# CAN MARINE PROTECTED AREAS RESTORE AND CONSERVE STOCK ATTRIBUTES OF REEF FISHES?

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## ABSTRACT

One of the proposed benefits of marine protected areas (MPAs) is to conserve genetic diversity for life-history traits and to restore some semblance of the life history that was expressed before intense exploitation. Strong size-selective mortality from fishing has promoted an earlier age and smaller size at maturity in many species and a concomitant reduction in subsequent adult body sizes. These attributes are less economically desirable than those of fish from less heavily exploited stocks. We attempted to determine whether the establishment of marine protected areas, and the resulting relaxation of the directional selection produced by fishing mortality, would promote a substantial restoration of later ages at maturity. Our quantitative genetic models, calibrated with historical data from Gulf of Mexico populations of red snapper, Lutjanus campechanus, indicated that adequate variation should remain for life-history traits like age at maturity to respond to new fitness profiles. Marine species with planktonic larvae, including most economically important fishes, have high gene-flow rates that will preclude genetic differentiation between the no-take MPAs and the rest of the population. Any changes in the life history that are promoted by the no-take area may therefore ramify through the entire population. The establishment of no-take MPAs will promote substantial increases in the age at maturity if recruitment into them is not limited by density-dependent mortality. If it is, the benefit of no-take areas for increasing the age at maturity will be decreased. The no-take MPAs must serve as the major source of recruits for nearby fishing areas to produce the proposed benefits. The creation of MPAs will not replace the benefits of limiting age or size biases in harvesting by traditional fisheries management.

The global decline in quantity and quality of fishing stocks has created a need for new methods of stock management (Botsford et al., 1997). Marine protected areas (MPAs) and fishing no-take zones are proving to be valuable tools for management of marine fishery resources (Roberts, 1997; Allison et al., 1998; Lauck et al., 1998). The proposed virtues of MPAs include protection of spawning stock, elevation of recruitment rates, maintenance of the age and size structures of stocks, and preservation of a balance in the frequencies of predatory and prey species (Ballantine, 1991; Bohnsack, 1992; Gubbay, 1995; Shackell and Willison, 1995; Bohnsack and Ault, 1996). One possible benefit of no-take reserves that has received little attention is the protection of genetic resources for life-history patterns within stocks (Plan Development Team, 1990). This benefit is related to the attempt to conserve stock structure, as indicated by molecular genetic markers (Avise, 1998), but is distinct in referring to the genetic basis of the attributes of individual fish that make them economically desirable and sustain higher population numbers (Stokes et al., 1993).

The most important life-history characters for fishery stocks include the size and age at which individuals mature, the distribution of reproductive effort during life, and agespecific survivorship. Changes in these traits can change the size and age structure of a stock, altering its population dynamics and economic value. For example, a decrease in age at maturity appears to entail maturation at smaller sizes and an overall decrease in the adult body-size distribution (Trippel, 1995). Although earlier maturation can be associated with more rapid population growth, the exponential nature of the size-fecundity relationship in many species will combine with the smaller body sizes to reduce substantially the maximum possible yields and the economic value of the fishery (Law and Grey, 1989).

Size-structured mortality, a common result of fishing, can greatly alter the age and size distribution of the spawning population and, potentially, the genetic composition of subsequent generations (Nelson and Soulé, 1987; Bergh and Getz, 1989; Smith et al., 1991; McAllister and Peterman, 1992; Law and Rowell, 1993; Rijnsdorp, 1993). There are two reasons to believe that important fisheries have been altered genetically by size-selective removal of individuals from the spawning pool. First, fisheries are commonly age and size biased, removing the largest and oldest individuals preferentially (see, e.g., Ricker, 1981) and causing marked declines in the average size and age in many heavily fished stocks (Pauly, 1979; Policansky and Magnuson, 1998). Second, the estimated age at sexual maturity is declining in many heavily fished stocks (Trippel, 1995). This change is consistent with predictions from life-history theory about the effects of age-specific mortality (Roff, 1992). Although some of these changes may be attributable to phenotypic plasticity (Reznick, 1993) or other environmental changes, the repetition of the patterns across dozens of species in many locations and the consistency of those patterns with the predictions of life-history theory implicate an evolutionary effect.

Here, we explore the hypothesis that MPAs can protect a stock against further undesirable evolutionary changes and promote a partial restoration of the pre-exploitation life history, particularly restoring later ages at maturity. We base our exploration on the premise that directional selection by fisheries has been promoting earlier age and smaller size at maturity and that this selection pressure will be reversed within the MPAs (cf. Horppila and Peltonen, 1994). We evaluate this hypothesis by attempting to answer three questions. First, is there likely to be enough genetic variation remaining for the age at maturity to respond to selection? Second, will stocks within an MPA be connected strongly enough with those outside of it to overcome the divergent selection pressures in each habitat type such that the age at maturity can increase in the entire fishery? Third, which features of the selection process are most important in promoting an overall increase in the age at maturity? Our approach is to use standard models of quantitative genetics, calibrated with data from red snapper (Lutjanus campechanus) populations in the Gulf of Mexico (Goodyear, 1994), to find likely answers to each question. We will focus on age at maturity because there is ample evidence for an evolutionary effect of fishing pressure and because it is so influential on adult size-structure and consequent economic value of the fishery. Our simulations assume that size and age are tightly linked throughout the fish's life cycle so that selection on size is also selection on age. This expedient assumption is undoubtedly violated in many cases, but we argue that this problem does not limit the generality of our results.

