Catch-and-release and size limit regulations for blue, white, and striped marlin: the role of postrelease survival in effective policy design

William E. Pine III, Steven J.D. Martell, Olaf P. Jensen, Carl J. Walters, and James F. Kitchell

Abstract: Catch-and-release fishing as a management and conservation tool for billfish (family Istiophoridae) is practiced in many recreational fisheries, and mandatory release of billfish has been implemented for some commercial fisheries. Inherent in these approaches is the observation that survival of released fish is greater than those that are landed. Recent studies using pop-up satellite tags have begun to quantify postrelease survival rates for billfish, yet the efficacy of management measures that require some or all billfish to be released have not been evaluated. Using an age- and size-structured population model that accounts for individual variability in growth, we simulated the effects of postrelease mortality on yield, risk of recruitment overfishing, efficiency (i.e., ratio of harvest to postrelease mortality), and probability of catching trophy-sized individuals for three marlin species. Regulations such as size limits, catch-and-release, and mandatory release are likely to provide some benefit to billfish populations, but our results show that the effectiveness of these strategies is reduced when release survival is less than 100%. The management approaches most likely to benefit billfish populations are ones that focus on maximizing postrelease survival in the recreational fishery and minimize the billfish catch in commercial fisheries.

Résumé : La méthode de capture et de remise en liberté est utilisée comme outil de gestion et de conservation pour les voiliers (famille Istiophoridae) dans plusieurs pêches sportives et la remise en liberté des voiliers est obligatoire dans quelques pêches commerciales. Cette stratégie se fonde sur l'observation que la survie des poissons remis en liberté est plus grande que celle des poissons remontés à bord. Des études récentes utilisant des étiquettes détachables reliées aux satellites ont commencé à mesurer les taux de survie des voiliers après leur remise en liberté; néanmoins, l'efficacité des mesures de gestion qui requièrent que l'ensemble ou une partie des voiliers soit remis en liberté reste à évaluer. À l'aide d'un modèle démographique structuré en fonction de l'âge et de la taille qui tient compte de la variation individuelle de la croissance, nous avons simulé les effets de la mortalité après la remise en liberté sur le rendement, le risque de surpêche du recrutement, l'efficacité (c'est-à-dire le rapport de la récolte sur la mortalité après la remise en liberté) et la probabilité de capture des individus de taille-trophée chez trois espèces de voiliers. Les règlements sur les tailles limites, la prise et la remise en liberté et la remise en liberté obligatoire sont vraisemblablement bénéfiques aux populations de voiliers, mais nos résultats montrent que l'efficacité de ces procédures est réduite lorsque la survie après la mise en liberté est inférieure à 100 %. Les méthodes de gestion qui risquent le plus de bénéficier aux populations de voiliers sont celles qui cherchent à maximiser la survie après la remise en liberté lors de la pêche sportive et de minimiser la capture de voiliers lors des pêches commerciales.

[Traduit par la Rédaction]

Introduction

Effects of fishing on marine resources are an increasing area of focus for the development of ecosystem-based fishery management practices (National Research Council 2006). In many recreational and commercial fisheries, catch-and-release practices have been implemented as a conservation action both through the use of minimum size limits and the development of catch-and-release only fisheries (either by angler ethic or regulation; Muoneke and Childress 1994; Lucy and Studholme 2002; Bartholomew and Bohnsack 2005). These approaches clearly have some conservation benefits, as a fish released alive has an infinitely greater chance of surviving and contributing to future generations than one that is harvested. However, as fishing effort increases, individual fish are exposed to repeated risk of

Received 8 June 2007. Accepted 30 December 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 15 April 2008.
J20039

W.E. Pine III.[1] Department of Fisheries and Aquatic Sciences, University of Florida, 7922 NW 71st Street, Gainesville, FL 32653, USA.
S.J.D. Martell and C.J. Walters. Fisheries Centre, The University of British Columbia, 2202 Main Mall, Vancouver, BC V6T1Z4, Canada.
O.P. Jensen and J.F. Kitchell. Center for Limnology, University of Wisconsin, 680 N Park Street, Madison, WI 53706, USA.

[1]Corresponding author (e-mail: billpine@ufl.edu).

 doi:10.1139/F08-020

postrelease mortality. The ultimate success of catch-and-release as a management measure depends on a complex interplay among fishing effort, postrelease survival, and fish life-history characteristics (Coggins et al. 2007; Goodyear 2007).

Billfishes (family Istiophoridae; note: we are not including swordfish (*Xiphias gladius*) as "billfish" because of differences in habitat and fishery targeting and management) are pelagic, apex predators, which as a group are thought to have declined globally in abundance because of direct and indirect exploitation by commercial fisheries (Myers and Worm 2003; Hampton et al. 2005). Recreational fisheries for billfish represent economically important fisheries in North and Central America and in Australia (Squire and Au 1990; Ditton and Stoll 2003). Interest in these recreational fisheries is growing as evidenced by large and active billfish conservation organizations (Kitchell et al. 2006) and organized efforts by these groups to mandate fishery closures to protect billfishes, including legal action to protect some Atlantic billfishes (white marlin, *Kajikia albidus*; Venizelos et al. 2003).

Conservation efforts for billfish species in recreational fisheries in the USA and abroad include the use of length limits, catch-and-release, and gear modifications, including the use of circle hooks (Prince et al. 2002). Recreational length limits for blue marlin (*Makaira nigricans*) (251 cm) and white marlin (168 cm) are in place in US Atlantic waters, and the International Committee for the Conservation of Atlantic Tunas (2007) has recommended that all nations with recreational fisheries for these species adopt length limits. Catch-and-release practices for marlin are nearly universal in some US recreational fisheries (e.g., 99% for white marlin, Goodyear and Prince 2003) and lower but increasingly common elsewhere (e.g., 72%–87% for billfish tournament anglers in Puerto Rico, Ditton et al. 1999). The use of circle hooks is motivated by studies showing that circle hooks lead to higher incidences of jaw hooking and likely increased survival rates than traditional J-style hooks (Prince et al. 2002; Cooke and Suski 2004; Horodysky and Graves 2005). The use of circle hooks to reduce billfish postrelease mortality has also been mandated in some recreational billfish tournaments (Prince et al. 2002; Cooke and Suski 2004) and by some countries when recreationally fishing for billfish (e.g., Costa Rica, Cooke and Suski 2004). Regulations requiring the use of circle hooks in natural baits for all US Atlantic billfish tournaments are scheduled to take effect on 1 January 2008 (National Marine Fisheries Service 2007).

In commercial fisheries, a combination of gear changes, mandatory release, and closed areas have been used to reduce mortality of billfishes. The use of circle hooks (which appear to reduce hooking mortality of many pelagic fishes, Kerstetter and Graves 2006*a*) is mandated for the US Atlantic longline fleet (National Marine Fisheries Service 2004*a*) and for shallow sets in the Hawaii-based Pacific longline fleet (National Marine Fisheries Service 2004*b*) to reduce sea turtle bycatch. Commercial closed areas are used in Mexico (Sosa-Nishizaki 1998) and Australia (Findlay et al. 2003). Bans on commercial landings of all billfish from territorial waters began in 1991 in New Zealand (Holdsworth et al. 2003), and Australia banned commercial landings of blue and black marlin (*Istiompax indica*) in 1997 (Findlay et al. 2003). Longline-caught billfish are often alive when the gear is retrieved (Jackson and Farber 1998; Lee and Brown 1998), and all billfish are required to be released when caught in the US Atlantic longline fishery (National Marine Fisheries Service 1988). The International Committee for the Conservation of Atlantic Tunas (2007) has recommended the release of all live blue and white marlin caught in Atlantic commercial fisheries. Australia has mandated reduced longline soak times (the amount of time longline gear is in the water) to improve billfish survival at the time that gear is retrieved (Findlay et al. 2003).

Changes in fishing practices affect many species at once, and ecosystem models suggest that predator–prey interactions may play a large role in shaping the outcome of different conservation measures. Kitchell et al. (2004) showed that shifting longline fisheries to greater depths to reduce encounter rates with billfish would likely increase blue marlin biomass nearly threefold and biomass of other billfish species by nearly 200%. Kaplan et al. (2007), using an ecosystem model of the Pacific, found that striped marlin (*Kajikia audax*) and blue marlin populations would benefit from mandatory release from longline gear with or without changes in hook type that might improve survival or reduce catchability of marlins. However, under a scenario of reduced marlin catchability using circle hooks, marlins recovered much higher biomasses. The effects of circle hooks on billfish catch rates are unclear; one large study suggests that catch rates may increase (Hoey 1996), while another found no difference (Kerstetter and Graves 2006*a*). Billfish conservation efforts may lead to ecosystem and economic tradeoffs as changes in fisheries management practices to reduce bycatch of species such as marine turtles and billfish may lead to changes in foodweb dynamics because of interactions between species. For example, increases in billfish abundances may lead to reductions in tuna abundances (billfish feed on tuna) (Cox et al. 2002); yet these increases in billfish populations could have positive benefits on recreational fisheries through increases in billfish recreational catch rates (Kitchell et al. 2006).

