

1 Optimum lionfish yield: A non-traditional management concept for invasive lionfish (*Pterois*
2 spp.) fisheries

3 Alex K. Bogdanoff¹, Kyle W. Shertzer², Craig A. Layman¹, Jennifer K. Chapman³, Marc L.
4 Fruitema³, Jennifer Solomon⁴, Julie Sabattis⁴, Stephanie Green⁵, and James A. Morris, Jr⁶

5
6 ¹North Carolina State University, Department of Applied Ecology, Raleigh, NC 27695

7
8 ²NOAA, National Marine Fisheries Service, Southeast Fisheries Science Center, 101 Pivers
9 Island Road, Beaufort, NC 28516

10
11 ³Blue Ventures Conservation, 39-41 North Road, London N7 9DP, UK

12
13 ⁴Colorado State University, Department of Human Dimensions of Natural Resources, Fort
14 Collins, CO 80523

15
16 ⁵University of Alberta, Department of Biological Sciences, CW 405 Biological Sciences
17 Building, Edmonton, Alberta, T6G2E9

18
19 ⁶NOAA, National Ocean Service, National Centers for Coastal Ocean Science, 101 Pivers Island
20 Road, Beaufort, NC 28516

21
22 Corresponding author: AKB, akbogdan@ncsu.edu

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37

38 **Abstract:** This paper describes a non-traditional fisheries management concept and an indicator-
39 based framework to encourage and guide management of invasive lionfish (*Pterois* spp.)
40 fisheries in the temperate and tropical western Atlantic. We introduce the concept of optimum
41 lionfish yield (OLY) – an extension of the concept of ecologically sustainable yield – which
42 considers local ecological health in the establishment of fishery management targets. In contrast
43 to traditional fishery targets, OLY is a target exceeding maximum sustainable yield (MSY) that
44 still provides relatively high sustainable yield, but further contributes to population suppression
45 beyond what is achievable through targets at or below MSY. Thus, OLY seeks to balance
46 management trade-offs from both natural resource and invasive species management
47 perspectives. In this study, we developed an age-structured population model and applied the
48 concept of OLY to quantify targets to initiate management of a nationally-managed lionfish
49 fishery in Belize. Socioeconomic and ecological data were used as indicators to formulate OLY
50 values. The model indicates that lionfish in Belize are biologically robust to fishing pressure,
51 which corroborates previous findings. Fishing lionfish at rates above MSY levels is expected to
52 substantially reduce population abundance, much more so than fishing at rates below MSY
53 levels, while having relatively minimal impacts on yield. Population suppression can be further
54 enhanced by reducing size at selection, but this is expected to be done at a significant cost to
55 landings. Together, these data support continued establishment of (managed) commercial
56 lionfish fisheries throughout the invaded range to (1) provide an alternative sustainable fishery
57 resource and (2) serve as a means of national- and international-level control. While the concept
58 and framework described here is introduced for management of invasive lionfish, it could be
59 applied to management of other invasive species, both aquatic and terrestrial.
60

61 **1. Introduction**

62 Numerous studies indicate invasive lionfish (*Pterois* spp.) negatively affect reef
63 communities in the temperate and tropical western Atlantic through predation on, and
64 competition with, native species (Albins and Hixon 2008, Green *et al.* 2012, Albins 2015,
65 Ballew *et al.* 2016, Chagaris *et al.* 2017). To regulate population densities and mitigate
66 ecological impacts, researchers and coastal managers have established lionfish control and
67 management programs that focus on direct removals (*e.g.*, Johnston *et al.* 2015). These
68 programs, as well as community-based efforts such as recreational fishing tournaments, have
69 been successful at reducing lionfish densities and minimizing impacts on local reefs (Frazer *et al.*
70 2012, Dahl *et al.* 2016, Green *et al.* 2017). Lionfish are, however, established in most marine
71 habitats from North Carolina, USA to Brazil, and densities can exceed 300 fish/hectare (Côté *et*
72 *al.* 2013). Consequently, wide-scale eradication no longer seems plausible without major
73 technological advances for capture and a significant increase in the scale and magnitude of
74 removal efforts.

75 To increase the scale and magnitude of removal efforts, researchers and managers have
76 been promoting commercialization of lionfish over the last decade, particularly as seafood. Not
77 only are lionfish plentiful, they are safe to consume and a nutritious source of protein (Tremain
78 and O'Donnell 2014, Hardison *et al.* 2018, Morris *et al.* 2011a). Lionfish are now being harvested
79 recreationally and commercially throughout much of the invaded region, but are not being
80 managed as a fishery resource. Similar to other natural resource markets, as demand increases so
81 too does the number of people who exploit the resource and, therefore, the number of individuals
82 who may become (more) reliant on the resource. For this reason, lionfish fisheries would benefit
83 from science-based management (Merrick 2018). Through proper management, invasive lionfish

84 could serve as an alternative fishery resource, which could help create more diversified markets
85 and potentially reduce fishing pressure on traditional native fishery species. Lionfish fisheries
86 could also indirectly improve stocks of fishery species impacted by lionfish.

87 The objective of traditional fisheries management is to maintain high sustainable yield
88 without causing overfishing. This is often accomplished by setting management targets at or
89 below a population's maximum sustainable yield (MSY) (Larkin 1977, Mace 2001) (Figure 1).
90 Maximum sustainable yield is defined as the maximum yield (or, harvest) that a population can
91 sustain without having adverse effects on its ability to replenish itself. In United States fisheries
92 management, for example, MSY and its associated fishing rate F_{MSY} , are typically treated as
93 upper limits with target levels set somewhat lower (Prager and Shertzer 2010). There exists,
94 however, a paradox with the management of invasive lionfish fisheries. From a natural resource
95 management perspective, lionfish fisheries should be managed to maintain high sustainable yield
96 at levels that meet socioeconomic demand; however, from an invasive species management
97 perspective, the fishery should also be managed to suppress populations to levels that mitigate
98 ecological impacts. In the context of traditional fisheries management, these two objectives are
99 not sought in tandem.

100 This paper describes a non-traditional fisheries management concept and an indicator-
101 based framework to encourage and guide management of invasive lionfish fisheries throughout
102 the western Atlantic. We propose the concept of optimum lionfish yield (OLY), which seeks to
103 balance the competing objectives of high sustainable yield and population suppression, and
104 describe one potential approach for formulating OLY values using the lionfish fishery in Belize
105 as a case study. In contrast to traditional fisheries management targets, OLY is a target exceeding
106 MSY that still provides relatively high sustainable yield, but further contributes to population

107 suppression beyond what is achievable through targets at or below MSY (Figure 1). Thus, OLY
108 balances management trade-offs from both natural resource and invasive species management
109 perspectives. Optimum lionfish yield is an extension of the concept of ecologically sustainable
110 yield (ESY) – a target yield that a community or ecosystem can sustain without shifting to an
111 undesirable ecological state (Zabel *et al.* 2003). While OLY targets lie above MSY and ESY
112 targets lie below MSY, both concepts suggest that traditional fishery management practices that
113 set single-species targets based solely on MSY can be insufficient. OLY and ESY suggest that
114 managers establish fishery targets that also consider overall ecological health.

115 Since 2011, the Belize Fisheries Department and its partners have worked to establish a
116 nationally managed lionfish fishery as a means of national-level control and to diversify local
117 markets (Chapman *et al.* 2019, Searle *et al.* 2012). Commercial lionfish markets have been
118 developed (*e.g.*, as seafood and for jewelry) and the number of fishers targeting lionfish has
119 grown, but management of the fishery has not yet begun (Chapman *et al.* 2019). One of the
120 essential steps in establishing a well-managed fishery is understanding the population's response
121 to fishing pressure, which is typically achieved through application of population and stock
122 assessment models. Thus, we developed an age-structured population model and applied the
123 concept of OLY to quantify benchmark targets to initiate management of the lionfish fishery in
124 Belize. Available socioeconomic and ecological data for lionfish in Belize were used as indicators
125 to quantify and then validate that the proposed values of OLY satisfied the two general
126 objectives of lionfish fishery management – high sustainable yield that meets socioeconomic
127 demand and population suppression that mitigates ecological impacts. Data from the fishery are
128 not currently available to model temporal dynamics of the population, but do exist to examine
129 equilibrium behavior in response to fishing pressure and size at selection – two variables that

130 fishery managers can regulate. Although no real population is ever in true equilibrium, reference
131 points derived under this assumption are useful as long-term targets even if met with non-
132 equilibrium dynamics in practice (Goodyear 1993, Mace 2001). Model results are discussed
133 within the context of tradeoffs between sustainable yield and population suppression.

