STAGE STRUCTURE, DENSITY DEPENDENCE AND THE EFFICACY OF MARINE RESERVES

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ABSTRACT

The habitat requirements of fishes and other marine organisms often change with ontogeny, so many harvested species exhibit such extreme large-scale spatial segregation between life stages that all life stages cannot be protected within a single marine reserve. Nevertheless, most discussions of marine reserves have focused narrowly on single life-history events (e.g., reproduction or settlement) or a single life stage (e.g., adult or recruit). Instead, we hypothesize that an effective marine reserve system should often include a diversity of protected habitats, each appropriate to a different life stage. In such a case, the spatial configuration of habitats within reserves, and of separate reserves across larger spatial scales, may affect how marine resources respond to reserve design. We explored these issues by developing a mathematical model of a fish population consisting of two benthic life stages (juvenile and adult) that use spatially distinct habitats and examined the population's response to various management scenarios. Specifically, we varied the sizes of reserves protecting the two life stages and the degree of coupling between juvenile and adult reserves (i.e., the fraction of the protected juvenile stock that migrates into the adult reserve upon maturation). We examined the effects when density dependence operated in only the juvenile stage, only the adult stage, or both. The results demonstrated that population stage structure and the nature of density dependence should be incorporated into the design of marine reserves but did not provide robust support for the general tenet that all life stages must be protected for an effective reserve system. The results indicated that biological considerations, alone, were insufficient for design of the optimal marine reserve. Instead, it was necessary to consider the value (e.g., socioeconomic or ecological) of each biological outcome; under some value functions, a mixed strategy (i.e., protecting both life stages) was best, whereas for others, the best solution focused on a single life stage. Resolving issues of marine reserve design, especially for stage-structured populations, will require more detailed study of stage-structured populations and a more explicit integration of biological and socioeconomic models.

Marine reserves are often touted as a panacea for resource management. Presumed benefits include stock preservation and increased fisheries yields resulting from transport of larval production (and migration of older fishes) out of reserves (see, e.g., Plan Development Team, 1990; Roberts and Polunin, 1993; Clark, 1996; Lauck et al., 1998; but see also Allison et al., 1998; Bohnsack, 1998). The design of marine reserves is sometimes guided by model systems involving specific target species, such as gag grouper (*Mycteroperca microlepis*) (Koenig et al., this issue). This approach assumes that reserves will have similar benefits for other target species. Because their implementation can be difficult, both politically and economically, it is essential that reserves live up to expectations. They cannot simply be evaluated empirically after they are established. Indeed, tremendous resources can be wasted, and public confidence eroded, by a hit-and-miss approach. Mathematical models can provide initial insight into the implications of alternative strategies and can reveal how the implications depend on specific characteristics

of the managed system. Thus, theoretical investigations can help improve the design of marine reserves and clarify the type of empirical data needed to evaluate their efficacy.

Most exploited fishes exhibit complex habitat requirements that change with ontogeny. The segregation of the life cycle of a 'typical' marine fish into a planktonic larval stage and a subsequent benthic stage is often recognized in existing models of marine reserves. Yet, because planktonic stages are not easily subject to management action, attention is generally focused on the benthic stage (see, e.g., Attwood and Bennett, 1995; Man et al., 1995). Within the benthic stage, however, many fishes continue to undergo ontogenetic changes in their habitat use and spatial distribution. Sometimes these changes are so dramatic that all benthic life stages could not possibly be included within any single reserve (see, e.g., Koenig et al., this issue). For example, in the Gulf of Mexico, gag typically recruit to estuarine seagrass beds, where they spend the first several months of their benthic life. Juvenile gag then migrate 10–30 mi offshore to hard-bottom reefs, where they spend an additional 2–6 yrs. Upon maturation, gag disperse further offshore (60–100 mi) to join other reproductive individuals at traditional spawning sites. Thus, gag use at least three potentially critical, and spatially segregated, benthic habitats at different stages in their life history (Hood and Schlieder, 1992; Ross and Moser, 1995; Coleman et al., 1996; Koenig and Coleman, 1998; Lindberg and Loftin, 1998; Koenig et al., this issue). Any of these spatially separated habitats might be considered "essential" sensu the Magnuson-Stevens Fishery Conservation and Management Act (Magnuson-Stevens Act, 1996) and worthy of a reserve.

This sort of complex life cycle is not unique and probably occurs in many, if not most, harvested marine species (e.g., fishes, Koenig et al., this issue; crustaceans, Herrnkind et al., in press; the obvious exceptions are sessile invertebrates such as bivalves). As a result of these ontogenetic habitat shifts, populations become segregated into ecologically distinct life stages, giving rise to what we call 'population stage structure'. Importantly, theoretical and empirical work in a variety of aquatic systems demonstrates that stage structure can have serious implications for population dynamics and the response of populations to environmental change (e.g., Crouse et al., 1987; Osenberg et al., 1992; Marschall and Crowder, 1996; Nisbet et al., 1996; Herrnkind et al., in press). Thus, the success of marine reserves is likely to depend critically on the life history of the target species, yet existing theory on marine reserves largely ignores the effect of habitat shifts and population stage structure (but see, e.g., Mangel, this issue; Stockhausen et al., this issue). This limitation is particularly noteworthy given the emphasis on habitat relations in the reauthorization of the Magnuson-Stevens Act (1996).

