

## A simulation model to explore the relative value of stock enhancement versus harvest regulations for fishery sustainability

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### ABSTRACT

Harvest restrictions and stock enhancement are commonly proposed management responses for sustaining degraded fisheries, but comparisons of their relative effectiveness have seldom been considered prior to making policy choices. We built a population model that incorporated both size-dependent harvest restrictions and stock enhancement contributions to explore trade-offs between minimum length limits and stock enhancement for improving population sustainability and fishery metrics (e.g., catch). We used a Murray cod *Maccullochella peelii peelii* population as a test case, and the model incorporated density-dependent recruitment processes for both hatchery and wild fish. We estimated the spawning potential ratio (SPR) and fishery metrics (e.g., angler catch) across a range of minimum length limits and stocking rates. Model estimates showed that increased minimum length limits were much more effective than stock enhancement for increasing SPR and angler catches in exploited populations, but length limits resulted in reduced harvest. Stocking was predicted to significantly increase total recruitment, population sustainability, and fishery metrics only in systems where natural reproduction had been greatly reduced via habitat loss, fishing mortality was high, or both. If angler fishing effort increased with increased fish abundance from stocking efforts, fishing mortality was predicted to increase and reduce the benefits realized from stocking. The model also indicated that benefits from stock enhancement would be reduced if reproductive efficiency of hatchery-origin fish was compromised. The simulations indicated that stock enhancement was a less effective method to improve fishery sustainability than measures designed to reduce fishing mortality (e.g., length limits).

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### 1. Introduction

Sustainability of open-access recreational fisheries is an increasing concern in both freshwater and marine systems. There is growing evidence of overfishing from recreational fishing across broad spatial and temporal scales (Post et al., 2002; Cooke and Cowx, 2004). Limiting angler effort to reduce overfishing in public resource fisheries is difficult, therefore resource managers have often adopted aggressive management strategies such as stringent length limits and bag limits (e.g., walleye *Sander vitreus* in Wisconsin, Beard et al., 2003), and increased use of closed areas and seasons after contentious debates. Stock enhancement programs are often favored by angler groups for restoration and sustainability of fisheries that have undergone overfishing and/or loss in habitat

quantity and quality (Grimes, 1998; Molony et al., 2003; Lorenzen, 2005).

Despite positive intentions of stock enhancement programs, substantial evidence shows that stock enhancement can be ineffective or cause harm to the fisheries which are targeted for improvement. Hilborn and Eggers (2000) showed that one of the world's largest hatchery operations (i.e., pink salmon *Oncorhynchus gorbuscha* stocking in Prince William Sound) resulted in replacement of wild stocks rather than additive effects to natural recruitment. Lorenzen (2005) gave an overview of the potential benefits and pitfalls of stock enhancement and showed that stocking large, recruited fish can substantially increase fishery yields, whereas stocking maladapted hatchery fish can cause substantial negative impacts via introgression with native fish and reduce population abundance. Hilborn (1999) commented that responsible use of hatcheries in management should focus on (1) testable objectives for the hatchery programs including a plan for evaluation of those objectives, (2) measures of survival of stocked fish via tagging programs and monitoring, and (3) an assessment of whether the hatchery program produces a net augmentation to the wild stock. Leber (2002) also called for thorough evaluation and

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hypothesis testing in stock enhancement before production-level operations begin. Public and private institutions stock billions of fish worldwide annually, but the relative role of stock enhancement compared to other tools for sustaining fisheries (e.g., harvest restrictions) has seldom been evaluated.

The purpose of this study was to use simulation modeling to evaluate the role of stock enhancement relative to other common management strategies for sustaining and improving recreational fisheries. We used Murray cod *Maccullochella peelii peelii*, a large freshwater predator in Australia, as a test case for this evaluation. Murray cod are long-lived (likely exceeding 50 years) and late maturing (ages 4–5) species (Lintermans et al., 2005). Murray cod spawn on hard substrates and exhibit a short period of male nest guarding, whereafter, larvae free drift downstream for 5–7 days (Humphries et al., 2002; Lintermans et al., 2005). Murray cod populations have undergone large population declines over the past century, likely due to a combination of overfishing, introduction of exotic species, and habitat alterations (Lintermans et al., 2005; Rowland, 2005). Murray cod have been managed with a combination of closed seasons, length limits, bag limits, and stock enhancement in the Murray–Darling Basin (Lintermans et al., 2005). Thus, Murray cod fisheries are an excellent example for evaluating the value of stock enhancement relative to other management tools. Our objectives were to: (1) evaluate the potential for stock enhancement to improve fishery sustainability and angler catch metrics relative to minimum length limits, (2) explore effects of stocking rates and stocked fish sizes for producing fishery benefits, and (3) evaluate the potential for negative impacts of stocking via density dependence and/or genetic changes in the stock.

## 2. Methods

### 2.1. Model background and strategy

We modified an age structured simulation model for Murray cod (Allen et al., 2009) to include stock enhancement and provide equilibrium predictions of stocking effects on fishery sustainability and angler catch metrics. Modifications included changes to the stock-recruitment function used by Allen et al. (2009) to allow for the introduction of hatchery-reared fish, density-dependent survival for both pre-recruit wild and hatchery fish, and contributions of stocked fish to the spawning stock. We also incorporated methods to evaluate relative reproductive fitness effects on population total recruitment that could result from hatchery selection for maladapted fish (Fig. 1).

