

Lewis Eaton, Katherine A. Sloman, Rod W. Wilson, Andrew B. Gill, and Alastair R. Harborne

## Non-consumptive effects of native and invasive predators on juvenile Caribbean parrotfish

L. Eaton • K. A. Sloman

School of Science and Sport, University of the West of Scotland, Paisley, PA1 2BE, UK

### Present Address:

L. Eaton

WALTHAM Centre for Pet Nutrition, Freeby Lane, Waltham-on-the-Wolds, LE14 4RT, Leicestershire, UK.

R. W. Wilson

Biosciences, College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4PS, UK

A. B. Gill

COREE, School of Energy, Environment and Agrifood, Cranfield University, Cranfield, Bedfordshire, MK4 4AL, UK

A. R. Harborne (Corresponding author)

Marine Spatial Ecology Laboratory and Australian Research Council Centre of Excellence for Coral Reef Studies, School of Biological Sciences, Goddard Building, The University of Queensland, Brisbane, QLD 4072, Australia

### Present Address:

Department of Biological Sciences, Florida International University, Biscayne Bay Campus, 3000 Northeast 151 Street, North Miami, Florida 33181, USA

email: [alastair.harborne@fiu.edu](mailto:alastair.harborne@fiu.edu) | Tel: +1-305-919-4232 | Fax: +1-305-919-4030

## Abstract

Non-consumptive effects of predators can have important impacts on aquatic food webs, but there are few data on how predators change the behaviour of Caribbean reef fishes. Such changes may include behavioural responses to the invasive predatory lionfish (*Pterois volitans* / *P. miles*). This study used an aquarium experiment to examine the behaviour of herbivorous parrotfish (*Scarus iseri*) in the absence of other fish (control), with a non-piscivore present, and with a predatory threat from a native grouper or a lionfish. Treatments were repeated with and without additional parrotfish shelters to examine the potential effects of degraded reefs (loss of refuges). Using video, parrotfish behaviours (sheltering, swimming in open areas, foraging, aggressive interactions, bite rates, and shoaling behaviour) were recorded for groups of four parrotfish. Compared to the control, the average number of parrotfish hiding was reduced by 65% and foraging shoals were 10% larger when threatened by grouper, likely as a specific response to an ambush predator. When exposed to lionfish, parrotfish reduced their bite rates by 50%, possibly to be more vigilant of this predator's unique stalking behaviour. The absence of additional shelter had limited effects although parrotfish formed 10% larger shoals when swimming in open water, potentially as a defensive behaviour because of a perceived lack of refuges. The reduction in parrotfish bite rates caused by lionfish may have important demographic consequences. Furthermore, parrotfishes are important grazers of macroalgae, and these behavioural changes may exacerbate the direct effects of lionfish predation and potentially affect reef benthic dynamics.

**Keywords** Grazing • Grouper • Lionfish • *Scarus iseri* • The Bahamas

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**Ethical approval:** All applicable international, national, and institutional guidelines for the care and use of animals were followed.

## Introduction

Predation is a key process structuring fish assemblages and regulating populations on coral reefs (Hixon 1991; White et al. 2010). Although much of the research on reefs has focused on mortality from predation, there is a growing recognition that predators also have important sub-lethal effects by modifying the behaviour of their prey. These behavioural changes are an example of potentially energetically costly non-consumptive effects (Sih et al. 2010). For example, the foraging behaviours of four prey species from different trophic groups were altered by varying abundances of their predators across a gradient of fishing pressure (Madin et al. 2010). Changes in prey behaviour when exposed to increased predation risks may also impact lower trophic levels. This trophic cascade has been demonstrated on reefs by large groupers reducing the foraging of meso-predators and consequently increasing fish recruitment rates (Stallings 2008), and predators decreasing feeding rates by herbivores and reducing macroalgal grazing (Madin et al. 2011; Rizzari et al. 2014). These studies complement literature from other ecosystems demonstrating analogous effects of predators on prey behaviour (e.g. Preisser et al. 2005), which can be categorised as ‘trait-mediated interactions’ (TMIs) that represent strategic changes in prey phenotype or behaviour, or ‘trait-mediated indirect interactions’ (TMIIs) representing the effect of a predator on the resources of its prey (see discussion of terminology in Abrams 2007). Meta-analyses of the impact of TMIs and TMIIs (subsequently ‘non-consumptive effects’) within predator-prey interactions suggest they are at least as important as direct consumption, and may be more important in aquatic systems (Preisser et al. 2005).

