

1 **Resolving differences in observed impacts of**
2 **invasive lionfish and clarifying advice to**
3 **managers**

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23 ABSTRACT

24 Hackerott et al. (2017) report that Indo-Pacific lionfish “had no apparent effect on native
25 prey communities” (p. 9) on continuous reef-sites of the Belizean Barrier Reef (BBR).
26 Based on a lack of observational evidence, they challenge existing evidence for the
27 effects of predation by lionfish on native prey community structure and assert that
28 previous experimentally measured effects are inflated by “unnaturally high lionfish
29 densities” (p. 10). Managers may mistakenly interpret these conclusions as evidence
30 that invasive lionfish are of little concern and that active management of lionfish should
31 not be a conservation priority. We find the arguments presented in Hackerott et al.
32 (2017) unconvincing and potentially misleading. Here, we seek to re-evaluate their
33 conclusions in the context of the body of work on the lionfish invasion, and clarify advice
34 to marine resource managers in the invaded range. Specifically, we argue that (1) the
35 low lionfish densities observed in Hackerott et al. (2017) are not predicted to cause
36 observable lionfish effects—so the results offer no countervailing evidence; (2) the study
37 design is ill-suited to identify lionfish-induced changes in prey abundance, were they to
38 occur; (3) the analytical methods employed (correlation between lionfish and prey
39 densities) do not represent a BACI design nor offer a reliable test of predatory effects;
40 and (4) the authors minimize potentially important regional management activities that
41 could affect lionfish population densities and mischaracterize the body of lionfish
42 research that has come before. Scientists should rigorously challenge popular scientific
43 narratives. However, the foundation of such challenges must be carefully designed
44 experiments, sound methodology, and conservative interpretation of one’s findings.

45 INTRODUCTION

46 Hackerott et al. sought to evaluate the effects of invasive Indo-Pacific lionfish (*Pterois* spp.) on
47 fish communities at continuous reef sites in the Belizean Barrier Reef by conducting repeated,
48 yearly censuses before and after the arrival of lionfish. They report changes in fish density,
49 species richness, and community composition over five field-seasons and conclude “fish
50 communities appear unaffected by lionfish” (p. 13) based on marginal p-values. They contrast
51 these findings with the results of prior field experiments throughout the invaded range that have
52 demonstrated strong and significant effects of lionfish predation on native prey communities, and
53 speculate on the mechanisms that may have produced such disparate results. Finally, they
54 suggest a course correction in lionfish research, calling for a re-evaluation of the importance of
55 lionfish effects relative to other coral-reef conservation issues.

56 While we agree that the context-dependency of lionfish effects is an important area of
57 ongoing research, and that other threats to reef ecosystems should not be ignored, we fear that
58 the broad conclusions from Hackerott et al. (2017) may lead managers to dismiss active lionfish
59 management as a conservation priority. We believe that it is important to place Hackerott et al.’s

60 analysis and conclusions in context, and seek to clarify the message to managers in the invaded
61 range. Specifically, we argue that (1) the low lionfish densities observed in Hackerott et al.
62 (2017) are not predicted to cause observable lionfish effects—so the results offer no
63 countervailing evidence; (2) the study design is ill-suited to identify lionfish-induced changes in
64 prey abundance, were they to occur; (3) the analytical methods employed (correlation between
65 lionfish and prey densities) do not represent a BACI design nor offer a reliable test of predatory
66 effects; and (4) the authors minimize potentially important regional management activities that
67 could affect lionfish population densities and mischaracterize the body of lionfish research that
68 has come before. We therefore recommend that managers *not* suspend efforts to remove lionfish
69 on the basis of the results of Hackerott et al. (2017) but rather employ existing and field-tested
70 decision-support tools (Green et al., 2014) to determine the appropriate level of mitigation effort.

