Abstract.—We used fishery population models to assess the potential for marine fishery reserves, areas permanently closed to fishing, to enhance long-term fishery yields. Our models included detailed life history data. They also included the key assumptions that adults did not cross reserve boundaries and that larvae mixed thoroughly across the boundary but were retained sufficiently to produce a stock-recruitment relationship for the management area. We analyzed the results of these models to determine how reserve size, fishing mortality, and life history traits, particularly population growth potential, affected the fisheries benefits from reserves. We predict that reserves will enhance catches from any overfished population that meets our assumptions, particularly heavily overfished populations with low population growth potential. We further predict that reserves can enhance catches when they make up 40% or more of fisheries management areas, significantly higher proportions than are typical of existing reserve systems. Finally, we predict that reserves in systems that meet our assumptions will reduce annual catch variation in surrounding fishing grounds. The fisheries benefits and optimal design of marine reserves in any situation depended on the life history of the species of interest as well as its rate of fishing mortality. However, the generality of our results across a range of species suggest that marine reserves are a viable fisheries management alternative.

Fisheries benefits and optimal design of marine reserves

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Fishing activity impacts the marine environment in several ways. Individual species risk severe declines from overexploitation. Over two-thirds of all fisheries world-wide are classified as fished beyond capacity or in danger of becoming so (FAO, 1995), and higher trophic levels are particularly affected (Pauly et al., 1998). Along with target species, fishing can reduce the populations of nontarget species that are caught and discarded. The ecosystems that support the fisheries also face risks. Fishing can cause biological damage to ecosystems when the reduction of key species or trophic levels causes ecological shifts (e.g. Hay, 1984; Castilla and Durán, 1985; Hay and Taylor, 1985; Durán and Castilla, 1989; McClanahan and Shafir, 1990; Roberts, 1995; McClanahan et al., 1996; Pauly et al., 1998). Fishing can also cause physical damage to ecosystems, particularly when dwindling fish catches promote the incentive to use damaging fishing practices (McAllister, 1988).

Reserves can protect the ecosystems within them from damaging fishing practices and have the potential to reestablish a natural ecosystem balance (Russ, 1985; Plan Development Team, 1990; Roberts and Polunin, 1991; Dugan and Davis, 1993; Roberts and Polunin, 1993; Rowley, 1994; Roberts et al., 1995; Bohnsack, 1996). Field studies have generally demonstrated that fish stocks build up within a protected area (Roberts and Polunin, 1991; Dugan and Davis, 1993; Rowley, 1994; Bohnsack, 1996, and references within) but much less information exists on fishery enhancements.

In theory, reserves can maintain productive fisheries by protecting a critical stock within their borders. These stocks may enhance catches through adults that grow larger in the reserve and then migrate to fishing areas (adult spillover), or through enhanced recruitment in fishing areas due to increased population fecundity from the reserve (larval transport). In practice, fisheries benefits from reserves have rarely been demonstrated or even measured. This lack of field evidence reflects the difficulty of performing controlled and replicated experiments in unpredictable political and biological systems.

The few existing field studies addressing fisheries benefits from reserves show promise. A marine fishery reserve encompassing over 60% of the former fishing grounds north of Mombasa, Kenya, showed a 110% increase in catch per unit of effort after only two years (McClanahan and Kaunda-Arara, 1996). Total catches had not yet met those prior to reserve establishment, but trends looked favorable. On Apo Island, Philippines, total fish density and

species richness had increased by over 400% in both the reserve and the fishing grounds after 11 years of reserve protection (Russ and Alcala, 1996). Large fish were particularly abundant in the fishing grounds near the border of the reserve, possible evidence of adult spillover. These same authors showed previously that overall catches dropped more than 50% two years after the re-opening of a closed area on Sumilon Island, Philippines, despite the increased fishing area (Alcala and Russ, 1990), suggesting that the reserve had provided enhancements to surrounding fishing grounds.

These field studies show that under certain circumstances, reserves are likely to produce fisheries enhancements. However, models are also necessary because they allow more general analyses of the conditions under which reserves are likely to produce benefits and of the design attributes that will maximize these benefits. By making use of controlled replicates and large-scale manipulations, models can provide a theoretical background on which to interpret field results.

Several authors have built and analyzed models of marine fishery reserves. These models can be classified as those examining adult spillover (Beverton and Holt, 1957; Polacheck, 1990; DeMartini, 1993) and those examining larval transport (Quinn et al., 1993; Man et al., 1995; Holland and Brazee, 1996; Sladek Nowlis and Roberts, 1997; Holland et al.[1]). All of these models predict fisheries enhancements from reserves in at least some situations, particularly under heavy exploitation. However, the predicted enhancements were small and uncommon for the adult spillover models. Previous models have examined a variety of factors that influence potential reserve benefits, including adult movement tendencies (Polacheck, 1990; DeMartini, 1993), individual growth rate (DeMartini, 1993), Allee effects (Quinn et al., 1993), metapopulation patch dynamics (Man et al., 1995), and socioeconomic factors (Holland and Brazee, 1996; Holland et al.[1]). None of these examined the effect of population growth potential on reserve benefits.

In order to fill this gap, we built a set of models looking at reproductive enhancement and larval transport as mechanisms for providing reserve benefits. We analyzed these models with particular emphasis on how reserve size, fishing mortality, and life history traits, particularly population growth potential, affect long-term fishery yields. We also analyzed the short-term consequences of reserve establish-

ment and these results are presented elsewhere (Sladek Nowlis and Roberts, 1997).

