

Article

Ontogenetic shifts in perceptions of safety along structural complexity gradients in a territorial damselfish

Yinny CHAN[†], Sara LO[†], Alyssa QUAN[†], and Daniel T. BLUMSTEIN*

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA

*Address correspondence to Daniel T. Blumstein. E-mail: marmots@ucla.edu

[†]These authors contributed equally to this work.

Handling editor: Grant Brown

Received on 24 February 2018; accepted on 29 May 2018

Abstract

Age and body size can influence predation risk and hence habitat use. Many species undergo ontogenetic shifts in habitat use as individuals grow larger and have different age-specific predation pressures. On coral reefs, a number of fish species are more tolerant of threats in structurally complex habitats that contain more refuges than in less structurally complex habitats. However, we do not know how risk perception varies with age, and whether age interacts with habitat complexity. Adults and juveniles, because of their size, may face different risks in structurally simple versus complex habitats. We used flight initiation distance as a metric to analyze perceptions of risk in a species of damselfish *Stegastes nigricans*. All else being equal, fish fleeing at greater distances are inferred to perceive higher risk. We targeted juvenile and adult damselfish to assess whether there are ontogenetic shifts in perceptions of safety in relation to structural complexity, inferred based on percent coral cover and rugosity. We found that adult damselfish tolerated closer approach in more complex habitats as measured by percent coral cover, but not rugosity, whereas juvenile fish always allowed closer approach than adult fish regardless of complexity. This ontogenetic shift in habitat use may result from juvenile fish taking bigger risks to maximize growth, whereas older animals, who are closer to their maximum body size, can afford to take fewer risks and protect their assets.

Key words: *Stegastes nigricans*, habitat complexity, risk assessment, ontogenetic shifts, antipredator behavior, flight initiation distance.

Habitats influence the behavior and distribution of prey in that they vary in the degree to which they provide refuges from predators and other required resources (Crowder and Cooper 1982). More structurally complex habitats provide greater shelter for prey and lead to higher species abundance and diversity due to reduced predation risk (Gratwicke and Speight 2005). In young mammals with limited mobility such as white-tailed deer fawns *Odocoileus virginianus*, neonate fallow deer *Dama dama*, and North American porcupines *Erethizon dorsatum*, having suitable shelter has a major impact on survival (Grovenburg et al. 2012; Kjellander et al. 2012; Mabilie and Berteaux 2014). Habitat structural complexity is particularly

important for predator avoidance in aquatic systems (Hixon and Beets 1993; Lehtiniemi 2005). Aquatic species tend to avoid high predation risk areas that have scarce protective cover (Dill 1987), though intermediate cover may allow more efficient foraging and higher growth rates (Crowder and Cooper 1982). On coral reefs, habitat complexity influences the behavior and distribution of reef fish that depend on coral for protection, resources, or reproduction (Komyakova et al. 2013). For instance, juvenile Australasian snappers *Pagrus auratus* choose more structurally complex habitats in the presence of a predatory threat over less complex habitats (Ross et al. 2008). Two labrid fish species, Brazilian wrasse *Halichoeres*

brasilensis and gray parrotfish *Sparisoma axillare*, respond to lower perceived predation risk in areas of higher structural complexity by tolerating closer approach from a simulated threat (Nunes et al. 2015). However, while juveniles may benefit from hiding in more complex habitats, decreased habitat complexity may facilitate detection of predators by adult fish (Rilov et al. 2007).

Animals that experience ontogenetic shifts in predator risk assessment after reaching a particular size or age (Dahlgren and Eggleston 2000) are expected to choose, at each size and age, the habitat that would maximize the ratio of growth to mortality (Werner and Gilliam 1984). In fish, juveniles are smaller and adults are larger, which may influence the perceived security of a given habitat (Catano et al. 2015) because small fish are generally more vulnerable to predators (Laegdsgaard and Johnson 2001), whereas large fish may have problems finding suitable refuges because of their size (Ménard et al. 2012).

However, fish, like other animals, must balance the tradeoff between fulfilling their energetic requirements and avoiding predation. Juvenile dusky damselfish *Stegastes nigricans* have higher feeding activities than adults (Letourneur 1996) and use a greater range of habitat types than adults (Bay et al. 2001). This may be related to the high energetic needs of juveniles for rapid growth (Letourneur et al. 1997). In addition, though flexibility in growth rates can increase survival (Gagliano and McCormick 2007), small juveniles value faster growth to limit the amount of time they are vulnerable to predators that target small prey (Werner and Gilliam 1984). By comparison, adults tend to be more risk-averse since they have more stored resources that are worth protecting (Clark 1994). Thus, juveniles may tolerate greater foraging risks than adults because the benefits to growth are greater.

