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Short-Term Pain and Long-Term Gain: Using Phased-In Minimum Size Limits to Rebuild Stocks—the Pacific Bluefin Tuna Example

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Abstract

Like many stocks, the Pacific Bluefin Tuna *Thunnus orientalis* has been considerably depleted. High exploitation rates on very young fish have reduced the spawning stock biomass (SSB) to 2.6% of the unexploited level. We provide a framework for exploring potential benefits of minimum size regulations as a mechanism for rebuilding stocks, and we illustrate the approach using simulations patterned after Pacific Bluefin Tuna dynamics. We attempt to mitigate short-term losses in yield by considering a phased-in management strategy. With this approach, the minimum size limit (MSL) is gradually increased as biomass rebuilds, giving fishing communities time to adjust to new restrictions. We estimated short- and long-term effects of different MSLs on yield and biomass by using data from the 2016 assessment. A variety of scenarios was considered for growth compensation, discard mortality, and interest rates. The long-term value of the fishery was maximized by setting an MSL of 92 cm FL, which resulted in a 70% loss in yield during the first year (short-term pain). By implementing the MSL in two phases (64 cm FL in year 1; 92 cm FL in subsequent years), the long-term value of the fishery was maintained, and the short-term pain was reduced to a maximum 46% loss in yield during any 1 year. Under a three-phase implementation (55 cm FL in year 1; 77 cm FL in year 2; and 92 cm FL in subsequent years), the short-term pain was further reduced to a maximum loss of 30% during any 1 year. With no discard mortality, long-term yield increased by 165% and SSB increased 13-fold (to 33% of virgin SSB), regardless of the number of phases used. Long-term benefits were quickly diminished with increasing discard mortality. This simulation approach is widely applicable to cases where minimum size changes are contemplated; for Pacific Bluefin Tuna, our simulations demonstrate that size limits should be considered.

Minimum size limits (MSLs) have been widely used as a management tool to limit fishing pressure, increase yield per recruit, and prevent recruitment overfishing by allowing

a larger number of fish to reach sexual maturity (Woodward and Griffin 2003; Froese et al. 2016). Less often, MSLs have also been used in a rebuilding context to aid in

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the recovery of overfished stocks, such as Hogfish *Lachnolaimus maximus* (NOAA 2017a), Gray Triggerfish *Balistes capriscus* (NOAA 2017b), Swordfish *Xiphias gladius* (NOAA 1999), and Atlantic Bluefin Tuna *Thunnus thynnus* (Fromentin et al. 2013). Size limits have been shown to be particularly effective for relatively long-lived, slow-growing, late-maturing species with short spawning durations because these species require a large spawning stock reserve and a protracted age structure to persist (Fromentin and Fonteneau 2001; Secor 2007). Size limits are also particularly attractive for managing highly migratory species (Venizelos et al. 2003; Neilson et al. 2013; Trzcinski and Bowen 2016), as they require no spatial or temporal control of catch and effort. However, MSLs work under the assumption that undersized fish can be avoided or that their postrelease mortality rates are negligible. Violating this assumption can substantially influence the success of the regulation (Coggins et al. 2007; Pine et al. 2008). In this paper, we develop an analytical framework for examining trade-offs between conservation and yield after the implementation of a minimum size regulation, and we demonstrate its application to the Pacific Bluefin Tuna *Thunnus orientalis* stock, whose sustainability has been compromised by high levels of fishing effort on very young fish (ISC 2016a). This example is presented in enough detail to demonstrate the versatility of the approach. Through simulation, we explore how various assumptions about growth compensation, discard mortality, tolerance for undersized fish, and interest rates might affect the success of such a regulation, and we discuss the implications of our results in the context of the Pacific Bluefin Tuna fishery. This approach can be extended to allow for harvest slot limits or harvest exclusion slot limits; these are minimum and maximum size limits between which harvest is either contained (i.e., all harvest is in the slot) or excluded (i.e., no harvest in the slot).

Prized for its high-quality meat, the Pacific Bluefin Tuna is one of the most sought-after fishes in the world, with wholesale prices having routinely fetched upwards of US\$50 per kilogram (Deere 2000; Bayliff et al. 2004). This species, which consists of a single Pacific-wide stock, is harvested throughout its range, with the highest effort occurring in the western North Pacific Ocean (WPO) and eastern North Pacific Ocean (EPO; ISC 2016a). Historically, the stock has experienced considerable fluctuations in catch, ranging from a high of 40,383 metric tons in 1965 to a low of 8,653 metric tons in 1990. In recent years (2005–2014), landings have averaged 19,863 metric tons (Sakai et al. 2016). Five principal countries target the stock: Japan (50–80% of the annual catch), Taiwan, and Korea in the WPO; and Mexico and USA in the EPO, with catches in the EPO ranging from just over 40% of Pacific-wide catches in the mid-1970s to under 15% in the early 2000s and close to 20% in recent years (Maunder and Aires-da-Silva 2014). The

U.S. purse seine fishery was responsible for a large portion of catches prior to 1980 (ISC 2016a), but its importance rapidly declined with the development of the sashimi market, as the fishery was not able to meet the demand for high-quality fish. The implementation of the Mexican Exclusive Economic Zone in 1976 also contributed to the reduction of the U.S. purse seine fleet and was followed by an increase in Mexican purse seine catches (Aires-da-Silva et al. 2007). Purse seines predominately target juveniles and are responsible for the majority of the catch annually ($\approx 70\%$), while longlines, which target adults, typically account for less than 10% of the annual catch (ISC 2016b).

Adult Pacific Bluefin Tuna spawn in areas between the Ryukyu Islands and the Philippines in late spring and in the Sea of Japan during mid- to late summer (Suzuki et al. 2014). At age 0, juveniles stay close to the location where they were spawned; by the end of their first year, they begin to expand their range into neighboring waters. At age 1 or 2, a portion of the population migrates to the western coast of the USA and Mexico (Itoh et al. 2003), where they generally reside for 1–2 years and up to 7 years before returning to the WPO to spawn (age at 50% maturity = 4 years; Bayliff et al. 1991; Boustany et al. 2010; ISC 2016a; Madigan et al. 2017). Within the EPO, Pacific Bluefin Tuna are targeted by both commercial and recreational fishers, and a portion of the catch is brought back to Mexican grow-out pens, where fish are kept for a few weeks to a few months (but not longer than 6 months) before being sold when market conditions are favorable (Volpe 2005; Robadue and Del Moral Simanek 2007).

Though historical data indicate that juveniles have always dominated the catch of Pacific Bluefin Tuna, the fishery experienced a sharp increase in the catch of age-0 fish starting in 1990. The year 1990 coincided with an unusually high recruitment event that sparked the development of WPO purse seine fisheries specifically targeting age-0 and age-1 fish (Maunder and Aires-da-Silva 2014; Maunder et al. 2014). In 1994, the stock experienced a second peak in recruitment, maintaining high catches for a few more years. However, since 1994, the stock has not been able to produce such high levels of recruitment, and in the past 10 years, recruitment has reached near historical lows. Another major development in the Pacific Bluefin Tuna fishery occurred in the early 2000s, when large Japanese purse seiners, which had historically targeted mackerels and sardines in the Sea of Japan, shifted their effort toward Pacific Bluefin Tuna after the depletion of those stocks (Sanada 2015). Today, high levels of effort persist, with more than 90% of the catch (in numbers) comprising age-0 and age-1 fish (ISC 2016a). Results from the latest stock assessment indicate that Pacific Bluefin Tuna spawning stock biomass (SSB) is presently at 2.6% of unexploited levels (ISC 2016a) and is composed almost entirely of one strong cohort (Maunder et al. 2014).

The historical increase in effort after the expansion of purse seine fisheries and the consequential shift toward targeting smaller or younger fish are not particular to the Pacific Bluefin Tuna fishery. Other closely related species, including Yellowfin Tuna *Thunnus albacares* and Bigeye Tuna *Thunnus obesus*, have experienced a similar harvest pattern (Polacheck 2006; Wang et al. 2009). Recent increases in the use of fish-aggregating devices have brought about an increase in the catchability of juvenile Bigeye Tuna and Yellowfin Tuna, which are caught as bycatch in the purse seine fishery primarily targeting Skipjack Tuna *Katsuwonus pelamis* and adult Yellowfin Tuna (Bailey et al. 2013). Other species with very different life history traits, such as the Pacific Jack Mackerel *Trachurus symmetricus* stock and historical Northern Anchovy *Engraulis mordax* fishery off southern California (Mais 1981; Mason 1991), have also experienced a similar shift in harvest pattern.

Concerns over initial losses in yield resulting from more conservative management measures can create strong resistance from the fisheries sector and can prevent the implementation of management actions (Rosenberg 2003; Rosenberg et al. 2006; Beddington et al. 2007). Using a gradual approach in which the management measure is implemented in steps can make the solution more attractive and more likely to be implemented (Hannesson 1993). This concept has been studied in the past with ideas of dynamic adaptive quotas (Ussif and Sumaila 2005) and gradual implementation of marine reserves through incremental increases in reserve size, number of species being protected, or length of time an area is closed to fishing (Brown et al. 2015). Shertzer and Prager (2007) demonstrated, however, that delaying management can also be risky, as it may increase the probability of stock collapse, especially for stocks exhibiting depensation and those whose catchability (unknown to the assessment) is density dependent and for which fishing is concentrated on juveniles. In this paper, we explore ways to lessen the maximum annual loss in yield elicited by the introduction of a minimum size regulation (i.e., “short-term pain”). We examined the trade-offs between the short-term pain and long-term gains and investigated whether a gradual phasing in of MSLs over several years might help to reduce short-term losses in yield while gradually meeting long-term conservation goals.

