



# Sit and survive: predation avoidance by cryptobenthic coral reef fishes

Michalis Mihalitsis<sup>1,2,3,4</sup> · David R. Bellwood<sup>1,2,3</sup> · Peter C. Wainwright<sup>4</sup>

Received: 10 August 2023 / Accepted: 21 October 2023

© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2023

## Abstract

Predation is a crucial ecosystem function, transferring nutrients and shaping the abundance and diversity of animals within communities. On coral reefs, fish–fish predation (i.e., piscivory) is arguably one of the best known ecosystem functions, yet is also one of the least well quantified. Recent work has suggested that the prey capture performance of piscivorous fishes may differ when feeding on actively swimming vs. cryptobenthic fish prey. However, the extent of this difference remains unquantified. Our goal, therefore, was to conduct performance-based experiments comparing piscivorous fishes feeding on two different fish prey types, namely, actively swimming vs. cryptobenthic prey (i.e., prey sitting on the benthos). While predators were able to immediately detect actively swimming prey, when feeding on cryptobenthic prey, predators were generally unable to detect the prey until it moved. Both focal predators, the grabber *Pseudochromis fuscus* and the engulfer *Pterois volitans* were less successful at capturing cryptobenthic prey (mean 28% probability of capture), compared to actively swimming prey (85%). Overall, our study demonstrates the heterogeneous nature of fish predation on coral reefs, and the challenges of feeding on different prey functional groups.

**Keywords** Sensory · Prey · Crypsis · Piscivory · Camouflage · Prey detection

## Introduction

Predator–prey interactions are a major driver in shaping communities which, in turn, shape ecosystem processes (Estes and Palmisano 1974; Ripple et al. 2001; Mihalitsis et al. 2022). In highly diverse systems, such as coral reefs, fish predation by fishes (i.e., piscivory) has been found to have a significant impact on population dynamics (Hixon and Carr 1997; Almany and Webster 2004; Albins and Hixon 2008). Predation may also influence trophodynamics at an ecosystem process level (Brandl et al. 2019). However,

predation success may vary among species. There is, therefore, a need to explore the basis for variation in predation success. One of the most promising avenues is from a functional approach.

Recent work has identified functional groups in coral reef fishes, both as predators (Mihalitsis and Bellwood 2021) and prey (Mihalitsis et al. 2021), and found these groups can broadly reflect predator–prey interactions at a community level (Mihalitsis et al. 2022). These studies suggested that functional groups of predator and prey may not interact homogeneously, due to functional performance differences in both the predators (i.e., prey capturing) and prey (i.e., predator detection and escaping). Specifically, while small-bodied, elongate, benthic ‘sitting’ fishes (from here on referred to as cryptobenthic) are highly abundant on coral reefs (Depczynski and Bellwood 2004; Brandl et al. 2018) they may not be equally accessible (i.e., their capture probability compared to other prey) to different types of predators (i.e., grabbers vs. engulfers, sensu Mihalitsis and Bellwood (2021)).

Cryptobenthic fishes are important for coral reef ecosystems, as they provide both energy and nutrients to other fishes (Brandl et al. 2019). These fishes die at exceptionally high rates (Steele and Forrester 2002; Depczynski and Bellwood 2005, 2006; Hernaman and Munday 2005;

Responsible Editor: K.D. Clements.

✉ Michalis Mihalitsis  
mmihalitsis@ucdavis.edu

- <sup>1</sup> Research Hub for Coral Reef Ecosystem Functions, James Cook University, Townsville, Qld, Australia
- <sup>2</sup> College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia
- <sup>3</sup> Australian Research Council, Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia
- <sup>4</sup> Department of Evolution and Ecology, University of California, Davis, CA 95616, USA

Winterbottom and Southcott 2008). While many of these fishes can be found in 'open' reef areas, sitting on turfs, rubble, or coral (Depczynski and Bellwood 2004; Hernaman and Munday 2005; Doll et al. 2021; Hemingson et al. 2022), they manage to stay hidden from the numerous predators long enough to breed and sustain viable populations. However, the specific mechanism through which this is achieved, remains unknown. Previous work has suggested that high growth rates (Gillooly et al. 2001), constant year-round settlement (Lefèvre et al. 2016), and abundant larvae (Brandl et al. 2019) are all important. While these factors are likely to be contributing to the ability of cryptobenthic fishes to persist as viable populations on coral reefs, the predation pressure these fishes face at the exact moment of predation is poorly understood. Goatley and Bellwood (2016) showed that cryptobenthic fishes spend almost all their lives in the vulnerable high-predation size classes. This raises the question: do they have any predation avoidance mechanisms and if so, how effective are they?

