Incorporating Mortality from Catch and Release into Yield-per-Recruit Analyses of Minimum-Size Limits

JAMES R. WATERS AND GENE R. HUNTSMAN

SEDAR68-RD11

North American Journal of Fisheries Management 6:463–471, 1986

Incorporating Mortality from Catch and Release into Yield-per-Recruit Analyses of Minimum-Size Limits

JAMES R. WATERS AND GENE R. HUNTSMAN

National Marine Fisheries Service, Southeast Fisheries Center, Beaufort Laboratory
Beaufort, North Carolina 28516, USA

Abstract.—We evaluated the effect on yield per recruit of mortality from catch and release of fish smaller than a legal minimum length. Catch-and-release mortality reduces the potential effectiveness of minimum size limits for increasing yield per recruit by an amount that depends on the fishing mortality coefficient, the minimum size limit, and the probability that undersized fish survive if released. For a given probability of survival, catch-and-release mortality has its greatest influence when fishing mortality and the minimum size limit are large, because these factors determine the number of undersized fish that are caught and released. As the survival probability declines, minimum size limits become less effective for increasing yield per recruit because greater numbers of undersized fish die and cannot contribute to future catches. With low survival probabilities, minimum size limits may actually reduce yield per recruit. We calculated yield per recruit for red snapper (*Lutjanus campechanus*) in the Gulf of Mexico for minimum size limit ranging from 254 to 635 mm total length, survival probabilities ranging from 0.20 to 1.00, and several natural (M) and fishing mortality coefficients. A recently implemented 330-mm minimum size limit is predicted to increase yield per recruit as long as the survival probability exceeds 50% if $M = 0.25$; the survival probability must exceed 60% if $M = 0.35$.

An extremely important factor affecting the success of a minimum size limit for increasing yield is the ability of undersized fish to survive after release. Numerous authors have investigated the magnitude of catch-and-release mortality (Wydoski 1979; Dotson 1982; Feathers and Knable 1983). Others have described, in general terms, the effects of catch-and-release regulations on the fish population and angling quality (e.g., Barnhart and Roelofs 1979; Anderson and Nehring 1984), but few authors have modeled the catch-and-release process. Clark et al. (1980) included hooking mortality in their analyses of alternative size regulations for trout, but they did not study the implications of hooking mortality for the success or failure of those regulations. Clark (1983) documented the theoretically beneficial effects of voluntarily releasing legal-sized fish. Lenarz et al. (1974) described the effects on yield per recruit of a minimum size limit when undersized fish are discarded and killed.

Our interest in modeling catch-and-release mortality derives from a controversial minimum size limit of 330-mm total length implemented recently for red snapper (*Lutjanus campechanus*) in the Gulf of Mexico. Red snappers are reef fish landed primarily by hook and line in both commercial and recreational fisheries. Over time, continued heavy fishing has resulted in significant evidence of growth overfishing (Gulf of Mexico Fishery Management Council 1981).

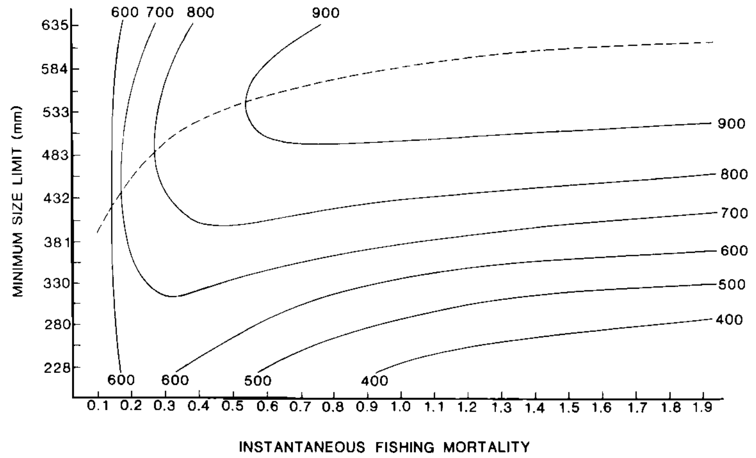
One objective of the minimum size limit is to increase yield in weight by reversing the effects of growth overfishing. However, red snappers can be injured during capture and may not survive if released. Opponents of the minimum size limit argued that releasing undersized red snappers may waste rather than conserve fish if too many die when released. Field studies are underway to determine postrelease survival probabilities, but criteria are needed with which to judge whether or not experimentally observed survival rates support the size limit.