The age-structured model incorporated a Beverton and Holt stock-recruitment function and predicted number-at-age matrices for wild produced and hatchery-origin fish. The model assumed that wild fish progeny, progeny from fish that originated in a hatchery and matured in the wild, and hatchery released age-0 fish would all contribute to density-dependent survival and structure year class strength at age-1. Annual recruitment to age-1 from wild adults and hatchery-origin adults in the population was estimated using a Beverton–Holt function:

$$R_{w,t} = \frac{a \times Fry_{net,t}}{1 + b \times Fry_{tot,t}} \quad (1)$$

where  $R_{w,t}$  is the recruitment of wild spawned fish in year  $t$ ,  $a=0.22$  (Allen et al., 2009),  $Fry_{net,t}$  is the net reproductive output to size  $i$  in year  $t$  from three potential adult matings in the wild: wild  $\times$  wild, hatchery  $\times$  wild, and hatchery  $\times$  hatchery (see below), and  $b=2.11 \times 10^{-6}$  (Allen et al., 2009). The quantity  $Fry_{tot,t}$  is the total reproductive output to size  $i$  in year  $t$  from all matings as:

$$Fry_{tot,t,i} = S_{fry,i} \times \sum_g f_g N_{w,g,t} + S_{fry,i} \times \sum_g f_g N_{h,g,t} \quad (2)$$

where  $S_{fry,i}$  is the survival of wild-hatched fish from egg to size  $i$ , the size at stocking. The  $f_g$  was the age-specific fecundity (Rowland, 1998; Allen et al., 2009), and  $N_{w,g,t}$  is the number of wild fish of age  $g$  at time  $t$ , and  $N_{h,g,t}$  is the number of hatchery-released fish at age  $g$  at time  $t$  in the population. Values  $N_{w,a,t}$  and  $N_{h,g,t}$  were predicted by applying a survivorship schedule from Allen et al. (2009) to the age-1 recruits for each group in each year. Thus, the model simply tracked hatchery-origin and wild fish as adults in the population, and the progeny from both sources entered the population as wild recruits.

The parameter  $S_{fry}$  reflected higher mortality in the wild from egg to the stocking length  $i$  relative to mortality in hatcheries during that period because of intense culture (i.e., a “hatchery advantage”, Lorenzen, 2005). We estimated  $S_{fry}$  with a size-based mortality model (Lorenzen, 1996; Lorenzen, 2006) using the mean annual instantaneous natural mortality at one gram ( $M=3.13$ ) at temperate latitudes reported by Lorenzen (1996). We converted Lorenzen’s annual rates of  $M$  to daily instantaneous mortality values, and estimated  $S_{fry}$  for a range of potential stocking lengths assuming a juvenile growth rate of 0.5 mm/day based on pond experiments (Ingram, 2009).

Recruitment to age-1 for fish released from the hatchery was modeled with a Beverton–Holt function such that the strength of density dependence determining their survival depended on their abundance (i.e., the stocking rate) and wild-spawned juvenile abundance:

$$R_{h,t} = \frac{a \times Fry_{h,t}}{1 + b \times Fry_{tot,t}} \quad (3)$$

where  $R_{h,t}$  is the predicted recruitment of hatchery released fish in year  $t$ ,  $Fry_{h,t}$  is the number of hatchery released fish in year  $t$ , and  $a$ ,  $b$ , and  $Fry_{tot,t}$  were the same as in Eq. (1). Total age-1 recruitment in year  $t$  was then found by  $R_{w,t} + R_{h,t}$ . Hatchery released fingerlings and wild-spawned fish that survived to age-1 were assumed to have equal survival, maturity, growth, and fishing vulnerability schedules to their maximum age.

Using three mating combinations allowed for potentially reduced offspring viability for fish with hatchery genotypes (per Walters and Martell, 2004). The distribution of reproductive output in a year was generated from three mating types and the production for each mating in each year was estimated by assuming the genetic composition of the population was at Hardy–Weinberg equilibrium. The proportion of annual fingerling output from wild fish relative to total fingerling production ( $P_{ww}$ ) was used to partition the total annual fingerling production for the three possible mating combinations. Annual fingerling production for each combination was estimated as:

$$Fry_{ww} = P_{ww}^2 \times Fry_{tot} \quad (4)$$

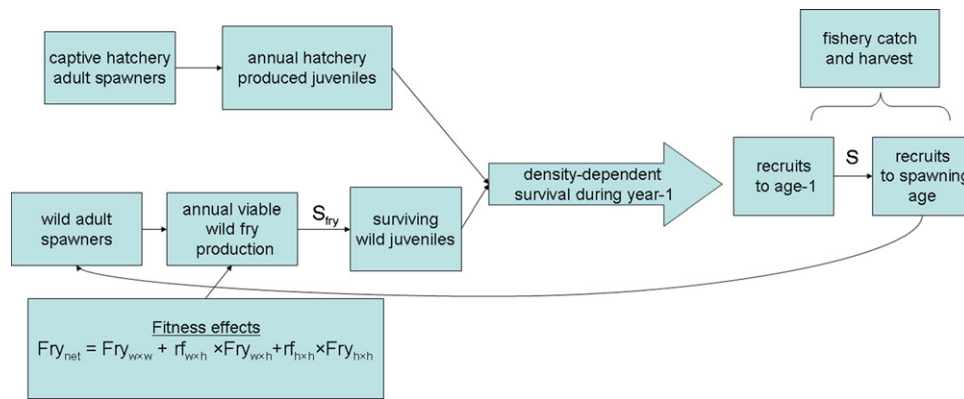
$$Fry_{wh} = 2 \times P_{ww} \times (1 - P_{ww}) \times Fry_{tot}$$

$$Fry_{hh} = (1 - P_{ww})^2 \times Fry_{tot}$$

Using these results, we could estimate net viable fry production while accounting for potentially reduced reproductive success stemming from hatchery effects (e.g., selective breeding for unfit wild genes in the hatchery, Walters and Martell, 2004) with the equation:

$$Fry_{net} = Fry_{ww} + Rf_{wh} \times Fry_{wh} + Rf_{hh} \times Fry_{hh} \quad (5)$$

where  $Rf_{wh}$  and  $Rf_{hh}$  are the reproductive success for wild  $\times$  hatchery and hatchery  $\times$  hatchery matings, respectively, relative to wild  $\times$  wild matings. Relative fitness values equaled one for all mating combinations and simulations (i.e.,  $Fry_{net} = Fry_{tot}$ ) except for our specific evaluation of reproductive fitness effects (see below).