71 **EVALUATING LIONFISH PREDATORY EFFECTS**

72 **Low lionfish densities are not predicted to affect prey biomass**

73 Assessing predatory effects of lionfish requires knowledge of the relationship between invader-
74 induced predation mortality and the composition and productivity of the prey community. Green
75 et al. (2014) introduced a tool for managers to assess the density of lionfish at which prey
76 populations will experience declines, given local prey productivity. This mass-balanced model
77 estimates the relationship between invasive lionfish prey consumption (incorporating lionfish
78 body size, density, and temperature-specific predation rates on mass-specific consumption) and
79 the biomass productivity of native reef fishes they consume (incorporating the effect of body size
80 and temperature on biomass production over time). The model predicts that predation effects are
81 nonlinear (i.e., lionfish effects begin to occur beyond a particular threshold of predation
82 mortality). Application of the model to estimating the densities at which lionfish consumption
83 outstrips prey production on both continuous (Green, 2013) and patch reefs (Green et al., 2014)
84 reveals that the magnitude of change in prey-sized fishes is well predicted by properties of both
85 resident lionfish and their prey community. Taken together, this work highlights contexts in
86 which invasive lionfish are *not* likely to cause measurable changes in the density or biomass of
87 prey species. In particular, effects are unlikely in fish communities with high standing biomass
88 and/or larger size classes and low densities/small size classes of invasive lionfish. Therefore,
89 given that density alone does not dictate the magnitude of expected predation effects (as
90 Hackerott et al. acknowledge), it is not appropriate to compare densities between experiments
91 and among regions without also accounting for predator body size distribution, the
92 composition/standing biomass of prey, and environmental temperature.

93 Studies applying this framework for lionfish in northern Belize (Valderrama & Fields, 2015)
94 and across multiple regions in the archipelago (Chapman et al., 2016) found that lionfish
95 densities are currently below levels predicted to affect the standing biomass of available prey
96 species. As such, the results presented by Hackerott et al. (2017) do not provide evidence

97 countervailing results observed from other locations within the invaded range, as the authors
98 suggest. Rather, they pose a different question:

99 **Why are lionfish densities too low to cause observable predation effects along**
100 **the BBR?**

101 There are several possible explanations for the lack of an effect of lionfish on prey fishes in this
102 region. On one hand, substantial culling across the BBR since the start of the invasion may have
103 served to limit population increases (and thus predatory effects) on continuous fore-reef
104 environments. Culling by the dive industry, through lionfish ‘derbies’, and by lobster and fin-fish
105 fishers occurs regularly across many parts of this region (Chapman et al. 2016). As a single
106 example, from 2009 to 2012, volunteer divers with the Reef Environmental Education
107 Foundation surveyed for and removed 960 lionfish from 20 sites along BBR, with annual
108 removal increasing from zero lionfish in 2009 (when none were sighted) to 63 lionfish in 2010,
109 peaking at 505 in 2011, and dropping to 392 lionfish in 2012. A recent evaluation of culling
110 efficacy from Florida and the Bahamas has demonstrated that even a single-day culling event can
111 reduce lionfish densities below the threshold at which they are predicted to overconsume native
112 prey (Green, Underwood & Akins, 2017). Rather than challenge existing evidence of lionfish
113 effects, the results of Hackerott et al. (2017) may therefore highlight a case of successful regional
114 management of lionfish along the BBR.

115 On the other hand, the standing biomass of prey-sized reef fish at the fore-reef sites examined
116 by Hackerott et al. may also be at a level that exceeds what resident lionfish in the region can
117 overconsume. Given that Hackerott et al. do not present data on the density and standing biomass
118 of prey fishes, it is difficult to compare the fish communities on the reefs they studied with others
119 in the region, or to assess the extent to which this study represents a departure from previously
120 observed lionfish effects.

121 **OBSERVATIONAL DESIGN REDUCES THE LIKELIHOOD OF**
122 **DETECTING LIONFISH EFFECTS**

123 Hackerott et al. employed a repeated-measures, observational approach in which transects on
124 continuous reefs were censused for native prey before and during the invasion of lionfish. To
125 quantify lionfish effects, native prey abundance was modeled as a function of lionfish density
126 (among other predictors). However, the study design makes the detection of lionfish effects
127 unlikely by inappropriately restricting “potential lionfish prey” in terms of both species and size,
128 and by employing annual surveys that fail to capture the peak period of prey-fish recruitment.