These conservation efforts are all designed to reduce mortality induced by stress, injuries, or increased predation risk that result from being captured on a hook, retrieved to a vessel, unhooked, and released — yet even at some of the higher postrelease survival rates reported in the literature, population-level effects of reduced survival may still be large. Estimates of postrelease survival of billfish from recreational fisheries vary widely based on hook type, study design, and treatment of nonreporting tags, with published survival rates ranging from 65% to 100% (Pepperell and Davis 1999; Domeier et al. 2003; Graves and Horodysky 2008). Similar postrelease survival rates have been reported for longline fisheries. For example, 63%–89.5% of white marlin and 77.8%–100% of blue marlin (depending on treatment of nonreporting tags) released from pelagic longline gear survived (Kerstetter et al. 2003; Kerstetter and Graves 2006*b*). For longline fisheries, the survival at haulback (when gear is retrieved) must also be considered. For white marlin, survival when longline gear is retrieved may be on the order of 51%–71% (Cramer 2000; Beerkircher et al. 2004), with the lower estimate coming from scientific observers. The population-level impacts of postrelease mortality are poorly understood, and postrelease mortality could prevent catch- and-release practices in both the recreational and commercial sectors from having their intended effects of aiding billfish population recovery.

We evaluated population-level effects of postrelease survival for the three species of billfish most commonly encountered globally in commercial and recreational fisheries: striped marlin, white marlin, and blue marlin. Our purpose is to (*i*) evaluate population sensitivity to different postrelease survival levels for each billfish species and (*ii*) examine the trade-offs between implementing minimum size limits to conserve billfish populations and the population-level impacts of postrelease survival. The model is designed to explore trade-offs across a range of potential size limits, postrelease survival rates, and levels of fishing effort, not to evaluate the management approach of any single billfish fishery.

Materials and methods

We constructed age- and size-structured population models for striped, blue, and white marlins across a range of minimum length limits, release rates, and fishing mortalities for each species. The model was originally developed by Coggins et al. (2007) to evaluate population impacts of size-selective fisheries for two generalized life-history types that represented a range of longevity, growth, and recruitment compensation rates. Below we provide a summary of model input parameters and overall approach, but refer the reader to Coggins et al. (2007) for additional details on the model used.

Model parameters

Model input parameters for each species (Table 1) included basic population dynamics parameters related to growth (i.e., von Bertalanffy growth parameters), maximum age, instantaneous natural mortality rates, length at maturity, length at recruitment to the fishery, and parameters for the allometric length–weight relationship (Coggins et al. 2007). Each species was divided into subpopulations, and each subpopulation had different growth trajectories to account for widely observed variability in length within age classes (Walters and Martell 2004, p. 119; Coggins et al. 2007). Including growth variability for each species also accounts for size-specific differences in fecundity and fishery vulnerability among age classes. Equilibrium abundance for each growth trajectory was calculated by multiplying age-specific survivorship and equilibrium total recruitment. Recruitment was calculated using Botsford equilibrium solutions (Botsford 1981; Walters and Martell 2004, p. 56) for the Beverton–Holt and the Ricker stock–recruitment models. Fish were assigned to each growth trajectory following a normal probability distribution.

Fecundity was specified for each age–growth trajectory following Coggins et al. (2007). For each growth trajectory, fecundity was calculated as a function of weight using standard fecundity–weight relationships (Quinn and Deriso 1999, p. 203). Survivorship for each age and growth trajectory was recursively calculated where each simulated population was subject to natural mortality, harvest mortality, and a range of postrelease mortalities. Harvest and postrelease survival varied among subpopulations based on length-dependent vulnerability schedules (Coggins et al. 2007). The vulnerability to harvest was calculated based on the proportion of fish for each age in each growth trajectory whose size exceeded the length limit, and vulnerability to release was calculated as the proportion of fish larger than the minimum size vulnerable to the gear, but smaller than the minimum legal vulnerable size.

Because of uncertainty over the recruitment compensation rate for these species, we followed suggestions from Schnute and Kronlund (1996) and Martell et al. (2008) to treat F_{MSY} (the fishing mortality rate that results in maximum sustainable yield) as a leading parameter instead of a recruitment compensation parameter such as Goodyear's (1980) compensation ratio or a from Myers et al. (1999). For each species, we assume that the optimal fishing mortality rate (Table 1) that would maximize the long-term yield is roughly approximated by $F_{\mathrm{MSY}} = 0.6M$ (M defined from life-history invariants as in most billfish stock assessments, Table 1). Given F_{MSY}, basic life-history parameters, and a selectivity curve (which represents the size-specific probability of capture), we then proceed to derive the recruitment compensation ratio that is consistent with the specified F_{MSY} value. For the Beverton–Holt stock (S) recruitment (R) model of the form

$$(1) \qquad R = \frac{aS}{(1 + BS)}$$

where a and B are constants, and the analytical expression for the recruitment compensation ratio (κ) is given by

$$(2) \qquad \kappa = \frac{\phi_e}{\phi_f} - \frac{F_{\mathrm{MSY}}\,\phi_Q \dfrac{\phi_e}{\phi_f^2} \dfrac{\partial \phi_f}{\partial F_{\mathrm{MSY}}}}{\phi_Q + F_{\mathrm{MSY}} \dfrac{\partial \phi_Q}{\partial F_{\mathrm{MSY}}}}$$

where ϕ_f, ϕ_Q, $\dfrac{\partial \phi_f}{\partial F_{\mathrm{MSY}}}$, and $\dfrac{\partial \phi_Q}{\partial F_{\mathrm{MSY}}}$ are evaluated at F_{MSY} (see Appendix A for full derivation of eq. 2; see List of symbols for definitions of terms).

This was done for two reasons: (*i*) recruitment compensation parameters are generally calculated to provide the compensation slope from eggs to age-1. In our model, we are interested in recruits to the fishery, which varies with the size limits imposed on the stock; (*ii*) our purpose is to evaluate how specific billfish species may respond to different levels of discard mortality. If a range of recruitment compensation parameters were used, the uncertainty would then fall on which compensation parameter was correct — this is not our study objective. Our approach allowed us to choose values of F_{MSY} based on a commonly used rule of thumb ($F_{\mathrm{MSY}} = 0.6M$, Walters and Martell 2004, p. 60) rather than having to estimate a recruitment compensation value by fitting a stock assessment model to time-series data. Because of uncertainty around estimates of M and, as a result, F_{MSY}, we evaluated a range of fishing rates that likely include the true estimate of F_{MSY}. To initialize the model, we set discard mortality to equal 0 and the size limit as the size at first capture. Model results at each discard mortality rate are then scaled to these initial values and are expressed across a range of F/F_{MSY} values. Because of this scaling, results are qualitatively the same across a wide range of values for F_{MSY}.

Table 1. Life-history parameter values used for model simulations for striped marlin (*Kajikia audax*), white marlin (*Kajikia albidus*), and blue marlin (*Makaira nigricans*).

Parameter	Description	Striped	White	Blue
A	Maximum age (years)	11[a]	18[e]	25[i]
M	Instantaneous natural mortality rate	0.38[b]	0.48[b]	0.41[b]
G	Number of growth trajectories	11	11	11
$\bar{L}_\infty$	Average asymptotic length (cm)	221[a]	204	244[j]
k	von Bertalanffy growth coefficient (year^{-1})	0.23[a]	0.32	0.28[j]
t_0	von Bertalanffy time at zero length (years)	–1.6[a]	–0.002	–3.9[j]
CV_L	Coefficient of variation for asymptotic length	0.1	0.1	0.1
L_{mat}	Length at 50% maturity (cm)	140[c]	150[f]	160[c]
L_{min}	Length at recruitment to the fishery (cm)	110[d]	160[g]	160[k]
α	Allometric length–weight parameter	8.0×10^{-5}[a]	3.9×10^{-6}	1.2×10^{-6}
β	Allometric length–weight parameter	2.523[a]	3.069[h]	3.37[h]

Note: Growth parameters for blue marlin represent an average of male and female growth rates.
[a]Melo-Barrera et al. (2003).
[b]Pauly (1980) method applied to growth parameters using mean temperature of 26 °C.
[c]Kume and Joseph (1969).
[d]Hinton and Bayliff (2002): length at first mode in length frequency of longline catches.
[e]International Committee for the Conservation of Atlantic Tunas (2001): based on time at liberty of 15 years for a fish tagged at 2–3 years of age.
[f]Arocha et al. (2005).
[g]Goodyear and Arocha (2001).
[h]Prager et al. (1995).
[i]Hill et al. (1989) gives a range of 20–30 years.
[j]Goodyear (2003): based on fitting von Bertalanffy growth curve to data from Prince et al. (1991) and Wilson (1984) for individuals 1 year of age and older.
[k]Kleiber et al. (2003): length at first mode in length frequency of longline catches.

Approach

We evaluated effects of postrelease mortality on blue, white, and striped marlin stocks by calculating a variety of utility metrics (Die et al. 1988), including spawning potential ratio (SPR), yield, efficiency (biomass lost to potential future harvest because of postrelease mortality; the ratio of yield to total deaths due to fishing), and probability of catching a trophy billfish (a goal of many, but not all, recreational and tournament anglers) across a range of sizes at recruitment to the fishery (i.e., length limits), postrelease mortality rates, and catch rates. SPR is a common stock assessment tool to evaluate the degree to which fishing has reduced the potential population reproductive output (Goodyear 1993). Recruitment overfishing generally occurs when SPR ≤ 0.35 (Mace 1994; Clark 2002), although highly reproductive stocks can sustain lower values. We evaluated how different postrelease survival levels would affect fishery performance metrics by examining changes in equilibrium yield, fishery efficiency, and catch rate of trophy marlin. Efficiency is a way to evaluate conservation goals, as low efficiency values indicate that the majority of biomass losses are due to postrelease mortality rather than harvest. We considered trophy billfish as fish that are greater than 80% of their asymptotic length (L_∞).

