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Biogeography of near-shore reef fishes in northern New Zealand

F. J. Brook[1]

Abstract Species composition and richness of near-shore reef fish faunas around northern New Zealand were examined at different spatial scales. This comparison indicated a primary subdivision of faunas into three regional biogeographic groups: western North Island coast; north-eastern North Island coast and offshore islands; and Three Kings Islands. The western North Island reef fish fauna had low species richness, a predominance of widespread species over warm temperate species, and lacked subtropical and tropical species. North-eastern North Island and Three Kings faunas were richer, and incorporated mixes of widespread, warm temperate, subtropical, and rare tropical fish. Some frequent north-eastern North Island species were absent or rare in the Three Kings fauna; conversely, some species that were frequent at the Three Kings, including the restricted endemic *Odax cyanoallix*, were rare on the north-eastern North Island coast. The reef fish fauna of north-eastern Northland was further subdivided into three ecological-biogeographic subgroups, representing species assemblages of: headlands and islands strongly influenced by oceanic watermasses; open coasts predominantly influenced by coastal watermasses; and harbours and sheltered bays. Overall species richness and numbers of subtropical-tropical species were highest in the first subgroup, intermediate in the second, and lowest in the last-mentioned. The species assemblages of harbours and sheltered bays in north-eastern Northland had similar composition and richness to harbour and exposed open coast assemblages in western Northland.

Keywords reef fish; diversity; species associations; warm temperate; subtropical; biogeography; northern New Zealand; Three Kings Islands; Poor Knights Islands

INTRODUCTION

The present study was undertaken to examine patterns of geographic variation in species composition, at spatial scales ranging from individual reef sites to regions, among near-shore (<45 m depth) reef fish faunas around northern New Zealand. The main objective was to develop a hierarchical biogeographic classification of faunas, based on comparisons of species composition at different spatial scales, that could be included in a New Zealand-wide biogeographic classification scheme being developed by the Department of Conservation (see Walls & McAlpine 1993; Walls 1995). This stems from initiatives by the International Union for the Conservation of Nature and Natural Resources (IUCN) advocating development of national marine biogeographic and ecological classification schemes, which can provide a

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basis for assessing representativeness and uniqueness of marine areas for marine conservation planning, and for determining appropriate regional or ecosystem management regimes (e.g., Salm & Clark 1984; Kelleher & Kenchington 1992; IMCRA Technical Group 1998).

The regional biogeographic distributions and relationships of New Zealand coastal marine fish faunas have previously been described by Moreland (1959), Paulin & Roberts (1992, 1993) and Francis (1996a). Moreland (1959) recognised four main types of species distribution among New Zealand shore fishes: widespread species found throughout New Zealand; northern species restricted to the North I. and northern South I.; southern species restricted to the South I. and Stewart I.; and subtropical species confined to the north-eastern North I. north of East Cape.

Paulin & Roberts (1992, 1993) recognised three main distributional types on mainland rocky coasts: widely distributed species, found from North Cape to Stewart I.; northern species, mostly found north of Cook Strait; and southern species, mostly found south of Cape Egmont and Hawke Bay. However, they noted that about a third of the northern species were restricted to the north-eastern North I. coast between North Cape and East Cape.

Francis (1996a) identified two distinct regional faunal groups in northern New Zealand. The first incorporated the Three Kings Is fauna and north-eastern North I. fauna between Cape Maria van Diemen and East Cape. The second incorporated the fauna of western and south-eastern North I. coasts (i.e., south of Cape Maria van Diemen and East Cape).

In addition to these New Zealand-wide biogeographic studies, others have described the species composition of reef fish faunas at various locations around northern New Zealand, especially along the north-eastern North I. coast including, in the northern part of that geographic region, Karikari Peninsula (Willan et al. 1979), Cavalli Is (Nicholson 1979), Bay of Islands (Nicholson & Roberts 1980), Mimiwhangata (Ballantine et al. 1973), Poor Knights Is (e.g., Russell 1971; Kelly 1983), Hen I. (Grace & Grace 1978a; Willis 1995), Leigh (Russell 1969; Gordon & Ballantine 1977), Mokohinau Is (Housley 1980), and northern Great Barrier I. (Roberts et al. 1986). The composition of the reef fish fauna at the Three Kings Is has also been described in detail (Hardy et al. 1987), but the north-western North I. coast has received little attention except for studies in the Kawerua and New Plymouth areas (Dickson 1986; New Plymouth Underwater Club 1989).

Species lists compiled for these various locations, along with other descriptions of reef fish distributions (e.g., Ayling & Grace 1971; Russell & Ayling 1976; Ward & Roberts 1986; Choat & Ayling 1987; Kingsford 1989), indicate the existence of latitudinal and across-shelf differences in species composition and biogeographic affinities among north-eastern North I. and Three Kings Is reef fish faunas. In particular, they show that the diversity of subtropical fish species differs within and among island groups and along the mainland coast of eastern Northland.

The present study examines reef fish species composition: along the north-eastern North I. mainland coast and offshore islands north of c. 36.3°S; at the Three Kings Is, 60 km north-west of the northern tip of the North I. (34.2°S); and at Hokianga (35.7°S) and Sugarloaf Is (39.1°S) on the west coast of the North I. (Fig. 1, 2). These geographic areas lie within the north-east North I., Three Kings Is, and north-west North I. geographic regions examined by Francis (1996a, fig. 1).

Physical setting

Near-shore rocky reefs are present along much of the mainland eastern Northland coastline, and islands fringed by rocky reefs are scattered along the coast, of which the Mokohinau Is and Poor Knights Is are the furthest offshore. Mainland and island coastal reefs in eastern Northland are mostly moderately to steeply sloping, and are typically fringed by aprons of

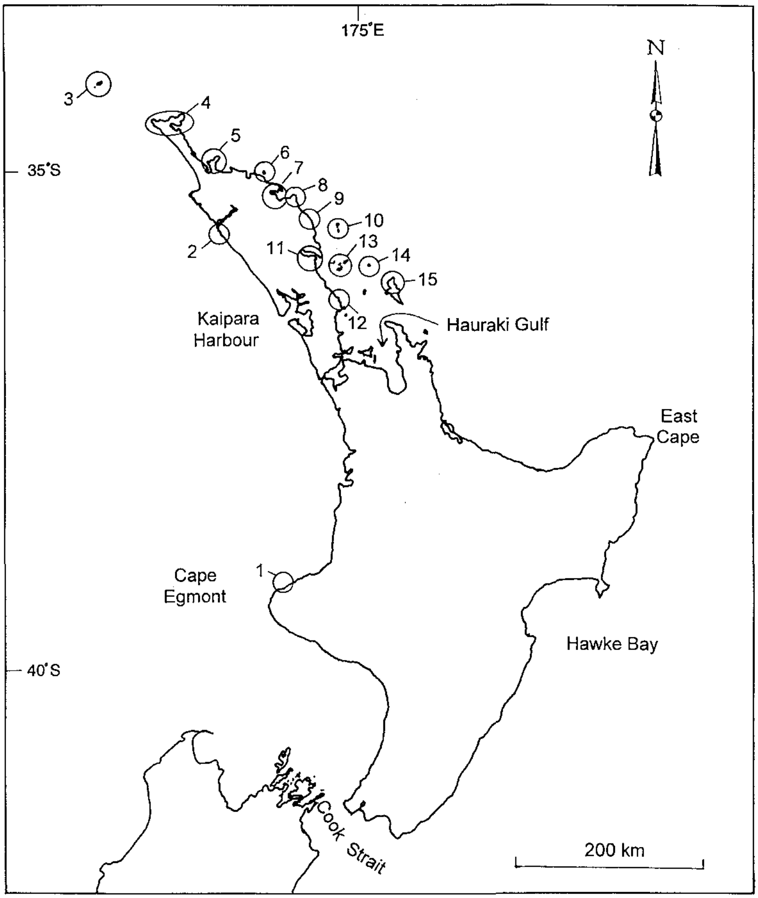


Fig. 1 North Island, New Zealand, showing locations 1–15 described in text. 1, Sugarloaf Is; 2, Hokianga; 3, Three Kings Is; 4, Reinga; 5, Karikari; 6, Cavalli Is; 7, Bay of Islands; 8, Brett; 9, Mimiwhangata; 10, Poor Knights Is; 11, Whangarei; 12, Leigh; 13, Hen & Chickens Is; 14, Mokohinau Is; 15, Great Barrier I.

bioclastic and lithic gravel. The 45 m depth contour lies close inshore along most bold rocky coasts, and is within a few tens to hundreds of metres of some mainland headlands (e.g., Karikari, Brett) and offshore islands (e.g., Cavalli, Poor Knights, Hen & Chickens, Mokohinau, and Great Barrier). A number of harbours and estuaries are present along the eastern Northland coast, and most contain shallow rocky reefs. Deeper reefs, extending to 15 m or more, are present in some of the larger harbours (i.e., Whangaroa, Bay of Islands, Whangarei).

Much of the western Northland coastline consists of long sandy beaches, but near-shore rocky reefs are present locally. Most open coastal reefs drop onto sand or gravel at depths of only a few metres, but deeper subtidal patch reefs and rocky banks are present offshore. Three harbours are present, one of which (Hokianga) contains reefs extending deeper than 30 m.

There is a marked difference in wave exposure between the east and west coasts of Northland. The former generally has a low energy wave climate, but is subjected intermittently to episodes of high energy, easterly and northerly quarter, storm and swell waves, whereas the latter has a high-energy wave climate dominated by westerly and southerly swell and storm waves (Pickrill & Mitchell 1979; Harris 1985).

The Three Kings Is, located 60 km north-west of Cape Reinga, are encircled by rocky reefs that drop steeply to depths of 20–50 m. Reefs are mostly bounded by aprons of lithic cobble gravel and boulder talus, but fringing patches of finer lithic and bioclastic sediment are present locally. The Three Kings Is are exposed to oceanic swell and storm waves from every compass direction and, as a consequence, probably have the most exposed coastline of anywhere in the Northland region.

Northern New Zealand lies in the path of east to north-eastward flowing subtropical watermasses, collectively referred to as the Tasman Current, which cross the Tasman Sea as part of a large, subtropical, anticyclonic gyral system (Wyrtki 1960; Carter et al. 1998; Uddstrom & Oien 1999). Oceanic circulation patterns along the western Northland coast are temporally variable. Tasman Current watermasses either flow north from Cape Egmont, or south-east (Stanton 1973; Carter et al. 1998). Upwelling zones characterised by lowered sea surface temperatures (SSTs) and high primary productivity and biomass are common in the Three Kings and Reinga areas (Garner 1959, 1961; Bradford 1969; Stanton 1973; Bradford & Roberts 1978). Around northernmost New Zealand, the Tasman Current flows south-east to form a western boundary current, known as the East Auckland Current, that flows along the continental slope between North Cape and East Cape (Carter et al. 1998; Uddstrom & Oien 1999). Along the inner margin of the East Auckland Current, flow is generally to the south-east, but is commonly retroflected eastwards offshore from Karikari Peninsula (Denham et al. 1984; Harris 1985). The inner margin of the current is apparently mostly located offshore, but impinges intermittently on prominent coastal headlands and islands nearest the edge of the continental shelf (e.g., Sharples 1997).

SSTs of open coastal watermasses around Northland and the Three Kings typically range from minima of 14–16°C in August–September, to maxima of c. 20–22°C in February–March, with temperatures off western Northland and around the Three Kings slightly cooler on average than along the north-eastern Northland coast (e.g., Garner 1961; Booth 1974; Mercer 1979; Chiswell 1994; Uddstrom & Oien 1999). Seasonal SST ranges within harbours and estuaries are greater than on open coasts (e.g., Booth 1974; Heath 1985), and thermal stratification of coastal waters is generally more pronounced in summer than winter, with the greatest seasonal temperature fluctuations occurring in near-surface waters (e.g., Garner 1961; Stanton 1973; Booth 1974).

