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Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand

Marti J. Anderson*, Russell B. Millar

Department of Statistics, Tamaki Campus, University of Auckland, Private Bag 92019, Auckland, New Zealand

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Abstract

Reef-associated fishes can respond to changes in habitat structure and the nature of their response can change with different spatial scales of observation. A structured hierarchical mensurative sampling design was used to sample temperate reef fish assemblages in northeastern New Zealand at several spatial scales over 2 years. The three spatial scales examined were tens of meters (transects), hundreds to thousands of meters (sites) and hundreds of kilometers (locations). We tested the hypothesis that fish assemblages differed between kelp forest habitat (relatively dense stands of the kelp, *Ecklonia radiata* (C. Agardh) J. Agardh, median depth=13.5 m) and barrens habitat (rocky reef dominated by turfing and encrusting red algae and the grazing urchin, *Evechinus chloroticus* (Valenciennes), median depth=6.7 m). Recently developed multivariate techniques were used to test for and quantify multivariate variation at different spatial scales. There were significant effects of habitat on the spatial distribution of fish assemblages, characterised by greater abundances or frequencies of *Parika scaber*, *Chromis dispilus*, *Trachurus novaezelandiae*, *Nemadactylus douglasii*, *Bodianus unimaculatus*, *Odax pullus* and *Pseudolabrus miles* in kelp forest habitat, and greater abundances or frequencies of *Notolabrus celidotus*, *Notolabrus fucicola*, *Girella tricuspidata*, *Coris sandageri*, *Chironemus marmoratus*, *Parma alboscapularis*, *Scorpis violaceus* and *Kyphosus sydneyanus* in barrens habitat. Some of the more common species, including *Upeneichthys lineatus*, *Scorpis lineolatus* and *Cheilodactylus spectabilis* showed no strong consistent effects of these two differing habitats on their distributions. There was, however, a significant Habitat×Locations interaction: effects of habitat did not occur at all locations. Variability was highest at the scale of individual transects and variability from site to site and from location to location was comparable. Spatial variation was large compared to inter-annual variation, which was minimal, and spatial patterns were consistent in the 2 years examined. Further experiments, including manipulations, are required to

* Corresponding author. Tel.: +64-9-373-7599x85052; fax: +64-9-373-7000.
E-mail address: mja@stat.auckland.ac.nz (M.J. Anderson).

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understand what mechanisms and processes might be driving these patterns. This study, coupled with results from previous studies, suggests that there may be a dynamic inter-play between effects of habitat on fish and effects of fish on biogenic habitat, such as kelp forests.

Keywords: Hierarchical experimental design; Kelp forest; Multivariate analysis; Temperate reef fish; Urchin grazing; Variance components

1. Introduction

An important goal in ecology is to understand patterns of distributions of organisms by reference to the habitat available to them in the environment. For reef-associated fishes, there is abundant evidence that the structure of the habitat has important effects on spatial distributions of populations, both in tropical coral reefs (Roberts and Ormond, 1987; Tolimieri, 1995; Caley and St. John, 1996; Friedlander and Parrish, 1998; Tolimieri, 1998a; Holbrook et al., 2000; McClanahan and Arthur, 2001) and in temperate rocky reef systems (Choat and Ayling, 1987; Jones, 1988; Holbrook et al., 1990; Connell and Jones, 1991; Carr, 1989; Levin and Hay, 1996; Tupper and Boutilier, 1997; García-Charton and Pérez-Ruzafa, 2001). For example, for temperate reefs in northeastern New Zealand, Choat and Ayling (1987) described two distinct assemblages of fishes associated with two different habitat types: (i) areas dominated by grazing urchins (*Evechinus chloroticus* (Valenciennes)), with cover by encrusting and turfing red algae (called "barrens" habitat) and (ii) areas of relatively dense stands of the laminarian kelp *Ecklonia radiata* (C. Agardh) J. Agardh (referred to as "kelp forests"). They found that small wrasses were more abundant in the shelter of kelp forests and increased with increases in kelp density, while larger carnivores were more abundant in urchin-grazed areas (Choat and Ayling, 1987). Jones (1984a) found that juveniles of the wrasse, *Notolabrus celidotus* (spotty), were positively associated with the density of macroalgae on New Zealand reefs. Furthermore, densities of recruits decreased with the experimental removal of kelp and increased with the experimental addition of kelp (through removal of urchins, Jones, 1984a). The consequences of the use of kelp forests by younger fish for predicting distributions of adult populations are, however, largely unknown.

There is some evidence for the effects of kelp habitat on reef fishes in other parts of the world. However, Holbrook et al. (1990) found only weak differences in species composition among reefs with different types of algal habitats in Southern California, and mixed results were obtained by other workers in this region (e.g., Stephens et al., 1984; Carr, 1989; DeMartini and Roberts, 1990). In addition, in New Zealand, Choat and Ayling (1987) suggested that the differences found between habitats in their study were independent of species identity, being driven instead by differences in the biology of feeding preferences of fishes at different ontogenetic stages. Thus, it is unclear whether the species composition and relative abundances of individual fish species differ in consistent or predictable ways between these two identifiable habitats

in northeastern New Zealand. A structured mensurative experiment is needed to investigate this.

A further important aspect of understanding spatial distributions with respect to habitat characteristics is to recognize that observed patterns are dependent on the spatial scale of observation (e.g., Andrew and Mapstone, 1987; Wiens, 1989; Tolimieri, 1995; Chesson, 1998; Sale, 1998). There have been several studies of spatial patterns of distributions of fish at several spatial scales, from meters up to hundreds or thousands of kilometers (e.g., Choat and Ayling, 1987; Doherty, 1987; Fowler et al., 1992; Tolimieri, 1998a; Ault and Johnson, 1998; Connell and Kingsford, 1998; García-Charton and Pérez-Ruzafa, 2001; Connell, 2002). Effects of habitat at small spatial scales can provide predictive power at larger spatial scales for some coral reef fish species (i.e., damselfish, Tolimieri, 1995; Holbrook et al., 2000), but not for others (i.e., stoplight parrotfish, Tolimieri, 1998a,b). Jones (1988) suggested that it is the comparison of the magnitude of variation at each spatial scale of interest that will provide the necessary framework for formulating hypotheses about relevant processes for reef fishes. Hierarchical spatially structured sampling programs provide a means of partitioning and quantifying the magnitude of variation at different spatial scales (Andrew and Mapstone, 1987; Underwood and Chapman, 1996; Underwood et al., 2000). Indeed, it may not be possible to understand effects of habitat, which is a spatial phenomenon, involving patchiness and heterogeneity, without an understanding of variability at different spatial scales (Kotliar and Wiens, 1990; Underwood and Chapman, 1996; Underwood et al., 2000). For example, Fowler-Walker and Connell (2002) demonstrated scale-dependent associations of understorey algae in *E. radiata* forests, with weak or variable local-scale responses to habitat, but strong and consistent patterns at regional scales (thousands of kilometers). Although some explicit measurements of variation in effects of habitat on fish species at different spatial scales have been made by certain workers (e.g., Tolimieri, 1998a; Doherty, 1987; Fowler et al., 1992; García-Charton and Pérez-Ruzafa, 2001), this has not generally been done using structured hierarchical designs, such as those used to advantage for benthic invertebrate and algal assemblages (e.g., Underwood and Chapman, 1996; Menconi et al., 1999; Benedetti-Cecchi, 2001; Fowler-Walker and Connell, 2002), but see Connell and Kingsford (1998) and Connell (2002).

One stumbling block towards measuring spatial variation in fish or other kinds of assemblages has been the lack of an appropriate method for assessing multivariate variation for several species simultaneously, that is, to measure and quantify variation in multivariate assemblages in each scale of a hierarchy of spatial scales. Available distance-based multivariate methods that are realistic for non-normal counts of species abundances are either unable to obtain independent partitions of multivariate variation for such complex designs (such as ANOSIM, Clarke, 1993; or Mantel correlograms, Legendre and Fortin, 1989), or require large numbers of replicates to avoid problems of non-independence (Underwood and Chapman, 1998).

Recent developments in non-parametric multivariate analysis provide a method for analyzing multivariate assemblages on the basis of any distance or dissimilarity measure, while also allowing the data to be partitioned according to any experimental design, including nested hierarchies (Anderson, 2001a; McArdle and Anderson, 2001).

Non-parametric multivariate analysis of variance (NPMANOVA, Anderson, 2001a) can be used to partition variability and to provide measures of multivariate variability at different scales in a structured hierarchical design, in a manner directly analogous to univariate partitioning using ANOVA (e.g., Searle et al., 1992; Benedetti-Cecchi, 2001). The statistical significance of multivariate variance components can also be tested using appropriate methods of permutation (Anderson, 2001b; Anderson and ter Braak, 2003).

The purpose of the present investigation was to conduct a mensurative, observational experiment (sensu Hurlbert, 1984) to examine the potential effects of habitat on fish assemblages in northeastern New Zealand at several spatial scales. Before hypotheses concerning any potential emerging patterns or processes can be developed, good observational data and quantitative measures of spatial variability in fish assemblages are extremely useful—for individual species and for the multivariate assemblage as a whole (Underwood et al., 2000). More specifically, we wished to test the null hypothesis (following Choat and Ayling, 1987) that there are no differences in the composition of fish assemblages in kelp forest habitat vs. barrens habitat on subtidal rocky reefs (i.e., that differences are "independent of species identity"). To determine the generality of any potential patterns, effects of habitat need to be examined at several locations and at several times (e.g., Yates and Cochran, 1938; Snedecor, 1946; Underwood and Petraitis, 1993). Furthermore, as effects of habitat on fish may or may not "scale up" to provide good prediction at larger spatial scales (e.g., Tolimieri, 1998a), depending on the species (e.g., Ault and Johnson, 1998), we predicted that the multivariate effects of habitat would interact with variability at different spatial scales and that different species would show different patterns in this regard. We also tested the hypothesis that there is a significant relationship between fish assemblage structure and the density of kelp forests, as a relationship with kelp density was observed for total numbers of large carnivorous fish by Choat and Ayling (1987).

The spatial scales of investigation included in the study were tens of meters (transects), hundreds of meters to kilometers (sites) and hundreds of kilometers (locations). These large-scale surveys were performed in each of 2 years using a structured hierarchical experimental design to investigate effects of habitat on reef fishes. This is the first study, to our knowledge, that uses multivariate methods to obtain independent quantitative measures of variability in fish assemblages at different spatial scales.

