

## Effects of cryptic mortality and the hidden costs of using length limits in fishery management

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### Abstract

Fishery collapses cause substantial economic and ecological harm, but common management actions often fail to prevent overfishing. Minimum length limits are perhaps the most common fishing regulation used in both commercial and recreational fisheries, but their conservation benefits can be influenced by discard mortality of fish caught and released below the legal length. We constructed a computer model to evaluate how discard mortality could influence the conservation utility of minimum length regulations. We evaluated policy performance across two disparate fish life-history types: short-lived high-productivity (SLHP) and long-lived low-productivity (LLLP) species. For the life-history types, fishing mortality rates and minimum length limits that we examined, length limits alone generally failed to achieve sustainability when discard mortality rate exceeded about 0.2 for SLHP species and 0.05 for LLLP species. At these levels of discard mortality, reductions in overall fishing mortality (e.g. lower fishing effort) were required to prevent recruitment overfishing if fishing mortality was high. Similarly, relatively low discard mortality rates (>0.05) rendered maximum yield unobtainable and caused a substantial shift in the shape of the yield response surfaces. An analysis of fishery efficiency showed that length limits caused the simulated fisheries to be much less efficient, potentially exposing the target species and ecosystem to increased negative effects of the fishing process. Our findings suggest that for overexploited fisheries with moderate-to-high discard mortality rates, reductions in fishing mortality will be required to meet management goals. Resource managers should carefully consider impacts of cryptic mortality sources (e.g. discard mortality) on fishery sustainability, especially in recreational fisheries where release rates are high and effort is increasing in many areas of the world.

**Keywords** catch and release, discard mortality, length limits, recruitment overfishing, spawning potential ratio, yield

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**Introduction**

The ability of human users to alter aquatic ecosystems through direct and indirect consequences of harvest fisheries has received substantial attention from conservationist, scientist and international regulatory agencies (Stevens *et al.* 2000; Jackson *et al.* 2001), and has led to a growing shift in the conceptual framework for managing fisheries. This shift is reflected in recent international and US Federal fisheries policy discussions (FAO 2005) that acknowledge the role of fishing in causing significant and possibly irreversible ecosystem change (NRC 2006a). Humans have a long and successful history of efficiently harvesting marine organisms, even to the point of extinction (Jackson *et al.* 2001), and currently about 24% of the world's fisheries are considered imperilled (FAO 2005).

Recruitment overfishing (where harvest exceeds the ability of a population to replace itself) of fish stocks has major ecological and economic impacts on both aquatic ecosystems and the human users who depend on these ecosystems (Walters and Maquire 1996; Fogarty and Murawski 1998; Pauly *et al.* 1998; Lotze and Milewski 2004; Bearzi *et al.* 2006). The global scope of overfishing extends beyond well-documented marine commercial fisheries examples (cod and herring) and has recently been examined in freshwater and marine recreational fisheries (Post *et al.* 2002; Coleman *et al.* 2004). Thus, overfishing impacts transcend commercial and recreational fisheries in both marine and freshwater environments, and effective management strategies to prevent overfishing are critical.

Efforts to regulate fisheries for sustainability have ranged from calls to end directed fishing for certain species (e.g. orange roughy, *Hoplostethus atlanticus*, Trachichthyidae), to management of fishing activities with spatial and temporal fishing closures, or (most commonly) regulations limiting fish harvest based on quotas, length limits, gear restrictions, or a combination of each. However, in many fisheries, regulating spatial and temporal dynamics or total catch and effort are extremely costly or politically unfeasible. In such situations, length limits are an

attractive management tool because they require no control of spatial and temporal fishing effort patterns. Instead, length limits operate under the assumption that undersized (or oversized) fish can be released alive and survive to either contribute to the breeding stock or grow and be harvested at a more desirable size in future.

However, if this assumption is not met, cryptic sources of fishing mortality via discard deaths from physical injury, handling stress or post-release predation, can influence the efficacy of length limits to sustain fisheries. Despite much research effort to quantify discard mortality rates across a range of fisheries (reviewed by Bartholomew and Bohnsack 2005) and recent reviews of fish life-history parameters (Goodwin *et al.* 2006), no review has evaluated the population-level consequences of discard mortality on fishery sustainability and performance across a range of life-history types. This is of particular concern for recreational fisheries as effort is increasing in many parts of the world and release rates for some fish species are very high (>90%, Bartholomew and Bohnsack 2005). We evaluated the effects of discard mortality (i.e. the proportion of released fish that die) on the efficacy of minimum length regulations to conserve fish stocks and optimize fishery performance. Our evaluation used a simulation model to examine trade-offs that occur between fisheries performance and conservation goals when managing stocks using length limits. Results of this study have broad implications for the sustainability and performance of fisheries where regulations require release of some portion of captured fish.

**Methods**

We constructed an age- and size-structured population model to evaluate recruitment overfishing and fishery performance across a range of minimum length limits, discard mortality rates and fishing mortality rates for two life-history types. These life-history types were based on recent meta-analyses of globally important fisheries (Myers *et al.* 1999; Goodwin *et al.* 2006) and represent a wide spectrum in longevity, growth and recruitment compensation.

The two life-history types were a short-lived and high-productivity species and a long-lived and low-productivity species. Recruitment overfishing was evaluated by calculating spawning potential ratio (SPR) and fishery performance was assessed by calculating yield and efficiency (i.e. proportion of fishery-related biomass losses attributable to harvest). The model segregated the populations into subpopulations with differential growth trajectories to account for variability in length within age classes (Walters and Martell 2004).

### Model formulation

The model simulated an age-structured population composed of  $G$  growth trajectories, each with a different growth curve [von Bertalanffy (LVB) growth function; Bertalanffy 1938]. The set of curves differ from one another only in terms of the asymptotic length parameter as:

$$L_{a,g} = L_{\infty,g}(1 - e^{-k(a-t_0)}), \quad (1)$$

where  $L_{a,g}$  is the length of an age- $a$  fish ( $a = 1$  to  $A$ ) in growth trajectory  $g$  ( $g = 1$  to  $G$ ),  $L_{\infty,g}$  is the asymptotic length of fish belonging to trajectory  $g$ ,  $k$  and  $t_0$  have conventional interpretations in fisheries with  $k$  determining how fast length approaches the maximum and  $t_0$  predicting the fish age at length equal to zero (Quinn and Deriso 1999). To define the  $L_{\infty,g}$  for each growth trajectory, we first specified a population-level mean asymptotic length ( $\bar{L}_{\infty}$ ). We then specified minimum,  $L_{\infty,\min}$ , and maximum,  $L_{\infty,\max}$ , values representing 20% variation around  $\bar{L}_{\infty}$  and assigned  $L_{\infty,g}$  values for each growth trajectory by choosing  $G$  equally spaced values between  $L_{\infty,\min}$  and  $L_{\infty,\max}$ . A key motivation to include growth variability as different growth trajectories was to explicitly account for differences in size-specific fecundity and fishery vulnerability among different growth trajectories.

Equilibrium abundance for each growth trajectory was calculated by multiplying age-specific survivorship and equilibrium recruitment using:

$$N_{a,g} = p_g l_{a,g} R, \quad (2)$$

where  $p_g$  is the proportion of fish recruited to growth trajectory  $g$ ,  $l_{a,g}$  is the age- and growth trajectory-specific survivorship, and  $R$  is the equilibrium total recruitment. Proportions,  $p_g$ , recruited to each growth trajectory were calculated from a normal

probability density with standard deviation,  $\sigma_g$ , and  $g$  equally spaced intervals between  $-2$  and  $2$ .

