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High population density recruitment and survival of a harvested coral reef fish

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1 *Running head:* Inverse density dependence in harvested fish

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4 **High population density enhances recruitment and survival of a harvested coral reef**
5 **fish**

6

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15 **ABSTRACT**

16 A negative relationship between population growth and population density (direct density
17 dependence) is necessary for population regulation and is assumed in most models of
18 harvested populations. Experimental tests for density dependence are lacking for large-
19 bodied, harvested fish because of the difficulty of manipulating population density over large
20 areas. We studied a harvested coral reef fish, *Lutjanus apodus* (schoolmaster snapper) using
21 eight large isolated natural reefs (0.4-1.6 ha) in the Bahamas as replicates. An initial
22 observational test for density dependence was followed by a manipulation of population
23 density. The manipulation weakened an association between density and shelter-providing
24 habitat features, and revealed a positive effect of population density on recruitment and
25 survival (inverse density dependence), but no effect of density on somatic growth. The
26 snappers on an individual reef were organized into a few shoals, and we hypothesize that
27 large shoals on high-density reefs were less vulnerable to large piscivores (groupers and
28 barracudas) than the small shoals on low-density reefs. Reductions in predation risk for
29 individuals in large social groups are well documented but, because snapper shoals occupied
30 reefs the size of small marine reserves, these ecological interactions may influence the
31 outcome of management actions.

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35 **KEYWORDS:** coral reef fish, critical habitat, demographic rate, density dependence, inverse
36 density dependence, large-scale experiment, marine protected area, recruitment, survival.

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39 INTRODUCTION

40 Density dependence is central to population dynamics and is required for population
41 regulation (Murdoch 1994). Most models for harvested populations assume that per-capita
42 population growth rates will increase when and where harvesting reduces population density
43 by increases in rates of growth, reproductive output, or survival (Sissenwine 1984, Rose et al.
44 2001). This direct density-dependent feedback is expected because unharvested populations
45 are assumed to be at their carrying capacity set by limited resources (Rose et al. 2001). This
46 assumption may, however, be false in situations where unharvested populations are kept
47 below carrying capacity by predators, disturbance, or changing environmental conditions.

48 Evidence for direct density dependence in harvested marine species is limited because
49 testing is difficult for several reasons. Firstly, many stocks have been so depleted that there
50 are simply no high-density populations to study (Myers and Cadigan 1993). Secondly, it is
51 sometimes difficult to isolate effects of density using observational studies because
52 population density often covaries with other variables (Shima and Osenberg 2003). For
53 example, animals tend to select better quality habitats and so they are often naturally more
54 crowded in better quality habitat. Experimental manipulation of population density can
55 mitigate these difficulties, but it is logistically challenging with harvested species, and so has
56 only been done using small juveniles (reviewed in White et al. 2010). In contrast, density-
57 manipulations have been performed many times using small-bodied reef fishes because they
58 are abundant, have small home ranges, and can be stocked on small experimental habitat
59 replicates to create gradients of density (Hixon and Webster 2002, Osenberg et al. 2002). It is
60 hoped that insights into density dependence learned from these “model species” apply to
61 larger harvested species that are more difficult to work with, but there is no empirical basis to
62 conclude that they do.

63 Studies on “model species”, like small coral-reef fishes, have revealed that direct
64 density dependence is common (Hixon and Webster 2002), but not universal. Some studies
65 have revealed no effects of density (e.g., Doherty 1983), and others have revealed inverse
66 density dependence (e.g., Booth 1995, Sandin and Pacala 2005, White and Warner 2007).
67 White et al. (2010) hypothesized that inverse density dependence was more likely in
68 schooling species, which benefit from group living, whereas direct density dependence might
69 be more prevalent in solitary species. Extrapolating to harvested fishes, we might expect that
70 species living in schools are more likely to experience inverse density dependence (Clark
71 1974, Murphy 1980).

72 Because density-dependent interactions determine how populations respond to
73 thinning or crowding, a better understanding of their effects is necessary for successful
74 management and conservation. For example, the relative efficacy of marine reserves versus
75 more traditional fisheries regulations in maximizing harvest hinges on the form and intensity
76 of density dependence (Hastings and Botsford 1999). The crowding that follows the build-up
77 of harvested fish populations within no-take reserves (Halpern 2003, Lester et al. 2009) is
78 predicted to induce direct density dependence (Sanchez Lizaso et al. 2000), which in turn
79 should decrease the fisheries yield from reserves via the export of young to fished areas
80 (Hastings and Botsford 1999, Gerber et al. 2003). If, instead, the steady build-up inside
81 reserves leads to increased survival or reproductive rates (inverse density dependence) this
82 may increase fisheries production in surrounding areas through reproductive export. With
83 inverse density dependence, a network of marine reserves might produce higher overall
84 yields than more traditional management tools, such as catch limits.