**Fig. 1.** Conceptual diagram of the population dynamics model that incorporates stock enhancement contributions to a wild spawning population, relative fitness of mating combinations, and fishery effects.  $S_{fry}$  = parameter for reduced survival from egg to size at stocking in the wild relative to high survival owing to intensive hatchery culture (i.e., “hatchery advantage”, Lorenzen, 2005).  $S$  is the post-recruitment survival (i.e., after age-1) assumed the same for wild and hatchery-origin fish.  $Fry_{net}$  is the viable wild fry production from three possible matings that can occur in the wild (wild  $\times$  wild,  $w \times w$ ; wild  $\times$  hatchery,  $w \times h$ ; and hatchery  $\times$  hatchery,  $h \times h$ ) multiplied by the relative fitness ( $rf$ ) for each mating ( $rf$  for  $w \times w = 1$ ).

We primarily used parameters from Allen et al. (2009) to parameterize our model, but used historical stocking and creel survey data from the Goulburn River, Victoria, Australia to apply our model to one specific fishery that was actively stocked with 50 000 fingerlings (45–55 mm total length) per year on average. The Goulburn River is a tributary to the Murray River with moderate angler effort (132 angler h/ha) and average angler catch rates (6.12 fish/ha) relative to other Murray cod fisheries (effort range: 253–58 angler h/ha, catch range: 12.7–1.9 fish/ha) monitored with creel surveys (Brown, 2009). The river has natural reproduction of fish and is considered a relatively stable to slightly increasing Murray cod population (Koster et al., 2004). All simulations started with 40 000 fish recruiting to age-1 in the unfished condition, which resulted in a predicted catch that was similar to estimated angler catches from 2007 creel surveys on the Goulburn River (Brown, 2009). The fishing mortality rate was not known, and we used  $F=0.15$  as a hypothesized moderate level of fishing mortality per Allen et al. (2009) for the base case model.

## 2.2. Model scenarios

We used the model to evaluate benefits of stocking relative to using minimum length limits (MLL) for maintaining population viability (i.e., potential reproductive output relative to unfished conditions) and fishing quality metrics at the Goulburn River. The Goulburn River was annually stocked with 25 000–72 500 Murray cod fingerlings (i.e., 50 mm TL) from 2001 to 2008, and we simulated a range of 30 000–300 000 stocked fingerlings into the modeled population. We compared effects of stocking to a range of minimum length limits from 500 to 800 mm TL. Our base model (i.e., stocking large numbers of 50 mm fingerlings) used average juvenile survival ( $S_{fry}$ ) for temperate fishes from Lorenzen (1996). This resulted in an average egg to 50 mm TL survival of 0.0048 for wild fish. We modified our base case scenario by changing the  $S_{fry}$  survival parameter to evaluate the impact of stocking fewer, larger Murray cod. We simulated a range of 2000–16 000 stocked advanced fingerlings (i.e., 150 mm TL), where wild fish survival from egg to 150 mm was  $9.1 \times 10^{-5}$  via Lorenzen (1996). Model outputs included spawning potential ratio (SPR), catch of trophy fish (i.e., total length exceeding one meter), total harvest (number of fish), and percent contribution of stocked fish to age-1 in the population. Spawning potential ratio was estimated as the ratio of  $Fry_{net}$  in the fished condition relative to  $Fry_{net}$  at time zero. The SPR is the reproductive capacity of the stock in the fished relative to unfished condition, and values of  $SPR \geq 35\%$  are desired to decrease recruitment overfish-

ing risks (Mace, 1994; Clark, 2002; Walters and Martell, 2004). We also assessed the model’s ability to emulate situations where stocking was hypothesized to have the largest influence on population abundance (e.g., a recruitment limited population) and compared harvest regulations to stock enhancement for fisheries sustainability.

Lastly, we evaluated the potential for angler effort responses to influence the effectiveness of stock enhancement for a recruitment limited population with high fishing mortality. Annual fishing mortality ( $F_t$ ) was estimated as a function of the vulnerable biomass ( $B$ ) available to anglers in year  $t$  as:

$$F_t = 1 - e^{-q^* B_t} \quad (6)$$

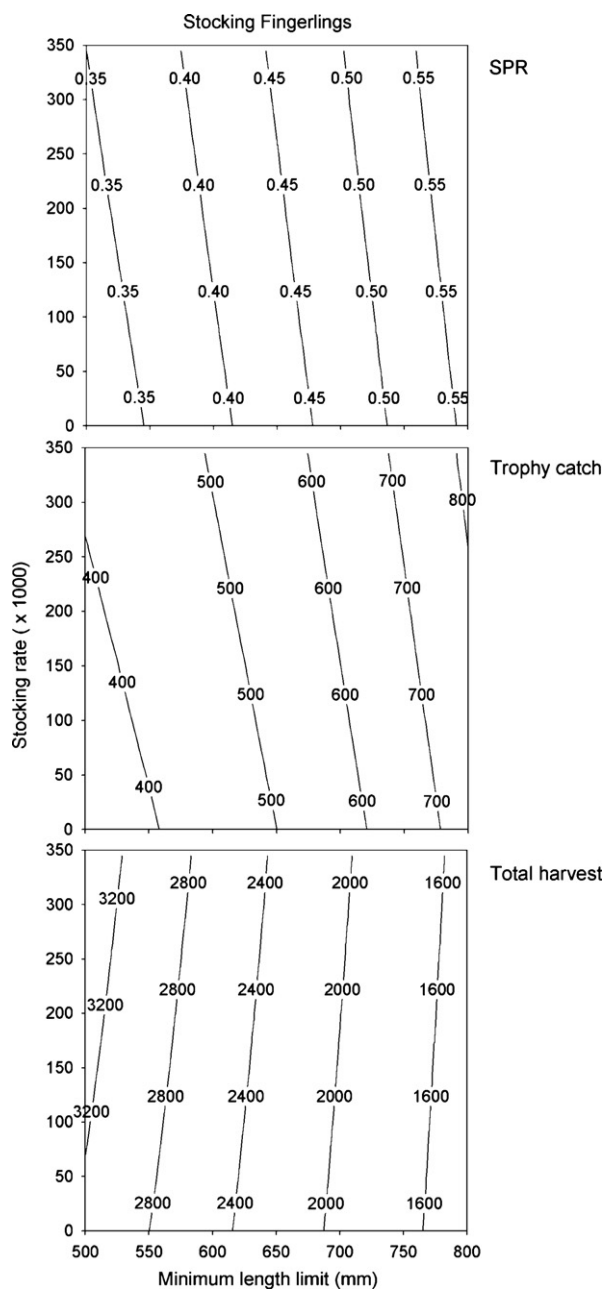
and

$$q^* = -\frac{\log_e(1 - 0.4)}{B_{equ}} \quad (7)$$

where  $B_{equ}$  was the equilibrium vulnerable biomass in the fished condition with stocking at 50 000 fingerlings per year to enhance the population (i.e., at the new equilibrium). Thus, the angler effort dynamics model assumed that anglers could detect annual changes in the vulnerable biomass that would arise from a range of stocking rates (i.e., relative to stocking 50 000 fingerlings per year and  $F=0.4$ ) and effort would respond linearly to those vulnerable biomass changes. Angler effort effects were modeled at a fixed minimum length limit of 600 mm (i.e., the current minimum length limit in Victoria, Australia) across the range of stocking rates described above. We predicted annual fishing mortality and SPR and compared these results to simulations without angler effort responses.

## 3. Results

The base case model indicated that stocking fingerlings was not likely to influence population sustainability or angler catch metrics for the fishery, especially relative to length limits. Values of SPR increased substantially as the minimum length limit increased, but stocking had only a minor influence on SPR values (Fig. 2). Similarly, catch of trophy fish was not influenced by stocking rates up to 300 000 fish per year. Number of fish harvested declined with increasing length limit as expected, but stocking up to 300 000 fingerlings did not substantially increase harvest for any hypothesized length limit. Under these scenarios, the percent of total age-1 fish that were predicted to be hatchery fish reached 7% at 300 000 stocked fingerlings. Thus, our base case model suggested that recent stocking rates of fingerlings would not substantially influence the Murray cod fishery at the Goulburn River, given an



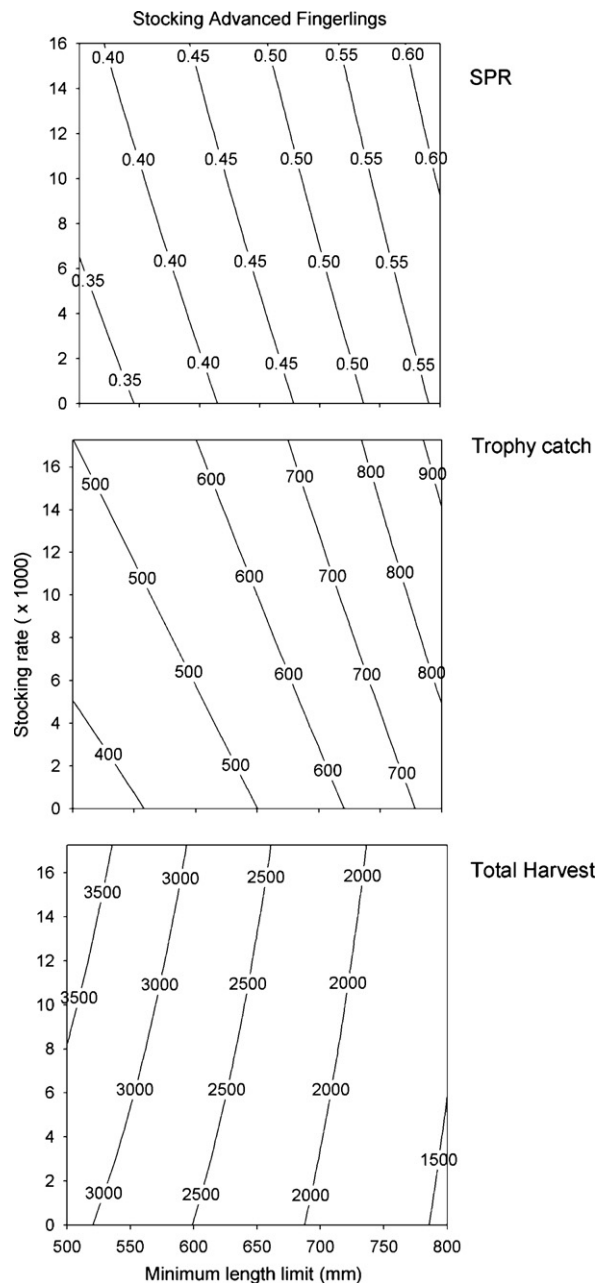
**Fig. 2.** Model predictions of spawning potential ratio (SPR, top panel), number of trophy fish caught (center panel), and total harvest (number of fish, bottom panel) plotted on the number of fingerlings stocked (y-axes) and the minimum length limit (x-axis). Simulations are for the base case scenario of  $F=0.15$  with fingerlings stocked at 50 mm TL.

annual exploitation rate of 0.15 and recruitment values required to produce observed catches.