Recognizing different stages in the benthic life phase refocuses the question of interest away from "should we establish a reserve?" toward "should we establish a reserve for this stage, or that stage, or should we set up multiple reserves each focused on a different life stage?" If multiple reserves are the best strategy, then we must ask whether it matters how these reserves are arranged in space (i.e., how distant they are from reserves protecting the other life stage). Again, we use gag to provide a hypothetical example. Movement from seagrass beds to offshore reefs may occur in such a way that particular seagrass beds primarily supply adults to particular reefs (e.g., those most directly offshore from the seagrass). This potential coupling between seagrass beds and reefs could be used in designing a marine reserve system. For example, seagrass and reef reserves could be set up such that seagrass reserves supply juveniles primarily to the reef reserves, or they could be set up such that the reef reserves receive juveniles that matured in nonreserve seagrass

habitat. The benefits associated with reserve coupling will probably depend on the life-history features of the target species and the effects of density dependence.

In this paper we present a stage-structured model in which we recognize two distinct benthic life stages, 'juveniles' and 'adults', and evaluate the efficacy of marine reserves designed to protect juveniles only, adults only, or both juveniles and adults. In the latter context, we examine the effect of coupling between the juvenile and adult reserves. We also consider how the results are affected by where in the life history density dependence operates most strongly, and we discuss further theoretical and empirical investigations motivated by our initial theoretical exploration.

THE MODEL

The model we developed considers abundance within four spatially separated compartments of the population: juveniles in the reserve (J_R), juveniles not in the reserve (J_N), adults in the reserve (A_R), and adults not in the reserve (A_N). We assumed that adult and juvenile habitats were spatially separated so that a particular reserve included only one habitat or the other. We also assumed that the only movement between compartments resulted from maturation (the production of adults from juveniles) and reproduction (the production of juveniles from adults). Thus, there was no movement, within a stage, into or out of the reserve. A reserve consisted of a portion of the total usable habitat for a life stage, and for simplicity, we assumed that the total amount of area available to juveniles and adults was equal (and gave each a standardized value of 1). The dynamics of juveniles and adults inside and outside the reserve were modeled as:

$$\frac{dJ_R}{dt} = p_J\Big[r_R\big(A_R,p_A\big)A_R + r_N\big(A_N,p_A\big)A_N\Big] - \Big[d_{J,R} + m_R\big(J_R,p_J\big)\Big]J_R \qquad \text{Eq. 1}$$

$$\frac{dJ_N}{dt} = \big(1-p_J\big)\Big[r_R\big(A_R,p_A\big)A_R + r_N\big(A_N,p_A\big)A_N\Big] - \Big[d_{J,N} + m_N\big(J_N,p_J\big)+f_J\Big]J_N \qquad \text{Eq. 2}$$

$$\frac{dA_R}{dt} = b_R\big(\alpha,p_A\big)m_R\big(J_R,p_J\big)J_R + p_A m_N\big(J_N,p_A\big)J_N - d_{A,R}A_R \qquad \text{Eq. 3}$$

$$\frac{dA_N}{d_t} = \Big[1-b_R\big(\alpha,p_A\big)\Big]m_R\big(J_R,p_J\big)J_R + \big(1-p_A\big)m_N\big(J_N,p_A\big)J_N - \big(d_{A,N}+f_A\big)A_N \qquad \text{Eq. 4}$$

where p_J is the proportion of the juvenile habitat in the juvenile reserve; p_A is the proportion of the adult habitat in the adult reserve; $r(A,p_A)$ is the reproductive rate, which is a function of adult density; d is the natural mortality rate; $m(J,p_J)$ is the maturation rate, which is a function of juvenile density; f is the additional mortality rate outside the reserve; and $b_R(\alpha,p_A)$ is the portion of juveniles in the juvenile reserve that move to the adult reserve upon maturation, which is a function of a coupling parameter (α) and the size of the adult reserve (p_A). All rates are habitat and stage specific and are summarized in Table 1. Because of the complexities inherent in this model (i.e., stage structure,

Table 1. Parameters and variables. Ranges and values are provided for parameters and variables, respectively.

Symbol	Meaning	Values
Parameters		
$d_{J,R} = d_{J,N}$	natural juvenile per capita mortality rates	0.2
$d_{A,R} = d_{A,N}$	natural adult per capita mortality rates	0.2
$f_J = f_A$	additional per capita mortality on juveniles	
	and adults in nonreserve habitats	0.4
m_{max}	maximum per capita maturation rate	0.2
r_{max}	maximum per capita reproductive rate	20.0
Variables		
A_N	the number of adults outside the reserve	unconstrained
A_R	the number of adults in the reserve	unconstrained
J_N	the number of juveniles outside the reserve	unconstrained
J_R	the number of juveniles in the reserve	unconstrained
c_J	intensity of density dependence in juvenile stage	0–1 (see text)
c_A	intensity of density dependence in adult stage	0–1 (see text)
P_A	the proportion of adult habitat in the reserve	0–1
p_J	the proportion of juvenile habitat in the reserve	0–1
α	degree of coupling between juvenile and adult reserves	0–1
b_R	probability that juveniles in the reserve will	
	mature into the adult reserve	see Eq. 5
m	the density-dependent maturation rate	see Eq. 6
r	the density-dependent reproductive rate	see Eq. 7

stage-specific reserves, and coupling), we necessarily left out other factors (e.g., fisheries redirection, habitat differences between reserve and nonreserve) that are dealt with elsewhere in this volume (e.g., Crowder et al., this issue; Mangel, this issue; Walters, this issue). Provided below is some additional discussion of the model and its assumptions.