Surface waters around the Three Kings Is and headlands and offshore islands in eastern Northland typically have high salinities and very low levels of suspended sediment (Garner 1961; Stanton 1973; Booth 1974; Harris 1985). Watermasses in eastern Northland harbours generally have lower salinities and higher levels of suspended sediment than on adjacent open coasts, and are strongly influenced by seasonal changes in precipitation and fluvial run-off (e.g., Booth 1974). Coastal waters in western Northland generally contain higher levels of suspended sediment than on the east coast as a consequence of greater fluvial run-off and wave turbulence.

METHODS

I examined reef fish faunal composition at two different spatial scales: sites, to determine the species composition of fish communities on individual reefs; and locations, to determine overall faunal composition across a variety of environmental settings within local geographic areas (coastline lengths ranging from c. 15 to 65 km).

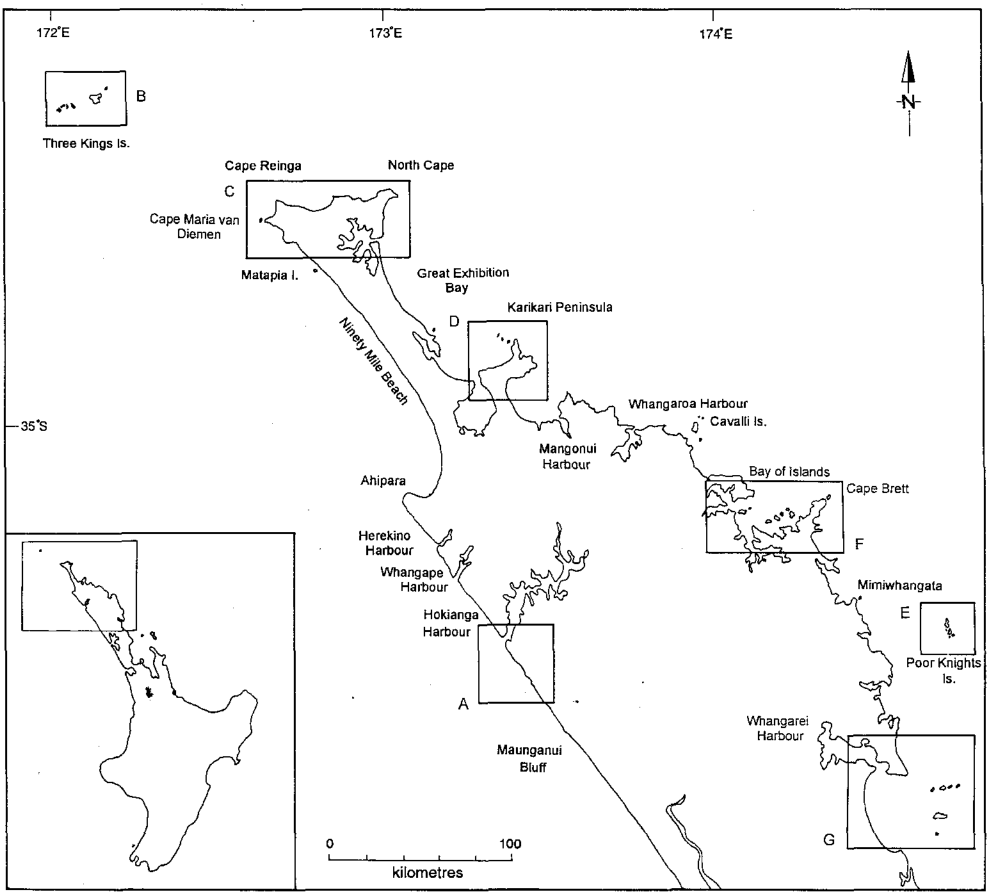


Fig. 2 Northland and the Three Kings Is, showing distribution of site study areas. **A**, Hokianga; **B**, Three Kings Is; **C**, Reinga; **D**, Karikari; **E**, Poor Knights Is; **F**, Bay of Islands–Brett. **G**, Whangarei–Hen & Chickens Is.

Site surveys

Between June 1990 and April 1993, underwater surveys of fish faunas were carried out (using SCUBA) at 119 reef sites around the Northland coast. Site record data are held on file at the Department of Conservation, Whangarei. Sites were located in the following geographic areas (Fig. 2–4): Hokianga to Kawerua (6 sites); Three Kings Is (12); Cape Maria van Diemen to Parengarenga Harbour (17); Karikari Peninsula (20); Bay of Islands to Cape Brett (24); Poor Knights Is (10); Whangarei Harbour to Bream Is (15); and Hen & Chickens Is (15). Each site comprised a band of reef up to 50 m wide, oriented at right angles to the coastline, and extending from the base of the intertidal zone (or from the shallowest point on subtidal pinnacle reefs), to the deepest part of the reef system (or to a maximum depth of 45 m). Site selection was made with the objective of sampling reef habitats in as wide a range of environmental settings as possible within each local area. However, because the surveys were based on visual searches, sites with underwater visibilities of <2 m were excluded. In western Northland and at the Three Kings Is, site selection was also constrained by difficulty of access and rough sea conditions.

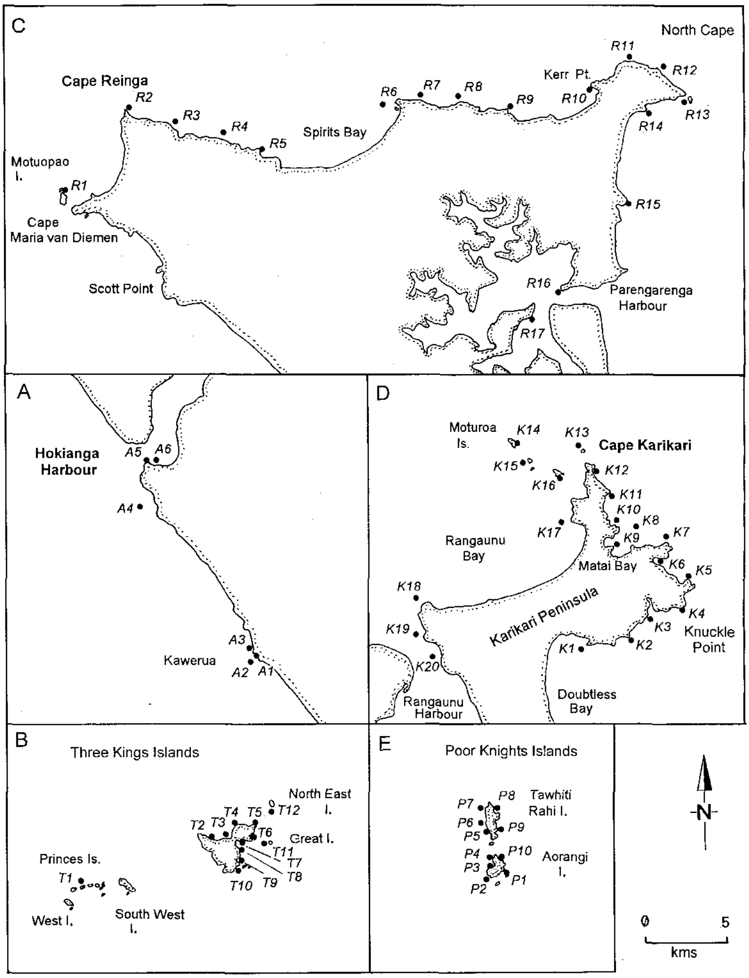


Fig. 3 Distribution of reef fish survey sites at **A**, Hokianga; **B**, Three Kings Is; **C**, Reinga; **D**, Karikari; **E**, Poor Knights Is.

The species composition of fish faunas at reef sites was surveyed using 15-minute timed visual searches within depth intervals of 0–6, 6–15, 15–30, and 30–45 m below low water mark. This method allowed reefs shallower than 30 m to be surveyed during a single no-decompression SCUBA dive, whereas reefs extending deeper than 30 m required two separate dives. At each site, and within the depth intervals represented, the range of physical habitat types present, including caves and crevices, were searched for a total of 15 minutes, and all fish species seen within each depth interval were recorded. Water depths were determined using a dive computer, with values recalculated to depth below low water mark.

From the survey data, I compiled lists of fish species seen at each site. These lists were then standardised to include only those fish species that could be reasonably easily and consistently located, if present, using the search methods described above. Following Willan et al. (1979), cryptic fish species (e.g., in Syngnathidae, Clinidae, Gobiesocidae, Gobiidae, and some tripterygiids), soft-substrate species only occasionally associated with coastal reefs (e.g., *Ophisurus serpens*, *Paristiopterus labiosus*, *Nemadactylus macropterus*, uranoscopids),

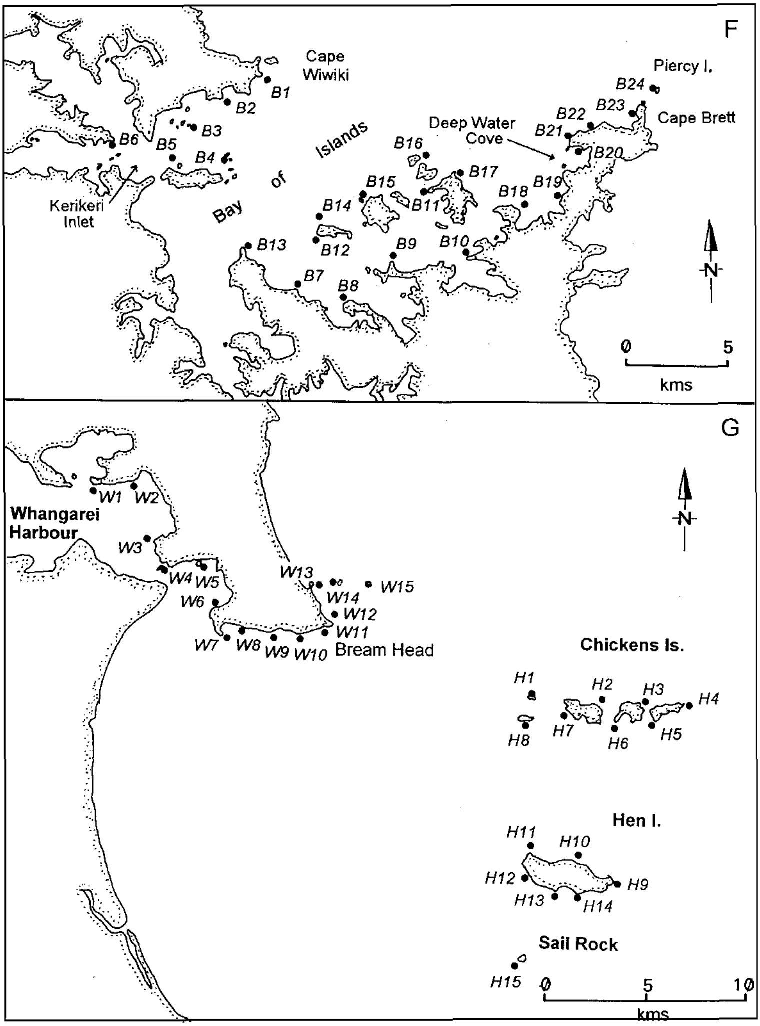


Fig. 4 Distribution of reef fish survey sites at **F**, Bay of Islands–Brett; and **G**, Whangarei–Hen & Chickens Is.

and oceanic pelagic species were excluded. Further, I also excluded some widely ranging, and/or typically highly mobile coastal fish, including rays (*Dasyatis brevicaudata*, *D. thetidis*, *Myliobatis tenuicaudatus*), mullet (*Aldrichetta forsteri*, *Mugil cephalus*), piper (*Hyporhamphus ihi*), some carangids (*Decapterus koheru*, *Seriola lalandi*, *Trachurus novaezelandiae*), and kahawai (*Arripis trutta*), because their presence could not be consistently determined by rapid visual searches.