129 **Lionfish have the strongest effects on 1-5cm TL prey**

130 Hackerott et al. focus their analyses on fish species that have been previously documented as
131 lionfish prey and that are in the 6-10cm TL size range. First, it is unclear why they exclude other
132 potential prey fish species rather than examining all species within the known size range of
133 lionfish prey, especially given the generalist diet of lionfish (Layman & Allgeier, 2012; Valdez-

134 Moreno et al., 2012; Côté, Green & Hixon, 2013; Green & Côté, 2014; Rocha et al., 2015;
135 Harms-Tuohy, Schizas & Appeldoorn, 2016). This is problematic given that Hackerott et al.
136 analyze the densities of documented lionfish prey from only ten studies, of which only one was
137 conducted in Belize (seven were from The Bahamas).

138 Furthermore, their rationale for focusing on the 6-10cm TL size range is based on the
139 argument that lionfish can consume prey up to half of their body length (Albins & Hixon, 2008;
140 Morris & Akins, 2009). While lionfish *can* consume prey that large, there is abundant evidence
141 that lionfish predation disproportionately affects smaller prey (Albins & Hixon, 2008; Morris &
142 Akins, 2009; Muñoz, Currin & Whitfield, 2011; Albins, 2013; Green et al., 2014; Green & Côté,
143 2014; Albins, 2015; Benkwitt, 2016). For example, Morris and Akins (2009) found that the mean
144 size of teleost prey for all lionfish in their study, including lionfish up to 40cm TL, was between
145 1.5 and 2.5cm TL. Many of the fish families that suffer the greatest reductions (Albins & Hixon,
146 2008; Albins, 2013; Benkwitt, 2015; Ingeman & Webster, 2015; Benkwitt, 2016; Palmer et al.,
147 2016; Kindinger & Albins, 2017; Tuttle, 2017) and comprise the largest proportion of lionfish
148 gut contents (Layman & Allgeier, 2012; Valdez-Moreno et al., 2012; Côté, Green & Hixon,
149 2013; Green & Côté, 2014; Rocha et al., 2015; Harms-Tuohy, Schizas & Appeldoorn, 2016)
150 either seldom achieve 6cm TL (many apogonids, blenniids, gobiids, etc.) or are far more
151 vulnerable to lionfish predation as 0-5 cm TL juveniles (labrids, pomacentrids, grammatids, etc.).

152 Especially given the modest size (mostly less than 20cm TL) of lionfish observed at the study
153 sites of Hackerott et al., removing these small prey species and families from the focal analyses
154 severely limits the ability to detect lionfish-caused changes in prey abundance and species
155 richness. Hackerott et al. report that individuals of the 0-5cm TL range were “potentially too
156 variable at the scale of our study for meaningful conclusions” (p. 5). We argue that if the study
157 design precludes inference on precisely the segment of the fish community most likely to show
158 an effect of the treatment, it may not be appropriate for addressing the research question.
159 Monitoring programs are emerging across the invaded region that focus specifically on recruit
160 and small-bodied size classes (e.g. standardized protocols in Green 2012) because of the body of
161 evidence showing the vulnerability of these size classes to lionfish predation.

162 **Annual late-spring surveys miss primary window of prey vulnerability**

163 Hackerott et al. conducted their reef fish censuses annually in late spring, potentially missing the
164 peak recruitment season for many of the prey-sized fishes that inhabit the region (Shulman &
165 Ogden, 1987; Robertson, Green & Victor, 1988; Caselle & Warner, 1996; Robertson et al.,
166 1999). Immediate post-settlement predation accounts for the vast majority of overall reef-fish
167 mortality (Almany & Webster, 2006) and previous research has demonstrated the strongest
168 lionfish effects on small prey immediately after this window of post-settlement vulnerability
169 (Albins, 2015). The timing of surveys, set after a long winter of mortality and prior to substantial
170 new settlement, essentially reflects a measure of the *survivors* of the annual predation gauntlet
171 and is thus poorly timed to detect lionfish effects. Although it is important to examine the extent
172 to which reduction in summer recruitment alters long-term patterns in the adult reef-fish

173 community, this is not a stated goal of Hackerott et al.'s study. In any case, it is important to
174 acknowledge the role of seasonality in potentially masking lionfish predation effects.

