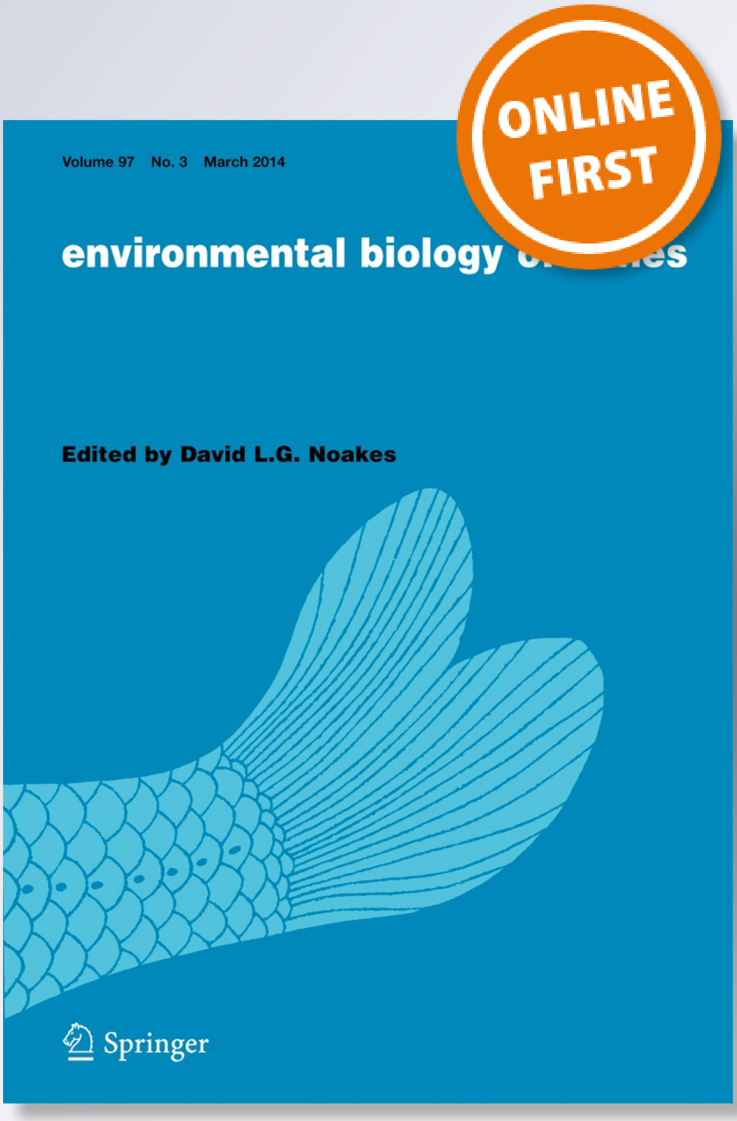
Competitive interactions for shelter between invasive Pacific red lionfish and native Nassau grouper

Wendel W. Raymond, Mark A. Albins & Timothy J. Pusack

Environmental Biology of Fishes

ISSN 0378-1909

Environ Biol Fish
DOI 10.1007/s10641-014-0236-9



Springer

Environ Biol Fish
DOI 10.1007/s10641-014-0236-9

Competitive interactions for shelter between invasive Pacific red lionfish and native Nassau grouper

Wendel W. Raymond · Mark A. Albins ·
Timothy J. Pusack

Received: 12 September 2013 / Accepted: 14 January 2014

Abstract The invasive Pacific red lionfish (*Pterois volitans*) poses a threat to western Atlantic and Caribbean coral reef systems. Lionfish are small-bodied predators that can reduce the abundance and diversity of native fishes via predation. Additionally, native predators or competitors appear to have a negligible effect on similarly sized lionfish. Nassau grouper (*Epinephelus striatus*) are a regionally endangered, large predator found throughout lionfish's invasive range. Because lionfish and Nassau grouper occupy similar habitats and use similar resources, there is potential for competition between these two species. Using large, outdoor in-ground tanks, we investigated how lionfish and Nassau grouper affect each other's behavior by comparing their distance from and use of shelter when in isolation versus when both species were in the presence of each other with limited shelter. We found that Nassau grouper, which displayed a high affinity for shelter in isolation, avoided lionfish in two distinct ways; (1) groupers positioned closer to and used limited shelter more when paired with similarly sized lionfish and (2) grouper moved much further away from shelter when paired with smaller lionfish. We also found that neither large lionfish nor large Nassau grouper preyed upon smaller individuals of the opposite species suggesting that Nassau grouper do not recognize small lionfish as prey. This study highlights how invasive lionfish may affect native Nassau grouper, and suggests that competition for shelter between these two species may be size dependent.

Keywords Avoidance · Bahamas · Refuge · Shelter dominance · Size dependence

Introduction

Marine biological invasions are increasingly common and result in many negative effects on native systems (Ruiz et al. 1997). Most marine invaders are invertebrates; however, invasions of marine fishes can have drastic ecological effects (Helfman 2007). The invasion of Pacific red lionfish (*Pterois volitans*, Linnaeus, 1758) is arguably the most serious marine fish invasion to date, and its effects on native fish communities via direct predation have already been well documented (e.g. Albins and Hixon 2008; Albins 2013). However, there has been little research on non-predatory interactions between invasive lionfish and native fish species. In the present study we focus on the potential competitive interactions between invasive lionfish and native Nassau grouper (*Epinephelus striatus*, Bloch, 1792) for limited shelter space.