134 **2. Methods**

135 *2.1 General overview of approach*

136 An age-structured population model was developed to quantify benchmark management
137 targets, including values of OLY and its associated fishing rate F_{OLY} , to initiate management of a
138 nationally-managed lionfish fishery in Belize. The model was used to evaluate trade-offs
139 between equilibrium landings and abundance of lionfish in response to fishing pressure and size
140 at selection. Available socioeconomic and ecological data for lionfish in Belize were used as
141 indicators to quantify and then validate that the proposed values of OLY satisfied the two general
142 objectives of lionfish fishery management. Functional forms and parameter values used in the
143 population model were derived from Belize survey data when possible, but also drew on
144 published data from nearby Little Cayman Island (Edwards *et al.* 2014, Gardner *et al.* 2015).
145 Like Belize, lionfish were first observed at Little Cayman Island in 2008, and were considered
146 established in 2009 (Schofield 2010). Data used for parameter values in this study were obtained
147 through various surveys conducted in both locations in the period between 2011 and 2015. Age-
148 specific parameter values are summarized in Table 1. The overall approach described here serves
149 as a model framework for formulating lionfish fishery management targets throughout the
150 western Atlantic.

151 *2.2 Model description*

152 Lionfish abundance at age (N_a) was computed as

153
$$N_a = N_{a-1}e^{-Z_a-1} \quad (1)$$

154 where Z_a is total instantaneous mortality at age a . The model included ages 1–7 years, with the
 155 oldest age treated as an accumulator class. The ages modeled were chosen based on the time
 156 since introduction to Belize and the initiation of this study (2008 – 2015). A plus group (7+) was
 157 used to account for older fish that may exist in the population, since we assume maximum age is
 158 20 years (see below). The abundance of recruits (N_1 , age-1 fish) was computed using the
 159 steepness formulation of the Beverton-Holt spawner-recruit function (Beverton and Holt 1957)

160
$$N_1 = \frac{(0.8R_0hS)}{[0.2R_0\Phi_0(1-h)+S(h-0.2)]} \quad (2)$$

161 where R_0 is the asymptotic recruitment of age-1 fish, h defines the steepness of the curve, S is
 162 population fecundity (total egg production), and Φ_0 is the number of spawners (eggs) per recruit
 163 in an unfished population. Population fecundity (S) was computed as

164
$$S = \sum_a 0.5N_a m_a f_a \quad (3)$$

165 where 0.5 is the proportion of females in the population, m_a is maturity at age a , and f_a is
 166 fecundity at age a . Given a fishing mortality rate (F), total landings by number at age a (λ_a) was
 167 derived using the Baranov catch equation (Baranov 1918)

168
$$\lambda_a = \frac{F_a}{Z_a} N_a (1 - e^{-Z_a}) \quad (4)$$

169 where F_a is the fishing mortality rate at age a , computed as the product of F and selectivity at age
 170 a (s_a). Total landings in weight (Y_F), as a function of F , was then computed as

171
$$Y_F = \sum_a \lambda_a W_a \quad (5)$$

172 where W_a is weight in kilograms at age a .

173 Length at age (L_a , total length in mm) was modeled using the von Bertalanffy growth
 174 equation (von Bertalanffy 1957)

175
$$L_a = L_\infty (1 - e^{-K(a-a_0)}) \quad (6)$$

176 where L_∞ is asymptotic total length, K is the growth coefficient, and a_0 is the theoretical age at
177 which length is zero. The growth parameters provided by Edwards *et al.* (2014) for both sexes
178 combined were used: $L_\infty = 349$, $K = 0.42$, and $a_0 = -1.01$. The relationship between total length
179 (mm) and weight (W , in g) was described by fitting a power function to data from Belize (n=352,
180 sexes combined),

$$181 \quad W = \alpha L^\beta \quad (7)$$

182 The resulting parameter estimates were $\hat{\alpha} = 0.000007$ and $\hat{\beta} = 3.11$ (Figure 2).

183 Maturity at age (m_a) followed the logistic function from Gardner *et al.* (2015)

$$184 \quad m_a = \frac{1}{1 + e^{-(L_a - L_{50})/\sigma}} \quad (8)$$

185 where L_a is total length at age, $L_{50} = 190$ mm is length at 50% maturity, and $\sigma = 13.1$ is the
186 parameter characterizing the slope of the fitted curve. Sex ratio was determined from 375
187 lionfish captured throughout Belize from 2011–2015. Forty-nine percent (n=184) were females
188 and 51% (n=191) were males. This proportion of females was not distinguishable from 0.5 (exact
189 binomial test; $p=0.76$) and thus the sex ratio in the model was assumed to be 50:50. A 50:50 sex
190 ratio is consistent with lionfish population sex structure reported elsewhere (*e.g.*, Edwards *et al.*
191 2014, Morris 2009). Annual fecundity at age (f_a) was computed using the batch fecundity model
192 from Gardner *et al.* (2015)

$$193 \quad f_a = B(b_1 L_a - b_2) \quad (9)$$

194 where $B = 152$ is the mean number of batches per female per year and parameters $b_1 = 308.67$ and
195 $b_2 = 58,265$ define the number of eggs per batch as a function of fish total length. The range of
196 values used in this study are consistent with estimates of lionfish fecundity from other locations
197 (*e.g.*, Morris 2009, Fogg *et al.* 2017).

198 Age-independent natural mortality (M) was computed using the mortality estimator
199 recommended by the meta-analysis in Then *et al.* (2015)

$$200 \quad M = 4.889 * t_{max}^{-0.916} \quad (10)$$

201 where t_{max} is maximum age. Maximum age of lionfish in the wild is unknown. The longest
202 observed lifespan of lionfish in captivity is 30 years (Potts *et al.* 2010). The oldest recorded
203 lionfish in the western Atlantic was 8 years and was captured off of North Carolina (Potts *et al.*
204 2010). Given the lack of studies on maximum age of lionfish in the wild, their maximum
205 observed age in captivity, and the presence of predation defense mechanisms, we assumed $t_{max} =$
206 20 yrs and, therefore, $M = 0.3$. The M value used here is typical of a moderately short-lived reef
207 fish and is consistent with the natural mortality values used in other lionfish population modeling
208 studies (*e.g.*, Barbour *et al.* 2011, Edwards *et al.* 2014, Johnston and Purkis 2015, Morris *et al.*
209 2011b).

210 Selectivity at age (s_a) was computed based on a normal distribution of sizes around the
211 mean length at age, computed from equation 6 (SD = 28.2; Johnson and Swenarton 2016), with
212 parameter $L_{vuln} = 250$ mm defining a threshold of vulnerability to harvest. That is, for each age,
213 s_a is the probability that length exceeds the vulnerability threshold, computed from the normal
214 cumulative distribution function with mean L_a and SD = 28.2 mm. The value of $L_{vuln} = 250$ mm
215 was derived from catch and fishing data obtained through semi-structured fisher and
216 restaurateur interviews conducted throughout Belize in 2015 and 2016 (Chapman *et al.* 2019).
217 Without data to estimate steepness (h), we assumed a value of 0.75. This value is consistent with
218 that of other reef fish populations that have similar life histories as lionfish, including rockfish
219 and scorpionfish (Scorpaenidae) (Forrest *et al.* 2010, Shertzer and Conn 2012, Thorson 2020).

