New Zealand Journal of Marine and Freshwater Research, 2004, Vol. 38: 163–182
0028–8330/04/3801–0163

Fish species composition on seamounts and adjacent slope in New Zealand waters

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Abstract Datasets from deep-water fisheries abundance surveys on the commercially important species—orange roughy (*Hoplostethus atlanticus*), smooth oreo (*Pseudocyttus maculatus*), and black oreo (*Allocyttus niger*) —were used to compare fish fauna between seamounts in 10 different parts of the New Zealand region. For five of these areas, fauna was also compared between the seamounts and nearby areas of the relatively flat slope. Dominant species were listed for each area. Diversity was compared between seamount complexes, and between seamount and slope areas. Differences between the species taken in different seamount areas were investigated using similarity analysis. Total species richness was similar in all seamount regions, but mean species richness was found to be much higher in southern areas. Species richness was consistently higher on the relatively flat slope than on seamounts. Five seamount areas south of 41°S were found to have similar fish fauna, as compared with three seamount areas north of 41°S which were different from the southern areas and from each other.

Keywords deep sea; seamounts; slope; deep-water fish; diversity, distribution; species richness

M03045; Online publication date 15 March 2004
Received 11 August 2003; accepted 22 October 2003

INTRODUCTION

Seamount features are very prominent in the New Zealand marine environment. Over 500 seamounts with an elevation greater than 250 m, and a further 300 between 100 and 250 m, have been identified in the New Zealand region (Clark et al. 1999a; Wright 1999). These seamounts vary in shape and size, occur singly or in groups, some have steep slopes with rugged tops, others are more knoll like in their appearance with large relatively flat tops (NIWA unpubl. data). Seamounts within the New Zealand Exclusive Economic Zone (EEZ) provide an important habitat for deep-water fish such as orange roughy (*Hoplostethus atlanticus*), smooth oreo (*Pseudocyttus maculatus*), black oreo (*Allocyttus niger*), and black cardinalfish (*Epigonus telescopus*) (Clark et al. 2001; Clark & O'Driscoll in press).

Deep-water fisheries were initially developed for orange roughy on relatively flat slope. Increased knowledge of bathymetry and improved fishing techniques (Clark 1999; Clark & O'Driscoll in press) led to an expansion of the fishery onto seamounts. Seamounts are the focus of commercially important orange roughy and oreo fisheries, as a result of their high biological productivity (Clark 1999; Clark & O'Driscoll in press), but numerous by-catch species are also caught. Research trawl and acoustic surveys have regularly been carried out in several areas around New Zealand and, although primarily monitoring the change in relative abundance of the major deep-water commercial species over time (e.g., Clark & Tracey 1994; McMillan & Hart 1994a,b,c, 1995; Clark et al. 1999b; Doonan et al. 1999; Bull et al. 2000; Doonan et al. 2001), have recorded information on the composition of fish assemblages on seamounts and on the adjacent slope areas. These surveys provide an opportunity to compare and examine such variables as species dominance, diversity, fish density, and faunal rarity. In addition, data from these surveys have enabled an examination in trends in abundance between the seamounts and between the seamounts and neighbouring flat areas.

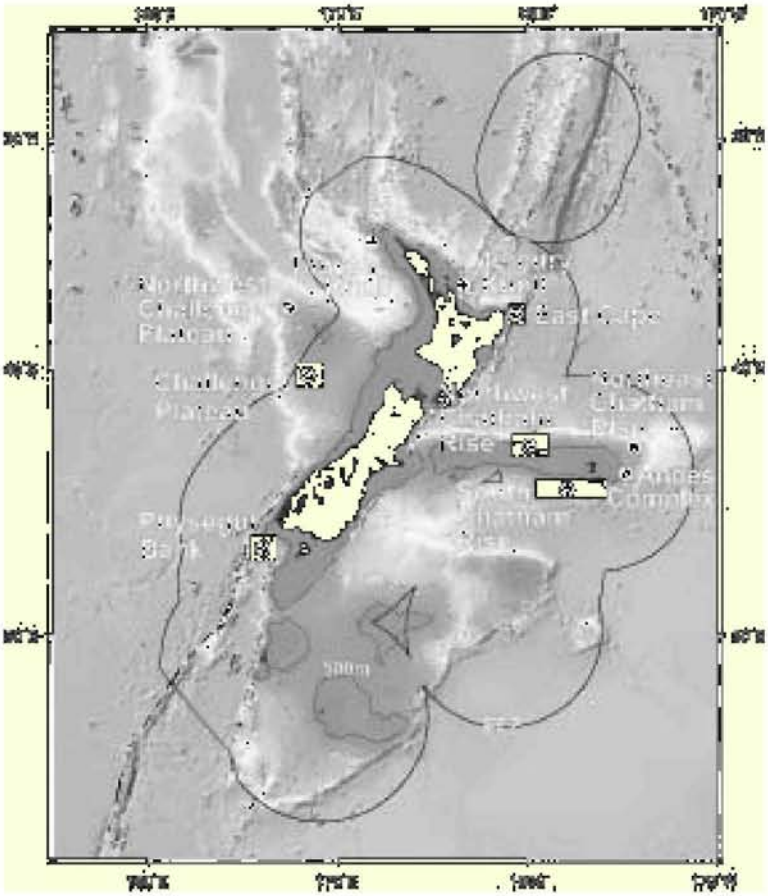

Fig. 1 Ten regions included in this study. Seamount complexes are indicated by black dots, and adjoining slope areas by pale rectangles.

Table 1 Number of trawl stations, and range of years in which they were carried out, by area.

Area	No. of stations		Years
	Seamounts	Slope	
South-east Chatham Rise	42	–	1994, 2000
Challenger Plateau	15	590	1987–90
North-east Chatham Rise	39	–	1998, 2000
East Cape	56	23	1995, 1997
Mercury Knoll	54	–	1995, 1998, 2000
North-west Chatham Rise	82	64	1994, 1996, 1999
North-west Challenger Plateau	5	–	1990
Puysegur Bank	130	66	1992, 1994
South Chatham Rise	50	310	1988, 1991–93, 1998
Tauroa Knoll	5	–	1999

Numerous studies have described the species richness and diversity of fish fauna on seamounts, but few have included deep-water species taken below 600 m. Wilson & Kaufman (1987) reviewed seamount biota worldwide and included a description of fishes collected from more than 60 seamounts. More than 60% of the seamounts described were over 300 m in depth. Rogers (1994) reviewed the biology of seamounts and included several works describing the species diversity and commercial exploitation of seamount fisheries. Koslow (1997) and Koslow et al. (2000) describe the high productivity and worldwide focus of important commercial fisheries on seamounts. Recent work by Grandperrin et al. (1999) described 263 fish species found on seamount features between 230 and 1860 m in the New Caledonian region, and Richer de Forges et al. (2000) describe fish and macroinvertebrates from the New Caledonian area as well as from several Tasmanian seamounts. Richer de Forges et al. (2000) found highly localised distributions of many seamount species and noted that sampling effort had a large influence on the species richness. These studies have generally examined deep seamount biota in general, and often covered a range of organisms on seamounts. There have been few specific studies on fishes on seamounts, or comparison of fish assemblages in the mid-slope area with those found on neighbouring seamounts.

In this paper we report on dominant fish species in the New Zealand EEZ, about how species composition and diversity on the seamounts differs from that of the neighbouring slope areas, and how species composition varies between seamounts. In describing the deep-sea assemblages, we differentiate between fish taken over seamount features and those caught over drop offs, relatively flat slope, and rugged slope (all referred to as slope in the text).

