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Intruder identity alters the response of territorial damselfish protecting algal farms

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Abstract Herbivorous damselfish that cultivate algal farms frequently exhibit aggressive territorial behaviour to defend their investment from intruders, particularly against other herbivorous fish and invertebrates. On a coastal coral reef in New Caledonia, the response of the damselfish *Hemiglyphidodon plagiometopon* to intruders of varying type and level of threat to their algal farm was tested. Responses to live and dead coral fragments, carnivorous whelks, shells, and rocks varied from no response to biting and extrusion from farms. Damselfish elicited the strongest defensive response to the herbivorous sea urchin *Echinometra mathaei*, rapidly attacking the urchin by biting and lifting it from farms, before extruding it up to 3.5 m away. *H. plagiometopon* responded in a similar manner to dead urchins (no threat of herbivory) as to live urchins, but typically did not extrude them as far. Ultimately, damselfish responded to intruders in a manner largely consistent with the level of threat posed to their algal farm, with the similar response between live and dead urchins suggesting such strong defensive behaviours may be combination of 'hard-wired' and learned behaviours in reaction to the level of realised threat.

Keywords Algae · Habitat structure · *Hemiglyphidodon plagiometopon* · Herbivory · Sea urchin · Territorial behaviour · Turf

Introduction

Many animal species modify habitats through their behaviours and interactions, sometimes driving wholesale changes that have lasting consequences to habitat structure and functioning. Familiar examples include sea urchins that over-graze diverse kelp forests to create and maintain relatively unproductive coralline barrens (Steneck et al. 2002; Ling 2008), beavers that topple riverbank trees to dam rivers and create lakes (Naiman et al. 1988), and humans, who have extensively modified habitats in almost all biomes on Earth (Vitousek et al. 1997; Jackson 2001; Wohl et al. 2017). Sometimes cited as keystone species (Power et al. 1996) due to the far-reaching consequences of their actions for the broader community, such organisms often modify habitats directly (e.g., the creation of beaver dams), but may also indirectly facilitate habitat change by modifying behaviours in other species (e.g., reducing herbivory; Irving and Witman 2009).

Damselfish (Family Pomacentridae) are a common feature of coastal fish communities on tropical and temperate shores around the world (Frederich and Parmentier 2016). Many of the approximately 385 species are small, rocky/coral reef-dwelling fish that can locally modify habitats due to a combination of their own manipulation of the substratum, as well as their

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often aggressive defensive behaviour toward other species (Ceccarelli et al. 2001). Many herbivorous damselfish modify the primary rock or coral habitat by cultivating and maintaining discrete ‘farms’ of filamentous algae, akin to a marine turf or lawn (Lassuy 1980; Hata and Kato 2002; Hata and Ceccarelli 2016). Farms, and the small benthic invertebrates they contain, are typically the primary source of food for the damselfish (Wilson and Bellwood 1997; Hata and Umezawa 2011), may be used to attract mates and protect eggs (Navarrete-Fernandez et al. 2014), and have been observed to occupy up to 70% of the reef area (Ferreira et al. 1998; Ceccarelli 2007). As such, damselfish may present as a key determinant of reef habitat structure, capable of killing corals to increase the amount of suitable substrata for their farms (Wellington 1982), but also indirectly facilitating local coral establishment through aggression toward corallivores (Kamath et al. 2019).

Given the investment damselfish typically put into their farms, they are often vigorously defended from other herbivorous fish (including conspecifics) and invertebrates through aggressive territorial behaviours (Ceccarelli et al. 2001; Jan et al. 2003; Hattori and Shibuno 2013). Intruding fish are typically chased away from the local area by being charged at and/or bitten (Hourigan 1986), while invertebrates that encroach into farms are bitten, dragged out and/or picked up and swum away from the farm (Sammarco and Williams 1982; Glynn and Colgan 1988; Irving and Witman 2009). While such territorial behaviours of damselfish have been well documented (see review in Hata and Ceccarelli 2016), there is limited evidence showing how the type of response may be broadly intruder-specific (e.g. fish vs invertebrate), as well as species-specific (e.g. among species of sea urchin), eliciting responses ranging from no reaction to rapid and vigorous defence/removal (Jan et al. 2003; Irving and Witman 2009). One general explanation for such variation is that damselfish modify their response according to the level of perceived threat, with the most vigorous and aggressive responses most likely to be associated with intruders recognised as the most direct threat. While this hypothesis is largely untested, there is evidence that damselfish aggression is greater between conspecifics vs heterospecifics on coral reefs, with conspecifics likely to represent a greater threat to farms due to similarities in diet, farming behaviour, and territory requirements (Eurich et al. 2018; Robles et al. 2018).