From the standardised species lists, I determined total species richness of sites and the numbers of species present within each of the depth intervals 0–6, 0–15, 0–30, and 0–45 m. The overall standardised species lists for sites were combined into a presence-absence data matrix comprising 119 sites and 85 species. Species presence and absence were denoted by ones and zeros, respectively, in the data matrix.

Location data

To assess regional biogeographic variation in reef fish faunal composition, species distributional information for 15 locations around northern New Zealand was collated: Sugarloaf Is (New Plymouth); Hokianga; Three Kings Is; Reinga; Karikari; Cavalli Is; Bay of Islands; Brett; Mimiwhangata; Poor Knights Is; Whangarei; Leigh; Hen & Chickens Is; Mokohinau Is; and Great Barrier I. (Fig. 1). Most records were from published and unpublished literature reports and dive survey records obtained during the present study, but unpublished fish sightings by other divers were also used for Hokianga, Cavalli, Poor Knights, Hen & Chickens, and Mokohinau Is (Table 1). I then compiled a standardised species list for each location; firstly, following Willan et al. (1979), by excluding cryptic, predominantly soft-substrate, and oceanic pelagic fish species, and secondly, by excluding vagrant tropical and subtropical reef species known from northern New Zealand only by single or very few records (e.g., *Pterois volitans*, *Epinephelus lanceolatus*, *Forcipiger flavissimus*, *Cyprinocirrhites polyactis*,

Table 1 Descriptions of 15 coastal locations used for determining reef fish distributions around northern New Zealand, and sources of distributional data.

Location number, name and geographic extent		Data sources
1	Sugar Loaf Is (New Plymouth)	New Plymouth Underwater Club 1989
2	Hokianga (Kawerua to Hokianga Harbour)	Dickson 1986; A. Dawn, E. Neho, and M. Pinkney pers. comm. 1993; this study
3	Three Kings Is	Hardy et al. 1987; Francis et al. 1999; this study
4	Reinga (Cape Maria van Diemen to Parengarenga Harbour)	Hardy et al. 1987; Francis 1988; Francis et al. 1999; this study
5	Karikari (Rangaunu Harbour to Tokerau Beach)	Willan et al. 1979; Francis & Evans 1993; Francis et al. 1999; this study
6	Cavalli Is	Nicholson 1979; A. Walker pers. comm. 1999
7	Bay of Islands (Cape Wiwiki to Rawhiti Point)	Nicholson & Roberts 1980; Brook & Carlin 1992; Francis & Evans 1993; Francis et al. 1999; this study
8	Brett (Cape Brett Peninsula and Piercy I.)	Brook & Carlin 1992; Francis & Evans 1993; Francis et al. 1999; this study
9	Mimiwhangata (Mimiwhangata Marine Park)	Ballantine et al. 1973; Grace & Grace 1978b; F. J. Brook unpubl. data
10	Poor Knights Is	Stephenson 1970; Russell 1971; Moreland 1975; Russell & Ayling 1976; Ritchie et al. 1979; Kelly 1983; Ayling & Paxton 1983; Randall & Guézé 1992; Francis 1988; Francis & Evans 1993; Francis et al. 1999; M. Conmee pers. comm. 1993; this study
11	Whangarei (Whangarei Harbour to Bream Is)	This study
12	Leigh (Leigh Marine Reserve)	Russell 1969; Russell & Ayling 1976; Gordon & Ballantine 1977; Thompson 1981; Francis & Evans 1993
13	Hen & Chickens Is	Grace & Grace 1978a; Willis 1995; T. Willis pers. comm. 2000; this study
14	Mokohinau Is	Housley 1980; Francis et al. 1999; M. Francis pers. comm. 1999; T. Willis pers. comm. 2000
15	Great Barrier I. (Needles Pt to Whangapoua and Rakitu I.)	Roberts et al. 1986; Jeffs & Irving 1993; Francis et al. 1999

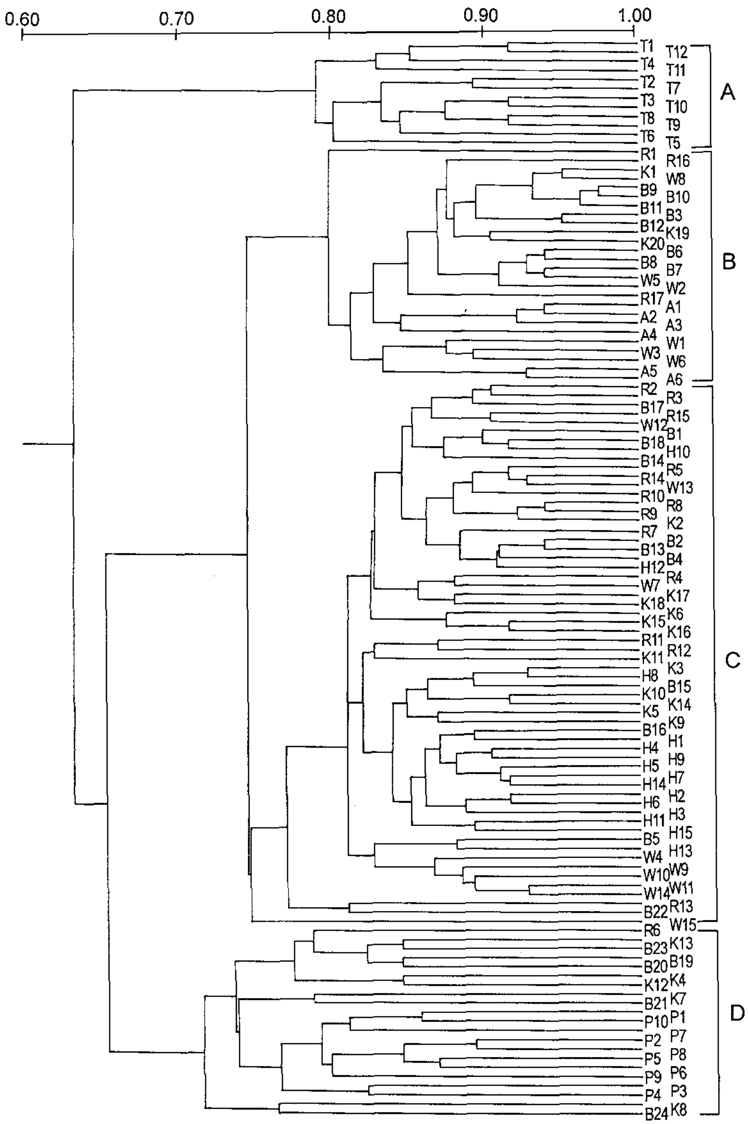


Fig. 5 Dendrogram classification of 119 sites by cluster analysis of species presence-absence data using the simple matching coefficient.

Abudefduf vaigiensis, *Chromis flavomaculata*, *C. vanderbilti*, *Chrysiptera rapanui*, *Parma kermadecensis*, *Stegastes gascoynei*, *Coris dorsomacula*, *Leptoscarus vaigiensis*, *Thamnaconus analis*) and species known only from juveniles (e.g., *Upeneus francisi*, *Thalassoma amblycephalum*, *T. lunare*, *T. lutescens*, *Acanthurus dussumieri*) (see Russell & Ayling 1976; Francis & Evans 1993; Francis et al. 1999). The fish lists for the 15 locations were used to compile a presence-absence data matrix, in which species presence and absence were denoted by ones and zeros, respectively (Appendix 1).

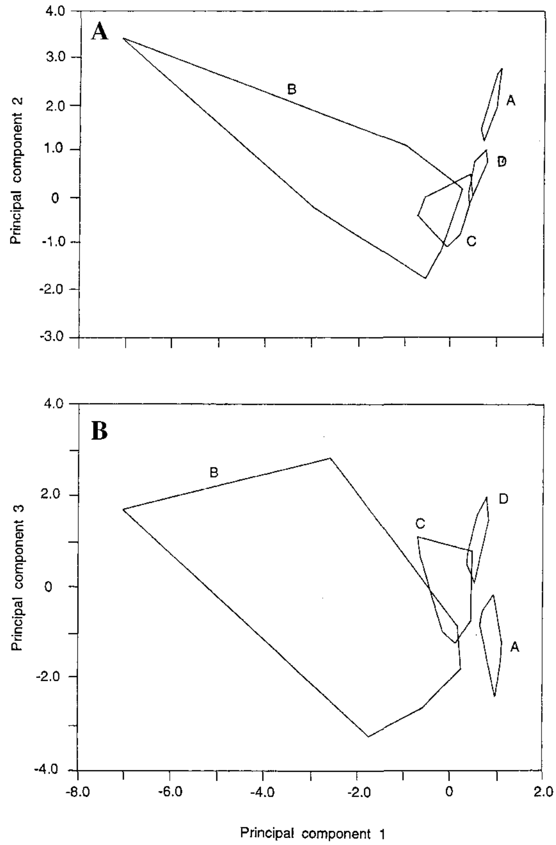


Fig. 6 Principal components ordination of the 119 reef sites in northern New Zealand, showing convex hulls for Associations A–D. **A**, first and second principal components; **B**, first and third principal components.

Data analysis

Compositional similarity among the fish faunas of (a), the 119 Northland reef sites, and (b), the 15 northern New Zealand locations, was explored using multivariate statistical analyses. Following the methods of Francis (1996a), principal components analyses (PCA) of sites and locations were performed using χ^2 transformed data matrices. The matrices of both data sets were transformed by dividing each element by column (site, location) totals, and then by the square root of row (species) totals. PCAs were carried out on the covariance matrices of the respective transformed data sets using SPSS (1999).

For comparison with the PCA, a cluster analysis was also carried out on the site data using the NTSYS-pc package of Rohlf (1989). Similarity of the presence-absence data matrix was calculated using the simple matching coefficient, and clustering was by the unweighted pair group method.

Relationships between depth and species richness among sites were investigated by examining patterns of total species richness versus maximum depth at sites, and by comparing means ± standard errors for species richness at depth intervals of 0–6, 6–15, 15–30, and 30–45 m, within and among each of the main groupings of sites identified by cluster analysis. For sites where only part of the depth range within a given depth zone was sampled, I assumed that the actual recorded diversity was representative of the full depth zone, and included these actual diversities in the calculations of means.

Variation in the biogeographic composition of fish faunas in northern New Zealand was also investigated using the New Zealand-wide species distributional categories of Francis (1996a): tropical, subtropical, warm temperate, widespread, or cool temperate. Numbers of species in each category at each of the 119 sites and 15 locations (Appendices 1, 2) were determined. For comparison among sites, I expressed the number of "northern" species (defined as the sum of the tropical, subtropical, and warm temperate categories) as a percentage of the species total for each site, and then compared values among the main groupings of sites identified by cluster analysis. Regional biogeographic trends were also

Table 2 Frequent reef fish species (present at >80% of sites) in Associations A–D.

	Association			
Species	A	B	C	D
Gymnothorax nubilus				X
Gymnothorax prasinus				X
Optivus elongatus			X	X
Centroberyx affinis	X			X
Scorpaena cardinalis				X
Caesioperca lepidoptera	X			X
Caprodon longimanus				X
Hypoplectrodes sp.				X
Upeneichthys lineatus			X	X
Pempheris adspersus			X	X
Scorpis lineolatus			X	
Scorpis violaceus	X		X	X
Girella tricuspidata		X	X	
Chironemus marmoratus			X	X
Aplodactylus arctidens	X		X	X
Cheilodactylus spectabilis	X		X	X
Nemadactylus douglasii	X			X
Chromis dispilus	X		X	X
Bodianus unimaculatus				X
Coris sandageri				X
Notolabrus celidotus		X	X	
Notolabrus fucicola	X		X	X
Pseudolabrus luculentus				X
Pseudolabrus miles	X			X
Suezichthys aylingi	X			X
Odax cyanoallix	X			
Parapercis colias	X			
Forsterygion flavonigrum				X
Forsterygion lapillum		X	X	
Forsterygion malcolmi			X	
Forsterygion varium		X	X	
Notoclinops segmentatus			X	X
Notoclinops yaldwyni				X
Obliquichthys maryannae			X	X
Ruanoho whero		X	X	X
Parablennius laticlavius			X	X
Parika scaber	X		X	X
Canthigaster callisterna				X

examined by comparing relative proportions of tropical+subtropical, warm temperate, widespread, and cool temperate species among the 15 locations, calculated as percentages of the total species diversities recorded for each location.

