RESEARCH ARTICLE

Determinants of habitat association in a sympatric clade of marine fishes

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Abstract Triplefin fishes reach their greatest diversity in New Zealand with 26 endemic species, and habitat diversification has been implicated as a key factor in the divergence of this group. Despite this, it is unknown whether species-specific habitat patterns in these sympatric fishes are established by passive processes (e.g. differential mortality) or by habitat selection during settlement. We investigate this question by comparing the habitat associations of new recruits with those of conspecific adults in five species. In addition, the amount of variation in habitat use of conspecific recruits and adults was calculated to identify ontogenetic shifts in habitat association. The results indicated that while there were some differences between recruit and adult habitats, these differences were small in magnitude and habitat use of new recruits was similar to that of adult conspecifics. This finding was further supported by the small difference in variation of habitat use between conspecific recruits and adults. The study suggests that new recruits are actively involved in the selection of habitats at settlement and maintain the use of these throughout demersal life. Habitat use in these territorial species has a large influence on mate choice, thus habitat selection by new recruits would provide a powerful mechanism for prezygotic isolation between individuals with different habitat preferences. Together these findings support the notion that habitat diversification has been a major component in the radiation of this sympatric group.

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Introduction

The evolution of habitat differences among closely related species has received considerable attention (Morris 2003). This is partly because habitat partitioning can result in prezygotic isolation when mating requires sufficient proximity between individuals (Johnson et al. 1996; Funk et al. 2002; Bierne et al. 2003). For example, divergent preferences for coral hosts reduces the probability of hybridization in coral dwelling gobies (Munday et al. 2004), and divergent preferences for distinct lake habitats cause almost complete reproductive isolation between cichlid species (Schliewen et al. 2001). However, while many studies have investigated animal-habitat associations in detail, less attention has been given to whether divergent habitat use is the result of active or passive processes (see Montgomery et al. 2001 and references therein). In philopatric species, a high degree of habitat similarity between conspecific adults and settlers would indicate active processes, while different ontogenetic patterns of habitat use in a species would suggest that passive processes, such as habitat dependent mortality, shape abundance and distribution patterns over time.

Triplefin fishes (Tripterygiidae) reach their highest regional diversity in New Zealand with 26 endemic species (Clements 2003). Previous studies have shown that New Zealand triplefin species are highly philopatric throughout ontogeny (Connell and Jones 1991) and have diversified in habitat use over evolutionary timescales, with different species displaying only limited habitat overlap as adults (Syms 1995; Feary and Clements 2006; Wellenreuther et al. 2007a, 2008). The use of distinct habitats by adults of each species occurs despite the fact that New Zealand triplefins have an 8–12-week pelagic larval phase (Kingsford and Choat 1989; Tolimieri et al. 2000; Hickford and Schiel 2003), during which the different species are largely sympatric

(*sensu* Futuyma and Mayer 1980). Thus divergence in habitat use also takes place on an ecological time scale within each generation as larvae of each species settle and shift from a relatively homogeneous pelagic distribution to their more heterogeneous demersal distributions.

While it is well established that adults of New Zealand triplefin species are associated with specific habitat types (Syms 1995; Feary and Clements 2006; Wellenreuther et al. 2007a), it is unclear whether this is the result of active processes at settlement (i.e. behaviour), passive post-settlement processes (e.g. mortality), or both. Work on *Forstergion varium* has shown that movement of juveniles between habitats is extremely rare (Connell and Jones 1991). Tolimieri et al. (2000) demonstrated that light traps with reef noise attracted substantially more triplefin larvae than traps without reef noise, indicating that pre-settlement larvae use sound as a cue in the selection of habitat. Hickford and Schiel (2003) sampled triplefin larval abundance at various distances from the shore, and found several distinct species-specific larval distribution patterns. Furthermore, triplefin larvae have been observed to swim actively in the water column and clearly maintain their position, even in strong currents (Kingsford and Choat 1989). Together, these studies suggest that larval behaviour plays a role in determining settlement location.

On the other hand, Connell and Jones (1991) found that newly settled larvae of *F. varium* occurred in a much wider range of habitats than adults, and concluded that higher post-settlement mortality in some habitat types led to a more restricted habitat distribution of adults. Conversely, Syms (1995) found that newly settled triplefins were generally found in habitats (i.e. depth and biotic zonation) similar to those of adult conspecifics, and suggested that this pattern was likely to be determined by habitat preference exerted at settlement (Syms 1992). Thus, it remains unclear whether the species-specific pattern of habitat use in New Zealand triplefins is the result of active choice by individual fish or differential mortality between habitats. The hypothesis that habitat associations may have been involved in the evolution of this group of fishes (Wellenreuther et al. 2007a) is consistent with the former of these alternatives (i.e. active choice), but not the latter.

This study aims to improve the understanding of the causal factors determining habitat associations in triplefin species by comparing the habitat use of new recruits with that of adults. Two hypotheses concerning the distribution of newly settled recruits (<1 week post-settlement) of five triplefin species were tested. The first hypothesis addressed whether triplefin recruits occupy habitats similar to those occupied by conspecific adults by comparing the depth and exposure, substratum and microhabitat selection of recruits to that of conspecific adults. If recruits occur in same habitats as adults, then this suggests that habitat associations are largely established at the time of settlement. In contrast, if recruits occur in a different and wider range of habitats to adults then this would indicate that post-settlement modification influences patterns of habitat use. Recruit and adult density can be accurately assessed in the field, as triplefins are highly philopatric (Clements 2003) and thus exhibit minimal movement after settlement (Connell and Jones 1991). The second hypothesis addressed whether the amount of variation in habitat use is similar between new recruits and conspecific adults. If settlement occurs in a wider range of habitats than those occupied by adults then the degree of variation is expected to be higher. Conversely, if recruits settle into a similar range of habitats that are occupied by adult fish, then the amount of variation is expected to be similar between recruits and adults.