Given the likely importance of non-consumptive effects in marine ecosystems, it is critical to understand their characteristics and impacts in diverse coral-reef fish assemblages. Existing data on reef-fish non-consumptive effects are relatively limited, and have focused on the impacts of over-fishing predators (Madin et al. 2010; Madin et al. 2011; Rizzari et al. 2014) and how fish learn and use predatory threat cues (Leahy et al. 2011; Lönnstedt and McCormick 2011; Manassa et al. 2013). However, the introduction of additional predators into fish assemblages has received little attention. Perhaps the highest profile invasive species on reefs is the introduction of the Indo-Pacific species *Pterois volitans* (Linnaeus 1758) and *P. miles* (Bennett, 1828) (subsequently ‘lionfish’) into the Caribbean. The history of the invasion is reviewed in detail elsewhere (Côté et al. 2013), but in summary lionfish were recorded in Floridian waters in 1985, entered The

Bahamas in 2004, and have colonised the majority of the western Atlantic, Caribbean Sea and Gulf of Mexico. The ubiquity and high densities of lionfish on many Caribbean reefs has led to concern about their effects on native fishes and invertebrates, and a growing literature has demonstrated that these impacts are significant (Albins and Hixon 2008; Green et al. 2012; Layman et al. 2014; Albins 2015). In contrast to studies of direct predation on native fishes, the effects of lionfish on native fish behaviours are less well known. However, a study of predator-cue use by two goby species demonstrated that behavioural responses to native species and lionfish varied (Marsh-Hunkin et al. 2013), although it is not clear if the response to invasive predators is maladaptive or is simply a different response to a different threat. In contrast, the damselfish *Stegastes planifrons* (Cuvier, 1830) had no measurable behavioural response to lionfish, but clear aggressive behaviours towards native predators and competitors (Kindinger 2015).

In the present study, we conducted an aquarium experiment to examine the behavioural response of juvenile striped parrotfish (*Scarus iseri*, Bloch 1789) to predation threats from a native carnivorous grouper, an invasive lionfish and a non-predatory fish. Non-consumptive effects on parrotfishes are particularly important to the ecology of Caribbean reefs, because they are now the major grazer of macroalgae following the disease-induced reduction of the urchin *Diadema antillarum* (Philippi, 1845) (Mumby 2006). An overabundance of macroalgae on reefs can significantly alter the demographics of reef-building corals through processes such as limiting the survival of juvenile corals (Birrell et al. 2008), and consequently reduce reef resilience (Mumby et al. 2007). Since juvenile fishes appear to have the ability to discriminate among predators and non-predators (Chivers et al. 2014), we hypothesised that parrotfish would only alter their behaviour when threatened by the predators. There is some evidence of Caribbean fishes responding differently to native and invasive predators (Marsh-Hunkin et al. 2013), so we hypothesised that the behaviour of parrotfish following exposure to the grouper or lionfish would vary. In addition to varying predator identity, we examined the effect of refuge availability. There are myriad potential changes in behaviour that could be adopted by prey fishes exposed to predators, including spending more time in refuges within the reef to reduce mortality rates (e.g. Hixon and Beets 1993). Any links between fish behaviour and habitat quality are important given the continuing reduction of complexity on many Caribbean reefs (Alvarez-Filip et al. 2009). We hypothesised that parrotfish threatened by predators would spend more time hiding when additional shelter was available.

## Methods

### Experimental design

The study was conducted in south Eleuthera, The Bahamas, in July 2013. A total of 24 *S. iseri* individuals were captured using a barrier net from patch reefs where they are likely to have been exposed to predation threats from lionfish (Green et al. 2011) and grouper. A lionfish (assumed to be *P. volitans*), Nassau grouper (*Epinephelus striatus*, Bloch 1792) and non-piscivorous white grunt (*Haemulon plumierii*, Lacepède 1801) were caught using either hand nets or fish traps. After a minimum of 72 hours acclimation to laboratory conditions, experiments took place in 900 litre cylindrical tanks continuously supplied with seawater (mean water parameters: pH  $8.25 \pm 0.01$  SD; DO<sub>2</sub>  $78.8\% \pm 2.87$  SD; temperature  $27.2^{\circ}\text{C} \pm 0.3$  SD).

