Home-range size in juveniles of the temperate reef fish, the common triplefin (*Forsterygion lapillum*)

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Abstract. An organism’s home range dictates the spatial scale on which important processes occur (e.g. competition and predation) and directly affects the relationship between individual fitness and local habitat quality. Many reef fish species have very restricted home ranges after settlement and, here, we quantify home-range size in juveniles of a widespread and abundant reef fish in New Zealand, the common triplefin (*Forsterygion lapillum*). We conducted visual observations on 49 juveniles (mean size \(= 35\text{-mm total length}\)) within the Wellington harbour, New Zealand. Home ranges were extremely small, \(0.053 \text{ m}^2 \pm 0.029 \text{ (mean \pm s.d.)}\) and were unaffected by adult density, body size or substrate composition. A regression tree indicated that home-range size sharply decreased, \(4.5 \text{ juveniles m}^{-2}\) and a linear mixed model confirmed that home-range sizes in high-density areas (\(>4.5 \text{ juveniles m}^{-2}\)) were significantly smaller (34%) than those in low-density areas (after accounting for a significant effect of fish movement on our home-range estimates). Our results suggest that conspecific density may have negative and non-linear effects on home-range size, which could shape the spatial distribution of juveniles within a population, as well as influence individual fitness across local density gradients.

Additional keywords: animal movement, density-dependent space use, intraspecific interactions, marine reef fish, New Zealand.

Received 17 December 2014, accepted 8 May 2015, published online 30 September 2015

Introduction

The spatial extent of an organism’s movements and activities has important implications for population structure and abundance (Adams 2001), predator–prey interactions (de Roos et al. 1998) and the relationship between individual fitness and local site quality (Germain and Arcese 2014). Marine reef fish can disperse great distances during their pelagic larval stage (Planes et al. 2009), but following the transition of larvae into reef habitats, many species show limited movement from their immediate settlement sites (Apo gonidae, Marnane 2000; Chaetodontidae, Reese 1973; Pomacentridae, Sale 1971; Chapman and Kramer 2000; Gobiidae, Luckhurst and Luckhurst 1978; Cole 1984; Tripterygiidae, Thompson 1983). Such species are among the most diverse and abundant groups in many reef ecosystems (Munday and Jones 1998) and quantifying their typical range of movement may provide valuable insights into their population dynamics and distributions. In particular, the spatial scale of movement of juveniles of these species may shape density-dependent demographic rates and contribute to local population regulation. Density-dependent mortality is strongly scale dependent (Hixon and Carr 1997; Shima and Osenberg 2003; White et al. 2010) and typically most intense during the juvenile stage for many reef fishes (Hixon and Jones 2005). Space use in juvenile reef fish may be negatively correlated with increasing density (Norman and Jones 1984), which could have important implications for the spatial scale of density-dependent processes after settlement. The common triplefin, *Forsterygion lapillum* (Tripterygiidae), is a small-bodied temperate reef fish (maximum total length \(\sim 70\text{ mm}\)) and is one of the most widespread and abundant species on shallow rocky reefs around New Zealand (Willis 2001; Feary and Clements 2006; Wellenreuther et al. 2007, 2008). Densities of juveniles of the common triplefin are relatively high when compared with related species of similar size (Wellenreuther and Clements 2008) and the numerical dominance of this species has repeatedly facilitated its use as a model to explore the recruitment dynamics of marine reef fish (e.g. Shima and Swearer 2010; Smith and Shima 2011; Morton and Shima 2013). However, we currently lack basic information about space use in this species or how this may be influenced by conspecific density. Results from preliminary tagging studies suggest recent settlers (<30 mm) stay within \(1.5 \text{ m}^2\) of their settlement sites (Smith 2010); however, home-range estimates from other triplefin species (e.g. *Enneanectes atrorus*, 15–30 mm,
High densities (Mensink and Shima 2014) however, juveniles and adults appear to have similar substrate preferences (Syms 1995; Feary and Clements 2006), although it is typically most abundant within sheltered cobble habitats (Syms 1995; Feary and Clements 2006; Wellenreuther and Clements 2008). Juveniles and adults may leave the habitats into which they settled after maturity (McDermott and Shima 2006). The diet of adult common triplefins is dominated by gammarid amphipods, limpets and ostracods (Feary et al. 2009), whereas the dietary composition of juvenile common triplefins has not been formally quantified. As adults, common triplefins are strongly site-attached (Clements 2003) and during the breeding season (August–December), males defend nests located underneath cobbles (Feary and Clements 2006), whereas females range further to find mating opportunities (Clements 2003). Triplefins are demersal fish and their typical movement consists of short bouts of swimming, followed by resting periods on the substrate. Currently, we lack information about the amount of home-range overlap among conspecifics of the common triplefin or the level to which these areas are defended; however, previous studies on the closely related species, Forsterygion varium, have found that adults defend overlapping territories year round (Thompson 1979; Thompson and Jones 1983).