Materials and methods

Census methods

This study was conducted over three recruitment seasons from January 2002 to May 2005 in the Hauraki Gulf (36°36′S, 174°50′E) in north eastern New Zealand using 4×4 m transects. Habitat associations of new recruits and adult triplefins were sampled as frequently as logistically possible, with most months being sampled within each year. Sites were selected to sample as broad a range of habitats as practically possible. In each year, regular transects were conducted at various onshore sites from the Whangaparaoa Peninsula to the Leigh Marine Reserve, and at selected offshore islands (Mokohinau Islands, Little Barrier and Great Barrier Island, Fig. 1). Between three and six transects were laid out at each site. The first transect was conducted at the deepest depth that could safely be sampled (maximum depth dived 30 m), and the two subsequent transects were done at approximately 33 and 66% of the deepest depth. Additional transects were conducted in variable depths if time and logistic constraints permitted. This design was employed to allow sampling flexibility at a range of sites. A minimum distance of approximately 50 m between transects was maintained to eliminate dependent samples.

In total, 151 randomly placed transects at 36 sites were sampled to examine the distribution patterns of newly settled recruits and adults. Newly settled recruits could be distinguished from older individuals and adults by their small size (≈ 30 mm) (Connell and Jones 1991; McDermott and Shima 2006) and lack of fully developed pigmentation (Connell and Jones 1991). Pigmentation starts to develop 4–7 days after settlement (Connell and Jones 1991), and can thus be used as a reliable indicator of recent settlement (i.e. <1 week old).
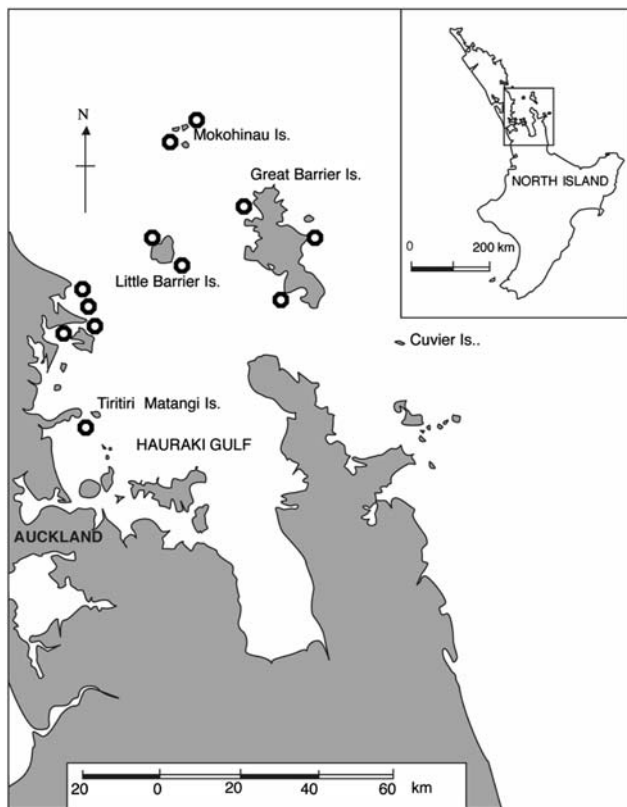
Fig. 1 Map of study sites in the Inner and Outer Hauraki Gulf. *Black circles* indicate study areas

Prior to sampling, a location fix was taken for each site using a handheld Garmin® 12 global positioning system, and a physically derived ocean swell exposure index (fetch) was calculated based on the total sum of the fetch (maximum radial distance 300 km). Fetch calculations were performed with the program "Fetch Effect Analysis" (available at request from the author CR_Pickard@hotmail.com), a measure that describes fetch distance from a given point (GIS fix) for each 20° compass sector (Thomas 1986). The centre line of each transect was marked with a leaded line, and a steel quadrat was used to outline each 1 m². Habitat use of new recruits and adults was recorded for each 4 × 4 m transect. For each 1 × 1 m quadrat within each transect, the depth was recorded, and seven habitat variables were estimated visually as percent cover of the substratum: rock (rocks > 7 cm), cobbles (rocks < 7 cm), gravel (rocks < 4 cm), sand, mud, macroalgae, and coralline and turfing algae. The first five variables always summed to 100%, while algal coverage could range from 0 to 100%. Triplefins within each 1 × 1 m quadrat were identified and their micropositions recorded as follows: on the side/top of rock, free swimming, under rock or in crack, on cobbles, on algae, on mud/sand, and under overhang. Micropositions were defined as the substratum upon which >50% of a fish's body rested (Feary and Clements 2006).

Analysis of habitat use of new recruits and conspecific adults

The analysis included only species for which new recruits were observed in each of the three recruitment seasons, and in which the total number of new recruits exceeded 50 observations over the duration of the study. This ensured that observations spanned more than two recruitment years and that habitat use could be estimated with some certainty. Species that met these criteria were *Forsterygion lapillum* (adults: 2,871; new recruits: 578), *F. varium* (adults: 830; new recruits: 353), *Notoclinops segmentatus* (adults: 1,894; new recruits: 291), *Obliquichthys maryannae* (adults: 596; new recruits: 196) and *Ruanoho whero* (adults: 1,371; new recruits: 358). Details on sampling sites and the densities of adults and settlers observed can be found in Figs. 1 and 2, respectively.

Habitat associations were investigated in three ways. First, we compared the habitat association of conspecific recruits and adults among 4 × 4 m transects using Canonical Correlation to identify any broad-scale differences in habitat use. This ordination technique is useful for identifying correlations between species and habitat variables. If habitat variables and species are plotted in the same direction on the plot, then there is a positive correlation between those variables. In contrast, negative correlations are indicated by species and habitat vectors in opposite directions to each other.