Parrotfish were divided into six replicate groups of four individuals, and there was no difference in total length of fish between replicates (mean total length was  $7.6 \text{ cm} \pm 0.9$  SD): one-way ANOVA;  $F_{1,18}=0.758$ ,  $P=0.591$ ). A shoal of four individuals is within the typical range of group sizes observed for this species on shallow reefs (Wolf 1985; Overholtzer and Motta 1999). The focus of this study was on sub-lethal effects of predation, so to ensure that the parrotfish reacted to the threat of predators, but were not actually eaten, each replicate group of parrotfish was housed within a 61 x 41 x 41 cm mesh cage within the main cylindrical tank. The mesh cage contained an algal-covered rock (~15 x 15 x 10 cm, with naturally regenerating turf algae that are preferred by juvenile parrotfishes), along with a 15 cm length of PVC pipe in treatments where additional shelter was provided. Addition of the PVC pipe provided greater and more varied sheltering opportunities for the parrotfishes, which distinguished between the two treatments. Parrotfish were kept within these mesh cages for seven days. Parrotfish were subjected to four different treatments (one per day) in which a native predator (Nassau grouper: 26 cm, one day), a non-native predator (lionfish: 35 cm, one day), a native non-predator (white grunt: 21 cm, one day) and a no-fish control (four days) were placed into the main cylindrical tank outside of the mesh cage. The order of these treatments was randomised across each of the six replicates, but each treatment involving adding a grouper, lionfish or grunt was separated by at least one control day. This design aimed to provide replicate baseline data on parrotfish behaviour in the

absence of any other fishes throughout the experiment, and avoid predator exposures on consecutive days. Since only three experimental tanks were available, treatments with three replicates of four parrotfishes were conducted over the first seven days of the experiment, followed by the final three replicates in the second seven days of the experiment (fourteen days in total, see Online Resource 1 for detailed schedule).

Each day at noon, the parrotfish were recorded from above using GoPro video cameras for one hour. Recordings were then paused and the PVC pipe (additional shelter) was either placed within, or removed from, the mesh cage. The parrotfish were then allowed another hour to acclimate to the replacement or removal of the PVC pipe before recordings continued for a further hour (each treatment lasted for 3 hours on each day). The order in which the PVC pipe was removed or replaced was randomised within each replicate. Consequently, on each day of the experiment, each group of parrotfish was exposed to only one of the four treatments (lionfish, grouper, grunt or control), but both the 'no shelter' and 'added shelter' treatments.

As predators were separated from the parrotfish, there were no concerns about predators learning to hunt more efficiently within the aquaria and, therefore, only a single individual of each predatory species and grunt was necessary for the entire experiment. Furthermore, using a single individual of each predatory species ensured a consistent threat across all replicates. The predators and grunt were fed regularly during the experiment, but not during observational periods. During almost all observations, the lionfish and the Nassau grouper were positioned within a small gap between the mesh cage and the wall of the cylindrical tank, looking into the mesh cage. Predators were very rarely observed more than a body length away from the mesh cage, and were presumed to always be visible to the parrotfish and to represent a threat. In contrast, the grunt continually swam around the main tank, and the mesh cage was not a focal area of activity. No change in predator behaviour was observed over the duration of the experiment.

#### Behavioural analyses

The total number of bites made by parrotfish on the rock, and aggressive interactions among parrotfish, were counted for each hour of observation. In addition, recordings were stopped every minute and the number of fish undertaking different behaviours within the mesh cage was counted. This resulted in a maximum of 120

measurements from each video (60 with no added shelter and 60 with added shelter) of how many fish were behaving in each of the following ways: 1) hiding against or under the rock or within the PVC pipe (only possible when the pipe was present); 2) feeding on, or within a body length of, the algae covered rock; and 3) swimming in open areas of the mesh cage away from the rock or artificial shelter (Fig. 1). In addition, at the same 1 min time points, the presence or absence of a shoal (two or more individuals within a body length of each other) and the number of fish in the shoal were recorded. Shoal occurrences and sizes were recorded for both foraging fish and fish swimming in open areas.