We used our models to achieve several goals. First, we wanted to identify conditions that favored the success of reserves at enhancing fisheries. Second, we wanted to establish design criteria to help maximize the benefits that could accrue from a closed fishing area. Third, we wanted to assess whether reserves can decrease year-to-year variation in catches. Finally, we wanted to provide guidelines for future field research through the identification of important but poorly understood biological processes and through the generation of testable predictions about the design and function of marine fishery reserves.
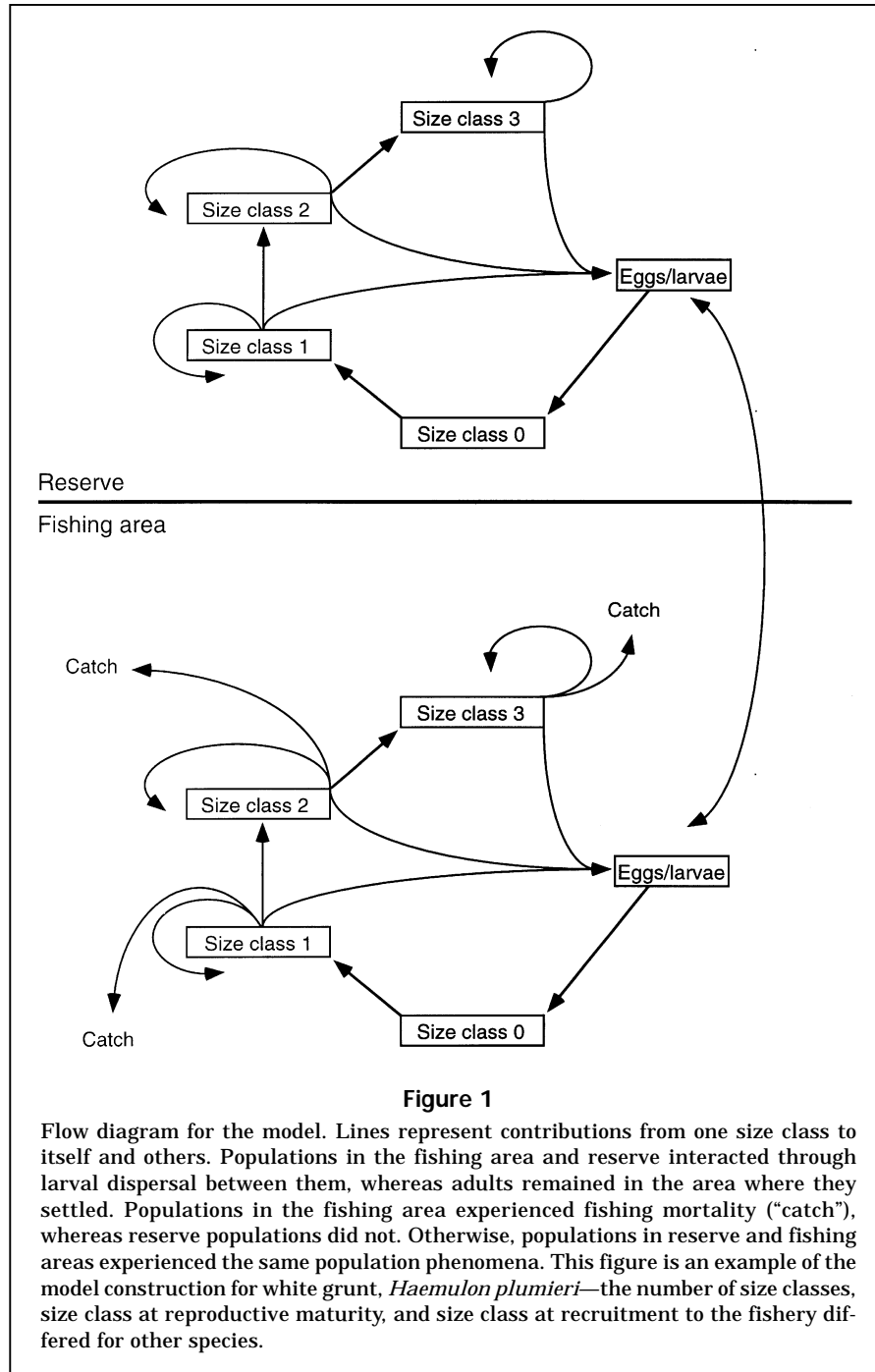
Methods

Our basic model followed yearly changes in a population separated into size categories. Although categorization by age is more common than by size, we felt size better represented size-dependent processes such as reproduction and fishing mortality (Polunin and Roberts, 1996). Each size category contributed to future populations through some simple rules (Fig. 1).

We used the best-available estimates of size-based fecundity and larval survivorship for various species (see Table 1). Little is known about larval survivorship in fish, especially for coral reef species (Boehlert, 1996). The best estimates we could find came from an analysis of larval performance across a global array of ambient temperatures (Houde, 1989). Houde used linear regression on data from various studies to relate ambient temperature to fish larval duration and daily survivorship. This process produced statistically significant and predictive, but crude, relationships that could then be combined to estimate total larval survivorship. At a temperature of 26°C, Houde's estimate of survivorship for larvae through the entire larval stage was 5×10^{-5} (see Appendix for equations). Whenever we had additional information about larval stage duration, we used it along with Houde's temperature-based estimate for daily survivorship to produce our estimate of total larval survivorship.

Natural mortality estimates were also taken from the literature (see Table 1). Those adults that survived had the additional possibilities of either growing to the next size class or staying in the same one. We used von Bertalanffy growth parameters (Ricker, 1975) to determine the chance that a fish of one size class grew to the next in a given year (Fig. 2). Von Bertalanffy parameters describe the growth of individual fish and are widely estimated in the literature (see Table 1 for the estimates that we used and

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[1] Holland, D. S., J. B. Braden, and R. J. Brazee. 1995. Managing artisanal fisheries with marine fishery reserves: an alternative to managing catch or effort. Environmental and Natural Resources Policy and Training/Midwest Universities Consortium for International Activities Supplementary Paper 3, 36 p.

Figure 1

Flow diagram for the model. Lines represent contributions from one size class to itself and others. Populations in the fishing area and reserve interacted through larval dispersal between them, whereas adults remained in the area where they settled. Populations in the fishing area experienced fishing mortality ("catch"), whereas reserve populations did not. Otherwise, populations in reserve and fishing areas experienced the same population phenomena. This figure is an example of the model construction for white grunt, *Haemulon plumieri*—the number of size classes, size class at reproductive maturity, and size class at recruitment to the fishery differed for other species.

Appendix for relevant equations). To convert these continuous measures into probabilities, we used the standard von Bertalanffy parameters to estimate the lengths of the smallest and largest individual in each size category for the following year. We calculated the proportion of this size range that fell into the next size class and used this value to represent the probability that a fish of this size class grew to the next size class. The remaining individuals stayed the same size over the next year, with a probability determined by subtracting the probability of growing from 1. We chose the size-class interval for each species such that newly settled fish had exactly 100% chance of growing to the next size class during the first year (see Appendix for formula). Consequently, fish were never able to grow more than one size class in a year. As with all von Bertalanffy growth relationships, growth slowed with age—in our case from

Table 1

Parameter values for four fishery species. See Appendix for detailed explanation of parameters. Parameter values were taken from the literature where available. Where we could not find values in the literature, we made our best educated guess by looking at a related species, by running several values until we got realistic population growth (i.e. growth in the absence of fishing), or by measuring some other consequence, for example length at recruitment, to check for realism. References: [1] Plaut (1993); [2] Houde (1989); [3] Plaut and Fishelson (1991); [4] Aiken (1983); [5] Darcy (1983); [6] Thompson and Munro (1983); [7] best guess.