Second, we compared substratum selection of conspecific adults and recruits by calculating the differences in substratum use association (rock, cobble, gravel, sand, mud, macroalgae, and coralline and turfing algae) by recruits and conspecific adults within each transect. Differences were calculated simply by subtracting the proportional use of habitats of recruits from that of adults. The number of transects for which both newly settled recruits and conspecific adults were present was relatively high, namely 134 for *F. lapillum*, 120 for *F. varium*, 117 for *N. segmentatus*, 39 for *O. maryannae* and 26 for *R. whero*. The advantage of this approach is that it takes substratum availability into account, and thus is a powerful method to detect differences in habitat selection between adult and recruits of a species. The calculated differences in substratum association between recruits and adults were subsequently analysed with an intercept-only MANOVA (one for each species), where the dependent variables were the differences between habitat use of adults and recruits for each habitat type. This analysis explicitly tested whether the difference between adult and juvenile habitat use was zero. We followed the multivariate analysis with separate intercept-only ANOVA's to assist interpretation of results. Recruits of two species, *N. segmentatus* and *O. maryannae*, were never found to occupy habitats with mud so this habitat was excluded from the analysis of these two species. Third, we compared the fine-scale habitat

Fig. 2 Adult and settler density m^{-2} of *F. lapillum*, *F. varium*, *N. segmentatus*, *O. maryannae* and *R. whero* at different months. *Error bars* show standard error
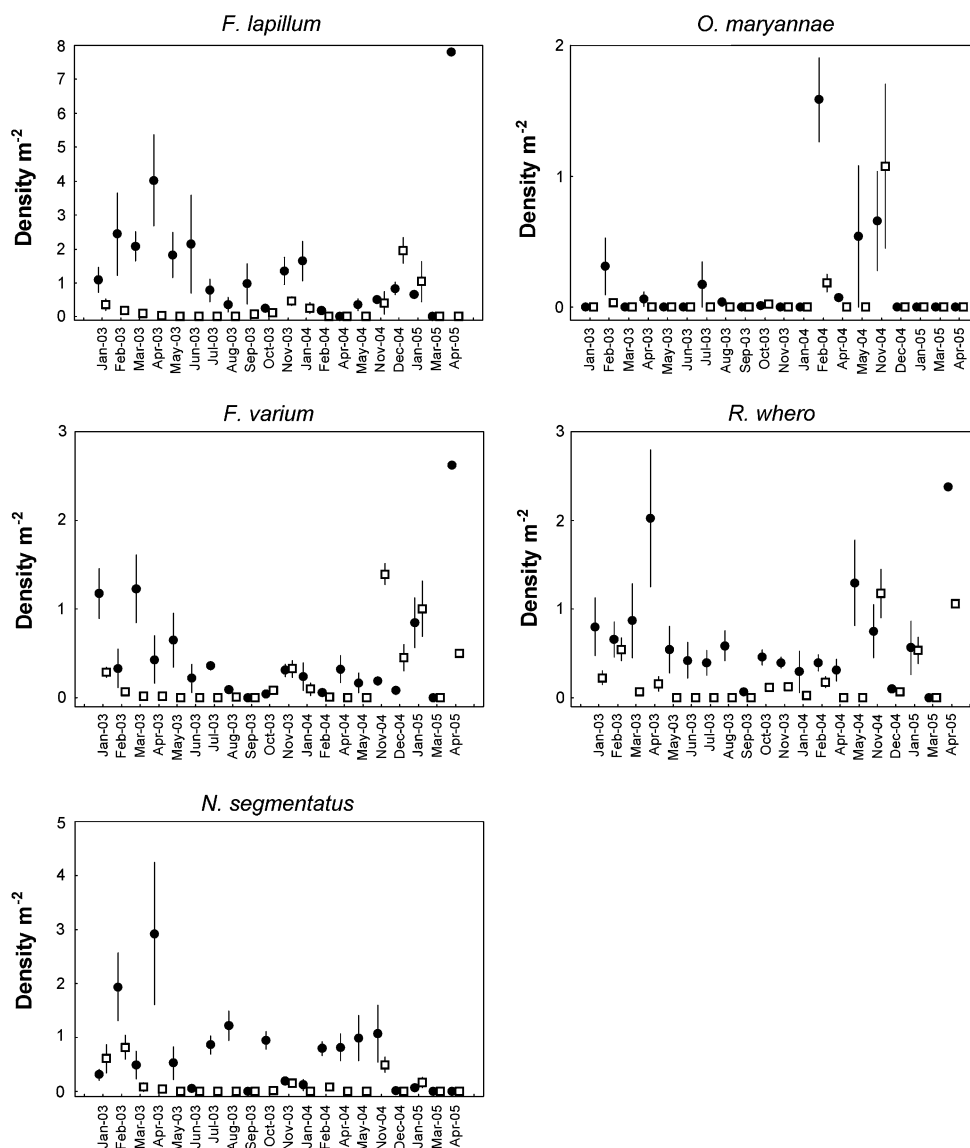
associations of recruits and adults by comparing the micro-position between and within species using a Correspondence Analysis. Canonical Correlations and Correspondence Analysis were carried out in Statistica (Statsoft, version 8), and ontogenetic differences in substratum association were analysed in SAS (SAS, version 9).

Variation in habitat use

The degree of variation in habitat use of recruits and adults was calculated by comparing each individual of a group (recruits or adults) to all other individuals within that group using the computer program HDA-1 (can be obtained from http://www.pbarrett.net/). Thus, the raw data of the within group comparison consisted of $(N^2–N)/2$ comparison coefficients, where N equals the number of individuals within a group. The similarity between two individuals within each group was expressed as double-scaled Euclidean distance,

and was scaled between 0 and 1 (where 0 stands for no distance and 1 denotes maximum possible distance between variables, Wellenreuther et al. 2007a). The double-scaled distance was subsequently expressed as a similarity index by subtracting it from 1, thereby yielding a double-scaled Euclidean similarity (DSE-S) measure, where 0 indicates that all individuals within a group use completely different magnitudes of habitat variables, and 1 that individuals use exactly the same habitat variables. The variable mud was not used by new recruits of *N. segmentatus* and *O. maryannae*, and was excluded from the comparisons for these two species.

