

Consumptive and non-consumptive effects of an invasive marine predator on native coral-reef herbivores

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Abstract Invasive predators typically have larger effects on native prey populations than native predators, yet the potential roles of their consumptive versus non-consumptive effects (CEs vs. NCEs) in structuring invaded systems remains unclear. Invasive lionfish (*Pterois volitans*) may have ecosystem-level effects by altering native fish grazing on benthic algae that could otherwise displace corals. Lionfish could reduce grazing by decreasing the abundance of herbivorous fishes (CEs), and/or the predation risk posed by lionfish could alter grazing behavior of fishes (NCEs). To test for these CEs, we manipulated lionfish densities on large reefs in The Bahamas and surveyed fish populations throughout June 2009–2011. In July 2011, NCEs of lionfish were measured by observing

fish grazing behavior on algal-covered substrata placed in microhabitats varying in lionfish presence at different spatial scales, and quantifying any resulting algal loss. Lionfish reduced small herbivorous fish density by the end of the 2010 summer recruitment season. Grazing by small and large fishes was reduced on high-lionfish-density reefs, and small fish grazing further decreased when in the immediate presence of lionfish within-reefs. Lionfish had a negative indirect effect on algal loss, with 66–80 % less algae removed from substrata in high-lionfish-density reefs. Parrotfishes were likely driving the response of herbivorous fishes to both CEs and NCEs of lionfish. These results demonstrate the importance of considering NCEs in addition to CEs of invasive predators when assessing the effects of invasions.

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Introduction

Predators can affect prey population dynamics both through direct consumption (i.e., consumptive effects [CEs]; Taylor 1984; Sih et al. 1985; Murdoch et al. 2013) and alteration of prey behavior, morphology, or life history traits (i.e., non-consumptive effects [NCEs]; Peacor and Werner 1997; Lima 1998). NCEs

are induced when prey are faced with a tradeoff between predation risk and activities such as resource acquisition, habitat use and movement, or mating (Dill 1987; Lima and Dill 1990; Sih and Wooster 1994), and are generally as strong, or stronger than, CEs on prey demography (Peacor and Werner 2001; Preisser et al. 2005). Invasive predators typically have effects on native prey populations that are larger than the effects of native predators (Salo et al. 2007; Paolucci et al. 2013), yet the role of CEs versus NCEs of invasive predators in structuring invaded communities and ecosystems remains unclear.

Negative impacts of invasive predators are most commonly attributed to CEs (Ruiz et al. 1999; Strayer et al. 2006), because these predators often cause large declines in native species (Grosholz 2002; Snyder and Evans 2006; Pitt and Witmer 2007; Cucherousset and Olden 2011; Gallardo et al. 2016) that can even reach local or global extinction (Clavero and García-Berthou 2005; Medina et al. 2011; Pringle 2011; Woinarski et al. 2015). However, the prevalence and importance of NCEs of these predators are seldom considered. The existence of NCEs hinges on the ability of prey to both perceive and respond to predation risk (Lima and Steury 2005; Berger 2010). Therefore, a lack of evolutionary history between native prey and invasive predators reduces the expectation of NCEs (Sih et al. 2010). Studies that fail to corroborate the existence of such NCEs (e.g. Pearl et al. 2003; Smith et al. 2008; Gomez-Mestre and Díaz-Paniagua 2011) typically infer that native prey are naïve (*sensu* Diamond and Case 1986; Cox and Lima 2006; Banks and Dickman 2007) toward the novel predator. However, a growing number of studies illustrate the importance of considering NCEs in addition to the CEs of invasive predators in order to accurately assess both the acute and chronic effects of invasions. For example, Freeman and Byers (2006) demonstrated that an invasive crab induces the defense mechanism of shell thickening in a native mussel in regions of New England where the predator has invaded. And, some native species of freshwater zooplankton exhibit shifts in vertical distribution in the presence of an invasive predatory cladoceran (Bourdeau et al. 2011).

The ongoing invasion of Western Atlantic and Caribbean coral reefs by Pacific red lionfish (*Pterois volitans*; Schofield 2009, 2010) constitutes one of the rare occurrences of a successful invasion by a marine

fish (Côté et al. 2013a), which has been recognized as a major conservation issue in a global assessment (Sutherland et al. 2010). Lionfish are novel predators in the Atlantic both in their appearance (coloration and morphology) and use of unique hunting strategies, including herding prey with widely-fanned pectoral fins (Côté and Maljković 2010; Green et al. 2011; Cure et al. 2012) and blowing directed jets of water at prey (Albins and Lyons 2012). Lionfish are generalist predators that hunt (Côté and Maljković 2010; Green et al. 2011; Cure et al. 2012) and consume (Morris and Akins 2009; Muñoz et al. 2011; Côté et al. 2013b) a variety of small native fishes at high rates (Albins and Hixon 2008; Côté and Maljković 2010), that can cause large reductions in native fish abundance and richness on smaller patch reefs (Albins and Hixon 2008; Albins 2013; Green et al. 2014; Benkwitt 2015) and large coral reefs (Albins 2015).

While the CEs of invasive lionfish on small native fishes have been well-documented, few studies have considered the potential role of their NCEs on a broader size range of fishes. Without considering these potential NCEs, the documented effects of invasive lionfish on native systems could be greatly underestimated. Albins and Hixon (2013) postulated invasive lionfish could have ecosystem-level effects on invaded coral reefs similar to those caused by overfishing of native parrotfishes and other herbivores (Mumby et al. 2006; Mumby and Steneck 2008), whereby a reduction in grazing of algae indirectly enhances the ability of algae to outcompete and/or interfere with corals. Invasive lionfish could reduce native fish grazing on reefs by depleting the abundance of grazers (CEs). Small herbivorous fishes have frequently been found in the stomachs of invasive lionfish (e.g. Morris and Akins 2009; Côté and Maljković 2010; Layman and Allgeier 2012; Côté et al. 2013b), including parrotfishes which are the dominant grazers on Caribbean coral reefs (Carpenter 1986; Steneck 1994). Large parrotfish are especially effective at removing noticeable quantities of algae from reefs (Mumby et al. 2006), and the grazing behavior of these individuals (in addition to smaller, prey-sized fishes) could potentially be influenced by the predation risk posed by invasive lionfish (NCEs). Therefore, we tested for both CEs and NCEs of invasive lionfish on this important ecosystem function of native herbivorous fishes for maintaining coral-dominated reefs.

