

Trophic ecology of New Zealand triplefin fishes (Family Tripterygiidae)

David A. Feary · M. Wellenreuther · K. D. Clements

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Abstract In many vertebrate radiations, food partitioning among closely related taxa is a key factor in both the maintenance of species diversity and the process of diversification. We compared diet composition and jaw morphology of 18 New Zealand triplefin species (F. Tripterygiidae) to examine whether species have diversified along a trophic axis. These fishes predominantly utilised small, mobile benthic invertebrates, and interspecific differences in diet composition appeared to be mainly attributable to habitat- or size-dependent feeding behaviour. Although there were differences in the relative size of the bones comprising the oral jaw apparatus between species, the majority showed an apparatus consistent with a relatively high velocity, low

force jaw movement indicative of a diet of evasive prey. Phylogenetic comparative analyses showed that the evolution of jaw lever ratios and diet breadth was best explained by a non-directional model in which character changes have occurred randomly and independent of phylogeny. The mode of diet breadth evolution was gradual and the tempo has not accelerated or slowed down over time. The mode of evolution for the jaw lever ratios has been gradual for the opening but punctuated for the closing levers, suggesting that evolutionary changes have occurred rapidly for the latter trait. The tempo of trait evolution for the jaw opening levers has not accelerated or slowed down over time, while the tempo for the jaw closing levers has accelerated towards the tips of the tree, which is suggestive of species level adaptation. The lack of phylogenetic signal in diet breadth and jaw lever ratios appears most likely to be a correlated response to the marked habitat diversification in this group, and is thus the passive outcome of prey availability in species-specific habitat types. Overall, the trophic ecology of New Zealand's triplefin fauna parallels the generalist strategy typical of the family worldwide, suggesting that trophic resource partitioning has not been an important factor in the evolution of these fishes.

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D. A. Feary
School of Biological Sciences, University of Auckland,
Private Bag 92019, Auckland, New Zealand

Present Address:
D. A. Feary (✉)
International Network on Water, Environment and Health,
PJSC, United Nations University, P.O. Box 17777,
Dubai, United Arab Emirates
e-mail: dfeary@inweh.unu.edu

M. Wellenreuther
Section for Animal Ecology, University of Lund,
Ecology Building, Solvegatan 36, 223 02 Lund, Sweden

K. D. Clements
School of Biological Sciences, University of Auckland,
Private Bag 92019, Auckland, New Zealand

Introduction

Understanding the factors that permit the coexistence of species has been a central question in both community ecology (Ross 1986; Carr et al. 2002) and evolutionary biology (Schluter 2000). Within many vertebrate radiations, trophic resource partitioning has been found to play a key role in adaptive diversification (Streelman and Danley 2003), maintaining the coexistence of species-rich assemblages in both terrestrial (Denoel and Schabetsberger 2003;

Levesque et al. 2003) and aquatic environments (Duftner et al. 2005; Vanderklift et al. 2006). Within the marine environment, partitioning of trophic resources is apparent in a range of highly diverse fish communities (Platell and Potter 2001; Zekeria et al. 2002). However, the majority of this work has focused on coral-associated reef fish communities (Longnecker 2007), which form large, species-rich assemblages on relatively small habitat patches (see review in Sale 2002). In comparison, few studies have investigated trophic resource partitioning in temperate reef fish assemblages (but see Grossman 1986; Angel and Ojeda 2001; Wennhage and Pihl 2002; Floeter et al. 2004), despite the fact that temperate reefs can support diverse fish communities (Anderson and Millar 2004).

Although a range of factors can maintain trophic partitioning within fish communities (Ross 1986), variations in feeding morphology between species, including both dentition and jaw morphometrics, may be particularly important (Westneat et al. 2005), and can indicate substantial partitioning of food resources between species (Castillo-Rivera et al. 1996; Hyndes et al. 1997). Consequently, interspecific differences in feeding morphology have been used to describe trophic partitioning in temperate reef fishes (Wainwright and Richard 1995; Karpouzi and Stergiou 2003; Platell et al. 2006); however, few of these studies have examined the extent to which variation in trophic apparatus and feeding ability are important in structuring this diversity (but see Angel and Ojeda 2001; Boyle and Horn 2006).

Triplefins (F. Tripterygiidae) are small, blennioid teleosts that reach their highest diversity and disparity in New Zealand waters (Fricke 1994). Of the approximately 30 genera and 140 species recognised worldwide (Fricke 1997; Fricke 2002), 14 genera and 26 endemic species are currently recognised in New Zealand (Clements 2003). Three of these species have been reported from Australian waters, but molecular analyses show that these were introduced from New Zealand (Hickey et al. 2004). Phylogenetic analyses based on molecular data suggest that at least 18 New Zealand triplefin species are closely related (Hickey and Clements 2005), indicating that these endemic species have evolved in close association. Most New Zealand triplefin species occur all around coastal New Zealand, and show no latitudinal trends in abundance (Paulin and Roberts 1992; Fricke 1994; Clements 2003). Previous work has shown that the New Zealand triplefin fauna has diverged considerably in habitat use (Syms 1995; Feary and Clements 2006; Wellenreuther et al. 2007), and that species-specific habitat associations are consistent throughout New Zealand, even across environmental gradients (Wellenreuther et al. 2008). In contrast, little is known of how trophic resources are partitioned between species (but see Russell 1983).

The aim of the present study was to investigate diet composition and feeding morphology of New Zealand triplefin species to determine the level of interspecific divergence in these factors. Divergence in feeding morphology was assessed in terms of oral jaw morphology and jaw lever ratios. We then used a phylogenetic comparative framework to investigate the evolution of both diet breadth and jaw lever movement in the group.

Materials and methods

Adult triplefin specimens were collected from around New Zealand to minimise location effects on diet composition. Collections were supplemented by specimens from the collection of the National Museum of New Zealand ‘Te Papa Tongarewa’ where necessary [see Appendix (electronic supplementary information) for full description of all study specimens]. A total of 18 species were examined, all of which belong to endemic genera: *Bellapiscis lesleyae* Hardy, 1987; *Bellapiscis medius* (Günther, 1861); *Blennodon dorsale* (Clarke, 1879); *Cryptichthys joettae* Hardy, 1987; *Forsterygion capito* (Jenyns, 1842); *Forsterygion flavonigrum* Fricke and Roberts, 1994; *Forsterygion gymnota* (Scott, 1977); *Forsterygion lapillum* Hardy, 1989; *Forsterygion malcolmi* Hardy, 1987; *Forsterygion maryannae* (Hardy, 1987); *Forsterygion nigripenne* (Valenciennes, 1836); *Forsterygion varium* (Schneider: in Bloch and Schneider 1801); *Karalepis stewarti* Hardy, 1984; *Notoclinops caerulepunctus* Hardy, 1989; *Notoclinops segmentatus* (McCulloch and Phillipps, 1923); *Notoclinops yaldwyni* Hardy, 1987; *Ruanoho decemdigitatus* (Clarke, 1879); and *Ruanoho whero* Hardy, 1986.

