Consistent spatial patterns across biogeographic gradients in temperate reef fishes

Maren Wellenreuther, Craig Syms and Kendall D. Clements

M. Wellenreuther (Maren.Wellenreuther@zooekol.lu.se) and K. D. Clements, School of Biological Sciences, Univ. of Auckland, Private Bag 92019, Auckland, New Zealand. (Present address of M. W.: Dept of Animal Ecology, Lund Univ., Ecology Building, Sölvegatan 37, SE-223 62 Lund, Sweden.) – C. Syms, School of Marine and Tropical Biology, James Cook Univ. of North Queensland, Townsville, Queensland, Australia.

Biogeographic gradients may facilitate divergent evolution between populations of the same species, leading to geographic variation and possibly reproductive isolation. Previous work has shown that New Zealand triplefin species (family Tripterygiidae) have diversified in habitat use, however, knowledge about the consistency of this pattern throughout their geographic range is lacking. Here we examine the spatial habitat associations of 15 New Zealand triplefin species at nine locations on a latitudinal gradient from 35°50′S to 46°70′S to establish whether distant populations differ in habitat use. Triplefin diversity and density varied between locations, as did habitat variables such as percentage cover of the substratum, onshore-offshore location, microposition, depth and exposure. Canonical discriminant analysis identified specific species-habitat combinations, and when habitat was statistically partialled from location, most species exhibited consistent habitat associations throughout their range. However, the density of a few species at some locations was lower or higher than expected given the habitat availability. This indicates that the habitat variables recorded were not the sole predictors of assemblage structure, and it is likely that factors influencing larval dispersal (e.g. the low salinity layer in Fiordland and geographic isolation of the Three Kings Islands) play an additional role in structuring assemblage composition. Together these results suggest that New Zealand triplefin species show strong and consistent habitat use across potential biogeographical barriers, but this pattern appears to be modified by variation in larval supply and survival. This indicates that species with broad geographic distributions do not necessarily show phenotypic variation between populations.

Many species have wide ranging distributions and thus are subject to strong biogeographic gradients, particularly at the limit of their distributional range (Rosenzweig 1995). As a consequence, different populations of a species may experience selection in opposing directions, which might present an opportunity for the generation and maintenance of phenotypic variation between them (Endler 1977). Phenotypic differences between populations have been demonstrated for a wide variety of species (Cox and Moore 2005), and may over time lead to the splitting of a subdivided species into reproductively isolated units in spite of migration (Endler 1977).

Many marine fishes have pelagic larvae that disperse over long distances (Kinlan et al. 2005) and this has caused local selection to be neglected as a potential source of variation. However, growing evidence suggests that a long pelagic larval phase does not necessarily result in even recruitment among sub-populations (Taylor and Hellberg 2003). Larval exchange between geographic areas is affected by a number of factors, including the behavioural and physiological capabilities of larvae (Leis and McCormick 2002, Taylor and Hellberg 2003) and habitat availability at locations

(Kinlan et al. 2005). Thus, interindividual variation in larval capabilities in combination with environmental differences across biogeographic gradients provides a fertile ground for the evolution of geographic differences between populations.

The purpose of this study was to investigate the habitat use of New Zealand triplefin fishes (Family Tripterygiidae) across a latitudinal and biogeographical gradient to assess geographic variation in this endemic group. Previous work has shown that New Zealand triplefin species use species-specific habitats (Syms 1995, Feary and Clements 2006, Wellenreuther et al. 2007a, b) and that spatial differences affect mate choice (Wellenreuther and Clements 2007), but data on the consistency of this pattern around coastal New Zealand are lacking. New Zealand's temperate reefs occur as far north as the Three Kings Islands (34°S latitude) and as far south as Campbell Island (52°S latitude), imposing a strong biogeographic gradient in environmental conditions, which is reflected in the abundance and distribution of many New Zealand reef fishes (Paulin and Roberts 1992, Francis 1996). Most coastal fishes are either distinctly northern or southern in distribution, with few species

equally abundant throughout New Zealand (Paulin and Roberts 1992, Francis 1996, Francis and Nelson 2003). Triplefin fishes form an exception, with 23 of the 26 New Zealand triplefin species being sympatric all around coastal New Zealand, and no species are known to display latitudinal trends in abundance (Paulin and Roberts 1992, Fricke 1994, Francis 2001, Clements 2003). The three species for which the distribution is not sympatric with the rest of the New Zealand triplefin assemblage are *Enneapterygius kermadecensis*, *Apopterygion oculus* and *Matanui bathytaton* (Fricke 1994). *Enneapterygius kermadecensis* is endemic to the subtropical Kermadec Islands, *A. oculus* is restricted to the southern half of the North Island and south-east of the South Island and *M. bathytaton* has not been recorded north of the subtropical convergence (Fricke 1994, Jawad and Clements 2004). The remaining 23 New Zealand triplefin species are distributed circumcoastally over 13° of latitude where there is suitable habitat (Fricke 1994, Clements 2003). The wide ranging distribution of all New Zealand triplefin species is presumably related to the long larval dispersal phase, with estimates ranging between 2 and 3 months (Kingsford and Choat 1989, McDermott and Shima 2006). Given the wide distribution of triplefin fishes in New Zealand and the environmentally diverse coastline (Francis and Nelson 2003), it becomes apparent that triplefin populations are exposed to biogeographic gradients that provide the potential for geographic variation.

The overall aim of this study was to determine if, and to what extent, habitat use of New Zealand triplefin fishes is consistent across biogeographical scales along a latitudinal gradient from 35°50′S to 46°70′S. Our first objective was to describe the triplefin assemblage composition and habitat availability at different locations, and to examine the habitat associations of populations of the same species exposed to different biogeographic gradients. The second objective was to account for the effect of local habitat characteristics on triplefin habitat use by partialling out the habitat effects from the location. This approach enabled us to identify whether populations differ in habitat use, and whether the presence of habitat types at particular locations could limit or enhance the relative density of species. Strongly divergent habitat characteristics between populations of the same species would be interpreted as evidence for geographic variation in habitat traits, whereas uniform habitat use of a species across biogeographic gradients would be seen as evidence for consistent habitat selection by a species.

Materials and methods

Collection of data

The habitat use of adult triplefin species was quantified at nine locations around coastal New Zealand from 2002 to 2004 (Fig. 1). Although some locations were sampled in different years it is unlikely that this confounded the results because triplefin abundance patterns are temporally stable over small (between transects: Connell and Jones 1991, Syms and Jones 1999) and large scales (between locations: Wellenreuther et al. unpubl.). The habitat measures ranged

from large between-site (e.g. exposure) to intermediate within-site scale (e.g. depth) and to fine-scale microhabitat characteristics (substratum types and fish microposition). The locations covered a geographic range from 35°50′S to 46°70′S and included the Three Kings Islands (35°50′S, 172°10′E), the Coromandel Peninsula (36°29′S, 175°19′E), exposed offshore islands in the Hauraki Gulf (36°94′S, 174°57′E), sheltered Hauraki Gulf (36°70′S, 175°68′E), mainland Hauraki Gulf (36°32′S, 174°51′E), Napier (39°29′S, 176°55′E), Wellington (41°16′S, 174°51′E), Fiordland (45°30′S, 167°00′E) and Stewart Island (46°70′S, 168°20′E). The characteristic features of the locations have been described in detail elsewhere (Wellenreuther et al. 2007a).