Recruitment was calculated using equilibrium solutions developed by Botsford (1981) for the Beverton–Holt model using the compensation ratio (Walters and Martell 2004) form of the model such that equilibrium recruitment is:

$$R = R_0 \frac{CR - (\Phi_0/\Phi_f)}{CR - 1}, \quad (3)$$

where  $R_0$  is the average recruitment in the unfished population,  $CR$  is the compensation ratio describing the ratio of juvenile survival at low spawner abundance to juvenile survival in the unfished population (Goodyear 1980), and  $\Phi_0$  and  $\Phi_f$  represent equilibrium lifetime egg production per recruit for the unfished and fished stocks respectively. Equilibrium expected egg production was calculated as:

$$\Phi = \sum_a \sum_g p_g l_{a,g} f_{a,g}, \quad (4)$$

where  $f_{a,g}$  is the fecundity.

To model the common relationship between fecundity and weight (Quinn and Deriso 1999), fecundity was calculated as:

$$f_{a,g} = \left( \frac{W_{a,g}}{W_{\text{mat}}} \right) f_{\text{mat}}, \quad (5)$$

where  $W_{a,g}$  is the weight of an age- $a$  fish belonging to growth trajectory  $g$ ,  $W_{\text{mat}}$  is the weight of a mature fish, and  $f_{\text{mat}}$  is the fecundity of a fish that has just reached maturity (i.e. a fish of mass  $W_{\text{mat}}$ ). The age- and growth trajectory-specific fecundity ( $f_{a,g}$ ) is set to zero if  $W_{a,g} < W_{\text{mat}}$ . Finally, we calculated weight at a particular length as:

$$W = \alpha L^\beta, \quad (6)$$

where  $\alpha$  is a length–weight constant and  $\beta$  is the allometric parameter.

Survivorship was calculated recursively as:

$$l_{1,g} = 1 \quad l_{a,g} = l_{a-1,g} e^{-Z_{a,g}}, \quad (7)$$

where  $Z_{a,g}$  is the instantaneous total mortality rate. Each simulated population experienced natural mortality, harvest mortality and discard mortality. Instantaneous natural mortality rate  $M$  was constant across ages, but instantaneous harvest  $H_{a,g}$  and discard mortality  $D_{a,g}$  rates varied among ages and growth trajectories via length-dependent

vulnerability schedules. Instantaneous total mortality rate was partitioned into its additive components using:

$$Z_{a,g} = M + H_{a,g} + D_{a,g}. \quad (8)$$

Formulating the fishery-specific mortality components as instantaneous rates allowed the possibility that individual fish may be captured and discarded multiple times within a year.

Instantaneous harvest mortality rate was calculated as:

$$H_{a,g} = Fv_{h(a,g)}, \quad (9)$$

where  $F$  is an overall instantaneous fishing mortality rate and  $v_{h(a,g)}$  is the age- and growth trajectory-specific relative vulnerability to harvest. Similarly, instantaneous discard mortality rate was calculated as:

$$D_{a,g} = Fdv_{d(a,g)}, \quad (10)$$

where  $d$  is the discard mortality rate (proportion of discards not surviving), and  $v_{d(a,g)}$  is the vulnerability to discarding. The vulnerability to harvest  $v_{h(a,g)}$  was calculated as the proportion of fish of age  $a$  in growth trajectory  $g$  whose total length (TL) exceeded the minimum length limit (MLL) assuming TL is normally distributed with mean  $L_{a,g}$  and coefficient of variation  $cv_L$ . The vulnerability to discard was similarly calculated as the proportion of fish whose TL was less than MLL but larger than the minimum size vulnerable to the fishing gear  $L_{vul}$ . We approximated changes in vulnerability with growth throughout the year by calculating mean length  $L_{a,g}$  at mid-year (i.e. age =  $a + 0.5$ ).

Spawning potential ratio is a commonly used reference to assess fisheries sustainability and measures the extent to which fishing mortality has reduced the potential reproductive output (Goodwin 1993):

$$SPR = \frac{\Phi_f}{\Phi_0}. \quad (11)$$

Recruitment overfishing is generally prevented by maintaining an  $SPR \geq 0.4$  (Mace 1994). However, target SPR values vary with stock resiliency, with lower SPR required for sustaining highly productive stocks (e.g.  $SPR \geq 0.35$ ; Clark 2002).

Fishery performance was evaluated by calculating equilibrium yield and fishery efficiency. Equilibrium yield ( $Y$ ) was calculated as:

$$Y = \sum_a \sum_g N_{a,g} W_{a,g} H_{a,g} \frac{(1 - e^{-Z_{a,g}})}{Z_{a,g}}. \quad (12)$$

Fishery efficiency ( $E$ ) was used to assess waste due to discard mortality and was calculated as the ratio of yield to total deaths attributable to the fishing process (i.e. harvest + discard deaths):

$$E = \frac{Y}{\sum_a \sum_g N_{a,g} W_{a,g} (H_{a,g} + D_{a,g}) [(1 - e^{-Z_{a,g}})/Z_{a,g}]}, \quad (13)$$

where the denominator represents the total biomass lost to fishing mortality. Low efficiency values would indicate that most losses are due to discard mortality.

We evaluated SPR, yield and efficiency across a range of length limits, discard mortality rates and fishing mortality rates. Minimum length limits ranged from  $0.4\bar{L}_\infty$  to  $\bar{L}_\infty$  and fishing mortality ( $F$ ) ranged from 0 to 2 years<sup>-1</sup>. We simulated six discard mortality rates ( $d$ ): 0, 0.05, 0.10, 0.20, 0.35 and 0.80. Equilibrium solutions for SPR, yield and efficiency were calculated for all combinations of length limits, discard mortality rates and fishing mortality rates.

### Parameter value specification

We expected fish life-history strategy to influence the efficacy of length regulations across a range of discard and fishing mortality rates. Therefore, we simulated two species that could be placed roughly at opposite ends of a life-history continuum bounded by a short-lived high-productivity strategy (SLHP) at one extreme, and a long-lived low-productivity strategy (LLP) at the other. The SLHP strategy represented a small-bodied, early-maturing species, with a relatively weak compensatory recruitment process. The LLP represented a large-bodied, late-maturing species, with relatively strong compensatory recruitment. These strategies generally reflect life-history categorizations from a recent meta-analysis of exploited fish species (Goodwin et al. 2006).

To assign parameters to each life-history strategy, we first defined longevity ( $A$ ) for each and used published correlations among vital rates of fish species to assign natural mortality rate, growth parameters and maturity schedules based on  $A$  (Table 1). We chose a maximum age of 10 years for the SLHP and 30 years for the LLP. Following

**Table 1** Parameter values used for model simulations.

Parameter	Description	SLHP	LLLP
<i>A</i>	Maximum age (years)	10	30
<i>M</i>	Natural mortality rate (years <sup>-1</sup> )	0.44	0.15
<i>G</i>	Number of growth trajectories	11	11
CR	Compensation ratio	5	25
$\sigma_g$	Standard deviation to calculate $\rho_g$	0.9	0.9
$\bar{L}_\infty$	Average asymptotic length (mm)	500	1000
$\bar{L}_{\infty,\min}$	Minimum asymptotic length (mm)	400	800
$\bar{L}_{\infty,\max}$	Maximum asymptotic length (mm)	600	1200
<i>k</i>	von Bertalanffy growth coefficient (years <sup>-1</sup> )	0.35	0.1
<i>t</i> <sub>0</sub>	von Bertalanffy age at zero length (years)	0	0
<i>cv</i> <sub>L</sub>	Coefficient of variation for length-at-age	0.1	0.1
<i>L</i> <sub>mat</sub>	Length at maturity (mm)	200	400
<i>L</i> <sub>min</sub>	Length at recruitment to the fishery (mm)	200	400
$\alpha$	Length–weight constant	$3.5 \times 10^{-5}$	$3.5 \times 10^{-5}$
$\beta$	Allometric parameter	2.8	2.8

Values are given for a short-lived high-productivity species (SLHP) and a long-lived low-productivity species (LLLP).