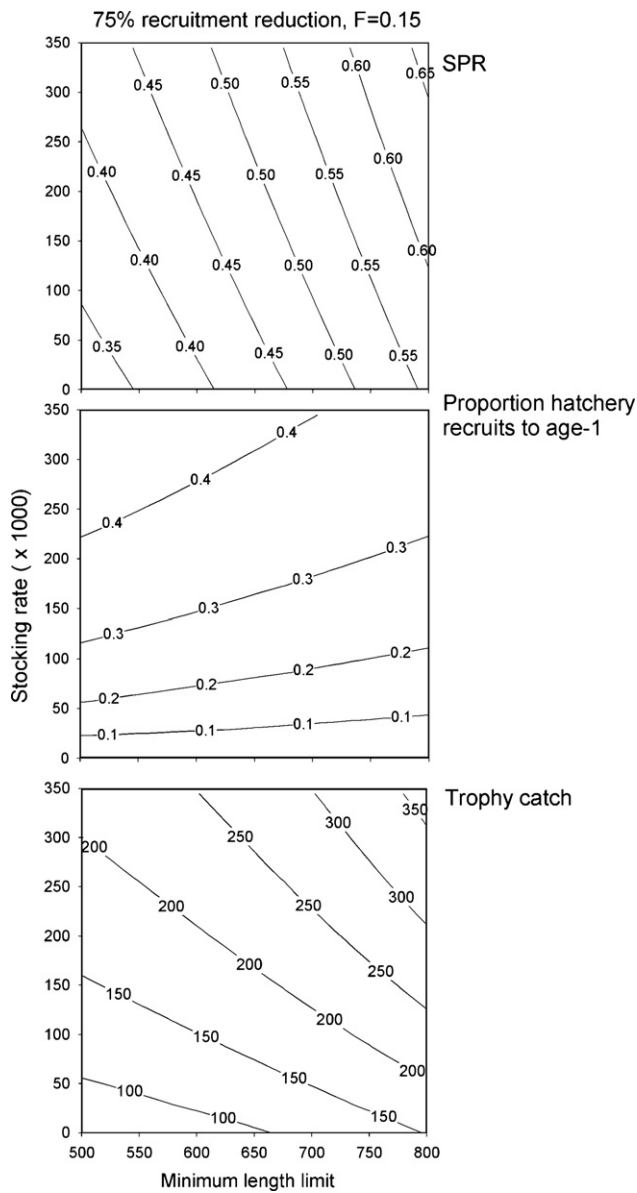
Stocking advanced fingerlings had slightly more influence on fishery metrics than stocking high numbers of fingerlings. For example, stocking 2000 versus 16000 advanced fingerlings was predicted to increase SPR from 0.38 to 0.45 with a 600 mm minimum length limit (Fig. 3). Stocking advanced fingerlings also had the potential to increase catch of trophy fish, and slightly mediated declines in harvest as the minimum length limit increased (Fig. 3). The percent of total age-1 fish that were predicted to be hatchery fish ranged from 2% at 2000 advanced fingerlings to 15% at 16000 advanced fingerlings. Thus, the model suggested that stocking smaller numbers of advanced fingerlings caused larger fishery benefits than stocking fingerlings. This resulted because

larger fish underwent less density-dependent interactions with wild pre-recruits, and thus had better survival. For our base model, length limits showed substantially more power to protect stocks from overfishing than stocking fish of either size because SPR values were more strongly influenced by the length limit than the stocking scenarios we considered (Figs. 2 and 3).

Stocking programs are sometimes implemented to rebuild stocks that have low recruitment and/or high rates of fishing mortality (Leber, 2002), and we explored scenarios where stocking programs could improve Murray cod populations. We simulated a low recruitment system by lowering average wild fish recruitment to 25% of the equilibrium value in our base model. Reduced recruitment simulated poor habitat quality relative to the average



**Fig. 3.** Model predictions of spawning potential ratio (SPR, top panel), number of trophy fish caught (center panel), and total harvest (number of fish, bottom panel) plotted on the number of advanced fingerlings stocked (y-axes) and the minimum length limit (x-axes). Simulations are for the base case scenario of  $F=0.15$  with advanced fingerlings stocked at 150 mm TL.



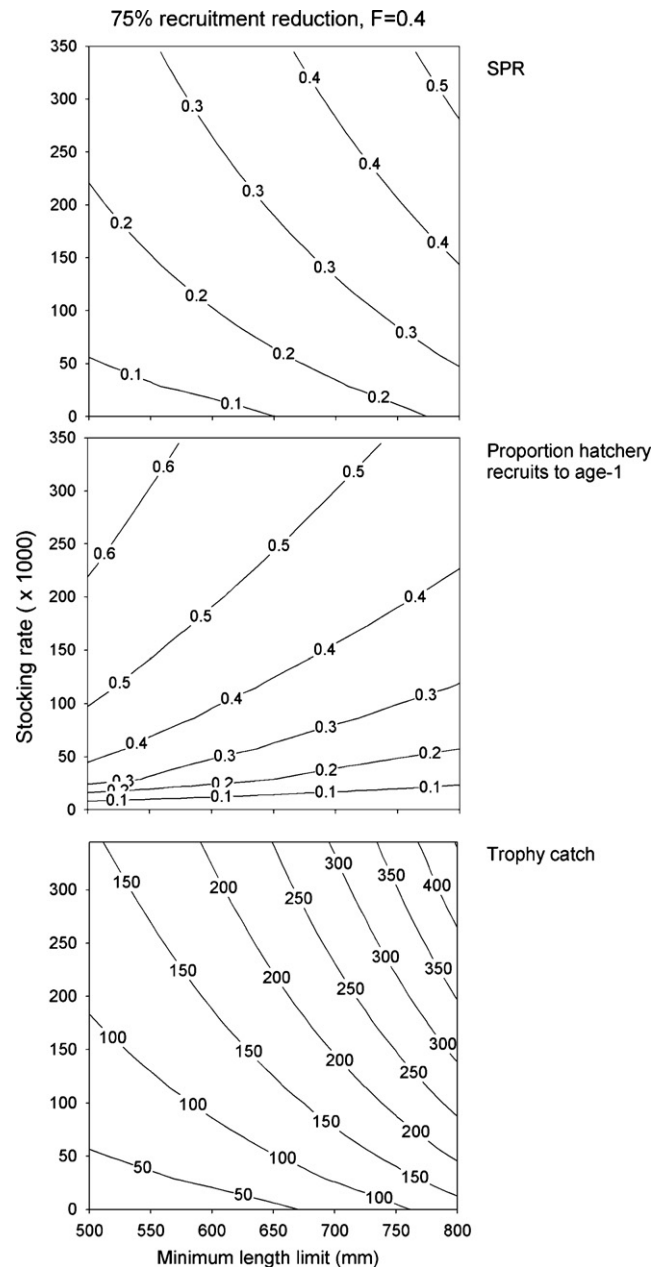
**Fig. 4.** Model predictions of spawning potential ratio (SPR, top panel), proportion hatchery recruits to age-1 (center panel), and trophy catch (number of fish, bottom panel) plotted on the number of fingerlings stocked (y-axes) and the minimum length limit (x-axes). Simulations are for the base case scenario of  $F=0.15$  with 25% of equilibrium recruitment and fingerlings stocked at 50 mm TL.