175 **STATISTICAL METHODS DO NOT PRODUCE RELIABLE ESTIMATES** 176 **OF LIONFISH PREDATION EFFECTS**

177 Several statistical issues limit the reliability of the conclusions drawn by Hackerott et al. (2017).
178 These issues include (1) mischaracterization of the observational approach as a “modified BACI
179 design,” (2) the fact that lionfish density and year are confounded in the statistical model, (3)
180 inconsistent survey locations among years that introduce variability and could potentially bias
181 estimates of lionfish effects, and (4) the absence of power analysis to support the conclusion that
182 lionfish have no effect on prey communities.

183 **BACI design requires evaluation of the interaction between treatment and time**

184 Hackerott et al. mischaracterize their study as a “modified BACI design” (p 1) and make an
185 unsupportable distinction between their study and previous large-scale correlational work, which
186 they characterize as “uncontrolled observational studies” (p 1). The Before-After, Control-
187 Impact (BACI) design (Green, 1979; Stewart-Oaten, Murdoch & Parker, 1986; Underwood,
188 1994) represents the gold-standard for measuring the effects of an event or management action
189 on a biological community. The central question for BACI experiments involves the *interaction*
190 between treatment and time: How does the variable of interest change from before to after the
191 event at a control site compared to an impact site? The power of a BACI design is that it controls
192 for site differences and therefore provides strong inferential power.

193 While Hackerott et al. report that they employed a “modified BACI design” (p 1), in fact,
194 their approach cannot address the key prediction of a BACI experiment: a significant interaction
195 between lionfish density (“treatment”) and year (“time”). The authors report that, over the five
196 years of observations, lionfish came to occupy all sites, having been completely absent at the
197 outset of the study (p. 6). Thus, unlike a BACI design, this study has no lionfish-free control sites
198 with which to compare responses through time to reefs subject to lionfish effects. In essence,
199 each of the 16 reef locations is both a “control” and a “treatment” site and lionfish density is
200 entirely confounded with year, precluding any quantification of their interaction. This lack of
201 true controls makes it possible for some unknown variable to have an effect on both the
202 treatment (lionfish density) and the response (native prey-fish density) confounding any attempt
203 to draw conclusions about how one affects the other.

204 Although the design employed by Hackerott et al. allows for the possible detection of a
205 simple correlation between site-averaged lionfish density and prey abundance, it remains unclear
206 exactly what such a correlation would signify mechanistically. For example, a positive
207 correlation between lionfish density and prey density might result when sites (or time periods)
208 that support high prey fish abundance also support high lionfish abundance, whereas a negative
209 correlation might result when lionfish have a negative effect on prey. Of course, if both of these

210 hypothesized mechanisms are in play, they could offset one another, and we may not see any
211 relationship between the two variables. In any case, we stress emphatically that Hackerott et al.
212 did not employ BACI design, or even a modified BACI design. Labeling it as such is inaccurate
213 and misleadingly suggests that their approach provides stronger inference than other
214 “uncontrolled observational studies.”

215 **Statistical model produces spurious parameter estimates and confidence** 216 **intervals**

217 Rather than accounting for the covariance between time and lionfish density, the statistical model
218 employed treats these two variables as independent predictors of prey-fish density. In essence,
219 this approach requires the model to determine the magnitude of contributions caused by both
220 invader density and time on prey responses without any means to separate the effects of each.
221 Further, their model treats year as a continuous predictor: an examination of the model residuals
222 plotted against time illustrates the inappropriateness of this statistical choice. The clear annual
223 pattern in model residuals is an indication of model mis-specification. In essence, treating time as
224 continuous imposes a monotonic relationship between the response and time, when there is no
225 reason to assume such. It seems likely from both their boxplots (Hackerott et al., 2017, Fig 2)
226 and their model residuals that prey densities in 2009 were influenced by either very low
227 recruitment or very high mortality, yet the model, as specified, is unable to adequately fit
228 processes that cause substantial inter-annual variability.