In northeastern New Zealand, it is known that patches of kelp forest habitat tend to occur at deeper depths than patches of barrens habitat, although there is some overlap in their natural depth ranges (e.g., Schiel, 1990). Brook (2002) found a significant positive relationship between depth (up to 45 m) and species richness of fishes, while depth-stratified sampling by Meekan and Choat (1997) showed significant differences in abundances of several prominent herbivorous fishes among different depth strata. It is not known, however, the extent to which effects of depth may mediate effects of habitat. The present study therefore also measured depth as a covariable for analyses, to test the hypothesis that significant differences in assemblages due to habitat, if present, could not be fully explained by a relationship of assemblages with depth.

2. Methods

2.1. Underwater visual sampling of fish

The study used a structured hierarchical experimental design. Four locations, separated by hundreds of kilometers, were sampled along the northeastern coast of New Zealand (Fig. 1). These included, from South to North, Hahei (36°50.86′S, 175°49.32′E), Leigh (36°17.43′S, 174°48.82′E), Home Point (35°19.38′S, 174°21.38′E) and Berghan Point (34°55.78′S, 173°32.72′E) (Fig. 1). Within each location, fish were sampled at each of four different randomly located sites, separated by hundreds to thousands of meters. At each site, two habitats were investigated: kelp forests (i.e., areas characterised by relatively dense cover of the kelp *E. radiata*) and "barrens" (i.e., areas characterised by little or no macroalgal cover and dominated by the grazing urchin *E. chloroticus*). The range of depths was 2–20 m, although the majority of the observations were in the range from 5 to 15 m.

Within each habitat, divers on SCUBA did a visual survey by swimming along a transect and identifying and recording the number of each species of fish observed within a distance of 2.5 m on either side of the transect. Taxonomic authorities for all fish species named herein are available in Paulin et al. (1989). All fish seen were recorded except for notoriously cryptic or very small species (e.g., Tripterygiidae and Gobiidae), which were not included, as we could not be confident that they were being reliably seen over these spatial scales (e.g., Lincoln-Smith, 1989; Willis, 2001). Each diver carried a tape measure and swam a "run-in" distance of 5 m before beginning the actual survey for each transect, which was 25 m long after the run-in. Thus the total area sampled per transect was 5×25 m. There were n=10 transects sampled haphazardly within each habitat at each site. Although there are some known biases inherent in using the method of underwater visual surveys to count fish (e.g., Brock, 1982; Sale and Sharp, 1983; Lincoln-Smith, 1989; Thompson and Mapstone, 1997; Willis et al., 2000), this same sampling methodology was used across the entire experimental design. This allows valid comparisons to be made across habitats and across different spatial scales, even though unbiased estimates of population densities may not be obtained for some fish species from these data. It was not possible logistically for a single diver to perform the entire sampling design, so several divers participated in the study. There was likely variation due to different observers, although this was not explicitly measured. This was not, however, related in any systematic fashion with differences across habitats because each diver involved in the study sampled both types of habitat. Divers also recorded the depth at the beginning and at the end of each transect (in meters), which generally differed by no more than 1–2 m. The average depth measured for each transect was used for analyses. Also, in the first year of sampling for kelp habitats, the density of kelp in the forests was estimated. This was done by a second diver swimming behind the diver counting fish. A 1-m^2 quadrat was placed alongside the transect tape (used by the diver counting fish) at each of five positions along the tape (approximately 5, 10, 15, 20 and 25 m) and the number of kelp plants of the species *E. radiata* per quadrat was recorded. The average and the standard deviation for kelp density were then calculated for each transect based on these five observations.

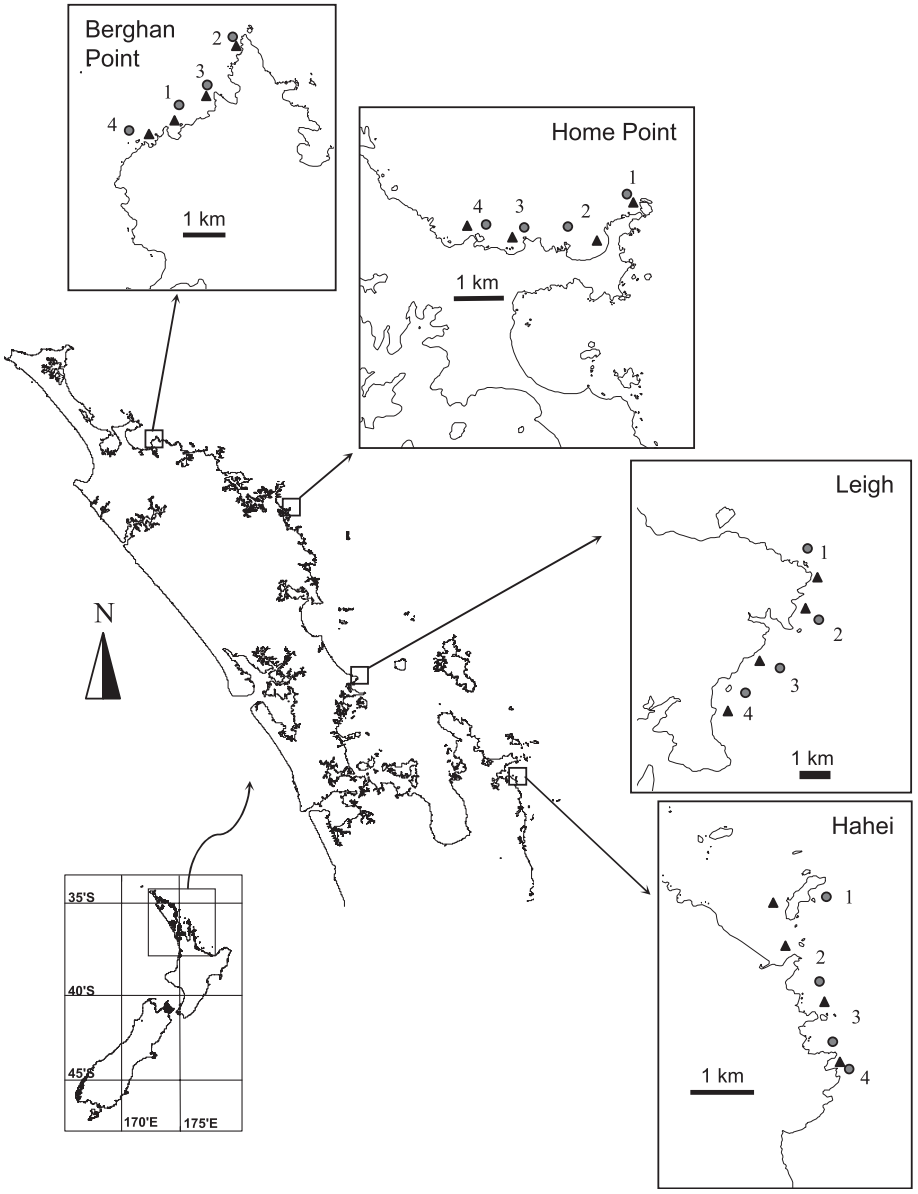

Fig. 1. Map of northeastern New Zealand showing the four locations for the study and the sites where surveys were done. Grey circles indicate kelp habitat and black triangles indicate barrens habitat sampled at each site.

The sampling was done within a 1-month period in each of 2 consecutive years during the southern hemisphere's (austral) summer: from 30 November to 21 December 2000 (year 1) and from 7 January to 5 February 2002 (year 2). The locations were not sampled consecutively from north to south or vice versa, so as not to confound the latitudinal

gradient (if any) with time of sampling within the month. In addition, all sites were located outside of any established marine reserves (i.e., at Hahei and Leigh). GPS coordinates were recorded at each site in year 1 and the same sites (although not the same transects) were re-visited in year 2 by reference to these GPS coordinates. Due to the high mobility of fish, the 2 years were considered as independent samples.

2.2. Multivariate statistical methods

The experimental design therefore consisted of four factors: year (two levels, fixed), location (four levels, random), site (four levels, random, nested in location) and habitat (two levels, fixed, crossed with all other factors). Thus, with n=10 transects, there were a total of 640 observation units in the data set. There were 46 species of fish (variables) recorded in the study that were included in multivariate analyses (listed in Appendix A). Although it would have been logical to treat the factor "year" as random in the present design, with only 2 years of data, inferences concerning inter-annual variation in general could not be viewed as very precise. Thus, "year" was treated as a fixed factor, which focused our analyses on results obtained for these 2 years only. With a greater number of years of sampling anticipated in the future, we would treat this as a random effect.

The fish species variables were highly skewed and contained a great many zeros, making traditional analyses (which assume normality of errors) unsuitable, so non-parametric approaches were used. NPMANOVA (Anderson, 2001a; McArdle and Anderson, 2001) was used to analyse the multivariate data set in response to the complete experimental design (including interactions). This method allows multivariate data to be analysed on the basis of any distance or dissimilarity measure of choice, in response to any complex experimental design, with P-values obtained using permutations. We used scale-invariant binomial deviance as a dissimilarity measure (described below) for the NPMANOVA. The tests do not assume that the original variables conform to a multivariate normal or to any other specified distribution. Although the approach does not explicitly assume common variances among groups, it will (like ANOSIM, Clarke, 1993) be sensitive to differences in multivariate dispersion. In addition, the results of NPMANOVA were also used to estimate the sizes of multivariate pseudo variance components from the analyses, relying on the analogy of NPMANOVA as an ANOVA based on distances and univariate ANOVA estimators based on mean squares (e.g., Searle et al., 1992). Doing this (and indeed applying NPMANOVA to a complex multi-factorial design in general) does require us to assume that the linear ANOVA model can be applied successfully to achieve a partitioning of the squared inter-point dissimilarities for inferences to be made about the multivariate assemblage. We feel this is reasonable provided the choice of dissimilarity measure accurately reflects relevant qualities of the multivariate assemblage of interest.

For each term in the analysis, 4999 permutations of raw data units were done to obtain P-values (e.g., Manly, 1997). Care was taken to ensure that the correct permutable units were used to obtain a valid permutation test of each term in the analysis (Anderson, 2001b; Anderson and ter Braak, 2003). For example, to test the following term: Year×Location×Habitat, the 64 cell units corresponding to the 64 combinations of Year×Site(Location)×Habitat were permuted (i.e., the 10 transects within each of these cells were kept together as a unit). This is because the denominator mean square for the

test of Year×Location×Habitat is the mean square for Year×Site(Location)×Habitat, thus it is these units (indicated by the denominator of the *F*-ratio) that are appropriate to permute under the null hypothesis (Anderson, 2001b; Anderson and ter Braak, 2003). An important assumption underlying each test is therefore the exchangeability of the correct errors (for each particular term being tested in the analysis) under each null hypothesis of interest. In some cases, this restriction on the permutable units meant that there were not enough possible permutations to get a reasonable test. For these situations, a Monte Carlo sample was drawn from the theoretical asymptotic permutation distribution (Anderson and Robinson, 2003). We re-iterate that these permutation tests assume not just exchangeability, but also that a linear model on dissimilarities is appropriate for choosing reasonable test-statistics for testing multivariate hypotheses in an ANOVA framework, analogous to those used in univariate ANOVA. All analyses were done using specialised software, written in FORTRAN.