In the current study, we test the ability (through aquarium-based performance experiments) of two piscivorous coral reef fishes (a grabber *Pseudochromis fuscus* and engulfer *Pterois volitans*), to feed on both cryptobenthic and actively swimming fishes as prey. We test the ability of these predators to both successfully detect, and capture these different types of prey fishes. Overall, we test whether predators exhibit different capture success when feeding on different fish prey groups.

## Materials and methods

### Performance experiments

All experiments were carried out at the James Cook University (JCU) between 2020 and 2021. Housing and experimental protocols were in accordance with the JCU Animal Ethics Committee (A2523). Holding and experimental tanks were connected to a flow-through filtration system, with lighting in tanks between 9 a.m. and 6 p.m. All fishes were fed commercially available food (prawns or pellets) daily (unless predators were in the experimental phase, see below). All tanks were allowed to grow algae turfs on the bottom and sides to reduce reflection. It also provided a more natural substratum mirroring the algal turfs over which many reef gobies reside (Hemingson et al. 2022).

We studied two predator species. The first, *Pseudochromis fuscus* has been categorized in the functional group of grabbers, which primarily capture prey tail-first, through a long-distance strike, using their caniniform teeth (Mihalitsis and Bellwood 2021). The second, *Pterois volitans* has been categorised in the functional group of engulfers, capturing prey head-first by having a large mouth, high upper jaw protrusion

and no visible teeth (Mihalitsis and Bellwood 2019, 2021). We used the pomacentrid *Acanthochromis polyacanthus* as an actively swimming (AS) prey fish. The functional group of cryptobenthic substratum dwellers (sensu Mihalitsis et al. 2021) (hereby referred to as cryptobenthic) encompasses small-bodied, elongate, fishes, that 'sit' on the benthos, for which the likely anti-predatory benefits are discussed in (Mihalitsis et al. 2021). In our study, we used the goby *Eviota zebrina* for experiments with *P. fuscus*. For experiments with *P. volitans*, we primarily used larger *Eviota zebrina*, but also the goby *Asterropteryx semipunctatus*, and the blenny, *Ecsenius sp.*, for larger predator individuals. This was done to ensure that all predators fed on similar relative prey sizes, as relative prey size is perhaps one of the strongest influences on the ability of predators to capture prey (Pepin et al. 1992; Christensen 1996). A total of 31 *A. polyacanthus*, 21 *Eviota zebrina*, 5 *Asterropteryx semipunctatus*, and 4 *Ecsenius sp.* were used in our experiments. The potential for differences among cryptobenthic species in attack response latency was tested, and was found to be non-significant (see Supplemental Fig. S1). The average prey size used for the experiments, in terms of prey body depth/predator gape size, was  $0.71 \pm 0.04$  S.E (Standard Error), closely reflecting natural prey sizes (Mihalitsis and Bellwood 2021). Experiments were carried out in 20L aquaria. Only a single predator was held in an aquarium at a time, and was acclimatised for at least one week prior to experiment initiation.

Predators were starved for 24 h prior to experimental feeding. Prior to the experiment, an opaque tank separator divided the tank into two arenas, to ensure the predator and prey could not see each other. A single prey fish was then measured (Standard Length, SL and Body Depth, BD) in a zip-lock bag (thus avoiding skin contact and preventing potential effects of handling, on predator behaviour due to olfactory cues). The prey fish was then introduced to the empty side of the tank and was allowed one minute to orient itself before the tank separator was removed. The feeding event was then filmed using a Go-Pro camera to film in real time, and a Sony RX100 IV to capture the strike of the predator in slow motion (250 fps). Prey fish were removed after one minute if the predator failed to strike. If the predator made a non-lethal strike, the prey was immediately removed from the tank, and euthanised. A successful capture by the piscivore was defined as the piscivore capturing and holding the prey in its mouth for  $\geq 3$  s upon the first strike (i.e., performance). After a successful feeding event, the predator had to fully digest the prey before another feeding trial could commence. This usually took two to four days and was assessed by visually inspecting for swelling in the stomach area of the predator and the behaviour of the predator upon a researcher approaching the tank. We used three *P. fuscus* (Standard Length =  $56.4 \text{ mm} \pm 1.008$  S.E) and four *P. volitans* (Standard Length =  $99.5 \text{ mm} \pm 20.7$  S.E) individuals. Each