Species	Fecundity	Larval survival	Adult survival	Growth
Panulirus penicillatus, Red Sea spiny lobster	r = 4 spawns per year $\times$ 2.715 $\times L^{2.581}$ eggs per spawn. Mature at L = 50 mm ([1])	D = 35.5 days ([1]) Z = 0.3454 ([2]) $N = 5 \times 10^{-6}$ ([2])	v = 0.8 (M=0.223) Fishery recruitment = 25.7 mm ([7])	k = 0.1066 L_∞ = 84.7 mm t_0 = 0 c = 6.43×10^{-4} y = 2.89 ([3])
Balistes vetula, queen triggerfish	r = 3 spawns per year $\times$ 73 per g body weight. Mature at size 23.5 cm ([4])	D = 28.7 days ([2]) Z = 0.3454 ([2]) $N = 5 \times 10^{-5}$ ([2])	v = 0.07427 (M=2.6) ([4]) Fishery recruitment = 17 cm ([7])	k = 0.57 ([4]) L_∞ = 45 cm ([4]) t_0 = −0.5 ([7]) c = 0.05164 ([4]) y = 2.875 ([4])
Haemulon plumieri, white grunt	r = 1 spawn per year $\times$ (626 per g body weight − 93000). Mature at size = 22 cm ([5])	D = 28.7 days ([2]) Z = 0.3454 ([2]) $N = 5 \times 10^{-5}$ ([2])	v = 0.17 (M=1.77) Fishery recruitment = 14.9 ([5])	k = 0.34 ([5]) L_∞ = 42 ([5]) t_0 = −1 ([7]) c = 0.0238 ([5]) y = 2.93 ([5])
Epinephelus guttatus the red hind	r = 1 spawn per year $\times$ 873.454 per g body weight − 194086). Mature at size < 25 cm ([6])	D = 28.7 days ([2]) Z = 0.3454 ([2]) $N = 5 \times 10^{-5}$ ([2])	v = 0.5066 (M=0.68) Fishery recruitment = 31 cm ([6])	k = 0.24 ([6]) L_∞ = 52 ([6]) t_0 = −0.5 ([7]) c = 0.0107 ([6]) y = 2.96 ([6])

100% growth for new settlers to 0% for fish in the largest size class.

Adults in the fishing area that grew larger than the minimum catch size experienced fishing mortality. We represented fishing mortality using the parameter u, equal to the proportion of fishery-recruited individuals caught per year, and related to the more common F by the equation:

$$u = 1 - e^{-F}.$$

We independently varied the two key parameters in our models: fishing mortality (u) and reserve proportion (s).

We made settlement a density-dependent process by incorporating a negative exponential function into survivorship for new settlers during their first year (see Appendix for equation). There is evidence to suggest that shelter is limiting for coral reef fish, especially new settlers (Hixon, 1991; Hixon and Beets, 1993; Hixon and Carr, 1997)—a process that would fit well with our density dependence assumptions. We also performed runs in which larval rather than new settler survivorship was density-dependent and
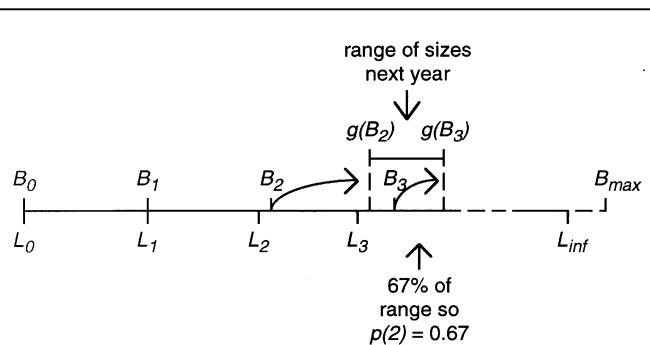

Figure 2

Determination of growth probabilities. The probability $p(x)$ that a fish of size class x grows to size class $x+1$ is the proportion of the range of sizes that size class x individuals will span one year later. Using von Bertalanffy growth parameters (see Appendix), we determined one year in the future the size of the smallest and largest fish in size class x. All other fish in x would fall between these two values. We then determined what proportion of these sizes fell into size class $x+1$, 0.67 in the case illustrated. In this hypothetical example, we would assume that $p(x)$ = 0.67, or that 67% of the fish from size class x grew to class $x+1$ by the next year. L_t represents the sizes attained at age t and B_x represents the lower bounds of each size class. We begin counting age at the moment of settlement (so $L_0 = B_0$).

obtained qualitatively identical results. Little information exists on density-dependent relationships for tropical fish; therefore we were forced to use a standard theoretical logistic equation (see Appendix). For simplicity in analysis and in recognition of this knowledge gap, we constructed the models with a fixed carrying capacity of 1000 one-year-old individuals per unit area. We modeled population processes on the basis of density measures in reserve and fishing areas and used relative proportions of each to calculate catches and population fecundity. Thus, yields are expressed as kg per year from the whole management area.