We used a range of potential length limit values from $0.2L_\infty$ to L_∞. However, recreational fisheries for billfishes are primarily catch-and-release, with release rates in some fisheries (e.g., Atlantic white marlin) approaching 99% (Goodyear and Prince 2003). In our model, catch-and-release fisheries are simulated by examining population responses to length limits that are equal to the mean L_∞. It is important to realize how the model is operating at high length limits. Fish above the minimum vulnerable size to capture but below the size limit are subjected to the postrelease mortality rate only. At the high length limits, few fish are harvested, but the fish that are caught are subject to the specified postrelease mortality rates. Natural mortality always operates on both groups. To evaluate conservation efforts within the commercial and recreational fisheries, we simulated three different postrelease survival scenarios (99%, 75%, and 50%) that cover the range of published estimates of postrelease survival rates with different hook types from commercial longline and recreational hook-and-line fisheries.

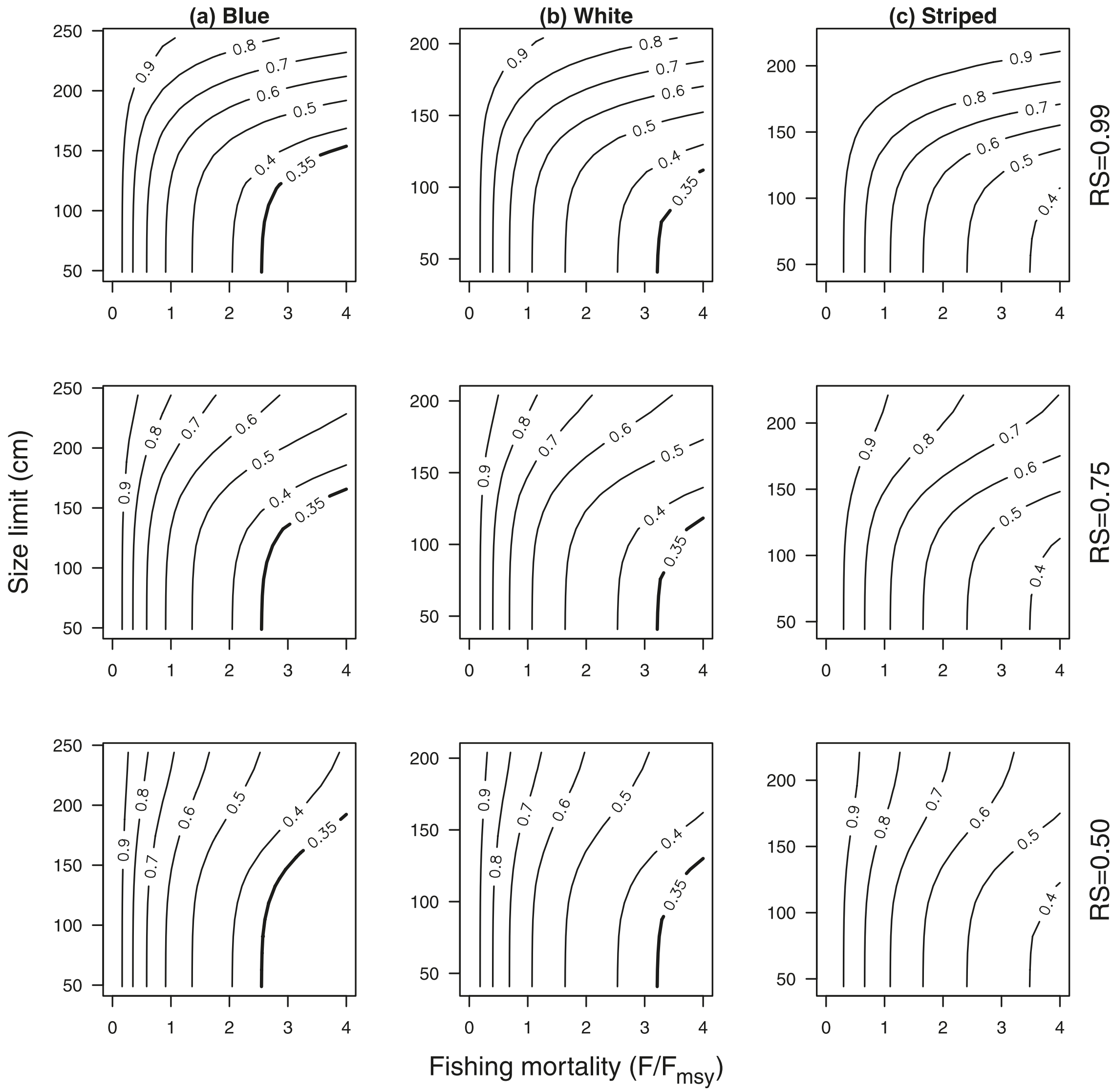
Results

Postrelease mortality decreased the ability of size limits to prevent recruitment overfishing. As postrelease survival decreased, the effectiveness of size limits for maintaining SPR above 0.40 declines for a given F (Fig. 1). For example, as postrelease survival decreased from 99% to 50% (Figs. 1*a*, 1*b*, 1*c*), the shape of the SPR response curve changed drastically across the range of simulated length limits and F/F_{MSY} fishing mortality ratios.

This relationship at high postrelease survival rates is generally asymptotic where length limits are effective at preventing SPR < 0.35 across a range of F/F_{MSY} ratios up to 4. Yet as postrelease survival decreases, the F/F_{MSY} ratio must decline to prevent recruitment overfishing even with very high size limits (Fig. 1). These patterns are similar for each of the three species we examined.

Billfish population biomass as measured in yield demonstrates a surprising response. As postrelease survival decreased, the eumetric fishing line (Quinn and Deriso 1999,

Fig. 1. Spawners-per-recruit for different size limits (cm) and fishing rates (F/F_{MSY}) and postrelease survival rates (RS, figure rows) for (*a*) blue marlin (*Makaira nigricans*), (*b*) white marlin (*Kajikia albidus*), and (*c*) striped marlin (*Kajikia audax*).

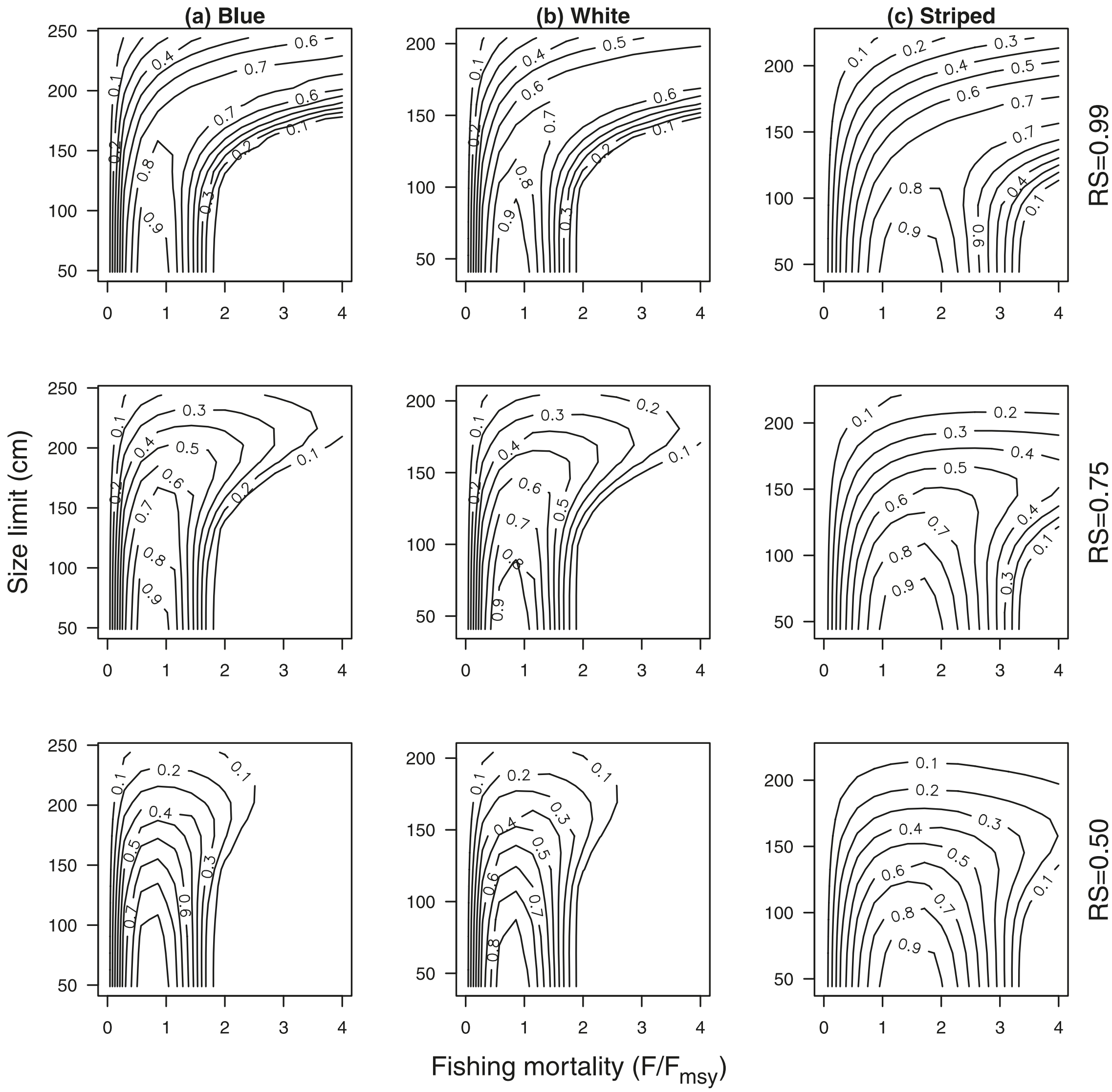


pp. 246–247) along the yield isopleths shifted from the expected asymptotic shape seen in the 99% postrelease survival plots to a nearly vertical orientation, where length limits are ineffective at conserving billfish biomass and fishing mortalities must be drastically reduced (Fig. 2). This pattern also shows a surprising effect where the yields are maximized at lower fishing mortality rates and lower size limits.

