: 15–25

Green, J. M. (1971). Local distribution of Oligocottus maculosus Girard and other tidepool cottids of the west coast of Vancouver Island, British Columbia. Can. J. Zool. 49: 1111–1128

Grossman, G. D. (1982). Dynamics and organization of a rocky intertidal fish assemblage: the persistence and resilience of taxocene structure. Am. Nat. 119: 611–637

Gustavsson, U. (1972). A proposal for a classification of marine rockpools on the Swedish west coast. Bot. Mar. 15: 210–214

Haeggström, C.-A., Skytén, R. (1987). Two successional stages of the vegetation in a rock-pool in the Aland Islands, SW Finland. Ann. bot. fenn. 24: 311–316

Hanski, I., Ranta, E. (1983). Coexistence in a patchy environment: three species of Daphnia in rock pools. J. anim. Ecol. 52: 263–279

Hawkins, S. J., Hartnoll, R. G. (1983). Grazing of intertidal algae by marine invertebrates. Oceanogr. mar. Biol. A. Rev. 21: 195–282

Hawkins, S. J., Hartnoll, R. G. (1985). Factors determining the upper limits of intertidal canopy-forming algae. Mar. Ecol. Prog. Ser. 20: 265–271

Hill, A. S., Hawkins, S. J. (1991). Seasonal and spatial variation of epilithic microalgal distribution and abundance and its ingestion by Patella vulgata on a moderately exposed rocky shore. J. mar. Biol. Ass. U.K. 71: 403–423

Huggett, J., Griffiths, C. L. (1986). Some relationships between elevation, physico-chemical variables and biota of intertidal rock pools. Mar. Ecol. Prog. Ser. 29: 189–197

Janke, K. (1990). Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). Helgoländer Meeresunters. 44: 219–263

Jernakoff, P. (1983). Factors affecting the recruitment of algae in a midshore region dominated by barnacles. J. exp. mar Biol. Ecol. 67: 17–31

Jernakoff, P. (1985). An experimental evaluation of the influence of barnacles, crevices and seasonal patterns of grazing on algal diversity and cover in an intertidal barnacle zone. J. exp. mar. Biol. Ecol. 88: 287–302

Johnson, D. S., Skutch, A. F. (1928). Littoral vegetation on a headland of Mt. Desert Island, Maine. II. Tide-pools and the environment and classification of submersible plant communities. Ecology 9: 307–338

Kooistra, W. H. C. F., Joosten, A. M. T., van den Hoek, C. (1989). Zonation patterns in intertidal pools and their possible causes: a multivariate approach. Bot. Mar. 32: 9–26

Lami, R. (1931). Sur l'hétérogénéité saline de l'eau des cuvettes littorales pendant les pluies. C. r. Acad. Sci., Paris 192: 1579–1580

Lawrence, J. M., McClintock, J. B. (1987). Intertidal invertebrate and algal communities on the rocky shores of the Bay of Morhiban, Kerguelen (southern Indian Ocean). P.S.Z.N. I: Mar. Ecol. 8: 207–220

Lewis, J. R. (1954). Observations on a high-level population of limpets. J. anim. Ecol. 23: 85–100

Lively, C. M., Raimondi, P. T. (1987). Desiccation, predation, and mussel barnacle interactions in the northern Gulf of California. Oecologia 74: 304–309

Lubchenco, J. (1978). Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112: 23–39

Lubchenco, J. (1982). Effects of grazers and algal competitors on fucoid colonization in tide pools. J. Phycol. 18: 544–550

Lubchenco, J. (1983). Littorina and Fucus: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64: 1116–1123.