85 Here we report the results of an observational test for density dependence in a
86 harvested coral reef fish, followed immediately by a field manipulation of population density.
87 We used a set of large isolated natural reefs as replicates, each of which was comparable in

88 size to a small marine reserve. By working in a lightly fished area, we were able to create a
89 gradient of density that spanned most of the natural range for the study species. Specifically,
90 our goals were to (1) perform a correlational test for density dependence under natural
91 conditions, 2) test the relationship between density and habitat attributes, and 3) manipulate
92 density to reduce its correlation with habitat attributes to get a stronger test for density
93 dependence.

94

95 **METHODS**

96 *Study populations*

97 The study species, *Lutjanus apodus* Walbaum (the schoolmaster snapper) is one of the
98 most abundant large generalist carnivores on reefs in the Caribbean and subtropical Atlantic.
99 *L. apodus* is harvested from coral reefs throughout the region (Anderson 2002) and is found
100 in schools of several to hundreds of individuals. We studied populations of *L. apodus* on 8
101 natural reefs in the Bahamas (23°46' N, 76°10' W) that were spread over a 25-km long area
102 and sufficiently isolated to serve as natural replicates (Appendix A). Each study reef was
103 separated from other suitable habitat for *L. apodus* by at least hundreds of meters of sand
104 plains or seagrass beds, and from other study reefs by 1 – 6 km (Appendix A). Other small
105 fragments of suitable back-reef habitat existed in the study area, but our study sites contained
106 the largest expanses and the majority of suitable habitat for *L. apodus* in the area. Individual
107 reefs contained between 0.4 and 1.6 hectares of suitable habitat for our study species, and so
108 were comparable in size to small marine reserves (IUCN and UNEP 2010). The study reefs
109 were all back reefs in shallow water (1-10 m), and were primarily composed of coral heads,
110 soft corals and sponges on sand, rubble or pavement substrata. They ranged in shape from
111 rings of reef habitat surrounding small islands, to long, isolated patch reefs, to large expanses

112 of reef off the shores of islands. The study populations are fished infrequently, because
113 human population densities are low in this area and fishers still target higher value fisheries
114 for conch, lobster and Nassau grouper, which are no longer viable in much of the Caribbean
115 (Chiappone et al. 2000).

116 *Study design*

117 Our study was conducted in two phases: an observational phase and an experimental
118 phase. The 2-year observational phase (June 2002 – June 2004) mimicked the typical design
119 of tests for density dependence in harvested species. In the third year (July 2004 – August
120 2005), densities of *L. apodus* were manipulated to provide a stronger test of density-
121 dependent feedbacks (detailed below). During both phases, survival and growth were
122 measured by standard mark-recapture methods (described later). Recruitment was measured
123 with underwater visual censuses (described below) only during the experimental phase. We
124 tested for density dependence by correlating per-capita vital rates (survival, recruitment and
125 somatic growth) with spatio-temporal fluctuations in snapper density.

126 *Estimating population density of L. apodus*

127 Population density and size structure (standard length (SL)) of *L. apodus*, were
128 assessed by underwater visual census along 3–7 permanent 50 x 10 m band transects at each
129 site. Transects were counted by a single observer (the first author) on 18 occasions between
130 June 2002 and August 2005. A pilot study showed that underwater visual estimates of fish
131 length were quite accurate. The first author visually estimated the SL of individually
132 recognizable (externally tagged) *L. apodus* during a census and the same fish were then
133 captured and measured. The mean difference between estimated and actual SL was 0.7 cm,
134 and paired measurements were statistically indistinguishable (paired *t*-test, $n = 44$, $t = 1.5$, df
135 $= 43$, $P = 0.14$; Wormald and Steele 2008).