This counterintuitive response is driven by the effects of declining postrelease survival. At lower postrelease survival rates, a large amount of biomass that would otherwise have been available for later harvest is instead lost to postrelease mortality. The maximum yield is at smaller, younger sizes versus the traditional expectation to maximize yield at larger sizes. Simply put, there is no point restricting the harvest of younger fish if their release is unlikely to result in survival and future harvest at a larger size. This is particularly evident in the white marlin example (Fig. 2*b*), where much of the yield in our simulation is coming from young fish when they first enter the fishery. This nonharvest fishing mortality is a cryptic source of mortality that is not widely considered in using size limits to reduce the impacts of fishing.

Our evaluation of fishery efficiency as a conservation goal shows that as postrelease survival declines, then the usefulness of size limits to conserve billfish stocks declines greatly across a wide range of size limits and F/F_{MSY} rates (Fig. 3). Basically, efficiency declines as release survival declines, and size limits and fishing mortality increase for the same reasons seen in the yield plots; fishery efficiency is driven down by waste from nonharvest mortality related to postrelease mortality. The yeild per recruit and efficiency plots are combined (Fig. 3) and show that for each marlin species, there is a relatively narrow range of F/F_{MSY} and size limit combinations that can be used to conserve marlin stocks by reducing the likelihood of recruitment overfishing while maximizing yield and fishing efficiency. For example, striped marlin (Fig. 3, right column) shows a narrow range of size limits and fishing mortality rates that maximize yield

Fig. 2. Equilibrium yield for different size limits (cm) and fishing rate rates (F/F_{MSY}) and postrelease survival (RS, figure rows) rates for (*a*) blue marlin (*Makaira nigricans*), (*b*) white marlin (*Kajikia albidus*), and (*c*) striped marlin (*Kajikia audax*).



and efficiency without substantial risk of recruitment overfishing.

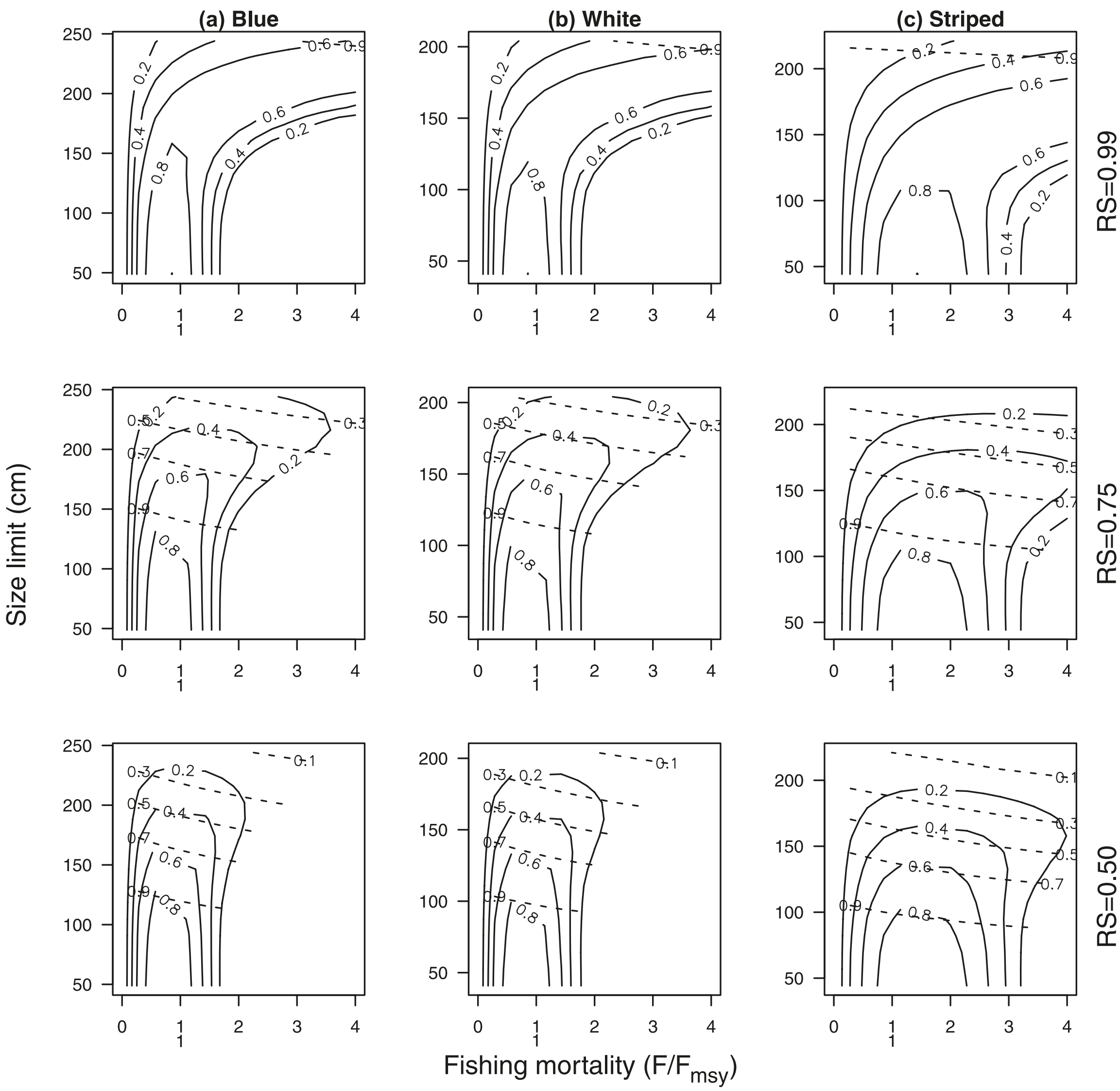
The probability of catching a trophy fish also declines as postrelease survival decreases (Fig. 4). With postrelease survival of about 99%, we found that about 1 in every 100 blue marlin caught will be a trophy individual across a wide range of size limits and fishing mortality rates (Fig. 4*a*). As postrelease survival decreases, the probability of catching a trophy blue marlin declines, as does the utility of size limits as a management tool. For postrelease survival rates of 50% or more, size limits are completely ineffective for maintaining trophy fisheries. Even at postrelease survival rates of 75%, size limits are only effective for populations experiencing overfishing (i.e., $F/F_{MSY} > 1$).

Discussion

We found that postrelease mortality can have major population level effects on key billfish species at higher exploitation rates and may limit the effectiveness of existing conservation measures designed to aid population recovery such as length limits. Postrelease mortality, even at relatively low levels, can lead to counterintuitive outcomes from conservation actions designed to improve fishery efficiency. Most conservation efforts for billfishes are motivated by catch-and-release fishing practices where fish are released with the expectation that they are very likely to survive. Our results suggest that even at postrelease survival rates as high as 75%, cumulative effects of postrelease mortality can seriously reduce the benefits of catch-and-release practices intended to reduce the chance of recruitment overfishing, increase yield, and increase the probability of catching a trophy fish. Additionally, these conservation efforts may lead to a waste of harvestable biomass and ultimately a failure of an intended conservation action.