### **DOES ENOUGH GENETIC VARIATION REMAIN?**

ESTIMATING ORIGINAL HERITABILITY.—In order to assess the likelihood that a species will be able to respond genetically to relaxation of directional selection, we must estimate the present heritability of age at maturity. To do so, however, we must first estimate its value before mass exploitation and then estimate the amount of genetic variation lost through the process of evolving the lower ages at maturity. The data available for red snapper are the estimated average age at maturity and its variance in unfished and fished stocks. To estimate the original heritability, we assume that the differences in these values represent the cumulative changes that have occurred in the fished stocks through the selective pressure generated by size- and age-selective harvesting.

We begin with the breeder's equation of quantitative genetics, which describes the standardized response to selection as a function of the heritability and the standardized selection differential (Falconer and Mackay, 1996). This equation is

 $R/\sigma = h^2(S/\sigma)$ 

where R is the change in the average value of the trait across a single generation;  $\sigma$  is the standard deviation (SD) of the trait before selection acts; S is the selection differential, the difference in the average trait value between the selected and the original, unselected cohort; and h<sup>2</sup> is the heritability of the trait, the ratio of the additive genetic to phenotypic variance.

To apply this equation, we must make indirect estimates of the response as well as the differential. We will estimate the cumulative response by the difference between the average ages at maturity in fished and unfished populations. For red snapper, at most six generations have passed (estimated generation time = 14 yrs, Goodyear, 1994) since the onset of heavy exploitation at the beginning of this century. To estimate the cumulative differential, we begin by assuming that fishing exerts complete truncation selection against individuals who are above the average age at maturity. For a symmetric distribution, this assumption means that fishing selectively removes the upper 50%, leaving the lower 50% to contribute to the next generation. For a distribution skewed to the right (as are many distributions of age at maturity), the fraction removed would actually be less, but we will use the assumption of 50%. This level corresponds to a standardized selection intensity (S/ $\sigma$ ) of about 0.80 (Falconer and Mackay, 1996:190, fig. 11.3). The basic equation is therefore converted to

 $R/\sigma = 0.80h^2$ 

To express the cumulative response, we rewrite R as  $x_1-x_0$ , the difference between the average trait value in the original population  $(x_0)$  and that in the first generation after selection  $(x_1)$  and rewrite the basic equation as

$$\left(\mathbf{x}_{1}-\mathbf{x}_{0}\right)/\sigma=0.80\mathrm{h}^{2}$$

or

 $x_1 = 0.80 \sigma h^2 + x_0$ 

If we assume for the moment that parameter values are constant from one generation to the next, then we can express the average value of the trait in the second generation as

$$x_2 = 0.80 \sigma h^2 + x_1$$

and, after x, is rewritten, as

$$x_2 = 0.80 \sigma h^2 + 0.80 \sigma h^2 + x_0$$

or

$$x_2 = 2(0.80 \text{ sh}^2) + x_0.$$

We can write a comparable equation for the average value of the trait after six generations and then rearrange that equation to estimate the heritability as

$$h^2 = (x_6 - x_0)/4.80\sigma$$

This method will provide a conservative (i.e., low) estimate of the original heritability for three reasons. First, weaker selection, perhaps more realistic, would decrease the denominator on the right-hand side and increase our estimate of the original realized heritability. Second, we may have overestimated the number of generations embraced by the period of intense exploitation. Goodyear's (1994) estimates of generation time range up to 20 yrs; if either the 20-yr duration is a better estimate or heavy exploitation began much later than we have surmised, our estimate of heritability will be too low. The estimate is too low because the same difference in average values would have been achieved in fewer generations. Third, the heritability itself is likely to decrease every generation as the population responds to strong selection over such a short period (see below). An underestimate will generate a conservative (i.e., low) assessment of the potential response of current populations to a relaxed selection pressure and therefore offer a conservative assessment of the potential benefits of MPAs.

We used life-table data compiled by Goodyear (1994) and supplemented by information provided by Michael Schirrippa (pers. comm.) to estimate the ages at maturity in fished and unfished populations and their variances. We used as our estimator the age at which 50% of the population is sexually competent because the data are in the form of fish of known age that are or are not sexually competent. For the age in fished populations, this median value is 3 yrs (Moran, 1988, gives a value of 2 yrs). The estimate for unfished populations, which is derived from historical data and modeling of natural mortality rates, is 5 yrs (SD, 2 yrs). These values produce an estimated heritability of age at maturity of 0.21, which is comparable in magnitude to direct estimates for life-history traits from a wide variety of species (Mousseau and Roff, 1987).