136 *Quantifying habitat quality*

137 Structural attributes of the habitat were quantified to assess the influence of the
138 physical environment on *L. apodus* density. Preliminary observations revealed that this
139 species congregated near large coral heads or limestone boulders (lithified carbonate
140 sediments fallen from adjacent islands). Coral and limestone boulders were distinguished
141 because coral boulders usually include a larger number of internal voids than similarly sized
142 limestone boulders and our observations suggested they provide more shelter space for *L.*
143 *apodus*. The height, width and breadth of all coral heads and limestone boulders larger than
144 0.5 m in any dimension was measured on each of the permanent 50 x 10 m band transects
145 surveyed for *L. apodus*. These habitat features were surveyed only once because they did not
146 change perceptibly over the study period. Since we did not know beforehand which specific
147 features of the coral heads and boulders *L. apodus* might be responding to, we evaluated a
148 number of metrics: total number of coral and limestone boulders per m², the sum of coral and
149 limestone boulder heights per m², sum of coral and limestone boulder volume per m², total
150 number of coral boulders per m², sum of coral boulder heights per m², and the sum of coral
151 boulder volume per m². Models including only limestone boulders and not coral boulders
152 were not evaluated because limestone boulders were relatively rare and present at only 3 of
153 the 8 sites. Each metric was related to the density of *L. apodus* using linear regression and the
154 best metric was defined as the one that explained most variation in density (highest *r*² value)
155 and had the highest model likelihood (lowest corrected Akaike Information Criterion (AICc)
156 value; Burnham and Anderson 2002).

157 *Recruitment to the study reefs*

158 *L. apodus* juveniles occupy mangroves and shallow inshore areas nursery areas before
159 recruiting to coral reefs. Most recruitment to the study reefs occurred between July and
160 November and recruits are between 8-14 cm SL when they first appear (Nagelkerken et al.,

161 2002, Wormald 2007). Operationally, we defined all *L. apodus* less than 14 cm SL counted
162 during the underwater visual transects as recruits. Our analysis of recruitment used data only
163 from 2004 and 2005 (after the density manipulation), because we did not collect data in
164 autumn of the previous two years.

165 General linear models were used to test whether recruit density was a function of
166 post-recruit (*L. apodus* \geq 14 cm SL) density, habitat quality (coral boulder volume m⁻²) or
167 differed among years (2004 and 2005). Site means each year were replicates for the analysis
168 (8 sites x 2 years; $n = 16$). Different combinations of independent variables were tested, and
169 the best model was chosen based on relative model likelihood (AICc values) and variance
170 explained (r^2 values).

171 *Mark-recapture sampling for growth and survival*

172 Capture-mark-recapture (CMR) methods were used to measure growth and estimate
173 survival throughout the study (Lebreton et al. 1992). Twelve CMR sessions were conducted
174 between June 2002 and August 2005, each lasting between 1 and 4 weeks. During each
175 session, fish were sampled using unbaited 2.5-cm square-mesh fish traps with a 24-hour soak
176 time and all *L. apodus* captured were given unique passive integrated transponder (PIT) tags
177 (12 mm, 125kHz; Allflex USA Inc., Dallas, Texas). Captured *L. apodus* were first
178 anaesthetized in a 200 mg/L solution of tricaine methanesulfonate (MS-222) in seawater
179 buffered with sodium bicarbonate. Once anaesthetized, they were measured (SL) and scanned
180 for a PIT tag. A PIT tag was injected into the abdominal cavity of all untagged fish. In a
181 previous double-tagging study ($n = 376$), PIT tag loss was $< 6\%$ in the first week and 0% in
182 the subsequent year, so we assumed loss of PIT tags was negligible (Wormald and Steele
183 2008). After processing, each fish was placed into a holding tank with fresh seawater for 10
184 to 20 minutes. The fish were then released by placing them in an opened trap near a coral
185 head at the capture site. This method was developed during a 2001 pilot study and, based on

186 our observations, ensured that *L. apodus* were able to safely rejoin their school upon release.
187 A total of 1,863 *L. apodus* were tagged, ranging in size from 10-40 cm SL. Seven hundred
188 and sixty nine individuals were recaptured at least once, and the interval between recaptures
189 ranged from 1-809 days.

190 *Experimental phase: density manipulation*

191 In the initial observational phase of the study, *L. apodus* populations were denser at
192 sites with abundant shelter (Fig. 1) so we manipulated population densities to reduce the
193 correlation between fish density and habitat. The 8 study sites were divided into 4 pairs that
194 had similar densities and habitat characteristics. One member of each pair was randomly
195 assigned for reduction of density and the other for density-elevation (Appendix A). We
196 moved fish from reduction to elevation reefs 4 times over a span of 12 months to maintain
197 differences between the treatments (a press manipulation, sensu Bender et al. 1994).