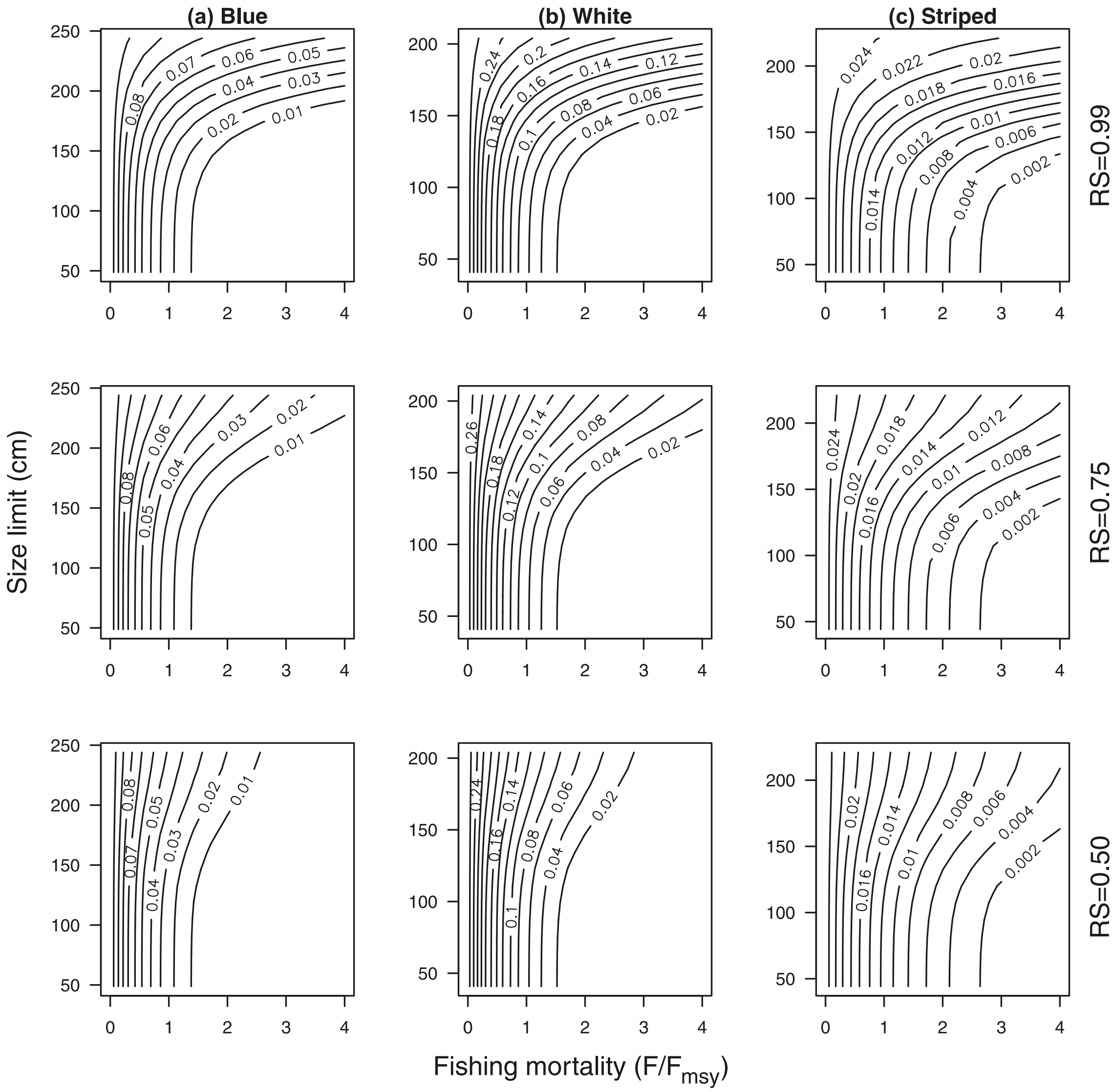
The use of catch-and-release practices has increased drastically over the last 30 years in recreational and commercial fisheries in both freshwater and marine systems (Barnhart 1989; Radomski 2003; Bartholomew and Bohnsack 2005). This increase is related both to changes in angler motivation (Clark 1983; Barnhart 1989) and also to the increasing use

Fig. 3. Efficiency (i.e., ratio of release mortality to harvest mortality) (broken line) and yield for different size limits (cm) and fishing rates (F/F_{MSY}) and postrelease survival (RS, figure rows) rates for (*a*) blue marlin (*Makaira nigricans*), (*b*) white marlin (*Kajikia albidus*), and (*c*) striped marlin (*Kajikia audax*).



of length limits as a regulatory tool to reduce fishing mortality and conserve fish stocks (Radomski 2003; International Committee for the Conservation of Atlantic Tunas 2007). Catch-and-release practices in recreational fisheries are heavily motivated by the premise that releasing smaller individuals will increase the probability of catching more and larger individuals in the future. Clark (1983) predicted that catch rates of trophy brook trout (*Salvelinus fontinalis*), largemouth bass (*Micropterus salmoides*), northern pike (*Esox lucius*), and brown trout (*Salmo trutta*) populations would increase as anglers voluntarily chose to release fish that were legal to harvest simply because as total mortality declined (because of declines in harvest) then more fish would survive to trophy size. Coggins et al. (2007) found that postrelease mortality rates above 20% for short-lived, highly productive species and above 5% for long-lived, low productivity species substantially decreased the effectiveness of size limits in preventing recruitment overfishing and greatly reduced fishery yield and efficiency. Goodyear (2007) highlights the competing objectives of maximizing catch rates and maximizing sustainable harvest, which occurs frequently in fisheries when commercial and recreational fisheries target the same species. This study shows that this objective can be met for both groups if recreational groups release their catch and the commercial harvest is not allowed to increase above MSY (Goodyear 2007). Nelson (2002) describe how the recreational common snook (*Centropomus undecimalis*) fishery in Florida is managed using a combination of restrictive seasonal closures, bag limits, and size limits that effectively create long annual periods of catch-and-release only fishing for common snook. Postrelease mortality for common snook is currently estimated at about 3% (Muller and Taylor 2006), and combined with the high and increasing angler effort, mortality of fish caught and released is now equal to about one-third of all fishing mortality for this species. Because of the large number of extensive regulations already in place designed to reduce fishing mortality for common snook in Florida, man-

Fig. 4. Fraction of population consisting of trophy-sized individuals (i.e., individuals greater than 80% of their asymptotic length (L_∞)) for different size limits (cm) and fishing rates (F/F_{MSY}) and postrelease survival (RS, figure rows) rates for (*a*) blue marlin (*Makaira nigricans*), (*b*) white marlin (*Kajikia albidus*), and (*c*) striped marlin (*Kajikia audax*).



agers may be forced to evaluate alternative regulations, such as limiting effort to protect common snook populations from overfishing, partially driven by postrelease mortality.

Blue and white marlin populations have experienced large population declines from historical levels to the point that white marlin in the Atlantic have been considered for protection under the US Endangered Species Act. The most recent assessment for these species suggests that Atlantic blue and white marlin populations may be stabilizing or even recovering (International Committee for the Conservation of Atlantic Tunas 2006). At the higher exploitation rates experienced by Atlantic marlins, size limits and catch-and-release may be effective management tools if postrelease survival is high. Stringent regulations requiring mandatory release of all commercially caught white marlin and a variety of minimum size limits in the recreational fishery implemented in the late 1980s and 1990s have likely been part of the apparent recovery. The most recent assessment of striped marlin in the eastern Pacific (Hinton and Maunder 2003) determined that F/F_{MSY} was probably less than 1. Although catch-and-release practices are becoming increasingly common in recreational fisheries for striped marlin, length limits and mandatory commercial releases of billfish have not been as widely used in the Pacific.

The central assumption of regulations requiring the release of white marlin caught in commercial fisheries is that a released white marlin has a higher probability of survival than one that is retained and that releasing white marlin leads to a reduction in *F*. Recent stock assessments have suggested increases in white marlin stocks, which may be partially attributed to reductions in *F*. Our findings suggest that if postrelease survival is low, then regulations mandating release of marlin are likely leading to inefficient fishing practices. This is because a substantial amount of fishery yield is discarded as waste when it could represent a marketable product. The ban on retention or sale of billfish in the US domestic Atlantic longline fishery is estimated to have resulted in a loss of gross revenue of approximately $660 000 per year (National Marine Fisheries Service 1999). Incentives could be developed such that a portion of the revenue from this previously discarded yield (US discards of dead billfish) could be used to fund research on new methods to reduce marlin catch in the longline fishery or increase postrelease survival by modifying fishing practices, locations, or seasons. One key to this being effective is that the incentive must not lead to reductions in the release rate of fish landed live as fishers moved towards claiming the incentive for dead fish.

A large amount of recent and ongoing billfish research is focused on finding ways to maximize postrelease survival by focusing on hook types used in both the recreational and commercial fisheries. Striped marlin, blue marlin, black marlin, and white marlin have all been subjects of recent studies using a variety of passive, acoustic, and satellite tags to estimate postrelease mortality (Pepperell and Davis 1999; Domeier et al. 2003; Horodysky and Graves 2005). While the methods and assumptions of these studies differ, the general results have shown that circle hooks have lower incidences of hooking-related injury and thus likely have higher postrelease survival rates (Graves et al. 2002; Prince et al. 2002; Cooke and Suski 2004). The use of J hooks in recreational fisheries for billfish may result in postrelease survival rates as low as 65% (Horodysky and Graves 2005). Our results suggest that survival rates this low are likely to compromise the value of catch-and-release and size limits as conservation tools where fishing effort is high. Designing studies to estimate postrelease survival with high precision is quite difficult (Pollock and Pine 2007), and the high cost of satellite archival tags often limits sample sizes. However, understanding differences in postrelease survival rates from different fishing gears is of critical importance if catch-and-release is to be an effective management tool.

The vast majority of the US billfish effort is from recreational tournament and charter fisheries that operate along the South Atlantic, Gulf of Mexico, and southern California. In both the charter and tournament fleets, goals of many anglers are to catch large marlin (i.e., a 1000 lb (454 kg) “grander”), tag the fish, and release these individuals to catch them again in the future. Trophy marlin are those that have survived long enough to reach a large size, and the probability of catching a trophy-sized individual is particularly sensitive to the cumulative effects of postrelease mortality. Our evaluation of the probability of catching a trophy individual shows that length limits are only likely to help if postrelease survival is high.