To compare whole fish assemblages to quantitative variables (i.e., depth, average kelp density and the standard deviation of kelp density), non-parametric multivariate multiple regression was used on the basis of the binomial deviance dissimilarity measure, using 4999 random permutations (McArdle and Anderson, 2001). We were particularly concerned to test for any significant effects of habitat over and above the potential effect of depth, as kelp forests and barrens habitats occur naturally at different depths, on average. Thus, the effect of habitat was tested, with depth as a covariable in the analysis, using non-parametric multivariate multiple regression and 4999 permutations of residuals under the reduced model (e.g., Anderson, 2001b). We also used ordinary least squares regression to compare each of the three quantitative variables to the total number of species per transect and the total number of individuals (the latter after transforming to $\ln(x+1)$). Individual transects were removed from the analysis whenever the quantitative predictor variable of interest was missing. Also, for these and any other analyses of the total number of fish (as a univariate variable), the following schooling species that can occur sporadically in clumps of thousands were not included: *Trachurus novaezelandiae* (jack mackerel), *Aldrichetta forsteri* (yellow-eyed mullet) and *Decapterus koheru* (koheru). Far from being dominant species, mullet and koheru, for example, were only observed in 4 and 16 out of 640 transects, respectively. More importantly, these species were excluded from sums of the total number of individuals primarily because no certainty regarding the precision of estimates of their numbers was warranted (Choat and Ayling, 1987). These species were not, however, omitted from the multivariate analyses, as such large numbers do not pose a problem for the dissimilarity measure used here. Although there still may be some difficulty in interpreting analyses of total numbers of individuals among sites with different species composition, as the underwater visual sampling method may be biased in different ways for different fish species, we nevertheless considered that it was a measured variable worth investigating, with this caveat in mind.

2.3. Binomial deviance as a dissimilarity measure

For the fish abundance data, we developed and used a new dissimilarity measure, based on likelihood theory. Let y_{1k} and y_{2k} be the count for species k in transects 1 and 2, respectively, and let $n_k=(y_{1k}+y_{2k})$. We may then consider the null hypothesis that the two

transects do not differ in their composition and relative abundance of species. That is, for each species, we expect that half of the counts (i.e., half of n_k) will fall into each transect. The binomial deviance of our observed data from this hypothesis is defined, under likelihood theory, as

$$\text{deviance} = y_{1k} log\left(\frac{y_{1k}}{n_k}\right) + y_{2k}\log\left(\frac{y_{2k}}{n_k}\right) - (y_{1k} + y_{2k})\log\left(\frac{1}{2}\right)$$

Thus, a useful measure of ecological dissimilarity between the two transects is the sum of these deviances across all species. To take account of the fact that different species may be varying on different scales, a scale-invariant measure may be obtained by considering this quantity on a per-observation basis, which is achieved by simply dividing by n_k:

$$d_{1,2} = \sum_{k=1}^{p} \frac{1}{n_k}\left\{y_{1k}\log\left(\frac{y_{1k}}{n_k}\right) + y_{2k}\log\left(\frac{Y_{2k}}{n_k}\right) - (y_{1k} + y_{2k})\log\left(\frac{1}{2}\right)\right\}$$

This measure, which we will refer to as the binomial deviance dissimilarity, resembles somewhat the measure proposed by Cao et al. (1997) as an improvement on the Bray-Curtis measure, but has the added advantage of being based in likelihood theory.

The null hypothesis from which the binomial deviance dissimilarity is derived could also be tested using the chi-square test statistic for the equality of expected counts in the two transects for all species. In this context, the chi-square test statistic is equivalent to the dissimilarity measure known as the coefficient of divergence (Clark, 1952). Hence, the binomial deviance and the coefficient of divergence should have similar properties. The coefficient of divergence, along with the Canberra metric and the Bray-Curtis measure, were recommended by Gower and Legendre (1986) for use with species abundance data. For further details on the properties of these measures, see Legendre and Legendre, (1998, e.g., p. 298).

2.4. Ordination

Metric multi-dimensional scaling (MDS) (principal coordinate analysis) on the basis of the binomial deviance dissimilarity measure was used as an unconstrained ordination method to visualize multivariate patterns. In addition, canonical analysis of principal coordinates (CAP, Anderson and Willis, 2003; Anderson and Robinson, 2003) was used as a constrained ordination procedure to visualize patterns by reference to particular hypotheses. The CAP analyses were only done on appropriate terms found to be significant using NPMANOVA. These analyses were also done using specialised software written in FORTRAN.

2.5. Univariate analyses

Frequencies of occurrence were examined for each fish species across the relevant factors of interest in the study (Appendix A). Six species of fish were abundant enough to be analysed using univariate analysis of variance (ANOVA): *Parika scaber* (leather

jacket), *Cheilodactylus spectabilis* (red moki), *Scorpis lineolatus* (sweep), *Upeneichthys lineatus* (goatfish), *N. celidotus* (spotty) and *Chromis dispilus* (demoiselle). The total number of fish and the total number of species per transect were also analysed using univariate ANOVA. Due to the predominance of zeros, extremely large variability at the level of individual transects and the highly skewed nature of these data, normality was not a reasonable assumption for any of these single variables except for the total number of species. Thus, in each case, all tests were done using a permutation procedure (with 4999 permutations of appropriate units), as described for the NPMANOVA above. These tests using permutations will be sensitive to differences in dispersion, so results should be interpreted with caution in this regard. Where appropriate, significant terms were investigated with a posteriori pair-wise comparisons, which also used 4999 random permutations to obtain *P*-values. These univariate tests were done using the same software as that used for the multivariate tests, but with only one variable and (appropriately) basing the analysis on Euclidean distance. The *F*-ratios used for tests done in this way are equivalent to those of traditional ANOVA (Anderson, 2001a), although the *P*-values are not obtained using traditional tables.

3. Results

3.1. Effects of depth and density of kelp

The two habitats sampled did differ in their spatial distributions with respect to depth (Fig. 2). The median depth of transects in kelp habitat was 13.5 m (inter-quartile range = 11.5–15 m), while for barrens habitat the median depth was 6.7 m (inter-quartile

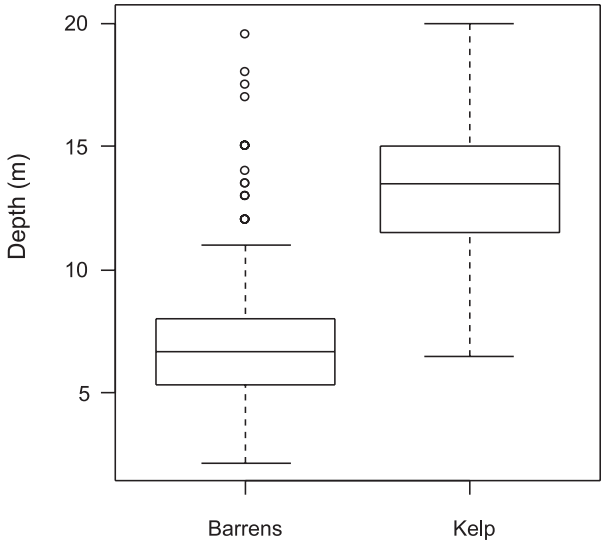

Fig. 2. Boxplots of the depth of transects (in metres) for each habitat: barrens (n=316) and kelp (n=318).

Table 1
Relationships between the total number of fish species (*tot sp*) and the total number of fish (*tot fish*) vs. depth, average kelp density (*kelp av*) or standard deviation of kelp density (*kelp sd*)

	n	r^2	*F*	*P*
Year 1				
tot sp vs. *depth*	309	0.0043	1.325	0.2506
tot fish vs. *depth*	309	<0.0001	0.003	0.9538
tot sp vs. *kelp av*	159	0.0711	12.022	0.0007
tot fish vs. *kelp av*	159	0.0167	2.700	0.1043
tot sp vs. *kelp sd*	159	0.0774	13.171	0.0004
tot fish vs. *kelp sd*	159	0.0349	5.673	0.0184
Year 2				
tot sp vs. *depth*	325	0.0057	1.869	0.1726
tot fish vs. *depth*	325	0.0157	2.691	0.0238

The total number of fish was transformed to ln(x+1) before analysis. Note that kelp densities were not recorded in year 2.

range = 5.35 – 8 m). There was no significant relationship, however, between the total number of species and depth for either year 1 or for year 2 (Table 1). The total number of fish (transformed to ln(x+1)) was significantly and positively related to depth for year 2 only (Table 1). There was also a significant relationship between the depth of transects and the multivariate fish assemblages (Table 2). Depth only explained 3.5% of the variation in the multivariate assemblage structure and only 1.6% of the variation in total numbers of fish. Furthermore, effects of habitat (kelp vs. barrens) were significant over and above effects of depth (Table 2). Thus, although some effects of habitat (described in greater detail below) may be attributable to differences in depth, this analysis shows there were significant effects of habitat on fish assemblages (e.g., structural or other differences) that were unrelated to depth. Depth was not treated as a covariable in subsequent analyses (e.g., Table 3 below), as we wished to examine overall effects of habitat, including those aspects that may have been related to depth.

