The role of dispersal and demography in determining the efficacy of marine reserves[1]

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Abstract: Marine reserves are rapidly becoming an important tool for protection and recovery of depleted marine populations. However, the relative value of reserves to particular species is strongly dependent on its life history and behavior. We present a general conceptual framework for considering dispersal in simple demographic models. This framework includes transition matrices that consist of two age-structured models connected by transition probabilities for general migration, ontogenetic shifts, and recruitment in both a reserve and an unprotected area. We show that life history characteristics and perturbation analysis can be used to predict changes in growth rate due to a decrease in adult mortality resulting from a marine reserve for different levels and types of dispersal. Reserves enhanced growth rate for all species irrespective of net dispersal between the reserve and surrounding matrix habitat, but the efficacy of reserves relative to catch reduction depended significantly on the magnitude and sign of net dispersal across the reserve boundary. Patterns of reserve efficacy across different dispersal types were strongly species specific. Given the paucity of spatially explicit data for many marine systems and species, this simple approach represents a first step in applying life history information to advance current theory and provide practical considerations for marine reserve management.

Résumé : Les réserves marines sont vite en train de devenir des outils importants pour la protection et la récupération des populations marines décimées. Cependant, la valeur relative des réserves pour une espèce en particulier dépend de son cycle biologique et de son comportement. Nous présentons un cadre conceptuel général pour examiner la dispersion dans des modèles démographiques simples. Ce cadre comprend des matrices de transition qui consistent en deux modèles structurés d'après l'âge reliés par des probabilités de transition pour la migration générale, les changements ontogéniques et le recrutement dans une zone de réserve et dans une zone sans protection. Nous montrons que les caractéristiques démographiques et l'analyse de perturbation peuvent servir à prédire les changements du taux de croissance causés par un déclin de la mortalité des adultes associé à la présence d'une réserve marine pour divers degrés et types de dispersion. Les réserves font augmenter le taux de croissance chez toutes les espèces, quelle que soit la dispersion nette entre la réserve et la matrice d'habitats avoisinants; cependant, l'efficacité de la réserve, par comparaison à une réduction des captures, dépend de façon significative de l'importance et du signe de la dispersion nette à travers les frontières de la réserve. Les patrons d'efficacité des réserves en fonction des types de dispersion varient fortement selon les espèces. Étant donné le peu de données spatiales spécifiques sur de nombreux systèmes marins et espèces de mer, cette approche simple représente un premier pas vers l'application des données démographiques pour améliorer la théorie actuelle et pour fournir des informations pratiques pour la gestion des réserves marines.

[Traduit par la Rédaction]

Introduction

The benefits of no-take marine reserves are many, including an increase in size and biomass of target species and local enhancement of fisheries (Allison et al. 1998; National Research Council 2001; Gell and Roberts 2003). The role of dispersal in marine protected area design has been addressed by a number of researchers, both empirically (e.g., Martell et al. 2000; Grantham et al. 2003) and theoretically (Quinn et al. 1993; Stockhausen et al. 2000; Botsford et al. 2001), although rarely in a comparative framework (but see Polacheck 1990; Acosta 2002; Lockwood et al. 2002). Dispersal may be modeled simply as diffusion into and out of a reserve, spillover in response to density dependence, or directed dispersal due to migration or ontogenetic shifts in habitat use that are life history dependent. The latter, in particular, has been overlooked in most theoretical treatments of marine reserves, in spite of the fact that most marine spe-

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cies undergo major habitat shifts at least once in their life history.

Because marine species typically exhibit complex life histories with multiple ontogenetic shifts (e.g., directed spillover between habitats that occurs when individuals move from one life stage to the next), only under rare circumstances would a reserve encompass the entire life cycle of a species or population. Likewise, patchy distribution of resources forces many marine species to disperse long distances, even within a life stage, and migration across reserve boundaries that are fixed in space and (or) time is certain to impact population dynamics. Theoretical studies suggest that reserves should provide fewer benefits to species with greater rates of dispersal as adults (see review by Gerber et al. 2003). Therefore, species with moderate rates of dispersal are good candidates for reserves because high adult dispersal allows for too little protection of reproductive output within reserves, and low adult dispersal does not increase catch outside reserves. But, from a purely conservation standpoint, evidence suggests that marine reserves appear to be most effective for both preventing extinction and promoting recovery for those species that exhibit a low population growth rate (λ) and a low dispersal rate (Gerber et al. 2002).

Any approach to comparing the efficacy of reserves has to be developed in the context of the objective of the reserve (Agardy 1994). Possible objectives for enhancement of particular species could be to maximize population abundance and yield, to minimize rate of population decline, or to minimize the probability that the population falls below some quasi-extinction threshold. The potential effects of reserves on single species can only be determined with the incorporation of spatial and demographic information. The previously popular assumption of a common pool of larval dispersal is inadequate (Gaines et al. 2003) owing to species-specific differences in the spatiotemporal distribution of larvae; hence, metapopulation structure and connectivity (via migration or larval dispersal) need to be incorporated into reserve design and evaluation. In addition, demography needs to be taken into account because reserve effects vary as a function of life histories (Hooker and Gerber 2004).

