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

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

1. Introduction

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

To increase the scale and magnitude of removal efforts, researchers and managers have been promoting commercialization of lionfish over the last decade, particularly as seafood. Not only are lionfish plentiful, they are safe to consume and a nutritious source of protein (Tremain and O'Donnell 2014, Hardison *et al.* 2018Morris *et al.* 2011a). Lionfish are now being harvested recreationally and commercially throughout much of the invaded region, but are not being managed as a fishery resource. Similar to other natural resource markets, as demand increases so too does the number of people who exploit the resource and, therefore, the number of individuals who may become (more) reliant on the resource. For this reason, lionfish fisheries would benefit from science-based management (Merrick 2018). Through proper management, invasive lionfish could serve as an alternative fishery resource, which could help create more diversified markets and potentially reduce fishing pressure on traditional native fishery species. Lionfish fisheries could also indirectly improve stocks of fishery species impacted by lionfish.

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

This paper describes a non-traditional fisheries management concept and an indicator-based framework to encourage and guide management of invasive lionfish fisheries throughout the western Atlantic. We propose the concept of optimum lionfish yield (OLY), which seeks to balance the competing objectives of high sustainable yield and population suppression, and describe one potential approach for formulating OLY values using the lionfish fishery in Belize as a case study. In contrast to traditional fisheries management targets, OLY is a target exceeding MSY that still provides relatively high sustainable yield, but further contributes to population suppression beyond what is achievable through targets at or below MSY (Figure 1). Thus, OLY balances management trade-offs from both natural resource and invasive species management perspectives. Optimum lionfish yield is an extension of the concept of ecologically sustainable yield (ESY) – a target yield that a community or ecosystem can sustain without shifting to an undesirable ecological state (Zabel *et al.* 2003). While OLY targets lie above MSY and ESY targets lie below MSY, both concepts suggest that traditional fishery management practices that set single-species targets based solely on MSY can be insufficient. OLY and ESY suggest that managers establish fishery targets that also consider overall ecological health.

Since 2011, the Belize Fisheries Department and its partners have worked to establish a nationally managed lionfish fishery as a means of national-level control and to diversify local markets (Chapman *et al.* 2019, Searle *et al.* 2012). Commercial lionfish markets have been developed (*e.g.*, as seafood and for jewelry) and the number of fishers targeting lionfish has grown, but management of the fishery has not yet begun (Chapman *et al.* 2019). One of the essential steps in establishing a well-managed fishery is understanding the population's response to fishing pressure, which is typically achieved through application of population and stock assessment models. Thus, we developed an age-structured population model and applied the concept of OLY to quantify benchmark targets to initiate management of the lionfish fishery in Belize. Available socioeconomic and ecological data for lionfish in Belize were used as indictors to quantify and then validate that the proposed values of OLY satisfied the two general objectives of lionfish fishery management – high sustainable yield that meets socioeconomic demand and population suppression that mitigates ecological impacts. Data from the fishery are not currently available to model temporal dynamics of the population, but do exist to examine equilibrium behavior in response to fishing pressure and size at selection – two variables that fishery managers can regulate. Although no real population is ever in true equilibrium, reference points derived under this assumption are useful as long-term targets even if met with non-equilibrium dynamics in practice (Goodyear 1993, Mace 2001). Model results are discussed within the context of tradeoffs between sustainable yield and population suppression.

2. Methods

2.1 General overview of approach

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

2.2 Model description

Lionfish abundance at age (N_a) was computed as

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

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

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

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

$$\mathrm{S} = \sum_a 0.5 N_a m_a f_a \quad (3)$$

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

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

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

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

where W_a is weight in kilograms at age *a*.

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

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

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

$$W = \alpha L^{\beta} \tag{7}$$

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

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

$$m_a = \frac{1}{1+e^{-(L_a - \mathrm{L50})/\sigma}} \tag{8}$$

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

$$f_a = B(b_1 L_a - b_2) \tag{9}$$

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

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

$$M = 4.889 * t_{max}^{-0.916} \tag{10}$$

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

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

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

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

Given total mortality at age (Z_a) and $N_{tot} = \sum_a N_a = 733{,}257$, the recursive relationship of Equation 11 provides $\widehat{R_{eq}} = 266{,}000$. This value was then used to compute $\widehat{R_0} = 289{,}900$ as a function of equilibrium recruitment

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

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

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

where ψ_a is the number of fish per recruit at age a computed using Equation 11 with N_1 = 1. The number of spawners per recruit of an unfished population (Φ_0) is computed similarly, but with F = 0.

2.3 Model application

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

2.4 Formulation of OLY values

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

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

2.5 Sensitivity analysis

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

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

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

3. Results and Discussion

Overall, the model indicates that harvest of lionfish effectively reduces population abundance (Figure 3). Equilibrium abundance at $\mathrm{F_{LOW}} = 0$ was estimated at 1.5 million lionfish, while abundance at $\mathrm{F_{HIGH}} = 5.0$ was 220,000 lionfish. The model suggests that the current fishing effort in Belize has already reduced lionfish abundance by 34%, but increasing effort to $\mathrm{F_{MSY}} = 0.67$ could reduce abundance by an additional 21% (Figure 3). The model also suggests that the population in Belize can withstand high rates of fishing without collapse, as indicated by the relatively high abundance of lionfish predicated at F_{HIGH} – an improbable fishing mortality rate (Figure 3). Other lionfish population modeling studies have reported similar findings. Morris *et al.* (2011b) predicted monthly exploitation of 27% of the adult population in the temperate and tropical western Atlantic would result in zero net growth; Barbour *et al.* (2011) predicted annual exploitation rates between 35 and 65% of the total population in North Carolina would be required to cause recruitment overfishing; Edwards *et al.* (2014) predicted annual exploitation rates between 15 and 35% of the total population at Little Cayman Island would be required to cause recruitment overfishing; and Chagaris *et al.* (2017) predicted fishing mortality rates greater than F = 1.0 are required to cause population declines on the West Florida Shelf. The results from these studies, which vary in terms of model design, data inputs, and geographic and spatial scales, all indicate a key population characteristic – invasive lionfish are biologically robust to fishing pressure. This population characteristic is likely due to lionfish biology and ecology (Côté *et al.* 2013) and is an important finding in terms of both lionfish control and establishing managed lionfish fisheries. This finding highlights the (1) biological sustainability of lionfish as a fishery resource and (2) indicates that the level of fishing effort required to overfish lionfish is substantial and unlikely to be achieved, especially without commercial-scale fishing practices. These data support continued establishment of (managed) commercial lionfish fisheries throughout the invaded range to provide an alternative sustainable fishery resource and serve as a means of national- and international-level control.