On a coastal coral reef in Noumea, New Caledonia, the response of territorial damselfish to a variety of intruders was tested. Intruders represented varying levels of grazing threat to algal farms, ranging from no threat (e.g. rocks, coral fragments) to an explicit threat (e.g. live sea urchins). Damselfish response to each intruder was measured as i) the time taken for the damselfish to bite the intruder, ii) the number of bites given to the intruder, iii) whether the intruder was extruded from the farm (and how), and iv) the distance that the intruder was extruded. Intrusion by sea urchins was predicted to elicit the strongest aggressive response from damselfish given they are capable of rapidly overgrazing farms and are known to be forcibly removed by damselfish (Sammarco and Williams 1982), sometimes even cooperatively with neighbours (Irving and Witman 2009). While this response highlights that damselfish can perceive a significant threat from urchins, it was also tested whether damselfish were responding to a perceived or realised threat of sea urchins by comparing their response to dead urchin tests (no realised threat of herbivory) with that of live urchins.

Materials and methods

Study site and species description

All research was done on a shallow (~ 4 m deep) coastal coral reef in Anse Vata, Noumea, New Caledonia (Fig. 1, 22° 18′ 26.70″ S, 166° 26′ 49.87″ E). The reef extends ~ 50 m out to sea, comprising a mix of predominantly branching staghorn coral (*Acropora spp.), millepora* spp., and large *Porites* spp. corals at the fore-reef, which give way to sand and sparse seagrass meadows. A wide diversity of herbivorous and carnivorous fish occupy the reef, including the territorial damselfish *Hemiglyphidodon plagiometopon*, which grows to ~ 20 cm and is known to actively cultivate and defend farms of filamentous algae from conspecifics and other intruders (Wilson and Bellwood 1997; Lassuy 1980; Hattori and Shibuno 2013).

The most abundant herbivorous invertebrate observed on the reef was the sea urchin *Echinometra mathaei*, which grows to a test diameter of ~ 5 cm and grazes on filamentous algae (Mills et al. 2000). While *E. mathaei* often creates a burrow for protection by using its spines and teeth to bioerode coral and rock (Mokady et al. 1996), urchins at the study site were

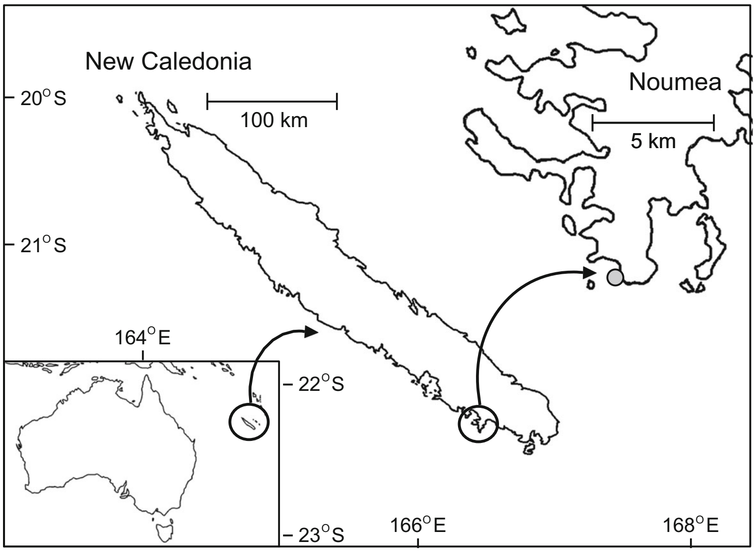


Fig. 1 Map of New Caledonia showing the location of the study site (grey circle) at the southern point of Noumea. Inset: Map of Australia and New Caledonia