198 Fish were moved among reefs during trapping sessions. At reduced density sites, a
199 subset of captured *L. apodus* was haphazardly selected for relocation. Selected fish were
200 placed in holding tanks in the boat and driven to the designated density-elevation reef. At the
201 elevation reef, the fish were placed in a closed fish trap near to coral heads harboring other
202 schoolmasters and allowed to acclimate for 20 minutes before being released by a freediver.
203 In a separate analysis, we detected no difference in growth and survival of PIT tagged fish
204 that were relocated from those remaining at their home site (Wormald 2007).

205 Based on the 18 underwater visual censuses (7 before the manipulation and 11 after
206 it), we succeeded in altering densities at the study sites, as indicated by a significant
207 interaction between treatment (density elevation or reduction) and time period (pre- or post-
208 manipulation) (ANOVA: $F_{1,123} = 19.92$, $P < 0.001$) (Appendix B); and in weakening the
209 correlation between density and habitat attributes (Fig. 1).

210 *Estimating somatic growth rates*

211 Growth was estimated using PIT tagged individuals that were recaptured at least once.
212 Daily growth was calculated as the change in SL divided by the number of days at liberty. To
213 test the precision of SL measurements made in the boat, we compared repeated measurements
214 of fish recaptured after less than 7 days at liberty (based on the conservative assumption that,
215 over such a short time, differences reflect only measurement error). Repeated measurements
216 of the same fish differed by 0.14 cm SL on average ($n = 61$). To minimize the influence of
217 this slight measurement error, we only analyzed growth for individuals at liberty for more
218 than 38 days (mean growth after 38 days = 0.37 cm). Growth estimates were obtained from
219 299 individuals in the pre-manipulation period and 187 in the post-manipulation period. For
220 individuals recaptured more than once, we used a single growth estimate derived from the
221 change in length over the longest at-liberty span. Average growth was 1.66 cm, considerably
222 more than our measurement error.

223 To test the effect of density on growth rate, it was necessary to correct for the effect of
224 a fish's initial size on its daily growth rate because growth declined with size. To remove this
225 effect of size, rather than analyze absolute growth in mm/day, we used residuals from the
226 relationship between daily growth and initial size. These residuals were not normally
227 distributed and so to meet this assumption they were log transformed (after adding 0.002 to
228 each residual to make them all positive). We used linear regression to test for an effect of
229 density and habitat (coral boulder volume m^{-2}) on growth rate. Separate regressions were run
230 for the pre- and post-density manipulation periods, and mean growth rates per reef were used
231 as replicates ($n = 8$ per period). We tested models that included terms for adult density,
232 habitat, and both factors.

233 *Estimating survival rates*

234 Per-capita rates of apparent survival (Φ) were estimated using the recapture histories
235 of the 1863 PIT-tagged fish (Lebreton et al. 1992). We refer to Φ as apparent survival, since
236 the permanent disappearance of tagged fish could represent either mortality or emigration.
237 Because there were 12 recapture sessions and some fish were recaptured more than once
238 (maximum = 9 recaptures), we were able to model both Φ and the probability that a fish
239 would be captured if present (p) using the Cormack-Jolly-Seber (CJS) model (White and
240 Burnham 1999). The time step for the CJS models was one month (i.e., Φ and p are
241 probabilities measured over 30 days).

242 The CJS model assumes p is a function of site and time. Preliminary modeling of
243 recapture histories revealed that *L. apodus* captured in the preceding trapping session had a
244 slightly higher capture probability in the next session than other individuals (i.e., they were
245 “trap-happy”) (Wormald and Steele 2008). To account for this bias in capture probability, p
246 was modeled as a function of m (whether a fish was captured in the preceding session)
247 (following Pradel 1993). Tests of model fit showed that p was well described as an additive
248 function of site, time, and m (Wormald 2007); and Φ was modeled as such in all analyses of
249 factors affecting Φ .

250 We assessed effects of density and habitat on Φ over the entire study period by
251 constructing a candidate set of plausible CJS models for Φ that incorporated different
252 combinations of covariates (density and habitat) plus relevant grouping variables (site and
253 time). Relative fit of the models to the data was assessed using AICc, which is particularly
254 useful when comparing models with varying numbers of parameters because it reflects both
255 model fit to the data and simplicity (few parameters) (Burnham and Anderson 2002).