Results

New recruits of all species were primarily observed from October to April, with a noticeable peak from November to February (Fig. 2). The new recruits were presumably

offspring from eggs that were laid between July and August, as triplefin larvae are thought to have a pelagic larval phase of approximately 2–3 months (Kingsford and Choat 1989; McDermott and Shima 2006). Adult density was usually highest just before the start of the triplefin breeding season, and started to decline at the end of the breeding season. This pattern was particularly clear in *F. varium* and *F. lapillum*, and less clear in *N. segmentatus* and *R. whero* (Fig. 2).

Habitat use of new recruits and conspecific adults

Triplefin species were found to occupy distinct habitats, while habitat associations of conspecific recruits and adults were similar (Fig. 3). Adults and new recruits of *F. lapillum* were found in shallow and sheltered habitats dominated by soft and mobile benthic substrata such as gravel, cobble and sand, while *F. varium* were strongly associated with macro-algal cover and stands of coralline and turfing algae (Fig. 3). The habitat of adults and new recruits of *R. whero* were generally similar to *F. varium*, though individuals of *R. whero* tended to be more closely associated with large rocks (Fig. 3). Adults and recruits of both *N. segmentatus* and *O. maryannae* were negatively correlated with the presence of mud, presumably because they were found in deeper and more exposed habitats than the remaining species (Fig. 3). Rock was an important predictor for the presence of *N. segmentatus*, while the schooling species *O. maryannae* was not obviously associated with any substratum type (Fig. 3).

Habitat associations of conspecific recruits and adults were also highly similar within transects (Fig. 4). However, three of the five global MANOVA's detected significant
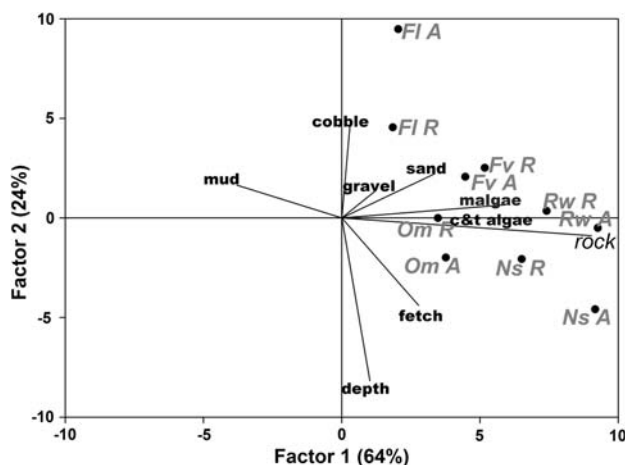
Fig. 3 Species habitat associations of adults (A) and new recruits (S) of five triplefin species. The names are abbreviated by the first letter of the genus followed by the first letter of the species name. Coralline and turfing algae is denoted by *c&t* algae and macroalgae by malgae

differences in substratum selection (Table 1), namely for *F. lapillum* (Pillai Trace = 0.1023, $F_{6,177}$ = 3.36, P = 0.0037), *O. maryannae* (Pillai Trace = 0.1920, $F_{5,530}$ = 2.52, P = 0.0406), and *R. whero* (Pillai Trace = 0.0325, $F_{6,600}$ = 3.36, P = 0.0029). Univariate ANOVA's showed that the habitats of recruits and adults of *F. lapillum* differed in the coverage of coralline and turfing algae and macroalgae. It should be noted, however, that differences in algal coverage were in both cases less than 5% (Fig. 4). Similarly, recruits and adults of *O. maryannae* differed by less than 10% in their use of rock, and less than 5% in their use of cobble and gravel. Lastly, habitats of recruits and adults of *R. whero* differed in rock, cobbles, gravel, mud and coralline algae, but all differences were less than 4%. Together, these results suggest that the magnitude of differences between conspecific recruits and adults are negligible and thus unlikely to be biologically important. Unlike the MANOVA, univariate ANOVA's found significant differences in the amount of coralline and turfing algae between the habitats of recruits and adults of *F. varium* (difference is less than 4%). This discrepancy may be related to an increased chance of Type I errors being present in the univariate analyses. *N. segmentatus* was the only species for which no significant ontogenetic differences in habitat were found.

Interspecific habitat associations were less differentiated on the microposition scale compared to the relative clear partitioning seen in depth, fetch and the substratum variables. Specifically, *F. varium*, *F. lapillum* and *N. segmentatus* showed high overlap in the use of micropositions, with all three species being strongly associated with the following micropositions: on the side/top of rock, on sand/mud, on algae, on cobbles, and under overhang (Fig. 5). Despite the high interspecific overlap in these three species, *R. whero* and *O. maryannae* showed pronounced interspecific differences in microposition use, with adults and new recruits of both species having the same preferences for micropositions (Fig. 5). The microposition use of *O. maryannae* recruits and adults was associated with the free swimming category, and *R. whero* recruits and adults were associated with the microposition under rock or in crack (Fig. 5).