We developed a method for establishing the needed criteria by evaluating the effect of catch-and-release mortality on yield per recruit. First, we modified the traditional Beverton and Holt (1957) yield-per-recruit model to include catch-and-release mortality and briefly described the implications of the new model for fishery management. We then used the model to describe the effect of alternative minimum size limits on yield per recruit for red snapper and several other species of reef fish, assuming various survival probabilities for undersized fish that are caught and released.

Incorporating Catch-and-Release Mortality into the Beverton and Holt Yield-per-Recruit Model

Yield-per-recruit models are used to calculate the theoretical value of yield in weight from a year

(a) Ps = 1.0



(b) Ps = 0.9

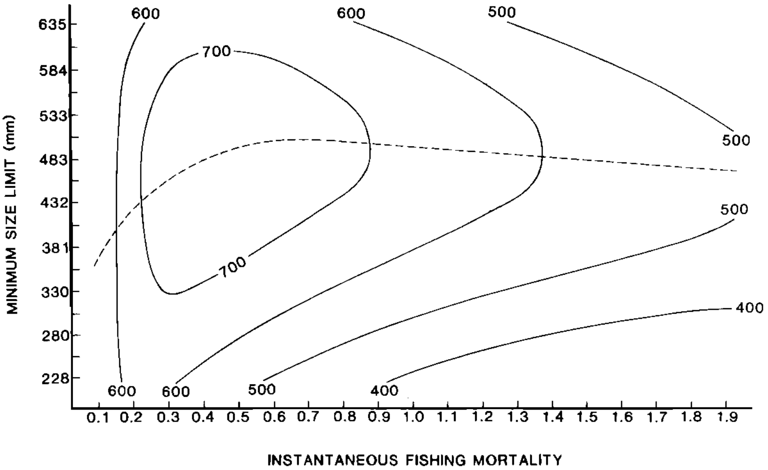


FIGURE 1.—Yields per recruit in weight (g) for red snapper for $M = 0.25$ and probabilities of survival (Ps) of 1.0, 0.9, 0.6, and 0.3 for released fish. Dotted lines indicate maximum yield per recruit for each fishing mortality coefficient.

TABLE 1.—Instantaneous total mortality coefficients for red snapper.[a]

Ages	Without size limit	With size limit
t_r–t_c	M	M
t_c–t_m	$M+F$	$M+F(1-Ps)$
t_m–t_λ	$M+F$	$M+F$

[a] t_r = age at recruitment; t_c = age at first catch; t_m = age at minimum size limit; t_λ = maximum age; M = natural mortality; F = fishing mortality; Ps = probability of survival for released fish.

class of fish during its lifetime on the fishing grounds divided by the initial number of fish recruited to the grounds. In the traditional yield-per-recruit model, the age at first capture t_c is an independent variable that is controllable by fishery managers, and implementation of a minimum size limit effectively increases t_c. Fishing mortality is assumed to be nonexistent for fish smaller than the legal minimum. However, we treated t_c as a parameter whose value is determined as a characteristic of the fishery and the commonly employed fishing gear. We then defined a new variable t_m to rep-

