

Body size and ecological diversification in a sister species pair of triplefin fishes

Maren Wellenreuther · Craig Syms · Kendall D. Clements

Received: 13 July 2006 / Accepted: 14 May 2007 / Published online: 6 June 2007
© Springer Science+Business Media B.V. 2007

Abstract The effect of body size on spatial resource competition and reproductive isolation was examined in a sister species pair of subtidal triplefin fishes (F. Tripterygiidae) in New Zealand. *Ruanoho decemdigitatus* and *Ruanoho whero* have overlapping sympatric distributions and differ in body size, attaining a total length of 12 cm and 9 cm, respectively. *R. decemdigitatus* was most commonly found in sheltered areas shallower than 5 m, while *R. whero* was frequently found in sheltered to moderately exposed areas down to 20 m. In sites where the species co-occurred, *R. whero* was less associated with rock substratum. The effect of body size on substratum use was investigated using laboratory trials based on the field data to test habitat preference and competitive ability in a common setting. Reproductive behaviour was assessed in courtship, mate choice and hybridisation trials. Both species exhibited similar habitat preferences, but large *R. decemdigitatus* were dominant in inter- and intraspecific contests for the preferred rock habitat, while small *R. whero* were displaced into less preferred habitats. Courtship behaviour in *R. whero* was a subset of that displayed by *R. decemdigitatus*, while no mating behaviour was observed in heterospecific trials. Female *R. whero* showed a strong preference for smaller males, while female *R. decemdigitatus* had no preference for male size. Results suggest that body size differences in the *Ruanoho* pair are consistent with female choice for smaller males in *R. whero* and competition for habitat in both species. Body size in the *Ruanoho* species appears to be influenced by conflicting selection pressures that may differ between the species.

Keywords Ecological diversification · Competition · Body size · Assortative mating · Reproductive isolation · Tripterygiidae · Courtship behaviour

M. Wellenreuther (✉) · K. D. Clements
School of Biological Sciences, The University of Auckland, Private Bag 92019,
Auckland, New Zealand
e-mail: Maren.Wellenreuther@zoekol.lu.se

C. Syms
School of Marine and Tropical Biology, James Cook University, Townsville 4811 QLD, Australia

Introduction

Ecological diversification, the evolution of divergent ecological characteristics within a lineage, is a topic central to the study of evolutionary ecology (Schluter 2000). Diversification is facilitated in heterogeneous environments where variable resource distribution allows specialized individuals to evolve and coexist (Dobzhansky 1951). Spatial variation in habitat availability has been shown to be a potent force in the evolutionary diversification of animals both theoretically (Doebeli and Dieckmann 2003) and experimentally (Nevo et al. 1998).

Diversification in habitat use is often linked with divergence in other phenotypic traits (e.g. Langerhans et al. 2003), such as body size. Divergence in body size has been linked with ecological diversification in several fish species (e.g. Lu and Bernatchez 1999; Schliewen et al. 2001; Knouft 2003; Knudsen et al. 2006), presumably because body size directly affects competitive dominance within populations (Beaugrad and Zayan 1985) and between closely related species (Robertson 1998). Competition for habitat is intense when individuals are highly territorial, and generally in these situations large body size gives individuals an advantage in contests and territorial defence (Wilson 1975). This effect is particularly strong when individuals with better territories not only obtain better resources, but also increase the quantity of mates and produce offspring with higher survival (Lindström 1992). Because male mating success in many fishes is related to territory quality (reviewed in Jennions and Petrie 1997), it can be expected that larger males typically have a competitive advantage over smaller males, thereby gaining better resources and more matings. While the advantages of large body size are well established, there is a substantial lack of studies on the costs of having a large body size. These can include increased foraging costs and predation risk before reaching sexual maturation size (Abrams et al. 1996); increased parasitism and starvation because of reduced agility; increased detectability and predation (Ghiselin 1974); higher energy requirements (Blanckenhorn 1998), heat stress and intrinsic costs of reproduction; decreased mating success of large males due to reduced agility (Blanckenhorn 2000); and lastly reduced mating success in females and males due to late reproduction (Westendorp and Kirkwood 1998).

Reproductive isolation between species may arise as a correlated response to divergent selection between different habitats, even where female choice is not under selection (Rice and Hostert 1993). A more direct path to reproductive isolation can be achieved when the phenotypic traits that lead to ecological divergence are also involved in mate choice (Schliewen et al. 2001; Knudsen et al. 2006). In this case, sexual selection on diverging phenotypic traits can lead directly to the evolution of premating isolation between populations (Kondrashov and Shpak 1998). For example, Schluter (1993) showed that two stickleback forms, known as the small 'limnetic' and the large 'benthic' ecotype, diverged in body size due to differences in their respective limnetic and benthic habitats. Work on reproductive isolation showed that the ecotypes were reproductively isolated from one another, and that interspecific mate preferences were primarily linked with differences in male body size (Nagel and Schluter 1998).

Body size is a likely candidate for a linkage between ecological divergence and mate choice for two reasons. First, recent studies have shown that body size in many animals is highly plastic (Peters 1983) and the likely target of divergent selection pressures between contrasting environments (Ratcliffe and Grant 1983; Schluter et al. 1991). Second, differences in body size can affect intra- and intersexual selection (Andersson 1994).

In the former case, differences in body size may influence the dominance status of individuals, and thus male-male competition within a species. In the latter case, body size differences between males may directly affect the probability of heterospecific matings if species possess species-specific preferences for male size, thereby leading to assortative mating. Size-assortative mate choice has been observed in many invertebrate and vertebrate taxa, including snails (Cruz et al. 2004), birds (Ratcliffe and Grant 1983), lizards (Richmond and Reeder 2002), and fishes (Nagel and Schluter 1998; McKinnon et al. 2004). Consequently, ecological divergence in body size has been linked with reproductive isolation of closely related species pairs (e.g. Ratcliffe and Grant 1983; Rice and Hostert 1993; Nagel and Schluter 1998), demonstrating a direct link between ecological divergence in phenotypic traits and the evolution of premating isolation. The importance of body size in premating isolation is illustrated in cases where reproductive isolation between diverging populations is incomplete (Richmond and Reeder 2002). In these cases, the level of reproductive isolation between populations is usually directly related to differences in body size.

Here we investigate the relationships between resource competition and premating isolation in *Ruanoho decemdigitatus* and *Ruanoho whero* (F. Tripterygiidae), two sympatric marine blennioid fishes from New Zealand. The genus *Ruanoho* was described by Hardy (1986) to include these two species, which were separated on the basis of differences in body size, lateral line scale morphology, length of spines in the first dorsal fin, and colour pattern. Fricke (1994) experienced difficulty in differentiating the two species, and subsequently treated *Ruanoho* as synonymous ecological forms. Other authors (e.g. Francis 2001) continued to recognise two species. Recently, Hickey and Clements (2005) showed that *R. decemdigitatus* and *R. whero* (i) differ significantly in genome size, and (ii) form reciprocally monophyletic lineages in both mitochondrial and nuclear DNA. These data provide strong support for Hardy's original description of these forms as distinct biological species. *R. decemdigitatus* and *R. whero* display the least amount of genetic divergence seen among the six sister-species pairs of New Zealand triplefins included in the analysis of Hickey and Clements (2005). This divergence is less than "cryptic" genetic divergences reported from Mediterranean triplefins (Carreras-Carbonell et al. 2005), suggesting that the mechanisms that led to the ecological divergence of the *Ruanoho* species are comparatively recent and may still be in evidence (Schluter 2000).