In order to ask the general questions we intended, we used two simple movement assumptions that emphasized the benefits accruing from larval transport rather than from adult spillover. Larvae dispersed widely across reserve boundaries, resulting in an even density of new fish settlement in reserve and nonreserve areas. This assumption does not negate the possibility that larvae drift to the open ocean and become lost—these can be accounted for in larval mortality. Rather, the assumption implies that settlement in the reserve and the management area are equally affected by the stock averaged over both areas. We also assumed that adults did not move across reserve boundaries; that is to say fish spent their entire lifetime in the area in which they settled. These assumptions specifically addressed the case where enhanced fecundity within the reserve was exported to fishing areas through larval transport. Thus they complemented previous models that focused on enhancements from adult spillover (Polacheck, 1990; DeMartini, 1993). These models also examined potential increases in reproductive output by means of increased spawning stock biomass per recruit. However, they were unable to examine the equilibrium consequences with their particular model construction.
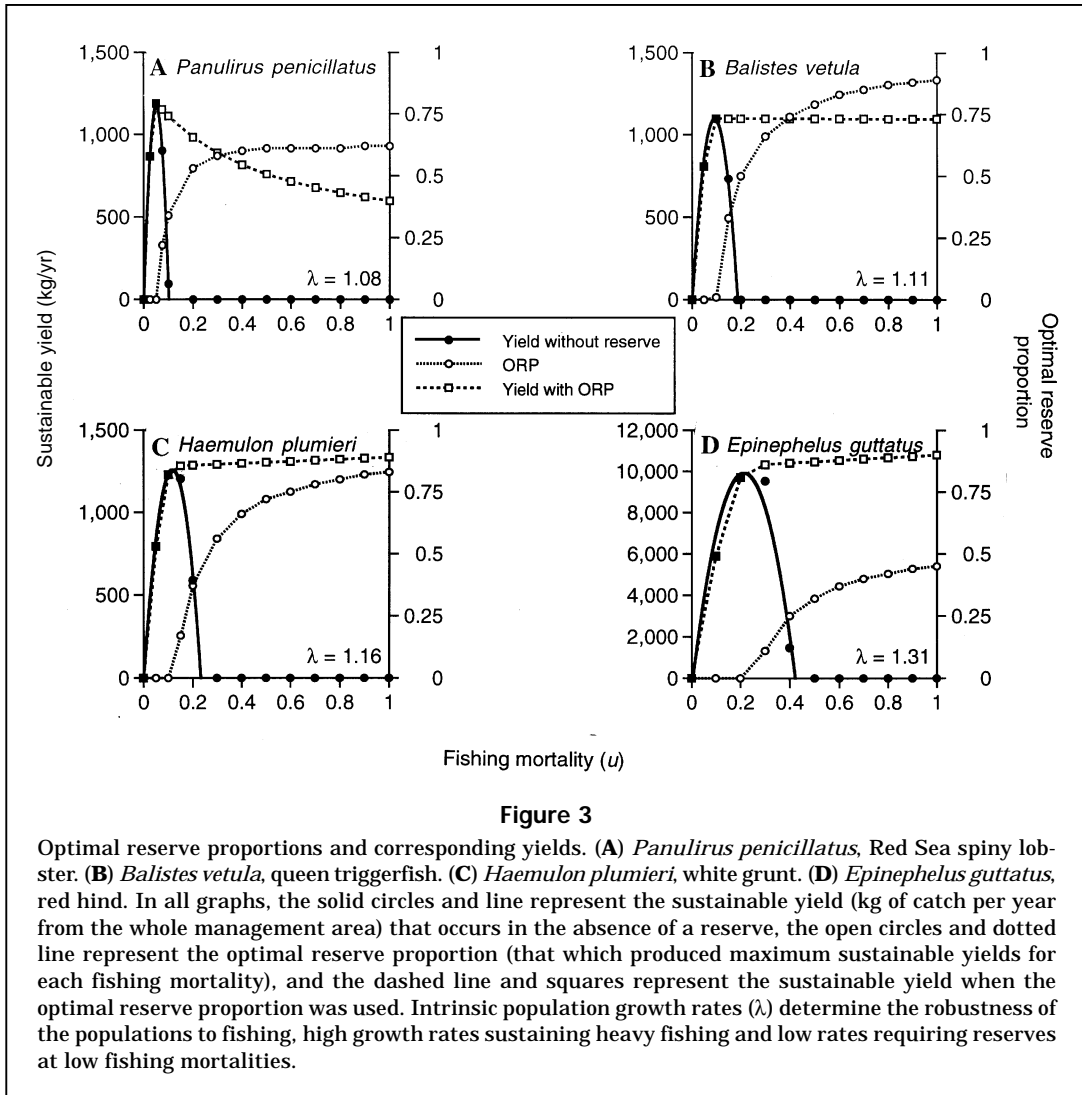
Our movement assumptions apply to the majority of fishery species on at least some spatial scales. Most aquatic species disperse more widely as larvae than as adults (Boehlert, 1996). Consequently, larvae are more likely to cross boundaries than are adults. As long as individual reserve units stretch beyond the dispersal distance of adults but remain well within the dispersal distance of larvae for a given species, the model assumptions will approximate reality. For large reserve proportions, our assumptions could still be met if the reserve area were partitioned into several smaller units. Some areas of concern here include ontogenetic and reproductive migrations. To fit the assumptions of this model, reserves must be designed with these movements in mind so that fish are likely to remain in the reserve during the phase of their life in which they are vulnerable to fishing.

We ran the models over reserve proportions varying from 0 to 99% of the management area (s=0 to 0.99), and fishing mortalities varying from 1% to 100% mortality of fishery-recruited individuals per year (u=0.01 to 1.00). For each combination of fishing mortality and reserve proportion, the model ran until the fish catch—calculated for the whole management area rather than per km^2 of available fishing area—had stabilized at the long-term sustainable yield. The model stored the yield, fishing mortality, and reserve proportion. It sometimes took hundreds of years to reach stability, and those interested in our model's predictions about the short-term dynamics of reserve creation should refer to Sladek Nowlis and Roberts (1997).

We used these results to determine the optimal reserve proportions and fishing mortalities for individual fishery species. For each fishing mortality, we found the reserve proportion that maximized sustainable yields and stored it and the yield. We compared these yields when an optimally-sized reserve was used with the yields without a reserve (s=0) to establish fisheries benefits. We plotted this information using fishing mortality as an independent variate.

We also examined the effects of marine fishery reserves on year-to-year catch variability. Bohnsack (1996) suggested that marine fishery reserves could dampen natural fluctuations in catches, thus making fisheries more stable and easier to manage. We tested this hypothesis by adding a stochastic component to larval survivorship in our model. These new models drew larval survivorship randomly from a normal distribution around the mean larval survivorship whose standard deviation we could define. We examined all species over a range of fishing mortalities and present the results from $u = 0.2, 0.4, 0.6,$ and 0.8 to illustrate the pattern. We also examined some of these conditions at three levels of environmental variation, with standard deviations of 5, 10, and 20% of the mean larval survivorship, to gain insight into whether reserve benefits are influenced by the degree of environmental variability.

For each possible combination of fishing mortality and reserve proportion, we performed 10 replicate runs of our stochastic models. In each run, we ran the models for 500 years to allow the fisheries to stabilize to the maximum extent possible and thus minimize the influence of our arbitrarily chosen initial state. The mean and standard deviation of the catches were measured over the next 100 years. We examined the ratio of the standard deviation to the average catch over this period because this measure gave us an estimate of the likelihood of percentage fluctuations in catches rather than absolute changes.