220 Data from Belize on total lionfish abundance (N_{tot}) and total catch (C_{tot}) in numbers were
 221 used to estimate R_0 and the current fishing mortality rate (F). Total initial abundance was
 222 estimated using geospatial data on marine habitat sizes across Belize (provided by the Belize
 223 Coastal Zone Management Authority and Institute) and habitat-specific lionfish density estimates
 224 derived from Belize-wide surveys conducted in 2015 (Chapman *et al.* 2019). The habitat-specific
 225 densities were scaled up to total habitat-specific abundances using the area of each habitat type.
 226 Total area of the main barrier reef, back reef areas, and atolls was estimated to be 60,704
 227 hectares, which scaled total abundance to $N_{\text{tot}} = 733,257$ lionfish. Based on information obtained
 228 through the semi-structured interviews mentioned above, total (or current) catch in 2015 was
 229 estimated to be $C_{\text{tot}} = 89,902$ lionfish (Chapman *et al.* 2019). Given N_{tot} , natural mortality,
 230 selectivity, and the relative abundance at age implied by Equation 1, we solved the Baranov
 231 catch equation in terms of numbers (*i.e.*, Equation 5 without the weight term) for the value of F
 232 that provided $C_{\text{tot}} = 89,902$ lionfish. We refer to this value, $F=0.32$, as the current F . This
 233 procedure was then used to back-calculate equilibrium recruitment (R_{eq})

$$234 \left(\begin{array}{l} N_1 = R_{eq} \\ N_2 = N_1 e^{-Z_1} \\ N_3 = N_2 e^{-Z_2} \\ N_4 = N_3 e^{-Z_3} \\ N_5 = N_4 e^{-Z_4} \\ N_6 = N_5 e^{-Z_5} \\ N_{7+} = N_6 e^{-Z_6} / (1 - e^{-Z_{7+}}) \end{array} \right) \quad (11)$$

235 Given total mortality at age (Z_a) and $N_{\text{tot}} = \sum_a N_a = 733,257$, the recursive relationship of
 236 Equation 11 provides $\widehat{R}_{eq} = 266,000$. This value was then used to compute $\widehat{R}_0 = 289,900$ as a
 237 function of equilibrium recruitment

$$238 R_0 = \frac{R_{eq}(h-0.2)\Phi_F}{0.8h\Phi_F - 0.2(1-h)\Phi_0} \quad (12)$$

239 where Φ_F is the number of spawners per recruit of a population fished at rate F . For any F , Φ_F is
240 computed as

$$241 \quad \Phi_F = \sum_a 0.5\psi_a m_a f_a \quad (13)$$

242 where ψ_a is the number of fish per recruit at age a computed using Equation 11 with $N_l = 1$. The
243 number of spawners per recruit of an unfished population (Φ_0) is computed similarly, but with F
244 = 0.

245 *2.3 Model application*

246 The population model was developed and implemented using R Statistical Software (R
247 Core Team 2017) and applied to evaluate and identify initial lionfish fishery management targets
248 for Belize, including values of OLY and F_{OLY}. More specifically, the model was used to quantify
249 equilibrium landings and abundance of lionfish across a range of fishing mortality rates from
250 $F_{LOW} = 0.0$ (no fishing effort) to $F_{HIGH} = 5.0$ (the maximum rate modeled). Fishing rates of
251 particular interest were $F_{CURRENT}$ (the fishing rate in 2015), F_{MSY} , and F_{OLY} . The model was also
252 used to explore how lionfish size at selection (L_{vuln}) affects landings and abundance. For this
253 analysis, fishing mortality was fixed at $F = F_{OLY}$ and selectivity was adjusted as described above,
254 but with L_{vuln} set to different values across the range of 200 – 300 mm.

255 *2.4 Formulation of OLY values*

256 OLY and F_{OLY} values will vary among management areas throughout the western
257 Atlantic due to differences in local lionfish biology, socioeconomics, resources, data availability,
258 and lionfish fishery management objectives (*i.e.*, desire for greater yield vs population
259 suppression or vice versa). This paper describes one possible indicator-based approach for
260 formulating OLY targets. Available socioeconomic and ecological data for lionfish in Belize
261 were used as indicators to quantify and then cross-check or validate that the proposed values of

262 OLY and F_{OLY} would satisfy the two general objectives of lionfish fishery management – high
263 sustainable yield that meets socioeconomic demand and population suppression that mitigates
264 ecological impacts. More specifically, OLY values were quantified and validated based on the
265 estimated MSY, current yield levels (i.e., yield in 2015) (Chapman *et al.* 2019), fisher and
266 restaurateur satisfaction of current yield (Chapman *et al.* 2019), and Belize-specific lionfish
267 ecological threshold density estimates (Chapman *et al.* 2019).

268 2.5 Sensitivity analysis

269 Sensitivity (Z_i) of model results to parameter values were computed using local
270 perturbation analysis (Ellner and Guckenheimer 2006)

$$271 \quad Z_i = \frac{Y(1.05p_i) - Y(0.95p_i)}{0.1Y(p_i)} \quad (14)$$

272 where Y is the model output of interest and $Y(p_i)$ is the value of Y as a function of the i th
273 parameter p_i . A positive value of Z_i shows that an increase in parameter p_i leads to an increase in
274 Y , while a negative value shows the opposite effect. A value of $|Z_i| \geq 1.0$ indicates that a 10%
275 change in parameter p_i results in a >10% change in output Y . The larger the $|Z_i|$, the greater the
276 sensitivity. We examined sensitivity of MSY, F_{MSY} , and N_{MSY} , the expected total abundance when
277 fishing at F_{MSY} . Model results were considered sensitive to parameter values when $|Z_i| \geq 1.0$.
278 Sensitivities were also used to identify lionfish fishery research needs in Belize.

279 3. Results and Discussion

280 Overall, the model indicates that harvest of lionfish effectively reduces population
281 abundance (Figure 3). Equilibrium abundance at $F_{LOW} = 0$ was estimated at 1.5 million lionfish,
282 while abundance at $F_{HIGH} = 5.0$ was 220,000 lionfish. The model suggests that the current fishing
283 effort in Belize has already reduced lionfish abundance by 34%, but increasing effort to $F_{MSY} =$
284 0.67 could reduce abundance by an additional 21% (Figure 3). The model also suggests that the

285 population in Belize can withstand high rates of fishing without collapse, as indicated by the
286 relatively high abundance of lionfish predicated at F_{HIGH} – an improbable fishing mortality rate
287 (Figure 3). Other lionfish population modeling studies have reported similar findings. Morris *et*
288 *al.* (2011b) predicted monthly exploitation of 27% of the adult population in the temperate and
289 tropical western Atlantic would result in zero net growth; Barbour *et al.* (2011) predicted annual
290 exploitation rates between 35 and 65% of the total population in North Carolina would be
291 required to cause recruitment overfishing; Edwards *et al.* (2014) predicted annual exploitation
292 rates between 15 and 35% of the total population at Little Cayman Island would be required to
293 cause recruitment overfishing; and Chagaris *et al.* (2017) predicted fishing mortality rates greater
294 than $F = 1.0$ are required to cause population declines on the West Florida Shelf. The results
295 from these studies, which vary in terms of model design, data inputs, and geographic and spatial
296 scales, all indicate a key population characteristic – invasive lionfish are biologically robust to
297 fishing pressure. This population characteristic is likely due to lionfish biology and ecology
298 (Côté *et al.* 2013) and is an important finding in terms of both lionfish control and establishing
299 managed lionfish fisheries. This finding highlights the (1) biological sustainability of lionfish as
300 a fishery resource and (2) indicates that the level of fishing effort required to overfish lionfish is
301 substantial and unlikely to be achieved, especially without commercial-scale fishing practices.
302 These data support continued establishment of (managed) commercial lionfish fisheries
303 throughout the invaded range to provide an alternative sustainable fishery resource and serve as a
304 means of national- and international-level control.

305 The model indicates that fishing lionfish at rates above F_{MSY} is expected to contribute
306 substantially to population suppression, much more so than fishing at rates below F_{MSY} , while
307 having relatively minimal impacts on yield (Figure 3). Fishing at F_{HIGH} is predicted to further

308 reduce lionfish abundance by an additional 63%, while only reducing landings by 42% relative
309 to fishing at F_{MSY} (Figure 3). While any harvest of lionfish beyond MSY can be considered
310 beneficial for local reef ecology, the model indicates that trade-offs exist where increased
311 population suppression is done at a cost to landings (Figure 3). OLY seeks to balance these
312 trade-offs to meet socioeconomic demand, while suppressing populations to levels that mitigate
313 ecological impacts. OLY values in this study were formulated using available socioeconomic
314 and ecological data for lionfish in Belize. These data were used as indicators to quantify and then
315 validate that the proposed values of OLY and F_{OLY} would satisfy the two general objectives of
316 lionfish fishery management. While distribution challenges exist in Belize, Chapman *et al.*
317 (2019) reported that Belizean fishers and restaurateurs were, in general, satisfied with catch
318 levels in 2015 due to relatively sufficient supply to meet demand and the fact that lionfish are
319 predominately caught and sold opportunistically. For these reasons, and because the current
320 catch level was only 10% below the estimated MSY, yield in 2015 was used as a benchmark for
321 quantifying OLY and F_{OLY} . OLY, and subsequently F_{OLY} , was quantified as the yield above MSY
322 that produced equivalent yield as the current catch level. The proposed value of $F_{OLY} = 1.51$ for
323 lionfish in Belize is predicted to provide the same yield as the current fishing levels, thus
324 generally satisfying current socioeconomic demand in Belize, while reducing abundance by an
325 additional 42% relative to current levels (Figure 3).