predator individual was fed between 3 and 5 individuals of each prey type (active swimmer vs. cryptobenthic).

We first quantified the ability of predators to detect the two types of prey. Prey detection was quantified based on the behaviour of the predator, i.e., turning towards the prey and approaching or striking at it. Immediate detection was quantified as the predator detecting prey within the first 2 s of the tank separator being removed. We also quantified the onset of prey escape relative to the predator strike initiation. Predator strike initiation was quantified from the slow motion footage (250 fps), and was defined as the frame at which the predator significantly increased its velocity, through a visible s-shaped bending on the posterior end of its body. Prey escape onset was defined as the frame at which the prey began to turn its body away from the predator, as a response to the predator striking. If there was no evident reaction by the prey, this variable was given the value of the predator strike duration (given that zero would mean the prey initiated an escape upon the predator initiating the strike). Only strikes where the prey did not appear to be influenced by the glass of the aquarium at the moment of strike, were used in this analysis.

## Statistical analysis

Statistical analyses were all carried out in a Bayesian framework, in the software R (R Core Team 2017). Experimental data were analysed using Bayesian Generalised Linear Models (BGLM) in the packages '*stan*' (Team 2018) and '*rstanarm*' (Goodrich et al. 2018). For both (1) immediate detection probability, and (2) probability of successful capture upon first strike (as response variables), predator species and prey groups were the explanatory variables, and a binomial distribution was used. For the onset of prey escape (response variable) predator species and prey groups were again the explanatory variables, using a gaussian distribution (based on the distribution and nature of the data). All models were analysed with three chains, 5000 iterations (warmup = 2000), a thinning factor of 5, and an adapt delta value of 0.99. All models were then compared using the 'leave one out (loo)' cross validation method, in the '*loo*' package (Vehtari et al. 2020). Model diagnostics were conducted using the '*DHARMa*' package (Florian 2020). Model predictions were examined using the '*emmeans*' package (Lenth 2019), and visualisation was explored using the '*ggplot2*' package (Wickham 2016).

## Results

In all but one trial, actively swimming prey were immediately detected upon experiment initiation, whereas for cryptobenthic prey, immediate detection occurred in less

than half of all strikes, and the prey was only detected following prey movement (Fig. 1a). Specifically, the immediate detection probability for an actively swimming prey fish was 94% (78–100 Highest Posterior Density, HPD) by *Pseudochromis fuscus*, and 99% (92–100 HPD) by *Pterois volitans* (Fig. 1a). By contrast, for cryptobenthic prey, the immediate detection probability was 37.5% (15–63 HPD) by *P.fuscus*, and 41% (20–65 HPD) by *P.volitans* (Fig. 1a). For model details, please see Supplemental Table 2. In summary, while actively swimming prey were immediately detected, for the majority of predation events involving cryptobenthic prey, neither predator species were able to detect the prey until it moved (by a burst-and-coast swim).

Upon detection, predators approached the prey and prepared to initiate a strike. For strikes by *P.fuscus*, the escape onset by prey (relative to predator strike initiation), was -9.2 ms (-26.9–9.03 HPD) for cryptobenthic prey, and 11.18 ms (-12.2–32.01 HPD) for active swimming prey (Fig. 1b). For strikes by *P.volitans*, the escape onset by prey, was 61.27 ms (42.2–78.31 HPD) for cryptobenthic prey, and 38.69 ms (16–61.85 HPD) for active swimming prey (Fig. 1b). The model with the best predictive accuracy (using the loo criterion) was one with an interaction term between predator species and prey as explanatory variables, indicating that prey escape onset was dependant on both the predator type and the prey type (for detailed model see Supplemental Table 2). In summary, for *P.fuscus*, both prey types initiated escapes faster (sometimes before the predator initiated the strike), compared to their reaction times to strikes from *P.volitans*.