Within each location underwater visual counts (UVC, 4 × 4 m) were conducted at randomly selected sites with the aim of sampling as much of the exposure gradient as was practically possible. All UVC were done by the same diver and consisted of a close, rigorous and systematic searching pattern, spending at least 1 min on each quadrat (1 × 1 m), with all interstices and overhangs examined to ensure a complete census. Because all sites were surveyed by the same observer, the data were comparable and could be used in the analyses. Prior to sampling, a location fix was taken for each site using a handheld Garmin® 12 global positioning system (accuracy ± 15 m) and a physically derived exposure index was calculated based on the total sum of the fetch (maximum radial distance 300 km). Fetch calculations were performed with the program "Fetch Effect Analysis" (program available from: < cr_pickard@hotmail.com >), which measures fetch distance for each 20 degree sector on a compass rose from a given point.

At least three 4 × 4 m quadrats were laid out on each site, and the minimum distance between quadrats was 50 m. The first quadrat at each site was done at the deepest depth that could safely be sampled, and the two subsequent quadrats at approximately 33 and 66% of the deepest depth. Any additional quadrats were conducted in intermediate depths, but were always at least 50 m from any other quadrat that had been sampled. This design was employed to allow sampling flexibility throughout sampling locations and avoided dependent sampling. The centre line of each quadrat was marked with a leaded line, and a steel quadrat used to outline each 1 m² along the quadrat. For each 1 m² quadrat the depth was recorded and eleven habitat variables estimated visually as percent cover of the substratum: rock (rocks >7 cm); horizontal rock face (rocks >7 cm); vertical rock face (rocks >7 cm); cobbles (rocks <7 cm); gravel (rocks <4 cm); sand; mud; *Ecklonia radiata*; *Carpophyllum* spp.; other macroalgae; and coralline and turfing algae. While the first seven variables always sum to 100%, algal coverage could range from 0 to 100%.

The fish within each quadrat were identified. Triplefin species that were found in at least two locations were analysed and included *Bellapiscis lesleyae* (n = 176), *Cryptichthys jojettae* (n = 235), *Forsterygion flavonigrum* (n = 942), *F. lapillum* (n = 3886), *F. malcolmi* (n = 346), *F. varium* (n = 2102), *Grahamina capito* (n = 879), *G. nigripenne* (n = 337), *Karalepis stewarti* (n = 75), *Obliquichthys maryannae* (n = 1495), *Notoclinops segmentatus* (n = 2328),
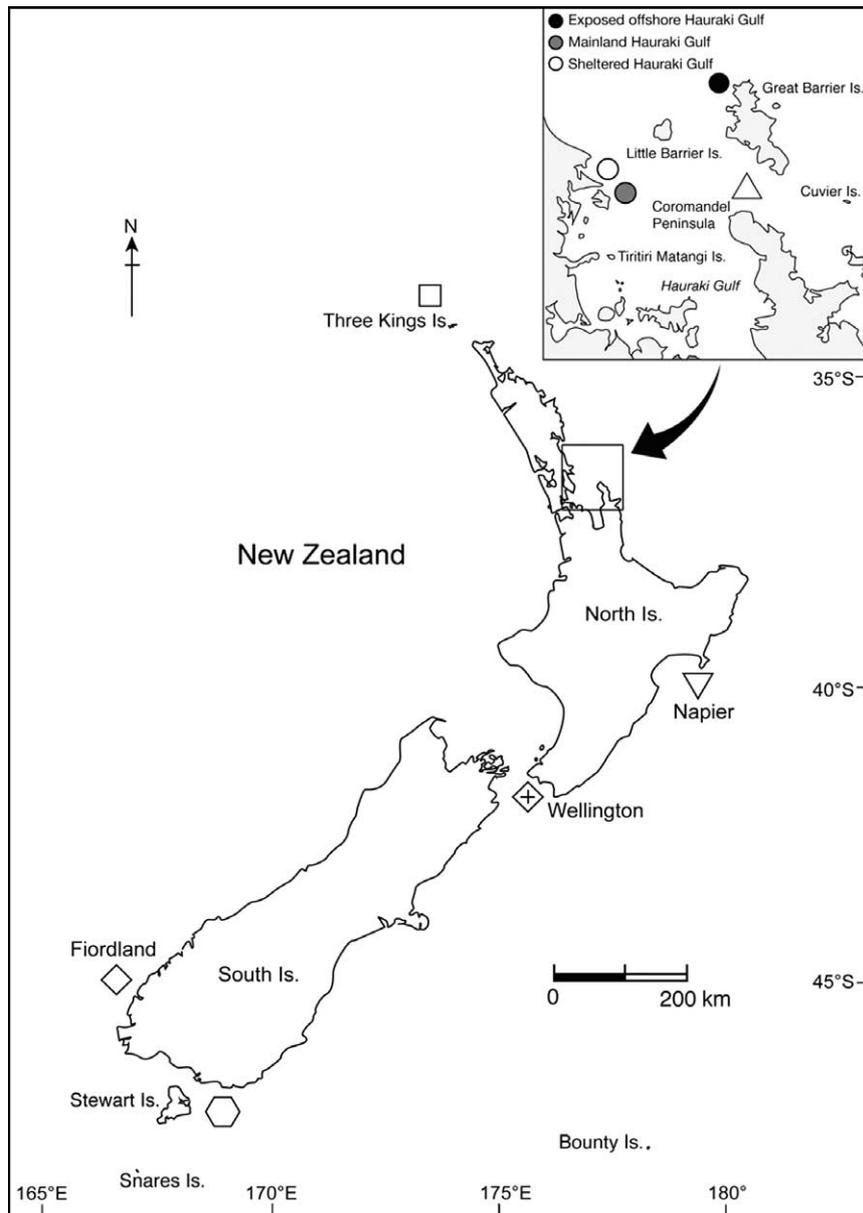
Fig. 1. Location of study areas in New Zealand. □ Three Kings Islands; △ Coromandel Peninsula; ⬩ Wellington; ● exposed offshore Hauraki Gulf; ⬤ mainland Hauraki Gulf; ○ sheltered Hauraki Gulf; ▽ Napier; ◇ Fiordland; ⬡ Stewart Island.