Hoenig (1983), we assigned an *M* of 0.44 years<sup>-1</sup> for the SLHP and 0.15 years<sup>-1</sup> for the LLLP. We assigned LVB *k* parameter values of 0.35 for the SLHP and 0.1 for the LLLP based on Jensen's (1996) relationship between *M* and *k*.

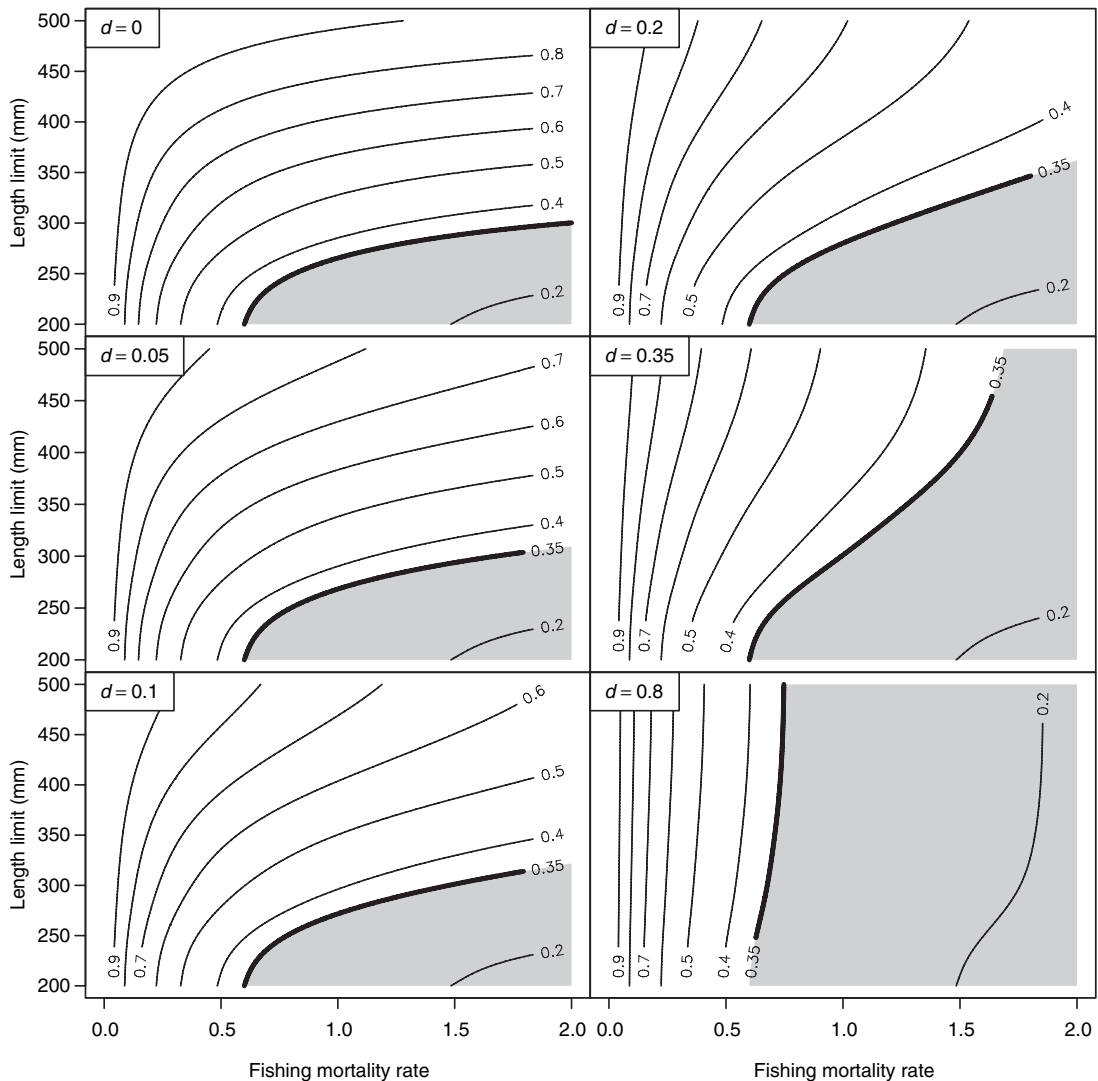
We simulated a total of 11 growth trajectories for each life-history strategy, set *t*<sub>0</sub> = 0, and allowed *L*<sub>∞,g</sub> to vary between 400 and 600 mm for the SLHP and between 800 and 1200 mm for the LLLP. These values were chosen to reflect variability in maximum size common with maximum fish age for important exploited fish stocks. Coefficient of variation in length at age (*cv*<sub>L</sub>) was set at 0.1. We used allometric parameters  $\alpha = 3.5 \times 10^{-5}$  and  $\beta = 2.8$  for both life-history strategies based on a survey of the online database FISHBASE (Froese and Pauly 2006). Minimum size of fish vulnerable to the fishery was defined to equal length at maturity *L*<sub>min</sub> = *L*<sub>mat</sub> as is frequently observed. Finally, we assigned *L*<sub>mat</sub> = 0.4*L*<sub>∞</sub> based on general results from Beverton's (1992) meta-analysis of the life-history characteristics for a large number of fish stocks.

We specified the strength of density dependence in the recruitment process via the compensation ratio parameter (CR). We assigned a relatively low CR to the SLHP life-history type (CR = 5) and a relatively high CR for the LLLP (CR = 25) based on meta-analyses across species (Myers *et al.* 1999; Goodwin *et al.* 2006). We arbitrarily defined *R*<sub>0</sub> as one million and *f*<sub>mat</sub> as one because these are scaling parameters that have no influence on the overall behaviour of the simulated

populations. We used target SPR values of 0.35 and 0.4 for the SLHP and LLLP life-history types, respectively, to determine which combinations of length limit, discard mortality and fishing mortality resulted in recruitment overfishing (i.e. SPR < target value).