W. W. Raymond · M. A. Albins · T. J. Pusack
Department of Zoology, Oregon State University,
3029 Cordley Hall, Corvallis, OR 97331-9214, USA

Present Address:
W. W. Raymond (✉)
Friday Harbor Laboratories, University of Washington,
620 University Road, Friday Harbor, WA 98250, USA
e-mail: wraymond@u.washington.edu

Present Address:
M. A. Albins
School of Fisheries Aquaculture and Aquatic Sciences,
Auburn University,
8300 State Highway 104, Fairhope, AL 36532, USA

Lionfish were first recorded in Atlantic waters in the mid-1980s, and were likely introduced via aquarium releases or escapes (Morris and Whitfield 2009). Currently, their established range includes the southeastern seaboard of the United States, the Gulf of Mexico, the Caribbean, and much of the tropical and sub-tropical Western Atlantic (Schofield 2009, 2010). Lionfish are predicted to continue to expand southward along the east coast of South America (Morris and Whitfield 2009; Luiz et al. 2013). Throughout the invaded range, lionfish are found in diverse habitats, including coral and rocky reefs (Whitfield et al. 2007), seagrass beds (Claydon et al. 2012), mangrove forests (Barbour et al. 2010; Claydon et al. 2012), estuaries (Claydon et al. 2012; Jud and Layman 2012), and mesophotic reefs (Lesser and Slattery 2011). Local populations of invasive lionfish exhibit exponential population growth (Albins and Hixon 2011; Claydon et al. 2008) and occur at far greater densities than lionfish in their native range (Green and Côté 2009; Kulbicki et al. 2012). Given their broad invasive range and high densities, lionfish have the potential to interact with a wide variety of species across many different habitats (Côté et al. 2013).

Invasive lionfish have severe direct effects on native species, which may cause cascading indirect effects (Albins and Hixon 2011). They are known to consume at least 41 native fish species in 21 families (Albins and Hixon 2008; Morris and Akins 2009; Valdez-Moreno et al. 2012). Moreover, lionfish in the Bahamas directly reduce the number of small reef-fishes on patch reefs by up to 93 % over short time periods (Albins and Hixon 2008; Albins 2013), and may reduce prey biomass by up to 65 % (Green et al. 2012). This reduction in small reef-fish abundance can be up to 2.6 times the reduction due to a native mesopredator, the coney grouper (*Cephalophous fulva*, Linnaeus, 1758) (Albins 2013). Additionally, lionfish predation on parrotfishes may indirectly increase algal growth, leading to decreased coral cover, and possibly trophic cascades (Albins and Hixon 2011). This potential shift to algal dominated habitats may already have occurred in mesophotic communities (Lesser and Slattery 2011).

While previous studies have examined interactions between invasive lionfish and native prey (Albins and Hixon 2008; Green et al. 2012; Albins 2013) and between lionfish and native mesopredators (Albins 2013), interactions between lionfish and larger coral-reef predators remain relatively understudied. Juvenile specimens of large-bodied grouper species have been found in the stomach contents of lionfish (Morris and Akins 2009), and anecdotal reports have found lionfish in the guts of two species of large native groupers (Maljković et al. 2008). Thus, intraguild predation may occur between lionfish and other native predators. In addition to predation, lionfish may also interact with large native predators via competition for shared resources, such as food and shelter. Shelter space is an important, potentially limiting resource for coral-reef fishes (reviewed by Hixon 1991). Field experiments show that shelter/refuge space can limit the local abundance of reef fishes (e.g. Hixon and Beets 1993) and can affect patterns of mortality in reef fishes (e.g. Forrester and Steele 2004). However, there has been little research concerning competition for shelter between native and invasive marine fishes.

Competition for shelter is often size dependent and most research examining competition for shelter in marine and freshwater fishes has indicated that larger individuals are dominant (e.g. O'Niell and Cobb 1979; Shulman 1985; Buchheim and Hixon 1992; Figler et al. 1999; Vorburger and Ribi 1999; Nakata and Goshima 2003). However, competitive interactions can shift as the size of competitors change through their respective life spans (e.g. Sebens 1982; Wootton 1994; Donahue 2004). In an invaded ecosystem it is likely that native species will encounter varying size classes of the invader and therefore size-dependent relationships may exist. Considering the documented patterns of competitive interactions between fishes it is critical to investigate varying size combinations of native and invasive species as a possible factor in competitive interactions. However, in at least one study of competition between native and invasive freshwater fishes, invaders outcompeted natives for shelter regardless of size (Van Kessel et al. 2011).