Some of the morphological differences between the *Ruanoho* species, especially body size and colour pattern (Hardy 1986), are known to affect mate selection by females in other fish species (Oliveira et al. 2000). Differences in colour pattern do not appear to be important for female mate selection in *Ruanoho*, as males of both species turn completely black during courtship and when guarding nests (Wellenreuther and Clements 2007). Conversely, differences in size are pronounced between the species, with *R. decemdigitatus* and *R. whero* attaining maximum lengths of about 12 cm and 9 cm, respectively (Francis 2001). The *Ruanoho* species show little differentiation in prey taxa and jaw morphology (Feary 2001), therefore it is unlikely that they have diverged markedly along a trophic axis. In contrast, the species have diversified considerably in habitat use (Feary and Clements 2006; Wellenreuther et al. 2007).

This paper explores two aspects of the relationship between ecological divergence in habitat use and reproductive isolation in the *Ruanoho* species. First, we investigated the habitat use of both species in the field. Second, we used competition trials in the laboratory to test whether species differ in their preference and competitive ability for the four most commonly used habitat types. Third, we tested whether ecological divergence is linked with the degree of reproductive isolation between the species. The courtship behaviour of each species was recorded, then we assessed whether male body size affects female mate

choice. Finally, we used hybridisation trials, in which each species was denied a conspecific mate, to establish the extent of reproductive isolation between the species. Hybrids of the *Ruanoho* species have never been reported, although it is unclear whether this is due to inadequate sampling, hybrid inviability, or the lack of hybridisation.

Materials and methods

Study species

R. decemdigitatus and *R. whero* are benthic, marine fishes that occur sympatrically around coastal New Zealand (Fricke 1994). All New Zealand triplefin species establish a small territory (1–2 m²) after settlement in which breeding and feeding is carried out, and this area is defended year round (Wellenreuther and Clements 2007). Previous work on the *Ruanoho* sister species pair has shown that the species have diversified in habitat use (Feary and Clements 2006; Wellenreuther et al. 2007). *R. decemdigitatus* is found typically in shallow habitats in coastal mainland areas and seldom on offshore islands, while *R. whero* is found in a range of depths and is a common inhabitant of offshore islands and coastal mainland areas. Due to these habitat differences in, *R. decemdigitatus* are exclusively found in sympatry with *R. whero*, while *R. whero* commonly occurs in allopatric populations. Reproduction in triplefins occurs in the same small territory that they occupy at other times of the year and takes place during the winter-spring season (Fricke 1994; Francis 2001; Wellenreuther and Clements 2007). During the breeding season, the males of both *Ruanoho* species assume a jet-black spawning colouration over the whole body (Paulin and Roberts 1992; Francis 2001; Wellenreuther and Clements 2007). Unlike male colouration, female colouration is consistent throughout the year, and is indistinguishable from the colouration of non-reproductive males. The mating system in New Zealand triplefins is polygynandrous, with different clutches simultaneously present in a nest (Thompson 1979). Males build nests on different types of hard substrata, and when encountering a female the male displays intensively and tries to lead the female to the nest to initiate spawning (Thompson 1986). Males spend the majority of their time in close proximity to the nest until the larvae hatch, with the exception of occasional feeding forays (Thompson 1979).

Habitat use

Overlap in habitat use was investigated in the Inner Hauraki Gulf (36°36'S, 174°50'E) in north-eastern New Zealand. Quadrats were sampled at 49 sites between the Whangaparaoa Peninsula and the Leigh Marine Reserve to a depth of 30 m (Fig. 1). The geographic position of each quadrat was noted using a handheld Garmin® 12 global positioning system (GPS) (accuracy ± 15 m). Exposure of each quadrat was calculated based on the total sum of the fetch using the program 'Fetch Effect Analysis' (Pickard 2000), which measures fetch distance (i.e. distance to land up to a maximum of 300 km) for each 20° sector on a compass rose from a given point (Thomas 1986). Quadrats were sampled via SCUBA using a 4 × 4 m sampling area. For each quadrat the depth and microposition of all *R. whero* and *R. decemdigitatus* were recorded. Based on the depth distribution of the *Ruanoho* species (see results), the microposition use of *R. whero* was investigated in the absence (deeper than 5 m) and in the presence (shallower than 5 m) of *R. decemdigitatus*.

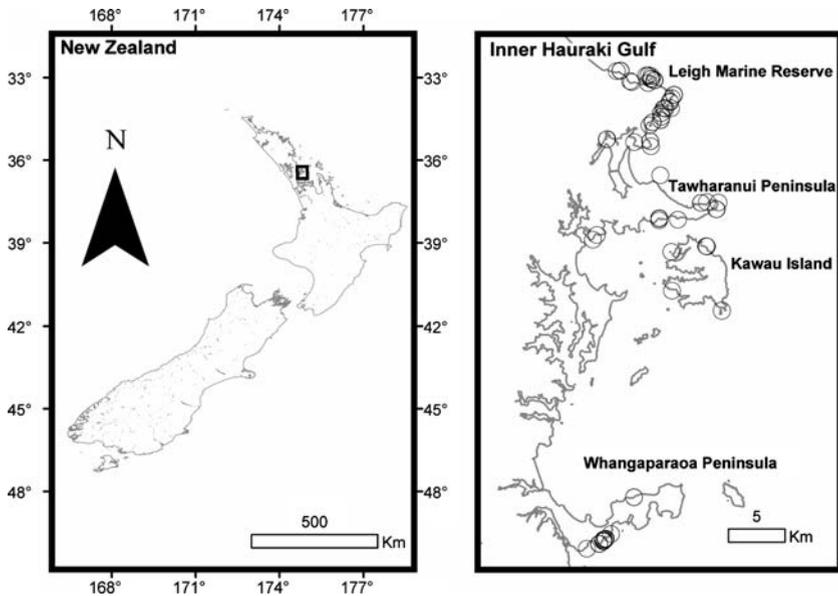


Fig. 1 Map of the study sites. The black rectangle in the New Zealand map indicates the position of the Inner Hauraki Gulf. Circles in the Inner Hauraki Gulf map indicate the position of study sites. Specimens for the competition and mate choice trials were caught at the Tawharanui and Whangaparaoa Peninsulas

Differences in microposition use were analysed using Chi-square analysis, and the densities of both species were calculated as the number of individuals m^{-2} .

Holding procedures

Individuals of *R. whero* and *R. decemdigitatus* were collected from the Whangaparaoa ($36^{\circ}36'S$, $174^{\circ}50'E$) and Tawharanui ($36^{\circ}22'S$, $174^{\circ}48'E$) Peninsulas (Fig. 1) during the triplefin spawning season from late June to the end of August using slurp guns and hand nets. Fish were transported immediately to the Leigh Marine Laboratory of the University of Auckland and maintained in holding aquaria. The total length (L_T) of all fish was measured with vernier calipers and males were sexed visually on capture by the jet-black spawning colouration. Holding aquaria contained sand, gravel and different-sized stones to simulate natural habitat. Each aquarium received seawater from a flow-through circulation system at ambient temperature ($15\text{--}17^{\circ}C$), salinity ($34\text{--}34.7\text{‰}$) and photoperiod. Fish were fed daily *ad libitum* with a variety of different prey types including *Artemia* sp. nauplii, frozen bloodworms (*Chironomid* sp.), frozen adult brine shrimp (*Artemia* sp.) and New Zealand green lip mussels (*Perna canaliculus*).