Variation in habitat use

Analysis of intraspecific variation in depth, fetch and substratum types showed that the variation in habitat use by conspecific recruits and adults (DSE-S) was comparable (Fig. 6). While the median DSE-S values of adult *F. lapillum*, *F. varium*, *N. segmentatus* and *R. whero* were higher than those of recruits, the difference was negligible (difference in median DSE-S values between conspecific adults and settlers 0.01–0.04), indicating similar levels of variation in the use of habitat by adults and recruits. Recruits of
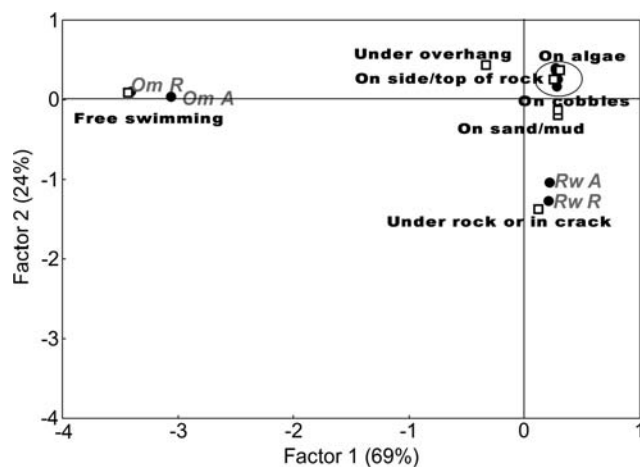
Fig. 4 Percentage difference of substratum selection by recruits and conspecific adults. *Positive* values represent selection and *negative* values avoidance of substratum types based on their relative availability. A *star* denotes substratum types that were selected to different degrees by recruits and conspecific adults
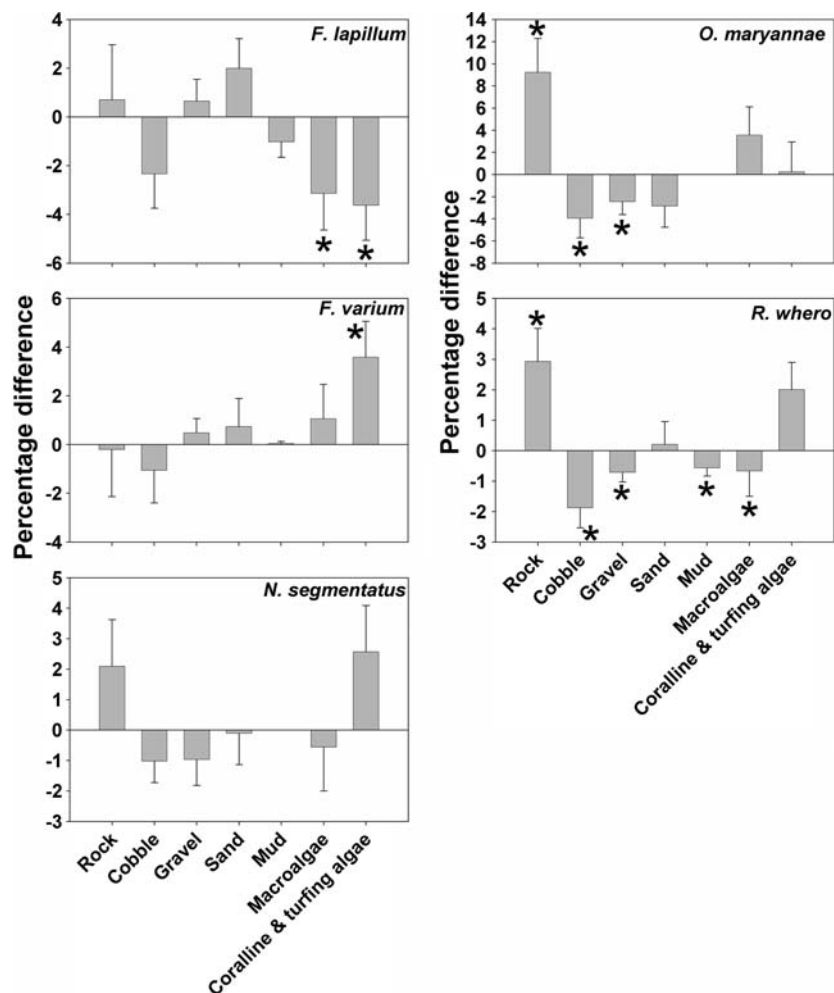
Table 1 Results of MANOVA's testing for differences in habitat use between conspecific recruits and adults within transects

Species	Pillai's trace	F value	df	P
F. lapillum	0.1023	3.36	6,177	0.0037
F. varium	0.0439	1.31	7,200	0.2465
N. segmentatus	0.0258	1.12	5,212	0.3498
O. maryannae	0.1920	2.52	5,530	0.0406
R. whero	0.0325	3.36	6,600	0.0029

Fig. 5 Microposition use of triplefin adults and new recruits. The *circle* shows the position of new recruits and adults of the species *F. lapillum*, *F. varium* and *N. segmentatus*, which could not be displayed individually due to high overlap

O. maryannae had an apparently lower variance in depth and exposure use than adults, although again this difference was small (0.03). A similar pattern was found for substratum type use, with *F. lapillum* (0.01), *F. varium* (0.02), *N. segmentatus* (0.03) and *R. whero* (0.02) showing a negligible difference between new recruits and adults in the variation in substratum use. New recruits of *O. maryannae* showed also a higher median value than conspecific adults, but this difference was again small (0.02, Fig. 6). A consistent pattern that emerged was that new recruits and adults showed less variation in the use of depth and exposure than variation in the use of substratum types. This was evident in the overall higher mean DSE-S value for depth and exposure (0.84) compared to substratum types (0.77).