229 **Inconsistent annual survey locations produce unreliable statistical inference**

230 Although not reported in manuscript, the site-level data is averaged from a variable number of
231 transects year-to-year, with some transects censused only in 2009. This design introduces
232 unnecessary year-to-year, within-site variability. More importantly, because lionfish density is
233 strongly correlated with year, any difference in response variables that results from changing the
234 survey locations could spuriously be attributed to lionfish. To illustrate this, imagine a transect
235 with a low density of prey that is only surveyed in 2009, when lionfish densities are reportedly
236 zero. In subsequent years, the omission of this depauperate transect would artificially inflate site-
237 averaged fish densities contemporaneously with increasing lionfish density, leading to an
238 underestimate of invader effects. We acknowledge the converse situation is equally possible and
239 use this scenario only to illustrate the unreliability parameter estimates derived from an
240 inconsistent set of survey locations.

241 **Marginal p-values do not provide evidence that lionfish effects are absent**

242 Given the limitations of their study, we disagree with several of the conclusions presented in
243 Hackerott et al. (2017), in particular the inference that fish communities “appear unaffected by
244 lionfish” (p. 13) on their study sites. Despite the fact that the lionfish densities they report are an
245 order of magnitude lower than those commonly reported in other locations in the invaded region,
246 the results of Hackerott et al. nonetheless suggest negative relationship between lionfish and

247 native prey density. For example, their Figure 3 shows a significant negative correlation between
248 lionfish and damselfish densities, which the authors dismiss as “marginally significant” (p. 7)
249 despite a p-value of 0.03. Further, while not statistically significant given a $p < 0.05$ cutoff, the
250 direction and magnitude of their observed effects on all species (Fig. 3A) and on Labridae (Fig.
251 3B) are consistent with the hypothesis that lionfish predation causes reductions in these groups.

252 It is also instructive that as they increase the arbitrary cutoff between “low” and “high”
253 lionfish reefs from 10/ha to 25/ha—still far lower than natural densities observed in most other
254 studies—the resultant p-values approach significance. This is a clear illustration of the statistical
255 relationship between effect size, noise, and sample size. Increasing the cutoff value for density of
256 lionfish in the “high” category increased the effect size to a point that approaches significance,
257 despite the concomitant loss of replication in the “high” category itself.

258 The authors mistakenly cite lack of evidence of a lionfish effect as evidence that effects are
259 absent, citing marginal p-values as evidence that native prey communities are unaffected by
260 lionfish. The hypothesis testing approach employed here sets a relatively high bar ($p < 0.05$) for
261 avoiding Type I error—mistakenly identifying a difference among treatments that is, in fact, due
262 to chance. However, the probability of *not* finding a difference that actually exists (a Type II
263 error) is not addressed by p-values but by calculating the power of the test. As the authors do not
264 report the probability of such a “false negative,” the assertion that prey communities are
265 unaffected by lionfish is unsubstantiated.

266 **CORRECTING THE RECORD ON EXPERIMENTAL AND** 267 **OBSERVATIONAL EVIDENCE FOR LIONFISH PREDATION EFFECTS**

268 Hackerott et al. suggest that previous experimental studies, which have documented severe
269 declines in native reef-fish communities, (1) employ unnaturally high lionfish densities, (2) do
270 not apply to larger or continuous reef habitats, and (3) should not be extended to management-
271 relevant scales. We disagree and counter each claim in turn.