Competition trials

All fish were maintained in holding aquaria for at least two days prior to trials. Aquaria for the experiments were of identical dimensions ($50\text{ cm} \times 40\text{ cm} \times 35\text{ cm}$) and differed only

in their placement within the room. Four substratum types (rocks (rocks > 7 cm), cobbles (rocks < 7 cm), gravel (rocks < 4 cm), and sand) were placed in equal amounts in discrete sections of each aquaria to a depth of approximately 7 cm. These substratum types were chosen because they were frequently found in the habitats of both species in the wild.

The first experiment (no competition) was designed to determine substratum use of individual fish of each species per aquarium in the absence of a competitor. The second experiment (intraspecific competition) consisted of two individuals of each species to estimate the extent of intraspecific competitive interaction by each species. The third experiment (interspecific competition) consisted of one individual of each species to test the substratum use of each species in the presence of an interspecific competitor. The fourth experiment (high density competition) consisted of four individuals of each species per aquarium to test substratum use of each individual in a high density sympatric situation. The no competition, intraspecific competition and interspecific competition experiments were conducted with eight replicate aquaria, however, the high density competition experiment was run with five aquaria because fish availability limited the number of trials at the higher density.

Before every trial, each aquarium was assigned a designated number of fish. Prior to introduction into the centre of the aquarium, each fish was measured (L_T) to the nearest mm. The size distribution of each species did not differ between experiments (*R. whero* [$F_{3,40} = 1.83, P = 0.16$] and *R. decemdigitatus* [$F_{3,40} = 0.79, P = 0.51$]), and individuals were never used more than once in each experiment. All experiments started at 0800 h and observations of substratum and microposition use were made after 24 h. Individual fish were easily recognised by length, colouration and markings. Each observation consisted of the numbers of individuals on each substratum, and microposition on rock (if rock was selected as a substratum type). Two different rock micropositions were recorded, namely the 'side or top of rock' and 'under rock'.

A categorical linear model was used to analyse the (i) substratum and (ii) microposition use data of all four experiments:

$$\text{Habitat} = \text{Treatment Species Treatment*Species Size}$$

There was a strong potential for body size effects, in addition to treatment and species effects, so 'Treatment' and 'Species' were included as categorical factors, with a simple covariate of 'Size'. The habitat variable was a multinomial variable corresponding to either the substratum or microposition categories respectively, weighted by the number of individuals in each category. The generalised logit was used as the link function. The displacement of each species was calculated as the natural log of the ratio of its trait mean in interspecific competition and its mean in the absence of a heterospecific competitor, the larger divided by the smaller. Symmetry of displacement was computed as the ratio of the displacements for each species, the smaller divided by the larger (Schluter 2000). Symmetry ranged from 0 (only one of two species shifted in habitat use in response to heterospecific competition) to 1 (both species shifted equally).

Mate choice trials

Mate choice trials were conducted to test whether females of the two *Ruanoho* species showed a preference for male size. Individuals for the mate choice trials were selected on the basis that they had spawned previously to ensure that (i) sex was accurately determined,

and (ii) individuals were reproductively active. The design of the mate choice apparatus followed LaFleur et al. (1997) except for slight modifications in the aquarium dimensions. The main apparatus consisted of a 45-l glass aquarium (50 cm × 30 cm × 30 cm) situated between two smaller chambers (8 cm × 30 cm × 30 cm). Two transparent and removable Plexiglas sliding walls, placed 16 cm from each end, divided the main aquarium into three compartments. Several small perforations were made in the Plexiglas walls to allow water flow between the compartments. Black plastic sheets were placed on the back and distal sides of the end compartments to minimise any visual interference.

At the start of each trial, two homospecific males were selected from the holding aquaria and allocated randomly to each end compartment. For each trial the males were labelled as ‘large’ or ‘small’ depending on their size relative to each other. A female of the same species was placed in the inner compartment between the two Plexiglas sliding walls. Before the commencement of the trial all fish were allowed to acclimate and observe each other for 10 min. After the acclimation period, the Plexiglas partitions were slowly lifted simultaneously by pulling a string from another room and the female was allowed to move freely. Movement of the female was recorded for 10 min with a digital Sony video camera (model number: DCR-PC10E) placed 1.5 m in front of the apparatus. Data recording commenced after the female started to move. Female fish encountered each male only once during the experiments. The data collection consisted of 20 trials for each species. To quantify the strength of the female mate choice the tank was divided into three zones. Two zones were labelled ‘preference zones’ and consisted of the areas 12.5 cm from each end of the aquarium. The presence of the female in one of these zones indicated a preference for the nearest male. The middle zone was labelled the ‘no preference zone’ as the presence of the female in this zone was assumed to indicate no preference for either male. Ten min of videotape were analysed and the time the female spent in each zone was quantified for each trial.

Two complementary tests of size-assortative mating were investigated: (i) the initial choice, and (ii) the overall choice. Initial choice was measured as the number of times females spent the first 15 consecutive seconds in the ‘preference zone’ with the ‘small’ or the ‘large’ male and was analysed using Chi-square tests. The overall mate choice was analysed using percentages of summed time counts for each zone during a trial. Preference was assessed using paired dependent *t*-tests on the difference of the time spent on the side of the ‘small’ male and the time spent on the side of the ‘large’ male.

Courtship behaviour

A pilot study was used to determine the male courtship characteristics of both *Ruanoho* species. Individuals for the courtship trials ($n = 6$ per species) were chosen on the basis that they had spawned previously, and each male was only used once. After 2 weeks in the holding tanks all female fish were put in a separate holding aquarium and each male was allocated to a single aquarium (50 cm × 30 cm × 30 cm) so that the males could establish a territory and nest site. After at least 2 days a single female was then added to the aquarium with the male and any courtship behaviour was recorded for 10 min immediately following introduction using a digital Sony video camera (model number: DCR-PC10E).

Hybridisation trials

Specimens were kept in holding aquaria for at least four days prior to the commencement of conspecific and heterospecific mating trials. A total of 16 conspecific mating trials were

run for each species. At the start of each trial, males were placed individually in aquaria and were given the opportunity to establish a nest. A conspecific female was then introduced and monitored daily over 10 days to determine if mating took place.

Heterospecific trials were conducted as above, and consisted of eleven pairs of female *R. whero* and male *R. decemdigitatus*, and nine pairs of male *R. decemdigitatus* and female *R. whero*. Only individuals that had spawned previously in a conspecific trial were used in heterospecific trials to ensure that (i) sex was accurately determined, and (ii) individuals were reproductively active. This has the possible limitation that prior experience could lead to behavioural imprinting of mate choice (Jennions and Petrie 1997), and thus decrease the probability of hybridisation. As triplefins are short lived and mature within the first year (Thompson 1979), the use of naïve animals would require fish to be caught within the first few months of their life and kept in isolation in captivity for an extended period to eliminate the possibility of prior mating experience. Determining sex and reproductive maturity in such naïve individuals would also be problematical, and could lead to false negative results in the hybridisation trials. To avoid these problems we used reproductively active individuals, despite the possibility of behavioural imprinting of mate choice.