326 Belize-specific lionfish ecological threshold densities reported in Chapman *et al.* (2019)
327 were then used to cross-check that the proposed OLY targets would sufficiently reduce lionfish
328 populations to a level that is expected to mitigate their ecological impacts. Threshold densities
329 were estimated for the five major Belizean marine protected areas (MPAs) in 2015 following the
330 approach in Green *et al.* (2014). The approach in Green *et al.* (2012) estimates location-specific

331 lionfish densities at which their ecological impacts are predicted to be mitigated. Threshold
332 densities are quantified based on local sea surface temperature, reef fish densities, lionfish prey
333 consumption rates, and lionfish prey production rates. Estimated threshold density across the
334 Belizean MPAs ranged from 10 to 40 fish/hectare (Chapman *et al.* 2019). The predicted
335 abundance of lionfish at F_{OLY} , converted to density, is 7 fish/hectare. Thus, the proposed OLY is
336 expected to substantially reduce the ecological impacts of lionfish in Belize. OLY in this study
337 was quantified and validated based on available ecological and socioeconomic indicators. When
338 ecological and socioeconomic data are not available to formulate OLY targets, setting OLY
339 targets based on a percent yield below MSY is a good initial approach. Based on the trade-offs
340 identified in this study (Figure 3), OLY targets based on percent yields closer to MSY are
341 expected to favor higher yields while percent yields further from MSY are expected to favor
342 population suppression.

343 Encouraging and/or achieving fishing effort beyond MSY levels will likely be a
344 challenge for lionfish fishery managers. From the perspective of single-species fisheries
345 management, fishing at rates beyond F_{MSY} is economically counterproductive because more
346 fishing effort is needed to obtain the same yield. However, from a broader management
347 perspective, fishers, managers, researchers, and the public can view the effort beyond F_{MSY} as
348 effort devoted to marine conservation and control of an invasive species. This additional effort
349 can be viewed and marketed as an investment in native species that are negatively affected by
350 lionfish and/or are overfished. One approach to achieve target F_{OLY} values is to set the target
351 commercial $F = F_{MSY}$, then make up the additional effort needed through recreational fishing.
352 Regularly scheduled and well-advertised recreational lionfish derbies and tournaments, which
353 almost always incorporate some form of marine conservation messaging, have been highly

354 successful at reducing lionfish densities and impacts on local reefs throughout the invaded range
355 (e.g., Green *et al.* 2017). Making up this effort deficit through recreational fishing is much more
356 likely than through commercial fishing, given that recreational fishing priorities are based more
357 on angler satisfaction than on economic efficiency. Monitoring fishing effort and determining
358 fishing mortality rates from these events would not be difficult; not only would these efforts aid
359 in achieving increased fishing mortality, they can also enhance awareness and education of
360 marine conservation issues.

361 In addition to fishing mortality and landings, size at selection is a variable that fishery
362 managers often regulate. Typically, the objective is to allow juveniles to reach maturity and
363 spawn before becoming susceptible to the fishery. Like fishing mortality (Figure 3), the model
364 indicates that a trade-off exists in which increased harvest of smaller lionfish can significantly
365 reduce abundance, and theoretically reduce the potential for ecological impact, but comes with a
366 significant cost to landings (Figure 4). Equilibrium landings and abundance at the current size
367 selection threshold of 250 mm were estimated at 28.3 t (1000 kg) and 422,000 lionfish (Figure
368 4). A shift in size selection to smaller lionfish (*i.e.*, 200 mm fish) indicated a 68% reduction in
369 landings as well as a 72% reduction in abundance, whereas an increase in size selection to larger
370 lionfish (*i.e.*, 300 mm fish) indicated a 20% increase in landings and a 56% increase in
371 abundance (Figure 4). This result is consistent with model predictions in Barbour *et al.* (2011),
372 Morris *et al.* (2011b), and Edwards *et al.* (2014), all of which indicated that the removal of
373 smaller (juvenile) lionfish may have the strongest effect on population abundance. As with other
374 fish species, this characteristic is attributed to lionfish reproductive biology, particularly their age
375 and size at maturity and their fecundity at age and size. Lionfish become mature at age 1 or ~100
376 mm (Edwards *et al.* 2014), and annual egg production per female generally increases with size

377 and age (Morris 2009). As such, increased harvest of smaller lionfish reduces total annual egg
378 production. While this population characteristic is common among fishery species, it is an
379 important characteristic for both lionfish control and lionfish fishery management. For general
380 lionfish control, it supports the need to target smaller lionfish to enhance population suppression.
381 For lionfish fishery management, it indicates that size selection thresholds could help managers
382 balance the trade-offs between sustainable yield and population suppression.

383 Overall, the model results were relatively sensitive to the growth and fecundity
384 parameters (Table 2), which is consistent with other lionfish population modeling studies (*e.g.*,
385 Barbour *et al.* 2012, Edwards *et al.* 2014). While growth and fecundity estimates for lionfish
386 from nearby Little Cayman Island were used in this study, robust age, growth, and fecundity data
387 for lionfish in Belize could improve model predictions and overall management of the fishery,
388 particularly estimates of F_{MSY} . The largest sensitivity described the response of MSY to changes
389 in the length-weight parameter β ($|Z_i| = 19.9$, Table 2), indicating the importance of precise β
390 estimates. This level of sensitivity is due to the exponential relationship between length and
391 weight and, therefore, the potential for β to strongly influence estimates of yield in weight.
392 However, given the well-defined relationship between length and weight described in this study
393 (Figure 2), we do not view this as a critical research need in Belize. In general, model results
394 were not sensitive to natural mortality, suggesting the model provided by Then *et al.* (2015) is
395 adequate for describing natural mortality of lionfish, at least until lionfish-specific estimates
396 become available. Data derived from several surveys conducted to develop Belize's National
397 Lionfish Management Strategy (Chapman *et al.* 2019) were used in this study. These included
398 data on current landings, total lionfish abundance, fisher and restaurateur satisfaction of current
399 landings, and lionfish ecological threshold densities. While these data are informative and

400 satisfactory for model development and initiation of management, establishment of systematic
401 and regular fishery-dependent and fishery-independent monitoring is imperative for successful
402 long-term lionfish fishery management in Belize and elsewhere.

403 **4. Conclusions**

404 This paper describes the application and extension of fishery management concepts to the
405 management of an invasive species. This paper introduces the concept of optimum lionfish yield,
406 which seeks the balance management trade-offs from both the natural resource and invasive
407 species management perspectives. We applied this concept to quantify initial lionfish fishery
408 management targets in Belize. This case study highlights an alternative approach to invasive
409 species management and is an illustrative example of a sentiment summarized by Oficialdegui *et*
410 *al.* (2020): “Legal instruments regulating the commercial use of non-native invasive species need
411 to overcome simplistic approaches (full exploitation or complete ban) and involve more flexible
412 and adaptive strategies because there is no one-size-fits-all solution.” Through proper
413 management, invasive lionfish can serve as a biologically robust alternative fishery resource,
414 which could help create more diversified markets and potentially reduce stress on traditional
415 native fishery species. While the concept and framework described here is introduced for
416 management of invasive lionfish, it could be applied to management of other invasive species,
417 both aquatic and terrestrial.

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568 **Tables and Figures**

569 Table 1: Age-specific parameter values used in the population model

Parameter values	1	2	3	4	5	6	7+
Maturity (<i>m</i>)	0.665	0.990	0.999	0.999	0.999	0.999	0.999
Fecundity (<i>f</i> , eggs)	478,705	2,892,869	4,479,088	5,521,309	6,206,096	6,656,034	6,951,664
Natural mortality (<i>M</i>)	0.30	0.30	0.30	0.30	0.30	0.30	0.30
Mean Length (<i>L</i> , mm)	198.97	250.42	284.23	306.44	321.04	330.63	336.93
Mean Weight (<i>W</i> , g)	98.69	201.82	299.23	378.13	437.00	478.90	507.85
Selectivity (<i>S</i>)	0.035	0.507	0.889	0.978	0.995	0.999	1

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583 Table 2: Sensitivity of model results to parameter values. Values > 1.0 or < -1.0 indicate that a
 584 10% change in the parameter results in a $>10\%$ change in the model output, which were
 585 considered significant in this study (*). The larger the absolute value, the greater the sensitivity.

