



# Composition, distribution and regional affinities of the deepwater ichthyofauna of the Lord Howe Rise and Norfolk Ridge, south-west Pacific Ocean

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## ABSTRACT

Fishes were collected from seamounts and insular slopes of the northern Tasman and southern Coral Seas in the environs of the Reinga Ridge, Norfolk Ridge and Lord Howe Rise, at depths ranging from 49 to 1927 m. A total of 348 demersal fish species in 99 families, which were collected from 135 samples taken with a variety of sampling gear, greatly improved taxonomic knowledge of this poorly known area. Twenty five percent of the fish sampled are considered to be potentially new species. Relatively high levels of regional endemism and diversity are attributed to geological history, and the complexity of contemporary climatology, hydrography and habitat diversity of the region. Fish assemblages were highly structured by depth, but across regions, deep-water fish faunas showed stronger taxonomic affinities than shallower faunas. Although less pronounced, spatial differences pointed towards distinct faunas between the southern and northern parts of the area. The distribution patterns and affinities to regions adjacent to the survey area indicate that (1) the fish fauna on the Lord Howe Rise near Lord Howe Island and further north is distinct from the rest of the survey regions, and exhibits eastern Australian and northern (Coral Sea) affinities, (2) the Northern Norfolk Ridge fauna is distinct from the other regions and has strong affinities with New Caledonia, (3) fishes on the Southern Norfolk Ridge, Western Norfolk Ridge and Lord Howe Plateau have more shared species compared to the other regions indicating a high level of connectedness and affinities with New Zealand fauna, and (4) some species have a wide distribution along the Norfolk Ridge providing a possible deepwater pathway between New Caledonia and New Zealand. Survey data is also useful for assessing the regions' conservation values by identifying rare or unusual components of the fauna, those with very limited distributions, those with low productivity that may be vulnerable to human disturbance (fishing, mining), and for defining bioregions.

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## 1. Introduction

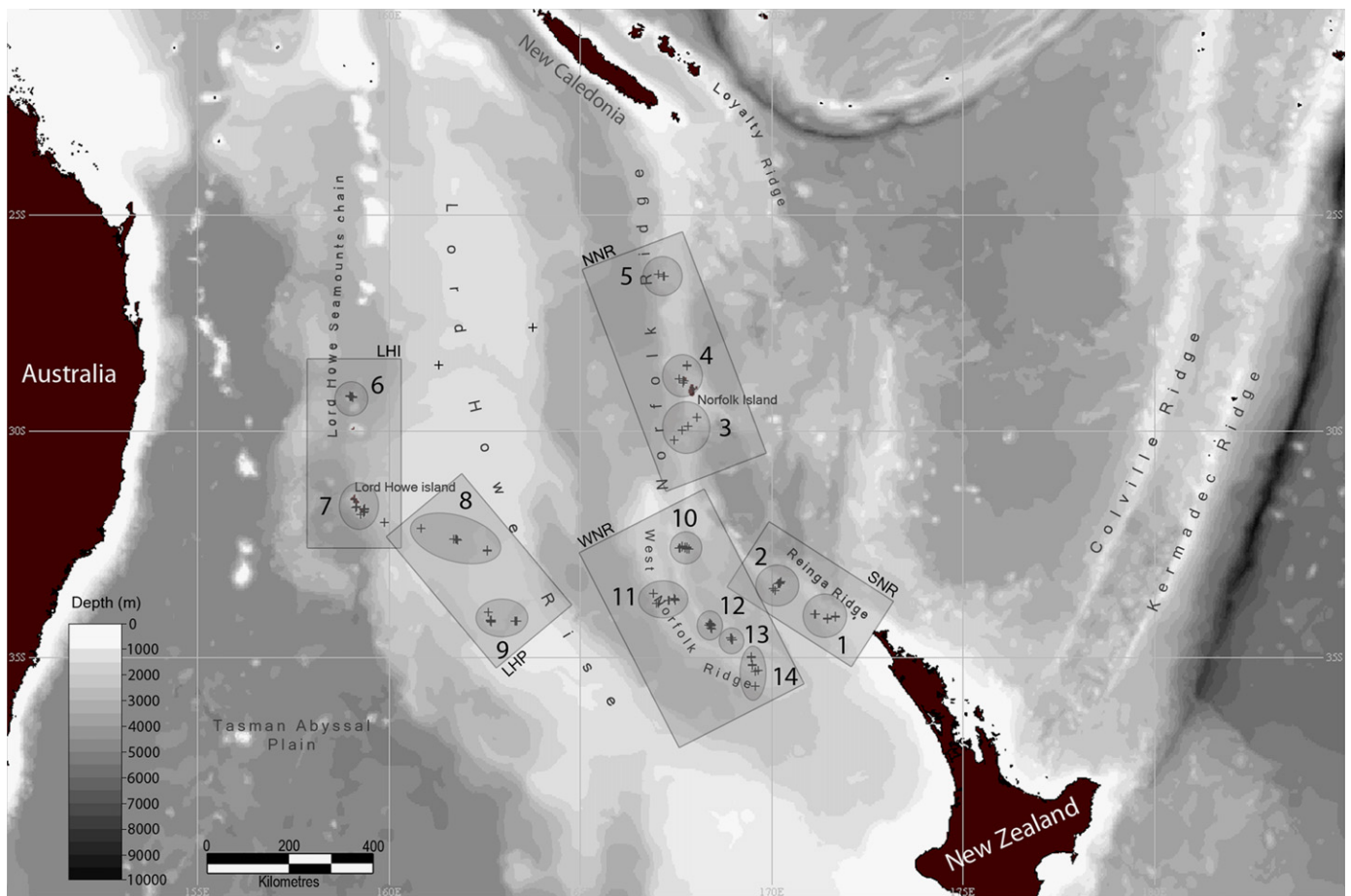
The Lord Howe Rise and Norfolk Ridge are prominent chains of seamounts, plateaus, banks, ridges and submerged escarpments rising from 3500 m to depths of 200–1200 m between New Zealand, New Caledonia and Australia (Fig. 1). They provide large areas of diverse habitats in relatively shallow depths in the central Tasman and Coral Sea basins (Richer De Forges, 1990). The Lord Howe Rise and Norfolk Ridge, which were once part of the coastline of Gondwana, have existed in one form or another for over 80 million years (Stevens, 1980; Eade, 1988). Prior to the Miocene, when the Norfolk Ridge subsided by over 400 m, most seamounts

were emergent and New Zealand and New Caledonia were contiguous at 1000 m depth or less (Stevens, 1980).

The deep-water fish faunas of the Lord Howe Rise and Norfolk Ridge were known from just a few recent fisheries surveys of the Wanganella Bank, on the southern Norfolk Ridge (Clark, 1988; Yano, 1991), and French led exploratory voyages in the northern sector (e.g., Richer De Forges, 1990; Grandperrin and Lehodey, 1992; Lehodey et al., 1993). New Caledonian waters were also surveyed more recently down to 1800 m (Grandperrin et al., 1997a, 1997b). Hence, distribution patterns of the region's fishes remain poorly known, except for a few areas revealing some unusual patterns after being repeat sampled (e.g. French Beryx 1 to 11 and HALIPRO 2 voyages, southern New Caledonian EEZ).

In addition to horizontal spatial gradients for fish distributions, increased sampling over the past two decades has confirmed the global presence of depth zonation of the continental margin, in the

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**Fig. 1.** Sampling stations (+) and sites (1–14) regrouped under regions. WNR: Western Norfolk Ridge, SNR: Southern Norfolk Ridge, NNR: Northern Norfolk Ridge, LHI: Lord Howe Islands, LHP: Lord Howe Plateau.

sense that individual species and assemblages occupy restricted depth bands (Carney, 2005). Distinct assemblages of demersal fishes at upper (500 m) and mid-slope depths (800–1200 m), each with distinct depth related sub-communities, have been identified in Australia and New Zealand (Koslow et al., 1994; Williams et al., 2001; Francis et al., 2002). The dominant mid-slope fish fauna was thought to comprise an identifiable community within a biogeographic province that extends at least from the Great Australian Bight to the Chatham Rise, a distance of 5000 km (Koslow et al., 1994). However, for fauna from deeper strata (including non-commercial or by-catch species of both fishes and invertebrates), knowledge is more limited, and it is uncertain whether discrete communities exist across the plateaus, ridges and seamounts of the Tasman Sea between Australia and New Zealand.

Knowledge of deep-sea fish distributions is of prime importance for fisheries and conservation management because commercial fishing on these seamounts has increased recently (e.g., Grandperrin et al., 1997b), especially on the West Norfolk Ridge where there has been a rapid expansion of effort for orange roughy fishing since 2002 (Clark, 2004). There is increasing concern about the impacts of fishing and mineral exploration on the deep-sea environment because the rate of exploitation is often faster than the acquisition of biological knowledge needed to guide sustainable development. This is particularly true in deep-sea fisheries, which have expanded rapidly in the last 25 years causing rapid depletion of target species and destruction of associated faunas and their habitats, particularly on seamounts (Koslow et al., 2001; Clark and O'Driscoll, 2003; Lack et al., 2003; Althaus et al., 2009; Clark et al., in press). It is recognised that there is an increasing need for

the conservation and management of deep-sea biodiversity at both national and international levels, and associated research to provide accurate data on which to base effective management strategies study (Probert, 1999; Gislason et al., 2000).

In 2003, a major biodiversity survey of fishes and benthic invertebrates of the Lord Howe Rise and Norfolk Ridge addressed the obvious lack of rigorous biodiversity information from this area. Initiated by an international team of scientists from France, Australia and New Zealand, this survey was termed “NORFANZ”. Preliminary data and outcomes have already been published in post-voyage reports (Williams et al., 2006b; Clark and Roberts, 2008), but more complete taxonomic identifications and more extensive analyses have now been conducted.

This paper characterises the biodiversity of the demersal ichthyofauna at depths from 50 to ~2000 m along the Lord Howe Rise and Norfolk Ridge. Our specific objectives are to: (1) detail the composition and structure of fish assemblages of the area, (2) describe their diversity and distribution, (3) identify boundaries delineating the major assemblages and their environmental determinants, and (4) discuss other biogeographic patterns of the area.