Lubchenco, J., Gaines, S. D. (1981). A unified approach to marine plant-herbivore interactions. I. Populations and communities. A. Rev. Ecol. Syst. 12: 405–437

Lubchenco, J., Menge, B. A. (1978). Community development and persistence in a low rocky intertidal zone. Ecol. Monogr. 48: 67–94

MacArthur, R. H., Wilson, E. O. (1967). The theory of island biogeography. Princeton University Press, Princeton

Marsh, B., Crowe, T. M., Siegfried, W. R. (1978). Species richness and abundance of clinid fish (Teleostei; Clinidae) in intertidal rockpools. Zool. Afr. 13: 283–291

McCook, L. J., Chapman, A. R. O. (1991). Community succession following massive ice-scour on an exposed rocky shore: effects of Fucus canopy algae and of mussels during late succession. J. exp. mar. Biol. Ecol. 154: 137–169

McGregor, D. D. (1965). Physical ecology of some New Zealand rockpools. Hydrobiologia 25: 277–284

McGuinness, K. A. (1987a). Disturbance and organisms on boulders. I. Patterns in the environment and the community. Oecologia 71: 409–419

McGuinness, K. A. (1987b). Disturbance and organisms on boulders. II. Causes of patterns in diversity and abundance. Oecologia 71: 420–430

McGuinness, K. A., Underwood, A. J. (1986). Habitat structure and the nature of communities on intertidal boulders. J. exp. mar. Biol. Ecol. 104: 97–123

Menge, B. A. (1976). Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecol. Monogr. 46: 355–393

Menge, B. A. (1978). Predation intensity in a rocky intertidal community. Relation between predator foraging activity and environmental harshness. Oecologia 34: 1–16

Menge, B. A. (1983). Components of predation intensity in the low zone of the New England rocky intertidal region. Oecologia 58: 141–155

Menge, B. A. (1991). Relative importance of recruitment and other causes of variation in rocky intertidal community structure. J. exp. mar. Biol. Ecol. 146: 69–100

Menge, B. A., Farrell, T M. (1989). Community structure and interaction webs in shallow marine hard-bottom commu-

nities: tests of an environmental stress model. Adv. ecol. Res. 19: 189–262

Menge, B. A., Lubchenco, J., Ashkenas, L. R. (1985). Diversity, heterogeneity and consumer pressure in a tropical rocky intertidal community. Oecologia 65: 394–405

Menge, B. A., Sutherland, J. P. (1976). Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am. Nat. 110: 351–369

Menge, B. A., Sutherland, J. P. (1987). Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am. Nat. 130: 730–757

Metaxas, A., Lewis, A. G. (1992). Diatom communities in tidepools: the effect of intertidal height. Bot. Mar. 35: 1–10

Mgaya, Y. D. (1992). Density and production of *Clinocottus globiceps* and *Oligocottus maculosus* (Cottidae) in tidepools at Helby Island, British Columbia. Mar. Ecol. Prog. Ser. 85: 219–225

Minchinton, T. E., Scheibling, R. E. (1991). The influence of larval supply and settlement on the population structure of barnacles. Ecology 72: 1867–1879

Moore, P. G., Seed, R. (1986). The ecology of rocky coasts. Columbia University Press, New York

Moring, J. R. (1990). Seasonal absence of fishes in tidepools of a boreal environment (Maine, USA). Hydrobiologia 194: 163–168

Morris, S., Taylor, A. C. (1983). Diurnal and seasonal variation in physico-chemical conditions within intertidal rock pools. Estuar. coast. Shelf Sci. 17: 339–355

Nakamura, R. (1976). Temperature and vertical distribution of two tidepool fishes (*Oligocottus maculosus, O. snyderi*). Copeia 1976: 143–152

Naylor, E., Slinn, D. J. (1958). Observations on the ecology of some brackish water organisms in pools at Scarlett Point, Isle of Man. J. anim. Ecol. 27: 15–25

Ostmann, M., Rönnberg, O. (1991). Effects of ships' waves on rock-pools in the Aland Archipelago, northern Baltic Sea. Sarsia 76: 125–132

Paine, R. T. (1966). Food web complexity and species diversity. Am. Nat. 100: 65–75

Paine, R. T (1974). Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15: 93–120

