On the relationship between native grouper and invasive lionfish in the Caribbean

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Abstract

The Indo-Pacific lionfish, *Pterois volitans*, has invaded most of the Tropical Western Atlantic in the last few years. The degree to which populations of this invasive species can be controlled by native predatory fish (mostly grouper), is controversial with conflicting reports. Here, we review the evidence of two recent papers and point out some of the difficulties in inferring predator-limitation purely from observational data. A negative relationship has been found between large-bodied grouper and lionfish during early colonisation though the degree to which this is caused by direct predation versus behavioural mechanisms is unclear. Evidence to the contrary from a recent study suffers confounding effects of habitat quality, fishing, and dispersal and therefore remains equivocal.

Introduction

The rapid invasion of predatory lionfish (*Pterois volitans*) in the Atlantic (Schofield 2010) has led to concern over their impact on native fish stocks (Albins and Hixon 2008). Not surprisingly, this has prompted interest in whether native predators can exert some biocontrol upon lionfish. In 2011, we published a study from the central Bahamas, a region that has managed to attain some of the highest biomasses of large groupers in the Caribbean (Mumby et al. 2011). Fish surveys were undertaken three years after the invasion began and revealed a strong, nonlinear, and negative relationship between the biomass of large-bodied grouper and that of lionfish. We interpreted this pattern as occurring because of a predatory impact of grouper upon lionfish and also noted a consistent change in lionfish behaviour such that they exhibited risk-sensitive foraging behaviour at sites with the greatest abundance of potential predators.

Recently, a second paper was published on this topic (Hackerott et al. 2013) which purported to find no effect of grouper on lionfish abundance in the Caribbean. The authors of this paper made a number of assertions of confounding effects in the previous study (Mumby et al. 2011) but as we show here, these assertions were factually incorrect and belied an inattentive reading of our paper. Here, we discuss some of the assertions made by Hackerott et al (2013) and consider whether their results really provide evidence that grouper and lionfish

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abundances are unrelated. In so doing, we hope to clarify the level of evidence on this question and discuss putative mechanisms.

Confounding effects of habitat, larval dispersal, and fishing

Hackerott et al. aim to prove a 'negative' result of grouper on lionfish while failing to account for a multitude of processes that could likely obscure any relationship that might exist. The numbers of grouper and lionfish will vary from site to site for many reasons other than whether they exhibit a predator-prey relationship. Fishing has a major effect on grouper (Coleman et al. 2000) and increasingly, a significant effect on lionfish. Habitat quality, particularly rugosity, is a major driver of fish abundance and mediates predator-prey interactions (Hixon and Beets 1993). Larval dispersal is likely to be an important factor for lionfish, particularly given the very recent colonisation of the species. All of these factors will vary dramatically among study sites around the Caribbean yet none are measured nor accounted for. The only attempt to control for fishing is to include reserve effects but it is well established that very few reserves have any significant effect on grouper (see AGRRA dataset, included in Mumby et al 2011).

Hackerott et al's attempt to stratify data by reef zone is inadequate. It is well established that forereef slopes in the Caribbean encompass at least two contrasting habitats: structurally complex “*Montastraea*” reefs (i.e., *Orbicella* reefs) versus structurally simple hardbottom dominated by gorgonians (Chollett and Mumby 2012). The fish assemblages differ dramatically between these habitats (Harborne et al. 2008, Mumby et al. 2008) and failure to distinguish which sites lie in one habitat versus the other constitutes a genuine confounding effect. The authors also mix reef slopes with spur and groove zones, and again the additional large-scale complexity offered by coral spurs intersected by sand grooves can affect fish communities. The varying geomorphology between spur and groove zones and reef slopes are also typically driven by their location in different physical environments, which needs to be accounted for in any analysis pooling across reef zones. Finally, 25 (35%) of the sites are shallow patch reefs from The Bahamas. Large grouper have well-established habitat preferences for deeper water and during extensive surveys on these patch reefs, one of us (ARH) has rarely seen large grouper comparable to those found in the ECLSP. Therefore, while high density might allow the total biomass of grouper on patch reefs to be high, the sizes of grouper - and therefore their predatory capacity - is substantially less than that of forereef populations and likely incomparable to our study of the ECLSP. Moreover, the fish assemblages on patch reefs, which include high densities of lionfish, tend to be concentrated and heavily influenced by patch size, shape (Acosta and Robertson 2002), and connectivity, all of which comprise confounding variables in the analysis of Hackerott et al. In short, any extrapolation of patterns seen on shallow patch reefs to deep forereefs should be made with caution.

Our study in the ECLSP (Mumby et al 2011) involved a series of sites along a single reef tract in the central Bahamas. The only major difference among sites was the level of fishing and amount of algal cover (a trophic cascade that followed from the level of parrotfish fishing). Several sites were within one of the oldest and most effective MPAs in the

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Caribbean. Previous papers had tested whether there was any systematic bias in rugosity, damselfish abundance, and potential larval dispersal and found none (Mumby et al. 2006, Mumby et al. 2007). In 2010, we reported that sites with more parrotfish (mostly in the ECLSP) had a faster rate of coral recovery but coral cover was still low at all sites (<10%) and even a modest change in absolute cover (a few %) is unlikely to have any detectable impact on lionfish or grouper. Thus, while our comparison of lionfish and grouper biomass was still only correlative in nature, we could at least argue that obvious confounding effects of habitat and larval dispersal were not present. This also included potential effects of fishing upon lionfish but we'll return to that point later.