METHODS

Study areas

Ten geographical areas (Fig. 1), each containing a seamount feature or a complex of seamounts, were selected for analysis. The areas were the "Andes" complex on the south-east Chatham Rise (SECR), Challenger Plateau (CHAL), north-east Chatham Rise (EACR), East Cape (ECAP), Mercury Knoll (MERC), the "Graveyard" seamounts on the north-west Chatham Rise (NWCR), north-west Challenger Plateau (NWCH), Puysegur Bank (PUYS), south Chatham Rise (STHR), and Tauroa Knoll (TAUR).

Trawl data are available for seamounts in all 10 areas, although the number of stations varies widely (from 5 on the north-west Challenger Plateau to 130 on Puysegur Bank: see Table 1).

Table 2 provides the number of seamounts within each region along with information on the ranges of depth at base and vertical elevation.

For 5 of the 10 areas, trawl data are also available for the slope areas in the vicinity of the seamounts. This allows us to make comparisons of species composition between seamount complexes and the adjoining slope. Again, the number of stations on the slope varies widely (from 23 at East Cape to 590 on the north-east Chatham Rise).

Data extraction

Species composition and catch rate data were derived from deep-water research voyages carried out to estimate the abundance of orange roughy, smooth oreo, and black oreo in various parts of New Zealand between 1987 and 2000. The surveys were either stratified random trawl surveys or acoustic surveys with a trawling component for mark identification. The data volume is shown in Table 1.

Data came from 1531 stations over 23 voyages. Most of these voyages were carried out on *Tangaroa*, the fisheries research vessel owned by the National Institute of Water and Atmospheric Research Limited (NIWA), the rest from chartered commercial trawlers carrying out survey work. All of these vessels used similar trawl gear, a standard six-panel, rough bottom orange roughy trawl with cut away lower wings (McMillan 1996). A cod-end mesh size of 100 mm was used on all surveys. Headline height was fairly consistent around 7 m, as was the towing speed at 3.0 knots. Trawling was carried out at all times of the day and night.

All fish caught were identified when possible to species, and all weights recorded in the Ministry of Fisheries "trawl" database. Data extraction was based on a similar method to that of Anderson et al. (1998). Station records were excluded where gear performance was unsatisfactory. Species records were excluded if there was uncertainty in the identification of a species, or if the species was predominantly midwater in distribution (and hence was probably caught while shooting or hauling the trawl, rather than near the sea floor).

All species caught in the research surveys that met the selection criteria are listed in Appendix 1. This comprises elasmobranchs (sharks, rays, chimaeras, and ghost sharks), squids and octopi, deep-water crustaceans (crabs), and teleost fishes, caught in depths between 586 and 1707 m. The final edited dataset contained 84 species, plus 5 genera and 1 family which were pooled as they had not been consistently identified to species. Those identified to genus only were *Xenodermichthys* spp., *Moroteuthis* spp., *Histioteuthis* spp., and *Helicolenus* spp., and to family only, the Cranchiid squids which are likely to be *Teuthowenia pellucida* or species belonging to the genera *Taonius* and *Galiteuthis*. The two *Lepidion* species (*L. schmidti* and *L. inosimae*) were combined, as were *Bassanago bulbiceps* and *B. hirsutus*, as species differentiation was unreliable. Throughout this paper we refer to the above 90 taxa as "species".

Data analysis

The analysis compares fauna between the 10 seamount complexes, and between the 5 slope regions and the corresponding 5 seamount complexes. Fauna in each region are characterised in terms of dominant species, diversity, and the list of all species present.

A shortlist of 10 "dominant" species is given for each region. Species dominance was determined by the mean catch rate, which is taken as a rough measure of the local abundance of the species assuming all species were equally catchable. Catch rate was defined as catch per tow (kg). Note that these catch rates were not divided by tow length or swept area. The reason is that some tows on fish aggregations over seamounts had very short tow lengths, which would lead to extremely high catch rates if a swept-area method was used. Occurrence (on a presence/absence basis) is also shown for the dominant species in each region.

Species were also ranked in terms of occurrence on seamount complexes, from those occurring on all 10 seamount complexes to those occurring on only one complex. This was to investigate the gradient from widespread species that occur in all study areas (e.g., orange roughy) to rare species which only occur in a few areas.

We then proceeded to analyses of diversity. The total species richness in each area was estimated by fitting a "species accumulation curve" to the data, as described in a review paper by Colwell & Coddington (1994). The species accumulation curve $S(n)$ represents the expected number of species found in n stations, and takes the hyperbolic form.

$$S(n) = \frac{S_{max.} n}{B + n}$$

The $S_{max.}$ parameter is the asymptote of the curve, representing the estimated number of species that would theoretically be found if a very large number of stations were completed. This is our estimate of species richness.

We randomised the order of stations and then used the method of Raaijmakers, as described by Colwell & Coddington (1994), to estimate the parameters of the species accumulation curve. We found it necessary to make one modification to this method. The original version fits the hyperbolic curve to data points $(n, S(n))$ for each value of n from 1 to the total number of stations completed. We found that this technique leads to poor fits for higher values of n because it tries to achieve a good fit to small values of n. As a result, the estimated value of $S_{max.}$ can commonly be less than the actual number of species observed. To avoid this problem, we discarded the first 10 values of n and $S(n)$ before fitting the curve.

As recommended by Colwell & Coddington (1994), a resampling standard error was calculated for each estimate of S_{max}. This is an easy and appealing method of estimating the errors in estimates of species richness, though Colwell & Coddington note that it has not yet been evaluated in the statistical literature. The stations were permuted into a random order, $S(n)$ is recalculated for each n, and $S_{max.}$ is recalculated. This process was repeated 200 times and the resulting values of $S_{max.}$ were collated. The standard deviation of these randomisations is our resampling estimate of standard error, indicating the accuracy of our estimate.

Mean species richness (i.e., average number of species caught in a single tow) is also presented for seamounts in each area. This is a measure of the diversity which can be expected within a single

Table 2 Number of seamounts and the range of height and elevation for the seamounts within each region.

Area	No. of seamounts	Depth range (m)	Elevation range (m)
Tauroa Knoll	1	950	400
Mercury Knoll	1	906	344
Challenger Plateau	2	790–833	117–160
North-west Challenger Plateau	3	578–874	130–300
East Cape	12	742–1012	127–485
North-west Chatham Rise	12	748–1265	150–405
North-east Chatham Rise	6	784–1032	180–358
South-east Chatham Rise	7	644–1008	458–625
South Chatham Rise	13	588–1123	100–418
Puysegur Bank	7	740–964	104–1136

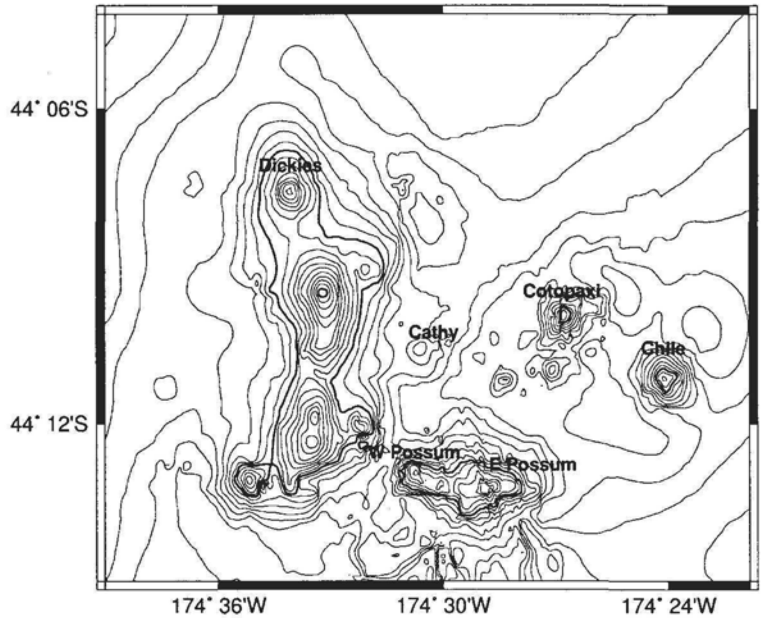

Fig. 2 The Andes Complex, south-east Chatham Rise.

sample, as opposed to the diversity which would be found over many samples.