256 RESULTS

257 During the initial observational phase, the density of *L. apodus* was positively
258 associated with various metrics quantifying the availability of large coral boulders on a reef
259 (Fig.1, Appendix C). The volume of coral boulders per m² was a slightly better predictor of *L.*
260 *apodus* density than either the height or number of boulders per m², suggesting that *L. apodus*
261 responds to the three-dimensional structure of the corals (Appendix C). Coral boulders were
262 common at all 8 sites, whereas terrigenous limestone boulders occurred at only 3 sites and
263 were relatively rare. Adding the availability of limestone boulders to regression models for *L.*
264 *apodus* density always weakened the prediction (lower r^2 , Appendix C). *L. apodus* was thus
265 more strongly associated with coral boulders, which contain internal voids suitable as shelter,
266 than with terrigenous solid limestone boulders. Our manipulation of density succeeded in
267 weakening the relationship between habitat (coral boulders) and density (Fig. 1), and
268 broadened the range of *L. apodus* densities on the reefs to span the range reported throughout
269 the Caribbean (Appendix B, Appendix D). The manipulation was thus successful in creating
270 a stronger test of the effect of density, and isolating the relative effects of density and habitat.

271 Recruitment of small *L. apodus* (< 14 cm SL) after the density manipulation was
272 positively related to the density of larger *L. apodus* ($F_{1,13} = 7.37$, $P = 0.018$; Fig. 2), and this
273 relationship was consistent across the two years studied (2004 and 2005) ($F_{1,12} = 2.0$, $P =$
274 0.19). There was no compelling evidence that habitat availability (volume of coral boulders)
275 affected recruitment (Appendix E). Models to predict recruit density that included a term for
276 the effect of habitat in addition to, or instead of, a term for the density of larger *L. apodus*
277 were less well supported (model likelihood 0.11 and 0.13, respectively) than the model
278 including only density. In addition, the term for the effect of habitat was not significant in
279 either model (model with habitat only: $F_{1,12} = 0.01$, $P = 0.95$; model with habitat and density
280 $F_{1,13} = 2.82$, $P = 0.12$, respectively).

281 Growth of 486 *L. apodus* was measured over intervals from 38-809 days (mean = 214
282 days) and growth rates ranged from -0.01 to 0.05 cm SL/day (mean = 0.01 cm SL/day). We
283 found no evidence that daily growth was density-dependent. Growth rates in the
284 observational phase of the study, and after the density manipulation, were unrelated to
285 population density, habitat (coral volume per m²) or these two factors combined, ($t < 1.12$, P
286 > 0.12) (Appendix F).

287 Although we cannot completely rule out the possibility that disappearance of tagged
288 fish from the 8 study reefs was due to emigration, three observations suggest that Φ is
289 primarily a measure of survival. First, none of the 769 recaptured PIT tagged fish moved
290 among the 8 study sites. Second, in a pilot mark-recapture study from 2001-2002, 199 of 376
291 visually tagged *L. apodus* were resighted, but no resightings occurred in thorough searches of
292 other reef habitat in the study region. Third, repeated recaptures of PIT tagged individuals at
293 the same site over 4 years, coupled with repeated observations of other recognizable
294 individuals (identified based on scars or other unique visual marks) suggested that site
295 fidelity was high.

296 Comparison of candidate models for Φ revealed the strongest support for a model in
297 which Φ was a simple function of density (Appendix G). The model that included only the
298 covariate density was almost three times better supported than the model that included terms
299 for site and time (to capture unmeasured sources of spatio-temporal variation in Φ); and more
300 than thirty times better supported than a model where Φ was constant (the simplest possible
301 model). Substituting the term for density with a term for habitat (volume of coral boulders per
302 m²) markedly reduced model support (Appendix G). Models including terms for both habitat
303 and density, in additive or multiplicative combinations, produced no improvements in fit over
304 the model just containing density (Appendix G). Reconstituting estimates of Φ across a
305 gradient of *L. apodus* density revealed that Φ increased at higher densities (i.e., was inversely

306 density dependent) (Fig. 3). The apparent monthly survival of *L. apodus* was thus higher at
307 sites and/or during months when their population was dense (Fig. 3).