A large bodied native predator that could potentially compete with lionfish for shelter space is the Nassau grouper. Despite being severely overfished and regionally endangered throughout most of the greater Caribbean region (Cornish and Eklund 2003), Nassau grouper are relatively common in the Bahamas and are of high ecological and economic importance (Sadovy and Eklund 1999). Nassau grouper are known to behave aggressively towards conspecifics as well as other species (Sadovy and Eklund 1999; Stallings 2008). Furthermore, the presence of Nassau grouper has been shown to have negative effects on the growth rate of native mesopredators, such as small groupers (Stallings

2008). Juvenile Nassau grouper, between 12 and 50 cm total length (TL), tend to inhabit small patch reefs and rocky coral outcroppings and are known to use reef holes for shelter (Beets and Hixon 1994; Eggleston 1995; Sadovy and Eklund 1999). Invasive lionfish tend to inhabit similar habitats and also use reef holes for shelter (Schultz 1986; Whitfield et al. 2007). Due to this overlap in habitat preference, shelter use, large populations of lionfish around our study site, lionfish and Nassau grouper have the potential to compete for shelter. Furthermore, Nassau groupers as well as other large Caribbean reef predators have been a logical potential source of biological control of the lionfish invasion. Reports of lionfish in the guts of large groupers (Maljković et al. 2008) offer some support for this hypothesis but there is little other research regarding predation on invasive lionfish. However, to date there has been no direct documentation of grouper predation on lionfish in the wild.

The objective of this study was to investigate whether invasive lionfish compete with Nassau grouper for limited habitat space. Following the general consensus in the literature, we hypothesized that competitive interactions will follow the trend that larger individuals will dominate, regardless of native or invasive status. We used relative distance from shelter and shelter use as metrics to monitor lionfish and Nassau grouper behavior, when in isolation and when sharing a space together. The distance measure provided us with data to indirectly investigate the potential for competition between Nassau grouper and invasive lionfish, and the proportion of shelter use data allowed us to test for direct competition. Because previous studies found that individual size can play an important role in competitive interactions, (e.g. Buchheim and Hixon 1992; Donahue 2004) we examined these interactions for different size combinations of the two species. By virtue of size discrepancies in two of our treatments we also assessed whether larger individuals of each species would consume smaller individuals of the other species.

Methods

Study area and collections

Our study was conducted during the summer of 2010 at the Perry Institute for Marine Science (PIMS) on Lee Stocking Island, Bahamas where lionfish were first reported in 2005 (Albins and Hixon 2008). SCUBA divers used nets to collect lionfish and Nassau groupers from surrounding shallow reefs (2–10 m depth). The TL of each fish was recorded, and the fish were transported in coolers with seawater to PIMS, where they were held separately (by species) in 100 cm wide × 100 cm long × 43 cm high cages submerged in large, outdoor, flow-through seawater tanks.

Experimental design

We conducted all experimental trials in mesh cages measuring 86 cm wide × 258 cm long × 43 cm high. Two removable partitions divided these cages into three equal 86 cm wide × 86 cm long × 43 cm high areas to allow for both isolation and interaction periods in each trial (Fig. 1). We constructed shelters by placing two 20 × 20 × 20 cm cinder blocks end-to-end, creating one continuous hole measuring 15 × 15 × 40 cm open at both ends. We placed one of these shelters into each partitioned area of each experimental cage. The cages were submerged in a large in-ground tank, measuring approximately 10 m long × 7 m wide × 1 m deep, with continuous flow-through seawater.

We ran multiple trials using one of three size-ratio treatments: (1) similarly sized fish (1:1 size ratio of lionfish:grouper—hereafter referred to as L:G), (2) juvenile lionfish and substantially larger juvenile grouper (1:4 size ratio of lionfish:grouper—hereafter referred to as smL:lgG), and (3) adult lionfish and much smaller juvenile grouper (3:1 size ratio of lionfish:grouper—hereafter referred to as lgL:smG) to examine lionfish-grouper interactions. Size ratios were within ±0.1 of the target ratio. We completed 9 L:G trials with lionfish ranging in size from 7.7 to 31.7 cm TL and Nassau grouper ranging in size from 8.3 to 34.1 cm TL (L:G size-ratios ranged from 0.92 to 1.10). We also completed 8 smL:lgG trials with lionfish ranging in size from 5.6 to 12.3 cm TL and Nassau grouper ranging in size from 18.4 to 42.1 cm TL (smL:lgG size-ratios ranged from 0.18 to 0.30). Due to the difficulty of locating and collecting small Nassau grouper, and to repeated escapes of small Nassau groupers from cages, we were unable to complete a sufficient number of lgL:smG trials to produce meaningful statistical inferences for shelter competition. However, we were able to evaluate whether large lionfish consumed small Nassau grouper. To avoid experimental fish becoming familiar with the experimental cage set up we used different individuals for each replicate.