Mean species richness was not calculated for slope areas. This is because individual tows on the slope were not directly comparable with seamount tows, as they typically swept a much greater area. Mean species richness would be higher in slope areas for this reason alone, so the comparison was not attempted.

The next phase of the analysis compared species lists between seamounts and slope areas, and between the 10 seamount complexes. First, species lists were compared between seamounts and adjacent slope areas for the five areas where these data were available. The analysis identifies all species which occurred significantly more often on each seamount complex than on the adjoining slope area, and conversely those which occurred significantly more often on slope areas. Differences in occurrence were tested using Fisher's exact test if the area included less than 200 stations, or the standard Chi-squared approximation otherwise. The 99% significance level was used throughout, to compensate for the massively multiple significance testing. Note that this analysis was purely based on presence/absence data—catch rate data were not used.

A group of "slope" species was identified, including species which occurred significantly more commonly on the slope in three or more of the five areas. Similarly, a group of "seamount" species which occurred more commonly on seamounts in three or more areas was identified.

The similarities between fauna on different seamount complexes were assessed by comparing species lists for each pair of seamount areas. The P_{pos} statistic (e.g., Graham & Bull 1998) was used to measure the similarity of each pair of species lists. P_{pos} number of species in common on both lists divided by the average length of the two lists; if there were no species in common then $P_{pos} = 0$, and if the species lists were identical then $P_{pos} = 1$.

The resulting similarity table was displayed graphically using classical metric multidimensional scaling, as implemented in S+ (Venables & Ripley 1999). This technique attempts to place the areas on a 2-dimensional plot so that areas with high faunal similarity are close together and less similar areas are further apart.

A comparison of fauna between individual seamounts within a complex was also included. Trawl samples were taken on the Andes seamount complex on the south-east Chatham Rise during an acoustic abundance survey (Doonan et al. 2001; Tracey et al. 2001). Six seamounts in this area were sampled, known as East Possum, West Possum, Chile, Cotopaxi, Cathys, and Dickies. The seamounts are closely spaced, with a maximum distance of 25 km between peaks (Fig. 2). Depths of the peaks range from 644 to 1008 m. These data have been used to describe differences in faunal composition between the six seamounts. However we have not carried out extensive statistical analysis due to the relatively small amount of trawl data available.

RESULTS

Dominant species

The 10 species with the highest mean catch rates in each area are shown in Fig. 3. Catch rates are given on the log-scale. Occurrence figures are also shown (i.e., the percentage of stations where each species was recorded).

In every area, orange roughy (ORH) or smooth oreo (SSO) is the most dominant species. As noted earlier, this is at least partly because of the timing and design of the surveys. Other very abundant species include Baxter's lantern dogfish (*Etmopterus baxteri*, ETB), Plunket's shark (*Centroscymnus plunketi*, PLS), seal shark (*Dalatias licha*, BSH), longnose velvet dogfish (*Centroscynmus crepidater*, CYP), shovelnose spiny dogfish (*Deania calcea*, SND), leafscale gulper shark (*Centrophorus squamosus*, CSQ), spiky oreo (*Neocyttus rhomboidalis*, SOR), black oreo (*Allocyttus niger*, BOE), ribaldo (*Mora moro,* RIB), black cardinalfish (*Epigonus telescopus*, EPT), four-rayed rattail (*Coryphaenoides subserrulatus*, CSU), unicorn rattail and white rattail (*Trachyrincus* spp., WHR/WHX), Johnson's cod (*Halargyreus johnsonii*, HJO), and warty squid (*Moroteuthis* spp., WSQ). The full list of species and species codes is given in Appendix 1.

Comparison of species rarity

A total of 70 species were found on the 10 seamount complexes. Orange roughy was the only species to be found in all 10 areas, but 10 species were present on nine out of 10 complexes (Table 3). Fifteen of the 70 species were found on only one complex.

No clear distributional pattern is seen with the rarer species, i.e., those found at only 1 or 2 seamount complexes) (Table 4). Of those that occur more than once, some appear to have a more southern distribution, e.g., abyssal rattail (*Coryphaenoides murrayi*) was present only in the south and south-east Chatham Rise, spineback eel (*Notacanthus sexspinis*) in the south Chatham Rise and Puysegur. Others display a more northern occurrence, e.g., prickly dogfish (*Oxynotus bruniensis*) was present only in the Challenger areas (NWCH and CHAL), Portuguese dogfish (*Centroscymnus coelolepis*) on Challenger and Mercury seamounts, black ghost shark (*Hydrolagus* sp. *a*) in East Cape and Northwest Challenger, and *Talismania longifilis* on East Cape and Mercury seamounts. However the deep-water crabs *Lithodes murrayi* and *Neolithodes brodei* are

Table 3 Species found on all 10 seamount complexes, on nine out of ten, and so on, down to those found in only one area (see Appendix 1 for species code and scientific name when not listed).

No. of complexes	Count of species	List of species
10	1	orange roughy
9	10	basketwork eel, Owston's dogfish, longnose velvet dogfish, black cardinalfish, Johnson's cod, hoki, ribaldo, shovelnose spiny dogfish, spiky oreo, smooth oreo
8	6	brown chimaera, serrulate rattail, Baxter's lantern dogfish, giant lepidion, Plunket's shark, unicorn rattail
7	5	seal shark, Mahia rattail, leafscale gulper shark, widenosed chimaera, warty squid
6	3	black oreo, bigscale brown slickhead, *Tubbia tasmanica*
5	6	black javelinfish, giant chimaera, four-rayed rattail, ridge scaled rattail, small-headed cod, smallscaled brown slickhead
4	8	slender rattail, robust cardinalfish, pale ghost shark, hake, javelin fish, long-nosed chimaera, *Shedophilus* sp., violet squid
3	5	blue cusk eel, notable rattail, sea perch, *Trachyscorpia capensis*, warty oreo
2	11	abyssal rattail, Portuguese dogfish, deep-water spiny skate, black ghost shark, *Lithodes nurrayi*, *Neolithodes brodiei*, prickly dogfish, *Psychrolutes* sp., rudderfish, spineback eel, *Talismania longifilis*
1	15	black slickhead, Bollons rattail, black lip rattail, banded rattail, pink frogmouth, electric ray, lucifer dogfish, filamentous rattail, pointynose blue ghost shark, *Mastigoteuthis* sp., umbrella octopus, longnosed deep-sea skate, ragfish, spinyfin, violet cod