272 First, they argue that a single lionfish on a 1 m³ artificial reef or a 4 m² natural patch-reef is
273 an unnaturally high experimental density, equivalent to 10,000 or 2,500 lionfish per hectare (p.
274 10). In fact, observations of multiple individuals on similar structures are common in many parts
275 of the invaded range, including The Bahamas (Benkwitt, 2013; Benkwitt et al., 2017), and the
276 Gulf of Mexico (Dahl & Patterson, 2014). Thus, a single lionfish on a small patch reef accurately
277 and conservatively reflects naturally occurring densities and is justifiable given typical reef
278 configurations in a variety of locales across the invaded region. Further, we are unaware of any
279 researchers claiming that typically high patch-reef densities are directly comparable to densities
280 on continuous reef habitats. Clearly, in patchy habitats, lionfish (like most reef fishes) aggregate
281 disproportionately to high relief structures relative to the surrounding low relief sand and
282 seagrass. Experimental work integrating the timing and magnitude of lionfish effects on focal
283 patches and surrounding habitats has provided the first steps toward integrating an “effective
284 lionfish density” in patchy habitats (Benkwitt, 2016; Dahl & Patterson, 2014). Resolving

285 differences in both lionfish density measurements and the magnitude of prey effects between
286 patch and continuous reefs are both important steps for lionfish research. However, neither goal
287 is served by mischaracterizing the design and interpretation of previous work.

288 Second, while a growing list of experimental studies on small ($< 10 \text{ m}^2$) coral patch reefs
289 have indeed resulted in some of the strongest measured effects of invasive lionfish (Albins &
290 Hixon, 2008, Albins, 2013, Benkwitt, 2015), evidence for strong, negative lionfish effects is not,
291 as claimed by Hackerott et al., limited to studies conducted on small reefs. Studies in a variety of
292 habitats and at a variety of spatial scales have also demonstrated strong negative effects
293 (experimental studies) or strong negative relationships (observational studies). In a controlled
294 experiment, Albins (2015) demonstrated that lionfish caused declines in prey density, biomass,
295 and species richness on large, isolated coral reefs ranging in area from 1400 to 4000 m^2 . Palmer
296 et al. (2016) report the results of a non-replicated manipulative BACI experiment, also conducted
297 on large, isolated coral reefs ($> 1200 \text{ m}^2$), which demonstrated a strong, negative effect of
298 lionfish on two-of-three native prey species examined. Other experimental manipulations on
299 medium-to-large coral patch reefs (Benkwitt, 2016: 8 to 33 m^2 , Green et al., 2014: 100 to 150
300 m^2 , Ingeman, 2016: 140 to 1400 m^2 , Tuttle, 2017: 12 to 35 m^2) and in karst solution holes (Ellis
301 & Faletti, 2016: 1.7 to 7 m^2) have demonstrated strong negative effects of lionfish on native
302 fishes. Two separate observational studies conducted on continuous reefs have shown reductions
303 in native prey biomass (65% decline: Green et al., 2012), native predator and prey abundance
304 (including herbivores), and shifts in the benthic community (Lesser & Slattery, 2011)
305 concomitant with the lionfish invasion. An observational study using small reef ledges (within
306 continuous reef habitat) as observational units (Ingeman & Webster 2015) found a large (52%)
307 reduction in the abundance of a coral-reef fish after lionfish invaded the area. Finally, a regional-
308 scale observational BACI study demonstrated a strong negative relationship between invasive
309 lionfish and the change in abundance of tomtate (*Haemulon aurolineatum*) over a 17-year time
310 period (Ballew et al., 2016). Conversely, there has been a single observational study in addition
311 to Hackerott et al. (2017) that has failed to find evidence of a negative relationship between
312 lionfish and native fish on continuous reefs (Elise et al., 2015). While all studies have
313 limitations, the preponderance of evidence suggests that lionfish have negative effects on native
314 reef fishes across a broad range of scales and habitat types.