### Statistical analyses

The effects of predator identity and shelter availability on parrotfish behaviour were analysed using linear mixed-effects models. The response variables were: number of fish sheltering (mean number of fish hiding at each sampling point), number of fish in open areas (mean number of fish swimming in open cage areas at each sampling point), number of fish foraging (mean number of fish foraging close to rocks at each sampling point), number of interactions per minute (number of aggressive interactions per minute of filming), number of bites per foraging fish per minute (number of bites divided by the mean number of fish foraging and the number of minutes of filming, i.e. the bites rates of those fish that were foraging), probability of shoal formation in either foraging or open water fish (number of occurrences of shoal formation divided by the number of sampling points), and mean number of fish within a shoal when one had been formed by either foraging or open water fish. Explanatory factors were fish treatment (lionfish present, grouper present, grunt present or control) and shelter (not added or added), and the interaction between these factors. Random factors were experimental run (either day 1-7 or day 8-14) and replicate (six groups of fish, to account for repeated measures of each group), with 'replicate' nested in 'run'. All response and explanatory model variables were log transformed when necessary to improve normality of residuals.

All models were fitted in the nlme package in R (R Core Team 2014). Models were fitted using the procedure outlined by Crawley (2007). Briefly, a maximal model was fitted including all factors and interactions. Least significant terms were then removed in turn, starting with the interaction. After each term was removed, models were compared to ensure that term removal did not lead to a significant increase in

deviance or Akaike information criterion (AIC). Terms were removed until the model contained only significant terms or removal of any non-significant terms caused a significant increase in deviance or AIC (minimal adequate model). Minimal adequate models were checked for violations of assumptions.

## Results

Across all replicates and treatments, there were a mean of 0.61 fish hiding (SD = 0.77), 0.93 fish foraging on the algal-covered rock (SD = 0.65), and 2.46 fish swimming in the open (SD = 0.96) (summaries of all variables are provided in Online Resource 2). There was a mean of 0.84 interactions among the fish  $\text{min}^{-1}$  (SD = 0.56), and the foraging fish took 8.97 bites  $\text{fish}^{-1} \text{min}^{-1}$  (SD = 6.64). Foraging fish formed shoals for 44.9% of the survey period, and mean shoal size was 3.04 fish (SD = 0.35). Fish in open water formed shoals for 13.9% of the time, and mean shoal size was 2.76 fish (SD = 0.44).

The presence of groupers led to parrotfish spending less time hiding than during the control treatment (no other fish present) or when lionfish were present (Table 1, Fig. 2a, Online Resource 3). In the control treatment there was an average of 0.84 fish hiding, compared to an average of 0.29 fish in grouper treatments. Furthermore, when foraging parrotfish shoaled in the presence of grouper they tended to form larger shoals (average shoal size 3.2 fish) than in any other treatment (average shoal size 3.0 fish across all other treatments), although this result was only marginally significant (Table 2, Fig. 3a, , Online Resource 3). In contrast, the presence of lionfish led to foraging parrotfish taking fewer bites  $\text{min}^{-1}$  than during the control treatment or exposure to any other fish (Table 1, Fig. 2b). This led to a reduction of bites by each foraging fish of ~50% (10.1 bites  $\text{fish}^{-1} \text{min}^{-1}$  in control, grouper, and grunt treatments compared to 5.6 bites  $\text{fish}^{-1} \text{min}^{-1}$  when lionfish were present). Combining these rates with the number of fish actually foraging in each treatment also led to a reduction of overall bite rates of ~50% (7.6 bites  $\text{min}^{-1}$  in control, grouper, and grunt treatments compared to 3.9 bites  $\text{min}^{-1}$  when lionfish were present). The provision of additional shelter had a limited effect on parrotfish behaviour, but when fish shoaled while swimming in open water the shoals were larger when additional shelter was not available (Table 1, Table 2, Fig. 3b). Across all treatments, average shoal size without additional shelter decreased from 2.9 fish to 2.6 fish when additional shelter was available.