## 2. Material and methods

### 2.1. Data collection and dataset

In 2003, the New Zealand FRV *Tangaroa* was used to collect data on fishes from the seamounts and insular slopes along the Reinga Ridge, Lord Howe Rise and Norfolk Ridge, located between the

**Table 1**

Sampling intensity by site, region and depth. The number of samples with no fish caught are in brackets. Five additional samples were taken between 1500 and 2000 m, including one ORH sample. WNR: Western Norfolk Ridge, SNR: Southern Norfolk Ridge, NNR: Northern Norfolk Ridge, LHI: Lord Howe Islands, LHP: Lord Howe Plateau.

| Site  | Region | Depth (m) |          |           |          | OHR only Depth (m) |          |           |        |
|-------|--------|-----------|----------|-----------|----------|--------------------|----------|-----------|--------|
|       |        | 0–500     | 500–1000 | 1000–1500 | Total    | 0–500              | 500–1000 | 1000–1500 | Total  |
| 1     | SNR    | 2         | 3        | 3         | 8        | 1                  | 1        | 1         | 3      |
| 2     | SNR    | 3         | 5        | 2         | 10       | 1                  | 2        | 1         | 4      |
| 3     | NNR    | 2         | 5 (2)    | 2 (1)     | 9 (3)    | 1                  | 1        | 1         | 3      |
| 4     | NNR    | 3         | 3        | 4 (1)     | 10 (1)   | 2                  | 2        | 2         | 6      |
| 5     | NNR    | 0         | 4        | 2 (1)     | 6 (1)    | 0                  | 1        | 1         | 2      |
| 6     | LHI    | 4 (2)     | 4        | 1 (1)     | 9 (3)    | 2 (2)              | 1        | 0         | 3 (2)  |
| 7     | LHI    | 5         | 3        | 1         | 9        | 2                  | 2        | 0         | 4      |
| 8     | LHP    | 0         | 3        | 5         | 8        | 0                  | 1        | 1         | 2      |
| 9     | LHP    | 1         | 7        | 3         | 11       | 1                  | 2        | 1         | 4      |
| 10    | WNR    | 6         | 4        | 5 (1)     | 15 (1)   | 1                  | 1        | 1         | 3      |
| 11    | WNR    | 4 (2)     | 3        | 4         | 11 (2)   | 2 (1)              | 1        | 1         | 4 (1)  |
| 12    | WNR    | 3         | 3        | 3         | 9        | 2                  | 1        | 1         | 4      |
| 13    | WNR    | 0         | 4        | 3         | 7        | 0                  | 1        | 1         | 2      |
| 14    | WNR    | 0         | 4        | 4 (2)     | 8 (2)    | 0                  | 2        | 1         | 3      |
| Total |        | 33 (4)    | 55 (2)   | 42 (7)    | 130 (13) | 15 (3)             | 19 (0)   | 13 (0)    | 47 (3) |

**Table 2**

Total fish catch and distribution of the catch between the different fishing gears.

| Gear type   | Total     | Orange roughy trawl | Full wing bottom trawl | Beam trawl | Sherman sled | NIWA sled |
|---|-----------|---------------------|------------------------|------------|--------------|-----------|
| # stations sampled                                    | 135       | 48                  | 27                     | 21         | 36           | 3         |
| # stations with fish catch                            | 122       | 44                  | 26                     | 20         | 30           | 2         |
| Species distribution over the different gear types    |           |                     |                        |            |              |           |
| # families  | 135       | 102                 | 96                     | 55         | 30           | 3         |
| # species   | 501       | 283                 | 277                    | 147        | 74           | 3         |
| # demersal species                                    | 348 (69%) | 193 (68%)           | 179 (64%)              | 127 (86%)  | 65 (88%)     | 3 (100%)  |
| # demersal specimens                                  | 27,687    | 5,765               | 18,895                 | 2,875      | 148          | 4         |
| # pelagic species                                     | 153 (31%) | 91 (32%)            | 98 (36%)               | 19 (14%)   | 9 (12%)      | 0 (0%)    |
| # pelagic specimens                                   | 17,200    | 387                 | 16,754                 | 46         | 13           | 0         |
| Number of demersal species caught per sample          |           |                     |                        |            |              |           |
| Maximum   | 38        | 29                  | 38                     | 31         | 12           | 2         |
| Minimum   | 1         | 1                   | 4                      | 1          | 1            | 1         |
| Average   | 11.9      | 11.4                | 25.0                   | 9.7        | 3.0          | 1.5       |
| Stations with less than five demersal species sampled |           |                     |                        |            |              |           |
| # stations  | 44        | 11                  | 1                      | 5          | 25           | 2         |
| # species excluded                                    | 15        | 6                   | 1                      |            |              |           |

Tasman Basin and the south-west Pacific Basin (Fig. 1). Fourteen sites (i.e. individual features or seamounts) were evenly spread among five regions: Northern Norfolk Ridge (NNR), Southern Norfolk Ridge (SNR – Reinga Ridge), Western Norfolk Ridge (WNR), Lord Howe Islands (LHI), and Lord Howe Plateau (LHP). This geographical grouping was based on a subjective assessment of the location of sites along the different ridge systems. Samples were taken in 0–499 m, 500–999 m and 1000–1500 m depth strata at each site and sampling intensity varied from 0 to 7 (Table 1). Additionally, five samples were taken between 1500 and 2000 m depth (two on transit between NNR and LHI (see Fig. 1), one on transit between site 7 and 8, one on the Southern end of WNR, and one on site 6). Multiple gear types were used for sampling demersal species, a compromise being made between the minimum mesh size for adequate towing speed and the maximum size for adequate sampling of small species. They included: (1) an “orange roughy” rough-bottom trawl (ORH trawl, 60 mm cod-end), (2) a full-wing bottom trawl (40 mm cod-end), (3) a beam trawl (50 mm mesh size), and (4) two types of benthic sledges, a Sherman Sled and a NIWA Sled, specially designed to work on rough bottoms (30–50 mm mesh size).

The sampling strategy aimed to maximise diversity, and relied on different types of gear with different selectivities to sample over a variety of often hard and rocky terrains. The demersal ORH trawl was used consistently on all seamounts, with three trawls per site (where the depth range was appropriate). Smaller benthic fishes and invertebrates were sampled with the full-wing trawl, beam trawl and epibenthic sleds. Overall, 135 samples were taken including the five samples deeper than 1500 m (Table 2). Of these, 37 caught less than five fish species and 13 samples caught nothing. Those 50 samples were excluded from some of the analysis because they were judged to be unrepresentative samples of the local fauna. However, all samples were used to describe the diversity of the region's fishes.

Tows were generally short (15–30 minutes) at 2–3 knots speed to avoid damaging specimens and were carefully monitored with Netsonde sensors to record the operating depth in each case. Tows usually followed depth contours in order to avoid large variations in depth within a single sample unit; average towing depth was used to provide a single value for each sample. Onboard, specimens were identified to the lowest possible taxonomic level. Sixty-five percent of the taxa were identified with confidence to species, while 30%

were confidently identified to genus. The remaining 5% of taxa were recorded to a coarser taxonomic level. Operational taxonomic units (OTUs) are referred to herein as species. Gear types were designed to catch benthic or demersal species, so pelagic species were omitted prior to analysis (see Table 2). A more complete description of the locations, gear, sampling methods and treatment of specimens is given elsewhere (Clark and Roberts, 2008).

Environmental data were generated from data recorded on board ship – latitude, longitude and depth (mean of start and end depth) of the gear while sampling – and from modelled oceanographic data. Depth-specific means and standard deviation of temperature, salinity and oxygen, silicate, phosphate and nitrate concentrations were extracted for the location of each sample from the CSIRO Atlas of Regional Seas – an interpolated oceanographic data set (CARS 2006 – <http://www.marine.csiro.au/~dunn/cars2006/>).

## 2.2. Analysis

To explore biogeographic patterns of the fish assemblages, each species was assigned to one of the following distributional categories based on an extension of analyses presented by Clark and Roberts (2008). These include:

- (1) northern species – sampled at the NNR and near LHI, but not elsewhere;
- (2) southern species – sampled at the SNR, WNR and LHP, but not elsewhere;
- (3) widespread species – found at least once at each of the five regions (NNR, SNR, WNR, LHI and LHP);
- (4) restricted species – only sampled at one region and not elsewhere;
- (5) Norfolk species – sampled at the WNR, SNR and NNR but not elsewhere;
- (6) Lord Howe species – sampled at the LHI and LHP but not elsewhere;
- (7) Western species – sampled at Lord Howe (Islands or Plateau) and WNR, but not elsewhere.

Mean species accumulation curves and their standard deviation were produced for the different gears using 999 randomized iterations in PRIMER. Extrapolations of species richness for increased sample size were estimated using the Logarithmic Series method which is an iterative non-linear regression process developed by Efron and Thisted (1976) following Fisher et al. (1943). This method has been shown to be the most robust among a series of estimators in estimating species richness for a range of data sets and for extrapolation up to two times the size of the initial sample size (Keating et al., 1998; Melo et al., 2003). Mean species accumulation curves were also produced to compare species richness between the different regions using the most commonly used gear type (i.e. ORH trawl), but in this case, extrapolation was impossible due to the low number of replicates.

Assemblage analyses were produced on a subset of the dataset encompassing the samples taken with the ORH trawl. This sampling gear was chosen because it was consistently used in each site and sampled many individuals from a wide variety of taxa which was not necessarily the case with the other sampling gear.

Variation in the structure of fish assemblages along the depth gradient and between sites were examined on the basis of their taxonomic dissimilarity ( $\Gamma^+$ , Clarke et al., 2006). Taxonomic dissimilarity ( $\Gamma^+$ ) is a natural extension of the measure of average taxonomic distinctness (Clarke and Warwick, 1998). It is defined as:

$$\Gamma^+ = 100 \frac{\sum_i \min_j(\omega_{ij}) + \sum_j \min_i(\omega_{ji})}{s_1 + s_2}$$

where  $\omega_{ij}$  is the path length between species  $i$  and  $j$  and  $s_1$  and  $s_2$  are the numbers of observed species in samples 1 and 2, respectively.  $\Gamma^+$  is the mean of all path lengths through a tree (in our case, a standard Linnaean taxonomic tree with the levels species, genus, family, order and class) between each species in one sample and its closest relation in the other sample. For example, the closest relation of *sp1* (sample 1) in sample 2 could be the same species (in this case  $\omega_{1,2}=0$ ). If *sp1* is not found in the second sample, then its closest relation could be a species belonging to the same genus and  $\omega_{1,2}=25$ . If the genus to which *sp1* belongs to is not found in sample 2, then there might be a species belonging to the same family in sample 2 and  $\omega_{1,2}$  will take the value 50. This process continues until the extreme case of  $\omega_{1,2}=100$  where *sp1* has its closest taxonomic neighbour in a different class. The use of this dissimilarity measure is particularly useful for comparing samples having zero or few species in common. As the entire taxonomic structure is used to compute  $\Gamma^+$ , samples with no species in common can have dissimilarities  $<100$  if they share some branches of the taxonomic structure (e.g., if some of their species belong to the same family). This is a desirable property for data sets covering a large area like the present study and in a context of biogeographic rather than strictly assemblage pattern analysis.

To build the Linnaean tree, the latest taxonomic information available was used. Specific and generic determinations were based on novel research by NORFANZ fish taxonomists, and family level and higher classifications were based on Eschmeyer (2008) and Nelson (2006).

A dissimilarity matrix obtained from the  $\Gamma^+$  resemblance measure was then used to explore the patterns of differences in assemblage structure among samples by means of ordination with non-metric multidimensional scaling (nMDS). The goodness-of-fit of the resulting two-dimensional nMDS plot was measured using Kruskal's stress formula I (Kruskal and Wish, 1978).

Differences in the assemblage structure between the three depth strata, sites and regions were studied using PERMANOVA with taxonomic dissimilarities as an input matrix (Anderson, 2001). The factors of the model were sites (random, 14 levels, nested within location), location (fixed, 5 levels) and depth strata (fixed, 3 levels). Because of the low level of replications, pair-wise tests used Monte Carlo permutation to obtain meaningful p levels.

Linking the environmental dataset to the fish data was implemented indirectly by superimposing environmental variables on nMDS plots of the fish data for those variables deemed important from the BEST procedure. This link was explored in a direct way through the BEST procedures in PRIMER which searches the best match of a subset of the environmental data to explain the biotic data set by calculating a rank coefficient (Spearman) between the produced biotic and abiotic dissimilarity matrices (Clarke and Ainsworth, 1993). The environmental dissimilarity matrices used in the BIO-ENV analysis were calculated with the normalized Euclidean distance after inspection of draftsman plots (Clarke and Warwick, 2001). The plots suggested that no transformation was necessary to approximate normality but that several variables were highly correlated ( $\rho > 0.95$ ). In particular, Si, PO<sub>4</sub>, and NO<sub>3</sub> were all positively correlated with average depth. In order to give meaningful interpretation of the results, only average depth was retained in the analysis.