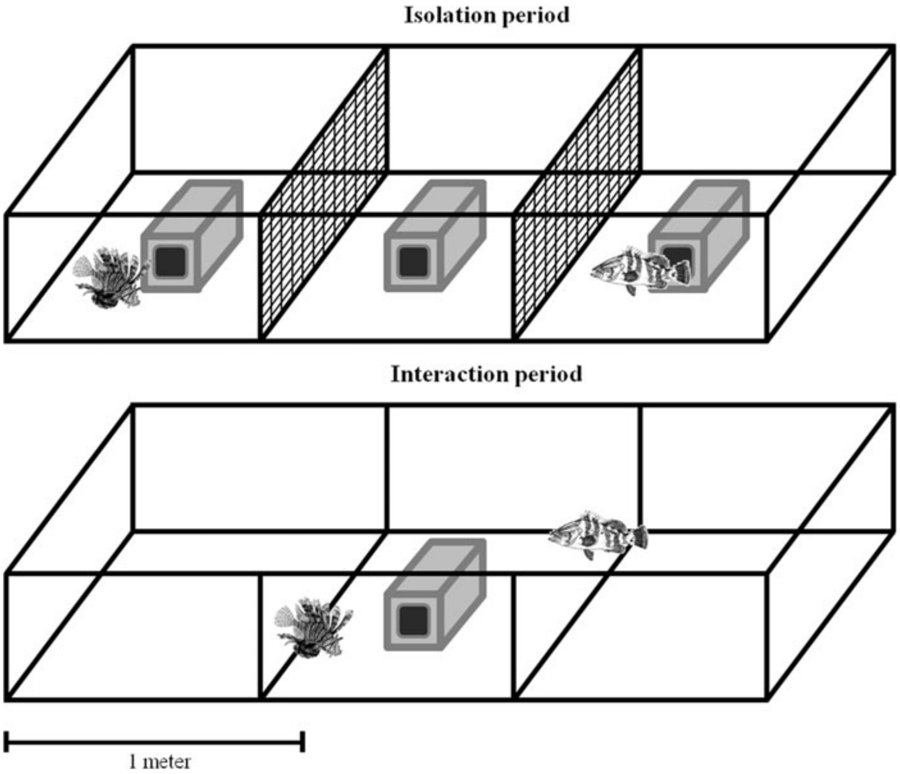


Fig. 1 Configuration of experimental cages. Isolation period shows partitions (*checkerboard patterned areas*) in place and each partition with its own shelter (*small grey box*). Interaction period shows partitions removed and one, centrally located shelter. Lionfish image from http://www.inkart.net/illustration/wildlife/red_lionfish/and Nassau grouper image from Sadovy and Eklund (1999)

Each trial consisted of a 24-h isolation period and 48-h interaction period. During the isolation period, one lionfish and one Nassau grouper were physically separated from one another in opposite ends of the partitioned cage (Fig. 1). During this time, the position of each fish in the cage area was recorded three times a day: once in the morning, between the times of 07:00–08:00, once during early afternoon, between the times of 12:30–13:30, and once in the evening, between the times of 18:30–19:30. After the 24-h isolation period, the partitions and outer shelter blocks were removed. This left the two fish to occupy the same space with a single shelter during the interaction period (Fig. 1). At the beginning of the interaction period, we observed the fish for the first 20 min, recorded their movements around the enclosure, and recorded any visible interactions between the two species such as aggressive posturing or chasing. Thereafter, occupation of the shelter, distance between each fish and the shelter, and any behavioral interactions between the fishes, were recorded three times a day as in the isolation period. We used distance from and occupation of the shelter as our metrics to evaluate changes in positioning from isolation to interaction periods. This allowed us to indirectly assess any competitive interaction between the two species for limited shelter. To reduce observer effects, observers approached the cages slowly with minimal movement and remained at least 3 m away from the experimental cages.

To test for predation between lionfish and Nassau grouper, we had to ensure that the larger specimen of each species would eat while in the cages. Therefore, we introduced an alternative small (<10 cm TL) prey fish, a slippery dick wrasse (*Halichoeres bivittatus*, Bloch, 1791), into the cage for each of the lgL:smG and smL:lgG trials after the completion of the 48 h interaction period. This test was conducted for all six attempts of the lgL:smG trials, and for seven of the 8 smL:lgG trials.

Statistical analysis

To test for evidence of a change in distance from shelter between isolation to interaction periods for lionfish and

Nassau grouper, we first needed to determine whether fish were spending time closer to (or further from) shelter than would be expected by chance during the initial isolation period. We could then do the same for the interaction period and compare the results to determine whether presence of the potential competitor resulted in a shift in positioning relative to shelter. For each species, we compared the average observed distance to the shelter to a distribution of mean distances calculated from simulated data. Due to the different sizes and shapes of the isolation and interaction arenas we were unable to directly compare observations between isolation and interaction periods. Additionally, we assumed that the error distribution of the distance from shelter metric would be constrained substantially by the arena size and shape and would therefore not be easy to approximate using standard distributions. We overcame this limitation by comparing observed distances to the distribution of mean distances generated from random draws.

Using the *R* statistical environment (R Core Team 2012), data were simulated using random draws from a uniform distribution for both x and y coordinates within the cage. The mean distance of the corresponding positions to the central shelter was then calculated. This process was repeated 5,000 times for both isolation and interaction arenas for each trial type. Since the null mean distance from the shelter was calculated for both cage dimensions (isolation and interaction) it allowed us to control for change in total size of the experimental cage. This gave us a distribution of expected mean distances from the shelter given random positioning with respect to shelter. The numbers of simulated positions used to create these means were based on the numbers of actual trials conducted for that particular type (9 positions for L:G; 8 positions for smL:lgG).