This model does not explicitly consider the planktonic larval stage. It is, however, equivalent to a three-stage model with density-independent larval survival in which larval survival is subsumed within the fecundity function (e.g., Nisbet et al., 1996). Furthermore, we assumed that the overall system was closed: i.e., that input of larvae from outside the reserve and designated nonreserve areas was negligible, as is the case for extremely large spatial scales and might be appropriate for some systems, such as the eastern Gulf of Mexico. We also assumed that the larvae were completely mixed and settled in proportion to the relative areas inside and outside the juvenile reserve. Once in the juvenile habitat, juveniles died at a constant per capita rate (d_J) independent of whether the habitat was protected or not. Outside the reserve, mortality was increased by a factor f, representing fishing on juveniles, by-catch of juveniles in other fisheries, and the effect of any other human activity excluded from the reserve. Juveniles matured into the adult stage at a rate m, which was a decreasing function of juvenile density. Although we did not explicitly consider effects of density on individual growth, some of these effects could be subsumed in the maturation rate.

Juveniles that matured outside the reserve migrated to areas within and outside the adult reserve in proportion to their relative areas (p_A and $1 - p_A$). In contrast, the proportion of juveniles that matured within the juvenile reserve that migrated to the adult re-

serve (b_R) reflected the relative accessibility of the adult reserve and nonreserve areas. In this case, the degree of coupling between the juvenile and adult reserves was represented by α, which is analogous to a dietary preference index that accounts for differences in habitat availability and ranges from 0 to 1 (see Manly, 1974; Chesson, 1983). Thus, the fraction of maturing juveniles from the juvenile reserve that migrated into the adult reserve was described by:

$$b_R(\alpha, p_A) = \frac{\alpha p_A}{(1-\alpha)(1-p_A) + \alpha p_A}$$

Eq. 5

When $\alpha = 0$, none of the maturing juveniles from the reserve migrated to the adult reserve ($b_R = 0$). When $\alpha = 0.5$ migration from the juvenile reserve occurred in proportion to the areas inside and outside the adult reserve ($b_R = p_A$), and when $\alpha = 1$ all juveniles that matured within the reserve area migrated to the adult reserve ($b_R = 1$).

Density dependence was included in the model at the juvenile stage, in the form of density-dependent maturation rates, and at the adult stage, in the form of density-dependent reproductive rates. In both cases we used the Beverton-Holt form of density dependence (Getz and Haight, 1989):

$$m_i(J_i, p_i) = \frac{m_{max}}{1 + \left(\dfrac{c_J J_i}{p_i}\right)}$$

Eq. 6

and

$$r_i(A_i, p_i) = \frac{r_{max}}{1 + \left(\dfrac{c_A A_i}{p_i}\right)}$$

Eq. 7

where c_J and c_A are constants that reflect the strength of density dependence, and the subscript i refers to either the reserve (R) or the nonreserve (N) area. We assumed that the competition parameter, c, and the form of density dependence were the same inside and outside reserves. Further, we assumed that habitats inside and outside reserves did not differ from one another and that adults and juveniles incurred similar mortality rates: i.e., $d_{J,N} = d_{J,R} = d_{A,N} = d_{A,R} = 0.2$, and $f_J = f_A = 0.4$. The primary differences between individuals in a reserve and outside were their local density and their susceptibility to additional mortality (e.g., fishing). Thus, the overall strength of density dependence inside and outside the reserve was mediated entirely by the difference in density inside and outside the reserve.

We analyzed the models primarily by finding equilibria using the NSolve function in Mathematica 3.0 (Wolfram, 1996). This function provides numerical approximations to all roots of a polynomial equation. In the cases involving density dependence in only one life stage, this approach was successful and resulted in three roots: one negative, one

zero, and the other positive. We selected and report nonzero positive roots. Thus, we are confident that, in each of these analyses, we have identified the only nonzero, positive model equilibrium. Simulations confirmed that these solutions were stable, although we did not do a formal stability analysis. In the few cases involving density dependence in both stages, NSolve was not effective in identifying solutions. We instead used the FindRoot function to search for solutions. This function searches for a solution in the vicinity of a seed value and reports only the first solution encountered. We used $A_R = A_N = 30$ and $J_R = J_N = 50$ as seeds and did not do a more exhaustive search.

APPLICATION AND ANALYSIS OF THE MODEL

Our evaluation of the model required three interrelated steps: (1) specification of the various management scenarios (i.e., identification of the parameters that can be managed, such as reserve size and the constraints on these parameters); (2) application of the model to determine the results associated with each particular management scenario (e.g., specifying how the fish stock responded to different reserve sizes); and (3) specification of the socioeconomic or ecological value of each of these results, so that the best solution could be identified. Together, parts (1) and (2) define the ecological component of the modeling exercise. Part (3) defines the socioeconomic/policy component. Together, these components represent an important interdisciplinary integration critical to fisheries management. Because our expertise is ecological, we emphasize parts (1) and (2). Our ultimate goal is in guiding management, so here we outline the integration of the parts and are pursuing a more integrated study built on this preliminary analysis.