## 3. Results

### 3.1. Taxonomic diversity

Taxonomic diversity of demersal fishes from the NORFANZ survey included 23 orders, 99 families, 192 genera and 348 species (Table 3; Appendix 1) based on 27,687 specimens with a weight of



11,843 kg; about 61% of these species are valid nominal taxa, 39% have OTU status, being identified to genus and given an informal epithet. Ordinal groups, Gadiformes (68 spp.) and Perciformes (62 spp.), had the highest species richness, and together comprised 39.5% of the total number of reported species (Table 3). However, relative diversity within these two orders differs at higher taxonomic levels. At the family level, Gadiformes diversity was very low (4 families) compared to the Perciformes (29), with a similar but less pronounced trend at the genus level (24 genera cf. 45). Most (16) orders exhibited moderate species richness (6–27 spp. each) and a range of generic (4–16) and familial (2–7) diversity. Highest familial taxonomic diversity was found in the gadiform family Macrouridae, with 14 genera and 51 species. Lowest taxonomic diversity was found in five orders, each with one species.

Based on the samples taken with a single gear type (ORH trawl), Perciformes were most abundant in the shallowest depth stratum and were absent from the deepest (Table 4). Occurrences of families also varied with depth. Macrouridae was a dominant family in all but the shallowest depth stratum. In the 500–999 m and 1000–1500 m depth strata, it accounted for 24.3 and 36.9%, respectively, of the total occurrences in these strata. Moridae and Alepocephalidae were also important families at the two deepest strata. For the 0–499 m stratum, the partition of

occurrences was more evenly spread across a set of families, the Scorpaenidae and Serranidae being collected most frequently.

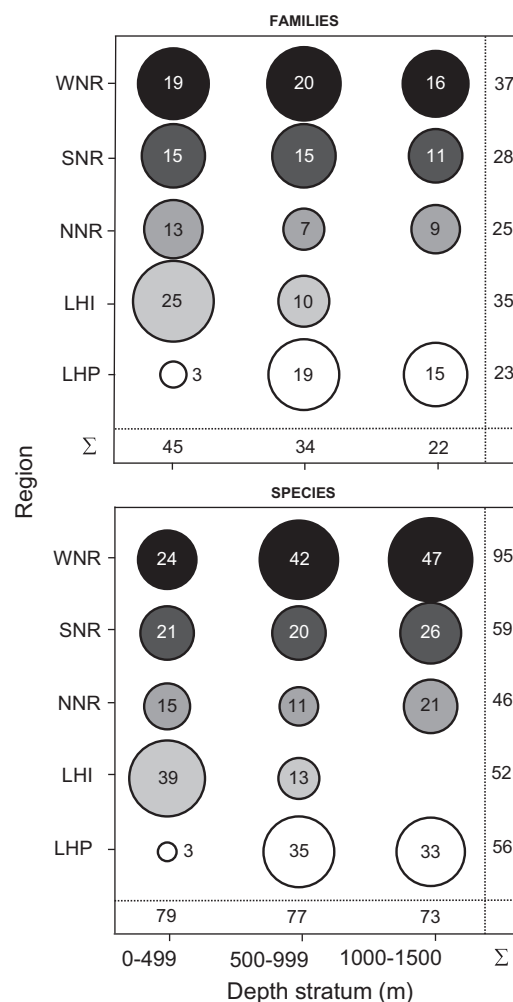
Taxonomic diversity of families and species captured by the ORH trawl varied between regions and with depth (Fig. 2). Despite differences in sampling effort, combined family richness strongly decreased with depth whereas species richness was similar in all strata; species richness was 79, 77 and 73 at the 0–499 m, 500–999 m and 1000–1500 m depth strata, respectively, while family richness was 45, 34 and 22. However, these patterns did not hold up

**Table 3**  
Taxonomic diversity of demersal fishes ranked by species occurrences.

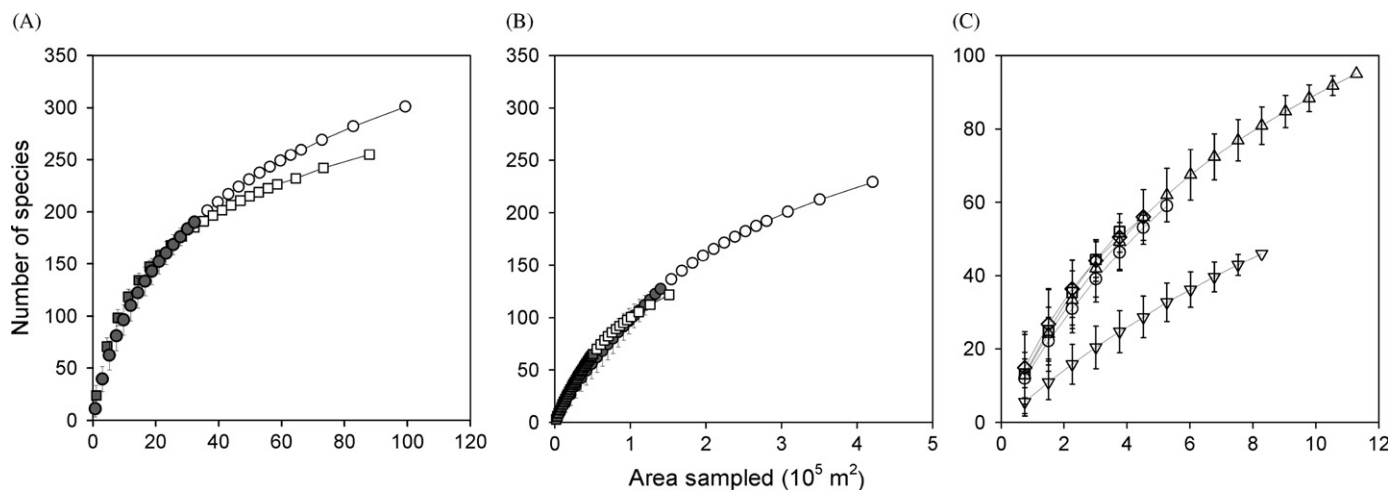
| Orders            | Family count | %    | Genus count | %    | Species count | %    |
|-------------------|--------------|------|-------------|------|---------------|------|
| Gadiformes        | 4            | 4.0  | 24          | 12.5 | 68            | 19.5 |
| Perciformes       | 29           | 29.3 | 45          | 23.4 | 62            | 17.8 |
| Scorpaeniformes   | 7            | 7.1  | 16          | 8.3  | 27            | 7.8  |
| Squaliformes      | 6            | 6.1  | 9           | 4.7  | 24            | 6.9  |
| Osmeriformes      | 2            | 2.0  | 10          | 5.2  | 19            | 5.5  |
| Tetraodontiformes | 4            | 4.0  | 12          | 6.3  | 18            | 5.2  |
| Anguilliformes    | 5            | 5.1  | 7           | 3.6  | 16            | 4.6  |
| Aulopiformes      | 4            | 4.0  | 8           | 4.2  | 15            | 4.3  |
| Carcharhiniformes | 4            | 4.0  | 6           | 3.1  | 12            | 3.4  |
| Rajiformes        | 4            | 4.0  | 5           | 2.6  | 12            | 3.4  |
| Zeiformes         | 5            | 5.1  | 8           | 4.2  | 11            | 3.2  |
| Beryciformes      | 3            | 3.0  | 5           | 2.6  | 10            | 2.9  |
| Lophiiformes      | 3            | 3.0  | 5           | 2.6  | 10            | 2.9  |
| Chimaeriformes    | 2            | 2.0  | 4           | 2.1  | 9             | 2.6  |
| Ophidiiformes     | 3            | 3.0  | 8           | 4.2  | 9             | 2.6  |
| Pleuronectiformes | 3            | 3.0  | 5           | 2.6  | 8             | 2.3  |
| Notocanthiformes  | 2            | 2.0  | 5           | 2.6  | 7             | 2.0  |
| Syngnathiformes   | 4            | 4.0  | 5           | 2.6  | 6             | 1.7  |
| Gobiesociformes   | 1            | 1.0  | 1           | 0.5  | 1             | 0.3  |
| Gonorynchiformes  | 1            | 1.0  | 1           | 0.5  | 1             | 0.3  |
| Hexanchiformes    | 1            | 1.0  | 1           | 0.5  | 1             | 0.3  |
| Lampriformes      | 1            | 1.0  | 1           | 0.5  | 1             | 0.3  |
| Siluriformes      | 1            | 1.0  | 1           | 0.5  | 1             | 0.3  |
| Grand Total       | 99           |      | 192         |      | 348           |      |

**Table 4**  
Dominant 10 families sampled with ORH trawl (ranked by occurrences of species in samples) in each of the three depth strata.

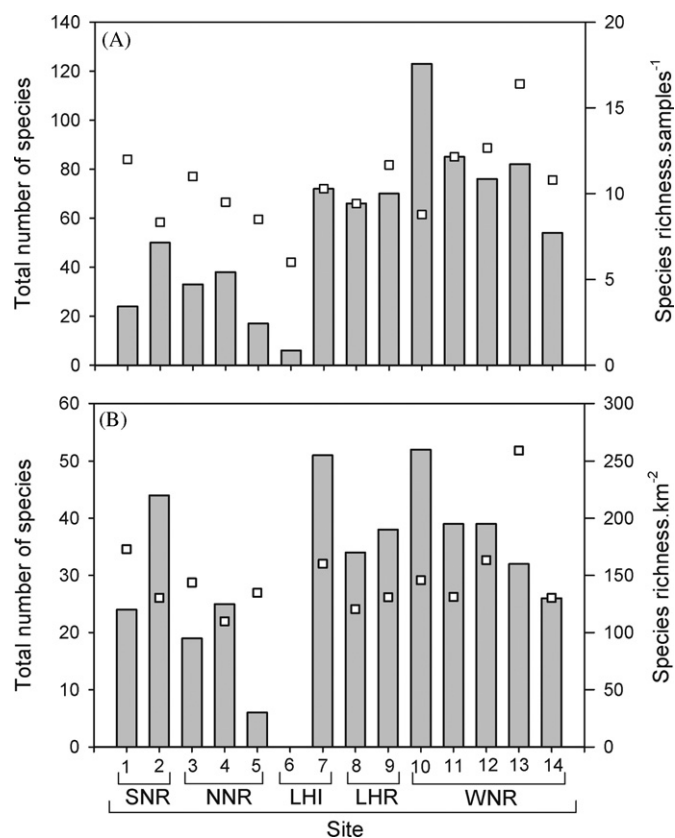
| 0–499 m                 | 500–999 m              | 1000–1500 m             | All strata              |
|-------------------------|------------------------|-------------------------|-------------------------|
| Scorpaenidae (6.5%)     | Macrouridae (24.3%)    | Macrouridae (36.9%)     | Macrouridae (24.0%)     |
| Serranidae (6.5%)       | Trachichthyidae (7.7%) | Alepocephalidae (19.0%) | Alepocephalidae (9.6%)  |
| Berycidae (5.6%)        | Centrophoridae (7.1%)  | Moridae (6.2%)          | Moridae (5.1%)          |
| Ostraciidae (5.6%)      | Moridae (6.5%)         | Scyliorhinidae (6.2%)   | Etmopteridae (4.1%)     |
| Pentacerotidae (4.8%)   | Alepocephalidae (5.9%) | Synphobranchidae (5.6%) | Scorpaenidae (3.9%)     |
| Caproidae (4.0%)        | Etmopteridae (5.9%)    | Etmopteridae (5.1%)     | Trachichthyidae (3.7%)  |
| Macroramphosidae (4.0%) | Scorpaenidae (5.9%)    | Chimaeridae (3.6%)      | Centrophoridae (3.3%)   |
| Monacanthidae (4.0%)    | Berycidae (3.6%)       | Oreosomatidae (3.6%)    | Scyliorhinidae (3.3%)   |
| Zeidae (4.0%)           | Somniosidae (3.0%)     | Somniosidae (3.1%)      | Berycidae (2.7%)        |
| Diodontidae (3.2%)      | Chimaeridae (2.4%)     | Centrophoridae (2.1%)   | Synphobranchidae (2.5%) |



**Fig. 2.** Taxonomic diversity of demersal fishes at the family and species level in relation to depth strata and regions taken by the ORH trawl during the NORFANZ voyage. The five samples taken beyond the 1500 m depth contour line are not included. WNR: Western Norfolk Ridge, SNR: Southern Norfolk Ridge, NNR: Northern Norfolk Ridge, LHI: Lord Howe Islands, LHP: Lord Howe Plateau.

