

Effects of freshwater input on shallow-water infaunal communities in Doubtful Sound, New Zealand

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ABSTRACT: Infaunal community structure is sensitive to both the range of salinity values and timing of exposure wrought by the time course and magnitude of freshwater input to estuaries. We sampled macro-infauna (>1 mm) from soft sediment habitat at 8 shallow sites (2 m below MHW; mean high water) within 4 regions in the Doubtful–Thompson Sound complex, a fjord in southwestern New Zealand. This fjord receives a large influx of freshwater from natural and anthropogenic sources that form a distinct low salinity surface layer and drive mean estuarine circulation. Shallow water soft sediment habitat in the fjord is highly fragmented and subject to strong environmental gradients shaped by freshwater input patterns. Infaunal community structure in the inner region of Doubtful Sound was consistently different from other regions of the fjord. This was evidenced by a low abundance of bivalves, decapods, and polychaetes in the family Orbiniidae, and elevated abundance of amphipods and polychaetes in the family Neredidae. An analysis of taxonomic richness among regions revealed that the inner regions of Doubtful Sound are also the least rich in the complex. Both taxonomic richness and patterns in abundance of the major taxa covary with physical information on the return times for low salinity events, thickness, and patterns in mixing in the freshwater layer. These results are consistent with a large impact of the persistent discharge of freshwater from the Manapouri power station on shallow water infaunal communities in the fjord. The loss of bivalves in particular has large implications for patterns in food-web structure and function in this system.

KEY WORDS: Fjord · Infauna · Diversity · Salinity

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INTRODUCTION

The influence of salinity on the distribution of organisms has been a central theme in studies of estuarine faunal diversity (Kinne 1966, 1975, Remane & Schlieper 1971, McLusky & Elliot 2004). Generally, these studies report a diminishing number of benthic species along gradients from marine to brackish water, with lowest taxonomic richness occurring in waters of salinity 4 to 6, though seasonality and variations in the salinity regime are important components of the observed relationship (Boesch 1977, Gainey & Greenberg 1977, McLusky et al. 1993, Ysebaert et al. 1993, Schlacher & Wooldridge 1996, Attrill & Power 2000). A corollary is that changes brought to the salinity gradient and pattern in salinity variation can induce large shifts in community composition and ecosystem func-

tion within estuaries (e.g. Kowalewski et al. 2000, Rodriguez et al. 2001, Lercari & Defeo 2003, Tallis et al. 2004). Such environmental change may interact strongly with sediment dynamics and carbon flux in these systems (e.g. Thrush et al. 2003). The influence of salinity on biological communities is particularly apparent in the estuarine regions of Fiordland, New Zealand where freshwater input from natural and anthropogenic sources is extreme.

The high annual rainfall (>7000 mm yr⁻¹) in the Fiordland region results in a well-defined surface low salinity layer (LSL) that drives estuarine circulation in each of the region's 14 fjords (Stanton & Pickard 1981). The presence of the LSL is a common feature but is more pronounced and persistent in Doubtful Sound due to the additional input of freshwater (450 to 510 m³ s⁻¹) by the Manapouri hydroelectric power plant to

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Deep Cove (McCully 1996, Gibbs et al. 2000, Peake et al. 2001, Wing et al. 2003). Although the variability in thickness of the LSL is strongly correlated to wind and rainfall events (Gibbs et al. 2000), Boyle et al. (2001) noted that changes correspond well to variability of the power plant outflow. Comparisons with the nearby Thompson-Bradshaw Sound reveal that low surface salinity (<5) is more persistent at Deep Cove over the course of drought and high rain periods than at Precipice Cove and Gaer Arm, at the head of Bradshaw Sound, which has natural freshwater inputs (McCully 1996, Tallis et al. 2004, Wing et al. 2003).

The power plant, established in 1969, has more than doubled the input of freshwater to the head of the Sound (Stanton & Pickard 1981), reducing the relative contribution from the natural rainfall and runoff to a third of the total input in the fjord complex (McCully 1996). Subsequent changes included a drop in surface salinity levels by as much as 20 units for the inner parts of Doubtful Sound, as well as a reduction in variability of the salinity regime. Although the range of salinity at 3 m depth in Deep Cove has been found to vary between almost fresh and oceanic conditions (Gibbs et al. 2000), the chance of oceanic salinity occurring in the intertidal area of the inner parts of Doubtful Sound is now small (Tallis et al. 2004). The thickness of the LSL ranges from approximately 1 m at the entrance of the fjord to between 5 and 12 m at Deep Cove, thus exceeding the tidal amplitude of 2 m at the head of the Sound (e.g. McCully 1996). Intertidal and, in some places, shallow, subtidal communities are thus likely to be continuously exposed to low salinity conditions (<5) at Deep Cove.

These observed changes in the salinity regime are large relative to similarly affected systems worldwide. In other systems where freshwater discharge has altered temperature, salinity and nutrient regimes investigators have observed significant changes in feeding and mortality of grazers (Irlandi et al. 1997); composition of meiofaunal (Montagna & Kalke 1992) and macrofaunal communities (Lercari & Defeo 1999, 2003); and abundance and distribution of nekton and hyperbenthos (Attrill & Power 2000, Drake et al. 2002). Within these studies, investigators observed effects of the magnitude and timing of salinity fluctuations (e.g. Irlandi et al. 1997) and differential effects on key community members (Lercari & Defeo 2003). Since salinity is one of the primary environmental influences on species distribution and abundance, changes wrought by canal discharge and other water management schemes can have widely distributed effects on coastal marine systems (e.g. Lercari et al. 2002).

This is apparent in Doubtful Sound where the persistent LSL has been identified as a dominant physical feature and important structuring factor for biological

communities. Direct effects include observed influences on predation (Witman & Grange 1998, Smith & Witman 1999), larval transport (Lamare 1999, Wing et al. 2003), phytoplankton productivity (Goebel et al. 2005), benthic productivity (Wing et al. 2001) and invertebrate zonation patterns (Grange et al. 1981, Smith & Witman 1999). Effects on the distribution and abundance of benthic organisms along the axis of Doubtful Sound have been addressed in a number of studies (McCully 1996, Witman & Grange 1998, Smith 2001, Boyle et al. 2001, Tallis et al. 2004). Boyle et al. (2001) observed changes in species composition in the intertidal rocky shore communities, as compared to the descriptions made in 1965 before the power plant outflow commenced (Batham 1965), and concluded that the observed displacement of a number of species to the outer parts of the fjord likely reflect an impact from the power plant outflow. Similarly, Tallis et al. (2004) found the littleneck clam *Austrovenus stutchburyi* to be locally rare and unable to survive in the shallow subtidal in the inner region of Doubtful Sound. Oxygen isotope analysis of carbonates from remnant shells indicated that higher salinity levels were present before the power plant was established.

In the present study, we focus on patterns of taxonomic richness and abundance of shallow water infauna across environmental space, in particular physical indicators of the dynamics of the LSL. To quantify spatial patterns in the salinity regime, we used fine scale CTD surveys and time series from moorings to calculate the depth of freshwater, a novel mixing index, and the return times of low salinity events. We then tested several hypotheses on the relationship between infaunal community composition and the salinity regime. We expect to see a decline in taxonomic richness in areas where the LSL is thick, persistent and the surface salinity is low. As a corollary, we expect to see a general gradient in community composition between inner and outer fjord regions. We test whether this gradient in community structure, and abundance of selected taxa is similar between Doubtful Sound, where the LSL is enhanced and persistent, and Thompson-Bradshaw Sound where the LSL has more natural variability. These analyses provide an investigation of the likely consequences of the altered salinity regime in Doubtful Sound for infaunal community structure.

MATERIALS AND METHODS

Study sites. Study sites were established within each fjord at 2 inner and 2 outer locations, overlapping those used by Tallis et al. (2004). Due to the near vertical rock walls, shallow water fans of sediment tend to be arranged as isolated islands of habitat at the mouths of

rivers and streams where alluvium collects in the glacial valleys and extends into the deep basins of the fjords. Each pair of sites was nested within 1 of 4 regions within the fjord complex. These regions represent the extremes of a gradient in surface salinity within each fjord from the persistently stratified LSL near the head of each fjord, particularly in Doubtful Sound, to a well-mixed surface layer and more oceanic salinity near the entrances (Fig. 1). Emphasis was placed on identifying covariates for differences in community structure between the 2 inner regions, particularly differences in local salinity regime. In this case, the Thompson-Bradshaw Sound sites functioned as a naturally varying reference region.