Diet analysis

Triplefins lack a distinct stomach (Silberschneider and Booth 2001), thus the entire alimentary tract was examined in 20 individuals of each of the 18 study species. Total length (TL) and standard length (SL) in each specimen were measured and all dietary items were identified to the lowest taxonomic level. To measure the relative importance of dietary categories within and between species, the relative contributions of each dietary category to the volume (%V) of the diets were calculated (Platell and Potter 2001). Dietary breadth of each species was determined using Levins’ standardised index for diet breadth, and then standardised from 0 to 1. Values close to 0 indicate diets dominated by a few prey categories, whereas values close to 1 indicate diets containing a large variety of prey categories (Krebs 1999).

Non-parametric multivariate analyses based on the mean %V contributions of each dietary category (excluding

unidentifiable crustaceans and incidental items) were used to test differences in diet. Classification (group-average sorting of the Bray-Curtis similarity measures based on $\log(x + 1)$ transformed volumetric data) and ordination (CLUSTER) on the above similarity matrices were used (Clarke and Warwick 1994). In addition, the contribution of each dietary category to the average similarity within each species group was examined using SIMPER (similarity percentages) (Clarke and Warwick 1994).

Morphological analysis

To examine whether there were differences in the morphological structures associated with feeding, we described the four bones comprising the oral jaw apparatus (premaxilla, maxilla, dentary and articular) and their associated dentition and then examined and compared nine morphological characteristics within each species (Table 1). All measurements were recorded on specimens that had been preserved in 70% ethanol. A grey-scale image of each jaw was captured and all measurements were taken using a video image analysis system (OPTIMAS v. 6.5) linked to a dissecting microscope. Opening and closing lever ratios were calculated following Westneat (1994): (a) quadratomandibular joint to the attachment of the interopercular ligament on the lower jaw (opening in-lever), (b) quadratomandibular joint to the insertion of the A3 section of the adductor mandibulae on the articular (closing in-lever), and (c) quadratomandibular joint to the most ventral tooth on the dentary (out-lever) (Fig. 1). Mechanical advantage of jaw opening is the opening in-lever divided by the out-lever; mechanical advantage

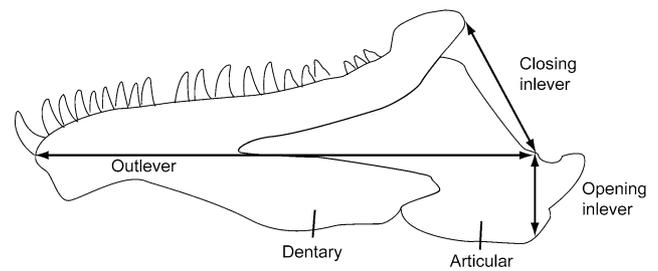


Fig. 1 Measurements taken to calculate closing (closing in-lever/out-lever) and opening lever ratios (opening in-lever/out-lever) (modified after Bellwood and Wainwright 2002)

of lower jaw closing is then the closing in-lever divided by the out-lever. All morphological measurements were standardised by the SL (mm) of each species to allow comparisons between species. The composition of species groups, based on jaw morphology, was explored by reducing the dimensionality of the data with a principal component analysis (PCA) based on the co-variance matrix. The morphological structures responsible for grouping species were expressed in the vector plot, enabling structures responsible for segregation of species to be identified.

Phylogenetic comparative analysis

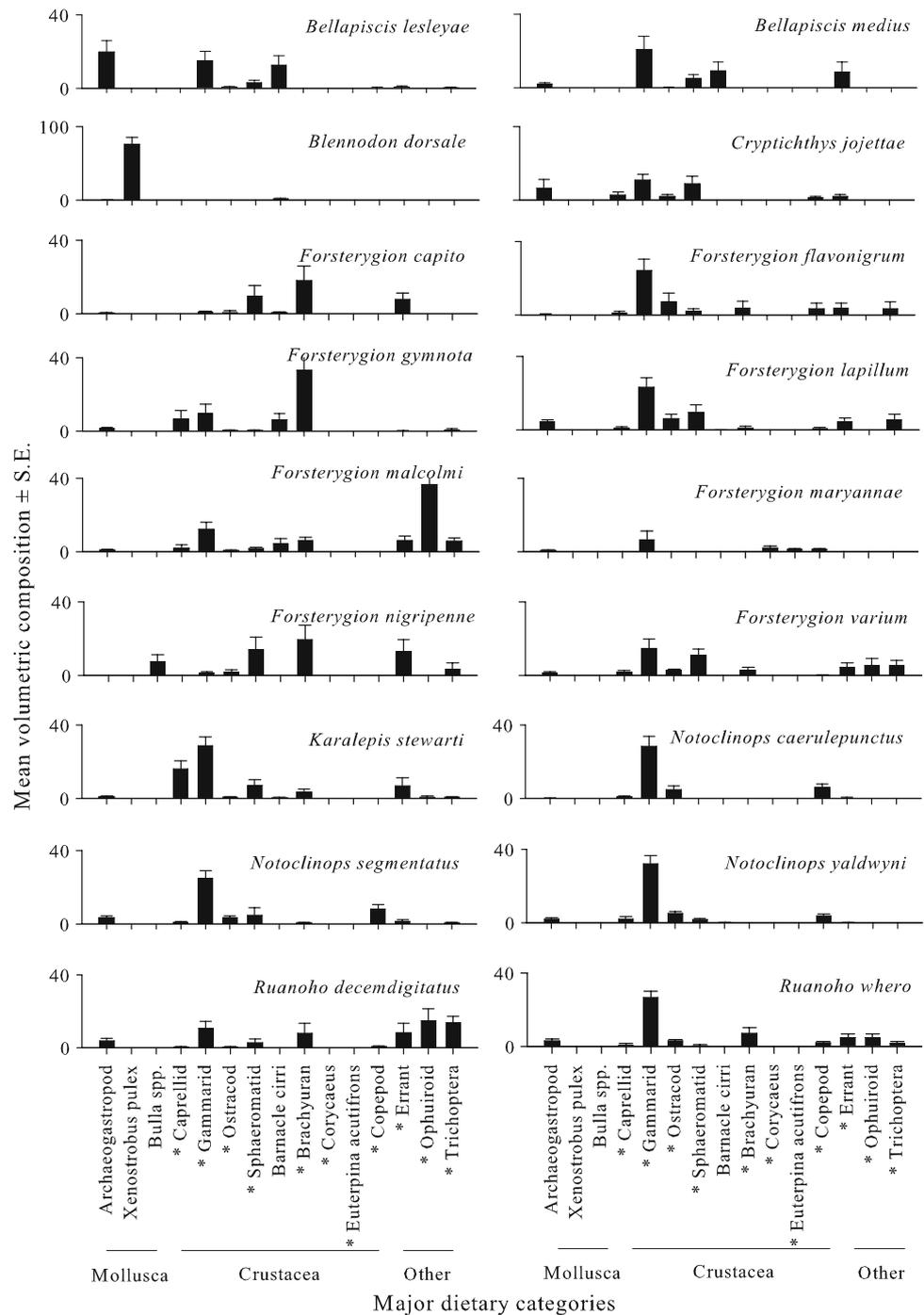
A phylogenetic comparative framework was used to analyse the evolution of both diet breadth and jaw lever ratios (mechanical advantage for lower jaw opening and closing) in the 18 study species. A phylogeny and branch lengths for the 18 triplefin species were constructed using MrBayes (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) based on sequence fragments from three mitochondrial genes (12S, 16S and control region) and a nuclear gene (ETS2) (Hickey and Clements 2005; see Fig. 2). Monte Carlo analysis was used to calculate the posterior probability distribution using the program BayesPhylogenies (Pagel and Meade 2004; Pagel et al. 2004), with the sister species pair *R. whereo* and *R. decemdigitatus* as an outgroup (following the topology of Hickey and Clements 2005). Trees were generated for 10 million generations, with sampling every 50,000 generations, and the first 2 million generations were discarded as ‘burn-in’ (20% of the trees).

