

# Fisheries Sustainability via Protection of Age Structure and Spatial Distribution of Fish Populations

**ABSTRACT**

Numerous groundfish stocks in both the Atlantic and Pacific are considered overfished, resulting in large-scale fishery closures. Fishing, in addition to simply removing biomass, also truncates the age and size structure of fish populations and often results in localized depletions. We summarize recent research suggesting that an old-growth age structure, combined with a broad spatial distribution of spawning and recruitment, is at least as important as spawning biomass in maintaining long-term sustainable population levels. In particular, there is evidence that older, larger female rockfishes produce larvae that withstand starvation longer and grow faster than the offspring of younger fish, that stocks may actually consist of several reproductively isolated units, and that recruitment may come from only a small and different fraction of the spawning population each year. None of these phenomena is accounted for in current management programs. We examine alternative management measures that address these specific issues and conclude that the best and perhaps only way to ensure old-growth age structure and complex spatial structure in populations of groundfish is through interconnected networks of marine reserves.

## Introduction

The objective of U.S. fisheries management, as mandated by National Standard 1 of the Sustainable Fisheries Act of 1996, is to maintain fish stocks at levels sufficient to produce maximum sustainable yields (MSY). Mandated levels of fishing may be less than MSY but are not to exceed these levels. MSY, of course, has been a highly elusive goal (Larkin 1977). Operationally, National Standard 1 has been interpreted by most fisheries management plans to mean that fishing should maintain some minimum spawning biomass deemed adequate to ensure that recruitment is not limited by insufficient egg or larval production. In the Pacific groundfish fishery and elsewhere, management is based on maintaining egg or larval output per recruit at or above 40% of the unfished level, referred to as  $B_{40}$  (while the unfished level is  $B_0$ ). Functionally this means maintaining the spawning biomass at 40% of the estimated virgin stock level, with adjustment for age-specific fecundity. Other biological reference points used in managing this fishery are  $B_{25}$  (25% of the unfished level), which is the overfishing threshold, and  $B_{10}$  (10% of the unfished level), which is the threshold at which the fishery is closed (even though bycatch mortality may continue).

Despite these guidelines, periodic population assessments, and attempts at careful regulation of fisheries, many rockfish and other groundfish stocks declined, some severely, and consequently were declared “overfished” (Table 1). These declines have resulted in very restrictive rebuilding plans that include large-scale fishery closures. Estimated rebuilding times, even with no further fishing, are quite long and in some cases may not be achieved within our lifetimes (Table 1).

How did such widespread stock declines occur? Was this challeng-

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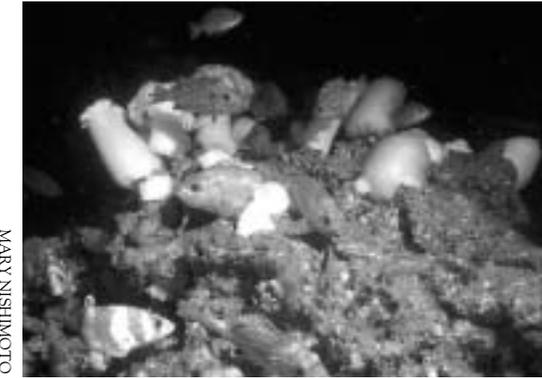
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**Table 1.** Overfished groundfish stocks on the west coast of the United States and estimated rebuilding times with no fishing mortality (PFMC 2003a,b). Of the 82 species in the Pacific Fisheries Management Council plan, 19 have undergone recent reliable stock assessments, so these 9 overfished species comprise about half the well-assessed species (S. Ralston, NOAA Fisheries, pers. comm.).

Species	Year Declared Overfished	Percent of $B_0$	Recovery Time (yr) if Fishing Mortality=0
Bocaccio rockfish ( <i>Sebastes paucispinus</i> )	1999	7.4	18
Canary rockfish ( <i>S. pinniger</i> )	2000	8	54
Cowcod rockfish ( <i>S. levis</i> )	2000	7	59
Darkblotched rockfish ( <i>S. crameri</i> )	2000	14	11
Pacific Ocean perch ( <i>S. alutus</i> )	1999	21.7	8
Widow rockfish ( <i>S. entomelas</i> )	2001	23.6	20
Yelloweye rockfish ( <i>S. ruberrimus</i> )	2002	24	24
Lingcod ( <i>Ophiodon elongates</i> )	1999	15–17	1–2
Pacific hake ( <i>Merluccius productus</i> )	2002	24	1

ing situation a failure of science or management, or merely a result of naturally occurring environmental conditions? While it is likely that all of these factors were at work, we believe that at least part of the explanation for stock collapses is the result of our failure to appreciate the value of both large old fish and fine-scale spatial dynamics of recruitment in the replenishment of fish populations. We discuss recent research that provides what we believe to be a compelling case that the age structure of a stock combined with the spatial distribution of recruitment are as important as spawning biomass in maintaining long-term sustainable population levels. In particular, there are an increasing number of examples of complex population structure in species currently managed as a unit stock, and increasing evidence that only a small fraction of spawners in a stock—those that spawn in the right time and place, which varies annually—successfully contribute to each new cohort. Moreover, it is large, old female fish that produce offspring most likely to recruit successfully

to these new cohorts. Based on this evidence, we believe that the best and perhaps only way to ensure old-growth age structure and complex spatial structure in populations of groundfish is through interconnected networks of fully protected marine reserves.