Surface salinity at the 2 sites in inner Doubtful Sound is heavily influenced by the outflow of freshwater from the hydroelectric plant tailrace ($510.0 \text{ m}^3 \text{ s}^{-1}$). Hall Arm (HA, $45^\circ 30.270' \text{ S}$, $167^\circ 03.641' \text{ E}$) and Deep Cove (DC, $45^\circ 27.858' \text{ S}$, $167^\circ 09.549' \text{ E}$) are located 39 and 35 km from the open ocean, respectively (Fig. 1). Natural influx of freshwater comes to the Hall Arm site from a small creek ($3.8 \text{ m}^3 \text{ s}^{-1}$) and to the Deep Cove site from the Lyvia River and other nearby tributaries ($8.5 \text{ m}^3 \text{ s}^{-1}$). Both sites receive a large input of terrestrial detritus from the surrounding forested catchments.

The 2 sites in outer Doubtful Sound are in a more oceanic salinity regime; nevertheless, surface salinity is influenced by freshwater outflow from the tailrace (Fig. 1). Corset Cove (CC, $45^\circ 17.2' \text{ S}$, $166^\circ 53.9' \text{ E}$) and Grono Bay (GB, $45^\circ 17.128' \text{ S}$, $166^\circ 56.580' \text{ E}$) are located 4.6 and 7.5 km from the entrance of Doubtful Sound, respectively. Natural freshwater input to Corset Cove comes from a small catchment on Bauza Island ($0.5 \text{ m}^3 \text{ s}^{-1}$), and to Grono Bay from small tributaries ($1.2 \text{ m}^3 \text{ s}^{-1}$). The sediment at each site contained relatively small amounts of terrestrial detritus.

The 2 sites at inner Bradshaw Sound have a more naturally varying salinity regime than similar sites at inner Doubtful Sound (e.g. Wing et al. 2003, Tallis et al. 2004). Shoal Cove, Camelot (C, $45^\circ 18.955' \text{ S}$, $167^\circ 11.233' \text{ E}$) and

Rum Cove (RC, $45^\circ 15.786' \text{ S}$, $167^\circ 07.615' \text{ E}$) are located 34.2 and 27 km from the entrance of Thompson Sound, respectively. Freshwater input to Shoal Cove comes from the Camelot River ($16.0 \text{ m}^3 \text{ s}^{-1}$), and to Rum Cove from the Rum River ($3.6 \text{ m}^3 \text{ s}^{-1}$). There is a large amount of terrestrial material in the sediments similar to the condition at Deep Cove.

The 2 sites at outer Thompson Sound are in a more oceanic salinity regime, with surface salinity influenced by the LSL. Deas Cove North (DN, $45^\circ 11.440' \text{ S}$, $166^\circ 58.500' \text{ E}$) and Deas Cove South (DS, $45^\circ 11.8' \text{ S}$, $166^\circ 58.4' \text{ E}$) are situated on each side of a small headland, approximately 6 and 7 km from the Thompson Sound entrance. The northern site is slightly exposed to oceanic swell from the northwest, and receives freshwater from a small tributary ($0.3 \text{ m}^3 \text{ s}^{-1}$). The southern site is located in a southward facing bay, which gives the flat protection from wave action. Freshwater is received from a small stream ($0.2 \text{ m}^3 \text{ s}^{-1}$)

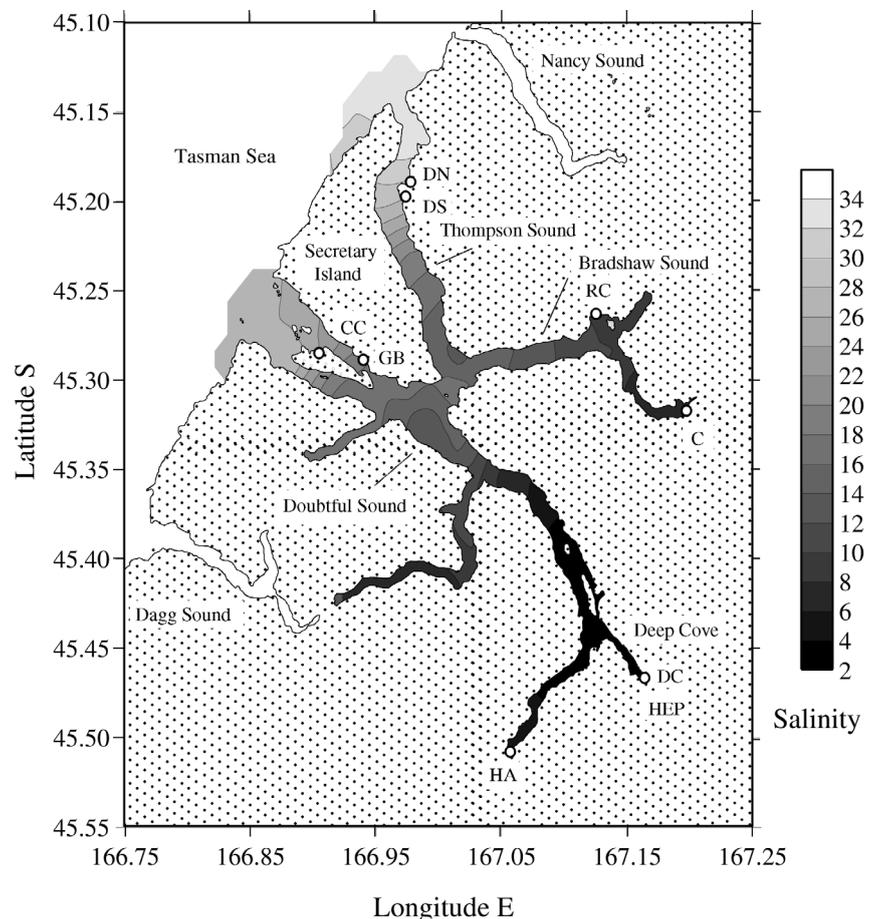


Fig. 1. Map of the Doubtful Sound complex showing contours of surface salinity in the top 2 m, and location of 8 study sites in 4 regions. Study sites are indicated by open circles at Deep Cove (DC), Hall Arm (HA), Corset Cove (CC), Grono Bay (GB), Deas Cove North (DN), Deas Cove South (DS), Rum Cove (RC) and Camelot (C). The outflow from the hydroelectric plant is indicated by HEP

and from Doubtful Sound through the Pendulo Reach. Only small amounts of detritus were observed in the sediments from both Deas Cove sites.

Physical data. Analysis of sediment composition:

Data on sediment characteristics such as mean phi-size and sediment composition were obtained from 3 to 5 random samples collected using a syringe (2.7 cm i.d., 7 cm deep) at each of the sites included in this study. Sediment samples were frozen before analysis. Mean grain size was calculated according to Folk & Ward (1957). The composition was calculated as the percentage of 5 different grain size categories of sand present, based on the Udden–Wentworth scale: very coarse (2 to 1 mm), coarse (1 to 0.5 mm), medium (0.5 to 0.25 mm), fine (0.25 to 0.125 mm) and silt/clay (<0.063 mm). Differences in mean phi-size for each collection were analysed using an ANOVA with fjord and position as factors; however, uneven replication with time prevented a full orthogonal treatment of the data.

Properties of the LSL: We conducted 6 fine-scale hydrographic surveys of the Doubtful–Thompson Sound complex using a Seabird SBE 19 conductivity, temperature and depth profiler (CTD) with a Wetstar fluorometer. These surveys took place in October 1997, August 1997, April 1998, July 1998, August 1998, October 1998 and February 1999. For each survey, we collected salinity, temperature and fluorescence at 0.5 m increments from the upper 100 m of the water column with 12 to 48 separate casts distributed at intervals throughout the fjord complex and associated arms. Data were post-processed using standard Seabird processing algorithms for the pumped SBE-19. These surveys were scheduled during periods of high average rainfall and low average rainfall, based on fortnightly running averages. Rainfall data were obtained from the National Institute of Water and Atmosphere (NIWA) weather station on Secretary Island #F56280 (45° 13.26' S, 166° 53.16' E). Surface salinity was calculated as the mean salinity in the upper 2 m of the water column from fine scale CTD surveys carried out in 1997, 1998 and 1999 (Wing et al. 2003).

