Comparative behavior of red lionfish (*Pterois volitans*) on native Pacific vs. invaded Atlantic coral reefs

Running head: *Native vs. invasive lionfish behavior*

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ABSTRACT: Pacific red lionfish (*Pterois volitans*) have invaded Atlantic reefs and reached much greater population densities than on native reefs. We hypothesized that lionfish on invaded reefs would (1) experience higher kill rates and thus spend less time hunting, given the naïveté of Atlantic prey, (2) consume a greater variety of prey, given the lack of native prey defenses, and (3) display less pronounced crepuscular patterns of hunting, given the ease of capturing Atlantic prey. Comparative behavioral observations were conducted in two native regions (Philippines and Guam) and two invaded regions (Cayman Islands and Bahamas) to assess lionfish time budgets and diurnal activity patterns, and to explore correlations between environmental variables and lionfish behavior. Contrary to our first hypothesis, total time allocated to hunting and kill rates showed no difference between native and invaded reefs, despite considerable regional variation. However, Atlantic prey of lionfish were twice as large as Pacific prey, suggesting that despite similar hunting behavior, invasive lionfish are receiving greater nutritional input. Furthermore, consistent with our second hypothesis, lionfish on invaded reefs

30 had broader diets, and also relied less on "blowing" behavior for prey capture, pointing to

31 substantial prey naïveté in the invaded range. Importantly, only in the invaded range did we

32 observe lionfish consuming parrotfishes, the decline of which could have indirect effects on

33 interactions between seaweeds and corals. Finally, lionfish overall tended to exhibit a

34 crepuscular pattern in behavior whereby hunting peaked at sunrise and/or sunset, with no

35 differences attributable to native vs. invasive status.

36

37 KEY WORDS: Native vs. invasive behavior; Diurnal hunting pattern; Crepuscular hunting;

38 Time budget

39

40 **INTRODUCTION**

41 In the mid 1980´s Pacific red lionfish (*Pterois volitans*) invaded the Western Atlantic via the

42 aquarium trade (Semmens et al. 2004), and beginning in the early 2000´s extended their range

43 throughout the Caribbean, Gulf of Mexico, and down the South American coastline (Schofield

44 2010). Despite local attempts at removal, invasive lionfish reached local population densities far

45 greater than in their native Pacific (Whitfield et al. 2007, Green & Côté 2008, Kulbicki et al.

46 2012). At invaded locations, lionfish consume a broad diversity of small fishes and crustaceans

47 including juveniles of herbivores (Morris & Akins 2009) and have caused substantial reductions

48 in the recruitment and abundance of reef fishes (Albins & Hixon 2008, Green et al. 2012).

49 Invasive lionfish can also negatively affect native piscivorous predators through both predation

50 on juveniles and competition with adults (Albins 2012). Thus, lionfish may ultimately cause

51 drastic changes in Atlantic coral-reef ecosystems (Albins & Hixon 2011).

52   Lionfish are likely protected from predators by their cryptic coloration and numerous

53   venomous spines (Allen & Eschemeyer 1973). Predators rarely target adult lionfish at either

54   native or invaded locations, despite anecdotal evidence of occasional predation (Bernadsky &

55   Goulet 1991, Maljkovic & Van Leeuwen 2008). Because natural controls have not been

56   definitively identified at either the native Pacific or invaded Atlantic, direct removals of lionfish

57   by humans have to date been the only effective way to reduce invasive populations. Because

58   invasive lionfish are widespread geographically and occur far deeper than usual SCUBA depths

59   (Whitfield et al. 2007, Lesser & Slattery 2011), complete eradication is unlikely.

60   Before the invasion, little was known about the ecology and behavior of lionfish, due in part

61   to their rarity in their native range (Kulbicki et al. 2012). Lionfish use two types of hunting

62   methods: slow stalking of prey aided by fanlike pectoral fins that herd prey, and sit-and-wait

63   ambush (Randall 2005). Blowing behavior, by which lionfish produce jets of water directed at

64   prey while approaching them, enhances predatory efficiency by confusing or distracting prey

65   (Albins & Lyons 2012). Lionfish diets are well documented in the invasive range and include a

66   broad variety of coral reef fishes, crustaceans (Morris & Akins 2009, Côté & Maljkovic 2010,

67   Green et al. 2012), and even conspecifics (Valdez-Moreno et al. 2012). These records coincide

68   with diet reported from qualitative descriptions in the native range (Myers 1999). Hunting takes

69   place during crepuscular periods (Myers 1999, Randall 2005) when low light levels impede

70   visually adapted prey (Helfman 1986). During the daytime, native lionfish become inactive in

71   holes and crevices (Fishelson 1997), a pattern common to a variety of other predatory fishes and

72   often influenced by ambient light levels (Belovsky & Slade 1986). Invasive lionfish in the

73   Bahamas also display this crepuscular pattern of hunting behavior (Green et al. 2011).

74   Behavioral comparisons between populations in native vs. invaded ranges are highly

75   informative because they may identify factors that foster invasion success (Holway & Suarez

76   1999, Morris & Whitfield 2009, Meyer & Dierking 2011), and may help in developing control

77   measures (Guo 2006). Changes in diel activity of fishes are a common response to differences in

78   biotic and abiotic environmental factors, including predator abundance, prey availability,

79   presence/absence of competitors, habitat structure, depth, and abiotic conditions such as

80   temperature and light levels (Chen et al. 1999, Reebs 2002, Hansen et al. 2004, Andrews et al.

81   2009, Côté & Maljkovic 2010).   Because these factors may vary regionally, and because

82   invasion is often accompanied by release from the natural controls of competition and predation

83   (Mack et al. 2000), behavioral differences in invasive species are therefore likely between native

84   and invaded locations. For invasive predators, such differences can mean access to more

85   abundant or higher quality prey (Meyer & Dierking 2011), enhanced by the substantial

86   advantages novel invasive predators usually have over native naïve prey (Cox & Lima 2006).

87   We conducted replicate comparative field observations in two regions in the native Pacific

88   Ocean and two regions in the invaded Atlantic Ocean in an effort to determine whether there are

89   any inter-ocean differences in lionfish behavior. Assuming native Atlantic prey are naïve to

90   invasive lionfish, we hypothesized that lionfish would have higher success at killing prey at

91   invaded regions. If so, we further hypothesized that higher success at killing prey would result in

92   concomitant changes to predatory behavior in the invaded Atlantic, including less time spent

93   hunting as lionfish satiated more rapidly, and hunting being less restricted to the low-light levels

94   of crepuscular times often exploited by native predators (Helfman 1986). We also predicted that,

95   as an efficient and voracious generalist predator, lionfish would consume a greater variety of

96   prey in their invaded Atlantic range compared to their native Pacific range.

97

MATERIALS AND METHODS

Data collection

100   We observed *in situ* behavior of lionfish in two regions within each ocean: the Philippines

101   and Guam in the native range, and the Cayman Islands and the Bahamas in the invaded range

102   (Fig. 1). Invasive lionfish were first detected in the Bahamas in 2004 and in the Caymans in 2008

103   (Schofield 2009). Sampling was conducted over a 3-year period, mostly during June to

104   September 2009-2011. We selected sites known to have lionfish, including sandy slopes with

105   coral patches, continuous reef walls, and a few artificial habitats (*e.g.*, piers, small wrecks, tire

106   reefs, and old fish traps). Maximum depth at these sites was 25 m.

107   The number of sites sampled depended on lionfish frequency encountered at those sites. In

108   the native range, where the probability of encountering lionfish was low, 20 sites were sampled

109   in the Philippines and 13 on Guam. In the invasive range, 5 sites were sampled in the Bahamas

110   and 4 in the Cayman Islands.