recruitment conditions at the Goulburn River, a viable Murray cod fishery. Stocking under a scenario with a 75% recruitment reduction and  $F=0.15$  showed a higher potential for stocking to improve sustainability and the fishery. Increased stocking rates showed potential to increase SPR, the percentage of age-1 fish of hatchery origin, and trophy catches for all minimum length limits (Fig. 4). Beneficial effects from stocking were negatively related to the MLL. For example, trophy catch at a 500 MLL was predicted to double as fingerling stocking rate was increased from 50 000 to 300 000, but the same increase in stocking only increased trophy catch by about 60% if the MLL was 800 mm TL (Fig. 4). High length limits protected adult fish from harvest and resulted in decreased proportional contributions of stocking to recruitment, thus decreasing the efficiency of stock enhancement.

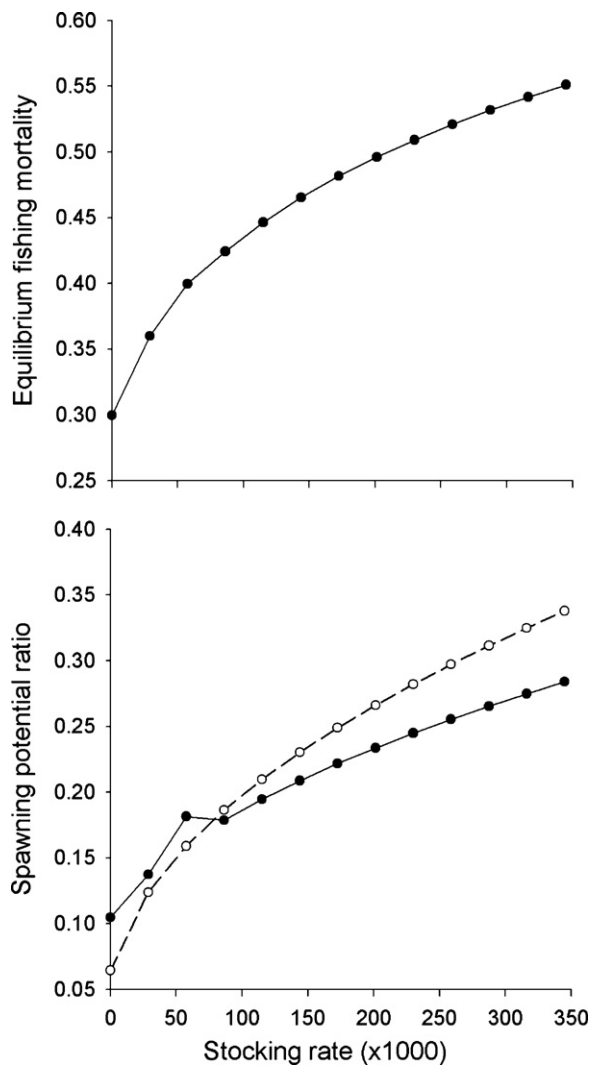
We then increased fishing mortality from the base case of 0.15–0.4 combined with the 75% recruitment reduction to simulate intense fishing effects on a population with low recruitment.

This scenario showed stronger contributions of a hatchery program to sustainability and fishery metrics relative to the lower exploitation scenario. Beneficial effects from stocking were again negatively related to the MLL (Fig. 5). Thus, the model showed that stocking could have benefits for populations that are undergoing very low recruitment and/or high fishing mortality, but an interaction between stocking rate and MLL will affect the total contribution of the stocking program. Benefits from stocking were stronger under low MLL's than high MLL's. However, length limits over 700 mm were required to prevent recruitment overfishing (i.e.,  $SPR < 0.35$ ) if fishing mortality was 0.4 (Fig. 5).

Incorporating angler effort responses influenced annual fishing mortality rates and SPR for a fixed 600 mm minimum length limit (Fig. 6). Angler effort responses were predicted to reduce annual

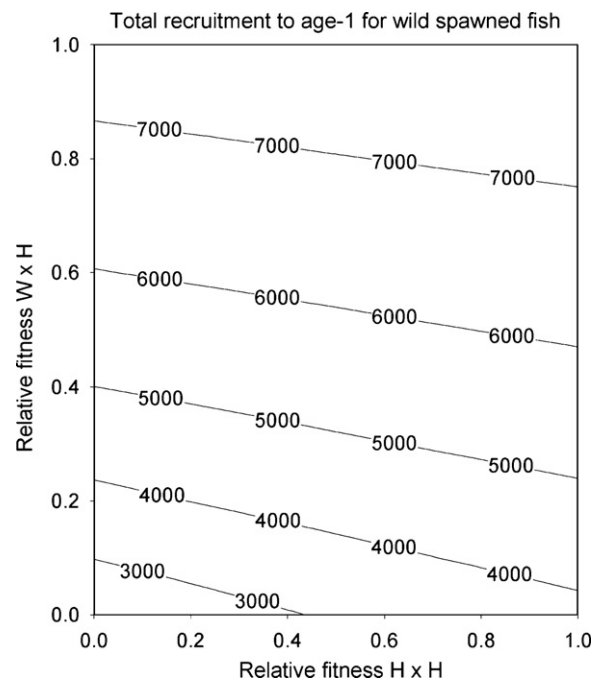


**Fig. 5.** Model predictions of spawning potential ratio (SPR, top panel), proportion hatchery recruits to age-1 (center panel), and trophy catch (number of fish, bottom panel) plotted on the number of fingerlings stocked (y-axes) and the minimum length limit (x-axes). Simulations are for the scenario of  $F=0.40$  with 25% of equilibrium recruitment and fingerlings stocked at 50 mm TL.