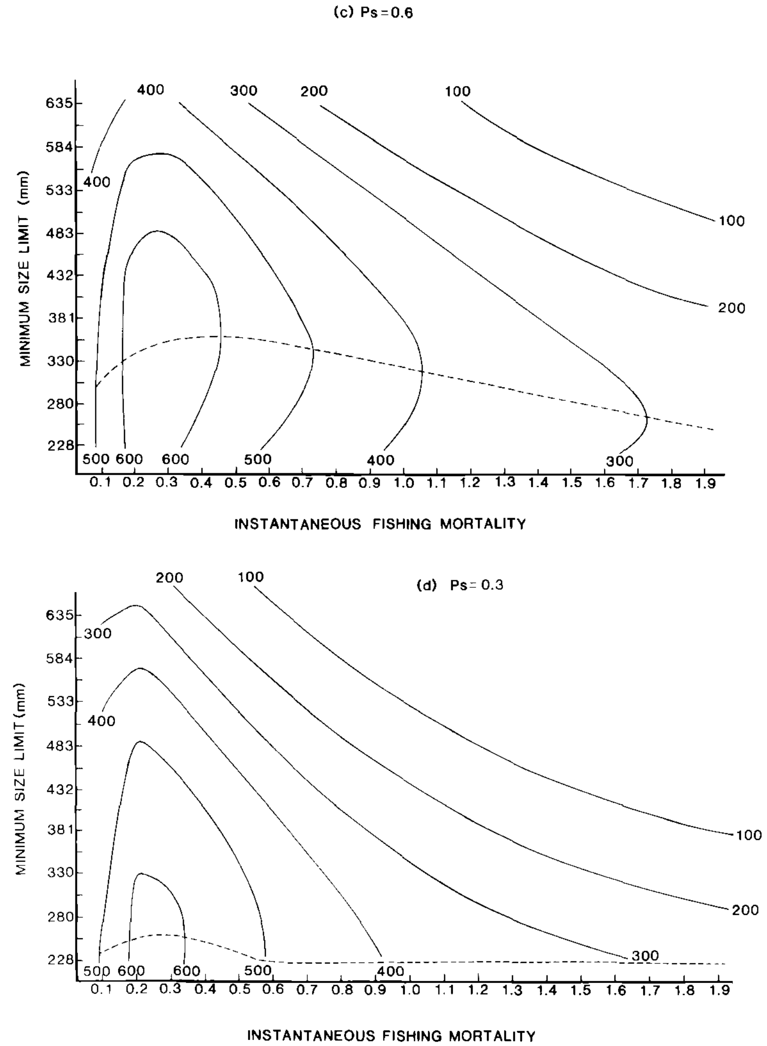


FIGURE 1.—Continued.

resent the age corresponding to a particular minimum size limit, and calculated yield per recruit as a function of t_m and fishing mortality and coefficient F.

The additional age variable enabled us to include a component for catch-and-release mortality. Between ages t_c and t_m, the instantaneous coefficient of catch-and-release mortality $F(1 - Ps)$ is defined as the rate at which undersized fish are caught F multiplied by the probability that they will die when released $(1 - Ps)$ (Table 1). Because fish cannot be identified as legal or sublegal until they have been caught, our initial hypothesis was that undersized fish are caught at the same rate F as without a size limit but that they are released and survive with a probability of $Ps \leq 1.0$. This hypothesis overestimates mortality from catch and release if fishermen minimize the catch of sublegal fish by using larger hooks and by avoiding areas with large concentrations of undersized fish. In this event, the coefficient of catch-and-release mortality is $F'(1 - Ps)$, where $F' < F$. In addition, we assumed that the probability Ps that undersized fish would survive if released is not a function of size, and that fishermen fully comply with the minimum size limit by voluntarily releasing all undersized fish.

We incorporated catch-and-release mortality into the Beverton and Holt (1957) yield-per-recruit model, which implicitly assumes that all fish would survive if released ($Ps = 1.0$). In this case, the minimum size limit would be completely effective because there is no fishing-related mortality between ages t_c and t_m. In models where $Ps = 0$, the regulation would be completely ineffective because fishing mortality between ages t_c and t_m would be undiminished. For other survival probabilities, $0 < Ps < 1$, minimum size limits would be partially effective in reducing mortality rates for undersized fish. An analytical solution for yield per recruit in the presence of catch-and-release mortality is presented in the Appendix.

Parameter Values in the Yield-per-Recruit Analyses for Red Snapper

We illustrated the effect of catch-and-release mortality by examining yield-per-recruit response surfaces for red snapper in the Gulf of Mexico. We assumed alternative minimum size limits ranging from 254 to 635 mm, survival probabilities ranging from 0.2 to 1.0, and several natural and fishing mortality coefficients.