111   Because capturing and tagging lionfish observed in this study was logistically impractical,

112   and because tagging can possibly alter lionfish behavior towards the observer (personal

113   observation), we chose to observe untagged animals. At each site during any given time of day,

114   we ensured that different animals were sampled by swimming over the site unidirectionally and

115   sampling lionfish encountered haphazardly along the way. Each site was sampled only once

116   within a day, and if we returned to that same site on another day, we sampled different parts of

117   the site and different time periods. Therefore, we assumed that our observations were statistically

118   independent and representative, even when we had no way of knowing with certainty whether

119   we resampled the same fish between days.

120   In each region, we conducted a series of standardized ten-minute observations taken from

121   sunrise to sunset (between ~0600 and ~1830 h). During each period, lionfish behavior was

122   recorded by trained observers using either SCUBA or snorkel. There were 5 observers in the

123   native range and 8 in the invaded range (1 observer in the Pacific and 2 observers in the Atlantic

124   completed 60% of the total observations). Care was taken to minimize the influence of observer

125   presence on lionfish behavior by keeping a distance of approximately 3 m from each fish. We

126   attempted to sample equally all times of day, sites, habitats and environmental conditions,

127   subject to logistic constraints.

128   Eight lionfish behaviors were quantified, following an initial ethogram constructed from a

129   pilot study in the Bahamas. Behaviors were quantified as either proportion of time (*i.e.*

130   proportion of each 10 minute observation period) or counts (*i.e.* number of events per each 10

131   minute observation period). Proportion of time was recorded for each of four activities: inactive,

132   minimal activity, active, and hunting. The first three range from lionfish being stationary, to

133   short distance movements, to long distance movements, respectively, but in all instances pectoral

134   fins are relaxed (*i.e.* not flared and in position for hunting). Hunting activity was obvious as

135   lionfish focused on particular prey with fully flared pectoral fins (Green et al. 2011). Counts

136   were recorded for aggressive interactions (chasing other lionfish or other fish species), strikes

137   (successful and unsuccessful attacks on potential prey), kills (successful capture of prey, *i.e.* prey

138   consumed), and blows (water current directed at prey). During each observation period, we

139   identified all prey approached by lionfish to at least the family level as well as the species level

140   where possible, and estimated prey body size as total length (TL) to the nearest cm.

141   For each 10-min observation we also measured five environmental variables known to

142   influence fish behavior. (*i*) We recorded the microhabitat within which each observation

143   occurred, mostly hard coral, rock-boulder/cave and sand/rubble, and less frequently seagrass

144   beds, sponge fields, soft coral fields, and artificial structures. Lionfish usually did not move

145   outside of the identified microhabitat during the observation time. In the few cases where such

146   movement did occur, microhabitat was classified as the area where lionfish spent most of the

147   observation time. During each sample period, we also recorded (*ii*) cloud cover (clear: 0 to 25%,

148   partly cloudy: 25 to 75%, overcast: >75%), (*iii*) current (low: diver barely kicking to maintain

149   position, medium: periodic kicking required by diver to maintain position, high: constant kicking

150   by diver required to maintain position), (*iv*) estimated lionfish size (TL) and (*v*) depth.

151   Temperature was measured *in situ* using HOBO® temperature loggers every 30 min in Guam

152   and the Bahamas, while temperature data for the Philippines and the Cayman Islands were

153   recorded   from   NOAA   virtual   stations

154   (http://coralreefwatch.noaa.gov/satellite/current/products_vs.html).

155   **Statistical analyses**

156   Frequency distributions for each of the quantified behaviors were highly skewed and had

157   high proportions of ones and zeros, so data transformation did not result in either normality or

158   homoscedasticity. The two most common behaviors (inactive and hunting), were therefore

159   analyzed with a logistic regression using a generalized linear mixed-effects model (GLMM), in

160   which region (random effect) was nested within ocean (fixed effect). The model was robust to

161   the skewed nature of the data and allowed us to explore the cumulative effects of putative

162   explanatory variables. Cumulative effects of ocean, time period, habitat, cloud cover, current,

163   lionfish size (TL), and depth on lionfish behavior, were assessed.

164   Despite the reduction in detail from the conversion of proportions to binary data, a logistic

165   regression model was chosen in part because a lionfish that is exhibiting inactivity or hunting is

166   doing so exclusively (*i.e.*, if a lionfish is inactive, it cannot hunt, and vice versa). The behaviors

167   categorized as "minimal activity" and "active" (both not involving hunting) accounted for less

168   than 10% of the total time budgets for all regions, so these were excluded from further analysis,

169   as well as rates of aggressive behavior toward conspecifics, which were very low in all regions.

170   Data for *y* were binary variables created for lionfish behavior (0 = inactive and 1 = hunting).

171   An observation was considered as inactive if >50% of the ten minute period was spent inactive,

172   and as hunting if >50% of the ten minutes were spent hunting; 75% of all observation periods

173   were dominated by one behavior or the other (*i.e.* either hunting or inactive represented >80% of

174   the observation period). All logistic regressions were done in *R* (*R* Development Core Team

175   2010) using the package "lme4" (Bates et al. 2011) and following the guidelines of Rossiter &

176   Loza (2010) and Peng et al. (2002). Model fit was assessed by examination of model residuals,

177   predicted outcomes, likelihood ratio tests and chi-square statistics (Quinn & Keough 2002).

178   Validation of the model by comparing predicted probabilities to observed outcomes was also

179   performed (70% of outcomes were correctly predicted by the model).

180   Partitioning of variance to determine the relative importance of each explanatory variable in

181   the model was calculated using the *R* package "hier.part" (Walsh & MacNally 2008).

182   Hierarchical partitioning is a technique that, rather than seeking a best fit, uses all possible

183   models in a regression hierarchy to distinguish variables that have the highest independent

184   correlations with the response variable; these variables are most likely to influence variation

185   (MacNally 1996).

186   One-way univariate permutational analyses of variance (PERMANOVA, Anderson et al.

187   2008) were used to compare strike and kill rate means at the level of ocean vs. ocean, with region

188   nested within ocean. These were chosen because of their robustness to deviations from normality

189 and homoscedasticity, characteristic of our data. PERMANOVAs were run for 9999

190 permutations in PRIMER 6 (PRIMER-E Ltd., 2009) with the following specifications:

191 Euclidean distance, sequential sums of squares, and permutation of residuals under the reduced

192 model (Anderson et al. 2008).

193

194 **RESULTS**

195 We observed lionfish ranging in size from 5 to 35 cm TL during a total of 192 hours of time

196 budgeting at native reefs (Philippines 37 hr, Guam 28 hr) and invaded reefs (Cayman Islands 73

197 hr, Bahamas 54 hr). Variation in lionfish time budgets was not substantial between oceans, but

198 considerable between regions within each ocean (Fig. 2, Table 1). Lionfish were usually more

199 active in the Philippines (native) and the Cayman Islands (invaded), and more sedentary in Guam

200 (native) and the Bahamas (invaded). In all regions, we never observed predators attacking

201 lionfish. Temperature was similar both between oceans (pooling regional means ±SE: Pacific =

202 28.13 ± 0.02 °C, Atlantic = 28.69 ± 0.01 °C) and between regions within oceans (mean ± SE:

203 Philippines = 30.23 ± 0.04 °C, Guam = 28.12 ± 0.01 °C, Cayman Islands = 29.72 ± 0.06 °C,

204 Bahamas = 28.68 ± 0.02 °C).

205 **Hunting behavior and prey consumed**

206 Lionfish hunting behavior contradicted *a priori* expectations of inter-ocean differences. Time

207 spent hunting throughout the day was equal between the Atlantic and the Pacific (Table 1),

208 although maximum hunting time was nonetheless observed in the Pacific (Philippines = 70%

209 hunting) and minimum hunting time in the Atlantic (Bahamas = 17.6% hunting) (Fig. 2). Diurnal

210 patterns of lionfish behavior showed that, irrespective of native vs. invaded range, hunting was

211 greater and inactivity lower during sunrise and/or sunset (Fig. 3, Table 1). A strongly crepuscular

212   hunting pattern was most evident for lionfish in Guam and the Bahamas, while lionfish hunting

213   in the Philippines and the Cayman Islands peaked at sunrise (Fig. 3, A & C).