In their paper, Hackerott et al argue that our study could be confounded by differences in habitat quality inside and outside the ECLSP. Strangely, they attempt to substantiate that point by citing our papers that actually show no correlation between grazing (which correlates with fishing) and habitat quality. Further, our 2006 paper showed that there was no significant bias in rugosity between fished and reserve sites. So, not only is their argument factually incorrect, but their argument should actually be directed towards their own study because measurements of habitat quality were not included in their analysis.

Confounding effects of lionfish control by marine park staff

Hackerott et al. assert that the most likely reason we found fewer lionfish in areas with higher grouper biomass - mostly at sites within the reserve - was because marine park staff might have controlled (speared) the lionfish. This assertion constitutes an inattentive representation of our paper and further personal communications. We specifically addressed the issue of active culling in our article, and found it to be negligible, but Hackerott et al. make no mention of this. As for the facts, the Bahamas National Trust and Department of Marine Resources have never sanctioned control of lionfish in the ECLSP. Hackerott et al. communicated with the ECLSP administrator, who confirmed that lionfish control inside the park was insignificant, but the Park’s response was ignored (Andrew Kritz, pers. comm.). Second, there is one tour operator that dives in the area with whom we have worked since 2004. By agreement, he forbid his staff from spearing lionfish in the Park until we completed our survey. Third, even if there was some control at the most popular dive site, our results were robust to a deletion of this data point.

Do did large-bodied grouper impact the density of lionfish in the ECLSP?

As mentioned above, the strength of our study lay in comparing a broad range of grouper densities across a narrow geographical area, thus keeping as many other confounding geographical variables as limited as possible. With a range in grouper biomass from 160 g 100 m^{-2} to 3030 g 100m^{-2} across 12 sites, the pattern we observed in 2010 was strong and could not be explained by other potential predators of lionfish or the usual metrics that influence fish abundance. In contrast, the Hackerott et al. study, including 71 reefs across three biogeographic regions with substantial potential for site-specific variation, only measured greater grouper biomass at 3 sites.

In our previous paper (Mumby et al. 2011), we stated that it was not clear whether the negative relationship between grouper and lionfish occurred because of direct predation or competitive mechanisms, a point reinforced by Cote et al (2013). However, we argued that predation by large-bodied grouper was at least partly responsible for the pattern observed in the ECLSP. Here, we list key reasons for this, but return to competitive mechanisms later.

A) It has already been documented that grouper can consume living lionfish (Maljkovic et al. 2008).

B) The sizes of grouper in the ECLSP are large and perfectly capable of consuming lionfish, particularly at juvenile stages.

C) Densities of lionfish during our surveys were actually quite low - a point made by Hackerott et al. The reason for the overall low level of abundance is not clear but there certainly existed a strong negative association with grouper biomass. When lionfish densities are low, predation rates do not have to be high in order to have a demographic impact. So, even if laboratory or mesocosm studies struggle to find predation events of grouper upon lionfish, this does not show that infrequent events do not occur on open forereef environments and have a corresponding demographic effect. To resolve this question, we need data on settlement rates of lionfish together with migration rates from neighbouring habitats (e.g., seagrass beds which lie at least a kilometre away). With such data, it might transpire that only very occasional predation can have a significant demographic effect.

D) We observed a striking change in lionfish behaviour between park and non-park sites. In the Park, lionfish were cryptic, often remaining close to the substrate and near crevices - i.e., risk sensitive foraging. Outside the park, lionfish were found high above the substrate and they appeared to show no obvious fidelity to crevices. Unfortunately we did not quantify this formally but we did cite this as a personal observation. The behavioural observations are entirely consistent with a predator effect, particularly when you consider that many of the locations had virtually no history of human observation let alone spear fishing.

Do large grouper control lionfish abundance in the Caribbean?

The key point we made in our 2011 paper was that grouper abundance and size was so low throughout the Caribbean that it is extremely unlikely that grouper are controlling lionfish in the region. Grouper biomass at our sites in the Bahamas were within the top 1 percentile of reported values for the Caribbean as a whole. Thus, the paper of Hackerott et al. is actually consistent with our original conclusion. At no point did we assert that grouper would be controlling lionfish in places like the Mesoamerican Barrier Reef (one of their study areas) that have very low levels of grouper (Mumby et al. 2012). We also point out that the ability of grouper to have a demographic impact on lionfish might only occur at the early stages of lionfish invasion, when densities are relatively low. We have not attempted to resurvey our sites and test this possibility.