We chose natural mortality coefficients of $M = 0.25$ and $M = 0.35$, values we assumed to bracket the true but unknown value of M. Nelson and Manooch (1982) reported M values from 0.19 to 0.20 for red snapper in the Gulf of Mexico, but these values are now considered to be underestimates (R. S. Nelson, National Marine Fisheries Service, Beaufort, North Carolina, personal communication). A minimum size limit would be more favorable than our analyses indicated if the true M were less than 0.25, and it would be less favorable if the true M exceeded 0.35. We assumed fishing mortality coefficients ranging from 0.1 to 1.9 and present tabular results for $F = 0.2$, 0.3, 0.6, and 0.8 because Nelson and Manooch (1982) estimated that fishing mortality coefficients ranged from 0.2 to 0.3 in Florida and from 0.58 to 0.74 in Louisiana.

Length–age and weight–length curves for red snapper in the Gulf of Mexico have been estimated by Nelson and Manooch (1982):

$$L(t) = 941[1 - e^{-0.17(t+0.1)}]; \qquad (1)$$

$$W(t) = 1.82 \times 10^{-5} L(t)^{2.966}; \qquad (2)$$

$L(t)$ denotes total length (mm) and $W(t)$ represents weight (g) at age t (years). The Beverton and Holt (1957) assumption of an isometric weight–length relationship appears to be justified. We calculated W_∞ based on the estimated exponent in equation (2).

We also assumed that fish recruit to the fishing grounds at a length of approximately 178 mm, and that they are not usually caught until attaining a length of 228 mm (inferred from Figures 2–4 and Appendix E in McEachron 1983). The ages corresponding to the 178-mm length at recruitment ($t_r = 1.132$ years), the 228-mm length at first capture ($t_c = 1.537$ years), and the 330-mm minimum legal length ($t_m = 2.442$ years) were found from the length–age equation.

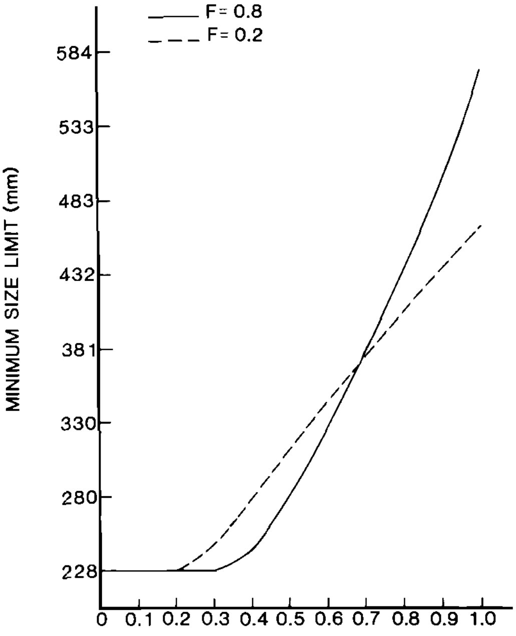


FIGURE 2.—Minimum size limits (mm) that would approximately maximize yield per recruit for red snapper as a function of the probability of survival (Ps) for released fish, based on instantaneous fishing mortality coefficients (F) of 0.2 and 0.8, a natural mortality of 0.25, and a length at first capture of 228 mm.

Effect of Catch-and-Release Mortality on Yield per Recruit

In the traditional Beverton and Holt model, yield-per-recruit isopleths become open-ended at the right (Figure 1a). The implication is that an appropriately chosen minimum size limit would effectively achieve and maintain yield per recruit at a relatively high level unless F is very small. Furthermore, yield per recruit would increase quickly toward an asymptote if fishery managers could optimally adjust the minimum size limit whenever F increased (Figure 1a).

Catch-and-release mortality changes the shape of the yield-per-recruit response surface and its

TABLE 2.—Percentage gains in yield per recruit for red snapper based on 100% survival (Ps = 1.0) for released fish, alternative minimum size limits, various natural (M) and fishing (F) mortality coefficients, and the assumption that the length at first capture is 228 mm.