ESTIMATING THE REMAINING LEVEL OF GENETIC VARIATION.—Strong truncation selection, like that described above, exercised repeatedly over six generations, will erode the genetic variation for a trait under selection. The current heritability of age at maturity will be lower than the original heritability if the phenotypic variance has changed more slowly than the genetic variance. The precise estimation of this loss for a finite population requires complex calculations with parameter estimates that we cannot obtain for these systems (Hospital and Chevalet, 1996). If we assume, however, that the original target population was very large and that the genetic variation in age at maturity is formed from many loci, we can estimate the erosional effect rather simply.

To do so, we return to our earlier assumption that truncation selection removes 50% of the population. For simplicity, we assume that age at maturity has a normal distribution; only a radical departure from this assumption would change our broad result. Under these assumptions, following Bulmer (1985:154), we can calculate the level of genetic variation after a round of selection and response as

$$V_{A}(t) = 0.5[1-h^{2}(t-1)]V_{A}(t-1)+0.5[V_{A}(0)]$$

where  $V_A(t)$  is the additive genetic variance in generation t,  $V_A(0)$  is the additive genetic variance at the start of selection, and  $h^2(t)$  is the heritability in generation t. If we assume that the phenotypic variance is unchanged by the selection process, then we can estimate the present heritability of age at maturity at approximately 0.18, a drop of about 14% from the estimated initial value.

Data from Goodyear (1994) suggest, however, that the phenotypic variance is half of what it appears to have been before intensive exploitation. If we take the initial value of the additive genetic variance to be 0.84 (our estimate of the original  $h^2$  multiplied by the estimated phenotypic variance), then we can estimate the magnitude of additive genetic variance available in the first generation after selection as 0.75. We can continue through six generations, allowing each new phenotypic variance to be 0.89 times that in the previous generation (to yield a net halving after six generations, reflecting the data). Under these conditions, we would estimate the present magnitude of additive genetic variance to be approximately 0.65, yielding an estimated heritability of 0.33. This value is higher than our estimate of the original heritability because the additive genetic variance may have decreased more slowly than the phenotypic variance.

We can make another assessment of the evolutionary potential of the present stock of red snapper that is divorced from any concerns about the change in the phenotypic variance. To do so we can compare the 'evolvability' (Houle, 1992) of the age at maturity of fished with unfished stocks. The 'evolvability' is the ratio of the additive genetic variance to the average trait value; these numbers for the unfished and fished populations are approximately 0.17 and 0.22 respectively, and, conservatively, we conclude that the evolvability of present stocks is comparable to that in the ancestral stocks.

These calculations indicate that red snapper populations will in fact have enough genetic variation in age at maturity to rebound after a relaxation of the directional selection imposed by fishing mortality. This conclusion is likely to extend to most fishery species, because, under the assumptions of very large populations and polygenic control, the cumulative loss of genetic variation across many generations is unlikely to exceed 20% of the original level of variation even with 50% selective mortality (Bulmer, 1985; Roff, 1997). This is good news for fisheries in general, especially for species with long generation times relative to the duration of intense exploitation because of the small number of generations actually selected. CAVEATS.—We are obliged to offer a few caveats about these calculations. First, our conclusions may not hold if the genetic variation in age at maturity is based on only a few loci with large effects on the phenotype (Turelli and Barton, 1990). In this case, strong truncation selection over a few generations could remove virtually all of the genetic variation for a character, leaving current populations unable to respond to any relaxation of directional selection. At present, we have no way to evaluate the validity of assuming polygenic control, although the general success of polygenic methods in predicting short-term responses to selection offers some support (Roff, 1997).

Second, our calculations do not include any attempt to integrate a lag in the response to selection created by the considerable age structure of unfished populations (see Charlesworth, 1994). This lag would bias our estimate of present genetic variation downward and so contribute to its conservatism. However, there is likely to be an even greater lag in any upward response to relaxed selection, so the age at maturity may not rebound as quickly in real time as our estimates of heritability or evolvability would imply.

Third, our conclusions could also be vitiated if the genetic effective sizes of these populations are small or became reduced through the process of selection (Turelli and Barton, 1990). Again, strong selection in a population of small effective size could remove all of the genetic variation for age at maturity, but population sizes for most fishery species, at least for these reef fishes, appear to be large in genetic terms (Table 1, see below), even at present levels of exploitation. It is possible that the size-fecundity relationship in females, particularly in unfished populations, created an effective size far below what census numbers would suggest because of the enormous contribution of a few very large females (Hedgecock, 1994). On the other hand, the reproductive value of large females appears quite low despite their vast fecundity (see Goodyear, 1994), so the importance of this effect is unclear to us.

On the whole, we believe most species will have the genetic capacity to respond to the altered selection pressure produced by MPAs, although the lag time in that response may not be negligible.

WILL THE STOCK STRUCTURE ALLOW THE AGE AT MATURITY TO RESPOND IN THE ENTIRE FISHERY?