It is also possible that much of the pattern we observed was attributable to behavioural effects as well as predation (Cote et al. 2013). As stated, we observed a significant change in

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lionfish behaviour inside the park and it is possible that fewer lionfish choose to settle in this habitat because of higher predation risk. Similarly, it is also possible that some lionfish undertake ontogenetic migrations away from sites with large predators, though this would entail a migration of several kilometres. Unfortunately, there are no data to evaluate either of these possibilities but they should be examined in future. Should either prove to be correct, then it would still imply that large grouper can reduce the density of lionfish but through mechanisms other than direct predation. There is a precedent for this. Experiments have shown that the foraging activity of smaller grouper is disrupted in the presence of large-bodied grouper, which is a potential predator (Stallings 2008). As a result, the biomass of large-bodied grouper (e.g., *Epinephelus striatus*), and small grouper (e.g., *Epinephelus guttatus*) are often inversely related in space (Chiappone et al. 2000) or time (Mumby et al. 2012).

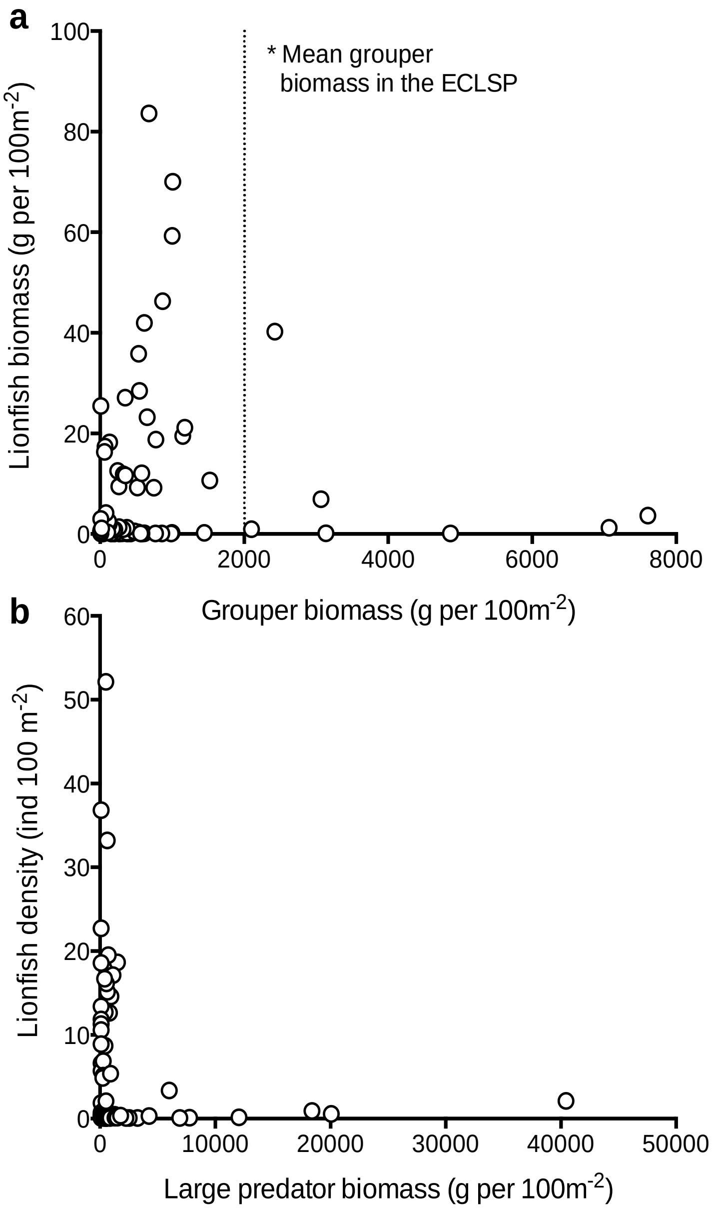

Fig. 1 The relationship between lionfish biomass and the biomass of large groupers (a) and that between lionfish density and the biomass of large predators in general (b). Data replotted from Hackerott et al (2013).

Re-examining the results of Hackerott et al., there appears to be a clear breakpoint in predator biomass and lionfish abundance which makes the reader wonder whether their interpretation is correct. While a detailed analysis of these data is impossible without site-level information on habitat, etc, we extracted their data for the two large-predator plots (Figure 2b and Figure 7 of Hackerott et al.) and present it on untransformed axes (Fig. 1). At low levels of predator biomass, there is no clear relationship between grouper and lionfish biomass (Fig. 1a). This is not surprising as the abundance / size of each taxon will be controlled differently by a wide range of processes (e.g., fishing, recruitment, habitat quality, prey availability). However, lionfish biomass is virtually zero at all higher levels of grouper biomass, such as the levels of biomass observed in the ECLSP (Fig. 1a). Lionfish density is also virtually zero at high levels of apex predator biomass (Fig. 1b). We interpret these results as a constraint upon lionfish under high predator biomass, though alternative interpretations should also be tested.

To conclude, whether grouper control lionfish or not is likely to be a moot point unless grouper populations are dramatically restored, which is unlikely outside of well protected areas. For now, human control is the only feasible mechanism of controlling lionfish. While it is important to test the generality of studies from one region to another, it is always difficult to 'prove a negative', particularly when alternative hypotheses or drivers are not measured or tested.

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