Minimum size limit (mm)	$M = 0.25$				$M = 0.35$			
	$F = 0.2$	$F = 0.3$	$F = 0.6$	$F = 0.8$	$F = 0.2$	$F = 0.3$	$F = 0.6$	$F = 0.8$
254	3	5	9	11	2	4	7	10
280	6	9	18	22	5	8	15	19
305	9	14	27	34	6	11	22	28
330	11	18	35	45	8	13	28	36
356	14	22	44	56	9	16	34	44
381	16	26	52	67	9	17	39	51
406	17	29	60	78	9	18	42	57
432	18	31	67	87	8	18	45	61
457	19	33	73	96	6	17	47	64
483	19	34	77	103	4	15	47	65
508	18	35	81	109	1	13	46	65
533	16	34	84	113	−3	9	43	63
559	14	32	84	115	−8	4	39	59
584	11	30	83	115	−13	−1	33	53
610	7	26	81	113	−20	−8	26	46
635	2	21	76	109	−26	−15	17	36

management implications. For a given $Ps < 1.0$, mortality from catch and release reduces the potential effectiveness of minimum size limits for increasing yield per recruit for all fishing mortality coefficients and minimum size limits, but the reductions are greatest when F and t_m are large. Hence, the previously open-ended sections of each isopleth bend toward each other where F and t_m are largest and join to form closed-loop contours. The response surface indicates a maximum yield per recruit that shifts closer to the origin as the survival probability declines (Figure 1). Hence, maximum yield per recruit would be achieved at smaller size limits than when $Ps = 1.0$. As Ps declines, the size limit that maximizes yield per recruit diminishes rapidly, especially when F is large (Figure 2). Therefore, when Ps is low, minimum size limits may actually reduce yield per recruit. There is no reason for a minimum size limit if few fish survive when released. Fishery managers then would be forced to reduce fishing effort rather than implement minimum size limits to increase yield per recruit.

Our calculations suggest that if $Ps = 1.0$, the 330-mm minimum size limit will increase yield per recruit by 8–45%, depending on the levels of M and F considered (Table 2). However, the anticipated increases in yield per recruit would fall far short of the potential maxima (Figure 1a, Table 2) that could be achieved with minimum size limits as large as 381–559 mm, depending on M and F.

The decision to implement a 330-mm rather than a larger minimum size limit anticipates the existence of catch-and-release mortality. The 330-mm minimum size limit is predicted to increase

TABLE 3.—Percentage gains in yield per recruit for red snapper based on a 330-mm minimum size limit, alternative survival probabilities (Ps) for released fish, various natural (M) and fishing (F) mortality coefficients, and the assumption that the length at first capture is 228 mm.

Probability of survival (Ps)	$M = 0.25$				$M = 0.35$			
	$F = 0.2$	$F = 0.3$	$F = 0.6$	$F = 0.8$	$F = 0.2$	$F = 0.3$	$F = 0.6$	$F = 0.8$
1.0	11	18	35	45	8	13	28	36
0.9	9	15	28	35	6	10	21	27
0.8	8	12	21	26	4	8	15	18
0.7	6	9	15	17	2	5	9	10
0.6	4	6	9	9	0	2	3	2
0.5	2	3	3	1	−2	−1	−2	−5
0.4	0	0	−2	−6	−3	−4	−8	−12
0.3	−2	−2	−7	−13	−5	−6	−12	−18
0.2	−4	−5	−12	−19	−7	−9	−17	−24

TABLE 4.—Minimum size limits (MSL) in millimeters that would approximately maximize yield per recruit for red snapper and the corresponding percentage gains in yield per recruit (ΔYPR), given alternative survival probabilities (*Ps*) for released fish, various natural (*M*) and fishing (*F*) mortality coefficients, and a 228-mm length at first capture.

Probability of survival (*Ps*)	$F = 0.2$ MSL	$F = 0.2$ ΔYPR	$F = 0.3$ MSL	$F = 0.3$ ΔYPR	$F = 0.6$ MSL	$F = 0.6$ ΔYPR	$F = 0.8$ MSL	$F = 0.8$ ΔYPR
				$M = 0.25$				
1.0	457	19	508	35	559	84	559	115
0.9	432	14	457	24	508	52	508	65
0.8	406	10	432	17	432	31	432	36
0.7	381	6	381	11	381	18	381	19
0.6	330	4	356	6	356	9	330	9
0.5	305	2	305	3	305	4	280	3
0.4	280	1	280	1	254	1	228	0
0.3	254	0	254	0				
				$M = 0.35$				
1.0	381	9	406	18	457	47	483	65
0.9	356	6	381	12	432	29	432	38
0.8	330	4	356	8	381	17	381	20
0.7	305	2	330	5	330	9	330	10
0.6	280	1	305	2	305	4	280	3
0.5	254	0	254	1	254	1	254	1

yield per recruit as long as survival probability exceeds 50% of $M = 0.25$ or 60% if $M = 0.35$, with the potential gains in yield per recruit increasing as *Ps* increases (Table 3).