N. yaldwyni (n = 453), *N. caerulepunctus* (n = 245), *Ruanoho decemdigitatus* (n = 232) and *R. whero* (n = 1644).

Data analysis

Fish and habitat variables were initially examined for excessive skew and bivariate non-linearities. Square-root transformations were found to decouple variance-mean relationships and improve bivariate linearity for both fish and habitat measures, so this transformation was used across all habitat variables. Analysis of abiotic (e.g. substratum type, depth, exposure) and biotic habitat (e.g. macroalgal cover) was carried out by canonical discriminant analysis

(CDA) of the variables using the location as the classification variable, in combination with summary graphs of mean habitat types across localities. The appropriateness of the constrained (by location) analysis was checked by comparing CDA results with a principal components analysis of the same data. The dominant signals in the data were associated with location differences, so the constrained CDA ordination was used to display habitat differences between locations.

Habitats differed between locations, which presented a problem in quantifying triplefin assemblages and habitat associations independent of habitat distributions at locations. Therefore, we used an approach based on partial canonical correlation to independently measure the relative

effects of continuous habitat variables and categorical location differences on triplefin assemblages, and calculated the variance explained by habitat, location, and their interaction (see for a related example Borcard et al. 1992). One computational difficulty with this approach was that location was a categorical variable, and could not be used either as a partial or a correlation variable in the software. This problem was resolved by recoding location as a set of effects-coding variables, which replaced a single categorical variable with a set of $n-1$ variables. These variables were assigned a value of 1 if the sample came from the location associated with the new variable or zero otherwise – except for the last location category which was assigned a value of -1 for each variable. This was necessary to avoid linear dependency of the variables. This approach is implicitly used in most general linear model software (e.g. Littell et al. 2002), and a canonical correlation on variables coded in this way is indeed mathematically equivalent to a CDA. Two canonical correlations were carried out: 1) the correlation of triplefins with habitat variables after partialling location effects (standard partial canonical correlation, which assesses the effect of the habitat alone), and 2) the correlation of triplefin species with the multiple location variables, after partialling habitat effects (equivalent to a partial CDA, to assess the effect of the spatial variability (location) alone). Statistical significance of the variance fractions was assessed by a permutation test, in which the fish rows of the data table were randomly reordered 1000 times, and the analysis recalculated. The observed sum of the Eigenvalues for a given fraction (i.e. the amount of variation explained in the fish data by the habitat and location effects) was compared to the distribution of the Eigenvalue sums of the permuted data sets to yield a significance test. Confidence intervals of the variance fractions were calculated using a bootstrap approach (n = 100).

Results

Most locations contained mixed amounts of hard and mobile substrata such as rocks, cobbles and gravel, and soft sediments like sand and mud (Fig. 2). Similarly, most locations contained varying amounts of coralline and turfing algae as well as brown macroalgal types (Fig. 3). In combination, however, both biotic and abiotic habitat types were typical of particular locations with no clear correlation with latitude. For example, the habitat structure at the Three Kings Islands, beyond the northern tip of mainland New Zealand (Fig. 1), was similar to habitat at exposed sites of the Hauraki Gulf in north-eastern and Stewart Island in southern New Zealand (Fig. 4). These exposed locations were characterised by a combination of high density of *Ecklonia radiata,* and coralline and turfing algae (Fig. 4), and hard substratum categories such as rock, vertical rock faces, and horizontal rock faces (Fig. 2). Some deep and sheltered sites at Stewart Island, however, differed from the Three Kings Islands and exposed Hauraki Gulf sites, in being dominated by mud and sand (Fig. 2). In contrast, sheltered sites in the Hauraki Gulf were more similar to sheltered sites in Wellington and Napier and characterised by shallow depths, *Carpophyllum* spp. (Fig. 3, Fig. 4), and soft and mobile benthic substrata such as gravel, cobble and mud (Fig. 2). Fiordland sites were unique in
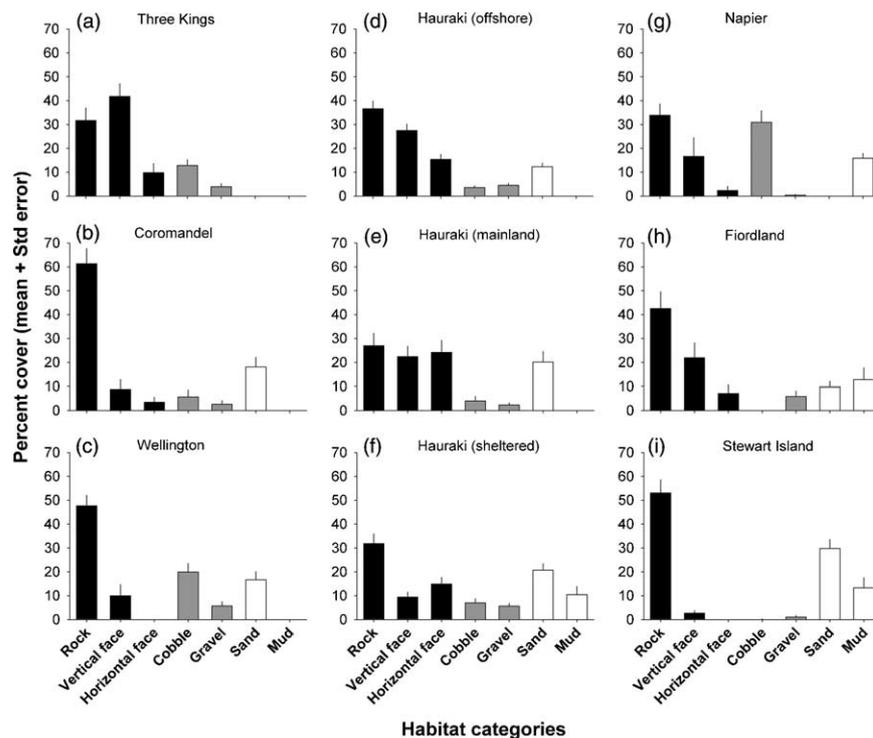

Fig. 2. Abiotic habitat composition at different biogeographic locations in New Zealand. Hard substratum classes are depicted with black shading, mobile hard substratum with grey shading, and soft sediment classes with white shading.
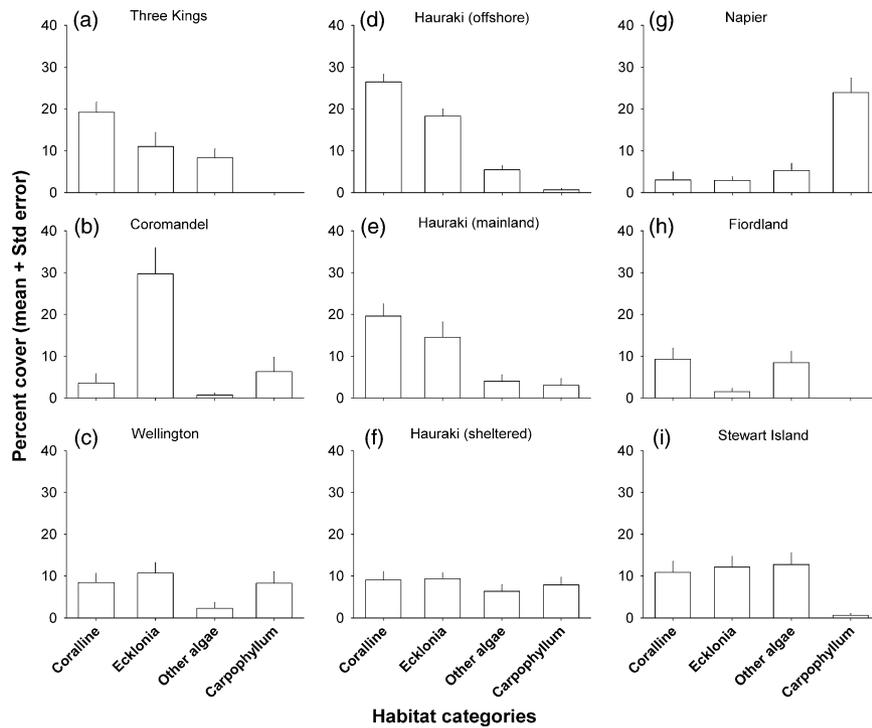
Fig. 3. Biotic habitat composition at different biogeographic locations in New Zealand. The coralline category includes encrusting and turfing forms.