214   Also contradicting expectations, both strike and kill rates were similar between oceans

215   (Strikes: *Pseudo-F* = 0.051, df = 1,1146, p = 1; Kills*: Pseudo-F* = 0.081, df = 1,1146, p = 0.834)

216   (Fig. 4A), although there was considerable regional variation. Successful kill rates (% of total

217   strikes that resulted in prey being consumed = [number of kills / number of strikes]*100) were

218   highest in the Bahamas (51.2%), followed by Philippines (50.0%), the Cayman Islands (25.6%),

219   and Guam (22.9%) (Fig. 4A).

220   Despite lionfish time budgets and kill rates varying more between regions than between

221   oceans, there were several clear differences in hunting behavior between the native Pacific and

222   invaded Atlantic ranges. First, mean blowing rates were three times lower in the invaded range

223   vs. the native range (Fig. 4B). Second, mean prey size was nearly double in the invaded vs. the

224   native range (mean ± SEM: Atlantic = 2.45 ± 0.42 cm, Pacific = 1.50 ± 0.35 cm).   Third,

225   observed diets (kill rates) were broader in the invaded range than in the native range (total # of

226   prey taxa killed/1000 min: Atlantic = 1.6, Pacific = 0.9), even though strikes targeted a greater

227   diversity of fishes in the native Pacific (total # of prey taxa targeted/1000 min: Atlantic = 2.5,

228   Pacific = 3.8). Lionfish successfully killed prey in 6 fish families in the invaded range

229   (Apogonidae, Blenniidae, Gobiidae, Labridae, Pomacentridae and Scaridae), vs. only 2 in the

230   native range (Pomacentridae and Trichonotidae) (Table 2). Strikes were mostly towards gobies

231   (Gobiidae), wrasses (Labridae) and parrotfishes (Scaridae) in the invaded range, and towards

232   cardinalfishes (Apogonidae), gobies, and marine catfishes (Plotosidae) in the native Pacific.

233   Successful kills in the Atlantic included ecologically important species such as juvenile

234   parrotfishes, which were not targeted by lionfish in the Pacific. These differences in diet breadth

235 occurred despite the fact that there are far more potential prey fish species in the native range

236 compared to the invaded range of lionfish (Roberts et al. 2002).

237 **Lionfish size**

238 Overall, body size had no statistical effect on lionfish behavior (Table 1). However, the

239 coefficient estimate for size was negative, suggesting that smaller lionfish spent more time

240 hunting (β = -0.014, p = 0.102, Table 1). Furthermore, when individual regions were analyzed

241 separately, smaller lionfish (5 to 15 cm TL) in the Philippines and the Cayman Islands spent

242 more time hunting than larger fish (Spearman Rank Correlations: $\dot\rho$ = -0.145, p = 0.040 for the

243 Philippines; $\dot\rho$ = -0.131, p = 0.036 for the Cayman Islands). Lionfish size distributions differed

244 across regions, with larger lionfish found in Guam and the Bahamas (mean ± SD: Philippines =

245 17.69 ± 6.15 cm TL, Guam = 22.08 ± 7.22 cm TL, Cayman Islands = 15.63 ± 5.57 cm TL,

246 Bahamas = 22.66 ± 5.44 cm TL; Kruskal-Wallis H = 219.191, df = 3, 1146, p < 0.001).

247 **Environmental effects**

248 Between-ocean comparisons revealed that native Pacific and invasive Atlantic lionfish

249 responded similarly to measured environmental factors (Table 1). Hunting activity was greatest

250 when overcast (Table 1), and this response to changes in cloud cover was most evident for

251 lionfish on Guam and the Bahamas (Fig. 5A). Together with the Caymans, these two regions

252 were sampled at shallower depths (mean ± SEM: Philippines = 19.3 ± 0.3 m, Guam = 10.9 ± 0.4

253 m, Cayman Islands = 9.4 ± 0.3 m, Bahamas = 3.1 ± 0.1 m; Kruskal-Wallis H = 925.1, df = 3,

254 1146, p < 0.001), where the effects of cloud cover on ambient light levels were most obvious to

255 the observers. High currents had a consistent effect across all regions, resulting in less time spent

256 hunting and greater inactivity when compared to both low and medium currents (Table 1),

257 especially on Guam (Fig. 5B). Habitat had only slightly significant effects in both inactivity and

258 hunting patterns (Table 1, Fig. 5C). However, lionfish in rock-boulder habitats tended to hunt

259 less and be more inactive, in contrast to lionfish over hard coral and sand/ rubble, where hunting

260 peaked, especially in the Atlantic (Fig. 5C).

261   When all variables were examined simultaneously, hierarchical partitioning analyses

262 indicated that time-of-day, followed by depth and habitat, were most important in explaining

263 variation in lionfish behavior (Fig. 6). Although coefficient estimates for depth in the logistic

264 model were not significant, depth accounted for almost 20% of total model deviance (Fig. 6) and

265 coefficient estimates indicated a trend towards greater time spent hunting with increasing depth

266 ($\beta = 0.028$, p = 0.499) (Table 1).

267

268 **DISCUSSION**

269   Despite initial expectations of interoceanic differences in lionfish behavior related to

270 native vs. invasive status, our field observations from two regions in each of two oceans suggest

271 that overall patterns in lionfish time budgets, daily activity patterns, and success rates at killing

272 prey are similar in the native Pacific and the invaded Atlantic. These results show that if ease of

273 prey capture is higher for invasive lionfish due to naïve prey, this is not reflected in either kill

274 rates, hunting time or crepuscular hunting patterns.

275   Instead, lionfish behavioral patterns are determined more by regional differences in a

276 suite of environmental factors, which act synergistically to affect behavior. The most pronounced

277 of these factors was the low light level associated with crepuscular times, during which time

278 spent hunting was maximal, regardless of ocean of residence. Twilight foraging is a feature

279 common among coral-reef piscivores, and is probably related to the advantages that low light

280 levels confer to predators vs. their prey (Helfman 1986). The largely crepuscular hunting pattern

281 found, despite peaks occurring in either sunrise and sunset (Guam and Bahamas) or sunrise alone

282 (Philippines and Caymans), confirms earlier descriptions of lionfish in both their native range

283 (Fishelson 1975, Myers 1999) and invaded range (Green et al. 2011).

284 **Between-ocean differences**

285 While lionfish time budgets and kill rates did not vary appreciably between oceans, there

286 were nonetheless differences in diet breadth, prey size and use of blowing behavior between the

287 native and invaded ranges. Although coral-reef fishes are far more diverse in the Pacific than in

288 the Atlantic (Roberts et al. 2002), we observed invasive lionfish successfully consuming a

289 broader diversity of fishes in the Atlantic than native lionfish in the Pacific. Diet was broader in

290 the Atlantic despite the fact that lionfish strikes were directed at a greater diversity of prey in the

291 Pacific. Atlantic prey species composition was similar to that previously observed in Bahamian

292 lionfish (Albins & Hixon 2008, Morris & Akins 2009). We observed only invasive lionfish

293 consuming parrotfishes (Scaridae). Parrotfishes are ecologically important herbivores that help to

294 keep seaweeds from overgrowing corals (Mumby 2006). Declines in such herbivores in the

295 invaded range could have severe indirect effects on Atlantic coral reefs (Albins and Hixon 2011).

296 There are at least three possible (not mutually exclusive) explanations for increased diet

297 breadth in invasive relative to native lionfish. The first is based on optimal foraging theory,

298 which predicts that diet breadth is determined by the encounter rate of preferred prey (Stephens

299 & Krebs 1986). It is possible that crustaceans and juvenile pomacentrids are preferred prey in the

300 Pacific and are present in sufficiently high densities that diet breadth is reduced in native Pacific

301 lionfish. The higher availability of fish recruits during the dates we sampled in the Philippines

302 (Abesamis & Russ 2010) compared to other regions is consistent with this hypothesis, yet the

303 fact that lionfish targeted a greater diversity of prey in the Pacific but successfully killed a lower

304 diversity of prey, tends to falsify this hypothesis.