Within kelp forest habitats for year 1, fish assemblages were also significantly related to the average kelp density per transect (pseudo $F_{1,\ 157}$=4.788, P=0.0008, 4999 permutations), but were not related to the variation (standard deviation) in kelp density along transects (pseudo $F_{1,\ 157}$ = 1.214, P = 0.3134, 4999 permutations). The total number of

Table 2
Sequential non-parametric multivariate multiple regression showing the relationship between multivariate fish species abundance data (based on the binomial deviance dissimilarity measure) and depth, followed by the effect of habitat, taking depth into account as a covariable

Source	*df*	SS	MS	*F*	*P*
Depth	1	32.660	32.660	22.942	0.0002
Habitat/depth	1	10.050	10.050	7.128	0.0078
Residual	631	889.665	1.410		
Total	633	932.375			

Table 3
Non-parametric multivariate analysis of variance of 46 fish species abundance variables, based on the binomial deviance dissimilarity measure

Source	*df*	SS	MS	*F*	*P*	Denominator MS	Permutable units
Year (Ye)	1	8.280	8.280	0.979	*0.4608*	Ye×Lo	8 Ye×Lo units
Location = (Lo)	3	87.368	29.123	5.765	0.0002	Si(Lo)	16 Si(Lo) units
Site(Location) = Si(Lo)	12	60.620	5.052	4.388	0.0002	Res	640 observation units
Habitat = Ha	1	25.708	25.708	2.264	*0.0650*	Lo×Ha	8 Lo×Ha units
Ye×Lo	3	25.384	8.461	2.975	0.0012	Ye×Si(Lo)	32 Ye×Si(Lo) units
Ye×Si(Lo)	12	34.130	2.844	2.470	0.0002	Res	640 observation units
Ye×Ha	1	4.117	4.117	1.598	0.1948	Ye×Lo×Ha	16 Ye×Lo×Ha units
Lo×Ha	3	34.065	11.355	3.684	0.0002	Si(Lo)×Ha	32 Si(Lo)×Ha units
Si(Lo)×Ha	12	36.983	3.082	2.677	0.0002	Res	640 observation units
Ye×Lo×Ha	3	7.728	2.576	1.256	0.2248	Ye×Si(Lo)×Ha	64 Ye×Si(Lo)×Ha units
Ye×Si(Lo)×Ha	12	24.609	2.051	1.781	0.0004	Res	640 observation units
Residual	576	663.153	1.151				
Total	639	1012.145					

P-values were obtained using 4999 permutations of given permutable units for each term or using 4999 Monte Carlo samples from the asymptotic permutation distribution (given in italics) when there were few possible permutations.

species was significantly positively related to the average and to the standard deviation in kelp density per transect, while the total number of fish (transformed to $\ln(x+1)$) was significantly positively related only to the standard deviation in kelp density (Table 1). However, these relationships, although statistically significant, were very weak, with a large amount of scatter and very low values of r^2 (Table 1). This indicates that kelp density and depth, while apparently contributing to explain small amounts of observed variation in fish assemblages, do not provide the means to generate predictions at the scale of individual transects.

3.2. Measured variation

Non-parametric MANOVA on the fish data showed that there was significant small-scale variability in the fish assemblages from site to site and year to year in different habitats (i.e., a significant Year×Site(Location)×Habitat interaction, Table 3). This significant small-scale variation was reflected in the analysis of several of the relatively abundant individual species as well, namely: *N. celidotus*, *S. lineolatus* and *C. dispilus* (see Tables 6 and 8 below). The greatest multivariate variability occurred at the scale of individual transects (i.e., residual, Table 4). The next-greatest

Table 4
Estimated multivariate pseudo variance components for each term in the model based on sums of squared dissimilarities (binomial deviance) for 46 fish species and the analogous univariate ANOVA estimators using mean squares (i.e., using multivariate mean squares in Table 1), ordered from largest to smallest

Source	MS	Variance components
Residual	1.1513	1.1513
Lo	29.1227	0.1504
Lo×Ha	11.3551	0.1034
Si(Lo)	5.0516	0.0975
Si(Lo)×Ha	3.0819	0.0965
Ye×Si(Lo)×Ha	2.0507	0.0899
Ye×Si(Lo)	2.8441	0.0846
Ha	25.7084	0.0449
YexLo	8.4614	0.0702
Ye×Lo×Ha	2.5760	0.0131
Ye×Ha	4.1171	0.0096
Ye	8.2796	0.0000

All components are random variance components except for habitat, year and Ye×Ha which are sums of squared fixed effects.

measured source of variation was that across locations, followed by the random interaction of location with habitat, and then the variation from site to site within locations. Considerable variation was also contributed by the random interaction of sites with habitats (Table 4). Other measured sources of variation included interactions of spatial effects with years; however, overall changes in assemblages from year to year were not strong compared to the other effects. In fact, the estimated variation due to years was slightly negative (−0.0006) using the ANOVA estimator and thus was estimated as zero (Table 4).

3.3. Effects of habitat

The effects of habitat (kelp forest vs. barrens) on fish assemblages varied significantly across locations (Table 3). In particular, the effects of habitat appeared to be strongest at Hahei and Home Point. This is shown by a greater separation of the points representing assemblages in kelp vs. barrens assemblages for these two locations, compared to Berghan Point and Leigh in the unconstrained ordinations: the two-factor metric MDS plot (Fig. 3) and in each of the one-factor metric MDS plots (Fig. 4, left-hand side). In addition, the CAP analysis showed larger canonical correlation coefficients for Hahei and Home Point than for Leigh or Berghan Point (Table 5, Fig. 4, right-hand side). Furthermore, the allocation success showed that fish assemblages from the two habitats at either Leigh or Berghan Point were not as distinct as that seen for the other locations. For example, Leigh had only 69% allocation success compared to Hahei, which had 94% success (Table 5). Pair-wise comparisons showed that there were significant differences in assemblages of fishes between barrens and kelp habitats at either Hahei or Home Point, but not at Berghan Point or Leigh (Table 5). It is interesting to note that the CAP analysis for Leigh shows a fairly distinct separation due to habitat, although its allocation success was poor and there was no significant effect detected by NPMANOVA. This is essentially due to the selection

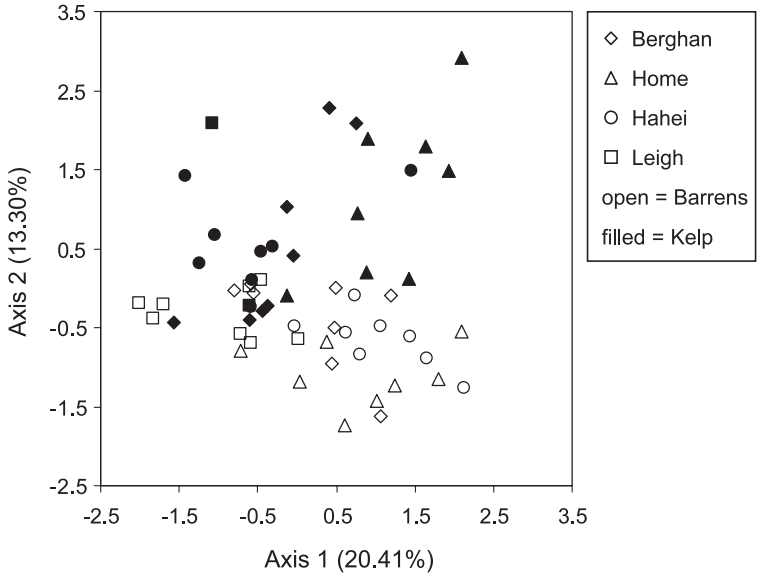

Fig. 3. Two-factor metric MDS plot of the pooled fish assemblages for each site on the basis of the binomial deviance dissimilarity measure, showing the factors of location and habitat. There are eight points for each combination of the factors, which correspond to the four sites in each of 2 years.

effects occurring in high-dimensional space, which can cause canonical plots to paint a "rosy" picture of the results. It further emphasizes the importance of using a technique like the leave-one-out method (e.g., Lachenbruch and Mickey, 1968) for assessing the distinctness of groups and independent tests rather than relying solely on the canonical plot.

There were no consistent effects of habitat on the total number of fish; these effects varied from site to site and from year to year (Table 6a, Fig. 5a). Despite the significant three-way interaction of Year×Location×Habitat (Table 6b), there were no statistically significant pair-wise differences detected in the total number of species in kelp forest vs. barrens in either year at any location (pair-wise comparisons, $P > 0.05$, Fig. 5b). In contrast, average numbers of *P. scaber* (leather jackets) were significantly higher in kelp forests than in barrens habitats for both years at the two northern locations of Berghan Point and Home Point (Table 6c, Fig. 5c, $P < 0.05$). Their frequency of occurrence was also greater in kelp forests, as was that of *C. dispilus* (demoiselle), *T. novaezelandiae* (jack mackerel), *Nemadactylus douglasii* (porae), *Bodianus unimaculatus* (pigfish), *Odax pullus* (butterfish) and *Pseudolabrus miles*

Fig. 4. Unconstrained metric MDS plots (left) and constrained CAP plots (right) done separately at each location (rows) on the basis of the binomial deviance dissimilarity measure, in each case comparing fish assemblages in two different habitats: barrens vs. kelp. There are eight points for each combination of the factors, which correspond to the four sites in each of 2 years.

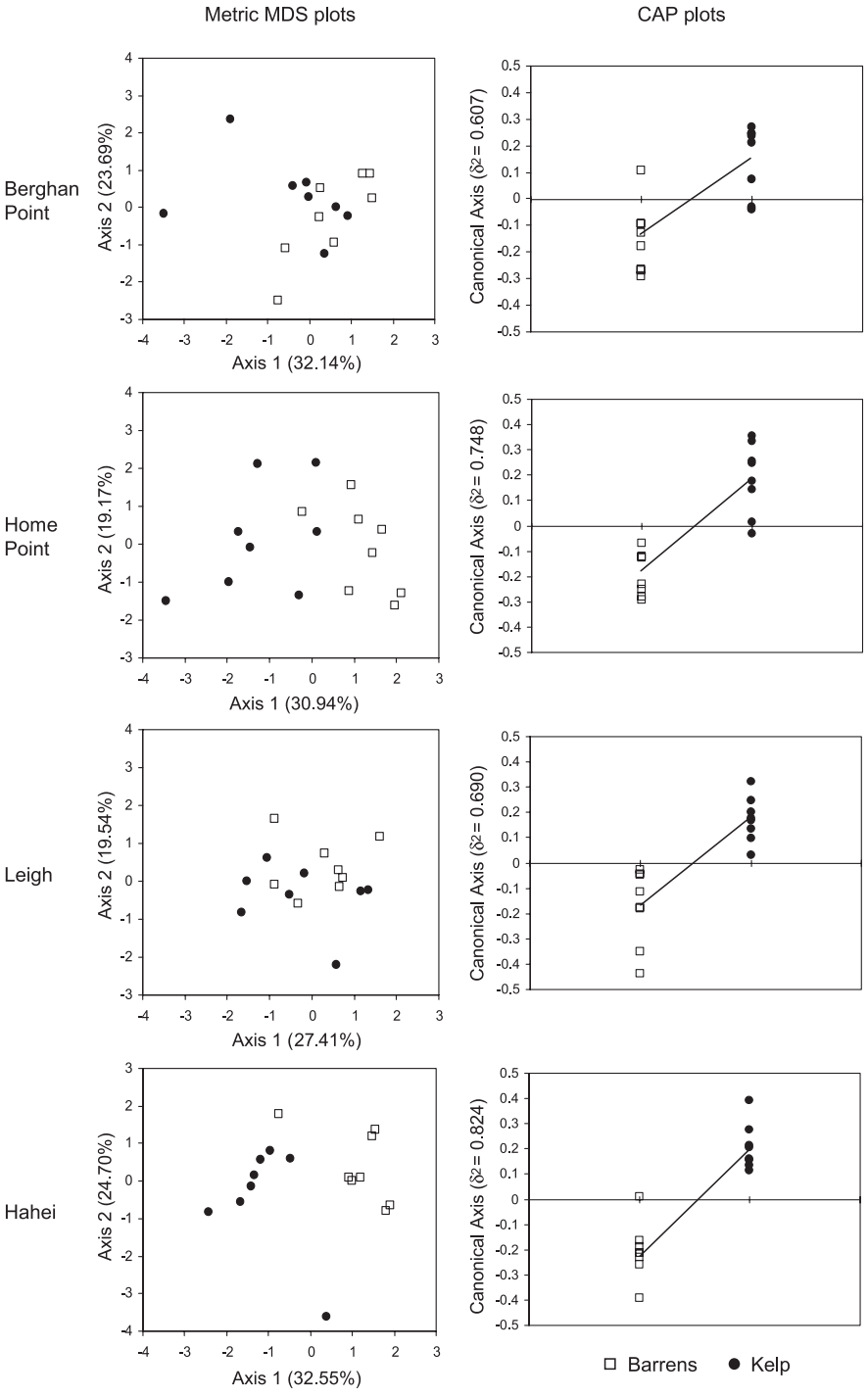
Metric MDS plots
CAP plots
Berghan Point
Home Point
Leigh
Hahei
Axis 2 (23.69%)
Axis 1 (32.14%)
Axis 2 (19.17%)
Axis 1 (30.94%)
Axis 2 (19.54%)
Axis 1 (27.41%)
Axis 2 (24.70%)
Axis 1 (32.55%)
Canonical Axis (δ²= 0.607)
Canonical Axis (δ²= 0.748)
Canonical Axis (δ²= 0.690)
Canonical Axis (δ²= 0.824)
Barrens
Kelp