## Discussion

Reef fishes are exposed to a range of predators that use strategies such as crypsis, ambush, and pursuit (reviewed by Hixon 1991), although there are few data considering how prey change their behaviour depending on different predator hunting methods. Biological invasions of novel predators provide additional challenges to native prey, and any anti-predator responses may be sub-optimal because of the limited evolutionary history between the invasive predator and the invaded assemblage (Sih et al. 2010). Any examination of the response of Caribbean prey fish to the lionfish invasion inevitably cannot distinguish between their effects as an invasive predator that is relatively unfamiliar to native prey (i.e. being a novel predator) and the effects caused by their hunting style being unlike any other native predator (i.e. having a unique hunting style). Lionfish are stalking predators that use a slow, hovering hunting style with pectoral fins spread out and angled forward, which is unique among Atlantic fishes (Green et al. 2011; Côté et al. 2013). Furthermore, lionfish blow jets of water at their prey, perhaps to confuse or distract prey and increase the probability of capturing and swallowing the prey items head-first (Albins and Lyons 2012), which also appears to be unique among Caribbean predators. In contrast, Nassau grouper is typically an ambush predator, using bursts of speed to catch invertebrates and fishes on reefs or in adjacent soft-bottom habitats (Eggleston et al. 1998). Despite their different hunting modes, both lionfish and grouper represent a clear predation risk to juvenile parrotfish, as parrotfish have been found in the stomachs of both species (Randall 1967; Eggleston et al. 1998; Albins and Hixon 2008; Morris and Akins 2009). Indeed, field observations have documented lionfish feeding on juvenile striped parrotfish on the patch reefs used to collect our experimental fish (Green et al. 2011).

In this study, parrotfish were only exposed to the presence of the predator, rather than actually being hunted, but this was sufficient to induce changes in parrotfish behaviour that may be even stronger in natural habitats with a real risk of predation-induced mortality. These behavioural changes were relatively subtle and only identifiable in some of the observed behaviours, namely time spent hiding, bite rate of foraging fishes, and shoal size. Furthermore, the behavioural response varied with predator identity, which is consistent with the differential behaviour of native gobies (Marsh-Hunkin et al. 2013). Juvenile fishes also have sophisticated abilities to distinguish predators from non-predators (Chivers et al. 2014), and the behaviour of parrotfish

juveniles was indistinguishable from the control when exposed to the non-piscivorous grunt. When the grouper was present, parrotfish spent significantly less time hiding. The reduction in hiding behaviour may be a function of the tendency of striped parrotfish to associate with groups of conspecifics when threatened by a predator, and these groups are formed by non-hiding fish (Wolf 1985; Clifton 1989). Although there was no change in the number of fish foraging, and foraging parrotfish did not shoal more frequently when threatened by grouper, they did tend to form larger shoals. Presumably these larger shoals reflect a larger proportion of foraging fish seeking the anti-predator benefits of being within a group. Irrespective of the reason, the response of parrotfish to the presence of a grouper is likely to have been refined through a long evolutionary history of exposure to native predators.

Parrotfish have a much shorter evolutionary history with lionfish, as the first records of lionfish being present in the study area were in 2005 (Green et al. 2011). However, parrotfish altered their behaviour when lionfish were present by reducing their bite rates, indicating that parrotfish have responded to the novel threat or unique hunting style of this invasive species. Although we cannot assess whether this anti-predator behaviour is more or less effective than the strategy used when exposed to grouper, we suggest it is likely to reduce predation rates by lionfish, given the strong selection pressure exerted by the abundance of lionfish on the reefs of south Eleuthera (Green et al. 2011). However, it may represent the parrotfish incorrectly assigning lower threat levels to lionfish, as seen in gobies (Marsh-Hunkin et al. 2013). Parrotfish typically graze algae in a head-down manner, which is likely to leave them vulnerable to predation. Given the stalking behaviour of hunting lionfish where they move slowly towards the prey item (Albins and Lyons 2012; Côté et al. 2013), increasing vigilance by reducing bite rates may allow parrotfish to continue to forage but still flee when the lionfish gets close enough to strike. Whether this is a novel behaviour used by parrotfish only when lionfish are present, or is also adopted when threatened by other stalking predators, is not known. However, working with another stalking species (trumpetfish, *Aulostomus maculatus*, Valenciennes, 1841), Wolf (1985) demonstrated that their predation threat typically led to striped parrotfish rapidly associating with large groups of conspecifics and ceasing to feed, but bite rates were not measured.