Figure 3

Optimal reserve proportions and corresponding yields. (**A**) *Panulirus penicillatus*, Red Sea spiny lobster. (**B**) *Balistes vetula*, queen triggerfish. (**C**) *Haemulon plumieri*, white grunt. (**D**) *Epinephelus guttatus*, red hind. In all graphs, the solid circles and line represent the sustainable yield (kg of catch per year from the whole management area) that occurs in the absence of a reserve, the open circles and dotted line represent the optimal reserve proportion (that which produced maximum sustainable yields for each fishing mortality), and the dashed line and squares represent the sustainable yield when the optimal reserve proportion was used. Intrinsic population growth rates (λ) determine the robustness of the populations to fishing, high growth rates sustaining heavy fishing and low rates requiring reserves at low fishing mortalities.

This measure is better than standard deviation alone which would treat a 10-kg fluctuation equally, regardless of whether it occurred in a 100 kg or 1,000,000 kg per year fishery. We graphed these results with reserve proportion as the independent variate and examined the graphs for trends.

We performed these analyses on four coral reef fishery species for which we obtained relatively complete parameter sets. These included *Balistes vetula*, queen triggerfish; *Epinephelus guttatus*, red hind; *Haemulon plumieri*, white grunt; and *Panulirus penicillatus*, Red Sea spiny lobster (see Table 1 for parameter estimates).

Results

When we ran the models without a reserve (s=0), they produced standard yield-effort curves (Fig. 3). These curves are characterized by steep initial gains in long-term sustainable yields with increases in fishing mortality (and thus effort), followed by equally steep declines (Clark, 1990). The curves peaked at the maximum sustainable yield, one of several goals a manager might try to achieve with a fishery (Clark, 1990), and we will refer to the corresponding fishing mortality as the MSY mortality for the rest of this paper. Above the MSY mortality, the fishery can be defined as overfished because it is less productive than it would be with less fishing activity.

When a reserve was present, the yield-mortality curves were still parabolas passing through the origin but spread farther to the right, and the larger the reserve, the more pronounced were these shifts. Consequently, larger reserves required higher fishing mortalities to maximize long-term sustainable yields (remember that this mortality only affected fish in fishing areas), whereas the sustainable yields

decreased more slowly as fishing mortality increased past the MSY mortality.

Our analyses of optimal reserve proportions produced several key results. First, reserves produced fisheries enhancements, meaning that the overall catches with a reserve exceeded those without one, whenever the fisheries were overfished (Fig. 3), here defined as fished above the MSY mortality level. When fisheries were overfished, they produced higher yields with a reserve even though the reserve decreased the amount of fishing area. The optimal reserve proportion increased with increasing fishing mortality, and heavily exploited fisheries required particularly large reserves to remain productive. The fishery benefit attributable to reserves, calculated by subtracting the yield without a reserve from that with an optimally sized reserve, increased with increasing fishing mortality up to a near-maximum yield in most cases (Fig. 4). Consequently, a wide span of reserve sizes (up to 80% of the management area for some species) pro-

duced similarly high yields for most species as long as fishing mortalities were chosen accordingly.

Using this information (Fig. 3), we predicted optimal reserve proportions under real-life fishing mortalities. For queen triggerfish, the fishing mortality estimate of $u = 0.45$ from Puerto Rico and the Virgin Islands (Aiken, 1983) corresponded to an optimal reserve proportion of approximately $s = 0.8$. For white grunt, a reported heavy fishing mortality of $u = 0.99$ from Jamaica (Darcy, 1983) corresponded to an optimal reserve proportion of just over $s = 0.75$. Thus, for these species in these locations, our models predicted that 75–80% of the fishing grounds should be made off-limits to fishing in order to maximize long-term sustainable yields. These numbers may seem unrealistically high, especially since most models predict maximum yields when approximately 50% of the population density at carrying capacity is protected from fishing (see Clark, 1990, for an overview). In the case of our models, populations within the reserve did not reach carrying capacity when fishing was heavy outside, and the conditions of peak production corresponded to those that protected approximately 50% of the population density at carrying capacity.

The qualitative conclusions outlined above were consistent across all the species we examined. However, the model's quantitative predictions of the long-term fishery yields and optimal reserve proportion varied from species to species for any given fishing mortality (Fig. 3). The key differences between species were the speeds at which the yield and optimal reserve proportion changed with increasing fishing mortality (Fig. 3). These differences reflected differences in intrinsic population growth rates (λ)—the maximum growth rate of a population with no density-dependent constraints or fishing mortality. This summary parameter integrates most of the life history data that we used. It does not include the growth rate of individuals in the population and consequently does not adequately predict yields. However, it is a useful summary of the ability of a population to sustain harvesting. For example, life history parameters from the literature suggested that the Red Sea spiny lobster had a relatively low $\lambda = 1.08$, just above the $\lambda = 1$ necessary for a population to sustain itself with no fishing pressure. This species had a low MSY fishing mortality because its slow population growth could
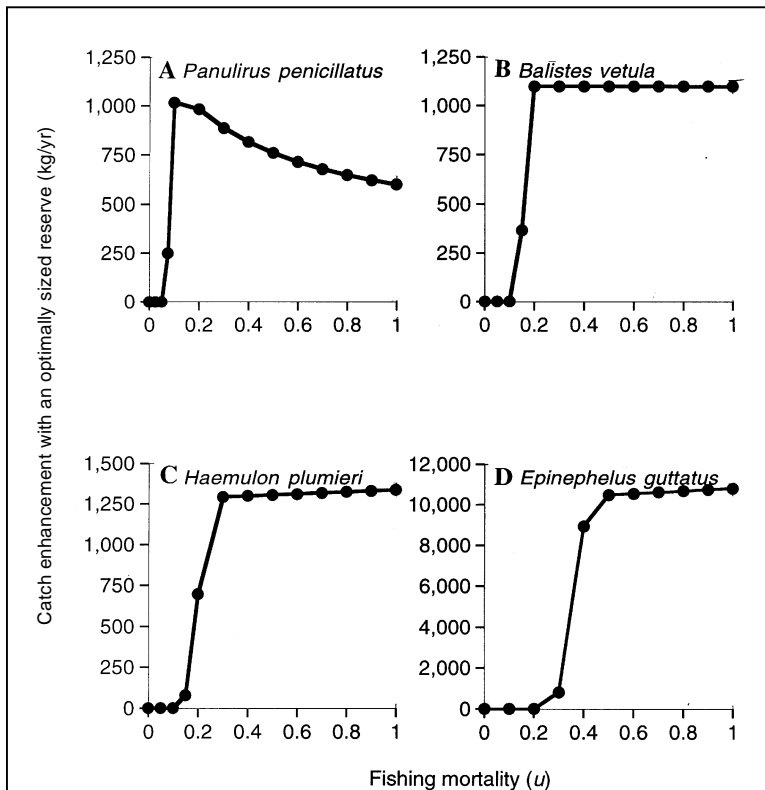