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

Belize-specific lionfish ecological threshold densities reported in Chapman *et al.* (2019) were then used to cross-check that the proposed OLY targets would sufficiently reduce lionfish populations to a level that is expected to mitigate their ecological impacts. Threshold densities were estimated for the five major Belizean marine protected areas (MPAs) in 2015 following the approach in Green *et al.* (2014). The approach in Green *et al.* (2012) estimates location-specific lionfish densities at which their ecological impacts are predicted to be mitigated. Threshold densities are quantified based on local sea surface temperature, reef fish densities, lionfish prey consumption rates, and lionfish prey production rates. Estimated threshold density across the Belizean MPAs ranged from 10 to 40 fish/hectare (Chapman *et al.* 2019). The predicated abundance of lionfish at F_{OLY}, converted to density, is 7 fish/hectare. Thus, the proposed OLY is expected to substantially reduce the ecological impacts of lionfish in Belize. OLY in this study was quantified and validated based on available ecological and socioeconomic indicators. When ecological and socioeconomic data are not available to formulate OLY targets, setting OLY targets based on a percent yield below MSY is a good initial approach. Based on the trade-offs identified in this study (Figure 3), OLY targets based on percent yields closer to MSY are expected to favor higher yields while percent yields further from MSY are expected to favor population suppression.

Encouraging and/or achieving fishing effort beyond MSY levels will likely be a challenge for lionfish fishery managers. From the perspective of single-species fisheries management, fishing at rates beyond F_{MSY} is economically counterproductive because more fishing effort is needed to obtain the same yield. However, from a broader management perspective, fishers, managers, researchers, and the public can view the effort beyond F_{MSY} as effort devoted to marine conservation and control of an invasive species. This additional effort can be viewed and marketed as an investment in native species that are negatively affected by lionfish and/or are overfished. One approach to achieve target F_{OLY} values is to set the target commercial $F = F_{MSY}$, then make up the additional effort needed through recreational fishing. Regularly scheduled and well-advertised recreational lionfish derbies and tournaments, which almost always incorporate some form of marine conservation messaging, have been highly successful at reducing lionfish densities and impacts on local reefs throughout the invaded range (e.g., Green *et al.* 2017). Making up this effort deficit through recreational fishing is much more likely than through commercial fishing, given that recreational fishing priorities are based more on angler satisfaction than on economic efficiency. Monitoring fishing effort and determining fishing mortality rates from these events would not be difficult; not only would these efforts aid in achieving increased fishing mortality, they can also enhance awareness and education of marine conservation issues.

In addition to fishing mortality and landings, size at selection is a variable that fishery managers often regulate. Typically, the objective is to allow juveniles to reach maturity and spawn before becoming susceptible to the fishery. Like fishing mortality (Figure 3), the model indicates that a trade-off exists in which increased harvest of smaller lionfish can significantly reduce abundance, and theoretically reduce the potential for ecological impact, but comes with a significant cost to landings (Figure 4). Equilibrium landings and abundance at the current size selection threshold of 250 mm were estimated at 28.3 t (1000 kg) and 422,000 lionfish (Figure 4). A shift in size selection to smaller lionfish (*i.e.*, 200 mm fish) indicated a 68% reduction in landings as well as a 72% reduction in abundance, whereas an increase in size selection to larger lionfish (*i.e.*, 300 mm fish) indicated a 20% increase in landings and a 56% increase in abundance (Figure 4). This result is consistent with model predictions in Barbour *et al.* (2011), Morris *et al.* (2011b), and Edwards *et al.* (2014), all of which indicated that the removal of smaller (juvenile) lionfish may have the strongest effect on population abundance. As with other fish species, this characteristic is attributed to lionfish reproductive biology, particularly their age and size at maturity and their fecundity at age and size. Lionfish become mature at age 1 or ~100 mm (Edwards *et al.* 2014), and annual egg production per female generally increases with size and age (Morris 2009). As such, increased harvest of smaller lionfish reduces total annual egg production. While this population characteristic is common among fishery species, it is an important characteristic for both lionfish control and lionfish fishery management. For general lionfish control, it supports the need to target smaller lionfish to enhance population suppression. For lionfish fishery management, it indicates that size selection thresholds could help managers balance the trade-offs between sustainable yield and population suppression.

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

4. Conclusions

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

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Literature Cited

Albins MA. 2015. Invasive Pacific lionfish *Pterois volitans* reduce abundance and species richness of native Bahamian coral-reef fishes. *Marine Ecology Progress Series 522:231-243.*

Albins MA & MA Hixon. 2008. Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series* 367: 233-238.

Ballew NG, NM Bacheler, GT Kellison, and AM Schueller. 2016. Invasive lionfish reduce native fish abundance on a regional scale. *Scientific Reports* 6:32169.

Barbour AB, MS Allen, TK Frazer, and KD Sherman. 2011. Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. *PLoS ONE* 6(5):e19666.

Baranov FI. 1918. On the question of the biological basis of fisheries. *Izvestiya* 1:81–128.

Beverton RJH and SJ Holt. 1957. On the dynamics of exploited fish populations. *Fish. Invest. Minist. Agric. Fish. Food* G.B. Ser. II 19.533 p.

Chagaris D, S Binion-Rock, AK Bogdanoff, K Dahl, J Granneman, H Harris, J Mohan, MB Rudd, MK Swenarton, R Ahrens, WF Patterson, JA Morris, and M Allen. 2017. An ecosystem based approach to evaluating impacts and management of invasive lionfish. *Fisheries* 42(8):421-431.

Chapman JK, L Anderson, ML Fruitema, J Solomon, S Green, AK Bogdanoff, J Sabattis, & D Bueso. 2019. Belize National Lionfish Management Strategy, 2019-2023. *Blue Ventures Conservation*, London, UK. 102 pages.