RESULTS

Site classification

A standardised total of 85 fish species was recorded from the 119 reef sites surveyed around Northland. Species distributions are listed in Appendix 2.

A classification of the 119 Northland reef sites produced by cluster analysis of species presence-absence data is illustrated as a dendrogram in Fig. 5. The analysis divided sites into three primary groups, with the largest group itself incorporating two main subgroups. These four clusters of sites are labelled Associations A–D on the dendrogram.

In the PCA carried out on the same data set, the first three principal components explained 19.1, 10.1, and 6.2% of the variation in the data. These three components thus accounted for only a small portion of the total variability. On plots of the first three principal components, the sites grouped in Associations B, C, and D by cluster analysis formed a gradational configuration with slight overlap between convex hulls of Associations B and C, and between those of C and D. However, Association A sites of the cluster analysis also formed a discrete cluster on the PCA plot (Fig. 6).

The four site Associations (A–D) identified by cluster analysis have the following characteristics.

Association A

Distribution: Three Kings Is (Sites T1–12).
Depth range: The shallowest site extended down to 6 m; the deepest to 45 m.
A total of 50 species was recorded from the 12 sites in this association. Species richness at sites ranged from 21–36, with a median of 27 and a mean of 27.4 ± 3.5 SD. Thirteen species were frequent, found at >80% of sites (Table 2).

Association B

Distribution: Hokianga (A1–6); Reinga (R1, R16, R17); Karikari (K1, K19, K20); Bay of Islands (B3, B6–12); Whangarei (W1–3, W5, W6, W8).
Depth range: The shallowest site extended down to 2 m; the deepest to 30 m.
A total of 44 species was recorded from the 25 sites. Species richness ranged from 7–24, with a median of 15 and a mean of 14.3 ± 4.2 SD. Five species were frequent (Table 2), and one species (*Grahamina capito*) was recorded only from this association.

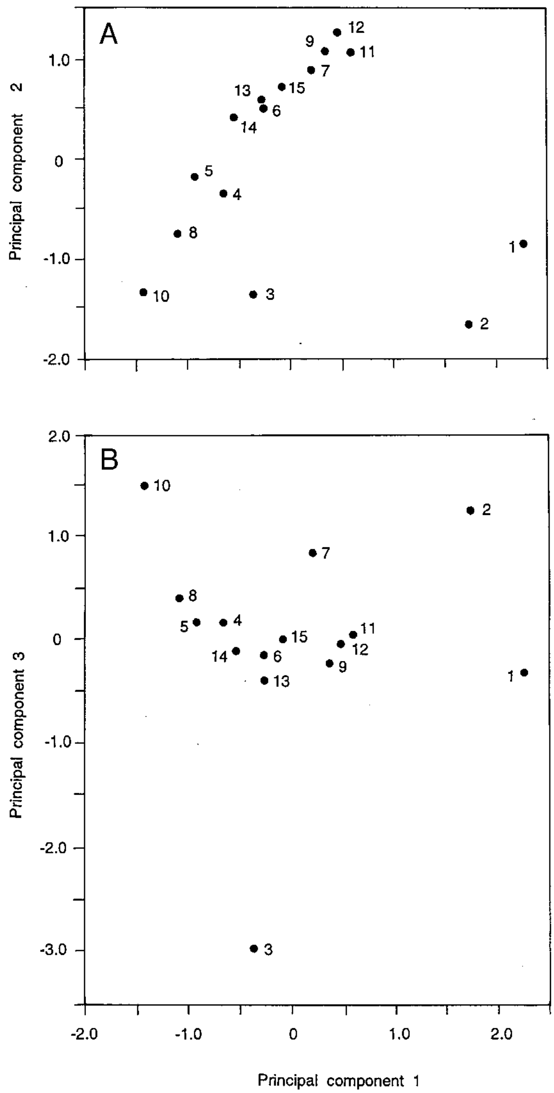
Association C

Distribution: Reinga (R2–5, R7–15); Karikari (K2, K3, K5, K6, K9–11, K14–18); Bay of Islands (B1, B2, B4, B5, B13–18); Brett (B22); Whangarei (W4, W7, W9–15); Hen & Chickens Is (H1–15).
Depth range: The shallowest sites extended down to 6 m; the deepest to 45 m.
A total of 75 species was recorded from the 60 sites. Species richness ranged from 20–45, with a median of 31 and a mean of 31.3 ± 6.0 SD. Twenty species were frequent (Table 2).

Association D

Distribution: Reinga (R6); Karikari (K4, K7, K8, K12, K13); Brett (B19–21, B23, B24); Poor Knights Is (P1–10).

Fig. 7 Principal components ordination of the 15 coastal locations in northern New Zealand based on comparison of species compositions. **A**, first and second principal components; **B**, first and third principal components.



Depth range: The shallowest site extended down to 18 m; the deepest to 45 m.

A total of 81 species was recorded from the 21 sites. Species richness ranged from 39–57, with a median of 43 and a mean of 44.4 ± 4.5 SD. Thirty species were frequent (Table 2). Six species (*Epinephelus rivulatus*, *Amphichaetodon howensis*, *Zanclistius elevatus*, *Latridopsis forsteri*, *Bodianus* sp., *Coris picta*), were recorded only from Association D. The richest sites, with 54–57 species, were on the mainland coast near Cape Brett and on Karikari Peninsula. Sites at the Poor Knights Is contained between 41 and 46 species and formed a discrete subgroup separate from other Association D sites in the cluster analysis.

Associations B–D represent stages in a faunal continuum, ranging from impoverished species assemblages in sheltered bays, harbours, and exposed west coast sites (Association B), to moderately diverse assemblages of open coasts of northern and eastern Northland (Association C), and higher diversity assemblages around some headlands, islands, and pinnacle reefs off northern and eastern Northland (Association D). The increased richness from Associations B to C to D mostly involved simple addition of species. However, one tripterygiid species (*Grahamina capito*) was found only at some Association B sites, and another (*Ruanoho decemdigitatus*) was found at some Association B and C sites but not any Association D site. Similarly, *Girella tricuspidata*, *Notolabrus celidotus*, *Forsterygion lapillum* and *Forsterygion varium* were more frequent among Association B and C sites than Association D (especially Poor Knights Is) sites.

Association A, restricted to the Three Kings Is, showed some similarities with Association D (e.g., frequent *Centroberyx affinis*, *Caesioperca lepidoptera*, *Nemadactylus douglasii*, *Pseudolabrus miles*, *Suezichthys aylingi*; Table 2). However, it differed from Association D, and also from Associations B and C, in two main ways: firstly, by the frequent presence of species that were absent from or infrequent in the other three associations (*Odax cyanoallix*, *Parapercis colias*); and, secondly, by the species absences listed previously and also by the rarity of some species that were widely distributed in other associations (e.g., *Zeus faber*, *Pagrus auratus*, *Upeneichthys lineatus*, *Pempheris adspersus*, *Kyphosus sydneyanus*, *Scorpis lineolatus*, *Coris sandageri*, *Forsterygion flavonigrum*, *Parablennius laticlavius*; Appendix 2).

Location classification

The results of the PCA on a χ^2 transformed species presence-absence data set (total of 104 species) incorporating the 15 locations in northern New Zealand, are illustrated in Fig. 7. The first principal component described 46.9% of total variation and the first three principal components cumulatively described 67.5% of variation. There were three main regional clusters: Group 1, North I. west coast (Locations 1, 2); Group 2, Three Kings Is (Location 3); Group 3, north-eastern North I. (Locations 4–15).

The two west coast locations in Group 1 (Sugarloaf Is, Hokianga) had the lowest species richness among the 15 locations examined (Table 3), with about half the number of species recorded from the two richest locations (Poor Knights Is, Brett). With the exception of

Table 3 Percentages of widespread, cool temperate, warm temperate, and subtropical-tropical reef fish species in faunas at northern New Zealand locations.

	Location	No. of species	% widespread species	% cool temperate species	% warm temperate species	% subtropical-tropical species
1	Sugarloaf Is	51	80.4	0	19.6	0
2	Hokianga	46	71.7	0	28.3	0
3	Three Kings Is	69	46.4	1.4	24.6	27.5
4	Reinga	80	46.3	0	23.7	30.0
5	Karikari	86	43.0	0	24.4	32.6
6	Cavalli Is	71	47.9	0	28.2	23.9
7	Bay of Islands	63	55.6	0	30.2	14.3
8	Brett	93	41.9	0	23.7	34.4
9	Mimiwhangata	64	54.0	0	27.0	19.0
10	Poor Knights Is	98	37.8	0	24.5	37.8
11	Whangarei	61	54.1	0	31.1	14.8
12	Leigh	62	54.8	0	29.0	16.1
13	Hen & Chickens Is	72	50.0	0	27.8	22.2
14	Mokohinau Is	78	47.4	0	26.9	25.6
15	Great Barrier I.	68	50.0	0	26.5	23.5

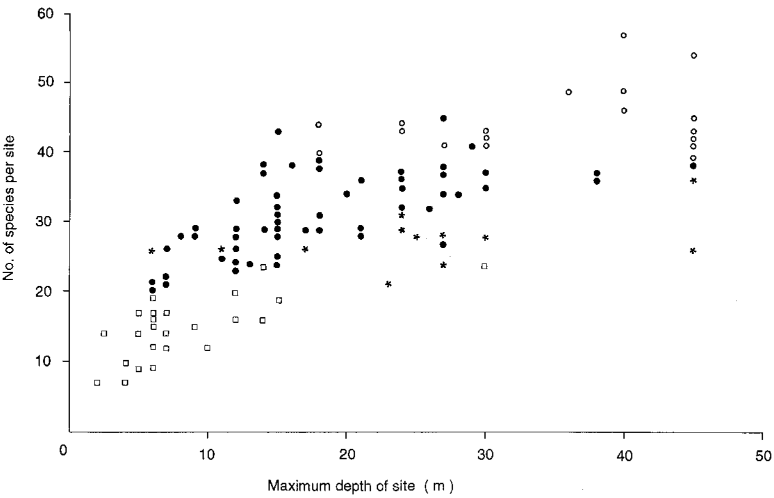


Fig. 8 Relationship between maximum depth and species richness in reef fish assemblages at sites in northern New Zealand. Association A sites denoted by asterisks; Association B sites by squares; Association C sites by solid circles; Association D sites by empty circles.

Pseudophycis bachus, present at the Sugarloaf Is, all other west coast species were also recorded from north-eastern North I. locations.

The Three Kings Is (Group 2) lacked several species widely distributed elsewhere around northern New Zealand (*Gymnothorax prasinus*, *Hyporhamphus ihi*, *Trachurus novaezelandiae*, *Girella tricuspidata*, *Chironemus marmoratus*, *Bodianus unimaculatus*, *Notolabrus celidotus*, *Odax pullus*, *Forsterygion lapillum*, *Notoclinops caerulepunctus*, *N. segmentatus*). Species richness was within the range recorded for north-eastern North I. locations (Table 3).