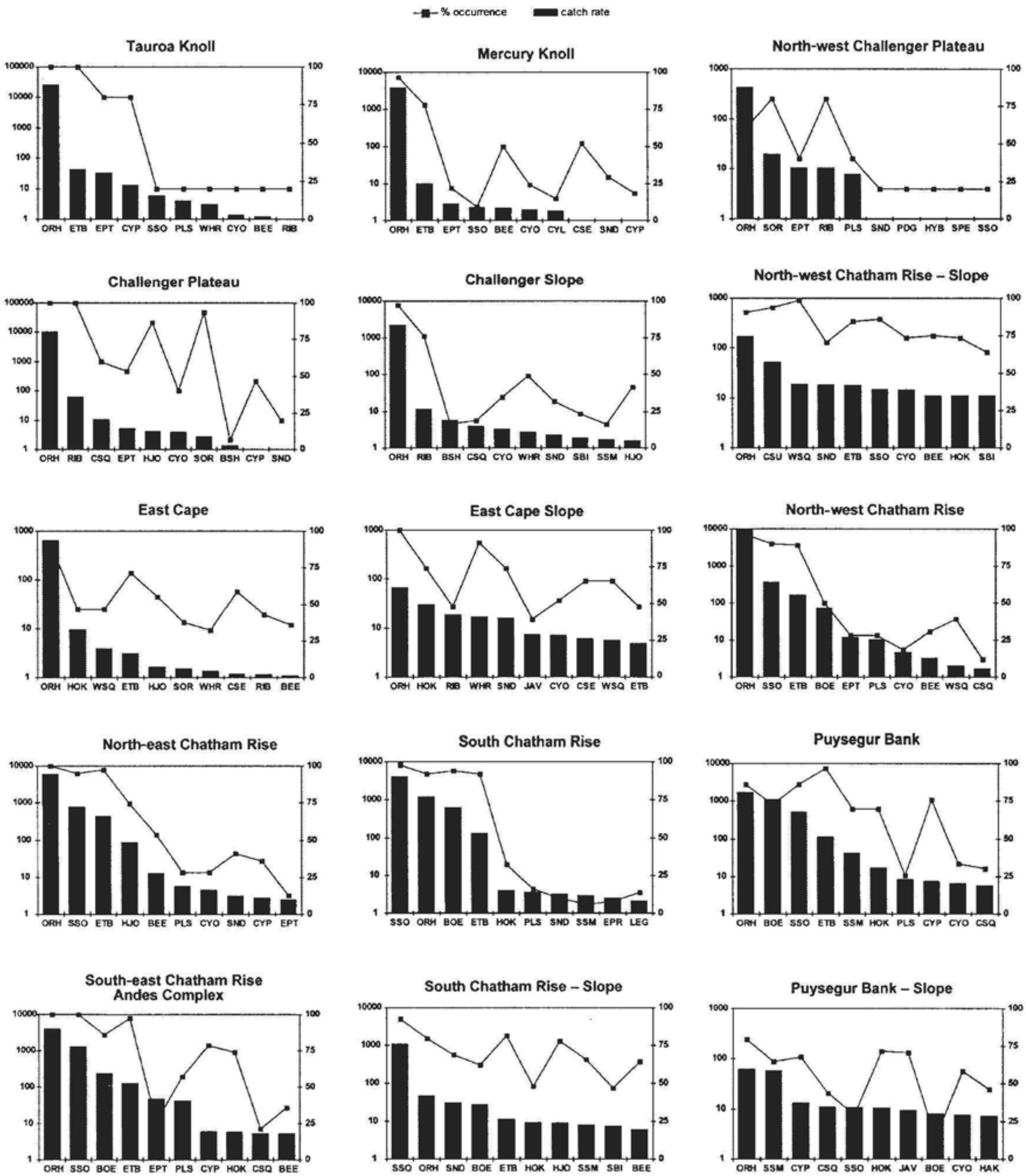

Fig. 3 Catch rate on the log-scale (left axis) and percentage occurrence (right axis) for the 10 species with the highest catch rates in each area. Species are identified by Ministry of Fisheries codes: see Appendix 1 for species names.

rare in the north (East Cape) as well as the south (Puysegur). Overall, the East Cape seamounts have a high number of rarer species present.

Species diversity

Total species richness estimates are shown in Table 5. Results from the Challenger Plateau seamounts (both areas) and Tauroa Knoll have been omitted, as the number of samples was small and the resampling standard errors were enormous.

Total species richness is estimated as 60–70 species for all five slope areas. This is a substantially greater diversity than in all seven seamount areas with enough data to carry out the analysis, where the species richness ranges from 38 to 57. In all four areas where figures are available for both seamounts and slope, the estimated species richness is greater on the slope, with the difference ranging from 7 (north-west Chatham Rise) to 23 (south Chatham Rise).

The mean species richness at each seamount complex is shown in Table 6. Figures range from 4.0 species per station (north-west Challenger Plateau, though with just 5 stations) to 11.4 species per station (Puysegur Bank). A trend with latitude is evident, with southern areas having higher mean species richness (Fig. 4).

Differences in species lists between seamounts and slope

The numbers of species with significantly higher percentage occurrence on seamounts than on the adjoining slope, and vice versa, are given in Table 7. Comparisons are based entirely on presence/absence, and do not take account of differences in catch rate.

For many species a statistically significant difference could not be established either way. Sometimes this was because occurrence percentages were similar on the seamounts and the slope;

Table 4 List of rarer species found on the seamount complexes (see Appendix 1 for species code and where scientific names are not given).

Seamount	Species
South-east Chatham Rise	abyssal rattail, spineback eel
Challenger Plateau	Portuguese dogfish, prickly dogfish
East Cape	black lip rattail, pink frogmouth, lucifer dogfish, black ghost shark, *Lithodes nurrayi*, *Neolithodes brodiei*, umbrella octopus, *Psychrolutes* sp., ragfish, spinyfin, *Talismania longifilis*
Mercury Knoll	Portuguese dogfish, filamentous rattail, pointynose blue ghost shark, *Mastigoteuthis* sp., *Psychrolutes* sp., *Talismania longifilis*
North-east Chatham Rise	deep-water spiny skate, electric ray, rudderfish
North-west Challenger Plateau	black ghost shark, prickly dogfish
North-west Chatham Rise	rudderfish
Puysegur Bank	Bollons rattail, banded rattail, *Lithodes nurrayi*, *Neolithodes brodiei*, spineback eel, violet cod
South Chatham Rise	black slickhead, abyssal rattail, deep-water spiny skate, longnosed deep-sea skate

Table 5 Estimated total species richness of each area, based on an asymptotic fit to the species accumulation curve. Areas with very small data volume are omitted. Standard errors (SE) are given in parentheses.

	Number of stations		Species richness (SE)	
Area	Seamounts	Slope	Seamounts	Slope
South-east Chatham Rise	42	–	38.3 (2.6)	–
Challenger Plateau	–	590	–	65.4 (1.4)
North-east Chatham Rise	39	–	44.0 (7.7)	–
East Cape	56	53	49.3 (4.8)	64.6 (7.5)
Mercury Knoll	54	–	42.7 (4.2)	–
North-west Chatham Rise	82	64	56.6 (4.2)	63.4 (2.1)
Puysegur Bank	66	130	46.1 (2.3)	61.2 (1.8)
South Chatham Rise	50	310	40.6 (6.8)	73.4 (1.6)

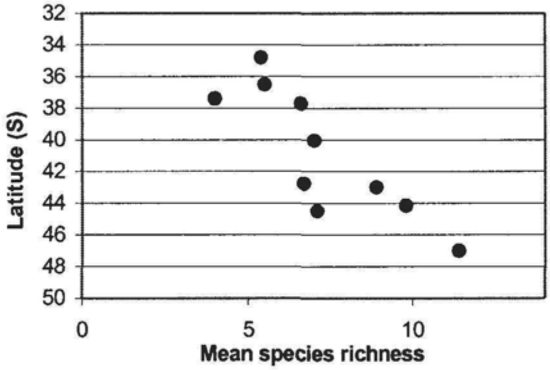

Fig. 4 Relationship between latitude and mean species richness on seamount complexes, as listed in Table 6. Latitude figures are approximate.

otherwise it was because there were insufficient data to establish a significant result.