The L_T of all fish used in the conspecific and heterospecific trials was recorded to estimate the size at which *R. whero* and *R. decemdigitatus* show reproductive activity. To verify the behavioural observations of reproductive behaviour, all specimens used in the trials were subsequently killed and dissected to determine gonad maturity. Maturity was determined by visual inspection of gonad anatomy following Neat (2001). The length data from the hybridisation trials and field observations of nesting males were further used to test for sexual size dimorphism in the two species.

Results

Habitat use

In the field *R. decemdigitatus* used a subset of the habitat of *R. whero*. *R. decemdigitatus* occurred in shallow (0–6 m) and sheltered (0–119 km fetch) habitats, whereas *R. whero* was found in a range of depths (0–21 m) and exposures (0–247 km fetch). A comparison of the mean fetch of sites containing *R. decemdigitatus* with the mean fetch of sites containing *R. whero* showed that the *Ruanoho* species differ in fetch use ($t(60) = -2.15$, $P = 0.04$, Fig. 2). Depth differences between species were also significant ($t(60) = -3.58$; $P < 0.001$, Fig. 2).

Four micropositions were used by both species, namely ‘under rocks’, ‘side or top of rocks’, ‘on sand’ and ‘on cobbles/gravel’. *R. decemdigitatus* was almost exclusively (95%) found ‘under rocks’ (Fig. 3). *R. whero* preferred the microposition ‘under rocks’ (70%) and the ‘side or top of rocks’ (22%) in areas deeper than 5 m (allopatric populations, Fig. 3). The use of the microposition ‘under rocks’ was lower (58%) and ‘side or top of rocks’ higher (33%) in areas shallower than 5 m, which were areas where *R. decemdigitatus* co-occurred (sympatric populations, Fig. 3). These differences in microposition use were significant between species ($\chi^2 = 37.4$, $df = 6$, $P < 0.0001$). Relative densities of *R. whero* were similar in habitats deeper and shallower than 5 m (0.68 m^{-2} and 0.63 m^{-2} , respectively), although both densities were higher than that of *R. decemdigitatus* (0.25 m^{-2}).

Fig. 2 Depth and exposure (fetch) use of *R. decemdigitatus* and *R. whereo* in the Hauraki Gulf. Black square shows the median, the box around the mean shows 25–75% percentiles and the whiskers show the non-outlier range

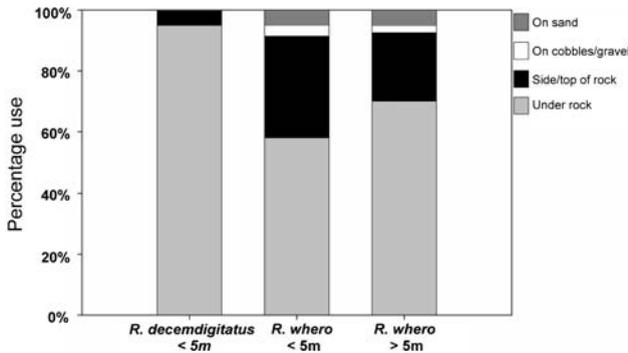
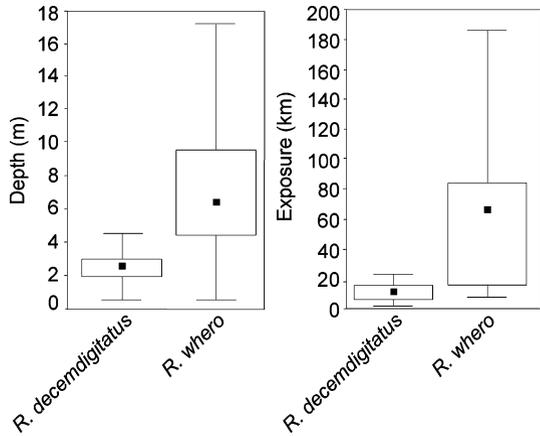


Fig. 3 Percentage microposition use of *R. decemdigitatus* (<5 m), *R. whereo* (<5 m) and *R. whereo* (>5 m) in the field. Both species co-occur in areas that are shallower than 5 m, however, *R. whereo* occur allopatrically in areas deeper than 5 m

Competition trials

The results of the ‘no competition’ experiment showed that both species exhibit almost identical substratum preferences. Both species preferred rock as a substratum, and only *R. whereo* selected cobbles. Neither of the species selected gravel or sand (rock>>cobble>sand = gravel, Fig. 4). In the ‘intraspecific competition’ experiment *R. whereo* occupied all four substratum types, of which rock was used predominantly (Fig. 4). Similarly, *R. decemdigitatus* used a wider range of substratum types when in the presence of conspecifics, and rock was again the preferred substratum type (Fig. 4). In the ‘interspecific competition’ experiment, the use of the preferred substrate by *R. whereo* (i.e. rock) decreased greatly in the presence of *R. decemdigitatus*, while the substratum use by *R. decemdigitatus* remained unchanged, with 100% of the *R. decemdigitatus* individuals using rock (Fig. 4). The mean use of cobble, gravel and sand in the ‘high density competition’ experiment was much higher by both species, however, rock was still the most preferred substratum type (rock > cobble > gravel > sand, Fig. 4). The categorical linear model showed that body size was significant ($P = 0.01$), while both ‘species’ and ‘treatment’ were

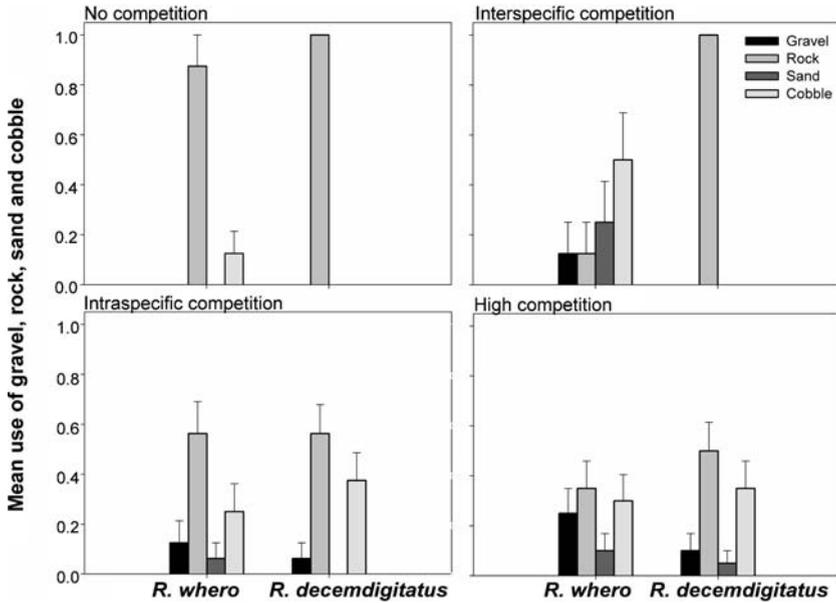


Fig. 4 Percentage use of gravel, rock, sand and cobble by *R. decemdigitatus* and *R. whero* in the four competition experiments

not significant (Table 1), in habitat use. This finding demonstrates that habitat use is driven primarily by the body size of an individual, rather than by species identity or experiment type.