Fig. 6 Histogram of the DSE-S coefficient distribution of new recruits (*black bars*) and adults (*white bars*) based on intraspecific variation in the use of all habitat variables. The *open circle* shows the median DSE-S value for adults and the *closed circle* the median DSE-S value for new recruits
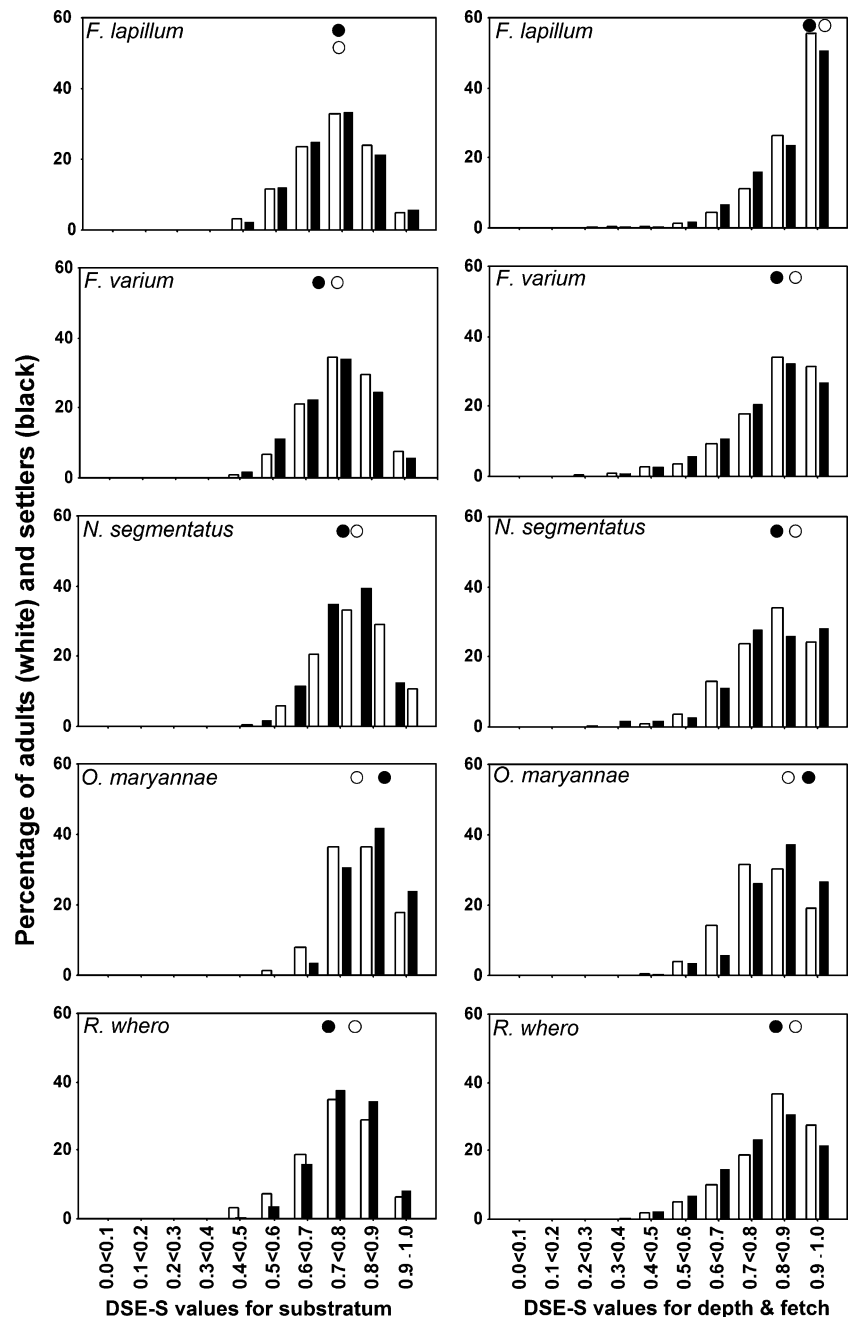
Discussion

This study investigated whether newly settled recruits of five triplefin species show habitat associations similar to those of conspecific adults. This was done in two parts. First, tests were conducted to determine whether habitat use by newly settled recruits matched that of conspecific adults. Second, we tested whether variation in habitat use of recruits was similar to the variation seen in conspecific adults. These two parts will be discussed in turn.

All species studied were clearly associated with particular habitat types. Examination of habitat associations between 4 × 4 m transects indicated that recruits generally selected the same types of habitats used by conspecific adults. The same pattern was found within transects. Although some differences in substratum selection between conspecific recruits and adults were found, the variation was less than 5% for *F. varium*, *F. lapillum*, *N. segmentatus* and 10% for *O. maryannae*, and thus can be considered negligible. Therefore, new recruits and adults of a given species had similar habitat use between and within transects. Not only were the habitat depth, exposure and substratum use similar between adults and new recruits, but also the use of micropositions, showing that habitat

selection occurs even at a very fine spatial scale. Of all of the variables measured the depth and exposure exhibited the lowest amount of variance between new recruits and conspecific adults, meaning that depth and exposure were most similar between these ontogenetic age classes. It would appear therefore, that habitat depth and exposure is of particular importance, while selection for substratum variables appeared to be less marked. Species-specific differences in haemoglobins (Brix et al. 1999) and metabolic physiology (Hickey and Clements 2003) are related to habitat depth in New Zealand triplefins, thus suggesting that physiological constraints might be important factors in determining habitat depth in these fishes. Studies of other fish assemblages have documented a similarly strong role of depth (Bean et al. 2002) and exposure (Thorman 1986; La Mesa and Vacchi 2005) in accounting for most of the spatial variation apparent. Therefore, we can reject the possibility that settlement occurs into a wider range of habitat types in these five triplefin species.

An important question is whether the patterns of habitat use are determined actively (e.g. by larval behaviour) or passively (e.g. by predation), and also whether the methods employed in this study were sufficient to discriminate between these mechanisms. These points will be discussed separately. Many reef fishes sample habitat prior to settlement (Kauffman et al. 1992; Carr and Syms 2006), demonstrating that larvae are competent to make active choices about where to settle. New Zealand triplefin species exhibit differences in horizontal and vertical distributions as pelagic larvae (Kingsford and Choat 1989; Hickford and Schiel 2003), and pre-settlement larvae actively use reef sound as a settlement cue (Tolimieri et al. 2000). Furthermore, a recent study demonstrated that newly recruited *F. lapillum* exhibited habitat selection under both experimental and field conditions (McDermott and Shima 2006). Larval behaviour is thus likely to be involved in determining settlement habitat in all species of New Zealand triplefins.

Studies on both tropical reef fishes (Tupper and Boutilier 1997; Almany and Webster 2006) and New Zealand triplefins (Connell and Jones 1991) show that predation can have strong impacts on the density of newly settled recruits. However, the effects of predation would have to be highly species-specific to create distinct patterns of habitat use. The five triplefin species examined in this study are closely related (Hickey and Clements 2005). Although they differ markedly in habitat use (Syms 1995; Feary and Clements 2006; Wellenreuther et al. 2007a), they share many morphological and ecological characters (Paulin and Roberts 1992; Fricke 1994; Francis 2001), suggesting that the susceptibility of recruits to predators of these species is similar with the possible exception of the schooling *O. maryannae*. Furthermore, the local abundance of predators would have to be spatially and temporally consistent for predation to

shape the habitat distribution of triplefin recruits in a species-specific manner. Data on the ecology of potential predatory species of New Zealand triplefin fishes (Jones 1988) suggest that this is very unlikely to be the case.