Data were analysed using the generalised least squares model in the program BayesContinuous (Pagel and Meade 2004; Pagel et al. 2004) that assumes a Brownian motion model of evolution, whereby non-independence of data is accounted for by reference to a matrix of the expected covariances among species. Specific hypotheses about trait evolution were investigated using three scaling parameters implemented in BayesContinuous: lambda, kappa and delta, which test for the contribution of the phylogeny, the mode and the tempo in trait evolution, respectively.

Table 1 Morphological characteristics used to compare feeding morphology between 18 triplefin species

Characteristic	Explanation
Premaxilla length	Length from anterior to posterior of alveolar process of premaxilla
Maxilla length	Length from medial head to lateral wing of maxilla
Ascending process length	Length of ascending process from dorsal tip to articulation with alveolar process of premaxilla
Angle ascending process	Inner angle between ascending process and alveolar process of premaxilla
Dentary length	Length from anterior to posterior of dorsal arm of dentary
Articular length	Length from anterior of pointed projection to quadratomandibular joint
Opening jaw lever	See Fig. 1
Closing jaw lever	See Fig. 1
Tooth height	Length of longest tooth in dentary

Fig. 3 Mean volumetric contribution \pm SE of major prey items to diet composition of 18 triplefin species. Note change in y-axis of *Blennodon dorsale*. Asterisk indicates elusive prey items



dominated the majority of species diets, contributing up to 35% in volume between species (Fig. 3). Other commonly ingested taxa included both sedentary and free-living invertebrates (Fig. 3). The most diverse diet was that of *F. nigripenne* (0.65) and the least diverse diet was found in *F. maryannae* (0.06) (Table 2).

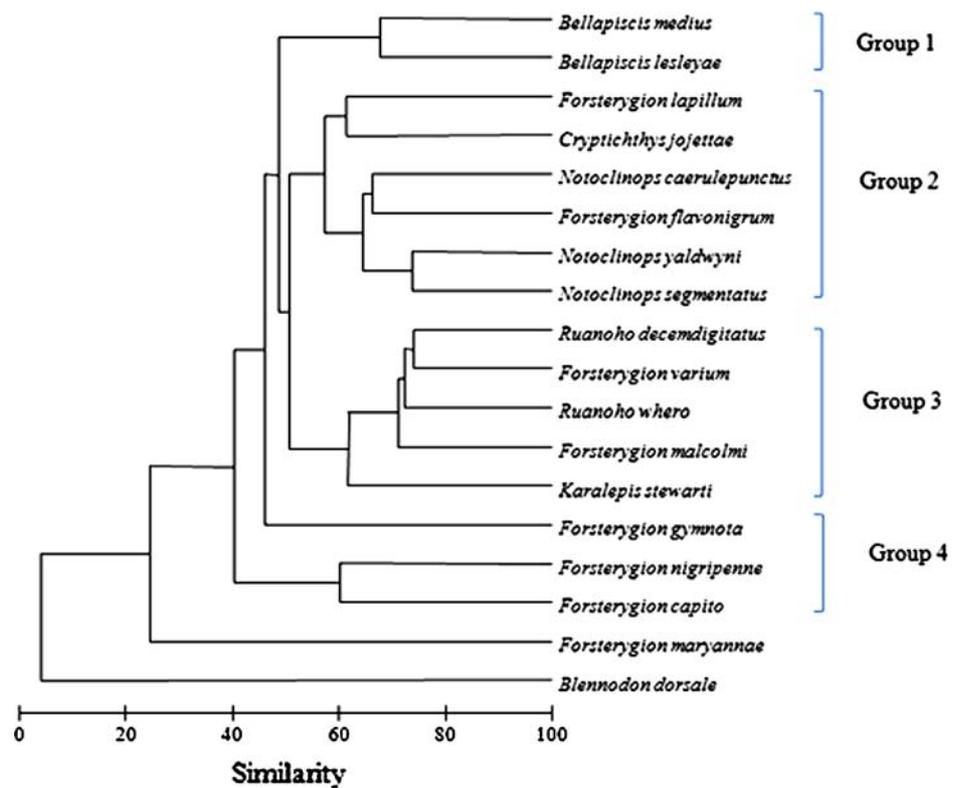
Interspecific differences in diet composition were apparent and four distinct groups were evident (Fig. 4). *B. lesleyae* and *B. medius* showed 68% similarity in diet composition