Table 5
Results of CAP analyses examining effects of habitat within each location for 46 species of fish on the basis of the binomial deviance dissimilarity measure

Location	*m*	%Var	Allocation success (%)			δ^2	*P*
			Barrens	Kelp	Total		
Berghan Point	4	78.56	75	75	75	0.607	0.0564
Home Point	5	84.81	88	75	81	0.748	0.0018
Leigh	6	86.97	63	75	69	0.690	0.1080
Hahei	4	86.89	88	100	94	0.824	0.0006

m = the number of principal coordinate (PCO) axes used in the CAP procedure, %Var = the percentage of the total variance explained by the first *m* PCO axes, Allocation success = the percentage of points correctly allocated into each group, δ^2 = the squared canonical correlation. *P*-values given are the results of pair-wise comparisons of assemblages in kelp forest vs. barrens habitat at each location, using NPMANOVA, with 4999 permutations of individual sites as units (i.e., permuting each set of $n = 10$ transects together as a unit).

(scarlet wrasse) (Appendix A). Correlations of species with canonical axes also suggested that *Zeus faber* (john dory) and *Seriola lalandi* (kingfish) were associated with kelp forest habitats (Table 7). Although average numbers of *C. dispilus* also tended to be greater in kelp forest habitat (Fig. 5d), this pattern was not statistically significant (Table 6d).

Fish that occurred more frequently in barrens habitats were *N. celidotus* (spotty), *Notolabrus fucicola* (banded wrasse), *Girella tricuspidata* (parore), *Coris sandageri*

Table 6
Results of univariate ANOVAs on selected variables and species

Source	*df*	(a) Total no. fish			(b) Total no. species			(c) *Parika scaber*			(d) *Chromis dispilus*		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Ye	1	8917.0	4.779	*0.1114*	3.025	0.070	*0.8108*	2.336	0.892	*0.4206*	4944.4	4.565	*0.1164*
Lo	3	13056.2	4.065	0.0370	98.173	5.342	0.0170	15.135	2.789	0.0888	9972.5	7.064	0.0088
Si(Lo)	12	3211.7	4.916	0.0002	18.377	4.853	0.0002	5.427	2.674	0.0014	1411.7	4.575	0.0002
Ha	1	17.2	0.010	*0.9332*	32.400	0.388	*0.5752*	43.403	2.908	*0.1788*	3048.9	4.761	*0.1084*
Ye×Lo	3	1866.0	1.934	0.1824	43.050	9.156	0.0026	2.618	1.329	0.3076	1083.2	1.516	0.2600
Ye×Si(Lo)	12	965.1	1.477	0.1268	4.702	1.242	0.2538	1.970	0.970	0.4858	714.4	2.315	0.0068
Ye×Ha	1	1196.5	0.586	0.5122	12.656	0.762	0.4538	9.344	8.959	0.0572	3032.5	5.714	0.0948
Lo×Ha	3	1794.5	0.564	0.6510	83.508	7.402	0.0032	14.924	6.991	0.0036	640.4	0.738	0.5406
Si(Lo)×Ha	12	3184.4	4.874	0.0002	11.281	2.979	0.0010	2.135	1.052	0.4020	867.2	2.810	0.0022
Ye×Lo×Ha	3	2043.5	1.335	0.3046	16.606	4.516	0.0278	1.043	0.900	0.4670	530.7	0.523	0.6790
Ye×Si(Lo)×Ha	12	1530.7	2.343	0.0062	3.677	0.971	0.4762	1.159	0.571	0.8830	1013.9	3.286	0.0002
Residual	576	653.4			3.787			2.030			308.6		
Total	639												

P-values were obtained by 4999 permutations of appropriate units, as shown in Table 3 for each term in the analysis.
P-values in italics were obtained using 4999 Monte Carlo samples from the asymptotic permutation distribution. Mean squares used in the denominator for each test are also shown in Table 3.

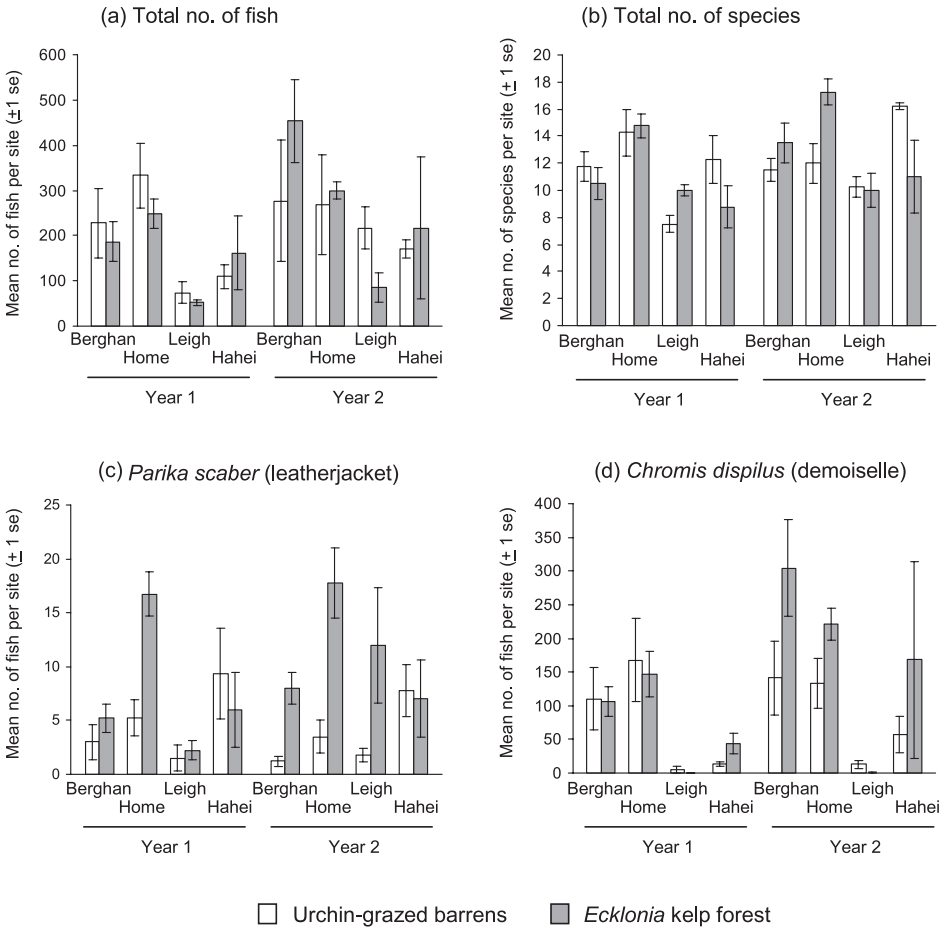

Fig. 5. Means (±1 S.E.) for (a) the total number of fish, (b) the total number of species, (c) the number of *P. scaber* (leather jacket) and (d) the number of *C. dispilus* (demoiselle) in each combination of Year×Location×Habitat ($n=4$ sites per combination of levels and a site consisted of counts summed across 10 transects).

(Sandager's wrasse), *Chironemus marmoratus* (hiwihiwi), *Parma alboscapularis* (black angelfish), *Scorpis violaceus* (blue maomao) and *Kyphosus sydneyanus* (silver drummer) (Appendix A). All of these fish had strong correlations with canonical axes, as did *Pempheris adspersus* (big eye) (Table 7). Average numbers of *N. celidotus* also tended to be greater in barrens habitats (Fig. 6a), although this trend was only statistically significant at Hahei ($P<0.05$), but not at the other locations (Table 8a).

Some of the common species did not show any strong consistent patterns or differences across the two habitats, including *U. lineatus* (goatfish, Fig. 6b, Table 8b), *S. lineolatus* (sweep, Fig. 6c, Table 8c) and *C. spectabilis* (red moki), which was significantly more

Table 7
Correlations of individual species with the canonical axis for habitat for each of the four locations, as shown in Fig. 4 (right-hand side)

Name	Berghan	Home	Leigh	Hahei	Average
Positive correlation (kelp)					
Bodianus unimaculatus	0.489	0.639	–	0.232	0.453
Seriola lalandi	0.499	–	0.218	0.561	0.426
Parika scaber	0.681	0.856	0.384	−0.226	0.424
Zeus faber	0.356	0.425	0.475	0.417	0.418
Nemadactylus douglasii	0.491	0.776	0.333	−0.245	0.338
Trachurus novaezelandiae	0.420	0.305	0.250	0.060	0.259
Pseudolabrus miles	–	0.270	0.075	0.398	0.247
Chromis dispilus	0.435	0.286	−0.269	0.237	0.172
Odax pullus	0.104	0.456	0.248	−0.172	0.159
Negative correlation (barrens)					
Parma alboscapularis	−0.409	−0.495	–	−0.539	−0.481
Chironemus marmoratus	−0.552	−0.023	−0.681	−0.591	−0.462
Coris sandageri	−0.352	−0.303	−0.438	−0.551	−0.411
Notolabrus celidotus	−0.340	−0.083	−0.380	−0.694	−0.374
Girella tricuspidata	−0.414	−0.499	−0.056	−0.442	−0.353
Pempheris adspersus	−0.124	−0.102	−0.569	−0.261	−0.264
Notolabrus fucicola	−0.119	0.062	−0.028	−0.822	−0.227
Kyphosus sydneyanus	−0.125	−0.358	0.218	−0.488	−0.188
Scorpis violaceus	0.347	−0.415	−0.090	−0.456	−0.153

A positive correlation indicates species associated with kelp habitat, while a negative correlation indicates species associated with barrens habitat. Species are given in decreasing order of the absolute value of their average for the correlation across the four locations. Dashed lines indicate a species did not occur at that location. Species that occurred in fewer than 7 transects (out of a total of 640) were not included.

abundant in barrens habitats but only in year 2 and only at Hahei (Fig. 6d, Table 8d, pair-wise comparisons, $P < 0.05$).