For each sample, data effective freshwater depth (EFD) was calculated as:

$$EFD = -z_0 + \int_0^{-z_0} \frac{\sigma(z)S(z)}{\sigma_0 S_0} dz$$

where z_0 equals the depth of the salinity reference S_0 and corresponding density σ_0 .

We derived a measure of the relative mixing of the LSL from the ratio of the potential energy anomaly of the water column (PEA) to the maximum potential energy anomaly that could be achieved by the sampled water column (PEA_{\max}). This ratio was scaled to 1 so that perfectly mixed water columns have a value of

1 and perfectly stratified water columns have a value of 0. For this derivation, we used a value of PEA where:

$$PEA = \int_{-d}^0 (\sigma_t - \sigma_z) g dz$$

PEA_{\max} describes the potential energy anomaly of a perfectly stratified water column where:

$$PEA_{\max} = \int_{EFD}^0 (\sigma_t - \sigma_z) g dz + \int_{-d}^{EFD} (\sigma_t - \sigma_z) g dz$$

Here, σ_t is the value for density and σ_z is the density at a reference depth z . In these calculations, the reference depth was 48 m, where salinity changes very slightly with increasing depth.

Time series of temperature and salinity, analysis of extreme values: We deployed moorings at each study site from which temperature time series of 10 min increments were collected through the winter months (April to October 2000) with Tidbit® temperature loggers (Onset Computer) from every 2 m below mean high water mark to 20 m. In winter, the cold (8 to 10°C) low salinity (0 to 10) layer is distinct from the relatively warm (12 to 14°C) underlying seawater (25 to 34) (Gibbs 2001). These temperature data were then used to measure the depth of the cold, low salinity surface layer during a series of rainfall events. Temperature–salinity relationships were established from CTD data series collected in winter and from published values (Gibbs et al. 2000). We used the statistics of extreme values (e.g. Gaines & Denny 1993, Leichter & Miller 1999) to calculate return times of temperature anomalies with depth at each of the 4 study regions. Negative anomalies (–3°C from 13°C) indicate that cold (<10°C), low salinity (<10) water is present at depth.

Biological data. Infaunal sampling: Benthic sampling was carried out in the Doubtful–Thompson Sound complex in April and November 2002, each sampling occasion spanning 4 consecutive days. Replicate samples ($n = 6$ to 8) were taken at each site during the 2 sampling periods. At each site, 2 cores (785 or 625 cm²) were randomly distributed (using random number of fin kicks) at 2 m below high water mark and sediment to 10 cm depth was sieved with a Venturi sampler made from PVC-pipe with a SCUBA air supply (Coyer & Witman 1990). Fauna and sediment >1 mm was collected on a screen made from 1 mm Nytex®. James et al. (1995) reported that little information is lost by using 1 mm rather than 0.5 mm sieve mesh-size, and this larger mesh made processing the highly organic sediment feasible in the remote location. The samples were preserved in 50 to 70% isopropanol alcohol with Rose-Bengal added to aid in faunal sorting.

Sorting and identification of the infauna from benthic samples took place at the Portobello Marine Laboratory. Due to difficulties associated with specific

taxonomic identification, polychaetes and amphipods were identified to family level only. It has been suggested that little resolution of diversity pattern is lost by such an approach (James et al. 1995, Karakassis & Hatziyanni 2000, Roach et al. 2001, Defeo & Lercari 2004). References used for identification were Melrose (1975), Fauchald (1977), Powell (1979), Poore & Taylor (1997) and Glasby et al. (2000). A general rule of counting only specimens with heads was applied in the case of polychaetes and amphipods to calculate the minimum number of individuals.

Taxa-accumulation curves: Curves of cumulative number of taxa versus quadrat sample number were plotted for each region to investigate whether the number of taxa present had been sufficiently sampled. This was done by plotting the average number of taxa found in random combinations of progressively increasing number of replicates (e.g. Magurran 1988). Log-normal taxonomic richness models were fitted to the data. Simple linear regression and non-linear regression was used to investigate the relationship between effective freshwater depth (*EFD*), surface salinity, mixing ($(PEA_{max} - PEA)/PEA_{max}$) and the estimated taxonomic richness at each site.

Analysis of abundance patterns: Site replication as well as replication of regions and sample periods was achieved through the nested sampling scheme. We tested for differences in taxonomic richness between regions using the Mann-Whitney *U*-test for unmatched samples (Fowler & Cohen 1992). Differences in abundance of taxa were tested using a 4-factor mixed model ANOVA with fjord (2 levels random), position (2 levels, fixed, orthogonal), site (2 levels, random, nested in position) and time (2 levels, fixed, orthogonal) as factors. In the absence of statistical significance for time and site, we simplified the model to a 2-factor ANOVA on fjord and position, and tested for the interaction between factors. The data were transformed with $\ln(\text{abundance} + 1)$, before analysis to remove heterogeneity of variance and to obtain normal distributions of abundance. ANOVA algorithms in Systat 11 were used for each analysis.

Analysis of size distribution of bivalves: Shell length was measured for the most abundant species of bivalve *Paphies australis*, which occurred at 5 of the 8 sites (Grono Bay, Shoal Cove, Rum Cove, Dea's Cove North and South). A Kolmogorov-Smirnov 2-sample test (Sokal & Rolf 1981) was used to detect differences in clam size distributions between sites.

MDS and ANOSIM: Non-metric multidimensional scaling (NMDS) of a Bray-Curtis similarity matrix of family composition and abundance data was used to visualise the degree of similarity between communities among sites and regions. A 1-way multivariate analysis of similarity (ANOSIM) was used on the same matrix to

test for community level differences between regions and sampling occasions, respectively (Clark & Warwick 1994). We used the SIMPER routine to highlight the specific families accounting for up to 90% of the observed dissimilarity pattern between regions. No transformation of the data was applied prior to analysis in this case.

RESULTS

Sediment composition and mean phi-size

Analysis of the sediment composition data revealed that each of the biological collections was made in areas with predominately fine (0.25 to 0.125 mm) sediment. We did not analyse the sediments for organic content, though differences in gross amounts of terrestrial detritus were observed among sites. There were no significant differences in mean phi-size detected by ANOVA ($F = 4.17$, $p > 0.05$). However these results are for sediment data collected at a single time period within each site and because of the small sample size have low power to detect spatial differences in sediment types within areas.

Analysis of extreme temperature values

Analysis of the temperature time series reveals that the sites in the inner parts of Doubtful Sound are more likely to experience low salinity (temperature below

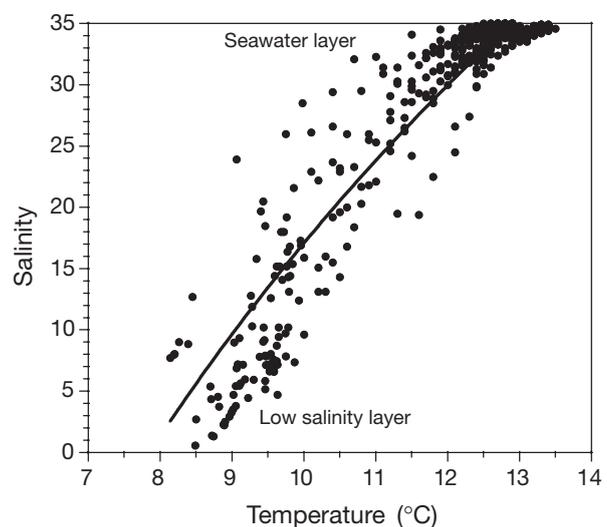


Fig. 2. Temperature–salinity relationship from June to August in Doubtful Sound. Grouping of temperature and salinity into relatively cold (8 to 10°C) low salinity (0 to 10) and relatively warm (12 to 14°C), high salinity (25 to 34) water masses clearly indicates the 2-layered structure of the water column