(Group 1; Fig. 4) and were distinct from all other species in containing high abundances of barnacle cirri, archaeogastropods and flabelliferan isopods (Table 3). *N. yaldwyni*, *N. segmentatus*, *F. lapillum*, *F. flavonigrum*, *N. caerulepunctus* and *C. jojettae* shared a similar diet (57% similarity) (Group 2; Fig. 4) dominated by not only gammarid amphipods but also ostracods and limpets (Table 3). *F. varium*, *R. whereo*, *R. decemdigitatus*, *F. malcolmi* and *K. stewarti* were similar in diet (62%) (Group 3; Fig. 4) and utilised a

Table 2 Standardised dietary breadth using Levins' index and lever ratios (mechanical advantage) for opening and closing the lower jaw for 18 species of New Zealand triplefin \pm SE

Species	Standardised niche breadth	Mechanical advantage		Average SL \pm SE
		Jaw opening	Jaw closing	
<i>Bellapiscis lesleyae</i>	0.357	0.183 \pm 0.008	0.294 \pm 0.014	42.70 \pm 1.302
<i>Bellapiscis medius</i>	0.573	0.184 \pm 0.011	0.307 \pm 0.007	51.80 \pm 1.759
<i>Blennodon dorsale</i>	0.099	0.243 \pm 0.008	0.280 \pm 0.013	114.00 \pm 3.480
<i>Cryptichthys jojettae</i>	0.136	0.183 \pm 0.006	0.268 \pm 0.010	33.85 \pm 0.955
<i>Forsterygion capito</i>	0.236	0.207 \pm 0.011	0.272 \pm 0.003	52.65 \pm 4.475
<i>Forsterygion flavonigrum</i>	0.390	0.161 \pm 0.007	0.238 \pm 0.012	37.35 \pm 1.340
<i>Forsterygion gymnota</i>	0.343	0.186 \pm 0.005	0.274 \pm 0.012	58.80 \pm 2.024
<i>Forsterygion lapillum</i>	0.299	0.175 \pm 0.013	0.258 \pm 0.018	45.50 \pm 1.252
<i>Forsterygion malcolmi</i>	0.219	0.193 \pm 0.009	0.293 \pm 0.017	68.90 \pm 4.877
<i>Forsterygion maryannae</i>	0.064	0.179 \pm 0.006	0.213 \pm 0.003	41.50 \pm 0.949
<i>Forsterygion nigripenne</i>	0.655	0.185 \pm 0.008	0.277 \pm 0.015	55.65 \pm 1.865
<i>Forsterygion varium</i>	0.430	0.193 \pm 0.008	0.239 \pm 0.014	73.00 \pm 5.710
<i>Karalepis stewarti</i>	0.241	0.204 \pm 0.007	0.245 \pm 0.007	82.70 \pm 6.068
<i>Notoclinops caerulepunctus</i>	0.148	0.211 \pm 0.007	0.257 \pm 0.007	27.80 \pm 0.667
<i>Notoclinops segmentatus</i>	0.175	0.209 \pm 0.005	0.291 \pm 0.007	33.50 \pm 1.113
<i>Notoclinops yaldwyni</i>	0.174	0.207 \pm 0.006	0.295 \pm 0.009	40.05 \pm 1.194
<i>Ruanoho decemdigitatus</i>	0.499	0.169 \pm 0.005	0.288 \pm 0.005	67.45 \pm 3.927
<i>Ruanoho whero</i>	0.343	0.195 \pm 0.006	0.279 \pm 0.008	46.80 \pm 1.849

Fig. 4 Cluster analysis of mean volumetric contribution of major dietary categories to the diet composition of 18 triplefin species



range of benthic invertebrates including ophiuroids, archaeogastropods, trichoptera and errant polychaetes (Table 3). Diets of *F. nigripenne* and *F. capito* displayed 60% similarity (Group 4; Fig. 4) due to their inclusion of brachyuran

spp., errant polychaetes and flabellifera isopods (Table 3). *F. gymnota* and *F. maryannae* were more distinct from the remainder of the species (46 and 24% similarity, respectively) (Fig. 4). The diet composition of *B. dorsale*

Table 3 Volumetric contribution (\pm SE) and contribution of each dietary category to the average similarity within each species group of 10 diet categories within 18 species of triplefin

	Group 1			Group 2			Group 3			Group 4		
	Mean	SE	Input (%)									
Archaeogastropod	14.0	4.1	18.6				2.2	0.4	6.6			
Barnacle cirri	15.4	4.3	19.2									
Brachyuran spp. ^a										20.3	5.8	42.2
Errant spp. ^a							6.2	1.5	6.1	10.5	3.9	20.9
Sphaeromatid spp. ^a	4.7	1.4	12.5							10.3	4.5	17.3
Gammarid spp. ^a	20.4	4.8	37.9	23.2	1.9	62.3	18.8	2.0	46.2	1.9	0.8	11.1
Limpet spp.				3.9	0.8	6.2						
Ophiroid spp. ^a							11.8	2.2	11.3			
Ostracod spp. ^a				4.9	1.0	13.5						
Trichoptera spp. ^a							4.5	0.9	6.1			

<5% contribution excluded

^a Elusive prey

showed little similarity to any other species (4%), (Fig. 4; Table 3), due to the almost exclusive use of the blue-black mussel, *Xenostrobus pulex* (Fig. 3).

Description of jaw morphology

The premaxilla in the majority of species had a long ascending process (Fig. 5a), which was most slender in *F. maryannae* (Fig. 5b). The alveolar process was robust at its anterior margin and moderately long in all species (Fig. 5a). A relatively well-formed dentary comprising asymmetrical posterior arms and a medially curved anterior shaft was also found throughout the species (Fig. 5a). The dentary was most slender and elongate in *F. maryannae* (Fig. 5b), and sturdiest with reduced arms in *B. dorsale* (Fig. 5c). Similar-shaped maxillae were apparent between species, though differences in length and size were evident. The maxilla of *B. dorsale* was short and robust (Fig. 5c), while that of *F. maryannae* was elongate and slender (Fig. 5b). The maxilla was intermediate in all remaining species. The articular was shallow in all species, with a pointed projection reaching halfway along the dentary (Fig. 5a). This projection was blunt in *B. dorsale*, extending only one-third of the length of the dentary (Fig. 5c).