their habitat structure in that the inner fiords were characterised by deep and sheltered basins that were covered with mud and little *Ecklonia radiata* cover (Fig. 4), although shallow vertical rock faces were present. Coralline and turfing algae were either numerically dominant or equally abundant to brown algal cover across most exposed
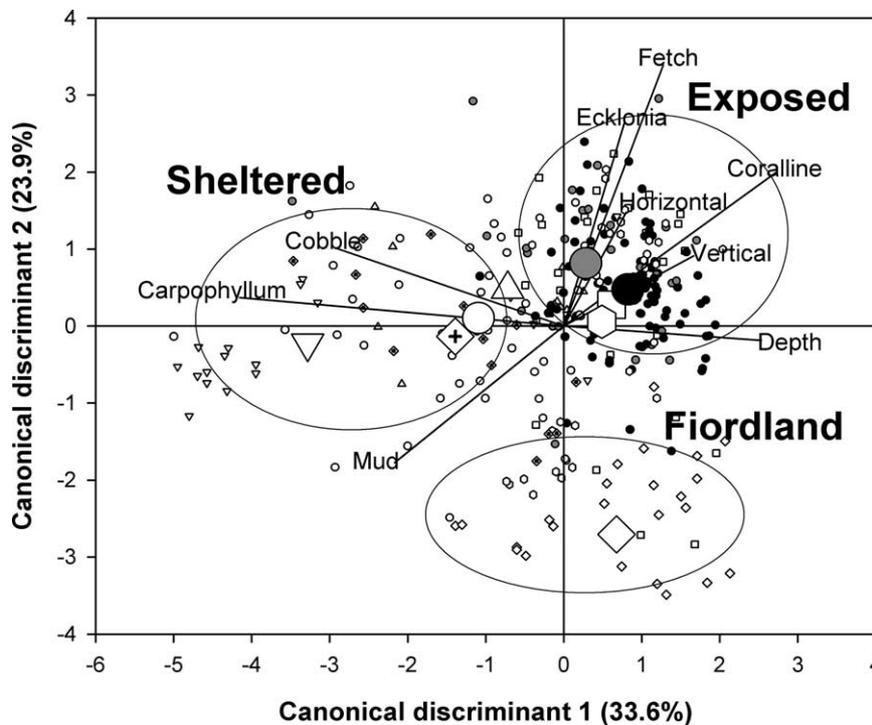

Fig. 4. Canonical discriminant analysis of habitat variables among biogeographic locations in New Zealand. □ Three Kings Islands; △ Coromandel Peninsula; ⨁ Wellington; ● exposed offshore Hauraki Gulf; ● mainland Hauraki Gulf; ○ sheltered Hauraki Gulf; ▽ Napier; ◇ Fiordland; ⬡ Stewart Island. Habitat vectors are structure coefficients, multiplied by 5 to improve clarity. Rock, gravel, sand and other macro algae were not strongly associated with either axis, and are not presented on the plot.

sites, with sheltered sites such as Napier characterized by the brown algae *Carpophyllum* spp., and the Coromandel sites dominated by the brown alga *Ecklonia radiata* (Fig. 3).

Different locations contained different densities of triplefin species (Fig. 5). However, as biotic and abiotic variables differed between locations it was important to distinguish between differences in triplefin assemblage due to habitat versus other intrinsic and perhaps unmeasured location differences. Habitat, independent of location, explained $15.42 \pm 0.31\%$ of the variation in the data set and was characterised by a set of predictable species-habitat associations (Fig. 6). *Forsterygion lapillum* and *R. decemdigitatus* were associated with shallow cobble and *Carpophyllum* spp. habitats (Fig. 6). In contrast, *N. segmentatus, R. whero,* and *N. yaldwyni* were associated with *Ecklonia radiata*-covered rocky and exposed habitats (Fig. 6). *Notoclinops caerulepunctus* and *F. malcolmi* were associated with deep rocky habitats, and *F. flavonigrum* were associated with deep habitats with either rocky or soft substrata (Fig. 6). *Grahamina nigripenne* and *G. capito* were primarily found on mud and sand in shallow and sheltered sites (Fig. 6).

Although fish-habitat associations were obviously important predictors of the triplefin assemblage location effects, $12.12 \pm 0.24\%$ of the variance was explained by the location, after partialling habitat. Three partial canonical discriminant axes, each explaining approximately equal amounts of variation (from 21.5 to 27.3%), identified three location-specific differences in triplefin assemblage composition that were not accounted for by habitat variables (Fig. 7). On the first axis, Napier, Wellington, and some quadrats in the Coromandel locations had greater densities of *F. varium, R. decemdigitatus,* and *F. malcolmi* than would be predicted by habitat alone compared to other locations

(Fig. 7a), however these differences were generally due to small changes in density of these species (Fig. 5). The second axis reflected differences between the Three Kings Islands and the offshore and mainland Hauraki Gulf locations (Fig. 7a). The Three Kings Islands had a comparatively depauperate fauna, with relatively low fish densities and the notable absences of numerically dominant mainland Hauraki Gulf species such as *N. segmentatus* and *F. lapillum* and small but notably higher densities of *C. jojettae* (Fig. 5). The third axis distinguished Fiordland from other sites due to higher densities of *G. capito, F. flavonigrum,* and *O. maryannae* than would be predicted by habitat alone (Fig. 7b). In general, location differences that were independent of habitat were usually idiosyncratic, and occasionally due to differences in the density of species that were relatively uncommon. In addition to main effects of habitat and location, there was also an interaction effect between habitat and location that explained $11.35 \pm 0.23\%$ of the variation. This fraction had no obvious biological interpretation, and probably reflected the uniqueness of some habitat and site combinations, such as the presence of mud habitats at some deep sites in Fiordland and Stewart Island.