308

309 **DISCUSSION**

310 We found positive effects of conspecific density on the demography of *L. apodus*.
311 Our density manipulation weakened the association between *L. apodus* density and habitat
312 availability (volume of large coral boulders) with the result that, over the entire study period,
313 spatio-temporal fluctuations in apparent survival were better described as a simple function of
314 density than as a function of habitat availability. Model selection analysis, which rewards
315 increased model fit but penalizes increased model complexity, indicated that the
316 improvement in model fit by including a term for the effect of habitat was not sufficient to
317 outweigh the “cost” of increasing model complexity. Although we routinely observed *L.*
318 *apodus* congregating near coral boulders, our results suggests that any density-independent
319 effect of this habitat feature on apparent survival is relatively weak compared to the influence
320 of conspecific density. *L. apodus* is a long-lived fish and small, positive effects of habitat
321 quality on survival of this species might accumulate over several years to generate the
322 correlation between density and coral boulders that we detected.

323 Although we did not quantify the causes of loss of *L. apodus* during our study, we
324 suggest predation by larger fish as a simple and plausible agent of the inversely density-
325 dependent survival we observed. Circumstantial evidence supporting this hypothesis is as
326 follows. Firstly, the fact that apparent survival was density-dependent, whereas somatic
327 growth was not, is consistent with predation as the main agent of mortality rather than factors
328 with an obvious energetic component to their effect, such as food supply or infection with
329 pathogens. Second, although a systematic study of *L. apodus* behavior was not our intent,
330 observations amassed over more than 3000 hours on SCUBA during the study revealed that

331 *L. apodus* were grouped into a few schools, which appeared to function as coherent social
332 groups when avoiding or escaping attacks from barracudas and large groupers, which were
333 the predators most frequently observed attacking *L. apodus* in the area. Larger predatory
334 fishes such as reef sharks (*Carcharhinus perezii*) and lemon sharks (*Negaprion brevirostris*)
335 though occasionally sighted on these reefs were relatively rare, as is the case in most of the
336 Caribbean (Stallings 2009, Ward-Paige et al. 2010). Barracuda and large grouper densities at
337 our sites were relatively lightly impacted by fishing. Although their densities were not as high
338 as found in some marine reserves (Chiappone and Sealey 2000), they were similar to those at
339 other lightly fished sites in the Caribbean (Appendix D), and these predatory fishes should
340 have the potential to control *L. apodus* populations. The density of these predators was not
341 correlated with density of *L. apodus* on the study reefs (Appendix D), which is expected
342 because barracuda and large groupers consume a variety of fish species. Lastly, alternate
343 mechanisms known to generate inverse density dependence are not consistent with our
344 results. Cooperative feeding can generate inverse density dependence but is not consistent
345 with the density-independent growth we observed (Courchamp et al. 1999). Demographic
346 stochasticity, genetic inbreeding and reduced heterozygosity can also generate inverse density
347 dependence in very small populations, but are unlikely to be expressed across the wide range
348 of densities we studied (Lande 1998).

349 We also observed a positive association between the densities of new recruits and
350 older individuals. One possible mechanism is recruitment facilitation, a common
351 phenomenon in other group-living reef fishes, in which juveniles select sites with high adult
352 density when they first colonize the reef habitat (reviewed in Hixon and Webster 2002).
353 Alternatively, early survival of recruits (from the time of arrival at a reef to the time of
354 census) might be inversely density-dependent, as shown for larger *L. apodus*.

355 It is well known that some vertebrates forming social groups survive better in large
356 groups because they detect predators earlier, recognize and assess predator intent more
357 effectively, are better able to inhibit predator attacks, or are more confusing to attacking
358 predators than their counterparts in small groups (Pulliam 1973, Bertram 1978, Crawley
359 1992, Pitcher and Parrish 1993). A rich array of these social behaviors have been linked to
360 population level dynamics for small reef fishes and other vertebrates whose behaviors are
361 readily observable (Sutherland 1996). Recent studies have indicated that large, harvested
362 fishes also have complex and varying social organization (Rowe and Hutchings 2003, Egli
363 and Babcock 2004). *L. apodus* may thus be an example of a harvested species whose
364 antipredator strategies become more effective in large groups.

365 Inverse density dependence expressed only at very low densities, the Allee effect,
366 occurs in many taxa (Courchamp et al. 1999) but is rarely detected in harvested fish (Myers
367 et al. 1995). Models of the Allee effect typically assume that per capita population growth
368 rate is positive below a carrying capacity (set by limited resources) until density drops to a
369 threshold, below which per capita growth becomes negative. An important implication of the
370 Allee effect is that populations dropping below the threshold are less likely to recover, and
371 more likely to go extinct (Dennis 1989, Lande 1998). Inverse density dependence spanning
372 the normal density range, as observed in *L. apodus*, has been reported relatively infrequently
373 (Courchamp et al. 1999) and has different implications for management.

