Abstract.—The potential use of marine fishery reserves (MFRs) for managing fisheries on tropical Pacific coral reefs was assessed with an extension of the Beverton-Holt model. The effects of year-round fishery closures on harvests in adjacent, exploited areas were evaluated. Potential changes in spawning stock biomass per recruit (*SSB/R*) and yield per recruit (*Y/R*), when varying fractions of exploitable reef area were closed to fishing, were estimated from published data, approximated natural and fishing mortality rates, size- and maturity-at-age distributions, and "transfer" (emigration and immigration) rates. For select cases, fundamental transfer rates were adjusted for possible density-dependent emigration from closed areas as relative densities decreased in surrounding non-closed areas because of continued fishing. Three hypothetical "fish types" were constructed, bracketing the likely extremes in fundamental transfer rates and related life-history parameters of Pacific coral reef fishes: a small-bodied, fast-growing and short-lived, strongly philopatric species of damselfish was contrasted with a large-bodied, relatively slow-growing, long-lived, vagile species of jack. A "surgeonfish" type was used to represent intermediate parameter values.

Simulations corroborate previous observations that MFRs contribute little, if anything, towards increasing Y/R. Results for the highly vagile jack confirm that rapid transfer rates will negate potential gains in *SSB/R* resulting from closures. At the opposite extreme, small reef philopatriots like damselfishes would almost never be harvested, because of negligible transfer rates, unless the MFR was periodically opened to fishing. The simulations suggest that the *SSB/R* of the surgeonfish type is the most likely to benefit from MFRs, because moderate vagility allows biomass to accumulate within the closure despite harvesting in the non-closed area. Results further suggest that growth rate, fishing effort in the non-closed (open) area, natural mortality, and maturity and harvesting schedules importantly influence the potential of MFRs to augment SSB when transfer rates are low to moderate.

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Modeling the potential of fishery reserves for managing Pacific coral reef fishes

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Marine fishery reserves (MFRs), areas closed to harvesting and adjacent to fished areas, have recently been touted as enforceable and cost-effective alternatives to conventional fisheries management measures such as size and bag limits, closed seasons, and limited entry (Davis, 1989; Plan Development Team 1990; Polacheck, 1990; Bohnsack, in press; Davis et al.[1]; Russ et al., in press). MFRs are recognized worldwide as providing sanctuaries in which local populations of desirable species can increase in abundance or attain larger body sizes (McCormick and Choat, 1987; Alcala, 1988; Buxton and Smale, 1989; Clark et al., 1989; Russ 1985, 1989; Alcala and Russ, 1990; Cole et al., 1990; Bennett and Attwood, 1991). In contrast, harvesting is known to alter the abundance and body size distributions (Craik, 1981; Katnik, 1982; Koslow et al., 1988; Plan Development Team 1990) and assemblage structure (Bell, 1983; Russ and Alcala, 1989) of fishes on coral reefs and other localized regions of fishery exploitation.

By providing havens from exploitation within which organisms can attain large adult body sizes, designated refuges protect the most valuable segments of spawning stocks (Plan Development Team, 1990). For most marine organisms with lengthy (≥2 wk-long) planktonic larval stages, MFRs can function as sources of benthic recruits to exploited, often distant, sink populations. The subsequent contribution of these recruits to the fishery might counteract (or forestall) the effects of recruitment overfishing (Carr and Reed, in press; Russ et al., in press). Through the directed movements of settled stages, MFRs might also augment the standing biomass of stocks, including spawning adults, in exploited areas adjacent to MFRs as well as within the MFRs themselves (Polacheck, 1990; Roberts and Polunin, 1991). MFRs thus might provide a management tool that addresses growth overfishing, particularly for multispecies fisheries on tropical coral reefs where conventional management is ineffective (Roberts and Polunin, 1991).