Finally, could high early post-settlement mortality influence our ability to differentiate between active habitat selection and post-settlement processes as determinants of habitat use patterns? Repeated surveys by Connell and Jones (1991) and Syms and Jones (1999) indicated that the habitat distribution of newly settled recruits was stable over at least 3 days, suggesting that habitat surveys of new recruits are suitable to detect settlement signals. Connell and Jones (1991) found that mortality was highest during the first week after settlement. Similar results have been obtained in tropical reef fishes, where some species suffer a mortality rate of over 50% in the first 2 days after settlement (Almany and Webster 2006). If mortality is highest immediately after settlement then cohort density is also highest immediately after settlement, and consequently our ability to observe individuals within a cohort (and their habitat associations) is highest during this period. Patterns of habitat association produced by post-settlement mortality by definition will involve a diminished proportion of each cohort. Thus, the probability of detecting the patterns of habitat association through ontogeny are a balance between cohort density and temporal stability. In other words, even if habitat distribution was heavily modified by mortality in the first few days after settlement, we nevertheless had a good likelihood of detecting the original (i.e. pre-mortality) pattern of habitat association.

The ability to find a suitable habitat directly at settlement is critical to individual fitness, since growth and survivorship of juvenile fish is affected by habitat structure (Jones 1988; Hixon and Beets 1989). Habitat selection at settlement may therefore be an evolved response to fitness trade-offs and patterns of post-settlement mortality (Keough and Downes 1982). However, the finding that triplefin recruits have similar patterns of habitat use to conspecific adults conflicts with the conclusions of Connell and Jones (1991). This discrepancy may be attributable to differences in the spatial and temporal scales used to examine habitat selection in the respective studies. Connell and Jones (1991) sampled over 2 years at a single site, and their habitat comparisons between new recruits and adults were based on a single species (*F. varium*) at a single depth stratum (10 m). In the present study, habitat associations of new recruits and adult triplefins were compared in five species that were observed over 3 years in a wide range of habitat types at multiple sites, thereby allowing more comprehensive sampling of habitat associations.

New Zealand triplefin fishes are highly philopatric (Clements 2003) and occupy the same territories (1–2 m^2) for their entire life (Thompson 1983), and recent work has

shown that species specific habitat associations are consistent across biogeographic gradients (Wellenreuther et al. 2007b). Mating takes place within the territory (Wellenreuther and Clements 2007) and thus show parallels to phytophagous insects and coral dwelling gobies (Berlocher and Feder 2002; Munday et al. 2004; Nosil 2007). As a consequence of this linkage between habitat and mate choice, individuals with different habitat use are spatially isolated from one another and may not encounter each other during the reproductive season (Wellenreuther and Clements 2007). Habitat use in New Zealand triplefins is highly divergent even between sister-species pairs (Wellenreuther et al. 2007a), suggesting that habitat use in triplefins may be a "magic trait" (sensu Gavrilets 2004). Both theoretical (Kirkpatrick 2000; Schneider and Bürger 2006) and experimental (Rice and Salt 1988; Nagel and Schluter 1998) studies have shown that magic trait models are one of the most plausible paths for speciation in the presence of gene flow. Examples of such magic traits include body size in sticklebacks (McKinnon et al. 2004) and in sea horses (Jones et al. 2003), and habitat use in fish (Munday et al. 2004) and phytophagous insects (Bush 1969; Feder 1998; Nosil 2007). The results of this study suggest that the New Zealand triplefin radiation may present another example where pre-zygotic isolation was facilitated by divergent preferences in habitat use.

Conclusions

New triplefin recruits displayed habitat use that was consistent with habitat associations of conspecific adults, and the level of variation in habitat use was comparable through ontogeny. This consistency suggests that settlement patterns are species-specific, and that new recruits maintain the use of particular habitats throughout post-settlement life. Therefore, species specific habitat associations appear to be mainly the result of active selection during settlement, while passive processes, such as mortality, are unlikely to account for the specific habitat associations in these species. Habitat use in these territorial species has a strong influence on mate choice, thus habitat selection by new recruits would provide a powerful mechanism for pre-zygotic isolation. This supports the view that diversification of habitat selection may have been involved in the evolution of this sympatric group of fishes (Feary and Clements 2006; Wellenreuther et al. 2007a, c).

References

Almany GR, Webster MS (2006) The predation gauntlet: early post-settlement mortality in reef fishes. Coral Reef 25:19–22. doi:10.1007/s00338-005-0044-y

Bean K, Jones GP, Caley JM (2002) Relationships among distribution, abundance and microhabitat specialisation in a guild of coral reef triggerfish (family Balistidae). Mar Ecol Prog Ser 233:263–272

Berlocher SH, Feder JL (2002) Sympatric speciation in phytophagous insects: moving beyond controversy. Annu Rev Entomol 47:773–815. doi:10.1146/annurev.ento.47.091201.145312

Bierne N, Bonhomme F, David P (2003) Habitat preference and the marine speciation paradox. Proc R Soc Ser B 270:1399–1406. doi:10.1098/rspb.2003.2404

Brix O, Clements KC, Wells RMG (1999) Haemoglobin components and oxygen transport in relation to habitat distribution in triplefin fishes (Tripterygiidae). J Comp Physiol 169:329–334

Bush GL (1969) Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). Evolution 23:237–251

Carr M, Syms C (2006) Recruitment. In: Allen LG, Pondella DJ, Horn MH (eds) The ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley, pp 411–427

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

Connell SD, Jones GP (1991) The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. J Exp Mar Biol Ecol 151:271–294

Feary DA, Clements KC (2006) Habitat use by triplefin fishes (family Tripterygiidae) on rocky reefs in New Zealand. J Fish Biol 69:1031–1046. doi:10.1111/j.1095-8649.2006.01178.x