instead mostly found sheltering among dead coral fragments collecting on the reef floor. *E. mathaei* typically forages at night to avoid predation by carnivorous fish (Mills et al. 2000; Young and Bellwood 2011), yet the presence of empty urchin tests, typically only broken on the oral surface where spines are small and the urchin is more readily accessible, suggests fish predators are a local threat for exposed urchins at the study site (see Dee et al. 2012). Herbivorous gastropods were not observed at the study site despite intensive searching, with carnivorous whelks observed only rarely.

Habitat sampling and species abundance

The abundance of *H. plagiometopon* farms was quantified on replicate 10 × 1 m belt transects ($n = 8$) oriented perpendicular to the shore and between 1 and 3 m depth. For each transect, a tape measure was laid over the reef and the number of individual farms encountered within 0.5 m either side of the tape was counted. Concurrently, the number of *H. plagiometopon* individuals was counted along each transect, up to 1 m in height above the reef substratum given their propensity for swimming close to the reef structure. To estimate the size of farms, 20 were haphazardly selected across the reef area and measured across their longest dimension. It was observed that the majority of farms were approximately circular, so the area of each farm was estimated as πr^2.

The densities of *E. mathaei* sea urchins and gastropods were estimated by counting individuals within 1 m^2 quadrats ($n = 15$) placed haphazardly on the reef. Coral rubble and corals with a branching architecture (e.g. *Acropora, Millepora*) were targeted since these habitats appeared to support the greatest densities, presumably due to more hiding spaces among branches and therefore greater protection from fish predators. Targeted sampling in this manner may over-estimate urchin abundance on a per-reef-area basis, but this may be countered somewhat by the cryptic day-time behaviour of sea urchins during the sampling period.

Experimental tests

The response of *H. plagiometopon* to intruders was tested by placing rocks, bivalve shells, dead coral fragments, live coral fragments, predatory whelks, live *E. mathaei*, and dead *E. mathaei* tests (an almost-whole urchin test presumably left over from a fish predation event) into isolated algal farms maintained by a single adult *H. plagiometopon*. While rocks, shells, and coral fragments could not be considered functionally as intruders that deliberately choose to occupy algal farms, they were conceptually considered intruders for this study as a reference to any object not usually found within an algal farm. For each replicate trial ($n = 10$ per intruder type), a single intruder was placed into the centre of a haphazardly selected farm with the ensuing behaviour of the resident *H. plagiometopon* observed for a maximum of 60 s (preliminary observations suggested aggressive responses would occur within this time frame, if at all). While *H. plagiometopon* often retreated among the coral as the intruder was placed by the diver, they usually immediately returned to the farm once the diver retreated a metre or two. If the damselfish did not immediately return, the trial was abandoned and a new trial begun elsewhere. Individual farms/ *H. plagiometopon* were only ever tested once to avoid biasing results (e.g. learned behaviours), and effort was made to use intruders of similar dimensions (approximately 4–5 cm across the longest axis) to minimise possible size-related influences on the damselfish response.

The time taken for *H. plagiometopon* to respond to the intruder was quantified as the duration between placing the intruder into a farm and the first bite of the intruder by the damselfish. The number of additional bites, if any, and whether the intruder was extruded by *H. plagiometopon* during the 60 s trial was subsequently recorded. Additionally, the method of extrusion (nudging and dragging vs picking up and swimming away) and the resulting distance of extrusion from the edge of the farm was recorded. Differences in the response of *H. plagiometopon* to this suite of intruders were analysed using one-way ANOVA, with *post-hoc* Student-Newman-Keuls tests used to identify the hierarchy of differences among intruder types where main effects were detected.