Côté IM, SJ Green, and MA Hixon. 2013. Predatory fish invaders: insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. *Biological Conservation* 164:50-61.

Dahl KA, WF Patterson, and RA Snyder. 2016. Experimental assessment of lionfish removals to mitigate reef fish community shifts on northern Gulf of Mexico artificial reefs. *Marine Ecology Progress Series* 558: 207-221.

Edwards MA, TK Frazer, and CA Jacoby. 2014. Age and growth of invasive lionfish (*Pterois* spp.) in the Caribbean Sea, with implications for management. *Bulletin of Marine Science* 90: 953-966.

Ellner SP and J Guckenheimer. 2006. Dynamic models in Biology. *Princeton University Press*, 352 pp.

Fogg AG, NJ Brown-Peterson, and MS Peterson. 2017. Reproductive life history characteristics of invasive red lionfish (*Pterois volitans*) in the northern Gulf of Mexico. *Bulletin of Marine Science* 93(3):791-813.

Forrest RE, MK McAllister, MW Dorn, SJD Martell, RD Stanley. 2010. Hierarchical Bayesian estimation of recruitment parameters and reference points for Pacific rockfishes (*Sebastes* spp.) under alternative assumptions about the stock-recruit function. *Canadian Journal of Fisheries and Aquatic Science* 67(10): 1611-1634.

Frazer TK, CA Jacoby, MA Edwards, SC Barry, and CM Manfrino. 2012. Coping with the lionfish invasion: Can targeted removals yield beneficial effects? *Reviews in Fisheries Science* 20:185-191.

Gardner PG, TK Fraser, CA Jaconby, and RPE Yanong. 2015. Reproductive biology of invasive lionfish (*Pterois* spp.). *Frontiers in Marine Science* 2:7.

Goodyear CP. 1993. Spawning stock biomass per recruit in fisheries management: Foundation and current use. *In*: Risk Evaluation and Biological Reference Points for Fisheries Management Ed Smith, SJ, JJ Hunt, D Rivard. *Canadian Special Publication of Fisheries and Aquatic Sciences*, pp. 67-81.

Green SJ, JL Akins, A Maljkovi, and IM Côté. 2012. Invasive Lionfish Drive Atlantic Coral Reef Fish Declines. *PLoS One* 7(3): e32596.

Green SJ, NK Dulvy, ALM Brooks, AB Cooper, JL Akins, S Miller and IM Côté. 2014. Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecological Applications* 24(6): 1311-1322.

Green SJ, EM Underwood, and JL Akins. 2017. Mobilizing volunteers to sustain local suppression of a global marine invasion. *Conservation Letters* 10: 726-735.

Hardison DR, WC Holland, HT Darius, M Chinain, PA Tester, D Shea, AK Bogdanoff, JA Morris, HAF Quintana, CR Loeffler, D Buddo, and RW Litaker. 2018. Investigation of ciguatoxins in invasive lionfish from the greater Caribbean region: Implications for fishery development. *PLoS ONE* 13(6): e0198358.

Johnston MA, SR Gittings, and JA Morris, Jr. 2015. NOAA National Marine Sanctuaries Lionfish Response Plan (2015-2018): Responding, Controlling, and Adapting to an Active Marine Invasion. *Marine Sanctuaries Conservation Series ONMS-15-0*1. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries, Silver Spring, MD. 55 pp.

Johnston MW and SJ Purkis. 2015. A coordinated and sustained international strategy is required to turn the tide on the Atlantic lionfish invasion. *Marine Ecology Progress Series* 533: 219-235.

Johnson EG and MK Swenarton. 2016. Age, growth and population structure of invasive lionfish (*Pterois volitans/miles*) in northeast Florida using a length-based, age-structured population model. *PeerJ* 4: e2730.

Larkin PA. 1977. An Epitaph for the Concept of Maximum Sustained Yield. *Transactions of the American Fisheries Society* 106(1): 1-11.

Mace P. 2001. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. *Fish and Fisheries* 2: 2-32.

Merrick R. 2018. Mechanisms for science to shape US living marine resource conservation policy. *ICES Journal of Marine Science* 75: 2319-2324.

Morris JA. 2009. The Biology and Ecology of invasive indo-pacific lionfish. Ph.D. Thesis, North Carolina State University, Raleigh, NC, 168 pp.

Morris JA, A Thomas, AL Rhyne, N Breen, L Akins, and B Nash. 2011(a). Nutritional properties of the invasive lionfish: a delicious and nutritious approach for controlling the invasion. *Aquaculture, Aquarium, Conservation, & Legislation* 5:99-102.

Morris JA, KW Shertzer, and JA Rice. 2011(b). A stage-based matrix population model of invasive lionfish with implications for control. *Biological Invasions* 13: 7-12.

Oficialdegui FJ, M Delibes-Mateos, AJ Green, MI Sanchez, L Boyero, and M Clavero. 2020. Rigid laws and invasive species management. *Conservation Biology* 34: 1047-1050.

Potts JC, D Berrane, and JA Morris. 2010. Age and growth of lionfish from the western north Atlantic. *Proceedings of the Gulf and Caribbean Fisheries Institute* 63:314.

Prager MH and KW Shertzer. 2010. Deriving acceptable biological catch from the overfishing limit: Implications for assessment models. *North American Journal of Fisheries Management* 30: 289-294.

R Core Team. 2017. R: A language and environment for statistical computing. https://www.R-project.org/

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

Searle L, N Chacon, and L Bach. 2012. The Belize Lionfish Management Plan: An Overview of the Invasion, Mitigation Activities and Recommendations. *ECOMAR* Technical Publication No 1. 80 p.

Shertzer KW and PB Conn. 2012. Spawner-recruit relationships of demersal marine fishes: Prior distributions of steepness. *Bulletin of Marine Science* 88: 39-50.

Then AY, JM Hoenig, NG Hall, DA Hewitt. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES Journal of Marine Science* 72(1): 82-92.

Thorson JT. 2020. Predicting recruitment density dependence and intrinsic growth rate for all fishes worldwide using a data-integrated life-history model. *Fish and Fisheries* 21: 237-251.