Our results provide a framework in which to compare ongoing field studies designed to evaluate techniques to reduce postrelease mortality in billfishes in both commercial and recreational fisheries. Our model results are conditional on the life-history input parameters drawn from a wide variety of sources. Life-history information for billfishes is generally uncertain, and as new information becomes available for these species, our model will need to be updated. Billfish fisheries are unique in that most directed fisheries are recreational and motivated by the experience of catching and releasing the fish. In commercial fisheries, billfish are mostly bycatch and are not widely targeted. This difference suggests that properly designed incentive programs may be a highly effective way to reduce commercial catch rates and improve postrelease survival in both sectors.

While the use of size limits (recreational fisheries) and mandatory release (commercial fisheries) regulations are part of the management solutions for protecting billfish, the best approach is likely one that focuses on reducing catch rates of billfish in commercial fisheries (either through gear modifications or time–area closures; Goodyear 1999) and increasing postrelease survival rates in the recreational fishery through the use of circle hooks or in-water release methods that minimize stress and injury and maximize survival of recreationally caught billfish.

Acknowledgements

We thank the staff of the National Marine Fisheries Service office in Honolulu for their hospitality in developing this manuscript. We also thank R. Ahrens, C. Boggs, L. Coggins, M. Catalano, P. Goodyear, and M. Allen for helpful discussion on this manuscript. This manuscript was funded by a National Science Foundation Grant OCE 9731531 to JFK.

References

Arocha, F., Bárrios, A., Silva, J., and Lee, D.W. 2005. Preliminary observations on gonad development, sexual maturity and fecundity estimates of white marlin (*Tetrapturus albidus*) from the Western Central Atlantic. Int. Comm. Cons. Atl. Tunas (ICCAT) Coll. Vol. Sci. Pap. **58**(5): 1567–1573.

Barnhart, R.A. 1989. Symposium review: catch-and-release fishing, a decade of experience. N. Am. J. Fish. Manag. **9**: 74–80.

Bartholomew, A., and Bohnsack, J.A. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Rev. Fish. Biol. Fish. **15**(1–2): 129–154.

Beerkircher, L.R., Brown, C.J., Abercrombie, D.L., and Lee, D.W. 2004. SEFSC Pelagic Observer Program data summary for 1992–2002. NOAA Tech. Memo. NMFS-SEFSC 522. pp. 1–25.

Botsford, L.W. 1981. Optimal fishery policy for size-specific density-dependent population models. J. Math. Biol. **12**(1): 265–293.

Clark, R.D. 1983. Potential effects of voluntary catch and release of fish on recreational fisheries. N. Am. J. Fish. Manag. **3**(1): 306–314.

Clark, W.C. 2002. $F_{35\%}$ revisited ten years later. N. Am. J. Fish. Manag. **22**: 251–257.

Coggins, L.G., Catalano, M.J., Allen, M.S., Pine, W.E., and Walters, C.J. 2007. Effects of cryptic fishing mortality on fishery sustainability and performance. Fish Fish. **8**: 1–15.

Cooke, S.J., and Suski, C.D. 2004. Are circle hooks an effective tool for conserving marine and freshwater recreational catch-and-release fisheries? Aquat. Conserv. Mar. Freshw. Ecol. **14**(3): 299–326.

Cox, S.P., Martell, S.J.D., Walters, C.J., Essington, T.E., Kitchell, J.F., Boggs, C., and Kaplan, I. 2002. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. I. Estimating population biomass and recruitment of tunas and billfishes. Can. J. Fish. Aquat. Sci. **59**(11): 1724–1735.

Cramer, J. 2000. Species reported caught in the U.S. commercial pelagic longline and gillnet fisheries from 1996–1998. NMFS Sustain. Fish. Div. Publ. SFD-99/00 No. 78. pp. 1–33.

Die, D.J., Restrepo, V.R., and Hoenig, J.M. 1988. Utility-per-recruit modeling: a neglected concept. Trans. Am. Fish. Soc. **117**(3): 274–281.

Ditton, R.B., and Stoll, J.R. 2003. Social and economic perspective on recreational billfish fisheries. Mar. Freshw. Res. **54**: 545–554.

Ditton, R.B., Clark, D.J., and Chaparro, R.S. 1999. A human dimensions perspective on the billfish fishery in Puerto Rico. Proceedings of the Gulf and Caribbean Fisheries Institute, **46**: 274–288.

Domeier, M.L., Dewar, H., and Nasby-Lucas, N. 2003. Mortality rate of striped marlin (*Tetrapturus audax*) caught with recreational tackle. Mar. Freshw. Res. **54**(4): 435–445.

Findlay, J., Cross, C.M., and Bodsworth, A.G. 2003. Marlin fisheries management in Australia. Mar. Freshw. Res. **54**: 535–543.

Goodyear, C.P. 1980. Compensation in fish populations. *In* Biological monitoring of fish. *Edited by* C.H. Hocutt and J.R. Stauffer. D.C. Heath and Company, Lexington, Mass. pp. 253–280.

Goodyear, C.P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D. Rivard. NRC Research Press, Ottawa, Ont., Canada. Can. Spec. Publ. Fish. Aquat. Sci. 120. pp. 67–81.

Goodyear, C.P. 1999. An analysis of the possible utility of time–area closures to minimize billfish bycatch by US pelagic longlines. Fish. Bull. **97**: 243–255.

Goodyear, C.P. 2003. Blue marlin mean length: simulated response to increasing fishing mortality. Mar. Freshw. Res. **54**(4): 401–408.

Goodyear, C.P. 2007. Recreational catch and release: resource allocation between commercial and recreational fisherman. N. Am. J. Fish. Manag. **27**: 1189–1194.

Goodyear, C.P., and Arocha, F. 2001. Size composition of blue and white marlins taken in selected fisheries in the western north Atlantic. Int. Comm. Cons. Atl. Tunas (ICCAT) Coll. Vol. Sci. Pap. **53**(4): 249–257.

Goodyear, C.P., and Prince, E.D. 2003. U.S. recreational harvest of white marlin. Int. Comm. Cons. Atl. Tunas (ICCAT) Coll. Vol. Sci. Pap. **55**: 624–632.

Graves, J.E., and Horodysky, A.Z. 2008. Does hook choice matter? The effects of three circle hook models on post-release survival of white marlin. N. Am. J. Fish. Manag. In press.

Graves, J.E., Luckhurst, B.E., and Prince, E.D. 2002. An evaluation of pop-up satellite tags for estimating postrelease survival of blue marlin (*Makaira nigricans*) from a recreational fishery. Fish. Bull. **100**(1): 134–142.

Hampton, J., Sibert, J.R., Kleiber, P., Maunder, M.N., and Harley, S.J. 2005. Decline of Pacific tuna populations exaggerated? Nature (London), **434**(7037): E1–E2.

Hill, K.T., Cailliet, G.M., and Radtke, R.L. 1989. A comparative analysis of growth zones in four calcified structures of Pacific blue marlin, *Makaira nigricans*. Fish. Bull. **87**(4): 829–843.

Hinton, M.G., and Bayliff, W. 2002. Status of striped marlin in the Eastern Pacific Ocean in 2001 and outlook for 2002. Inter-American Tropical Tuna Commission, La Jolla, Calif.

Hinton, M.G., and Maunder, M.N. 2003. Status of striped marlin in the Eastern Pacific Ocean in 2002 and outlook for 2003–2004. Inter-American Tropical Tuna Commission, La Jolla, Calif.

Hoey, J. 1996. Bycatch in the western Atlantic pelagic longline fisheries. *In* Alaska Sea Grant. 1996. Solving bycatch: considerations for today and tomorrow. Alaska Sea Grant College, University of Alaska – Fairbanks, Alaska. Prog. Rep. No. 96-03. pp. 193–203.

Holdsworth, J., Saul, P., and Browne, G. 2003. Factors affecting striped marlin catch rate in the New Zealand recreational fishery. Mar. Freshw. Res. **54**: 473–481.

Horodysky, A., and Graves, J. 2005. Application of pop-up satellite archival tag technology to estimation of postrelease survival of white marlin (*Tetrapturus albidus*) caught on circle and straight-shank ("J") hooks in the western North Atlantic recreational fishery. Fish. Bull. **103**: 84–96.

International Committee for the Conservation of Atlantic Tunas. 2001. Report of the fourth ICCAT billfish workshop. Int. Comm. Cons. Atl. Tunas (ICCAT) Coll. Vol. Sci. Pap. **53**: 1–130.

International Committee for the Conservation of Atlantic Tunas. 2006. Executive summary of the 2006 stock assessment for blue and white marlin. Int. Comm. Cons. Atl. Tunas (ICCAT) Coll. Vol. Sci. Pap. PLE/014 2006. pp. 68–77.

International Committee for the Conservation of Atlantic Tunas. 2007. Recommendation by ICCAT to further strengthen the plan to rebuild blue marlin and white marlin populations. *In* ICCAT 2007. Compendium of management recommendations and resolutions adopted by ICCAT for the conservation of Atlantic tunas and tuna-like species. Int. Comm. Cons. Atl. Tunas (ICCAT) Coll. Vol. Sci. Pap. **60**: 55–57. Available from www.iccat.int/Documents/Recs/ACT_COMP_2007_ENG.pdf [accessed December 2007].