The preference for the micropositions was equally clear. When rock was selected as a substratum type both species preferably selected the microposition ‘under rock’ in the absence of a competitor, though *R. whero* also appeared to use the side and tops of rocks (Fig. 5). In the ‘intraspecific competition’ experiment the use of the microposition ‘under rock’ decreased in both species, while the use of ‘side and top of rock’ increased (Fig. 5). In the presence of a heterospecific competitor, fewer *R. whero* used the microposition

Table 1 Categorical linear model analysis of the use of substratum (rock, cobble, gravel and sand) and microposition types (‘under rock’ and ‘side or top of rock’)

Effect	DF	Wald chi-square	P-value
Substratum types			
Species	3	0.000	1.000
Treatment	9	3.393	0.947
Species*Treatment	9	0.025	1.000
Body size	3	11.310	0.010
Microposition use			
Species	1	0.000	0.999
Treatment	3	3.678	0.298
Species*Treatment	3	0.282	0.963
Body size	1	3.912	0.048

‘under rock’ and no individuals were observed to use the microposition ‘side or top of rock’, whereas the use of micropositions by *R. decemdigitatus* remained virtually unchanged from the ‘no competition’ experiment (Fig. 5). Microposition use by both species in the ‘high density competition’ experiment differed considerably from that in the three other experiments, in that more individuals of both species used the microposition ‘side or top of rocks’ (Fig. 5). The categorical linear model analysis of the ‘side/top of rock’ versus ‘under rock’ categories showed again that body length is the main determinant of habitat use in *R. decemdigitatus* and *R. whero* ($P < 0.05$), while species and treatment were not significant (Table 1).

Interspecific character shifts from no competition to high density interspecific competition were strongly asymmetric for the most preferred substratum type rock (symmetry of character shift: 0.76), since *R. decemdigitatus* was competitively superior to *R. whero*. The shifts in resource use for sand, gravel and cobble could not be calculated as either one or both species did not use these substratum types at all in the no competition, interspecific competition or the high density competition experiments.

Mate choice trials

The ‘initial choice’ analysis showed that the species differ significantly in their choice of larger and smaller males ($\chi^2 = 5.6$, $df = 1$, $P < 0.05$). Females of *R. whero* chose to be next to the smaller-sized males 17/20 times, indicating a strong response. This demonstrates that *R. whero* females have an initial preference for smaller males. While in the ‘initial choice’ test *R. whero* females preferentially chose smaller-sized males, *R. decemdigitatus* females selected larger- and smaller-sized males in equal proportions. The ‘overall choice’ test

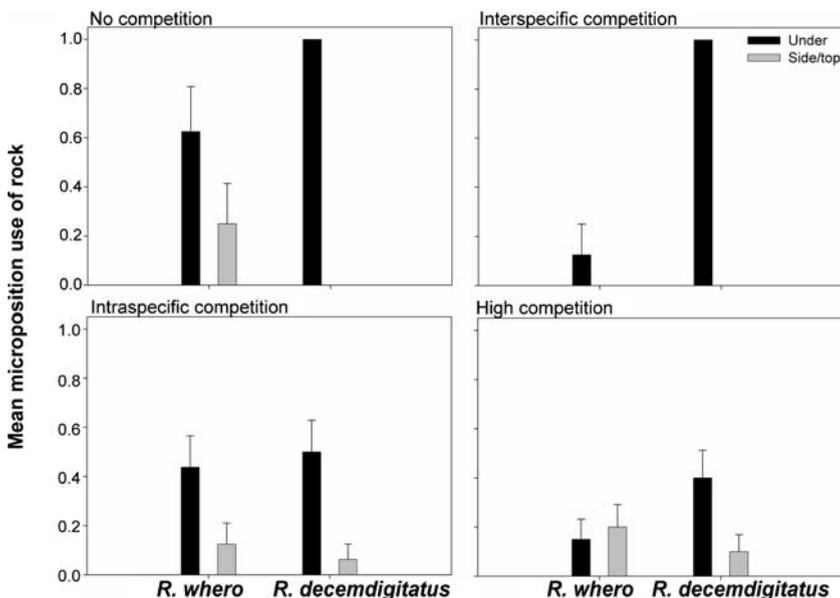


Fig. 5 Percentage use of the microposition ‘under rock’ and ‘on the side or top of rock’ by *R. decemdigitatus* and *R. whero* in the four competition experiments. Note that the percentages only sum to 1 if a species was found in all experimental replicates on rock

showed that *R. whero* females have a significant preference for smaller-sized males ($t(19) = -3.53, P < 0.01$), whereas *R. decemdigitatus* showed no preference for either larger or smaller males ($t(19) = -1.25, P = 0.23$).

Courtship behaviour

Courtship displays of *R. decemdigitatus* consisted of 11 steps: (i) darkening of breeding colours and erection of anal, caudal and all dorsal fins, (ii) increase in opercular movements, (iii) movement towards the female, (iv) flicking of the first dorsal fin, (v) opercular spread displays, in which the male widely opens and closes the operculum, (vi) lateral displays, in which the male swims close to the female with erect dorsal and pectoral fins, shivering his body, (vii) pectoral fin waving, (viii) lead displays, in which the male swims from the female to the nest with exaggerated, undulating fin and body movements, (ix) biting of the female and swimming into her, (x) male swims to the nest and female follows, and (xi) lateral shivers of the male in the nest (Fig. 6). The courtship of *R. whero* (Fig. 6) consisted of a subset of the display in *R. decemdigitatus*, including steps i-iii and viii-x, with steps iv-v and vii entirely absent, and step vi only present in two of the six individuals examined.

Hybridisation trials

Males in conspecific trials showed increased activity and territoriality, assumed a jet-black spawning colouration, and displayed frequently to the female. Conspecific pairs of *R. decemdigitatus* spawned 12 of 16 times and *R. whero* 11 of 16 times. Both *Ruanoho* species selected the microposition ‘under rock’ for all nests. In contrast, no evidence of nest

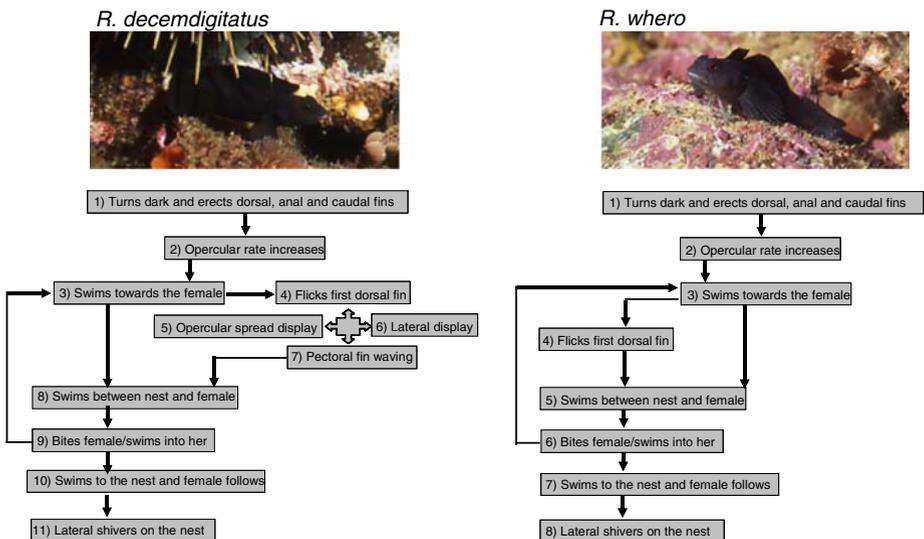


Fig. 6 Ethogram of the male courtship display in *R. decemdigitatus* and *R. whero*. Photographs show both species in jet-black spawning colouration