METHODS

General approach.—An age-structured model with annual time steps and stochastic recruitment was constructed to simulate the impact of various MSLs (0–130 cm FL) on stock status and fisheries returns over 20 years, with the ultimate goal of determining the optimal MSL to be imposed on the fishery. Alternative scenarios with differing assumptions on tolerance for undersized fish, discard mortality, growth compensation, and interest rates were used to

evaluate the sensitivity of the results to these assumptions (Figure 1). In each scenario, the short- and long-term management performance of the regulation was evaluated by assessing model results for SSB, yield, and economic value of the fishery (Figure 1). The benefits of introducing the MSL in phases was also explored—that is, gradually increasing the MSL over 2 years (two-phase approach) or 3 years (three-phase approach) to reach the optimal long-term MSL. One-hundred simulation runs were carried out for each scenario being considered to observe the range of plausible outcomes given different recruitment histories. The analysis was performed in R version 3.3 (R Foundation for Statistical Computing, Vienna).

Input parameters.—Input parameters and results from the 2016 assessment’s base case scenario were used to parameterize the model (ISC 2016a; detailed in Table 1). To adequately account for changes in the age structure of the population as SSB rebuilds, a plus group of 20 (grouping of all age-20 and older fish) was used instead of a plus group of 10, which was used in the assessment. Estimates of numbers at age and fishing mortality rates at age were averaged (geometric mean) over a 5-year reference period (2010–2014) to provide stability to the estimates and were used as a starting point for the simulations.

Base case scenario.—At the start of each year, the numbers-at-age estimates (N_a) were divided between undersized ($N_a[<\text{MSL}]$) and legal-sized ($N_a[\geq \text{MSL}]$) fish so that the two groups could be projected forward separately. A cumulative normal distribution function was used to calculate the fraction of fish that fell below the MSL in each age-class (see Figure 2 for size distributions of cohorts and relationship to MSL). These fractions (R_a) and their complement ($1 - R_a$) were then multiplied by numbers at age to obtain the number of fish corresponding to each group:

$$N_a(<\text{MSL}) = N_a R_a \quad (1a)$$

$$N_a(\geq \text{MSL}) = N_a(1 - R_a). \quad (1b)$$

Numbers at age were projected forward by a year (y ; before considering growth) by using an exponential survival model,

$$N_{a,y+1}(<\text{MSL}) = N_{a,y}(<\text{MSL})e^{-[F_a(<\text{MSL})+M_a]} \quad (2a)$$

$$N_{a,y+1}(\geq \text{MSL}) = N_{a,y}(\geq \text{MSL})e^{-(F_a+M_a)}, \quad (2b)$$

where M_a is the natural mortality rate at age a ; F_a is the fishing mortality rate at age a assuming that no MSL is in place; and $F_a(<\text{MSL})$ is the fishing mortality rate affecting fish of age a that are below the MSL. In the base case scenario, it is assumed that the MSL is being strictly enforced

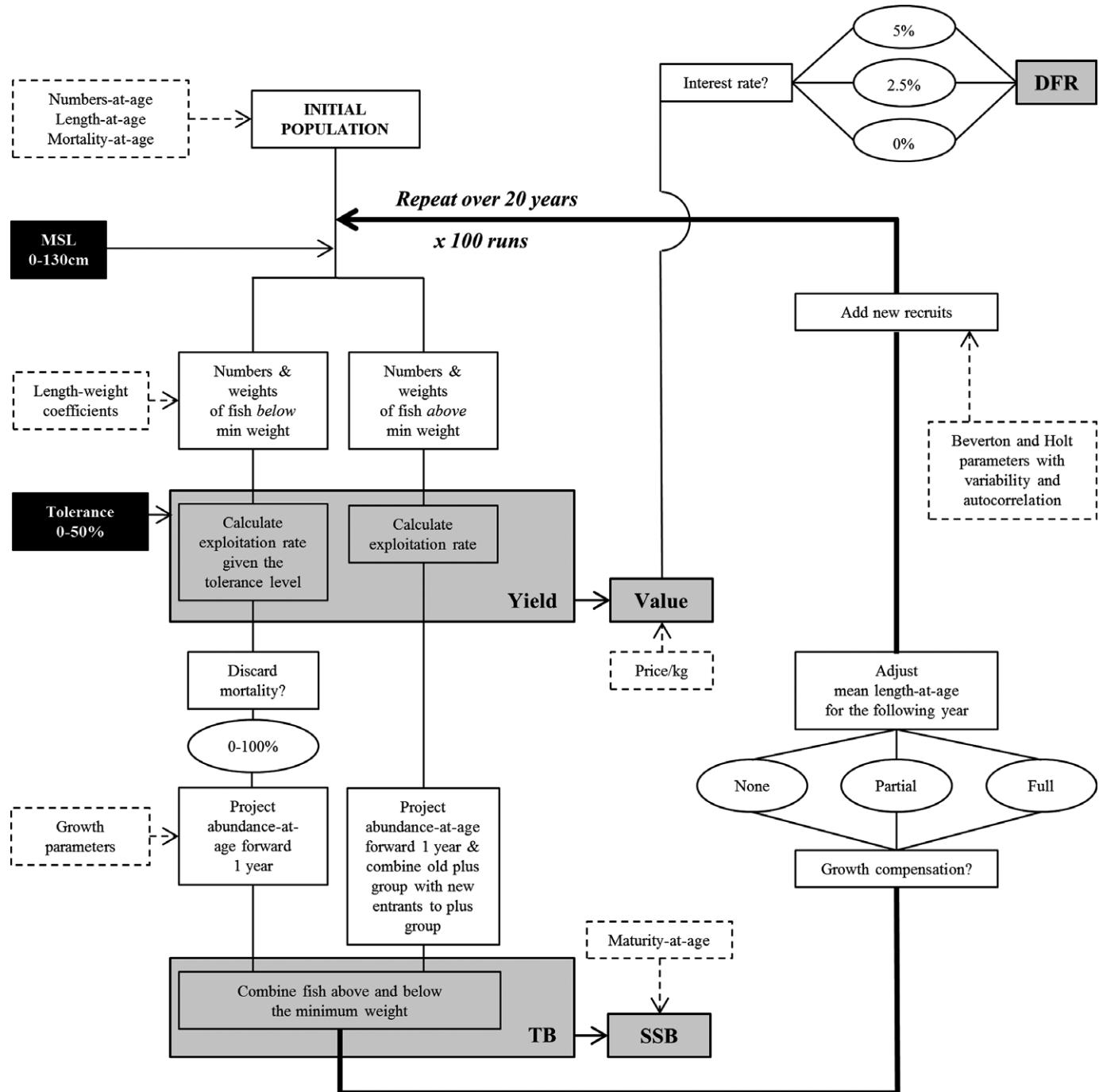


FIGURE 1. Pacific Bluefin Tuna simulation outline. Dashed lines represent input parameters, circles indicate assumptions, and gray boxes indicate outputs. Black-filled boxes represent the regulation scenario simulated in the run (MSL = minimum size limit; TB = total biomass; SSB = spawning stock biomass; DFR = discounted future revenues of the fishery; see equation 7).

and that there is zero tolerance for catching undersized fish; thus, $F_d(<\text{MSL}) = 0$. Any fish of age 20 in year y that was still alive in year $y + 1$ was added to the number of age-20 fish in year $y + 1$. We also assumed perfect growth compensation, meaning that the undersized fish

within a specific cohort are advanced to the following year assuming that they will have the same mean length as the size distribution for the next age-group. This assumption was later relaxed (see *Alternative scenarios: compensatory growth*).

TABLE 1. Description of parameters used in the Pacific Bluefin Tuna analysis (ISC 2016a). Parameter values for alternative scenarios are shown in bold italics.