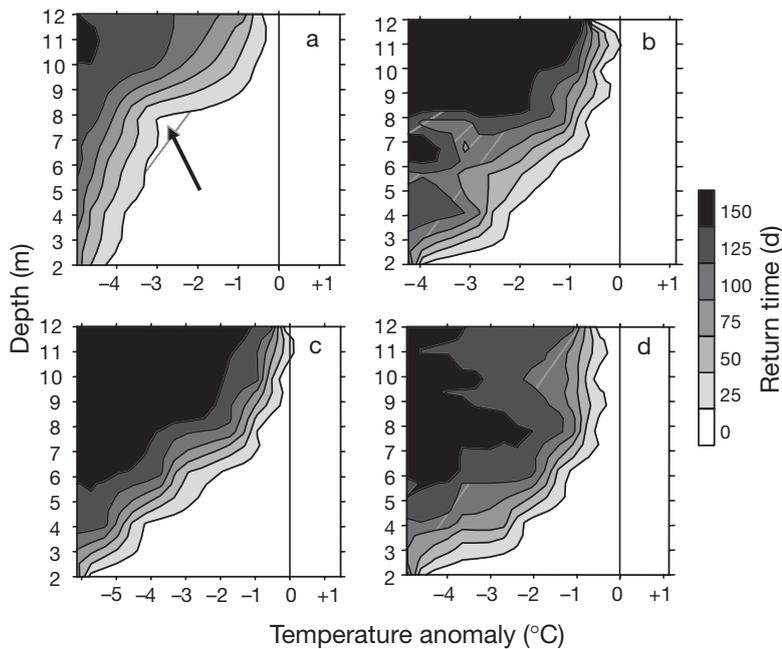


Fig. 3. Return times for temperature anomalies from 13°C (zero anomaly as indicated by the vertical line) across depth for (a) Inner Doubtful Sound, (b) Inner Thompson Sound, (c) Outer Doubtful Sound and (d) Outer Thompson Sound. A -3°C anomaly indicates the presence of low salinity water (<10). The arrow in (a) indicates the penetration of cold, low salinity water to depth at inner Doubtful Sound sites

10°C , anomaly of -3°C) events (Figs. 2 & 3a) at deeper depths than sites in the inner reaches of Thompson-Bradshaw Sound (Fig. 3b). This is born out by examining return times, or average time between events, for -3°C anomalies at similar depths from each site. For example at the inner site in Thompson-Bradshaw a -3°C anomaly is observed with a return time of 25 d at approximately 2.5 m while at the site in the inner region of Doubtful Sound a -3°C anomaly is seen with a return time of 25 d at 8 m. This indicates that the upper parts of the water column are more consistently cold, low-salinity water in Doubtful Sound and that infaunal organisms would be exposed to more frequent and longer periods of low salinity in inner Doubtful Sound. Both of the inner fjord sites show low temperature events at deeper depths than the entrance sites (Fig. 3c,d).

Taxa-accumulation curves

The taxa accumulation curves show a log-normal distribution of taxa with increasing sample size, and equivalent saturation of taxa discovery among sites (e.g. Magurran 1988). Because the 2 similar-sized cores were distributed randomly in equal sample num-

ber this does not affect the randomisation procedure used to calculate taxa accumulation by sample size. Sites range in taxonomic richness along a log-normal accumulation curve from outer Thompson, outer Doubtful, inner Thompson to inner Doubtful Sound (Fig. 4). Taxonomic richness for the regions combined follows a log-normal distribution with 210 taxa discovered from 112 samples ($y = -1.544 + 35.342[\log x]$, $r^2 = 0.9932$). The outer regions of the fjord complex combined had a significantly greater number of taxa than the inner regions combined (Table 1).

Properties of the low salinity layer vs. richness and abundance of taxa

Taxonomic richness covaried with surface salinity (Fig. 5), the effective freshwater depth, and mixing index ($(PEA_{\max} - PEA)/PEA_{\max}$). Each of these relationships was significant with a large fraction of the variance in taxonomic richness explained by the physical data (no. of

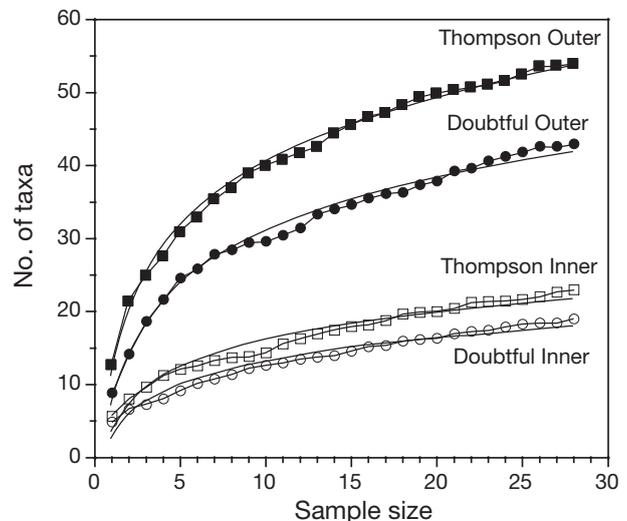


Fig. 4. Log-normal distributions of taxonomic richness versus sample size for each region. Sites range in taxonomic richness along a log-normal accumulation curve from outer Thompson ($y = 11.186 + 29.347[\log x]$, $r^2 = 0.99$), outer Doubtful ($y = 7.1863 + 23.992[\log x]$, $r^2 = 0.98$), inner Thompson ($y = 3.553 + 12.567[\log x]$, $r^2 = 0.96$) to inner Doubtful ($y = 2.575 + 10.63[\log x]$, $r^2 = 0.96$). Taxonomic richness for the regions combined follows a log-normal distribution with 210 taxa discovered from 112 samples ($y = -1.544 + 35.342[\log x]$, $r^2 = 0.99$)

Table 1. Mann-Whitney U -test for unmatched samples on pair-wise differences in species richness between 4 regions in the Doubtful–Thompson fjord complex

| Regions | U_1/U_2 | $U_{crit} = 12$ | p |
|-----------------------------------|-----------|-----------------|-------------|
| Inner Doubtful vs. Outer Doubtful | -10.5 | 37 | ≤ 0.05 |
| Inner Doubtful vs. Inner Thompson | 63.5 | 37 | ns |
| Inner Doubtful vs. Outer Thompson | 2.5 | 37 | ≤ 0.05 |
| Inner Thompson vs. Outer Doubtful | 11 | 37 | ≤ 0.05 |
| Inner Thompson vs. Outer Thompson | 10 | 37 | ≤ 0.05 |
| Outer Doubtful vs. Outer Thompson | 64 | 37 | ns |

taxa = $8.0475 e^{0.053679(\text{surface salinity})}$, $r^2 = 0.83$, $p = 0.0017$;
 no. of taxa = $49.598 e^{-0.34697(EFD)}$, $r^2 = 0.82$, $p = 0.0021$;
 no. of taxa = $6.639 e^{3.0753((PEA_{max} - PEA)/PEA_{max})}$, $r^2 = 0.89$,
 $p = 0.0005$). We observed strong linear relationships between EFD and abundance of bivalves and amphipods ($r^2 = 0.966$, $p < 0.05$ and $r^2 = 0.695$, $p < 0.05$).

