

# Consumptive and Non-consumptive Effects of an Invasive Marine Predator on Native Coral-reef Herbivores

## Efectos Consuntivos y No Consuntivos de un Depredador Marino Invasiva en los Herbívoros de Arrecifes de Coral Nativos

## Effets Consommatrices et Non Consommatrices d'un Prédateur Marin Invasive sur les Herbivores des Récifs Coralliens Indigènes

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### EXTENDED ABSTRACT

Predators can affect prey population dynamics through both direct consumptive effects (CEs; Taylor 1984, Murdoch et al. 2013) and non-consumptive effects (NCEs), or energetically-costly phenotypic alterations in prey. Invasive predators typically have larger effects on native prey populations than native predators (Salo et al. 2007), yet the role and relative importance of their CEs versus NCEs in structuring invaded systems remains unclear. Without considering potential NCEs, the overall effects of invasive predators on native communities and ecosystems could be greatly underestimated. We tested for both CEs and NCEs of the invasive red lionfish (*Pterois volitans*) on an important ecosystem function of native herbivorous fishes: reducing the abundance of benthic algae that could otherwise displace corals on reefs.

We selected 10 large (1400 - 4000 m<sup>2</sup>), isolated coral reefs located on the Great Bahama Bank near Lee Stocking Island, Bahamas. These reefs ranged in depth from 2 to 11 m and were paired by similarity in habitat type. To quantify CEs of lionfish, we manipulated lionfish densities (*low* versus *high*) on paired reefs and surveyed fish populations from June 2009 to June 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:

- i) Low-lionfish-density reef with lionfish absent from the observed microhabitat (n = 100),
- ii) High-lionfish-density reef with lionfish absent from the microhabitat (n = 50), and
- iii) High-lionfish-density reef with lionfish present in the microhabitat (n = 50).

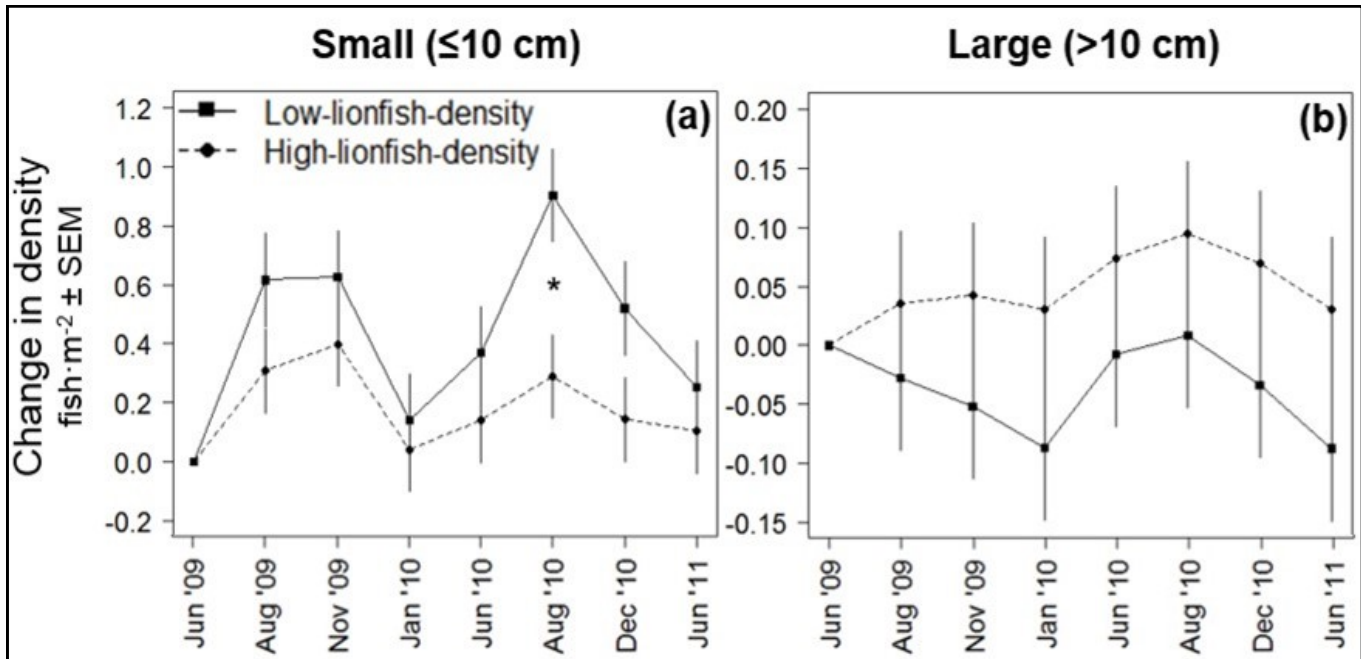
We also used before-and-after photographs of each substrate to estimate the percent loss of algal cover from observed grazing.