Methods

We selected 10 large (1400–4000 m²), isolated coral reefs located on the Great Bahama Bank near Lee Stocking Island, Bahamas, which ranged in depth from 2 to 11 m and were paired by similarity in habitat. We estimated reef area using the software, Image J, to calculate the area of hard substrate per reef from satellite images obtained with Google Earth. In June 2009, we performed baseline surveys of the fish community at each reef using SCUBA (survey methods below), and then manipulated invasive lionfish densities as part of a long-term experiment (see Albins 2015 for further reef descriptions and methodological details). We haphazardly assigned reefs in each pair to low- or high-lionfish-density treatments. Lionfish were removed from low-lionfish-density reefs using hand nets and pole spears, and we released live lionfish onto high-lionfish-density reefs. Artificially augmented lionfish densities were never greater than the highest baseline density (0.43 lionfish/m²) observed across the system prior to manipulation. Every 3–5 months thereafter, a pair of SCUBA divers maintained lionfish treatments at all experimental reefs.

Reef fish surveys and analyses

Visual surveys of reef fishes were conducted by a pair of SCUBA divers throughout (seafloor to surface) two permanent square plots (10 × 10 m) and four permanent strip transects (2 × 25 m), for a total area of 400 m² per reef (see Albins 2015 for detailed description). We positioned square plots to include areas of the reef with the highest apparent relief, and strip transects were placed randomly across the remaining hard substrate, with the intent of including all important high-relief habitat features. Divers conducted censuses of each sampling unit whereby each fish was identified to the species-level and total length (TL) was visually estimated to the nearest cm. Paired reefs (low- and high-lionfish-densities) were surveyed within 24 h by the same set of observers, and all reefs were surveyed by the author (M. Albins). Every 3–5 months thereafter, we resurveyed the fish community at all experimental reefs.

We quantified CEs of invasive lionfish on native herbivorous fish populations throughout the 2-year experiment by comparing the change in density and

biomass of small and large herbivorous fishes between lionfish-density treatments. *Small* fish were ≤ 10 cm TL, which encompasses the majority of prey fish sizes reported in invasive lionfish gut-content studies for the size range of lionfish (2–35 cm TL) observed on our experimental reefs (Morris and Akins 2009; Muñoz et al. 2011). Responses of fish >10 cm TL were consistent, regardless of whether individuals were binned into medium (11–20 cm TL) and large (>20 cm TL) size classes, so hereafter we refer to all fish >10 cm TL as *large*. To determine the relative response of different subguilds of herbivorous fishes, we also calculated the change in small and large fish density and biomass by fish family: (1) *parrotfishes* (Labridae); (2) *surgeonfishes* (Acanthuridae); (3) *angelfishes* (Pomacanthidae); and (4) *damselishes* (Pomacentridae). We used published length-weight conversions to calculate fish biomass; parameters of closely related species were used when conversions were not available (Online Resource 1). We calculated changes in fish density and biomass at every survey interval by subtracting the baseline value (prior to initial lionfish manipulation) for each sub-sample (plots and transects) from the corresponding value of each subsequent survey.

To test for an effect of invasive lionfish through time on changes in density and/or biomass of each group of native fishes (described above), we fitted linear mixed effects models (LMMs) with *lionfish-density* treatment and *time* as categorical fixed effects, and *sub-sample* nested within *reef* as random effects (Pinheiro and Bates 2000; Bolker et al. 2009; Zuur et al. 2009). *Time* was a categorical variable because we had no a priori reason to assume any linear relationships with response variables. Full models included weighted terms allowing variances to differ among reefs and AR1 covariance structures to account for temporal autocorrelation (Zuur et al. 2009). We fitted full and reduced models (with vs. without weighted terms and/or AR1 structures) using restricted maximum likelihood (REML) and compared full and reduced models using Akaike's Information Criterion (AIC) and likelihood ratio tests (LRTs, Online Resource 2). Visual examination of residuals of the best-fit models indicated that the assumptions of normality, homogeneity, and independence were all met.

To assess the significance of fixed effects, we refit each model using maximum likelihood estimation

(ML) and applied LRTs (Zuur et al. 2009). Fixed effects that were not significant were sequentially dropped from models. The resulting best-fit models in terms of variance structure, temporal correlation, and fixed effects were refit using REML in order to estimate the fixed-effects parameters and associated effect sizes. If LRTs indicated the *lionfish* \times *time* interaction was significant, we made simultaneous inferences about the marginal effects of the lionfish treatment at each survey period, and adjusted the associated *p* values to maintain an approximately 5 % family-wise error rate (Hothorn et al. 2008).

Regardless of whether the *lionfish* \times *time* interaction was significant, we estimated expected values and standard error of the means (SEMs) for all response variables from low- and high-lionfish-density treatments during each survey period. We also fit LMMs to compare the baseline levels of each response variable between lionfish-density treatments using a similar procedure to the one outlined above, but with density and biomass of each group of small and large fishes (described above) as the response (rather than the change in these variables). Additionally, we fit LMMs to assess whether small (≤ 10 cm) and large (> 10 cm) native *mesopredators* (Online Resource 1) that are potentially ecologically-similar to invasive lionfish differed between the reefs assigned to each lionfish-density treatment at the baseline survey (mesopredator density and biomass) and at each subsequent survey period (change in mesopredator density and biomass).