On coral reefs, many species of fish have ontogenetic shifts in habitat preference. Fish prefer and survive better in habitats consisting of size-appropriate refuges (Hixon and Beets 1993). Though increased cover may obstruct the ability of adults to visually detect predators, juveniles may benefit from the crypsis that complex habitats provide (Rilov et al. 2007). Three-spot damselfish *Stegastes planifrons* shifted habitat preferences as a function of age whereby juveniles preferred dead foliose coral structures, whereas adults preferred live foliose coral structures (Lirman 1994). These preferences may enhance survivorship and reduce predation (Jones 1988). Whether these shifts could be driven in part by changes in perceptions of security has not been widely studied.

Territorial damselfish play an important role in structuring coral reef communities, having both positive and negative impacts on the living coral (Casey et al. 2014). As grazers they can benefit coral reefs by providing a defense for certain coral species from coral feeding species (Gochfeld 2010) and reducing algal growth on coral through herbivory (Hughes et al. 2007). However, herbivorous damselfish also damage coral reefs by promoting algal diversity which reduces the amount of substrate to which juvenile coral can attach (Hixon and Brostoff 1983). In addition, by farming turf, other herbivores are attracted and may create incidental damage to the coral (Traçon et al. 2013).

Although studies have investigated how habitat complexity influences fish risk assessment, the interaction between structural complexity and potential ontogenetic shifts in antipredator behavior of damselfish has not been explored. To test this, we pushed an object to create a looming stimulus towards individual dusky damselfish to stimulate them to flee (Oliva and Tomsic 2012) and used flight initiation distance (FID), the distance at which an individual flees from an approaching threat (Ydenberg and Dill 1986; Cooper and

Blumstein 2015), to assess risk perception by juveniles and adults as a function of rugosity and percent coral and hard substratum cover. Structural rugosity and percent coral cover have been shown in previous studies to be accurate measurements of habitat complexity, which is correlated with the availability of shelters (Luckhurst and Luckhurst 1978; Rilov et al. 2007; Ménard et al. 2012).

We tested 2 related hypotheses about ontogenetic shifts in antipredator behavior as a function of different structural complexities. Our null hypothesis is that if juveniles and adults do not have ontogenetic shifts in their predation risk assessment in different habitat complexities, then they should have similar FIDs in different habitats. This may be a result from individuals preferring to live in areas with appropriately sized shelters. Our alternative hypothesis is that if juveniles and adults, because of their size differences, have different perceptions of risk in different habitat complexities, then FID should vary across size and age classes in different habitats.

Materials and Methods

Study site and subjects

We measured the FID of dusky damselfish at 2 fringing reef sites with abundant damselfish next to the Ta'ahiama Public Beach (17° 29' S, 149° 51' W) and next to Maharepa (17° 29' S, 149° 48' W) in Mo'orea, French Polynesia from 20 January to 3 February 2018. All experiments were conducted between 07:00 h and 16:00 h every other day and thus avoided dawn and dusk. These fringing reefs have experienced shifts in algal communities from dominant algal turf to dominant foliose macroalgae, as well as declining live coral cover (mainly *Acropora* spp. and *Porites lobata*) since 2010 after perturbations from a crown-of-thorns sea star *Acanthaster planci* outbreak (Adam et al. 2011; Han et al. 2016). Damselfish defend individual, non-overlapping territories that form colonies with adjacent territories occupying the same reef structure (Williams 1978; Karino and Nakazono 1993). These territories consist of both live and dead coral (Gochfeld 2010) covered with filamentous algae which damselfish farm and feed (Hata and Kato 2004). Dusky damselfish are ideal for these experiments because they were abundant at our Mo'orean study site, and because they were pugnaciously territorial (Hata and Kato 2002), we could avoid resampling individuals by moving to a different coral structure after collecting data on an individual. We targeted individuals that were <4.0 cm and those >8.5 cm long to allow us to focus on the differences in risk assessment between younger and older individuals. We categorized each subject into size classes "small" (presumably younger damselfish) and "large" (presumably older damselfish).