Methods

Study species

After hatching from small benthic eggs, common triplefin larvae remain in the pelagic phase for ~1–3 months (Shima and Swearer 2009; Kohn and Clements 2011). In our study area, late-stage larvae settle near macroalgal habitats at ~26-mm total length (Mensink and Shima 2014) during the recruitment season (November–March; McDermott and Shima 2006). The common triplefin may use a variety of substrate types (Feary and Clements 2006), although it is typically most abundant within sheltered cobble habitats (Syms 1995; Feary and Clements 2006; Wellenreuther and Clements 2008). Juveniles and adults appear to have similar substrate preferences (Syms 1995; Wellenreuther and Clements 2008) and frequently co-occur in high densities (Mensink and Shima 2014); however, juveniles may leave the habitats into which they settled after maturity (McDermott and Shima 2006). The diet of adult common triplefins is dominated by gammarid amphipods, limpets and ostracods (Feary et al. 2009), whereas the dietary composition of juvenile common triplefins has not been formally quantified. As adults, common triplefins are strongly site-attached (Clements 2003) and during the breeding season (August–December), males defend nests located underneath cobbles (Feary and Clements 2006), whereas females range further to find mating opportunities (Clements 2003). Triplefins are demersal fish and their typical movement consists of short bouts of swimming, followed by resting periods on the substrate. Currently, we lack information about the amount of home-range overlap among conspecifics of the common triplefin or the level to which these areas are defended; however, previous studies on the closely related species, Forsterygion varium, have found that adults defend overlapping territories year round (Thompson 1979; Thompson and Jones 1983).

Home-range size

We quantified home ranges in juvenile common triplefins by conducting 10-min visual observations of fish movements in the field, a technique widely used to measure home ranges for a variety of small-bodied benthic reef fish (Norman and Jones 1984; Jones 2005; Buckle and Booth 2009). In our study, we chose to use the definition of home ranges as ‘the area of daily activity’ (Burt 1943). We did observe individuals swimming outside of their main area of activity (e.g. chasing another conspecific), but noticed that they would generally return to the area they had previously occupied to rest on the substrate (P. J. Mensink, pers. obs.). Therefore, during our 10-min observation periods, we recorded the resting place of the focal fish (regardless of the total amount of time spent there) and used the largest perimeter of those resting areas to define our home-range boundaries (e.g. Norman and Jones 1984).

In contrast to home ranges, properly defining territorial borders requires multiple observations of territory defence behaviour (Adams 2001), which may have occurred too infrequently during our short observation periods (e.g. Weeden 1965). Therefore, we chose to classify our areas of activity as home ranges; however, we recorded several aggressive interactions between conspecifics during our observations, which suggest that individuals may be defending territorial space. We recorded all agonistic behaviours observed, including displays, charges and chases. In between resting periods, we also noticed that individuals appeared to be feeding in the water column by swimming up above the substrate (~10–15 cm), making short biting motions and repeatedly opening their mouths while maintaining their position in the water column. We recorded each of the biting movements our focal fish made over the 10-min observation period as ‘feeding bites’.

We completed surveys on snorkel in shallow sheltered bays within the harbour area surrounding Wellington, New Zealand. We selected two north-facing focal sites for our study to ensure they were protected from strong southerly swells, namely, Shark Bay (41°18′05″S, 174°49′00″E) and Kau Bay (41°17′15″S, 174°49′44″E). Both of these sites have a continuous and mixed stand of macroalgae (consisting of Carophyllum maschalocarpum and Cystophora retroflexa) running parallel to the shore at ~2–3-m depth. On the shore side of these algal stands is a large, subtidal and contiguous rocky reef, composed mainly of rock rubble and cobbles. Densities of the common triplefin reach their highest in these reef and cobble habitats (Wellenreuther and Clements 2008) and we conducted our surveys on these open cobble habitats ~1–2 m shoreward of the shore-side edge of the algal stands. We surveyed fish on these open cobble habitats because of the difficulty associated with properly tracking the movements of focal fish within the macroalgae itself. This also allowed observers to take accurate observations from the sea surface on snorkel, which minimised disturbance to our focal fish.