374 Because many small, no-take reserves are similar in size to our study reefs, our results
375 suggest that a reduction in fishing mortality within reserves should allow *L. apodus* densities
376 to increase, which may in turn produce increased natural survival. This synergistic effect
377 should magnify the build-up of fish within reserves beyond that expected if natural mortality
378 is either density-independent or directly density-dependent (Sanchez Lizaso et al. 2000). Our
379 finding of a strong correlation of density with coral boulder volume, emphasizes the need to

380 include high-quality habitat within reserves (e.g., Parnell et al. 2006). Ultimately, of course,
381 the benefit to *L. apodus* of being in larger schools within reserves depends on the biological
382 mechanism for inverse density dependence. If, as we hypothesize, interactions between *L.*
383 *apodus* and their predators are the cause, reserve effects on *L. apodus* will depend on whether
384 reserves promote recovery of top predators that consume *L. apodus* (Abrams et al. 2011).
385 Although logistically challenging, further experimental and behavioral studies to identify the
386 biological mechanisms creating density-dependent feedbacks will thus help predict the
387 response of harvested fishes to alternate management actions.
388

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540

541 **APPENDICES**

542

543 **Appendix A**

544 A table and a figure showing the location and approximate size of the 8 study reefs in the
545 central Exuma Cays, Bahamas.

546 **Appendix B**

547 A figure showing that the manipulation of *L. apodus* density succeeded in increasing density
548 at density elevation sites and reducing density at density reduction sites.

549 **Appendix C**

550 A table showing relationships between *L. apodus* density and habitat features used as shelter.

551 **Appendix D**

552 A table documenting densities of *L. apodus* and two of their predators at sites throughout the
553 Caribbean and tropical Atlantic.

554 **Appendix E**

555 Comparison of general linear models relating recruit density of *L. apodus* to density of older
556 conspecifics or habitat features used as shelter.

557 **Appendix F**

558 A figure showing that growth in standard length was unrelated to *L. apodus* density across the
559 natural range of densities and across a broader range of experimentally established densities.

560 **Appendix G**

561 A table showing mark-recapture models testing the effects of *L. apodus* density, habitat, site,
562 and time on survival probability.

563

564 **FIGURES**

565

566 Fig. 1. Relationship between *L. apodus* density and coral boulder volume at $n = 8$ study sites.

567 Mean densities (number of individuals per $m^2 \pm SE$) of *L. apodus* and coral boulder volume

568 (per m^2) are shown for the (a) pre-manipulation period of the study, based on 7 visual

569 censuses between June 2002 and June 2004 ($r^2 = 0.78$, $P = 0.002$) and the (b) post-

570 manipulation period based on 11 visual censuses from August 2004 to August 2005 ($r^2 =$

571 0.52 , $P = 0.05$). Coral volume (per m^2) is based on a single survey (see Methods). The

572 manipulation weakened the relationship between *L. apodus* density and coral volume,

573 allowing isolation of the effects of population density and habitat quality on survival rates.

574

575 Fig. 2. Relationship between density of recruit and adult *L. apodus* (number of individuals

576 per $m^2 \pm SE$) ($r^2 = 0.34$ and $P = 0.02$) at $n = 8$ study sites. There was no significant difference

577 in the relationship between the years 2004 (open circles) and 2005 (closed circles)

578 (ANCOVA: $F_{1,12} = 2.0$, $P = 0.19$).

579

580 Fig. 3. Relationship between survival and density of *L. apodus*. Survival values (Φ) were

581 reconstituted from parameters estimated by Program MARK, from the model $\Phi(\text{density})$,