Tremain M and D O'Donnell. 2014. Total mercury levels in invasive lionfish, *Pterois volitans* and *Pterois miles* (Scorpaenidae), from Florida waters. *Bulletin of Marine Science* 90(2): 565-578.

Von Bertalanffy L. 1957. Quantitative laws in metabolism and growth. *Quarterly Review in Biology* 32:217 – 2331.

Zabel RW, CJ Harvey, SL Katz, TP Good, and PS Levin. 2003. Ecologically Sustainable Yield: Marine conservation requires a new ecosystem-based concept for fisheries management that looks beyond sustainable yield for individual fish species. *American Scientist* 91(2): 150-157.

Tables and Figures

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

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

Table 2: Sensitivity of model results to parameter values. Values > 1.0 or < -1.0 indicate that a 10% change in the parameter results in a >10% change in the model output, which were 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

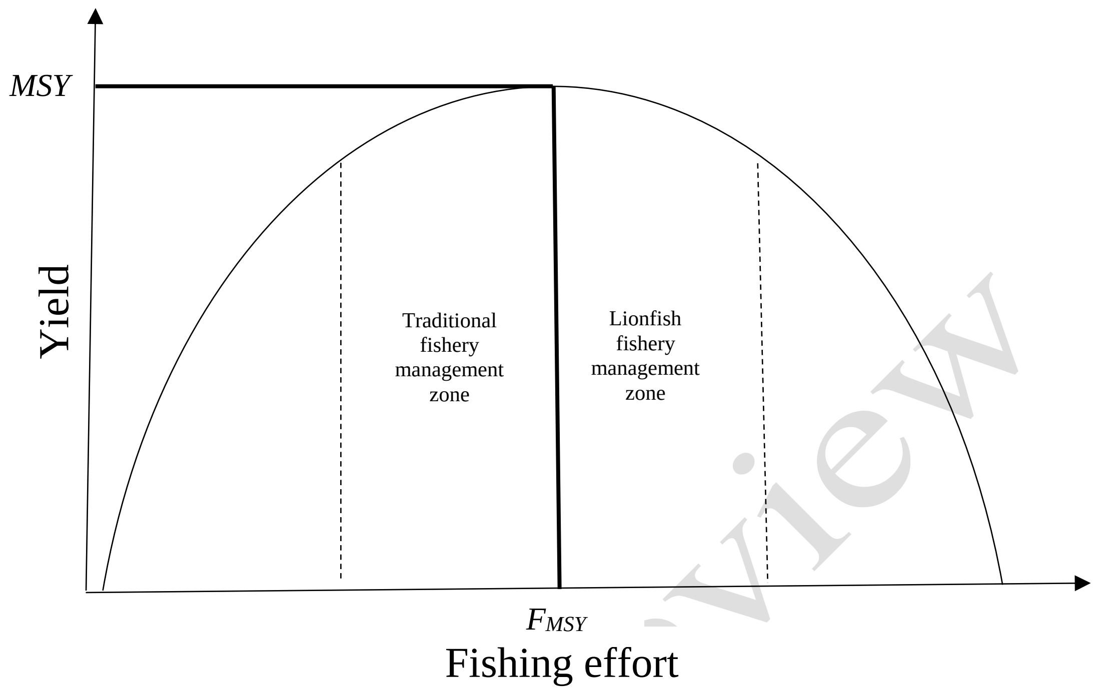


Figure 1: A generalized sustainable yield curve depicting the approximate zones of traditional fishery management targets compared to proposed lionfish fishery management targets

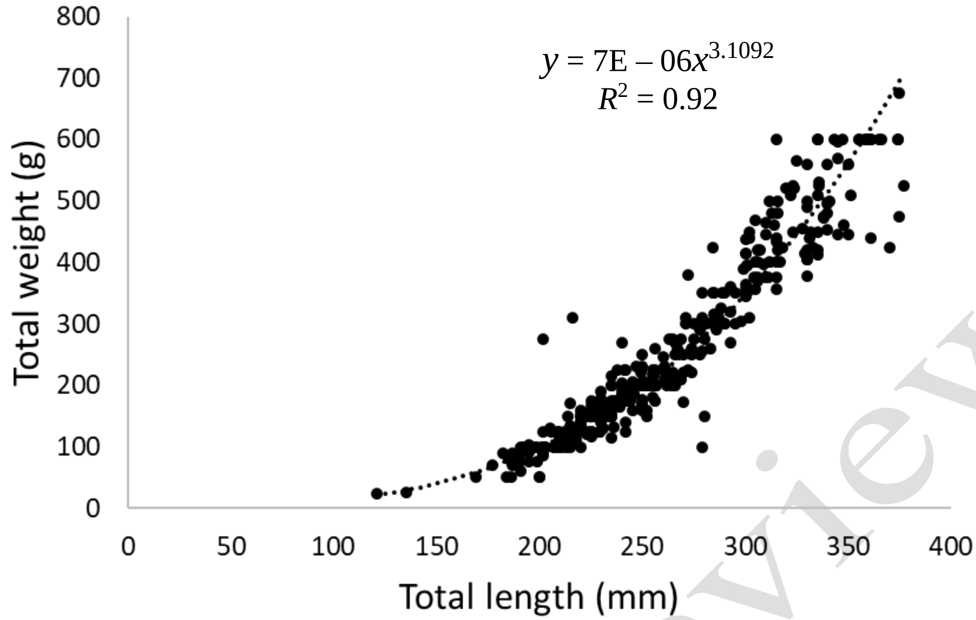


Figure 2: The relationship between lionfish length and weight in Belize (n=352)