The limited change in parrotfish behaviour when additional shelter was available was surprising, given the strong correlations between the abundance of this species and reef rugosity and the potential benefits of

increased shelter for avoiding predation (Mumby and Wabnitz 2002). The lack of additional shelter did lead to fish forming larger shoals when swimming in open water, as seen in bluegill sunfish (*Lepomis macrochirus*, Rafinesque, 1819) that switch from schooling to dispersed distributions with increasing habitat structure (Crowder and Cooper 1982). Potentially, parrotfish undertaking this risky behaviour felt less threatened when additional refuges from predators were available, and therefore less inclined to seek the anti-predator benefits of being within a group. The tendency of juvenile striped parrotfish to form groups when threatened by native predators (Wolf 1985) may have reduced any further functional importance of refuges within this experiment. Fish did hide in the PVC pipe approximately as frequently as they hid under the algal-covered rock, but the total number of fish hiding did not increase significantly when it was present. It is possible that the rock alone provided sufficient shelter for the four fish when they wanted to hide, and the additional shelter may have been more important for a larger group of parrotfish. Furthermore, all our observations were during the day, and shelter may be functionally more useful at night when parrotfish require sleeping shelters, or during the crepuscular periods when both groupers and lionfish are particularly active (Randall 1967; Green et al. 2011). Similarly, if the predators had actually been hunting the parrotfish the additional refuges may have been important to avoid feeding strikes.

Irrespective of whether the reduced bite rate of parrotfish when lionfish were present was caused by the invasive predator's novelty or hunting mode, this study clearly highlights the potential for a non-consumptive effect between the species. Definitions of non-consumptive effects typically involve demographic consequences for the prey species (Preisser et al. 2005), which we have not demonstrated. However, it is reasonable to assume that a lower bite rate will lower a fish's energy intake and consequently affect growth rate, body condition, or other demographic processes. In contrast, the response of parrotfish when faced with a native predator was to spend less time hiding, but still spend the same amount of time foraging and feeding as when no other fish was present. Furthermore, even if the behavioural response of parrotfish when exposed to lionfish is not unique and is also adopted for other native predators, the high biomass of lionfish on Bahamian reefs (Green and Côté 2009) means that this invasive predator is likely to cause a significant increase in predator-induced reductions in bite rates. Consequently, it is possible that lionfish are driving a trophic cascade by reducing the grazing pressure on reefs and potentially increasing algal cover. The majority of grazing on reefs is typically undertaken by adult parrotfishes, which are less

likely to be directly threatened by lionfish, but their abundance could be reduced both by the slower growth rate of juveniles and lionfish predating on recruits (Albins and Hixon 2008). Fewer parrotfish of all sizes because of the lionfish invasion may be sufficient to affect benthic dynamics (Lesser and Slattery 2011; Albins and Hixon 2013), and this impact may be exacerbated if small parrotfish have lower bite rates when lionfish are present. Further work to understand the effects of lionfish on the behaviours of all parrotfish life phases, and how increased mortality changes parrotfish population dynamics, could potentially demonstrate the full impacts of lionfish on trajectories of coral cover by simulating altered parrotfish grazing rates within models of benthic dynamics (Mumby et al. 2007), and how these effects may be ameliorated by lionfish removals.

Extrapolating from aquarium experiments to reef communities is problematic because in reality both prey and predatory species are embedded within a wider food web of additional predators and competitors. However, the reduction in parrotfish bite rates when threatened by lionfish highlights an additional impact of the invasion, and that more research is warranted on non-consumptive effects throughout reef assemblages. This study also underscores the need to control lionfish abundances as a key aim of Caribbean reef conservation (Côté et al. 2013).