**Fig. 6.** Model predictions of equilibrium annual fishing mortality ( $F$ , top panel), SPR (bottom panel) plotted on the number of fingerlings stocked (y-axes) at a fixed minimum length limit (600 mm). Simulations were conducted with angler effort responses to deviations from equilibrium vulnerable biomass when  $F=0.4$  at annual stocking rate of 50 000 fingerlings (solid line in both panels). For SPR, the predictions for fishing effort responses (solid line) are shown with comparison to a fixed fishing mortality rate (dashed line,  $F=0.4$ ) at 25% base case recruitment and fingerlings stocked at 50 mm TL.

fishing mortality to 0.3 if stocking was eliminated or increase fishing mortality to 0.55 at our highest stocking rates (Fig. 6). The SPR values suggested that angler effort responses could reduce the magnitude of recruitment overfishing at low stocking rates (i.e., <50 000 fingerlings per year), but also lower the potential of rebuilding the population to a sustainable level at higher stocking rates. Thus, the model showed that if stocking increased fish abundance and attracted anglers, it could result in low population abundance and SPR. We simulated the effect of reduced reproductive fitness, relative to wild  $\times$  wild mating, for hatchery  $\times$  wild and hatchery  $\times$  hatchery matings in a population with a 75% recruitment reduction,  $F=0.15$ , and an annual stocking rate of 50 000 fingerlings (i.e., a scenario where stocking had high success, Fig. 4). We predicted total recruitment to age-1 by varying relative fitness from 0.0 to 1.0, where 1.0 represented an equal reproductive fitness to wild  $\times$  wild mating. Results showed that reduced fitness of hatchery  $\times$  hatchery crosses had minor impacts on total recruitment to age-1 in the population (Fig. 7). Conversely, reduced fitness of hatchery  $\times$  wild caused large impacts to total recruitment



**Fig. 7.** Model predictions of the number of recruits to age-1 for fish hatched in the wild plotted on the relative fitness of wild  $\times$  hatchery crosses ( $W \times H$ , y-axis) versus the relative fitness of hatchery  $\times$  hatchery ( $H \times H$ , x-axis) crosses. Simulations were conducted at 25% of base case recruitment,  $F=0.15$  and 50 000 fish stocked at 50 mm TL.

to age-1 in the population (Fig. 7). This occurred because hatchery  $\times$  hatchery crosses would be relatively rare in the population at an annual stocking rate of 50 000 fingerlings, but reduced fitness of hatchery  $\times$  wild crosses resulted in large numbers of fish with reduced effective reproductive output. Thus, in cases where stocked fish represented a significant fraction of the total recruits (15–20%), either due to very high stocking densities or very low natural recruitment, reduced fitness of hatchery fish would have substantial population-level consequences.

#### 4. Discussion

Our population model expanded on an existing simulation model to include a popular fisheries management strategy (i.e., stock enhancement) whose effects were largely unknown. Simulations showed that interactions between wild population abundance (e.g., natural recruitment), stocking strategy (i.e., size at stocking and stocking density), and the fishery (i.e., management regulations and fishing mortality) determined the potential for stocking to contribute to sustainability and fishery metrics. In most cases, increasing minimum length limits had larger positive effects than stocking. However, the model illustrated cases where stocking could substantially benefit fisheries, such as those with very low natural recruitment (e.g., due to habitat loss) or overfishing. The model also highlighted the importance of considering angler effort dynamics and relative fitness among mating combinations for scenarios where stocking was predicted to enhance Murray cod populations.

We found a lack of benefits from stocking under our base case scenario, which resulted from density-dependent mortality during the juvenile life stage. The strength of density-dependent mortality for stocked fish depended on the abundance and size at stocking, the abundance of wild spawned fish, and total juvenile recruitment regulation. Stocking fish at 50 mm TL in our base model caused stocked fish to undergo high mortality along with pre-

recruit wild-hatched fish. Stocking advanced fingerlings increased the contribution of stocked fish to the population, because larger fish underwent less density-dependent mortality, however they still made a minor contribution relative to wild-hatched fish. Thus, the influence of stocking fingerlings in our example was low due to (1) high juvenile mortality and (2) stocking rates that were not substantial relative to the model-predicted natural recruitment to age 1. Our base case model suggested that hatchery fingerlings could partially replace but would not significantly augment wild recruits because stockings were small relative to wild production. Similarly, Scharf (2000) found no population level effects of stocking early juvenile red drum *Sciaenops ocellatus* in Texas estuaries, and hypothesized that density-dependence during juvenile stages limited the potential for small stocked fish to contribute to a year class. This was also shown empirically by Hilborn and Eggers (2000) for the Kodiak Island pink salmon hatchery, where increasing the size at stocking improved hatchery contributions, but additive population level effects were minimal.