Jackson, T.L., and Farber, M.I. 1998. Summary of at-sea sampling of the western Atlantic Ocean, 1987–1995, by industrial longline vessels fishing out of the port of Cumana, Venezuela: ICCAT Enhanced Research Program for Billfish 1987–1995. Int. Comm. Cons. Atl. Tunas (ICCAT) Coll. Vol. Sci. Pap. XVVII. pp. 203–228.

Kaplan, I.C., Cox, S.P., and Kitchell, J.F. 2007. Circle hooks for Pacific longliners: not a panacea for marlin and shark bycatch, but part of the solution. Trans. Am. Fish. Soc. **136**(2): 392–401.

Kerstetter, D., and Graves, J.E. 2006*a*. Effects of circle versus J-style hooks on target and non-target species in a pelagic longline fishery. Fish. Res. **80**: 239–250.

Kerstetter, D., and Graves, J.E. 2006*b*. Survival of white marlin (*Tetrapturus albidus*) released from commercial pelagic longline gear in the western North Atlantic. Fish. Bull. **104**: 434–444.

Kerstetter, D.W., Luckhurst, B.E., Prince, E.D., and Graves, J.E. 2003. Use of pop-up satellite archival tags to demonstrate survival of blue marlin (*Makaira nigricans*) released from pelagic longline gear. Fish. Bull. **101**: 939–948.

Kitchell, J.F., Kaplan, I.C., Cox, S.P., Martell, S.J.D., Essington, T.E., Boggs, C.H., and Walters, C.J. 2004. Ecological and economic components of managing rare or endangered species in a tropical pelagic ecosystem. Bull. Mar. Sci. **74**(3): 607–619.

Kitchell, J.F., Martell, S.J.D., Walters, C.J., Jensen, O.P., Kaplan, I.C., Watters, J.R., Essington, T.E., and Boggs, C.H. 2006. Billfishes in an ecosystem context. Bull. Mar. Sci. **79**(3): 669–682.

Kleiber, P., Hinton, M.G., and Uozumi, Y. 2003. Stock assessment of blue marlin (*Makaira nigricans*) in the Pacific using MULTIFAN-CL. Mar. Freshw. Res. **54**(4): 349–360.

Kume, S., and Joseph, J. 1969. Size composition and sexual maturity of billfish caught by the Japanese longline fishery in the Pacific Ocean east of 130W. Bull. Far Seas Fish. Res. Lab. **2**: 115–162.

Lee, D.W., and Brown, C.J. 1998. SEFSC pelagic observer program data summary for 1992–1996. NOAA Tech. Memo. NMFS-SEFSC 408. pp. 1–21.

Lucy, J.A., and Studholme, A.L. (*Editors*). 2002. Catch and release in marine recreational fisheries. American Fisheries Society, Bethesda, Md. Am. Fish. Soc. Symp. 30.

Mace, P.M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. Can. J. Fish. Aquat. Sci. **51**(1): 110–122.

Martell, S.J.D., Pine, W.E., III, and Walters, C.J. 2008. Parameterizing age-structured models from a fisheries management perspective. Can. J. Fish. Aquat. Sci. **65**. In press.

Melo-Barrera, F.N., Felix-Uraga, R., and Quinonez-Velazquez, C. 2003. Growth and length–weight relationship of the striped marlin, *Tetrapturus audax* (Pisces: Istiophoridae), in Cabo San Lucas, Baja California Sur, Mexico. Cienc. Mar. **29**: 305–313.

Muller, R.G., and Taylor, R.G. 2006. The 2005 stock assessment update of common snook, *Centropomus undecimalis*. Fish and Wildlife Conservation Commission, Florida Marine Research Institute, St. Petersburg, Fla.

Muoneke, M.I., and Childress, W.M. 1994. Hooking mortality: a review for recreational fisheries. Rev. Fish. Sci. **2**(2): 123–156.

Myers, R.A., and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature (London), **423**(6937): 280–283.

Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rates of fish at low population sizes. Can. J. Fish. Aquat. Sci. **56**(12): 2402–2419.

Nelson, R.S. 2002. Catch and release: a management tool for Florida. *In* Catch and release in marine recreational fisheries. *Edited by* J.A. Lucy and A.L. Studholme. American Fisheries Society, Silver Spring, Md. pp. 11–14.

National Marine Fisheries Service. 1988. The Atlantic billfish fishery management plan. NOAA-NMFS-F/SF – Highly Migratory Species Division, Silver Spring, Md.

National Marine Fisheries Service. 1999. Ammendment 1 to the Atlantic billfish fishery management plan. NOAA-NMFS-F/SF – Highly Migratory Species Division, Silver Spring, Md.

National Marine Fisheries Service. 2004*a*. Atlantic highly migratory species (HMS); pelagic longline fishery; final rule. **69** F.R. 40733–40758.

National Marine Fisheries Service. 2004*b*. Fisheries off west coast states and in the Western Pacific, Western Pacific pelagic fisheries, pelagic longline fishing restrictions, seasonal area closure, limit on swordfish fishing effort, gear restrictions, and other sea turtle take mitigation measures. **69** F.R. 17329–17354.

National Marine Fisheries Service. 2007. Atlantic highly migratory species (HMS); U.S. Atlantic billfish tournament management measures. **72** F.R. 26735–26741.

National Research Council. 2006. Dynamic changes in marine ecosystems: fishing, food webs, and future options. The National Academies Press, Washington, D.C.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer, **39**(2): 175–192.

Pepperell, J.G., and Davis, T.L.O. 1999. Post-release behaviour of black marlin, *Makaira indica*, caught off the Great Barrier Reef with sportfishing gear. Mar. Biol. **135**(2): 369–380.

Pollock, K.H., and Pine, W.E., III. 2007. The design of field studies to estimate catch and release mortality. Fish. Ecol. Manag. **14**(2): 1–8.

Prager, M.H., Prince, E.D., and Lee, D.W. 1995. Empirical length and weight conversion equations for blue marlin, white marlin, and sailfish from the North Atlantic Ocean. Bull. Mar. Sci. **56**: 201–210.

Prince, E.D., Lee, D.W., Zweifel, J.R., and Brothers, E.B. 1991. Estimating age and growth of young Atlantic blue marlin, *Makaira nigricans*, from otolith microstructure. Fish. Bull. **89**(3): 441–459.

Prince, E.D., Ortiz, M., and Venizelos, A. 2002. A comparison of circle hook and "J" hook performance in recreational catch-and-release fisheries for billfish. *In* Catch and release in marine recreational fisheries. *Edited by* J.A. Lucy and A.L. Studholme. American Fisheries Society, Bethesda, Md. Am. Fish. Soc. Symp. 30. pp. 66–79.

Quinn, T.J., II, and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Radomski, P. 2003. Initial attempts to actively manage recreational fishery harvest in Minnesota. N. Am. J. Fish. Manag. **23**(1): 1329–1342.

Schnute, J.T., and Kronlund, A.R. 1996. A management oriented approach to stock recruitment analysis. Can. J. Fish. Aquat. Sci. **53**(3): 1281–1293.

Sosa-Nishizaki, O. 1998. Historical review of the billfish management in the Mexican Pacific. Cienc. Mar. **24**: 95–111.

Squire, J.L., and Au, D.K.W. 1990. Striped marlin in the northeast Pacific — a case for local depletion and core area management. *In* Planning the Future of Billfishes: Research and Management in the 90s and Beyond. Proceedings of the Second International Billfish Symposium, Kailua-Kona, Hawaii, 1–5 August 1988, Part 2. Contributed Papers. National Coalition for Marine Conservation, Savannah, Ga. pp. 199–214.

Venizelos, A., Sutter, F., and Serafy, J. 2003. Use of minimum size regulations to achieve reduction targets for marlin landings in the Atlantic Ocean. Mar. Freshw. Res. **54**(3): 567–573.

Walters, C.J., and Martell, S.J.D. 2004. Fisheries ecology and management. Princeton University Press, Princeton, N.J.

Wilson, C.A. 1984. Age and growth aspects of the life history of billfishes. Ph.D. thesis, University of South Carolina, Columbia, S.C.

List of symbols

Subscripts and superscripts

a	index for age
(f)	fished equilibrium
e	steady state or equilibrium conditions

Age schedules

w_a	mean weight-at-age
$l_a, (l_a^{(f)})$	unfished, (fished) survivorship to age a
v_a	vulnerability-at-age

Equilibrium variables

R_o, (R_e)	unfished (fished) equilibrium recruits
$B_{a,e}$	equilibrium age-specific biomass
MSY	maximum sustainable yield
F_{MSY}	fishing mortality rate that achieves MSY
κ	recruitment compensation parameter
F	instantaneous fishing mortality rate
M	instantaneous natural mortality rate
Y_e	equilibrium yield

Incidence functions

$\phi_B, (\phi_B^{(f)})$	unfished, (fished) biomass per recruit
ϕ_Q	per recruit shield
$\phi_e, (\phi_f)$	unfished, (fished) eggs per recruit

Appendix A appears on the following pages.