Measuring FID

By snorkeling in shallow water (<2.0 m), 3 observers worked together to collect the FID and habitat complexity measurements. We located an appropriate area without a predator present and identified a suitable subject. One observer approached the focal subject whereas the other observers remained >3.0 m away. All individual damselfish were oriented towards us at the start of the experiment, and all were in immediate vicinity of shelter during approach. Once approximately 2.0 m from the subject (2.16 m ± 0.15 m) the first observer pushed, at 0.5 m/s, a black, 18 cm-diameter funnel attached to a 2.0 m pole (marked in cm increments) towards the subject until the subject fled. A second observer then swam up and held the looming object in place whereas the first observer measured the FID, given by the distance from the end of the object to the initial

location of the fish. We also measured the extension distance (ED), the distance that the pole was extended from the first observer's body, from which we calculated the starting distance, the distance between the funnel and the subject at the start of the experiment by adding ED and FID. We defined flight as the instance at which an alerted damselfish darted away from the looming object. Similar to Nunes *et al.* (2015), we recorded the actions of the fish immediately after it fled as “flee to hole” if the fish sought shelter in a hole or under a structure, “swim away” if the fish swam away from the looming object without retreating to shelter, or “return” if the fish returned less than 5 s after fleeing. The first observer estimated fish size by measuring the distance between protruding structures on the coral that the fish passed. We also recorded the number of conspecifics on the same coral structure during the FID trial and the depth of the fish (all depths were between 0.2 m and 1.4 m and the effect of depth was not analyzed further). Water temperature varied within 8°F during our study.

Quantifying habitat complexity

After completing an FID trial, we measured rugosity and percent coral cover. We measured rugosity along 4 radiating directions 90° apart, centered at the subject's initial position. For each measurement, we draped a weighted fine-link chain along the benthic topography and measured the length of the chain adhering to the benthos across 1.0 linear meter (Risk 1972). We calculated the total rugosity as the sum of the 4 surface distances, with terrain becoming flatter as total rugosity approached 4.0 m.

One observer measured percent coral cover by centering a 1.0 m × 1.0 m gridded quadrat with 81 equally-spaced intercepts over the subject's initial position. At each of the intercepts, we tallied the number of occurrences of each type of benthos in the following mutually exclusive categories: macroalgae, sand, rubble, live coral, and hard substratum. We defined “macroalgae” as any visible algae that had a holdfast and was not algal turf (Bruno *et al.* 2009), and “rubble” as benthos that consisted of broken down pieces of coral fragments or rock that were larger than sand particles (Rasser and Riegl 2002). We defined “live coral” as living coral structure that could provide refuge, and “hard substratum” as dead reef structure, typically covered in algal turf, that could provide refuge and was not rubble nor covered by macroalgae. For our analyses we summed the intercepts over live coral and hard substratum to represent the total amount of coral in which fish could presumably shelter.

Statistical analyses

We explained variation in log₁₀ transformed FID by fitting a traditional general linear model in SPSS version 24 (IBM Corp 2016). Our independent variables included size classes small (mean ± SD: 2.62 ± 0.60 cm; *n* = 38) and large (10.5 ± 0.95 cm; *n* = 31), for which 95% confidence intervals did not overlap, as well as starting distance (216.51 ± 15.01 cm; range 191–249 cm), number of conspecifics (2.29 ± 2.26 individuals per structure; range 0–10 individuals), water temperature (mean 84.1°F; range 82°F–90°F), total rugosity, percent cover of live coral and hard substratum combined, and the interaction between size and rugosity as well as the interaction between size and percent live coral and hard substratum cover. We report adjusted R² values and set our alpha to 0.05. Variances between these groups were homogeneous (Levene's test of equality of error variances, *P* = 0.097), and residuals from our analysis appeared normal. To determine whether escape strategy varied

by size, we created a size by escape behavior frequency contingency table and tested it with a Chi-square test.

Results

Overall, we flushed 69 damselfish; 38 small and 31 large (mean ± SD: FID small 18.24 ± 11.58 cm; FID large 54.26 ± 16.53 cm). After controlling for other potentially important independent variables (Table 1), there was no significant interaction between size and total rugosity (616.13 ± 87.01 cm; *P* = 0.332; Table 1), but there was a significant interaction between size and percent cover of live coral and hard substratum (71.03 ± 15.94%; *P* = 0.026; Table 1). The estimate for the interaction of percent coral and hard substratum cover and size category was negative, indicating a decreasing FID as size and coral and hard substratum cover increased for large fish (Figure 1). There was no significant effect on the FID of small fish as size and coral and hard substratum cover increased (Figure 1). This model (*P* < 0.001) significantly explained 64.4% of the variation in FID. Small and large damselfish did not employ categorically different escape strategies (*P* = 0.423; Table 2). In our contingency table, one data point was removed as it did not have an escape response recorded.