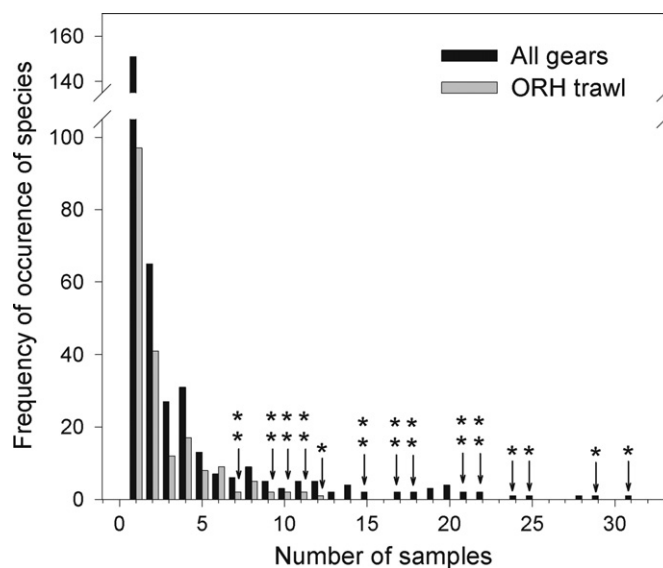


**Fig. 3.** Species accumulation curves (grey symbols) and extrapolation of species richness for additional sampling effort estimated with the Log-Series method (open symbols). Interpretation of extrapolation of species richness is limited to two times the initial sampling effort. (A) Full-wing bottom trawl (□) and orange roughy trawl (○), (B) Beam trawl (□) and Sherman sled (○) and (C) orange roughy trawl samples by regions (▽: Northern Norfolk Ridge, □: Lord Howe Rise, ◇: Lord Howe Plateau, ○: Southern Norfolk Ridge, △: Western Norfolk Ridge).



**Fig. 4.** Species richness of demersal fish catch according to site. (A) Total number of species and species richness averaged over the sampling intensity using all gear combined, and (B) total number of species and species richness adjusted for tow length using orange roughy trawl catch data only. The vertical bars are for total species richness and the squares points are for adjusted species richness. Samples with less than five species were excluded.

within regions. The WNR, which was the most heavily sampled region ( $n=25$ ), had the highest species and family diversity and its highest species richness in the deepest depth stratum (1000–1500 m). In the other regions, family richness tended to decrease with increasing depth but with no obvious co-occurring decrease in species richness.



**Fig. 5.** Frequency of occurrence of demersal fish species in samples for all five gears combined and for samples taken by orange roughy trawl (ORH) alone. \* and \*\* indicate that the frequency of occurrence of the species is equal to one and two, respectively.

Species accumulation curves were not asymptotic, indicating that many additional species would be caught with further sampling (Fig. 3). The full-wing bottom trawl and ORH trawl accumulated species in a very similar way and the two curves only started to differentiate on their extrapolated section (Fig. 3A). The beam trawl and Sherman sled also accumulated species in a similar trend, but in a steeper way than what was observed for the ORH and full-wing bottom trawl (Fig. 3B). The extrapolation of the species richness for a sampling effort equivalent to two times the realised sampling would increase the number of collected species with ORH trawl from 192 to 259 (35% increase). For the full-wing bottom trawl, the species richness would increase from 179 to 226 (26% increase), for the beam trawl from 127 to 192 (51%) and for the Sherman sled from 65 to 101 (55%). Using a single gear type (ORH trawl) to compare species richness between regions, the NNR region showed a decreased mean species richness compared to the other regions which, on the other hand, accumulated species in a similar way (Fig. 3C).

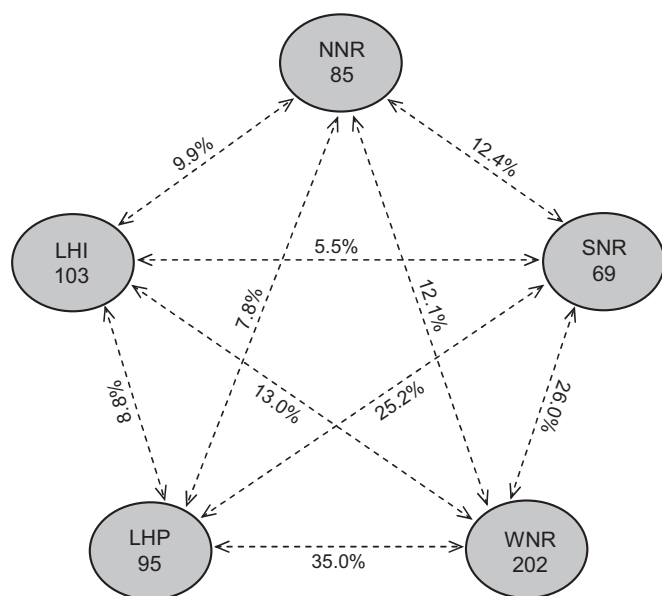
At the site spatial unit, species richness adjusted for sampling effort displayed a relatively uniform pattern (Fig. 4). Taking all gears into account (Fig. 4A), adjusted species richness ranged from 8.3 to 12.7 sp. sample<sup>-1</sup>, except for site 6 which had a lower (6.0 sp. sample<sup>-1</sup>) and site 13 which had a higher adjusted richness (16.4 sp. sample<sup>-1</sup>). Comparing sites with a single gear type (ORH trawl, Fig. 4B), adjusted species richness ranged from 110 to 173 sp. km<sup>-2</sup>, again with the exception of site 13 which had species richness of 259 sp. km<sup>-2</sup>. These values are only relative values and are not true species richness per area. They should only be used for relative comparisons.

Most species occurred only once (42% of the stations) or twice (18%) (Fig. 5). The proportions of single and double occurrences in ORH samples were higher, 48 and 21% respectively. Few species occurred commonly: most frequent was *Diastrorhynchus capensis* (23% of the stations) with *Alepocephalus antipodanus*, *Allocyttus verrucosus*, *Coelorhynchus innotabilis*, *Deania calcea*, *Mora moro*, *Alepocephalus australis*, *Gadomus aoteanus* and *Hoplostethus mediterraneus*, all caught in more than 20 samples (15%).

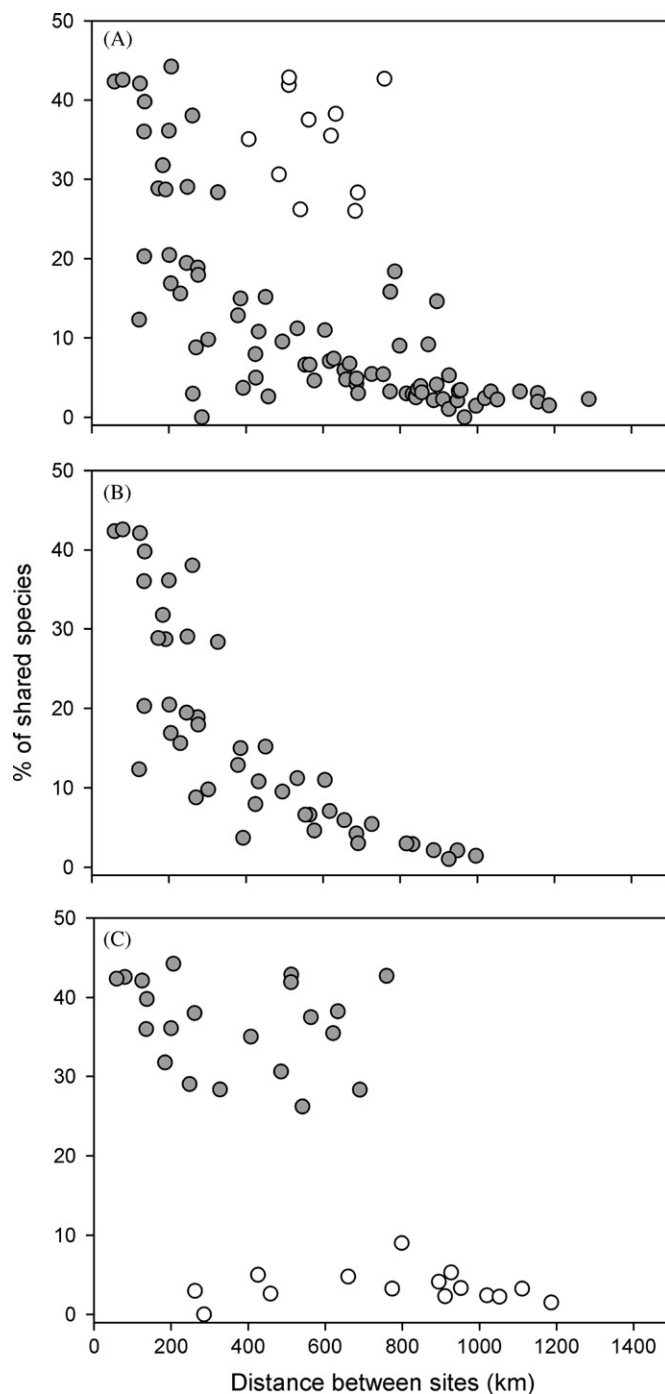
### 3.2. Distribution

Comparing the species shared between regions showed the southern regions were most similar: WNR–LHP (35% species shared), WNR–SNR (26%) and SNR–LHP (25.2%) (Fig. 6). Least similar were LHI and all other regions (5.5–9.9%), and NNR and all other regions (7.8–12.4%). Those results from LHI should be tempered by the fact that sampling in the depth stratum 1000–1500 m for this region was poor (table 1). Apart from the links between SNR, WNR and LHP, the number of shared species was generally low (< 13.0%). Some adjacent regions also had very few species in common: SNR and NNR (12.4% shared), and Lord Howe Island and LHP (8.8%). Indeed, even the two regions with most shared species (WNR–LHP) were remarkably dissimilar (65% of species not shared).