3.4. Effects of locations

Although locations were originally chosen randomly and so treated as a random factor in the analyses, it was nevertheless of interest to compare the 4 locations in terms of the fish assemblages found there, for biogeographic reasons and to compare results with those of previous studies. Due to its interaction with habitat (Table 3), the potential differences among locations were considered separately for each habitat. For each habitat, unconstrained ordinations did not separate assemblages from different locations very clearly (non-metric MDS plots, Fig. 7, right-hand side), while constrained (CAP) ordinations appeared to successfully separate Leigh, Hahei and Home Point, with assemblages from Berghan Point being less distinct (Fig. 7, right-hand side). The separation in multivariate space of assemblages from different locations was slightly more successful for barrens habitats than for kelp forests (Table 9). For barrens habitats, fish assemblages from each location differed significantly from all other locations, except for Berghan Point and Home Point, which did not differ significantly

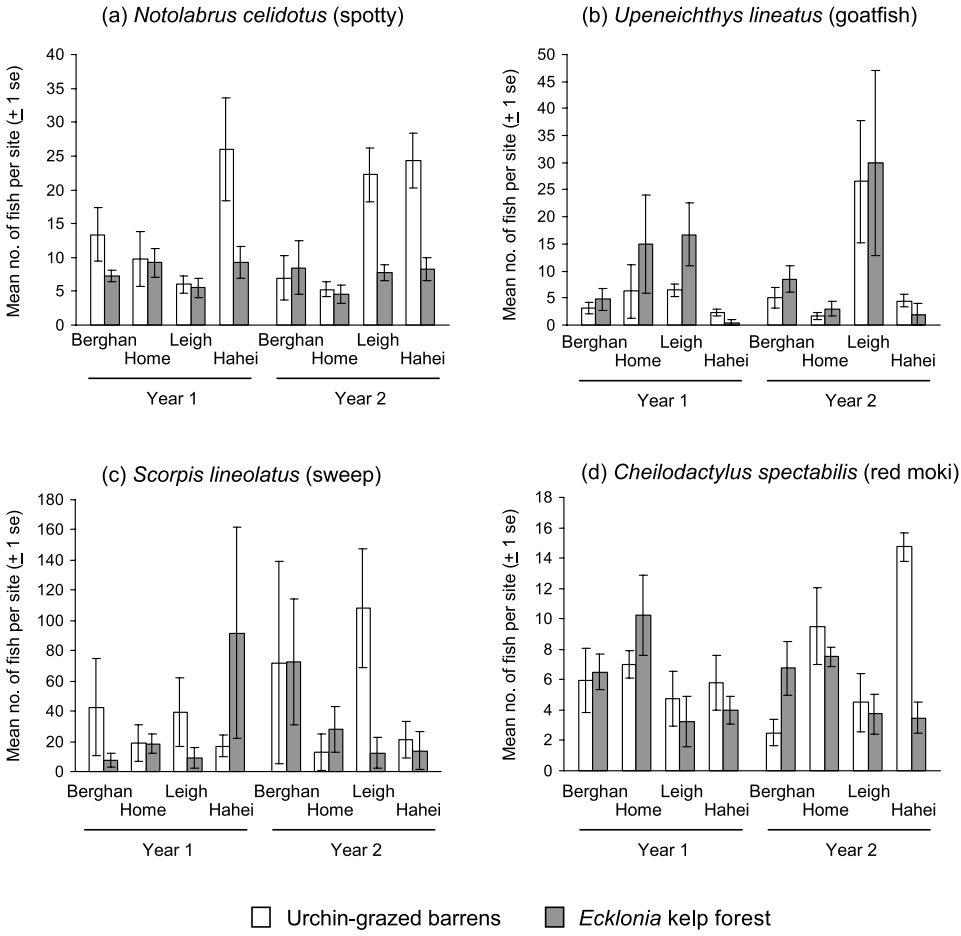

Fig. 6. Means (±1 S.E.) for (a) the number of *N. celidotus* (spotty), (b) the number of *U. lineatus* (goatfish), (c) the number of *S. lineolatus* (sweep) and (d) the number of *C. spectabilis* (red moki) in each combination of Year×Location×Habitat ($n=4$ sites per combination of levels and a site consisted of counts summed across 10 transects).

(Table 10). For kelp forest habitats, fish assemblages did not differ between Berghan Point and Hahei, but all other comparisons among locations were statistically significant (Table 10).

The average total number of fish observed per transect was significantly greater at the two northern locations, Berghan Point and Home Point, than at either Leigh or Hahei (pair-wise comparisons, $P<0.05$, Table 6a, Fig. 5a). The greatest average number of species was found at Hahei for barrens habitats and at Home Point for kelp forests (Table 6b, Fig. 5b). In year 1, Home Point had a significantly greater average number of species than Leigh or Hahei, for kelp or barrens habitats. In year 2, this was only true for kelp habitats: in barrens

Table 8
Results of univariate ANOVAs on selected species

Source	*df*	(a) *Notolabrus celidotus*			(b) *Upeneichthys lineatus*			(c) *Scorpis lineolatus*			(d) *Cheilodactylus spectabilis*		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Ye	1	0.046	0.003	*0.9584*	17.150	0.411	*0.5706*	228.1	0.398	*0.5770*	0.693	0.277	*0.6396*
Lo	3	28.859	6.164	0.0114	97.709	5.018	0.0038	249.9	0.675	0.6062	6.076	3.401	0.0506
Si(Lo)	12	4.682	2.122	0.0126	19.471	2.397	0.0044	370.4	2.275	0.0072	1.787	2.248	0.0104
Ha	1	71.939	3.579	*0.1430*	15.242	2.524	*0.2014*	152.0	0.224	*0.6660*	2.132	0.358	*0.5912*
Ye×Lo	3	15.374	5.017	0.0204	41.756	1.506	0.2226	573.7	1.733	0.2080	2.499	2.860	0.0786
Ye×Si (Lo)	12	3.064	1.388	0.1678	27.726	3.414	0.0002	331.1	2.034	0.0142	0.874	1.099	0.3466
Ye×Ha	1	0.858	0.105	0.8190	4.350	2.096	0.2594	232.9	0.684	0.4786	2.634	0.753	0.4688
Lo×Ha	3	20.103	3.849	0.0334	6.040	0.963	0.4586	678.0	1.391	0.2984	5.949	5.654	0.0126
Si(Lo)× Ha	12	5.223	2.366	0.0064	6.270	0.772	0.7356	487.3	2.994	0.0008	1.052	1.324	0.2068
Ye×Lo× Ha	3	8.201	2.050	0.1578	2.076	0.402	0.7866	340.6	0.984	0.4448	3.497	6.829	0.0048
Ye×Si (Lo)Ha	12	4.001	1.813	0.0436	5.166	0.636	0.8532	346.3	2.127	0.0068	0.512	0.644	0.8154
Residual	576	2.207			8.123			162.8			0.795		
Total	639												

P-values were obtained by 4999 permutations of appropriate units, as shown in Table 3 for each term in the analysis.
P-values in italics were obtained using 4999 Monte Carlo samples from the asymptotic permutation distribution. Mean squares used in the denominator for each test are also shown in Table 3.

habitats, Hahei had a significantly greater average number of fish species than either Berghan Point or Leigh (Fig. 5b, pair-wise comparisons).

Significantly greater numbers of *P. scaber* were found at Hahei than at other locations for barrens habitats, while for kelp forests, there were significantly greater average numbers at Home Point compared to the other locations (Fig. 5c, Table 6c). There were no significant differences among locations in numbers of *S. lineolatus*, but *C. dispilus* was significantly more abundant at the two northern locations: Berghan Point and Home Point, compared to Leigh and Hahei (Fig. 5d, Table 6d, pair-wise comparisons, $P<0.05$). *N. celidotus* was significantly more abundant at Hahei than at the other locations in barrens habitats, while there were no significant differences in its average abundances at different locations for kelp habitats (Table 8a, Fig. 6a, pair-wise comparisons). *U. lineatus* was significantly more abundant at Leigh than at the other locations (Table 8b, Fig. 6b). The only statistically significant differences among locations for *C. spectabilis* occurred in year 2 and in barrens habitat only, where Hahei had significantly greater numbers, on average, than either Leigh or Berghan Point (Fig. 6d, Table 8d).