Despite the recognized importance of MFRs as sanctuaries for conserving biomass, their contribution to fishery stocks and yields in adjacent exploited areas is poorly understood (Davis, 1989; Polacheck, 1990; Roberts and Polunin, 1991; Russ et al., in press). An introduction to the problem is provided by Polacheck (1990), who expands the Beverton-Holt equation (Beverton and Holt, 1957) describing the effects of a year-round refuge on the spawning stock biomass (*SSB*) and yield of a cohort in a surrounding exploited area. Although areal closures on coral reefs are one identified application, Polacheck's (1990, Table 1) simulations use empirical data on the growth, matu-

[1] Davis, G. E., S. C. Jameson, and J. E. Dugan. Potential benefits of harvest refugia in Channel Islands National Park and Channel Islands Marine Sanctuary. Unpubl. manuscr., 25 p. U.S. Natl. Park Service, Channel Islands National Park, CA 93001.

rity, and harvesting schedules of Georges Bank cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*. The growth and mortality dynamics of tropical coral reef fishes, however, may be quite unlike those of higher-latitude species (Munro and Williams, 1985; Longhurst and Pauly, 1987). Further simulations using growth and mortality data of other fishes are needed.

Observations of traditional practices by marine islanders (Johannes, 1978) suggest that reserves can augment the *SSB*, and perhaps the yield of tropical reef fishes. To date, controlled empirical measurements of fishery yields in an area adjacent to a MFR have been published for only one study site (Sumilon Island, central Philippines; Alcala and Russ, 1990). The changes in catches that Alcala and Russ (1990) observed, however, were based on yield, not yield per recruit (Y/R), over a 1-year period and therefore may not have represented equilibrium conditions.

The present paper evaluates the effects of permanently closed MFRs of different sizes on net changes in *SSB* and yield for several types of tropical Pacific reef fishes. The author simulated various combinations of fishing mortality and emigration-immigration ("transfer") rates for fishes having different but typical natural growth and mortality schedules. Because tropical reef fishes have higher natural growth and death rates than do temperate zone fishes, the focus is on the relative sensitivity of spawning stock biomass per recruit (SSB/R) and Y/R to MFR size, transfer rates, variations in natural mortality and growth, fishing effort, and age at first capture. Another objective is to compare the management potential of "single large or several small" (SLOSS) (Simberloff, 1988) reserves of equal total area. Finally, the potential of MFRs on island reefs is discussed, with particular reference to reef areas surrounding the island of Oahu, Hawaii.

Methods

Parameter values for von Bertalanffy growth rates, derived mortality rates, and maturity and harvesting schedules were chosen to bracket the spectrum of life histories and exploitation characteristics of tropical Pacific reef fishes. At one extreme, values were assembled to describe a reef transient (e.g., a jack of the family Carangidae) that is relatively slow-growing but long-lived and large-bodied is likely to travel rapidly over relatively large distances. Such species often support valuable commercial fisheries. Values used for growth and mortality rates of the jack resemble those of many species of commercially important snappers, groupers, and jacks from the South Pacific and other tropical seas (Munro, 1983; Munro and Williams, 1985).

A short-lived, fast-growing but small-bodied reef damselfish (family Pomacentridae), with limited movements after settlement, was used to represent the opposite extreme. Such small tropical reef species are collected for the aquarium fish trade.

In between these two extremes lies a broad continuum of fishes with intermediate longevities, body sizes, and movement rates. These fishes probably represent most species targeted by recreational and artisanal fisheries on tropical reefs. The few data available (Galzin, 1987; Ralston and Williams[2]; Russ and St. John, 1988; Dalzell, 1989) suggested a range of moderate growth and mortality rates for a number of Pacific parrotfishes (family Scaridae) and surgeonfishes (family Acanthuridae). For convenience, these fishes were labeled the "surgeonfish" type.

The growth parameters used in this study were based partly on published values for a particular species population, complemented by data for other Pacific populations of the same species. For the pomacentrid, the author used a Moorean population of *Stegastes nigricans* (Galzin, 1987). He selected *Ctenochaetus striatus* as the surgeonfish; the length-weight relation was based on a Moorean population (Galzin, 1987), and a Samoan population provided the VBGF parameters (Ralston and Williams, 1988). Sudekum et al.'s (1991) data for NWHI *Caranx ignobilis* were used to represent the jack. Thus the degree to which values were population-specific varied among the three fish types. Natural mortality rates (M) were estimated using Pauly's (1980) multiple regression of M on maximum size, growth coefficient, and mean water temperature (Pauly and Ingles, 1981); 25°C was chosen as representative for shallow, tropical Pacific waters. All parameter values used are listed by fish type in Tables 1 and 2.