305   A second explanation is that prey are naïve to lionfish as a novel predator in the newly

306 invaded Atlantic, allowing generalist lionfish to successfully capture a broader diversity of prey,

307 even when kill rates and hunting times were equal between native and invaded locations. This

308 explanation goes in line with our initial hypothesis that invasive lionfish would consume greater

309 variety of prey given the lack of native prey defenses. As observed for invasive lionfish (Albins

310 & Hixon 2008, Green et al. 2011), native prey may exhibit weak or nonexistent responses to

311 newly introduced predators (Cox & Lima 2006, Smith et al. 2008). Lionfish are new to the

312 Atlantic and do not resemble any native Atlantic predators. Therefore, prey types that normally

313 may not be available to native Pacific lionfish are present in invasive lionfish diet. Our findings

314 of broader targeted species in the native Pacific Ocean, yet greater success at killing more

315 diverse prey in the Atlantic, lends credence to this hypothesis. The prey naïveté explanation is

316 also supported by the larger prey size accessed by invasive lionfish. It is possible that, because

317 prey in the Pacific are more likely to recognize lionfish as predators, only the smallest and/or

318 least mobile species and individuals are vulnerable to predation. Still further evidence of prey

319 naïveté in the invaded range comes from differences in the use of blowing behavior by lionfish.

320 Lionfish employed blowing while stalking prey three times more often in the native Pacific range

321 compared to the invaded Atlantic range. Blowing behavior may confuse prey and facilitate head-

322 first capture as prey face upcurrent (Albins & Lyons 2012). Greater use of this hunting technique

323 may be required in the Pacific because prey recognize lionfish and are more wary. In contrast,

324 because lionfish are new to the Atlantic, they need not employ such secondary hunting methods

325 as frequently to capture naïve Atlantic prey. Given that native prey can adapt to invasive

326   predators by rapid evolution of behavioral responses to predator presence (Schlaepfer et al. 2005,

327   Freeman & Byers 2006), we suggest that future research focus on whether invasive lionfish and

328   native prey alter their attack and evasion behavior, respectively, through time.

329   A third explanation for increased diet breadth in invasive relative to native lionfish is the

330   competitive and/or predatory release that often accompanies invasions (Mack et al. 2000). For

331   example, the introduced grouper *Cephalopholis argus* fed on larger prey as a response to lower

332   competitor densities in non-native vs. native reefs (Meyer & Dierking 2011). A similar pattern

333   could affect lionfish hunting, given the larger prey sizes consumed at invaded reefs and the

334   higher diversity of ecologically similar reef fishes (i.e., potential competitors) in the native

335   Pacific relative to the invaded Atlantic (Roberts et al. 2002). Additionally, Albins (2012) has

336   demonstrated that invasive lionfish compete effectively with native grouper. Regarding release

337   from predation, although venomous spines appear to be an effective prey defense for larger

338   lionfish (Allen & Eschmeyer 1973), we hypothesize that new lionfish recruits (which have

339   flexible spines with less venom) may be the target of co-evolved, specialized, smaller predatory

340   fishes in the Pacific that do not occur in the Atlantic, thereby providing a source of biotic control

341   that is absent in the Atlantic.

342   **Conclusions**

343   Generally, lionfish are crepuscular predators in both their native Pacific and invaded

344   Atlantic ranges. Invasive lionfish seem to have maintained their native behaviors that generally

345   vary with environmental conditions, and therefore display no major inter-ocean differences in

346   overall activity patterns. Lionfish nonetheless exhibit substantial behavioral and ecological

347   differences between Pacific and Atlantic locations. First, invasive lionfish spend far less time

348   using blowing behavior, perhaps indicating prey naïveté in the Atlantic. Second, invasive

349   lionfish have far broader diets (measured by kill rates) despite the fact that (a) native lionfish

350   hunted greater variety of prey, and (b) the Pacific Ocean supports a far greater species diversity

351   of potential prey reef fishes. Importantly, only invasive lionfish were observed consuming

352   ecologically important parrotfishes. Third, Atlantic prey of lionfish are larger, even though prey

353   consumption rates are comparable to native Pacific lionfish, therefore implying that invasive

354   lionfish ingest a greater daily ration in terms of prey biomass than do native lionfish. Overall, it

355   is clear that red lionfish display a substantial capacity for behavioral adaptation to local

356   environmental conditions, likely contributing to their enormous success as an invasive species.

357

366

367   LITERATURE CITED

368   Abesamis RA, Russ GR (2010) Patterns of recruitment of coral reef fishes in a monsoonal
369   environment. Coral Reefs 29:911-921
370
371   Albins MA, Hixon MA (2008). Invasive Indo-Pacific lionfish (*Pterois volitans*) reduce
372   recruitment of Atlantic coral-reef fishes. Mar Ecol Prog Ser 367:233-238
373

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

Albins MA (2012) Effects of invasive Pacific red lionfish *Pterois volitans* versus a native predator on Bahamian coral-reef fish communities. Biol Inv DOI:10.1007/s10530-012-0266-1

Albins MA, Lyons PJ (2012) Invasive red lionfish *Pterois volitans* blow directed jets of water at prey fish. Mar Ecol Prog Ser 448:1-5

Allen GR, Eschmeyer WN (1973) Turkeyfishes at Eniwetok. Pac Discov 26:3-11

Andrews KS, Williams GD, Farrer D, Tolimieri N, Harvey CJ, Bargmann G, Levin PS (2009) Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator. Anim Behav 78: 525-536

Anderson MJ, Gorley RN, Clarke RK (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods. Primer-E Ltd., Plymouth/UK

Bates D, Maechler M, Bolker B (2011) Linear mixed-effects models using S4 classes. Package ´lme4´. R Foundation for Statistical Computing, Springer, New York

Belovsky GE, Slade JB (1986) Time budgets of grassland herbivores: body size similarities. Oecologia 70: 53-62

Bernadsky G, Goulet D (1991) A natural predator of the lionfish, *Pterois miles*. Copeia 1991(1): 230-231

Chen WM, Purser J, Blyth P (1999) Diel feeding rhythms of greenback flounder *Rhombosolea tapirina* (Günther 1862): the role of light-dark cycles and food deprivation. Aquac Res 30: 529-537

Côté IM, Maljkovic A (2010) Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. Mar Ecol Prog Ser 404: 219-225

Cox JG, Lima SL (2006) Naïveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. TREE 21:674-680

Fishelson L (1975) Ethology and reproduction of pteroid fishes found in the Gulf of Aqaba (Red Sea), especially *Dendrochirus brachypterus* (Cuvier) (Pteroidae, Teleostei). PSZNI: Mar Ecol 39:635–656

Fishelson L (1997) Experiments and observations on food consumption, growth and starvation in Dendrochirus brachypterus and Pterois volitans (Pteroinae, Scorpaenidae). Environ Biol Fish 50: 391-403

419 Freeman AS, Byers JE (2006) Divergent induced responses to an invasive predator in marine
420 mussel populations. Science 313: 831-833

421

422 Green SJ, Côté IM (2008) Record densities of Indo-Pacific lionfish on Bahamian coral reefs.
423 Coral Reefs 28: 107

424

425 Green SJ, Akins JL, Côté IM (2011) Foraging behavior and prey consumption in the Indo-Pacific
426 lionfish on Bahamian coral reefs. Mar Ecol Prog Ser 433:159-167

427

428 Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish
429 declines. PLOS One 7(3): e32596. doi:10.1371/journal.pone.0032596

430

431 Guo Q (2006) Intercontinental biotic invasions: What can we learn from native populations and
432 habitats? Bio Invasions 8:1451-1459

433

434 Hansen EA, David BO, Closs GP (2004) Diel patterns of feeding and prey selection in giant
435 kokopu (*Galaxias argenteus*). N Z J of Mar Freshw Res 38:341-345

436

437 Helfman GS (1986) Fish behaviour by day, night and twilight. In: Pitcher TJ (ed) Behavior of
438 Teleost Fishes. Pp. 479-512. Chapman & Hall, London.