Comparison of the observed mean distances for each fish to the distribution of means from the simulated data allowed us to generate two-sided p-values representing the probability—under the null hypothesis of random positioning with respect to shelter—of observing distances as extreme or more extreme than those observed for each species in each trial type during both isolation and interaction periods of the trials. If the average observed distance to shelter was less than the mean distance from the simulations, with a p-value<0.025, then we concluded that the species spent more time closer to the shelter than would be expected by chance. We used a 0.025 p-value cutoff as evidence of a position differing from random because we also wanted to account for the possibility that a fish could also have been further away from the shelter than would be expected by chance. This approach created a two-tailed distribution with our total cutoff for the null hypothesis of random positioning at $\alpha=0.05$.

To test for a change in shelter use we compared proportion of sampling times that each species was using the shelter (fish was inside or resting on top of the shelter) or not (fish was elsewhere in the cage, not inside or on top of the shelter) between isolation and interaction periods. We used a Pearsons's Chi-squared test with a Yates continuity correction in the *R* statistical environment (R Core Team 2012) to identify if each species had changed its proportion of shelter use from isolation to interaction.

Results

Distance from limited shelter

During the isolation period of the smL:lgG trials, the average (± SEM) distance of lionfish from the shelter was 6.10±3.12 cm and the average distance of Nassau grouper from the shelter in the isolation period was 6.20±6.10 cm. Results of the randomization test demonstrated that both lionfish and Nassau grouper were closer to the shelter during the isolation period than would be expected by chance ($p=0.004$ and $p=0.005$ respectively, Fig. 2). During the interaction period in these trials, the average distance of lionfish from the shelter was 2.10±13.16 cm and the average distance of Nassau grouper from the shelter was 45.60±16.70 cm. Results of the randomization test indicated that lionfish continued to spend time closer to the shelter than would be expected by chance ($p=0.002$), but on average, Nassau grouper changed their position and shifted further away from the shelter in the presence of lionfish ($p=0.393$, Fig. 2).

During the isolation period of the L:G trials, the average (± SEM) distance of lionfish from the shelter was 12.70±3.56 cm and the average distance of Nassau grouper was 5.16±4.52 cm. During the interaction period, the average distance of lionfish from shelter was 44.20±14.43 cm and the average distance of Nassau grouper from the shelter was 29.49±15.57 cm. The distance between lionfish and the shelter was not different from the null expectation in either the

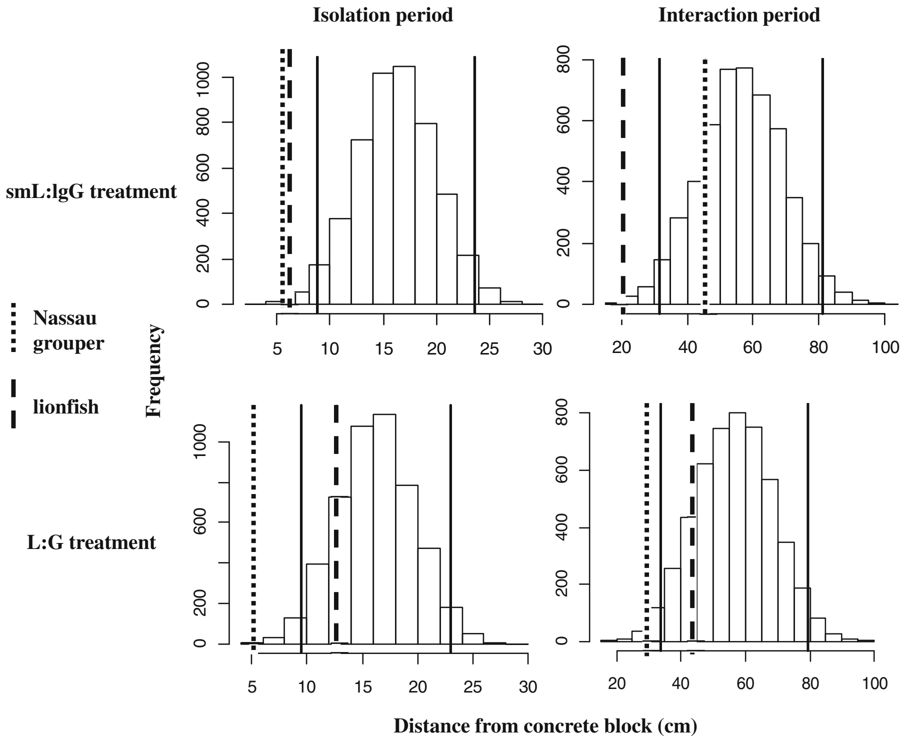


Fig. 2 Distribution of random mean distances from the shelter generated from the computer simulation of random positions within an experimental cage. The y-axis measures frequency of random mean distances, and the x-axis is distance from the shelter in centimeters. The range of distances between each set of *solid lines* are distances that would not be considered any closer to or further from shelter than expected at random at $\alpha=0.05$. *Dotted lines* indicate mean Nassau grouper distance from the shelter and *dashed lines* indicate mean lionfish distance from the shelter for both the isolation period,when each species was alone, and the interaction period, when the species were together. *Top row* is the treatment comparing smaller lionfish to larger grouper (smL:lgG) and the *bottom row* is the treatment comparing lionfish and grouper of approximately the same sizes (L:G)

isolation ($p=0.332$) or interaction ($p=0.274$) periods, while the distance between Nassau grouper and the shelter was closer than would be expected by chance during both the isolation ($p<0.001$) and interaction ($p=0.018$) periods (Fig. 2).