Abundance of taxa

Marked differences in bivalve abundance between the inner region of Doubtful Sound and the other regions were observed (Fig. 6a). Bivalves were essentially absent from the former with no effect of time or site. A significant outcome of the ANOVA analysis was found for the factors fjord and position with significant interaction effects (Table 2). Amphipod abundance was significantly different for the factors fjord and position with a significant interaction effect (Table 2). There was no effect of time or site. The inner region of Doubtful Sound had a significantly greater abundance of amphipods compared to all other regions (Fig. 6b, Table 2). Decapod abundance was significantly differ-

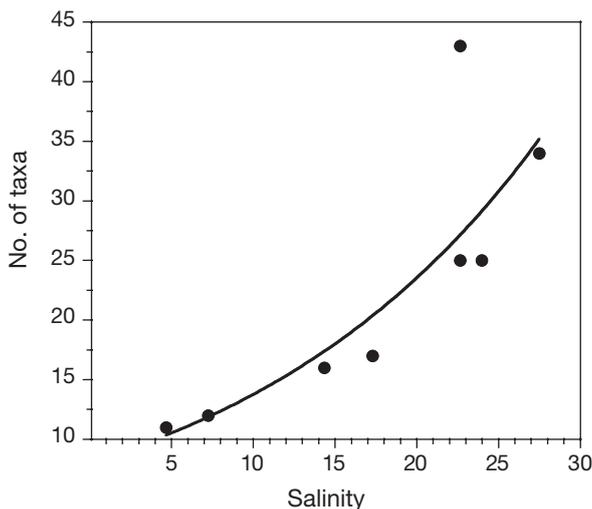


Fig. 5. Observed numbers of taxa by site vs. surface salinity

ent between inner fjord positions and outer fjord positions, with no significant effect of fjord (Fig. 7a, Table 2). There was no effect of time or site. Gastropod abundance was significantly greater in the 2 inner regions of the fjords compared to the 2 outer regions; there were significant effects of fjord and time but not of site in the analysis and significant interactions (Fig. 7b, Table 2).

Polychaete abundance had significant effects of fjord, position and time with a significant interaction of fjord and position (Table 2). The abundance of polychaetes in the family Neredidae had significant effects of fjord, position and time with a significant interaction of fjord and position (Table 2) while abundance of the family Orbiniidae had a significant effect of fjord and position with a significant interaction between the two

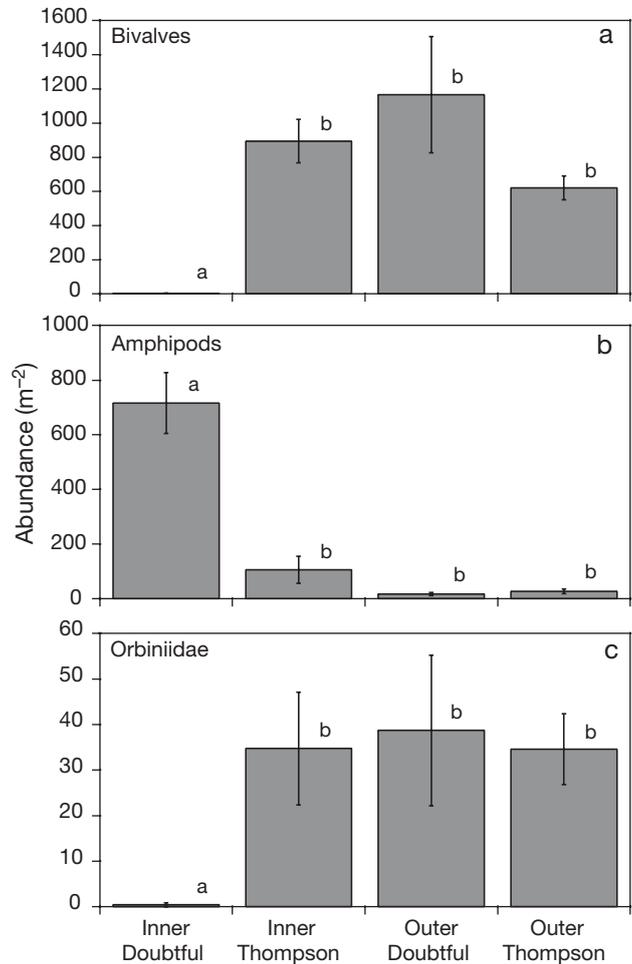


Fig. 6. Abundance of (a) bivalves, (b) amphipods and (c) polychaetes from the family Orbiniidae from each of the study regions. Each abundance estimate is based on 28 samples from 2 sites taken over 2 time periods. Error bars indicate 1 SE of the mean. Letters above each bar indicate significant groupings

Table 2. Results of ANOVA on abundance of invertebrates among regions within the Doubtful–Thompson fjord complex. Factors were Fjord (df = 1), Position (df = 1), Time (df = 1) and Site (df = 2). Significant interactions are **bold**

| Taxon | Factor | F | p |
|-----------------|------------------|--------|---------------|
| Bivalvia | Fjord | 151.59 | 0.0001 |
| | Position | 91.86 | 0.0001 |
| | Fjord × Position | 110.67 | 0.0001 |
| Amphipoda | Fjord | 20.63 | 0.0001 |
| | Position | 33.75 | 0.0001 |
| | Fjord × Position | 28.17 | 0.0001 |
| Gastropoda | Fjord | 5.16 | 0.025 |
| | Position | 305.73 | 0.0001 |
| | Time | 25.65 | 0.0001 |
| | Fjord × Position | 5.88 | 0.017 |
| | Fjord × Time | 13.43 | 0.0001 |
| Decapoda | Position × Time | 10.06 | 0.002 |
| | Fjord | 0.26 | 0.61 |
| | Position | 8.47 | 0.004 |
| Polychaeta | Fjord × Position | 0.03 | 0.86 |
| | Fjord | 7.06 | 0.009 |
| | Position | 31.73 | 0.0001 |
| Fam: Neredidae | Time | 47.38 | 0.0001 |
| | Fjord × Position | 15.70 | 0.0001 |
| | Fjord | 14.50 | 0.0001 |
| | Position | 5.17 | 0.025 |
| Fam: Orbiniidae | Time | 23.24 | 0.0001 |
| | Fjord × Position | 35.12 | 0.0001 |
| | Fjord | 9.36 | 0.003 |
| Fam: Spionidae | Position | 23.24 | 0.0001 |
| | Fjord × Position | 4.53 | 0.036 |
| | Fjord | 1.81 | 0.18 |
| | Position | 31.16 | 0.0001 |
| | Fjord × Position | 3.07 | 0.08 |

(Fig. 6c, Table 2). There were significantly fewer Orbiniids at inner Doubtful Sound than the other regions (Fig. 6c). Abundance of the family Spionidae had a significant effect of position not of fjord (Fig. 7c, Table 2). There were significantly fewer Spionids in the inner fjord regions than the outer regions (Fig. 7c).

Analysis of size distribution of bivalves

Size distributions for populations of the clam *Paphies australis* were significantly different between inner fjord and outer fjord sites when tested using the Kolmogorov-Smirnov 2-sample test (Fig. 8).

NMDS and ANOSIM

The NMDS model provided a useful description of the communities with a stress value of 0.10 in 3D space and 0.16 in the 2D case (Fig. 9). The ordination clearly separated the inner region of Doubtful Sound from the other regions of the fjord complex with a tight group-

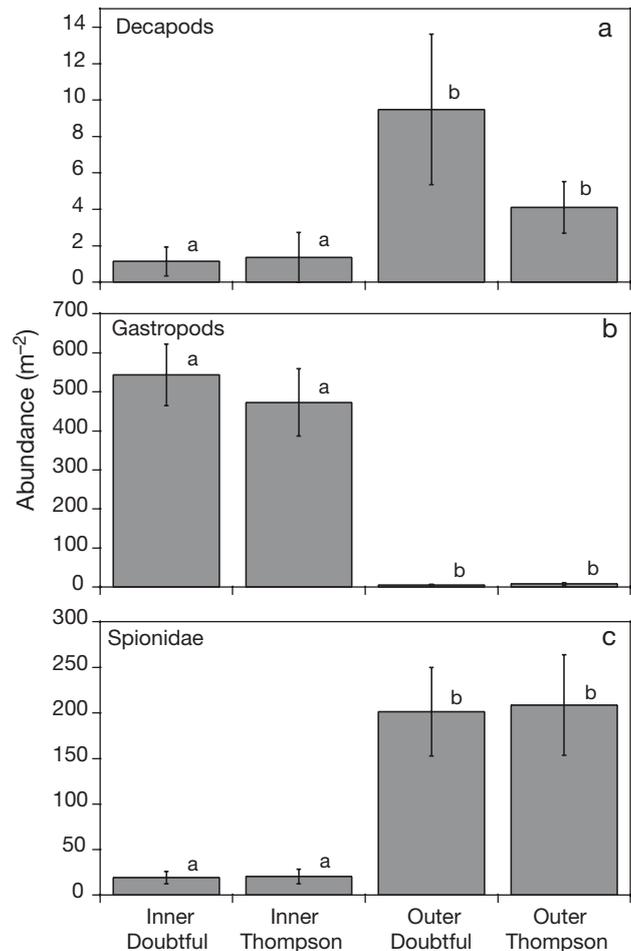


Fig. 7. Abundance of (a) decapods, (b) gastropods and (c) polychaetes from the family Spionidae from each of the study regions. Each abundance estimate is based on 28 samples from 2 sites taken over 2 time periods. Error bars indicate 1 SE of the mean. Letters above each bar indicate significant groupings

ing of samples. The inner region of Thompson-Bradshaw Sound was somewhat less distinct and had a much less clumped distribution of samples indicating more dissimilarity among samples. Communities from the 2 outer regions overlap in the NMDS model indicating the greatest degree of similarity among the 4 groupings. There was no apparent temporal separation among the samples.