Parameter type	Parameter description	Parameter symbol	Parameter value(s)
Growth	Age	a	0–20 + years
	Mean asymptotic length	L_∞	249.917 cm FL
	Brody's growth coefficient	K	0.188 year ⁻¹
	Theoretical age at a length of zero	t_0	-0.4217 year
	Coefficient of variation in length at age	CV_a	$CV_0 = 0.26, CV_1 = 0.18,$ $CV_2 = 0.10, CV_{3-20} = 0.04$
	Level of growth compensation	γ	0 (0.5, 1.0)
Length-weight relationship	Regression coefficient	α	1.7117×10^{-5}
	Exponent	β	3.0382
Mortality	Natural mortality rates at age	M_a	$M_0 = 1.6, M_1 = 0.39, M_{2+} = 0.25$
	Fishing mortality rates at age	F_a	$F_0 = 0.65, F_1 = 0.82, F_2 = 0.60,$ $F_3 = 0.20, F_4 = 0.22, F_5 = 0.18,$ $F_6 = 0.15, F_7 = 0.15, F_8 = 0.12,$ $F_9 = 0.17, F_{10-20} = 0.15$
Maturity and recruitment	Proportion mature at age a	P_a^m	$P_{0-2}^m = 0, P_3^m = 0.2, P_4^m = 0.5,$ $P_{5-20}^m = 1.0$
	Unexploited spawning stock biomass	SSB_0	644,466 metric tons
	Unexploited recruitment	R_0	13,739,000 fish
	Steepness	h	0.999
	Autocorrelation coefficient	ρ	0.466
	Variability in recruitment	σ_R	0.6
Undersized fish	Tolerance for undersized fish	t	0% (1–50%)
	Discard mortality rate	d	0% (1–100%)
Economic factors	Interest rate	I	2.5% (0%, 5%)

Recruitment (R) was modeled as a first-order autoregressive stochastic process about a Beverton–Holt stock–recruitment relationship,

$$R_y = \frac{0.8R_0hSSB_{y-1}}{0.2SSB_0(1-h) + (h-0.2)SSB_{y-1}} e^{\varepsilon_y - 0.5\sigma_R^2}, \quad (3)$$

where R_y is recruitment of age-0 fish (in numbers) at the beginning of year y ; R_0 and SSB_0 are the mean recruitment and SSB, respectively, under unfished conditions; SSB_{y-1} is the SSB remaining at the end of the previous year; and h is the steepness parameter. The recruitment deviation term ε_y is expressed as

$$\begin{cases} \varepsilon_y = \rho\varepsilon_{y-1} + \phi_y \sqrt{1-\rho^2} & \text{for } y > 1 \\ \varepsilon_y = \phi_y & \text{for } y = 1, \end{cases}$$

where ρ controls the level of autocorrelation in recruitment deviations; and $\phi_y \sim N(0, \sigma_R^2)$ represents process error (Wiedenmann et al. 2015; Johnson et al. 2016). Steepness was set at 0.999; the SD of stochastic errors in recruitment (σ_R) was set at 0.6; and the unexploited recruitment (R_0) and SSB_0 were set at 13,739,000 fish and 644,466 metric

tons, respectively, to match the values in the stock assessment (ISC 2016a). The autocorrelation coefficient ρ was set at 0.466, the mean of the predictive distribution for Perciformes obtained from a recent meta-analysis of recruitment (Thorson et al. 2014).

At the end of each year, numbers at age of fish above and below the MSL were added together and multiplied by the weight at age (assuming perfect growth compensation) and maturity at age for the next-older age. This amount was then summed over all ages to obtain SSB. To place our results in the context of rebuilding the stock, SSB was also expressed as a percentage of unexploited condition (% SSB_0), with SSB_0 obtained from the assessment.

Annual yield (Yld_y) was computed as for a type II (continuous) fishery, with weights at age assumed to be those at mid-year as follows:

$$Yld_y = \sum_{a=0}^{20} \left[N_{a,y}(<\text{MSL}) W_{a,y_{midy}}(<\text{MSL}) U_a(<\text{MSL}) \right. \\ \left. + N_{a,y}(\geq\text{MSL}) W_{a,y_{midy}}(\geq\text{MSL}) U_a(\geq\text{MSL}) \right], \quad (5)$$

where $W_{a,y_{midy}}(<\text{MSL})$ and $W_{a,y_{midy}}(\geq\text{MSL})$ are the average weights of age- a fish midway through year y that are

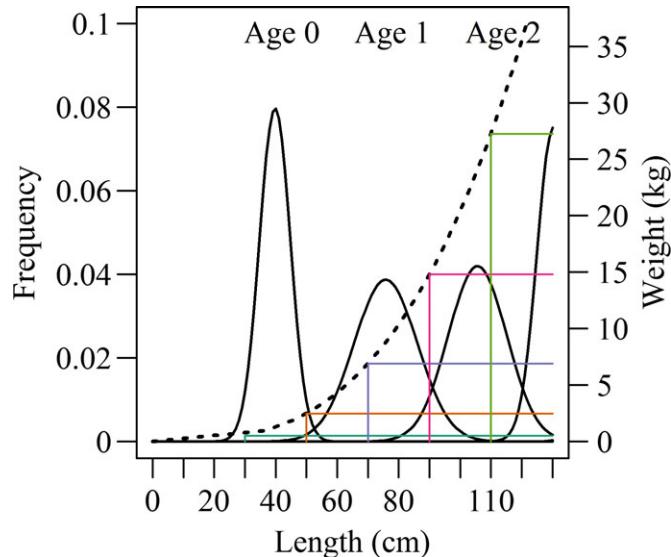


FIGURE 2. Relationship between Pacific Bluefin Tuna length at age (mid-year) for three illustrative cohorts and five minimum size limits (MSLs). Dashed line overlaid on top of the length-at-age curves represents the length-weight relationship. The horizontal and vertical lines show how MSLs relate to weight (e.g., a minimum size of 90 cm FL corresponds to a minimum weight of around 15 kg and affects nearly all age-0 and age-1 fish and a small portion of age-2 fish).

below and above the minimum size, respectively (calculated by converting lengths to weights and taking the means of the truncated distributions of weight at age created by the size limit); and $U_a(<\text{MSL})$ and $U_a(\geq\text{MSL})$ are the exploitation rates affecting age- a fish that are below and above the MSL, calculated from the Baranov catch equation as

$$U_a(<\text{MSL}) = \frac{F_a(<\text{MSL})}{F_a(<\text{MSL}) + M_a} \{1 - e^{-(F_a(<\text{MSL}) + M_a)}\} \quad (6a)$$

$$U_a(\geq\text{MSL}) = \frac{F_a}{F_a + M_a} [1 - e^{-(F_a + M_a)}]. \quad (6b)$$

Net overall economic gain was defined as the discounted future revenues of the fishery n years after implementation (DFR_n). It was calculated by summing annual fishery values over the years and discounting future values according to an interest rate (I) using the conventional equation,

$$\text{DFR}_n = \sum_{y=1}^n \frac{V_y}{(1+I)^{y-1}}, \quad (7)$$

where V_y is the value of the fishery in year y , calculated by multiplying the yield in year y by the price per kilogram (round weight) of fish caught. An I of 2.5% was

chosen for the base case scenario, an appropriate rate for discounting near-future gains like those measured here (Weitzman 2001). The price per kilogram of fish was set to \$12, reflecting the whole-weight price of U.S. exports of Pacific Bluefin Tuna averaged over the period 2003–2013 (NOAA 2014). The economics of the Pacific Bluefin Tuna fishery are undoubtedly more complicated than is suggested by equation (7). A variety of factors influences Pacific Bluefin Tuna value: from meat quality (resulting mainly from the method of capture, slaughtering process, and storage conditions; Jerret et al. 1996; Addis et al. 2009; Secci et al. 2011; Torrieri et al. 2011) and fat content (typically linked to fish size, catch location, time of year, and fattening process, in the case of ranched tunas; Carroll et al. 2001; Mourente et al. 2001; Ottolenghi 2008; Goñi and Arrizabalaga 2010) to fishing costs and availability. However, our intention was not to provide a detailed economic assessment of the regulation; rather, we sought to provide a number that could be looked at in relative terms when comparing the performance of the regulation under various scenarios. To that end, economic gains are presented in the Results as a percent change in DFR 20 years after implementation of the MSL compared to having no size regulations in place ($\% \Delta \text{DFR}_{20}$). Once the range of possible minimum size regulations was explored, the optimal MSL was determined as that which produced the highest DFR over 20 years. Other factors, such as the SSB achieved and the loss in yield and value immediately after implementation of the regulation, were also examined.

The 20-year time frame was chosen to afford the population of Pacific Bluefin Tuna enough time to reach equilibrium. In the United States, the 1996 Sustainable Fisheries Act amendments to the Magnuson–Stevens Fishery Conservation and Management Act of 1976 mandate that federally managed species that have been declared overfished must be rebuilt to levels that support maximum sustainable yield in as short a time as possible, not to exceed 10 years. This rule is made more flexible in the case of internationally managed species like bluefin tunas, for which the socioeconomic background and the stock life history characteristics can be used as grounds to argue for longer rebuilding periods (Pilling et al. 2016). For the Atlantic Bluefin Tuna and Southern Bluefin Tuna *Thunnus maccoyii*—the two species most closely related to Pacific Bluefin Tuna—the rebuilding time frames were established based on the mean generation time of the stocks, since it takes at least one generation for the impacts of management actions to be fully realized. As such, rebuilding programs were built on an approximately 20-year time frame, which justifies the use of a 20-year projection in this study.

Alternative scenarios: compensatory growth.—Compensatory growth, the process by which individual growth

rates increase as a response to more favorable conditions (in this case, the removal of the largest fish in a cohort), is believed to occur in a variety of fishes (Rose et al. 2001; Ali et al. 2003; Hazlerigg et al. 2012). For Southern Bluefin Tuna, Polacheck et al. (2004) linked changes in growth rates to changes in juvenile abundance over time, suggesting that density dependence could be one of the mechanisms behind observed changes in growth over time. This mechanism has also been shown to increase SSB growth rates in depleted groundfish populations, helping to accelerate the speed of stocks' recovery (Morgan et al. 2016). It is likely that some level of compensation occurs in the growth rate of Pacific Bluefin Tuna, but the degree to which this mechanism takes place remains unknown. In the base case scenario, full compensation was assumed: the undersized fish within a specific cohort had the normal size distribution about the von Bertalanffy curve when they reached the next age. However, full compensation in growth is likely to be overly optimistic, so for the alternative scenarios, the average lengths of fish (beginning of the year for biomass calculations; middle of the year for yield calculations) were adjusted on a yearly basis to account for both a lack of compensation and partial compensation in growth.