building, courtship behaviour or increase in territoriality was observed in heterospecific *Ruanoho* pairs. The results from the conspecific trials also indicated that individuals of *R. decemdigitatus* less than 8.5 cm L_T were not reproductively active. Males below this size did not become territorial, were less aggressive and did not establish a nest site. Female *R. decemdigitatus* below 8.5 cm L_T did not produce any eggs. In contrast, *R. whero* individuals started to become reproductively active slightly below 5 cm L_T . Visual inspection of gonad maturity in 18 individuals of each species confirmed that *R. whero* mature at a smaller size than *R. decemdigitatus*, however, the species' size ranges show slightly more overlap compared to the behavioural indications of maturity. The L_T data from the hybridisation trials and nesting males in the wild showed that there was no evidence for sexual size dimorphism in either *R. whero* ($F_{1, 118} = 0.20$, $P = 0.65$) or *R. decemdigitatus* ($F_{1, 53} = 3.38$, $P = 0.071$).

Discussion

The results of this study show that body size differences between the *Ruanoho* species affect both habitat use and reproductive isolation. Field observations demonstrated that the species differ in habitat use and that *R. whero* shifts in substratum use in the presence of *R. decemdigitatus*. Laboratory trials showed that the use of substratum types was related to body size. Despite having similar preferences for substratum type, inter- and intraspecific competition for the mutually-preferred rock habitat resulted in the displacement of small individuals of both species because the larger sized *R. decemdigitatus* had greater competitive ability in interspecific contests, a pattern that has been shown to apply in other species (Munday et al. 2001; Young 2004). The competitive dominance of *R. decemdigitatus* was illustrated by the highly asymmetric displacement ratio between the two species. The larger body size and consequent competitive superiority in interspecific contests is undoubtedly the main factor allowing *R. decemdigitatus* to exploit the preferred rock habitat when the species co-occur.

In the laboratory competition experiments small *R. whero* had to compete with larger *R. decemdigitatus* and with large conspecifics for suitable habitat space. The displacement of *R. whero* into habitats devoid of rocks is likely to increase predation risk because these habitats are less complex and offer less shelter (Forrester and Steele 2004; Gratwicke and Speight 2005). These negative effects are presumably magnified during the spawning season as both *Ruanoho* species usually use rocks as nesting substrata (Clements 2003). Substrata other than rock may not have enough area for the attachment of the eggs and are less stable, therefore nests would have a greater risk of physical damage (Piller and Burr 1999). In many fish species that exhibit paternal care, male body size is positively correlated with the size of the nesting substratum (Konishi and Takata 2004), and therefore body size is directly related to fitness (Andersson 1994). When body size is an important factor in interspecific competition between ecologically similar species, the larger species is usually a superior competitor and is more successful in establishing territories (Barlow 1992; Robertson 1996) and attracting females (McKaye 1986; Barlow 1992; Seehausen and van Alphen 1998). In contrast, a smaller body size gives individuals access to a higher quantity of shelter places (Hixon and Beets 1989), and thus may offer increased protection from predation. Competition for resources has been implicated both theoretically (Rosenzweig 1978; Doebeli and Dieckmann 2003) and empirically (Bolnick 2004; Friesen et al. 2004; Munday et al. 2004; Bernardi 2005) in the divergence of ecological traits and reproductive isolation. The finding that the *Ruanoho* species have similar substratum

preferences but differ in competitive ability is consistent with ecological competition being a factor in the evolution of these species.

The results also demonstrated that ecological diversification was linked with reproductive isolation between the species. The mate choice trials demonstrated that *R. whero* females have a preference for smaller males, while *R. decemdigitatus* females showed no general preference for either smaller- or larger-sized males. Larger males are often preferred in species with female mate choice due to the competitive advantage of large males in contests over mates (Oliveira et al. 2000; Candolin and Voigt 2001), and few exceptions to this rule are known (Andersson 1994). These exceptions include moorhens, where small, fat males are preferred by females (Petrie 1983), and in some Diptera small males have a greater chance to pair with females, possibly as a consequence of their greater agility (MacLachlan and Allen 1987). Because *R. whero* females prefer smaller males and *R. decemdigitatus* matures at a relatively large size, the likelihood of hybridisation between *R. decemdigitatus* males and *R. whero* females is very low. This suggests that body size may have been a major factor leading to premating isolation in the *Ruanoho* species. Thus, it appears that body size in the *Ruanoho* species strongly affects not only the exploitation of different habitats but also reproductive isolation. This suggests that natural selection arising from resource competition could have contributed to divergence in body size in the *Ruanoho* species. Furthermore, it appears that sexual selection in *R. whero* favours smaller males, suggesting that body size in this species may be affected by two contrasting selection pressures. Theory suggests that sexual selection for smaller male body size in *R. whero* should result in males being smaller than females (Andersson 1994), however, this study found no evidence for sexual size dimorphism in this species. An interesting topic for future work would be to test whether body size in the *Ruanoho* sister species pair is under divergent natural selection. Differential ecological adaptations are also linked with body size in other species pairs of fishes (Lu and Bernatchez 1999; Schliewen et al. 2001; Knudsen et al. 2006) and thus may form a common characteristic of reproductive isolation in fishes.

Body size differences are likely to affect mate choice in many animals because, unlike many other traits, size is easy to assess visually during courtship. In Galapagos finches (Ratcliffe and Grant 1983) and sticklebacks (Nagel and Schluter 1998; Boughman et al. 2005) morphological aspects such as shape or colour also contribute to the frequency of mating between individuals. However, it is unlikely that shape or colour of males influences mate choice in the *Ruanoho* species, as the species are very similar in shape and males of each are indistinguishable in colour during the breeding season (Francis 2001; Wellenreuther and Clements 2007).

The courtship trials showed that the premating courtship sequence differs between species, indicating divergence in behavioural traits. The courtship behaviour of *R. whero* consisted of a subset of that of *R. decemdigitatus*, as it did not include opercular and lateral spread displays or pectoral fin waving. Several studies have found strong courtship differentiation between stickleback populations (e.g. Ishikawa and Mori 2000), while others have shown that males adjust courtship in part based on female body size (Albert and Schluter 2004). Our study did not test for the effect of single traits such as size or colour on male courtship behaviour, and can thus not distinguish between these effects. However, the small magnitude of variation in courtship behaviour in both *Ruanoho* species suggests that these differences in mating sequence are likely to contribute to assortative mating between the species.

The hybridisation trials suggested that reproductive isolation between the *Ruanoho* species is complete. Avise and Saunders (1984) proposed that the absence of conspecific partners may be an important factor in increasing the likelihood of interspecific hybridisation. The present study showed a complete absence of any signs of interspecific

courtship, even in the absence of a conspecific mate, thereby indicating that the *Ruanoho* species are true biological species sensu Mayr (1999). Furthermore, our results illustrate unequivocally that assortative mating can persist in the absence of ecological and environmental cues such as microhabitat choice and seasonality.