MARY NISHIMOTO

Miscellaneous rockfish.

## Spatial heterogeneity and recruitment

Although marine populations are obviously affected by the vagaries of larval survival (Houde 1987), the spatial and temporal features of year-class formation are not yet clearly understood. Hedgecock (1994a,b) proposed the “sweepstakes hypothesis” to explain small-scale genetic heterogeneity observed in some widely distributed marine populations. According to this hypothesis, most spawners fail to

produce surviving offspring because their reproductive activity is not matched in space and time to favorable oceanographic conditions for larval survival during a given season. As a result of this mismatch (*sensu* Cushing 1969, 1975), the surviving year class of new recruits is produced by only a small minority of adults that spawned within those restricted temporal and spatial oceanographic windows that offered good conditions for larval survival and subsequent recruitment. If this is indeed the case, then quotas that apply stock-wide (for most U. S. west coast groundfishes, that would be coastwide), without regard to how the catch is spatially distributed, could lead to increased recruitment variability and to occasional recruitment failure if concentrated fishing results in local depletions.

One testable prediction of Hedgecock’s hypothesis is that a cohort of new recruits should show less genetic diversity than the adult population, reflecting the underlying pattern of only a few adults successfully passing their genome to each new cohort. This hypothesis was tested during 1994, when the National Marine Fisheries Service Tiburon Lab conducted a sampling survey of the entire pelagic stage of shortbelly rockfish (*Sebastes jordani*) combined with juvenile and adult surveys (Larson et al. 1995; Julian 1996). Results supported the Hedgecock hypothesis (Table 2): levels of genetic diversity were lower for later stage (“June” and “Farallon”) pelagic juveniles and their haplotype frequencies were different from both adults and most of the earlier stages of larvae and juveniles. Results also indicated that these differences were not due to seasonal spawning by a unique portion of the adult population, but were in fact the result of differential survival during the pelagic larval stage. In contrast, Gilbert (2000) found no reduction in genetic diversity within a very strong year class of kelp rockfish (*S. atrovirens*). Burford (2001) also found no reduction in genetic diversity in a year class of blue rockfish (*S. mystinus*) but did find genetic differences among recruits from different locations that were not matched by differences among adult populations.

Gomez-Uchida and Banks (in press), studying the population genetics of darkblotched rockfish (*S. crameri*), found that the breeding population was several orders of magnitude smaller than the spawning stock size indicated by the stock assessment. Only several thousand breeders, rather than the millions of

**Table 2.** Genetic diversity (diagonals in bold) within samples and genetic differentiation between samples for different developmental stages of shortbelly rockfish. Single asterisk (\*):  $p < 0.10$ , and double asterisk (\*\*):  $p < 0.05$  for Monte Carlo chi square contingency tests for differences in haplotype frequencies (Larson et al. 1995).

	Adults	Larvae	March Juveniles	Total June Juveniles	Farallon June Juveniles
Adults	<b>0.6844</b>				
Larvae	0.0070	<b>0.7355</b>			
March Juveniles	0.0148	0.0161	<b>0.6211</b>		
Total June Juveniles	0.0549*	0.0447*	0.0247	<b>0.5887</b>	
Farallon Juveniles	0.0677**	0.0572**	0.0316*	—	<b>0.5532</b>

adults in the whole population, would successfully reproduce. While not a direct test of Hedgcock's hypothesis, these results nevertheless suggest that recruitment is not uniformly distributed throughout the adult population.

Thus, although the generality of Hedgcock's hypothesis remains in question, indications are that it may be true under at least some circumstances, and that the genetic composition of recruits may otherwise be quite complicated spatially. This suggests that the geographic source of successful recruits may differ from year to year. Based on these considerations, management should strive to preserve a minimal spawning biomass throughout the geographic range of the stock (Larson and Julian 1999).

### Complex population structure

Most continuously distributed groundfish species are assumed to comprise a unit stock throughout their range or at least throughout their range within the management unit. Recent studies using genetic and otolith microchemistry analytical techniques on a broad array of rockfish species indicates that there may be considerable reproductive isolation at regional spatial scales. Miller and Shanks (2004), using chemical signatures in the otoliths of black rockfish to infer larval origin, determined that larval dispersal was much more limited than previously believed, and showed that there were four different population subdivisions between southern Oregon and central Washington.

Buonaccorsi et al. (2002), using microsatellite DNA, showed very similar results for copper rockfish (*S. caurinus*); significant population subdivision was detected among four coastal locations. Despite the wide distribution of this species, they concluded that there was limited oceanographic exchange among geographically proximate locations. Perhaps even more surprisingly, Withler et al. (2001) studying the genetics of Pacific Ocean perch (*S. alutus*), one of the most widely distributed of all rockfish species, being found from Japan and the Bering Sea through Baja California, discovered three genetically distinct populations just off the coast of British Columbia. Similarly, Gomez-Uchida and Banks (in press), found three population subdivisions in darkblotched rockfish along the U.S. west coast.

These results suggest that current stock assessments will not adequately represent the status of the "stock" for species that exhibit complex population structure.