Lack of compensation was modeled using the growth function described by Methot (2000), which was a modification of the von Bertalanffy growth equation (as parameterized by Schnute 1981) made to account for size-specific survivorship caused by fishery size-selectivity,

$$L_{y+1,a+1} = \pi_{y,a} \{ L_{y,a} + [L_{y,a} - L_{\infty}(\prod_{\beta=0}^a \pi_{y-a+\beta,\beta})] (e^{-K} - 1) \}, \quad (8a)$$

where $L_{y,a}$ is the mean length of age- a fish in year y ; $\pi_{y,a}$ is the ratio of the mean size of age- a fish that survived to the end of year y (i.e., $\{ \text{numbers at age of undersized fish} \times \text{mean length at age of undersized fish} \} + \{ \text{numbers at age of legal-sized fish} \times \text{mean length at age of legal-sized fish} \} / \text{total numbers at age} \)$ to the mean size of age- a fish present at the beginning of year y ; and K is the growth coefficient that describes the rate of approach to the asymptotic length (L_{∞}) toward which the cohort is growing. This function includes an adjustment (π) to both the mean size at age in any 1 year ($\pi_{y,a}$) and L_{∞} through the cumulative effect of the different π values experienced by a specific cohort over the years ($\prod_{\beta=0}^a \pi_{y-a+\beta,\beta}$; the β index is used here to loop over all of the ages through which each cohort has gone).

The equation was modified here to allow for partial compensation by raising π to the power of γ ($0 < \gamma < 1$),

$$L_{y+1,a+1} = \pi_{y,a}^{\gamma} \{ L_{y,a} + [L_{y,a} - L_{\infty}(\prod_{\beta=0}^a \pi_{y-a+\beta,\beta}^{\gamma})] (e^{-K} - 1) \}. \quad (8b)$$

An intermediate value of $\gamma = 0.5$ was chosen to represent partial compensation in growth. At the extremes, a value of $\gamma = 1$ leaves the equation unchanged, thus representing a lack of compensation in growth; a value of $\gamma = 0$ makes the equation revert back to a simple von Bertalanffy growth equation, thus representing full compensation as in the base case scenario.

Alternative scenarios: tolerance for undersized fish and discard mortality.—Fishing mortality rates affecting fish below the MSL were modified to account for (1) situations where the regulation would allow a certain level of fishing mortality on undersized fish (expressed as a tolerated fraction [t] of F for each age, where $0 \leq t \leq 1$); and (2) discard mortality (d , where $0 \leq d \leq 1$; the proportion of discards not surviving capture or release, assumed constant across ages and years). Fishing mortality rates at age affecting fish below the MSL, $F_{a,t,d}(<\text{MSL})$, were expressed in two parts: $F_{a,t}^H(<\text{MSL})$, the fishing mortality rate at age resulting from harvest; and $F_{a,t,d}^D(<\text{MSL})$, the fishing mortality rate at age resulting from discards,

$$F_{a,t,d}(<\text{MSL}) = F_{a,t}^H(<\text{MSL}) + F_{a,t,d}^D(<\text{MSL}) \quad (9)$$

with

$$F_{a,t}^H(<\text{MSL}) = F_{a,t} \quad (10a)$$

$$F_{a,t,d}^D(<\text{MSL}) = F_{a,t} (1 - t) d. \quad (10b)$$

We approached the issue of discard mortality in two ways: (1) by assuming that a certain level of discard mortality was occurring in the fishery and accounting for it when calculating the optimal MSL; and (2) by assuming a certain level of discard mortality was occurring in the fishery but not accounting for it when establishing the regulation (i.e., setting the MSL equal to the optimal MSL determined under the assumption of 0% discard mortality).

Alternative scenarios: interest rates.—Interest rates are inherently variable and difficult to predict. We therefore tested the sensitivity of the results to both higher ($I = 5\%$) and lower ($I = 0\%$) interest rates to cover the range of plausible values (Weitzman 2001).

Alternative scenarios: phases of implementation.—We explored the short- and long-term impacts of introducing the MSL in phases—that is, gradually increasing the minimum size over 2 years (two-phase approach) or 3 years (three-phase approach) to reach the optimal long-term MSL. Short-term pain was defined as the maximum annual loss in yield incurred by implementing an MSL, and long-term gain was defined as the DFR₂₀. We first determined the optimal MSL for all years (single-phase approach). For the two-phase approach, the optimal MSL

in year 1 was chosen as the size that minimized short-term pain given that the MSL in all subsequent years was the optimal MSL established in the single-phase approach. For the three-phase approach, the minimum sizes in years 1 and 2 were searched over a grid given the constraint that $(\text{MSL in year 1}) \leq (\text{MSL in year 2}) \leq (\text{optimal MSL established in the single-phase approach})$ and were chosen as the combination of sizes that minimized the maximum short-term pain to the fishery.

RESULTS

Base Case Scenario

Simulation results showed that there are large potential gains to be realized in the long run, both in terms of yield and SSB, across a wide range of MSLs (Figure 3). The values are presented as the median of 100 runs unless otherwise stated. Fifth to ninety-fifth interquartile ranges are listed in the supplementary material (Supple-

mentary Table S.1 available in the online version of this article). For the single-phase approach, the optimal MSL was identified as 92 cm FL. This resulted in an immediate 70% loss in yield in the first year, and losses turned into gains 4 years into the regulation (Table 2; Figure 3). In the long run, the optimal minimum size resulted in an average 165% increase in yield and 13-fold increase in SSB over 20 years, rebuilding the SSB back to 33% of SSB_0 (Table 2; Figure 3).

Alternative Scenarios

The optimal MSL for the single-phase approach (assuming a 0% tolerance level and no discard mortality) was almost identical across runs, ranging from 86 to 108 cm FL depending on the assumption made regarding growth compensation and the annual interest rate (Table 3). This equated to releasing almost all age-0 and age-1 fish and a portion of age-2 individuals (Figure 2). Higher compensation and interest rates generally resulted in slightly lower MSLs.

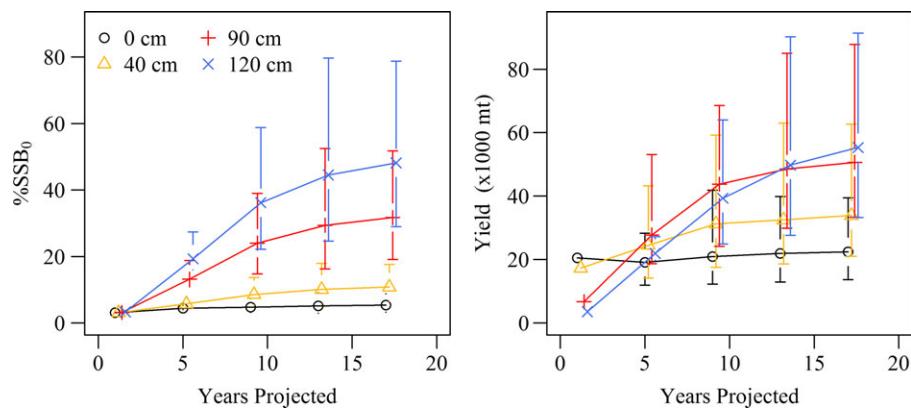


FIGURE 3. Effect of minimum size regulation on Pacific Bluefin Tuna spawning stock biomass (SSB) and yield over the 20-year projection ($\%SSB_0$ = SSB expressed as a percentage of unexploited SSB; mt = metric tons). Results are from the base case scenario. Points and whiskers show the median and 95% tails over the 100 runs, respectively.

TABLE 2. Comparative outcomes of a single-phase approach to establishing minimum size limit (MSL) regulations given different discard mortality rates for Pacific Bluefin Tuna ($\%SSB_0$ = spawning stock biomass [SSB] expressed as a percentage of unfished SSB; $\%ΔDFR_{20}$ = percent change in discounted future revenues of the fishery over a 20-year period after implementation). Three cases are considered: discard mortality is absent from the fishery (0%); a 20% discard rate is affecting the fishery but is not accounted for when determining the optimal MSL; and a 20% discard mortality rate is affecting the fishery and is accounted for when determining the optimal MSL. “Rebuilding years” refers to the delay in the time taken by the fishery to produce yield that exceeds the status quo (i.e., no MSL in place). Median values (first number) and 5th and 95th percentiles (numbers in parentheses) from the 100 simulations are presented. All other assumptions from the base case scenario were maintained.

Discard mortality	MSL (cm)	Short-term losses		Long-term gains (20 years)		
		Maximum loss in yield in any 1 year (%)	Rebuilding years	$\%SSB_0$ achieved	Percent increase in yield	$\%ΔDFR_{20}$
0%	92 (79, 101)	-70 (-75, -60)	4 (2, 5)	33 (22, 51)	165 (64, 281)	82 (71, 91)
20%, not accounted for	92 (79, 101)	-70 (-75, -60)	4 (3, 7)	23 (16, 35)	88 (12, 163)	31 (26, 34)
20%, accounted for	74 (72, 77)	-56 (-58, -54)	4 (2, 5)	17 (11, 28)	76 (24, 143)	37 (31, 42)

TABLE 3. Optimal minimum size limits (MSLs) and percent change in discounted future revenues of the Pacific Bluefin Tuna fishery 20 years after MSL implementation ($\% \Delta DFR_{20}$) across scenarios (assuming 0% tolerance for undersized fish and 0% discard mortality). Median values (first number) and 5th and 95th percentiles (numbers in parentheses) from the 100 simulations are presented. Results from the base case scenario are highlighted in gray.