## Results

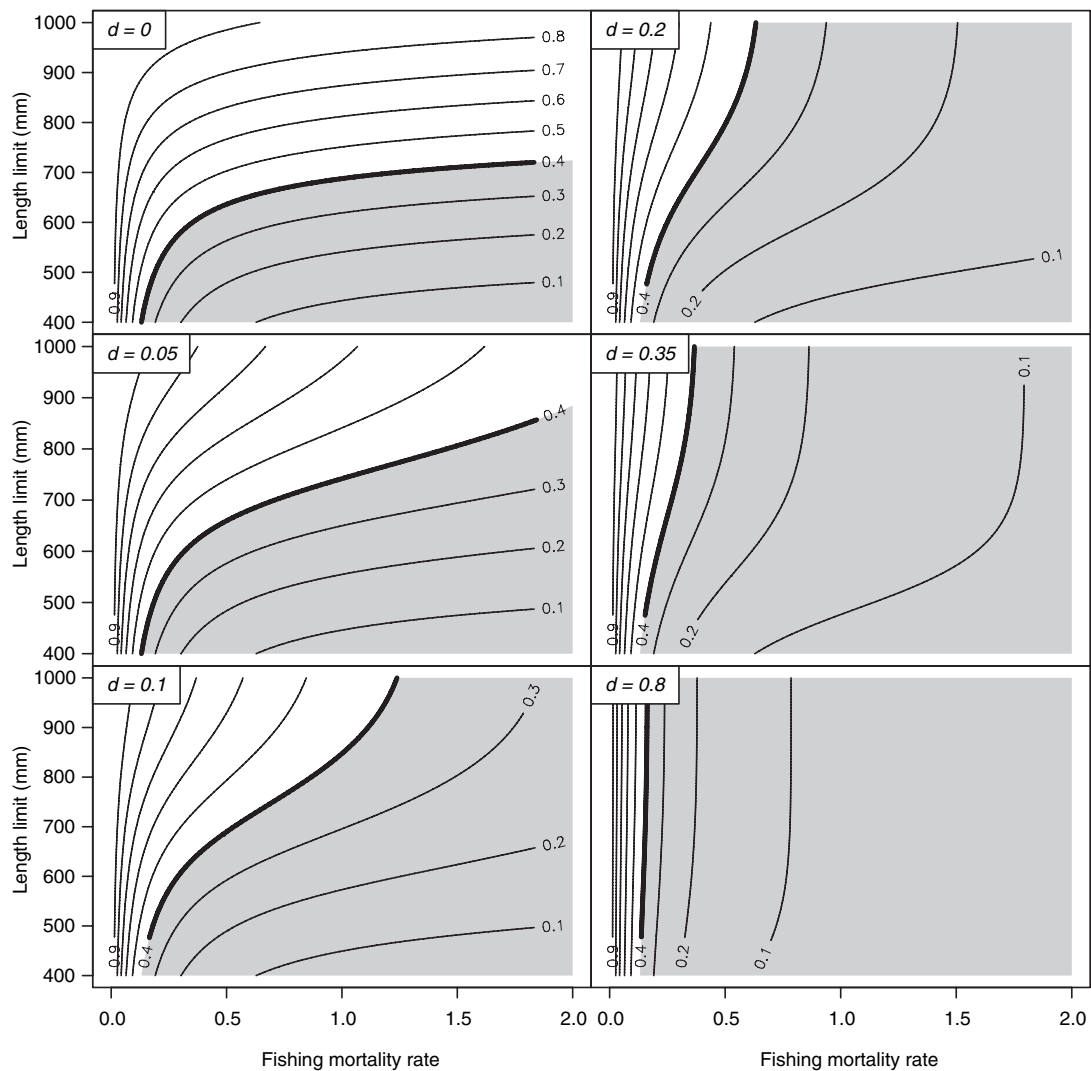
We found that relatively low levels of discard mortality can negate the ability of length limits alone to maintain fishery sustainability. Our results show that if *F* is high and discard mortality exceeds about 0.2 for short-lived high-productivity species or about 0.05 for long-lived low-productivity species, then measures to reduce *F* (i.e. effort) would be required to protect these fisheries from recruitment overfishing and to maximize fishery efficiency. In situations where fishing effort restrictions are not amenable to resource user groups, then discard mortality rates would need to be reduced to achieve sustainability and optimize yield. While these effects on fishery performance vary with length limit, discard mortality rate and fishing mortality rate, the overall pattern of large reductions in fishery performance was similar between life-history type. In general, increasing the length limit resulted in higher SPR values, especially when *d* was nil (Figs 1 and 2). For the SLHP strategy, discard mortality rate did not substantially influence SPR unless *d* > 0.2 (Fig. 1). However, length limits were ineffective in preventing recruitment overfishing (i.e.



**Figure 1** Spawning potential ratio (SPR) representing the ratio of exploited to unfished egg production per recruit across length limit (ordinate), fishing mortality rate (abscissa) and discard mortality rate ( $d$ , sub plots) for short-lived, high-productivity life-history strategists (SLHP). Shaded areas represent scenarios resulting in  $SPR < 0.35$  and potentially leading to recruitment overfishing.

$SPR < 0.35$ ) for the SLHP strategy at high fishing and discard mortality rates (Fig. 1). Effects of discard mortality rate on the LLP strategy were more pronounced, where  $d$  as low as 0.10 rendered length limits ineffective for maintaining sustainability if  $F$  exceeded about 1 (Fig. 2). Thus, discard mortality rate strongly influenced the efficacy of length limits to prevent recruitment overfishing, particularly for fisheries exploiting long-lived low-productivity species at moderate to high fishing mortality rates.

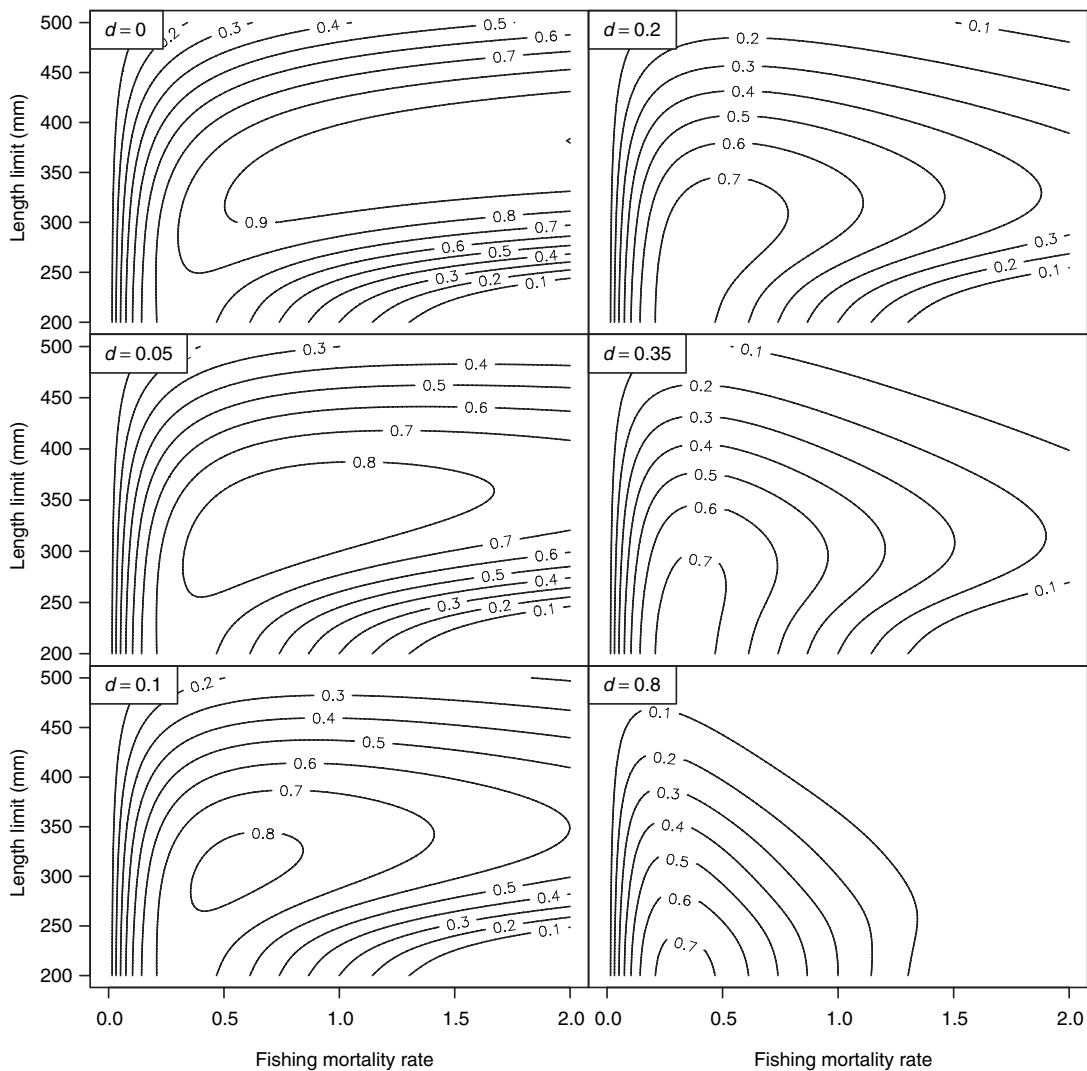
Discard mortality rate also strongly influenced yield. If  $d$  was zero, the maximum yield occurred at a high  $F$  ( $2 \text{ years}^{-1}$ ) and a length limit of about 375 mm for the SLHP strategy (Fig. 3). However, even slight increases in  $d$  to 0.05 and 0.1 caused the maximum yield to be unobtainable, and optimizing yield under these scenarios required reductions in  $F$  and length limit (Fig. 3). For example, increasing discard mortality rate from 0 to 0.05 changed the optimal length limit and  $F$  from 375 mm and  $2 \text{ years}^{-1}$ , to about 350 mm and  $< 1 \text{ years}^{-1}$