Results

Sampling of reef habitats revealed that there were 8.00 ± 1.21 (mean ± SE) *H. plagiometopon* algal farms per 10 m^2 of reef (i.e. per transect). Each farm appeared to be maintained by a single *H. plagiometopon*, with the counted abundance of *H. plagiometopon* averaging 10.38 ± 1.48 per transect, highlighting that some individuals were not clearly associated with algal farms. Farms averaged 60.95 ± 3.06 cm across their longest axis, and being approximately circular, gives an average farm area of 3057.20 ± 292.64 cm^2 per 10 m^2 of reef (~ 3% of reef area).

The urchin *E. mathaei* was sparsely distributed, averaging 1.00 ± 0.40 individuals per m^2. Given their cryptic day-time behaviour, however, they are likely more prevalent than what was observed and counted. Gastropods were very rare, averaging 0.13 ± 0.09 individuals per m^2 and comprising only carnivorous whelks (surprisingly, no herbivorous gastropods were ever observed).

Experimentally adding intruders into *H. plagiometopon* farms resulted in clear behavioural responses dependent on the identity of the intruder. The intrusion of either live or dead urchins resulted in the shortest response times from *H. plagiometopon* (average time to first bite = 2.9–3.2 s), followed by dead and live coral fragments (15.4–17.8 s), and lastly rocks, shells, and whelks (42.2–54.7 s) (Fig. 2a, Table 1a). In contrast, the number of bites upon an intruder until extrusion or within the 60 s observation period (if extrusion did not occur) was statistically similar among all intruders, generally averaging 2–4 bites (Fig. 2b, Table 1b). Based on the rank magnitude of the number of bites, rocks were bitten on average more than other intruders, but this was highly variable among trials and may also reflect that rocks were never extruded from farms, thus allowing more opportunity for *H. plagiometopon* to bite during the 60 s trial.

Among all types of intruders, rocks and whelks were never observed to be extruded from farms, and shells only extruded once, whereas live and dead urchins were always extruded (Fig. 3). The rapid extrusion of urchins was consistently characterized by *H. plagiometopon* biting onto an urchin spine and lifting the entire urchin off the farm before vigorously swimming it away, temporarily abandoning the farm in the process. Live and dead coral fragments were extruded in 90% of trials, most often by *H. plagiometopon* nudging and dragging the fragment out of the farm but occasionally by being lifted and swum away (Fig. 3).

Where extrusion occurred, there was a clear pattern in the distance that intruders were removed from farms. Urchins were extruded the furthest distance of all intruders, with live urchins swum further away than dead urchins (mean distance = 2.15 ± 0.25 m vs 0.90 ± 0.22 m; Fig. 4, Table 1c). Live and dead coral fragments were only extruded by 0.13 ± 0.03 m, on average, by predominantly being nudged and dragged to the edge of the farm, while rocks, shells and whelks were rarely or never extruded.

Discussion

Damselfish that farm algal turfs are a common feature of tropical coral reefs and temperate rocky coasts, often defending their investment with vigour (Ceccarelli et al. 2001; Jan et al. 2003). On a New Caledonian coral reef, the damselfish *Hemiglyphidodon plagiometopon*