A 2-way nested ANOSIM run for the factor position nested within fjord indicates that much of the dissimilarity among regions can be attributed to position rather than fjord. A test for differences between position groups averaged across all fjord groups was significant (Global R = 0.596), while a test for differences between fjord groups using position groups as samples was not significant (R = 0.0). The results of the

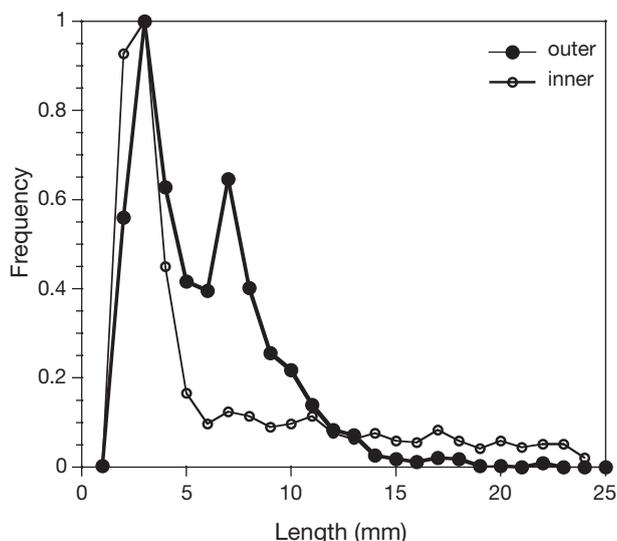


Fig. 8. *Paphies australis*. Size distributions of the bivalve collected from inner fjord regions ($n = 1134$, \circ) and outer fjord regions ($n = 1674$, \bullet)

1-way ANOSIM run for the factor region showed there was an overall difference (Global $R = 0.635$) and also provided the basis of pair-wise comparisons at the region level. Pair-wise comparisons of sample groups showed that all regions were significantly different from each other, though to different degrees (Table 3). Communities from inner Doubtful Sound were ranked as the most distinct followed by those from inner Thompson and the 2 outer coast sites. Each of these results is consistent with the patterns observed in the NMDS ordination.

In the comparisons of inner Doubtful Sound to the other regions, the same 3 families contributed to at least 60% of the average dissimilarity. These were the Corophiidae, Hydrobiidae and Mesodesmatidae of which the first 2, an amphipod and a gastropod family, are very abundant at the heads of the fjord complex. The family Mesodesmatidae includes the clam species *Paphies australis*, which is abundant at the outer sites

Table 3. One-way ANOSIM showing pair-wise comparisons of community similarity among regions (Global $R = 0.635$, significance level = 0.1%, no. of permutations = 999). Differences between regions were significant in all cases

| Region | R |
|-----------------------------------|------|
| Inner Doubtful vs. Outer Doubtful | 0.84 |
| Inner Doubtful vs. Inner Thompson | 0.74 |
| Inner Doubtful vs. Outer Thompson | 0.96 |
| Inner Thompson vs. Outer Doubtful | 0.42 |
| Inner Thompson vs. Outer Thompson | 0.49 |
| Outer Doubtful vs. Outer Thompson | 0.24 |

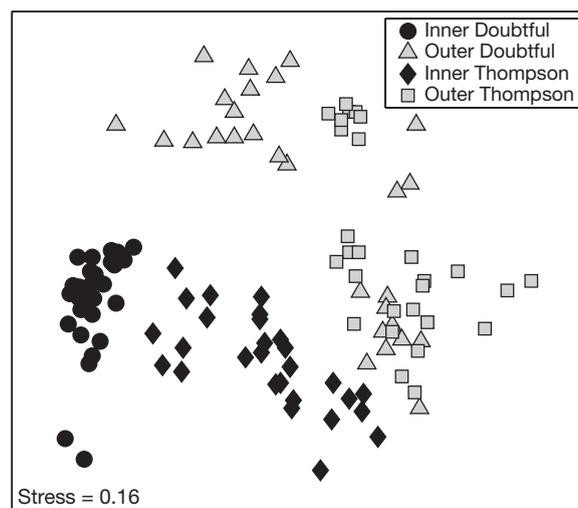


Fig. 9. Non-metric multiple dimensional scaling (NMDS) of a Bray-Curtis similarity matrix based on sample data from each of the 8 sites. Sites are identified by symbols corresponding to the 4 regions (see key in figure). Inner Doubtful: Deep Cove (DC), Hall Arm (HA); Outer Doubtful: Grono Bay (GB), Corset Cove (CC); Inner Bradshaw: Shoal Cove (C), Rum Cove (RC); Outer Thompson: Dea's Cove South (DS), Dea's Cove North (DN)

of the complex as well as at the inner sites of Thompson-Bradshaw Sound. Three other families adding a larger portion of the average dissimilarity in these comparisons were the polychaete families Spionidae, Capitellidae and Nereididae (10, 12 and 5 to 6%, respectively). The first 2 families are abundant at the entrance sites and Nereididae in the inner region of Doubtful Sound.

Comparing inner Thompson Sound with the outer regions of the fjord complex, the same families were listed but with a different ranking. The families Mesodesmatidae and Hydrobiidae contributed 50 to 60% in this case while either Spionidae or Capitellidae contributed 10 to 12% and the clam family Psammobiidae 4 to 5%. Corophiidae contributed only 4% as compared to 20 to 25% in the inner Doubtful Sound comparisons.

Comparing the 2 outer regions, the families Mesodesmatidae (35%), Capitellidae (13%), Spionidae (12%) and Psammobiidae (8%) were the top contributors. The families Lasaeidae, Nereididae and Orbiniidae all contributed 3 to 3.5% each.

DISCUSSION

The data presented in this study add support to the idea that the increased freshwater input by the Manapouri power station has led to habitat conversion through changes in the salinity regime and to large

changes in infaunal community structure in the inner regions of Doubtful Sound. We found that there were fewer taxa and lower abundances of key taxa, particularly bivalves, within the inner Doubtful Sound region. While no records similar to Batham's study (1965) of rocky shore communities exist for the soft sediment communities, the patterns in community structure strongly suggest a large influence of the modified salinity regime on these communities. In the case of the cockle *Austrovenus stutchburyi*, Tallis et al. (2004) clearly indicated a cause and effect relationship. The results showed the inability of *A. stutchburyi* to survive in the current salinity regime in the inner parts of the fjord as well as oxygen isotope evidence for a large shift in the salinity regime recorded in shell carbonates from historic populations. The present study examined differences in the infaunal community composition within this region and documented the large differences in both abundance of key taxa and community structure patterns across the fjord complex. Each of these patterns covaries with physical data on the dynamics and spatial pattern of the LSL.