When prey was detected, a strike was initiated, and the prey initiated an escape. *P. fuscus* had a median 71% (50–90% HPD) probability of successfully capturing damselfish prey; for *P. volitans* it was 92% (80–99% HPD). By contrast, *P. fuscus* had a median 15% (3.1–35% HPD) probability of successfully capturing cryptobenthic prey, whereas for *P.volitans* it was 46% (25–67% HPD) (Fig. 1c). The model with the best predictive accuracy (using the loo criterion) was one with predator species and prey as explanatory variables, without an interaction term, indicating the effect of prey type was the same for both predator species (for detailed model see Supplemental Table 2). In summary, while both predators were highly successful at capturing damselfish, they were less successful at capturing cryptobenthic prey.

## Discussion

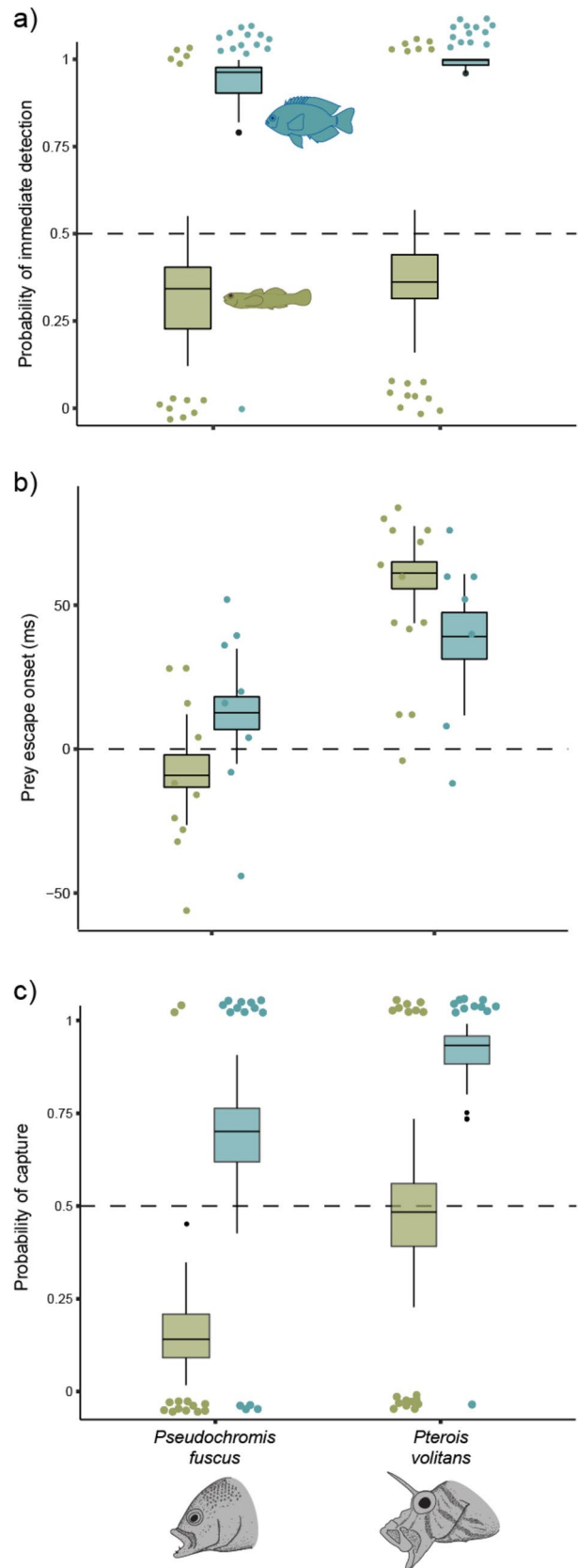
Our results demonstrate the ability of some cryptobenthic fishes, to reduce their vulnerability to predation. As a first barrier, these fishes are highly effective at crypsis, with predators primarily able to detect them when they move.