Fish grazing surveys and analyses

To quantify NCEs of invasive lionfish on native herbivores, we observed the grazing behavior of herbivorous fishes at each of the 10 experimental reefs over 10 consecutive days in July 2011, observing paired reefs on adjacent days. Each day, we collected 20 haphazardly selected pieces of algal-covered coral rubble (0.43–0.94 m² surface area) from a non-experimental reef containing an extensive area of dead *Acropora cervicornis* coral rubble inhabited by a high density of three-spot damselfish (*Stegastes planifrons*). This territorial fish maintains higher standing stocks of farmed palatable seaweeds via interspecific aggression in response to intruding herbivores (Ceccarelli et al. 2001).

Each piece of algal substratum was carefully placed into a plastic bag filled with seawater, photographed

out of water onboard a boat, returned to its plastic bag, and transported in a cooler of seawater to a nearby experimental reef. At high-lionfish-density reefs, we randomly assigned paired substrata to two similar, but separate microhabitats (e.g., next to a coral head, on a ledge, etc.) that differed only in the presence (< 0.25 m away) versus absence (> 3 m away) of lionfish at the time of observation. At low-lionfish-density reefs, we placed algal substrata in paired microhabitats that were similar to those used at high-lionfish-density reefs, except lionfish were always absent during observation. All replicates were therefore placed in types of microhabitats frequented by lionfish, regardless of actual lionfish presence. Overall, we observed grazing of translocated algal-covered substrata at three levels of lionfish presence: (1) low-lionfish-density reef with lionfish absent from the observed microhabitat ($n = 100$); (2) high-lionfish-density reef with lionfish absent from the microhabitat ($n = 50$); and (3) high-lionfish-density reef with lionfish present in the microhabitat ($n = 50$); hereafter referred to as *low-absent*, *high-absent*, and *high-present* treatments, respectively. These treatments were designed to provide insight on the spatial scale at which lionfish presence affects herbivorous fish behavior by allowing simultaneous comparisons of grazing behavior between (1) low- and high-lionfish-densities at the reef-scale while controlling for lionfish presence at the within-reef scale (i.e., low-absent vs. high-absent treatments) and (2) lionfish presence-absence at the within-reef scale while controlling for lionfish density at the reef-scale (i.e., high-absent vs. high-present treatments).

At each experimental reef, we monitored four of the translocated algal substrata—one pair in the morning (0900–1200) and one pair in the afternoon (1400–1600)—for 60 min each using automated underwater video cameras placed approximately 3 m away. Meanwhile, we observed the remaining 16 algal substrata with SCUBA (8 replicates per diver) one at a time for 20 min each, with observations divided evenly throughout the day (2 pairs in the morning and 2 pairs in the afternoon per diver). All observations were therefore performed during the day when the probability of lionfish predation is greatly reduced (Green et al. 2011; Cure et al. 2012) and all lionfish observed were inactive. We identified the species of each fish that visited these substrata, visually estimated its TL to the nearest cm, and counted the

number of times it took a bite of algae. Each fish was considered to be a unique individual once it entered the diver's field of view (approximately 2 m surrounding the focal rock), and continuing until the time it left the field of view and could no longer be visually tracked. At the end of each observation period, the algal substratum was carefully returned to its plastic bag full of fresh seawater and kept underwater until all 20 replicates had been observed. We then rephotographed each replicate onboard the boat.

Grazing behavior observed at each replicate algal substratum was comprised of the following response variables: (1) visitation rate (number of fish/minute); (2) percent visitation rate (percent fish/minute); (3) bite rate (number of bites/minute); and (4) individual bite rate (number of bites per fish/minute). The percent visitation rate and individual bite rate allowed us to account for any potential differences in herbivorous fish densities between low- and high-lionfish-density reefs. Percent visitation rates were calculated by dividing the total number of fish observed grazing (per substratum) by the total number of herbivorous fish counted at each reef during the reef fish surveys conducted just prior (June 2011) to the grazing observations (July 2011). For all the herbivorous fish that grazed on each experimental substrate, the number of bites each fish took during individual grazing bouts was averaged to measure the individual bite rate. We also used the before and after photographs of each substrate to estimate the percent loss of algal cover from observed grazing. We quantified percent cover from photographs using the image processing program, ImageJ.

We analyzed the response of all herbivorous fishes that grazed on the experimental substrate by fish size class (*small* and *large*, with *large* encompassing the response among fishes >10 cm TL, which remained consistent regardless of further size binning into *medium* and *large* size classes). Parrotfishes accounted for 69.2 % of the herbivorous fishes that we observed grazing. Therefore, the behavioral response (same variables as above) of this fish family was also analyzed by fish size class. The remaining fish families (surgeonfishes, angelfishes, and damselfishes) were not further divided by size class, because such extensive division of each response variable would have resulted in highly zero-inflated data. The percent loss of algae from substrata was not analyzed by fish size class nor by fish family, because individual

contributions of each fish to the overall algal loss could not be distinguished.

We fitted LMMs using a similar procedure as the one described above to account for the nested design of the fish grazing surveys when comparing grazing behavior of herbivorous fish among lionfish treatments. Random effects consisted of paired microhabitats nested within paired reefs. In addition to *lionfish* treatment (low-absent, high-absent, and high-present), all full models included the initial algal percent cover (*algae*) of each replicate substratum as a fixed factor in order to account for any influence this parameter could have on grazing behavior, as well as an *algae* \times *lionfish* interaction. With the exception of the model of percent loss in algal cover, we log-transformed all rate response variables and allowed variances to differ among reefs with weighted terms to meet all assumptions of normality, homogeneity, and independence. When lionfish treatment was significant in the model based on LRTs, we performed multiple comparisons of the response at every combination of lionfish treatments using Tukey's Honestly Significant Difference (HSD) method.

All statistical analyses of both reef fish surveys and fish grazing observations were conducted using the statistical software *R* (*R* Core Team 2014) with the associated packages, *nlme* (Pinheiro et al. 2014) and *multcomp* (Hothorn et al. 2008).