MANAGEMENT SCENARIOS AND CONSTRAINTS.—We assumed that resource managers designing a marine reserve system can designate: (1) the size of the juvenile reserve ($0 \leq p_J \leq 1$), (2) the size of the adult reserve ($0 \leq p_A \leq 1$), and (3) the degree of coupling between juvenile and adult reserve areas ($0 \leq \alpha \leq 1$). Although coupling is, in part, a function of the movement patterns of the target species, we assumed that it was under management control because the spatial proximity of the juvenile and adult reserves could be chosen specifically to increase or decrease movement between the reserves. After a preliminary analysis to explore how the fish population responded to the creation of juvenile and adult reserves, we imposed the constraint that the total area of reserves was constant and equal to 15% of the total area used by juveniles or adults: i.e., $p_J + p_A = 0.3$. In other words, 30% of juvenile habitat might be set aside or 30% of adult habitat, or some combination of the two summing to 30%. A fixed reserve area might result from social, economic, and legal constraints on the total area that can be initially placed into a reserve system, subsequently patrolled, and successfully protected from illegal activities. The choice of 15% is arbitrary, although we have explored the behavior of the population in response to the whole range of reserve sizes and believe that these results are qualitatively similar to those obtained with different reserve sizes.

APPLICATION OF THE MODEL.— We varied p_J, p_A, and α and calculated their effects on the equilibrium abundances of juvenile and adult stocks inside and outside the reserves (i.e., J_R, J_N, A_R, and A_N). We specifically focused on two results: the equilibrium adult stock outside the reserve (A_N), which can be thought of as a surrogate for the potential yield to the fishery, and the equilibrium total adult stock ($A_T = A_N + A_R$), which can be thought of as a measure of the long-term value of the fishery (stemming from future sustained ex-
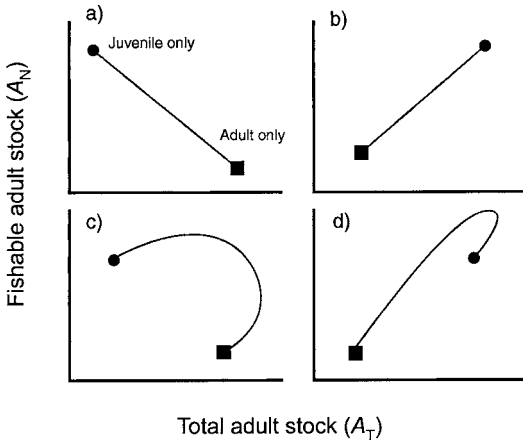
Figure 1. Four hypothetical relationships between two outcomes of interest to managers, the fishable adult stock, A_N, and the total adult stock, A_T, under different reserve designs. In each panel we indicate population responses as the allocation to juvenile and adult habitat is varied but the total reserve area is held constant. (A) Fishable stock and total adult stock are in direct conflict; maximization of one precludes maximization of the other. (B) Fishable stock and total stock respond similarly to reserve designs; a single strategy (juvenile reserves only) maximizes both outcomes simultaneously. (C) Fishable stock and total stock are generally in conflict, as in panel (A), but a reserve design that includes both juvenile and adult habitat can maximize A_N and A_T simultaneously. (D) A combination of (B) and (C) in which a reserve design that includes both juvenile and adult habitat unambiguously maximizes both A_N and A_T.

ploitation as well as other nonharvest uses). Thus, we asked how A_T and A_N varied as we altered the allocation of reserves to the juvenile and adult stages (i.e., as p_J changed from 0.3 to 0, and p_A concomitantly changed from 0 to 0.3) and as we varied the degree of coupling (from $\alpha = 0.05$ to 0.95). To visualize the response of the system to these management scenarios, we plotted A_N against A_T for all possible management strategies (e.g., hypothetical relationships are given in Fig. 1). We then used this same presentation to overlay the role of fisheries value in determining the best strategy.

We also explored the effects of density dependence by considering three cases: (1) density dependence only in the adult stage, (2) density dependence only in the juvenile stage, and (3) density dependence in both. When density dependence occurred in one stage, the value of the competition parameter, c_i, had little effect on the qualitative pattern of results. Therefore, we present results for $c = 1$ for the stage in which density dependence occurred. This assumption, and the others we made and discussed above, was designed to facilitate analysis of this model and presentation of the results. Our immediate goal is to develop a relatively simple case that highlights the possible effects of stage structure and stage-specific density dependence on reserve design and serves as a foundation for more detailed theoretical and empirical work on this problem. Because the framework we develop is general, we hope that it will facilitate future research leading to better-informed decisions about the design of marine reserves.

DEFINING VALUE OF THE FISHERY.—Management goals vary widely and might be focused on maximization of expected stock size, minimization of uncertainty, or some combination based on both short-term fishery yield and long-term exploitation (Mangel et al., 1996). Furthermore, the goals might focus on benefits accrued by commercial fisheries, recreational fisheries, or other societal or scientific groups (e.g., based on consideration

of tourism or biodiversity). As a consequence, the optimization or maximization criterion in a modeling exercise is not likely to be simple. In our example, we have two simple management goals (maximization of A_N and A_T; see above), and as we show below, maximizing the fishable adult stock (A_N) is often in direct conflict with maximizing the total adult stock (A_T) (e.g., Fig. 1A). Because the goals may not be simultaneously maximized, we must weight their relative contributions to obtain an aggregate 'value' associated with the outcome. Providing precise definitions of value is outside the scope of our paper; Mangel (this issue) presents one possibility. Instead, we chose a more general approach in which we recognized four basic shapes of value functions that may arise when two variables (e.g., A_N and A_T) are under consideration: (1) all value (V) resides in the fishable stock (i.e., $V = k_1 A_N$; Fig. 2A); (2) all value resides in the total stock, independent of its distribution between reserve and nonreserve areas (i.e., $V = k_2 A_T$; Fig. 2B); (3) both resources are valuable, but they are completely substitutable (i.e., $V = k_3 A_N + k_4 A_N$; Fig. 2C); and (4) resources are qualitatively substitutable, but the exchange rate increases as one resource becomes relatively low in abundance (e.g., Fig. 2D). We expect this last scenario to be most common, and as we show below, the shape of the value function plays a critical role in determining the optimal management strategy.