**Fig. 1** Predation events between two species of predator (*Pseudochromis fuscus* and *Pterois volitans*) and two types of prey (cryptobenthic 'sitting' vs. active swimming). **a** Probability of immediate detection by a predator, leading to a strike on cryptobenthic and active swimming prey. A value of one was assigned for strikes initiated by the predator immediately upon the prey being visible to the predator; a value of zero was assigned for detections/strikes by the predator that were initiated only after the prey moved by swimming. **b** Prey escape onset (ms) relative to the predator strike onset ( $t=0$ ). **c** Probability of predators successfully capturing different prey types. Model predictions are shown in boxplots and outlier points, coloured depending on the prey type; blue=actively swimming damselfish, brown=cryptobenthic. Dots represent raw data

Secondly, if they are detected, the identity (and likely striking behaviour) of the predator determined their escape onset, with both cryptobenthic and active-swimming prey reacting faster to strikes by *Pseudochromis fuscus*. Upon the predator striking, cryptobenthic prey were harder to capture, when compared to an actively swimming damselfish. Our findings support the hypothesis that piscivory on coral reefs may not be a 'one-prey fits-all' relationship when considering body size vs. mortality. Overall, we show that fish predation on coral reefs may be shaped by both predator and prey at the moment of capture.

It has been suggested that cryptobenthic fishes rely primarily on crypsis to avoid detection by predators (Brandl et al. 2018; Hemingson et al. 2022). Our results support this suggestion and emphasise the importance of crypsis in avoiding predation by the three cryptobenthic fishes that we studied. Cryptobenthic fishes, while highly abundant on reefs, may not be as easily detectable on the reef as freely swimming fishes. The visual abilities of predatory fishes has previously been studied with regards to acuity and sensitivity (Goatley and Bellwood 2009; Schmitz and Wainwright 2011; Fogg et al. 2022). Recent advances in technology have allowed us to view a reef through the eyes of a predator, showing how quickly acuity can decrease, further strengthening the hypothesis of crypsis as a highly effective anti-predatory strategy on reefs (Caves et al. 2017). Reef predators may therefore rely more on prey movement, as opposed to pattern recognition, in order to detect them. Indeed, in our study, the majority of strikes on cryptobenthic prey fishes (60%), by both functional groups of predators, occurred only after the prey moved.

Furthermore, our results show that even if a cryptobenthic prey fish is detected, it can still be more difficult to capture, compared to an actively swimming prey fish. The mechanistic basis for this has yet to be determined. Mihalitsis et al. (2021) suggest a link to the nature of the predators' strike, with a ram strike directed towards the substratum causing difficulties for the predators (i.e., potential of the predator damaging its teeth/jaws). However, here we find that an engulfing lionfish also showed decreased capture success on cryptobenthic prey. We suggest that our results may



be linked to the sensory and swimming abilities of cryptobenthic fishes, or the approaching/striking behaviour of the predator.

Changes in water flow are primary stimuli to which fishes respond, through multiple neurological tissues (Webb 2014). However, the speed at which fishes react to external stimuli changes depending on the detecting structure. For example, responses to visual stimuli in zebrafish (*Danio rerio*) were found to take approximately 200 ms (Burgess and Granato 2007), whereas for a flow stimulus, they were able to respond in less than 4 ms (Liu and Fetcho 1999). Indeed, visual stimuli are found to take a longer path to trigger the Mauthner (M-) cells (neuron cells responsible for initiating escape response), as opposed to mechano-acoustic stimuli (Mirjany and Faber 2011; Domenici and Hale 2019). Furthermore, fishes with faster escape responses (i.e., smaller escape latency) are known to have a higher survival probability (McCormick et al. 2018). Therefore, for fishes as prey, visual stimuli, as well as water flow-related detection of movement may be important against predators.