Figure 4

Catch enhancements with the use of an optimally proportioned reserve (OPR). (**A**) *Panulirus penicillatus*, Red Sea spiny lobster. (**B**) *Balistes vetula*, queen triggerfish. (**C**) *Haemulon plumieri*, white grunt. (**D**) *Epinephelus guttatus*, red hind. Values represent the increase in yield, in kg of catch per year from the whole management area, one could expect if an optimally sized reserve system were established in a management area that lacked reserves initially.

only sustain modest harvesting effort (Fig. 3). In contrast, life history parameters from the literature suggested that red hind had a relatively high $\lambda = 1.31$. Consequently, its maximum sustainable yield occurred at the highest fishing mortality of any species we tested (Fig. 3). The two other species we examined had intermediate intrinsic rates of population growth rates and responses to reserves.
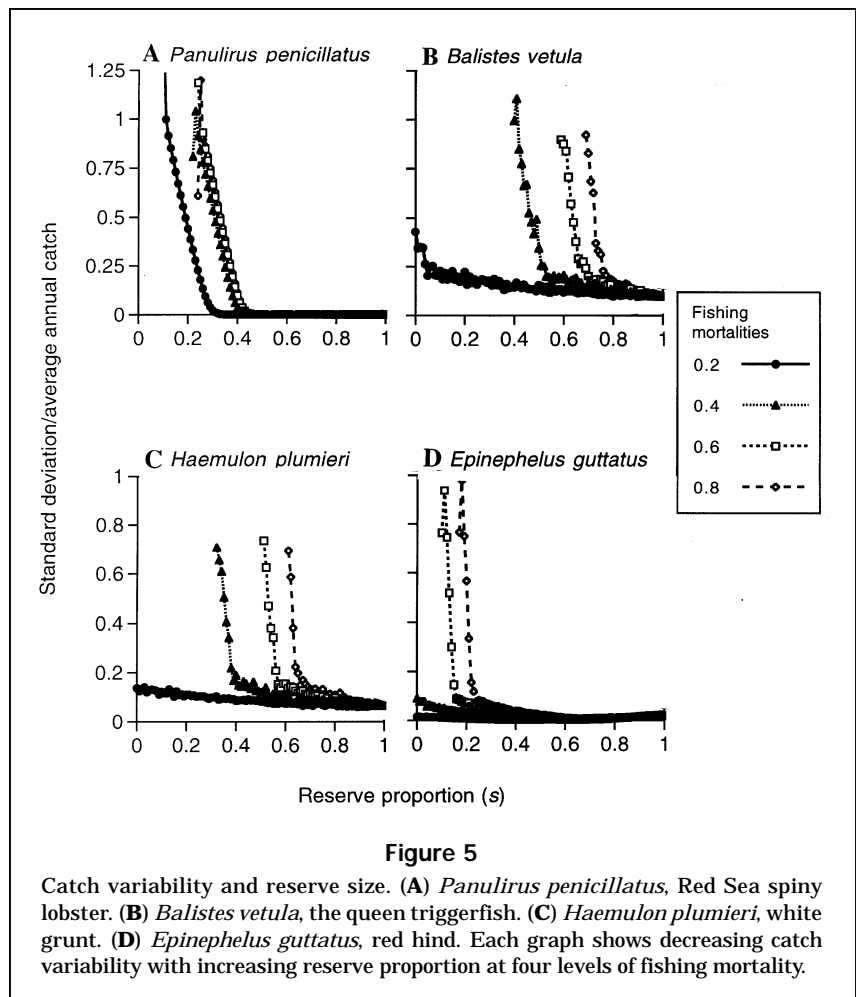
The sensitivity of our models' quantitative predictions was also clear within a species when we varied larval survivorship. For all species, optimal reserve proportion and yield without a reserve varied greatly (senior author's unpubl. data) because we varied larval survivorship from 10^{-5} to 10^{-4}. This sensitivity to poorly understood parameter values renders any quantitative estimates of optimal reserve proportion unreliable, whether the inaccuracy is in larval survivorship, the relationship, or parameters for density dependence, or any other life history parameter.

Finally, we examined how reserves might influence unpredictable catches resulting from environmental variation. Our stochastic models predicted that catches will be more stable with larger reserve proportions. In these models, we saw general decreases in catch variability with increasing reserve proportion (Fig. 5). The results presented here showed drops in variation that were more pronounced at higher fishing mortalities for all four species. We also tested these results at three levels of environmental variation. Our results showed that the drop in catch variability was most extreme when the environment was most variable, suggesting that the stability offered by reserves will be most valuable in highly variable fisheries.

Discussion

Effects of life history and fishing mortality on reserve benefits

Our models predicted that marine fishery reserves will provide catch enhancements to any overfished fishery that meets our basic assumptions regarding

Figure 5

Catch variability and reserve size. (**A**) *Panulirus penicillatus*, Red Sea spiny lobster. (**B**) *Balistes vetula*, the queen triggerfish. (**C**) *Haemulon plumieri*, white grunt. (**D**) *Epinephelus guttatus*, red hind. Each graph shows decreasing catch variability with increasing reserve proportion at four levels of fishing mortality.

the movement of adults and larvae. The results from previous modeling efforts by Man and colleagues (1995) and Holland and co-workers (Holland and Brazee, 1996; Holland et al.[1]) support these findings if one compares their results in specific cases to the patterns we found for a variety of species. Two key variables help determine whether a population is overfished: intrinsic population growth rate (λ) and fishing mortality. Managers can control fishing mortality to varying extents. Apparently, this control is inadequate in many industrial fisheries (FAO, 1995) and is probably even less effective in subsistence fisheries (Roberts and Polunin, 1993). Managers have no control over population growth potential but can take into account that species with low population growth have a greater tendency to be overfished and consequently show greater promise for fisheries enhancements from reserves.

Even in a well-managed fishery, it may be helpful to close large areas. This strategy could allow the relaxation of some fishing restrictions in remaining waters. Consequently, recreational and commercial

fishermen may feel greater equity with fewer restrictions on the number of participants or their catches. Moreover, reserves have the potential to reduce variability in catches from year to year and to enhance conservation of species and ecosystems. Fishing is not the only threat to marine ecosystems, though, and fisheries regulations are not sufficient to protect these systems (Allison et al., 1998).

To our knowledge, no field study has yet examined the effects of population growth potential or fishing mortality on reserve benefits. In part, such studies are made difficult by the uncontrolled nature in which reserves are established.