CONCEPTUAL MODEL.—The creation of MPAs will create two habitats, one in which fishing pressure continues to select for an early age at maturity and another (within the MPA) in which release from fishing pressure will presumably select for a later age. The habitats are connected by the gene flow that results from the wide larval dispersal characteristic of most reef species. Adult movements, at least in red snapper (Moran, 1988; Goodyear, 1994), are sufficiently limited that individuals are likely to remain in the immediate area where they have settled.

The long-term outcome of evolution in this situation depends on the relative strength of the divergent selection pressures compared to the rate of gene exchange between the habitats (Bulmer, 1971). If the divergent selection pressures in each habitat are so strong as to overwhelm the effect of gene flow between them, the subpopulations in the two habitats will remain genetically differentiated for age at maturity. The average ages in the two habitats may be more similar than the respective optimal ages because of the blending effect of gene flow, but the subpopulations will differ persistently. In this case, MPAs will be of little or no benefit in restoring a later age and large size at maturity in the entire fishery. If the strength of selection is sufficiently weak compared to gene flow, the subpopulations will be only weakly differentiated, if at all, for age at maturity. In this case, the effect of releasing the subpopulations within the MPAs from fishing pressure will diffuse throughout the stock and cause an overall elevation in the age at maturity. The average age at equilibrium may not equal exactly the optimal age for an unfished population, but it will be close to it.

To evaluate the likely outcome, we offer a conceptual model of a system of MPAs that exchange migrants with nearby areas where fishing takes place (Fig. 1). We envision MPAs on the order of several square kilometers surrounded by a much larger expanse of habitat where fishing takes place, consistent with the relatively small MPAs planned at present. We also assume high potential for long-distance larval drift, consistent with that for most economically important reef species. Our basic question can be rephrased in operational terms: Given a specific difference between habitats in their optimal ages at maturity, what fraction of this difference will actually be realized in the long run between habitats? If a substantial fraction of this difference will be realized, then the fishery is best characterized as a metapopulation system, and the benefit of the MPAs will not ramify throughout the fishery. If only a small fraction is realized, the fishery will be better characterized as a single evolutionary unit and the benefit of the MPAs may ramify through the fishery.

The mathematical version of this question is given by Bulmer (1971) as

$$(M_1 - M_2) = \frac{h^2 k (1 - 2m)}{h^2 k (1 - 2m) + 2m} \cdot (\theta_1 - \theta_2)$$

where  $M_1$  and  $M_2$  are the average trait values in the two subpopulations when genetic equilibrium has been attained,  $\theta_1$  and  $\theta_2$  are the optimal values of these traits in each subpopulation,  $h^2$  is the heritability of the trait, k is a measure of the intensity of selection on the trait, and m is the migration rate between the two habitat types, expressed as the proportion of individuals in one habitat that immigrated from the other. The intensity of selection is estimated from a Gaussian fitness profile, where fitness as a function of trait value y, denoted  $\omega(y)$ , is given as

$$\omega(\mathbf{y}) = \exp\left(-c(\mathbf{y}-\mathbf{\theta})^2\right)$$

The intensity of selection, k, is scaled between 0 and 1 (higher values indicate stronger selection) and is calculated as

$$\mathbf{k} = 2\mathbf{c}\mathbf{V}/(1+2\mathbf{c}\mathbf{V})$$

where V is the phenotypic variance and c measures the breadth of the fitness profile (smaller values of c imply a wider region of high fitness and weaker selection). The Bulmer equation expresses the level of equilibrium divergence as a function of the differ-



Figure 1. An illustration of our conceptual model for modeling life-history evolution in MPAs. We envision that MPAs will receive migrants from nearby areas experiencing fishing and that they will in turn send migrants back to those areas. Note that this model assumes some level of larval retention within the MPAs as discussed in the text. Fitness ( $\omega(y)$ ) is plotted against age at maturity with the optimal age at maturity ( $\Theta_{\rm F}$  for area with fishing and  $\Theta_{\rm MPA}$  for area inside MPAs). MPA and fished areas are exchanging migrants (m).

Species	N_m	N <sub>f(c)</sub>	Reference
North American Atlantic a	nd Gulf of Mexico	o Coastal	
Atlantic menhaden		800,000	Avise, 1992
Atlantic herring		273,000	Kornfield and Bogdanowicz, 1987
Gulf menhaden		250,000	Avise, 1992
Red drum	>>10	93-95,000	Gold et al., 1993, 1994a,b
Red snapper	>10		Gold et al., 1994b
Spotted seatrout		75,000	Gold et al., 1993
Greater amberjack		57,000	Gold et al., 1993
Black drum	>>10	17,000	Gold et al., 1993, 1994b
Red grouper	>>10	10,000	Gold and Richardson, 1994
Black sea bass		5,000	Avise, 1992
North American Pacific Co	oastal		
Woolly sculpin	5.7-7.5		Waples, 1987*
Island kelpfish	8.7-19.4		Waples, 1987*
Bluebanded goby	30.0-42.9		Waples, 1987*
Blacksmith chromis	12.0-87.4		Waples, 1987*
Opaleye chub	24.9-62.3		Waples, 1987*
California sheephead	14.4-23.5		Waples, 1987*
Halfmoon chub	26.1		Waples, 1987

Table 1. Examples of estimates of gene flow for marine fish species. This is not an exhaustive review; it is limited to North American coastal and reef-dependent species, especially economically important ones. Estimates of gene flow  $(N_em)$  and the effective number of females  $N_{fe}$  are reported, as appropriate.