Shelter use

In the smL:lgG treatment lionfish and Nassau grouper did not change the amount of time they used the shelter ($p=0.531$ and $p=0.160$, respectively). However, Nassau grouper slightly decreased the proportion of time that they used the shelter from 58 to 43 % of the time. In the L:G treatment lionfish did not change the proportion of time that they used the shelter between the isolation, 22 %, and the interaction period, 16 %, ($p=0.605$). However, Nassau grouper did change the proportion of time they used the shelter, from 16 % of the time in isolation to 63 % of the time during the interaction period ($p<0.001$, Table 1).

Predation and behavioral observations

Several times during the interaction period of smL:lgG trials we observed a Nassau grouper move from inside the cinder block shelter to outside the shelter as the smaller lionfish swam in. We did not observe any predation between large lionfish and small Nassau grouper, or between large Nassau grouper and small lionfish. We observed no obvious aggressive interactions between lionfish and Nassau grouper during the L:G trials. This was true during the initial 20 min of the interaction period and all observation times during the interaction period. However, in 7 out of 8 smL:lgG trials and in all 6 of the lgL:smG trails, the alternative prey fish was consumed by the large experimental predator in the trial.

Table 1 Number of observations that an individual fish using or not using shelter in both experimental periods. The *p*-values are calculated from a Pearson's Chi-squared test with Yates continuity correction

Species	Period	Using shelter	Not using shelter	*p*-value
L:G treatment				
Lionfish	Isolation	8	28	0.6051
	Interaction	10	53	
Nassau grouper	Isolation	6	30	<0.001
	Interaction	40	23	
smL:G treatment				
Lionfish	Isolation	18	18	0.5313
	Interaction	33	23	
Nassau grouper	Isolation	21	15	0.1604
	Interaction	23	33	

Discussion

Our findings suggest that Nassau grouper display avoidance behavior towards lionfish in two different ways. First, when Nassau grouper interact with much smaller lionfish (smL:lgG treatment) Nassau grouper avoid lionfish by moving further away from shelter occupied by a small lionfish and by using shelter slightly less. However, since our distance analyses support lionfish shelter dominance but our proportion analyses do not, these findings do not completely support that small lionfish outcompete much larger Nassau grouper for limited shelter. Second, when Nassau grouper interact with similarly sized lionfish (L:G treatment) Nassau grouper avoid lionfish by increasing their proportion of shelter use, avoiding the part of the experimental cage where lionfish were consistently present. In the sml:lgG treatment, Nassau grouper changed their pattern of positioning and shelter use when interacting with lionfish. Conversely, lionfish did not change their pattern of positioning and shelter use when interacting with Nassau grouper. We found that in both treatments Nassau grouper changed their positioning relative to shelter in the presence of lionfish and that lionfish did not change their positioning when interacting with Nassau grouper. These results indicate that Nassau grouper and lionfish may compete for limited shelter and that the manner in which Nassau groupers avoid lionfish is size dependent.

Lionfish and Nassau grouper shelter use and positioning also differed between treatments. In the L:G treatment, lionfish were not close to the shelter and were not observed using the shelter very often in both isolation and interaction periods, while in the smL:lgG treatment they did the opposite. In the smL:lgG treatment, lionfish displayed high affinity for shelter in both isolation and interaction periods. This may be due to much smaller size of lionfish in the smL:lgG treatment than the L:G treatment. Small lionfish may have a higher affinity to shelter than large lionfish. Nassau grouper also differed in their shelter use between treatments. This may be an explained by the different sizes of lionfish in the treatments. Nassau grouper responded differently to the two size pairings of lionfish, further supporting a size dependent interaction. It is interesting to note that Nassau grouper did not change their proportion of shelter use in the smL:lgG treatment, indicating that Nassau groupers were not completely excluded from shelter and still may occasionally use shelter when small lionfish are present.

Avoidance behavior is a documented form of competitive dominance in marine fishes (e.g. Hixon 1980). Our study indicates that Nassau grouper display this behavior towards lionfish at two size pairings. In previous studies of fishes competing for shelter, larger individuals usually dominate smaller ones (e.g. O'Niell and Cobb 1979; Shulman 1985; Buchheim and Hixon 1992; Figler et al. 1999; Vorburger and Ribi 1999; Nakata and Goshima 2003), however our results were not consistent with this hypothesis. Our study suggests that the native Nassau grouper may be avoiding the invasive lionfish by either seeking shelter more often from similarly sized lionfish or by vacating limited shelter when interacting with a small lionfish.