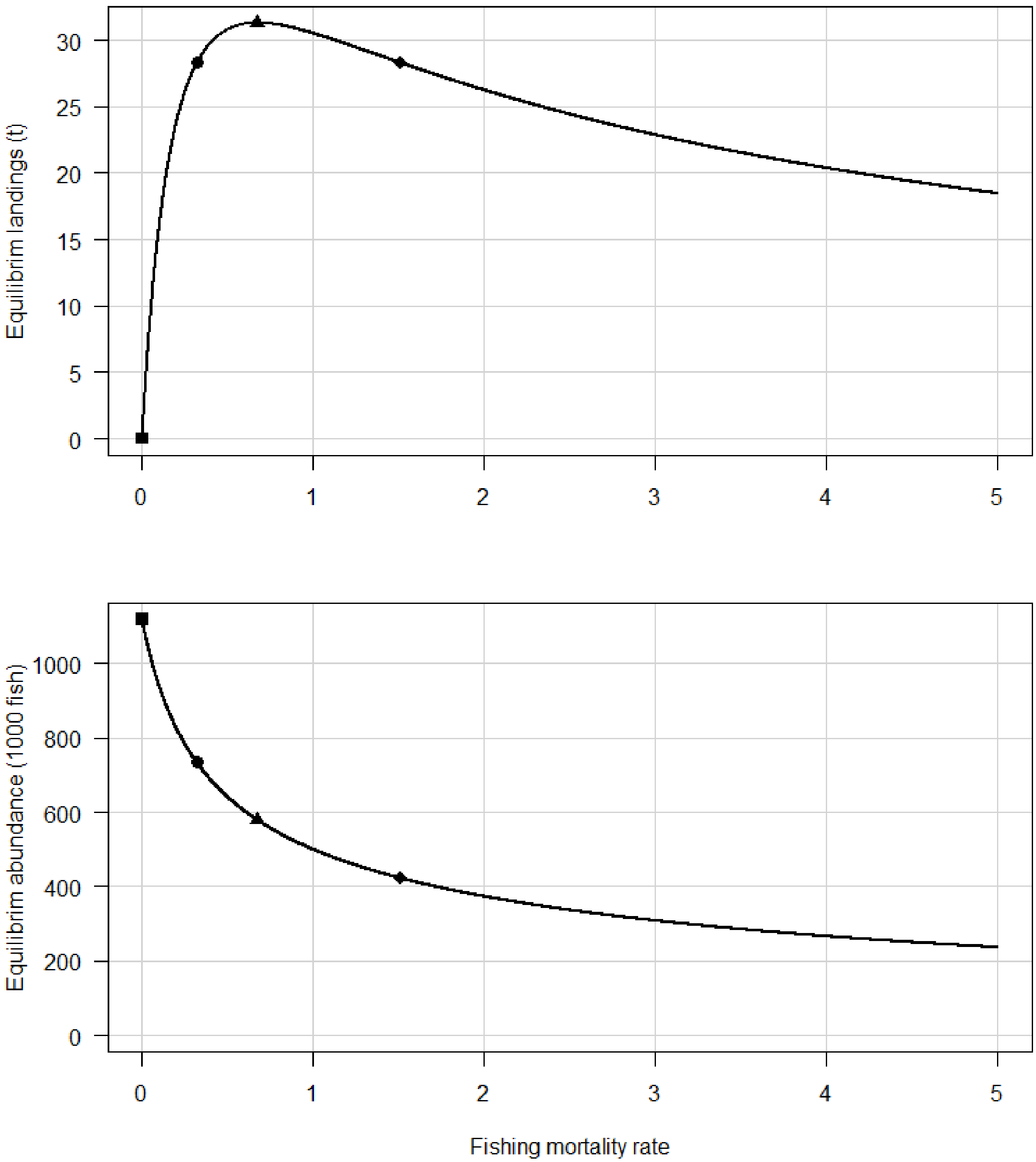


Figure 3: Equilibrium landings (top) and abundance (bottom) of lionfish in Belize across a range of fishing mortality rates: $F_{LOW} = 0$ (■), $F_{CURRENT} = 0.32$ (●), $F_{MSY} = 0.67$ (▲), $F_{OLY} = 1.51$ (♦), and $F_{HIGH} = 5.0$