Interest rate (%)	Compensatory growth	Optimal MSL (cm FL)	$\% \Delta DFR_{20}$
5.0	None	108 (72, 108)	68 (58, 77)
5.0	Partial	103 (75, 106)	70 (62, 78)
5.0	Full	86 (77, 95)	74 (66, 81)
2.5	None	108 (72, 108)	78 (63, 88)
2.5	Partial	104 (75, 106)	79 (67, 89)
2.5	Full	92 (79, 101)	82 (71, 91)
0.0	None	108 (72, 108)	88 (68, 100)
0.0	Partial	106 (75, 106)	89 (72, 101)
0.0	Full	101 (79, 104)	90 (76, 102)

The magnitude of economic gains (DFR_{20}) did not vary much across assumptions on interest rate and level of compensation (Table 3). Gains were highest under an I of 0% and full compensation in growth and were lowest under a high interest rate and no compensation in growth (Table 3; Figure 4). Full growth compensation led to higher economic gains, but the difference in DFR_{20} between a lack of growth compensation and full compensation was just 2–8% depending on the assumption placed on interest rates (Table 3; Figure 4). The choice of I had the largest impact on long-term gains. The DFR_{20} increased by 10–15% for every 2.5% decrease in I (Table 3).

The level of tolerance for undersized fish was shown to substantially affect yield and SSB projections (Figure 5). For an MSL of 92 cm FL, allowing undersized fish to be subjected to 20% of the F at age cut potential long-term gains in yield and SSB by one-third (long-term yield reached 43,000 metric tons rather than the 55,000 metric tons achieved under the zero-tolerance scenario, and $\%SSB_0$ dropped from 33% to 23%; Figure 5).

Accounting for discard mortality also substantially affected the results (Figure 6). If discard mortality was occurring in the fishery but was not accounted for when selecting the optimal MSL (i.e., choosing a minimum size of 92 cm for the base case scenario), the result was a decrease in long-term gains (Figure 6). Under an MSL of 92 cm FL, discard mortality of 20% resulted in a decrease in long-term economic gains from 82% to 31% and a reduction in SSB from 33% of SSB_0 to 23% of SSB_0 (Table 2). It also delayed the time taken by the fishery to recover and exceed the status quo yield (i.e., no MSL) from a range of 2–5 years (5th and 95th percentiles) to a range of 3–7 years (Table 2). If discard mortality was

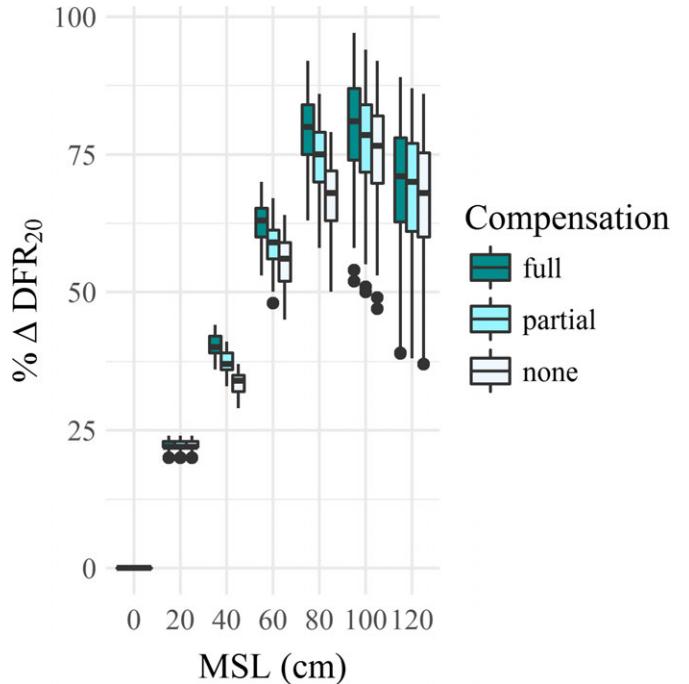


FIGURE 4. Effects of growth compensation on the percent change in discounted future revenues of the Pacific Bluefin Tuna fishery 20 years after MSL implementation ($\% \Delta DFR_{20}$) as a function of the minimum size limit (MSL) regulation. Results from the 100 runs are presented. All other assumptions from the base case scenario were maintained.

occurring and considered when selecting the optimal MSL, the result was a decrease in the optimal MSL (i.e., 78 cm FL for a 10% discard mortality rate, 74 cm FL for a 20% discard mortality rate, and 41 cm FL for a 40% discard mortality rate). Above a 50% discard mortality rate, there was little benefit to an MSL both in terms of increasing the value of the landings and rebuilding the SSB (Figure 6). Accounting for discard mortality in calculating the optimal size limit resulted in a lower MSL. For a discard mortality rate of 20%, the optimal MSL decreased to 74 cm FL (Table 2) and $\% \Delta DFR_{20}$ rose from 31% to 37%, with SSB declining even further to 17% of SSB_0 (Table 2). Thus, accounting for discard mortality when calculating the optimal MSL did help to recover some of the increased value, but these measures came at the cost of reduced conservation benefits, since the lower MSL chosen did not allow for SSB to achieve as high a level of rebuilding.

Two- and Three-Phase Approaches

The median optimal MSLs for the two-phase approach (using assumptions from the base case scenario) were 64 cm FL in year 1 and 92 cm FL in subsequent years (see Figure 7 for a visual example of the trade-off between short-term pain and long-term gain when selecting the optimal MSL in year 1). This maintained the long-term

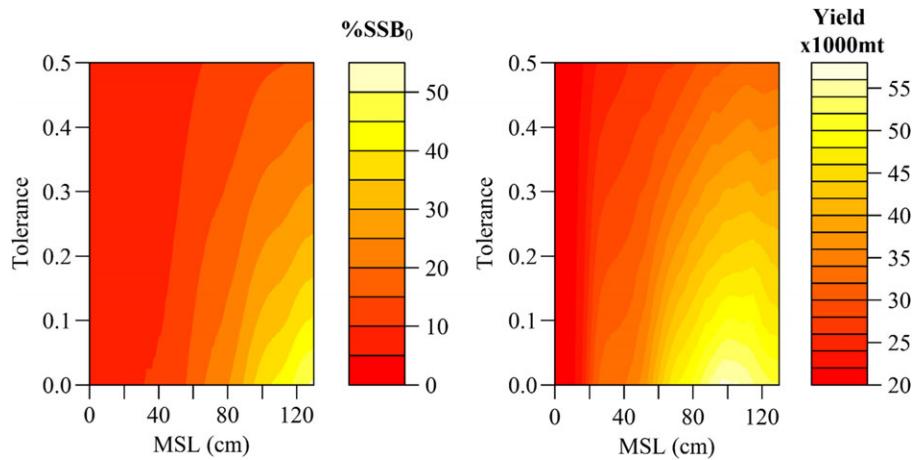


FIGURE 5. Isopleths of Pacific Bluefin Tuna equilibrium spawning stock biomass (SSB) and yield under different minimum size limit (MSL) regulations and tolerance levels ($\%SSB_0$ = SSB expressed as a percentage of unexploited SSB; mt = metric tons). Median values from the 100 simulations are presented. All other assumptions from the base case scenario were maintained.

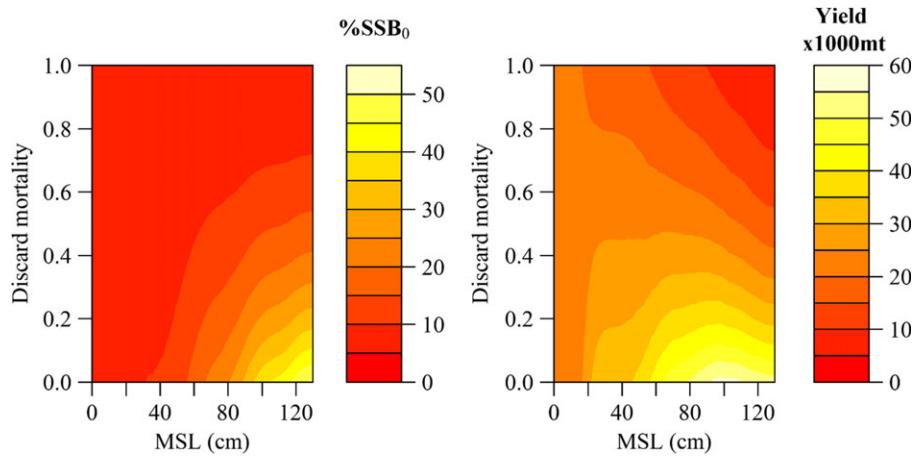


FIGURE 6. Isopleths of Pacific Bluefin Tuna equilibrium spawning stock biomass (SSB) and yield under different minimum size limit (MSL) regulations and discard mortality levels ($\%SSB_0$ = SSB expressed as a percentage of unexploited SSB; mt = metric tons). Median values from the 100 simulations are presented. All other assumptions from the base case scenario were maintained.

net present value of the fishery to within 1% of the value observed in the single-phase approach and reduced the short-term pain from 70% to a 46% maximum loss in yield in any 1 year (Figure 8; Table S.1). For the three-phase approach, median optimal MSLs were 55 cm FL in year 1, 77 cm FL in year 2, and 92 cm FL in year 3 and subsequent years (see Figure 9 for individual realizations of the simulation runs). With this approach, the short-term pain was further reduced to a maximum loss in yield of 30% compared to the status quo, and long-term gains were again maintained within 1% of the value observed in the single-phase approach (Figure 8; Table S.1). Across all assumptions made on growth, interest rate, and discard mortality, gradually increasing the MSL over the years consistently reduced the short-term pain while maintaining

long-term gains in yield, biomass, and profits (Figure 8). The amount by which short-term losses in yield were lessened as a result of phasing in the regulation was also fairly consistent across assumptions.