Length measurements of reproductively active individuals and macroscopic inspection of the gonads of both species showed that *R. whereo* mature at a smaller size than *R. decemdigitatus*. The larger body size of *R. decemdigitatus* at first maturity indicates that this species either (i) matures later or (ii) grows faster than *R. whereo*. This means that the reproductive period of *R. decemdigitatus* may be comparatively shorter, and therefore the chances of finding a mate lower. However, if *R. decemdigitatus* grows faster than *R. whereo* it may reach maturity at a similar age but at a higher energetic cost (Blanckenhorn 2000). This in turn may increase the risk of predation as more foraging is necessary to achieve a faster growth (Abrams et al. 1996; Blanckenhorn 2000).

In conclusion, our results suggest that the evolution of body size differences in the *Ruanoho* sister pair may be driven not simply by adaptation to habitat, but by subtle interactions between resource competition and sexual selection (Schluter et al. 1991). Hybridisation appears to be prevented by a combination of differences in courtship behaviour, size at first maturity, and female preference for male size. Differences in body size evolving in the context of ecological differentiation between species are wholly or partly responsible for premating isolation between sympatric stickleback species (Nagel and Schluter 1998), sockeye and kokanee salmon (Foote and Larkin 1988), and several species of Galapagos finches (Ratcliffe and Grant 1983). The linkage between ecological and morphological diversification may therefore be a simple and potentially widely applicable mechanism that can lead to reproductive isolation between diverging populations, providing that individuals exhibit an underlying tendency to mate assortatively by body size.

The effects of competition and mate selection on body size divergence described here have wider implications for our understanding of adaptive radiation in New Zealand triplefins. Other sister species pairs of New Zealand triplefins, e.g. *Notoclinops segmentatus* and *N. yaldwyni*, *Bellapiscis lesleyae* and *B. medius*, *Obliquichthys maryannae* and *Forsterygion malcolmi*, *F. lapillum* and *Grahamina nigripenne* (Hickey and Clements 2005), also show considerable interspecific differences in body length and habitat use (Francis 2001; Clements 2003; Wellenreuther et al. 2007, Wellenreuther and Clements 2007). This indicates that habitat and morphological differentiation in body size may be an important component of divergence in this clade. These findings invoke a role for ecologically based selection in speciation, and support the hypothesis that adaptation to habitat is a major factor in speciation in this system.

Acknowledgements We thank Zoë Hilton and Damian Moran for help with the collection of animals and Paul Barrett for statistical advice. Howard Choat, Mark Hauber, Damian Moran, Phil Munday, David Raubenheimer, Erik Svensson and two anonymous referees made helpful comments. We thank Arthur Cozens from the Leigh Marine Laboratory for providing facilities for this study. Laboratory experiments were conducted under the University of Auckland animal ethics permit AEC/11/2002/R83. This research was supported by a Marsden Grant from the New Zealand Royal Society to Kendall Clements. Maren Wellenreuther was supported by a Top Achiever Doctoral Scholarship from the Tertiary Education Commission and a doctoral scholarship from the University of Auckland of the New Zealand Government.

References

Abrams PA, Leimar O, Nylin S, Wiklund C (1996) The effects of flexible growth rates on optimal sizes and development times in a seasonal environment. *Am Nat* 147:381–395

- Albert AYK, Schluter D (2004) Reproductive character displacement of male stickleback mate preference: reinforcement or direct selection? *Evolution* 58:1099–1107
- Andersson M, (1994) Sexual selection. Monographs in behavior and ecology. New Jersey, Princeton University Press
- Avise JC, Saunders PT (1984) Hybridization and introgression among species of sunfish (*Lepomis*): analysis by mitochondrial DNA and allozyme markers. *Genetics* 108:237–255
- Barlow GW (1992) Is mating different in monogamous species? The midas cichlid fish as a case study. *Am Zool* 32:91–99
- Beaugrad JP, Zayan RC (1985) An experimental model of Aggressive Dominance in *Xiphophorus helleri* (Pisces, Poeciliidae). *Behav Processes* 10:1–52
- Bernardi G (2005) Phylogeography and demography of sympatric sister surfperch species, *Embiotoca jacksoni* and *E. lateralis* along the California Coast: historical versus ecological factors. *Evolution* 59:386–394
- Blanckenhorn WU (1998) Adaptive phenotypic plasticity in growth, development, and body size in the yellow dung fly. *Evolution* 52:1394–1407
- Blanckenhorn WU (2000) The evolution of body size: what keeps an organism small? *Q Rev Biol* 75:385–407
- Bolnick DI (2004) Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Am Nat* 58:608–618
- Boughman JW, Rundle HD, Schluter D (2005) Parallel evolution of sexual isolation in sticklebacks. *Evolution* 59:361–373
- Candolin U, Voigt H-R (2001) Correlation between male size and territory quality: consequence of male competition or predation susceptibility? *Oikos* 95:225–230
- Carreras-Carbonell J, Macpherson E, Pascual M (2005) Rapid radiation and cryptic speciation in Mediterranean triplefin blennies (Pisces: Tripterygiidae) combining multiple genes. *Mol Phylogenet Evol* 37:751–61
- Clements KC (2003) Triplefins. The living reef. The ecology of New Zealand's rocky reefs. N Andrew and M Francis. Nelson, Craig Potton Publishing, 160–167
- Cruz R, Carballo M, Condepadi P, Rolán-Alvarez E (2004) Testing alternative models for sexual isolation in natural populations of *Littorina saxatilis*: indirect support for by-product ecological speciation? *J Evol Biol* 17:288–293
- Dobzhansky T (1951). *Genetics and the origin of the species*. New York, Columbia University Press
- Doebeli M, Dieckmann U (2003) Speciation along environmental gradients. *Nature (London)* 421:259–264
- Feary D (2001). *Trophic morphology, diet and habitat use of New Zealand triplefins (Family Tripterygiidae)*. University of Auckland, New Zealand
- Feary DA, Clements KC (2006) Habitat use by triplefin fishes (family Tripterygiidae) on rocky reefs in New Zealand. *J Fish Biol* 69:1031–1046
- Foote CJ, Larkin PA (1988) The role of male choice in the assortative mating of sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka*. *Behaviour* 106:43–62
- Forrester GE, Steele ME (2004) Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. *Ecology (New York)* 85:1332–1342
- Francis MP (2001). *Coastal fishes of New Zealand. An identification guide*. Reed Books, Auckland
- Fricke R (1994). *Tripterygiid fishes of Australia, New Zealand and the Southwest Pacific Ocean (Teleostei)*. Koeltz Scientific Books, Königstein
- Friesen ML, Saxer G, Trivisano M, Doebeli M (2004) Experimental evidence for sympatric ecological diversification due to frequency-dependent competition in *Escherichia coli*. *Evolution* 58:245–260
- Ghiselin MT (1974). *The economy of nature and the evolution of sex*. University of California Press, Berkeley (CA)
- Gratwicke B, Speight M (2005) Effects of habitat complexity on Caribbean marine fish assemblages. *Mar Ecol Prog Series* 292:301–310
- Hardy GS (1986) Redescription of *Gilloblennius* Whitley and Phillipps, 1939 (Pisces: Tripterygiidae), and description of a new genus and two new species from New Zealand. *J R Soc N Z* 16:145–168
- Hickey AJR, Clements KC (2005) Genome size evolution in New Zealand triplefin fishes. *J Hered* 7:356–362
- Hixon MA, Beets JP (1989) Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull Mar Sci* 44:666–680
- Ishikawa M, Mori S (2000) Mating success and male courtship behaviors in three populations of the threespine stickleback. *Behaviour* 137:1065–1080
- Jennions MD, Petrie M (1997) Variation in mate choice and mating preferences: a review of causes and consequences. *Biol Rev* 72:283–327
- Knouft JH (2003) Convergence, divergence, and the effect of congeners on body size ratios in stream fishes. *Evolution* 57:2374–2382