Minimum length limits were substantially more effective at preventing overfishing and maintaining the fishery than stocking across all the scenarios we evaluated. Decreasing fishing mortality for spawners, by increasing the minimum length limit, resulted in much higher recruitment than high stocking rates despite a hatchery advantage that acted to increase per-capita survival from egg to stocking sizes in hatcheries. However, increased minimum length limits can fail to improve fishery sustainability if discard mortality is high (Coggins et al., 2007). Discard mortality for Murray cod appears low ( $\leq 10\%$ ), making length limits a viable management option, but potential mortality trade-offs should be considered when imposing length limit changes for species with higher levels of discard mortality. The model suggested that stocking could benefit fisheries with low recruitment and/or relatively high fishing mortality. Stocked fish could contribute substantially to a year class in these simulations, and these results were supported from field studies in some Victorian waters where stocked fish were common in angler catches. Hall and Douglas (2008) reported almost 50% of Murray cod collected in the Loddon River, Victoria were hatchery released fish and they concluded that stocking was likely making a large contribution to the fishery. The Loddon River was a low density population because the average angler catch rate in creel surveys was  $<0.01$  fish/h whereas average angler catch rates at other rivers ranged from 0.08 to 0.03 fish/h (Brown, 2009). The Loddon River also had one of the highest angler effort estimates (251 h/ha) among rivers sampled by creel surveys (range = 58–253 h/ha, Brown, 2009). Thus, those field observations support our model predictions of a type of system where stocking would have the highest potential to contribute substantially to fish abundance and angler catches.

The ability of stock enhancement to improve population sustainability was sensitive to potential angler effort responses and biomass dependent fishing mortality. Our angling effort response model implied that increased stocking rates could cause fishing mortality to increase, and vice versa. The potential for angler effort responses to fish abundance is dependent on many factors (e.g., harvest regulations, Beard et al., 2003; proximity to other opportunities, Cox et al., 2003; Post et al., 2008) that have been highlighted as an area of continuing research importance (Pereira and Hansen, 2003 and references therein). Of further importance is the need to recognize the potential for management strategies to mask population declines or result in counter-intuitive results (Lewin et al., 2006) as seen in our simulations where high stocking rates increased fishing mortality and reduced SPR relative to lower stocking rates. Leber (2002) and Walters and Martell (2004) warned that attracted fishing effort from stocking could increase fishing mortality on an already depressed wild population. In contrast, fishing mortality reductions at low stocking sizes increased SPR

relative to fixed F simulations, but SPR was still below a level considered sustainable. We did not have data to indicate how fishing effort would respond to management changes in Murray cod fisheries, and future use of this model should seek to measure these responses. However, angler effort dynamics should be expected to affect the efficiency of stock enhancement and regulation policies both within a system and across multiple systems.

Our results indicated that any reduction in reproductive fitness for hatchery progeny could have implications for realized recruitment to age-1. Realized recruitment could be less than 50% of potential recruitment if reproductive fitness of hatchery progeny was greatly reduced relative to wild progeny reproductive fitness. Catastrophic examples of hatchery genetic effects have been presented for multiple enhancement programs (see Walters and Martell, 2004). Our results showed that a stocking program could appear to be successful, even in the presence of reduced reproductive fitness for hatchery fish, because hatchery fish would represent a significant portion of the total population. However, realized recruitment would be much lower than potential recruitment due to reduced fitness of hatchery fish and the effects would not be apparent from evaluations of percent contribution of hatchery fish. Reduced fitness for hatchery  $\times$  wild crosses had much larger effects on potential recruitment than reduced fitness for hatchery  $\times$  hatchery matings. This occurred because of hatchery  $\times$  wild matings were much more common than hatchery  $\times$  hatchery matings in the simulated populations. We presume hatchery  $\times$  wild matings would commonly occur in wild populations experiencing stocking, indicating the importance of hatchery fish fitness for enhancing total recruitment.

Although our simulations demonstrated some scenarios where stocking was predicted to enhance population sustainability and the fishery, we included several assumptions that may restrict our results to a “best case” description. There were no data available on survival of hatchery released Murray cod to maturity, and thus, our assumptions of equal survival, growth, and maturity would likely overestimate stocking contributions if differences between wild and hatchery released fish existed. These important parameters have been shown to be lower for hatchery fish in many cases (Lorenzen, 2005), and much attention has been directed at increasing post-release performance of hatchery fish (e.g., Brown and Day, 2002). Our use of a Beverton–Holt stock-recruitment function to describe density-dependent pre-recruit survival could also contribute to our simulations being “best case” descriptions. For example, our estimated benefits of stocking for spawning potential ratio and recruitment would be overestimated if Murray cod exhibit overcompensation at highest stock abundances (e.g., a Ricker stock recruitment relationship). The form of the stock recruitment curve is not known for Murray cod, and our use of the Beverton and Holt curve served as a best case scenario for stocking to influence total fish abundance.

Our simulations demonstrated some cases where stock enhancement could benefit fisheries, but we caution that those cases represented best case scenarios rather than the expected outcomes for most conditions where stock enhancement is applied (e.g., existing wild fish recruitment, moderate fishing quality, etc.). Similar to Allen et al. (2009) we found our model's estimates to be most sensitive to changes in natural mortality and growth parameters and model estimates of SPR were robust to changes (i.e., 95% confidence intervals for natural mortality at length from Lorenzen, 1996, 2006) in our  $S_{fry}$  parameter.

## 5. Conclusions

Public and political support for stocking programs has generally been favorable even in the absence of impact evaluations (Leber,

2002), and stock enhancements to improve population sustainability are likely to continue in the future. Thus, our modeling approach and results should provide insight into the types of systems stocking could result in fishery improvements. Our model scenarios indicated that systems with low recruitment and/or high fishing mortality would provide the highest potential for stocking to cause a significant proportional increase in stock abundance. In contrast, stocking systems that currently have substantial natural recruitment will not benefit population sustainability or the fishery. Field experiments to test our results could use an adaptive experimental approach as described by Walters and Hilborn (1978) and suggested by Leber (2002). Potential treatments would include high minimum length limits or catch and release regulations at a range of stocking rates for some systems, and stocking without length limits in others. An experimental framework could isolate the impacts of stocking versus harvest regulations, which would reduce the ambiguity in uses of both practices simultaneously. Leber (2002) called for a predictive capability to determine the potential for stocking success. Modeling approaches, like those presented here, combined with adaptive experimental research are necessary for quantitatively resolving the role of stocking programs relative to other tools used for fisheries management.

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