Few species occurred in a higher proportion of seamount tows than slope tows (although some species such as orange roughy had a much higher average catch rate on seamounts). The only species that was significantly more common on three or more of the five seamount complexes was black oreo.

Many species occurred more commonly on the slope. Species which were significantly more common on the slope in three or more of the five areas were four-rayed rattail, unicorn rattail, white rattail, Owston's dogfish (*Centroscymnus owstoni*), shovelnose spiny dogfish, pale ghost shark (*Hydrolagus bemisi*), long-nosed chimaera (*Harriotta raleighana*), and bigscaled brown slickhead (*Alepocephalus* spp.).

Table 6 Mean species richness for the 10 seamount complexes. Standard errors (SE) are given in parentheses. The table is sorted by latitude from north to south. Latitude figures are approximate.

Seamount complex	Number of stations	Mean species richness	Latitude (S)
Tauroa Knoll	5	5.4 (0.18)	34° 48′
Mercury Knoll	54	5.5 (0.06)	36° 31′
North-west Challenger Plateau	5	4.0 (0.37)	37° 25′
East Cape	56	6.6 (0.07)	37° 42′
Challenger Plateau	15	7.0 (0.08)	40° 04′
North-west Chatham Rise	82	6.7 (0.04)	42° 45′
North-east Chatham Rise	39	8.9 (0.12)	43° 00′
South-east Chatham Rise	42	9.8 (0.06)	44° 10′
South Chatham Rise	50	7.1 (0.07)	44° 30′
Puysegur Bank	66	11.4 (0.06)	47° 00′

Table 7 Numbers of species occurring in a significantly higher proportion of tows on seamounts, the slope, or neither. Fisher's exact test is used for areas with less than 200 tows, or the standard chi-squared approximation otherwise. The 99% significance level is used throughout.

	Number of species		
Area	Significantly higher occurrence on seamounts	No significant difference	Significantly higher occurrence on slope
Challenger Plateau	4	54	8
East Cape	0	52	10
North-west Chatham Rise	3	28	33
Puysegur Bank	6	46	6
South Chatham Rise	2	59	11

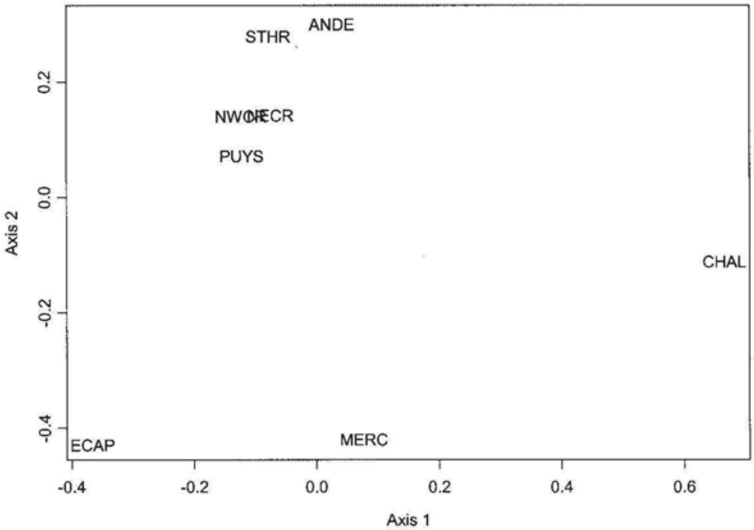

Fig. 5 Multidimensional scaling plot of similarity between the species lists of seamount complexes. Areas with the most similar species lists are plotted close together. The four Chatham Rise sites (NWCR, NECR, STHR, ANDE) and Puysegur Bank (PUYS) form a tight cluster, indicating strong mutual similarity. East Cape, Mercury Knoll and Challenger Plateau are all widely spaced, indicating weak similarities to all other areas.

Table 8 Pairwise similarity (P_{pos}) between seamount species lists of each pair of areas. Values close to 1 denote strong similarity.

	SECR	CHAL	ECAP	MERC	NECR	NWCR	PUYS	STHR
SECR	1.00	0.58	0.58	0.63	0.76	0.78	0.75	0.75
CHAL	0.58	1.00	0.45	0.60	0.57	0.57	0.56	0.55
ECAP	0.58	0.45	1.00	0.68	0.64	0.69	0.68	0.61
MERC	0.63	0.60	0.68	1.00	0.69	0.67	0.66	0.63
NECR	0.76	0.57	0.64	0.69	1.00	0.88	0.77	0.83
NWCR	0.78	0.57	0.69	0.67	0.88	1.00	0.82	0.85
PUYS	0.75	0.56	0.68	0.66	0.77	0.82	1.00	0.74
STHR	0.75	0.55	0.61	0.63	0.83	0.85	0.74	1.00

Comparing fauna between seamount complexes

The similarity in species lists, P_{pos}, is shown in Table 8 for each pair of seamount complexes. High values denote pairs of areas with very similar species lists. Lower values denote pairs of seamounts with fewer species in common. Areas with very little data are omitted. Note that this analysis is based only on the species list and does not incorporate any percentage occurrence or catch rate information. Examples of the calculation of P_{pos} are shown in Appendix 2.

There is strong similarity between the four Chatham Rise sites (south-east, north-west, north-east, south) and Puysegur Bank. The other three sites (Mercury Knoll, Challenger Plateau and East Cape) do not have strong similarity with any area. This situation is illustrated in the multidimensional scaling representation of the similarity matrix in Fig. 5. The Chatham Rise and Puysegur areas are grouped closely together, indicating relatively strong similarity; the other three sites are widely spread, indicating weak similarity with all other areas.

Variation within a seamount complex

The numbers of trawls carried out on six seamounts in the "Andes" complex on the south-east Chatham Rise are listed in Table 9. Species lists taken on each of these seamounts are given in Table 10.

Of the 35 species recorded, 5 (14%) were caught on every seamount, a further 18 (51%) occurred on 3 to 5 seamounts, and 5 (14%) "rarer" species occurred on only one seamount.

Orange roughy proportions by weight in the Andes complex were 62% on Dickies, 77% on Chile, 68% on East Possum, and 80% on West Possum. For the remaining seamounts, orange roughy proportions were low (<37%). High catches of smooth oreo were present on several seamounts and formed the highest proportion of the catch on Cotopaxi (65%). Black oreo catch comprised 8% of the catch on both

Table 9 Number of research trawls per seamount in the south-east Chatham Rise (Andes complex).

Area	Number of trawls
East Possum	7
West Possum	2
Chile/Sir Michael	6
Cotopaxi	5
Cathys	3
Dickies/Iceberg	3

Cotopaxi and East Possum. Baxter's dogfish was taken in quantity on Chile and Cotopaxi.

DISCUSSION

Dominant species in the slope and on the various seamounts were in reasonable agreement with the deep slope communities described in Francis et al. (2002) and Koslow et al. (1994). The top 10 fish

Table 10 Species composition by seamount in the south-east Chatham Rise, Andes complex (see Appendix 1 where scientific names are not provided). These data were recent and not used in the overall report analyses. Hence some species below (†) are referred to for the first time.