Discussion

The abundances of species with wide ranging distributions frequently vary across biogeographic gradients either as a result of local selection, variability in recruitment, or both (Endler 1977, Rosenzweig 1995, Taylor and Hellberg 2003, Kinlan et al. 2005). New Zealand triplefin fishes offer an opportunity to test the effects of biogeographic gradients on habitat use patterns in a diverse group of fishes,
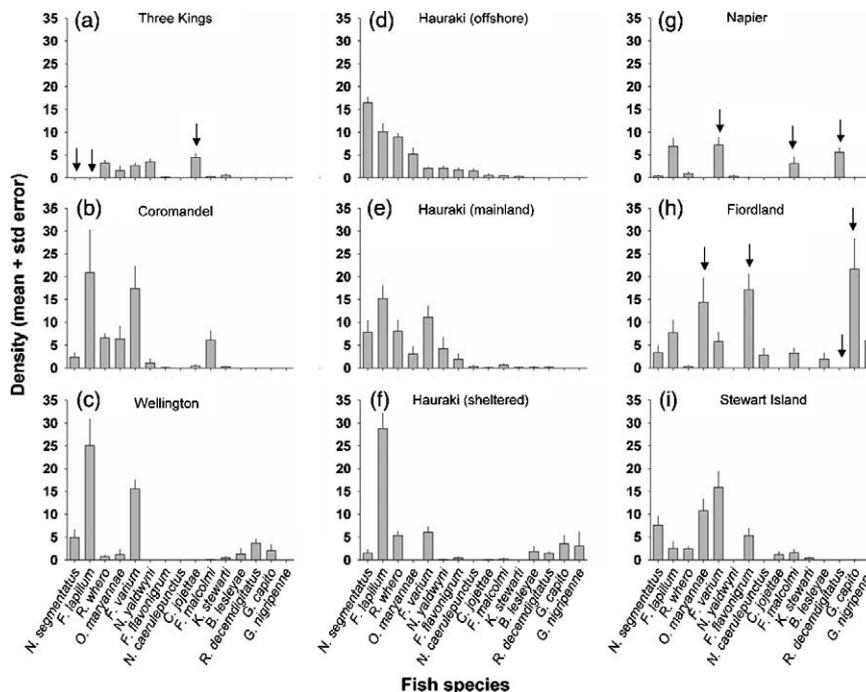

Fig. 5. Triplefin densities at different biogeographic locations in New Zealand. Density estimates are per quadrat (16 m^2). Arrows indicate species in which the density was lower or higher than expected given the habitat availability.
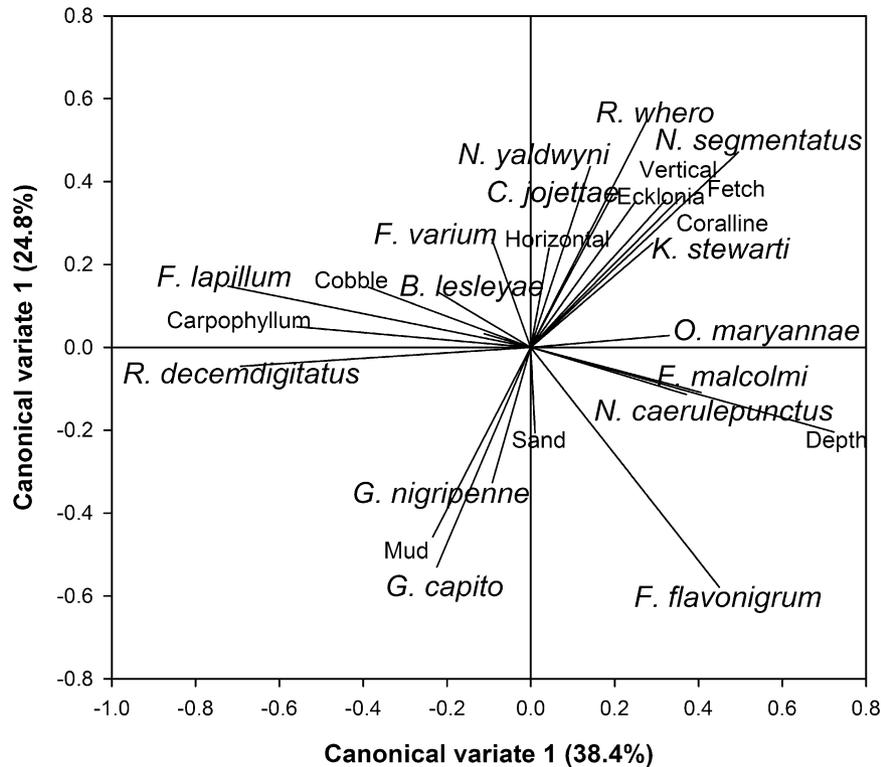
Fig. 6. Partial canonical correlation of fish and habitat variables, after correcting for biogeographic variation. Vectors are structure coefficients of variables in the ordination space defined by the habitat variables. Species with a structure coefficient of <0.15 were not presented on the plot.

as all species show species-specific habitat use (Syms 1995, Feary and Clements 2006, Wellenreuther et al. 2007a) and have broad distributions around coastal New Zealand (Paulin and Roberts 1992, Fricke 1994, Francis 2001, Clements 2003). The results of this study show that the density of triplefin species was highly variable between locations, but that this pattern could, in most cases, be explained by local habitat availability. Therefore, the close relationship between habitat availability and triplefin density suggested that habitat use was consistent across locations, indicating that potential biogeographical barriers in a species' range do not necessarily lead to geographic variation in habitat use, in particular for species with high dispersal abilities. The abundance of some species at the Three Kings Islands and Fiordland was higher or lower than expected by the habitat availability alone, probably due to distinct oceanographic conditions in these regions. For this reason these populations will be discussed prior to considering the mechanisms that are likely to be responsible for the absence of distinct triplefin ecotypes around New Zealand, and the generality of the patterns over large latitude.

Although habitat use appeared to be consistent across most locations, the density of a few triplefin species at some locations were lower or higher than expected given the habitat availability. Therefore, habitat availability alone did not determine density patterns in these species. Instead, differences in density were likely to be related to barriers to larval dispersal, such as the geographic isolation of the Three Kings Islands from the mainland and the high freshwater input in Fiordland. For example, although

F. lapillum and *N. segmentatus* were numerically dominant species at onshore locations throughout New Zealand, both species are absent from some offshore islands such as the Three Kings Islands and the Chatham Islands (Paulin and Roberts 1992, Fricke 1994). The absence of these species is interesting because congeners with similar habitat requirements are present at these islands (Clements 2003), suggesting that the absence was related to larval dispersal and survival. A long pelagic larval phase does not necessarily lead to larger spatial range, or population connectivity (Victor and Wellington 2000). There are several factors that can contribute to isolation of larvae from the mainland pool, such as physical isolation of the islands from the mainland, and the typically limited availability of shallow water habitat (<30 m) around the offshore islands. These factors, singly or in combination, could diminish the chances of larval input from coastal locations (Floeter et al. 2001). Indeed, populations of *F. varium* show reduced levels of gene flow between mainland sites and the Three Kings Islands (Hickey 2004).