Overfishing of one reproductively isolated population unit can remain undetected if the reproductive units are not assessed individually, which currently they are not. Stock assessment and traditional quota or effort-based management at this level of population subdivision will be very problematic.

### Age truncation and recruitment

Many marine fish species, such as those in the north temperate waters of the Pacific Ocean, exhibit long life spans, with the rockfishes being particularly striking in this regard (Table 3). The adaptive value of allocating reproductive output across many years (iteroparity) is generally thought to be a bet-hedging strategy that ensures some individual reproductive success despite long periods of environmental conditions unfavorable for larval survival (Leaman and Beamish 1984). At the population level, longevity ensures that there will be sufficient reproductive output for the population to maintain itself between favorable recruitment events (Longhurst 1999, 2002).

**Table 3.** Examples of long-lived fishes from the northeast Pacific (Cailliet et al. 2001; Love et al. 2002, O'Connell et al. 2003).

Family	Species	Common name	Estimated maximum age (yr)
Squalidae	<i>Squalus acanthias</i>	Spiny dogfish	75
Acipenseridae	<i>Acipenser transmontanus</i>	White sturgeon	104
Anoplopomatidae	<i>Anoplopoma fimbria</i>	Sablefish	114
Macrouridae	<i>Coryphaenoides acrolepis</i>	Pacific grenadier	73
Scorpaenidae	<i>Sebastes melanops</i>	Black rockfish	50
	<i>Sebastes levis</i>	Cowcod	55
	<i>Sebastes pinniger</i>	Canary rockfish	84
	<i>Sebastes alutus</i>	Pacific Ocean perch	100
	<i>Sebastes crameri</i>	Darkblotched rockfish	105
	<i>Sebastes ruberrimus</i>	Yelloweye rockfish	121
	<i>Sebastes aleutianus</i>	Rougeye rockfish	205
	<i>Sebastes alascanus</i>	Shortspine thornyhead	115

Age truncation—the removal of older age classes via fishing—occurs at even moderate levels of exploitation (Figure 1). Leaman and Beamish (1984) suggest that age truncation will be most detrimental when reproductive success is highly variable, since stock maintenance may be dependent on the relative stability of reproductive output that results from a broad spectrum of age classes. Most, if not all rockfish stocks on the U. S. west coast fall into this category of highly variable and episodic recruitment (Hollowed et al. 1987; Moser et al. 2000).

At the population level, longevity provides a storage effect similar to the seed bank of plants, ensuring extended survival of adults until favorable recruitment conditions return (Warner and Chesson 1985). MacCall (1996) also suggested that populations that are located near the extremes of their geographic ranges, such as the white seabass (*Atractoscion nobilis*) populations near San Francisco around the turn of the twentieth century, may be maintained by irregular

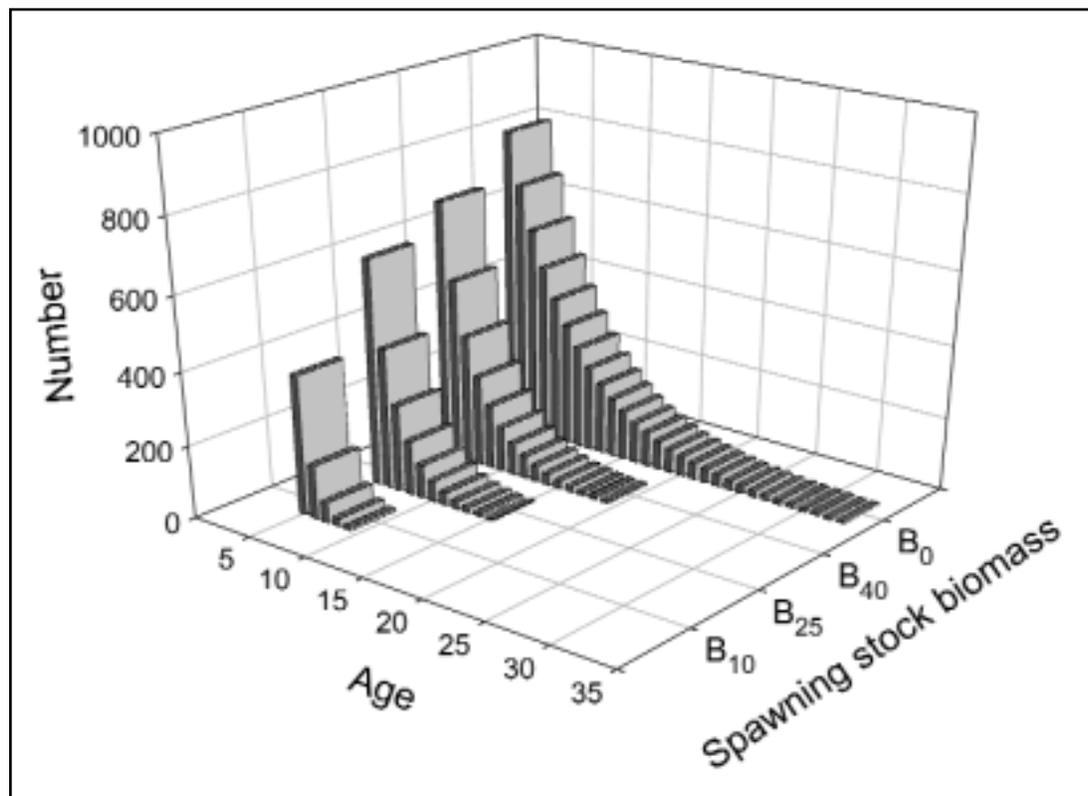
recruitment during climatically favorable conditions. The longevity of such species may allow the populations to persist during extended periods of adverse climatic conditions, when recruitment is essentially absent, but truncation of the age distribution due to fishing may make such irregular replenishment impossible. If individuals at the extremes of the geographic range contribute recruits to the population in the center of the range, as proposed by Cowen (1985) and Pringle (1986) for California sheephead (*Semicossyphus pulcher*) and spiny lobster (*Panulirus interruptus*), respectively, then longevity of populations near the extremes allows the continued production of larvae from these stock components that helps to maintain the central portion of the population.