Sites were surveyed 1 week apart and took two consecutive days to complete (Shark Bay, 6–7 June 2012; Kau Bay, 14–15 June 2012). At the time of the surveys, juveniles may have been on the reef anywhere between ~1 and 8 months; therefore, our surveys included individuals of a range of sizes, which facilitated our examination of the effects of body size on home ranges. However, we acknowledge that we are unable to disentangle the influence of size from either the order in which individuals arrived or individual age. All observations were made between 0900 and 1300 hours on days of southerly winds (i.e. while our north-facing sites were sheltered) to ensure that fish were active and not seeking refuge under cobbles.

At the beginning of each survey, a 50-m transect tape was laid out parallel to shore ~2 m shoreward from the shore side of the algal stand. At the completion of our surveys each day, we measured the depth at 5-m intervals along the transect line. All of our surveys commenced at approximately mid-tide; however, because of changes in tidal states, the water depth where surveys were conducted varied slightly among sites and days (mean ± s.d., 6 June, Shark Bay, 0.98 m ± 0.09; 7 June, Shark Bay, 1.40 m ± 0.18; 14 June, Kau Bay, 1.11 m ± 0.53; 15 June, Kau Bay, 1.41 m ± 0.15). To select a focal juvenile, each observer moved to a randomly assigned starting point...
along the transect tape and selected the first juvenile (total length <40 mm) they encountered. Juvenile common triplefins rarely move from an area of 1.5 m² (Smith 2010); therefore, we used random points that were at least 3 m apart on the transect tape to ensure that our replicates were independent from each other. Prior to the surveys, observers were trained to estimate fish total lengths by using a training set of common triplefins with known lengths collected from the study site.

Observers estimated the total length of the focal juvenile to the nearest 1 mm and then counted the number of conspecifics (juveniles <40 mm, adults >40 mm) located within a 1-m² area centred on the focal fish. Observers carried an L-shaped frame (two 1-m pieces of 10-mm PVC pipe connected at a right angle) to help them approximate the 1-m² area; however, so as to avoid disturbing the focal fish and conspecifics, this was not directly placed on the substrate. Home-range size in reef fish may be negatively influenced by increasing density of conspecifics (Norman and Jones 1984) and evidence suggests that adult conspecifics in particular may influence juvenile distributions in the common triplefin (Wellenreuther 2007; Mensink and Shima 2014); therefore, we hypothesised that juvenile home ranges would be smallest in areas of high conspecific density.

Prior to each observation, observers took a 3-min ‘acclimation’ period, during which the observer sketched an approximate map of the area of activity of the focal fish on waterproof paper. This map was later used as a reference during actual observations and was not used for analysis of home-range sizes. After 3 min had elapsed, the movements of the focal fish were recorded on the sketch map for a 10-min period. Observers on snorkel maintained their position outside of the 1-m² area and stayed on the surface during the entire observation period. At the end of the 10-min period, the observer placed weighted markers on the substrate to form a perimeter around the largest area marked out on the map (e.g. Norman and Jones 1984). The observer then photographed the marked home range along with a scale bar. Home ranges were later quantified by measuring the total area within the weighted markers on the digital photographs by using the image analysis software Image J (Schneider et al. 2012). Observers then placed the L-shaped frame on the substrate and recorded substrate variables (as percentage cover in 5% increments) in the 1-m² area centred on and surrounding the focal fish (rock, protruding bedrock or sediment particle size >7 cm; cobbles, sediment particle size <7 cm; gravel, sediment particle size <4 cm; and sand, as per Wellenreuther and Clements 2008).

**Statistical analysis**

To prepare substrate percentage cover for statistical analysis, we created a composite score of substrate composition for each 1-m² area by using principal component analysis (PCA). Mean percentage cover of sand was extremely low (<5%); therefore, the PCA was conducted on the percentage cover of rock, cobble and gravel alone. The first principal component axis (PC1) explained 84.2% of the variation and was positively correlated with rock cover (logit-transformed rock proportion, adjusted \( R^2 = 0.90, P < 0.01 \)) and negatively correlated with cobble cover (logit-transformed cobble proportion, adjusted \( R^2 = 0.91, P < 0.01 \)). In other words, positive scores for PC1 described quadrats with higher amounts of rock and lower amounts of cobble; subsequently, we used PC1 as a fixed effect for ‘sediment size’ in our statistical analysis.