RESULTS

Below we describe the effect of alternative reserves in terms of the consequences they have for equilibrium population sizes. As detailed above, we considered four alternative value functions, or maximization criteria (Fig. 2). The choice of value functions greatly influenced the best management scenario. Thus, as we describe and evaluate alternative reserve designs we explicitly refer to the alternative value functions.
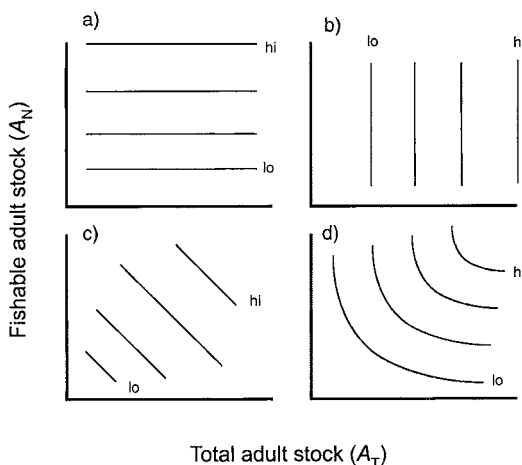

Figure 2. Four hypothetical families of value functions defined by the fishable stock, A_N, and the total adult stock, A_T. Lines connect combinations of stocks that yield the same value; lower values are nearer the origin. (A) The case in which only fishable stock is of value. (B) The case in which only total adult stock is of value. (C) The case in which both fishable stock and total adult stock are valued, and their value is equal and substitutable. (D) The case in which both fishable stock and total adult stock are valued, but they are not substitutable at a constant exchange rate—large amounts of one stock are not as valuable as intermediate amounts of both.
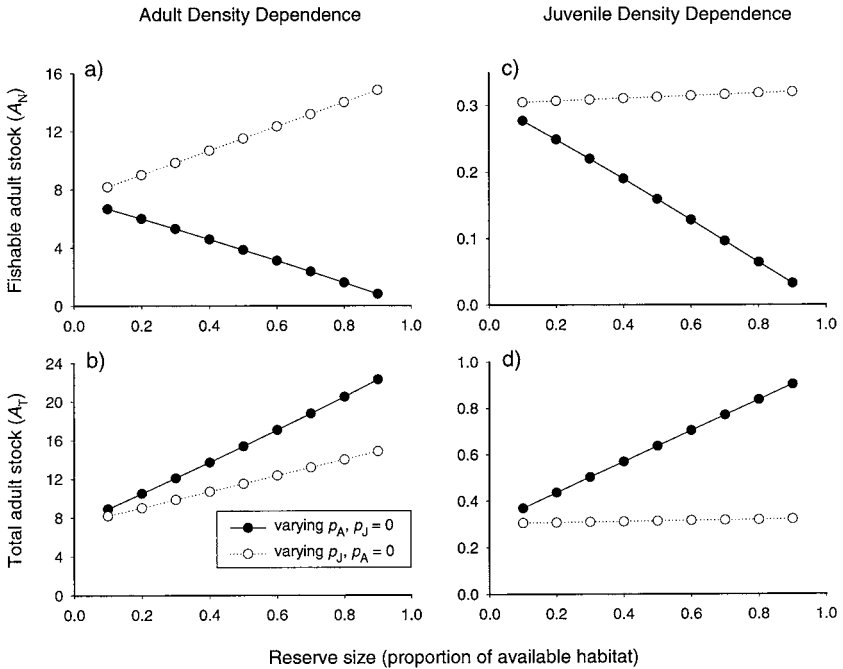
Figure 3. The effects of varying the size of adult or juvenile reserves on the fishable adult stock (panels A, C) and the total adult stock (C, D) under the assumptions of adult density dependence (A, B) or juvenile density dependence (C, D). In each panel the effect of adult reserves is presented in filled circles and the effect of juvenile reserves in open circles.

DENSITY DEPENDENCE IN THE ADULT STAGE ONLY ($c_J = 0$, $c_A = 1$).—In this case and in all but one of the others that we considered, our two simple maximization criteria, maximize adults outside the refuge (A_N) and maximize total adults (A_T), were in opposition to some degree (e.g., Fig. 1A,C). Increasing the size of the adult reserve, p_A, increased the total number of adults in the population, A_T, but decreased the fishable adult stock, A_N. Increasing the size of the juvenile reserve, p_J, increased both A_N and A_T (Fig. 3A,B). Thus, to maximize A_N, one could simply maximize the proportion of the juvenile habitat that is set aside. On the other hand, total adults increase as either reserve is increased in size, although at different rates.

When we explicitly consider the establishment of both juvenile and adult reserves, conflict arises when we attempt to maximize both A_N and A_T. Because we are concerned with allocation to both habitats, we must also consider the effect of reserve coupling. As part of this exercise, we evaluated the effect of coupling ranging from strong disassociation ($\alpha = 0.05$) to strong association ($\alpha = 0.95$), and as noted above, considered the constraint where $p_J + p_A = 0.3$. Notice first that, in general, the maximization criteria were in opposition—increasing the fishable adult stock (A_N) often led to a decrease in the total adult stock (A_T) (Fig. 4). Furthermore, these effects varied depending on the degree of coupling between juvenile and adult reserves (i.e., as α increased, the solutions shifted out away from the origin in Fig. 4).