In terms of strict shelter competition, our results are consistent with other studies of competition between native and invasive species. In fresh water, an invasive goby has been documented as competitively dominant and displaced the native goby from its preferred habitat type (Van Kessel et al. 2011). Our study also indicates that the invader displays competitive dominance, via avoidance behavior by the native species when the invader is smaller and of similarly size to the native competitor. Over time competitive displacement could lead to invasive lionfish becoming the dominant predator on invaded reefs instead of the large bodied native predator the Nassau grouper. Such a shift in the dominant predators could lead to trophic effects throughout the invaded range. This scenario, described in Albins and Hixon (2011), could contribute to the overall decline of coral reef ecosystems. Lionfish exert negative pressure on an apex predator (through shelter competition), and on native mesopredators and herbivores (through predation) leading to algal dominated communities, which smother corals.

Some reports have suggested that Nassau grouper and other groupers may provide a natural biological control for the lionfish invasion through competition and/or predation (Mumby et al. 2011). Reports of grouper caught in the Bahamas with lionfish in their guts (Maljković et al. 2008) are encouraging but appear to be rare events. To date there is no direct evidence that groupers seek out lionfish as prey. Furthermore, while Mumby et al. (2011) suggests that native groupers, which maintain relatively high biomass within a large Bahamian marine reserve, may have some negative effect on invasive lionfish, this study did not adequately account for lionfish culling within the reserve. Alternatively, Hackerott et al. (2013) found no relationship between the density or biomass of lionfish and that of native predators in the Caribbean. Since Nassau grouper in our study did not eat much smaller lionfish, we suggest that Nassau grouper do not recognize small lionfish as prey. Furthermore, our findings suggest that Nassau grouper may not be an effective biological control via either competition for shelter or predation and that lionfish appear to add an additional stressor to Nassau grouper populations, which have already been reduced substantially by heavy fishing pressure (Sadovy and Eklund 1999; Cornish and Eklund 2003; Stallings 2008).

The differing results in positioning and shelter use of invasive lionfish and native Nassau grouper between the L:G and smL:lgG treatments suggests a size dependent avoidance by Nassau grouper. Nassau grouper either stayed away from limited shelter when in the presence of lionfish (smL:lgG treatment) or stayed close to limited shelter (L:G treatment). While our study suggests Nassau grouper avoided lionfish and by extension shelter when large Nassau grouper are in the presence of much smaller lionfish, competition for shelter itself was not apparent when lionfish and Nassau grouper were similar in size. Evidence of competition for shelter between small lionfish and large Nassau grouper also suggests that, as the abundance of lionfish increases, there will be a loss of habitat for Nassau grouper. However, our study only investigated one-on-one competitive interactions. The effect of locally high densities of lionfish or Nassau groupers may alter the interactions we detected in our outdoor tanks. Our findings should be further examined in the field; focusing on persistence and survivorship of both Nassau groupers and lionfish, as well as other native mesopredators, in both one-on-one settings and at different relative densities. Such studies would elucidate the interactions between a threatening invader and an iconic native species in their natural setting.

Acknowledgments We thank the staff and interns of the Perry Institute for Marine Science at Lee Stocking Island, Bahamas for their help and logistical support. We thank S. Hixon and K. Ingemen for their expert cage building skills and assistance in setting-up the experiment, collecting data, and enduring hundreds of mosquito bites. We also thank M.A. Hixon, M. Errend, and A. Lowe for their constructive comments in the preparation of this manuscript. All fish handling procedures were approved by IACUC though Oregon State University. This study was funded by NSF research grants 08–51162 and 12–33027 awarded to M.A. Hixon, an NSF Graduate Research Fellowship awarded to M. Albins and an Oregon State University Undergraduate Research, Innovation, Scholarship & Creativity (URISC) grant awarded to W. Raymond.

References

Albins MA (2013) Effects of invasive Pacific red lionfish *Pterois volitans* vs. a native predator on Bahamian coral-reef fish communities. Biol Invasions 15:29–43

Albins M, Hixon M (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 (2011) Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. Enviro Biol Fish. doi:10.1007/s10641-011-9795-1

Barbour AB, Montgomery ML, Adamson AA, Díaz-Ferguson E, Silliman BR (2010) Mangrove use by the invasive lionfish *Pterois volitans*. Mar Ecol: Prog Ser 401:291–294

Beets J, Hixon MA (1994) Distribution, persistence, and growth of groupers (Pisces: Serranidae) on artificial and natural patch reefs in the Virgin Islands. B Mar Sci 55:470–483

Buchheim JR, Hixon MA (1992) Competition for shelter holes in coral-reef fish *Acanthemblemaria spinosa* Metzelaar. J Exp Mar Biol Ecol 164:45–52

Claydon JAB, Calosso MC, Jacob SE (2008) The red lionfish invasion of South Caicos, Turks & Caicos Islands. Proc Gulf Coast Fish Inst 61:400–402

Claydon JAB, Calosso MC, Traiger SB (2012) Progression of invasive lionfish in seagrass, mangrove and reef habitats. Mar Ecol: Prog Ser 448:119–129

Cornish A, Eklund AM (2003) Epinephelus striatus. In: IUCN 2013. IUCN Red list of threatened species. Version 2013.2. <www.iucnredlist.org>. Downloaded on 05 December 2013

Côté IM, Greene SJ, Hixon MA (2013) Predatory fish invaders: Insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. Biol Conserv 164:50–61

