

SPECIES DIVERSITY IN SUBTIDAL LANDSCAPES: MAINTENANCE BY PHYSICAL PROCESSES AND LARVAL RECRUITMENT

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Abstract. Heterogeneous patterns of species diversity are rarely linked to the processes that maintain them on spatial scales larger than tens of meters. In this study, subtidal landscapes of a New Zealand fjord were used to study the spatial patterns of epifaunal invertebrate species diversity and to test hypotheses about the mechanisms maintaining the patterns. Patterns of species diversity were quantified along 1000-m² sections of vertical rock wall habitat at three sites separated by 3–6 km of horizontal distance during April–August 1993. Species diversity data from random 0.25-m² quadrats at four depth strata (3, 5, 10, and 18 m) within a 20 × 50 m area were contoured to reveal spatial patterns at each site. General patterns consisted of localized patches of 300–660 m² of high diversity (i.e., H' [Shannon-Weiner diversity index] of 2.0–3.2/0.25 m² and S [species richness] of 28–32 species/0.25 m²) centered at 10 m depth. High-diversity patches, dominated by bryozoans, sponges, and ascidians, were bounded vertically by low-diversity mussel assemblages and horizontally by low-diversity assemblages dominated by encrusting calcareous algae with areas of bare rock. Vertical patterns of diversity were attributed to physical stress from a low-salinity surface layer impinging on shallow areas (e.g., 0–5 m depth) of the landscapes, while horizontal patterns could be partly attributed to large-scale landslides and severe grazing by sea urchins.

The hypothesis that the areas of high diversity could be maintained by larval recruitment was tested by deploying an array of recruitment tiles with predator exclusion treatments. Experiments were conducted on the same spatial scale as the documented patterns of diversity (e.g., at 3, 5, 10, and 18 m depth), with tiles placed in and out of the high-diversity patches. Recruitment densities of calcareous polychaetes, bryozoans, and hydroids showed significant depth and habitat effects (i.e., in vs. out of the high-diversity areas) after 3 mo, but no significant effects of predator exclusion treatment. A positive linear relationship between species diversity and number of recruit species in adjacent areas of wall explained 27–57% of the variance. These data also suggested that the size of the high-diversity patches and location within the fjord are important factors affecting this relationship.

We suggest that the localized patches of high diversity over hundreds of meters of continuous habitat can be maintained on temporal scales of months either by spatially limited recruitment of short-lived larvae from the patches or by recruitment near established conspecifics. Additionally, there may be a feedback mechanism involving the interaction of increased biogenic structure provided by the high-diversity patches enhancing recruitment. This feedback would then serve to maintain localized areas of high diversity within the extensive areas of low diversity on scales of hundreds to thousands of meters.

Key words: diversity; epifaunal invertebrates; fjords; landscape ecology; low-salinity surface layer; New Zealand; recruitment; rocky subtidal; species diversity; stratified water column.

INTRODUCTION

The distribution and abundance of organisms in natural communities are characterized by heterogeneous spatial patterns, whereby several theories (Janzen 1970, Connell 1971, 1979, Ricklefs 1977, Hubbell 1979) and empirical studies (Connell et al. 1984, Condit et al. 1992) have sought to explain mechanisms that allow for the coexistence of large numbers of species. The

realization of the importance of scale in ecological studies (Dayton and Tegner 1984, Wiens 1989, Levin 1992, Pickett and Cadenasso 1995) has stimulated new hypotheses about how species assemblages are maintained (Menge and Olson 1990, Barry and Dayton 1991, Holt et al. 1995). For example, one emerging area of research in community ecology that considers linkages across multiple scales is focused on determining how regional processes contribute to local patterns of species diversity (Ricklefs 1987, Schuler and Ricklefs 1993, Cornell and Karlson 1996).

Since most of the understanding of how communities are organized has been based on studies conducted in

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small plots or patches of habitat measuring <10's of square meters in area (Kareiva and Andersen 1988, Jackson 1991), it is uncertain how processes maintaining diversity of these local communities can be extrapolated to explain patterns of diversity over larger spatial scales (Ricklefs 1987, Schuller and Ricklefs 1993, Wiens et al. 1993). The predominance of research conducted within patch types or within landscape elements has focused the attention of ecologists on smaller scale structuring processes, such as competition and predation (Malanson 1993). Consequently, the importance of between-patch processes in maintaining patterns of species diversity has been largely overlooked.

Many factors can account for patterns of spatial heterogeneity observed in sessile marine communities on rocky substrata, including competition (Connell 1961), predation (Paine 1966), larval recruitment (Gaines and Roughgarden 1985, Underwood and Fairweather 1989), and physical or biological disturbances (Dayton 1971, Paine and Levin 1981, Dethier 1984, Sousa 1985, Wethey 1985, Witman 1992). Among these, physical disturbances, such as storm damage (Ayling 1984, Witman 1987), and larger scale biological disturbances, such as severe grazing by large urchin aggregations (Ayling 1981, Witman 1985), have been documented to influence patterns of species diversity over areas of hundreds of meters of continuous habitat. Strong species interactions, such as spatial competition (Sebens 1986), can also influence epifaunal diversity on smaller spatial scales (i.e., meters) but are unlikely to account for patterns observed over hundreds of meters.

Recruitment, regarded as the input of new individuals into a population or community, is another process that can influence community patterns over hundreds of meters of continuous habitat (e.g., Sale 1977, Connell et al. 1984, McGowan and Walker 1985, Condit et al. 1992). Recruitment is also an implicit assumption in several theories of the establishment and maintenance of populations within a disturbance regime (e.g., Connell 1978, Sousa 1984, Connell and Keough 1985, Menge and Sutherland 1987, Petraitis et al. 1989).

Sessile marine species are characterised by mobile dispersal stages, and recruitment of these larvae or propagules serves as a mechanism that can link spatially discrete populations or patch assemblages (Hansson 1991). Although the importance of larval dispersal and recruitment in structuring subtidal epifaunal communities has been demonstrated (Sutherland and Karlson 1977, Keough 1984a, Brault and Bouget 1985, Mullineaux 1988, Hurlbut 1991, Bingham 1992, Farnsworth and Ellison 1996), there is little explicit information relating patterns of species diversity to recruitment in these communities, particularly on scales over hundreds of meters.

In this paper, large-scale patterns of diversity of epifaunal assemblages in a New Zealand fjord were used to test the hypothesis that the patterns of diversity could be maintained by larval recruitment. Patterns of species

diversity over hundreds of meters of continuous habitat were quantified along sections of vertical rock wall at three sites separated by 3–6 km. Patterns of epifaunal diversity consisted of localized patches of high diversity bounded by extensive areas of low diversity. These patches were used to determine the relationship between diversity and recruitment. Recruitment was measured at these sites on the same spatial scale in areas of high and low epifaunal diversity on an array of recruitment tiles with predator exclusion treatments. Results demonstrated that areas of high diversity received higher densities and more species of recruits than areas at shallow depths and in adjacent low-diversity areas. Comparisons between caged and uncaged recruitment tiles showed that predation had minimal influence on the observed patterns of recruitment. The depth of a low-salinity surface layer present in the fjords was closely related to the vertical patterns of diversity at each of the three sites. Physical and biological disturbances, including landslides and severe urchin grazing, were related to horizontal patterns of diversity in these assemblages.

Study area and description of heterogeneity.—The drowned glacial valleys of the Fiordland region, located in the southwest corner of the South Island, New Zealand (Fig. 1), harbor rich and diverse subtidal sessile invertebrate assemblages (Grange et al. 1981). The steep topography of fjords created by glacial scouring provides extensive near-vertical rock wall habitat that extends hundreds of meters vertically and thousands of meters horizontally. These habitats offer little structural heterogeneity over hundreds of meters of habitat and thus provide an excellent system for studying the spatial patterns of epifaunal diversity (Grange et al. 1981, Lundälv 1985).

Patchiness of the epifaunal assemblages in the New Zealand fjords is extreme. Broad-scale diving surveys conducted throughout the Doubtful Sound complex during April–August 1993 revealed that kilometers of continuous rock wall habitat consisted of low-diversity areas dominated by calcareous algae and bare rock substrata. Within these extensive low-diversity areas, localized patches of high-diversity epifaunal assemblages (i.e., tens of meters of continuous habitat) were found to be dominated by bryozoans, sponges, and ascidians (F. Smith, *unpublished data*).