**Conflict of Interest:** The authors declare that they have no conflict of interest.

## References

- Abrams PA (2007) Defining and measuring the impact of dynamic traits on interspecific interactions. *Ecology* 88:2555-2562
- Albins MA (2015) Invasive Pacific lionfish *Pterois volitans* reduce abundance and species richness of native Bahamian coral-reef fishes. *Mar Ecol Prog Ser* 522:231-243
- 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, Hixon MA (2013) Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environ Biol Fishes* 96:1151-1157
- 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
- Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc R Soc B* 276:3019-3025
- Birrell CL, McCook LJ, Willis BL, Diaz-Pulido GA (2008) Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. *Oceanogr Mar Biol Ann Rev* 46:25-63
- Chivers DP, McCormick MI, Mitchell MD, Ramasamy RA, Ferrari MCO (2014) Background level of risk determines how prey categorize predators and non-predators. *Proc R Soc B* 281
- Clifton KE (1989) Territory sharing by the Caribbean striped parrotfish, *Scarus iserti*: patterns of resource abundance, group size and behaviour. *Anim Behav* 37:90-103

- Côté IM, Green SJ, Hixon MA (2013) Predatory fish invaders: Insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. *Biol Cons* 164:50-61
- Crawley MJ (2007) *The R Book*. John Wiley & Sons Ltd, Chichester, England
- Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802-1813
- Eggleston DB, Grover JJ, Lipcius RN (1998) Ontogenetic diet shifts in Nassau grouper: trophic linkages and predatory impact. *Bull Mar Sci* 63:111-126
- Green SJ, Akins JL, Côté IM (2011) Foraging behaviour and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. *Mar Ecol Prog Ser* 433:159-167
- Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. *PLoS ONE* 7:e32596. doi:10.1371/journal.pone.0032596
- Green SJ, Côté IM (2009) Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs* 28:107
- Hixon MA (1991) Predation as a process structuring coral reef fish communities. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press Limited, London, pp 475-508
- Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol Monogr* 63:77-101
- Kindinger TL (2015) Behavioral response of native Atlantic territorial three spot damselfish (*Stegastes planifrons*) toward invasive Pacific red lionfish (*Pterois volitans*). *Environ Biol Fishes* 98:487-498
- Layman CA, Jud ZR, Nichols P (2014) Lionfish alter benthic invertebrate assemblages in patch habitats of a subtropical estuary. *Mar Biol* 161:2179-2182
- Leahy SM, McCormick MI, Mitchell MD, Ferrari MCO (2011) To fear or to feed: the effects of turbidity on perception of risk by a marine fish. *Biol Lett* 7:811-813
- Lesser MP, Slattery M (2011) Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. *Biol Invasions* 13:1855-1868
- Lönstedt OM, McCormick MI (2011) Chemical alarm cues inform prey of predation threat: the importance of ontogeny and concentration in a coral reef fish. *Anim Behav* 82:213-218
- Madin EMP, Gaines SD, Warner RR (2010) Field evidence for pervasive indirect effects of fishing on prey foraging behavior. *Ecology* 91:3563-3571
- Madin EMP, Madin JS, Booth DJ (2011) Landscape of fear visible from space. *Sci Rep* 1:14; DOI:10.1038/srep00014
- Manassa RP, McCormick MI, Chivers DP, Ferrari MCO (2013) Social learning of predators in the dark: understanding the role of visual, chemical and mechanical information. *Proc R Soc B* 280:20130720
- Marsh-Hunkin KE, Gochfeld DJ, Slattery M (2013) Antipredator responses to invasive lionfish, *Pterois volitans*: interspecific differences in cue utilization by two coral reef gobies. *Mar Biol* 160:1029-1040
- Morris JA, Akins JL (2009) Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environ Biol Fishes* 86:389-398
- Mumby PJ (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecol Appl* 16:747-769
- Mumby PJ, Hastings A, Edwards HJ (2007) Thresholds and the resilience of Caribbean coral reefs. *Nature* 450:98-101
- Mumby PJ, Wabnitz CCC (2002) Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. *Environ Biol Fishes* 63:265-279
- Overholtzer KL, Motta PJ (1999) Comparative resource use by juvenile parrotfishes in the Florida Keys. *Mar Ecol Prog Ser* 177:177-187
- Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501-509
- R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria
- Randall JE (1967) Food habitats of reef fishes of the West Indies. *Stud Trop Oceanogr* 5:665-847
- Rizzari JR, Frisch AJ, Hoey AS, McCormick MI (2014) Not worth the risk: apex predators suppress herbivory on coral reefs. *Oikos* 123:829-836
- Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage JS, Vonesh JR (2010) Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos* 119:610-621