\*Ranges are derived from multiple estimates reported.

ence in optima; we will estimate the fraction of the difference in optima that can be obtained  $((M_1 - M_2)/(\theta_1 - \theta_2))$  by using estimates of k and m from the literature.

THE DATA AND CALCULATIONS.—We can estimate migration rates from estimates of the number of effective migrants per generation (N m, where m is the level of gene flow and N is the genetic effective population size) obtained from analysis of neutral or nearly neutral molecular markers in fishery species. The results of these studies universally indicate very open population structure (that is, very high gene flow) for estuary-dependent, reef-associated, and pelagic fish species (Table 1; Ward et al., 1994; Gold and Richardson, 1998). The published estimates of N m for economically important marine fish species all exceed 5, and most exceed 10. These estimates of high gene flow are consistent with the life history of most marine fish, which includes a drifting larval phase sometimes lasting several weeks (Allison et al., 1998). The exception to these estimates, *Acanthochromis polyacanthus*, is a reef species that is unusual in lacking a larval phase (Planes and Doherty, 1997).

An emerging knowledge of drift distances in the pelagic larval life stage of reef species suggests that many individuals (perhaps 10% or more of recruits) disperse and settle significant distances from the location of their birth (Fig. 2; Jones et al., 1999; Swearer et al., 1999; Warner et al., this issue). The balance of local and long-distance recruitment (i.e., recruitment not from adjacent reefs or islands) depends on poorly known factors including vertical migration, stratified current flows, and MPA location (Cowen et al., 2000). An argument for low gene-flow rates might be made from observations of regional stock collapses and failure of immigrants to recolonize an area. Normal gene flow and recolonization may, however, be quite different entities ecologically and can produce different genetic patterns (Wade and McCauley, 1988; Ewens, 1989; McCauley, 1992). Moreover, the spatial and temporal scales at which recolonization failed to replenish a



Figure 2. Three possible patterns of dispersal distance for marine fish. Only pattern A promotes local differentiation within MPAs with dimensions in the tens of kilometers. Patterns B and C necessitate strong selection in the MPA to prevent selection from distant areas from swamping local effects. A. Possibly appropriate for fish lacking pelagic larvae (Planes and Doherty, 1997). B. Possibly appropriate for reef species with some fraction of their larvae entrained in local currents or with very short larval period (e.g., Warner et al., this issue). C. Pattern predicted by population-genetic data and life cycle of many marine fishes with moderate to extended larval period.



Figure 3. The amount of realized phenotypic divergence between an MPA and fishing area, expressed as a proportion of the actual difference in fitness optima depicted as a function of the intensity of selection (k from the Bulmer equation) at three levels of gene exchange (topmost line downward: 0.01, 0.05, 0.10). The realized divergence is calculated as the difference in average ages at maturity that will be maintained between MPAs and the surrounding area  $(M_1 - M_2)$  divided by the difference in their optimal ages at maturity  $(\theta_1 - \theta_2)$ .

stock are much larger than the scales relevant to analyses of gene flow and normal migration (Pogson et al., 1995; Grant and Bowen, 1998).

An estimate of gene flow (m) from estimates of the effective number of migrants (N<sub>e</sub>m) requires some assessment of the effective population size. We can obtain these to an order of magnitude from estimates of the effective number of females (Nf<sub>e</sub>) obtained from mitochondrial DNA (Table 1). These numbers exceed 1000, and many are orders of magnitude higher. If we take the order of magnitude of N<sub>e</sub>m to be 10<sup>1</sup> or higher, and the order of Nf to be 10<sup>3</sup> or higher, then gene-flow rates could range in order of magnitude from  $10^{-3}$  to  $10^{-1}$ . However, what we require is an estimate of gene flow between the two habitat types, not the general level of gene flow among all locations within a species' range. Given the model for MPAs (Fig. 1), the gene flow rate between habitats is likely be at the upper end of the range (~ $10^{-2}$  to  $10^{-1}$ ). Except in embayments or island areas with locally isolated current patterns, existing and proposed MPAs are probably small enough to ensure that 10% or more of recruits will come from outside areas (adult fish, Attwood and Bennett, 1994; larvae, Warner et al., this issue). If MPAs serve as a significant source pool for recruitment outside the MPA, the movement rate outward will approach 1 to 10% or more, at least in areas adjacent to the MPAs.