Donahue MJ (2004) Size-dependent competition in a gregarious porcelain crab *Petrolisthes cinctipes* (Anomura: Porcellanidae). Mar Ecol: Prog Ser 267:219–231

Eggleston DB (1995) Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. Mar Ecol: Prog Ser 124:9–22

Figler MH, Cheverton HM, Blank GS (1999) Shelter competition in juvenile red swamp crayfish *Procambarus clarkii*: the influences of sex differences, relative size, and prior residence. Aquaculture 178:63–75

Forrester GE, Steele MA (2004) Predator, prey refuges and the spatial scaling of density-dependent prey mortality. Ecology 85:1332–1342

Green SJ, Côté IM (2009) Record densities of Indo-Pacific on Bahamian coral reefs. Coral Reefs 28:107

Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. PLoS ONE 7:3

Hackerott S, Valdivia A, Greene SJ, Côté IM, Cox CE, Akins L, Layman CA, Precht WF, Bruno JF (2013) Native predators do not influence invasion success of Pacific lionfish on Caribbean reefs. PloS ONE. doi:10.1371/journal.pone.0068259

Helfman GS (2007) Fish Conservation, A guide to understanding and restoring global aquatic biodiversity and fishery resources. Island Press, Washington DC

Hixon MA (1980) Competitive interactions between California reef fishes of the genuis *Embiotoca*. Ecology 61:918–931

Hixon MA (1991) Predation as a process structuring coral reef fish communities. The Ecology of Fishes on Coral Reefs. pp 475–508

Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish. Ecol Monogr 63:77–101

Jud ZR, Layman CA (2012) Site fidelity and movement patterns of lionfish, *Pterois* spp., in a Florida estuary. J Exp Mar Biol Ecol 79:198–178

Kulbicki M, Beets J, Chabanet P, Cure K et al (2012) Distributions of Indo-Pacific lionfishes *Pterois* spp. in their native ranges: implications for the Atlantic invasion. Mar Ecol: Prog Ser 446:189–205

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

Luiz OJ, Floeter SR, Rocha LA, Ferreira CEL (2013) Perspectives for the lionfish invasion in the South Atlantic: Are Brazilian reefs protected by currents? Mar Ecol: Prog Ser 485:1–7

Maljković A, Van Leeuwen TE, Cove SN (2008) Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. Coral Reefs 27:501–501

Morris JA, Akins JL (2009) Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. Enviro Biol Fishes 86:389–398

Morris JA, Whitfield PE (2009) Biology, ecology, control and management of the invasive Indo-Pacific Lionfish: An updated integrated assessment. NOAA Technical Memorandum NOS NCCOS 99

Mumby PJ, Harborne AR, Brumbaugh DR (2011) Grouper as a natural biocontrol of invasive lionfish. PloS ONE 6:1–4

Nakata K, Goshima N (2003) Competition for shelter of preferred sizes between the native crayfish species *Cambaroides japonicus* and the alien crayfish species *Pacifastacus leniusculus* in Japan in relation to prior residence, sex difference, and body size. J Crus Biol 23:897–907

O'Niell DJ, Cobb JS (1979) Some factors influencing the outcome of shelter competition in lobsters (*Homarus americanus*). Mar Behav Physiol 6:33–45

R Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2012 URL http://www.R-project.org. ISBN 3-900051-07-0

Ruiz G, Carlton J, Grosholz E, Hines A (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. Am Zool 632:621–632

Sadovy Y, Eklund A (1999) Synopsis of biological data on the nassau grouper, Epinephelus striatus (Bloch, 1792), and the Jewfish, E. itajara (Lichtenstein, 1822). FAO Fisheries Synopsis

Schofield PJ (2009) Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitan*s [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. Aquat Invasions 4:473–479

Schofield PJ (2010) Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) in the Western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. Aquat Invasions 5: S117–S122

Schultz ET (1986) *Pterois volitans* and *Pterois miles*: Two valid species. Copeia 1986:686–690

Sebens KP (1982) Competition for space: growth rate, reproductive output, and escape in size. Am Nat 120:189–197

Shulman MJ (1985) Coral reef fish assemblages: intra- and interspecific competition for shelter sites. Env Biol Fish 13:81–92

Stallings CD (2008) Indirect effects of an exploited predator on recruitment of coral-reef fishes. Ecology 89:2090–2095

Valdez-Moreno M, Quintal-Lizama C, Gómez-Lozano R, García-Rivas MDC (2012) Monitoring an alien invasion: DNA barcoding and the identification of lionfish and their prey on coral reefs of the Mexican Caribbean. PloS One. doi:10.1371/journal.pone.0036636

Van Kessel N, Dorenbosch M, De Boer MRM, Leuven RSEW, Van Der Velde G (2011) Competition for shelter between four invasive gobiids and two native benthic fish species. Curr Zool 57:844–851

Vorburger C, Ribi G (1999) Aggression and competition for shelter between a native and an introduced crayfish in Europe. Freshw Biol 42:111–119

Whitfield PE, Hare JA, David AW, Harter SL, Munoz RC, Addison CM (2007) Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the Western North Atlantic. Biol Invasions 9:53–64

Wootton JT (1994) Size-dependent competition: effects on the dynamics Vs. The end point of mussel bed succession. Ecology 74:195–206