Recent work has identified the potential for highly differentiated sensory abilities of some cryptobenthic fishes (e.g., *Elacatinus*) compared to other fishes, which include having a reduced lateral line system, a proliferation of superficial neuromasts, and the presence of a large sacculus, containing a large saccular otolith in the inner ear (Nickles et al. 2020; Majoris et al. 2021). The function of these saccular otoliths in gobies has been suggested to enhance the detection of sound pressure, or for the detection of particle motion (Popper et al. 2021). The superficial neuromasts, found along the body of the fish, have also been suggested to function as hydrodynamic water flow (velocity) detectors (Montgomery et al. 1997). For cryptobenthic fishes on coral reefs, the ecological function of this proliferation in neuromasts, has also been suggested to function for flow-refuging (avoiding areas with rapid water movement) (Goatley et al. 2021). Our results therefore suggest that the sensory abilities of cryptobenthic fishes in relation to predation, may be an interesting avenue for future research. In this context the presence of the substratum may be an additional feature reducing predation. The substratum represents a refuge of no water movement associated with a strong boundary layer. The closer the prey are to the substratum the harder it will be to suck them from a surface; the presence of the substratum may effectively neutralize some suction force.

Our results also suggest that the approach behaviour of the predator may impact the timing of prey escape initiation. *Pseudochromis fuscus* has been observed to frequently carry out a pursuit behaviour, resulting in a decreased capturing success rate (Feeney et al. 2012), as opposed to *Pterois volitans*, which is known to display more of an ambushing behaviour (Mihalitsis and Bellwood 2021). Furthermore, *P. volitans* is also known to display

a specialised feeding behaviour, where, upon detection and approaching prey, *P. volitans* blows water jets towards the prey (Albins and Lyons 2012) (also carried out by *P. volitans* in our study). This behaviour results in the prey sensing this water jet, turning towards/into the water flow (i.e., rheotaxis) and thus the predator coaxes the prey to face the predator, allowing the predator to capture the prey head-first (Albins and Lyons 2012), an essential component of prey capture in this functional group of piscivorous fishes (Mihalitsis and Bellwood 2017, 2021). Overall, our results suggest that the approaching behaviour of predators towards prey, can have significant effects on the escape onset of prey fishes.

It is suggested that fishes living in complex environments such as coral reefs, tend to have better fast-start performance skills than fishes living in structurally simpler environments (Domenici and Blake 1997). Complex environments reduce predator-prey interactions to brief encounters, where unsteady swimming and manoeuvrability is advantageous for both predator and prey (Domenici and Blake 1997). Our results also highlight the enhanced ability of *Pterois volitans*, an engulfer, to capture cryptobenthic prey, when compared to *Pseudochromis fuscus*, a grabber. While further work on other predator species will be needed to establish the generality of our results for the engulfer-grabber dichotomy.

Cryptobenthic fishes spend their whole life in the most vulnerable size classes, where they face significantly high mortality rates (Goatley and Bellwood 2016; Mihalitsis et al. 2021). Any traits resulting in predation reduction may, therefore, have far reaching impacts for fishes that may spend only a few weeks on the reef. It seems that crypsis, immobility and fast escape responses are crucially important for these species offering advantages against members of both major predator functional groups. In predator-prey interactions the prey can influence the outcomes as much, or potentially more, than the predators. Overall, our study demonstrates the heterogeneous nature of fish predation on coral reefs, by showing that predator and prey functional groups may not interact with the same outcomes. We suggest that, ultimately, the detection of prey may be determined by the eyesight performance of the predator, prey escape initiation by the approach behaviour of the predator, and the outcome of the strike by both predator and prey performance.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00227-023-04330-0>.

**Acknowledgements** We thank S. Brandl, C. Hemingson, V. Huertas, R. Morais, A. Siqueira, R. Streit, and S. Tebbett for insightful discussions; E. Fakan, J. Donnelson, R. Spinks, and M. Jarrold for providing prey fishes. We also thank two anonymous reviewers for helpful comments. Supported by the Australian Research Council (FL190100062 and CE140100020).

**Authors' contribution** MM and DRB conceived and designed the study, MM collected and analysed the data, MM, DRB, and PCW wrote the manuscript.

**Funding** Supported by the Australian Research Council (FL190100062 and CE140100020).

**Data availability** Data will be made available upon request.

## Declarations

**Conflict of interest** The authors declare no conflict of interest.

**Ethical approval** Housing and experimental protocols were in accordance with the James Cook University Animal Ethics Committee (A2523).