439

440 Holway DA, Suarez AV (1999) Animal behavior: an essential component of invasion biology.
441 TREE 14(8): 328-330

442

443 Kulbicki M, Beets J, Chabanet P, Cure K, Darling E, Floeter SR, Galzin R, Green A, Harmelin-
444 Vivien M, Hixon M, Letourneur Y, Lison de Loma T, McClanahan T, McIlwain J, MouTham G,
445 Myers R, O´Leary JK, Planes S, Vigliola L, Wantiez L (2012) Distributions of Indo-Pacific
446 lionfishes *Pterois spp*. In their native ranges: implications for the Atlantic invasion. Mar Ecol
447 Prog Ser 446: 189-205

448

449 Lesser MP, Slattery M (2011) Phase shift to algal dominated communities at mesophotic depths
450 associated with lionfish (Pterois volitans) invasion on a Bahamian coral reef. Bio Inv 13: 1855-
451 1868

452

453 Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions:
454 Causes, epidimiology, global consequences, and control. Ecol App 10: 689-710

455

456 MacNally, R (1996) Hierarchical partitioning as an interpretative tool in multivariate inference.
457 Aus Ecol 21(3): 224-228

458

459 Maljkovic A, Van Leeuwen T (2008) Predation on the invasive red lionfish, *Pterois volitans*
460 (Pisces: Scorpaenidae), by native groupers in the Bahamas. Coral Reefs 27: 501

461

462 Meyer AL and Dierking J (2011) Elevated size and body condition and altered feeding ecology
463 of the grouper *Cephalopholis argus* in non-native habitats. Mar Ecol Prog Ser 439: 203- 212

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

Morris JA, Whitfield PE (2009) Biology, ecology, control and management of the invasive Indo-Pacific lionfish: An updated integrated assessment. Tech Mem NOS NCCOS 99. National Oceanic and Atmospheric Administration, Washington DC

Mumby, P J (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecol App 16:747-769

Myers R (1999) Micronesian reef fishes: a field guide for divers and aquarists. Coral Graphics, Barrigada/Guam

Peng CJ, Lee KL, Ingersoll GM (2002) An introduction to logistic regression analysis and reporting. J. Educ Res 96(1): 3-14

Quinn GP, Keough MJ (2002) Experimental Design and Data Analysis for Biologists. Cambridge University Press, New York

R Development Core Team (2008) *R*: a language and environment for statistical computing. *R* Foundation for Statistical Computing, Vienna, Austria http://www.R-project.org

Randall J (2005) Reef and shore fishes of the South Pacific: New Caledonia to Tahiti and the Pitcairn Islands. University of Hawaii Press, Honolulu

Reebs SG (2002) Plasticity of diel and circadian activity rhythms in fishes. Rev Fish Biol Fish 12: 349-371

Roberts CM, McClean CJ, Veron JEN, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, Vynne C, Werner TB (2002). Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295:1280-1284

Rossiter DG, Loza A (2010) Technical note: analyzing land cover change with logistic regression in R. University of Twente, Faculty of Geo-Information Science & Earth Observation, Enschede, NL. http://www.itc.nl/~rossiter/teach/R/R_lcc.pdf

Schofield P (2009) Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennet 1828]) in the Western North Atlantic and Caribbean Sea. Aquat Invasions 4(3): 473-479

Schofield P (2010) Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennet 1828]) in the Western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. Aquat Invasions 5(1): S117-S122

Schlaepfer MA, Sherman PW, Blossey B, Runge, MC (2005) Introduced species as evolutionary traps. Ecol Lett 8: 241-246

511 Semmens BX, Buhle ER, Salomon AK, Pattengill-Semmens CV (2004) A hotspot of non-native
512 marine fishes: evidence for the aquarium trade as an invasion pathway. Mar Ecol Prog Ser 266:
513 239-244
514
515 Smith GR, Boyd A, Dayer CB, Winter KE (2008) Behavioral responses of American toad and
516 bullfrog tadpoles to the presence of cues from the invasive fish, *Gambusia affinis*. Biol Inv
517 10(5): 743-748
518
519 Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, New
520 Jersey
521
522 Valdez-Moreno M, Quintal-Lizama C, Gómez-Lozano R, García-Rivas MC (2012) Monitoring
523 an alien invasión: DNA barcoding and the identification of lionfish and their prey on coral reefs
524 of the Mexican Caribbean. Plos One 7(6): e36636
525
526 Walsh C, Mac Nally R (2008) hier.part: Hierarchical partitioning, R package version 1.0-3. R
527 Foundation for Statistical Computing, Springer, New York
528
529 Whitfield PE, Hare JA, David AW, Harter SL, Muñoz RC, Addison CM (2007) Abundance
530 estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the Western North
531 Atlantic. Biol Invasions 9: 53-64.
532

Table 1. Results of logistic regressions of lionfish time budgets between the native Pacific Ocean and the invaded Atlantic Ocean, using a general linear mixed-effects model (GLMM). Shown are coefficient estimates for each explanatory variable (ß) together with standard errors (SE), significance (*p*) and odd ratios ($e^ß$). Also presented are the independent effects of each explanatory variable (%) on the dependent variable (lionfish behavior), calculated by hierarchical partitioning. *P* values in bold italics are significant. Likelihood ratio and chi-square test statistics indicate logistic regression model fit. Reference levels for this regression were set as Atlantic for ocean, sunrise for time period, hard coral for habitat, clear for weather, and high for current.

| Coefficient		Estimate (ß)	SE	*p*	$e^ß$	Independent effects (%)
Intercept		-0.003	0.773	0.997		
Ocean						3.754
	Pacific	0.438	0.891	0.623	1.549	
Time Period						35.626
	Morning	-2.557	0.244	***<0.001***	0.078	
	Midday	-2.446	0.279	***<0.001***	0.087	
	Afternoon	-1.748	0.216	***<0.001***	0.174	
	Sunset	-0.719	0.271	***0.008***	0.487	
Habitat						13.715
	other	0.434	0.259	0.094	1.543	
	rock-boulder	-0.479	0.239	***0.045***	0.619	
	sand-rubble	0.451	0.271	0.096	1.569	
Cloud cover						7.567
	overcast	0.687	0.227	***0.002***	1.988	
	partly cloudy	-0.158	0.184	0.389	0.854	
Current						9.570
	low	1.210	0.326	***<0.001***	3.355	
	medium	1.125	0.346	***0.001***	3.079	
Size						10.055
		-0.014	0.013	0.102	0.258	
Depth						19.712
		0.028	0.024	0.499	0.241	
Likelihood ratio test statistic				420.736, ***p<0.001***		
Pearson Chi-square				1092.019, p=0.727		

Table 2. Reef-fish and crustacean prey targeted by lionfish (based on strikes, but not necessarily kills) while hunting in their native Pacific (Philippines, Guam) and the invaded Atlantic (Cayman Islands, Bahamas). Shown are species (or taxa when species identification was not possible) targeted with an indication of whether each prey type was accessible to lionfish in the Atlantic, Pacific or both, and with their respective species specific successful kill rates. The unidentified category includes both fishes and crustaceans.