In this paper, we propose that modeling tools based on life history theory can be used by decision makers to design marine reserves for target species and by managers to evaluate the efficacy of different reserve designs. Our measure of efficacy is the change in the maximum eigenvalue of a deterministic projection matrix with a proportional change in mortality. Our assumption is that maximizing the λ of a population should have a significant impact on population recovery and spillover, an important objective for fishery enhancement. We present a conceptual framework using simple spatial matrix population models that incorporate life history and dispersal information (Wooton and Bell 1992; Doak 1995) to determine the efficacy of marine reserves as a function of spatial and demographic parameters.

Methods

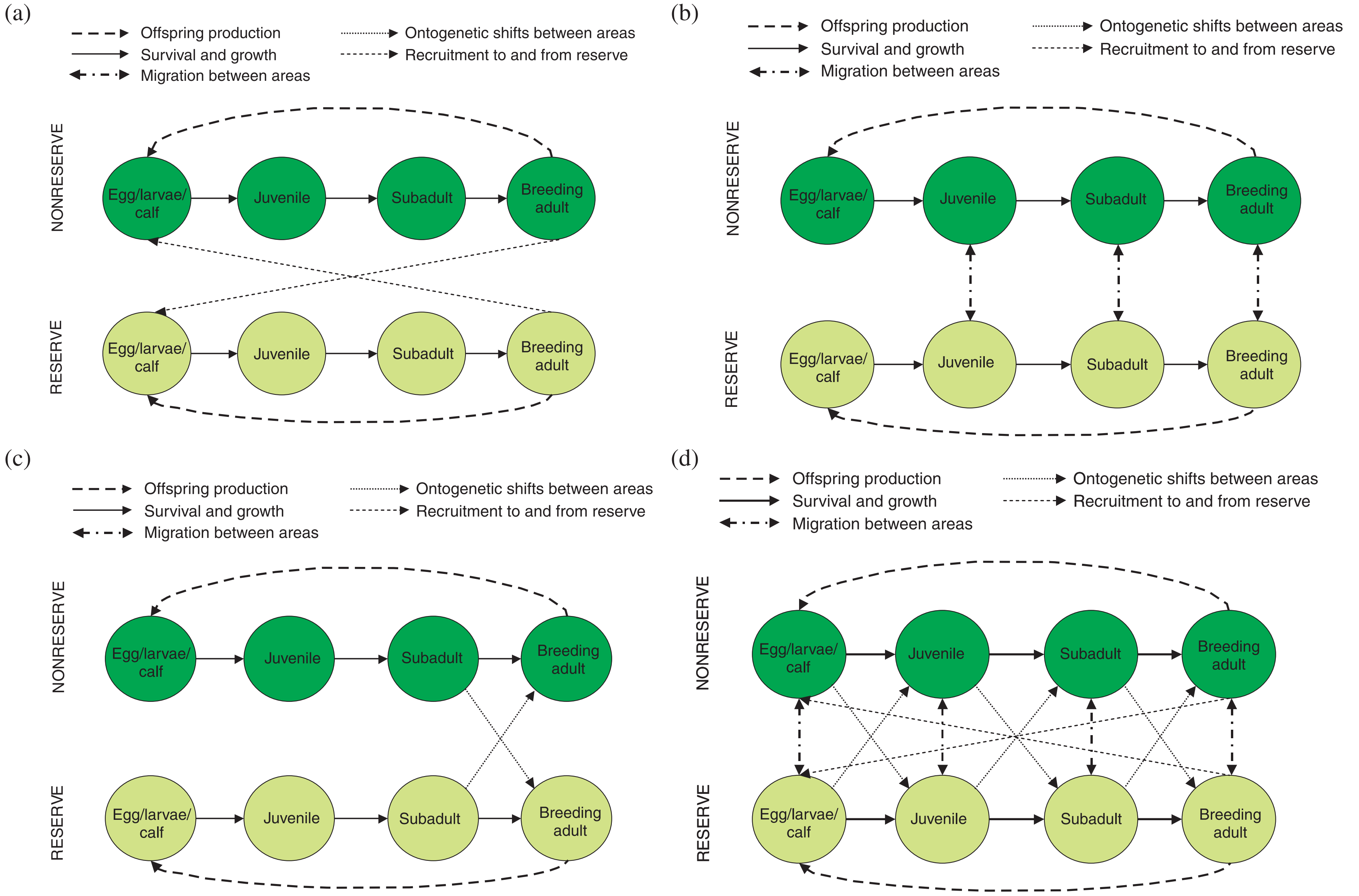
A conceptual framework for evaluating the importance of life history and dispersal in reserve efficacy