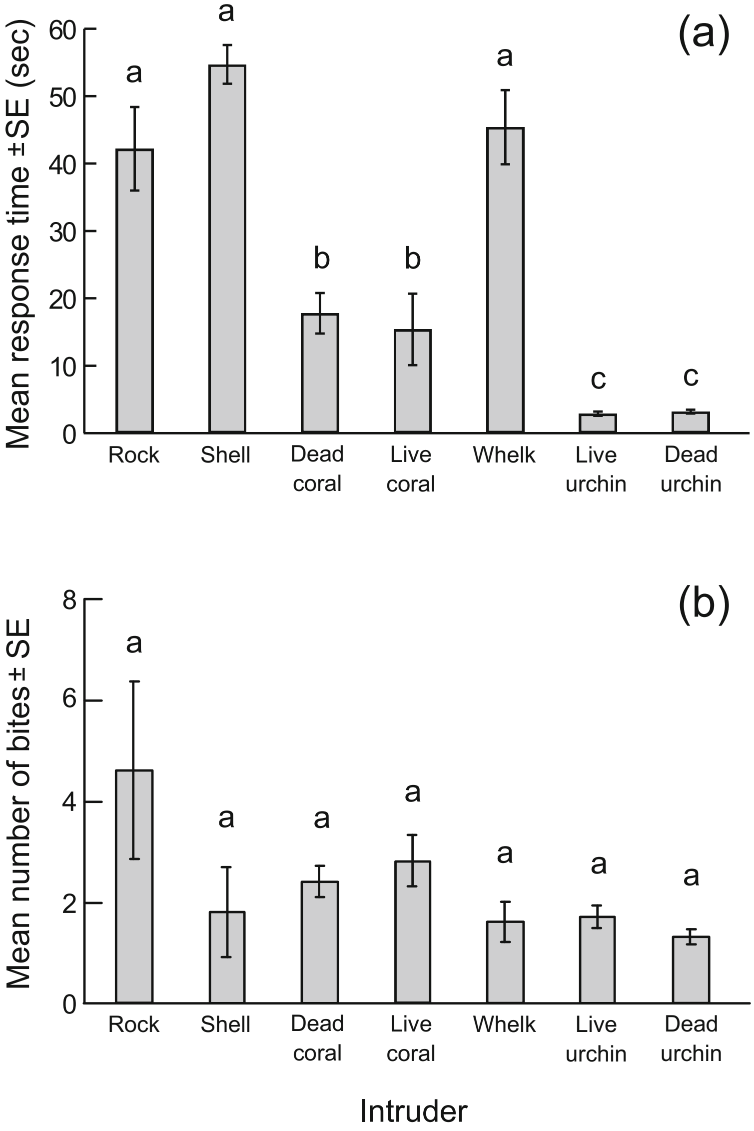


Fig. 2 Response of damselfish (*Hemiglyphidodon plagiometopon*) to different intruders into their algal farms, including the herbivorous sea urchin *Echinometra mathaei*. Data show the mean ± SE **a**) response time to each intruder (time to first bite), and **b**) the number of bites of the intruder over a 60 s observation period. Letters above bars indicate statistical similarities/differences in responses based on SNK tests

defended its farm most actively against intruding sea urchins *Echinometra mathaei*, moderately against live and dead coral fragments, and least against rocks, shells and whelks. This strong reaction of damselfish to urchins is consistent with previous studies (Sammarco and Williams 1982; Irving and Witman 2009), and might be expected given the fervour with which urchins can consume algae (Chapman and Johnson 1990; Ling 2008) and thus threaten damselfish farms.

H. plagiometopon not only responded strongly to the presence of *E. mathaei* urchins through biting, but also rapidly extruded them by biting on to a spine, lifting the entire urchin off the farm, and then swimming it up to 3.5 m away before dropping it and rapidly returning to their farm. In contrast, live and dead coral fragments were dragged or nudged to the edge of the farm (approximately 0.10 m away) and were only occasionally swum further away. Robustly transporting urchins away from farms suggests they are perceived as a significant threat, especially as damselfish are prepared to temporarily abandon their closely-guarded farm as part of the extrusion process. Indeed, in approximately half of all live urchin trials, urchins were swum past the reef edge and deposited over bare sand, which likely represents an environment with greatly enhanced predation risk for an otherwise cryptic urchin that hides among coral

Table 1 Results of ANOVAs testing the effect of intruder type on a) response time of the damselfish *Hemiglyphidodon plagiometopon* (measured as time to the first bite of the intruder), b) the number of bites of intruders over a 60 s observation period, and c) the distance the intruder was extruded by *H. plagiometopon*. *Post-hoc* SNK tests indicate the location of significant effects