So as to examine how substrate composition influenced patterns of fish density across our focal sites, we used generalised linear regressions with Poisson error distributions between fish density (adult and juveniles separately) and our composite score of sediment size. For the juvenile density regression, initial analysis indicated that there was a highly influential data point in the dataset (Cook’s \( D = 0.27 \), Cook’s \( D \) cut-off (4/n) = 0.066). Consequently, we analysed the influence of sediment size on juvenile density by using a robust generalised linear model with M-estimators, which is less sensitive to influential data points than is a generalised linear model (Valdora and Yohai 2014).

We hypothesised that home-range size would decrease linearly with increasing conspecific density; however, during our preliminary analysis, we noticed that home-range size was responding to conspecific density in a non-linear manner (declining after a particular threshold density). This type of non-linear response might be expected if home-range size becomes density-dependent only when available space becomes fully saturated with individuals (e.g. scramble competition, Hassan 1975). To further explore the relationship between home-range size and conspecific density, we analysed our dataset using a regression tree. Regression trees split continuous explanatory variables (e.g. juvenile density) into separate homogeneous groups based on their influence on the response variable (Breiman et al. 1984; De’ath and Fabricius 2000). After multiple splits are made in the explanatory variables, critical thresholds are identified by (1) testing the classification error of the resulting groups using a cross-validation test and (2) only selecting splits that create groups with the minimum amount of classification error (Quinlan 1987). To determine whether any significant density thresholds existed, we created a regression tree with home-range size as our response variable and included juvenile density and adult density as explanatory variables. The regression tree identified two groups by using a single cut-off point, 4.5 juveniles m⁻², above which the mean home-range size was 44% lower (n = 13) than those individuals found at densities below 4.5 juveniles m⁻² (n = 36, Fig. 1). We created a categorical variable of juvenile density by using this split (high density, >4.5 juveniles m⁻², n = 36; low density, ≤4.5 juveniles m⁻², n = 13) and used this as a fixed factor in our analysis of home-range size to statistically test whether home-range size responded to juvenile density past the identified threshold.

We used a linear mixed model to evaluate the influence of juvenile density (as continuous and categorical variables), adult density, substrate composition and focal fish total length on the size of juvenile home ranges. We included survey site (Shark Bay or Kau Bay) as a random factor because (1) we sampled sites from a wide selection of available sites and (2) we were not specifically interested in differences between our replicate sites, but did want to account for any potential influence that site had on home-range size. In addition, we included day of sampling as a random effect. All continuous explanatory variables were scaled and centred with a mean of zero and a standard deviation of 1, so as to make regression coefficients more interpretable (Schielzeth 2010). We conducted a model selection procedure...
that ranked a candidate set of biologically relevant models using Akaike information criterion (AIC, Akaike 1974). We constructed a ‘global model’, which included fixed factors of adult density, juvenile density (continuous), focal fish total length, number of movements by each individual (to examine how activity levels influenced our home-range estimates), and sediment size, including two interaction terms, to investigate how the influence of conspecific density varied depending on sediment size (adult density × sediment size, juvenile density × sediment size). To examine the possibility that home-range sizes responded to juvenile conspecific density only past a specific threshold, we created another global model with juvenile density as a categorical variable, using the split suggested by our regression tree analysis (high density, >4.5 juveniles m⁻², n = 36; low density, <4.5 juveniles m⁻², n = 13). From these two global models, we created a combined list of all possible candidate models with those fixed factors (removing any duplicated models) and ranked them using AIC with a correction for small sample sizes (AICc). This combined list allowed us to compare fits between models that had juvenile density as a continuous variable and those that had juvenile density as a categorical variable. We used a cut-off criterion of ΔAICc < 2 (Burnham and Anderson 2002; Grueber et al. 2011) for top model selection and we calculated profile confidence intervals to make inferences about each parameter in the top model (parameters with confidence intervals that did not overlap with zero were considered statistically significant).

All statistical analyses were completed using the statistical software R (R Core Team 2014). A robust generalised linear model was conducted with the package ‘robustbase’ (Rousseeuw and Leroy 2003) and the function glmrob. The function glm was used to conduct the generalised linear regression between adult density and the composite score of sediment size. The regression tree was fitted with the package ‘part’ using the function part and pruned with the function prune. The package ‘lme4’ (Bates et al. 2013) with the function lmer was used to conduct the linear mixed model investigating the influence of our independent variables on home-range size. Candidate models were generated from the global model using the dredge function in the ‘MuMIn’ package (Barton 2013).