Four conceptual models for the role of dispersal in simple life history models are illustrated (Fig. 1). The selection of the appropriate model will depend on the particular life history and dispersal mechanism of the focal organism. Our general conceptual model includes transition probabilities for general migration (spillover), ontogenetic shifts, and recruitment (e.g., larval dispersal) between a reserve and an unprotected area. We illustrate a situation in which the primary mechanism of dispersal between the protected area and unprotected area is recruitment (Fig. 1*a*). Here, animals spend their whole lives in one location or the other, with low mobility. This scenario might be appropriate for sessile invertebrates (e.g., urchins), where larval dispersal between sites outweighs adult and juvenile dispersal. We then describe a situation in which adults and (or) juveniles move between protected and unprotected sites, with insignificant larval or newborn exchange (Fig. 1*b*). Migration into and out of the reserve may occur as spillover in the adult, juvenile, or both adult and juvenile stages. Also depicted is a situation in which exchange between sites only occurs as individuals undergo an ontogenetic niche shift between protected and unprotected sites (Fig. 1*c*). Ontogenetic shifts in habitat use occur for many reef fish species, which move from estuarine to pelagic environments between the juvenile and adult life stages. Here, a reserve established for a particular habitat will have stronger impacts on the life stage that occupies that habitat. A variation of this scenario is one in which the reserve protects only the breeding or nesting grounds of species, such as the spawning sites of groupers (e.g., Sala et al. 2003) or turtle nesting beaches. In these cases, individuals tend to make their way into the reserve after a particular life stage and only for short periods of time. When spawning, calving, or pupping areas are protected, the net effect is that those adults are in the reserve for that year or portion of a year, with higher survival or offspring production rates, even if they are not physically in the reserve all the time. The generic model (Fig. 1*d*) allows explicit incorporation of any or all of these transition probabilities. Below, we illustrate the application of this framework for four representative life histories of species in the Gulf of California and Baja California to examine the role of dispersal at different life stages in reserve efficacy.

Developing a spatial demographic model for evaluating reserve efficacy

We used our conceptual framework to examine two questions: (*i*) does dispersal reduce the efficacy of reserves for species that are otherwise predicted to respond strongly assuming no dispersal, and (*ii*) how does dispersal increase the efficacy of reserves for species that are otherwise predicted to show very little response from their establishment because of slow demographic rates? For a representative range of life histories for marine species, we examined the degree to which dispersal between a reserve area and a nonreserve area mitigates the effect of a reduction in adult mortality on reserve efficacy using the approach of Gerber and Heppell (2004). The species we chose as case studies (goliath grouper (*Epinephalus itajara*), sea urchin (*Tripneustes ventricosus*), loggerhead sea turtle (*Caretta caretta*), and gray whale (*Eschrichtius robustus*)) (Table 1) exhibit different types of dispersal and a wide range of mortality, which could be reduced by protected areas.

Fig. 1. Conceptual framework for considering dispersal in simple demographic models. The model includes transition probabilities for general migration (spillover), ontogenetic shifts (directed spillover that occurs when individuals move from one life stage to the next), and recruitment (e.g., larval dispersal) in both a reserve and an unprotected area. (*a*) A situation in which the primary mechanism of exchange is recruitment of larvae or newborns; (*b*) a situation with random exchange (spillover) among adults and (or) juvenile life stages but insignificant larval or newborn exchange; (*c*) similar to *b*, but specifies an ontogenetic shift in habitat use between sites; (*d*) a generic model that allows explicit incorporation of any or all of these transition probabilities.



We constructed a two-site matrix model for each species, with two patches representing a reserve and an unprotected population (Morris and Doak 2002). Each patch matrix was age structured with adults grouped into a single stage (Heppell et al. 2000). Vital rates and stages are provided (Table 1). In our model, dispersal between populations can be incorporated into the same general form of simple matrix models. The inclusion of dispersal results in the following two-patch matrix, where M represents dispersal for each matrix transition:

$$\left[\begin{array}{ccccc|ccccc}
0 & 0 & \cdots & P_{\alpha-1}(1-M_{\mathrm{AB}})F_{\mathrm{A}} & P_{\alpha}(1-M_{\mathrm{AB}})F_{\mathrm{A}} & 0 & 0 & \cdots & P_{\alpha-1}M_{\mathrm{BA}}F_{\mathrm{A}} & P_{\alpha}M_{\mathrm{BA}}F_{\mathrm{A}} \\
P_0(1-M_{\mathrm{AB}}) & 0 & 0 & 0 & 0 & P_0M_{\mathrm{BA}} & 0 & 0 & 0 & 0 \\
0 & P_1(1-M_{\mathrm{AB}}) & \ddots & \vdots & \vdots & 0 & P_0M_{\mathrm{BA}} & \ddots & \vdots & \vdots \\
0 & 0 & P_x(1-M_{\mathrm{AB}}) & 0 & 0 & 0 & 0 & P_0M_{\mathrm{BA}} & 0 & 0 \\
0 & 0 & 0 & P_{\alpha-1}(1-M_{\mathrm{AB}}) & P_{\alpha}(1-M_{\mathrm{AB}}) & 0 & 0 & 0 & P_{\alpha-1}M_{\mathrm{BA}} & P_{\alpha}M_{\mathrm{BA}} \\
\hline
0 & 0 & \cdots & P_{\alpha-1}M_{\mathrm{AB}}F_{\mathrm{B}} & P_{\alpha}M_{\mathrm{AB}}F_{\mathrm{B}} & 0 & 0 & \cdots & P_{\alpha-1}(1-M_{\mathrm{BA}})F_{\mathrm{B}} & P_{\alpha}(1-M_{\mathrm{BA}})F_{\mathrm{B}} \\
P_0M_{\mathrm{AB}} & 0 & 0 & 0 & 0 & P_0(1-M_{\mathrm{BA}}) & 0 & 0 & 0 & 0 \\
0 & P_1M_{\mathrm{AB}} & \ddots & \vdots & \vdots & 0 & P_1(1-M_{\mathrm{BA}}) & \ddots & \vdots & \vdots \\
0 & 0 & P_xM_{\mathrm{AB}} & 0 & 0 & 0 & 0 & P_x(1-M_{\mathrm{BA}}) & 0 & 0 \\
0 & 0 & 0 & P_{\alpha-1}M_{\mathrm{AB}} & P_{\alpha}M_{\mathrm{AB}} & 0 & 0 & 0 & P_{\alpha-1}(1-M_{\mathrm{BA}}) & P_{\alpha}(1-M_{\mathrm{BA}})
\end{array}\right]$$