Consistently low salinity conditions in the surface waters of Deep Cove (<5) and intrusion of low salinity conditions to depths of 10 to 12 m have been measured by several oceanographic surveys (Stanton & Pickard 1981, McCully 1996, Gibbs et al. 2000, Gibbs 2001). Gibbs (2001) found that although the range of salinity encountered was similar at the different sites throughout Doubtful–Thompson Sound, low salinity events were more frequent (higher salinity events had shorter duration) in the inner parts of Doubtful Sound. These observations indicate that shallow water benthic organisms in the inner region of Doubtful Sound most likely experience low salinity more often and for longer periods in comparison to those from other sites in the fjord complex. This is consistent with our analysis of extreme temperature values during winter, using temperature as a proxy for the LSL, from each of the study regions. These data indicate that low salinity events penetrate deeper and more frequently in inner Doubtful Sound than other regions of the fjord. Because exposure tolerance of benthic organisms typically scales with duration of events (e.g. LD₅₀), this aspect of the salinity regime likely has a critical influence on community composition (e.g. Tallis et al. 2004). Frequency of exposure to low salinity at depth as indicated by this analysis of extremes is clearly linked to the thickness of the LSL.

Three factors have been identified as influencing the variability in thickness of the LSL in Doubtful Sound: (1) wind stress, (2) precipitation and (3) the tailrace discharge (Witman & Grange 1998, Gibbs et al. 2000, Boyle et al. 2001). Witman & Grange (1998) found a strong relationship between the thickness of the LSL

and the amount of rain accumulated the previous day. Gibbs et al. (2000) showed that strong wind events can mix the surface LSL and deepen the penetration of low salinity water. Wind events typically coincide with rain events so the effect of increased mixing and increased freshwater input can add to the depth penetration of the LSL. In their study, Boyle et al. (2001) noted that the thickness of the LSL was well correlated with the level of tailrace discharge but did observe less precipitation in association with a lower discharge rate and a thinner LSL. These studies indicate that natural variability interacting with the anthropogenic inputs of freshwater at Deep Cove result in the observed pattern of deep and prolonged penetration of low salinity events to subtidal habitats in inner Doubtful Sound.

Analysis of the relationships between these physical indicators of the dynamics of the LSL and the observed taxonomic richness and abundance patterns suggest some striking interactions between community structure and salinity regime (e.g. Figs. 5–7). These patterns are consistent with previous studies of the response of infaunal diversity along salinity gradients (e.g. Kinne 1966, Attrill & Power 2000, Lercari et al. 2002) and with previous observations from Doubtful Sound (e.g. Boyle et al. 2001, Tallis et al. 2004).

The most striking difference in abundance of taxa was the low abundance of bivalves from the inner shallow water sites of Doubtful Sound as compared to Thompson-Bradshaw Sound where the inner region supported one of the largest populations sampled in this study. These differences could not be attributed to differences in sediment composition (Tallis et al. 2004), or site effects; however, dramatic differences in the salinity regime suggest that the patterns observed for *Austrovenus stutchburyi* may be applicable to the other bivalves in the community. The ecosystem-level consequences of loss of bivalves in a benthic community are potentially large because bivalves serve as one important link between water column phytoplankton productivity and the benthic detrital food web (e.g. Herman et al. 1999). For example Tenore (1977) demonstrated that suspension feeding bivalves can capture 8 g C gdw⁻¹ d⁻¹ at typical phytoplankton concentrations. Much of this material (20 to 30%) is directly deposited as available carbon into the benthos (Tenore et al. 1982). In Fiordland, terrestrial detritus comprises a large fraction of relatively non-labile organic material in the sediment which may drive recycled carbon pathways and chemosynthetic pathways (e.g. Levin & Michener 2002, Sandberg et al. 2004). The contribution of more labile detritus by bivalves and other suspension feeders may be particularly important in these systems (e.g. Dame 1996).

Another important pattern was the low taxonomic richness and high relative abundance of amphipods at

the inner Doubtful Sound sites. At these sites, only 2 families of amphipods were recorded, Corophiidae and Melitidae; however, in the inner region of Bradshaw Sound, and at the 2 entrance regions, 5 different families were recorded. There were also consistent differences in the abundance patterns among families of polychaetes. Polychaetes in the family Nereididae were found to be significantly more abundant in the inner parts of Doubtful Sound while polychaetes in the families Orbiniidae and Spionidae were least abundant in this region. While these patterns in abundance and distribution of key taxa indicate strong environmental forcing on community composition, indirect effects on the community may also be important.

As shown by Bohle (1972), effects of altered salinity on benthic communities extend to sub-lethal effects, such as inhibited growth and reproduction. Tallis et al. (2004) suggested that growth of *Austrovenus stutchburyi* can only occur under relatively high salinity. These findings likely extend to other infaunal bivalve species in the fjord. For example, we observed significant differences in size distributions of the clam *Paphies australis* among inner and outer regions of the fjord that are consistent with large differences in growth, or other vital rates, among regions.

While the data and results from this study indicate a strong influence of salinity on community structure, there are several caveats that must accompany our conclusions. Our analyses of sediment composition do not reveal large differences in particle distributions among sites; however, because of low sample size the results should be viewed with some caution. Also, we have not resolved more subtle differences in sediment such as composition of detrital material which are important to diversity patterns (e.g. Thrush et al. 2003). We did observe gross differences in amounts of terrestrial detritus in the different regions. With 2 sample periods for the faunal sampling, we did not resolve seasonal changes in community structure; however, our sampling does reveal a robust spatial pattern.

While each of the patterns that we observe is consistent with large effects of the modified salinity regime in Doubtful Sound on community structure, there are no observations prior to the salinity change to compare with the present community. We must therefore limit our conclusions to the observed spatial patterns and the relationships between community structure and the properties of the LSL. However, Tallis et al. (2004) and Boyle et al. (2001) have both reported large temporal changes in communities associated with changes in salinity, and each of the patterns that we observe in the present study are consistent with these observations, as well as with those of more general studies of diversity across salinity gradients. Here we use salinity data from several different time periods to provide

information on the average spatial pattern (e.g. Gibbs et al. 2000).

The results of the present study indicate that average thickness and dynamics of the LSL likely have a strong influence on infaunal community structure in terms of taxonomic distribution, abundance and richness within Doubtful Sound. Each of these patterns is consistent with a large impact of the persistent discharge of freshwater from the Manapouri power station on shallow water infaunal communities in the fjord. The patterns in abundance and richness of bivalves in particular may have large consequences for links between water column productivity and the detrital food web extending to deeper regions of the fjord. It is likely that within Doubtful Sound, where abundance of bivalves is reduced and pelagic production may be less actively delivered into the benthos, that less labile carbon sources such as terrestrial detritus become relatively more important as a direct consequence of the loss in functional diversity within the community.

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LITERATURE CITED

- Atrill M, Power M (2000) Effects on invertebrate populations of drought-induced changes in estuarine water quality. *Mar Ecol Prog Ser* 203:133–143
- Batham E (1965) Rocky shore ecology of a southern New Zealand fjord. *Trans R Soc NZ* 6:215–227
- Boesch D (1977) A new look at the zonation of benthos along the estuarine gradient. In: Coull B (ed) *Ecology of marine benthos*. University of South Carolina Press, Columbia, SC
- Bohle B (1972) Effects of adaptation to reduced salinity on filtration activity and growth of mussels (*Mytilus edulis*). *J Exp Mar Biol Ecol* 10:41–49
- Boyle M, Jillett J, Mladenov P (2001) Intertidal communities in Doubtful Sound, New Zealand: changes over time. *NZ J Mar Freshw Res* 35:663–673
- Clark K, Warwick R (1994) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth
- Coyer J, Witman J (1990) *The underwater catalog: a guide to methods in underwater research*. Shoals Marine Laboratory, Ithaca, NY
- Dame RF (1996) *Ecology of marine bivalves: an ecosystem approach*. CRC Press, Boca Raton, FL
- Defeo O, Lercari D (2004) Testing taxonomic resolution levels for ecological monitoring in sandy beach macrobenthic communities. *Aquat Conserv* 14:65–74
- Drake P, Arias A, Baldo F, Cuesta J and 5 others (2002) Spatial and temporal variation of the nekton and hyperbenthos from a temperate European estuary with regulated freshwater inflow. *Estuaries* 25:451–468