Little information is presently available to determine all factors contributing to this large-scale pattern of isolated patches of high epifaunal diversity surrounded by low-diversity areas. More explicitly, there was no basis for determining whether the extensive areas of calcareous algae and bare rock (i.e., the low-diversity areas) were ever colonized by high-diversity epifaunal assemblages. However, several factors occurring on ecological time scales (i.e., hours to hundreds of years) within the fjords have been documented to influence epifaunal species distributions and abundances. The presence of a salinity-stratified water column within

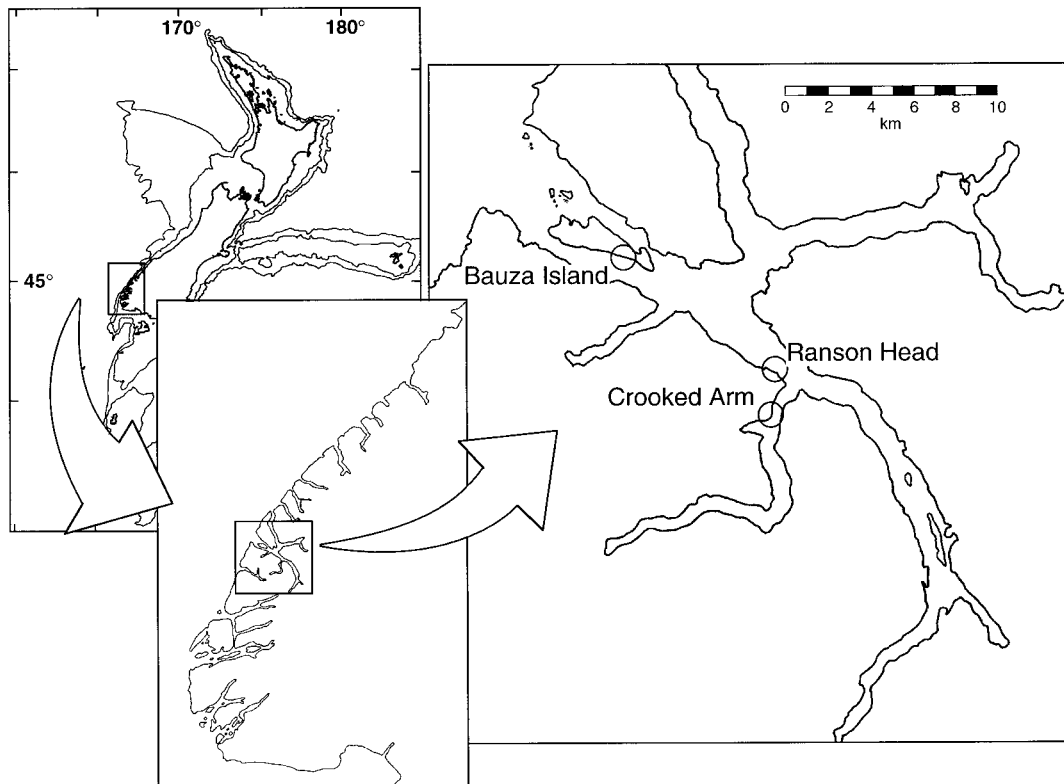


FIG. 1. Map showing location of study sites, Crooked Arm, Ranson Head, and Bauza Island, within Doubtful Sound, Fiordland, New Zealand.

the fjords has been shown to be correlated with patterns of vertical zonation (Grange et al. 1981, Witman and Grange, 1998). Physical and biological disturbances in the form of landslides and severe sea urchin grazing have been documented to remove epifaunal species over large spatial scales (Grange and Singleton 1988) and thus could create horizontal discontinuities in patterns of epifaunal diversity.

Water column stratification and vertical zonation.— Rainfall in the Fiordland region is prodigious, with a yearly average of ~6000 mm/yr, and characterized by intense rainfall events where over 50 mm of precipitation can fall during a 24-h period (Sansom 1984). This extreme rainfall, combined with the steep topographic features of the fjords, leads to the accumulation of runoff in the narrow inlets, forming a low-salinity surface layer (LSL), which is separated from the lower saline layer by a prominent pycnocline (Pickard and Stanton 1980, Stanton and Pickard 1981). The shallow-water hydrography of the fjords is dominated by the LSL, where the barotropically driven surface layer flows seaward, accompanied by entrainment in the lower saline layer (Pritchard 1952, Rattray 1967, Farmer and Freeland 1983). Currents within the surface layer can be substantial (i.e., up to 40–60 cm/s; J. D. Witman and F. Smith, *unpublished data*), while currents in the lower saline layer, mainly tidally driven, are generally

weak (i.e., mean spring tidal current of 3 cm/s; Stanton 1978). Many factors are important in determining water column stratification and oceanographic conditions in fjords, which involve complex interactions between winds (Buckley and Pond 1976), tides (Drinkwater and Osborn 1975) and local topography (Stigebrandt 1980, 1981) and have been the subject of several reviews (e.g., Freeland et al. 1980, Farmer and Freeland 1983, Skreslet 1996, see also recent work by Baker and Pond 1995).

In Doubtful Sound, the LSL is typically 3–5 m deep with fluctuating salinities of 0–14 ppt above the pycnocline, and tidal heights range from 1 to 2 m (Stanton and Pickard 1981, Grange et al. 1991, Witman and Grange 1998). The LSL plays an important role in determining the zonation patterns of subtidal invertebrates in the upper few meters by limiting the distribution of stenohaline species (Batham 1965, Gage 1974, Rosenberg and Möller 1979, Grange et al. 1981, Jensen et al. 1985) and by directly affecting the vertical distribution of key predators, such as seastars and urchins (Witman and Grange 1998). Gross vertical zonation patterns within the epifaunal communities consist of shallow assemblages (i.e., <3 m depth) dominated by mussels, barnacles, and algae; assemblages at intermediate-depths (i.e., 3–6 m) dominated by bryozoans, hydroids, and mussels; and deeper (i.e., >6 m)

assemblages, composed of sponges, bryozoans, brachiopods, cnidarians, and ascidians (Grange et al. 1981, Witman and Grange 1998; F. Smith and K. R. Grange, *unpublished manuscript*).

Physical and biological disturbances.—The Fiordland region represents an area of marked tectonic activity, as it is dissected by the Alpine Fault system, which runs the length of the South Island (Cox and Findlay 1995). Earthquakes frequently occur in the region, experiencing shaking levels according to the Modified Mercalli Intensity (MM) 6 every 30 yr and MM 7 every 100 yr (Smith and Berryman 1992). The steep topography and high precipitation also increase ground instability, which contributes to frequent, shallow-seated landslides that are able to denude areas over hundreds of meters (Grange and Singleton 1988, Van Dissen et al. 1994; R. A. Pickrill, *unpublished manuscript*). Disturbance to the subtidal epifaunal communities occurs directly under these landslides and indirectly in adjacent areas by the smothering of suspension-feeding invertebrates with sediment (Grange and Singleton 1988, F. Smith and J. D. Witman, *personal observations*).

Large aggregations of sea urchins, particularly *Pseudechinus huttoni* (Benham), represent a biological agent responsible for scouring extensive areas of rock wall (Grange and Singleton 1988) and are able to reduce epifaunal diversity by removing large numbers of species. There is little quantitative information on the distribution and abundance of these organisms available over large spatial scales within the New Zealand fjords. However, localized densities of *Pseudechinus* can be as high as 12 individuals per 0.25 m² in localized areas, and these urchins can denude large areas of substrata over a period of months (F. Smith, *personal observations*, Witman and Grange 1998).

Although these processes can partially account for aspects of the large-scale patchiness of epifaunal species diversity, there was no basis to unequivocally determine whether or not low-diversity areas were created by physical or biological disturbances. Firstly, the nature of landslide disturbance and intense grazing by urchins is highly variable with respect to the magnitude and spatial extent of the area disturbed. Secondly, there are extensive areas of low diversity present within the fjords that do not appear to have been impacted by landslides or severe grazing by sea urchins. The origins of this pattern are thus largely speculative.

Conceptual approach and preliminary investigations.—When viewed on large spatial scales (i.e., over kilometers), patterns of diversity of the subtidal epifaunal assemblages in the New Zealand fjords resembled type-2 patches of Connell and Keough (1985) or isolated patches of Holt et al. (1995), where isolated patches of high diversity were surrounded by large areas of low diversity. Although within-patch processes, such as competition and predation, occur within a given high diversity patch and may be important for main-

taining epifaunal diversity as in type-1 (Connell and Keough 1985) or embedded patches (Holt et al. 1995), these processes are more likely to be important for determining smaller scale spatial patterns (i.e., less than tens of meters). The focus of this study was to understand how isolated patches of high epifaunal diversity (resembling type-2 or isolated patches) were related to recruitment patterns and whether this relationship could serve as a mechanism maintaining the spatial structure of individual high-diversity patches over hundreds of meters.

A preliminary investigation of recruitment and community development was initiated at Tricky Cove, Doubtful Sound (45°20.95' S, 167°02.83' E) during March 1993. This investigation involved the deployment of recruitment tiles within two isolated epifaunal assemblages separated by ~450 m of substrata dominated by bare rock and calcareous algae. Recruitment tiles with predator exclusion cages were placed at stratified depths of 3, 5, 10, and 18 m and photographed quarterly to follow recruitment, growth, and community development. Results of this study indicated that substantial recruitment of calcareous polychaete worms and bryozoans occurred within 3 mo, and after 9 and 12 mo, a large percentage of tile surfaces (~80%) at 10 and 18 m depths were covered with erect and encrusting bryozoans, ascidians, and calcareous polychaete worms (J. D. Witman and F. Smith, *unpublished data*). This preliminary investigation was able to assess the timing of recruitment, growth rates, and the complexity of competitive interactions in the development of these diverse epifaunal assemblages and will be presented elsewhere.