Results

Consumptive effects of lionfish on native herbivorous fish populations

Lionfish reduced the density of small but not large herbivorous fishes (Table 1; Fig. 1), and this effect fluctuated over time (*lionfish* \times *time* interaction: LRT $p = 0.002$). While densities of small herbivorous fishes were always lower on high-lionfish-density reefs than low-lionfish-density-reefs (Fig. 1a), this difference was statistically significant only in August 2010 (-0.61 ± 0.17 fish $m^{-2} \pm SEM$, LMM $p_{cor} = 0.014$). Lionfish did not have an effect on the biomass of herbivorous fishes (Table 1). The response of parrotfishes was similar to the overall herbivorous fish community response (Table 1; Fig. 1) in that the density of small parrotfishes was generally lower on high-versus low-lionfish-density reefs, but this difference fluctuated over time (LRT $p = 0.017$, Fig. 1c)

Table 1 Results of hypothesis tests for the effect of lionfish-density-treatment (“lionfish”, *Pterois volitans*) and time on the density and biomass of small (≤ 10 cm TL) and large (> 10 cm

TL) herbivorous fish of all families combined and parrotfishes observed during reef surveys

Group	Size class	Response variable	Fixed effect	LRT p	Survey period	p_{adj}	
All herbivorous fishes	Small	Density	Lionfish \times time	0.002	Aug 2009	0.348	
					Nov 2009	0.593	
					Jan 2010	0.976	
					Jun 2010	0.585	
					Aug 2010	0.014	
					Dec 2010	0.203	
			Jun 2011	0.865			
		Large	Biomass	Lionfish \times time	0.053		
	Lionfish			0.211			
	Time			<0.001			
	Lionfish \times time			0.798			
	Lionfish			0.218			
Time	<0.001						
	Large	Density	Lionfish \times time	0.875			
Lionfish			0.396				
Time			<0.001				
Lionfish \times time			0.875				
Lionfish			0.396				
Time			<0.001				
Parrotfishes (Labridae)	Small	Density	Lionfish \times time	0.017	Aug 2009	0.857	
					Nov 2009	0.999	
					Jan 2010	0.999	
					Jun 2010	0.770	
					Aug 2010	0.048	
					Dec 2010	0.843	
			Jun 2011	0.999			
		Large	Biomass	Lionfish \times time	0.118		
	Lionfish			0.344			
	Time			0.113			
	Lionfish \times time			0.248			
	Lionfish			0.461			
Time	<0.001						
	Large	Density	Lionfish \times time	0.140			
Lionfish			0.662				
Time			<0.001				
Lionfish \times time			0.140				
Lionfish			0.662				
Time			<0.001				

The significance of fixed effects was calculated using likelihood-ratio tests (LRT) comparing nested models fit by Maximum Likelihood Estimation. If there was evidence of a significant interaction (lionfish \times time), p values from linear combinations were adjusted (p_{adj}) to achieve an approximate family-wise error rate of 5 %

with a statistically significant negative effect of lionfish detected only in August 2010 (-0.37 ± 0.14 fish $\text{m}^{-2} \pm \text{SEM}$, LMM $p_{\text{cor}} = 0.048$). Lionfish did not have an effect on the density or biomass of any other individual herbivorous fish families (Online Resource 3).

Throughout the experiment, lionfish densities at high-lionfish-density reefs consistently remained an order of magnitude greater than at low-lionfish-density reefs (mean \pm SEM: 0.031 ± 0.004 and 0.002 ± 0.0009 , respectively). Densities were calculated from lionfish counts conducted prior to lionfish

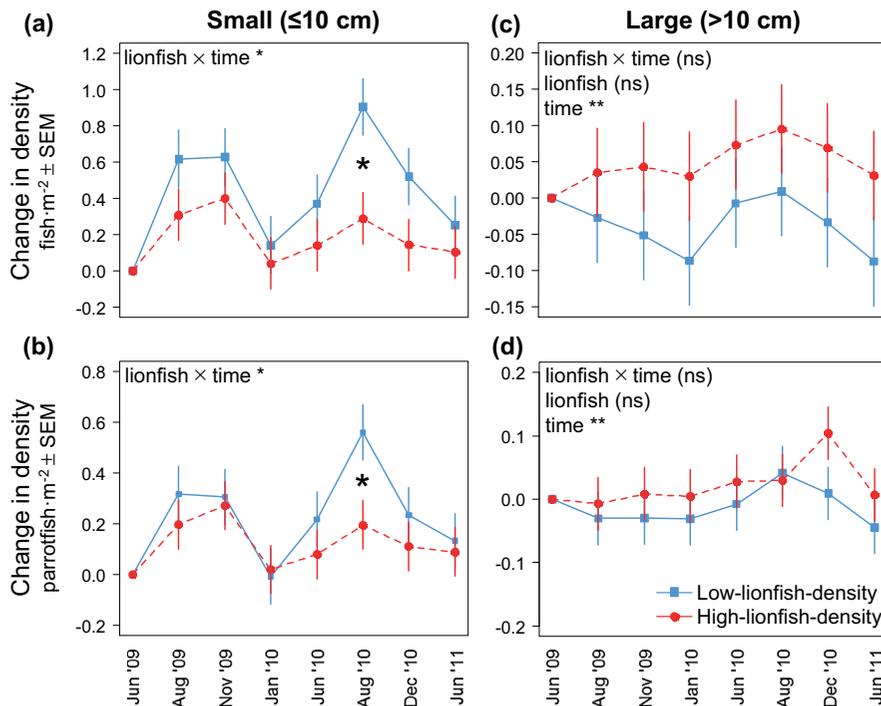


Fig. 1 Change in density of **a, c** small and **b, d** large herbivorous fish of **a, b** all families combined and **c, d** parrotfishes at low- and high-lionfish-density reefs ($n = 5$ reefs each). Means and SEMs were estimated from the full linear mixed effects models with the lionfish \times time interaction term. Results of likelihood ratio tests for the fixed effects are shown at

the *top left* of each plot. When the lionfish \times time interaction was significant, the marginal effects of lionfish treatment were examined at each survey date; adjusted p values to obtain an approximate family-wise error rate of 5 % are indicated for each date. Significance: ns: $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

manipulations performed during each survey period. The density and biomass of both small and large native mesopredators did not significantly differ between paired reefs (Online Resource 3). In addition, the baseline density and biomass of all groups and size classes of herbivorous fishes did not significantly differ prior to lionfish manipulation (Online Resource 4).