The anterior margin of both the premaxilla and the dentary held a single row of large, uniformly sized, medially recurved coniform teeth in the vast majority of species (Fig. 5a). *B. dorsale* was distinct from all other species in bearing very large, incisiform teeth (Fig. 5b).

There was relatively low variation in jaw mechanism values throughout the New Zealand triplefin fauna (Table 2). Biomechanical estimates of jaw opening force transmission (mechanical advantage) ranged from 0.16 in *F. flavonigrum* to 0.24 in *B. dorsale*, while estimates of jaw

closing force transmission ranged from 0.21 in *F. maryannae* to 0.31 in *B. medius* (Table 2).

Morphological analysis

The first two axes of the PCA explained over 60% of the variation in the data, with the first axis responsible for approximately 41% and the second axis responsible for 19% (Fig. 6a). PC1 was most influential in separating the majority of species into two major groups (Fig. 6a), one with high bone length and a small angle of the ascending process of the premaxilla (Fig. 6b) (which held *F. capito*, *F. gymnota*, *F. malcolmi*, *F. nigripenne*, *F. varium*, *K. stewarti* and *R. decemdigitatus*) and another with smaller bones and a large angle of the ascending process of the premaxilla (Fig. 6b) (which held *C. jojettae*, *F. flavonigrum*, *F. lapillum*, *F. maryannae*, *N. caerulepunctus*, *N. yaldwyni* and *R. whero*). The remaining species (*B. lesleyae*, *B. medius* and *B. dorsale*) were separated primarily along PC2, and were defined by large tooth height and high closing jaw lever values (Fig. 6b).

Phylogenetic comparative analysis

Diet breadth

Model fit of the diet breadth data was not significantly better when the directional model was used ($\chi^2 = 0.36$, $P = 0.551$), and, therefore, the model assuming a random walk was used for subsequent analysis. The model in which lambda was allowed to take its maximum likelihood value performed significantly better than the model with the default setting ($\chi^2 = 5.92$, $P = 0.015$). The mean estimate for lambda was 0.11, indicating that phylogenetic relationships



Fig. 5 Morphology of oral jaw apparatus of **a** *Forsterygion lapillum*, **b** *Forsterygion maryannae* and **c** *Blennodon dorsale*. PMX premaxilla, MX maxilla, DT dentary, ART articular. Bar 1 mm

had only a minimal effect on the evolution of diet breadth. Maximum likelihood estimates of kappa and delta did not provide a significantly better model fit, and thus the default settings were accepted for both (kappa: $\chi^2 = 2.79$, $P = 0.095$; delta: $\chi^2 = 1.87$, $P = 0.172$).

Mechanical advantage: opening and closing of jaw levers

The directional model did not fit the jaw opening ($\chi^2 = 0.483$, $P = 0.4871$) or jaw closing ($\chi^2 = 0.158$, $P = 0.691$) lever data significantly better than the random

walk model, and consequently the random model was used for all subsequent analyses. For both jaw opening and jaw closing lever values, log-likelihood tests of the random model versus the model in which lambda was allowed to take its maximum likelihood value showed that lambda differed significantly from the default setting 1 (jaw opening: $\chi^2 = 6.26$, $P = 0.0123$, lambda = 0.363; jaw closing: $\chi^2 = 11.590$, $P = 0.0007$, lambda = 0.221). For the jaw opening lever values, the scaling parameter kappa did not differ significantly from 1 ($\chi^2 = 1.404$, $P = 0.2361$). In comparison, for the jaw closing lever values, kappa values differed significantly from the default settings of 1 ($\chi^2 = 5.165$, $P = 0.023$), with a maximum likelihood value of kappa 0.000356. Lastly, for jaw opening lever values, the model in which delta was allowed to take its maximum likelihood value did not differ from the default model ($\chi^2 = 1.8912$, $P = 0.1691$), whereas the model in which delta was allowed to assume its maximum likelihood value fitted the jaw closing lever data significantly better ($\chi^2 = 7.4119$, $P = 0.0065$), and thus the maximum likelihood value of delta 3.349 was accepted.

Discussion

This work has shown a high level of dietary overlap among New Zealand triplefin species, with the majority of diets predominantly composed of mobile benthic invertebrates. This is consistent with earlier studies on triplefin species in New Zealand (Russell 1983) and elsewhere (Kotrschal and Thomson 1986). Crustaceans were the most important dietary taxon, found in the majority of species and dominating volumetric measurements. Such prey items are abundant within micro- and macro-algal beds (Taylor 1998), the dominant benthic-forming habitat around mainland and offshore islands in New Zealand (Taylor 1998). Although differences in diet composition were apparent between species, these differences could be explained with regards to their habitat distribution, or for the majority of species, their body size. For *B. lesleyae* and *B. medius*, both species were distinct in feeding on a range of epifauna abundant in the very shallow surge zones and mixed algae (Hilton et al. 2008), which is the habitat they are predominantly found (Paulin and Roberts 1992; Feary and Clements 2006). In parallel, the diets of *F. nigripenne* and *F. capito* were dominated by fauna abundant in their habitat of shallow harbours and estuaries (Clements et al. 2000; Wellenreuther et al. 2007). Such habitat-dependent feeding suggests that both groups of congeners are opportunistic, using dietary items that are readily available within their habitat. Both freshwater and marine fishes frequently display dietary opportunism (Liem 1990; Beyst et al. 2002), and such behavioural flexibility may increase