Feder JL (1998) The apple maggot fly, *Rhagoletis Pomonella*: flies in the face of conventional wisdom about speciation. In: Howard D, Berlocher S (eds) Endless forms: species and speciation. Oxford University Press, Oxford, pp 130–144

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

Funk DJ, Filchak KE, Feder JL (2002) Herbivorous insects: model systems for the comparative study of speciation ecology. Genetica 116:251–267

Futuyma DJ, Mayer GC (1980) Non-allopatric speciation in animals. Syst Zool 29:254–271

Gavrilets S (2004) Fitness landscapes and the origin of species. Princeton University Press, Princeton

Hickey AJR, Clements KC (2003) Key metabolic enzymes and muscle structure in triplefin fishes (Tripterygiidae): a phylogenetic comparison. J Comp Physiol B 173:113–123. doi:10.1007/s00360-002-0313-9

Hickey AJR, Clements KC (2005) Genome size evolution in New Zealand triplefin fishes. Heredity 7:356–362. doi:10.1093/jhered/esi061

Hickford MJH, Schiel DR (2003) Comparative dispersal of larvae from demersal versus pelagic spawning fishes. Mar Ecol Prog Ser 252:255–271

Hixon MA, Beets JP (1989) Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. Bull Mar Sci 44:666–680

Johnson PA, Hoppensteadt FC, Smith JJ, Bush GL (1996) Conditions for sympatric speciation: a diploid model incorporating habitat fidelity and non-habitat assortative mating. Evol Ecol 10:187–205. doi:10.1007/BF01241784

Jones AG, Kvarnemo C, Walker D, Avise JC (2003) Sympatric speciation as a consequence of male pregnancy in seahorses. Proc Natl Acad Sci USA 100:6598–6603. doi:10.1073/pnas.1131969100

Jones GP (1988) Ecology of rocky reef fish of north-eastern New Zealand: a review. NZ J Mar Freshwater Res 22:445–462

Kauffman L, Ebersole JP, Beets JP, McIvor CC (1992) A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. Environ Biol Fishes 34:109–118

Keough SJ, Downes BJ (1982) Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia 54:1432–1939. doi:10.1007/BF00380003

Kingsford MJ, Choat HJ (1989) Horizontal distribution patterns of pre-settlement reef fish: are they influenced by the proximity of reefs? Mar Biol 101:285–297. doi:10.1007/BF00428124

Kirkpatrick M (2000) Reinforcement and divergence under assortative mating. Proc R Soc Ser B 267:1649–1655. doi:10.1098/rspb.2000.1191

La Mesa G, Vacchi M (2005) Analysis of the blennioid assemblages associated with different rocky shore habitats in the Ligurian Sea. J Fish Biol 66:1300–1327. doi:10.1111/j.0022-1112.2005.00684.x

McDermott CJ, Shima JS (2006) Ontogenetic shifts in microhabitat preference of the temperate reef fish *Forsterygion lapillum*: implications for population limitation. Mar Ecol Prog Ser 320:259–266

McKinnon JS, Mori S, Blackman BK, David L, Kingsely DM, Jamieson L, Chou J, Schluter D (2004) Evidence for ecology's role in speciation. Nature 429:294–298. doi:10.1038/nature02556

Montgomery JC, Tolimieri N, Haine OS (2001) Active habitat selection by pre-settlement reef fishes. Fish Fisheries 2:261–277. doi:10.1046/j.1467-2960.2001.00053.x

Morris DW (2003) Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13. doi:10.1007/s00442-003-1241-4

Munday PL, Herwerden Lv, Dudgeon CL (2004) Evidence for sympatric speciation by host shift in the sea. Curr Biol 14:1498–1504. doi:10.1016/j.cub.2004.08.029

Nagel L, Schluter D (1998) Body size, natural selection, and speciation in sticklebacks. Evolution 52:209–218. doi:10.1126/science.287.5451.306

Nosil P (2007) Divergent host plant adaptation and reproductive isolation between ecotypes of *Timema* cristinae walking sticks. Am Nat 169:151–163. doi:10.1086/510634

Paulin CD, Roberts CD (1992) The rockpool fishes of New Zealand. Museum of New Zealand, Te Papa

Rice WR, Salt GW (1988) Speciation via disruptive selection on habitat preference: experimental evidence. Am Nat 131:911–917

Schliewen 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

Schneider KA, Bürger R (2006) Does competitive divergence occur if assortative mating is costly? J Evol Biol 19:570–588. doi:10.1111/j.1420-9101.2005.01001.x

Syms C (1992) Spatial scale and the structure and dynamics of a blennioid fish guild. MSc thesis, Zoology, Auckland

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

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

Thomas MLH (1986) A physically derived exposure index for marine shorelines. Ophelia 25:1–13

Thompson S (1983) Homing in a territorial reef fish. Copeia 3:832–834

Thorman S (1986) Physical factors affecting the abundance and species richness of fishes in the shallow waters of the southern Bothnian Sea, Sweden. Estuar Coast Shelf Sci 22:357–370

Tolimieri N, Jeffs A, Montgomery JC (2000) Ambient sound as a cue for navigation by the pelagic fish larvae of reef fishes. Mar Ecol Prog Ser 207:219–224. doi:10.3354/meps207219

Tupper M, Boutilier RG (1997) Effects of habitat settlement, growth, predation risk and survival of a temperate reef fish. Mar Ecol Prog Ser 151:225–236

Wellenreuther M, Barrett PT, Clements KD (2007a) 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. Mar Biol 152:619–630. doi:10.1007/s00227-007-0713-1

Wellenreuther M, Syms C, Clements KD (2007b) Consistent habitat use across biogeographic gradients. Ecography 30. doi:10.1111/j.2007.0906-7590.05270.x

Wellenreuther M, Syms C, Clements KD (2008) The role of body size in ecological diversification and reproductive isolation in a sister species pair of triplefin fishes. Evol Ecol. doi:10.1007/s10682-007-9183-7 (in press)