Some species were more frequently observed at Home Point than at any other locations, including *P. scaber*, *P. alboscapularis* and *N. douglasii* (Appendix A). Others had greater frequencies of occurrence at the two northern locations (Berghan Point and Home Point) than at the southern locations (Leigh and Hahei), such as *C. dispilus*, *C. sandageri* and *B.*

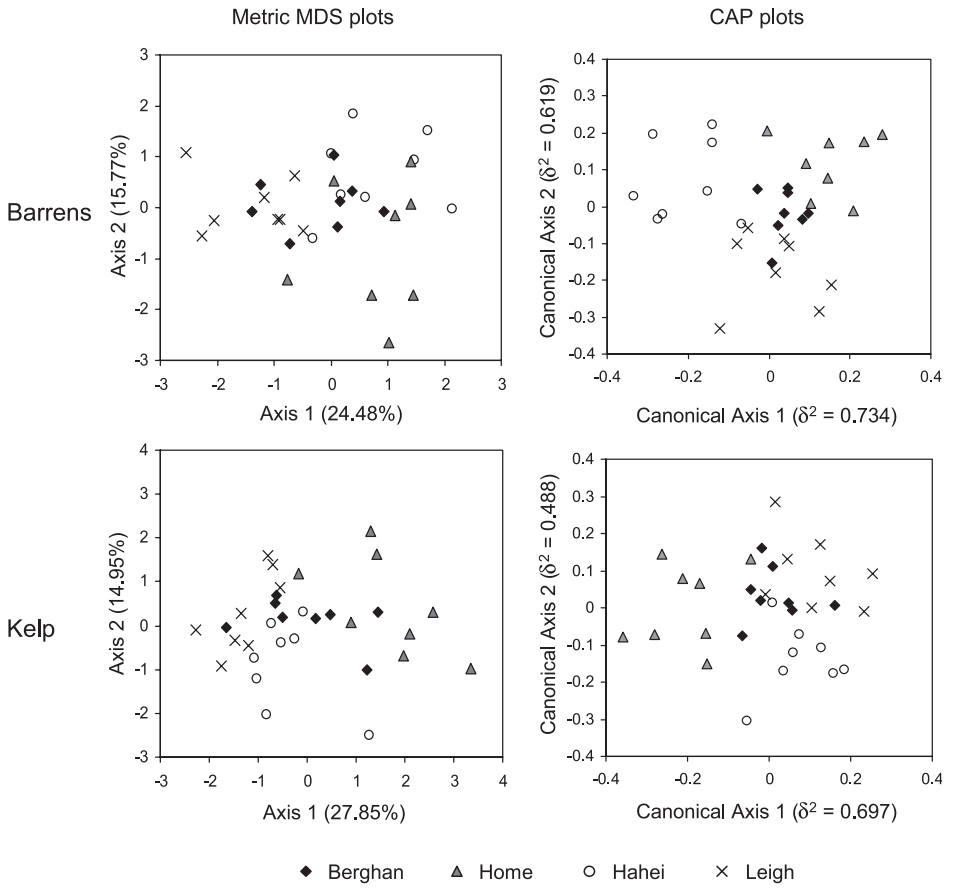

Fig. 7. Unconstrained metric MDS plots (left) and constrained CAP plots (right) done separately for each habitat (rows) on the basis of the binomial deviance dissimilarity measure, in each case comparing fish assemblages among four different locations: Berghan Point, Home Point, Leigh and Hahei. There are eight points for each combination of the factors, which correspond to the four sites in each of 2 years.

unimaculatus (Appendix A). Alternatively, some species were observed significantly more frequently at Home Point and Hahei than at any other location: *C. spectabilis*, *G. tricuspidata*, *C. marmoratus* and *Aplodactylus arctidens* (marblefish) (Appendix A).

Table 9
Results of CAP analyses examining effects of location within each habitat for 46 species of fish on the basis of the binomial deviance dissimilarity measure

Habitat	*m*	%Var	Allocation success (%)					δ^2
			B	Ho	L	Ha	Total	
Barrens	8	91.91	88	63	75	88	78	0.734
Kelp	8	94.56	63	88	50	63	66	0.697

Headings are as defined for Table 5, with B=Berghan Point, Ho=Home Point, L=Leigh, Ha=Hahei.

Table 10
P-values for NPMANOVA pair-wise comparisons among locations for each Habitat, using 4999 permutations

Habitat	Pair-wise comparison	*P*
Barrens	B vs. Ho	0.0618
	B vs. L	0.0228
	B vs. Ha	0.0106
	Ho vs. L	0.0002
	Ho vs. Ha	0.0014
	L vs. Ha	0.0008
Kelp	B vs. Ho	0.0228
	B vs. L	0.0050
	B vs. Ha	0.0608
	Ho vs. L	0.0002
	Ho vs. Ha	0.0004
	L vs. Ha	0.0006

In each case, the n=10 transects within a site were permuted together as a unit. For each test, there were eight such units per group (four sites observed per Lo×Ha combination in each of 2 years). No corrections have been made for multiple tests. B=Berghan Point, Ho=Home Point, L=Leigh, Ha=Hahei.

Finally, *U. lineatus* occurred more frequently at Leigh than anywhere else, and *N. fucicola* and *T. novaezelandiae* occurred more frequently at Hahei than anywhere else (Appendix A).

4. Discussion

There were significant differences in the multivariate structure of fish assemblages between kelp forest and barrens habitats. These were not independent of species identity. Differences between habitats included greater frequencies and/or abundances of *P. scaber*, *C. dispilus*, *T. novaezelandiae*, *N. douglasii*, *B. unimaculatus*, *O. pullus* and *P. miles* in kelp forest habitat, while *N. celidotus*, *N. fucicola*, *G. tricuspidata*, *C. sandageri*, *C. marmoratus*, *P. alboscapularis*, *S. violaceus* and *K. sydneyanus* were more frequent or abundant in barrens habitat. Some of the more common species, including *U. lineatus*, *S. lineolatus* and *C. spectabilis* showed no strong consistent effects of these two differing habitats on their distributions. These results differ somewhat from the results of Choat and Ayling (1987), who focused instead on the size classes and feeding groups, rather than on individual species, in their description. The present work examines species' overall patterns with a broad brush, while the work by Choat and Ayling (1987) recognized the importance of ontogenetic changes in diet and habitat use by individual species (e.g., Clements and Choat, 1993; Moran and Clements, 2002).

One of the most likely reasons for differences in fish assemblages between habitats is due to depth. Kelp forest and barrens habitats in northeastern New Zealand differ in their depth distributions (Fig. 2 and see Schiel, 1990). Previous studies have shown how the numbers and diversity of fish are affected by depth in temperate New Zealand (e.g., Meekan and Choat, 1997; Brook, 2002) and in tropical coral reefs (e.g.,

Roberts and Ormond, 1987; Friedlander and Parrish, 1998). We found that depth had a significant effect on fish assemblage composition (Table 2), although richness and the total numbers of fish were not significantly related to depth (Table 1). It was clear in the present study, however, that effects of habitat were not limited to effects of depth alone (Table 2), suggesting that other aspects of the habitat were important in structuring assemblages.

It may well be that fundamental biological differences in diet and patterns of foraging are driving differences in relative frequencies or abundances of species in different habitats, as suggested by Choat and Ayling (1987). For some species (e.g., *O. pullus*), the kelp *E. radiata* provides a source of food, although Clements and Choat (1993) suggested that the brown alga *Carpophyllum* spp. may be preferred by this species. In contrast, although *K. sydneyanus* is a herbivore that consumes *Ecklonia* (Moran and Clements, 2002), it was found more frequently in barrens habitat in the present study (Appendix A).

There are many other possible mechanisms that might also explain differences in fish assemblages in different habitats. There are natural differences in habitat complexity between kelp and barrens habitats, with kelp forests providing a more complex three-dimensional biogenic structure. As such, the kelp may provide a refuge from predation, particularly for juvenile stages (e.g., *P. scaber*). Also, within kelp forests, we found that diversity and total abundance of fish were each positively related to variation in kelp density (Table 1), indicating that the structure and heterogeneity of the habitat may play a role. Habitat complexity can modify the effects of predation on fish by providing refuges (e.g., Connell and Jones, 1991; Hixon and Beets, 1993; Caley and St. John, 1996; Beukers and Jones, 1997; Tupper and Boutilier, 1997; Steele, 1999). Alternatively, differences in kelp density can result in differences in understorey algae and invertebrate species, which fish may respond to positively or negatively (e.g., Carr, 1989). Connell (2002) and Wellenreuther and Connell (2002) have demonstrated such effects of habitat-driven prey availability on spatial patterns of a temperate reef fish (*Cheilodactylus nigripes*) from local through to broad scales (hundreds of kilometers). Habitat may also affect the frequency or intensity of inter-or intra-specific behavioural interactions (e.g., Levin et al., 2000).

It is important not to infer too much concerning processes that may be underlying observed patterns in the results reported here. What we have given is a ‘‘snapshot’’ of fish we happened to see when and where we saw them. First of all, not all potential habitats for these fish have been included in this study (e.g., sponge gardens, shallow areas with dense algal stands of *Carpophyllum* spp. or other algae, etc.). Thus, for example, observing increased frequencies of some species in *Ecklonia* forests should not be interpreted to mean that this is their ‘‘preferred’’ habitat. Furthermore, we expect individual species will occur in different habitats at different stages in their life history or during different behavioural stages (e.g., nesting, feeding, etc.), indeed even during different stages of the tide or time of day. Quantitative observations we have given here will have some biological basis, but this will require further and more detailed species-specific studies.

One important result obtained here is that effects of habitat, although relatively consistent for the 2 years of observation, did not occur at all locations. In fact,

multivariate effects of habitat were marginal at Berghan Point ($P = 0.0564$) and were not statistically significant ($P > 0.10$) for Leigh (Table 5). This could be one reason that Choat and Ayling (1987) concluded that habitat effects were independent of species identity, as many of their survey sites were around the Leigh area. We did find, however, that where effects of habitat were evident, the direction (i.e., the nature) of multivariate effects was similar (e.g., Fig. 3). This allowed us to make some generalisations about the nature of habitat differences, in terms of compositional changes, where they did occur. We must be cautious, however, in invoking any generalisations of processes that might have produced observed patterns. For example, Fowler-Walker and Connell (2002) have suggested that top-down processes are not as important in shaping shallow subtidal benthic coastal assemblages in South Australia as in New South Wales, because South Australia lacks the predominance of herbivorous grazers found in regions of New South Wales. Similarly, variations in effects of habitat among locations within New Zealand could be due to variation in the abundance or activity of invertebrate grazers and the relative strength and interactions of bottom-up vs. top-down processes (e.g., Menge, 1992).

Differences in fish assemblages among locations provided interesting biogeographic information that supports results from previous studies and provided some new insights. First, there were, on average, greater numbers of species at Home Point than at any other location, followed by Berghan Point and Hahei, with Leigh, on average, having the most depauperate fish communities. This is consistent with previous studies of North Island New Zealand fish fauna, where higher diversity at the Poor Knights Islands, the Karikari peninsula and Cape Brett was hypothesized to be a consequence of the influences of the East Auckland Current (e.g., Denham et al., 1984; Choat and Ayling, 1987; Brook, 2002), which does not appear to have much of an influence further south (i.e., at Leigh). However, in this study we found that, for kelp forest habitats, there was no significant difference between fish assemblages at Hahei (the southern-most location) and those at Berghan Point (the northern-most location). So, the influences of the East Auckland Current appear to extend, at least potentially, to areas as far south as Hahei, where species such as *B. unimaculatus* (pigfish), *Suezichthys aylingi* (crimson cleanerfish) and *Suezichthys arquatus* (rainbowfish) were all recorded in the present study. In contrast, Leigh may exist as a kind of oceanographic "backwater" of biodiversity for fish, potentially because of increases in turbidity and/or decreases in relative exposure as one moves southward into the Hauraki Gulf (Grace, 1983). It is also possible that there is greater fishing pressure around Leigh, which is not as isolated from human populations as the other locations in the study. Roberts et al. (1992) also found a non-linear gradient of fish assemblage structure with latitude in the Red Sea that was apparently caused by (or at least related to) a negative association of diversity with turbidity.