Within the 12 mo of monitoring this preliminary experiment, the area between the two isolated patches remained barren, despite dense recruitment and rapid community development documented within the high-diversity epifaunal patches. The hypothesis that emerged from this was that recruitment was largely occurring within the high-diversity patches and not in adjacent low-diversity areas. In this manner, recruitment could serve as a principle mechanism for maintaining observed spatial patterns of diversity. Alternately, recruitment was occurring in the adjacent low-diversity areas, but recruits were preyed upon, which would account for the lack of epifaunal invertebrates in adjacent areas.

METHODS

Patterns of epifaunal diversity.—Patterns of epifaunal species diversity were quantified at three locations separated by 3–6 km in Doubtful Sound, Fiordland, herein referred to as Crooked Arm, Ranson Head, and Bauza Island (Fig. 1). These three sites, situated on near-vertical rock wall habitat, were characterized by high-diversity epifaunal assemblages surrounded by areas of low diversity. Faunal transitions along a depth gradient have been documented in several other New

Zealand fjords (Grange et al. 1981) so a series of vertical transects were used to determine the depths of the major epifaunal zones for these sites. These zones were characterized by a mussel-dominated assemblage at ~3 m; a hydroid and bryozoan dominated assemblage at ~5 m; a sponge, bryozoan, and ascidian dominated assemblage at ~10 m; and a deeper assemblage of sponges, bryozoans, brachiopods, and ascidians at ~18 m depth (Witman and Grange 1998).

Species diversity patterns were quantified by photographing random 0.25-m² quadrats along horizontal transects at four depth strata (3, 5, 10, and 18 m). The photographic system used consisted of a Nikonos V camera fitted with a 15-mm lens and two strobes fixed to a rigid framer (Witman 1985), providing a high-resolution image able to identify organisms >2–3 mm in size. Although this method was ideal for sampling the majority of the fauna present in these rock wall assemblages, it was impractical for sampling a few species of more widely dispersed megafauna (e.g., antipatharian corals). These species were, therefore, under-represented in these samples.

Photo transects at 10 and 18 m were 50 m in length, having 34 random quadrats per transect, and photo-transects at 3 and 5 m depth were 25 m in length, having 17 random quadrats per transect. This strategy was adopted to ensure adequate sampling of species at the 10 and 18 m depth strata. Overall, 97 quadrats were sampled at Crooked Arm, 98 at Ranson Head, and 98 at Bauza Island during monthly sampling periods from December 1993 to May 1994.

The number of new species encountered in successive quadrats along a 25-m transect at 10 m depth was used to determine if the photo transect methodology was adequate for sampling the species of these assemblages. The asymptote of the species accumulation curve occurred near 12 quadrats, indicating that the area sampled was sufficiently large for diversity comparisons (Fig. 2).

Photographic images were used to quantify percent cover of species, identified to the lowest taxonomic level possible, using a variation of the random dot method (Menge 1976, Meese and Tomich 1992). In this method, a transparent acetate sheet with 200 random dots was placed over the backlit quadrat image, and organisms appearing under each dot were recorded. Percent cover for each species was then expressed as a percentage of the number of dots occupied over the total number of dots. For the purposes of this study, only organisms occupying primary substratum were counted, except in the cases where a species obscured the primary substratum, forming a "canopy" (as in Sebens 1986), typical of some arborescent bryozoans and hydroids. Categories of non-living substrata (e.g., bare rock, sediments, and detritus) were also included in the percent cover analysis. Species without positive taxonomic classifications were given pseudonyms based on field observations and kept consistent throughout the data analysis.

Percent cover data were used to compute species

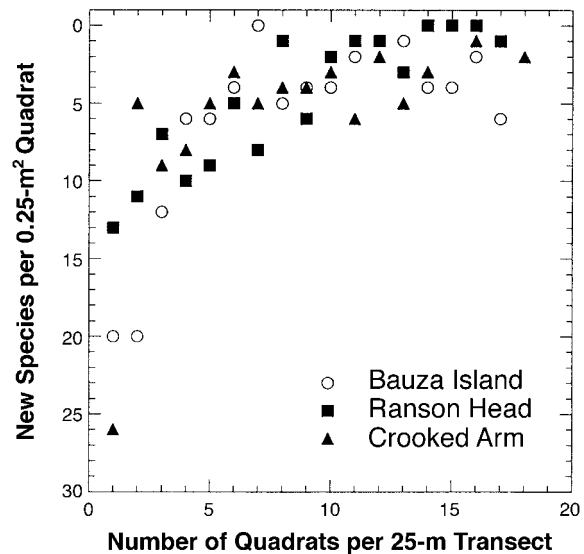


FIG. 2. Species accumulation curve showing the number of new species encountered in successive random 0.25-m² photo quadrats at 10 m depth at each of the three study sites. The asymptote occurred at ~12 quadrats, indicating that this methodology was adequate for sampling the species diversity within these assemblages.

richness (S) and Shannon-Weiner diversity (H') with an evenness component (J') per 0.25 m² using natural logarithms (Pielou 1966, 1974). In order to visualize the patterns of species diversity on large spatial scales, these data were contoured using a kriging interpolation (Spyglass Transform, Version 3.0, Spyglass Inc., Savoy, Illinois, USA), which optimally predicts unobserved values (Cressie 1991). Variance matrices, representing the variance for each datum within the resultant data matrix, were used to verify the accuracy of the kriging interpolation function (Robertson 1987). Areas of high variances, representing inaccuracies of the interpolation function, were contoured, measured, and expressed as a percentage of the total area sampled.

As transitions in faunal composition with depth were hypothesized to be influenced by the presence of the low-salinity surface layer, salinity profiles at each site were measured over 5 d during monthly sampling periods and used to relate water column structure to vertical patterns of species diversity. Since the LSL had been characterized as a dynamic feature of Doubtful Sound with daily and seasonal fluctuations in salinity (Grange et al. 1991), large depressions of the LSL were predicted to have the greatest influence on the upper limit of high-diversity patches.

Spatial patterns of recruitment diversity.—The hypothesis that the spatial patterns of epifaunal diversity could be maintained by recruitment was tested by measuring recruitment in areas of high and low epifaunal diversity on the same spatial scale (i.e., over hundreds of meters of continuous habitat). Supporting evidence

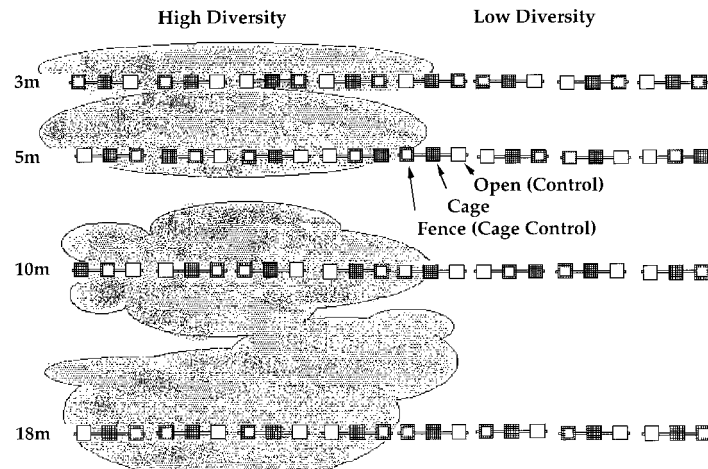


FIG. 3. Schematic diagram of the experimental recruitment rack array. Each depth stratum (i.e., 3, 5, 10, and 18 m) consisted of eight replicate recruitment racks per depth, with four in areas of high diversity and four in adjacent areas of low diversity, depicted by the shaded region. Each recruitment rack consisted of one of three treatments: predator exclusion cage, cage control, and open control. Refer to *Methods: Spatial patterns of recruitment diversity* for details and explanation of predator exclusion treatments and overall experimental design.

for this hypothesis would include higher recruitment densities and larger numbers of species recruiting into the areas of high epifaunal diversity, while if patterns of recruitment were random with respect to the pattern of epifaunal diversity, little or no spatial correspondence would be expected. Alternately, recruitment patterns could have a negative spatial correspondence to the pattern of epifaunal diversity, which would be indicated by higher recruitment into adjacent areas of low epifaunal diversity.

Recruitment was measured on an array of independent, randomly spaced slate tiles, placed both inside and outside of the high-diversity patches at each of the three sites (Fig. 3). Tiles were placed at the same depths of the epifaunal diversity surveys (i.e., 3, 5, 10, and 18 m) in order to detect trends in the pattern of recruitment with respect to depth. Slate tiles were coated with concrete to provide surface roughness similar to that of the natural rock wall substrata and deployed in triplicates of randomly assigned treatments: caged treatments to control for the effects of predation on newly settled recruits, fences (cage controls) as a control for potential hydrodynamic influences of the cage on recruitment, and open (control) tiles accessible to predators (Menge 1976). Cages were constructed of plastic mesh with square 15×15 mm openings, which was adequate to keep out key macropredators, such as fish, sea urchins, sea stars, and large gastropods. Eight replicate "triplets" (i.e., one of each treatment) were deployed at each depth stratum with four replicates placed within the high-diversity patches and four replicates outside the high-diversity patches within the 20×50 m study plots. This design was adopted to ensure adequate treatment dispersion (Hurlbert 1984). Treatments within each triplicate were spaced ~ 30 – 40 cm apart. Attachment of the recruitment tiles was achieved

by fixing each "triplet" to 15 mm diameter ABS (acrylonitrile butadiene styrene) pipes, which were then fastened to bolts drilled into the rock walls. This allowed for the tiles to be placed within 2.5 cm of the natural substrata.