**Figure 2** Spawning potential ratio (SPR) representing the ratio of exploited to unfished egg production per recruit across length limit (ordinate), fishing mortality rate (abscissa) and discard mortality rate ( $d$ , sub plots) for long-lived, low-productivity life-history strategists (LLP). Shaded areas represent scenarios resulting in  $SPR < 0.40$  and potentially leading to recruitment overfishing.

respectively (Fig. 3). If discard mortality rate was high (0.35 or 0.8), the yield potential was greatly reduced (0.6–0.8 of the maximum) and occurred only at low length limit combined with low  $F$  (Fig. 3). Similarly, for the LLP strategy the effects were more pronounced, with low values of  $d$  causing large changes in the optimal length limit and fishing mortality (Fig. 4). For example, increasing  $d$  from 0 to 0.05 changed the optimal length limit and  $F$  from 700 mm and 2 years<sup>-1</sup> to about 600 mm and <0.5 years<sup>-1</sup> (Fig. 4). Thus, discard mortality drastically reduced yield potential for both

life-history strategies. These general findings are a symptom of growth overfishing (i.e. removing fish prior to optimal size to maximize yield) and biomass lost to the discard process due to the interaction between length limits and discard mortality. When  $d > 0$ , the highest yield could be achieved only by reducing fishing mortality rate (Figs 3 and 4). In essence the imposition of a length limit with discard mortality creates two fisheries: one for fish that are caught (but not yet legal to harvest) and then discarded to die at a rate equal to  $d$ , and a second fishery on the fish that are legal to be harvested. As



**Figure 3** Yield (i.e. biomass of harvested fish) for the SLHP species across length limit, fishing mortality rate and discard mortality rate. All yield values are scaled to the simulated maximum yield across all values of length limit, fishing mortality rate and discard mortality rate.

discard mortality rates increase, the fishery operating on fish below the size limit removes many of the fish that would be available for harvest. As  $d$  approaches one, length limits confer no benefit to conservation goals and result only in reducing yield.

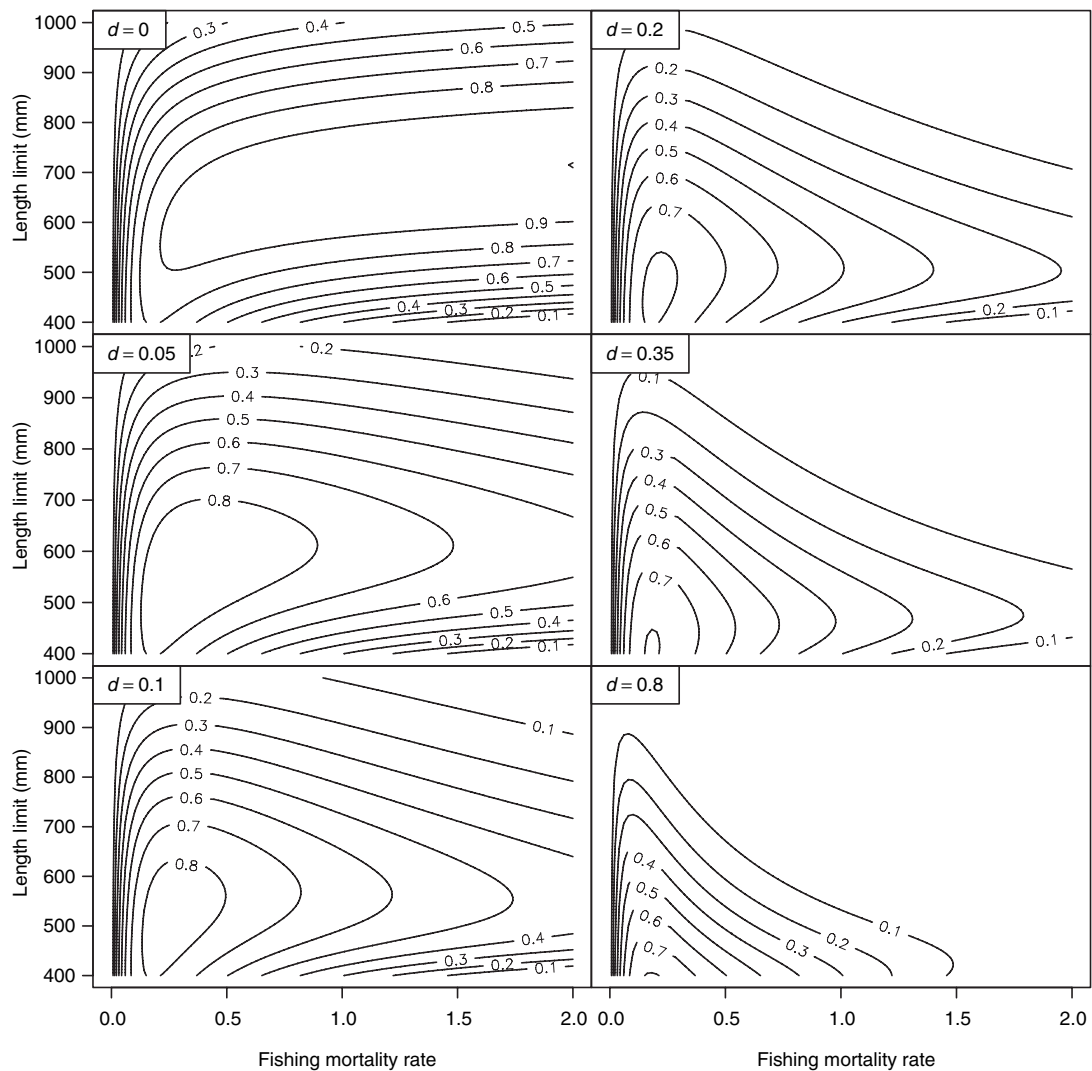
Fishery efficiency was strongly related to discard mortality and declined with increases in length limit,  $d$ , and  $F$  (Figs 5 and 6). The white areas in Figs 5 and 6 indicate the window of length limits and  $F$  that prevent recruitment overfishing (i.e. SPR above 0.35 or 0.40), and the lines indicate efficiency. Life-history strategy greatly influenced efficiency, the SLHP strategy having higher efficiency

than the LLLP for a given level of  $d$ ,  $F$  and length limit (Figs 5 and 6). These figures illustrate the trade-off between conservation and fishery performance when regulating a fishery with length limits. Although it may be possible to prevent recruitment overfishing with the imposition of length limits, the 'cost' to the fishery is reduced efficiency and yield with even small discard mortality rates.