Relation of fishery benefits to reserve size

Real-world fisheries span a range from lightly fished to heavily overfished, and the optimal reserve size will depend on the fishing mortality as well as the population growth potential of the target species. Because many fisheries involve multiple species with widely divergent population growth potentials, choosing a single best reserve size may be difficult. Moreover, key aspects of the life history of marine fish, the larval phase in particular, remain a mystery. Because of these gaps in knowledge, it would be difficult to make an accurate prediction of the optimal reserve size even in a well-studied single-species fishery.

Although our research sheds doubt on the use of a universal reserve proportion, it does lend support for the use of large reserve systems under certain circumstances. In the two real-world cases where the necessary information existed, our models predicted that reserves should encompass 75–80% of the management area. These proportions are enormous and may be unrealistic for several reasons. First, the short-term economic losses from closing 80% of a management area would be large, although our models predict that the recovery time for such heavily overfished fisheries would be rapid (Sladek Nowlis and Roberts, 1997). Second, the political challenges of establishing such large reserves would be a formidable barrier. Finally, we do not stand firmly behind these predictions because their accuracy is dependent on parameter values that are poorly understood. Nevertheless, consistent results across several species suggest that reserves encompassing 40% or more of a heavily fished management area could produce substantial fisheries benefits.

Though rare, at least one large reserve system does exist. The Mombasa Marine National Park closed over 60% of local fishing grounds (McClanahan and Kaunda-Arara, 1996). This example fits nicely with our model's assumptions because levels of fishing effort remained similar in the fishing grounds be-

fore and after the closure. After two years, total yields had not surpassed those prior to reserve establishment (McClanahan and Kaunda-Arara, 1996). However, catch per unit of effort had increased dramatically and total yields showed potential for future increases. In this case and others involving extensive use of marine reserves, our research encourages an adaptive approach that reflects the lack of knowledge about fish life histories and the high degree of uncertainty in these complex biological systems.

Relation of reserve size to catch variability

Our model supported Bohnsack's (1996) hypothesis that catch variability will decrease with increasing reserve size. Our models predicted decreases in catch variability across a variety of levels of environmental variability and fishing mortalities. Our results also complement other studies that showed that reserves could reduce catch variability,[2] decrease the likelihood of bad years (Lauck et al., 1998), and increase the persistence of fisheries vulnerable to overfishing (senior author's unpubl. data).

To our knowledge, no field study has yet examined the effects of reserves on catch variability. Although they may be confounded by variability in fishing effort, the necessary data should be practical to collect before and after reserve creation.

Assumptions revisited

As with all models, one must be careful in interpreting the results of this one. It is based on parameter values that in some incidences—larval survivorship in particular—are poorly understood. However, the model's predictions are qualitatively robust to parameter errors, meaning that its general predictions hold true across a wide range of values and a wide variety of species. Our assumptions regarding the movement of adults and larvae were far more critical in influencing the conclusions we have drawn here.

Our assumptions regarding adult movement have wide applicability. Many fisheries target sessile organisms such as harvested kelp (Bustamente and Castilla, 1990), slow-moving organisms including many invertebrates (Davis and Dodrill, 1980; Davis and Dodrill, 1989), and organisms with high site-specificity such as many reef fish (Polunin and Roberts, 1996). All of these systems are likely to approximate our assumptions of no adult movement. This model is not universally applicable, as highly mobile and migratory species, including many pelagic fisher-

[2] Mangel, M 1998. Environmental Studies Board, University of California, Santa Cruz, CA 95064. Unpubl. data.

ies (Safina, 1993), will only fit our adult movement assumptions if large reserves are established. Recent studies, though, have shown high site fidelity by fish species previously thought to range widely (Holland et al., 1993; Holland et al., 1996), demonstrating the need for more field data on adult movement patterns. Moreover, recent modeling efforts by Holland and colleagues[1] and others[3] suggest that reserves can benefit highly mobile species through enhanced population fecundity gained from temporary protection.

If adults do cross reserve boundaries, our predictions regarding fisheries benefits from reserves will be influenced in opposing ways. Under heavy fishing pressure and intermediate movement tendencies, minor yield enhancements may be possible from this adult spillover (Polacheck, 1990; DeMartini, 1993). However, this same movement would dilute the ability of reserves to enhance larval transport to fishing areas. As Polacheck showed (1990), spawning stock biomass, or the potential for fisheries enhancement through larval transport, is highest at lowest levels of adult movement. Because the potential benefits from larval transport presented here far outweigh those predicted from adult spillover (Polacheck, 1990; DeMartini, 1993), it is likely that adult movement across boundaries will decrease the predicted yields from reserves. Consequently, reserves will have the highest potential for enhancing surrounding fisheries if they are designed as a collection of units large enough to contain populations of adults with relatively little movement across boundaries.

Our assumptions regarding larval transport have less supporting evidence. Most aquatic species disperse more widely as larvae than as adults (Boehlert, 1996), and the potential for long-distance dispersal across reserve boundaries is great for species with long-lived larvae (Roberts, 1997), including most food fish. Consequently, larvae are likely to move from reserves to fishing areas as long as oceanographic conditions and larval behavior permit. Without larval transport, the potential for fisheries benefits from reserves is more limited, although Holland and colleagues[1] did show that a reserve system in which larvae stayed in place but adults moved widely across boundaries could produce some benefits. Reserves, especially in heavily overfished or large management areas, may need to be partitioned into several subunits that maintain adult populations within them but allow larvae to disperse to remaining fishing areas.

We also assumed a stock-recruitment relationship, implying that a significant portion of the population fecundity from reserves stays in or returns to the management area. The degree to which marine populations are locally sustained remains an active area of debate in marine ecology. Larvae of most tropical food fish are often found in greatest quantities offshore (Boehlert, 1996), suggesting the possibility of long-distance dispersal. However, studies that show this result may be biased because sampling within the complex structure of the reef itself is difficult (Boehlert, 1996). Therefore, reefs may harbor greater concentrations of larvae than are measured above the reef. This complexity (Wolanski and Sarsenski, 1997), along with potential for larval behavior to influence their distribution (e.g. Breitburg et al., 1995), suggests that larvae may be retained at higher concentrations than predicted by simple oceanographic models (e.g. Roberts, 1997). If recruitment dynamics are influenced on a much larger spatial scale than encompassed by the management area, such that the stock in the management area has a minimal impact on recruitment back to it, reserve benefits to the management area are likely to be much more limited. Cohort models, including those by Polacheck (1990) and DeMartini (1993), can be interpreted as situations in which larval supply is constant and not influenced by local stock. As has been discussed, these models show limited potential for fisheries benefits from reserves. It is necessary to think of reserve systems at a scale that fits stock-recruitment relationships. Yet our knowledge of these relationships remains poor. Even if larvae have the potential to disperse over large distances, stock-recruitment relationships could still exist on a local level if a significant portion of larval production is retained. The safest approach to this uncertainty is to design reserve systems at large scales. However, there is still the potential for reserves to produce fisheries benefits on small scales if larvae have the capacity to be retained. Further research on stock-recruitment relationships in marine populations will be invaluable for resolving this pressing issue along with many others in fisheries management.