Species	Cathy	Chile	Cotopaxi	Dickies	East Possum	West Possum
Catshark†	*	*	*	*		
Basketwork eel	*	*	*	*	*	
Black javelinfish		*				
Black oreo	*	*	*			
Seal shark				*		
Alfonsino†				*	*	*
Brown chimaera	*		*		*	
Giant chimaera		*				
Kaiyomaru rattail†				*	*	
Spottyfaced rattail†			*	*		
Mahia rattail		*		*	*	*
Serrulate rattail		*		*	*	
Leafscale gulper shark		*		*	*	*
Four-rayed rattail	*	*		*	*	
Longnose velvet dogfish	*	*	*	*	*	*
Deep-water octopus†		*			*	
Robust cardinalfish		*	*		*	
Black cardinalfish				*	*	
Baxter's lantern dogfish	*	*	*	*	*	*
Johnson's cod	*	*	*	*	*	
Hoki		*	*	*	*	*
Giant lepidion		*			*	
Ridge scaled rattail	*	*		*	*	*
Warty squid		*	*	*	*	
Orange roughy	*	*	*	*	*	*
Octopodidae†	*					
Plunket's shark	*	*	*	*	*	*
Ribaldo				*	*	
Small-headed cod	*	*	*	*		
Shovelnose spiny dogfish		*		*	*	
Spiky oreo		*	*	*	*	*
Smooth oreo	*	*	*	*	*	*
Todarodes filippovae†	*	*	*			
Tubbia tasmanica		*				
Violet squid	*	*				*

species from the mid slope assemblage (720–1320 m) reported by Francis et al. (2002) were orange roughy, Baxter's dogfish, Johnson's cod, four-rayed rattail, shovelnose spiny dogfish, serrulate rattail, smooth oreo, ribaldo, basketwork eel (*Diastobranchus capensis*), and longnose velvet dogfish. In Koslow et al. (1994) the top species in the mid-slope community (800–1200 m depth) by percentage occurrence were orange roughy, serrulate rattail, Johnson's cod, longnose velvet dogfish, warty oreo (*Allocyttus verrucosus*), four-rayed rattail, Owston's dogfish, shovelnose spiny dogfish, black oreo, and slickheads (*Alepocephalus* spp.). These lists bear a strong resemblance to our lists of dominant species (though there is some overlap between the datasets used by Francis et al. and ourselves).

Our selection of dominant species is heavily skewed towards orange roughy and smooth oreo, partly because much of the data were collected during research surveys designed to estimate the abundance of these species. Many tows were carried out at times of year when these species aggregate on seamounts to spawn, and some were targeted at marks seen on an echosounder and believed to represent orange roughy, black oreo, or smooth oreo aggregations. The dominance of dense populations of a relatively few species on the seamount features as opposed to the slope can also be explained by the fact that the seamount environment is more productive and so can support relatively large aggregations of species such as orange roughy and oreos (Clark 1999; Koslow et al. 2000). There is some discussion on species taking up residence around or close to seamounts. In these areas prey concentration may be enhanced, hence there would be more prey in these areas for the dominant species (Koslow 1994). This information helps us clarify the distinctions we see of species dominance between seamount and slope environments.

We present two comparisons of diversity between seamount complexes, using different measures—mean species richness and total species richness. These two analyses are complementary in that they are informative about different aspects of diversity. They probably also share some flaws, which lead to underestimation of true diversity. First, some very rare species will not have been successfully identified to species and so will not be included in our dataset. Second, some species may not have been caught in the trawl (because they were able to outswim the net or to pass through the 100 mm mesh). Third, our samples do not include all seasons of the year, and some migratory species may not have been present during our surveys.

We did not attempt to analyse diversity in terms of evenness of species distribution. This was because catches on seamounts were dominated by orange roughy and smooth oreo, for reasons noted above. Hence, we would see much lower evenness on seamounts than on the slope. It is unclear how much of this difference is related to timing and sampling methodology, and how much to real environmental differences.

The analysis based on mean species richness showed a strong correlation ($r = 0.84$) between diversity and latitude, with higher mean species richness observed in more southern (polar) latitudes. No such trend is observed in the analysis of total species richness, where the equivalent correlation is $r = -0.14$. In fact there is little difference between seamounts in terms of total species richness, with values ranging between 38 and 57 for the seven seamounts analysed. We conclude, then, that northern and southern seamount complexes have a similar diversity of fish, but that a single tow carried out on a northern seamount is likely to take fewer species of fish. This may indicate that northern seamounts are more dominated by a small number of highly abundant species, or that fish are more spatially segregated by species on northern seamounts.

There is a consistent pattern of lower total species richness on the seamounts than on the surrounding slope, across the four areas for which we were able to make the comparison. The differences range from 10% to 80%. Given the common view of seamounts being highly productive and highly bio-diverse (e.g., Rogers 1994) the opposite might have been expected.

We do note however that unlike much of the benthic fauna on seamounts, which appear to be largely restricted to the seamount environment, the fish most characteristic of seamounts are still not obligate seamount dwellers, rather they are found quite widely on the slope as well. It is likely this contributes to the relatively greater species richness of the slope fish fauna. There are relatively few fish species that are found only on seamounts but quite a fair number of slope fish species not found on seamounts.

There is a possibility that the species richness result may stem in part from difference in fishing techniques. The trawl rig is similar but it is fished more lightly (higher headline height) over seamounts and hard or rough bottom than on smooth and soft bottom on the adjacent slope. The tow direction is often dictated by how rough the bottom is over one or more sectors of the seamount or how steep the slope of the seamount is. This means that it is often impossible to sample all areas of a particular seamount. Tow length is often reduced when fishing seamounts because of the difficulty of sampling these features; often the top and/or slope of some of the seamounts can be very steep and rugged. Tow length is also reduced when fishing dense aggregations on the slope to avoid burst bags. Hence fishing gear performance on seamount terrain, over hard slope and in sampling dense aggregations, can differ from performance of the gear over the slope and in less dense fish marks. The implication from this variation in trawling is that some difference in the sampling methods and catchability of the fish occurs, but it would seem unlikely that this would invalidate the comparisons between slope and seamount fish fauna.

Another possible explanation for the lower number of fish species observed on seamounts is that the seamount complexes provide relatively small habitats, and that these may not be suitable for all species of fish. A number of species were identified which occur significantly less frequently on seamounts. We can form some hypotheses as to why the slope might be their preferred habitat, using information relating to body shape and diet, as well as visual observations made both in the New Zealand region and internationally (e.g., Trenkel et al. 2002). For example, several of the significantly more common slope species, such as ling (*Genypterus blacodes*), pale ghost shark, and shovelnose spiny dogfish, are benthic feeders (Mitchell 1984; Clark & King 1989; Horn 1997) and therefore are more suited to living above soft sediment, which is found more on the slope than seamount environment. Conversely, the high order shark predator Plunket's shark (*Centroscymnus plunketi*) is known to feed on orange roughy, and hence is often found over the top of seamounts (pers. obs.).

Body shape can also indicate ability to hover in strong currents, presumably taking advantage of enhanced water movement to maximise the supply of food. The oreosomatidae species *Neocyttus helgae* was observed by Trenkel et al. (2002) to be often associated with cliff faces and fields of deep-sea corals (gorgonians). The commercially important oreosomatidae black oreo is found in large numbers in the New Zealand region often aggregating over seamounts or near drop offs, areas that may produce strong currents. This was the only species on our list of fish with significantly higher occurrence on seamounts than on the slope.

Strong similarities are observed between the species present in the four Chatham Rise seamount areas and the Puysegur Bank area. The other three areas included in the faunal similarity analysis show distinct differences from the above five areas and from each other. The five similar areas are separated from the other three in terms of latitude, with the Chatham Rise and Puysegur areas south of 42°S and the Challenger, East Cape and Tauroa areas all near or above 40°S.