In this scenario, the value function could have major effects on the optimal design of the reserve. If the goal was to maximize the fishable adult stock, A_N (i.e., as in Fig. 2A),
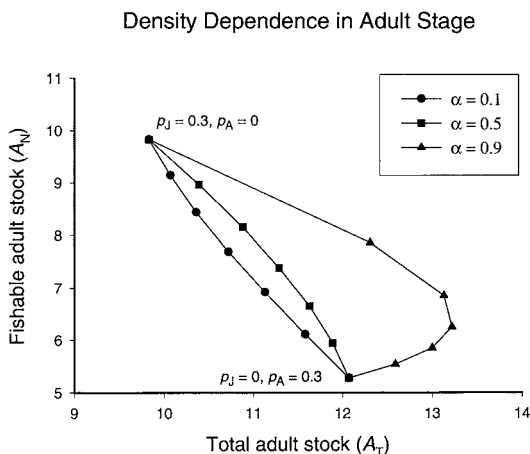
Density Dependence in Adult Stage

Figure 4. The relationship between two outcomes of interest to managers, the fishable adult stock, A_N, and the total adult stock, A_T, when density dependence acts only in the adult stage. The reserve is assumed to contain 15% of the total habitat, and here we consider combinations of juvenile and adult reserves ranging from 30% of the juvenile habitat (and no adult habitat) to 30% of the adult habitat (and no juvenile habitat). Results are presented for three degrees of coupling between juvenile and adult reserves: close association between juvenile and adult reserves, $\alpha = 0.9$ (triangles); random movement, i.e., no particular association between juvenile and adult reserves, $\alpha = 0.5$ (squares); and disassociated reserves, $\alpha = 0.1$ (circles).

the best management scenario would be to set aside only juvenile habitat. In this case, coupling is irrelevant. For other value functions (i.e., Fig. 2B–D), the strategy that yields the greatest value is likely to be one in which both adult and juvenile habitat are preserved (i.e., the greatest value function will be tangent to the result function at a point between the two endpoints). In these cases, coupling has a strong effect, and value is always enhanced with strong coupling between the reserves (Fig. 4).

DENSITY DEPENDENCE IN THE JUVENILE STAGE ONLY ($c_J = 1$, $c_A = 0$).—As observed above for the case with adult density dependence, an increase in the adult reserve area had a strongly negative effect on A_N but an even stronger positive effect on A_T (Fig. 3C,D). In this case, however, an increase in the juvenile reserve area had only a very small positive effect on A_N and A_T. The two management objectives are in direct conflict, and increases in one will inevitably lead to decreases in the other (Fig. 5). Furthermore, in contrast to the case with adult density dependence, the strategy that maximizes total adult stock is not a mixed strategy. Instead, the maximum adult population is achieved when only adult habitat is set aside (Figs. 3D,5A). Maximum fishable adult stock is achieved when only juvenile habitat is set aside.

More complex value functions (e.g., Fig. 2D), however, can lead to a mixed management strategy in which both habitats are protected. In these cases, coupling is important in determining the optimal design of the reserves (i.e., the fractions allocated to juvenile and adult habitat) but not in the maximal population size (i.e., value) that can be achieved from the marine reserve. For example, consider a curvilinear value function as shown in Figure 5B. The point at which this value function is tangent to the result function represents the marine reserve design with greatest value. If the adult and juvenile reserves are placed to achieve strong positive coupling (i.e., $\alpha = 0.9$), then this goal can be achieved with a juvenile reserve that is approximately four times the size of the adult reserve (i.e.,
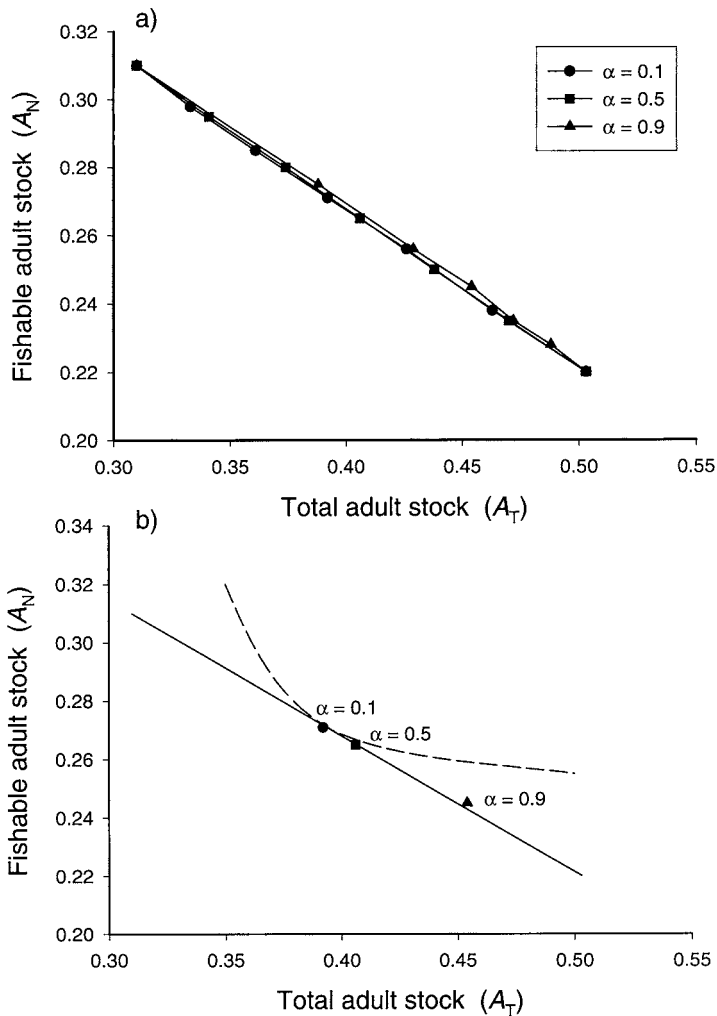
Density Dependence in Juvenile Stage