## Discussion

Discard mortality can render regulations designed to prevent overfishing ineffective. This could lead to unintended consequences of policy choices designed



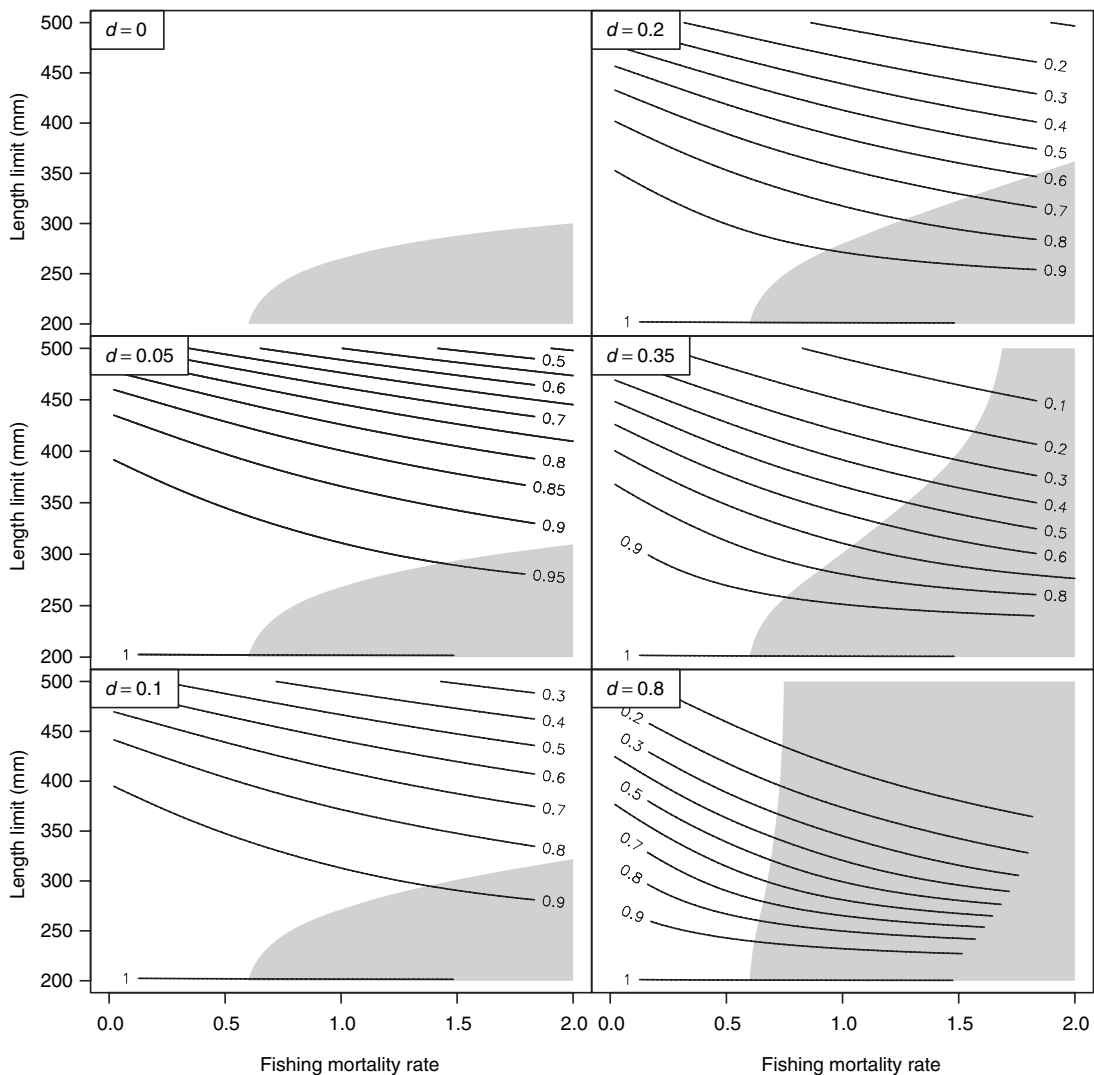


**Figure 4** Yield (i.e. biomass of harvested fish) for the LLLP species across length limit, fishing mortality rate and discard mortality rate. All yield values are scaled to the simulated maximum yield across all values of length limit, fishing mortality rate and discard mortality rate.

to reduce fishing mortality such as contributing to recruitment overfishing and possible associated ecosystem effects (Pauly *et al.* 1998; Essington *et al.* 2002). We show that the use of length limits failed to prevent growth and recruitment overfishing across a wide range of discard mortalities for both life-history strategies. This was especially true for the LLLP strategy, corresponding to some of the world's most important current and historical fisheries (FAO 2005). Life-history strategies generally similar to our LLLP include fish in families such as Gadidae (cod), Serranidae (groupers) and Lutjanidae (snappers), all of which are apex predators and

therefore major constituents of marine ecosystems. Although the specific life-history traits will not apply to all species in these groups, our analysis provided the contrast required to evaluate how life-history strategy would influence the effects of discard mortality.

Species life-history strategies strongly influenced population responses to discard mortality. We synthesized the effects of discard mortality on SPR by plotting the proportion of simulations (i.e. combinations of length limit and fishing mortality) resulting in SPR above the recruitment overfishing target as a function of discard mortality rate