Potential hydrodynamic effects of the cages on the flow environment of the tiles were assessed using the dissolution of alabaster blocks as a measure of relative flow at 5 m depth (Thompson and Glenn 1994, Leichter and Witman 1996). Results of one-way analysis of variance of the cage treatment on the mean dissolution rates were nonsignificant ($F = 1.358$, $P = 0.326$, $N = 9$), suggesting that the bulk fluid fluxes were similar for each of the cage treatments.

Recruitment tile arrays were deployed during 15–23 February 1994 and photographed on 3–6 May 1994, representing recruitment at each site after 3 mo. Results from our preliminary study showed that this time interval was adequate for assessing patterns of recruitment for many species in these assemblages, including calcareous polychaetes, bryozoans, and ascidians. A period of warm water temperature normally occurs within Doubtful Sound during late February and early March (Grange et al. 1991) and has been considered to be a reproductive cue for the sessile invertebrates of these rock wall assemblages. A well-studied example is the reproductive pattern of the antipatharian coral, *Antipathes fiordensis*, which typically spawns in early to mid-April (Grange and Singleton 1988). Thus, the experimental tile arrays were deployed during an appropriate time of year (i.e., late austral summer) and monitored for a sufficient time interval (i.e., for 3 mo) in order to determine the recruitment patterns for many species within these assemblages.

Tiles were sampled photographically with a Nikonos V fitted with a 35 mm close-up lens and framer, sam-

pling an area of 238 cm². Potential “edge-effects” of the tiles were minimized by photographing the center of the tile, typically 3–4 cm from all edges. Photographic images were used to quantify the density of recruits and the number of species recruiting onto the tiles. Species were identified to the lowest taxonomic level possible. White-colored encrusting bryozoans were often difficult to distinguish from the photographs, so these species (about seven) were designated as “*Schizomittina* complex,” where *Schizomittina* sp. was found to be the most abundant species in this group. This provided a conservative underestimation for the number of species recruiting onto the tiles.

To visualize the spatial patterns of recruitment at each of the sites, species diversity (H') of recruits per tile (238 cm²) was calculated and contoured using kriging interpolation against depth and distance along the wall (i.e., as with the diversity data). Contours of recruitment were constructed from 92 tile images at Crooked Arm, 89 at Ranson Head and 70 at Bauza Island. Fewer images were collected at the shallower depths (i.e., 3 and 5 m) due to equipment malfunctions and unavoidable loss of some tiles during storms.

Relationship between recruitment and epifaunal diversity.—Fully factorial analysis of variance was used to test the main effects of depth, predator exclusion treatment, and “habitat” (i.e., in vs. out of the high-diversity patches) with recruitment diversity (H') as the dependent variable. In order to identify areas of high recruitment diversity, Tukey multicomparison tests were conducted as planned pairwise comparisons between depth and “habitat” (Day and Quinn 1989). Separate hypotheses relating the spatial pattern of recruitment densities of commonly occurring species to the effects of depth, treatment, and habitat were tested using analysis of variance. Recruitment densities for individual species were $\sqrt{(x + 1)}$ transformed to satisfy the normality assumption (Zar 1996). For all analysis of variance tests, a Cochran’s C test was used to test the homoscedasticity assumption (Underwood 1981, Winer et al. 1991:105). As minor violations of the homoscedasticity assumption were detected with this test (i.e., increasing the Type I error rate), significant P values were decreased from the conventional $P < 0.05$ level to $P < 0.03$ for all three sites (Underwood 1981).

The relationship between the patterns of recruitment and diversity was further characterized by a linear regression between the numbers of species recruiting on the tiles and species diversity of proximal areas of rock wall. The regression analysis was based on independent quadrat measurements of epifaunal diversity in areas adjacent to the recruitment tiles. Data points were omitted where there were no matching data for epifaunal diversity. As the heterogeneous pattern of diversity was used as a natural means to determine the influence of the pattern of diversity on recruitment, the response variable used in this analysis was the number of species recruiting onto the tiles. Analysis of regression resid-

uals was used to verify that assumptions for the linear model were met (Wilkinson 1989). In addition, a deviation from linearity test was performed to determine whether the data with multiple values of Y for a single X conformed to the linear model (Zar 1996:338). In cases where the deviation from linearity was significant, second-order polynomials were used to characterize the relationship.

RESULTS

Patterns of epifaunal diversity.—At all three sites, there were localized patches of high diversity (i.e., $H' \geq 2.0/0.25$ m²) centered at 10 and 18 m depths with areas of 300–660 m² (Plate 1). High-diversity patches were bounded vertically by sharp diversity gradients from 3 to 7 m depth and horizontally by areas of low diversity. Areas of the lowest diversity values (i.e., $H' \leq 1.0/0.25$ m²) were predominantly located in shallow regions of 3–5 m, while diversity values in adjacent low-diversity areas were typically between 1.0 and 1.8/0.25 m². Overall patterns of high species richness (S) and evenness (J') corresponded to the patches of high diversity, indicating that both of these factors contributed to the high diversity in these patches (F. Smith, unpublished data).

The high-diversity patch at Crooked Arm encompassed an area of ~430 m² (Plate 1A) and was dominated by solitary ascidians (e.g., *Cnemidocarpa bicornuta*), brachiopods (e.g., *Notosaria nigricans*), and bryozoans (e.g., *Caberea* sp.) The upper depth limit of high diversity (i.e., $H' \geq 2.0/0.25$ m²) was at ~7 m depth at this site. Low-diversity areas at shallow depths (i.e., above 5 m depth) were composed of isolated groups of mussels (primarily of *Mytilus edulis galloprovincialis* [formerly *M. edulis aoteanus*]), barnacles (e.g., *Chamaesipho columna*), and encrusting algae. Adjacent low-diversity areas were dominated by *Lithothamnion* sp., encrusting ascidians (e.g., *Didemnum* sp. [red]), and encrusting sponges (e.g., *Tedania* sp.)

The large area of low diversity past 25 m in horizontal distance at Crooked Arm could be attributed, in part, to a previous landslide. This was evidenced above the waterline by fallen trees and scour marks visible on the upper slope. Subtidal evidence of this landslide consisted of terrigenous debris and accumulated rubble at deeper depths. The exact spatial extent of the landslide damage was difficult to ascertain in reference to the observed patterns of diversity, as there was a small region of relatively high diversity at ~18 m depth and 35 m horizontal distance (Plate 1A). Higher densities of urchins also occurred within the region of low diversity, particularly at 5 and 10 m depths (F. Smith, personal observations), suggesting that sea urchin grazing could contribute to the low epifaunal diversity in this area.

A patch of high diversity at Ranson Head encompassed an area of ~300 m², and the upper limit of high diversity occurred just below 5 m (Plate 1C). Dominant

species within the high-diversity patch included brachiopods (e.g., *Notosaria*) and massive (*Eurypon* sp.) and encrusting sponges (*Aegogropila* sp.) Numerous bryozoan species also characterized this patch of high diversity, including two species of *Tubulipora*, *Caberea* sp., and *Cellaria* sp. The shallow assemblages at this site were principally composed of mussels (i.e., *Mytilus* and *Aulacomya ater maoriana*) and bare rock substrata. The low-diversity areas on deeper sections of the wall were dominated by calcareous algae (e.g., *Lithothamnion* sp. and *Corallina officinalis*) and bare rock substrata. Severe grazing by large numbers of the sea urchin *Pseudechinus* in the low-diversity area could account for much of the bare rock and denuded substrata at this site (F. Smith, *personal observations*). However, the precise spatial extent of the grazed and nongrazed areas was difficult to discern.

The largest documented patch of high diversity occurred at Bauza Island, encompassing an area of ~660 m² (Plate 1E). The highest diversity values at this site were concentrated at deeper depths (18 m) with a short extension of high diversity between 5 and 10 m depth. Diversity contours were sharply demarcated from 3 to 5 m, with the upper bound of high diversity at ~4 m in depth (Plate 1E). The high-diversity patch at this site was largely dominated by erect bryozoans (e.g., *Hastingsia* sp., *Mucropetraliella lingulata*, and *Bugula* sp.) but also contained numerous ascidians (e.g., *Synoicum* sp. and *Aplidium* sp. IV) and sponges (e.g., *Cacospongia* sp.) The deeper areas of low diversity (i.e., at 10 and 18 m) were dominated by *Lithothamnion* sp. and encrusting ascidians (e.g., *Didemnum lithostrotum*). Shallow depths of relatively high diversity (i.e., at 5 m depth) were dominated by hydroids, encrusting sponges, and anemones (e.g., *Corynactis rupeola*). At shallow depths (i.e., 3 m), which are normally within the LSL, large beds of *Mytilus*, *Chamaesipho*, and encrusting sponges were dominant species in these assemblages. The area of lower diversity at this site could be partially attributed to a small landslide, which was evidenced by fallen trees and ferns above the waterline. Subtidally, large amounts of terrigenous debris and rubble were present on ledges in the area beyond 25 m in horizontal distance (Plate 1E). The exact spatial extent of the landslide damage at this site was impossible to determine.