| Subphylum/ Superclass	Family	Species/taxa	Access In	PACIFIC (Pac.)		ATLANTIC (Atl.)	
				Philippines % Success	Guam % Success	Caymans % Success	Bahamas % Success
Crustacea		Mysidacea	Both	-	-	50	-
Osteichthyes	Acanthuridae	*Acanthurus nigricans*	Pac.	-	0	-	-
	Apogonidae	*Apogon townsendi*	Atl.	-	-	100	-
		Apogon sp.	Pac.	0	0	-	-
		Cheilodipterus sp.	Pac.	0	-	-	-
	Blenniidae	*Malacoctenus triangulatus*	Atl.	-	-	100	-
		Meiacanthus atrodorsalis	Pac.	-	0	-	-
	Gobiidae	*Coryphopterus glaucofraenum*	Atl.	-	-	100	75
		Unidentified goby	Both	0	0	100	-
	Grammatidae	*Gramma loreto*	Atl.	-	-	0	-
	Labridae	*Halichoeres bivittatus*	Atl.	-	-	-	50
		Halichoeres garnoti	Atl.	-	-	100	0
		Labroides dimidiatus	Pac.	0	-	-	-
		Thalassoma bifasciatum	Atl.	-	-	-	33
	Plotosidae	*Plotosus lineatus*	Pac.	0	-	-	-
	Pomacentridae	*Chromis* recruits	Pac.	50	-	-	-
		Pomacentrus coelestis	Pac.	-	0	-	-
		Stegastes partitus	Atl.	-	-	-	100
	Scaridae	*Scarus iserti*	Atl.	-	-	-	75
		Sparisoma aurofrenatum	Atl.	-	-	-	100
		Unidentified parrotfish	Atl.	-	-	0	-
	Serranidae	*Serranus tigrinus*	Atl.	-	-	0	-
	Tetraodontidae	*Canthigaster rostrata*	Atl.	-	-	0	0
	Trichonotidae	*Trichonotus elegans*	Pac.	100	-	-	-
Unidentified			Both	36.2	29.2	20.9	22.7
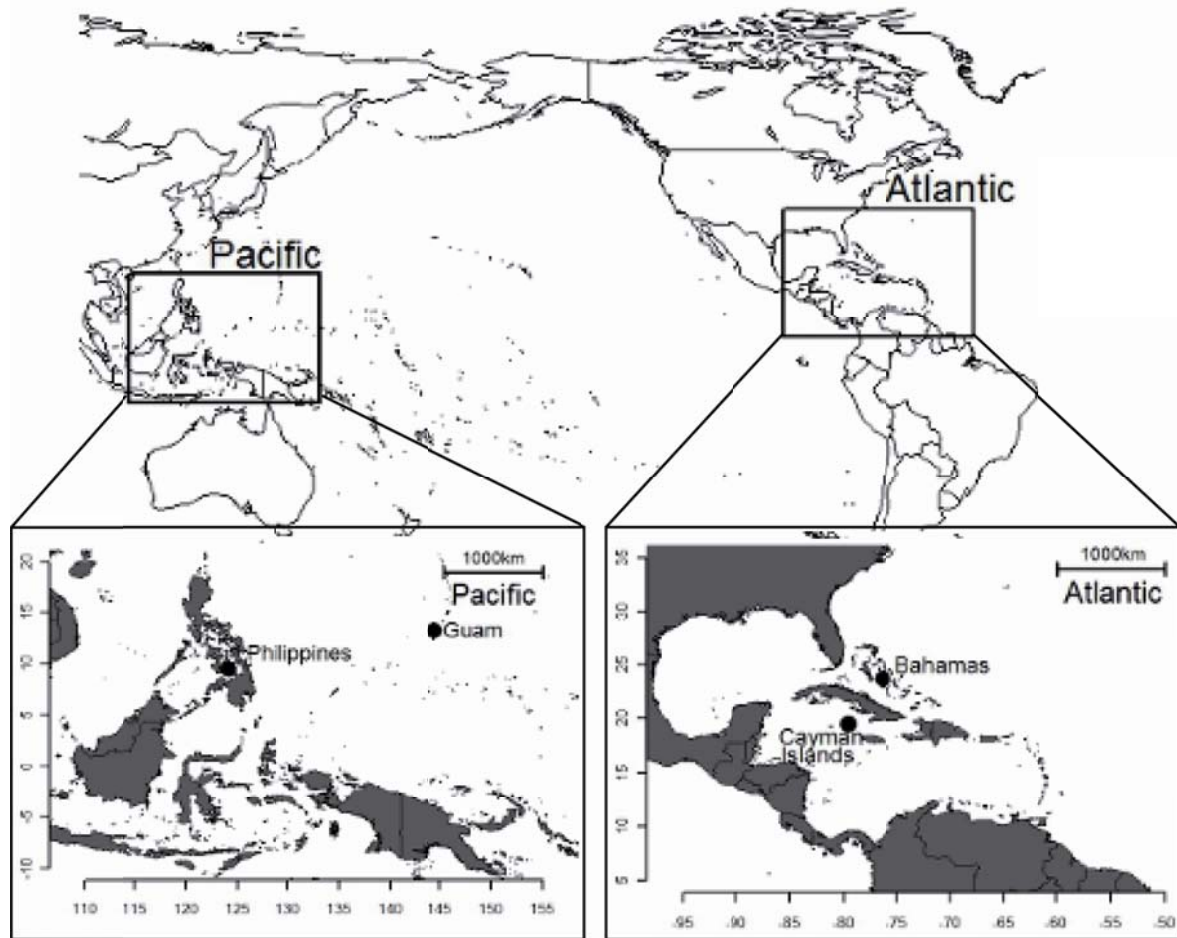
Fig. 1. Regions sampled: the Philippines and Guam in the Pacific Ocean, and the Cayman Islands and Bahamas in the Atlantic Ocean.
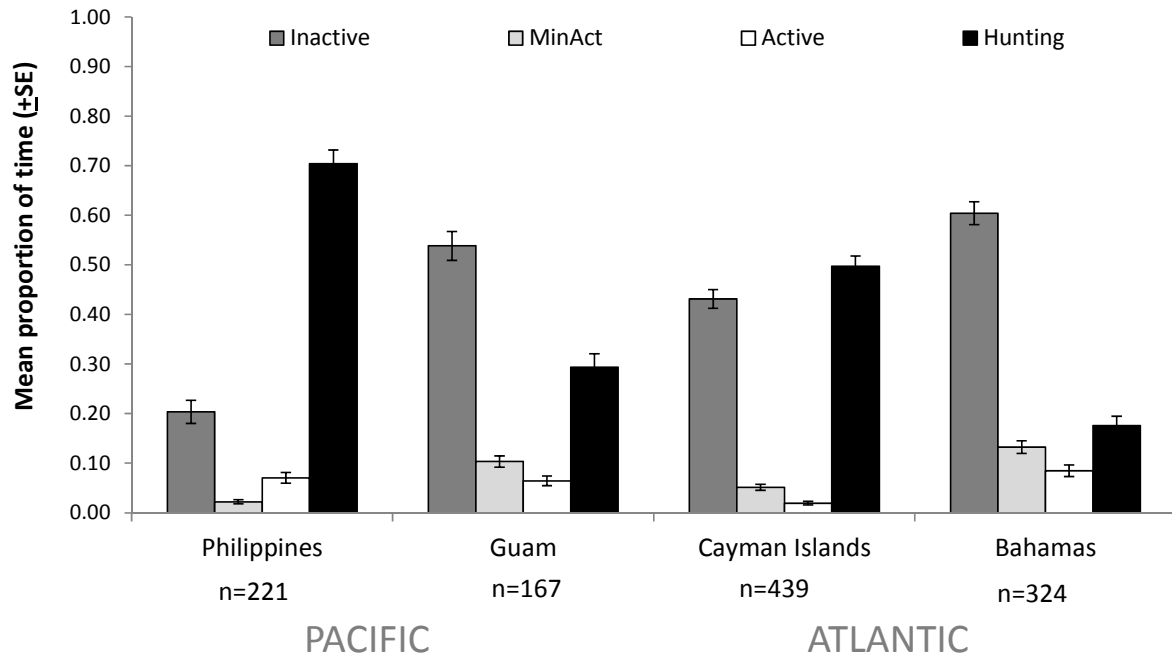
555
556 Fig. 2. Time budget summaries for lionfish in each of four regions, two per ocean. Shown are
557 mean proportions (± SEM, n = number of 10-minute samples) of dawn-to-dusk time in each of
558 the four activities recorded (inactive, minimal activity [MinAct], active and hunting).