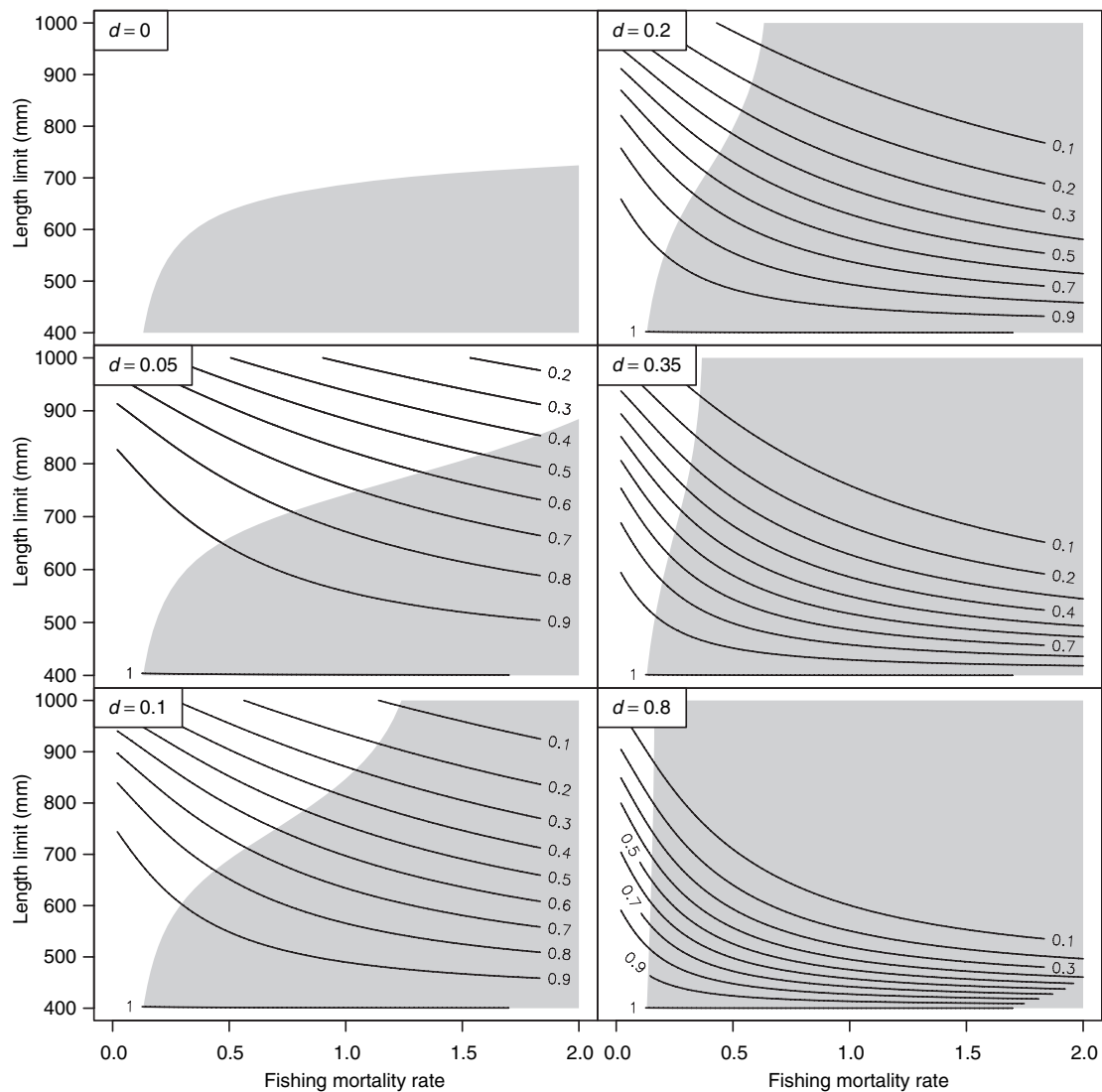


**Figure 5** Fishery efficiency across length limit, fishing mortality rate and discard mortality rate for SLHP strategists. Efficiency was calculated as the proportion of fishery-related biomass losses (i.e. harvest losses + discard losses) that were attributable to harvest. Shaded areas represent scenarios (i.e. values of length limit, fishing mortality and discard mortality) resulting in  $SPR < 0.35$  as an indicator of the potential for recruitment overfishing.

(Fig. 7). The response varied between life-history strategies, with SLHP strategists not influenced greatly until discard mortality rate exceeded about 0.2. Conversely, LLLP strategists were strongly influenced by minor changes in discard mortality rate up to 0.2. Thus, fish life-history strategy will influence the effect of discard mortality.

To place our simulation findings in a specific management context, we evaluated the population effects of discard mortality on striped bass (*Morone saxatilis*, Moronidae) and spotted seatrout (*Cynoscion nebulosus*, Sciaenidae), two species found along the

US Atlantic and Gulf of Mexico coast with well-established fisheries managed using length limits. All input parameters were taken from recent stock assessments, published manuscripts and unpublished agency reports (Table 2). These species represent contrasting life-history strategies with striped bass most closely approximating our LLLP species and spotted seatrout corresponding more to a SLHP species. As predicted, striped bass populations were more susceptible to population-level impacts of discard mortality than spotted seatrout primarily due to their longer life span and slower growth (Fig. 8). For

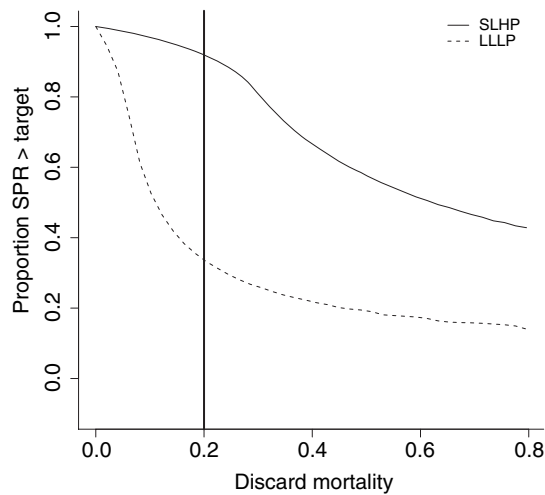


**Figure 6** Fishery efficiency across length limit, fishing mortality rate and discard mortality rate for LLLP strategies. Efficiency was calculated as the proportion of fishery-related biomass losses (i.e. harvest losses + discard losses) that were attributable to harvest. Shaded areas represent scenarios (i.e. values of length limit, fishing mortality and discard mortality) resulting in  $SPR < 0.4$  as an indicator of the potential for recruitment overfishing.

the fisheries exerting high  $F$  (bottom panels in Fig. 8), discard mortality rates well below the maximum observed were predicted to render these fisheries unsustainable. By contrast, for the fisheries exerting low  $F$  (top panels in Fig. 8), the imposition of length limits may serve mainly to lower yield and efficiency without providing a substantial conservation benefit.

Unintended fishing-associated mortality can influence sustainability of ecosystems through cascading trophic linkages. Our results suggest that discard mortality can represent a cryptic mortality

source capable of substantially increasing the likelihood of recruitment overfishing and decreasing fishery efficiency, even at low-to-moderate levels (i.e.  $d < 0.2$ ) when fishing mortality rate is high. Line fisheries (both commercial and recreational) usually target apex predators, which can have particularly important consequences for aquatic environments via top-down controls (Stevens *et al.* 2000; Schindler *et al.* 2002). Consequently, unintended mortality in these populations could further shift the structure and function of aquatic food



**Figure 7** Proportion of simulations scaled to a discard mortality equal to zero (ordinate; i.e. unique combinations of length limit, fishing mortality rate and discard mortality rate) resulting in  $SPR > \text{target}$  value for a given level of discard mortality rate (abscissa). Target  $SPR$  was 0.35 for SLHP and 0.4 for LLLP (dashed line). The solid vertical line indicates the approximate value for discard mortality rate 1) below which  $SPR$  for SLHP is relatively insensitive to changes in discard mortality and 2) below which  $SPR$  for LLLP is highly sensitive to changes in discard mortality.

webs, particularly when directed fishing mortality is already high for many fisheries (FAO 2005; NRC 2006a,b).

A growing concern related to discard mortality is the expansion of recreational fisheries, particularly in US, Canadian and Australian waters (Coleman *et al.* 2004; Walters and Martell 2004; NRC 2006b). These fisheries are commonly managed using increasingly stringent length limits (Radomski 2003). Bartholomew and Bohnsack (2005) evaluated the Marine Recreational Fishery Statistic Survey and found that recreational discards increased 97% from 1981 to 1999. They attributed the increased releases to more restrictive length and bag limits and to a lesser degree voluntary release of fish legal to harvest. Despite increased use of length limits over the past three decades (Radomski 2003), increasing fishing effort (e.g. person-days) in recreational fisheries still results in growth overfishing (Beard and Kampa 1999; Cox and Walters 2002) and potential for recruitment overfishing for important marine stocks (Coleman *et al.* 2004). Thus, increasing use of length limits to lower  $F$  will cause the proportion of total fishing mortality comprised of discards to increase for many sport fisheries.