Several other fish assemblage studies from recent years have found that assemblage structure in New Zealand waters depends on latitude (McClatchie et al. 1997; Anderson et al. 1998; Hurst et al. 2000; Bull et al. 2001; Beentjes et al. 2002; Francis et al. 2002). Depth, longitude, sediment type, bottom temperature, and current convergence zones were also found to be important in some of these studies. Several international studies, including those by Haedrich & Merrett (1990) and Merrett et al. (1991a,b), have also described deep-sea fish fauna and assemblages. Community structures of deep-sea fishes in the North Atlantic have been classified by these studies and then further described by Koslow (1993) and Koslow et al. (1994), showing that distinct communities are based on depth, latitude, and longitude (amphi-oceanically).

The latitudinal effect observed around 37° 42′S could possibly be explained by the different water masses in these regions, complex hydrographical factors such as bottom temperature and currents, or attributed to the depth, height, slope, and diameter of the various seamounts. The environmental variables are very complex within the New Zealand region and even more so on and around seamounts or seamount complexes. The presence of seamounts certainly affects local ocean circulation which although not fully understood (Roden 1987; Eriksen 1991) can affect biological processes. Several studies discuss the mean current flow being interrupted by seamounts with tidal mixing and localised upwellings and eddies commonly occurring around these features (e.g., Owens & Hogg 1980; Robinson 1981; Roden et al. 1982; Genin et al. 1989; Chiswell & Moore unpubl. data).

Other studies have addressed the effects of environmental data on seamount fauna to explain species diversity, dominance, or rarity, but most of these studies have carried out more general examinations and have included benthic fauna as well as fish in their studies. Rogers (1994) concluded that there was morphological and genetic evidence that populations of some organisms on seamounts are distinct from surrounding populations located on other seamounts, the abyssal plain and continental shelf. Wilson & Kaufman (1987) concluded that deep seamount biota were dominated by widespread or cosmopolitan species as opposed to shallow seamounts that comprised equal amounts of regional and widespread species. Boehlert et al. (1994) described seamount populations as "dependent" populations as a result of different larvae settling on different seamounts.

Clark et al. (2001) refer to the movement of species between seamounts. For a particular region, seamounts are often clustered with only a few nautical miles separating them. Species diversity on one seamount could be affected by fish movement between the various seamounts. For the analysis carried out on the Andes Complex, species composition data from the small individual seamounts within the complex could not be rigorously analysed because of an insufficient numbers of tows. However, there is a suggestion that there is substantial variability between seamounts within a particular complex. Differences in the species distribution on seamounts in the Andes region might also be explained by the depth, height, and slope of the seamounts. No species in this study indicated specific seamount endemism. Species that have shown endemism on seamounts have been species of the genera *Paralaemonena* (Moridae) and *Cataetyx* (Bythitidae) (Koslow pers. comm.) These two genera were not recorded on the surveys from which data were obtained for this report, probably because they are small bodied fish and their presence would be restricted by the gear type used on the surveys in this study. Small bodied animals restricted by the gear type will affect the diversity values.

The dataset used in this study has the advantage of a large volume of data, with over 1500 tows, including 527 seamount tows carried out in 10 different seamount complexes. A total of 84 species or closely related species groups were consistently identified. It does also have some disadvantages for the purpose of multispecies analysis. Most of the data came from targeted deep-water abundance surveys where the focus was on the main commercially important species, which were not designed to describe the general fish fauna. The survey trawls often sampled aggregations of commercial species during spawning season where these commercial species comprised over 90% of the catch because of their densely aggregated spawning behaviour. Tow duration was not standardised and was often shortened when fishing on aggregations to avoid overcatching—80 t bags are avoided when only a 10 t species identification sample is required. Some surveys had a very uneven spatial distribution of tows: fully randomised stations would be preferable for this sort of analysis.

A mix of sampling tools could add value to a study of this type. Cameras and videos would provide a better understanding of habitat specificity, and also provide information on fish species that can actively avoid trawls (e.g., Trenkel et al. 2000). Trawl nets with smaller cod-end mesh sizes and ROVs or submersibles with mechanical arms would aid sampling of the various-sized fauna. Understanding the preferred habitat of the fish fauna within an ecosystem, locating areas of high productivity, and capturing more data on the environmental processes will help provide reasons for the observed differences such as trends in abundance, species dominance, species richness, and rarity. Future work could also enable comparisons of seamount and slope fauna in terms of taxonomy and feeding mode to provide a real understanding as to why species richness and abundance is higher in the slope regions of the New Zealand EEZ.

ACKNOWLEDGMENTS

This work was funded by the Foundation for Research, Science and Technology, under contract CO1X0028 (Seamounts: their importance to fisheries and marine ecosystems). We thank the New Zealand Ministry of Fisheries for providing access to their database "trawl" and the Department of Conservation for allowing us to cite Client Reports. We acknowledge the many fisheries researchers from NIWA who were involved in data collection on the various surveys. Thanks to Martin Cryer, NIWA, for providing editorial comments on an earlier version of this report and helpful advice on the data analysis methodology; to referee Tony Koslow for his very thorough review; and an anonymous referee for useful comments particularly on a statistical component of this paper.

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Appendix 1 Codes, common name, and scientific name of all species used in the analyses.

Family and species code	Common name	Scientific name
Crustacea		
LMU	*Lithodes murrayi*	*Lithodes murrayi*
NEB	*Neolithodes brodiei*	*Neolithodes brodiei*
Opistoteuthidae		
OPI	Umbrella octopus	*Opisthoteuthis*
Graneledoninae		
OCTOPODIDAE		
OSQ	Deep-water octopus	Octopodidae
DWO	Deep-water octopus	*Graneledone* spp.
Onychoteuthidae		
WSQ	Warty squid	*Moroteuthis* spp.
Histioteuthidae		
VSQ	Violet squid	*Histioteuthis* spp.
Mastigoteuthidae		
MSQ	*Mastigoteuthis* sp.	*Mastigoteuthis* sp.
Ommastrephidae		
TSQ	*Todarodes filippovae*	*Todarodes filippovae*
Chranchiidae		
CHQ	Cranchiid squid	*Cranchiidae*
Squalidae		
APR	Catshark	*Apristurus* spp.
CSQ	Leafscale gulper shark	*Centrophorus squamosus*
CYL	Portuguese dogfish	*Centroscymnus coelolepis*
CYO	Owston's dogfish	*Centroscymnus owstoni*
CYP	Longnose velvet dogfish	*Centroscymnus crepidater*
ETB	Baxter's lantern dogfish	*Etmopterus baxteri*
ETL	Lucifer dogfish	*Etmopterus lucifer*
PLS	Plunket's shark	*Centroscymnus plunketi*
SND	Shovelnose spiny dogfish	*Deania calcea*
Dalatidae		
BSH	Seal shark	*Dalatias licha*
Oxynotidae		
PDG	Prickly dogfish	*Oxynotus bruniensis*
Rajiidae		
DSK	Deep-water spiny skate	*Amblyraja* sp.
PSK	Longnosed deep-sea skate	*Bathyraja shuntovi*
SSK	Smooth skate	*Dipturus innominatus*
Torpedinidae		
ERA	Electric ray	*Torpedo fairchildi*
Chimaeridae		
CHG	Chimaera, giant	*Chimaera lignaria*
CHP	Chimaera, brown	*Chimaera* sp.
GSP	Pale ghost shark	*Hydrolagus benisi*
HYB	Black ghost shark	*Hydrolagus* sp. *a*
HYP	Pointynose blue ghost shark	*Hydrolagus trolli*
Rhinochimaeridae		
LCH	Long-nosed chimaera	*Harriotta raleighana*
RCH	Widenosed chimaera	*Rhinochimaera pacifica*