Parameter	Description	F_{MSY}	MSY	N_{MSY}
R_0	Asymptotic recruitment level	0.00	1.02*	1.00*
h	Steepness of recruitment	2.24*	0.80	0.03
M	Natural mortality	1.49*	-0.58	-0.62
L_∞	Mean asymptotic length	-2.39*	2.97*	-0.41
K	Growth coefficient	0.00	1.18*	-0.48
a_0	Theoretical age of length 0	0.15	0.32	-0.20
α	Length-weight coefficient	0.00	1.02*	0.00
β	Length-weight exponent	-0.60	19.90*	0.21
B	Batches spawned per year	0.00	0.00	0.00
b_1	Batch fecundity coefficient	1.34*	0.32	-0.14
b_2	Batch fecundity intercept	-1.19*	-0.32	0.12
L_{50}	Length at 50% maturity	-0.30	-0.06	0.02
σ	Slope of maturity curve	0.00	0.00	0.00
L_{vuln}	Length of vulnerability to harvest	4.03*	0.58	0.26

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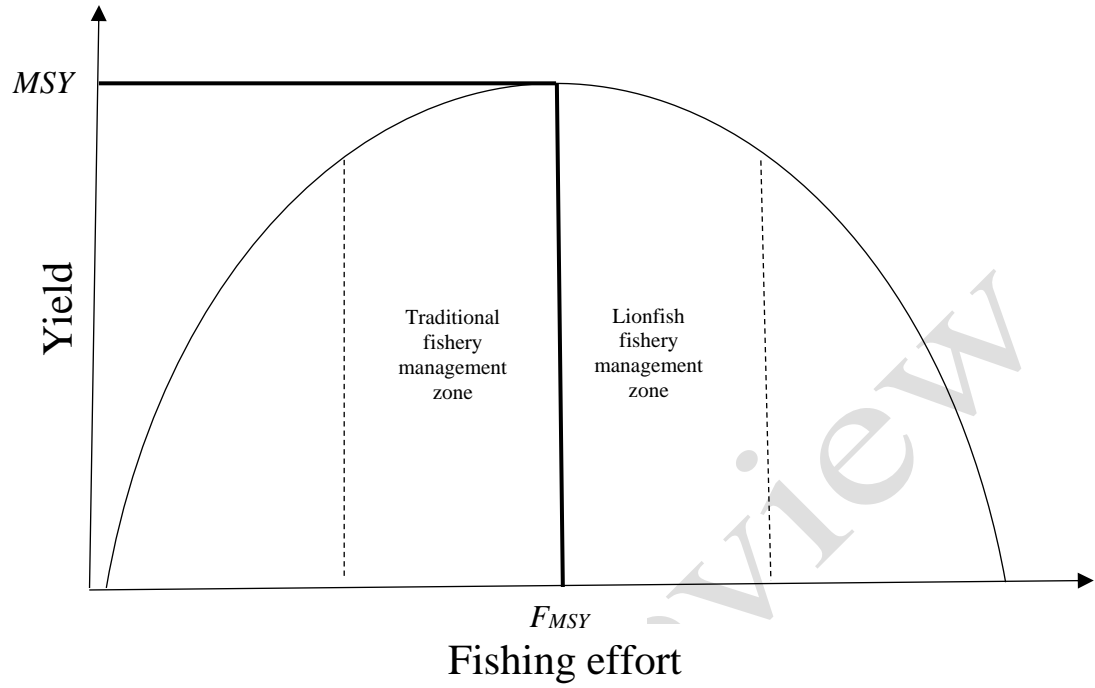
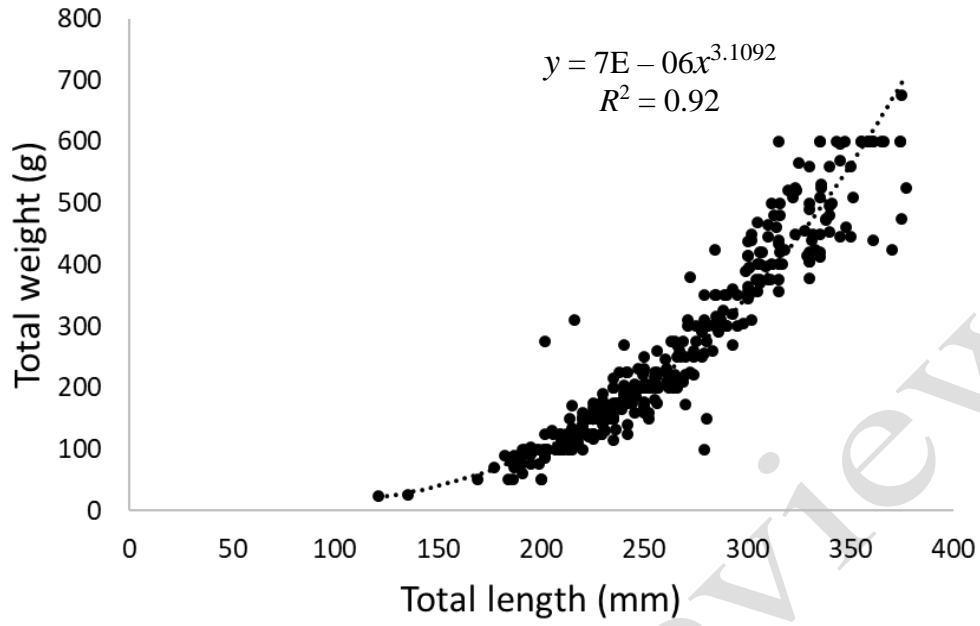


Figure 1: A generalized sustainable yield curve depicting the approximate zones of traditional fishery management targets compared to proposed lionfish fishery management targets



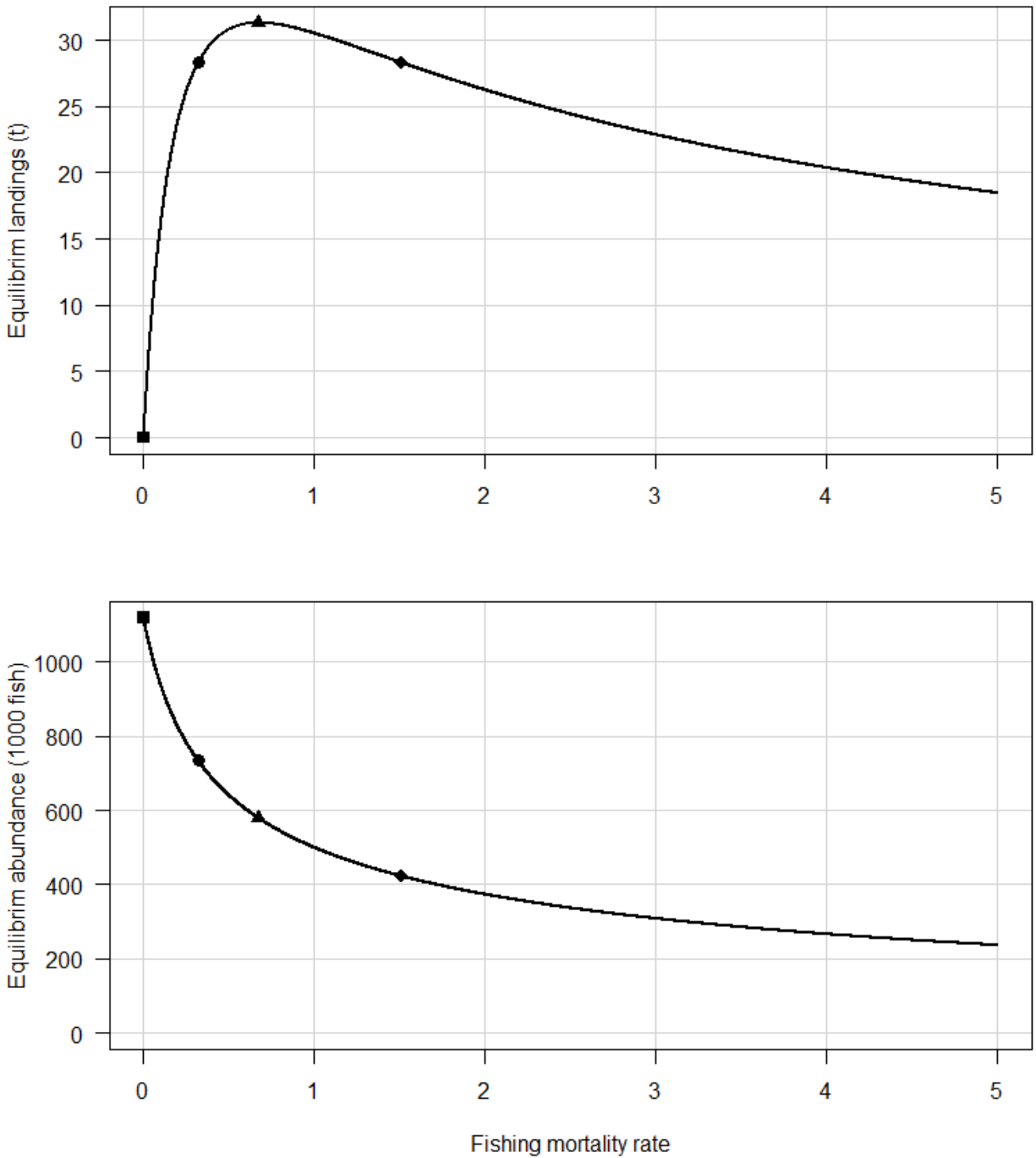
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Figure 2: The relationship between lionfish length and weight in Belize (n=352)