Appendix A

In an age-structured model the equilibrium yield is actually a sum over all ages multiplied by the fraction of age-specific mortality associated with fishing. Thus, the yield equation cab be written as

$$\text{(A.1)} \quad Y_e = \sum_{a=1}^{\infty} B_{a,e} \frac{F_{a,e}}{M_a + F_{a,e}} (1 - e^{-M_a - F_{a,e}})$$

where $F_{a,e} = F_e v_a$, and v_a is the age-specific probability of capture. Biomass-at-age at equilibrium ($B_{a,e}$) is defined as the product of numbers-at-age (N_a) and the mean weight-at-age (w_a). This can also be expressed as the product of the survivorship-at-age, the mean weight, and the unfished age-1 recruits (R_o). For unfished conditions, the age-specific survivorship is given recursively by

$$\text{(A.2)} \quad l_a = \begin{cases} 1, & a = 1 \\ l_{a-1} e^{-M_{a-1}}, & a > 1 \end{cases}$$

The age-specific biomass is then given by

$$\text{(A.3)} \quad B_{a,e} = R_o l_a w_a$$

An incidence function is simply the sum of the age-specific schedules (e.g., survivorship, length-at-age, weight-at-age, etc.) that expresses population units (e.g., biomass, numbers, fecundity, etc.) on a per recruit basis. For example, total biomass per recruit is given by

$$\phi_B = \sum_{a=1}^{\infty} l_a w_a$$

For notation purposes, we denote all of the incidence functions using ϕ and the subscripts correspond to the type of incidence function (e.g., ϕ_{E} = eggs per recruit, ϕ_{VB} = vulnerable biomass per recruit). The use of the incidence functions greatly simplifies the math required in subsequent calculations in that it is now possible to calculate total population abundances, fecundities, biomass, etc., based on an estimate or initial guess at the unfished recruitment R_o. For example, total biomass is given by $B = R_o \phi_B$.

Expressing the catch equation as a sum over ages of biomass that is vulnerable to harvest

$$\text{(A.4)} \quad Y = FR_o \sum_{a=1}^{\infty} l_a w_a \frac{v_a}{M_a + Fv_a} (1 - e^{-M_a - Fv_a})$$

the summation term can also be expressed as an incidence function, namely:

$$\text{(A.5)} \quad \phi_Q = \sum_{a=1}^{\infty} l_a w_a \frac{v_a}{M_a + Fv_a} (1 - e^{-M_a - Fv_a})$$

and the yield equation reduces to

$$\text{(A.6)} \quad Y = FR_o \phi_Q$$

Equilibrium recruitment for the Beverton–Holt stock–recruitment model can also be expressed as a function of equilibrium fishing mortality rate F_e, where total egg production has been reduced through the effects of fishing. Using incidence functions we can express equilibrium recruits as

$$\text{(A.7)} \quad R_e = R_o \frac{\kappa - \phi_e / \phi_f}{\kappa - 1}$$

where κ is the relative improvement in juvenile survival rate at low egg deposition rates (also referred to as the recruitment compensation ratio), ϕ_e is the eggs per recruit in unfished conditions, and ϕ_f is the eggs per recruit for a given equilibrium fishing mortality rate. To calculate the eggs per recruit under fished conditions (ϕ_f), we modify the survivorship calculation to include the effects of fishing ($l_a^{(f)}$):

$$\text{(A.8)} \quad l_a^{(f)} = \begin{cases} 1, & a = 1 \\ l_{a-1}^{(f)} e^{-M_{a-1} - F_e v_{a-1}}, & a > 1 \end{cases}$$

and ϕ_e and ϕ_f are given by

$$\phi_e = \sum_{a=1}^{\infty} l_a f_a, \quad \phi_f = \sum_{a=1}^{\infty} l_a^{(f)} f_a$$

where f_a is the age-specific fecundity at age. Note that is is not necessary to have the absolute fecundity values for each age class, but only the relative contribution, as the units cancel out in the ϕ_e/ϕ_f ratio in eq. A.7.

To determine the optimal fishing mortality rate (F_{MSY}) that achieves the maximum sustainable yield (MSY), we differentiate eq. A.6 with respect to F and set this derivative to 0 and solve for F. This corresponds to F_{MSY}, and MSY is determined by substituting F_{MSY} into eq. A.6. This calculation requires the leading parameters R_o and κ to determine the values of F_{MSY} and MSY.

To parameterize the model in terms of F_{MSY} and MSY directly, we differentiate eq. A.6 with respect to F, set it equal to 0, and solve for κ. Using the chain rule, the derivative of eq. A.6 is given by

$$\text{(A.9)} \quad \frac{\partial Y}{\partial F} = R_e \phi_Q + F\phi_Q \frac{\partial R_e}{\partial F} + FR_e \frac{\partial \phi_Q}{\partial F}$$

The partial derivative of R with respect to F_{MSY} is given by

$$\text{(A.10)} \quad \frac{\partial R}{\partial F} = \frac{R_o}{\kappa - 1} \frac{\phi_e}{\phi_f^2} \frac{\partial \phi_f}{\partial F}$$

Substituting eqs. A.7 and A.10 into eq. A.9 and setting the derivative equal to 0 and solving for κ results in

$$\text{(A.11)} \quad \frac{\partial Y}{\partial F_{\mathrm{MSY}}} = 0 = R_o \frac{\kappa - \phi_e/\phi_f}{\kappa - 1} \phi_Q + F\phi_Q \frac{R_o}{\kappa - 1} \frac{\phi_e}{\phi_f^2} \frac{\partial \phi_f}{\partial F} + FR_o \frac{\kappa - \phi_e/\phi_f}{\kappa - 1} \frac{\partial \phi_Q}{\partial F}$$

$$= \left(\kappa - \frac{\phi_e}{\phi_f} \right) \phi_Q + F\phi_Q \frac{\phi_e}{\phi_f^2} \frac{\partial \phi_f}{\partial F} + F \left(\kappa - \frac{\phi_e}{\phi_f} \right) \frac{\partial \phi_Q}{\partial F}$$

$$- F\phi_Q \frac{\phi_e}{\partial_f^2} \frac{\partial \phi_f}{\partial F} = \left(\kappa - \frac{\phi_e}{\phi_f} \right) \left(\phi_Q + F \frac{\partial \phi_Q}{\partial F} \right)$$

$$\kappa = \frac{\phi_e}{\phi_f} - \frac{F\phi_Q \dfrac{\phi_e}{\phi_f^2} \dfrac{\partial \phi_f}{\partial F}}{\phi_Q + F \dfrac{\partial \phi_Q}{\partial F}}$$

To determine R_o from MSY and F_{MSY}, use the following relationships:

$$\text{(A.12)} \quad R_e = \frac{\mathrm{MSY}}{F_{\mathrm{MSY}} \phi_Q}$$

$$R_o = R_e \frac{\kappa - 1}{\kappa - \dfrac{\phi_e}{\phi_f}}$$

With regards to the partial derivatives for ϕ_f and ϕ_Q, the analytical solution for these derivatives are a recursive function of survivorship given by

$$\text{(A.13)} \quad \frac{\partial \phi_f}{\partial F} = \sum_{a=2}^{\infty} f_a \frac{\partial l_a^{(f)}}{\partial F}$$

$$\text{(A.14)} \quad \frac{\partial \phi_Q}{\partial F} = \sum_{a=1}^{\infty} w_a \frac{v_a}{Z_a} (1 - \mathrm{e}^{Z_a}) \frac{\partial l_a^{(f)}}{\partial F} + \frac{l_a^{(f)} w_a v_a}{Z_a} \left(\mathrm{e}^{-Z_a} - \frac{1 - \mathrm{e}^{Z_a}}{Z_a} \right)$$

where $\dfrac{\partial l_a^{(f)}}{\partial F}$ is calculated recursively using

$$\text{(A.15)} \quad \frac{\partial l_a^{(f)}}{\partial F} = \begin{cases} 0, & a = 1 \\ \dfrac{\partial l_{a-1}^{(f)}}{\partial F} \mathrm{e}^{-Z_{a-1}} - l_{a-1} v_{a-1} \mathrm{e}^{-Z_{a-1}}, & a > 1 \end{cases}$$

Including postrelease survival

To include the effects of postrelease survival associated with size limits, the vulnerability at size–age has to be modified to account for the fraction of fish that are smaller (or larger in the case of slot limits) than the legal size limit that are caught and die subsequent to release. Given a specific age–size, there is a probability of capture that is usually described by a simple logistic curve. For any given age and size limit, there is also a probability of releasing the fish if the fish is less than the legal size. This simple joint probability can be described by

(A.16) $v_a = v_c[v_r + (1 + v_r)d]$

where v_a is the age-specific vulnerability of mortality associated with fishing, v_c is the vulnerability to capture, v_r is the probability of retention, and d is the postrelease mortality rate.

To implement the effects of size limits and postrelease mortality rates, the v_a term in eqs. A.5, A.8, and A.13 can be substituted with an expression similar to eq. A.16. Subsequent calculations leading to the derivation of κ are the same, but note that the estimates of κ and R_o assume that the MSY involves the retained portion of the catch.

Adding multiple groups

To represent variation in growth and the cumulative effects of size-selective fisheries, we assume that a population consists of a number of distinct groups (G) that have a unique asymptotic length (L_{∞_g}). We assume that the distribution of these L_∞ values are normally distributed with some mean and a coefficient of variation equal to 0.1. We further assume that new recruitment to each group g is normally distributed (p_g) and constant irrespective of the composition of the spawning population (i.e., we assume no genetic selection effects due to fisheries). The incidence functions (ϕ), and their respective partial derivatives, in the above equations are then modified to sum over both ages and groups to represent per recruit processes. For example the biomass per recruit is then given by

$$\phi_B = \sum_g \sum_{a=1}^{\infty} l_a w_a p_g$$