Rijnsdorp's (1993) work offers estimates of c and k that can be used in the Bulmer equation. Rijnsdorp estimated the fitness profiles for age at maturity of historical and contemporary stocks of North Sea plaice (*Pleuronectes platessa*) and calculated c = 0.004814 and k = 0.05675. We examined a range of realistic scenarios for c and V and found that k values tended to fall between 0.02 and 0.05, although very intense selection could drive k as high as 0.1. We evaluated the Bulmer equation for a heritability of 0.21 because the real heritabilities are likely to be close to this value (see previous section).

With these values, the Bulmer equation reveals that, for likely parameter values, only a small fraction of the difference in optima between habitats will be realized at equilibrium



Figure 4. Two models of spatially structured selection and homogenization of larvae in the water column, soft and hard selection. Production of larvae (r) and settlement into the juvenile population (S) are indicated by arrows, whereas MPA and fishing refer to habitats producing larvae (arrows away) or receiving recruits (arrows toward). Under both models, production is a function only of the area covered by each habitat and the numbers of individuals per unit area. Under soft selection, settlement is density dependent and thus may differ between habitats; under hard selection, there is no density dependence, and settlement rate is a function only of the area covered by each habitat. Modified from Hedrick (1983: 207).

(Fig. 3). If gene exchange values are of the order of  $10^{-1}$ , less than 9% of the actual difference between optima will be attained, even with strong selection. If selection is relatively weak (k ~ 0.02–0.04), the realized difference will be negligible, but if gene exchange rates are as low as  $10^{-2}$ , a substantial fraction of the difference between optima will be attained (~17% to 50%), even if selection is weak. Higher levels of heritability increase the likelihood of persistent differentiation, but the effect is weak relative to the major effect of variation in the gene exchange rate.

These calculations indicate that, if our model of MPAs and its concomitant presumptions about the order of magnitude of gene exchange between MPAs and the surrounding habitat is correct, evolution in a reef fishery like red snapper is best characterized as occurring within a single panmictic unit. The system will not behave as a metapopulation, at least in evolutionary terms. This conclusion will be stronger for species less sedentary than red snappers. The benefits of MPAs for life-history restoration may therefore ramify through the fishery.

# Which Features of the Selection Process Will Determine the Effect of MPAs on the Restoration of Historical Life-History Traits?

CONCEPTUAL MODEL.—Although the population will evolve as a panmictic unit, the issue to resolve is how to combine the contributions of the selected cohorts from each habitat and estimate the age at maturity that will be attained. This problem was first considered in mathematical terms by Levene (1953). To approach the problem with his method, we assume that larvae from inside and outside the MPAs are mixed randomly

before settlement (Fig. 4). Under Levene's model, termed soft selection, each niche (inside and outside the MPA, in our case) contributes a constant number of propagules per unit area to the larval pool, so the relative contribution of each niche to the larval pool is determined by its relative spatial coverage. This model assumes that settlement takes place at the same rate (number per unit area) in all niches, so the number of settlers from the pool is equal to the relative spatial coverage of each niche.

Dempster (1955) offered another view of the same scenario. He suggested that the density of individuals in each niche could depend on the niche's habitat quality. Variation would therefore be created between niches in the number of individuals per unit area that each contributes to the larval pool (Fig. 4). In this scenario, denoted hard selection, each niche's contribution depends not just on its respective spatial area but also on its carrying capacity; the niche with higher carrying capacity (numbers per unit area) contributes more to the pool. This view is more likely to reflect the effect of MPA's because we expect population sizes to increase inside their boundaries (Watson and Ormond, 1994; Russ and Alcala, 1996).

We used each selection regime to estimate the effects of MPAs on the final age at maturity to be attained. The logic of our procedure was to begin by estimating survivorship curves within and without the MPA. We combined these curves with estimates of age-specific fecundity in red snapper to estimate curves of the product of survivorship and per capita fecundity, from which we could estimate the optimal age at maturity in each niche. We then combined these curves for a hard-selection scenario and a variety of soft-selection scenarios to estimate the final age at maturity the fishery would attain. We examined the effect of combining curves under these scenarios for a range of areal coverage of MPAs from 0% (i.e., no MPAs) to 60% (admittedly unrealistic MPA coverage).

METHODS.—We used Goodyear's (1994) stock-assessment data to estimate survivorship curves for current red snapper stocks and 'unfished' snapper stocks (Fig. 5A). Goodyear's (1994) assessment includes information drawn from historical records of red snapper life expectancy (Camber, 1955) and estimates of natural mortality rates in the absence of fishing derived from modeling efforts (Nelson and Manooch, 1982). We combined these curves with data on age-specific fecundity (which we assume does not differ between niches) to develop curves for the product of age-specific survivorship (l(x)) and age-specific fecundity (m(x)) for each niche (Fig. 5B). In a stable population, a delay in the age at maturity is favored for all ages for which this product increases in the next age class (Bell, 1980; Roff, 1984, 1992). Thus the maximum point in the curve corresponds to the optimal age at maturity. Obviously we are assuming that eventually a stable equilibrium density will be reached within and without the MPA.