High-diversity patches at all sites were also characterized by a large percentage of species that only

occurred within these areas, indicating localized distributions within the 20 × 50 m plots. Of the total number of species found within high-diversity patches, 42% of these were locally restricted to the 430-m² patch at Crooked Arm, 40% in the 300-m² patch at Ranson Head, and 24% in the 660 m² patch at Bauza Island (F. Smith and K. R. Grange, *unpublished manuscript*).

The analysis of the kriging variance matrices showed that only 5–7% of the 20 × 50 m plots at all three sites were not well described by the interpolations. These areas were located in the upper right and left corners of the plots where there were lower numbers of replicate photo quadrats at 3 and 5 m depth. Visual surveys in these locations indicated that the diversity measures were similar across the entire depth strata (F. Smith, *personal observations*).

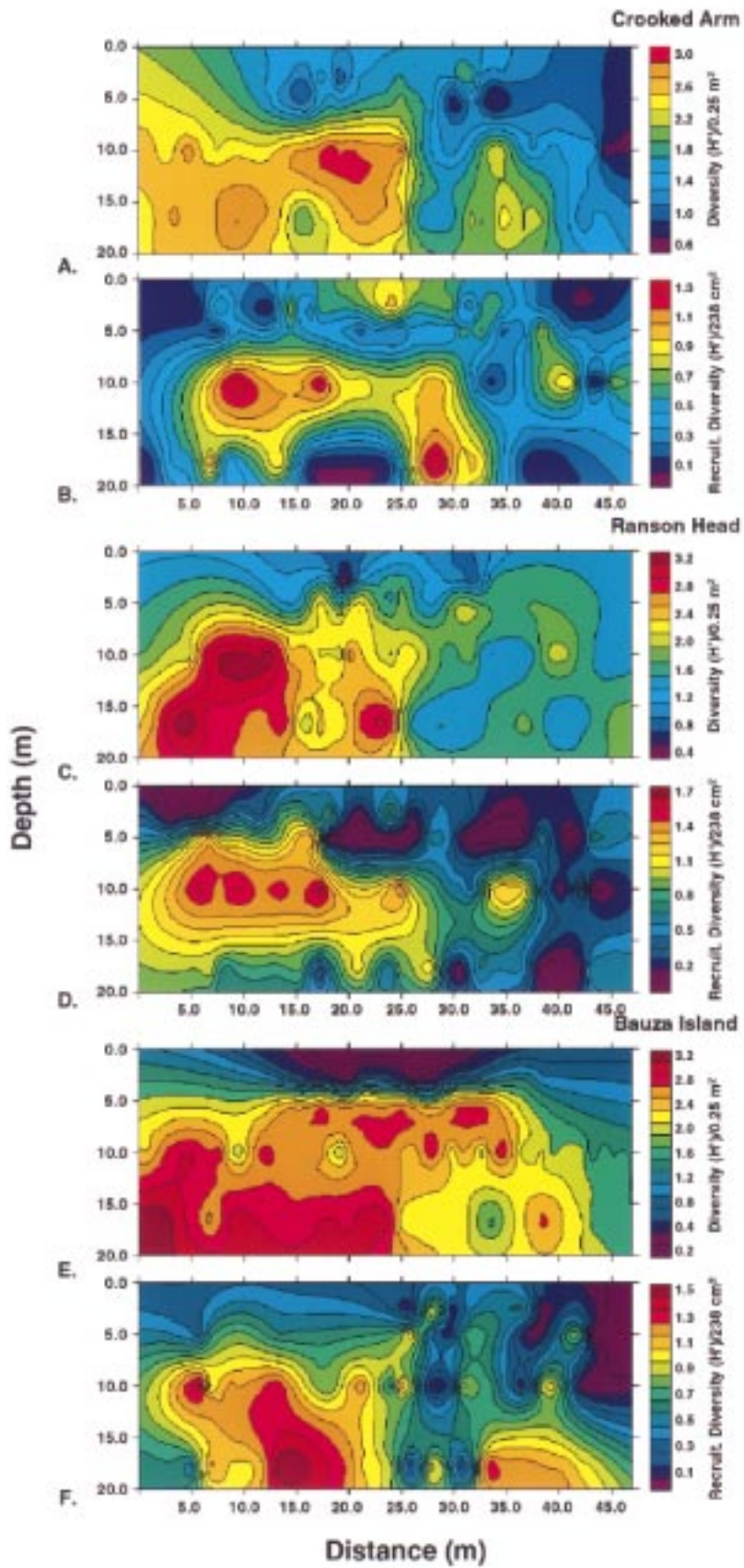
Trends in the vertical patterns of species diversity at each of the three sites indicated that the upper limits of high diversity ($H' \geq 2.0/0.25$ m²) were deeper with increasing distance from the mouth of the fjord (i.e., the open ocean). Crooked Arm, the innermost site, had the deepest upper limit of high diversity at 7.0 m, while the upper limit of high diversity at Ranson Head was just below 5 m depth and the upper limit at Bauza Island was just above 5 m depth. Corresponding depths of the low-salinity surface layer (LSL) were found to be extremely variable during the time of study, coinciding with more detailed time-series measurements of depth fluctuations of the LSL (Grange et al. 1991, Witman and Grange 1998). Variations of the depth of the LSL are largely dependent upon rainfall and runoff patterns within the Doubtful Sound region (Stanton and Pickard 1981). Salinity profiles taken during a single extreme rainfall event (~70 mm over a 24-h period) illustrated the dynamic characteristics of the LSL and showed a correspondence between the maximum depression of the LSL (i.e., 30 ppt) with the upper limit of high diversity (i.e., $H' \geq 2.0/0.25$ m²) at each of the three sites (Fig. 4).

Patterns of recruitment diversity.—The spatial patterns of recruitment diversity after 3 mo consisted of localized areas of high recruitment diversity (Plate 1). In general, recruitment diversity was lowest at shallow depths and decreased with increasing horizontal distance from the centers of high diversity at all three sites.

The pattern of recruitment at Crooked Arm consisted of two centers of high recruitment diversity: one at 10 m

→

PLATE 1. Contours of epifaunal species diversity (A—Crooked Arm, C—Ranson Head, and E—Bauza Island) and recruitment diversity (B—Crooked Arm, D—Ranson Head, and F—Bauza Island) after 3 mo within the approximated 20 × 50 m study plots. Crooked Arm (A, B) shows two localized areas of high recruitment diversity ($H' \geq 1.0/238$ cm²). The larger area of high recruitment diversity overlapped with high epifaunal diversity ($H' \geq 2.0/0.25$ m²), and the smaller area occurred in the adjacent low-diversity area past 25 m in horizontal distance. At Ranson Head (C, D), the pattern of high recruitment diversity ($H' \geq 1.0/238$ cm²) corresponded to the localized area of high epifaunal diversity ($H' \geq 2.0/0.25$ m²). At Bauza Island (E, F), the larger area of high recruitment diversity ($H' \geq 1.0/238$ cm²) corresponded to the area of higher epifaunal diversity ($H' \geq 2.0/0.25$ m²), and the smaller area occurred at deeper depths in an area of lower epifaunal diversity.



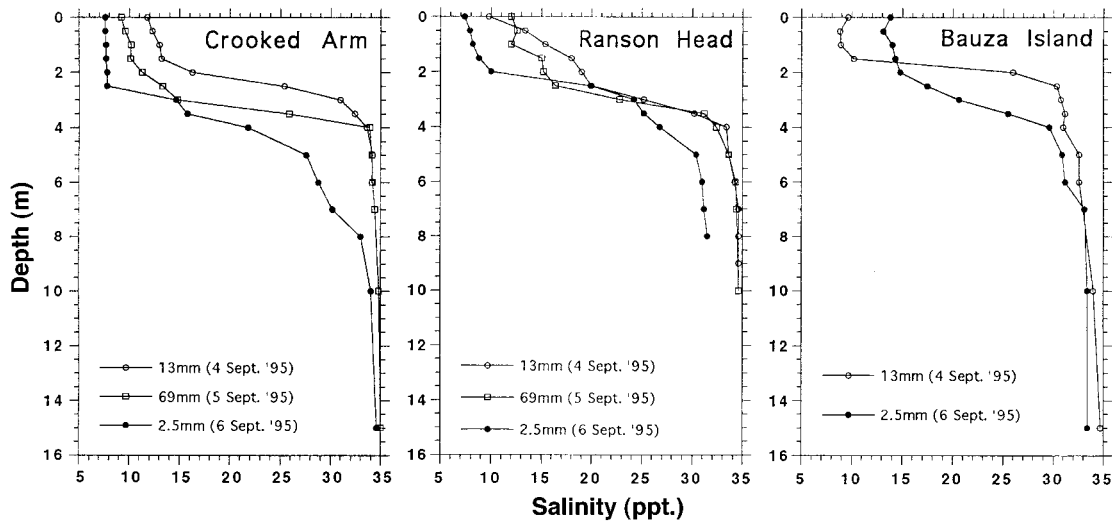


FIG. 4. Salinity profiles at each of the three study sites after a single large rainfall event (i.e., 69 mm over a 24-h period) that occurred on 5 September 1995. Note that the maximum depression of the 30 ppt corresponded to the upper limit of high epifaunal diversity ($H' \geq 2.0/0.25 \text{ m}^2$) at each of the three sites (Plate 1).