315 Finally, the idea that lionfish effects documented from patch reefs do not extend to
316 management-relevant scales ignores the fact that a significant proportion of the habitat in the
317 invaded range is composed of small to medium-sized patch reefs. Coral reefs are inherently
318 patchy habitats at multiple spatial scales. Unless one believes that continuous reef habitats are of
319 greater conservation value than patch reefs, there is no basis for claiming that Hackerott et al.
320 (2017) is any more relevant to management than those that occur in patchier habitats. It is clear
321 that lionfish densities and effects will vary across different spatial scales and reef configurations.
322 Rather than dismissing experiments from patch reefs, we argue that researchers should strive to
323 understand the ecological mechanisms underlying these potential differences, and provide

324 managers with evidence-based estimates of lionfish effects across a range of scales and habitat
325 configurations.

326 CONCLUSIONS

327 From abstract to conclusion, Hackerott et al. (2017) cast their findings as an iconoclastic
328 response to previous studies that have found strong negative effects of invasive lionfish on native
329 prey fish communities. In particular, the tone of their discussion suggests that the authors
330 perceive a false, or at least over-hyped, narrative regarding how the threats of invasive lionfish
331 have been characterized, especially in relation to other stressors that face coral reefs in the
332 Anthropocene. We agree that some of the popular coverage of the invasion has been
333 sensationalized and that lionfish effects should be evaluated in the context of other threats to
334 reef-fish community structure and function. With limited conservation funding available to
335 address overfishing, increased frequency and severity of bleaching events, ocean acidification
336 and warming, coastal pollution and sedimentation, managers should not be myopic in their
337 response to invasive species. However, these issues are surely not best addressed by over-
338 interpreting negative results nor by mischaracterizing previous research. The preponderance of
339 evidence from observational and experiment studies has demonstrated significant predatory
340 effects of lionfish at unmanipulated densities. Thus, despite preliminary evidence that lionfish
341 densities may have peaked in the core locations within the invaded range (Benkwitt et al., 2017),
342 we recommend that managers continue their efforts to remove lionfish via derbies and targeted
343 fisheries.

344 We further concur with the assertion of Hackerott et al. that the magnitude of lionfish effects
345 may be context-dependent, varying with factors such as reef configuration and complexity,
346 seasonality, recruitment dynamics, prey community richness, and especially lionfish density
347 itself (p. 10). Further, high densities of the lionfish following the invasion front may be transient
348 (Benkwitt, et al., 2017), and thus predatory effects may wane with increasing time of lionfish
349 occupancy at a given location. To evaluate management actions across the invaded range, we
350 must better understand the ecological mechanisms responsible for the patterns we see in different
351 contexts, and better integrate ecological theory into our evaluation of lionfish effects. One
352 productive area of future research concerns the scale of lionfish foraging in various habitat
353 configurations, and how their movement interacts with the distribution of prey in patchy versus
354 more continuous reef habitats. We suggest that valuable contributions could be made by
355 investigating the following questions:

- 356 (1) How is the magnitude of predatory effects mediated by spatial arrangement of habitat
357 (patchy versus continuous) and by the foraging scale of the predator?
- 358 (2) How well do the predation effects of lionfish documented by small-scale experiments
359 estimate the magnitude of region-wide, metapopulation-scale effects of lionfish on prey
360 dynamics?

- 361 (3) To what extent can uncontrolled, observational studies estimate the magnitude of
362 predator effects despite positive correlations between predator and prey due to common
363 responses to habitat (spatial correlation) and environmental conditions (temporal
364 correlation)?
- 365 (4) Given differences in stakeholder perspectives (local fishers, dive operators, marine
366 resource managers, conservation NGOs, etc.), at what spatial scale(s) should we evaluate
367 lionfish effects to determine whether and to what extent they represent a conservation
368 concern?

369 While contrasting one's findings with previous research can be illuminating, we believe that
370 Hackerott et al. set up an unnecessary dichotomy between studies that have observed strong vs.
371 weak effects of invasive lionfish. We argue that science is best served by integrating the work of
372 researchers who employ different approaches. Scientists should absolutely question the dominant
373 paradigms that could affect the allocation of limited conservation resources, yet they should do
374 so with carefully designed experiments, sound methodology, and conservative interpretation of
375 their findings. Failure to do so represents a disservice to managers who must make conservation
376 decisions based on the best available science.

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