This is a general model intended to illustrate the range of possible dispersal scenarios and ontogenetic shifts between different life stages to and from the protected area (see Fig. 2). The model (shown in age-structured form, where each row–column represents a single age-class for juveniles, and adults are grouped into one stage) contains two single-site matrices: A, the unprotected site, and B, the reserve site. The parameters P_i represent mean annual survival probabilities for age-class i, and F_{A} and F_{B} are the mean annual fertility rates outside and inside the reserve, respectively. The length of the juvenile stage is dependent on age at maturity, α (Table 1). The matrices in the other two quadrants reflect transitions between patches from A to B (lower left) or B to A (upper right). The postbreeding census format results in an annual sequence for each age-class of survival, migration, and reproduction. Thus, a reproduction term is applied to the last age-class of juveniles, which are animals that will mature (if they survive), migrate, and breed before the census. For example, $P_{\alpha-1}M_{\mathrm{AB}}F_{\mathrm{B}}$ represents the probability of maturing juveniles that are in the unprotected area migrating into the reserve and breeding for the first time (e.g., through an ontogenetic shift). Note that for our examples, ontogenetic shifts M_{AB} and M_{BA} only occur at age 0 or age $\alpha - 1$. Also, although movement probabilities from patch i to j are given by M_{ij}, we do not necessarily assume all of these to be the same.

For our four examples, the life stage in which dispersal occurs varies among species (Tables 1 and 2). A constant migration probability is assigned to the age 0 class (eggs or newborns), juvenile age-classes, or the adult stage for each submatrix. Because in the real world, reserves are much smaller than unprotected areas, our model allows the probability of moving in and out of the reserve probabilities to differ (i.e., M_{AB} need not be equal to M_{BA}).

The projection matrix maps a vector of population sizes in one time unit onto the vector of population sizes in the next unit. This vector represents population size in each age-class (e.g., the number of individuals in ages-classes 0, 1, 2,..., α, where α is adult) for sites A and B. The number of adults in one time unit in patch A is the sum of the number of last-stage juveniles in patch A the previous time unit that survive and do not move plus the number of adults from the previous time unit in patch A that survive and do not move plus the number of adults and subadults from the previous unit in patch B that survive and migrate out of the reserve. The time interval for all models is 1 year, so we assume that adults are either protected or not for an entire year. Adults that migrate to a reserve for breeding are not in that location year-round but do experience a lower annual mortality because they are there for part of the year. In the case of marine mammals, at least, this would also improve fecundity for those individuals that breed in the reserve.

Using this model, we evaluated how life history and a reduction in mortality interact to determine λ for the two-patch matrix created for each species (see Fujiwara and Caswell (2001), Kareiva et al. (2001), and Gerber and Heppell (2004) for an explanation of survival versus mortality sensitivity). For each case study, we made the simplifying assumption that establishing a reserve reduces adult mortality by 20% at site B, where mortality is 1 – annual survival probability. We then evaluated the effect of dispersal during different life stages on λ calculated for the entire two-patch matrix. We focus on a reduction in adult mortality because, in general, adults are the focus of a fishery, and thus, we seek to measure the potential impact of reserves based on protection of this life stage. For simplicity, we assume that all mortality is fishing mortality (e.g., $1 - P_{\alpha}$ is multiplied by 0.8). We compared the simplest reserve model with a generic reduction in adult mortality (e.g., as would occur with a constant mortality reduction analogous to a quota management scenario), where there is no effective reserve and mortality is reduced in sites A and B by 10%; we then included multiple forms of dispersal and timing of dispersal for two different dispersal rates.

How does dispersal rate interact with life history to determine reserve efficacy?

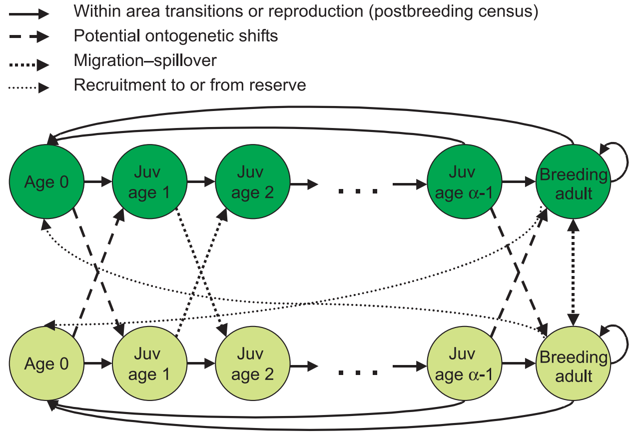
First, we compared population λ values for models with different dispersal rates to a constant mortality reduction (with no dispersal) in which mortality is reduced by 10% for both patches (versus the reserve system where mortality is reduced by 20% in one patch). For gray whales and sea turtles, we considered the effect of adult dispersal, and for sea urchins and groupers, we considered the effect of larval dis-

Table 1. Life history parameters assumed in demographic models.