depth, which corresponded to the patch of high epifaunal diversity, and the second centered at 18 m just outside the high epifaunal diversity patch (Plate 1A, B). Recruitment diversity at Ranson Head resembled the pattern of epifaunal diversity having large overlapping regions, and an abrupt decrease in epifaunal species diversity at $\sim 25 \text{ m}$ horizontal distance corresponded to a decline in the diversity of recruits (Plate 1C, D). The pattern of high recruitment diversity at Bauza Island had two relatively large centers located at $\sim 18 \text{ m}$ depth. The larger area of high recruitment diversity at Bauza Island was situated within the area of high recruitment diversity and the smaller area occurred in the area of lower diversity past 35 m in horizontal distance (Plate 1E, F).

At all three sites, the types of species found recruiting on the tiles were a subset of those found in the rock wall assemblages. Species commonly recorded included Polychaeta (*Spirorbis* sp., *Galeolaria hystrix*, *Pomatoceros carniferus*), Bryozoa (*Beania* sp., *Bitectipora* sp., *Schizomittina*, *Platonea* sp., *Tubulipora* sp., *Smittoidea maunganuiensis*, *Cellaria* sp.), Hydrozoa (Family Sertularidae), and Ascidiacea (*Didemnum* sp.).

Variance matrices of the recruitment diversity contours showed that areas of high variance were concentrated in the upper left- and right-hand corners of the plots, covering $<10\%$ of the plots. In these instances, fewer numbers of replicates were located in these areas due to storm damage or equipment malfunction (particularly at the Bauza Island site). The pattern of recruitment within these areas was therefore not well described by the interpolation function.

Relationship between recruitment and epifaunal diversity.—Analysis of variance of recruitment diversity indicated that main effects of depth and “habitat” (in vs. out of the high-diversity patches) were significant

at Crooked Arm, Ranson Head, and Bauza Island (Table 1). These results also showed nonsignificant main effects of cage treatment at all three sites, indicating that predation did not influence the observed patterns of recruitment. Tukey multicomparison tests illustrated that recruitment diversity was highest within high diversity patches, particularly at 10 m depth (Table 1).

Patterns of recruitment densities for individual species showed similar trends to the patterns of recruitment diversity, where there were significant main effects of depth and habitat for six species at Crooked Arm, five species at Ranson Head, and two species at Bauza Island (Table 2). *Spirorbis* showed the most coherent trend across all three sites, having significant main effects of depth and habitat. Results for bryozoans (e.g., *Schizomittina*, *Tubulipora*, and *Bitectipora*) were similar at Crooked Arm and Ranson Head, having significant main effects of depth and habitat. At Bauza Island, *Schizomittina* had a significant depth effect only while *Bitectipora* recruitment was nonsignificant. Densities of hydroids were significant at Crooked Arm and Bauza Island, with main and higher order interactions, and at Ranson Head there was a significant effect for depth only.

Since the depth of the LSL fluctuates over daily time scales and because the precise time of recruitment during the 3-mo period was unknown, there was no basis to determine more specifically the importance of water-column structure on the observed patterns of recruitment. However, the spatial patterns of recruitment diversity showed that the upper limits of high recruitment diversity (i.e., $H' \leq 1.0/238 \text{ cm}^2$) were shallower than the upper limit of high epifaunal diversity (Plate 1).

The relationship between the number of species recruiting onto the tiles and epifaunal diversity was characterized by a positive linear relationship. At depths of

TABLE 1. (A) Analysis of variance table for recruitment diversity (H')/238 cm² and (B) P values for Tukey multicomparison tests. Significant P values are shown in boldface type.

A)	Analysis of variance						
	Source	SS	df	MS	F	P	
Crooked Arm							
Depth (D)	2.678	3	0.892	10.204	< 0.001		
Treatment (T)	0.131	2	0.065	0.747	0.477		
Habitat (H)	1.917	1	1.917	21.908	< 0.001		
D × T	0.618	6	0.103	1.177	0.329		
D × H	2.541	3	0.847	9.683	< 0.001		
T × H	0.075	2	0.038	0.430	0.652		
D × T × H	0.349	6	0.058	0.666	0.678		
Error	6.036	69	0.087				
Cochran's C	0.1171						
Ranson Head							
Depth	5.991	3	1.997	12.297	< 0.001		
Treatment	0.376	2	0.188	1.158	0.320		
Habitat	2.759	1	2.758	16.987	< 0.001		
D × T	0.618	6	0.103	0.634	0.702		
D × H	2.437	3	0.812	5.001	0.003		
T × H	0.030	2	0.015	0.094	0.911		
D × T × H	1.221	6	0.204	1.253	0.291		
Error	10.718	66	0.162				
Cochran's C	0.1114						
Bauza Island							
Depth	2.914	3	0.971	5.686	0.002		
Treatment	0.368	2	0.184	1.078	0.349		
Habitat	0.856	1	0.856	5.013	0.030		
D × T	0.842	6	0.140	0.822	0.559		
D × H	0.769	3	0.256	1.501	0.226		
T × H	0.294	2	0.147	0.861	0.429		
D × T × H	1.672	6	0.279	1.631	0.160		
Error	8.029	47	0.171				
Cochran's C	0.1214						
B) Tukey multicomparison tests							
	3 m in	3 m out	5 m in	5 m out	10 m in	10 m out	18 m in
Crooked Arm							
3 m in	1.000						
3 m out	0.982	1.000					
5 m in	0.722	0.996	1.000				
5 m out	0.999	0.999	0.932	1.000			
10 m in	0.001	< 0.001	< 0.001	< 0.001	1.000		
10 m out	0.995	0.697	0.258	0.926	0.011	1.000	
18 m in	0.121	0.010	0.001	0.039	0.615	0.483	1.000
18 m out	0.056	0.390	0.834	0.163	< 0.001	0.006	< 0.001
Ranson Head							
3 m in	1.000						
3 m out	0.972	1.000					
5 m in	0.458	0.986	1.000				
5 m out	0.964	0.441	0.028	1.000			
10 m in	< 0.001	< 0.001	0.001	< 0.001	1.000		
10 m out	0.564	0.996	1.000	0.044	0.001	1.000	
18 m in	0.378	0.971	1.000	0.019	0.002	0.999	1.000
18 m out	0.999	0.997	0.622	0.778	< 0.001	0.733	0.000
Bauza Island							
3 m in	1.000						
3 m out	0.999	1.000					
5 m in	0.993	0.824	1.000				
5 m out	1.000	0.990	0.988	1.000			
10 m in	0.213	0.028	0.410	0.024	1.000		
10 m out	0.999	0.955	0.998	0.999	0.029	1.000	
18 m in	0.344	0.059	0.635	0.067	0.999	0.084	1.000
18 m out	0.558	0.139	0.881	0.204	0.975	0.262	0.000

TABLE 2. Analysis of variance P values and Cochran's C test values on $\sqrt{(x+1)}$ transformed recruitment densities/238 cm² for commonly occurring species at three sites within Doubtful Sound, Fiordland. Significant probabilities ($\alpha < 0.03$) are indicated in boldface type.