Discussion

Damselfish have ontogenetic shifts in their perceptions of risk. We found that larger damselfish increased their FID as percent coral and hard substratum cover decreased, indicating that they perceived higher risks in habitats with presumably fewer refuges. Smaller damselfish did not significantly modify FID as a function of percent coral and hard substratum cover; however, they consistently had significantly shorter FIDs than adults. This indicates that damselfish do not adjust their choice of habitat according to their individual size; rather, there is an ontogenetic shift in perceptions of risk that explains differences in antipredator behavior. These results suggest either that young fish perceived a lower risk of predation along these habitat gradients or that they were willing to take greater risks. Thus, it appears that as damselfish grow, habitat complexity influences their assessments of risk. There are at least 2, non-mutually exclusive, hypotheses that may explain these observed patterns.

First, juvenile fish may not have the experience to recognize certain predator cues and engage in appropriate antipredator behavior (Kelley and Magurran 2003). Many species of fish require experience to recognize predatory olfactory and visual cues (Karplus *et al.* 2006, Mitchell *et al.* 2011). However, learning may be rapid; in environments with novel predators, predator-naive juvenile damselfish learned to respond quickly to predatory threats and survived better (Mitchell *et al.* 2011; Ferrari *et al.* 2014). This shows that although adult fish may have more developed predator recognition and antipredator responses, juvenile fish can also rapidly learn, so it is unlikely that our ca. 2.6 cm long fish, which already have shown that they can survive in a predator rich environment, were entirely predator-naive.

Second, the asset protection principle predicts that the larger the reproductive asset, the more important it is to protect (Clark 1994). Juvenile damselfish accepted higher risks in the presence of a predator, whereas adult fish decreased foraging behavior and hid for longer periods (Lönstedt and McCormick 2011). This may be because adult fish have greater reproductive value since juveniles have not yet reached sexual maturity. In *S. nigricans*, the largest 25% of individuals in a colony reproduce (Karino and Nakazono 1993). Thus, large adult fish may generally be more wary as a way to maximize

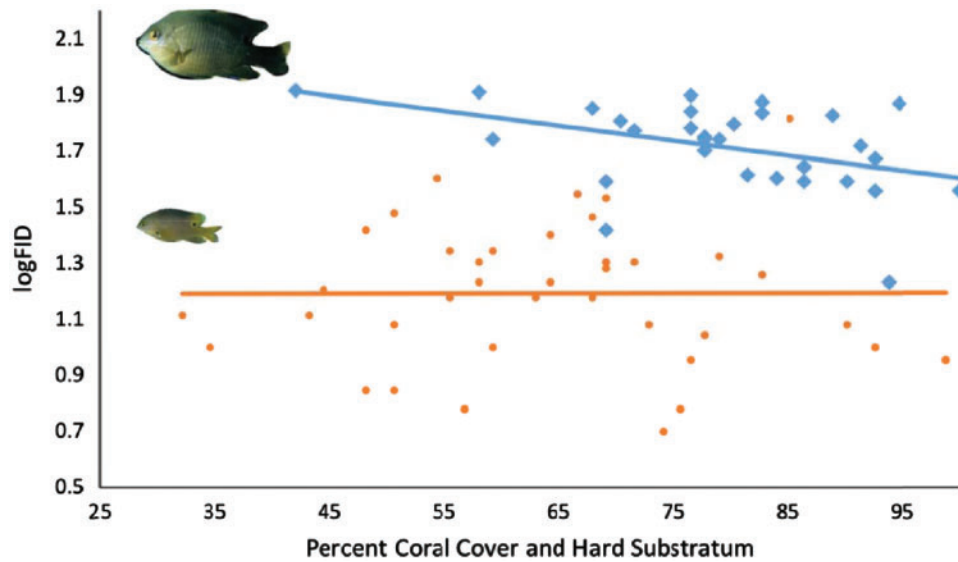


Figure 1. Effect of percent live coral and hard substratum cover on FID of dusky damselfish. Small damselfish and large damselfish are represented by orange circles and blue diamonds, respectively. Damselfish photographs modified from <http://fishbase.org>.