Species	Age categories (matrix dimensions)	Fecundity (eggs·year^{-1})	Age at maturity	Age 0 survival rate	Adult and juvenile survival	Juvenile habitat	Adult habitat	Type of dispersal modeled in Fig. 3
Goliath grouper (*Epinephelus itajara*)	0–5+ (12)	75 000[a]	4–6[b]	0.000 007[c]	0.85[c]	Shallow bays and estuaries	Structure in near and offshore	Recruitment
Sea urchin (*Tripneustes ventricosus*)	0–3+ (8)	2 000 000[a,d]	4[d]	0.000 001[d]	0.72, 0.5[d]	Rocky subtidal	Rocky subtidal to 30 m	Recruitment
Loggerhead sea turtle (*Caretta caretta*)	0–22+ (46)	153[e]	21[e]	0.5[e]	0.809, 0.705[e]	Open ocean, nearshore	Nearshore	Adult breeding reserve
Gray whale (*Eschrichius robustus*)	0–8+ (18)	0.47[f]	8[f]	0.893[f]	0.944, 0.893[f]	Shallow bays	Nearshore	Adult reserve

[a] Fertility estimated to solve for $\lambda = 1$; λ is population growth rate.
[b] Bullock et al. (1992).
[c] Sadovy and Eklund (1999).
[d] Pfister and Bradbury (1996).
[e] Crowder et al. (1994).
[f] Reilly (1984).

Fig. 2. General model used for perturbation analysis illustrating possible dispersal scenarios and ontogenetic shifts between different life stages to and from the protected area.



persal in reserve efficacy (Fig. 2), although we are aware that groupers can exhibit important spawning migrations (Sadovy and Eklund 1999). While limited data on dispersal distances are available for these species, we examined the sensitivity of reserve efficacy (i.e., increase in λ) to a range of dispersal scenarios to evaluate the relative importance of dispersal in predicting the effects of reserves based on life history. Parameter values for model scenarios are defined (Table 2*a*). This analysis helps to identify how changes in dispersal and vital rates affect reserve efficacy for each model. However, this simple approach does not allow for the additional dispersal patterns and ontogenetic shifts that exist in these four species (e.g., grouper exhibit juvenile ontogenetic shifts).

How does dispersal mechanism interact with life history to determine reserve efficacy?

To explore the degree to which the details of dispersal matter, we then evaluate how life history and various modes of dispersal interact to determine the efficacy of reserves. For each species, we considered the impact of including each single mechanism of dispersal as defined above on reserve efficacy. We examined the relative impact of each mechanism of dispersal for two different dispersal rates (low and high dispersal from reserve to unprotected site; Table 2*b*). In light of the paucity of dispersal data for these species, our intention here was not to parameterize realistic models for each species. Thus, while no single scenario encompasses the full range of biological complexity for the species considered, our intention is to compare the relative importance of each single dispersal mechanism to reserve efficacy.

Results

Results may be interpreted as general differences between four representative heuristic models for marine species. Models with dispersal may or may not differ from what we would predict from elasticity analysis of the life cycle (sensu Gerber and Heppell 2004). The spatial perturbation analysis approach used in this study is not specific to marine reserves as a management tool (i.e., perturbation analysis can be applied to examine a suite of hypothesized threats and po-

Table 2. Dispersal parameters in model scenarios used to generate (*a*) Fig. 3 and (*b*) Fig. 4.

(*a*) Model scenario.	M_{AB}	M_{BA}
No dispersal into reserve	0	0
High dispersal out of reserve (small reserve)	0.1	0.9
High dispersal into reserve (large reserve)	0.9	0.1
Total mixing (reserves are of equal size or attractiveness)	0.5	0.5
(*b*) Dispersal scenario.	High or low M applied to:	
Recruitment	P_0	
Adult spillover	P_α, $P_\alpha F$	
Juvenile spillover	P_0, P_1,..., $P_{\alpha-1}$	
Adult breeding reserve (ontogenetic shift)	$P_{\alpha-1}$, P_α, $P_{\alpha-1}F$, $P_\alpha F$	
All-age spillover	P_0, P_1,..., P_α, $P_{\alpha-1}F$, $P_\alpha F$	

Note: (*a*) For gray whales and turtles, dispersal is modeled as adult spillover; for urchins and groupers, dispersal is modeled as recruitment. Adult mortality is reduced by 20% in the reserve site for all dispersal scenarios and by 10% in both the reserve and nonreserve sites for the catch reduction scenario. (*b*) Dispersal parameters in model scenarios for high dispersal out of the reserve (Fig. 4*a*) and high dispersal into the reserve (Fig. 4*b*). For all scenarios, adult mortality is reduced by 20% in the reserve site.

tential management strategies that are species or location specific).