There was a significant decrease in the percentage of shared species with increasing distance between sites (regression on  $\ln(x)$ ,  $R^2=0.39$ ,  $p<0.001$ ) (Fig. 7A). Compared to the general trend in Fig. 7A, the sites from the WNR and LHP (open circles) shared a



**Fig. 6.** Fish species shared between regions. WNR: Western Norfolk Ridge, SNR: Southern Norfolk Ridge, NNR: Northern Norfolk Ridge, LHI: Lord Howe Islands, LHP: Lord Howe Plateau. The number under the region labels indicates the number of species sampled in this region.



**Fig. 7.** Percentage of shared fish species according to distance between sites. (A) All sites [1–14] combined (pale circles are a combination of sites from the Lord Howe Plateau [sites 8 and 9] and Western Norfolk Ridge [sites 10, 11, 12, 13 and 14]), (B) sites from the Norfolk Ridge only and (C) sites from the Southern/Western Norfolk Ridge and Lord Howe Rise/Plateau (pale circles are combinations of sites from the Lord Howe Islands [sites 6 and 7] with the other sites).

higher ratio of species, indicating a stronger link between these two regions. Along the Norfolk Ridge, the decrease of shared species closely followed a logarithmic trend (regression on  $\ln(x)$ ,  $R^2=0.74$ ,  $p<0.001$ ) (Fig. 7B). This is in opposition to the Southern/Western Norfolk and Lord Howe regions where the sites from the LHI shared very few species with every other site (open circles, Fig. 7C).

A large proportion of the species (78%) displayed one of the distribution patterns hypothesised to be found in the

**Table 5**  
Fish species distribution patterns (see text for definitions). For species with Restricted and Western distributions, only the 25 most abundant taxa (biomass) are presented.

| Species   | Family            | #specimens | Biomass (kg) |
|---|-------------------|------------|--------------|
| <b>NORTHERN SPECIES (8 spp.)</b>  |                   |            |              |
| <i>Pristipomoides filamentosus</i> (Cuvier & Valenciennes, 1830)        | Lutjanidae        | 3          | 25.5         |
| <i>Centroberyx</i> sp. A  | Berycidae         | 4          | 2.20         |
| <i>Scorpaena bulacephala</i> Motomura, Last & Yearsley, 2005            | Scorpaenidae      | 17         | 1.63         |
| <i>Bodianus unimaculatus</i> (Günther, 1862)                            | Labridae          | 7          | 0.45         |
| <i>Ventrifossa johnboborum</i> Iwamoto, 1982                            | Macrouridae       | 3          | 0.31         |
| <i>Amphichaetodon howensis</i> (Waite, 1903)                            | Chaetodontidae    | 2          | 0.22         |
| <i>Parapercis colemani</i> Randall & Francis 1993                       | Pinguipedidae     | 3          | 0.12         |
| <i>Plectranthias</i> sp. A  | Serranidae        | 3          | 0.03         |
| <b>SOUTHERN SPECIES (21 spp.)</b>                                       |                   |            |              |
| <i>Deania calcea</i> (Lowe, 1839)                                       | Centrophoridae    | 506        | 1465.6       |
| <i>Mora moro</i> (Risso, 1810)  | Moridae           | 594        | 740.1        |
| <i>Hoplostethus mediterraneus</i> Cuvier, 1839                          | Trachichthyidae   | 5,191      | 637.3        |
| <i>Halargyreus johnsonii</i> Günther, 1862                              | Moridae           | 214        | 151.8        |
| <i>Beryx splendens</i> Lowe, 1833                                       | Berycidae         | 214        | 99.0         |
| <i>Helicolenus barathri</i> Hector, 1875                                | Scorpaenidae      | 404        | 98.4         |
| <i>Rouleina eucla</i> Whitley, 1940                                     | Alepocephalidae   | 200        | 63.9         |
| <i>Chimaera</i> sp. NFZ1  | Chimaeridae       | 12         | 57.6         |
| <i>Hydrolagus homonycteris</i> Didier 2008                              | Chimaeridae       | 13         | 39.6         |
| <i>Etmopterus lucifer</i> Jordan & Snyder, 1902                         | Etmopteridae      | 138        | 34.7         |
| <i>Pleuroscopus pseudodorsalis</i> Barnard, 1927                        | Uranoscopidae     | 8          | 26.3         |
| <i>Rouleina guentheri</i> (Alcock, 1892)                                | Alepocephalidae   | 181        | 26.3         |
| <i>Coelorinchus acanthiger</i> Barnard, 1925                            | Macrouridae       | 69         | 18.9         |
| <i>Coelorinchus trachycarus</i> Iwamoto, McMillan & Shcherbachyev, 1999 | Macrouridae       | 43         | 8.40         |
| <i>Coelorinchus cookianus</i> McCann & McKnight, 1980                   | Macrouridae       | 171        | 5.77         |
| <i>Lepidion microcephalus</i> Cowper, 1956                              | Moridae           | 19         | 4.20         |
| <i>Nezumia namatahi</i> McCann & McKnight, 1980                         | Macrouridae       | 17         | 2.06         |
| <i>Trachonurus villosus</i> (Guenther, 1877)                            | Macrouridae       | 24         | 2.00         |
| <i>Tripterygopsis</i> sp. A   | Moridae           | 9          | 0.91         |
| <i>Coelorinchus horribilis</i> McMillan & Paulin, 1993                  | Macrouridae       | 8          | 0.45         |
| <i>Lucigadus nigromaculatus</i> (McCulloch, 1907)                       | Macrouridae       | 5          | 0.14         |
| <b>WIDESPREAD SPECIES (7 spp.)</b>                                      |                   |            |              |
| <i>Rouleina attrita</i> (Vaillant, 1888)                                | Alepocephalidae   | 2,789      | 1491.9       |
| <i>Diastobranchius capensis</i> Barnard, 1923                           | Synaphobranchidae | 698        | 496.8        |
| <i>Alepocephalus australis</i> Barnard, 1923                            | Alepocephalidae   | 855        | 431.3        |
| <i>Alloctytus verrucosus</i> (Gilchrist, 1906)                          | Oreosomatidae     | 641        | 356.4        |
| <i>Alepocephalus antipodanus</i> (Parrott, 1948)                        | Alepocephalidae   | 245        | 262.1        |
| <i>Rexea antefurcata</i> Parin, 1989                                    | Gempylidae        | 339        | 54.3         |
| <i>Etmopterus unicolor</i> (Engelhardt, 1912)                           | Etmopteridae      | 56         | 53.9         |
| <b>RESTRICTED SPECIES (191 spp.)</b>                                    |                   |            |              |
| <i>Centroscymnus cf coelelepis</i> Bocage & Capello, 1864               | Somniosidae       | 52         | 309.4        |
| <i>Macroramphosus scolopax</i> (Linnaeus, 1758)                         | Centriscidae      | 5,140      | 79.7         |
| <i>Pterygotrigla pauli</i> Hardy, 1982                                  | Triglidae         | 292        | 69.5         |
| <i>Caprodon</i> sp. C   | Serranidae        | 357        | 34.7         |
| <i>Dipturus</i> NFZ1  | Rajidae           | 4          | 26.7         |
| <i>Kathetostoma</i> sp.   | Uranoscopidae     | 16         | 25.4         |
| <i>Dasyatis thetidis</i> Waite, 1899                                    | Dasyatidae        | 2          | 25.0         |
| <i>Centroberyx</i> sp. B  | Berycidae         | 21         | 24.2         |
| <i>Nemadactylus</i> sp.   | Cheilodactylidae  | 24         | 20.5         |
| <i>Centroberyx affinis</i> (Günther, 1859)                              | Berycidae         | 15         | 20.3         |
| <i>Lepidion inosimae</i> (Günther, 1887)                                | Moridae           | 9          | 17.5         |
| <i>Epinephelus ergastularius</i> Whitley, 1930                          | Serranidae        | 1          | 16.0         |
| <i>Lepidion schmidtii</i> Svetovidov, 1936                              | Moridae           | 3          | 15.7         |
| <i>Coelorinchus kermadecus</i> Jordan & Starks, 1904                    | Macrouridae       | 15         | 12.8         |
| <i>Narcetes lloydi</i> Fowler, 1934                                     | Alepocephalidae   | 5          | 12.7         |
| <i>Polyprion americanus</i> (Bloch & Schneider, 1801)                   | Polyprionidae     | 1          | 12.2         |
| <i>Prionurus maculatus</i> Ogilby, 1887                                 | Acanthuridae      | 3          | 11.8         |
| <i>Bathyraja</i> sp.  | Arhynchobatidae   | 1          | 10.0         |
| <i>Callanthias australis</i> Ogilby, 1899                               | Callanthiidae     | 47         | 9.10         |
| <i>Apristurus cf herklotsi</i> (Fowler, 1934)                           | Scyliorhinidae    | 38         | 9.00         |
| <i>Etmopterus baxteri</i> Garrick, 1957                                 | Etmopteridae      | 3          | 8.30         |
| <i>Cephaloscyllium</i> sp. NFZ1   | Scyliorhinidae    | 1          | 8.20         |
| <i>Squalus</i> sp. cf <i>griffini</i>                                   | Squalidae         | 1          | 7.50         |
| <i>Gollum cf attenuatus</i> (Garrick, 1954)                             | Pseudotriakidae   | 3          | 6.80         |
| <i>Chilomycterus reticulatus</i> (Linnaeus, 1758)                       | Diodontidae       | 2          | 6.50         |
| <i>Thamnaconus cf modestoides</i> (Barnard, 1927)                       | Monacanthidae     | 8          | 6.40         |
| <i>Genypterus blacodes</i> (Bloch & Schneider, 1801)                    | Ophidiidae        | 1          | 6.30         |
| <i>Lepidoperca inornata</i> Regan, 1914                                 | Serranidae        | 39         | 6.00         |
| <i>Chimaera</i> sp. NFZ2  | Chimaeridae       | 3          | 6.00         |
| <b>NORFOLK SPECIES (7 spp.)</b>   |                   |            |              |
| <i>Beryx decadactylus</i> Cuvier & Valenciennes, 1829                   | Berycidae         | 59         | 59.1         |
| <i>Apristurus sinensis</i> Chu & Hu, 1981                               | Scyliorhinidae    | 88         | 42.8         |