The size limit that maximizes yield per recruit depends on the survival probability. The 330-mm minimum size limit would approximately maximize yield per recruit when $Ps = 0.6$ if $M = 0.25$ and when $Ps = 0.7$ if $M = 0.35$ (Table 4). For higher survival probabilities, larger size limits

TABLE 5.—Parameter values for yield-per-recruit analyses for nine species of reef fish.

Species	Length measurements	Size at recruitment (mm)	Size at first capture (mm)	Von Bertalanffy growth[a]				Natural mortality *M*	Maximum age (years)	Source of growth information
				K	t_0	L_∞ (mm)	W_∞ (g)			
Red snapper	Total	178	228	0.170	−0.100	941.0	12,105	0.25–0.35	17	Nelson and Manooch (1982)
Vermilion snapper	Total	178	203	0.198	0.128	626.5	2,983	0.25	11	Grimes (1978)
Yellowtail snapper	Fork	178	203	0.279	−0.355	450.9	1,297	0.25	15	Johnson (1983)
Red grouper	Total	280	330	0.110	0.0	917.0	20,614	0.20	30	Derived from Moe (1969)
Gag	Total	280	381	0.142	−1.330	1,193.0	21,566	0.20	20	Derived from Schlieder[b]
Scamp	Fork	280	305	0.092	−2.450	985.0	12,334	0.20	25	Matheson et al. (1986)
Black sea bass	Total	127	140	0.230	−0.301	465.0	1,283	0.30	11	Wenner et al.[c]
Red porgy	Total	228	254	0.096	−1.880	763.0	5,544	0.35	14	Manooch and Huntsman (1977)
White grunt	Total	203	228	0.108	−1.007	640.0	4,334	0.30	14	Manooch (1978)

[a] K = growth coefficient; t_0 = age at zero length (year); L_∞ = asymptotic length; W_∞ = asymptotic weight.

[b] Schlieder, R. Unpublished manuscript. Age, growth and reproduction of the gag (*Mycteroperca microlepis*) from the eastern Gulf of Mexico. Florida Department of Natural Resources, Marine Research Laboratory, 100 Eighth Avenue Southeast, St. Petersburg, Florida 33701, USA.

[c] Wenner, C. A., W. A. Roumillat, and W. Waltz. Unpublished manuscript. Biology of black sea bass (*Centropristas striata*) off the southeastern United States. South Carolina Wildlife and Marine Resources Department, South Carolina Marine Resources Research Institute, Post Office Box 12559, Charleston, South Carolina 29412, USA.

TABLE 6.—Minimum size limits (mm total length TL or fork length FL) that would approximately maximize yield per recruit for nine species of reef fish. M = natural mortality coefficient; F = fishing mortality coefficient; Ps = postrelease survival probability.

F	Red snapper (M=0.25) TL	Red snapper (M=0.35) TL	Vermilion snapper (M=0.25) TL	Yellowtail snapper (M=0.25) FL	Red grouper (M=0.20) TL	Gag (M=0.20) TL	Scamp (M=0.20) FL	Black sea bass (M=0.30) TL	Red porgy (M=0.35) TL	White grunt (M=0.30) TL
					Ps = 1.0					
0.2	457	381	305	254	432	635	432	228	228	228
0.4	533	432	356	280	483	686	483	254	254	254
0.6	559	457	381	305	508	737	508	280	280	280
0.8	559	483	406	305	533	762	533	280	305	305
					Ps = 0.8					
0.2	406	330	280	228	356	533	356	203		
0.4	432	356	305	254	381	559	381	203		
0.6	432	381	305	254	381	559	381	228		
0.8	432	381	305	254	356	559	356	228		
					Ps = 0.6					
0.2	330	280	228			432		152		
0.4	356	305	254			457		178		
0.6	356	305	254			432		178		
0.8	330	280	228			406		178		

would increase yield per recruit, each increment in the size limit producing successively smaller increases in yield per recruit until a maximum is achieved.