Non-consumptive effects of lionfish on grazing by native herbivorous fishes

When all families of herbivorous fishes were pooled, lionfish had a negative effect on both small and large fish grazing behavior in all response variables measured (Table 2). Small herbivorous fishes decreased grazing in response to lionfish at high-lionfish-density reefs (low-absent vs. high-absent and high-present lionfish treatments), and decreased grazing even further in the presence of lionfish at the within-reef scale (high-absent vs. high-present lionfish treatments, Online Resource 5, Fig. 2). Lionfish also caused a decline in large fish

grazing at the between-reef scale that was maintained regardless of lionfish presence within-reefs (Online Resource 5, Fig. 2). The response of both small and large parrotfishes decreased with increasing presence of lionfish, yet lionfish caused a reduction in all response variables (Table 2) that significantly differed only at the between-reef scale (Online Resource 5, Fig. 3). In addition to lionfish treatment, the amount of available *algae* affected the individual bite rates of large herbivorous fishes and large parrotfishes (Table 2), with increases of 0.98 ± 0.01 and 0.97 ± 0.01 bites fish⁻¹ - min⁻¹, respectively, with each percent increase in initial algal cover.

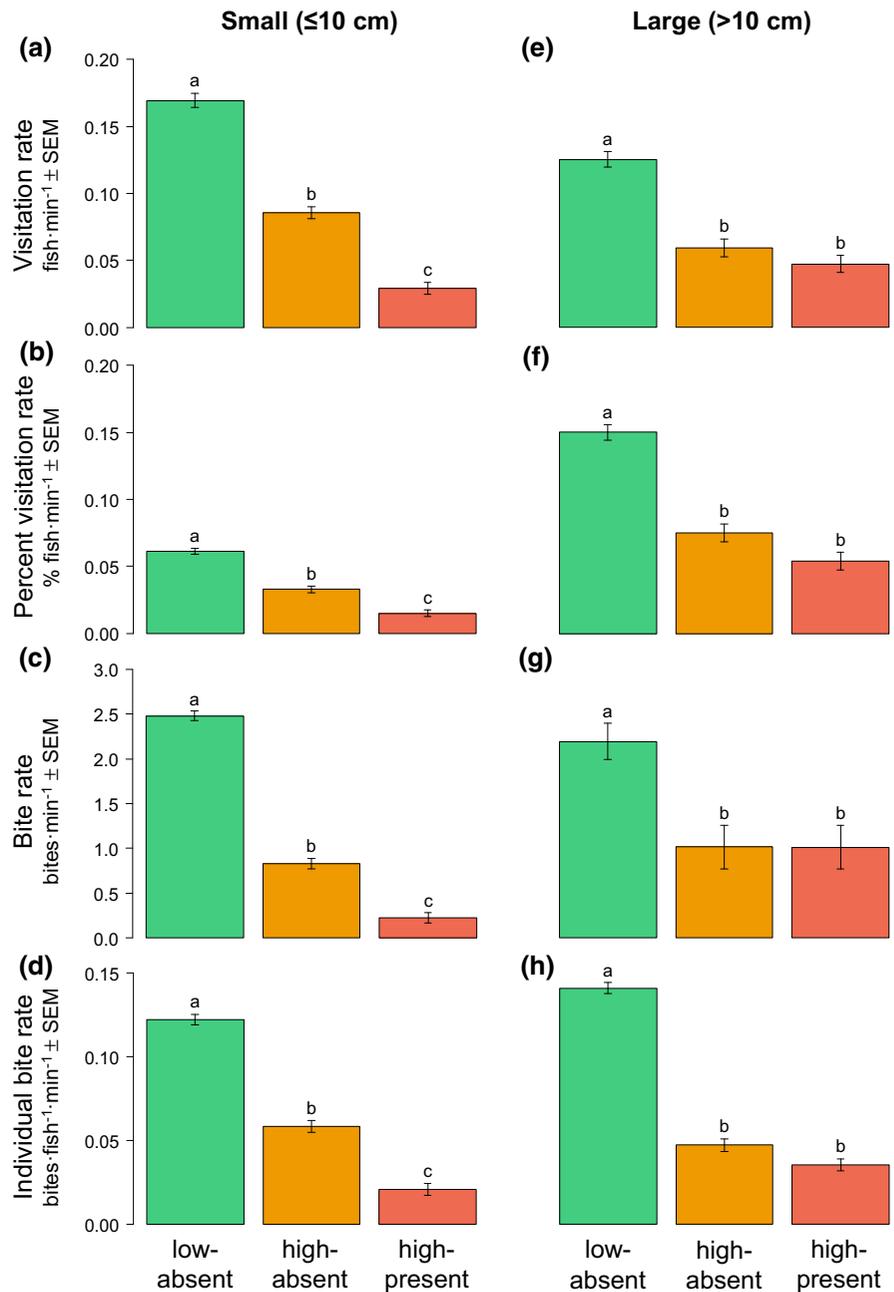
There was a positive relationship between the initial algal percent cover of substrata and the loss of algae from observed fish grazing that varied by lionfish treatment at the between-reef scale (*algae* \times *lionfish* interaction: LRT $p = 0.002$, Fig. 4). On low-lionfish-density reefs, the amount of algae removed from substrata (*algal loss*) increased by 0.56 ± 0.08 % per percent increase in initial algal cover. This

Table 2 Results of hypothesis tests for the effect of lionfish treatment (“lionfish”) and initial algal percent cover (“algae”) on response variables of small (≤ 10 cm TL) and large (> 10 cm TL) size classes of all herbivorous fish families combined and parrotfishes observed during grazing surveys