## References

- Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Mar Ecol Prog Ser* 367:233–238
- Albins MA, Lyons PJ (2012) Invasive red lionfish *Pterois volitans* blow directed jets of water at prey fish. *Mar Ecol Prog Ser* 448:1–5
- Almany GR, Webster MS (2004) Odd species out as predators reduce diversity of coral-reef fishes. *Ecology* 85:2933–2937
- Brandl SJ, Goatley CHR, Bellwood DR, Tornabene L (2018) The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs. *Biol Rev Camb Philos Soc* 93:1846–1873. <https://doi.org/10.1111/brv.12423>
- Brandl SJ, Tornabene L, Goatley CHR, Casey JM, Morais RA, Côté IM, Baldwin CC, Parravicini V, Schiettekatte NMD, Bellwood DR (2019) Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning. *Science*
- Burgess HA, Granato M (2007) Modulation of locomotor activity in larval zebrafish during light adaptation. *J Exp Biol* 210:2526–2539
- Caves EM, Sutton TT, Johnsen S (2017) Visual acuity in ray-finned fishes correlates with eye size and habitat. *J Exp Biol* 220:1586–1596
- Christensen B (1996) Predator foraging capabilities and prey antipredator behaviours: pre-versus postcapture constraints on size-dependent predator-prey interactions. *Oikos* 1:368–380
- Depczynski M, Bellwood D (2004) Microhabitat utilisation patterns in cryptobenthic coral reef fish communities. *Mar Biol* 145:455–463
- Depczynski M, Bellwood DR (2005) Shortest recorded vertebrate lifespan found in a coral reef fish. *Curr Biol* 15:R288–R289
- Depczynski M, Bellwood DR (2006) Extremes, plasticity, and invariance in vertebrate life history traits: insights from coral reef fishes. *Ecology* 87:3119–3127
- Doll PC, Munday PL, Bonin MC, Jones GP (2021) Habitat specialisation and overlap in coral reef gobies of the genus *Eviota* (Teleostei: Gobiidae). *Mar Ecol Prog Ser* 677:81–94
- Domenici P, Blake R (1997) The kinematics and performance of fish fast-start swimming. *J Exp Biol* 200:1165–1178
- Domenici P, Hale ME (2019) Escape responses of fish: a review of the diversity in motor control, kinematics and behaviour. *J Exp Biol* 222:jeb166009
- Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. *Science* 185:1058–1060
- Feeney WE, Lönnstedt OM, Bosiger Y, Martin J, Jones GP, Rowe RJ, McCormick MI (2012) High rate of prey consumption in a small predatory fish on coral reefs. *Coral Reefs* 31:909–918
- Florian H (2020) DHARMA: residual diagnostics for hierarchical (multi-level/mixed). Regression models. R package version 0.2. 7
- Fogg LG, Cortesi F, Lecchini D, Gache C, Marshall NJ, de Busserolles F (2022) Development of dim-light vision in the nocturnal reef fish family Holocentridae. II: Retinal morphology. *J Exp Biol* 225:244740
- Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. *Science* 293:2248–2251
- Goatley C, Bellwood DR (2009) Morphological structure in a reef fish assemblage. *Coral Reefs* 28:449–457
- Goatley CHR, Bellwood DR (2016) Body size and mortality rates in coral reef fishes: a three-phase relationship. *Proc R Soc B* 283:20161858
- Goatley CH, Brandl SJ, Wroe S, Bellwood DR (2021) Simple larvae sustain the world's smallest marine vertebrates. *Coral Reefs* 40:75–82
- Goodrich B, Gabry J, Ali I, Brilleman S (2018) rstanarm: Bayesian applied regression modeling via Stan. R Package Version 2:1758
- Hemingson CR, Mihalitsis M, Bellwood DR (2022) Are fish communities on coral reefs becoming less colourful? *Glob Change Biol* 28:3321–3332
- Hernaman V, Munday P (2005) Life-history characteristics of coral reef gobies. II. Mortality rate, mating system and timing of maturation. *Mar Ecol Prog Ser* 290:223–237
- Hixon MA, Carr MH (1997) Synergistic predation, density dependence, and population regulation in marine fish. *Science* 277:946–949
- Lefèvre CD, Nash KL, González-Cabello A, Bellwood DR (2016) Consequences of extreme life history traits on population persistence: do short-lived gobies face demographic bottlenecks? *Coral Reefs* 35:399–409
- Lenth R (2019) emmeans: Estimated Marginal Means, aka Least-Squares Means
- Liu KS, Fetcho JR (1999) Laser ablations reveal functional relationships of segmental hindbrain neurons in zebrafish. *Neuron* 23:325–335
- Majoris JE, Foretich MA, Hu Y, Nickles KR, Di Persia CL, Chaput R, Schlatter E, Webb JF, Paris CB, Buston PM (2021) An integrative investigation of sensory organ development and orientation behavior throughout the larval phase of a coral reef fish. *Sci Rep* 11:1–13
- McCormick MI, Fakan E, Allan BJ (2018) Behavioural measures determine survivorship within the hierarchy of whole-organism phenotypic traits. *Funct Ecol* 32:958–969
- Mihalitsis M, Bellwood DR (2017) A morphological and functional basis for maximum prey size in piscivorous fishes. *PLoS ONE* 12:e0184679
- Mihalitsis M, Bellwood DR (2019) Functional implications of dentition-based morphotypes in piscivorous fishes. *Royal Soc Open Sci* 6(9):190040
- Mihalitsis M, Bellwood DR (2021) Functional groups in piscivorous fishes. *Ecol Evol* 11:12765–12778
- Mihalitsis M, Hemingson CR, Goatley CH, Bellwood DR (2021) The role of fishes as food: a functional perspective on predator-prey interactions. *Funct Ecol* 35:1109–1119
- Mihalitsis M, Morais RA, Bellwood DR (2022) Small predators dominate fish predation in coral reef communities. *PLoS Biol* 20:e3001898
- Mirjany M, Faber DS (2011) Characteristics of the anterior lateral line nerve input to the Mauthner cell. *J Exp Biol* 214:3368–3377
- Montgomery JC, Baker CF, Carton AG (1997) The lateral line can mediate rheotaxis in fish. *Nature* 389:960–963
- Nickles KR, Hu Y, Majoris JE, Buston PM, Webb JF (2020) Organization and ontogeny of a complex lateral line system in a Goby (*Elacatinus lori*), with a consideration of function and ecology. *Copeia* 108:863–885