Figure 5. (A) The relationship between two outcomes of interest to managers, the fishable adult stock, A_N, and the total adult stock, A_T, when density dependence acts only in the juvenile stage. The variation in reserve design is as described for Figure 4. (B) The relationship described in panel (a) with a nonlinear value function (as depicted in Fig. 2D) superimposed (dashed line) on the typical result function from panel (a) (solid line). The maximum value that can be achieved occurs when the value function is tangent to the result function. That result can be achieved through alternative values of allocation to juvenile and adult habitat (p_A and p_J), which depends on the degree of coupling (compare with panel a). The three points (taken from panel a) correspond to equal juvenile and adult reserve sizes ($p_A = 0.15$ and $p_J = 0.15$), assuming negative coupling (circles: $\alpha = 0.1$), no association (squares: $\alpha = 0.5$), and strong coupling (triangles: $\alpha = 0.9$) between the reserves, respectively.

$p_A \cong 0.06$ and $p_J \cong 0.24$). However, if the reserves are set up to be negatively coupled (i.e., $\alpha = 0.1$), that same value can be achieved but only if the two reserves are of equal size (i.e., $p_J = p_A = 0.15$). This point is further illustrated by Figure 5B; the marked points represent a single combination of p_A and p_J (i.e., $p_J = p_A = 0.15$) at three levels of coupling.

In only one case ($\alpha = 0.1$) is the maximum value actually achieved. In the other two, the optimum value requires different allocation of the reserve area to juvenile and to adult habitats.

DENSITY DEPENDENCE IN BOTH STAGES.—When density dependence occurs in both stages, the results mirror the qualitative behavior of either of the extreme cases described above. For example, when $c_J = 1$ and $c_A = 1$, the predictions from the model are virtually identical to those of the case with juvenile density dependence (Fig. 5). This result arises, in part, because we modeled competition within both stages using similar functions and because juveniles are more abundant than adults. Thus, density dependence is stronger among juveniles. As c_J is reduced, the behavior of the model approaches that of the case with adult density dependence. Specifically, when c_J is reduced, and c_A is held at 1.0, the model predictions switch from those described in Figure 5 (density dependence in the juvenile stage only) to those described in Figure 4 (density dependence in the adult stage only) at $c_J \cong 0.1$.

DISCUSSION

It is premature to recommend a specific reserve design on the basis of this particular and preliminary modeling effort. Our model and its results do, however, provide a foundation and motivation for future empirical and theoretical work that should prove valuable in designing reserves. Again gag provide a useful example. When juvenile gag habitat is protected from fishing, gag densities can rise appreciably, causing decreases in fish growth and condition (Lindberg and Loftin, 1998). In addition, gag spawn offshore at traditional spawning grounds, which are heavily fished. This evidence for density dependence, the presence of extreme shifts in habitat, and the critical role of these habitats make gag a prime model species for further development and application of our model. In the long term, we hope to use the general framework laid out here to refine the model and to explore alternative reserve designs using parameter values and functions appropriate to gag. Below, we discuss some of the general insights that arise from our model exploration in hopes of stimulating additional research into the role of stage structure and density dependence. Our analyses were necessarily narrow, and the intriguing results demand further investigation.

DENSITY DEPENDENCE.—The timing of density dependence can clearly have significant effects on the response of stage-structured marine populations to the establishment of marine reserves. Our results suggest that, when density dependence is concentrated within the adult stage, reserves should protect both juvenile and adult life stages and be positioned to create positive coupling between reserves. This result is robust across a range of value functions. When density dependence is concentrated in the juvenile stage, however, the result is more equivocal—the greatest value was achieved by protection of only juveniles, only adults, or both. In these cases, the greatest value (in terms of fishable stocks or total stocks) was relatively insensitive to coupling, although the relative allocations to juvenile and adult habitat were greatly influenced (see Fig. 5B). These striking differences in the effects of reserves refocus attention on the relatively little-studied area of density dependence in the juvenile stages of fisheries species (but see Lindberg and Loftin, 1998). In the context of marine reserves, density dependence is likely to be even more important because population densities within reserves will generally be higher than those

outside reserves. Thus, we can expect density dependence to increase in intensity following the creation of a reserve.

We modeled density dependence in particular ways, however, which certainly also affected the results of our model. For example, we modeled juvenile density dependence through the effects of density on maturation rate. Because delayed maturation prolongs the time an individual spends in the juvenile stage, the through-stage juvenile survivorship increases as maturation rate declines. Thus, through-stage juvenile survival was density dependent even though juvenile survival (per some finite time interval) was not. In contrast, adult-stage density dependence in our models affected reproduction and had no direct feedback to adult survival. Our results involving density dependence in both stages suggest that density dependence in the juvenile stage is intrinsically more intense than that in the adult stage for two reasons: (1) the higher density of juveniles and, we suspect, (2) the compounding effects of delayed maturation and increased through-stage mortality. We conclude that the behavior of the system is determined by the stage at which density dependence has the strongest effect: i.e., where it creates a bottleneck in the life history (see also Mittelbach and Chesson, 1987; Nisbet et al., 1996).