- Stallings CD (2008) Indirect effects of an exploited predator on recruitment of coral-reef fishes. *Ecology* 89:2090-2095
- White JW, Samhouri JF, Stier AC, Wormald CL, Hamilton SL, Sandin SA (2010) Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observational scale. *Ecology* 91:1949-1961
- Wolf NG (1985) Odd fish abandon mixed-species groups when threatened. *Behav Ecol Sociobiol* 17:47-52

**Table 1** Minimal adequate linear mixed-effects models (fixed effects only) for behaviours of *Scarus iseri* when exposed to different predators and additional shelter. Results for predator identity are shown as comparisons to the control data (i.e. negative coefficients indicate a reduction in that behaviour compared to the control). Values are model coefficients with *P*-values in parentheses. ×: interaction term. ns: non-significant term ( $P>0.050$ )

Factor	Behaviour				
	Hiding	In open	Foraging	Interactions	Bite rate
<b>Intercept</b>	0.554 ( $<0.001$ )	16.417 (0.004)	0.610 ( $<0.001$ )	0.573 ( $<0.001$ )	2.266 ( $<0.001$ )
<b>Predator identity</b>	Grouper: -0.368 (0.017) Grunt: -0.249 (0.090) Lionfish: -0.051 (0.723)	ns	ns	ns	Grouper: -0.139 (0.581) Grunt: -0.015 (0.951) Lionfish: -0.688 (0.008)
<b>Shelter availability</b>	ns	ns	ns	ns	ns
<b>Predator × Shelter</b>	ns	ns	ns	ns	ns

**Table 2** Minimal adequate linear mixed-effects models (fixed effects only) for shoaling behaviour of *Scarus iseri* when exposed to different predators and additional shelter. Results for predator identity are comparisons to the control data (i.e. negative coefficients indicate a reduction in that behaviour compared to the control). Results for shelter availability are comparisons to no additional shelter. Values are model coefficients with *P*-values in parentheses. ×: interaction term. ns: non-significant term (*P*>0.050)

Factor	Probability of shoal formation		Number of fish in shoal when formed	
	Foraging	In open water	Foraging	In open water
<b>Intercept</b>	0.450 (<0.001)	0.138 (0.001)	2.901 (<0.001)	2.903 (<0.001)
<b>Predator identity</b>	ns	ns	Grouper: 0.271 (0.061) Grunt: 0.182 (0.192) Lionfish: 0.098 (0.478)	ns
<b>Shelter availability</b>	ns	ns	ns	Additional shelter: -0.294 (0.019)
<b>Predator × Shelter</b>	ns	ns	ns	ns

## Figure legends

**Fig. 1** Overhead view of parrotfish within the mesh cage, demonstrating different behaviours. A: swimming in open water; B: foraging on the algal-covered rock; C: hiding under the rock. Inset: hiding in the artificial shelter (D). The two foraging fish (B) are within a body length of each other and thus considered a shoal

**Fig. 2** Median, minimum, and maximum values, along with 25th and 75th percentiles, of a) the number of fish hiding (of 4) and b) bite rates of foraging fish when exposed to no predator (control), a non-predator (grunt), and native and invasive predators (grouper and lionfish respectively). + = mean value. Data were pooled across replicate parrotfish groups and for treatments where additional shelter was absent and present. Different letters indicate significant differences among means ( $P < 0.05$ )

**Fig. 3** Median, minimum, and maximum values, along with 25th and 75th percentiles, of a) the number of fish in a shoal of foraging fish when exposed to no predator (control), a non-predator (grunt), and native and invasive predators (grouper and lionfish respectively) and b) the number of fish in a shoal of fish in open water when additional shelter was absent and present. Maximum shoal size = 4 in both panels. + = mean value. Data were pooled across replicate parrotfish groups and for a) treatments where additional shelter was absent and present and b) for exposure to different fish species. Different letters indicate significant differences among means ( $P < 0.05$ ). Parentheses indicate marginal significance ( $P < 0.065$ )