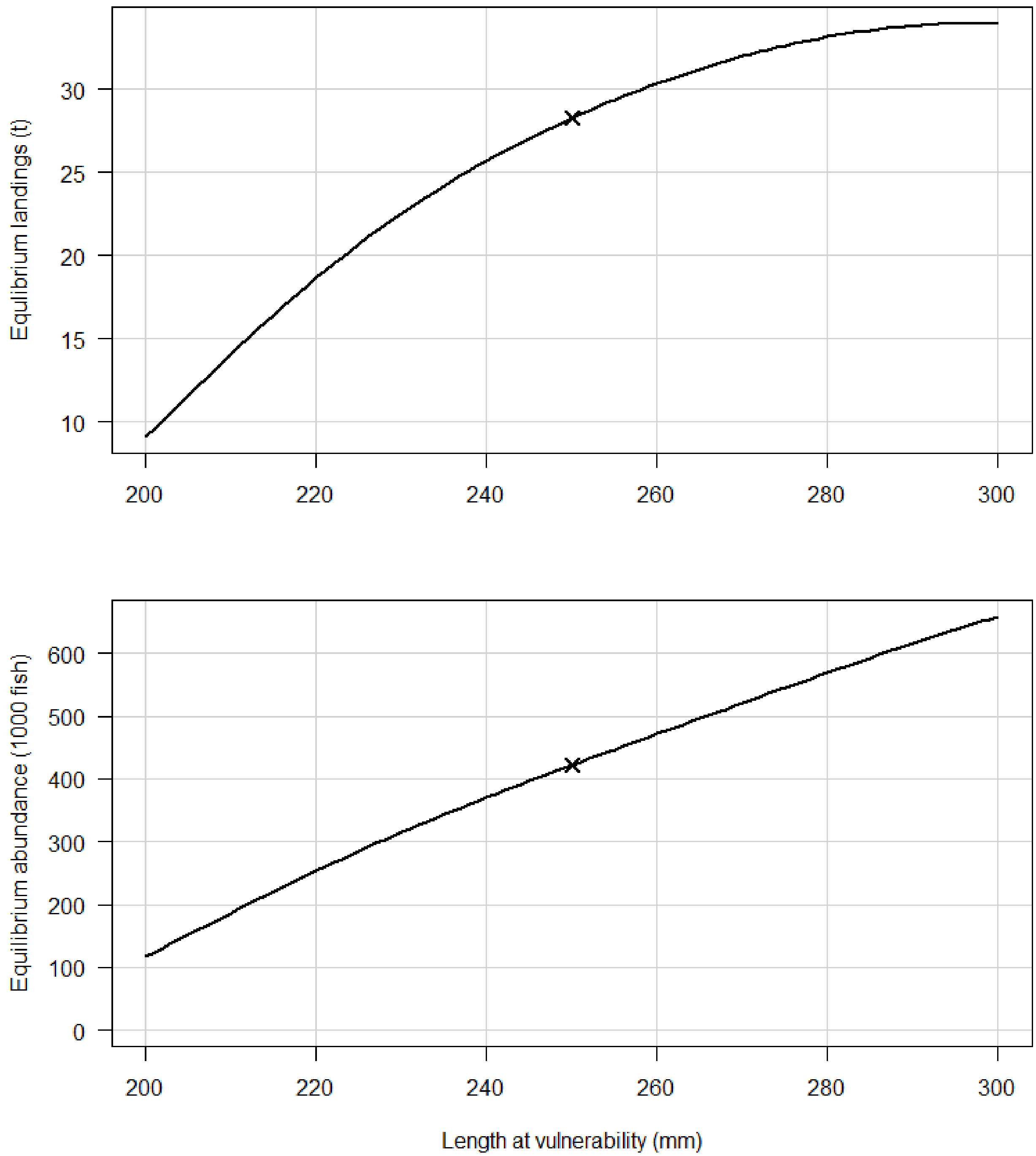


Figure 4: Equilibrium landings (top) and abundance (bottom) of lionfish in Belize across a range of sizes at selection with $F = F_{OLY} = 1.51$. The point on the graph indicates current size at selection = 250 mm

Appendix 1: Additional Analyses

Part 1: Exploring Uncertainty in Landings and Abundance

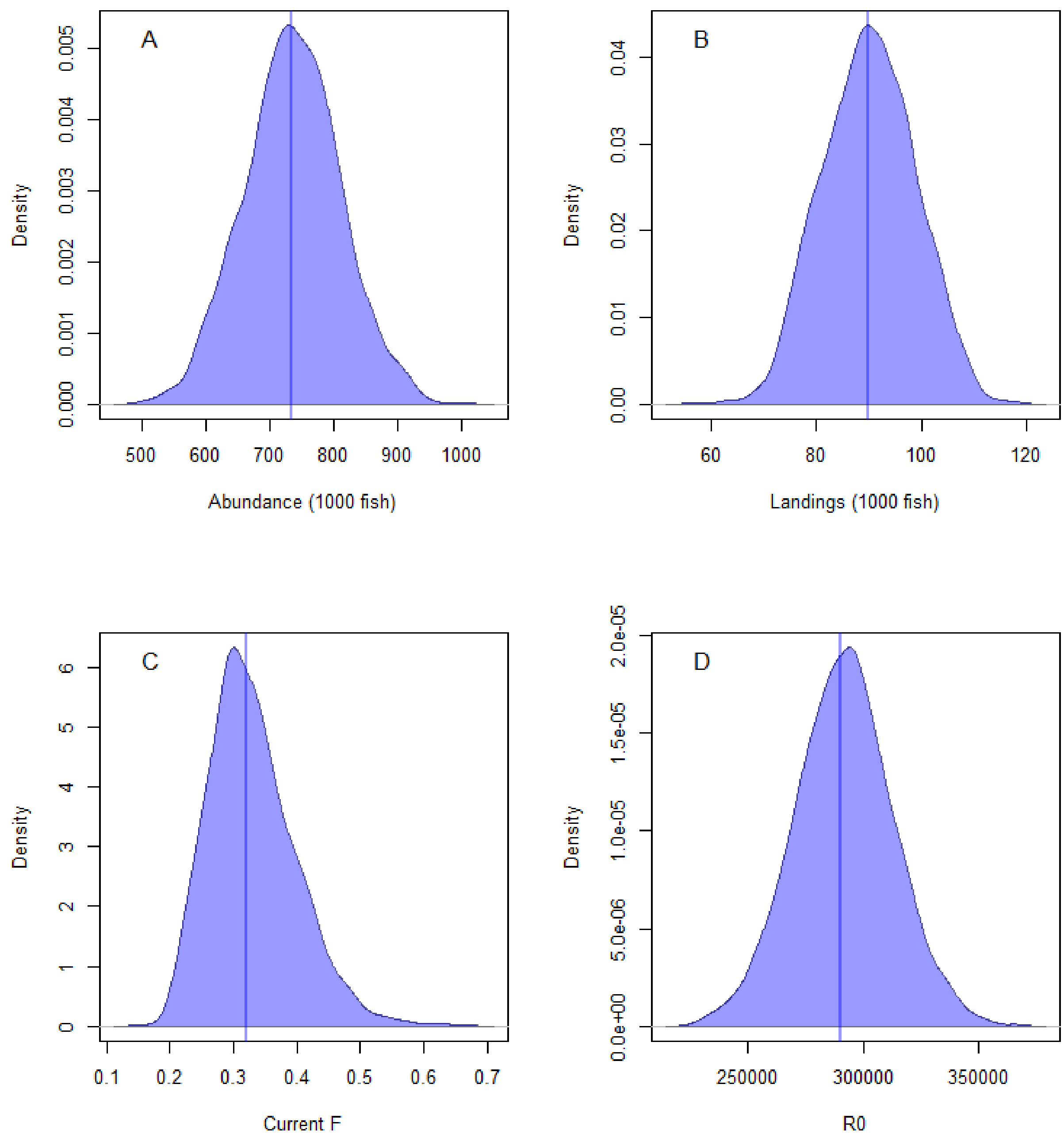
As described in the main text, the 2015 field estimates of abundance and landings were 733,257 lionfish and 89,902 lionfish. Abundance and landings directly affect estimates of the current fishing mortality rate (current F) and the asymptotic recruitment of age-1 fish (R0) and, therefore, model output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