- Pepin P, Shears T, De Lafontaine Y (1992) Significance of body size to the interaction between a larval fish (*Mallotus villosus*) and a vertebrate predator (*Gasterosteus aculeatus*). *Marine Ecology Progress Series*: 1–12
- Popper AN, Hawkins AD, Sisneros JA (2021) Fish hearing “specialization”—a re-evaluation. *Hearing Research*: 108393
- R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Ripple WJ, Larsen EJ, Renkin RA, Smith DW (2001) Trophic cascades among wolves, elk and aspen on Yellowstone National Park’s northern range. *Biol Cons* 102:227–234
- Schmitz L, Wainwright PC (2011) Nocturnality constrains morphological and functional diversity in the eyes of reef fishes. *BMC Evol Biol* 11:338
- Steele MA, Forrester GE (2002) Early postsettlement predation on three reef fishes: effects on spatial patterns of recruitment. *Ecology* 83:1076–1091
- Team SD (2018) RStan: The R interface to Stan. R package version 2.21.2 Online: <http://mc-stan.org>
- Vehtari A, Gabry J, Magnusson M, Yao Y, Bürkner P, Paananen T, Gelman A (2020) Efficient leave-one-out cross-validation and WAIC for Bayesian models. *R Package Version 2(3)*:1
- Webb JF (2014) Morphological Diversity, Development, and Evolution of the Mechanosensory Lateral Line System. In: Coombs S, Bleckmann H, Fay RR, Popper AN (eds) *The Lateral Line System*. Springer
- Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis*. In: Springer-Verlag (ed), New York
- Winterbottom R, Southcott L (2008) Short lifespan and high mortality in the western Pacific coral reef goby *Trimma nasa*. *Mar Ecol Prog Ser* 366:203–208

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.