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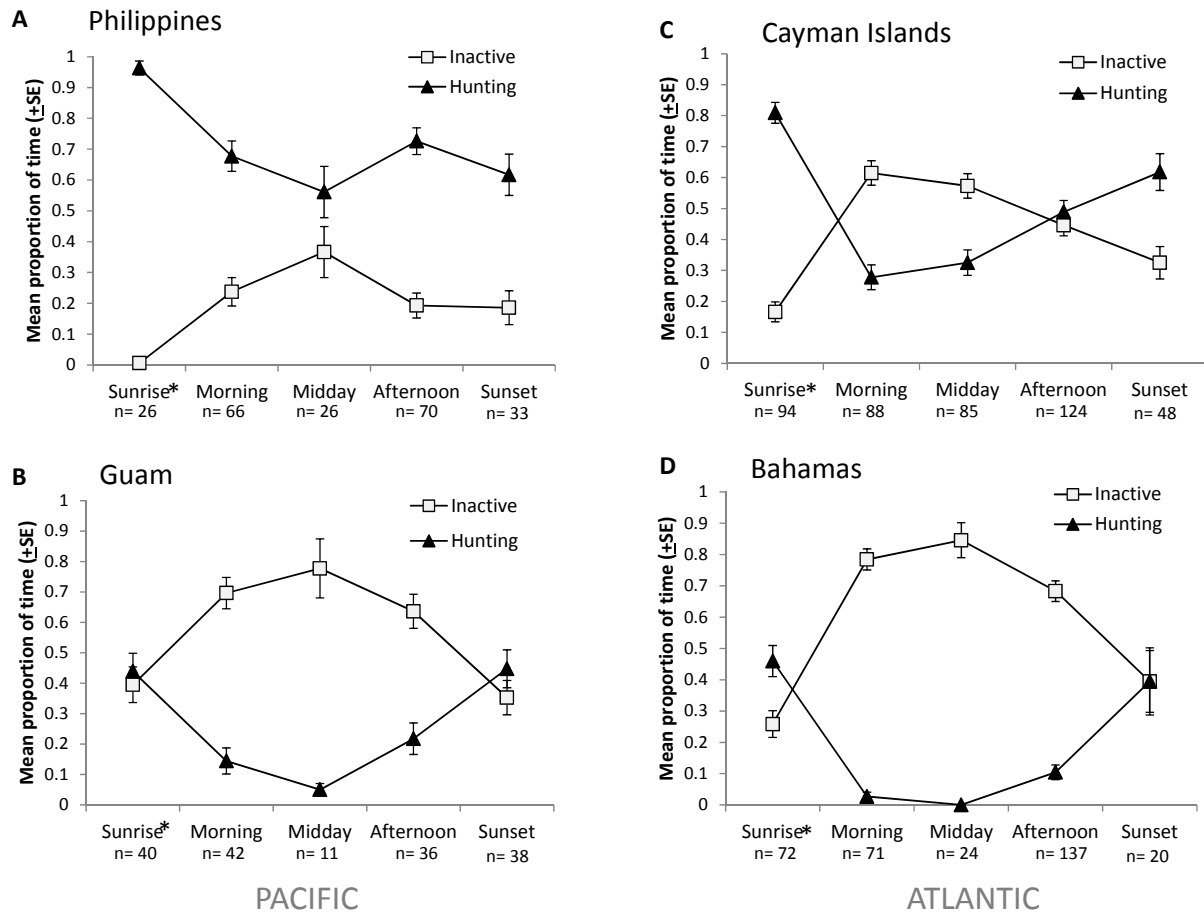
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561 Fig. 3. Time budgets of lionfish across time of day for inactivity and hunting behavior at each of
562 the four regions: (A) Philippines , (B) Guam, (C) Cayman Islands, and (D) Bahamas. Shown are
563 mean proportions (± SEM) of time spent in each behavior, standardized to regional sunrise and
564 sunset times: Sunrise = sunrise to 2 hr after sunrise, Morning = 2 to 5 hr after sunrise, Midday =
565 ca. 3-hour period midway between sunrise and sunset, Afternoon = 2 to 5 hr before sunset,
566 Sunset = 2 hr before sunset to sunset. n = # of 10-min samples. Asterisk (*) next to sunrise
567 represents significant differences in activity levels for this time period (p < 0.01; see GLMM
568 results Table 1).