- Knudsen R, Klemetsen A, Amundsen PA, Hermansen B (2006) Incipient speciation through niche expansion: an example from the Arctic charr in a subarctic lake. *Proc R Soc Lond B Biol Sci* 273:2291–2298
- Kondrashov AS, Shpak M (1998) On the origin of species by means of assortative mating. *Proc R Soc Biol Sci B* 265:2273–2278
- Konishi M, Takata K (2004) Size-dependent male-male competition for a spawning substrate between *Pseudorasbora parva* and *Pseudorasbora pumila*. *Ichthyol Res* 51:184–187
- Lafleur DL, Lozano GA, Sclafani M (1997) Female mate-choice copying in guppies, *Poecilia reticulata*: a re-evaluation. *Anim Behav* 54:579–586
- Langerhans RB, Layman CA, Langerhans AK, DeWitt TJ (2003) Habitat-associated morphological divergence in two Neotropical fish species. *Biol J Linn Soc* 80:689–698
- Lindström K (1992) The effect of resource holding potential, nest size, and information about resource quality on the outcome of intruder-owner conflicts in the sand goby. *Behav Ecol Sociobiol* 30:53–58
- Lu G, Bernatchez L (1999) Correlated trophic specialisation and genetic divergence in sympatric lake whitefish ecotypes (*Coregonus clupeaformis*): support for the ecological speciation hypothesis. *Evolution* 53:1491–1505
- MacLachlan AJ, Allen DF (1987) Male mating success in Diptera: advantages of small size. *Oikos* 48:11–14
- Mayr E (1999). Systematics and the origin of species from the viewpoint of a zoologist. Harvard University Press, Cambridge
- McKaye KR (1986) Mate choice and size assortative pairing by the cichlid fishes of Lake Jiloá, Nicaragua. *J Fish Biol* 29:135–150
- McKinnon JS, Mori S, Blackman BK, David L, Kingsley DM, Jamieson L, Chou J, Schluter D (2004) Evidence for ecology's role in speciation. *Nature (London)* 429:294–298
- Munday PL, Herwerden LV., Dudgeon CL (2004) Evidence for sympatric speciation by host shift in the sea. *Current Biol* 14:1498–1504
- Munday PL, Jones GP, Caley JM (2001) Interspecific competition and coexistence in a guild of coral-dwelling fishes. *Ecology (New York)* 82:2177
- Nagel L, Schluter D (1998) Body size, natural selection, and speciation in sticklebacks. *Evolution* 52:209–218
- Neat FC (2001) Male parasitic spawning in two species of triplefin blenny (Tripterygiidae): contrasts in demography, behaviour and gonadal characteristics. *Environ Biol Fishes* 61:57–64
- Nevo E, Rashkovetsky E, Pavliceck T, Korol A (1998) A complex syndrome in *Drosophila* caused by adaptation to microclimate contrasts. *Heredity* 80:9–16
- Oliveira RF, Miranda JA, Carvalhof N, Goncalves EJ, Grober MS, Santos RS (2000) Male mating success in the Azorean rock-pool blenny: the effects of body size, male behaviour and nest characteristics. *J Fish Biol* 57:1416–1428
- Paulin CD, Roberts CD (1992). The rockpool fishes of New Zealand. Museum of New Zealand, Te Papa, Tongarewa, Wellington
- Peters HR, (1983) The ecological implications of body size. Cambridge studies in Ecology. Cambridge University Press, Cambridge, UK
- Petrie M (1983) Female moorhens compete for small fat males. *Science (Washington D C)* 220:413–415
- Pickard R (2000) Fetch effect analysis computer program, version 1.01:E. Villouta
- Piller KR, Burr BM (1999) Reproductive biology and spawning habitat supplementation of the relict darter, *Etheostoma chienense*, a federally endangered species. *Environ Biol Fishes* 55:145–155
- Ratcliffe LM, Grant PR (1983) Species recognition in Darwin's finches (Geospiza, Gould). I. Discrimination by morphological cues. *Anim Behav* 31:1139–1153
- Rice WR, Hostert EE (1993) Laboratory experiments on speciation: What have we learned in 40 years? *Evolution* 47:1637–1653
- Richmond JQ, Reeder TW (2002) Evidence for parallel ecological speciation in scinid lizards of the *Eumeces skiltonianus* species group (Squamata: Scinidae). *Evolution* 56:1498–1513
- Robertson DR (1998) Implications of body size for interspecific interactions and assemblage organisation among coral-reef fishes. *Austral Ecol* 23:252–257
- Robertson RD (1996) Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology (New York)* 77:885–899
- Rosenzweig ML (1978) Competitive speciation. *Biol J Linn Soc* 10:275–289
- Schlieven UK, Rassmann M, Markmann J, Markert T, Kocher DT (2001) Genetic and ecological divergence of a monophyletic cichlid species pair under fully sympatric conditions in Lake Ejagham, Cameroon. *Mol Biol* 10:1471–1488
- Schluter D (1993) Adaptive radiation in sticklebacks: size, shape, and habitat use efficiency. *Ecol Appl* 4:699–709
- Schluter D (2000). The ecology of adaptive radiations. Oxford, Oxford University Press

- Schluter D, Price TD, Rowe L (1991) Conflicting selection pressures and life history trade offs. *Proc R Soc Biol Sci B* 246:11–17
- Seehausen O, van Alphen JJM (1998) The effect of male colouration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex). *Behav Ecol Sociobiol* 42:1–8
- Thomas MLH (1986) A physically derived exposure index for marine shorelines. *Ophelia* 25:1–13
- Thompson S (1986) Male spawning success and female choice in the mottled triplefin, *Forsterygion varium* (Pisces: Tripterygiidae). *Anim Behav* 34:580–589
- Thompson SM (1979). Ecological and behavioural factors influencing the distribution and abundance patterns of tripterygiid fishes with particular reference to *Tripterygion varium*. *Zoology*. Auckland, University of Auckland, New Zealand:80
- Wellenreuther M, Barrett PT, Clements KD (2007) Ecological diversification in habitat use in subtidal triplefin fishes (Tripterygiidae). *Mar Ecol Prog Ser* 330:235–246
- Wellenreuther M, Clements KD (2007) Reproductive isolation in temperate reef fishes. *Marine Biology* (in press) doi:10.1007/s00227-007- 0713-1
- Westendorp RGJ, Kirkwood TBL (1998) Human longevity at the cost of reproductive success. *Nature* 396:743–746
- Wilson DS (1975) The adequacy of body size as a niche difference. *Am Nat* 109:769–784
- Young KA (2004) Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. *Ecology* (New York) 85:134–149