Paine, R. T. (1984). Ecological determinism in the competition for space. Ecology 65: 1339–1348

Paine, R. T., Levin, S. A. (1981). Intertidal landscapes: disturbance and the dynamics of pattern. Ecol. Monogr. 51: 145–178

Paine, R. T., Vadas, R. L. (1969). The effects of grazing sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnol. Oceanogr. 14: 710–719

Pajunen, V. I. (1977). Population structure in rock-pool corixids (Hemiptera, Corixidae) during the reproductive season. Ann. zool. fenn. 14: 26–47

Pajunen, V. I. (1990). The population dynamics of rock-pool corixids living on supplementary food (Hemiptera, Corixidae). Ann. zool. fenn. 27: 337–350

Pajunen, V. I., Salmi, J. (1991). The influence of corixids on the bottom fauna of rock-pools. Hydrobiologia 222: 77–84

Petraitis, P. S. (1983). Grazing patterns of the periwinkle and their effect on sessile intertidal organisms. Ecology 64: 522–533

Petraitis, P. S. (1987). Factors organizing rocky intertidal communities of New England: herbivory and predation in sheltered bays. J. exp. mar. Biol. Ecol. 109: 117–136

Preston, A., Moore, P. G. (1988). The flora and fauna associated with *Cladophora albida* (Huds.) Kütz. from rockpools on Great Cumbrae Island, Scotland. Ophelia 29: 169–186

Pyefinch, K. A. (1943). The intertidal ecology of Bardsey Island, North Wales, with special reference to the recolonization of rock surfaces, and the rock-pool environment. J. anim. Ecol. 12: 82–108

Raffaelli, D. (1979). The grazer-algae interaction in the intertidal zone on New Zealand rocky shores. J. exp. mar. Biol. Ecol. 38: 81–100

Ranta, E. (1982). Animal communities in rockpools. Ann. zool. fenn. 19: 337–347

Ranta, E., Hallfors, S., Nuutinen, V., Hallfors, G., Kivi, K. (1987). A field manipulation of trophic interactions in rockpool plankton. Oikos 50: 336–346

Ranta, E., Nuutinen, V. (1984). Zooplankton predation by rock-pool fish (*Tinca tinca* L. and *Pungitius pungitius* L.): an experimental study. Ann. zool. fenn. 21: 441–449

Reed, D. C., Laur, D. R., Ebeling, A. W (1988). Variation in algal dispersal and recruitment: the importance of episodic events. Ecol. Monogr. 58: 321–335

Richkus, W. A. (1978). A quantitative study of interpool movement of the wooly sculpin *Clinocottus analis*. Mar. Biol. 49: 277–284

Roughgarden, J., Iwasa, Y., Baxter, C. (1985). Demographic theory for an open marine population with space limited recruitment. Ecology 66: 54–67

Sale, P. F. (1977). Maintenance of high diversity in coral reef fish communities. Am. Nat. 111: 337–359

Sale, P. F. (1979). Recruitment, loss and coexistence in a guild of territorial coral reef fishes. Oecologia 42: 159–177

Sale, P. F., Douglas, W. A. (1984). Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. Ecology 65: 409–422

Schonbeck, M. W., Norton, T. A. (1978). Factors controlling the upper limits of fucoid algae on the shore. J. exp. mar. Biol. Ecol. 31: 303–313

Schonbeck, M. W., Norton, T. A. (1980). Factors controlling the lower limits of fucoid algae on the shore. J. exp. mar Biol. Ecol. 43: 131–150

Singletary, R. L., Shadlou, R. (1983). *Balanus balanoides* in tide-pools: a question of maladaptation? Crustaceana 45: 53–70

Sousa, W. P. (1979a). Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 49: 227–254

Sousa, W. P. (1979b). Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60: 1225–1239

Sousa, W. P. (1984a). The role of disturbance in natural communities. A. Rev. Ecol. Syst. 15: 353–391