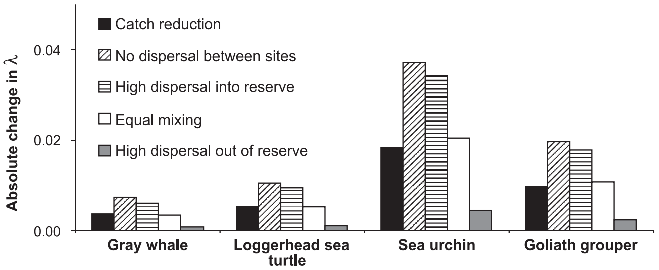
How does dispersal rate interact with life history to determine reserve efficacy?

For our first analysis, the change in λ resulting from a decrease in adult mortality and stage-specific dispersal varied for each representative life history (Fig. 3). It should be noted, however, that the effects on λ caused by vital rate values and age at maturity are confounded with model structure in the first analysis (e.g., dispersal occurs in different stages for urchins and whales). With this in mind, comparisons can be made between species and for different model scenarios for each species. Overall, sea urchins and groupers exhibited the most striking response to the establishment of a reserve, while whales and sea turtles exhibited a smaller absolute increase in λ following a decrease in adult mortality (also see Gerber and Heppell 2004). The maximum increase in λ is achieved when there is no dispersal, as the dominant eigenvalue for the metapopulation matrix is driven by the submatrix with the highest λ (site B).

The predicted change in λ for all species was reduced when dispersal was added to the model. The effect of dispersal is to proportionately reduce the maximum benefit attainable by the reduction in mortality that occurs in the reserve because individuals "leak out" and the net reduction in mortality is reduced. Thus, the magnitude and sign of net dispersal across the reserve boundary had strong effects on the efficacy of reserves for all species, but the responses took on the same shape for all four species. Under the reduced catch scenario, the change in λ was half of that expected from the no-dispersal scenario. The efficacy of reserves relative to catch reduction or the maximum benefit possible depended significantly on net dispersal (Fig. 3). When net dispersal was negative (i.e., higher dispersal out of reserve), efficacy was lower than that of catch reduction for all four species.

For these models, reserves were most effective when dispersal in both directions was zero. In this type of model, source (reserve) and sink (fished) habitats are disconnected and fisheries have no access to stocks protected within the reserve boundary; thus, the reserve effects are pronounced and the asymptotic population λ is entirely driven by dynamics inside the reserve. This is because the population size of the reserve eventually becomes arbitrarily large relative to the unprotected site so that the growth of the population as a whole approaches that of the reserve site. This dynamic may be prevented by finite patch size in real systems, where the protected area is likely to be smaller than the unprotected area. Thus, our method will be most useful for looking at responses to small changes in mortality when populations in both patches are initially rather close to equilibrium. Nonetheless, reserves have only slightly lower efficacy when dispersal is net positive (emigration < immigration) and still higher efficacy than fisheries reduction. When reserved and nonreserved populations mix equally, reserves and fisheries reduction have nearly equal efficacy for all case studies.

Fig. 3. Absolute change in population growth rate (λ) resulting from a 20% reduction in adult mortality due to reserves for different rates of migration modeled with four species life histories. The change in λ when there is no dispersal between the two sites is equal to the change expected from the mortality decrease alone. Mortality is reduced by 10% for both patches for the catch reduction scenario (no reserve). Parameter values for dispersal scenarios are defined in Table 2*a*.

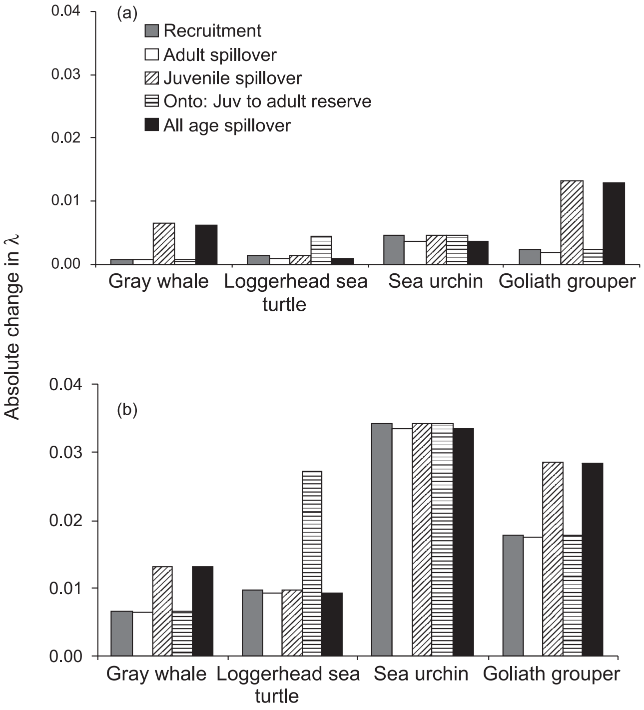


The consistency of reserve efficacy across taxa suggests that dispersal may indeed override life history considerations when setting reserves. More specifically, if the dispersal of a target species from a reserve is high relative to the replacement of these emigrants from external habitats, reserves may be a less effective tool than more traditional methods of fisheries management. In this case, reserves may be merely “show-and-tell” boundaries set over well-mixed fishing grounds.

How does dispersal mechanism interact with life history to determine reserve efficacy?