While the advantage of longevity for persistence of a population in a variable environment is intuitive, a growing body of evidence suggests that a broad age distribution can also reduce recruitment variability (Lambert 1990; Marteinsdottir and Thorarinsson 1998; Secor 2000a,b). There are at least two mechanisms by which stabilization of recruitment could occur: (1) there may be age-related differences in the time and location of spawning (Berkeley and Houde 1978; Lambert 1987; Hutchings and Myers 1993), thereby spreading larval production to cover temporal and spatial variability in favorable environmental conditions, and (2) older fish may produce larger, healthier, or otherwise more fit larvae (Hislop 1988; Marteinsdottir and Steinarsson 1998), which may survive under conditions that are inadequate for the survival of progeny from younger fish. Even slightly enhanced rates of early survival and growth have a

cumulative effect that can translate into a greatly increased probability of successful recruitment (Houde 1987).

Long life spans are necessarily associated with low rates of mortality during the adult stage (Stearns 1992). For most teleosts, size-dependent processes, especially lower risk of predation with increasing body size, result in decreasing natural mortality as fish grow older and larger (Hare and Cowan 1997; Sogard 1997). Fishing, however, generally selects for larger, older fish, imposing a selection pressure that works opposite to that of most natural mortality agents. One of the more predictable effects of fishing is the reduction or removal of the older age classes, i.e., age truncation (Figure 1). Prior to reaching a size acceptable to the fishery (either due to market demand or minimum size regulations intended to allow fish to attain reproductive maturity), younger age classes are reduced only through natural mortality, but once vulnerable to fishing gear, a cohort is reduced through both natural and fishing mortality. These sources of mortality are cumulative throughout the life of the cohort. As illustrated in Figure 1, even at moderate levels of fishing (e.g.,  $B_{40}$ , the target level), the number of age classes at equilibrium rapidly decreases. Although age truncation increases with increasing exploitation rates, it is essential to understand that older age classes are lost even at levels of fishing mortality that are currently considered sustainable (e.g., fishing at the target level, where spawning output is reduced to 40% of the level that would exist without fishing, or  $B_{40}$ ). More important, loss

**Figure 1.** Example of age truncation under increasing rates of exploitation of a hypothetical population of fish at equilibrium. The modeled population has the same size, growth, natural mortality, maturation, and age-specific fecundity characteristics as black rockfish (*Sebastes melanops*). Recruitment is assumed to remain constant (i.e., we start with the same number of fish at age 4 regardless of the population age structure). For simplicity we assume fishing mortality is knife-edged starting at age 4 (i.e., the cohort is reduced only through natural mortality until age 4 and through both fishing and natural mortality after age 4). Natural mortality, expressed as an instantaneous rate, is 0.18; instantaneous rates of fishing mortality that result in the biological reference points  $B_0$ ,  $B_{40\%}$ ,  $B_{25\%}$ , and  $B_{10\%}$  are 0.000, 0.165, 0.295, and 0.775, respectively. The cohort is considered eliminated when less than 0.5% of the initial cohort (at age 4) remains.



of older age classes may have severely negative ramifications for subsequent recruitment. As reviewed below, there can be crucial differences between young and old spawning females.

## Body Size and Adult Condition

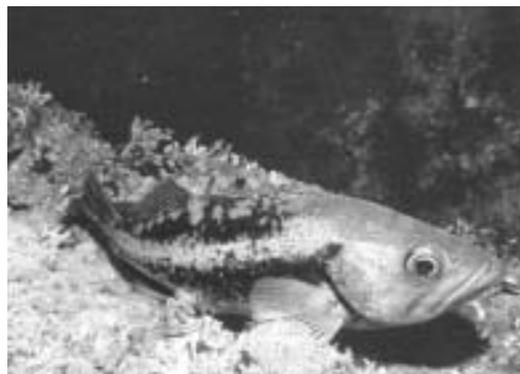
In rockfishes and in other teleosts, body condition and deposition of lipid reserves increase disproportionately with fish length or stage of maturity (Iles 1974; Eliasson and Vahl 1982; Larson 1991). If volumetric variables such as body weight, liver weight, and weight of fat reserves grow proportionately to the rest of the fish, they would increase with the cube of body length. In rockfish, Guillemot et al. (1985) found varying relationships between mesenteric fat weight and fish length (often with low  $R^2$  values). However, Larson (1991), benefiting from fish consistently collected in the same areas (in contrast to the fish available to Guillemot), found disproportionate relationships between measures of condition and fish length in kelp rockfish (*Sebastes atrovirens*) and black-and-yellow rockfish (*S. chrysomelas*). Body weight was proportional to slightly greater than the cube of length, liver weight to around the 4th power of length, and mesenteric fat weight to about the 6th power of length. Whether body reserves are utilized directly in reproduction (MacFarlane et al. 1993; Norton and MacFarlane 1994), for overwintering maintenance (Guillemot et al. 1985), or a combination of the two (Larson 1991), the amount of reserves may affect the timing (Lenarz and Wyllie Echeverria 1986) or amount (Eliasson and Vahl 1982; Lambert and Dutil 2000; Blanchard et al. 2003) of reproduction, and the potential for overwintering or post-spawning survival (Guillemot et al. 1985; Lambert and Dutil 2000). The positive allometry of reserves and body condition in fishes indicates that larger (and presumably older) fish may make greater reproductive contributions than smaller fish, and also that larger fish may be able to reproduce and survive reproduction under a greater range of environmental conditions than smaller fish.