Group	Size class	Response variable	Fixed effect	LRT <i>p</i>
All herbivorous fishes	Small	Visitation rate	Algae \times lionfish	0.641
			Algae	0.411
			Lionfish	<0.001
		Percent	Algae \times lionfish	0.590
			Algae	0.387
			Lionfish	<0.001
		Visitation rate	Algae \times lionfish	0.585
			Algae	0.348
			Lionfish	<0.001
		Bite rate	Algae \times lionfish	0.518
			Algae	0.698
			Lionfish	<0.001
	Large	Visitation rate	Algae \times lionfish	0.591
			Algae	0.994
			Lionfish	<0.001
		Percent	Algae \times lionfish	0.442
			Algae	0.840
			Lionfish	<0.001
		Visitation rate	Algae \times lionfish	0.530
			Algae	0.240
			Lionfish	<0.001
		Bite rate	Algae \times lionfish	0.441
			Algae	0.042
			Lionfish	<0.001
Parrotfishes (Labridae)	Small	Visitation rate	Algae \times lionfish	0.811
			Algae	0.796
			Lionfish	<0.001
		Percent	Algae \times lionfish	0.892
			Algae	0.789
			Lionfish	<0.001
	Large	Bite rate	Algae \times lionfish	0.957
			Algae	0.911
			Lionfish	<0.001
		Visitation rate	Algae \times lionfish	0.953
			Algae	0.994
			Lionfish	<0.001
Large	Visitation rate	Algae \times lionfish	0.581	
		Algae	0.367	
		Lionfish	<0.001	
	Percent	Algae \times lionfish	0.599	
		Algae	0.408	
		Lionfish	<0.001	
Large	Bite rate	Algae \times lionfish	0.516	
		Algae	0.135	
		Lionfish	<0.001	
	Visitation rate	Algae \times lionfish	0.220	
		Algae	0.002	
		Lionfish	<0.001	

The significance of fixed effects was calculated using likelihood-ratio tests (LRT) comparing nested models fit by Maximum Likelihood Estimation

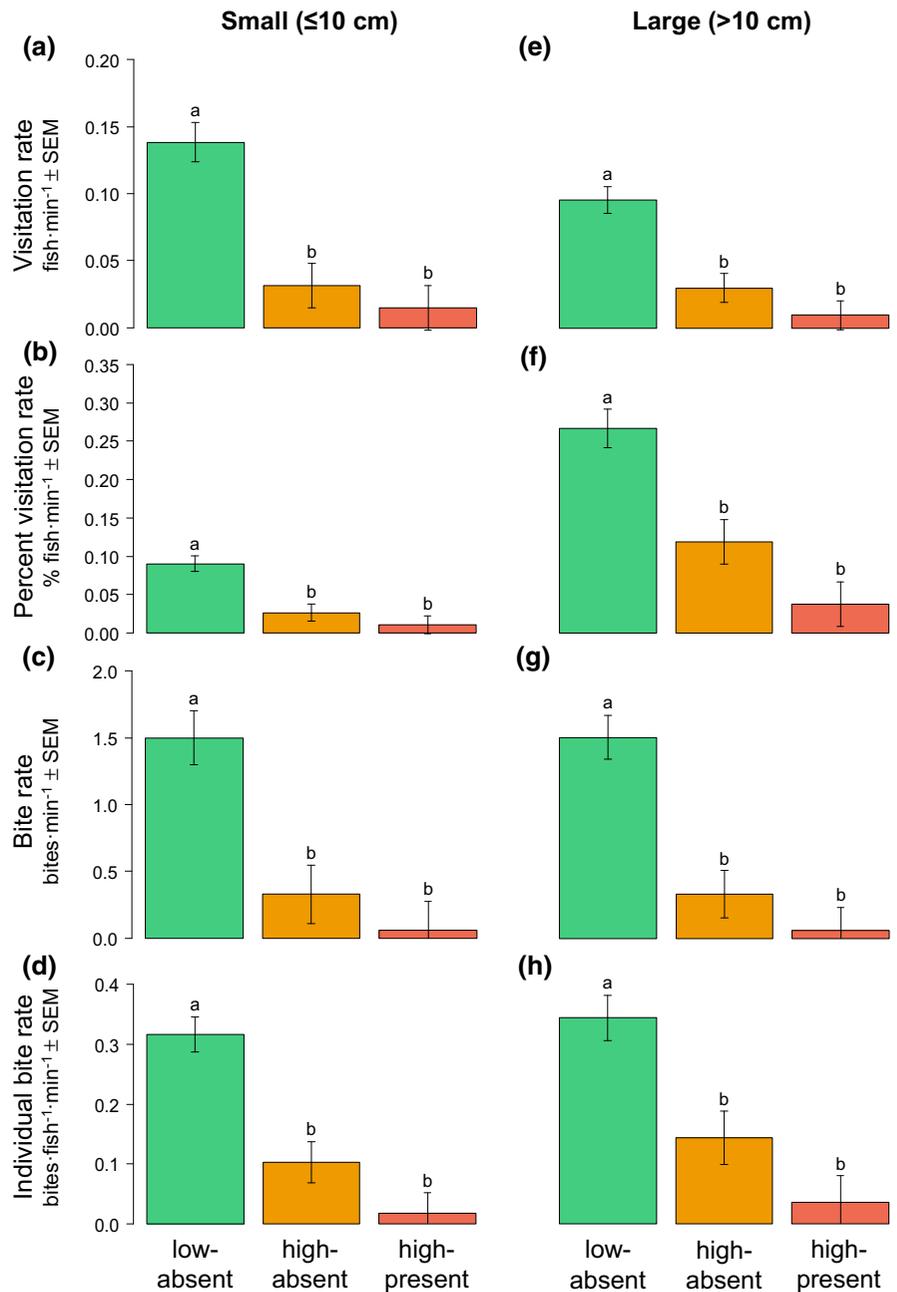
Fig. 2 Response of **a, c, e, g** small and **b, d, f, h** large herbivorous fishes of all families combined observed during grazing surveys in each lionfish treatment: low-absent ($n = 100$), high-absent ($n = 50$), and high-present ($n = 50$). Estimated mean values and SEMs were calculated from the final nested models fit by Restricted Maximum Likelihood. Letters within each plot indicate significant differences in response among lionfish treatments from the final models, with matching letters signifying a p value > 0.05