Table 1. Results of a general linear model to explain variation in FID

Source	Estimates	P	Partial η^2
Corrected Model		<0.001	0.685
Intercept	3.826	0.011	0.103
Size (large)	0.759	0.174	0.031
Starting distance (cm)	0.003	0.244	0.023
Temperature ($^{\circ}$ F)	-0.031	0.067	0.055
Number of conspecifics	-0.017	0.168	0.031
Total rugosity	-0.001	0.065	0.056
Percent live coral and hard substratum cover	0.003	0.326	0.016
Size (large) * Percent live coral and hard substratum cover	-0.009	0.026	0.080
Size (large) * Total rugosity	0.001	0.332	0.016

Table 2. Contingency table of the frequency of large and small damselfish that responded in each escape behavior category

	Small	Large
Flee to hole	25	24
Swim away	8	4
Return	5	2

their reproductive output, whereas juveniles take greater foraging risks so that they can have a chance to reproduce when mature. Therefore, as fish mature they have a greater need for refuges, indicated by an ontogenetic shift in their perceptions of security provided by varying coral cover.

In many species of fish, group size has been found to influence antipredator behavior (Larson and McCormick 2005; Brown et al. 2006). We used the number of conspecific damselfish in a colony as a reference for group size. However, we found that the number of conspecifics on the same structure did not have a significant effect on damselfish FID. Previous studies have also shown size of the subject and starting distance have an influence on FID (Catano et al. 2015; Cooper and Blumstein 2015; Nunes et al. 2015), however in our study neither of these were significant. Variation in temperature also did not have a significant effect. For *S. nigricans*, it seems that it

is coral and hard substratum cover, rather than other environmental factors, which has a profound influence on perceptions of security.

Although neither total rugosity nor percent cover of coral and hard substratum had any significant direct effect on FID, the interaction between percent cover and body size was significant whereas the interaction between rugosity and body size was not. This is notable because in several species of labrid fishes, variation in rugosity explained variation in their FIDs (Nunes et al. 2015). There are 2 possible explanations for this result. First, the 4 lines we measured for rugosity may have extended too far from an individual's territory to accurately characterize the focal subject's territory. However, previous studies on dusky damselfish have shown that the radius of an individual's territory, centered at a core algal mat, ranges from 0.55 to 2.80 m (Jan et al. 2003), which encompasses our rugosity measurements of 1.0 m. Indeed, we saw individual fish move >1 m from their territory. Second, percent cover of live and dead coral may be a more accurate measurement of the amount of crevices, and hence refuges, available than rugosity. Percent cover of live and dead coral measures the total substrate available for shelter while rugosity, measured with a chain, can produce the same value for structures with different amounts of protection (Nunes et al. 2015). Shorter coral structures with many holes may have the same rugosity as a taller coral structure with few holes, leading to different fish FIDs for the same rugosity estimate. However, rugosity has been shown

to correlate with habitat complexity and thus shelter and FID in previous studies (Luckhurst and Luckhurst 1978; Ménard *et al.* 2012; Nunes *et al.* 2015).

We have identified the importance of structural complexity on ontogenetic shifts in predator risk assessment. Adult damselfish seemingly perceive greater risk from predators because they are protecting their reproductive assets, whereas juveniles are expected to take greater risks in order to maintain high foraging and growth rates. However, some studies show that flexibility in growth rate, which may include slow growth in certain environments, can help individuals survive (Gagliano and McCormick 2007; Gagliano *et al.* 2007). In the future, understanding how variation in growth rate influences risk perception in juveniles would be valuable. In addition, quantifying the availability of specific refugia in coral crevasses that are available to each fish, and further differentiating between morphologically distinct coral species would help examine ontogenetic shifts in predator risk assessment along a more fine-scale and precise structural complexity gradient.

Acknowledgements

The authors thank H. Murphy and the rest of the staff at the UC Berkeley Richard B. Gump Research Station for logistical support, D. Williams for help with data analysis, P. Fong for help with methodology, and J. Nunes and 3 anonymous reviewers for comments on an earlier draft.

Funding

The authors thank the UCLA Office of Instructional Development and the UCLA Department of Ecology and Evolutionary Biology for partial support.