The absence of some otherwise common triplefin species from Fiordland is possibly related to the low salinity surface layer (Wing 2003), which may reduce the larval input of triplefins to the inner fiords. The low salinity layer is produced by high annual rainfall (>7000 mm yr^{-1}) in the Fiordland region, which results in a general decrease in invertebrate and vertebrate species diversity (Smith and Witman 1999). In particular, the pycnocline layer, which is associated with the bottom of the low salinity layer, has been suggested to act as a physical barrier to larvae (Smith and Witman 1999). In addition, the direction and
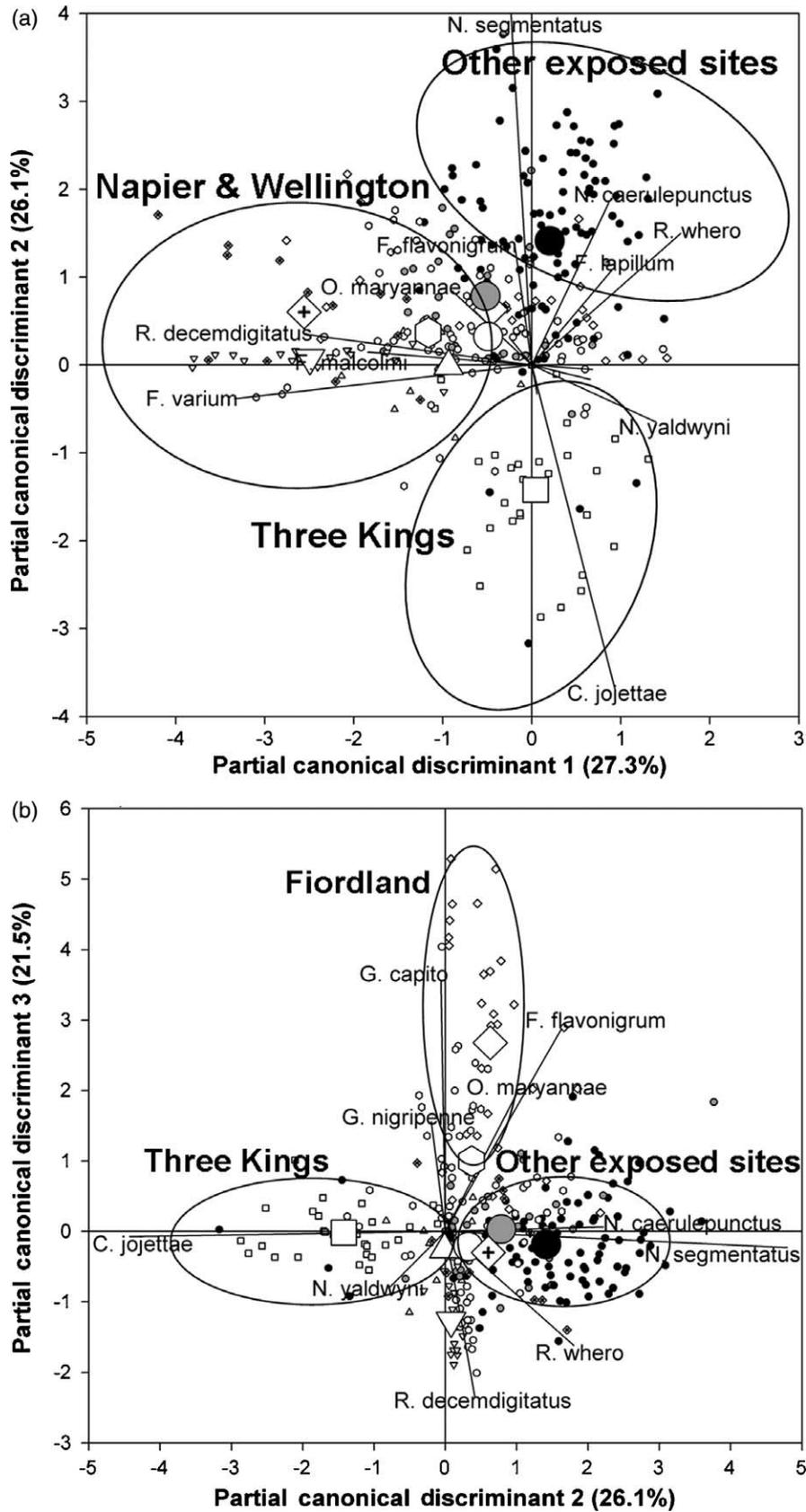
Fig. 7. Partial canonical discriminant analysis of triplefin species among biogeographic locations in New Zealand, after correcting for habitat differences. □ Three Kings Islands; △ Coromandel Peninsula; ⬙ Wellington; ● exposed offshore Hauraki Gulf; ● mainland Hauraki Gulf; ○ sheltered Hauraki Gulf; ▽ Napier; ◇ Fiordland; ⬡ Stewart Island. Species vectors are structure coefficients, multiplied by 3 to improve clarity.

magnitude of flow in the low salinity layer may have an important influence on the flow regime just below the pycnocline, which could directly influence dispersal and recruitment at shallow depths. Larvae or propagules entrained or released within the low salinity layer would be transported towards the mouth of the fiords (Smith and Witman 1999), during which time the increased tidal stirring towards the mouth causes the freshwater to become well-mixed with the rest of the seawater (Proctor and Hadfield 1998). It appears that although habitat availability may be the strongest modifier of assemblage composition, the offshore location of the Three Kings Islands and the freshwater layer in Fiordland generate dispersal barriers for some triplefin species, and thus are additional modifiers that contribute to assemblage composition around New Zealand.

Biogeographic barriers to dispersal are known to have a strong impact on the distribution of many marine species, with one of the best examples including the oceanographic barrier created by the Amazon freshwater and sediment outflow in Brazil (Floeter and Gasparini 2000, Rocha 2003). This barrier is marked with an abrupt change in hydrology, dissolved oxygen, topography and temperature, which profoundly affects species distribution and survival. Studies on this oceanographic break have shown that intraspecific phylogenies are often shaped by these biogeographic barriers to gene flow, leading over time to divergent populations on different sides of the barrier (Rocha et al. 2005). Despite potential biogeographic barriers around New Zealand's coastline, distinct triplefin ecotypes are absent even from the most distant offshore islands such as the Chatham Islands (Fricke 1994), although the remote location of these islands provide one of the most likely settings for such variants to evolve. This suggests that unlike the high inter-population variability in habitat associations of many widely distributed marine species (Floeter et al. 2001, Bouchon-Navaro et al. 2005), gene flow in New Zealand triplefin species may be sufficient to prevent local adaptation in broad-scale habitat use.