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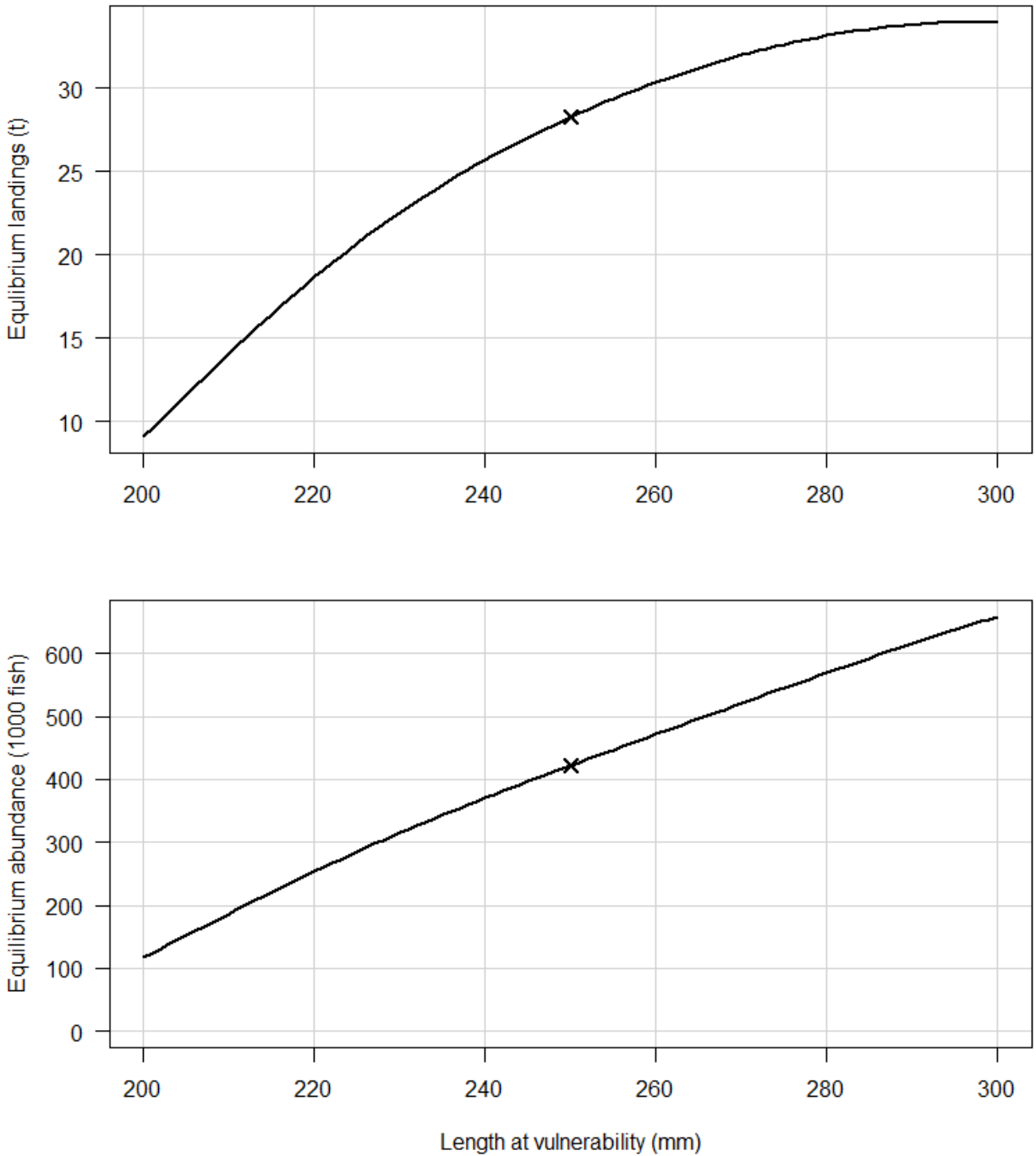
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616 Figure 3: Equilibrium landings (top) and abundance (bottom) of lionfish in Belize across a range
 617 of fishing mortality rates: $F_{LOW} = 0$ (■), $F_{CURRENT} = 0.32$ (●), $F_{MSY} = 0.67$ (▲), $F_{OLY} = 1.51$ (◆),
 618 and $F_{HIGH} = 5.0$
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623 Figure 4: Equilibrium landings (top) and abundance (bottom) of lionfish in Belize across a range
 624 of sizes at selection with $F = F_{OLY} = 1.51$. The point on the graph indicates current size at
 625 selection = 250 mm

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630 **Appendix 1: Additional Analyses**

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632 *Part 1: Exploring Uncertainty in Landings and Abundance*

633 As described in the main text, the 2015 field estimates of abundance and landings were
634 733,257 lionfish and 89,902 lionfish. Abundance and landings directly affect estimates of the
635 current fishing mortality rate (current F) and the asymptotic recruitment of age-1 fish (R0) and,
636 therefore, model output (see Section 2.2 in the main text). Here, we explore uncertainty in our
637 point estimates of abundance and landings on current F, R0, and model output.

638 To do this, we conducted Monte Carlo simulations (N=2000 iterations in each analysis)
639 in which each iteration repeated our analysis but with different values of (1) abundance and
640 landings and then (2) current F and R0. First, we drew a new value of abundance and a new
641 value of landings each from a normal distribution with mean equal to the 2015 field estimates
642 and an assumed coefficient of variation (CV) of CV=0.1 (Appendix Figure 1A,B). Using these
643 values, we computed distributions of current F (Appendix Figure 1C) and of R0 (Appendix
644 Figure 1D). We then propagated uncertainty in current F and R0 into the estimated management
645 quantities. Similar to above, we conducted Monte Carlo simulations (N=2000 iterations) in
646 which each iteration repeated our analysis but with different values of current F and R0 drawn
647 from their distributions produced above (i.e., Appendix Figure 1C,D). This produced
648 distributions of current landings (Lcurrent), MSY, and OLY (Appendix Figure 2A), as well as in
649 the levels of abundance associated with those values (Appendix Figure 2B). The general
650 conclusion presented in the main text remains the same as that inferred from the corresponding
651 point estimates - fishing at OLY provides current levels of landings (by design) while
652 suppressing the abundance to substantially lower levels than current.

653 We additionally propagated uncertainty in current F and R0 into estimates of equilibrium
654 landings and abundance as a function of fishing rate (Appendix Figure 3). We caution that this
655 analysis does not produce true confidence bands as it is predicated on our assumed value of
656 CV=0.1. It does, however, indicate the conditional degree of uncertainty in results stemming
657 from the field estimates of abundance and landings.

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659 *Part 2: Exploring Uncertainty in the standard deviation of size-at-age*

660 As part of our analyses in the main text, we examined effects of the size-at-selection on
661 equilibrium abundance and landings (Figure 4). The size-at-selection, along with growth
662 characteristics including the standard deviation of size-at-age, determined the pattern of
663 selectivity as the proportion of fish-at-age that were vulnerable to fishing. In Appendix Figure 4,
664 we show how size-at-selection and standard deviation of size-at-age affect the resulting
665 selectivity curves. In general, the curves are far more sensitive to the size-at-selection (our pivot)
666 than to the standard deviation.