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

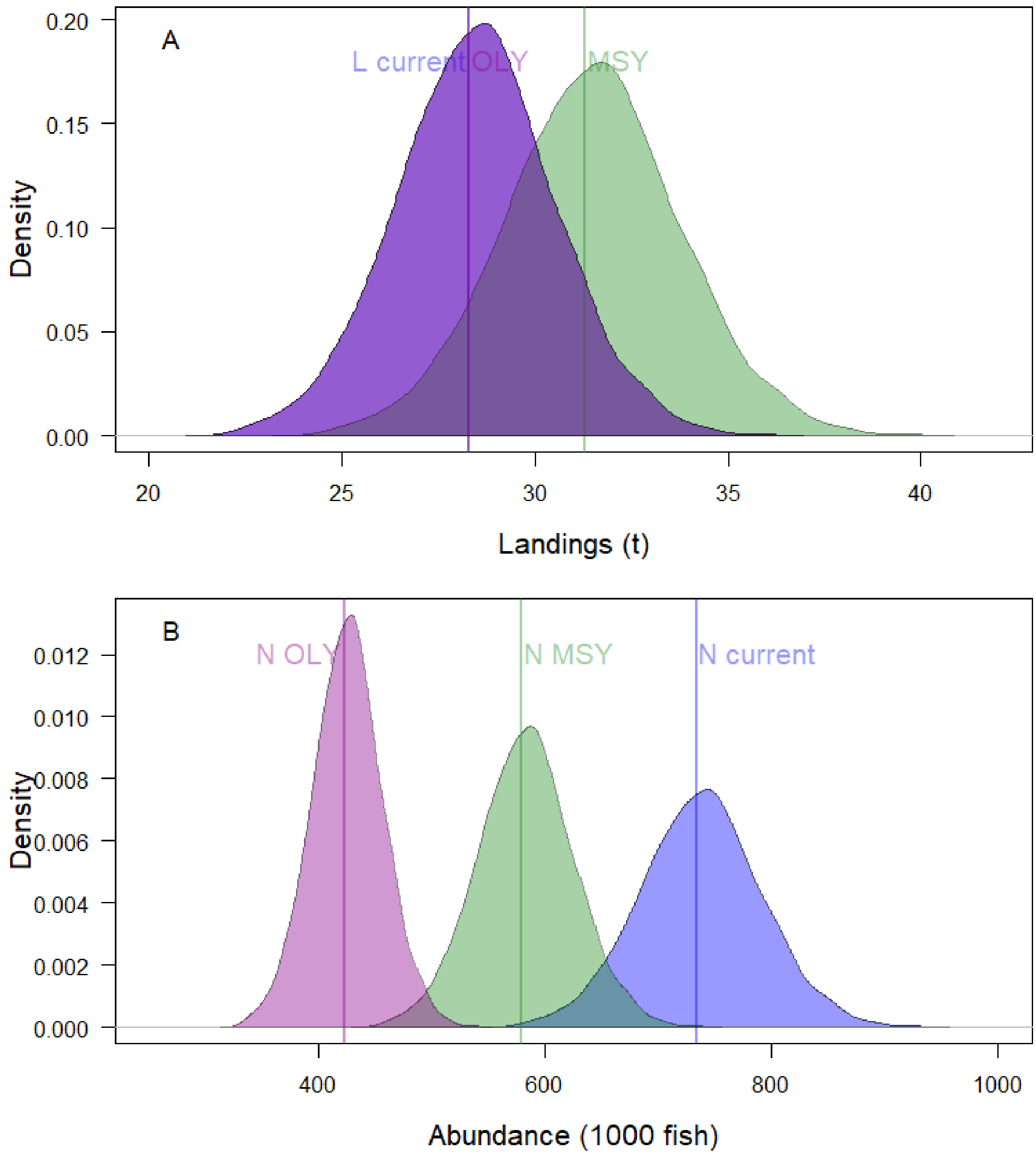
We additionally propagated uncertainty in current F and R0 into estimates of equilibrium landings and abundance as a function of fishing rate (Appendix Figure 3). We caution that this analysis does not produce true confidence bands as it is predicated on our assumed value of CV=0.1. It does, however,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

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

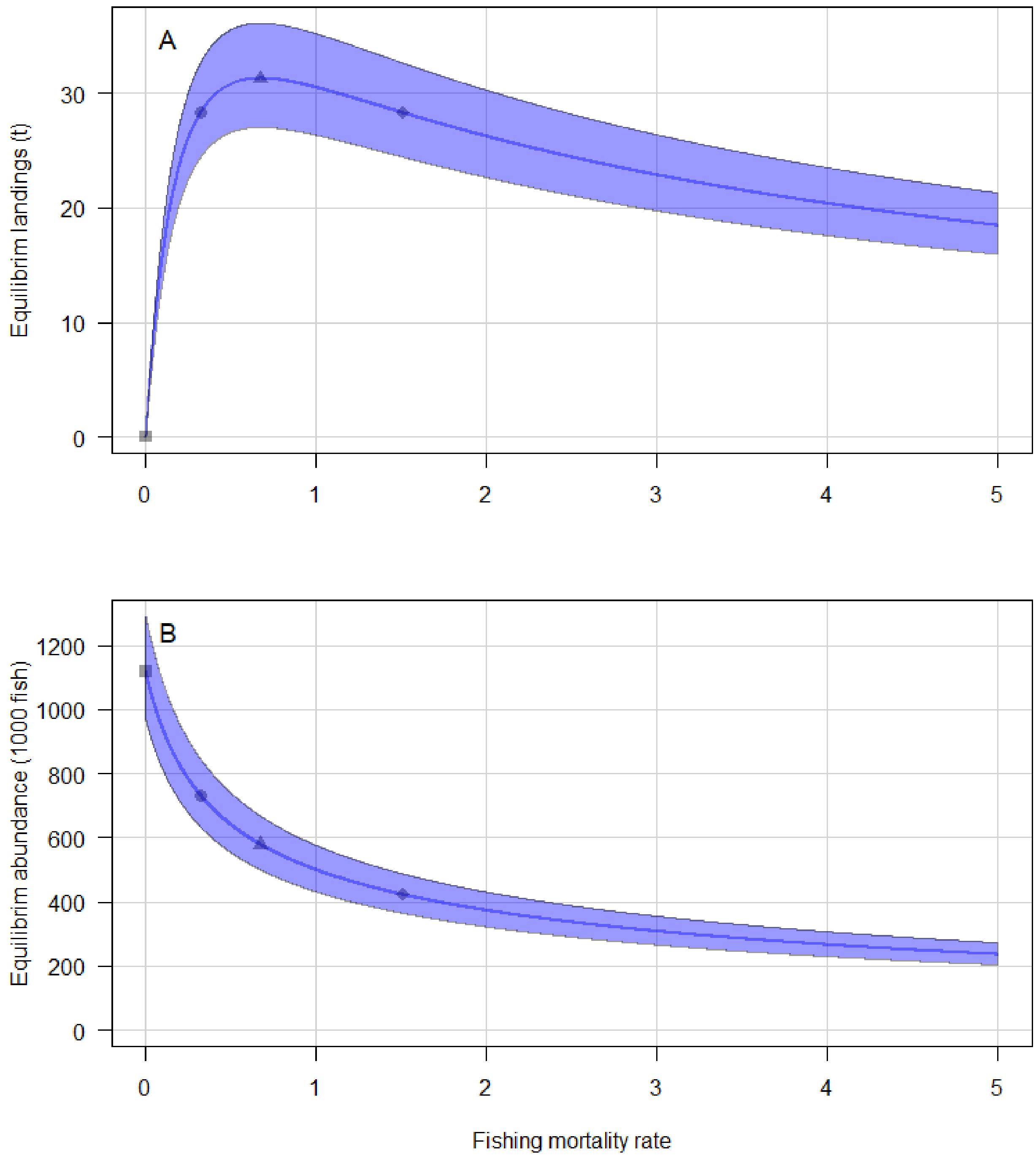
As part of our analyses in the main text, we examined effects of the size-at-selection on equilibrium abundance and landings (Figure 4). The size-at-selection, along with growth characteristics including the standard deviation of size-at-age, determined the pattern of selectivity as the proportion of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