relationship was significantly diminished on high-lionfish-density reefs (low-absent vs. high-absent lionfish treatments: LMM $p = 0.020$) with 66 % less algae removed from substrata (0.19 ± 0.13 % per percent increase in initial algal cover). 80 % less algae was removed from substrata in high-present (0.11 ± 0.12 % per percent increase in initial algal cover) versus low-absent lionfish treatments, yet this algal loss was not significantly greater than the loss

observed in the high-absent lionfish treatment (LMM $p = 0.615$). While not every species of herbivorous fish identified during the reef fish surveys were observed during the fish grazing surveys (Online Resource 7), the algal-covered substrata we used in this study were still sufficient for capturing substantial grazing behavior on our experimental reefs; over 75 % of the substrata (151 of 200 replicates) were grazed by an herbivorous fish at least once.

Fig. 3 Response of **a, c, e, g** small and **b, d, f, h** large parrotfishes observed during grazing surveys in each lionfish treatment: low-absent ($n = 100$), high-absent ($n = 50$), and high-present ($n = 50$). Estimated mean values and SEMs were calculated from the final nested models fit by Restricted Maximum Likelihood. Letters within each plot indicate significant differences in response among lionfish treatments from the final models, with matching letters signifying a p value > 0.05



Discussion

At this point in the invasion, our study indicates that the CEs of invasive lionfish affect small, but not large native herbivorous fishes, while their NCEs affect both size classes of these native fishes. Parrotfishes (the dominant grazers on Caribbean coral reefs) appeared

to drive the response of the overall herbivorous fish community to both the CEs and NCEs of lionfish.

Over the course of our 2-year study, we observed an expected seasonal trend in small herbivorous fish density, with increases in density occurring throughout the summer months when fish recruitment exceeds mortality, followed by declines in density during the

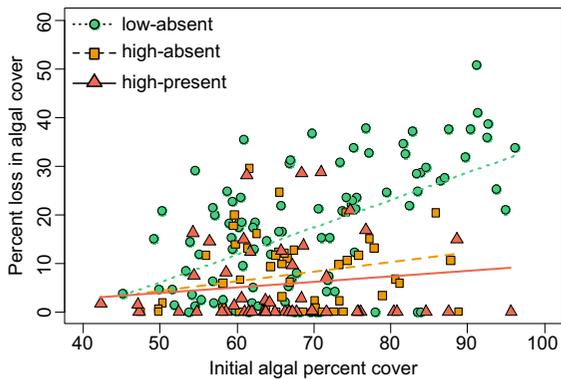


Fig. 4 Percent loss in algal cover due to grazing by herbivorous fishes during grazing surveys as a function of initial algal cover on translocated substrata. The result of a likelihood-ratio test indicated a significant initial algae \times lionfish treatment interaction ($p = 0.002$). Symbols represent the percent algal loss of each substratum observed in low-absent ($n = 100$), high-absent ($n = 50$), and high-present ($n = 50$) lionfish treatments. Corresponding lines for each lionfish treatment were calculated (estimated intercepts and slopes) from the full nested model fit by Restricted Maximum Likelihood

winter months when mortality exceeds recruitment and individuals leave the size class with growth. Changes in density of small herbivorous fishes did not differ through time between low- and high-lionfish-density reefs, with the exception of the end of the 2010 summer recruitment season. These findings are consistent with previous studies which demonstrate invasive lionfish cause reductions of small native fish populations by the end of the summer months (Albins and Hixon 2008; Albins 2013, 2015; Green et al. 2014; Benkwitt 2015). However, this effect of lionfish on herbivorous fishes that we observed was not consistent through time at two scales: the density of small herbivorous fishes no longer significantly differed between low- and high-lionfish-density reefs following August 2010, and having reduced populations of small herbivorous fishes did not result in reduced populations of large herbivorous fishes.

Importantly, while studies to date (including our study) that demonstrate reductions in native fish populations assume that these results occur because of lionfish CEs, lionfish NCEs or a combination of both CEs and NCEs may have also caused such declines in native fishes. Recruitment of coral-reef fishes can be influenced by the presence of predators and/or conspecifics (i.e., priority effects, Shulman et al. 1983; Almany 2003, 2004; Shulman 2015), thus

invasive lionfish may influence the recruitment of native herbivorous fishes on experimental reefs, either directly via their presence as a potential predator and/or indirectly by altering the abundance of conspecifics or other native fishes through time. In addition, the effect of lionfish presence on the foraging behavior of native herbivorous fishes demonstrated in this study likely represent associated costs of antipredator behavior (Peckarsky et al. 1993; Ruxton and Lima 1997; Creel et al. 2007; Pangle et al. 2007), which may have further contributed to the decline of small herbivorous fishes on high-lionfish-density reefs.

Herbivorous fishes decrease grazing behavior in response to predation risk (Madin et al. 2010), resulting in characteristic grazing halos surrounding coral reefs (Randall 1965; Hay et al. 1983; Madin et al. 2011). Despite lionfish being a novel predator, we have shown that the presence of invasive lionfish resulted in NCEs on both small and large herbivorous fishes: fewer fish grazed (visitation rate) and individuals that did graze took fewer bites (individual bite rate), which resulted in an overall decrease in grazing intensity (bite rate). Decreased visitation rates could be explained by lower densities of herbivorous fishes on high-lionfish-density reefs, yet when we accounted for this (percent visitation rate), we still found lower visitation rates. Additional decreases in grazing by small herbivorous fishes (but not large herbivorous fishes) when lionfish were present within-reefs may also suggest that the spatial scale of sensory data used in risk-based decision making likely varies with body size, and/or ontogenetic shifts in response to cues (Ferrari et al. 2010) of a gape-limited predator, whereby the level of perceived risk necessary to warrant a behavioral response may increase with herbivorous fish body size.