Regarding consumptive effects, lionfish reduced the density of small but not large herbivorous fishes (Figure 1), and this effect fluctuated over time (*lionfish* × *time* interaction: LRT  $p = 0.002$ ). Regarding non-consumptive effects, grazing by these small fishes was reduced on high-lionfish-density reefs, and further decreased when lionfish were present within reefs (Figure 2). Lionfish at high-lionfish-density reefs caused a decline in grazing by large herbivores that was maintained regardless of lionfish presence within reefs (Figure 2). Parrotfishes were likely driving the response of herbivorous fishes to both CEs and NCEs of lionfish. 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* × *lionfish* interaction: LRT  $p = 0.002$ ). Lionfish had a negative indirect effect on algal loss, with 66 - 80% less algae removed from substrata in high-lionfish-density reefs.

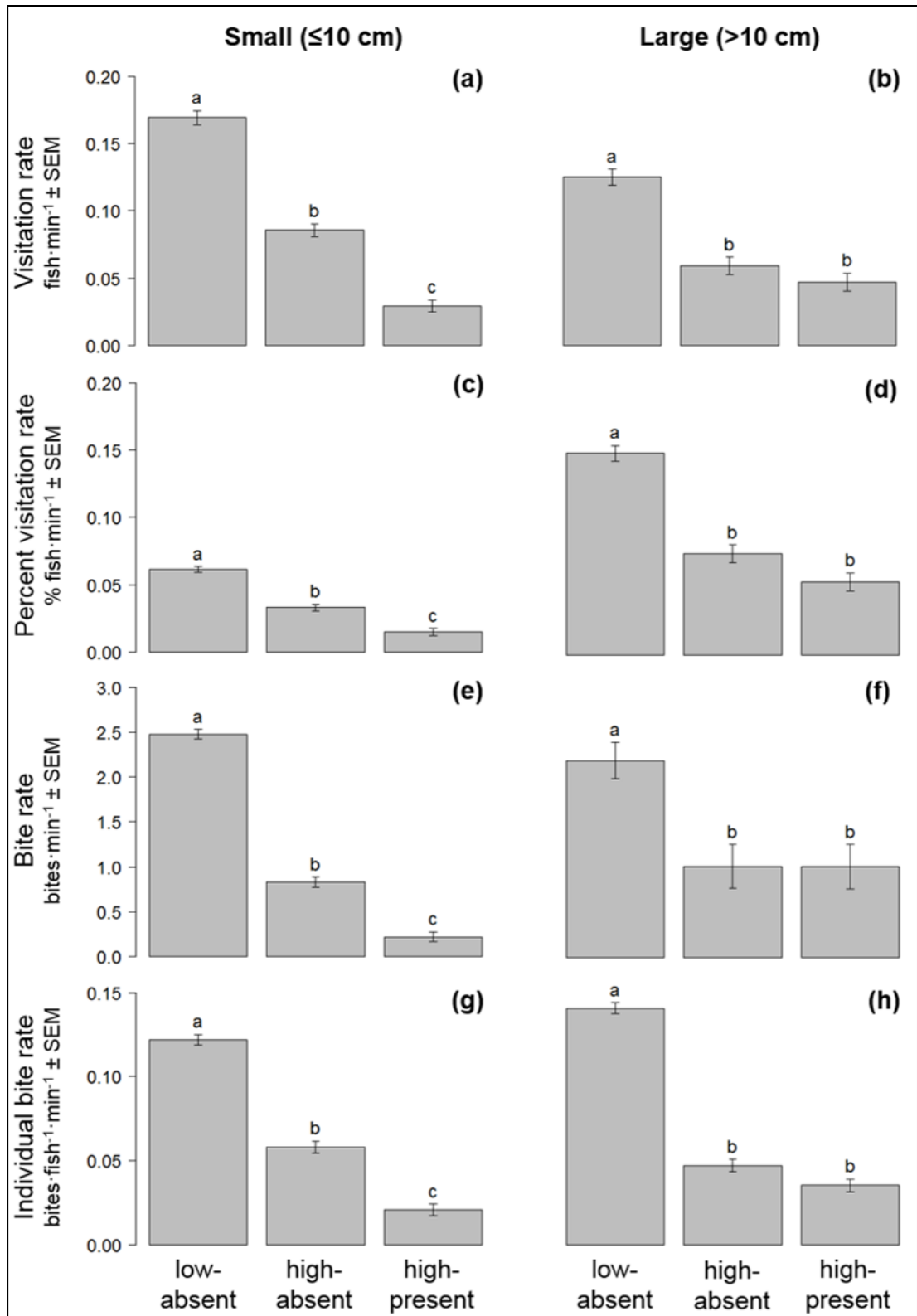
At this point in the invasion, our study indicates that the CEs of lionfish affect small, but not large native herbivorous fishes, while their NCEs affect both small and large native herbivorous fishes. Therefore, we conclude that the NCEs of lionfish currently have a larger role in diminishing the ecosystem function of native herbivorous fishes. 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). Our study further supports the potential for this lionfish trophic cascade, but also emphasizes the importance of distinguishing between lionfish CEs and NCEs as underlying mechanisms. Further testing of interactions between invasive predators and native prey at larger temporal and spatial scales will greatly inform our understanding of the effects of invasive predators on native communities and ecosystems, and enhance our ability to accurately predict both acute and chronic impacts of invasions.

## LITERATURE CITED

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**Figure 1.** Change in density of (a) small and (b) large herbivorous fishes 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. 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:  $*p < 0.05$ .



**Figure 2.** Response of (a, c, e, g) small and (b, d, f, h) large herbivorous fishes 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  $> 0.05$ .