Table 5 (continued)

| Species   | Family           | #specimens | Biomass (kg) |
|---|------------------|------------|--------------|
| <i>Squalus griffini</i> Phillipps, 1931                     | Squalidae        | 14         | 23.2         |
| <i>Paraulopus okamurai</i> Sato & Nakabo, 2002              | Paraulopidae     | 40         | 10.3         |
| <i>Nezumia coheni</i> Iwamoto & Merrett, 1997               | Macrouridae      | 35         | 6.38         |
| <i>Notopogon xenosoma</i> Regan, 1914                       | Macroramphosidae | 14         | 1.11         |
| <i>Physiculus cf luminosa</i> Paulin, 1983                  | Moridae          | 27         | 0.67         |
| <b>LORD HOWE SPECIES (1 sp.)</b>                            |                  |            |              |
| <i>Euclichthys</i> sp. NFZ1                                 | Euclichthyidae   | 2          | 0.20         |
| <b>WESTERN SPECIES (46 spp.)</b>                            |                  |            |              |
| <i>Allomycterus pilatus</i> Whitley, 1931                   | Diodontidae      | 710        | 521.5        |
| <i>Centroscyrnus</i> sp. NFZ1. cf <i>owstoni</i>            | Somniosidae      | 74         | 240.1        |
| <i>Cetonus globiceps</i> (Vaillant in Filhol, 1884)         | Macrouridae      | 1,164      | 224.5        |
| <i>Coelorinchus mycterismus</i> McMillan & Paulin, 1993     | Macrouridae      | 712        | 147.3        |
| <i>Hoplostethus atlanticus</i> Collett, 1889                | Trachichthyidae  | 149        | 116.2        |
| <i>Dalatis licha</i> (Bonnaterre, 1788)                     | Dalatiidae       | 9          | 52.9         |
| <i>Centrophorus squamosus</i> (Bonnaterre, 1788)            | Centrophoridae   | 5          | 45.8         |
| <i>Coryphaenoides serrulatus</i> Günther, 1878              | Macrouridae      | 204        | 44.9         |
| <i>Coryphaenoides rudis</i> Barnard, 1925                   | Macrouridae      | 7          | 41.2         |
| <i>Rhinochimaera pacifica</i> (Mitsukuri, 1895)             | Rhinochimaeridae | 9          | 36.9         |
| <i>Centroscyrnus crepidater</i> (Bocage & Capello, 1864)    | Somniosidae      | 63         | 35.2         |
| <i>Coelorinchus innotabilis</i> McCulloch, 1907             | Macrouridae      | 561        | 27.1         |
| <i>Epigonus telescopus</i> (Risso, 1810)                    | Epigonidae       | 12         | 23.4         |
| <i>Centroscyrnus owstoni</i> Garman, 1906                   | Somniosidae      | 4          | 23.2         |
| <i>Bathypterois longifilis</i> Günther, 1878                | Ipnopidae        | 103        | 21.7         |
| <i>Trachyscorpia</i> sp.                                    | Scorpaenidae     | 44         | 18.3         |
| <i>Torpedo macneilli</i> (Whitley, 1932)                    | Torpedinidae     | 2          | 16.1         |
| <i>Psychrolutes</i> sp. B                                   | Psychrolutidae   | 6          | 12.8         |
| <i>Mustelus</i> sp. NFZ1                                    | Triakidae        | 4          | 11.7         |
| <i>Metavelifer multiradiatus</i> Regan, 1907                | Veliferidae      | 23         | 10.4         |
| <i>Trachyscorpia capensis</i> (Gilchrist & von Bonde, 1924) | Scorpaenidae     | 10         | 9.90         |
| <i>Chaunax cf flammeus</i> Le Danois, 1979                  | Chaunacidae      | 65         | 9.03         |
| <i>Polyplacarus tyleri</i> Fujii & Uyeno, 1979              | Ostraciidae      | 41         | 8.20         |
| <i>Talismania longifilis</i> (Brauer, 1902)                 | Alepocephalidae  | 25         | 7.10         |
| <i>Gonorynchus greyi</i> (Richardson, 1845)                 | Gonorynchidae    | 19         | 5.00         |
| <i>Notacanthus sexspinis</i> Richardson, 1846               | Notacanthidae    | 22         | 4.55         |

Table 6

Numbers of fish species restricted to a single site.

| Site  | # of species | %     |
|-------|--------------|-------|
| 1     | 5            | 2.9   |
| 2     | 4            | 2.3   |
| 3     | 12           | 7.0   |
| 4     | 17           | 9.9   |
| 5     | 9            | 5.3   |
| 6     | 7            | 4.1   |
| 7     | 48           | 28.1  |
| 8     | 10           | 5.8   |
| 9     | 7            | 4.1   |
| 10    | 28           | 16.4  |
| 11    | 9            | 5.3   |
| 12    | 4            | 2.3   |
| 13    | 10           | 5.8   |
| 14    | 1            | 0.6   |
| Total | 171          | 100.0 |

area and described above (Table 5). The most frequent distribution pattern was a restricted distribution (191 spp.), followed by species with western (46 spp.), southern (21 spp.), widespread (8 spp.), northern (8 spp.), Norfolk (6 spp.) and Lord Howe distributions (1 sp.).

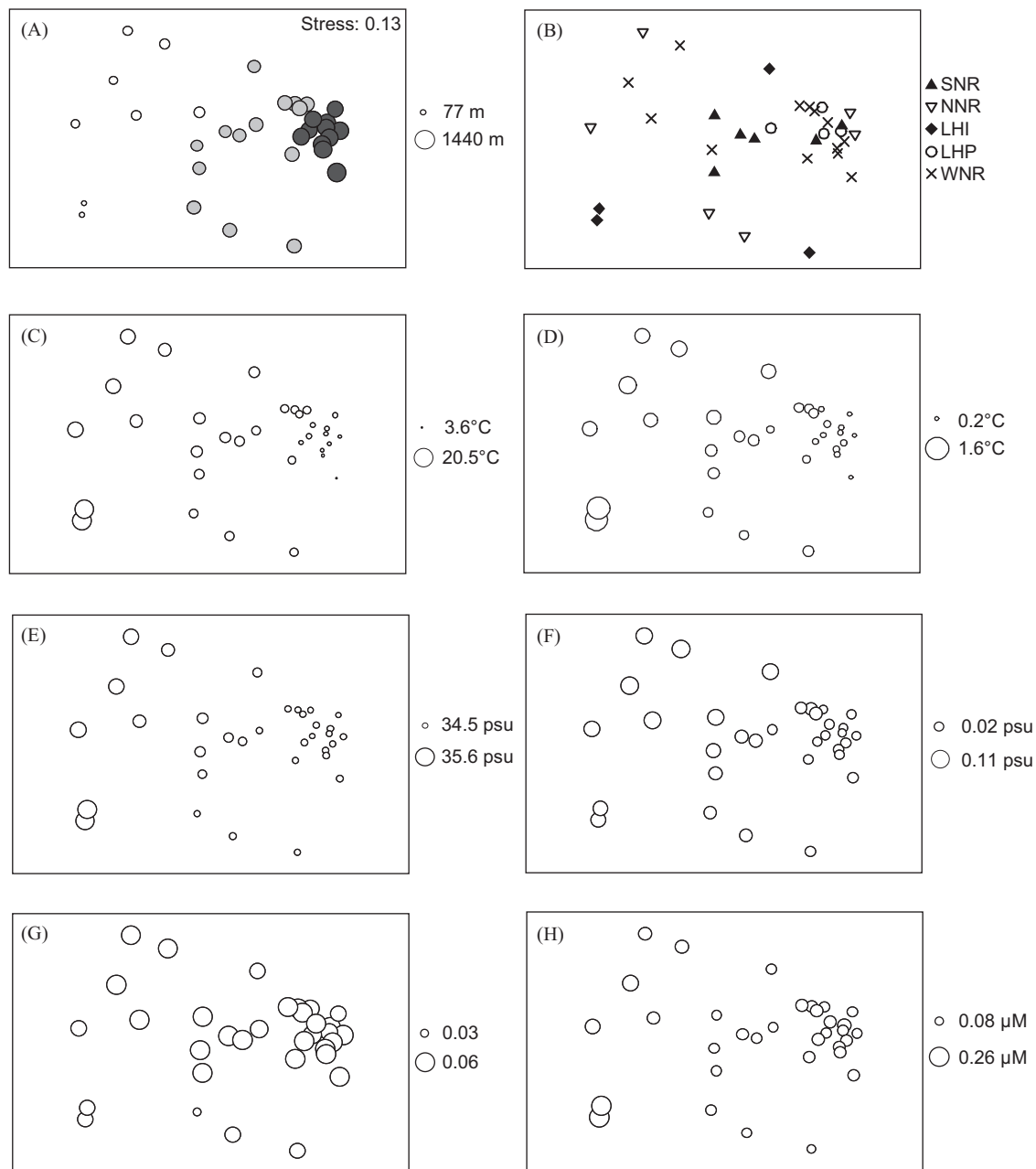
Those species which were recorded in only one site were not uniformly distributed among sites (Table 6). Sites 7 and 10 cumulated 44.5% of the species with restricted distributions; these two sites were also the shallowest sampled (minimum depths 48 and 116 m respectively). Although it is impossible to separate the

effect of sampling effort from true restricted distribution, the large values recorded at these two sites are notable.

### 3.3. Multivariate assemblage structure

In terms of taxonomic resemblance, there was a clear and significant gradient of change in the structure of fish assemblages with increases in depth (Fig. 8A). In contrast, there were no clear patterns of differences in the fish assemblages among different locations (Fig. 8B). A similar pattern was observed using a Bray-Curtis similarity approach.

This depth related structure in the dataset was confirmed by the permutational multivariate analysis of variance (PERMANOVA, Table 7). Samples taken in the three depth strata (0–499, 500–999 and 1000–1500 m) were significantly different from each other. The variation in the data cloud explained by the region factor was also highly significant. Pair-wise tests between regions showed the following patterns (the Monte Carlo simulations should be used here for reference to significance levels): (1) in terms of taxonomic structure, the assemblage of the WNR was significantly different from the LHI and NNR which in turn was different from the LHP ( $p(\text{MC}) < 0.05$ ), (2) the SNR, WNR and LHP fish fauna had strong taxonomic affinities with each other ( $p(\text{MC}) > 0.18$ ), (3) all the other pair-wise comparisons were at the limit of rejection at a 5–10% level, indicating that the taxonomic similarity between those regions might well be low. The factor site was not significant, and nor was its interaction with depth. However the interaction between regions and depth strata was significant. This interaction was clearly visible on the nMDS plot (Fig. 8B) where samples from deeper strata were more tightly clustered than shallower strata. Thus, across regions, the



**Fig. 8.** Non-metric MDS plot of orange roughy trawl catch data based on taxonomic dissimilarities  $\Gamma^*$ . Superimposed on the plots are (A) depth (open symbols: 0–499 m, light grey: 500–999 m, dark grey: 1000–1500 m), (B) symbols corresponding to location (as shown in the legends, WNR: Western Norfolk Ridge, SNR: Southern Norfolk Ridge, NNR: Northern Norfolk Ridge, LHI: Lord Howe Islands, LHP: Lord Howe Plateau), and circles representing the extent of, (C) temperature, (D) temperature standard deviation, (E) salinity, (F) salinity standard deviation, (G) export production and (H)  $O_2$  standard deviation.

deep fish fauna has stronger taxonomic affinities than shallower faunas.

The combination of abiotic variables that best explained the structure of taxonomic dissimilarities between ORH trawl samples was temperature, temperature standard deviation, salinity, depth, export production, salinity standard deviation, and  $O_2$  standard deviation (Table 8). The spearman correlation coefficient between fish catch and selected variables was high ( $\rho=0.868$ ), reflecting a good match between datasets. The structure in the fish assemblage was strongly dependant on variables having a clear gradient related to depth. It is illustrated in Fig. 8 where the values of those selected variables were superimposed on the ordination plot (plots c to h). Except for export production, all variables follow the depth related gradient. It would have been meaningful to search for those variables best explaining assemblage patterns by depth strata

(0–499, 500–999 and 1000–1500 m) but the amount of replication was insufficient to conduct this analysis.