## Maternal age and timing of spawning

Older marine teleosts generally spawn earlier during the reproductive season than younger fish (Berkeley and Houde 1978; Pedersen 1984; Lambert 1987). In a recent study of black rockfish (*Sebastes melanops*) off Oregon, Bobko and Berkeley (2004) found that older fish gave birth earlier in the year than progressively younger fish (a trend also noted in yellowtail rockfish, *Sebastes flavidus*, off southern California, Love et al. 1990). Black rockfish, like other rockfishes, are primitive livebearers and normally produce a single batch of larvae annually. Parturition dates were estimated from advanced stage gonads sampled during the pre-parturition period (Bobko 2002). These data

were applied to the age distribution of the population to estimate the percentage of larval production by age class for each week. Birthdates of young of the year benthic juveniles were then determined from daily growth rings on their otoliths, from which estimates were made of the relative contribution to recruitment by time period, and thus by implication, age group. By comparing birthdate distributions to adult spawning output, Bobko (2002) determined whether recruitment was proportional to spawning output or whether certain periods during the parturition season were responsible for a greater proportion of recruits. Results indicated that, in 1 of 3 years, significantly greater recruitment came from earlier in the spawning season, a time when few young fish were spawning.

Timing of spawning is likely to be a highly conserved trait in most fishes, as larval survival is highly dependent on larval production coinciding with peak zooplankton production (i.e., the “match-mismatch hypothesis” of Cushing 1969, 1975). For fishes that exhibit age-related temporal patterns of spawning, elimination of older age classes through fishing will effectively shorten the spawning season. In those years when successful recruitment is centered early in the season, elimination of older age classes could result in recruitment failure that would otherwise be avoidable if the age structure was intact. Indeed, Marteinsdottir and Thorarriison (1998) found that strong year classes of Icelandic cod (*Gadus morhua*) occurred only when the population contained a broad age distribution, suggesting that this relationship may be applicable to a variety of species.



RYAN BOEREMA

Black rockfish  
(*S. melanops*)

## Maternal age and egg production

It is well documented that fecundity increases nearly linearly with body mass in adult teleost fishes, and geometrically with body length, which is a decelerating function of age (Weatherley 1972; Wootton 1990). This relationship is due to larger fish not only having a greater body volume for holding eggs, but also devoting a greater proportion of energy stores to egg production. Thus, a 40-cm TL (0.65-kg) bocaccio rockfish produces an average of just over 200,000 eggs per year, whereas an 80-cm (5.41-kg) fish at double the length produces nearly 2 million eggs, nearly 10 times the fecundity (Love et al. 1990). In other words, considering only fecundity per se—let alone egg or larval quality—a single 80-cm bocaccio is worth nearly ten 40-cm fish.