In our second analysis we examine how dispersal at different life stages (versus different net rates; Fig. 3) determines the efficacy of reserves for the same four species. Reserves increased population λ values of all species much more strongly when net dispersal into the reserve was high (compare Figs. 4*a* and 4*b*), echoing results from our first analysis. Reserves had stronger effects on groupers and whales when the model assumed juvenile or adult and juvenile spillover (Fig. 4). Thus, as long as juveniles disperse from the reserve into the fished matrix, reserves will increase population λ values of whales and groupers more than catch reduction. By contrast, reserves had the strongest effect on turtles when dispersal occurred as an ontogenetic niche shift for maturing juveniles, and urchins showed similar responses to reserves for all dispersal scenarios (Fig. 4). This is most likely due to differences in the elasticity values of adults versus juveniles (see Gerber and Heppell 2004). Finally, the relative effects of ontogenetic dispersal were similar when net dispersal was negative (Fig. 4*a*) or positive (Fig. 4*b*). In general, patterns of reserve efficacy across different dispersal types were strongly species specific.

Fig. 4. Absolute change in population growth rate (λ) resulting from a 20% reduction in mortality due to reserves for each dispersal mechanism for (*a*) high dispersal out of the reserve and (*b*) high dispersal into the reserve. Parameter values for the scenarios for migration, ontogenetic shifts, and recruitment are defined in Table 2*b*.



Discussion

Studies of marine reserves have highlighted the importance of dispersal (especially larval transport; Gaines et al. 2003) and life history (Gerber and Heppell 2004) in maximizing conservation goals in the face of harvest. This paper illustrates how a more general theory of marine reserves should include both. Our results convey the importance of dispersal in determining reserve efficacy and more generally in interpreting the results of simple demographic models that ignore dispersal. In addition to the general message that dispersal matters, our results highlight the importance of understanding particular mechanisms of dispersal. Furthermore, the results convey the lack of generality among species in responses to relative importance of migration, ontogenetic shifts, and recruitment. This highlights the importance of including detailed information in both empirical and theoretical investigations of reserve efficacy.

Categorizing life histories according to their response to changes in stage-specific mortality may provide a useful method for considering conservation options (Heppell et al. 2000; Gerber and Heppell 2004). Demographic sensitivity analysis allows researchers to analyze a priori how much a small change in a demographic rate (here, adult survival) influences a population’s potential for recovery. Further, such approaches rely on minimal data (e.g., survival and fecundity rates) and may allow researchers to predict the effects of alternative management actions (Heppell et al. 1999). In the context of marine reserves, these analyses must be spatially explicit to cope with the connectivity between protected and unprotected populations determined by migration, larval transport, and ontogenetic habitat shifts. We showed that life history theory can be used to predict changes in λ resulting from a decrease in adult mortality following establishment of a marine reserve for four species with different life histories and further illustrate the complexity of including different types of dispersal for species with complex life histories. Given the paucity of spatially explicit data for many marine systems, our simple approach represents a first step in applying life history information to advance current theory and provide practical considerations for marine reserve management.

These results are consistent with current theory concluding that moderate rates of juvenile and adult dispersal render reserves more effective because high adult dispersal allows for too little protection of reproductive output within reserves, and low adult dispersal allows no increase in catch outside the reserves per unit area protected (Botsford et al. 2003; Gerber et al. 2003 and references therein). Furthermore, our results suggest that, in addition to higher population recovery rates following reserve implementation for species with high reproductive output (e.g., urchins and groupers), those with high larval dispersal may benefit more than those with high adult dispersal (e.g., whales and turtles). Our explicit consideration of recruitment from the unprotected area to the reserve has been largely ignored in theoretical and empirical studies of reserve efficacy.

Further assessment, both theoretical and empirical, is needed to develop driving principles for reserve design and life history attributes. A more systematic evaluation of the effect of variation in cofactors (e.g., stage-specific dispersal and demography) is an important next step. Explicitly incorporating uncertainty in vital rates is also critical to the application of demographic analysis to marine reserve design. Finally, an important next step will be to include density-dependent population growth in this type of modeling framework. While our model assumes that growing fast is more important than the ultimate population size reached, in the real world where protected areas are generally smaller than unprotected sites, density dependence is likely to be relevant. Thus, a more sophisticated density-dependent model may be more useful for assessing management policies. However, our comparative framework will be particularly effective for evaluating perturbation responses across species for which we do not have detailed information on dispersal and for those that exhibit clear changes in habitat through their life history.

Arguably, a species by species approach may have limited value when designing networks of reserves over a large ecoregion, where biodiversity protection accompanies fishery enhancement as a conservation goal. However, we believe that a representative group of species covering a wide range of life histories could be used to design a network of marine reserves at an ecoregional level. For example, the species treated here as case studies all inhabit, permanently or temporarily, the Gulf of California. In the Gulf of California, there is currently a move afoot among scientists, conservation organizations, and the Mexican government to establish new protected areas. Recent studies in the central and southern Gulf have proposed a design strategy for the establishment of such no-take reserves using data on biodiversity, ecological processes, and socioeconomic factors (Sala et al. 2002). However, there are no general formulae to decide how to prioritize establishment of reserves to maximize recovery of imperiled populations. Further, most existing reserves do not have explicit goals and expectations, and temporal changes in the species populations in the reserves are not consistently monitored. An important next step will be to use our conceptual framework as a basis for identifying relevant time frames for monitoring based on life history and dispersal data.