Source	<i>Spirorbis</i>	<i>Galeolaria</i>	<i>Beania</i>	<i>Schizomittina</i>	<i>Tubulipora</i> sp. 1	<i>Bitectipora</i>	<i>Cellaria</i>	Hydroid
Crooked Arm								
Depth	<0.001	<0.001	0.001	0.019	<0.001	<0.001	0.346	<0.001
Treatment	0.582	0.187	0.886	0.361	0.547	0.369	0.090	0.204
Habitat	0.003	0.408	0.377	0.002	0.018	<0.001	0.027	0.006
D × T	0.602	<0.001	0.972	0.228	0.944	0.713	0.786	0.554
D × H	0.643	0.103	0.029	0.150	0.123	0.001	0.995	0.008
T × H	0.368	0.250	0.436	0.757	0.914	0.177	0.247	0.075
D × T × H	0.298	0.858	0.927	0.743	0.324	0.488	0.612	0.440
Cochran's C	0.1992	0.2023	0.3835	0.3473	0.4390	0.3272	0.1905	0.4605
							Barnacles	
Ranson Head								
Depth	<0.001	<0.001	0.551	0.020	<0.001	<0.001	0.006	0.013
Treatment	0.415	0.033	0.223	0.877	0.654	0.173	0.943	0.265
Habitat	<0.001	0.002	0.015	0.007	0.002	<0.001	0.068	0.080
D × T	0.617	0.527	0.564	0.843	0.906	0.584	0.999	0.825
D × H	0.306	0.103	0.689	0.075	<0.001	<0.001	0.037	0.109
T × H	0.294	0.482	0.287	0.683	0.180	0.173	0.797	0.510
D × T × H	0.863	0.837	0.819	0.969	0.039	0.584	0.976	0.872
Cochran's C	0.2851	0.1790	0.4666	0.2561	0.6101	0.4546	0.5454	0.3724
					<i>Didemnum</i> sp.			
Bauza Island								
Depth	<0.001	0.005	0.092	0.010	<0.001	0.153		<0.001
Treatment	0.412	0.511	0.231	0.907	0.623	0.969		0.169
Habitat	0.015	0.152	0.790	0.060	0.729	0.097		0.732
D × T	0.739	0.729	0.627	0.800	0.685	0.998		0.016
D × H	0.321	0.371	0.372	0.069	0.894	0.270		0.003
T × H	0.796	0.984	0.987	0.954	0.913	0.731		0.125
D × T × H	0.492	0.816	0.919	1.000	0.893	0.819		0.099
Cochran's C	0.1458	0.2392	0.3280	0.1690	0.4686	0.2242		0.5964

the highest epifaunal diversity (i.e., 10 m), the linear model explained 27–57% of the variance (Fig. 5, Table 3). At 18 m depth at Crooked Arm and Ranson Head, 24 and 22% of the variance could be explained by the linear model, while at 18 m at Bauza Island only 1% of the variance was explained. In areas of low diversity, the relationship between recruiting species and wall diversity was not well explained by the linear model. Regressions from shallow depths (i.e., 3 and 5 m), where there was low epifaunal diversity and low recruitment, had low r^2 values and nonsignificant F ratios at all three sites. The deviation from linearity tests showed only two of the regressions significantly deviated from linearity (i.e., 18 m at Crooked Arm and 5 m at Bauza Island). Second-order polynomial fits were used to characterize these relationships, resulting in the equations: $y = 1.734 + 0.603x - 0.084x^2$, $r^2 = 0.497$ (Crooked Arm, 18 m) and $y = 2.086 + 0.429x - 0.083x^2$, $r^2 = 0.463$ (Bauza Island, 5 m).

DISCUSSION

Patterns of epifaunal diversity.—Epifaunal assemblages of the rock walls of Doubtful Sound, Fiordland, consisted of localized patches of high species diversity, having areas of 300–660 m², centered at ~10 m depth. Shallow-water assemblages of low diversity, dominated by mussels and bare rock, bounded the upper limit of high epifaunal diversity. The patches of high diver-

sity were bound horizontally by extensive low-diversity areas (i.e., over thousands of meters), dominated by calcareous algae and bare rock substrata. Although there are no data presently available to determine all factors important in creating this broadscale pattern, processes occurring on ecological time scales can account for some aspects of heterogeneity associated with these patches. Physical influences of the low-salinity surface layer may affect vertical diversity patterns, and large-scale physical and biological disturbances can create horizontal discontinuities in the patterns of epifaunal diversity.

The vertical patterns of epifaunal diversity were related to the depth of the low-salinity surface layer, where the upper limits of high diversity corresponded to the deepest recorded depths of the LSL (i.e., 30 ppt) at all three sites. A salinity of 30 ppt has been suggested to be a physiological limit that distinguishes between marine and estuarine species (Dahl 1956), and salinity has been recognized as an important variable influencing the distribution patterns for marine organisms (Kinne 1971, Boesch 1977). Fluctuations in salinity after large rainfall events have also accounted for the mass mortality of marine organisms (Goodbody 1961), and may be similarly important for shallow-water fjord assemblages.

The species composition of the fjord epifaunal assemblages also changes drastically at depths bounded

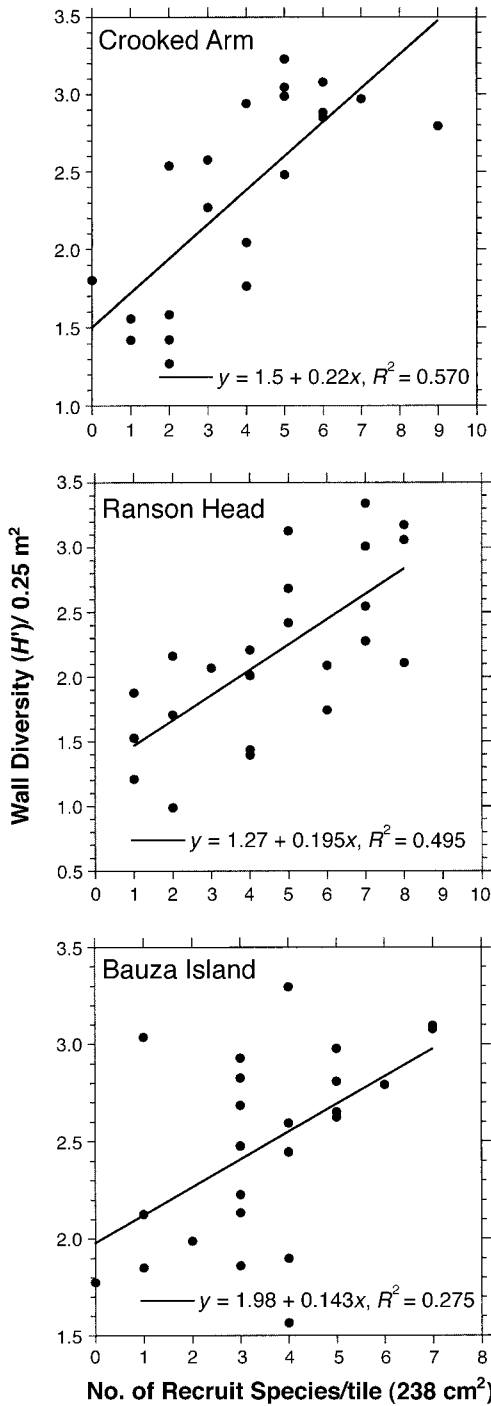


FIG. 5. Linear regressions of species diversity ($H'/0.25 \text{ m}^2$) and the number of species recruiting onto the tile (238 cm^2) from the 10 m depth at three replicate sites.

by the vertical displacements of the LSL, suggesting that both the number and the types of species are influenced by the LSL (F. Smith and K. R. Grange, unpublished manuscript). The presence of the LSL may also affect patterns of diversity by altering the distribution and abundance of macropredators (and, hence,

predation pressure), which could account for the changes in community composition and diversity along a depth gradient (Witman and Grange 1998). Since the LSL represents a dynamic feature of fjords and other estuarine regions, extreme rainfall events may play a significant role in influencing patterns of diversity over larger spatial scales (e.g., over an entire catchment area).

Both physical and biological disturbances can create horizontal discontinuities of epifaunal diversity. Landslides and intense sea urchin grazing have a similar influence on observed patterns over hundreds of meters, creating abrupt transitions between areas of high and low epifaunal diversity over a few meters. The extensive low-diversity areas created by landslides or large-scale sea urchin grazing are unlikely to recover through vegetative growth from the adjacent community, as in type-1 (Connell and Keough 1985) or embedded patches (Holt et al. 1995). This mechanism of recovery is more likely to occur on smaller spatial scales (i.e., $<1.0 \text{ m}$) and over longer time periods. The recovery of these extensive areas of low epifaunal diversity could therefore be largely dependent upon recruitment from epifaunal assemblages outside the immediate area.

Although there are obvious structuring processes within the fjords occurring on ecological time scales, the pattern of localized patches of high diversity surrounded by thousands of meters of low diversity cannot be explained solely by landslides and severe grazing by sea urchins. For example, there are extensive areas of low diversity within the fjords that do not appear to have been under the influence of landslides or intense urchin grazing. The initial colonization and development of a high diversity assemblage could be an important factor contributing to this pattern. Alternately, the indirect influences of landslide-derived sediments or limited food supply to the epifaunal assemblages could potentially affect diversity patterns over thousands of meters of habitat (Evans et al. 1980, Farrow et al. 1983).

Patterns of recruitment diversity.—At each of the three sites, high recruitment diversity occurred in localized areas and corresponded to the patterns of epifaunal diversity on a similar spatial scale. In general, areas of high recruitment diversity corresponded to the patches of high epifaunal diversity, and low recruitment diversity tended to occur at shallow depths. The occurrence of areas of high recruitment diversity slightly beyond the corresponding areas of high epifaunal diversity suggests that colonization of these areas may be taking place (i.e., over the scale of meters). For example, there was approximately a 7-m extension from the area of high diversity into the area of low diversity at Crooked Arm (Plate 1A, B). At Ranson Head, the high recruitment diversity extended $\sim 3 \text{ m}$ from the high epifaunal diversity patch, with a small isolated patch 10 m from the high epifaunal diversity

TABLE 3. Tabulated results of the regression analysis and ANOVA of the relationship between the number of species (S) in 3-mo recruitment (per 238 cm²) and diversity (H') of adjacent rock walls (per 0.25 m²). Regressions for the 10 m depth strata at each site are plotted in Fig. 5.