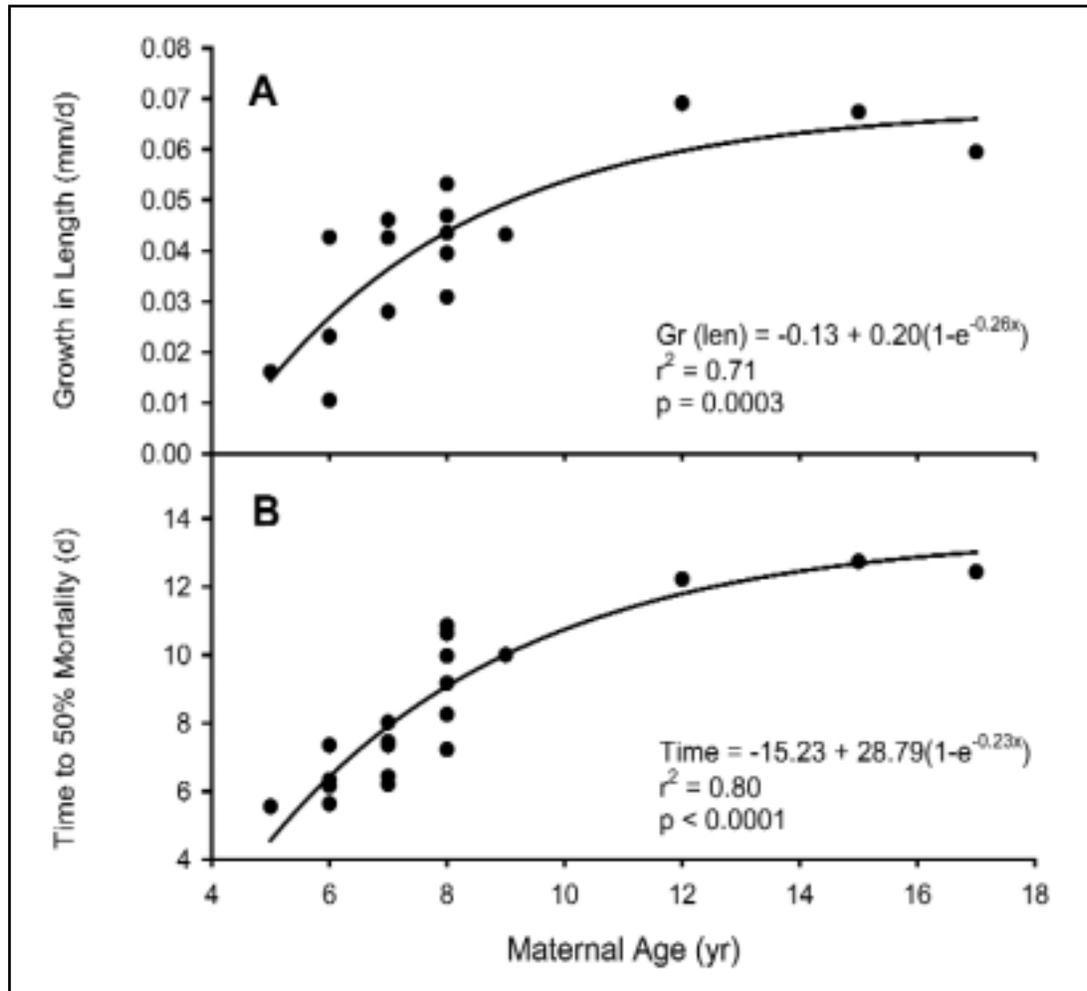
## Maternal age and larval quality

A variety of studies indicate that egg and larval size and/or viability also increase with female size and age (Chambers et al. 1989; Zastrow et al. 1989; Buckley et al. 1991). Recent experiments with black rockfish by Berkeley et al. (2004), in which gravid females were held until parturition and the larvae reared under controlled conditions, revealed that maternal age was much more predictive of larval growth and survival than either maternal size or condition index. Larvae from the oldest fish (age 17) survived starvation 2.5 times longer than those of the youngest fish (age 5) (Figure 2b), and grew more than 3 times as fast on the same diet (Figure 2a). These differences may be conservative since larvae were reared under constant environmental conditions, with ad libitum rations in fed treatments and no exposure to predators or competitors (other than their siblings). Results of a multiple regression analysis indicated that maternal age accounted for most of the variability in larval survival and growth. Maternal length provided a small but significant increase in goodness-of-fit. These results suggest that older females produce higher quality larvae, and that females that are both old and large produce the highest quality larvae. The

mechanism appears to be the volume of the larval oil globule at birth, which is strongly related to maternal age (Berkeley et al. 2004).

It seems likely that such large differences in growth and starvation tolerance have a profound effect on larval survival and subsequent recruitment (review by Heath 1992). The ability of larval fish to survive a period of starvation is often critical due to the spatial and temporal unpredictability of encountering patches of zooplankton prey (Letcher and Rice 1997). Fast growth has clear benefits in allowing larvae to more quickly pass through the most vulnerable life history stages and to develop more rapidly those morphological and physiological capabilities that improve detection and capture of prey, avoidance of predators, and resistance to other environmental challenges (Miller et al. 1988; Bailey and Houde 1989). Indeed, field studies on marine fish larvae have demonstrated that differences in growth rate, especially in the youngest larvae, can have a profound effect on survival. A doubling of the growth rate in larval bluefish (*Pomatomus saltatrix*) and Atlantic cod (*Gadus morhua*) can increase survival by a factor of 5-10 (Meekan and Fortier 1996; Hare and Cowen 1997). Larval quality can also vary in terms of behavioral attributes directly related to survival (Fuiman and Cowan 2003).

**Figure 2.** Relationships between maternal age and (A) larval growth rate in length and (B) median time to starvation in larval black rockfish (Berkeley et al. 2004).



## Fishing Induced Genetic Change

As shown above, fishing generally results in age truncation of the population. It has long been recognized that fishing, by removing the largest and oldest fish inadvertently removes fish that are genetically predisposed to fast growth and late maturation, creating a selection pressure that should theoretically favor early-maturing, slow-growing individuals. Nevertheless, this question has been largely ignored in fisheries management, which tacitly assumes that exploited populations will always retain their inherent rates of productivity and tend to return to their previous levels of abundance. A recent paper by Olsen et al. (2004) challenges these long-held beliefs. Results of this study strongly suggest that heavy and continuous fishing pressure in northern cod resulted in a rapidly-evolved, genetically-based shift in maturation patterns towards earlier and smaller sizes at maturity. The implications of this finding for management are profound. If evolutionary change in response to fishing turns out to be the rule rather than the exception, then, as Hutchings (2004) observed, we must address issues of reversibility of these changes, and their consequences for sustainable harvesting, population recovery and species persistence. At the very least, we believe that these results suggest that some portion of the population should be protected from the impacts of fishing, providing a sanctuary for the genes of fast-growing, late-maturing individuals.