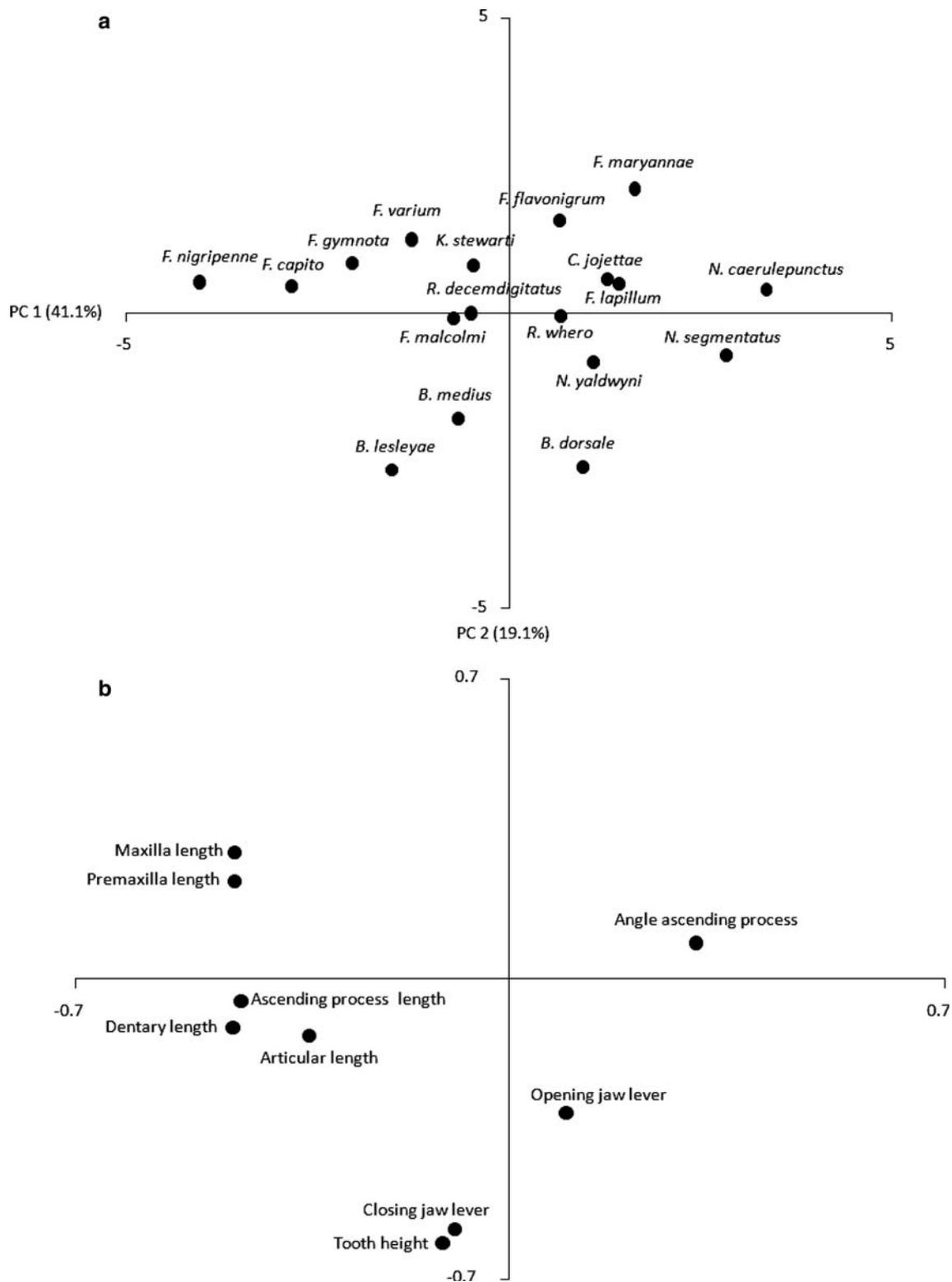


Fig. 6 Principal component analysis of morphology of oral jaw apparatus among the 18 study species. **a** Morphological groupings of species; **b** morphometric characteristics responsible for species loadings

both feeding opportunities and subsequent foraging success (Glasby and Kingsford 1994; Matic-Skoko et al. 2004).

Although differences in handling efficiency and feeding behaviour may have affected species foraging ability, differences in species ability to utilise prey items, dependent on

prey size, was apparent. For example, *N. caerulepunctus*, *N. yaldwyni*, *F. flavonigrum*, *N. segmentatus*, *C. jojettae* and *F. lapillum* are all relatively small to medium-sized fishes (4.5–8 cm), and their diets were dominated by a variety of small dietary categories (e.g. archaeogastropods and barnacle cirri), with very few large items apparent. This diet was complemented by a distinctive oral jaw apparatus structure, distinguished by its small size, relatively short bone length and high angle of the ascending process. In contrast, diets of the medium/large (8–15 cm)-sized species (i.e. *R. whero*, *F. varium*, *F. malcolmi*, *R. decemdigitatus* and *K. stewarti*) were composed of a range of larger-sized dietary categories (e.g. ophiroids and errant polychaetes). For these species, their oral jaw apparatus was distinguished by their large bone size, long bone length and a low angle of the ascending process.

When compared to primarily benthic-feeding taxa (e.g. Labridae), which exhibit species at both extremes of lower jaw lever ratios (Westneat et al. 2005), the range of morphological diversity apparent in New Zealand triplefins was indicative of a more generalised construction and function. In terms of jaw opening and closing, for the majority of species, the lever system is indicative of moving the lower jaw rapidly rather than forcefully (Westneat 1994). Although some of the study species foraged on non-elusive prey (i.e. bivalves and barnacle cirri), such jaw morphology is apparent in fishes that possess smaller mouths and feeding muscles that convey high velocity transmission, important in the capture of evasive prey (Westneat 1994).

Of the species examined, *B. dorsale* and *F. maryannae* were noticeably distinct in their diet and the structure of their oral jaw apparatus. Specifically, the diet and jaw morphology of *B. dorsale* were more indicative of an omnivorous feeding behaviour with a diet based solely on sessile prey and an oral jaw apparatus which would produce a relatively short, powerful bite (Westneat et al. 2005). Such trophic ecology is more indicative of the more advanced perciform families within the Blennioidei (Kotrschal 1988). In contrast to this wholly benthic ecology, the diet and jaw morphology of *F. maryannae* showed features more likely found in planktonic feeders, with a diet predominantly composed of zooplankton and an oral jaw apparatus that would increase biting speed, while reducing force (Motta 1985). Hickey and Clements (2003) have recently shown that the caudal trunk musculature of adult *F. maryannae* may be a paedomorphic characteristic. Such retention of the larval muscle architecture may have increased *F. maryannae* potential for sustained swimming, allowing this species to exploit a more pelagic lifestyle (Hickey and Clements 2003). In this respect, the variation in jaw morphology between *F. maryannae* and other triplefin species in the New Zealand fauna may also be due to the paedomorphic retention of larval jaw characteristics, with lowered bone

mineralisation and a more slender bone structure (Eastman 1997).