Lönstedt and McCormick (2013) demonstrated that a Pacific prey species (*Chromis viridis*) fails to respond to visual and chemical cues of lionfish (*P. volitans*) collected from the native range. Studies to date that document the ability of Atlantic prey to recognize and/or appropriately respond to the presence of invasive lionfish as a potential predator suggest antipredator response may be species-dependent (Marsh-Hunkin et al. 2013; Black et al. 2014; Kindinger 2015; Anton et al. 2016). Our study clearly demonstrates that both juvenile and adult native parrotfishes reduce their grazing activity when in the presence of invasive lionfish, which is consistent with

previous observations of grazing by juveniles of a native parrotfish when in the presence of invasive lionfish in aquaria (Eaton et al. 2016).

Differences in the antipredator responses of prey fishes between the native and invaded ranges of lionfish could be explained by the relative predation pressure of lionfish in each range. Population densities of lionfish are far greater in their invaded range, reaching over 390 fish/hectare versus 26.3 fish/hectare in their native range (Green and Côté 2009; Kulbicki et al. 2012). Therefore, the rate of encounter between lionfish and prey fishes is likely to be much higher on invaded reefs. As a result, the extent that survival outweighs the costs of antipredator behavior in response to lionfish is likely greater among Atlantic prey.

Throughout invaded systems, native prey that experience initial heavy predation by an invasive predator are expected to shift toward adaptive antipredator behavior (Sih et al. 2010). Studies consistently demonstrate that herbivorous fishes (especially parrotfishes) are among the native species on which invasive lionfish have the greatest effects (Albins and Hixon 2008; Albins 2013; Green et al. 2014; Benkwitt 2015), and thus may have an increased likelihood of adapting antipredator response to lionfish relatively sooner than fishes that are less affected. In addition, some herbivorous fishes, such as parrotfishes, often forage in groups (Itzkowitz 1977), which could further facilitate transmission of antipredator response among group individuals via social learning (Mathis and Chivers 2003).

Differences in antipredator behavior among native prey in response to invasive lionfish could also be explained by variance among species in the ability to recognize and respond appropriately to this novel predator. Aquatic prey may use general or specific cues when detecting predators (Petranka et al. 1987; Chivers and Smith 1998; Kats and Dill 1998; Brown 2003). General cues include signals from damaged conspecifics or heterospecifics, or the presence of any novel object larger than a minimum size threshold (Dill 1974; Sih 1986). Prey that rely upon general cues are more likely to exhibit an antipredator response to a novel predator (Sih et al. 2010), but are also more likely to unnecessarily respond to stimuli from non-threatening sources (e.g., Langerhans and DeWitt 2002). In our study, herbivorous fishes responded to lionfish throughout the day when lionfish are relatively

inactive and do not pose an actual predation threat (Côté and Maljković 2010; Green et al. 2011; Cure et al. 2012), which suggests these herbivorous fishes may use general cues.

Field observations of juvenile parrotfishes conducted during the day by Anton et al. (2016) indicated native individuals that approached invasive lionfish reached distances that were closer than those of individuals that swam near native predators. The authors conclude that this behavior suggests prey naiveté, but these findings could also suggest that parrotfishes in the invaded range have adapted an appropriate response to inactive lionfish in terms of parrotfish movement within reefs. Alternatively, antipredator response of native parrotfishes to invasive lionfish could consist of only altered grazing activity. Additional observations need to be conducted at dawn and dusk to observe both the movement and grazing behavior of native parrotfishes in the presence of invasive lionfish that are actively hunting. Further research is also needed to determine the types of cues (chemical and/or visual) of lionfish that cause (or fail to cause) a response in parrotfishes, and test which types of behaviors parrotfishes alter in response to these cues.

Albins and Hixon (2013) postulated invasive lionfish could have indirect effects on native benthic communities similar to those caused by overfishing of parrotfishes and other herbivores (Mumby et al. 2006; Mumby and Steneck 2008). Our study further supports the potential for this lionfish trophic cascade by demonstrating that lionfish have a negative indirect effect on algal loss via reduced fish grazing on substrata, which corresponded with herbivorous fish grazing behavior (likely driven by parrotfishes). Significantly less algae was removed from substrata at high-lionfish-density reefs where grazing was reduced by both small and large herbivorous fishes; whereas reduced grazing of small herbivorous fishes alone when lionfish were present within-reef failed to produce a corresponding significant reduction in the amount of algae removed. Therefore, we infer that the pattern in algal loss was largely driven by large herbivorous fish behavior, especially since larger parrotfishes have the biomechanical means to remove substantial quantities of algae (Hoey and Bellwood 2008). Additional testing is needed to determine whether this reduced grazing on substrata caused by the presence of lionfish is maintained at larger spatial scales and occurs on the natural reef landscape.

Further testing of CEs and NCEs of invasive predators on native prey at larger temporal and spatial scales will greatly inform our understanding of the effects of invasive predators on native communities and ecosystems. Over longer time periods, we predict that if invasive lionfish continue to cause increased prey mortality in addition to any potential survival and fitness costs related to antipredator behavior (Peckarsky et al. 1993; Ruxton and Lima 1997; Creel et al. 2007; Pangle et al. 2007), then native herbivorous fish populations could further decline in density and experience shifts in size and age structure, ultimately resulting in even greater reductions in fish grazing of algae throughout invaded ecosystems.

We have demonstrated the importance of considering and rigorously testing for NCEs in addition to CEs of invasive predators when assessing the effects of invasions. Understanding the roles of CEs and NCEs of invasive predators on native prey can also provide crucial insight for detecting novel indirect effects and trophic cascades that could potentially have ecosystem-level consequences. Further testing of these interactions between invasive predators and native prey will greatly enhance our ability to accurately predict both acute and chronic impacts of invasions.

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