Results

Juveniles ranged in size from 31 to 40 mm in total length, with an average total length of 36 mm ± 3 (n = 49, mean ± s.d.). The mean number of movements made by each individual during the 10-min observation period was 7.8 ± 3.6 (n = 49, mean ± s.d.). Juvenile home ranges were extremely small, ranging from 0.0014 to 0.122 m², with an average size of 0.053 ± 0.029 m² (mean ± s.d., ~26-cm circular diameter). The substrate surrounding juvenile home ranges was mainly composed of cobble (60% ± 20), with a smaller proportion of rock (30% ± 20), followed by gravel (10% ± 10) and sand (<5%). There was a positive correlation between juvenile density and sediment size; however, this was not statistically significant (P = 0.083). Adult density was unaffected by sediment size (P = 0.17). Conspecific densities were 1.2 adults m⁻² ± 1.0 (mean ± s.d.) and 3.7 juveniles m⁻² ± 1.8. We observed agonistic behaviour in 57% of our observation periods, including 21 flies, 12 chases and 7 fin displays. Feeding ‘bites’ occurred in 90% of our observations, with a mean occurrence of 5.0 ± 5.0 (mean ± s.d.) bites per individual.

Our selected model was reasonably well supported (the second-best model had a ΔAICc = 2.28), explained 31.2% of the variation in home-range size (fixed effects only) and included fixed effects of (1) juvenile density (categorical) and (2) the number movements made by an individual. Predicted home-range sizes in areas of high juvenile density (>4.5 juveniles m⁻²) were 34% smaller than home ranges in areas of low density (β = −0.018, profile confidence intervals = 0.002, 0.0346, Fig. 2). The number of movements made by an individual had a positive effect on estimates of home-range size (β = 0.011, profile confidence intervals = 0.004, 0.019), with an increase of 2.4 movements per observation period (1 s.d.) resulting in a 20% increase in estimated home-range size.

Discussion

We investigated how conspecific density, body size and substrate composition influenced the home-range size of juvenile common triplefins. Our statistical analysis detected a positive relationship between our estimates of home-range size and the number of movements a fish made during our observations. Although widely used, 10-min observation periods can underestimate home-range size (Bell and Kramer 2000) and, in our study, home-ranges sizes for less active fish (i.e. those who changed position less frequently) may have been slightly underestimated. However, home-range sizes were still very small (maximum home-range size <0.13 m², ~20-cm radius) and were consistent with those reported for the smaller black-edge triplefin, Enneanectes atraurus (20-cm radius or ~0.12 cm²), Luckhurst and Luckhurst (1978), and other similarly sized blennoid fish (0.05–0.15 m², Coryphopterus nicholsii; Cole 1984; ~0.2 m², Coryphopterus glaucofraenum; Luckhurst and Luckhurst 1978).
that juvenile home ranges are primarily maintained for feeding purposes, planktonic feeding could subsidise diets during development and decouple the scaling of body mass from home-range size. Indeed, Kroon et al. (2000) speculated that a switch to a more planktivorous diet may cause seasonal variation in home-range sizes of the blackeye goby (Coryphopterus nicholsii).

We chose to conduct our study on rocky-cobble substrates, where densities of our study species are typically the highest (Syms 1995; Feary and Clements 2006; Wellenreuther and Clements 2008). The common triplefin is found on a wide variety of substrate types (Feary and Clements 2006) and home-range sizes in other habitats may vary as a result of changes in conspecific density or environmental conditions such as food availability. The small home ranges we observed here, coupled with evidence that settlers remain within close proximity of their settlement sites during development (Smith 2010), suggest that extremely fine-scale (<0.1 m²) heterogeneity in the characteristics of local settlement sites (such as e.g. substrate composition, food availability) could shape patterns of variation in individual growth, quality and condition within local populations. Furthermore, our results also highlight the importance of considering intraspecific interactions in co-ordination with the spatial and temporal scale of sampling effort in relation to animal movements (e.g. Pittman and McAlpine 2003).

Acknowledgements
This research was funded by an ‘OBI Coasts and Oceans’ grant from the New Zealand Foundation for Research, Science and Technology that was awarded to the National Institute of Water and Atmospheric science (NIWA) with a subcontract to J. S. Shima, and a Marsden grant awarded to J. S. Shima. Logistic support was provided by the Victoria University Coastal Ecology Laboratory (VUCEL), of which this paper is a contribution. We gratefully acknowledge the dedicated field assistance of J. Oliver, C. Cardenas and S. Geange. Three anonymous reviewers provided helpful comments on earlier drafts of this manuscript.

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