## 4. Discussion

### 4.1. Taxonomic diversity

With an estimated 348 demersal fish species in 99 families from 135 samples (all gears combined), the Lord Howe Rise and Norfolk Ridge can be described as an area of high fish species richness. In addition, accumulation curves are very steep and truncated, showing that, despite the success of the NORFANZ voyage, sampling of the area is still less than comprehensive. This level of diversity is comparable to the Western Australian slope covering

**Table 7**

Results of the PERMANOVA, showing differences between sites, regions and depth strata. Similarities are based on taxonomic (dis)similarities  $\Gamma^+$  calculated from orange roughy catch samples, using 9999 permutations under a reduced model and type III sum of the squares. Depth strata are 0–499 m, 500–999 m and 1000–1500 m. Regions are the *a priori* defined regions of the NORFANZ voyage (WNR: Western Norfolk Ridge, SNR: Southern Norfolk Ridge, NNR: Northern Norfolk Ridge, LHI: Lord Howe Islands, LHP: Lord Howe Plateau). Monte Carlo tests were done on pair-wise comparisons. Bold indicates results significant at a 5% level.

| Source                       | df | SS     | MS     | Pseudo-F | P (perm)      | Unique perms |
|------------------------------|----|--------|--------|----------|---------------|--------------|
| Region                       | 4  | 7848.6 | 1962.1 | 2.7802   | <b>0.0007</b> | 9917         |
| Depth strata                 | 2  | 14716  | 7358.0 | 9.9726   | <b>0.0001</b> | 9942         |
| Site (region)                | 8  | 5493.8 | 686.73 | 0.8544   | 0.6633        | 9932         |
| Depth strata x Region        | 6  | 9226.6 | 1537.8 | 2.1481   | <b>0.0053</b> | 9913         |
| Depth strata x Site (region) | 9  | 6054.8 | 672.75 | 0.8371   | 0.6669        | 9948         |
| Res                          | 3  | 2411   | 803.67 |          |               |              |
| Total                        | 32 | 55965  |        |          |               |              |

PAIR-WISE TESTS FOR DIFFERENCES BETWEEN REGIONS

| Groups    | t       | P (perm) | Unique perms | P (MC)        | Average dissimilarity |
|-----------|---------|----------|--------------|---------------|-----------------------|
| NNR - WNR | 1.8362  | 0.0105   | 3183         | <b>0.0174</b> | 61.3                  |
| LHI - WNR | 2.0615  | 0.0001   | 60           | <b>0.0223</b> | 68.8                  |
| NNR - LHP | 2.0241  | 0.0505   | 60           | <b>0.0382</b> | 60.4                  |
| LHI - LHP | 2.0941  | 0.0001   | 3            | 0.0659        | 67.2                  |
| NNR - LHI | 1.917   | 0.0801   | 24           | 0.0784        | 69.7                  |
| SNR - LHI | 2.2384  | 0.0001   | 3            | 0.0812        | 65.9                  |
| SNR - NNR | 1.6093  | 0.1022   | 60           | 0.1044        | 58.9                  |
| SNR - LHP | 1.5125  | 0.0001   | 6            | 0.1775        | 45.7                  |
| SNR - WNR | 0.77843 | 0.7605   | 210          | 0.6599        | 49.5                  |
| LHP - WNR | 0.56645 | 0.9325   | 210          | 0.8822        | 43.0                  |

PAIR-WISE TESTS FOR DIFFERENCES BETWEEN DEPTH STRATA

| Groups                   | t      | P (perm) | Unique perms | P (MC)        | Average dissimilarity |
|--------------------------|--------|----------|--------------|---------------|-----------------------|
| 0–499 m vs 500–999 m     | 2.2223 | 0.0739   | 9143         | <b>0.0465</b> | 67.7                  |
| 0–499 m vs 1000–1500 m   | 3.166  | 0.0112   | 9949         | 0.121         | 74.5                  |
| 500–999 m vs 1000–1500 m | 3.2414 | 0.003    | 9951         | <b>0.0005</b> | 52.2                  |

**Table 8**

Results of the BIO-ENV/BV-STEP analysis linking orange roughy trawl taxonomic dissimilarities between samples to Euclidean distances between abiotic variables. The best matches for the combination of 1 to 7 abiotic variables are shown. The overall optimum (highest  $\rho$ ) was obtained after combining 7 variables.

| # of variables | Corr. ( $\rho$ ) | Variables   |
|----------------|------------------|---|
| 1              | 0.824            | Temperature   |
| 1              | 0.764            | Temperature SD  |
| 1              | 0.761            | Salinity  |
| 1              | 0.706            | Depth   |
| 2              | 0.829            | Temperature, Temperature SD   |
| 3              | 0.837            | Temperature, Temperature SD, Salinity   |
| 4              | 0.839            | Temperature, Temperature SD, Salinity, Depth  |
| 5              | 0.861            | Temperature, Temperature SD, Salinity, Depth, Export production                                 |
| 6              | 0.866            | Temperature, Temperature SD, Salinity, Depth, Export production, Salinity SD                    |
| 7              | 0.868            | Temperature, Temperature SD, Salinity, Depth, Export production, Salinity SD, O <sub>2</sub> SD |

the same range of latitude ( $\sim 10^\circ$ ) where 388 species in 109 families from 151 samples were caught at depths ranging from 200 to 1500 m (Williams et al., 2001). High diversity in that area was attributed to overlapping temperate and subtropical faunas. In contrast, 1163 hauls along the US Pacific continental slope (200–1200 m, 33–47°N), collected only 161 species in 68 families (Tolimieri, 2007), although in this area, isolating true geographical effect from the effect of historical intensive fishing activity is difficult.

Novelty of fishes was also high. More than a third of species were initially identifiable only to genus by a large team of taxonomic specialists who discovered key morphological

differences from known related taxa. Uncertain identifications mostly resulted from poor taxonomic knowledge of the fauna and inadequate diagnostic characters in closely related species. Since the survey, we now estimate that about 25% of the fishes collected are potentially new species. Nine examples (Zoarcidae, Trachichthyidae, Scorpaenidae, Cheilodactylidae, Labridae, Pinguididae and Chiasmodontidae) were given by Clark and Roberts (2008: 32–33), four most recently published (e.g. Arhynchobatidae: Séret and Last, 2009; Macrouridae: McMillan and Iwamoto, 2009; Scorpaenidae: Motomura and Last, 2009) and with others in prep (e.g. pers. comms. K. Nakaya and P. Last).

The most diverse groups in terms of species richness were the Gadiformes and Perciformes, but the latter had greater generic and familial diversity. The Perciformes are the most diversified of all fish orders (Nelson, 2006), while the Gadiformes were represented in deep water primarily by the highly diverse grenadiers (Macrouridae), and to a lesser extent Moridae. However, a depth effect was also evident, with Perciformes being better represented at shallow depths (0–499 m) and Gadiformes most abundant deeper (500–999 m and 1000–1499 m). This phylogenetic separation has been widely recognised in tropical and temperate seas, and reflects the divergent specialisations in the shallow-water evolution of spiny-rayed fishes (superorder Acanthopterygii) and the deep-water radiations of more primitive, soft-bodied teleosts (superorder Paracanthopterygii) (Helfman et al., 1997; Merrett and Haedrich, 1997; Weitzman, 1997).

#### 4.2. Drivers of distribution patterns and diversity

Depth was the most important variable identified in determining the assemblage composition for demersal fish species (expressed here in terms of taxonomic resemblance), which is consistent with observations on the distribution of fishes more

broadly (Moranta et al., 1998; Colloca et al., 2003; Bergstad et al., 2008) and in the Australasian region (Koslow et al., 1994; Francis et al., 2002). Depth is a dominant factor in seamount classification that incorporates both physical and biological attributes (Rowden et al., 2005). The effect of geographical location was less clear, although north-south differences appeared to be more important than longitudinal variation between the Lord Howe Rise and Norfolk Ridge. This is consistent with the pattern of water masses and oceanic currents in the area. The Tasman Front divides the study area into the warmer Coral Sea to the north and the cooler Tasman Sea to the south and marks the path of components of the East Australian Current. Antarctic Intermediate Water at depths of 600–700 m is represented by different ‘arms’ in the Tasman and Coral Seas that oppose each other along the path of the Tasman Front. This effectively separates the region into north (NNR and LHI sites) and south (west and south Norfolk Ridge sites), with some sites (LHP and the Wanganella Bank overlain by the Tasman Front (Ridgeway and Dunn, 2003)). Depth tended to attenuate the effect of these drivers, probably because the environment is less variable and less affected by surface-related heterogeneity in temperature, light, productivity, weather patterns and oceanographic waves or currents.

In addition to the hydrography of the area, high levels of fish diversity discovered in the Lord Howe Rise and Norfolk Ridge areas relative to other areas in the world can be attributed to a combination of several factors some of which are unique to the Tasman Sea-Coral Sea area.

A first factor is the unusually high habitat complexity and geomorphological diversity of the area. The Lord Howe Rise and Norfolk Ridge are very large oceanic features comprising chains of seamounts, banks, ridges and escarpments arising from abyssal depths. These large features form a great variety of complex habitats. Predominant substratum comprises volcanic rock, which in more sheltered areas is overlain by shell gravel and fine biogenic sediment. Oceanic circulation forms currents that become strong across elevated rocky structures. Such conditions support rich invertebrates communities and large schools of demersal species (Koslow, 1997; Clark et al., in press). In the NORFANZ area, a rich diversity of deep-sea habitats is associated with a rich diversity of marine life, including fishes (Clark and Roberts, 2008).

Second, palaeohistory has contributed to diversity through isolation, vicariant speciation and dispersal. Large regional features have existed for over 70 million years, since the break up of Gondwana and the opening of the Tasman Sea (Stevens, 1980; Eade, 1988). Their structures have had a dynamic history of volcanism, uplift, exposure, erosion, and submergence in the order of 200–400 m vertically (Stevens, 1980). Geologically active areas of the world, both in the sea and on land, are noted as centres of speciation and the evolution of new life. Conversely, the longevity of the Lord Howe Rise and Norfolk Ridge enable old Gondwanic communities of invertebrates and also fishes (which are not as easily dated and recognised) to survive to the present day in refuge communities (Richer De Forges, 1990).

Finally, biological highways have enabled particular processes of dispersal and speciation to occur through connectivity of suitable habitat. Long oceanic ridges and seamount chains provide pathways for biological dispersal, especially in fishes (Last and Yearsley, 2002). The species-rich, tropical Indo-Pacific to the north is connected via these features to the temperate Southern Ocean region, including the islands of New Zealand. Both northern and southern fish faunas have, over time, been able to radiate species along these features. Hence, the Lord Howe Rise and Norfolk Ridge are believed to have acted as biological highways for fishes, over a long period of geological time (Last and Séret, 1999), and also over shorter time spans for actively migrating fish species (Roberts, 1993; Roberts and Grande, 1999; Clark and Roberts, 2008). There is

growing taxonomic evidence to suggest that parts of the Lord Howe Rise and Norfolk Ridge support endemic species unique to these features (see below).

#### 4.3. Biogeographic patterns

This study detected three primary biogeographic patterns in the distribution of fishes within the northern Tasman Sea/ southern Coral Sea and adjacent regions. First, the fish fauna on the Lord Howe Rise, near Lord Howe Island and further north (site 6, around Middleton Reef), are distinct from the rest of the survey area and exhibit eastern Australian and northern (Coral Sea) affinities. This is true for the depth zone 50–1000 m where adequate sampling was achieved. Deeper, sites could not be adequately sampled due to rough bottoms. Second, the NNR demersal fish fauna was also clearly distinct from the other regions and had affinities with New Caledonia. Third, SNR, NNR, WNR and LHP have affinities with the northern New Zealand region. Patterns of fish distribution were dominated by a large number of species with a marked “southern” or “western” distribution, as also noted by Clark and Roberts (2008). Many of these predominantly deepwater species have a strong link with the northern New Zealand fauna and some also occur in Australian waters. Southern distributions largely comprise deepwater species from the two strata 500–999 m and 1000–1499 m, a few extending deeper, but none shallower. Most southern species also occur widely outside the NORFANZ survey area and are documented here at their northern limits of distribution. This limit is demarcated by a band at latitude 30–32°S, which is the approximate position of the Tasman Front (Ridgeway and Dunn, 2003).