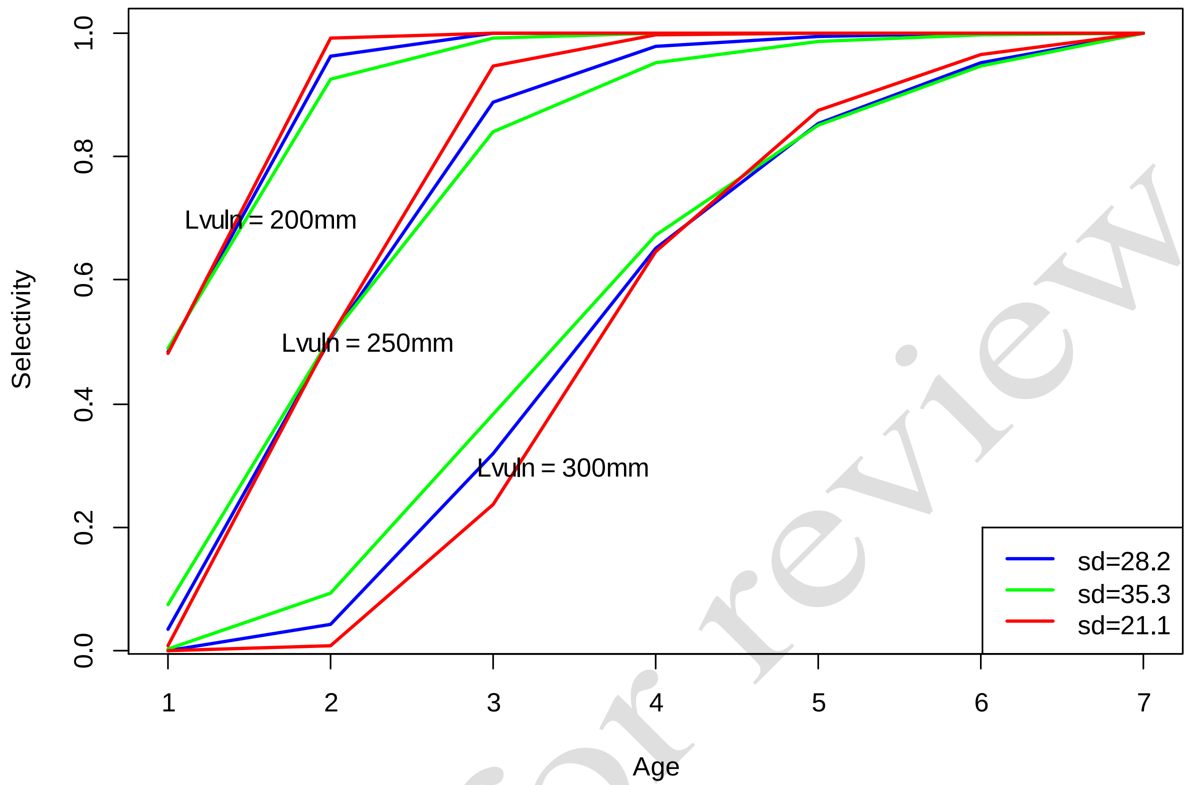
Appendix Figure 1. Assumed distributions of initial lionfish abundance (A) and landings (B) used to compute the current fishing rate (current F) (C) and the asymptotic recruitment of age-1 fish (R0) (D). Vertical lines indicate the 2015 field estimates of abundance and landings (A,B) and the point estimates of current F and R0 derived from those field estimates (C,D).



Appendix Figure 2. Distributions of results derived from assumed distributions of field estimates of abundance and landings. Panel A shows distributions of landings corresponding to Lcurrent (blue), OLY (purple), and MSY (green). Note that Lcurrent is not apparent because it overlaps entirely with OLY (by design). Panel B shows the levels of abundance that correspond to the landings in Panel A.



Appendix Figure 3. Equilibrium landings (A) and abundance (B) of lionfish in Belize across a range of fishing mortality rates: F_{MIN} = 0 (■), $F_{CURRENT}$ = 0.32 (●), F_{MSY} = 0.67 (▲), F_{OLY} = 1.51 (♦), and F_{HIGH} = 5.0. Intervals shown represent the 2.5^{th} and 97.5^{th} percentiles from N=2000 Monte Carlo simulations with variability in the 2015 field estimates of lionfish abundance and landings.



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