Appendix 1 (*Continued*)

Family and species code	Common name	Scientific name
Notacanthidae		
SBK	Spineback	*Notacanthus sexspinis*
Congridae		
CON	Swollen and hairy conger eel	*Bassanago bulbiceps* and *B. hirsutus*
Synaphobranchidae		
BEE	Basketwork eel	*Diastobranchus capensis*
Notocanthidae		
SBK	Spineback eel	*Notacanthus sexspinis*
Alepocephalidae		
BSL	Black slickhead	*Xenodermichthys* spp.
SBI	Slickhead, bigscaled brown	*Alepocephalus* sp.
SSM	Slickhead, smallscaled brown	*Alepocephalus australis*
TAL	*Talismania longifilis*	*Talismania longifilis*
Chauliodontidae		
CHA	Viper fish	*Chauliodus sloani*
Synodontidae		
BFE	Deep-sea lizardfish	*Bathysaurus ferox*
Chaunacidae		
CHX	Pink frogmouth	*Chaunax pictus*
Moridae		
HJO	Johnson's cod	*Halargyreus johnsonii*
LEG	Giant lepidion	*Lepidion schmidti* and *L. inosimae*
RIB	Ribaldo	*Mora moro*
SMC	Small-headed cod	*Lepidion microcephalus*
VCO	Violet cod	*Antimora rostrata*
Merlucciidae		
HAK	Hake	*Merluccius australis*
HOK	Hoki	*Macruronus novaezelandiae*
Ophidiidae		
BCR	Blue cusk eel	*Brotulotaenia crassa*
LIN	Ling	*Genypterus blacodes*
Carapidae		
ECR	Messmate fish	*Echiodon cryomargarites*
Macrouridae		
BJA	Black javelinfish	*Mesobius antipodum*
CBA	Slender rattail	*Coryphaenoides* sp. *B*
CBO	Bollons rattail	*Caelorinchus bollonsi*
CEX	Black lip rattail	*Caelorinchus celaenostoma*
CFA	Banded rattail	*Caelorinchus fasciatus*
CIN	Notable rattail	*Caelorinchus innotabilis*
CMA	Mahia rattail	*Caelorinchus matamua*
CMU	Abyssal rattail	*Coryphaenoides murrayi*
COL	Olivers rattail	*Caelorinchus oliverianus*
CSE	Serrulate rattail	*Coryphaenoides serrulatus*
CSU	Four-rayed rattail	*Coryphaenoides subserrulatus*
GAO	Filamentous rattail	*Gadomus aoteanus*
JAV	Javelin fish	*Lepidorhynchus denticulatus*
MCA	Ridge scaled rattail	*Macrourus carinatus*
NBU	Bulbous rattail	*Kuronezumia bubonic*
WHR	Unicorn rattail	*Trachyrincus longirostris*
CKA	Kaiyomaru rattail	*Caelorinchus kaiyomaru*
CKX	Spottyfaced rattail	*Caelorinchus trachycarus*
Trachichthyidae		
ORH	Orange roughy	*Hoplostethus atlanticus*
SRH	Silver roughy	*Hoplostethus mediterraneus*

Family and species code	Common name	Scientific name
SFN	Spinyfin	*Diretmoides parini*
Berycidae		
BYS	Alfonsino	*Beryx splendens*
Zeidae		
LDO	Lookdown dory	*Cyttus traversi*
Oreosomatidae		
BOE	Black oreo	*Allocyttus niger*
SOR	Spiky oreo	*Neocyttus rhomboidalis*
SSO	Smooth oreo	*Pseudocyttus maculatus*
WOE	Warty oreo	*Allocyttus verrucosus*
Macrohamphosidae		
BBE	Banded bellowsfish	*Centriscops humerosus*
Scorpaenidae		
SPE	Sea perch	*Helicolenus* spp.
TRS	Trachyscorpia capensis	*Trachyscorpia capensis*
Psychrolutidae		
COT	Bonyskull toadfish	*Cottunculus nudus*
PSY	Psychrolutes sp.	*Psychrolutes* sp.
TOP	Pale toadfish	*Neophrynichthys angustus*
Apogonidae		
EPR	Robust cardinalfish	*Epigonus robustus*
EPT	Black cardinalfish	*Epigonus telescopus*
Centrolophidae		
RAG	Ragfish	*Icichthys australis*
RUD	Rudderfish	*Centrolophus niger*
SUS	*Schedophilus* sp.	*Schedophilus* sp.
TUB	*Tubbia tasmanica*	*Tubbia tasmanica*
Bothidae		
MAN	Finless flounder	*Neoachiropsetta milfordi*

Appendix 2 overleaf

Appendix 2 Examples of the calculation of P_{pos}. Top panel shows agreement-disagreement matrix for the north-east and north-west Chatham Rise seamounts. These two areas have strong agreement in species lists ($P_{pos} = 0.88$). The bottom panel shows agreement-disagreement matrix for the Challenger Plateau and East Cape seamounts. These two areas have weak agreement in species lists ($P_{pos} = 0.45$).

$P_{pos} = 36 / ((41 + 41)/2) = 0.88$	Present on north-west Chatham Rise	Absent on north-west Chatham Rise
Present on north-east Chatham Rise	orange roughy, smooth oreo, Baxter's lantern dogfish, black oreo, black cardinalfish, Plunket's shark, Owston's dogfish, basketwork eel, warty squid, leafscale gulper shark, robust cardinalfish, giant chimaera, longnose velvet dogfish, hoki, four-rayed rattail, giant lepidion, widenosed chimaera, seal shark, brown chimaera, bigscale brown slickhead, serrulate rattail, shovelnose spiny dogfish, hake, Johnson's cod, rudderfish, spiky oreo, long-nosed chimaera, Mahia rattail, ridge scaled rattail, notable rattail, small-headed cod, *Tubbia tasmanica*, unicorn rattail, slender rattail, blue cusk eel, ribaldo ($n = 36$)	warty oreo, deep-water spiny skate, smallscaled brown slickhead, electric ray, violet squid ($n = 5$)
Absent on north-east Chatham Rise	pale ghost shark, *Shedophilus* sp., *Trachyscorpia capensis*, javelin fish, black javelinfish ($n = 5$)	all others

$P_{pos} = 14 / ((43 + 19)/2) = 0.45$	Present on Challenger Plateau	Absent on Challenger Plateau
Present on East Cape	orange roughy, ribaldo, black cardinalfish, Johnson's cod, Owston's dogfish, spiky oreo, longnose velvet dogfish, shovelnose spiny dogfish, basketwork eel, serrulate rattail, unicorn rattail, hoki, widenosed chimaera, giant lepidion ($n = 14$)	warty squid, Baxter's lantern dogfish, smallscaled brown slickhead, pale ghost shark, black javelinfish, warty oreo, brown chimaera, bigscale brown slickhead, umbrella octopus, smooth oreo, hake, long-nosed chimaera, black ghost shark, *Lithodes murrayi*, small-headed cod, *Neolithodes brodiei*, javelin fish, *Talismania longifilis*, black lip rattail, lucifer dogfish, spinyfin, *shedophilus* sp., Mahia rattail, black oreo, pink frogmouth, *Psychrolutes* sp., ragfish, *Trachyscorpia capensis*, violet squid ($n = 29$)
Absent on East Cape	leafscale gulper shark, seal shark, Portuguese dogfish, prickly dogfish, *Tubbia tasmanica* ($n = 5$)	all others