References

- Adam TC, Schmitt RJ, Holbrook SJ, Brooks AJ, Edmunds PJ *et al.*, 2011. Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS ONE* 6:e23717.
- Bay L, Jones G, McCormick M, 2001. Habitat selection and aggression as determinants of spatial segregation among damselfish on a coral reef. *Coral Reefs* 20:289–298.
- Brown GE, Bongiorno T, DiCapua DM, Ivan LI, Roh E, 2006. Effects of group size on the threat-sensitive response to varying concentrations of chemical alarm cues by juvenile convict cichlids. *Can J Zool* 84:1–8.
- Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW, 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90:1478–1484.
- Casey JM, Ainsworth TD, Choat JH, Connolly SR, 2014. Farming behaviour of reef fishes increases the prevalence of coral disease associated microbes and black band disease. *Proc R Soc B* 281:(2014)1032.
- Catano LB, Gunn BK, Kelley MC, Burkepile DE, 2015. Predation risk, resource quality, and reef structural complexity shape territoriality in a coral reef herbivore. *PLoS ONE* 10:e0118764.
- Clark CW, 1994. Antipredator behavior and the asset-protection principle. *Behav Ecol* 5:159–170.
- Cooper WE Jr, Blumstein DT, 2015. Escape behaviour: importance, scope, and variables. In: Cooper WE Jr, Blumstein DT, editors. *Escaping from Predators: An Integrative View of Escape Decisions*. 1st edn. Cambridge: Cambridge University Press, 3–14.
- Crowder LB, Cooper WE, 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813.
- Dahlgren CP, Eggleston DB, 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81:2227–2240.
- Dill LM, 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. *Can J Zool* 65:803–811.
- Ferrari MCO, McCormick MI, Meekan MG, Chivers DP, 2014. Background level of risk and the survival of predator-prey: can neophobia compensate for predator naivety in juvenile coral reef fishes? *Proc R Soc B* 282:(2014)2197.
- Gagliano M, McCormick MI, 2007. Compensating in the wild: is flexible growth the key to early juvenile survival? *Oikos* 116:111–120.
- Gagliano M, McCormick MI, Meekan MG, 2007. Survival against the odds: ontogenetic changes in selective pressure mediate growth-mortality trade-offs in a marine fish. *Proc R Soc B* 274:1575–1582.
- Gochfeld DJ, 2010. Territorial damselfishes facilitate survival of corals by providing an associational defense against predators. *Mar Ecol Prog Ser* 398: 137–148.
- Gratwicke B, Speight MR, 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J Fish Biol* 66:650–667.
- Grovenburg TW, Monteith KL, Klaver RW, Jenks JA, 2012. Predator evasion by white-tailed deer fawns. *Anim Behav* 84:59–65.
- Han X, Adam TC, Schmitt RJ, Brooks AJ, Holbrook SJ, 2016. Response of herbivore functional groups to sequential perturbations in Moorea, French Polynesia. *Coral Reefs* 35:999–1009.
- Hata H, Kato M, 2002. Weeding by the herbivorous damselfish *Stegastes nigricans* in nearly monocultural algae farms. *Mar Ecol Prog Ser* 237:227–231.
- Hata H, Kato M, 2004. Monoculture and mixed-species algal farms on a coral reef are maintained through intensive and extensive management by damselfishes. *J Exp Mar Bio Ecol* 313:285–296.
- Hixon MA, Beets JP, 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol. Monograph* 63:77–101.
- Hixon MA, Brostoff WN, 1983. Damselfish as keystone species in reverse: intermediate disturbance and diversity of reef algae. *Science* 220:511–513.
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O *et al.*, 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Biol* 17:360–365.
- IBM C, 2016. *IBM SPSS Statistics for Macintosh, Version 24.0*. Armonk (NY): IBM Corp.
- Jan RQ, Ho CT, Shiah FK, 2003. Determinants of territory size of the dusky gregory. *J Fish Biol* 63:1589–1597.
- Jones GP, 1988. Ecology of rocky reef fish of north-eastern New Zealand: a review. *N Z J Mar Fresh Res* 22:445–462.
- Karino K, Nakazono A, 1993. Reproductive behavior of the territorial herbivore *Stegastes nigricans* (Pisces: pomacentridae) in relation to colony formation. *J Ethol* 11:99–110.
- Karplus I, Katzenstein R, Goren M, 2006. Predator recognition and social facilitation of predator avoidance in coral reef fish *Dascyllus marginatus* juveniles. *Mar Ecol Prog Ser* 319:215–223.
- Kelley JL, Magurran AE, 2003. Learned predator recognition and antipredator responses in fishes. *Fish Fish* 4:216–226.
- Kjellander P, Svartholm I, Bergvall UA, Jarnemo A, 2012. Habitat use, bed-site selection and mortality rate in neonate fallow deer *Dama dama*. *Wildl Biol* 18:280–291.
- Komyakova V, Munday PL, Jones GP, 2013. Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLoS ONE* 8:e83178.
- Laegdsgaard P, Johnson C, 2001. Why do juvenile fish utilise mangrove habitats? *J Exp Mar Biol Ecol* 257:229–253.
- Larson JK, McCormick MI, 2005. The role of chemical alarm signals in facilitating learned recognition of novel chemical cues in a coral reef fish. *Anim Behav* 69:51–57.
- Lirman D, 1994. Ontogenetic shifts in habitat preferences in the three-spot damselfish *Stegastes planifrons* (Cuvier) in Roatan Island, Honduras. *J Exp Mar Biol Ecol* 180:71–81.
- Lehtiniemi M, 2005. Swim or hide: predator cues cause species specific reaction in young fish larvae. *J Fish Biol* 66:1285–1299.
- Letourneur Y, 1996. Dynamics of fish communities on Reunion fringing reefs, Indian Ocean. I. Patterns of spatial distribution. *J Exp Mar Biol Ecol* 195: 1–30.
- Letourneur Y, Galzin R, Harmelin-Vivien M, 1997. Temporal variations in the diet of the damselfish *Stegastes nigricans* (Lacepede) on a Reunion fringing reef. *J Exp Mar Biol Ecol* 217:1–18.