The different heights of the l(x)m(x) curves for each niche reflects the relative densities of individuals in each age class that we might expect to observe in each niche. This result allows us to calculate the age at maturity in the hard-selection scenario by simply weighting each curve by the proportional coverage of each niche. For example, in the 20% MPA case, we multiplied the unfished l(x)m(x) values by 0.2 and the fished l(x)m(x) values by 0.8 and then added them to produce a new curve of l(x)m(x) values. The optimal age at maturity for the fishery as a whole is then the age corresponding to the maximum point of this new curve. Although, at first glance, this procedure might appear to be the softselection procedure, we have performed the calculations so that the information about differential densities is carried by the l(x)m(x) curves, and thus no further modification is necessary.



Figure 5. Hypothetical red-snapper life-table parameters used in simulations. A. Survivorship curves for populations inhabiting fished and unfished (MPA) areas. B. L(x)m(x) curves for fished and unfished areas. Note the difference in height of the two curves and range of age classes present in each. Curves were fitted by LOWESS regression to illustrate general patterns.

We modeled the soft-selection scenario in two steps. First, we produced an l(x)m(x) curve for an MPA that included a density-dependent reduction in the number of age-class 0 recruits. This reduction will effectively lower the l(x)m(x) curve within an MPA toward the height of the curve for the fished niche. We performed this adjustment for four levels of recruitment limitation (50, 80, 99, and 99.8% decrements). We selected the final value (99.8%) because it brings the densities at each age class down to the levels outside the MPA. Our second step was to combine these l(x)m(x) curves for the MPA with the curves for the fished niche in the same way we combined them for the hard-selection scenario and proceed to estimate the optimal age at maturity for the entire fishery accordingly.

RESULTS.—Hard and soft selection yielded different prospects for MPAs (Fig. 6). Under hard selection (density-independent recruitment), the optimal age at maturity was 10 yrs in the MPA but only 5 yrs in the fished area. For the fishery as a whole, even a small amount of area in an MPA promotes a substantial increase in the final age at maturity. For example, with only 1% of the area in MPAs, the optimal age at maturity rises from 5 yrs, in the absence of MPAs, to 8 yrs. With 10% of the area in an MPA, the optimal age at

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Figure 6. The optimal age at maturity predicted by our simulations with different percentages of the habitat in MPAs. The percentage survival of recruits into the MPA from density-dependent limitation of settlement (soft selection) is indicated beside each curve (see text for more explanation). The results of hard selection (no density-dependent settlement limitation) are the same as the curve for 50% survival.

maturity in the entire fishery will be close to 9 yrs. Further increases in MPA area have diminishing effects.

The results under the soft-selection scenario resembled those for hard selection if the density dependence was weak. For example, recruitment limitations of up to 50% produce results indistinguishable from those of hard selection. The reason is that, even with 50% reduction in recruitment, the numbers in the MPA still exceed those in the surrounding area by a substantial amount (recall that the survivorship curves in Fig. 5A are on a logarithmic scale). Stronger density dependence reduces the benefits of the MPA by bringing the numbers of individuals inside and outside the MPA closer to one another. The benefits of the MPA are particularly reduced when the area in MPAs is within a realistic range (most probably below 10%). Restoration of the unfished age at maturity with strong density-dependent limitation only occurs at highly unrealistic levels of MPA coverage.

### DISCUSSION

We have made three points. First, exploited fish populations are likely still to retain sufficient genetic variation for life-history traits to respond to a relaxation of the selection pressure exerted by fishing mortality. Second, reef-fish populations inside and outside MPAs are likely to respond as a single, panmictic unit (there will be exceptions; see Kinsey et al., 1994; Conover, 1998). Third, under a variety of assumptions, MPAs are capable of contributing to the restoration of the original life history of heavily exploited species.

The first conclusion is consistent with traditional quantitative genetic theory (Roff, 1997). Despite the many assumptions we made in order to arrive at estimated parameter values, the conclusion we have drawn is a very general one and a conservative one. The most critical assumptions in our calculations are those of polygenic control and large effective population sizes during selection; if either is violated, our analyses could be incorrect.

The second conclusion is also drawn conservatively. The Gaussian selection model we employed produces strong selection and sharp divergence in selection pressures. Other models of optimizing selection, such as those using quadratic deviations of fitness from the optimum, would predict lower intensities of divergent selection and therefore even less divergence. It is quite likely that high levels of gene flow between habitats will be the rule; only in the central portions of very large MPAs are recruits likely to come solely from within the MPA. Indeed, gene flow may actually be asymmetrical. If MPAs do function as significant sources for larvae that will be recruited outside the MPA, and if the carrying capacities within the MPA are high, then a substantial level of gene flow out from the MPA to the surrounding area will result. This flow will connect the two habitats and will allow an easier restoration of a later age at maturity.

The first two conclusions provide the basis for the third. The beneficial effects of MPAs in reversing the effects of long-term directional selection depend on the differences between the survivorship curves inside and outside the MPA. Our modeling employed strikingly different curves; smaller differences would lead to smaller predicted benefits of the MPA. The modeling reveals the importance of estimating those curves in order to assess fully the potential value of the MPA.