The mechanisms responsible for the general absence of geographic variation in triplefin habitat use may be related to the long pelagic dispersal phase and the settlement behaviour of larvae. Previous studies have demonstrated that larvae of some New Zealand triplefin species are capable of wide dispersal, with the pelagic larval duration being estimated to last between 2 and 3 months (Kingsford and Choat 1989, McDermott and Shima 2006). There is also increasing evidence that some pre-settlement reef fish larvae have the capability to actively swim towards suitable settlement habitat (Leis and McCormick 2002, Taylor and Hellberg 2003). Additionally, studies on New Zealand triplefin fishes have shown that pre-settlement larvae are not randomly distributed in the surface waters (Tolimieri et al. 2000, Hickford and Schiel 2003), suggesting that larvae can actively influence their position during that time. In addition, work on post-settlement triplefin larvae showed that species select specific habitat types at settlement (McDermott and Shima 2006). It appears that while the long dispersal phase enables gene flow between distant locations, the highly species-specific larval behaviour may determine habitat associations in this group and possibly

counter local adaptation in habitat use across biogeographic discontinuities.

Strong species-specific and consistent habitat use across latitudinal gradients would be expected in species for which fitness trade-offs in alternative habitats are high (Rosenfeld and Boss 2001) so that particular habitats offer considerable fitness advantages for species and, therefore, individuals would strongly prefer to occupy these habitats (MacArthur 1972). In this context, strong species-habitat associations may be an evolved response to patterns of post-settlement mortality in sub-optimal habitats (Keough and Downes 1982). Availability of suitable habitat predicts spatial patterns in the damselfish *Dascyllus aruanus* at several spatial scales, and similar correlations were found for four other species of reef-associated fish (Holbrook et al. 2004). It should be noted, however, that while broad-scale habitat associations of triplefin species appear to be consistent across biogeographic gradients, it is unknown if triplefins possess any fine-scale behavioural, morphological, or physiological adaptations to adjust to environmental variation. Many species show adaptive fine-scale variation in traits (Stearns 1992), for example, latitudinal clines in quantitative traits such as female fecundity and egg size are common in many species with wide distributions (L'Abee-Lund and Hindar 1990). Investigating fine-scale clinal variation of New Zealand triplefin species would be an interesting future research area.

The spatial consistency in triplefin habitat associations may be seen as a mechanism to reduce interspecific competition (MacArthur and Levin 1964, Wiens 1977, Schoener 1982), as geographically uniform and species-specific habitat use would reduce interspecific resource overlap between otherwise ecologically similar species. Most studies demonstrating interspecific competition among reef fishes have measured shifts in local distribution or density of fishes in response to competitor density (Robertson 1996, Munday 2004). For example, work on the territorial damselfish *Stegastes planifrons* has shown that the presence of this species limits the abundance of four ecologically similar congeners (Robertson 1996). Thus, if competition is affecting space use in New Zealand triplefin species, then it may be expected that ecologically similar species expand their habitat range in locations, such as the Three Kings Islands and Fiordland, that lack species that are common elsewhere. For example, the absence of the dominant mainland species *F. lapillum* and *N. segmentatus* from the Three Kings Islands potentially enables other triplefin species to settle into unoccupied habitat space. The results of the present study, however, indicated no significant habitat shift or increase in habitat breadth of other triplefin species at these locations, suggesting that triplefin habitat use is highly species-specific and not obviously influenced by the absence of other species. The apparent release from interspecific competition at particular sites, coupled with an absence of expansion into the space available due to the absence of competitors strengthens the view that New Zealand triplefin species use highly species-specific habitats, and that fitness trade-offs in sub-optimal habitats are high. Despite the absence of marked habitat shifts, the relative density of *C. jojettae* at the Three Kings Islands was much higher than expected from the habitat availability alone. *Cryptichthys jojettae* were found in habitats that were highly

similar to the habitat occupied by *N. segmentatus* (present study and Wellenreuther et al. 2007a), therefore, the absence of *N. segmentatus* at the Three Kings Islands might explain the increase in density of *C. jojettae* at this location. A similar trend could be observed in Fiordland. Some common species (e.g. *R. whero*) were rare from the inner fiords, while other typically less abundant species (e.g. *G. nigripenne* and *F. flavonigrum*) reached their highest density in the fiords. This suggests than an increase in density may be linked to the habitat space left unoccupied by otherwise common species. However, this hypothesis remains to be tested.

Consistent habitat use across large spatial scales suggests that the processes driving this pattern are general and relatively homogenous across the biogeographic range of the species (Morris 1987). Density-dependent processes have been suggested to be the primary mechanisms in producing consistent habitat use patterns, as density-dependence leads to predictable quantitative and qualitative differences in the density of species across habitats (Morris 1988). Thus, while the species-specific habitat use patterns of adult triplefins (Syms 1995, Feary and Clements 2006, Wellenreuther et al. 2007a) may be largely due to active habitat preferences exhibited by individual fish (McDermott and Shima 2006), the overall density of triplefin species on reefs is presumably regulated by inter- and intraspecific density-dependent processes, such as competition and predation. This is because although individual fish can maximise their reproductive success by choosing those habitats which convey the greatest fitness rewards, an individual's fitness is an overall function of population and resource density. Therefore, the density of individuals across habitats will reflect the habitat-dependent trade-off between fitness and density (Morris 1988), so that as population density increases and resource density decreases, each habitat occupant will likely have a progressively negative effect on the available habitat space to other individuals in that habitat patch (Morris 1988). For example, Steele and Forrester (2005) found that localised habitat differences in refuge density can accurately be aggregated to describe larger-scale patterns in the bridled goby *Coryphopterus glaucofraenum*. A shortage of refuges from predation in this species causes density-dependent mortality (Forrester and Steele 2004), and so the strength of density-dependence at small scales is sensitive to changes in the local availability of shelter sites (Steele and Forrester 2005).

In conclusion, the current study demonstrated that New Zealand triplefin species showed consistent habitat use across biogeographic gradients, but that this pattern was modified in some cases by differences in larval dispersal and recruitment success at some locations. This indicated that species composition at locations could not be explained by a single factor, but appears to be mainly due to the combined influences of habitat availability and differences in recruitment. The marked absence of geographic variation in species habitat use indicated that species select particular habitats and that dispersal is strong enough to lead to sufficient larval exchange among sub-populations, thereby preventing local adaptation in habitat use on a broad-scale. Recognition that behaviour can generate similar patterns of distribution and density at multiples scales implicates habitat selection as an important factor affecting local and regional patterns of biodiversity. Habitat selection as a process thus forms a fundamental link between the dynamics of populations at the local scale, and the regional dynamics of communities at larger scales.

References

Borcard, D. et al. 1992. Partialling out the spatial component of ecological variation. – Ecology 73: 1045–1055.

Bouchon-Navaro, Y. et al. 2005. Biogeographic patterns of coastal fish assemblages in the West Indies. – J. Exp. Mar. Biol. Ecol. 315: 31–47.

Clements, K. C. 2003. Triplefins. – In: Andrew, N. and Francis, M. (eds), The living reef. The ecology of New Zealand's rocky reefs. Craig Potton Publ., pp. 160–167.

Connell, S. D. and Jones, G. P. 1991. The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. – J. Exp. Mar. Biol. Ecol. 151: 271–294.

Cox, B. C. and Moore, P. D. 2005. Biogeography. An ecological and evolutionary approach. – Blackwell.