DISCUSSION

The question of how much time should be taken to rebuild SSB is an important one. Rapid reductions in F are associated with high costs in short-term yield, whereas slow reductions in F are associated with high risks of recruitment failure (Rosenberg and Brault 1991). Intermediate strategies that dampen short-term losses while still allowing SSB to rebuild within an acceptable time frame are ideal (Rosenberg and Brault 1991). Phasing in the

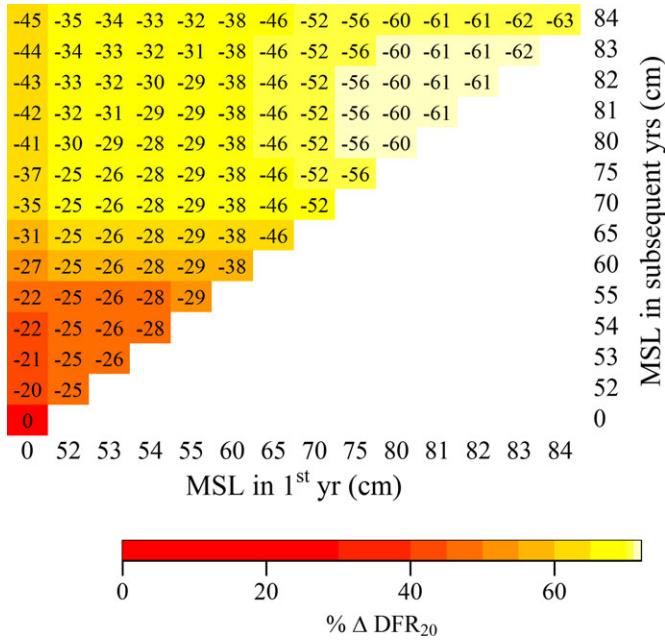


FIGURE 7. Trade-off between short-term pain and long-term gain in the Pacific Bluefin Tuna fishery given different combinations of minimum size limit (MSL) regulations in a two-phase approach. Results are shown for a single realization of the simulation where the optimal MSL in year 1 was 54 cm FL and the optimal MSL in subsequent years was 81 cm FL. Cell colors correspond to the percent change in discounted future revenues of the fishery over a 20-year period after implementation ($\% \Delta \text{DFR}_{20}$). Negative numbers in cells indicate maximum percentage loss in yield in any one year. All other assumptions from the base case scenario were maintained.

MSL increases over a 3-year period achieved marked reductions in short-term losses while still allowing the stock to rebuild. If the fishing communities were to require more time to adjust to the new regulation, additional phases could be added. However, the number of phases used should be given careful consideration given that any delay in implementing the optimal MSL will increase the recovery time frame of the stock and make it more susceptible to collapse (Caddy and Agnew 2004; Shertzer and Prager 2007). For Pacific Bluefin Tuna, recent low levels of spawning biomass have been associated with some of the lowest recruitment events ever observed, so there is concern that the stock may be—or will soon be—experiencing recruitment overfishing (Maunder et al. 2014). Furthermore, given that they are apex predators, Pacific Bluefin Tuna play a crucial role in the pelagic environment as important regulators of lower-trophic-level species (Heithaus et al. 2008). Thus, any further decrease in biomass or delay in rebuilding could seriously compromise the ecosystem's health and integrity.

The risk of recruitment failure is, by nature, tightly linked to the stock–recruitment relationship, which is an important factor in predicting long-term gains and risks of

stock collapse. The lack of contrast in the estimates of historical SSB and recruitment—coupled with the fact that the Pacific Bluefin Tuna is a highly productive species—has led scientists to assume that recruitment is largely independent of stock size. As a consequence, the point value chosen for h in the assessment was extremely high ($h = 0.999$; ISC 2016a). In an actual application of this simulation approach to Pacific Bluefin Tuna, one would want to evaluate alternative values for h , or possibly even different stock recruitment models, to cover the range of possible outcomes. It is difficult to predict exactly how our results would be affected by lower h -values. However, one can anticipate observing lower recruitment sizes at lower levels of SSB and a slightly higher value of equilibrium recruitment (ISC 2016a). This would translate into lower yields being observed in the earlier part of the rebuilding process but larger potential gains to be made in the long run. Furthermore, having assumed a relatively large recruitment variability in the simulation means that our recruitment estimates diverged considerably from the values predicted by the stock–recruitment model. As such, a wide range of possible recruitment values was observed across the various 100 runs of each scenario.

Our simulations suggest that an MSL protecting age-0 to age-2 fish can be beneficial if fishers avoid catching undersized fish. Since Pacific Bluefin Tuna tend to remain in schools of similar-sized individuals and since purse seines can be selective for the size of fish they catch, it should be possible to target fish of roughly a certain size, making an MSL a viable option for the fishery. Certain fleets seldom catch fish smaller than 92 cm (age 2 and below), such as the Taiwanese longline vessels (ages 5+) and Japanese longline vessels (ages 3+) operating in the spawning grounds off Okinawa and Taiwan during summer months (ISC 2002); for these fisheries, the Pacific Bluefin Tuna constitutes only a minor fraction of the catch (Z. Suzuki, National Research Institute of Far Seas Fisheries, personal communication). Others principally catch fish smaller than 92 cm, such as the Japanese troll, pole-and-line, and set-net fisheries (ages 0–2) and the Korean purse seiners operating in coastal waters (ages 0–1; ISC 2002). The small pelagic purse seines (Japanese and Korean), which catch the majority of young Pacific Bluefin Tuna, specifically target individuals less than 10 kg or 80 cm FL (Fukuda et al. 2014). The Mexican purse seines primarily target fish of ages 3–8, and the U.S. purse seines mainly target age 2 (ISC 2002).

One concern that has been raised about implementing a Pacific-wide MSL is the unequal distribution of losses and gains. Since fleets target different age-groups, not all countries exploiting the stock will be equally affected by a change in policy. Surface fleets that operate close to shore and target young fish will see their catches affected the most. Assuming no shift in targeting, the fleets or

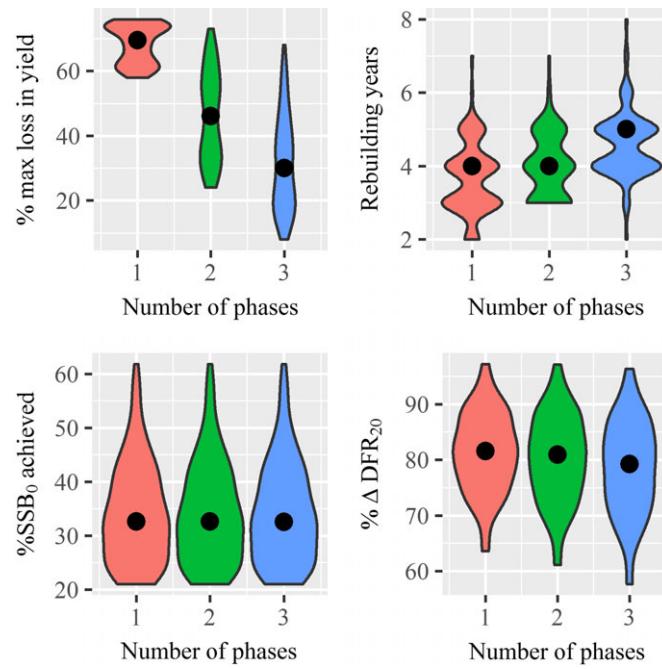


FIGURE 8. Comparison of the short-term pain and long-term gains associated with different phased-in approaches to implementing minimum size limit (MSL) regulations in the Pacific Bluefin Tuna fishery across the 100 simulation runs (using assumptions from the base case scenario; $\%SSB_0$ = spawning stock biomass [SSB] expressed as a percentage of unexploited SSB; $\%ΔDFR_{20}$ = percent change in discounted future revenues of the fishery over a 20-year period after implementation). “Rebuilding years” refers to the delay in the time it takes the fishery to produce yield that exceeds the status quo (i.e., no MSL in place).

countries that solely target very young fish would bear most of the hardship without reaping the benefits of a healthier stock. Conversely, longline fleets targeting larger individuals will feel none of the pain and reap all of the gain. A more detailed analysis of the impacts of various fleets defining the pains and gains of individual fleets falls beyond the scope of this paper but would be needed to define a workable management strategy and to measure the risk associated with choosing a particular MSL and phased-in strategy. The imposition of an MSL would only happen on the basis of a negotiated settlement. Such negotiations would likely include measures to prevent effort from shifting to target larger size-groups as well as the use of economic incentives to distribute the burden more evenly among the different fishing sectors. Incentives could include credit systems (Van Riel et al. 2013), taxes and subsidies (Gjertsen et al. 2010), or allowing for fishing nations that will see the benefits of improved stock sizes to compensate other countries for reduced catches through side payments.