Sousa, W. P. (1984b). Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology 65: 1918–1935

Stenton-Dozey, J. M. E., Brown, A. C. (1992). Clearance and retention efficiency of natural suspended particles by the rock-pool bivalve *Venerupis corrugatus* in relation to tidal availability. Mar. Ecol. Prog. Ser. 82: 175–186

Stephenson, T. A., Stephenson, A. (1950). Life between tidemarks in North America. I. The Florida Keys. J. Ecol. 38: 354–402

Stephenson, T. A., Stephenson, A. (1952). Life between tidemarks in North America. II. Northern Florida and the Carolinas. J. Ecol. 40: 1–49

Stephenson, T. A., Stephenson, A. (1954a). Life between tidemarks in North America. IIIA. Nova Scotia and Prince Edward Island: description of the region. J. Ecol. 42: 14–45

Stephenson, T. A., Stephenson, A. (1954b). Life between tide-marks in North America. IIIB. Nova Scotia and Prince Edward Island: the geographical features of the region. J. Ecol. 42: 46–70

Stephenson, T. A., Zoond, A., Eyre, J. (1934). The liberation and utilisation of oxygen by the population of rock-pools. J. exp. Biol. 11: 162–172

Sze, P. (1980). Aspects of the ecology of macrophytic algae in high rockpools at the Isles of Shoals (USA). Bot. Mar. 23: 313–318

Sze, P. (1982). Distributions of macroalgae in tidepools on the New England coast (USA). Bot. Mar. 25: 269–276

Thompson, D. A., Lehner, C. E. (1976). Resilience of a rocky intertidal fish community in a physically unstable environ-ment. J. exp. mar. Biol. Ecol. 22: 1–29

Underwood, A. J. (1976). Analysis of patterns of dispersion of intertidal prosobranch gastropods in relation to macro-algae and rock-pools. Oecologia 25: 145–154

Underwood, A. J. (1980). The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. Oecologia 46: 201–213

Underwood, A. J. (1981). Structure of the rocky intertidal community in New South Wales: patterns of vertical distri-bution and seasonal changes. J. exp. mar. Biol. Ecol. 51: 57–85

Underwood, A. J., Denley, E. J. (1984). Paradigms, explana-tions, and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong, D. R. Jr, Simberloff, D., Abele, L. G., Thistle, A. B. (eds.) Ecolog-ical communities: conceptual issues and the evidence. Princeton University Press, Princeton, p. 151–180

Underwood, A. J., Jernakoff, P. (1981). Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. Oecologia 48: 221–233

Underwood, A. J., Jernakoff, P. (1984). The effects of tidal height, wave exposure, seasonality and rock-pools on grazing and the distribution of intertidal macroalgae in New South Wales. J. exp. mar. Biol. Ecol. 75: 71–96

Vadas, R. L. (1985). Herbivory. In: Littler, M. M., Littler, D. S. (eds.) Handbook of phycological methods. Ecological field methods: macroalgae. Cambridge University Press, Cam-bridge, p. 531–572

Wethey, D. S. (1985). Catastrophe, extinction, and species diversity: a rocky intertidal example. Ecology 66: 445–456

Wilson, J. B., James, R. E., Newman, J. E., Myers, T. E. (1992). Rock pool algae: species composition determined by chance? Oecologia 91: 150–152

Wolfe, J. M., Harlin, M. M. (1988a). Tidepools in southern Rhode Island, U.S.A. I. Distribution and seasonality of macroalgae. Bot. Mar. 31: 525–536

Wolfe, J. M., Harlin, M. M. (1988b). Tidepools in southern Rhode Island, U.S.A. II. Species diversity and similarity analysis of macroalgal communities. Bot. Mar. 31: 537–546

Yoshiyama, R. M., Sassaman, C., Lea, R. N. (1986). Rocky intertidal fish communities of California: temporal and spatial variation. Environ. Biol. Fish. 17: 23–40