Field needs and testable predictions

Our results identify areas in need of additional field work and make testable predictions. The needs in regard to field work differ for our quantitative and qualitative predictions. The quantitative predictions were highly sensitive to all parameters that affected intrinsic population growth potential. The most important and least understood of these parameters is larval survivorship. We need significantly better information about the duration of the egg and larval stages of coral reef fishes and their daily mortality

[3] Guenette, S. 1998. Fisheries Centre, University of British Columbia, 2204 Main Mall, Vancouver, BC V6T 1Z4, Canada. Unpublished data.

risk. Until we understand these life history stages better, it will be impossible to make quantitatively accurate predictions of the optimal design of any fishery management strategy.

We also need better insight into how fecundity changes with size. Fecundity-size relationships should be fairly easy to measure and can be incorporated into any standard fishery study where adequate numbers of adults are sampled. We would further benefit from estimates of size-specific natural mortality. Few natural mortality estimates for coral reef fish species exist in the literature, and most that do are based on highly indirect methods of association. Marine fishery reserves actually offer the potential to generate more accurate predictions of natural mortality because fishing mortality does not confound the attempt in unfished areas. Moreover, despite numerous studies, we still have a poor understanding of population regulation and density dependence in coral reef fishes. This understanding is also necessary before we can generate accurate quantitative predictions of reserve benefits.

In contrast to the long list necessary to generate quantitative predictions, our qualitative predictions require additional knowledge in only one key area: fish movement. Because the qualitative predictions were robust across life history patterns, the key to knowing whether a fish species fits our assumptions is the movement of this species as eggs, larvae, and as adults. To some extent, we can skirt this issue because in our model, reserve size was based on proportion of coastline rather than actual size. Consequently, if we choose the management area to match the scale of fish movement, our model can fit most species. For example, a 20% reserve divided into areas of tens of hectares might ensure that adults of the species we examined here will stay in the area in which they settled while their larvae disperse widely among the reserve and nonreserve areas. In contrast, the management area might have to encompass whole ocean basins for the movement assumptions to fit bluefin tuna (Safina, 1993). Thus, we need to understand the movement dynamics of larvae and adults of a species to know the scales at which it will fit the assumptions of our model.

From the species that we ran and the resulting qualitative predictions of our model, we can generate a list of testable predictions. We predict that

1) Reserves will be beneficial for any over-fished population. Populations with low intrinsic growth rates and high fishing mortality stand to benefit the most, as is the case for the majority of reef fisheries in many regions of the world, such as the Caribbean. The location and size of the re-serve will also affect reserve benefits. For a fair test of this prediction, reserve should be representative of typical fish habitat and large enough to contain a viable population of adults.

2) Although no universal best reserve proportion exists, we predict reserves will enhance fishery productivity even when they encompass areas much larger than those of current reserve systems.

3) Reserves will reduce variation in catches resulting from unpredictability in fishing mortality as well as recruitment strength and larval survivorship. Such an effect will simplify fishery management and increase the ability of fishermen to predict future income.

Acknowledgments

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Appendix

Fecundities

Fecundities were size-specific, but the general form of the equation relating size to fecundity varied from species to species. The specific relationships are listed in Table 1 as r. These r values were set to zero for all classes smaller than the size at maturity.

Larval survival

We used equations developed by Houde (1989) that relate ambient temperature during development to duration of larval stage, daily mortality risk, and probability of surviving through the entire larval stage.

$$D = 952.5 \ T^{-1.0752} \qquad (1)$$

$$Z = 0.0003149 \ T \qquad (2)$$

$$N = e^{-ZD}, \qquad (3)$$

where T = ambient temperature during development, in degrees Celsius;
D = duration of larval stage, in days;
Z = probability of mortality, per day; and
N = probability of surviving through the entire larval stage.

Adult survival

We assumed that newly settled fish experienced density dependence. Thus, instead of surviving at a rate v_i like individuals in other size classes, their survival was weighted by a density-dependent function of the form $e^{-\rho/K}$ where ρ = the population density and K = a measure of carrying capacity arbitrarily set at 1000 due to a lack of information on carrying capacities for the fish we studied. Note that size-class-1 individuals included new recruits that survived and grew as well as old size-class-1 individuals that survived but did not grow to size class 2. Thus, at time t, the densities of size-class-1 individuals in the reserve ($S_{1,t}$) and the fishing area ($F_{1,t}$) are

$$S_{1,t} = v_0 \, p(0) \, S_{0,t-1} e^{-S_{0,t-1}/K} + v_1 \big(1 - p(1)\big) S_{1,t-1} \qquad (4)$$

$$F_{1,t} = v_0 \, p(0) \, F_{0,t-1} e^{-F_{0,t-1}/K} + v_1 \big(1 - p(1)\big) F_{1,t-1}, \qquad (5)$$

where v_x = the density-independent survival rate for individuals in size class x.

Note that the density in the fishing area is decreased later in the program to account for fishing mortality but only for size classes larger than the size at fishery recruitment. Also note that other size classes experience the density-independent survival rate v_x.

Growth

We began with standard von Bertalanffy equations (Ricker, 1975), relating length to age and weight to length (Fig. 2) and categorized them as described by Figure 2. Through algebraic manipulation, we established a formula for $g(B_x)$, the size of an individual projected one year in the future:

$$g(B_x) = e^{-k} \, B_x + (1 - e^{-k}) \, L_{inf}. \qquad (6)$$

We used this formula to establish the following calculation for $p(x)$, the probability that an individual in size class x grows to size class x+1 by next year.

$$p(x) = \frac{g(B_{x+1}) - B_{x+1}}{g(B_{x+1}) - g(B_x)} = \frac{L_\infty - B_{x+1}}{L_\infty - st - L_0} = \frac{L_\infty - B_{x+1}}{L_\infty - L_1}. \quad (7)$$