Introducing an MSL would likely cause fishers who solely target small Pacific Bluefin Tuna—or those who already operate on thin margins and thus cannot afford

even the smallest loss of catch—to leave the fishery. However, those that only incidentally catch small Pacific Bluefin Tuna (a minor fraction of the fleets) may not see a benefit in shifting their operation. If that is the case, undersized fish may continue to be caught as bycatch, and if the discard mortality is substantial, this will reduce potential gains in yield and impede efforts aimed at rebuilding the SSB. In fact, our results indicate little to no benefit from an MSL if discard mortality rates exceed 50%. However, this result is conservative since the model assumes that all fleets would remain active in the fishery.

This paper is not intended to describe how a management scheme should be implemented; rather, it aims to understand the biological and economic implications of different management schemes and to provide a useful tool for investigating optimal minimum size policies for stocks that are threatened with overfishing. The case of Pacific Bluefin Tuna is not an isolated one. Regulations aimed at curbing the fishing of young individuals were once a major source of contention in the Atlantic Bluefin Tuna fishery, when extremely high catches of juveniles in the Mediterranean were causing considerable stock declines. Today, these regulations are fully endorsed by member nations of the International Commission for the Conservation of Atlantic Tunas and have been successful at helping to rebuild SSB (Webster 2011; Fromentin et al. 2014). In a fishery as important and complex as that targeting Pacific Bluefin Tuna, it is especially helpful to be able to determine *a priori* whether a regulation is likely to benefit the rebuilding of the stock so that the contracting parties are not negotiating in vain. Based upon our

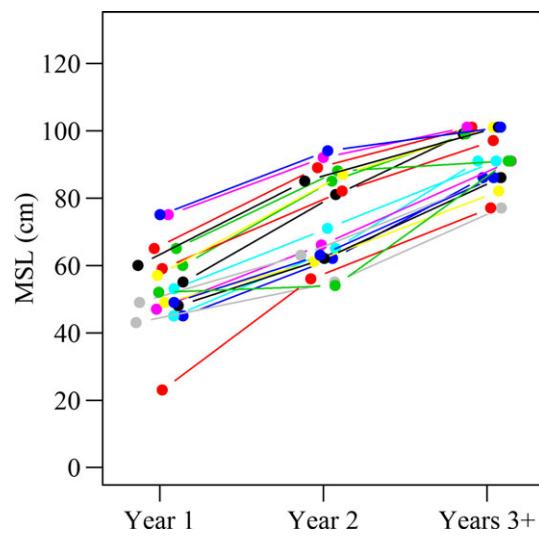


FIGURE 9. Optimal minimum size limits (MSLs) for the three-phase approach to implementing MSL regulations in the Pacific Bluefin Tuna fishery across 20 of the 100 runs; each line represents a different run (using assumptions from the base case scenario).

analysis, it is evident that the Pacific Bluefin Tuna fishery has the potential to be a more profitable and sustainable enterprise, and although rebuilding will come at a high cost in the short run, a phased-in management approach could be used to mitigate the pain.

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REFERENCES

Addis, P., I. Locci, A. Corriero, and A. Cau. 2009. Body temperature of the Atlantic Bluefin Tuna (*Thunnus thynnus* L.) in the western Mediterranean. Pages 195–207 in J. L. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutuvage, and J. Sibert, editors. Tagging and tracking of marine animals with electronic devices. Reviews: methods and technologies in fish biology and fisheries. Springer, New York.

Aires-da-Silva, A., M. G. Hinton, and M. Dreyfus. 2007. Standardized catch rates for Pacific Bluefin Tuna caught by United States and Mexican-flag purse seine fisheries in the eastern Pacific Ocean (1960–2006). International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean, Report ISC/07/PBFWG-3/01, Tokyo.

Ali, M., A. Nicieza, and R. J. Wootton. 2003. Compensatory growth in fishes: a response to growth depression. *Fish and Fisheries* 4:147–190.

Bailey, M., U. R. Sumaila, and S. J. Martell. 2013. Can cooperative management of tuna fisheries in the western Pacific solve the growth overfishing problem? *Strategic Behavior and the Environment* 3:31–66.

Bayliff, W. H., J. I. de Leiva Moreno, and J. Majkowski, editors. 2004. Management of tuna fishing capacity: conservation and socio-economics. Food and Agriculture Organization of the United Nations, Rome.

Bayliff, W. H., Y. Ishizuki, and R. B. Deriso. 1991. Growth, movement, and attrition of northern Bluefin Tuna, *Thunnus thynnus*, in the Pacific Ocean, as determined by tagging. *Inter-American Tropical Tuna Commission Bulletin* 20.

Beddington, J. R., D. J. Agnew, and C. W. Clark. 2007. Current problems in the management of marine fisheries. *Science* 316:1713–1716.

Boustany, A. M., R. Matteson, M. Castleton, C. Farwell, and B. A. Block. 2010. Movements of Pacific Bluefin Tuna (*Thunnus orientalis*) in the eastern North Pacific revealed with archival tags. *Progress in Oceanography* 86:94–104.

Brown, C. J., S. Abdullah, and P. J. Mumby. 2015. Minimizing the short-term impacts of marine reserves on fisheries while meeting long-term goals for recovery. *Conservation Letters* 8:180–189.

Caddy, J. F., and D. J. Agnew. 2004. An overview of recent global experience with recovery plans for depleted marine resources and suggested guidelines for recovery planning. *Reviews in Fish Biology and Fisheries* 14:43–112.

Carroll, M. T., J. L. Anderson, and J. Martinez-Garmendia. 2001. Pricing U.S. North Atlantic Bluefin Tuna and implications for management. *Agribusiness* 17:243–254.

Coggins, L. G., M. J. Catalano, M. S. Allen, W. E. Pine, and C. J. Walters. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish and Fisheries* 8:196–210.

Deere, C. 2000. Net gains: linking fisheries management, international trade, and sustainable development. International Union for Conservation of Nature and Natural Resources, Washington, D.C.

Froese, R., H. Winker, D. Gascuel, U. R. Sumaila, and D. Pauly. 2016. Minimizing the impact of fishing. *Fish and Fisheries* 17:785–802.

Fromentin, J.-M., S. Bonhommeau, H. Arrizabalaga, and L. T. Kell. 2014. The spectre of uncertainty in management of exploited fish stocks: the illustrative case of Atlantic Bluefin Tuna. *Marine Policy* 47:8–14.

Fromentin, J.-M., S. Bonhommeau, and B. Brisset. 2013. Update of the index of abundance of juvenile Bluefin Tuna in the western Mediterranean Sea until 2011. *ICCAT Collective Volume of Scientific Papers* 69:454–461.

Fromentin, J.-M., and A. Fonteneau. 2001. Fishing effects and life history traits: a case study comparing tropical versus temperate tunas. *Fisheries Research* 53:133–150.

Fukuda, H., I. Tsuruoka, Y. Tei, K. Oshima, H. Honda, and Y. Takeuchi. 2014. Preliminary population dynamics model for the updated stock assessment of Pacific Bluefin Tuna. International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean, Report ISC/14/PBFWG-1/03, Tokyo.

Gjertsen, H., M. Hall, and D. Squires. 2010. Incentives to address bycatch issues. Pages 225–248 in R. Allen, J. A. Joseph, and D. Squires, editors. Conservation and management of transnational tuna fisheries. Wiley-Blackwell, Ames, Iowa.

Goñi, N., and H. Arrizabalaga. 2010. Seasonal and interannual variability of fat content of juvenile Albacore (*Thunnus alalunga*) and Bluefin (*Thunnus thynnus*) Tunas during their feeding migration to the Bay of Biscay. *Progress in Oceanography* 86:115–123.

Hannesson, R. 1993. Fishing capacity and harvest rules. *Marine Resource Economics* 8:133–143.

Hazlerigg, C. R., K. Lorenzen, P. Thorbek, J. R. Wheeler, and C. R. Tyler. 2012. Density-dependent processes in the life history of fishes: evidence from laboratory populations of Zebrafish *Danio rerio*. *PLoS ONE* [online serial] 7(5):e37550.

Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* 23:202–210.

ISC (International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean). 2002. Report of the third meeting of the ISC Pacific Bluefin Tuna Working Group. ISC, Tokyo.

ISC (International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean). 2016a. Report of the Pacific Bluefin Tuna Working Group. ISC, Tokyo.

ISC (International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean). 2016b. Fisheries statistics [online database]. ISC, Tokyo. Available: http://isc.fra.go.jp/fisheries_statistics/index.html. (August 2018).

Itoh, T., S. Tsuji, and A. Nitta. 2003. Migration patterns of young Pacific Bluefin Tuna (*Thunnus orientalis*) determined with archival tags. U.S. National Marine Fisheries Service Fishery Bulletin 101: 514–534.

Jerret, A. J., J. Stevens, and A. J. Holland. 1996. Tensile properties of white muscle in rested and exhausted king salmon *Oncorhynchus tshawytscha*. Journal of Food Science 61:527–532.

Johnson, K. F., E. Councill, J. T. Thorson, E. Brooks, R. D. Methot, and A. E. Punt. 2016. Can autocorrelated recruitment be estimated using integrated assessment models and how does it affect population forecasts? Fisheries Research 183:222–232.