Source	df	MS	*F*	*P*
(a) response time				
Intruder type	6	50.09	38.41	< 0.0001
Residual	63	1.30		
SNK tests: live urchin = dead urchin < dead coral = live coral < whelk = shell = rock				
(b) number of bites				
Intruder type	6	0.48	1.25	0.2917
Residual	63	0.38		
SNK tests: rock = shell = dead coral = live coral = whelk = live urchin = dead urchin				
(c) extrusion distance				
Intruder type	6	1.79	59.06	< 0.0001
Residual	63	0.03		
SNK tests: rock = shell = dead coral = live coral = whelk < dead urchin < live urchin				

branches and rubble (Young and Bellwood 2011). In doing so, it is possible that *H. plagiometopon* are not only removing the immediate threat to their farm, but also reducing the future risk of *E. mathaei* by increasing their exposure to predators. Previous studies have noted a different type of antagonistic response to urchins, whereby spines are successively broken over the urchin's test until the urchin decides to leave the damselfish farm (Sammarco and Williams 1982). This type of territorial behaviour was not observed in this study, nor was cooperative removal of urchins by damselfish (Irving and Witman 2009).

Notably, *H. plagiometopon* responded to dead urchins in an almost identical way as to live urchins, suggesting that it is the perceived threat of the urchin to the algal farm that elicits such rapid and aggressive defensive behaviour in *H. plagiometopon*, rather than the realised threat of actual consumption of algae. Compared to live urchins, however, dead urchins were not swum as far away from the farm (less than half the distance). The reason for this difference is unknown, but one possible explanation is that *H. plagiometopon* are able to discern a dead urchin from a live one upon lifting it from the farm and recognising a difference in weight and associated ease of swimming with the urchin. The visual cue of an urchin shape, live or dead, is likely responsible for eliciting the primary defensive response from damselfish (Thresher 1976; Siebeck et al. 2009), but subsequent signals (e.g. weight of the urchin) may be important to determine continued defensive responses, such as swimming the intruder away, as opposed to renewed farm patrolling and maintenance.

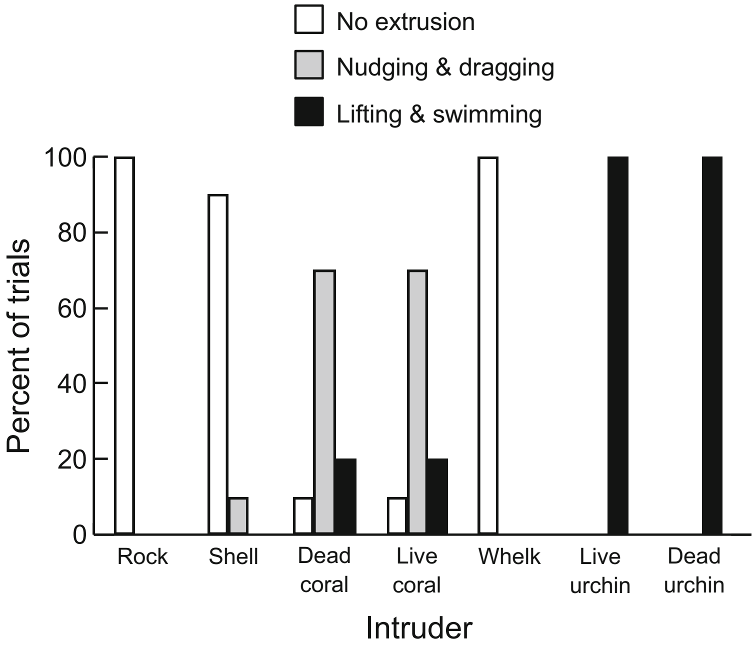
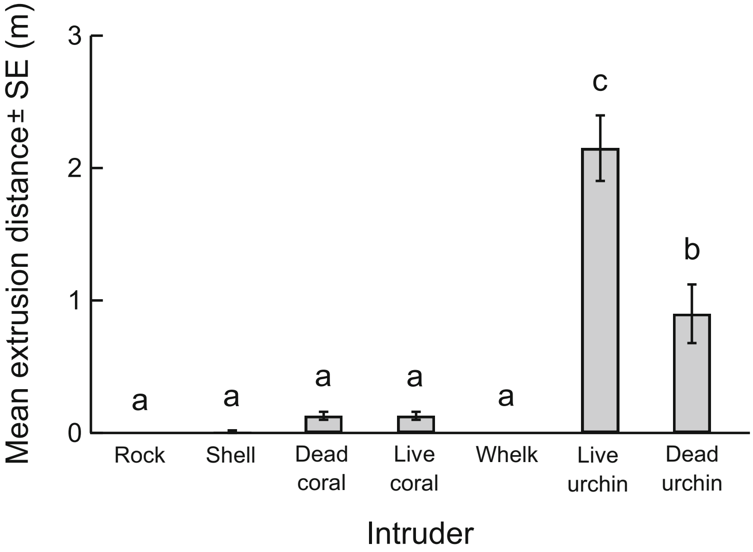