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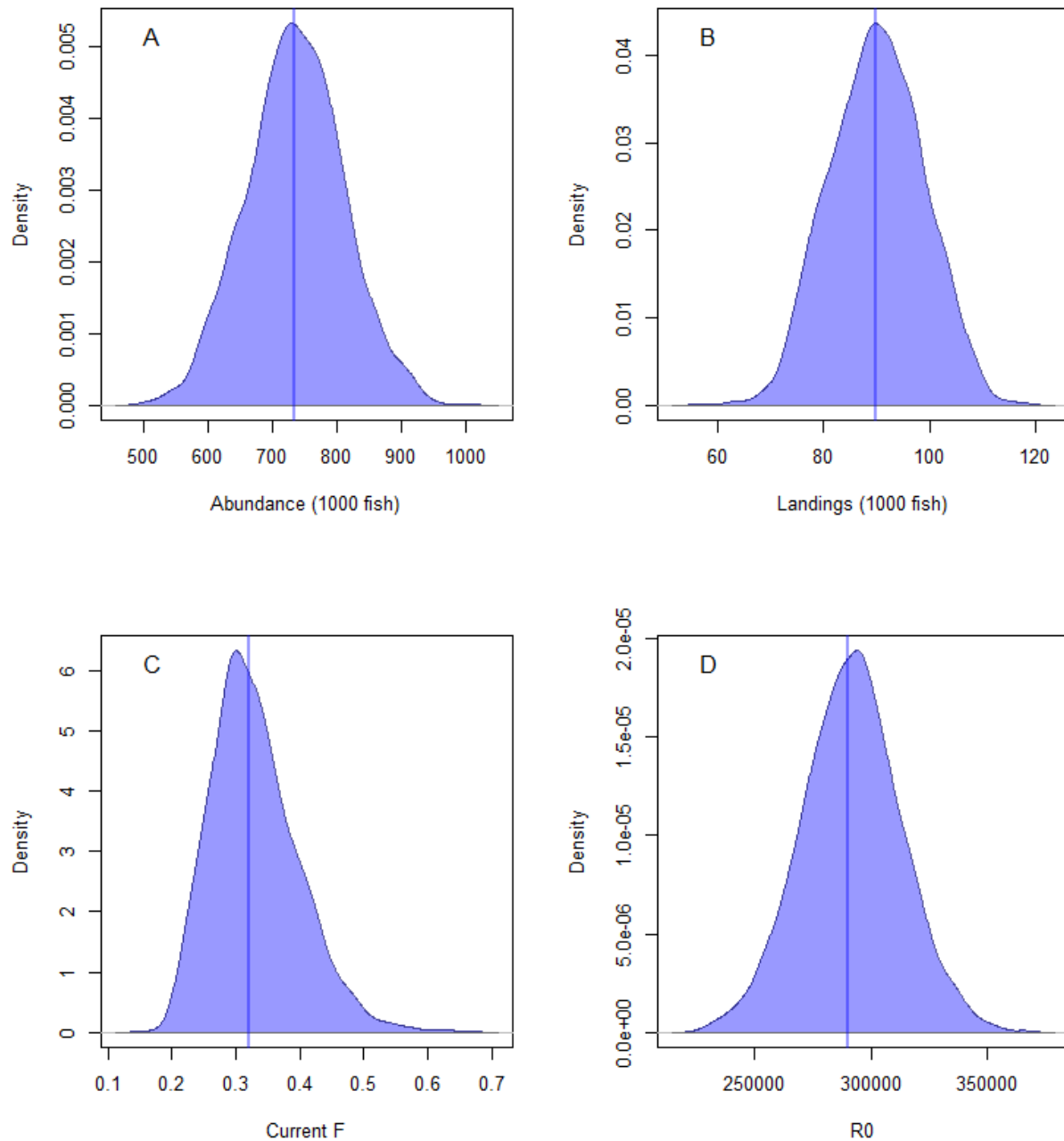
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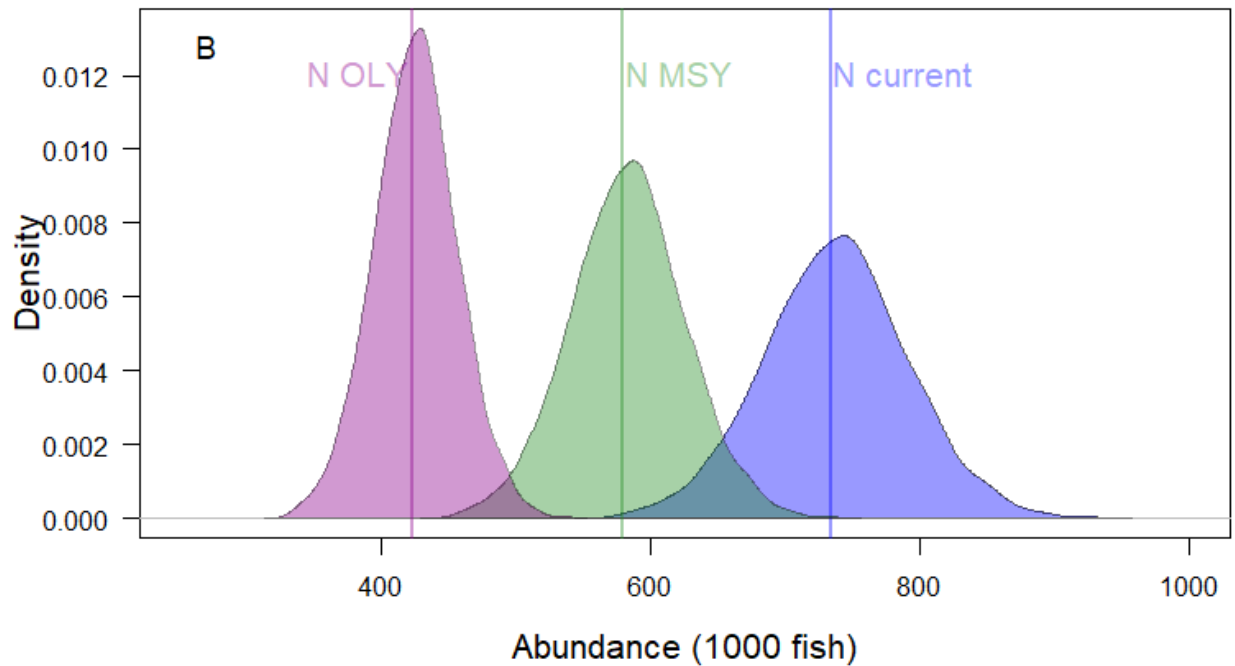
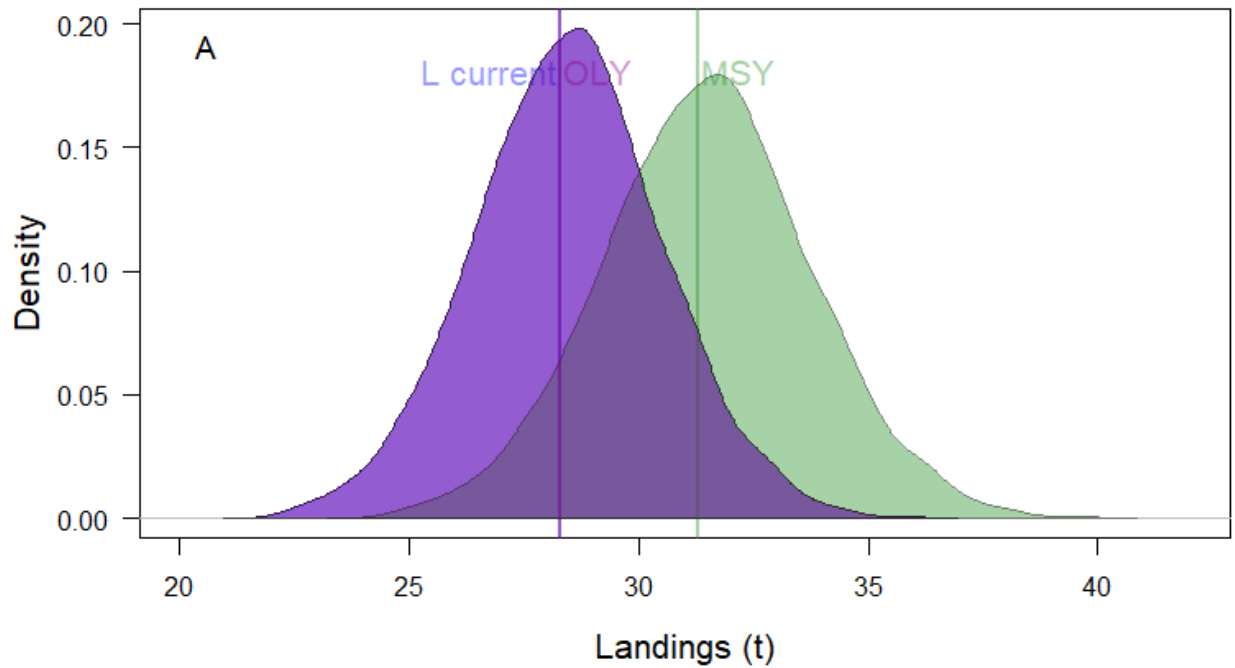
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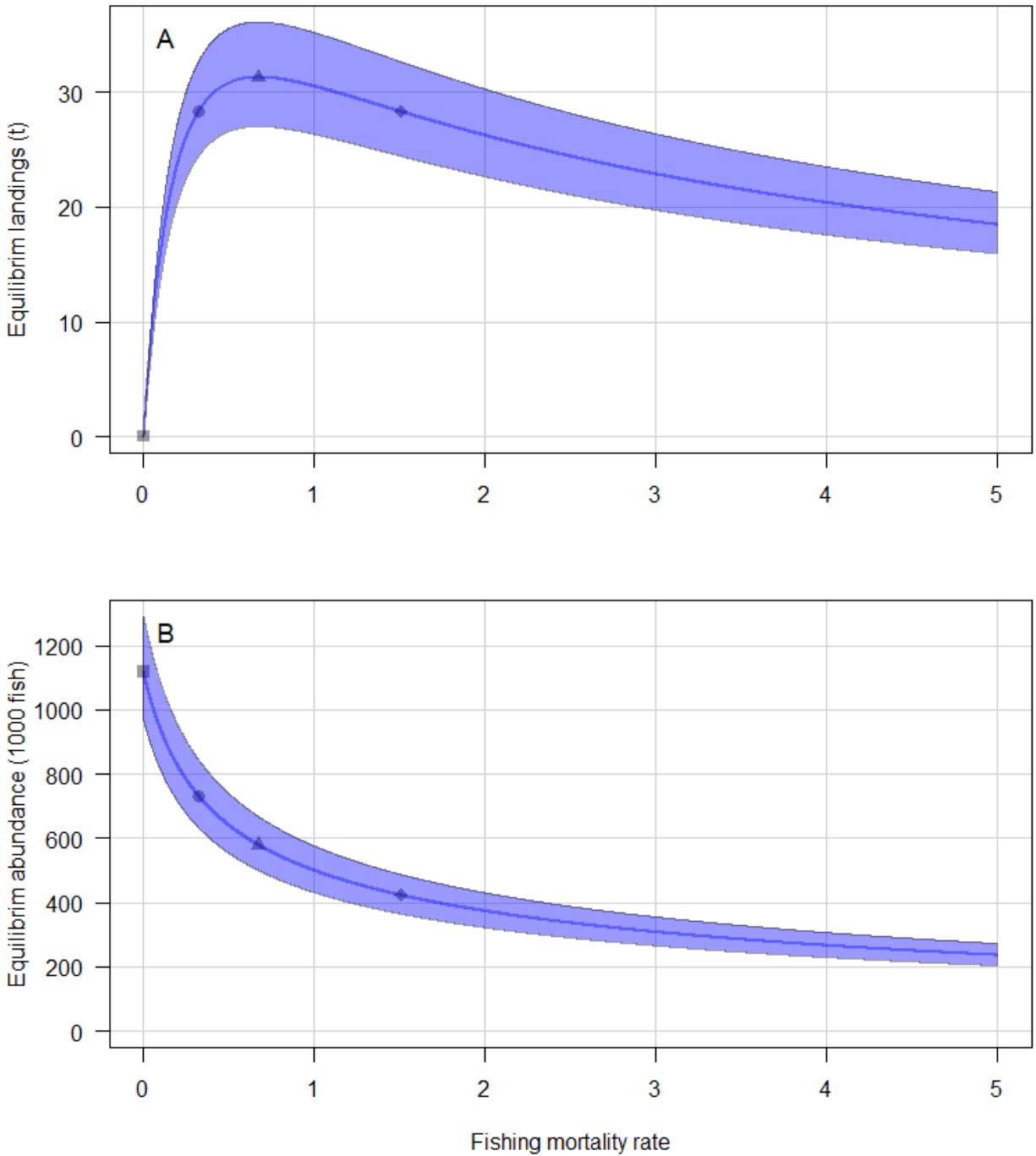
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675 Appendix Figure 1. Assumed distributions of initial lionfish abundance (A) and landings (B)
 676 used to compute the current fishing rate (current F) (C) and the asymptotic recruitment of age-1
 677 fish (R0) (D). Vertical lines indicate the 2015 field estimates of abundance and landings (A,B)
 678 and the point estimates of current F and R0 derived from those field estimates (C,D).
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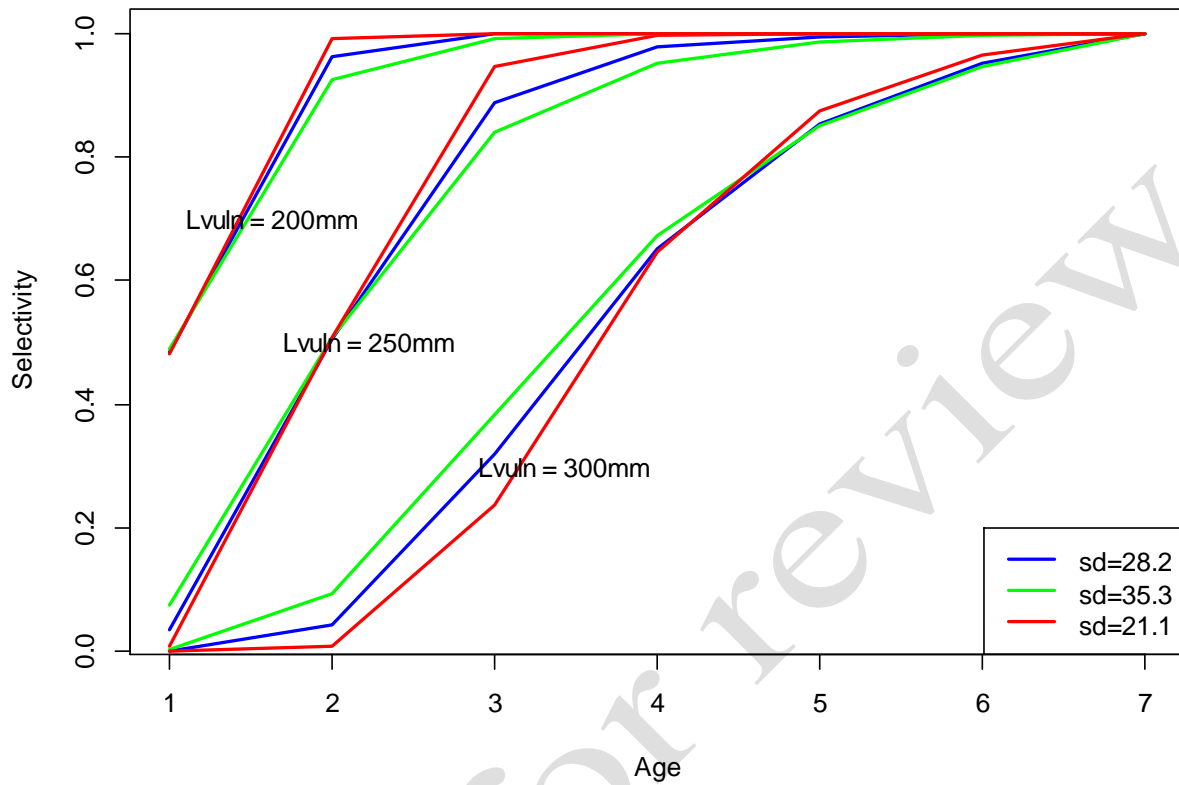
681 Appendix Figure 2. Distributions of results derived from assumed distributions of field estimates
 682 of abundance and landings. Panel A shows distributions of landings corresponding to Lcurrent
 683 (blue), OLY (purple), and MSY (green). Note that Lcurrent is not apparent because it overlaps
 684 entirely with OLY (by design). Panel B shows the levels of abundance that correspond to the
 685 landings in Panel A.
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689 Appendix Figure 3. Equilibrium landings (A) and abundance (B) of lionfish in Belize across a
 690 range of fishing mortality rates: $F_{MIN} = 0$ (■), $F_{CURRENT} = 0.32$ (●), $F_{MSY} = 0.67$ (▲), $F_{OLY} = 1.51$
 691 (◆), and $F_{HIGH} = 5.0$. Intervals shown represent the 2.5th and 97.5th percentiles from N=2000
 692 Monte Carlo simulations with variability in the 2015 field estimates of lionfish abundance and
 693 landings.

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 696 Appendix Figure 4. Selectivity as a function of the size-at-selection (L_{vuln}) and the standard
 697 deviation (SD) of size-at-age. Our base values were $L_{vuln} = 250$ mm and $SD = 28.2$, and values
 698 used to create Figure 4 (main text) varied L_{vuln} over the range 200mm to 300mm, with $SD =$
 699 28.2 in all cases. For this figure, we additionally varied $SD \pm 25\%$ of the base value.