The benefits under a hard-selection scenario are straightforward, whereas those under the soft-selection scenario would be weakened by strong density-dependent recruitment. The traditional wisdom of fisheries biology predicts a humped stock-recruitment curve for fishes (Everhart and Youngs, 1981). Therefore, although the soft-selection model is probably most appropriate for MPAs, the form of density dependence could be complex. For example, Quinn et al. (1993) argue for an Allee effect in the stock-recruitment curves of benthic marine invertebrates. Our reduction of recruitment and survivorship for all age classes would be too simple a form of soft selection in that case. Variation in the degree of mortality across age classes could alter the resulting optimal patterns of life-history allocations as well (Taylor and Gabriel, 1992) and would be a fruitful direction for future modeling, especially if empirical information delimiting the range of possible patterns were available.

All of our calculations that indicate a benefit for MPAs are based on the implicit assumption that they are 'source' sites for recruits. In fact, their role as 'sources' is the origin of their benefits. When density-dependent recruitment limitation was severe, in effect, the population size within the MPA did not differ from that outside the MPA. In this case it is not surprising that the MPA no longer provided a benefit for life-history conservation. Clearly, MPAs must be placed in areas with proper habitat to encourage and sustain large fish populations if they are to provide many of the benefits we desire (Crowder et al., this issue). Field studies of extant MPAs indicate that fishes are nonrandomly distributed around them and tend to accumulate inside (Polunin and Roberts, 1993; Watson and Ormond, 1994; Russ and Alcala, 1996). This effect would increase the prospects that the MPA would serve as a 'source', and perhaps even MPAs that cover a relatively small geographic area may serve to reseed a relatively large proportion of the population.

MPAs are not, however, limited to beneficial or neutral roles; in fact, an MPA could do harm if density dependence in juvenile survival or adult fecundity were extremely strong (cf. Forrester, 1995). These effects would have two negative effects for the fishery. First, they would limit the ability of the MPA to serve as a source for the remainder of the population. Second, such strong density-dependence could itself select for continued early maturity (Roff, 1997) and preclude any benefit at all from the relaxation of fishing pressure. Further modeling work ought to be undertaken to clarify the conditions under which this scenario might occur. Regardless of what further modeling might reveal, however, this possibility places a higher premium on empirical work that would illuminate the likely extent of density-dependent demographic processes within MPAs.

The allocation of protected area into patches of various sizes could affect the benefits of an MPA system in promoting a net relaxation of the directional selection pressure produced by fishing. If the density of fishes in MPAs is a linear function of area, the specific allocation is irrelevant under either hard or soft selection, but nonlinear functions imply that some allocations will outperform others. If densities increase with area at an accelerating rate, then fewer, larger reserves are preferable under either hard or soft selection. If densities increase with area at a decelerating rate, the optimal allocation may depend on whether a hard- or soft-selection scenario is more likely. Further modeling would serve to identify the locations of trade-offs between the number and size of MPA's under each scenario.

Finally, there is a distinct possibility that, even under the conditions most conducive to restoring the original life history (e.g., high migration among habitats, hard selection), the fishery as a whole may not respond or may respond too slowly for the MPA to be perceived as effective. First, there will always be a lag in the response of a trait to a shifting optimum (Taylor, 1989; Lynch and Lande, 1992), and the added spatial dimension of the shift in this case adds another type of lag effect (Pease et al., 1989). In addition, during the transition, fishing mortality may increase for immature fish from the MPA who are found outside the MPA; this effect would weaken any selection for later maturity. We note that we did not address the question of how long it might take for this restoration process to unfold; we addressed only the putative endpoint. More sophisticated work ought to be developed to address whether in fact this process could unfold fast enough, relative to changing economic conditions, that the MPA could be perceived as effective and therefore worth maintaining.

However beneficial an MPA might be in restoring the pre-exploitation life-history attributes of fisheries, the deployment of MPAs should not be seen as a substitute for other measures in stock management. At best, only a small percentage of suitable habitat will be deployed into MPAs, and their ecological as well as genetic benefits are likely to be circumscribed by this limited deployment. We believe, at least for the genetic benefits, the effectiveness of MPAs remains arguable. We have shown the circumstances under which they could be effective, but we have not fully investigated the real likelihood of success. In the face of this uncertainty, it would be decidedly unwise to abandon other measures and place our hopes on this single tactic.

#### ACKNOWLEDGMENTS

We thank J. Bohnsack for first encouraging us to pursue the relevance of gene-flow-selection balance to the management of marine fisheries with no-take areas. We also thank M. Schirrippa for his help with understanding red snapper life histories; T. Turner for sharing data on population structure; and C. Osenberg, C. St. Mary, and M. Wayne for valuable discussions of these ideas. Our research is supported by National Institutes of Health award NIH-MBRS S06 GM08205-11 (Trexler) and National Science Foundation award DEB 99-03925 (Travis).

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