**Table 2** Parameter values and information sources used for the spotted seatrout (*Cynoscion nebulosus*, Sciaenidae) and striped bass (*Morone saxatilis*, Moronidae) examples.

Parameter	Description	Spotted seatrout	Striped bass
$A^a$	Maximum age (years)	9	30
$M^a$	Natural mortality rate ( $\text{years}^{-1}$ )	0.3	0.15
$CR^b$	Compensation ratio	26.1	19
$\bar{L}_\infty^c$	Average asymptotic length (mm)	701	987
$k^c$	von Bertalanffy growth coefficient ( $\text{years}^{-1}$ )	0.2	0.158
$t_0^c$	von Bertalanffy age at zero length (years)	-0.44	0
$L_{\text{mat}}^d$	Length at maturity (mm)	271	395
$L_{\text{min}}^e$	Minimum size vulnerable (mm)	271	395
$\alpha^c$	Length-weight constant	8.5e-06	4.3e-06
$\beta^c$	Allometric parameter	2.99	3.153
$MLL^a$	Minimum length limits (mm)	300-380	450-750
$F$	Fishing mortality rate ( $\text{years}^{-1}$ )	0.3-0.79 <sup>f</sup>	0.1-0.4 <sup>a</sup>
$d$	Discard mortality rate	0-70% <sup>g</sup>	0-46% <sup>h</sup>

<sup>a</sup>ASMFC 2006b; ASMFC 2006a.

<sup>b</sup>Myers *et al.* 1999.

<sup>c</sup>Fishbase; Froese and Pauly (2007).

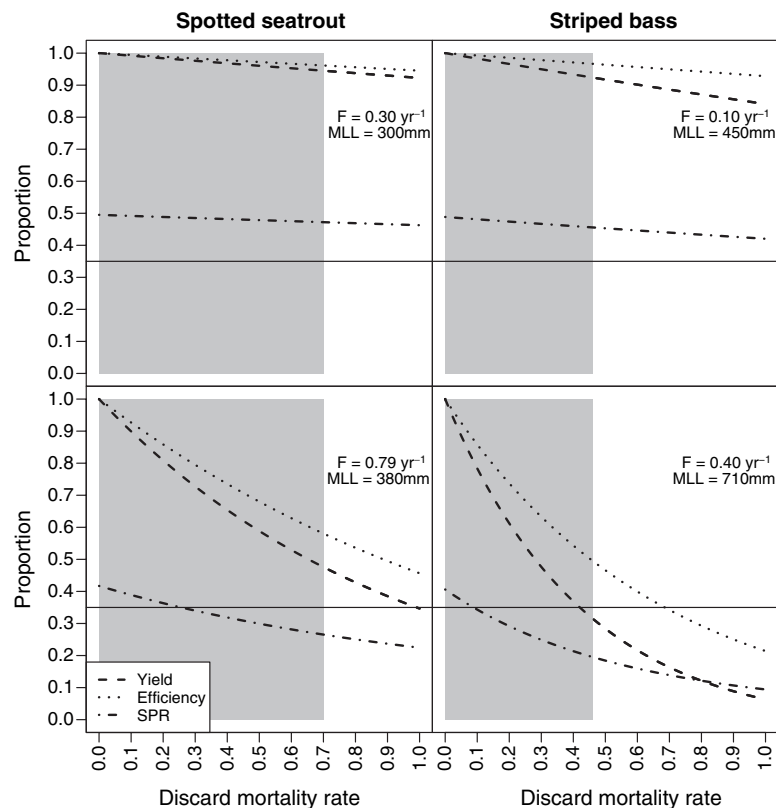
<sup>d</sup>Calculated as 40% L-infinity mean.

<sup>e</sup>Assumed to equal the size at maturity.

<sup>f</sup>Murphy (2003).

<sup>g</sup>Muoneke and Childress (1994).

<sup>h</sup>Bartholomew and Bohnsack (2005).



**Figure 8** Yield, efficiency and spawning potential ratio (SPR) as a function of discard mortality rate for spotted seatrout (left column) and striped bass (right column). The top panels are examples of low exploitation fisheries ( $F$  = fishing mortality) with liberal minimum length limits (MLL) and the bottom panels are more highly exploited fisheries with more restrictive MLL. Yield is calculated as a percentage of the yield at a discard mortality rate of 0.0 and corresponding values of  $F$  and MLL. The shaded region corresponds to reported discard mortality rates for these species. The  $SPR = 0.35$  is identified with the heavy dashed grey line for reference to the common conservation goal for that metric.

Estimates of discard mortality rates vary widely among fisheries. Bartholomew and Bohnsack (2005) reviewed 274 individual estimates of discard mortality rates from a wide range of species and life-history types. They found estimates ranging from 0% to 95%, with a median of 11% and a mean of 18%. Species from our LLLP strategy are sometimes caught from deep depth and exhibit barotrauma and high discard mortality rate, whereas other species caught from shallow water typically exhibit low discard mortality rate (<0.1; reviewed by Bartholomew and Bohnsack 2005). Thus, our results combined with this review suggest that the impacts of discard mortality rate on fisheries will vary widely, but that this mortality source is certainly significant in many cases.

The relationship between maximum yield, length limit and fishing mortality has long been studied in fisheries (Ricker 1975). Our results indicate that

discard mortality can substantially alter this relationship and lead to significant reductions in the maximum obtainable yields via growth overfishing and loss of biomass to discard mortality. Only small amounts of discard mortality (<0.1) were required to cause these effects, which shows that length limits alone cannot be used to maximize yield when discard mortality occurs. Waters and Huntsman (1986) evaluated the effects of catch-and-release practices on yield for red snapper (*Lutjanus campechanus*, Lutjanidae) and other reef fish across a range of specific length limits that were considered as part of a fishery management plan. These authors found that at the length limits and natural mortality rates evaluated, release mortality generally must be below 50% for the length limit to have the intended effect of increasing yield for a given level of  $F$ . These authors also examined the effects of discard mortality on other reef species and found

that release mortality must be less than 40% for length limits to increase yield.

Our results reveal important trade-offs between conservation and performance goals when making management decisions to reduce  $F$  in the face of discard mortality. In these situations, management options include either: (1) directly reducing fishing effort through restrictive harvest quotas, temporal or spatial closures and gear or fishing effort restrictions; or (2) requiring no change in directed fishing effort and attempting to reduce fishing mortality with length limits. The first option is appealing from the perspective of minimizing the ecosystem impacts of fishing, but it has been infrequently chosen due to political and economic pressures from communities that depend on the fisheries (Walters and Martell 2004). However, the second option reduces efficiency and yield if discard mortality is high, thereby exposing the target species and ecosystem to increased negative effects of the fishing process. Essington *et al.* (2002) showed how changes in tuna fishing practices, which were originally motivated by concerns over marine mammal interactions with the tuna fishing fleet, ultimately led to more destructive fishing practices from an ecosystem perspective. We demonstrate that discard mortality will strongly influence the efficiency of the harvest process. This may force fishers to increase effort in an attempt to maintain landings, which could lead to negative consequences to the target organism and ecosystem.

We suggest a third option is one where fishers and resource managers seek fishing practices that result in lower discard mortality rate. This may represent a 'best case' as in some fisheries it may be possible to maintain current fishing effort while still allowing high yield and efficiency fisheries. We further suggest that models such as ours can help to focus the discussion between managers and fishers on the key factors contributing to the realization of both fishery conservation and performance goals. Such examination of trade-offs will undoubtedly provide incentives to reduce discard mortality as an alternative to other more restrictive options such as direct effort controls, harvest quotas or closures.

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