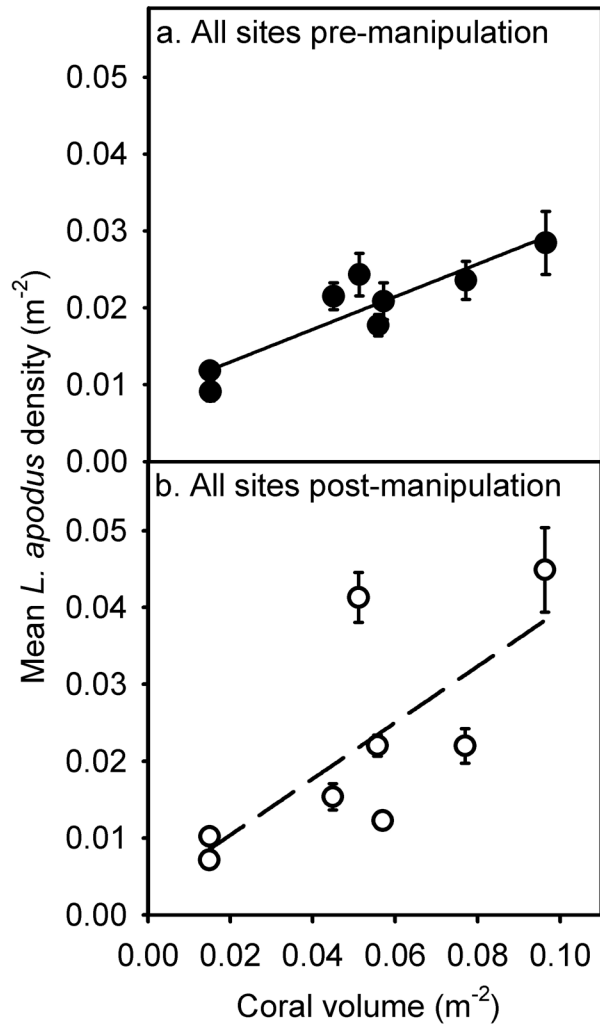
582 $p(\text{site} + m + \text{time})$ fit to the recapture histories of 1863 tagged *L. apodus* (see Methods).

583 Parameter m represents a short-term trap response in capture probability (p). Survival is the

584 probability of survival over a one-month time period. Broken lines represent the 95%

585 confidence interval of the survival estimate.

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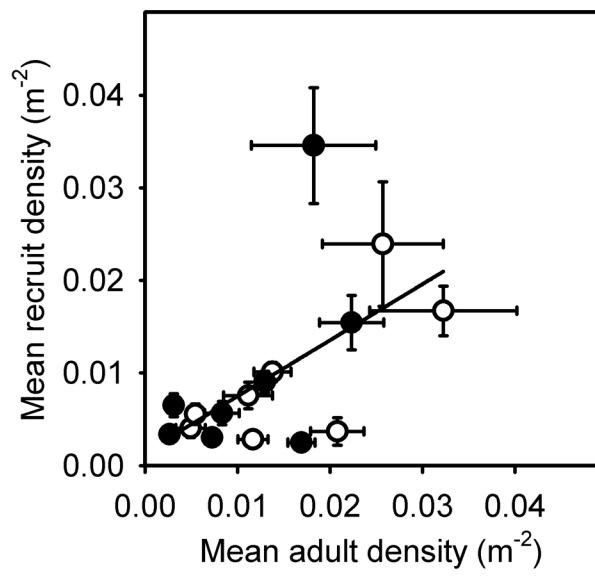


587

588

589 Fig. 1.

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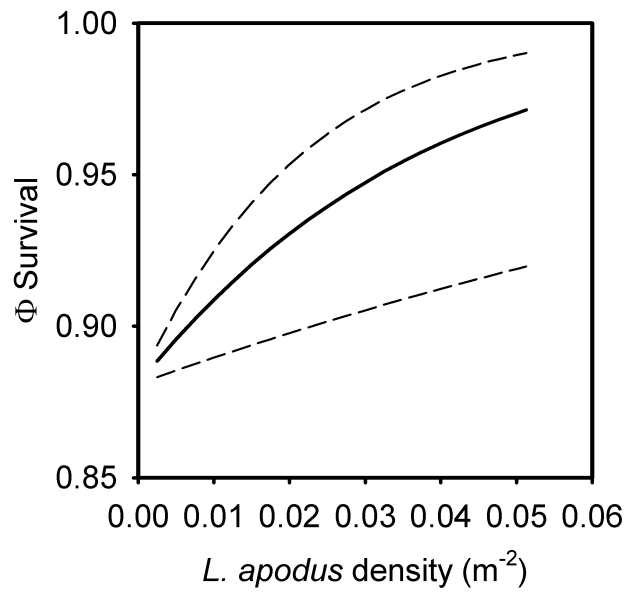


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592

593 Fig. 2.

594



595

596

597 Fig. 3.