Endler, J. A. 1977. Geographic variation, speciation, and clines. – Princeton Univ. Press.

Feary, D. A. and Clements, K. C. 2006. Habitat use by triplefin fishes (family Tripterygiidae) on rocky reefs in New Zealand. – J. Fish Biol. 69: 1031–1046.

Floeter, S. R. and Gasparini, J. L. 2000. The south-western Atlantic reef fish fauna: composition and zoogeographic patterns. – J. Fish Biol. 56: 1099–1114.

Floeter, S. R. et al. 2001. Geographic variation in reef-fish assemblages along the Brazilian coast. – Global Ecol. Biogeogr. 10: 423–431.

Forrester, G. E. and Steele, M. A. 2004. Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. – Ecology 85: 1332–1342.

Francis, M. P. 1996. Geographic distribution of marine reef fishes in the New Zealand region. – N. Z. J. Mar. Freshwater Res. 30: 30–55.

Francis, M. P. 2001. Coastal fishes of New Zealand. An identification guide. – Reed Books.

Francis, M. P. and Nelson, W. 2003. Biogeography. – In: Andrew, N. and Francis, M. (eds), The living reef. The ecology of New Zealand's rocky reefs. Craig Potton Publ., pp. 35–37.

Fricke, R. 1994. Tripterygiid fishes of Australia, New Zealand and the Southwest Pacific Ocean (Teleostei). – Koeltz Scientific Books.

Hickey, A. J. R. 2004. Evolution of New Zealand's triplefin fish (family Tripterygiidae). – Ph.D. thesis, School of Biological Sciences, Univ. of Auckland, New Zealand.

Hickford, M. J. H. and Schiel, D. R. 2003. Comparative dispersal of larvae from demersal versus pelagic spawning fishes. – Mar. Ecol. Prog. Ser. 252: 255–271.

Holbrook, S. J. et al. 2004. Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. – Oecologia 122: 109–120.

Jawad, L. A. and Clements, K. C. 2004. Matanui, a new genus of deepwater triplefin fishes (Pisces: Tripterygiidae) from New Zealand. – J. R. Soc. N. Z. 34: 81–103.

Keough, S. J. and Downes, B. J. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. – Oecologia 54: 1432–1939.

Kingsford, M. J. and Choat, H. J. 1989. Horizontal distribution patterns of presettlement reef fish: are they influenced by the proximity of reefs? – Mar. Biol. 101: 285–297.

Kinlan, B. P. et al. 2005. Propagule dispersal and the scales of marine community process. – Divers. Distrib. 11: 139–148.

L'Abee-Lund, J. H. and Hindar, K. 1990. Interpopulation variation in reproductive traits of anadromous female brown trout, *Salmo trutta* L. – J. Fish Biol. 37: 755–763.

Leis, J. M. and McCormick, M. I. 2002. The biology, behavior, and ecology of the pelagic larval stage of coral reef fishes. – In: Sale, P. F. (ed.), Coral reef fishes dynamics and diversity on a complex ecosystem. Academic Press, pp. 171–199.

Littell, R. et al. 2002. SAS system for linear models. – SAS Inst.

MacArthur, R. H. 1972. Geographical ecology. – Harper and Row.

MacArthur, R. H. and Levin, R. 1964. Competition, habitat selection and character displacement in a patchy environment. – Proc. Nat. Acad. Sci. USA 51: 1207–1210.

McDermott, C. J. and Shima, J. S. 2006. Ontogenetic shifts in microhabitat preference of the temperate reef fish *Forsterygion lapillum*: implications for population limitation. – Mar. Ecol. Prog. Ser. 320: 259–266.

Morris, D. W. 1987. Ecological scale and habitat use. – Ecology 68: 362–369.

Morris, D. W. 1988. Habitat-dependent population regulation and community structure. – Evol. Ecol. 2: 253–269.

Munday, P. L. 2004. Competitive coexistence of coral dwelling fishes: the lottery hypothesis revisited. – Ecology 85: 623–628.

Paulin, C. D. and Roberts, C. D. 1992. The rockpool fishes of New Zealand. – Museum of New Zealand, Te Papa, Tongarewa.

Proctor, R. and Hadfield, M. 1998. Numerical investigation into the effect of freshwater inputs on the circulation in Pelorus Sound, New Zealand. – N. Z. J. Mar. Freshwater Res. 32: 467–482.

Robertson, R. D. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damsel-fishes. – Ecology 77: 885–899.

Rocha, L. A. 2003. Patterns of distribution and processes of speciation in Brazilian reef fishes. – J. Biogeogr. 30: 1161–1171.

Rocha, L. A. et al. 2005. Ecological speciation in tropical reef fishes. – Proc. R. Soc. B 272: 573–579.

Rosenfeld, J. S. and Boss, S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. – Can. J. Fish. Aquat. Sci. 58: 585–593.

Rosenzweig, M. L. 1995. Species diversity in space and time. – Camebridge Univ. Press.

Schoener, T. W. 1982. The controversy over interspecific competition. – Am. Sci. 70: 586–595.

Smith, F. and Witman, J. D. 1999. Species diversity in subtidal landscapes: physical processes and larval recruitment. – Ecology 80: 51–69.

Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.

Steele, M. A. and Forrester, G. E. 2005. Small-scale field experiments accurately scale up to predict density dependence in reef fish populations at large scales. – Proc. Nat. Acad. Sci. USA 102: 13513–13516.

Syms, C. 1995. Multi-scale analysis of habitat association in a guild of blennioid fishes. – Mar. Ecol. Prog. Ser. 125: 31–43.

Syms, C. and Jones, G. P. 1999. Scale of disturbance and the structure of a temperate fish guild. – Ecology 80: 921–940.

Taylor, M. S. and Hellberg, M. E. 2003. Genetic evidence for local recruitment of pelagic larvae in a Caribbean reef fish. – Science 299: 635–645.

Tolimieri, N. et al. 2000. Ambient sound as a cue for navigation by the pelagic fish larvae of reef fishes. – Mar. Ecol. Prog. Ser. 207: 219–224.

Victor, B. C. and Wellington, G. M. 2000. Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean. – Mar. Ecol. Prog. Ser. 205: 241–248.

Wellenreuther, M. and Clements, K. D. 2007. Reproductive isolation in temperate reef fishes. – Mar. Biol. 152: 619–630.

Wellenreuther, M. et al. 2007a. Ecological diversification in habitat use in subtidal triplefin fishes (Tripterygiidae). – Mar. Ecol. Prog. Ser. 330: 235–246.

Wellenreuther, M. et al. 2007b. The role of body size in ecological diversification and reproductive isolation in a sister species pair of triplefin fishes. – Evol. Ecol., in press. DOI: 10.1007/s10682-007-9183-7.

Wiens, J. A. 1977. On competition and variable environments. – Am. Sci. 65: 590–597.

Wing, S. 2003. Fiordland. – In: Andrew, N. and Malcolm, F. (eds), The living reef. The ecology of New zealand's rocky reefs. Craig Potton Publ., pp. 238–247.