Site	Regression analysis		Analysis of variance		Deviation from linearity	
	N	R^2	F	P	F	P
Crooked Arm						
3 m	17	0.150	2.644	0.125	1.440	0.285
5 m	16	0.030	0.427	0.524	0.547	0.661
10 m	21	0.570	25.184	0.001	1.268	0.342
18 m	24	0.240	6.935	0.015	4.820	0.008
Ranson Head						
3 m	15	0.008	0.100	0.756	0.056	0.982
5 m	17	0.013	0.199	0.662	1.457	0.280
10 m	24	0.495	21.545	0.001	1.480	0.247
18 m	24	0.220	6.203	0.021	1.278	0.315
Bauza Island						
3 m	7	0.091	0.498	0.512	0.827	0.415
5 m	15	0.018	0.241	0.632	4.197	0.037
10 m	24	0.275	8.346	0.009	0.374	0.885
18 m	23	0.013	0.270	0.609	0.741	0.604

(Plate 1C, D). At Bauza Island, a broad, isolated patch of high recruitment diversity extended ~15 m from the high epifaunal diversity (Plate 1E, F). Following the development of the areas of high recruitment diversity in areas of low epifaunal diversity would determine whether epifaunal diversity is increasing in these areas.

Low recruitment diversity at shallow depths (i.e., 3 and 5 m) may reflect detrimental influences of the LSL on invertebrate larvae that could potentially recruit to shallow areas. The pycnocline associated with bottom of the LSL may act as a physical barrier to larvae (Harder 1968). Entrainment into this layer has been considered as a significant source of mortality for larvae, propagules, or newly settled recruits that are not physiologically tolerant of low-salinity conditions (Thorson 1966). Alternately, the microclimate created by the low salinity could deter recruitment at these depths.

The direction and magnitude of flow in the LSL may have an important influence on the flow regime just below the pycnocline (Rattray 1967, Farmer and Free-land 1983) which could directly influence dispersal and recruitment at shallow depths. Larvae or propagules entrained or released within the LSL would have a tendency to be transported towards the mouth of the fjord, following the directionality associated with barotropically-driven flows. Higher flow regimes within the LSL may also be an important factor limiting recruitment for some species (e.g., byzoans) at shallow depths through the failure of larvae or propagules to adhere to the substrata.

Dynamic aspects of the fjord water-column characteristics, with daily and seasonal variations in the depth of the LSL, could have important influences on observed patterns of recruitment. For example, larvae that recruit into shallow areas during times of higher salinities or lower flow regimes may encounter low-salinity

conditions or higher flow if the LSL depth increases. At present, the longer term influences of the LSL dynamics on community recruitment is poorly understood for these assemblages.

Although the 1-yr preliminary investigation at Tricky Cove suggested that recruitment patterns after 3 mo were representative for the species within these epifaunal assemblages, the timing of recruitment events may have implications for longer term dynamics of these assemblages. For example, species that recruit during different times of the year may play an important role in affecting the growth and recruitment of species documented within this study. Interannual variations in the reproductive output of species may also produce different patterns of recruitment.

Relationship between recruitment and epifaunal diversity.—Analysis of experimental results showed that the patterns of recruitment corresponded to the high-diversity patches on similar spatial scales, both in respect to density of recruits and the number of recruiting species. Analysis of variance also indicated that there were no significant effects of cage treatment on recruitment diversity, which indicates that predation plays a limited role in affecting the short-term recruitment patterns for these assemblages. These relationships were evident at all three sites (i.e., significant effects of depth and habitat with no significant effect of cage treatment), which were separated by 3–6 kilometers.

Although there is no information presently available to unequivocally determine the origin of the recruits, the relationship between epifaunal diversity and recruitment could be partially explained by the life history characteristics of organisms within these assemblages. Many of the organisms within these assemblages are characterized by short-lived, lecithotrophic larvae, such as ascidians (Olson 1985, Grosberg 1987),

sponges (Bergquist 1978, Ayling 1980, Battershill and Bergquist 1990), bryozoans (Ryland 1970), solitary corals (Gerrodette 1981), soft corals (Sebens 1986), serpulid polychaetes (Keough and Downes 1982), and brachiopods (Percival 1949, Rudwick 1970). Other species within these assemblages are characterized by having gregarious settlement patterns or by recruiting near conspecifics (e.g., Knight-Jones 1951, Keough 1984b). Although the duration of larval life has been estimated for some of these epifaunal taxa, our knowledge of how far these larvae actually disperse in nature is extremely limited (Obrebski 1979, Olson 1985, Olson and McPherson 1987, Graham and Sebens 1996). It is possible that the larvae or propagules in this system recruit soon after dispersal and remain within the patch of origin.

Reduced current flow within the fjords (Stanton 1978) could play a significant role in the limitation of larval dispersal, particularly with potentially short-lived larvae or propagules. Large current eddies or entrainment processes (Stancyk and Feller 1986, Bingham 1992) within the fjord may also concentrate or restrict propagules to certain areas of the fjord. Estimates from drifter studies suggest that hydrographic features on the scale of kilometers have a limited role in determining the recruitment patterns in relation to diversity patches of hundreds of square meters in area (F. Smith, *unpublished data*). However, alabaster dissolution studies suggest that flow over spatial scales of hundreds of meters may be important for recruitment on a similar scale (F. Smith, *unpublished data*).

Increased biogenic structure associated with the patches of high epifaunal diversity could also influence recruitment by reducing water motion and facilitating settlement (e.g., Dean 1981, Eckman 1983, 1990, Sebens 1991, Carr 1994). Larval association with substratum characteristics or the biogenic structure of the communities may result in higher abundances of larval forms in areas of high epifaunal diversity and decreased abundance with increasing distance from the wall (Marilave 1989, Graham and Sebens 1996). These factors could both contribute to higher recruitment in the high epifaunal diversity patches.

The linkage of recruitment and epifaunal diversity over scales of hundreds of meters suggests that recruitment does not function as a compensatory mechanism (*sensu* Connell et al. 1984) for these epifaunal assemblages. As patches of high epifaunal diversity are likely to represent regions of higher competition for newly settled recruits and regions of increased risk of mortality from ingestion by suspension-feeders and microcarnivores (Sebens and Koehl 1984, Young 1988), the selective advantages of recruiting into an area of high epifaunal diversity are uncertain. The limited areas of high recruitment diversity documented outside the high epifaunal diversity patches could represent areas of lower competition and predation by suspension-feeders and serve as a mechanism leading to the

development of high-diversity patches. The location of the high recruitment diversity may also be related to prevailing current flow in the lower saline layers, which underscores the importance of the LSL on altering the flow regimes of the lower saline layer and determining patterns of diversity.

We suggest that the spatial patterns of epifaunal diversity may be maintained by a feedback mechanism involving the interaction of the increased biogenic structure of the high-diversity patches, which enhances larval recruitment or restricts the dispersal of propagules. Additional feedback could occur through limited dispersal of short-lived lecithotrophic larvae or propagules and recruitment near conspecifics. Feedback between the organism and its environment has been addressed on smaller spatial scales (e.g., Southwood 1977, Buss 1981, Brault and Bouget 1985, Patterson 1991, Abelson et al. 1993) and may serve to maintain patterns on larger spatial scales. Such feedback mechanisms would tend to maintain localized patches of high diversity over hundreds of meters and play an important role in the dynamics of these assemblages.

For example, a preponderance of species characterized by limited dispersal of larvae or propagules and species that recruit near conspecifics supports the hypothesis that some populations within these assemblages are self-perpetuating. Without self-seeding recruitment, these patches would likely to disappear over time, assuming that asexual propagation is minimal (Pulliam 1988). However, to date, the actual larval dispersal distances for the majority of the New Zealand fjord epifaunal species are unstudied and unknown.

The high diversity of these epifaunal assemblages compared to those in regions of the North Island of New Zealand (Grange 1986) or regions of the Northeast Pacific, Northwest Atlantic, or Eastern Caribbean (J. D. Witman, *unpublished data*) may be partially explained by recruitment as a diversity maintaining mechanism. High densities and large numbers of species recruiting into a localized area may allow for the coexistence of larger numbers of species in localized areas over hundreds of meters of continuous habitat. The diversity of these assemblages may also be attributed to diverse habitat structure of the epifaunal patches (e.g., Kohn 1971, Roth 1976, Connell and Slayter 1977, Aronson and Precht 1995).

Although results of this study demonstrate how patterns of species diversity are related to processes operating over hundreds of meters of continuous habitat and between sites separated by kilometers, diversity patterns are likely to be influenced by processes operating on larger spatial and longer temporal scales than those considered in this study. For example, evolutionary and biogeographic factors that determine the regional species pool may have a strong influence on the diversity of local communities (Ricklefs 1987, Connell and Lawton 1992, Schluter and Ricklefs 1993, Connell and Karlson 1996) and may be similarly important

for rock wall assemblages (J. D. Witman, F. Smith, and R. J. Etter, *unpublished data*). How these results can be extended to explain patterns over larger spatial scales requires more information on the relationship between regional and local processes that influence these communities.

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