The group of north-eastern North I. locations showed gradational variation in faunal composition and richness, from the Poor Knights Is with the most diverse fauna, to Whangarei and Leigh with the least diverse faunas (Table 3). The four richest faunas (Poor Knights, Brett, Karikari, Reinga) included some species not found at any other locations (e.g., *Synodus doaki*, *Fistularia* cf. *commersonii*, *Aulacocephalus temmincki*, *Epinephelus rivulatus*, *Evistias acutirostris*, *Parma polylepis*, *Anampses elegans*, *Bodianus* sp., *Coris picta*, *Pseudojuloides elongatus*). However, all species present at other north-eastern North I. locations were also recorded from one or more of the four richest locations, indicating that the overall gradient in species composition and diversity within this region resulted from simple addition, rather than geographic replacement, of species.

Depth and species richness

Species richness showed an overall logarithmic increase with increasing maximum depth among sites (Fig. 8). However, for a given maximum depth, Association B sites generally contained fewer species than Association C or D sites, and Association D sites commonly contained more species than Association C sites. By contrast, Association A showed only slight variation in species richness between the shallowest and deepest sites examined.

There was no consistent variation in species richness among depth intervals within Associations A–D (Fig. 9). The curves for Associations B–D show similar trends with increasing depth, albeit with Association B sites containing fewer species than Association C and D sites for a given depth interval. Within Associations A and D, species richness was

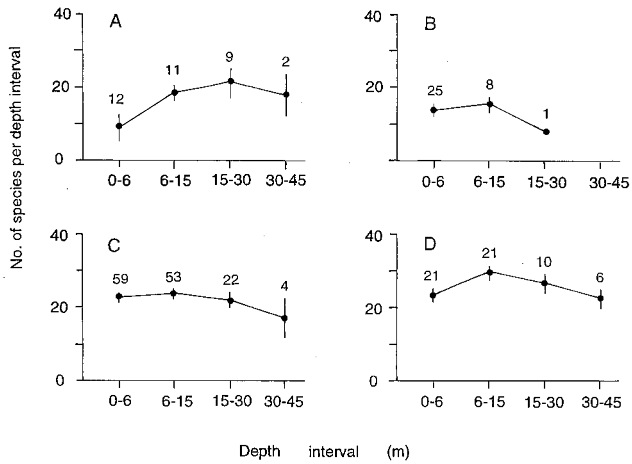


Fig. 9 Reef fish species diversity (mean ± 2 s.e.) at depth intervals of 0–6, 6–15, 15–30, and 30–45 m at Association A–D sites in northern New Zealand. No. of sites searched indicated on diagrams.

Table 4 Percentages of "northern" (i.e., warm temperate + subtropical + tropical) reef fish species at Association A–D sites.

		% of "northern" species at sites		
Association	No. of sites	Range	Median	Mean ± SD
A	12	33.3–51.6	42.3	42.3 ± 6.6
B	26	20.0–52.9	36.7	35.8 ± 11.0
C	60	34.3–55.6	45.1	44.7 ± 5.2
D	21	46.6–70.7	58.5	58.1 ± 6.0

consistently lower in the 0–6 m interval than at 6–15 m. Association A sites had similar species richness to Associations C and D in the 15–30 and 30–45 m intervals, but contained far fewer species in the 0–6 m interval. More than half the Association A sites contained six or fewer species at 0–6 m, the most frequently represented being *Scorpis violaceus*, *Aplodactylus arctidens*, *Notolabrus fucicola*, *Pseudolabrus miles*, *Suezichthys aylingi*, *Odax cyanoallix*, and *Notoclinops yaldwyni*.

Many reef fish species were found throughout the 0–45 m depth range covered in this survey, but some were restricted to shallower or deeper parts of this range. Species generally found shallower than 15 m included *Kyphosus bigibbus*, *K. sydneyanus*, *Girella tricuspidata*, *Bathystethus cultratus*, *Labracoglossa nitida*, *Parma alboscapularis*, *Aplodactylus etheridgii*, *Cheilodactylus ephippium*, *Forsterygion lapillum*, and *Notoclinops yaldwyni*. Species generally found deeper than 6 m included *Hypoplectrodes* sp., *Suezichthys arquatus*, and *Forsterygion flavonigrum*. Deeper still were *Pseudophycis barbata*, *Centroberyx affinis*, *Amphichaetodon howensis*, *Zanclistius elevatus*, *Latridopsis ciliaris*, *Coris picta*, and *Canthigaster callisterna*, generally found below 15 m, and *Helicolenus percoides*, *Callanthias australis*, and *Bodianus* sp. generally below 30 m.

Faunal composition

Relative proportions of widespread, warm temperate, subtropical, and tropical species (sensu Francis 1996a) in reef fish assemblages varied considerably among sites. Percentages of "northern" fish species (i.e., including tropical, subtropical, and warm temperate categories) at Association A–D sites are listed in Table 4. Associations B and D contained sites with the lowest and highest percentages of "northern" species, respectively. Associations A and C had very similar percentages of "northern" species, intermediate between B and D. Tropical species were absent from Association A and B sites, and rare in Associations C and D. Warm temperate species dominated the "northern" component of Associations A–C, and also most Association D sites, but were co-dominant with subtropical species at some Association D sites (e.g., B24, P3, P4, P7). North I. west coast sites at Hokianga and Kawerua had consistently low percentages of warm temperate species (range 20.0–29.2, mean 23.1 $\pm$ 3.4 SD), and lacked subtropical species.

Percentages of widespread, cool temperate, warm temperate, and subtropical-tropical fish species for the 15 locations are given in Table 3. The locations can be separated into two main groups based on similarity of biogeographic elements. The Sugarloaf Is and Hokianga faunas (Locations 1, 2) were dominated by widespread species (71.7–80.4%), and lacked cool temperate and subtropical-tropical species. The Three Kings and north-eastern North I. faunas (Locations 3–15) had lower proportions of widespread species (37.8–55.6%), and low to moderate proportions of subtropical-tropical species (14.3–37.8%).

Among the second group, Bay of Islands, Mimiwhangata, Whangarei, and Leigh (Locations 7, 9, 11, 12) all had relatively low proportions of subtropical-tropical species (14.3–19%). Cavalli Is, Hen & Chickens Is, Mokohinau Is, and Great Barrier I. (Locations 6, 13–15) had slightly higher proportions of subtropical-tropical species (21.7–25.7%), and ratios of warm temperate:subtropical-tropical species of >1. Three Kings Is, Reinga, Karikari, Brett, and Poor Knights Is (Locations 3–5, 8, 10) had the highest proportions of subtropical-tropical species (27.5–37.8%), and ratios of warm temperate:subtropical-tropical species of <1. Three Kings Is was the only location that included a cool temperate species (*Notolabrus cinctus*).

The separation of western (Sugarloaf Is, Hokianga) from north-eastern North I. locations in this classification is consistent with that based on the PCA of species presence-absence data (Fig. 7). However, whereas the Three Kings fauna was shown to differ from those of western and north-eastern North I. locations in species content, proportions of widespread, warm temperate and subtropical-tropical species were similar to those at north-eastern North I. locations, especially Reinga (Table 3).

DISCUSSION

Biogeographic patterns

Comparison of near-shore reef fish species distributions among the 15 locations examined in northern New Zealand indicated a three-way regional biogeographic subdivision of faunas: western North I.; north-eastern North I.; and Three Kings Is. Faunas at the two west coast locations (Sugarloaf Is, Hokianga) had low overall species diversity, a strong predominance of widespread species (72–80%) over warm temperate species, and an absence of subtropical and tropical species. By contrast, the faunas at north-eastern North I. locations were richer, and contained lower proportions of widespread species (38–56%) and between 14 and 38% subtropical-tropical species. The Three Kings fauna was similar to those of some north-eastern North Island locations in terms of overall species richness and relative proportions of subtropical-tropical species (27%), but it lacked many widespread and warm temperate species common elsewhere around northern New Zealand.

This regional subdivision agrees well with broad scale groupings of northern New Zealand reef fish faunas determined by Francis (1996a). The only point of difference is that Francis (1996a) grouped the Three Kings fauna together with north-eastern North I. faunas, although he noted that there were important compositional differences between the two. Findings of the present study indicate that biogeographic differences are even more pronounced if faunal comparisons are made at the level of sites rather than at larger spatial scales.

Within the north-eastern North I. region, I found considerable variation among locations in species composition and richness, and in the relative proportions of widespread, warm temperate, and subtropical-tropical species (Table 3). Species richness and relative proportions of subtropical-tropical species in fish faunas were highest at the Poor Knights Is and prominent coastal headlands in north-eastern Northland (Brett, Karikari, Reinga), intermediate at inshore islands off eastern Northland and islands in the outer Hauraki Gulf (Cavalli Is, Hen & Chickens Is, Mokohinau Is, Great Barrier I.), and lowest in the Bay of Islands and along the mainland coast south of Brett (Mimiwhangata, Whangarei, Leigh). In the south-eastern part of the study area, species richness and relative proportions of subtropical-tropical species in fish faunas were consistently higher at locations closer to the edge of the continental shelf than further inshore at similar latitudes (e.g., Brett > Bay of Islands; Poor Knights Is > Mimiwhangata; Mokohinau Is > Hen & Chickens Is > Whangarei). Similar patterns have been described previously by Ayling & Grace (1971), Ward & Roberts (1986), and Choat & Ayling (1987).

At the finer spatial scale of sites, four main ecological-biogeographic groupings (Associations A–D) were recognised. Association A was restricted to the Three Kings; Associations C and D were restricted to the north-eastern North I.; and Association B was present in both the western and north-eastern North I. Species richness and relative proportions of "northern" species were highest in Association D and lowest in Association B. Associations B–D represented a faunal continuum involving mainly species addition (i.e., of warm temperate and subtropical species) from B–C–D, whereas Association A differed markedly in species composition from the other three associations.

In western Northland, Association B sites were present in harbour mouth and exposed open coastal settings. Within the north-eastern North Island region, Association B sites were restricted to harbours and sheltered bays along the mainland coast; Association C sites were widely distributed on open mainland coasts and around some islands and reefs between Reinga and the Hen & Chickens Is; and Association D sites were present at the Poor Knights Is, Brett, and also locally at Reinga and Karikari (i.e., in the four locations with highest overall species richness within northern New Zealand). Within some locations there was a relatively high degree of faunal similarity among sites. For example, all sites surveyed at Three Kings Is, Hokianga, Hen & Chickens Is, and Poor Knights Is were classified in Associations A, B, C, and D, respectively. However, some north-eastern Northland locations showed greater faunal variation, as indicated by the presence of two or three different associations. Examples are Reinga and Karikari (Associations B–D), Bay of Islands and Whangarei (B, C), and Brett (C, D).

Comparison of biogeographic relationships among faunas at the different spatial scales of locations and sites indicates that the Three Kings reef fish fauna was compositionally distinct at both scales from faunas elsewhere in northern New Zealand. Some species frequent elsewhere around Northland were rare or absent at the Three Kings and, conversely, some species rare elsewhere were frequent there. The latter group included one species endemic to northernmost New Zealand, *Odax cyanoallix*, which was otherwise recorded from only a few sites in Reinga (although solitary individuals have also previously been recorded from Brett and the Poor Knights Is; Ayling & Paxton 1983; Brook & Carlin 1992).

Faunas of the two western North I. locations investigated differed from those of the north-eastern North I. locations in terms of both species composition and richness. However, species assemblages of open coast and harbour sites in western Northland were similar to those of harbours and sheltered bays on the north-eastern North I. coast, indicating a degree of faunal similarity at community scale between the two regions. It is probable that species assemblages similar to those recorded in Hokianga are present on open coastal and harbour mouth reefs at least as far north as Ahipara. Surveys are required between Ahipara and Cape Maria van Diemen to determine whether biogeographic affinities of the reef fish fauna in that geographic area lie with other west coast faunas or with north-eastern Northland faunas. On a wider geographic scale, the Hokianga fauna was found to be compositionally similar overall to the fauna at Sugarloaf Is, c. 450 km further south along the western North I. coast. This is in agreement with Francis's (1996a) classification, which suggested that western North I. reef fish faunas lie within an extensive biogeographic region that also includes the northernmost South I. and south-eastern North I. coasts. However, no information is available to indicate whether or not these broad faunal similarities also extend to the finer scale of communities, represented by species assemblages at sites, throughout the entire geographic extent of this region.