## Implications for fisheries management

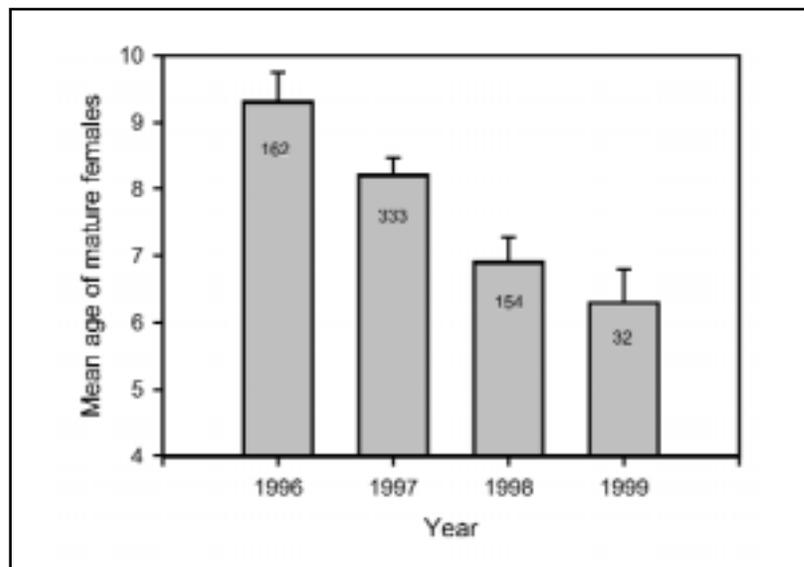
The findings discussed above have important implications for management of marine fish populations. Current management paradigms for a broad array of species assume, first, that each kilogram of spawning stock biomass is identical regardless of adult age, second, that all larvae have an equal probability of survival regardless of parental age, and third that the effects of fishing are reversible. Recent research reviewed here suggests that some or all of these simplistic assumptions are not true for rockfishes, cod, and striped bass (*Morone saxatilis*), and may not be true for other groundfish as well. Ongoing studies by the senior author are currently examining other species of *Sebastes* to determine whether there is a general pattern of maternal age effects among rockfishes. If so, fishing can have a much greater impact on the reproductive capacity of the stock than the simple reduction in spawning biomass. Maintaining a significant proportion of older fish may be critical to long term stability in exploited fish populations. Murawski et al. (2001) provide an elegant synthesis of these effects in Atlantic cod: fishing mortality rates estimated to cause a collapse in the population are markedly reduced if maternal effects on egg and larval quality are included in modeling analyses. Other studies have also concluded that spawner biomass alone may overestimate

the production of viable larvae (Trippel et al. 1997; Scott et al. 1999; Vallin and Nissling 2000).

Age truncation in fished populations is clearly a widespread problem for a broad variety of species (Apollonio 1994; Marteinsdottir and Thorarinnsson 1998; Longhurst 2002). For example, there was a severe decline in the abundance of older age classes of black rockfish off Oregon from 1996 to 1999 (Figure 3). These data were derived from nearshore reefs that received intensified recreational fishing pressure in conjunction with the decline and eventual prohibition of recreational fishing for salmon during the 1990s. Port sampling data collected by the Oregon Department of Fish and Wildlife (unpublished data) indicate that groundfish catches by recreational fishermen doubled in the 1990s compared to the 1980s after recreational fishing for coho salmon (*Onchorhynchus kisutch*) was prohibited in 1994. Although this shift in fishing effort was highly localized, and there was some evidence of partial recovery in 2000, the rapid removal of older fish was particularly striking.

Acceptance of the idea that older fish play a pivotal role in replenishing marine fish stocks in general is increasing, as evidenced by the recent reviews of Longhurst (2002) and Francis (2003). Although much of the data presented in this article are specific to Pacific rockfishes, similar findings in cod suggest that our conclusions are more generally applicable to other groundfish as well. Unfortunately, current fishery regulations under most methods of management generally do not protect older fish in the population. Three methods of management can help to conserve older fish in an exploited population: (1) very low rates of exploitation; (2) slot size limits in which there is both a minimum and a maximum size for retention; and (3) marine reserves that set aside areas in which fishing is prohibited and thus older fish can survive and spawn. Under the first scenario, reduced exploitation will allow more fish to reach old age. However, to be effective this strategy may need to reduce fishing to prohibitively low and economically unfeasible levels

**Figure 3.** Mean age and 95% CI of mature female black rockfish sampled off the central Oregon coast. Sample size is shown inside bars. All mature fish sampled in each year were included in age calculations.



(see Figure 1). This approach was used successfully in rebuilding Atlantic striped bass populations and restoring age structure (Secor 2000a; Richards and Rago 1999), but involved severe fishing restrictions including a virtual harvest moratorium lasting 5 years (Secor 2000a; www.asmf.org/).

The second option—a slot size limit—is available only for fishes that can be released unharmed after capture. Fishes that have a swimbladder (all *Sebastes* rockfishes, for example) typically do not survive due to the internal trauma of expansion and rupture of the swimbladder during capture. Swimbladder or not, the condition of many fishes after capture is too poor to ensure subsequent survival, generating the widespread fisheries issue of bycatch mortality (NMFS 1998). An example of the effect of a slot limit on the age composition of a population of fish similar to black rockfish is shown in Figure 4. In this example, we have assumed 25% release mortality for fish above the maximum size (age 12), which for rockfishes is almost certainly a conservative estimate. At  $B_{40}$ , a slot limit would increase the number of age classes in the population from 19 to 23 in this example, but the population would still be substantially age-truncated.