Fig. 3 Comparison of intruder extrusion frequency and method of extrusion among different types of intruders. When extruded from farms, *H. plagiometopon* either nudged and dragged intruders to the edge of the farm, or bit down on intruders to lift them from the farm and swim them away

Fig. 4 Mean ± SE distance that *H. plagiometopon* extruded intruders from their algal farm. Letters above bars indicate statistical similarities/differences in response based on SNK tests



H. plagiometopon rarely or never extruded rocks, shells, or whelks in this study, indicating little to no perceived threat from them. These objects were often investigated through multiple bites (Fig. 2b), but extrusion only occurred once (for a shell) in a total of 30 combined trials. When compared to a typical urchin shape, such intruders likely present very different visual cues to a damselfish, and may be tolerated inside farms because they may ultimately provide more surface area for farming algae (although whelks are likely transient). If so, the question must then be asked why *H. plagiometopon* wouldn't deliberately add such structures to a farm to enhance their investment. The general absence of such structures in farms observed across the study site suggest that these 'tolerated' intruders are either dislodged by wave action, remove themselves (i.e. for whelks), or are eventually extruded (i.e. beyond the 60 s observation period used here). If the latter, it would suggest such intruders are not seen as an immediate threat like urchins are, but are still something undesirable inside farms (e.g., rocks rolling around because of wave action may still crush and abrade algae within farms). Live and dead coral fragments were often extruded, but it is presently difficult to ascertain what threat *H. plagiometopon* perceived from them. While potentially able to also abrade algae due to rolling from wave action, coral fragments may also present a physical barrier that reduces farming efficiency, especially if that barrier might also provide a sting (live coral).

While efforts were made to keep the overall size of intruders similar among all trials, there were clearly broad differences in the overall shape among types of intruders. As such, an alternative explanation for the observed responses of *H. plagiometopon*, particularly the rapid response to urchins, is that urchins have numerous spines that may provide far more leverage points for extrusion than the other intruders tested. Previous research has shown that urchins with relatively blunt and thick spines (e.g., pencil urchins) are handled much faster by damselfish than urchins with sharp spines (Irving and Witman 2009). This would suggest that *E. mathaei* urchins, which possess many sharp and rigid spines, would be handled slower than intruders such as rocks and coral fragments (blunt 'spines') if extrusion was primarily a function of handling and leverage. In contrast, the rapid, consistent, and amplified response (e.g. swimming urchins up to 3.5 m away) of *H. plagiometopon* to urchins lends greater weight to the model that *E. mathaei* urchins are perceived as a critical threat to *H. plagiometopon* farms, at least above the other types of intruders tested.

In conclusion, the damselfish *H. plagiometopon* responded to intruders into its algal farm in a manner largely consistent with the threat posed. Herbivorous *E. mathaei* urchins were rapidly extruded, while inactive intruders posing no direct threat to algal farms (rocks and shells) were rarely extruded. Notably, the response to dead urchins was initially similar to live urchins in terms of response time, but the extrusion distance was approximately 42% of that measured for live urchins. These results suggest that *H. plagiometopon* initially responds to the perceived threat of urchins in general, perhaps as a 'hard-wired' behavioural response (also see Sammarco and Williams 1982), but that this behaviour can be subsequently modified upon discerning the realised threat of the intruder, perhaps as a learned response based on prior experience (Webster and Laland 2018). Prior research has shown that damselfish are able to discern an intruder's identity under circumstances other than the guarding of an algal farm, such as when protecting egg clutches (Souza and Ilarri 2014). Collectively, this growing body of evidence suggests that intruder recognition is an essential trait for multiple elements in the life cycle of territorial damselfish.

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