The north-eastern Northland region, which extended from Cape Maria van Diemen south-east along the eastern Northland coast including offshore islands, contained three broad ecological–biogeographic faunal groups representing species assemblages of harbours and sheltered bays (Association B); nearshore islands and open mainland coasts (Association C); and offshore islands and some prominent coastal headlands (Association D).

By extrapolation, I infer that Association C assemblages predominate on open coasts and Association B assemblages predominate in harbours and sheltered bays throughout north-eastern Northland. Association D assemblages are probably largely restricted to the geographic areas already identified, but may be present also in the outer Cavalli Is and at the Mokohinau Is.

The mosaic distribution of Association B and C assemblages within the north-eastern North I. region suggests that geographic patterning was strongly influenced by ecological factors operating at a local scale. By contrast, the more restricted distribution of Association D assemblages points to the operation of larger scale ecological and/or biogeographic controls on species composition at and within locations nearest the edge of the continental shelf.

In a wider context, previous studies have suggested that reef fish faunas of eastern Northland locations have close regional biogeographic affinities with other north-eastern North I. locations north of East Cape (Moreland 1959; Paulin & Roberts 1993; Francis 1996a). Further work is needed to determine whether or not subregional ecological and biogeographic variation in fish faunas, comparable to that described here, also exists between the Hauraki Gulf and East Cape.

Factors influencing faunal diversity and composition

The three biogeographic regions defined in northern New Zealand all have quite different broad-scale hydrological environments, as described in the Introduction. Significant features in the Three Kings region are contrasting influences of subtropical oceanic surface watermasses and cooler upwellings, a high degree of wave exposure, and low turbidity levels. The western North I. region has very high wave exposure on open coasts, and high turbidity levels in coastal watermasses. The north-eastern North I. region contains a greater range of geomorphological and hydrological variation than the other two regions. Offshore islands, and prominent coastal headlands in northern and eastern Northland, are at times bathed by south-eastward-flowing subtropical oceanic watermasses of the East Auckland Current, but the rest of the region is predominantly influenced by coastal watermasses. Wave exposure on open coasts is lower overall than in the other two regions, whereas turbidity levels are generally relatively high in harbours and inlets, low around offshore islands, and intermediate along mainland open coasts.

Three Kings Islands

The strong influence of subtropical Tasman Current watermasses in the Three Kings region was indicated by the relatively high number of warm temperate and subtropical fish species (17 and 18, respectively) recorded there. Most of the subtropical species were rare and probably transient members of the fauna (Hardy et al. 1987), but three (*Gymnothorax obesus*, *Epinephelus daemelii*, *Hypoplectrodes* sp.) were relatively common (F. Brook unpubl. data). Significantly, large individuals of *E. daemelii* over 1 m in length were present at the Three Kings, whereas records from elsewhere around northern New Zealand are of smaller fish. Given that individuals of this species change sex from female to male at a length of about 1.0–1.1 m (Francis 1996b), it is possible that the Three Kings Is supports the only breeding population of *E. daemelii* in the New Zealand region south of the Kermadec Is.

A feature of the Three Kings coastal marine biota noted by a number of previous workers was the coexistence of subtropical and cool temperate taxa (e.g., Adams & Nelson 1985; Hardy et al. 1987; Nelson 1994; Francis 1996a). The presence of cool temperate species in the region has generally been attributed to the influence of upwellings of cool waters around the islands. One cool temperate reef fish species (*Notolabrus cinctus*) has been recorded from the Three Kings. This species has a markedly disjunct distribution: it is otherwise known only from central and southern New Zealand, and the Chatham Islands (Francis 1996a,b). The Three Kings record is based on sightings made in January 1985 of a mixed sex group of c. 10 fish at c. 35 m depth at the western end of the island chain (C. Ward pers. comm. 1992). I know of no other records of *N. cinctus* from the Three Kings, suggesting that, like some subtropical fish, it is a rare and possibly also transient member of the fauna.

Another distinctive feature of the Three Kings reef fish fauna was the absence or rarity of some species that were widely distributed and common elsewhere around northern New Zealand. Possible reasons include:

1 Climatic instability caused by intermittent upwellings of cool water around the Three Kings.

2 The lack of continuous shallow water reef habitats between the Three Kings and the mainland Northland coast, coupled with a predominantly eastward current flow around northern New Zealand (Stanton 1973; Heath 1981), may prevent or severely restrict the northward dispersal of some shallow water species to the Three Kings (e.g., *Kyphosus sydneyanus*, *Odax pullus*, *Forsterygion lapillum*).

3 Some species may be unable to establish at the Three Kings because particular habitat types are not represented there. For example, the absence of *Girella tricuspidata* and *Notolabrus celidotus* might be related to a lack of the sheltered habitats required by juveniles.

4 Competitive exclusion. The labrids *Notolabrus fucicola*, *Pseudolabrus miles* and *Suezichthys aylingi* all live at high densities around the Three Kings compared with elsewhere around northern New Zealand (Choat & Ayling 1987; F. Brook unpubl. data) and, as a consequence, might prevent or limit the establishment of other small to medium sized reef fish species with similar feeding habits (e.g., *Chironemus marmoratus*, *Bodianus unimaculatus*, *Coris sandageri*, *Forsterygion varium*).

North-eastern North Island

Biogeographic variation in fish faunas among north-eastern North I. locations was clearly related to broad-scale hydrological patterns. As noted by previous workers, overall species richness and numbers of subtropical and tropical species were higher at locations influenced by subtropical oceanic watermasses of the East Auckland Current (i.e., offshore islands, and prominent coastal headlands in northern and eastern Northland) than at locations predominantly influenced by inshore coastal watermasses (e.g., Ayling & Grace 1971; Russell & Ayling 1976; Ward & Roberts 1986; Choat & Ayling 1987; Choat et al. 1988; Francis & Evans 1993; Francis 1996a). These faunal differences are generally attributed to direct influences of hydrology on fish distributions, and to the role of the East Auckland Current in transporting larvae of warm temperate, subtropical, and tropical fish species into and within the north-eastern New Zealand region.

At a finer spatial scale, there was also ecological differentiation in northern and eastern Northland between species assemblages of harbours and sheltered bays (Association B), and those of open coasts (Associations C and D). This correlates with, and was probably primarily caused by, differences in temperature, salinity, and turbidity. On open coasts, Association C was widespread, whereas Association D was much more restricted and common only at the Poor Knights Is, Brett, and outer Karikari Peninsula. The concentrations of Association D sites, at the headlands and islands presumably most strongly influenced by East Auckland Current watermasses, suggests that compositional differences between Associations C and D were determined partly by broad-scale patterns of larval dispersal and marine climate. However, the patchy distributions of the two associations at Reinga, Karikari, and Brett indicate that other ecological factors, probably including habitat, were also important.

Cluster analysis (Fig. 5) indicated that the fish assemblages at the Poor Knights Is, while most similar to some assemblages at Karikari and Brett, had unique faunal composition. Several widely distributed coastal species were infrequent (e.g., *Scorpaena papillosus*, *Girella tricuspidata*, *Notolabrus celidotus*, *Forsterygion lapillum*, *F. malcolmi*, *F. varium*) or absent (*Hypoplectrodes huntii*) at the Poor Knights. Conversely, some warm temperate and subtropical fish (e.g., *Gymnothorax obesus*, *Zanclistius elevatus*, *Girella cyanea*, *Parma alboscapularis*) were more frequent there than on the mainland coast. These differences were presumably related to the isolated offshore location, scarcity of shallow sheltered habitats, and greater exposure of the Poor Knights Is to East Auckland Current watermasses.

Western North Island

The lower overall species richness, and absence of subtropical and tropical species at western North Island locations, probably primarily reflected the influence of cooler sea temperatures. Differences in proportions of warm temperate species between the Hokianga and Sugarloaf Is faunas (Table 3) were presumably also temperature-related.

At a finer spatial scale within Hokianga, species composition and richness showed little variation between sheltered harbour mouth sites and highly exposed open coastal sites. This suggests environmental factors such as sea temperature, salinity, and turbidity probably had a greater influence than wave exposure on local distributions of the species concerned. However, the abundance of some fishes varied markedly between exposed and sheltered sites. For example, *Notolabrus fucicola* was far more abundant at exposed than sheltered sites, whereas *Notolabrus celidotus* showed the reverse pattern (F. Brook unpubl. data).

Depth distribution

Depth distributions of fish species observed during this study were closely similar to those reported elsewhere for northern New Zealand reefs (summarised in Ayling & Cox 1982; Francis 1996b), with some species found at 0–45 m and others restricted to shallower or deeper parts of that range. Species distributions within sites were presumably strongly influenced by habitat selection. Physical environmental factors (e.g., temperature, wave exposure, currents, reef topography, presence/absence of crevices, sand patches, boulders, etc.) and the distribution, composition, and structure of macroalgal stands and benthic encrusting communities were probably all important (e.g., Ayling 1978; Choat & Ayling 1987; Choat et al. 1988; Jones 1988). Similarly, patterns of depth-related variation in species richness among sites (Fig. 8, 9) probably resulted at least partly from the influence of bathymetric environmental gradients on the diversity and stratification of niches available for reef fish to occupy. For example, the differences in species richness between 0–6 and 6–15 m depth intervals at Association A and D sites (Fig. 9) correlated with and possibly resulted from depth-related gradients in wave exposure within shallow subtidal habitats around the offshore islands and coastal headlands.

Temporal variation

Fish distribution records, and long-term ecological studies, provide evidence of inter-annual changes in species compositions of reef fish faunas at some locations in north-eastern New Zealand (e.g., Russell & Ayling 1976; Choat et al. 1988; Francis & Evans 1993; Francis et al. 1999). This temporal variation has mostly involved changes in distribution and abundance of vagrant subtropical and tropical species, which are inferred to disperse to north-eastern New Zealand in watermasses of the Tasman and East Auckland Currents. Most of these species have apparently not established self-maintaining populations in New Zealand. Some are known only from juveniles that intermittently settle in summer months (e.g., *Thalassoma amblycephalum*, *T. lunare*, *T. lutescens*, *Acanthurus dussumieri*; Russell & Ayling 1976; Francis et al. 1999). Others form ephemeral local populations that persist for longer periods of up to several years before dying out (e.g., *Bathystethus cultratus*, *Labracoglossa nitida*, *Kyphosus bigibbus*, *Anampses elegans*, *Coris picta*, *Pseudojuloides elongatus*, *Suezichthys arquatus*; Choat et al. 1988; Francis et al. 1999; F. Brook pers. obs.).

Choat et al. (1988) and Francis & Evans (1993) have suggested that recruitment levels and diversities of such vagrant subtropical and tropical species within north-eastern New Zealand are influenced by long-term variations in sea temperatures, correlated with phases of the El Niño–Southern Oscillation cycle (Greig et al. 1988). They cited evidence for widespread recruitment of subtropical and tropical fish species in eastern Northland during the early 1970s and late 1980s, over periods when sea temperatures in the region were higher than average. However, Francis et al. (1999) noted that there was limited recruitment of subtropical and tropical fish in the region during periods of cooler than average sea temperatures.

The field surveys made for this study, undertaken from 1990 to 1993, coincided with a period of cooler than average sea temperatures that followed the positive temperature anomaly of the late 1980s (Francis et al. 1999, fig. 11). Even so, 26 subtropical and 4 tropical fish species were recorded from the reef sites surveyed in northern and eastern Northland, many of them represented by juveniles (e.g., *Epinephelus daemelii*, *Atypichthys latus*, *Bathystethus cultratus*, *Labracoglossa nitida*, *Kyphosus bigibbus*, *Parma polylepis*, *Anampses elegans*, *Coris sandageri*, *Pseudolabrus luculentus*).