Yield-per-Recruit Analyses for Other Species

To test the generality of our findings, we calculated yield per recruit for eight other species of reef fish, including vermilion snapper (*Rhomboplites aurorubens*), yellowtail snapper (*Ocyurus chrysurus*), red grouper (*Epinephelus morio*), gag (*Mycteroperca microlepis*), scamp (*Mycteroperca phenax*), black sea bass (*Centropristis striata*), red porgy (*Pagrus pagrus*), and white grunt (*Haemulon plumieri*) (Table 5). To determine approximate average sizes at first capture, we examined available data for the Gulf of Mexico; otherwise, we examined our own data from the south-Atlantic headboat fishery. For the reef fish considered here, the break-even survival probability is approximately 60% (Table 6). An appropriately chosen minimum size limit could increase yield per recruit for red snapper (M = 0.25), vermilion snapper, and gag if Ps is slightly less than 0.6, whereas red porgy and white grunt would require a Ps greater than 0.8.

Conclusions

Catch-and-release mortality reduces the effectiveness of minimum size limits but does not necessarily negate their usefulness as a management technique. By integrating this mortality into the yield-per-recruit model, we established a framework within which the results of field studies may be evaluated. If, for a given minimum size limit, experimentally determined survival rates fall within the range of values that theoretically would increase yield per recruit, then fishery managers can be reasonably certain that the minimum size limit would increase yield per recruit even when catch-and-release mortality exists. Alternatively, if Ps has already been estimated for several size limits, then managers could use the theoretical analyses to assist in the selection of an appropriate minimum size limit.

The break-even values for Ps are determined by the inherent ability of each species to respond to a minimum size limit. Those species with (1) a high percentage of potential growth yet to be realized at age t_c and (2) the ability to attain that growth quickly in relation to natural mortality are the prime candidates for a successful application of minimum size limits. According to Beverton and Holt (1966) and Gulland (1983), these species are characterized by low values for two ratios, $L(t_c)/L_\infty$ and M/K. Our analyses are subject to the same assumptions and limitations as traditional yield-per-recruit models.

References

Anderson, R. M., and R. B. Nehring. 1984. Effects of a catch-and-release regulation on a wild trout population in Colorado and its acceptance by anglers.

North American Journal of Fisheries Management 4:257–265.

Barnhart, R. A., and T. D. Roelofs, editors. 1979. Catch and release fishing as a management tool. Humboldt State University, Arcata, California.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fisheries Investigations Series II Marine Fisheries Great Britain Ministry of Agriculture Fisheries and Food 19.

Beverton, R. J. H., and S. J. Holt. 1966. Manual of methods for fish stock assessment, part 2: tables of yield functions. FAO (Food and Agriculture Organization of the United Nations) Fisheries Technical Paper 38.

Clark, R. D., Jr. 1983. Potential effects of voluntary catch and release of fish in recreational fisheries. North American Journal of Fisheries Management 3:306–314.

Clark, R. D., Jr., G. R. Alexander, and H. Gowing. 1980. Mathematical descriptions of trout stream fisheries. Transactions of the American Fisheries Society 109:587–602.

Dotson, T. 1982. Mortalities in trout caused by gear type and angler-induced stress. North American Journal of Fisheries Management 2:60–65.

Feathers, M. G., and A. E. Knable. 1983. Effects of depressurization upon largemouth bass. North American Journal of Fisheries Management 3:86–90.

Grimes, C. B. 1978. Age, growth, and length–weight relationship of vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina waters. Transactions of the American Fisheries Society 107:454–456.

Gulf of Mexico Fishery Management Council. 1981. Environmental impact statement and fishery management plan for the reef fish resources of the Gulf of Mexico. Gulf of Mexico Fisheries Management Council, Tampa, Florida.

Gulland, J. A. 1983. Fish stock assessment: a manual of basic methods. John Wiley and Sons, New York.

Johnson, A. G. 1983. Age and growth of yellowtail snapper from south Florida. Transactions of the American Fisheries Society 112:173–177.

Lenarz, W. H., W. W. Fox, Jr., G. T. Sakagawa, and B. J. Rothschild. 1974. An examination of the yield per recruit basis for a minimum size regulation for Atlantic yellowfin tuna, *Thunnus albacares*. U.S. National Marine Fisheries Service Fishery Bulletin 72:37–61.