The phylogenetic analyses showed that the evolution of diet breadth and jaw lever ratio has not followed any directional trends, but rather that it has evolved randomly in the New Zealand triplefin fauna. This general lack of phylogenetic signal in our diet breadth and jaw lever data suggests that trophic evolution has not been conserved in this clade, but instead has diverged in an unconstrained manner between the species. This means that sister species pairs in the New Zealand triplefin clade do not, on average, share more similarities in their trophic niche than less closely related species. The lack of any directional trend in the evolution of diet breadth is interesting, as it is contrary to the long held belief that radiations are typically founded by generalist species that steadily lead to more specialised species (see Futuyma and Moreno 1988; Schluter 2000 for a list of theoretical reasons). In this context, our results suggest that the evolution of diet breadth in this group has proceeded in both directions, towards one that favours increased specialisation and another that favours generalisation in diet breadth.

Although the New Zealand triplefin fauna occurs sympatrically throughout coastal New Zealand, most species show considerable diversification in habitat use (Syms 1995; Feary and Clements 2006; Wellenreuther et al. 2007). Recent phylogenetic comparative analyses of habitat use within this fauna have shown that species-specific habitat use patterns are unrelated to the phylogenetic relationships (Wellenreuther 2006), suggesting that selection has influenced the evolution of habitat use. Evolutionary changes in habitat use between species may then have corresponded with changes in the range of prey taxa available, leading to a correlated response in the evolution of their diet breadth. Given the overall lack of specialisation in diet and the strong diversification in habitat use in New Zealand triplefin species, therefore, it seems likely that diet breadth has evolved as a consequence of the marked divergence in habitat use in this group.

Our comparative analyses also showed that there were substantial differences in the evolutionary mode and tempo within each jaw lever system. Jaw opening levers appear to have undergone a relatively gradual evolution, whereas the jaw closing levers more closely fit a punctuated mode of evolution. Estimates of the tempo of trait evolution showed that jaw opening levers have evolved gradually over time, whereas evolution of the closing lever has accelerated near the tips of the tree, which is indicative of species level adaptations. These results suggest that the two jaw lever systems have evolved independently of one another in this fauna. Independent evolution of jaw lever systems has also been demonstrated in quantitative genetic analyses on cichlids (Albertson et al. 2005) and in biomechanical analysis

of the family Labridae (Westneat et al. 2005). Such decoupling in the evolution of biomechanical characters may be an important step in facilitating adaptive variation within ecologically related fish taxa, leading to increased functional diversity among fish communities (Westneat et al. 2005).

In conclusion, the broad dietary overlap combined with the similarities in jaw morphology in New Zealand triplefin species indicate that these fishes have not diversified greatly along a trophic axis. The evolution of both diet breadth and jaw lever ratios appears to have involved little phylogenetic signal, suggesting that the trophic niches were not constrained. Instead, triplefin species appeared to broadly consume all prey types available in their habitat, indicating that niche partitioning in this clade has been a correlated response to the pronounced interspecific diversification in habitat use in this group. Together these results suggest that interspecific partitioning of trophic resources was not an important mechanism in the evolution of the New Zealand triplefin fauna.

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References

- Albertson RC, Streebman JT, Kocher TD, Yelick PC (2005) Integration and evolution of the cichlid mandible: the molecular basis of alternate feeding strategies. *Proc Natl Acad Sci USA* 102:16287–16292
- Anderson MJ, Millar RB (2004) Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand. *J Exp Mar Biol Ecol* 305:191–221
- Angel A, Ojeda FP (2001) Structure and trophic organization of subtidal fish assemblages on the northern Chilean coast: the effect of habitat complexity. *Mar Ecol Prog Ser* 217:81–91
- Bellwood DR, Wainwright PC (2002) The history and biogeography of fishes on coral reefs. In: Sale PF (ed) *Coral reef fishes. Dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, pp 5–32
- Beyst B, Vanaverbeke J, Vincz M, Mees J (2002) Tidal and diurnal periodicity in macrocrustaceans and demersal fish on an exposed sandy beach, with special emphasis on juvenile plaice *Pleuronectes platessa*. *Mar Ecol Prog Ser* 225:263–274
- Boyle KS, Horn MH (2006) Comparison of feeding guild structure and ecomorphology of intertidal fish assemblages from central California and central Chile. *Mar Ecol Prog Ser* 319:65–84
- Carr MH, Anderson TW, Hixon MA (2002) Biodiversity, population regulation, and the stability of coral-reef fish communities. *Proc Natl Acad Sci USA* 99:11241–11245
- Castillo-Rivera M, Kobelkowsky A, Zamayoa V (1996) Food resource partitioning and trophic morphology of *Brevoortia gunteri* and *B. patronus*. *J Fish Biol* 49:1102–1111
- Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth
- Clements KD (2003) Triplefins. In: Andrew NL, Francis MP (eds) *The living reef. The ecology of New Zealand's rocky reefs*. Craig Potton Publishing, Nelson, pp 160–167
- Clements KD, Jawad LA, Stewart AL (2000) The New Zealand triplefin *Forsterygion signata* (Teleostei; Tripterygiidae): a junior synonym of *G. gymnota* from Tasmania. *J R Soc NZ* 30:373–384
- Denoeel M, Schabetsberger R (2003) Resource partitioning in two heterochronic populations of Greek Alpine newts, *Triturus alpestris veluchiensis*. *Acta Oecol* 24:55–64
- Duftner N, Koblmüller S, Sturmbauer C (2005) Evolutionary relationships of the Limnochromini, a tribe of benthic deepwater cichlid fish endemic to Lake Tanganyika, East Africa. *J Mol Evol* 60:277–289
- Eastman JT (1997) Phyletic divergence and specialization for pelagic life in the antarctic Nototheniid fish *Pleuragramma antarcticum*. *Comp Biochem Physiol A Mol Integr Physiol* 118:1095–1101
- Feary DA, Clements KD (2006) Habitat use by triplefin species (Tripterygiidae) on rocky reefs in New Zealand. *J Fish Biol* 69:1031–1046
- Floeter SR, Ferreira CEL, Dominici-Arosemena A, Zalmon IR (2004) Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. *J Fish Biol* 64:1680–1699
- Fricke R (1994) Tripterygiid fishes of Australia, New Zealand and the Southwest Pacific Ocean (Teleostei). Koeltz Scientific Books, Königstein
- Fricke R (1997) Tripterygiid fishes of the western and central Pacific, with descriptions of 15 new species, including an annotated checklist of world Tripterygiidae (Teleostei). Koeltz Scientific Books, Königstein
- Fricke R (2002) Tripterygiid fishes of New Caledonia, with zoogeographical remarks. *Environ Biol Fish* 65:175–198
- Futuyma DJ, Moreno G (1988) The evolution of ecological specialization. *Annu Rev Ecol Syst* 19:207–233
- Glasby TM, Kingsford MJ (1994) *Atypichthys strigatus* (Pisces: Scorpididae): an opportunistic planktivore that responds to benthic disturbances and cleans other fishes. *Aust J Ecol* 19:385–394
- Grossman GD (1986) Food resource partitioning in a rocky intertidal fish assemblage. *J Zool Soc Lond B* 1:317–355
- Hickey AJR, Clements KD (2003) Key metabolic enzymes and muscle structure in triplefin fishes (Tripterygiidae): a phylogenetic comparison. *J Comp Physiol B* 173:113–123
- Hickey AJR, Clements KD (2005) Genome size evolution in New Zealand triplefin fishes. *J Heredity* 96:356–362
- Hickey AJR, Lavery SD, Eyton SR, Clements KD (2004) Verifying invasive marine fish species using molecular techniques: a model example using triplefin fishes (Family: Tripterygiidae). *NZ J Mar Freshwat Res* 38:439–446
- Hilton Z, Wellenreuther M, Clements KD (2008) Physiology underpins habitat partitioning in a sympatric sister-species pair of intertidal fishes. *Funct Ecol* 22:1108–1117
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17:754–755
- Hyndes GA, Platell ME, Potter IC (1997) Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. *Mar Biol* 128:585–598
- Karpouzi VS, Stergiou KI (2003) The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *J Fish Biol* 62:1353–1365
- Kotschal K (1988) Evolutionary patterns in tropical marine reef fish feeding. *Zool Syst Evolut-forsch* 26:51–64
- Kotschal K, Thomson DA (1986) Feeding patterns in eastern Tropical Pacific blennioid fishes (Teleostei: Tripterygiidae, Labrisomidae, Chaenopsidae, Blenniidae). *Oecologia* 70:367–378
- Krebs CJ (1999) *Ecological methodology*. Benjamin/Cummings, California