The extent to which temporal variation in fish recruitment alters biogeographic patterning of reef fish faunas in northernmost New Zealand is not directly known. Intradecadal-scale turnover of subtropical-tropical species has been observed in Three Kings and north-eastern Northland faunas (e.g., Choat et al. 1988), but not, as yet, in western Northland faunas. Anecdotal evidence suggests that species turnover, and associated changes in local diversity, are greatest around prominent headlands and offshore islands in north-eastern Northland and, in particular, at the Poor Knights Is, Brett, and outer Karikari Peninsula, contingent on varying ecological influences of oceanic and coastal watermasses.

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Appendices over page

APPENDIX 1 Distribution of near-shore reef fish species at northern New Zealand locations. 1, Sugarloaf Is; 2, Hokianga; 3, Three Kings Is; 4, Reinga; 5, Karikari; 6, Cavalli Is; 7, Bay of Islands; 8, Brett; 9, Mimiwhangata; 10, Poor Knights Is; 11, Whangarei; 12, Leigh; 13, Hen & Chickens Is; 14, Mokohinau Is; 15, Great Barrier I. Biogeographic classification of species (in last column) follows Francis (1996a).

Family	Location															
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Biogeographic classification
Dasyatididae																
Dasyatis brevicaudata (Hutton)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Dasyatis thetidis Waite	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Myliobatididae																
Myliobatis tenuicaudatus (Hector)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Muraenidae																
Enchelycore ramosa (Griffin)	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	Subtropical
Gymnothorax nubilus (Richardson)	0	0	1	0	1	1	0	1	0	1	0	0	1	1	1	Subtropical
Gymnothorax obesus (Whitley)	0	0	1	1	0	0	0	1	0	1	0	0	0	0	1	Subtropical
Gymnothorax prasinus (Richardson)	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Gymnothorax prionodon Ogilby	0	0	0	0	1	1	1	1	0	1	0	0	1	1	0	Warm temperate
Congridae																
Conger verreauxi Kaup	1	1	1	1	1	0	1	1	0	1	1	0	1	1	0	Widespread
Conger wilsoni (Bloch & Schneider)	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	Subtropical
Synodontidae																
Synodus doaki Russell & Cressey	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	Subtropical
Synodus similis McCulloch	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	Subtropical
Moridae																
Lotella rhacinus (Bloch & Schneider)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Pseudophycis bachus (Bloch & Schneider)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Widespread[a]
Pseudophycis barbata Günther	0	0	1	0	1	0	0	1	0	1	1	0	1	1	0	Widespread
Hemiramphidae																
Hyporhamphus ihi Phillipps	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Trachichthyidae																
Optivus elongatus (Günther)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Paratrachichthys trailli (Hutton)	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	Widespread[a]
Berycidae																
Centroberyx affinis (Günther)	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Zeidae																
Zeus faber Linnaeus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Fistulariidae																
Fistularia cf. *commersonii* Rüppell	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	Tropical
Scorpaenidae																
Helicolenus percoides (Richardson)	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	Widespread
Scorpaena cardinalis Richardson	0	0	1	1	1	1	1	1	1	1	0	0	1	1	1	Warm temperate
Scorpaena papillosus (Bloch & Schneider)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Serranidae																
Acanthistius cinctus (Günther)	0	0	0	1	1	1	0	1	0	1	0	0	0	1	1	Subtropical
Aulacocephalus temmincki Bleeker	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	Tropical
Caesioperca lepidoptera) (Bloch & Schneider	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Caprodon longimanus (Günther)	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Epinephelus daemelii (Günther)	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	Subtropical
Epinephelus rivulatus (Valenciennes)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	Tropical
Hypoplectrodes huntii (Hector)	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	Widespread
Hypoplectrodes sp. (halfbanded perch)	0	0	1	1	1	1	0	1	0	1	1	0	1	1	0	Subtropical
Trachypoma macracanthus Günther	0	0	1	0	1	1	0	1	0	1	0	0	1	1	1	Subtropical

Continued

APPENDIX 1 *Continued*

Family Species	Location 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Biogeographic classification
Callanthiidae																
Callanthias australis Ogilby	0	0	1	0	1	1	0	1	0	1	1	1	1	1	0	Warm temperate
Carangidae																
Decapterus koheru (Hector)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Pseudocaranx dentex (Bloch & Schneider)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Seriola lalandi Cuvier & Valenciennes	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Trachurus novaezelandiae Richardson	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	Widespread
Sparidae																
Pagrus auratus (Bloch & Schneider)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Mullidae																
Parupeneus spilurus (Bleeker)	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	Tropical
Upeneichthys lineatus (Bloch & Schneider)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Pempheridae																
Pempheris adspersus Griffin	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Chaetodontidae																
Amphichaetodon howensis (Waite)	0	0	1	0	1	1	0	1	0	1	0	0	0	1	0	Subtropical
Pentacerotidae																
Evistias acutirostris (Temminck & Schlegel)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	Subtropical
Zanclistius elevatus (Ramsay & Ogilby)	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	Warm temperate
Microcanthidae																
Atypichthys latus McCulloch & Waite	0	0	1	1	1	1	0	1	1	1	1	1	0	1	0	Subtropical
Scorpididae																
Bathystethus cultratus (Bloch & Schneider)	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	Subtropical
Labracoglossa nitida McCulloch & Waite	0	0	0	1	1	0	1	1	0	1	1	0	1	1	0	Subtropical
Scorpis lineolatus Kner	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Scorpis violaceus (Hutton)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Girellidae																
Girella cyanea MacLeay	0	0	1	1	1	1	0	1	0	1	0	0	1	1	1	Subtropical
Girella tricuspidata (Quoy & Gaimard)	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Kyphosidae																
Kyphosus bigibbus (Lacépède)	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1	Tropical
Kyphosus sydneyanus (Günther)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Arripidae																
Arripis trutta (Bloch & Schneider)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Chironemidae																
Chironemus marmoratus Günther	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Aplodactylidae																
Aplodactylus arctidens Richardson	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Aplodactylus etheridgii (Ogilby)	0	0	1	1	1	1	1	1	1	1	0	0	1	1	1	Subtropical
Cheilodactylidae																
Cheilodactylus ephippium McCulloch & Waite	0	0	1	1	1	0	0	1	1	1	0	0	0	1	0	Subtropical
Cheilodactylus nigripes Richardson	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	Widespread[a]
Cheilodactylus spectabilis (Hutton)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Nemadactylus douglasii (Hector)	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Nemadactylus macropterus (Bloch & Schneider)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Latrididae																
Latridopsis ciliaris (Bloch & Schneider)	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	Widespread[a]
Latridopsis forsteri (Castelnau)	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	Widespread[a]

Continued over page

APPENDIX 1 *Continued*

Family Species	Location															Biogeographic classification
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Pomacentridae																
Chromis dispilus Griffin	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Chromis fumea Tanaka	0	0	0	1	1	0	1	1	0	1	0	0	1	0	0	Tropical
Chromis hypsilepis (Günther)	0	0	1	1	1	1	0	1	0	1	0	1	1	1	1	Subtropical
Parma alboscapularis Allen & Hoese	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	Subtropical
Parma polylepis Günther	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	Subtropical
Labridae																
Anampses elegans Ogilby	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	Subtropical
Bodianus unimaculatus (Günther)	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	Subtropical
Bodianus sp. (foxfish)	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	Warm temperate
Coris picta (Bloch & Schneider)	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	Subtropical
Coris sandageri (Hector)	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	Subtropical
Notolabrus celidotus (Bloch & Schneider)	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Notolabrus cinctus (Hutton)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	Cool temperate
Notolabrus fucicola (Richardson)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Notolabrus inscriptus (Richardson)	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	Subtropical
Pseudojuloides elongatus Ayling & Russell	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	Subtropical
Pseudolabrus luculentus (Richardson)	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	Subtropical
Pseudolabrus miles (Bloch & Schneider)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Suezichthys arquatus Russell	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	Subtropical
Suezichthys aylingi Russell	0	0	1	1	1	1	1	1	0	1	0	0	1	1	1	Warm temperate
Odacidae																
Odax cyanoallix Ayling & Paxton	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	Warm temperate[b]
Odax pullus (Bloch & Schneider)	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Pinguipedidae																
Parapercis colias (Bloch & Schneider)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Tripterygiidae																
Forsterygion flavonigrum Fricke & Roberts	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Forsterygion lapillum Hardy	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Forsterygion malcolmi Hardy	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Forsterygion varium (Bloch & Schneider)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Karalepis stewarti Hardy	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	Widespread
Notoclinops caerulepunctus Hardy	1	0	0	1	1	1	1	1	0	1	1	0	1	1	1	Widespread
Notoclinops segmentatus (McCulloch & Phillipps)	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Notoclinops yaldwyni Hardy	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Obliquichthys maryannae Hardy	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Ruanoho decemdigitatus (Clarke)	1	1	1	1	0	0	1	0	0	0	1	1	0	1	0	Widespread
Ruanoho whero Hardy	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Blenniidae																
Parablennius laticlavius (Griffin)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Warm temperate
Plagiotremus tapeinosoma (Bleeker)	0	0	1	1	1	0	0	1	1	1	1	1	1	1	0	Tropical
Acanthuridae																
Prionurus maculatus Ogilby	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	Subtropical
Monacanthidae																
Parika scaber (Bloch & Schneider)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	Widespread
Tetraodontidae																
Canthigaster callisterna (Ogilby)	0	0	0	1	1	0	0	1	0	1	0	0	0	1	1	Subtropical
Diodontidae																
Allomycterus jaculiferus (Cuvier)	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	Widespread

[a]Rare in northern and eastern Northland. [b]Restricted endemic; Three Kings Is and northern Northland.

APPENDIX 2 Distributions of reef fish species among Northland sites. Geographic areas: Hokianga (A1–6); Three Kings Is (T1–12); Reinga (R1–17); Karikari (K1–20); Bay of Islands (B1–18); Brett (B19–24); Poor Knights Is (P1–10); Whangarei (W1–15); Hen & Chickens Is (H1–15).