Madigan, D. J., Z. Baumann, A. B. Carlisle, O. Snodgrass, H. Dewar, and N. S. Fisher. 2017. Isotopic insights into migration patterns of Pacific Bluefin Tuna in the eastern Pacific Ocean. Canadian Journal of Fisheries and Aquatic Sciences 99:1–11.

Magnuson–Stevens Fishery Conservation and Management Act. 1976. U.S. Code, volume 16, sections 1801–1884.

Mais, K. F. 1981. Age-composition changes in the anchovy, *Engraulis mordax*, central population. California Cooperative Oceanic Fisheries Investigations Reports 22:82–87.

Mason, J. E. 1991. Variations in the catch of Jack Mackerel in the southern California purse seine fishery. California Cooperative Oceanic Fisheries Investigations Reports 32:143–151.

Maunder, M. N., and A. Aires-da-Silva. 2014. Developing conservation measures for Bluefin Tuna in the eastern and western regions of the Pacific Ocean: factors to consider and fishery impact analysis. IATTC (Inter-American Tropical Tuna Commission) Stock Assessment Report 15:74–99.

Maunder, M. N., K. R. Piner, and A. Aires-da-Silva. 2014. Stock status of Pacific Bluefin Tuna and the urgent need for management action. IATTC (Inter-American Tropical Tuna Commission) Stock Assessment Report 15:47–73.

Methot, R. D. 2000. Technical description of the Stock Synthesis Assessment Program. NOAA Technical Memorandum NMFS-NWFSC-43.

Morgan, M. J., P. A. Shelton, F. González-Costas, and D. González-Troncoso. 2016. Compensation potential in six depleted groundfish stocks from the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 73:257–269.

Mourete, G., C. Meginas, and E. Díaz-Salvago. 2001. Lipids in female Northern Bluefin Tuna (*Thunnus thynnus* L.) during sexual maturation. Fish Physiology and Biochemistry 24(4):351.

Neilson, J. D., F. Arocha, S. Cass-Calay, J. Mejuto, M. Ortiz, G. Scott, C. Smith, P. Travassos, G. Tserpes, and I. Andrushchenko. 2013. The recovery of Atlantic Swordfish: the comparative roles of the regional fisheries management organization and species biology. Reviews in Fisheries Science 21:59–57.

NOAA (National Oceanic and Atmospheric Administration). 1999. Atlantic highly migratory species fisheries; fishery management plan, plan amendment, and consolidation of regulations. Federal Register 64:103(March 28, 1999):29090–29160.

NOAA (National Oceanic and Atmospheric Administration). 2014. Stock assessment and fishery evaluation (SAFE) report for Atlantic highly migratory species. NOAA, National Marine Fisheries Service, Highly Migratory Species Management Division, Silver Spring, Maryland.

NOAA (National Oceanic and Atmospheric Administration). 2017a. Fisheries of the Caribbean, Gulf of Mexico, and South Atlantic; snapper–grouper fishery of the South Atlantic region; amendment 37. Federal Register 82:141(August 25, 2017):34584–34596.

NOAA (National Oceanic and Atmospheric Administration). 2017b. Fisheries of the Caribbean, Gulf of Mexico, and South Atlantic; reef fish fishery of the Gulf of Mexico; Gray Triggerfish management measures; amendment 46. Federal Register 82:167(August 30, 2017):41205–41206.

Ottolenghi, F. 2008. Capture-based aquaculture of Bluefin Tuna. Pages 169–182 in A. Lovatelli and P. F. Holthus, editors. Capture-based aquaculture. Food and Agriculture Organization of the United Nations, Rome.

Pilling, G., R. Scott, and J. Hampton. 2016. Biologically reasonable rebuilding timeframes for Bigeye Tuna. Western and Central Pacific Fisheries Commission, Report WCPFC-SC12-2016/MI-WP-02, Bali, Indonesia.

Pine, W. E., S. J. Martell, O. P. Jensen, C. J. Walters, and J. F. Kitchell. 2008. Catch-and-release and size limit regulations for Blue, White, and Striped marlin: the role of post-release survival in effective policy design. Canadian Journal of Fisheries and Aquatic Sciences 65:975–988.

Polacheck, T. 2006. Tuna longline catch rates in the Indian Ocean: did industrial fishing result in a 90% rapid decline in the abundance of large predatory species? Marine Policy 30:470–482.

Polacheck, T. J., P. Eveson, and G. M. Laslett. 2004. Increase in growth rates of southern Bluefin Tuna (*Thunnus maccoyii*) over four decades: 1960 to 2000. Canadian Journal of Fisheries and Aquatic Sciences 61:307–322.

Robadue, D. D. Jr., and R. del Moral Simanek. 2007. A system dynamics perspective on a global fishing enterprise: the case of tuna ranching in Mexico. Proceedings of the 25th International Conference of the System Dynamics Society 29:1–30.

Rose, K. A., J. H. Cowan, K. O. Winemiller, R. A. Myers, and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries 2:293–327.

Rosenberg, A. A. 2003. Managing to the margins: the overexploitation of fisheries. Frontiers in Ecology and the Environment 1:102–106.

Rosenberg, A. A., and S. Brault. 1991. Stock rebuilding strategies over different time scales. NAFO (Northwest Atlantic Fisheries Organization) Scientific Council Studies 16:171–181.

Rosenberg, A. A., J. H. Swasey, and M. Bowman. 2006. Rebuilding US fisheries: progress and problems. Frontiers in Ecology and the Environment 4:303–308.

Sakai, O., S. Nakatsuka, Y. Ishida, K. Oshima, and H. Fukuda. 2016. Input data of Pacific Bluefin Tuna fisheries for stock assessment model, stock synthesis 3; update for 2016 assessment. National Research Institute of Far Seas Fisheries, Fisheries Research Agency, Shizuoka, Japan.

Sanada, Y. 2015. A repeated story of the tragedy of the commons: a short survey on the Pacific Bluefin Tuna fisheries and farming in Japan. Organization for Regional and Inter-regional Studies, Waseda University, Tokyo.

Schnute, J. 1981. A versatile growth model with statistically stable parameters. Canadian Journal of Fisheries and Aquatic Sciences 38:1128–1140.

Secci, M., I. Locci, and P. Addis. 2011. Physiological responses in the Atlantic Bluefin Tuna, *Thunnus thynnus*, captured in the trap fishery of Sardinia (W. Mediterranean). Biologia Marina Mediterranea 18:228–229.

Secor, D. H. 2007. The year-class phenomenon and the storage effect in marine fishes. Journal of Sea Research 57:91–103.

Shertzer, K. W., and M. H. Prager. 2007. Delay in fishery management: diminished yield, longer rebuilding, and increased probability of stock collapse. ICES Journal of Marine Science 64:149–159.

Suzuki, N., T. Tanabe, K. Nohara, W. Doi, H. Ashida, T. Kameda, and Y. Aonuma. 2014. Annual fluctuation in Pacific Bluefin Tuna (*Thunnus orientalis*) larval catch from 2007 to 2010 in waters surrounding

the Ryukyu Archipelago, Japan. *Bulletin of the Fisheries Research Agency* 38:87–99.

Thorson, J. T., O. P. Jensen, and E. F. Zipkin. 2014. How variable is recruitment for exploited marine fishes? A hierarchical model for testing life history theory. *Canadian Journal of Fisheries and Aquatic Sciences* 71:973–983.

Torrieri, E., P. A. Carlini, S. Cavella, V. Fogliano, I. Attianese, G. G. Buonocore, and P. Masi. 2011. Effect of modified atmosphere and active packaging on the shelf-life of fresh Bluefin Tuna fillets. *Journal of Food Engineering* 105:429–435.

Trzcinski, M. K., and W. D. Bowen. 2016. The recovery of Atlantic Halibut: a large, long-lived, and exploited marine predator. *ICES Journal of Marine Science* 73:1104–1115.

Ussif, A. A. M., and U. R. Sumaila. 2005. Modeling the dynamics of regulated resource systems: a fishery example. *Ecological Economics* 52:469–479.

Van Riel, M. C., S. R. Bush, P. A. M. Zwieten, and A. P. J. Mol. 2013. Understanding fisheries credit systems: potentials and pitfalls of managing catch efficiency. *Fish and Fisheries* 16:453–470.

Venizelos, A., F. Sutter, and J. Serafy. 2003. Use of minimum size regulations to achieve reduction targets for marlin landings in the Atlantic Ocean. *Marine and Freshwater Research* 54:567–573.

Volpe, J. P. 2005. Dollars without sense: the bait for big-money tuna ranching around the world. *BioScience* 55:301–302.

Wang, S. P., M. N. Maunder, A. Aires-da-Silva, and W. H. Bayliff. 2009. Evaluating fishery impacts: application to Bigeye Tuna (*Thunnus obesus*) in the eastern Pacific Ocean. *Fisheries Research* 99:106–111.

Webster, D. G. 2011. The irony and the exclusivity of Atlantic Bluefin Tuna management. *Marine Policy* 35:249–251.

Weitzman, M. L. 2001. Gamma discounting. *American Economic Review* 91:260–271.

Wiedenmann, J., M. J. Wilberg, A. Sylvia, and T. J. Miller. 2015. Auto-correlated error in stock assessment estimates: implications for management strategy evaluation. *Fisheries Research* 172:325–334.

Woodward, R. T., and W. L. Griffin. 2003. Size and bag limits in recreational fisheries: theoretical and empirical analysis. *Marine Resource Economics* 18:239–262.

SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.