The analysis of multivariate variability in fish assemblages at different spatial scales revealed that the greatest variation occurred at the smallest spatial scale, between individual transects (Table 4). This is not terribly surprising, given that the spatial scale of individual transects is not large compared to the high mobility of many fish species included in these surveys. This result concurs with many studies of invertebrates and algae in intertidal and subtidal environments, which have also often found

the greatest variability to occur at small spatial scales (e.g., Archambault and Bourget, 1996; Underwood and Chapman, 1996; Menconi et al., 1999; Fowler-Walker and Connell, 2002). In addition, we found that some of the most abundant and ubiquitous species in the surveys had significant variability from year to year at different sites and in different habitats (i.e., a significant Year×Site(Locations)×Habitat term for each of *C. dispilus*, *N. celidotus* and *S. lineolatus*), meaning that predictability at small scales could prove very difficult for these species. Also, the spatial distribution of planktivores, such as *C. dispilus* and *S. lineolatus*, will likely be heavily dependent on temporal changes in currents, seasons and tides. We sampled only over a 1-month period in each of 2 years, but it is clear that variation at different temporal scales (e.g., tidal, within-day, daily, monthly, etc.) can also be quite large and can pose difficulties in the assessment of effects of habitat for fish (e.g., Labridae, Connell and Kingsford, 1998).

Variation from site to site in multivariate assemblages was about the same size as variability from location to location (Table 4), which concurs with the results of Choat and Ayling (1987). Observed spatial patterns in fish assemblages were consistent in the 2 years. These results are consistent with previous studies. Jones (1984b) indicated that, generally, variation in the densities of *N. celidotus* in different sites was greater than year-to-year variation over 4 years. Doherty (1987) indicated that, although temporal variation was detected at virtually every spatial scale found, recruitment was relatively consistent and hence predictable at geographic and regional scales and Fowler et al. (1992) found consistent spatial patterns of recruitment from year to year in butterflyfish on the Great Barrier Reef. In contrast, Tolimieri (1995) found no consistent patterns in recruitment of damselfish from year to year in the Caribbean and Sale et al. (1984) found significant year-by-reef interactions in recruitment for nine species of fish on the Great Barrier Reef. The number of years examined to date (only two) is still too small to make any inferences about inter-annual variation. Observations of New Zealand's fish fauna are needed over longer periods of time (i.e., over several years) and at various temporal scales to begin to understand potential spatio-temporal interactions or consistencies of patterns.

The observations of patterns given here and by Choat and Ayling (1987) provide a starting point for further investigations of effects of habitat on distributions of temperate New Zealand fishes (e.g., Underwood et al., 2000). Experiments, including manipulations of habitat, observations of feeding, behaviour, competition and predation, are needed for individual species and groups to further investigate the causal mechanisms behind any observed relationships or patterns. For example, Jones (1984a), Carr (1989), Levin and Hay (1996) and Wellenreuther and Connell (2002) have experimentally altered the presence and/or density of algae to investigate effects on temperate reef fish. In New Zealand, Jones (1984a) showed experimentally how juvenile spotties, *N. celidotus*, recruited in greater abundance in kelp forests and were negatively affected by decreases in kelp density. Although variation in recruitment among sites was apparently reflected in adult densities, Jones (1984b) reported nevertheless, on average, between 4.4 and 7.2 spotties (per 500 m^2) in kelp forest habitat sites, compared to 13.4 and 46.8 (per 500 m^2) in shallow broken rock habitat near Leigh (i.e., Table II therein). Thus, distributions of adult *N. celidotus* as reported in

Jones (1984b) support the results found here, that is, of greater numbers, on average, in barrens habitats.

Work along the coast of southern California and reviews of studies in other parts of the world have emphasised the idea that temperate reef fish, particularly through their predatory impacts on herbivores, such as urchins, can affect the distributions of kelp forests (e.g., Cowen, 1983; Holbrook et al., 1990; Tegner and Dayton, 2000). In contrast, previous studies in New Zealand (including the present study) have emphasised the idea that temperate reef fishes can respond to changes in habitat, and have not found much evidence to support the alternative idea that, instead, fish are affecting the structure and demography of the habitat (e.g., Andrew and Choat, 1982; Choat and Ayling, 1987; Jones, 1988; Schiel, 1990). However, recent studies of the large-scale effects of marine reserves have revealed that changes in densities of predatory fishes may have strong top-down effects on community structure (Babcock et al., 1999; Shears and Babcock, 2002). In particular, increases in predators, such as snapper (*Pagrus auratus*) and blue cod (*Parapercis colias*), inside of marine reserves resulted in increased rates of predation and decreases in densities of urchins (*E. chloroticus*), which in turn has been correlated with notable increases in the physical extent of kelp forest as opposed to barrens habitat within reserves (Babcock et al., 1999; Shears and Babcock, 2002). Thus, perhaps not surprisingly, it would appear that both processes occur: fish populations can affect habitat structure and habitat, in turn, can affect fish. This recent work, combined with the present study and the work of Choat and Ayling (1987), suggests that there may be dynamic feedback loops between indirect effects of fish on habitat structure (especially through predation on urchins) and direct and indirect effects of habitat structure (particularly the presence and varying density of kelp forest) on fish communities. However, the relative strength of these processes may be location-specific, and we must heed warnings of the potential dangers inherent in generalisations, particularly over large spatial scales (e.g., Underwood and Petraitis, 1993; Fowler-Walker and Connell, 2002). Clearly, more study is needed and of more components of the fish fauna in New Zealand to examine potential mechanisms and the relative importance of these processes.

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Appendix A

List of the 46 fish species recorded in the study and their frequencies of occurrence (a) at each location (out of a possible 160 transects) and (b) in each habitat (out of a possible 320 transects).

Family	Species	Common name	(a) Location				(b) Habitat	
			Berghan	Home	Leigh	Hahei	Barrens	Kelp
Aplodactylidae	*Aplodactylus arctidens*	Marblefish	1	12	1	8	14	8
Arripidae	*Arripis trutta*	Kahawai	0	1	0	5	3	3
Carangidae	*Decapterus koheru*	Koheru	2	5	0	2	4	5
Carangidae	*Pseudocaranx dentex*	Trevally	2	6	1	0	6	3
Carangidae	*Seriola lalandi*	Kingfish	2	0	1	5	0	8
Carangidae	*Trachurus novaezelandiae*	Jack mackerel	15	3	26	42	24	62
Chironemidae	*Chironemus marmoratus*	Hiwihiwi	13	22	7	20	47	15
Dasyatidae	*Dasyatis brevicaudata*	Short-tailed stingray	1	5	3	0	3	6
Dasyatidae	*Dasyatis thetidis*	Long-tailed stingray	0	3	0	0	1	2
Diodontidae	*Allomycterus jaculiferus*	Porcupinefish	1	2	0	0	2	1
Girellidae	*Girella tricuspidata*	Parore	13	33	9	21	61	15
Kyphosidae	*Kyphosus sydneyanus*	Silver drummer	2	4	1	4	10	1
Labridae	*Anampses elegans*	Elegant wrasse	1	0	0	0	1	0
Labridae	*Bodianus unimaculatus*	Red pigfish	8	12	0	1	4	17
Labridae	*Coris picta*	Combfish	0	2	0	0	2	0
Labridae	*Coris sandageri*	Sandager's wrasse	26	27	3	12	44	24
Labridae	*Notolabrus celidotus*	Spotty	71	69	84	99	175	148
Labridae	*Notolabrus fucicola*	Banded wrasse	18	24	4	52	69	29
Labridae	*Pseudolabrus luculentus*	Orange wrasse	1	4	2	0	3	4
Labridae	*Pseudolabrus miles*	Scarlet wrasse	0	5	4	9	4	14
Labridae	*Suezichthys arquatus*	Rainbowfish	1	0	0	1	1	1

(continued on next page)

Appendix A (*continued*)

Family	Species	Common name	(a) Location				(b) Habitat	
			Berghan	Home	Leigh	Hahei	Barrens	Kelp
Labridae	*Suezichthys aylingi*	Crimson cleanerfish	0	1	0	2	2	1
Latridae	*Cheilodactylus spectabilis*	Red moki	62	84	45	70	135	126
Latridae	*Latridopsis ciliaris*	Blue moki	1	0	0	0	0	1
Latridae	*Latridopsis forsteri*	Copper moki	0	1	0	1	1	1
Latridae	*Nemadactylus douglasii*	Porae	5	11	5	1	2	20
Latridae	*Nemadactylus macropterus*	Tarakihi	0	5	0	0	0	5
Monacanthidae	*Parika scaber*	Leatherjacket	47	83	28	59	82	135
Mugilidae	*Aldrichetta forsteri*	Yellow-eyed mullet	0	3	1	0	1	3
Mullidae	*Upeneichthys lineatus*	Goatfish	40	41	70	26	88	89
Muraenidae	*Gymnothorax prasinus*	Yellow moray	0	1	1	2	2	2
Myliobatidae	*Myliobatis tenuicaudatus*	Eagle ray	2	6	2	1	5	6
Odacidae	*Odax pullus*	Butterfish	4	7	1	8	7	13
Pempheridae	*Pempheris adspersus*	Big eye	14	9	10	4	21	16
Pinguipedidae	*Parapercis colias*	Blue cod	3	5	1	2	8	3
Pomacentridae	*Chromis dispilus*	Demoiselle	101	115	16	69	137	164
Pomacentridae	*Chromis fumea*	Yellow demoiselle	1	0	0	0	0	1
Pomacentridae	*Chromis hypsilepis*	Single-spot demoiselle	1	0	0	1	1	1
Pomacentridae	*Parma alboscapularis*	Black angelfish	7	21	0	7	35	0
Scorpaenidae	*Scorpaena cardinalis*	Northern Scorpionfish	0	0	0	2	2	0
Scorpidae	*Scorpis lineolatus*	Sweep	42	43	48	56	93	96
Scorpidae	*Scorpis violaceus*	Blue maomao	3	18	2	3	20	6
Serranidae	*Caesioperca lepidoptera*	Butterfly perch	0	0	3	0	0	3
Sparidae	*Pagrus auratus*	Snapper	19	14	48	3	42	42
Trachichthyidae	*Optivus elongatus*	Slender roughy	5	1	2	3	3	8
Zeidae	*Zeus faber*	John dory	2	1	2	2	0	7

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