Manooch, C. S., III. 1978. Age, growth and mortality of the white grunt, *Haemulon plumieri* Lacépède (Pisces: Pomadasyidae), from North Carolina and South Carolina. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 30:58–70.

Manooch, C. S., III, and G. R. Huntsman. 1977. Age, growth, and mortality of the red porgy, *Pagrus pagrus*. Transactions of the American Fisheries Society 106:26–33.

Matheson, R. H., III, G. R. Huntsman, and C. S. Manooch III. 1986. Age, growth, mortality, foods and reproduction of the scamp, *Mycteroperca phenax*, collected off North Carolina and South Carolina. Bulletin of Marine Science 38:300–312.

McEachron, L. W. 1983. Harvest estimates for Texas marine charter boats (September 1980–August 1981). Texas Parks and Wildlife Department, Coastal Fisheries Branch, Management Data Series 48, Austin.

Moe, M. A. 1969. Biology of the red grouper, *Epinephelus morio* (Valenciennes), from the eastern Gulf of Mexico. Florida Department of Natural Resources, Marine Research Laboratory, Professional Papers Series 10.

Nelson, R. S., and C. S. Manooch III. 1982. Growth and mortality of red snappers in the west central Atlantic Ocean and northern Gulf of Mexico. Transactions of the American Fisheries Society 111:465–475.

Wydoski, R. S. 1979. Relation of hooking mortality and sublethal hooking stress to quality fishery management. Pages 43–87 *in* R. A. Barnhart and T.D. Roelofs, editors. Catch and release fishing as a management tool. Humboldt State University, Arcata, California.

Appendix

To derive yield per recruit with catch-and-release mortality we incorporated catch-and-release mortality into the Beverton and Holt (1957) yield-per-recruit model by integrating catch in biomass from ages t_m and t_λ:

$$YPR = \int_{t_m}^{t_\lambda} F \cdot N(t) \cdot W(t)\, dt \tag{3}$$

$$= FW_\infty N(t_m) \sum_{j=0}^{3} \frac{G(j) e^{-jK(t_m - t_0)}}{(F + M + jK)} \left[1 - e^{-(M+F+jK)(t_\lambda - t_m)}\right];$$

YPR = yield per recruit in grams;
$N(t)$ = fraction of a recruit surviving at age t;
$N(t_m) = N(t_r)\exp[-M(t_c - t_r)]\exp\{-[M + F(1 - Ps)](t_m - t_c)\}$;
$N(t_r) = 1.0$;
t_r = age at recruitment;
t_c = average age when fish are first caught;
t_m = age corresponding to a minimum size limit;
t_λ = maximum age in the fishery;
M = instantaneous natural mortality coefficient;
F = instantaneous fishing mortality coefficient;
Ps = probability that undersized fish would survive if caught and released;
$W(t)$ = weight (grams) per fish at age t;
$= W_\infty\{1 - \exp[-K(t - t_0)]\}^3$;
W_∞ = maximum attainable weight;
K = growth parameter in von Bertalanffy equation;
t_0 = age parameter in von Bertalanffy equation;
$G(0) = 1$, $G(1) = -3$; $G(2) = 3$; $G(3) = -1$.

Catch-and-release mortality affects yield per recruit by reducing recruitment to the legal minimum size:

$$N(t_m) = e^{-M(t_m - t_r)} e^{-F(1-Ps)(t_m - t_c)}; \tag{4}$$

the term $\exp[-F(1 - Ps)(t_m - t_c)]$ represents the fraction of recruits that survive the catch-and-release process. Mortality from catch and release decreases yield per recruit by an amount that depends on the fishing mortality coefficient, the duration of time between ages t_c and t_m, and the survival probability

$$YPR(Ps < 1) = YPR(Ps = 1)e^{-F(1-Ps)(t_m - t_c)}. \tag{5}$$

The reduction in yield per recruit due to catch-and-release mortality is defined as

$$YPR(Ps = 1) - YPR(Ps < 1) = YPR(Ps = 1)(1 - e^{-F(1-Ps)(t_m - t_c)}). \tag{6}$$

For a given Ps, catch-and-release mortality has its greatest effect on yield per recruit when F and $(t_m - t_c)$ are large because these variables determine the proportion of undersized fish that are caught and released.