Perhaps more importantly, we included density dependence using a Beverton-Holt function (Eqs. 6,7), which results in rather mild density dependence. In a Beverton-Holt function, the output from a stage monotonically increases as input (i.e., density) increases. The exact form and general pattern of density dependence is not clear, although recent experimental field studies have found functions that closely resemble Beverton-Holt functions (e.g., Steele, 1997; Schmitt et al., in press). Other more intense forms of density dependence are possible (e.g., the Ricker function, which results in a humped output-input function). If density dependence acts more strongly than we have modeled, total stock might actually decline or exhibit cycles as reserves increase in size (see, e.g., Levin and Goodyear, 1980). These issues demand greater theoretical and empirical exploration.

RESERVE COUPLING.—Our research is among the first to consider explicitly the coupling between reserves designed to protect different life stages. Our results showed a consistently nonnegative effect of reserve coupling on reserve efficacy, leading to either no effect on fish stocks or an increase in stocks. Indeed under some assumptions, the effect of coupling was significant (Fig. 4). However, we are not willing to generalize from these results that coupling will never be detrimental. The coupling of reserves effectively acts to increase the density of individuals in the adult reserve (by augmenting the supply of maturing juveniles from the juvenile reserve). As a result, a tightly coupled reserve behaves much like a single reserve that protects both life stages, and we hypothesize that severe density dependence (e.g., based on a Ricker function) could lead to negative effects of coupling. For example, if juvenile maturation rates are density independent, but density dependence among adults follows a Ricker form, then coupling may force a large number of juveniles (protected in the juvenile reserve) into the adult reserve. This result could intensify competition, and greatly diminish reproductive output, leading to an overall decrease in stock sizes. This possibility provides a second motivation for exploring the effects of alternative forms of density dependence as well as greater empirical study of density dependence in target species.

DO RESERVES WORK THE WAY WE HYPOTHESIZE?—It is generally believed that marine reserves will increase fisheries yields through transport of larval production (and migration of older fishes) out of reserves (e.g., Plan Development Team, 1990; Roberts and Polunin, 1993; Clark, 1996; Lauck et al., 1998; Sumaila, 1998). The results of our model-

ing efforts provide reasons to reevaluate this view. The establishment of adult reserves led to declines in fishable adult stock in all cases, and juvenile reserves appreciably augmented fishable adult stocks only when they were accompanied by density dependence in the adult stage (Fig. 3). The consistent negative effect of adult reserves on fishable stocks arose because the benefit of reserves through reproductive output was insufficient to counterbalance the effect of removing habitat (and the associated stock) from the areas that could be fished. This result arose despite our assumption that the population was closed; in an open system we would expect local reproductive increases resulting from reserves to be largely exported from the study system. Our inability to find a beneficial effect of reserves on fishable stock may have two sources: (1) Although we allowed larval exchange between the reserve and nonreserve areas, and mixing during maturation, there was no dispersal within a stage, and (2) we focused on fishable adult stock, not on density outside the reserve. In fact, density of adults outside the reserve actually increased slightly as the fishable stock declined (i.e., the nonreserve area declined faster than the adult stock). Depending on how harvesting is modeled, this increase in density (but decrease in stock) could result in either increased or decreased yields (although certainly an increase in catch per unit effort).

We found that the population consequences of reserves varied dramatically with the underlying assumptions about target-species life history and ecology (e.g., with regard to the timing of density dependence and the degree of coupling). Thus, our results call into question the assertion that reserves will be particularly useful in the management of multiple target species through the identification of common 'essential' fish habitat (e.g., Plan Development Team, 1990; Roberts and Polunin, 1993; Clark, 1996; Lauck et al., 1998). The strength of density dependence, its occurrence in the life history, and the degree of movement between different habitats will probably vary considerably among target species. In these cases, the effect of a marine reserve is also likely to vary greatly among the target species. Although we agree that some model species may give qualitative insight into effective ways to manage other species, we believe it is overly optimistic to expect these generalizations to hold for species that exhibit substantially different life histories.

It is not our intention to denigrate reserves or to discourage their use as management tools. Instead we seek, through this work, to highlight some of the important considerations in their development. The results of this modeling exercise raise several critical points about the design of marine reserves. The first, and perhaps most important, is that reserves are not a panacea, either in the sense that their design is independent of the details of the system or that they generally have a positive effect on populations regardless of the particular management goals. Thus, explicit objectives and value functions must be articulated early in the design process. Indeed, a critical component to any comparison among alternative management strategies is the definition of the goal in management—what we call the value function. The value function interacts with the biological factors to define the optimum management strategy. Our results strongly suggest, not surprisingly, that consumptive use and conservation goals may often be in opposition. The goals in establishing a reserve must therefore be explicit and articulated from the beginning. Future ecological work should strive to incorporate more realistic value functions into models of stage-structured fish populations or at least provide results that can be considered under different value functions.

Future theoretical work should also strive to incorporate additional biological processes, including alternative forms of density dependence (as discussed above), movement into and out of reserves within a stage (a potentially important benefit of reserves to the fishery), stochasticity (e.g., in larval production or settlement, in the intensity of density dependence, or in fishing mortality), and fisher behavior (e.g., fishing redirection). However, the relative importance of these alternatives will probably depend on the empirical details of target systems, and many of these empirical data are lacking. For example, the form, intensity, and stage of density dependence acting on target species are largely unknown! A better understanding of these aspects of target species' ecology will be essential to the design of effective reserves. Furthermore, if coupling is to be considered in the design of marine reserves, then detailed knowledge of fish movements among stages and habitats will be needed for design of the most effective reserves.

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