- Fauchald K (1977) The polychaete worms: definitions and keys to the orders, families and genera, Vol 28. Natural History Museum of Los Angeles County, Los Angeles, CA
- Folk R, Ward W (1957) Brazos river Bar: a study in the significance of grain size parameters. *J Sediment Petrol* 27: 3–26
- Fowler J, Cohen L (1992) Practical statistics for field biology. John Wiley & Sons, New York
- Gaines S, Denny M (1993) The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. *Ecology* 74: 1677–1692
- Gainey L, Greenberg M (1977) Physiological basis of the species abundance—salinity relationship in molluscs. *Mar Biol* 40:41–49
- Gibbs M (2001) Aspects of the structure and variability of the low-salinity-layer in Doubtful Sound, a New Zealand fiord. *NZ J Mar Freshw Res* 35:59–72
- Gibbs M, Bowman M, Dietrich D (2000) Maintenance of near surface stratification in Doubtful Sound a New Zealand fjord. *Estuar Coast Shelf Sci* 51:683–704
- Glasby C, Hutchings P, Fauchald K, Paxton H, Rouse G, Watson R, Wilson R (2000) Polychaetes and allies: the southern synthesis, Vol 4A. CSIRO Publishing, Canberra
- Goebel N, Wing S, Boyd P (2005) A mechanism for onset of diatom blooms in a fjord with persistent salinity stratification. *Estuar Coast Shelf Sci* 64:546–560
- Grange, K, Singleton R, Richardson J, Hill P, del Main W (1981) Shallow rock-wall biological associations of some southern fiords of New Zealand. *NZ J Zool* 8:209–227
- Herman P, Middelburg J, Van de Koppel J, Heip C (1999) Ecology of estuarine macrobenthos. *Adv Ecol Res* 29: 195–240
- Irandi E, Macia S, Serafy J (1997) Salinity reduction from freshwater canal discharge: effects on mortality and feeding of an urchin (*Lyttechinus variegates*) and a gastropod (*Lithopoma tectum*). *Bull Mar Sci* 61:869–879
- James R, Lincoln-Smith M, Fairweather P (1995) Sieve mesh-size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. *Mar Ecol Prog Ser* 118:187–198
- Karakassis I, Hatzilyanni E (2000) Benthic disturbance due to fish farming analysed under different levels of taxonomic resolution. *Mar Ecol Prog Ser* 203:247–253
- Kinne O (1966) Physiological aspects of animal life in estuaries with special reference to salinity. *Neth J Sea Res* 3: 222–244
- Kinne O (1975) Physiological mechanisms. In: *Marine ecology*, Vol 2. John Wiley & Sons Chichester, p 594
- Kowalewski M, Guillermo E, Flessa K, Goodfriend G (2000) Dead delta's former productivity: two trillion shells at the mouth of the Colorado River. *Geology* 28:1059–1062
- Lamare M (1999) Origin and transport of larvae of the sea urchin *Evechinus chloroticus* Valenciennes (Echinodermata: Echinoidea) in a New Zealand fiord. *Mar Ecol Prog Ser* 174:107–121
- Leichter J, Miller S (1999) Predicting high-frequency upwelling: spatial and temporal patterns of temperature anomalies on the Florida coral reef. *Cont Shelf Res* 19:911–928
- Lercari D, Defeo O (1999) Effects of freshwater discharge in sandy beach populations: the mole crab *Emerita brasiliensis* in Uruguay. *Estuar Coast Shelf Sci* 49:45–468
- Lercari D, Defeo O (2003) Variation of a sandy beach macrobenthic community along a human-induced environmental gradient. *Estuar Coast Shelf Sci* 58S:17–24
- Lercari D, Defeo O, Celentano E (2002) Consequences of a freshwater canal discharge on the benthic community and its habitat on an exposed sandy beach. *Mar Pollut Bull* 44:1397–1404
- Levin L, Michener R (2002) Isotopic evidence for chemosynthesis-based nutrition of macrobenthos: the lightness of being at Pacific methane seeps. *Limnol Oceanogr* 47: 1336–1345
- Magurran A (1988) *Ecological diversity and its measurement*. Cambridge University Press, Cambridge
- McCully D (1996) The hydrography of Doubtful Sound. MSc thesis, University of Otago, New Zealand
- McLusky D, Elliot M (2004) *The estuarine ecosystem: ecology, threats, and management*, 3rd edn. Oxford University Press, Oxford
- McLusky D, Hull SC, Elliot M (1993) Variations in the intertidal and subtidal macrofauna and sediments along a salinity gradient in the upper forth estuary. *Neth J Aquat Ecol* 27:101–109
- Melrose M (1975) The marine fauna of New Zealand: Family Hymenosomatidae (Crustacea, Decapoda, Brachyura). *NZ Oceanogr Inst Mem* 34
- Montagna P, Kalke R (1992) The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces estuaries, Texas. *Estuaries* 15: 307–326
- Peake M, Walls D, Gibbs M (2001) Spatial variations in the levels of nutrients, chlorophyll *a*, and dissolved oxygen in summer and winter in Doubtful Sound, New Zealand. *NZ J Mar Freshw Res* 35:681–694
- Poore G, Taylor J (1997) *Introducing crustaceans*. Museum of Victoria Press, Melbourne
- Powell A (1979) *New Zealand mollusca marine land and freshwater shells*. William Collins Publishers, Auckland
- Remane A, Schlieper C (1971) *Biology of brackish water*. Wiley, New York
- Roach A, Jones A, Murray A (2001) Using benthic recruitment to assess the significance of contaminated sediments: the influence of taxonomic resolution. *Environ Pollut* 112: 131–143
- Rodriguez C, Dettman D, Flessa K (2001) Effects of upstream diversion of Colorado River water on the estuarine bivalve mollusk *Mulinia coloradoensis*. *Conserv Biol* 15: 249–258
- Sandberg J, Andersson A, Johansson S, Wikner J (2004) Pelagic food web structure and carbon budget in the northern Baltic Sea: potential importance of terrigenous carbon. *Mar Ecol Prog Ser* 268:13–29
- Schlacher T, Wooldridge T (1996) Axial zonation patterns of subtidal macrozoobenthos in the Gamtoos Estuary, South Africa. *Estuaries* 19:680–696
- Smith F (2001) Historical regulation of local species richness across a geographic region. *Ecology* 82:792–801
- Smith F, Witman J (1999) Species diversity in subtidal landscapes: maintenance by physical processes and larval recruitment. *Ecology* 80:51–69
- Sokal R, Rolf F (1981) *Biometry: the principles and practice of statistics in biological research*, 3rd edn. WH Freeman, New York
- Stanton B, Pickard G (1981) Physical oceanography of the New Zealand fiords. *NZ Oceanogr Inst Mem* 88:1–37
- Tallis H, Wing S, Frew R (2004) Historical evidence for habitat conversion and local population decline in a New Zealand fjord. *Ecol Appl* 14:546–554
- Tenore K (1977) Food chain pathways in detrital feeding benthic communities: a review, with new observations on sediment resuspension and detrital recycling. In: Coull B (ed) *Ecology of marine benthos*. University of South Carolina Press, Columbia, SC, p 37–53

- Tenore K, Cammen L, Findlay S, Phillips N (1982) Perspectives of research on detritus: Do factors controlling the availability of detritus to macroconsumers depend on its source? *J Mar Res* 40:473–490
- Thrush S, Hewitt J, Norkko A, Nicholls P, Funnell G, Ellis J (2003) Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. *Mar Ecol Prog Ser* 263:101–112
- Wing, S, Lamare M, Vasques J (2001) Population structure of sea urchins (*Evechinus chloroticus*) along gradients in primary productivity in the New Zealand fjords. In: Barker M (ed) *Echinoderms: Dunedin*. Balkema, Dunedin, p 569–575
- Wing S, Gibbs M, Lamare M (2003) Reproductive sources and sinks within a sea urchin (*Evechinus chloroticus*) population of a New Zealand fjord. *Mar Ecol Prog Ser* 248: 109–123
- Witman J, Grange K (1998) Links between rain, salinity, and predation in a rocky subtidal community. *Ecology* 79: 2429–2447
- Ysebaert T, Meire P, Maes D, Buijs J (1993) The benthic macrofauna along the estuarine gradient of the Schelde estuary. *Neth J Aquat Ecol* 27:327–341

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