The final option to prevent age truncation—marine reserves where all fishing of target species (including bycatch) is prohibited—has the potential to allow at least a segment of the population to age naturally and export larvae produced by a broad age range of female spawners (Murray et al. 1999). These benefits are not limited to rockfishes, but would apply more generally to other groundfish as long as the adults tend to stay in the reserve. Further, as reviewed

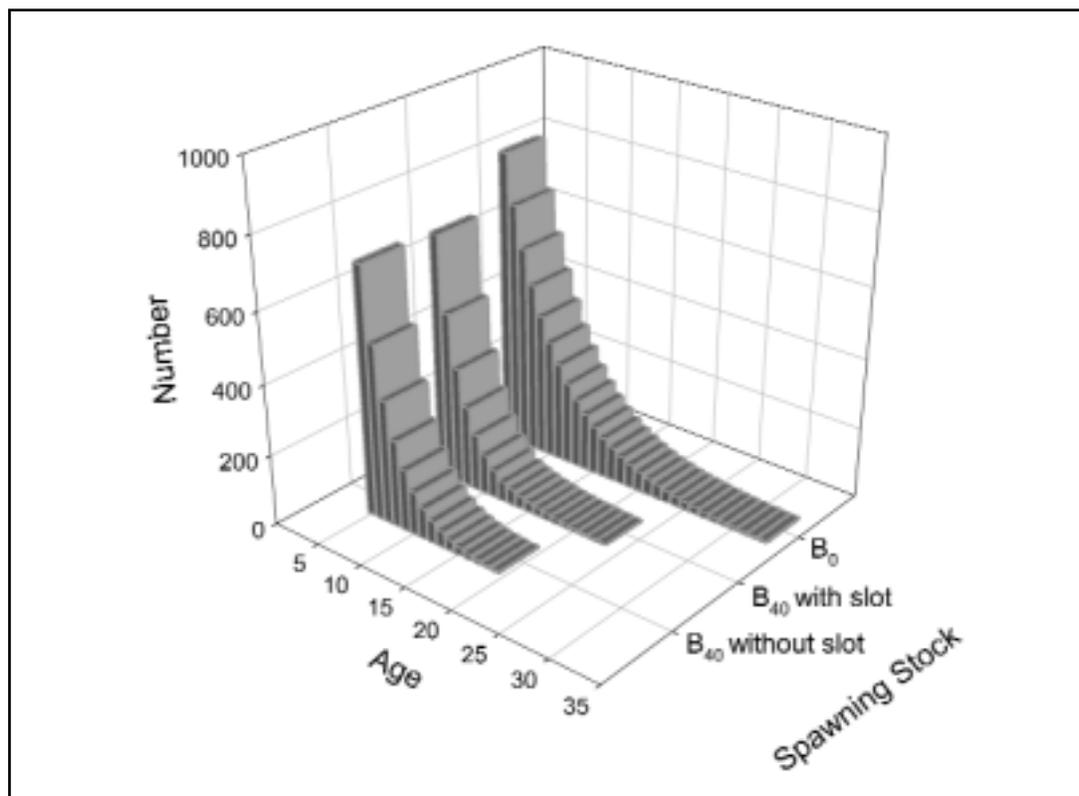


DONNA SCHROEDER

Bocaccio (*Sebastes paucispinus*)

here, successful recruitment may come from restricted temporal and spatial oceanographic windows that change from year to year (Larson et al. 1995), suggesting that management measures should be implemented to preserve minimal spawning stock sizes over the entire geographic range of the stock (Larson and Julian 1999). Marine reserves, placed to represent different habitats within biogeographic and oceanographic regions, therefore offer benefits to stocks that *cannot be achieved by any other means*. No other method of management, even slot limits, can preserve the potential for longevity as well as marine reserves and allow the unique contributions of older fish to accrue to the population. We believe that the implementation of such spatially explicit management tools, combined with conventional approaches, is essential for the replenishment and sustainability of groundfish stocks. 

**Figure 4.** Theoretical effect of a slot limit on the age composition of a population of fish with the same growth and natural mortality characteristics of black rockfish. In this example, the stock is fully vulnerable to fishing between ages 4 and 12 (the slot). Fish older than age 12 are assumed to experience 25% release mortality. Fishing mortality is set at a rate that will result in  $B_{40}$  ( $F = 0.184$  with the slot limit;  $F = 0.165$  without the slot limit). The cohort is considered eliminated when less than 0.5% of the initial cohort (at age 4) remains. For comparison, the theoretical age composition of the virgin stock ( $B_0$ ) is also shown. The unfished stock contains 33 age classes compared to 23 age classes with the slot limit and 19 age classes without the slot limit.



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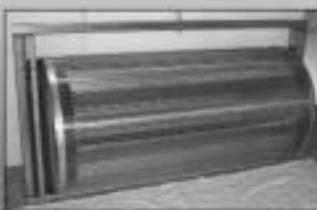
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