Family Species	Sites
Muraenidae	
Enchelycore ramosa	T4, R6, K10, K12, K13, P3, P6
Gymnothorax nubilus	T1, T2, T5, T10, K4, K5, K7–9, K11–13, B21, B23, B24, P1–10
Gymnothorax obesus	T1, T4–7, T11, T12, R5, R11–13, P1, P2, P4–6, P8
Gymnothorax prasinus	R2, R4, R6, R11–15, K3–8, K10–18, B1, B15–17, B19–23, P1–10, W4, W7, W9–15, H1–11, H14, H15
Gymnothorax prionodon	K4, K7, K13, B17, B19, B21, P6
Congridae	
Conger verreauxi	A5, A6, T2, T11, T12, K4, B5, B21, W1, W6, W7, W15
Conger wilsoni	R4, K2, K9, B1, B7, B14, B15, B18–20, W15, H2, H6, H7, H10, H11
Moridae	
Lotella rhacinus	A4, A6, T1, T3–5, T8–12, R7, K6, K7, B4, B6, B13, B14, B16, B20–23, P1, P4–7, W1, W9–11, H1, H4, H9, H12
Pseudophycis barbata	T1, T4–6, T11, T12, K4, K7, W15, H15
Trachichthyidae	
Optivus elongatus	A5, A6, T1, T2, T4, T5, T7–9, T11, T12, R2–15, K1–4, K6–18, B1–5, B7, B9–24, P1–9, W1, W4, W7–15, H1–15
Paratrachichthys trailli	A5, A6, T1, T12, B22
Berycidae	
Centroberyx affinis	T1–6, T8–12, K4, K7, K8, K12, K13, B1, B19–21, B23, B24, P2, P5–10, W15, H9, H11, H15
Zeidae	
Zeus faber	T4, R4, R6, R12, R13, K4, K8, K11, K12, K18, K20, B1, B5, B9, B15, B19, B20, B22, P3, P4, P9, W1, W3, W4, W6–8, W10–15, H5, H9, H11, H13–15
Scorpaenidae	
Helicolenus percoides	T11, K4, K12
Scorpaena cardinalis	T4, T5, T11, R2, R4, R6, R9, R11, R12, R14, R17, K4–8, K10–16, B17–24, P1–10, H3, H4, H8, H9, H11
Scorpaena papillosus	A1, A3–6, T1, T2, T4, T7–12, R3, R7, R10, R12, R13, R15, R16, K4, K5, K7–9, K11, K12, B1–5, B13, B16–19, B21, B22, B24, P4, P8, P9, W1, W3, W4, W6, W9–12, W14, W15, H1, H2, H4, H6, H9–15
Serranidae	
Acanthistius cinctus	R11, K12, K14, B21
Caesioperca lepidoptera	T1–4, T6–12, R11, K4, K7, K8, K11–13, B1, B5, B16, B18–24, P1–10, W1, W3, W4, W7, W9–11, W14, W15, H1–6, H9–11, H13–15
Caprodon longimanus	T1–4, T7, T8, T11, T12, K4, K7, K8, K11–13, B1, B21, B24, P1, P2, P4–10, W4, W15
Epinephelus daemelii	T1, T4, T12, R2, R13, R15–17, K11, K12, P5
Epinephelus rivulatus	P4
Hypoplectrodes huntii	A4–6, T1, T2, T4, T5, T7, T9, T12, R11, K4, B17, B19, B20, B24, W9–11, W14, W15, H2, H11, H13–15
Hypoplectrodes sp.	T1, T2, T4, T6–9, T11, T12, R6, K4, K7, K8, K11–13, B20, B21, B23, B24, P1–10, W15, H1, H4, H5, H9, H14, H15
Trachypoma macracanthus	K7, K11, B21, P1, P7, P9, P10, H4
Callanthiidae	
Callanthias australis	T11, K8, K12, B21, B24, P2, P8, W15
Carangidae	
Pseudocaranx dentex	A3–6, T2–4, T6, T7, T9, T11, T12, R1–3, R5–7, R10–15, K1, K2, K7, K8, K13–15, K19, K20, B1, B15, B17, B19, B20, B22–24, P2–4, P6, P8, W3, W11–14, H1, H12, H13

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APPENDIX 2 *Continued*

Family Species	Sites
Sparidae	
Pagrus auratus	T5, R6, R10, R12, R13, K3–7, K10–16, K18, K19, B1–3, B9–24, P1, P4, P10, W4, W11, W14, W15, H3, H4, H8, H11, H13
Mullidae	
Parupeneus spilurus	B22
Upeneichthys lineatus	A5, A6, T2–4, T7, R1–6, R8, R10–16, K1–16, K18–20, B1–5, B7–24, P1–10, W1–15, H1–15
Pempheridae	
Pempheris adspersus	T2, T7, R2–14, R16, K1–7, K9–18, K20, B1–24, P1–10, W4, W5, W7–15, H1–15
Chaetodontidae	
Amphichaetodon howensis	K7, K8, B21, B24, P6, P7
Pentacerotidae	
Zanclistius elevatus	P1, P2, P5, P6, P8
Microcanthidae	
Atypichthys latus	T2, T6, T8, K7, B21, B24, P3, P4, P6–8
Scorpididae	
Bathystethus cultratus	B21, H4
Labracoglossa nitida	R2–4, R6, K5, K8, K10, K11, K14, K18, B16, B24, W9, W14, H11
Scorpis lineolatus	A4–6, T2, T6, T7, R1–17, K1–5, K7–20, B1, B2, B4, B5, B7, B9–11, B13–19, B21–23, P2–7, P10, W1, W3–15, H1–15
Scorpis violaceus	T2–12, R1–15, R17, K1, K2, K4–12, K14, K15, K18, B1, B2, B4, B9–11, B13–19, B21–24, P1–10, W4, W7–15, H1–15
Girellidae	
Girella cyanea	T4, B24, P3, P4, P7, P10, H3, H11
Girella tricuspidata	A1, A3–6, R1–17, K1–7, K9–15, K17–20, B1–24, P1, P10, W1–15, H1–15
Kyphosidae	
Kyphosus bigibbus	K14, B21, P10
Kyphosus sydneyanus	A4, T5, R2, R7, R11, R12, K2, K3, K7, K9–12, K14, B2, B5, B11, B13, B15, B19, B21, P3, P6, P10, W8, W10, W11, W14, W15, H1–14
Chironemidae	
Chironemus marmoratus	A1–6, R1–12, R14–16, K1–15, K17–19, B1–5, B9–24, P1–8, W4, W7–15, H1–15
Aplodactylidae	
Aplodactylus arctidens	A1–4, T1–12, R1–15, K2, K4–19, B1, B13–24, P1, P2, P4–6, P8–10, W7, W10, W12–15, H1–11, H13–15
Aplodactylus etheridgii	R1, R7, R12, R13, K12–14, B16, B21, B22, B24, P1, P5, P7, P10, H1
Cheilodactylidae	
Cheilodactylus ephippium	T7, R10, R13, R14, K15, B22, P7
Cheilodactylus spectabilis	A1–6, T1–12, R1–17, K1–19, B1, B2, B4, B5, B9–11, B13–24, P1–10, W3, W4, W7–15, H1–15
Nemadactylus douglasii	T1–12, R4, R6, R13, R15, K3, K4, K7, K10, K12–14, K17, K18, B4, B5, B14, B16, B19–21, B23, P1–10, W10, W12, W15, H1–9, H11, H13–15
Latrididae	
Latridopsis ciliaris	T1, T4–6, T8, T9, T11, T12, R2, R10, R13, R15, K9, K12, B14, P1, P2, P9, W15
Latridopsis forsteri	B24
Pomacentridae	
Chromis dispilus	A5, T1–12, R3, R6, R7, R11–13, K3–16, B1, B2, B4, B5, B12–24, P1–10, W3, W4, W7, W9–15, H1–15

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APPENDIX 2 *Continued*

Family Species	Sites
Chromis hypsilepis	T4, T8, T11, R6, R13, K4, K7, K10–14, K18, B19, B20, B22, P2, P3, P5, P6, P8, P9, H1–3, H6
Parma alboscapularis	R2, R3, R7–9, R11, R12, R15, K2, K3, K5, K6, K9–14, B1, B15–19, B21–23, P1–10, W11, W12, W14, H1–11, H13–15
Parma polylepis	K5
Labridae	
Anampses elegans	B22, B23, P3
Bodianus unimaculatus	R11–13, K4–16, B5, B16, B19–24, P1–10, W15, H1–7, H9, H13, H14
Bodianus sp. (foxfish)	B24, P9
Coris picta	B24, P9
Coris sandageri	T2, T8, T9, R1, R2, R6, R8, R10–13, K3–5, K7–16, K18, B1, B14–24, P1–10, W10, W14, H1, H2, H4, H5, H7, H8, H10–12, H14, H15
Notolabrus celidotus	A1–3, A5, A6, R1–17, K1–6, K8–20, B1–23, P1–5, P10, W1–15, H1–15
Notolabrus fucicola	A1–6, T1–12, R1–15, K1–20, B1–4, B13–24, P1–10, W3, W4, W6–15, H1–12, H14, H15
Notolabrus inscriptus	K4, K7, K12, K17, B23, B24, P1–4, P7, P10, W10, W12, H2, H3, H11
Pseudolabrus luculentus	T4, T7, T8, R8, R11, R13, K4, K7, K8, K10–13, K15, B1, B16, B20–24, P1–10, H2, H4, H5, H9
Pseudolabrus miles	A4–6, T1–12, R6, R11, R12, K4, K5, K7, K8, K11–13, B4, B5, B21, B24, P1–10, W4, W9–11, W14, W15, H1–5, H9–11, H15
Suezichthys arquatus	R6, R13, K4, K7, K12, B4, B20, B23, P4, P6, P9
Suezichthys aylingi	T1–12, R6, R11, K4, K7, K11–13, B16, B19, B21, B23, B24, P1–10, H5
Odacidae	
Odax cyanoallix	T1–12, R1, R6
Odax pullus	A5, A6, R1–8, R10–13, R16, K2–5, K7, K9–14, K19, K20, B1, B2, B4, B5, B13, B15–17, B19–23, P1, P2, P5, P6, P8–10, W7–11, W13, W14, H1–6, H8, H10–12, H15
Pinguipedidae	
Parapercis colias	A4–6, T1–10, T12, R1, K2, K4, K7–10, K12, K14, K17, K18, B5, B21, P6, W1, W3, W4, W10, W11, H12, H14
Tripterygiidae	
Forsterygion flavonigrum	A5, A6, T3, T4, T8, T12, R1–3, R6, R7, R11–13, R15, R17, K4–14, B1, B2, B4, B5, B14–24, P1–10, W3, W4, W9–15, H1–15
Forsterygion lapillum	A1–3, A5, A6, R1–17, K1–6, K9–20, B1–23, P3, P4, W1–14, H1–15
Forsterygion malcolmi	A4–6, T1, T3, T4, T8–10, T12, R1–3, R6, R8, R9, R11, R13, R15, K2, K4–16, K18, B1–5, B7, B13–24, P2, W1, W3, W4, W9–12, W14, W15, H1–5, H7, H9–15
Forsterygion varium	A1, A3–6, T2, T3, T5–9, R1–15, K1–6, K8–20, B1–23, P1, P2, P8–10, W3–15, H1–15
Grahamina capito	A1, A5, K20, B8, W1, W2
Karalepis stewarti	T1, T3–6, T10, T12, R2–5, R11, R12, R15, K5, K7, K9–11, B5, B15, B17, B21–23, P3, P8, P10, H2, H3, H6, H8, H9, H11–13, H15
Notoclinops caerulepunctus	R2, R3, K4, K12, K13, K15, B1, B14, B16–21, B24, P1, P7–10, W9, W11, W14, H1, H10
Notoclinops segmentatus	R2–17, K1–20, B1–24, P1–10, W4, W7–15, H1–15
Notoclinops yaldwyni	A1, T2–10, R2–12, R14, R15, K2–5, K7–14, K18, B1, B4, B13, B14, B16–24, P1, P2, P4–10, W9, W12, W13, W15, H–12, H14–15
Obliquichthys maryannae	A6, T1–4, T6–10, R2, R3, R6–17, K2–20, B1–5, B11, B12, B14–24, P1–10, W3, W4, W6, W9–15, H1–15
Ruanoho decemdigitatus	A1, A2, A6, R4, R10, W2, W4, W5

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APPENDIX 2 *Continued*

Family Species	Sites
Ruanoho whero	A1, A2, A4–6, T2, T3, T5–10, R2–15, R17, K1–5, K7–20, B1–5, B7–24, P1–10, W1, W3–15, H1–15
Blenniidae	
Parablennius laticlavius	A1, A2, A5, T2, T6, R2–4, R6, R8, R9, R11–13, R15, R16, K1–5, K7–18, K20, B1, B2, B4, B8, B9, B11, B13–24, P1–10, W1–4, W7–11, W14, W15, H1, H3–7, H9–12, H14, H15
Plagiotremus tapeinosoma	R6, R12, B20, B21, P3, P5–7, W9, W14
Monacanthidae	
Parika scaber	T1–12, R1–16, K1–20, B1–5, B12–24, P1–10, W4, W7–15, H1–15
Tetraodontidae	
Canthigaster callisterna	R11, R12, K7, K8, K11–13, B19–21, B23, B24, P1–10
Diodontidae	
Allomycterus jaculiferus	T1, K8, K10, K13, B17, B18, B20, B22, B23, H3