- Levesque C, Juniper SK, Marcus J (2003) Food resource partitioning and competition among alvinellid polychaetes of Juan de Fuca Ridge hydrothermal vents. *Mar Ecol Prog Ser* 246:173–182
- Liem KF (1990) Aquatic versus terrestrial feeding modes: possible impacts on the trophic ecology of vertebrates. *Am Zool* 30:209–221
- Longnecker K (2007) Devil in the details: high-resolution dietary analysis contradicts a basic assumption of reef-fish diversity models. *Copeia* 3:543–555
- Matic-Skoko S, Antolic B, Kraljevic M (2004) Ontogenetic and seasonal feeding habits of the annular seabream (*Diplodus annularis* L.) in *Zostera* sp. beds, eastern Adriatic Sea. *J Appl Ichthyol* 20:376–381
- Motta PJ (1985) Functional morphology of the head of Hawaiian and mid-Pacific butterfly-fishes (Perciformes, Chaetodontidae). *Environ Biol Fish* 13:253–276
- Pagel M, Meade A (2004) A phylogenetic mixture model for detecting pattern-heterogeneity in gene sequence or character-state data. *Syst Biol* 53:571–581
- Pagel M, Meade A, Barker D (2004) Bayesian estimation of ancestral character states on phylogenies. *Syst Biol* 53:673–684
- Paulin CD, Roberts CD (1992) The rockpool fishes of New Zealand. Museum of New Zealand, Te Papa, Tongarewa, Wellington
- Platell ME, Potter IC (2001) Partitioning of food resources amongst 18 abundant benthic carnivorous fish species in marine waters on the lower west coast of Australia. *J Exp Mar Biol Ecol* 261:31–54
- Platell ME, Orr PA, Potter IC (2006) Inter- and intraspecific partitioning of food resources by six large and abundant fish species in a seasonally open estuary. *J Fish Biol* 69:243–262
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574
- Ross ST (1986) Resource partitioning in fish assemblages: a review of field studies. *Copeia* 2:352–388
- Russell BC (1983) The food and feeding habits of rocky reef fish of northeastern New Zealand. *NZ J Mar Freshw Res* 17:121–145
- Sale PF (2002) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, Amsterdam
- Schluter D (2000) The ecology of adaptive radiations. Oxford University Press, Oxford
- Silberschneider V, Booth DJ (2001) Resource use by *Enneapterygius rufopileus* and other rockpool fishes. *Environ Biol Fish* 61:195–204
- Streelman JT, Danley PD (2003) The stages of vertebrate evolutionary radiation. *Trends Ecol Evol* 18:126–131
- Syms C (1995) Multi-scale analysis of habitat association in a guild of blennioid fishes. *Mar Ecol Prog Ser* 125:31–43
- Taylor RB (1998) Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates. *Mar Ecol Prog Ser* 172:37–51
- Vanderklift MA, Kendrick GA, Smit AJ (2006) Differences in trophic position among sympatric sea urchin species. *Est Coast Shelf Sci* 66:291–297
- Wainwright PC, Richard BA (1995) Predicting patterns of prey use from morphology of fishes. *Environ Biol Fish* 44:97–113
- Wellenreuther M (2006) Ecological factors associated with speciation in New Zealand triplefin fishes (Tripterygiidae). PhD. School of Biological Sciences, Auckland
- Wellenreuther M, Barrett PT, Clements KD (2007) Ecological diversification in habitat use by subtidal triplefin fishes (Tripterygiidae). *Mar Ecol Prog Ser* 330:235–246
- Wellenreuther M, Syms C, Clements KD (2008) Consistent habitat use across biogeographic gradients. *Ecography* 31:84–94
- Wennhage H, Pihl L (2002) Fish feeding guilds in shallow rocky and soft bottom areas on the Swedish west coast. *J Fish Biol* 61:207–228
- Westneat MW (1994) Transmission of force and velocity in the feeding mechanisms of labrid fishes (Teleostei, Perciformes). *Zoomorphology* 114:103–118
- Westneat MW, Alfaro ME, Wainwright PC, Bellwood DR, Grubich JR, Fessler JL, Clements KD, Smith LL (2005) Local phylogenetic divergence and global evolutionary convergence of skull function in reef fishes of the family Labridae. *Proc R Soc B* 272:993–1000
- Zekeria ZA, Dawit Y, Ghebremedhin S, Naser M, Videler JJ (2002) Resource partitioning among four butterflyfish species in the Red Sea. *Mar Freshw Res* 53:163–168