Comparison of the fish fauna between New Zealand and New Caledonia shows that over 240 species are common to both regions, of which 22% are deep-water demersal or benthic (Roberts, 1993). *Gonorynchus forsteri* appears to migrate over 700 nm from New Zealand along the Norfolk Ridge to spawn in New Caledonian waters (Roberts and Grande, 1999). These examples suggest that the Norfolk Ridge could act like a “biological highway” connecting New Zealand and New Caledonia (Roberts, 1993; Clark and Roberts, 2008). However, several of the species exclusively found on this ridge during this study are also known outside the area, so are not Norfolk Ridge endemics. For example: *Nezumia coheni* (1013–1345 m depth), known from the Norfolk and Loyalty Ridges (south of New Caledonia), off the Kermadec Islands, and mid-slope grounds off New South Wales, Australia (Iwamoto and Graham, 2001); *Apristurus sinensis*, also known from the continental slope off southeast and west Australia (Last and Stevens, 2009); *Beryx decadactylus* and *Notopogon xenosoma* recorded further north in New Caledonian waters along Norfolk Ridge and/or Loyalty Ridge (Grandperrin et al., 1997a) and off New Zealand (Roberts et al., 2009).

The dominant component (taxonomic diversity and abundance) of the global deep sea demersal ichthyofauna is the family Macrouridae (grenadiers, rattails) (Merrett and Haedrich, 1997), which can be useful indicators of diversity, relationships and distributions in the southwest Pacific. During the NORFANZ voyage, 51 macrourid species were identified by specialist taxonomists P.J. McMillan and T. Iwamoto, based on 4334 specimens sampled at 322–1934 m bottom depth (e.g. Clark and Roberts, 2008). Complimentary collections (63 spp., 2055 specimens, 395–2105 m) from the adjacent New Caledonia area to the north (taken mostly during HALIPRO 2 by FRV *Tangaroa* with orange roughly bottom trawl) were reported by Iwamoto and Merrett (1997) and Merrett and Iwamoto (2000).

Out of a combined total of 95 macrourid species found in both areas, 30.5% were captured in both survey areas. This is a relatively high level of similarity based on the results of the NORFANZ survey



(maximum similarity of 35% was observed between WNR and LHP, fig.6) and supports one of the initial results of the HALIPRO 2 voyage (Grandperrin et al., 1997a) and other studies (Roberts, 1993) comparing the demersal ichthyofaunas of southern New Caledonia and New Zealand.

Based on 2055 specimens, Merrett and Iwamoto (2000) found dissimilarity increased with distance from New Caledonia and identified four biogeographic components to the macrourid fauna (63 spp.): widespread global, 32.3%; southern temperate, 27.4%; northern tropical, 25.8%; and endemic, 14.5%.

Comparing the two data sets combined, c. 15% of macrourids (14 spp., 348–1470 m depth range) exhibited a limited Norfolk Ridge (NR) distribution pattern. Half of these were endemic to New Caledonia and NNR and half to WNR and SNR. Four rattail species were distributed across the subtropical convergence area located at the mid-Norfolk Ridge; 3 were restricted to the north and 7 to the south of this convergence zone. Thus, indicating that this biogeographic barrier influenced some, but not all, Norfolk Ridge macrourid species, to at least 1500 m depth. Very similar NR distributions have been found in other unrelated deep-sea fish groups; for example, catsharks *Apristurus* spp., 700–1934 m (Nakaya pers. comm.) and arhynchobatin skates *Notoraja* spp., 800–1400 m (Last and Yearsley, 2002; Séret and Last, 2009) and should be examined in other taxa to test for similar generalised biogeographic patterns.

Besides broad biogeographic patterns linked to the NORFANZ area, three other within area patterns were observed. The most obvious one was that the fishes on the SNR, WNR and LHP have a higher proportion of shared species compared to the other regions which might indicate a privileged exchange between these regions. These stations form a trans-Tasman link for the species, which occur widely in slope waters of New Zealand and south-eastern Australia (including Cascade Plateau and South Tasman Rise) (Last and Stevens, 2009). For example, *Hydrolagus homonycteris* was caught at 1051–1345 m depth on the NNR, WNR and LHP. *Hoplostethus mediterraneus* has a wide depth distribution between 435 and 1340 m. The distribution extends from the New Zealand shelf to the SNR, WNR and southern LHP. Outside the survey area it is distributed widely in New Zealand and southeast Australian outer shelf and slope waters, and extends across the Indian and Atlantic oceans to the western Mediterranean Sea (Smith & Roberts, pers. com.). *Hoplostethus atlanticus* shows a similar distribution to *Hoplostethus mediterraneus* regionally and globally. It occurs on the WNR and LHP and is widely distributed throughout southern Australian and New Zealand but is not recorded from New Caledonia (Rivaton et al., 1989; Grandperrin et al., 1997a).

This study also confirmed that at least 14 species have a Norfolk Ridge (NNR, SNR, WNR) wide distribution indicating that this ridge could have provided dissemination of species between New Caledonia and New Zealand. NORFANZ species which have restricted Norfolk Ridge distributions are: catshark *Apristurus* sp. E (also found on NNR off New Caledonia, pers. comm. K. Nakaya); *Notoraja sapphira* Séret and Last, 2009 (as OTU *Notoraja* sp. D); *Coelorinchus obscuratus* McMillan and Iwamoto, 2009 (as *Coelorinchus* sp. NFZ3) and *Coelorinchus osipullus* McMillan and Iwamoto, 2009 (as *Coelorinchus* sp. 1). At least four species in four families not collected during the voyage have Norfolk Ridge distributions, providing independent support for this distribution: *Gollum attenuatus*, *Myroconger prolixus*, *Coelorinchus cylindricus* and *Hoplostethus* sp. nov. (Castle and Béarez, 1995; Iwamoto and Merrett, 1997; Compagno and Niem, 1998a; Compagno and Niem, 1998b).

Finally, another notable feature of fish biodiversity was that a high percentage of species occurred in only one or few samples in the NORFANZ study area leading to an apparently high endemism. Based on the number of restricted species that are unknown outside the survey area, it is possible that individual seamounts

or slope sites surveyed support their own unique suite of species, such as found on some parts of the Norfolk Ridge and Loyalty Island Ridge in New Caledonian waters (Roberts and Paulin, 1997; Richer De Forges et al., 2000). However, it should be stressed that on present knowledge true endemism at the level of sub-areas (ridges or individual seamounts) cannot be separated from the effect of a low sampling effort. Sampling adjacent non-seamount habitat is also required to evaluate true levels of seamount faunal endemism (e.g., McClain, 2007; O'Hara, 2007). Proof of this is that a portion of those species ( $n=60$ ) is known outside the survey area, including species that are widely recognised and have well recorded and globally extensive distributions (e.g. *Harriotta raleighana*, *Genypterus blacodes*, *Fistularia commersoni*, *Pterois volitans*, *Zeus faber* and *Polyprion americanus*). Either this group is comprised of species that are surprisingly rare within the survey area, or the fishes have not been adequately sampled to reflect their real occurrence.

#### 4.4. Management implications

The survey was not designed to assess commercial fish species abundances for fisheries purposes. However, it opportunistically extended knowledge of the distributions of species such as *Beryx splendens* (alfonsino), *Mora moro* (ribaldo), *Hoplostethus atlanticus* (orange roughy) and *Epigonus* spp. (cardinalfish), which are commercially fished in the EEZ's of New Zealand and Australia. Aggregations of major commercial species were not encountered, although the survey was not synchronous with the spawning period of the primary commercial species, *Hoplostethus atlanticus* (Pankhurst, 1998). A single large catch of a secondary commercial species, *Pseudopentaceros richardsoni*, was taken at a single station. Generally, catches of commercial species were low.

The survey also provided a full and quality assured catch composition from the ORH trawl, which gives a detailed indication of the likely bycatch from deepwater fisheries in the region. Compositions may vary if fishers target specific concentrations, but species recorded in the survey will be caught in the commercial fishery if fishers trawl more generally on seamounts. The relative abundance of *Deania calcea* (shovelnose dogfish), being the most abundant species by weight in the catches, may have management implications, as elasmobranchs have low fecundity, are usually long-lived, and hence vulnerable to overfishing as a bycatch of targeted commercial species (e.g. Graham et al., 2001). Fishing on seamounts, where such species are common, may need regulations limiting bycatch in order to reduce this risk.

A major use of NORFANZ data and research outputs relate to assessing conservation values of the ridges. This includes identifying rare or unusual components of the fauna, micro-endemics, those with low productivity vulnerable to human disturbance (fishing, mining), or defining areas which contain uniquely representative fauna. The data were used in a study of the Norfolk Seamounts region in the context of developing Australia's National Representative System of Marine Protected Areas (NRSMPA, Williams et al., 2006a). They found that the Norfolk Seamounts region possesses biodiversity values worthy of protection, and would contribute to the representativeness and comprehensiveness of the NRSMPA. Williams et al. (2006a) suggested that this could be part of a larger Tasman Sea deep-sea biodiversity conservation initiative, with the NORFANZ data providing an important baseline.

The results of this study indicate that northern and southern faunas differ, and there are smaller compositional differences between the ridge systems and individual sites. Management strategies need to address issues of scale, as well as geographical location, so any conservation measures need to factor in north-



south and depth related aspects and also small seamounts where there are indications of highly localised distributions or micro-endemic species. The NORFANZ project provides an important overview of the fauna and its biogeographic structure enabling more informed marine planning decisions to be taken.

## 5. Conclusions

The NORFANZ survey revealed diversity in the Lord Howe Rise and Norfolk Ridge fish faunas that appears unusually high in global terms. It considerably extended knowledge of the ichthyofauna of this poorly known area of the south-west Pacific, and estimated that 20% of the fishes sampled could either be new species or new records for the region. The variety of gear types deployed gave a much greater appreciation of faunal diversity than would have been gained from using just a single type of gear. The survey also showed clearly that further sampling will greatly increase the estimate and understanding of species richness of fishes in this area. Depth was a major variable in explaining taxonomic structure of fish assemblages and accounted for most of the variability in the dataset. Interestingly, the interaction between regions and depth was significant; across regions, deep-water fish faunas have stronger taxonomic affinities than shallower faunas. Although less pronounced, there were spatial differences that pointed towards distinct faunas between the southern and northern parts of the area, and complex regional biogeographic affinities. Overall, the percentage of shared species between locations was surprisingly low, despite an apparent privileged zone of exchange in the southern part of the area (LHP, WNR and SNR). Because sampling effort was low, given the relative size and scant prior knowledge of the region's ichthyofauna, we are presently unable to draw firm conclusions on levels of regional and local endemism.

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## Appendix 1. Supplementary data

Supplementary material related to this article can be found online at doi: 10.1016/j.dsr2.2010.10.049. For demersal fish species collected during the NORFANZ voyage, see Table A1.

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