- Lönstedt OM, McCormick MI, 2011. Growth history and intrinsic factors influence risk assessment at a critical life transition for a fish. *Coral Reefs* 30:805–812.
- Luckhurst BE, Luckhurst K, 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar Biol* 49:317–323.
- Oliva D, Tomsic D, 2012. Visuo-motor transformations involved in the escape response to looming stimuli in the crab *Neohelice* (= *Chasmagnathus*) *granulata*. *J Exp Biol* 215:3488–3500.
- Mabille G, Berteaux D, 2014. Hide or die: use of cover decreases predation risk in juvenile North American porcupines. *J Mammal* 95:992–1003.
- Ménard A, Turgeon K, Roche D, Binning SA, Kramer DL, 2012. Shelters and their use by fishes on fringing coral reefs. *PLoS ONE* 7:e38450.
- Mitchell MD, McCormick MI, Ferrari MCO, Chivers DP, 2011. Coral reef fish rapidly learn to identify multiple unknown predators upon recruitment to the reef. *PLoS ONE* 6:e15764.
- Nunes JCC, Sampaio CLS, Barros F, 2015. The influence of structural complexity and reef habitat types on flight initiation distance and escape behaviors in labrid fishes. *Mar Biol* 162:493–499.
- Rasser M, Riegl B, 2002. Holocene coral reef rubble and its binding agents. *Coral Reefs* 21:57–72.
- Rilov G, Figueira WF, Lyman SJ, Crowder LB, 2007. Complex habitats may not always benefit prey: linking visual field with reef fish behavior and distribution. *Mar Ecol Prog Ser* 329:225–238.
- Risk MJ, 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res Bull* 153:1–6
- Ross PM, Thrush SF, Montgomery JC, Walker JW, Parsons DM, 2008. Habitat complexity and predation risk determine juvenile snapper *Pagrus auratus* and goatfish *Upeneichthys lineatus* behaviour and distribution. *Mar Freshwater Res* 58:1144–1151.
- Trapon ML, Pratchett MS, Hoey AS, Baird AH, 2013. Influence of fish grazing and sedimentation on the early post-settlement survival of the tabular coral *Acropora cytherea*. *Coral Reefs* 32:1051–1059.
- Werner EE, Gilliam JF, 1984. The ontogenetic niche and species interactions in size-structured populations. *Ann Rev Ecol Syst* 15:393–425.
- Williams AH, 1978. Ecology of threespot damselfish: social organization, age structure, and population stability. *J Exp Mar Biol Ecol* 34: 197–213.
- Ydenberg RC, Dill LM, 1986. The economics of fleeing from predators. *Adv Study Behav* 16:229–249.