569
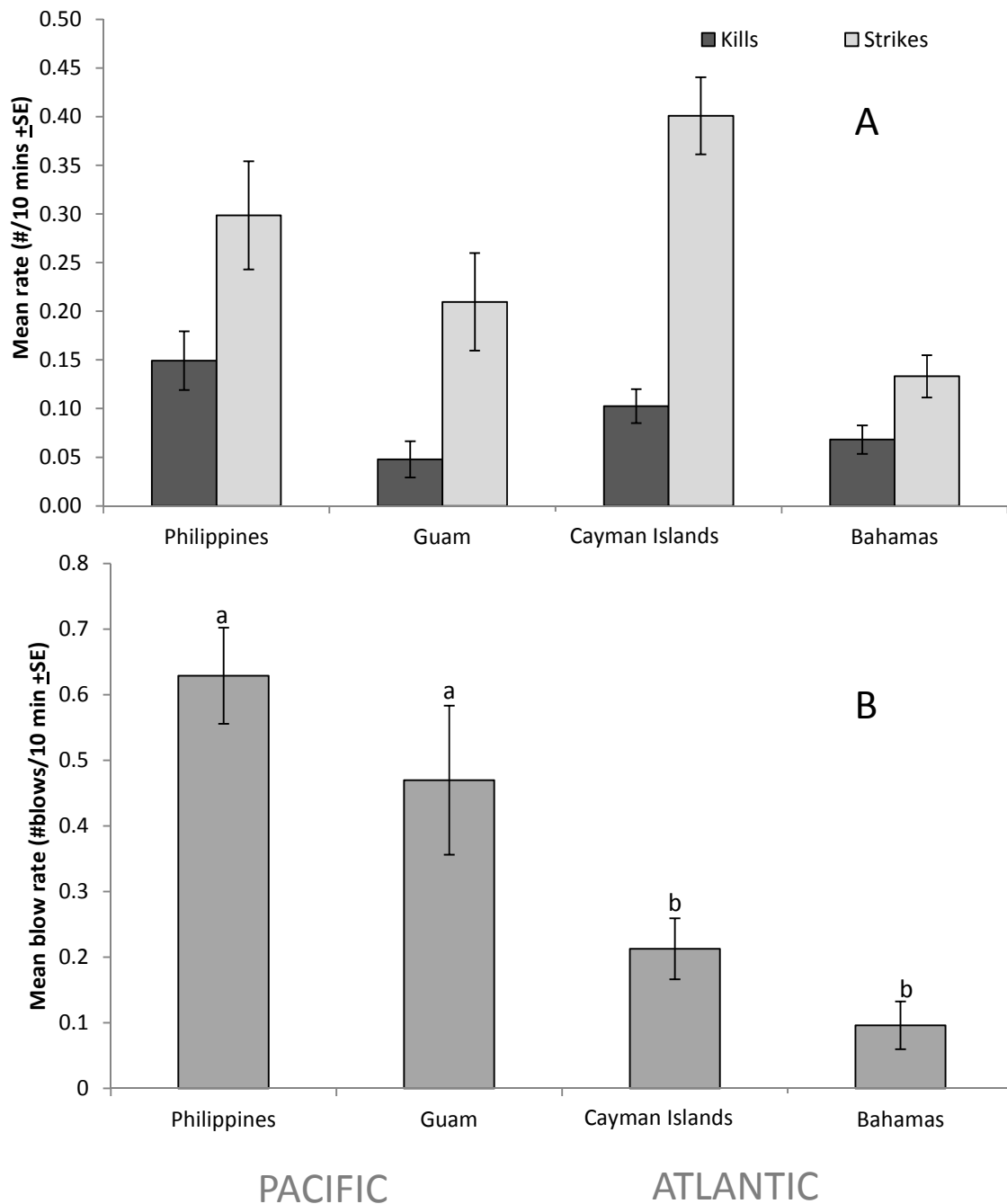
570
571 Fig. 4. Comparison of: (A) mean (± SEM) strike rates (successful and unsuccessful) and kill
572 rates (successful strikes, *i.e.* prey consumed), and (B) mean (± SEM) blow rate of lionfish in the
573 Pacific (left) and Atlantic (right). For (B) letters denote significant differences in blow rates
574 between Pacific and Atlantic Oceans (*Pseudo-F* = 13.234, df = 1, 1113, p = 0.001).
575
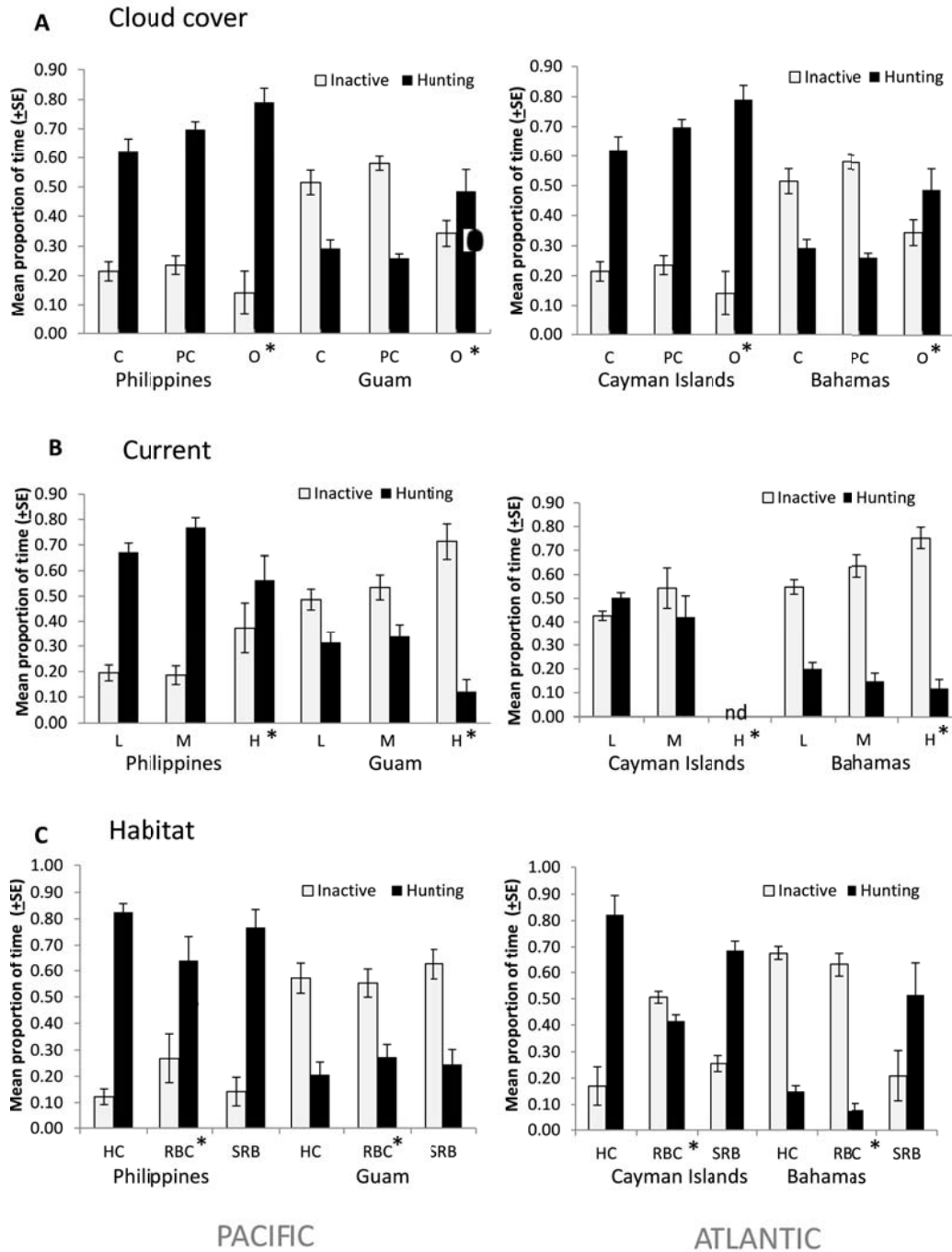
576
577 Fig 5. Mean proportion of time (± SEM) lionfish spent inactive or hunting in relation to: (A)
578 cloud cover (C = clear, PC = partly cloudy, O = overcast), (B) water current level (L = low, M =
579 medium, H = high), and (C) habitat (HC = hard coral, RBC = rock-boulder/cave, SRB =
580 sand/rubble) in the native Pacific (left) and invaded Atlantic (right). Asterisks next to letters (H,
581 O and RBC) represent significant differences in overall activity levels at this level for each
582 environmental factor (p< 0.05; see GLMM results Table 1).
583
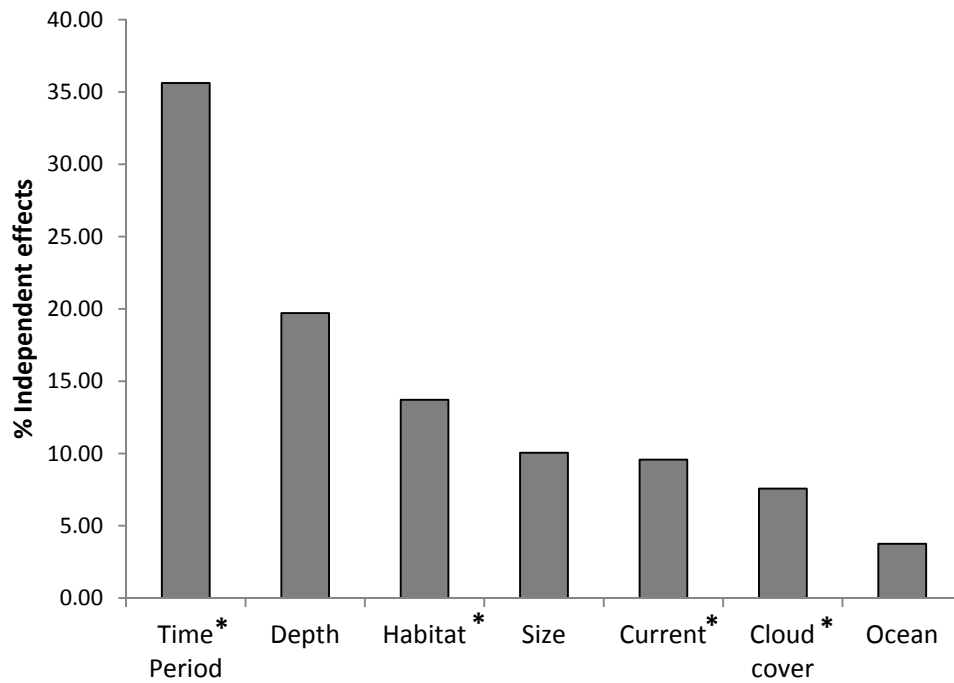
Fig. 6. The percent contribution of each explanatory environmental variable to the total variation in lionfish behavior detected by the hierarchical partitioning analyses of the logistic regression model (see Table S1 in the Supplement). Asterisks next to variables indicate which variables were significant in the logistic model.