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References

Acosta, C.A. 2002. Spatially explicit dispersal dynamics and equilibrium population sizes in marine harvest refuges. ICES J. Mar. Sci. **59**: 458–468.

Agardy, M.T. 1994. Advances in marine conservation: the role of marine protected areas. Trends Ecol. Evol. **9**: 267–270.

Allison, G.W., Lubchenco, J., and Carr, M.H. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecol. Appl. **8**: S79–S92.

Botsford, L., Hastings, A., and Gaines, S. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecol. Lett. **4**: 144–150.

Botsford, L.W., Micheli, F., and Hastings, A. 2003. Principles for the design of marine reserves. Ecol. Appl. **13**: S25–S31.

Bullock, L.H., Murphy, M.D., Godcharles, M.F., and Mitchell, M. 1992. Age, growth, and reproduction of Jewfish *Epinephelus itajara* in the Eastern Gulf of Mexico. Fish. Bull. **90**: 243–249

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Inc., Sunderland, Mass.

Crowder, L.B., Crouse, D.T., Heppell, S.S., and Martin, T.H. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecol. Appl. **4**: 437–445.

Doak, D.F. 1995. Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. Conserv. Biol. **9**: 1370–1979.

Fujiwara, M., and Caswell, H. 2001. Demography of the endangered North Atlantic right whale. Nature (Lond.), **414**(6863): 537–541.

Gaines, S., Gaylord, B., and Largier, J.L. 2003. Avoiding current oversights in marine reserve design. Ecol. Appl. **13**: S32–S46.

Gell, F.R., and Roberts, C.M. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol. Evol. **18**: 448–455.

Gerber, L.R., and Heppell, S.S. 2004. The use of demographic sensitivity analysis in marine species conservation planning. Biol. Conserv. **120**: 121–128.

Gerber, L.R., Kareiva, P.M., and Bascompte, J. 2002. The interplay of life history attributes and fishing pressure in evaluating efficacy of marine reserves. Biol. Conserv. **106**: 11–18.

Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R., and Andelman, S.J. 2003. Population models for reserve design: a retrospective and prospective synthesis. Ecol. Appl. **13**: S47–64.

Grantham, B.A., Eckert, G.L., and Shanks, A.L. 2003. Dispersal potential of marine invertebrates in diverse habitats. Ecol. Appl. **13**: S108–S116.

Heppell, S.S., Crowder, L.B., and Menzel, T.R. 1999. Life table analysis of long-lived marine species with implications for conservation and management. Am. Fish. Soc. Symp. **32**: 137–148.

Heppell, S.S., Caswell, H., and Crowder, L.B. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology, **81**: 654–665.

Hooker, S., and Gerber, L.R. 2004. Potential importance of megafauna: marine reserves as a tool for ecosystem-based management? BioScience, **54**: 29–41.

Kareiva, P., Marvier, M., and McClure, M. 2001. Recovery and management options for spring/summer chinook salmon in the Columbia River Basin. Science (Wash., D.C.), **290**: 977–979.

Lockwood, D.R., Hastings, A., and Botsford, L.W. 2002. The effects of dispersal patterns on marine reserves: does the tail wag the dog? Theor. Popul. Biol. **61**: 297–309.

Martell, S.J.D., Walters, C.J., and Wallace, S.S. 2000. The use of marine protected areas for conservation of lingcod (*Ophiodon elongatus*). Bull. Mar. Sci. **3**: 729–743.

Morris, W.F., and Doak, D.F. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Inc., Sunderland, Mass.

National Research Council. 2001. Marine protected areas: tools for sustaining ocean ecosystems. National Academy Press, Washington, D.C.

Pfister, C.A., and Bradbury, A. 1996. Harvesting red sea urchins: recent effects and future predictions. Ecol. Appl. **6**: 298–310.

Polacheck, T. 1990. Year round closed areas as a management tool. Nat. Resour. Model. **4**: 327–354.

Quinn, J.F., Wing, S.R., and Botsford, L.W. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. Am. Zool. **33**: 537–550.

Reilly, S. 1984. Observed and maximum rates of increase in gray whales, *Eschrichtius robustus*. Rep. Int. Whaling Comm. Spec. Issue, **6**: 389–400.

Sadovy, Y., and Eklund, A.E. 1999. Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichtenstein, 1822). NOAA Tech. Rep. NMFS 146.

Sala, E., Aburto, O., Paredes, G., Parra, I., Barrera, J.C., and Dayton, P.K. 2002. A general model for designing networks of marine reserves. Science (Wash., D.C.), **298**: 1991–1993.

Sala, E., Aburto, O., Paredes, G., and Thompson, G. 2003. Spawning aggregations and reproductive behavior of reef fishes in the Gulf of California. Bull. Mar. Sci. **72**: 103–121.

Stockhausen, W.T., Lipcius, R.N., and Hickey, B.M. 2000. Joint effects of larval dispersal, population regulation, marine reserve design, and exploitation on production and recruitment in the Caribbean spiny lobster. Bull. Mar. Sci. **3**: 957–990.

Wooton, J.T., and Bell, D.A. 1992. A metapopulation model of the peregrine falcon in California: viability and management strategies. Ecol. Appl. **2**: 307–321.