Modeling closure effects

Polacheck's (1990) model of the effects of closure size (1–50%), rates of fish transfer between closed and exploited areas, and fishing mortality rate on the biomass and production of fishes in an adjacent exploited area was used with one small but important difference: the use of a three- rather than a four-sided closed area. (Closures on island reefs usually extend seaward from the shoreline, so fishes can move across upcoast, downcoast, and offshore boundaries only. Other factors being equal, dispersion rates out of and into shore-

[2]Ralston, S., and H. A. Williams. 1988. Age and growth of *Lutjanus kasmira*, *Lethrinus rubrioperculatus*, *Acanthurus lineatus*, and *Ctenochaetus striatus* from American Samoa. Dep. of Commer., Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. H-88-18, 11 p.

Table 1

Length-weight relations, von Bertalanffy growth function parameters, and natural mortality rates used to simulate spawning stock biomass per recruit and yield per recruit contour surfaces for damselfish (based on Moorean *Stegastes nigricans* from Galzin, 1987); surgeonfish (length-weight relation: Moorean *Ctenochaetus striatus* from Galzin, 1987; VBGF parameters: Samoan *C. striatus* from Ralston and Williams[2]); and jack (NWHI *Caranx ignobilis* from Sudekum et al., 1991). *M* values were estimated after Pauly (1980) and Pauly and Ingles (1981; see Methods).

Variable	Damselfish	Surgeonfish	Jack
Length-weight relation (Total Length/g)	$W = 0.0195L^{3.07}$	$W = 0.0111L^{3.10}$	$W = 0.0072L^{2.96}$
L_∞ (Total Length, cm)	17.5	28.2	217
W_∞ (g)	128.9	348.6	120,139
K (1/year)	0.374	0.447	0.111
t_0 (year)	–0.042	–0.760	–0.097
M (1/year)	1.5	1.0	0.2

Table 2

Age-specific parameters used to simulate the standing stock and catch (yield) values for each of the reef fish types described in Table 1.

Fish type	Age (yr)	Mean weight[1] (g)	Percent mature[2]	Partial recruitment[3]
Damselfish	1.0	4.77	100	1.00
	2.0	32.40	100	1.00
	3.0	72.20	100	1.00
Surgeonfish	1.0	40.81	0	0
	2.0	101.87	100	1.00
	3.0	164.43	100	1.00
	4.0	217.18	100	1.00
	5.0	257.24	100	1.00
Jack	1.0	110.0	0	0
	2.0	861.7	0	0
	3.0	2587.0	0	0
	4.0	5348.6	100	1.00
	5.0	9061.8	100	1.00
	6.0	13,569.6	100	1.00
	7.0	18,688.4	100	1.00
	8.0	24,235.1	100	1.00
	9.0	30,042.0	100	1.00
	10.0	35,963.5	100	1.00
	11.0	41,878.8	100	1.00
	12.0	47,691.4	100	1.00
	13.0	53,327.1	100	1.00
	14.0	58,731.1	100	1.00
	15.0	63,865.3	100	1.00

[1] Based on mean weight-at-age estimated from weight-specific VBGF; see Table 1 for sources.

[2] Sexual maturity assumed 100% complete at age corresponding to the asymptote of the Von Bertalanffy growth function curve; all fish were assumed immature prior to this age.

[3] All species were defined as fully recruited to the fishery at the age of 100% sexual maturity, no fish entering the fishery prior to that age: Age-at-first-capture, A_c = 1.0, 2.0, and 4.0 years for the damselfish, surgeonfish, and jack, respectively.

line-bounded reef closures will be one-fourth slower than the respective rates for completely nested closures of equal areal extent.)

Polacheck's modified Equation 8 was

$$T_{12} = 3 \cdot T_{1s} \cdot (R_1 / R_s)^{-1/2}; \qquad (1)$$

where T_{12} is the instantaneous emigration rate from closed area 1 to exploited area 2; T_{1s} is the emigration rate from a closure of R_s standard size; and R_1 is the fractional closure size evaluated. As in Polacheck (1990), the initial fish densities were assumed homogeneous in both areas, and thus the number of fish initially present in area 1 at time t was defined as

$$N_{1,t} = R_1 \cdot N_{total,t} \qquad (2)$$

where $N_{total,t}$ = number of individuals in the cohort entering areas 1 and 2 at time t. T_{1s} was allowed to vary among fish types, as types surely differ in their fundamental emigration and immigration rates. Selected values of T_{1s} spanned realistic values for each fish type (damselfish: 0.001, 0.01, and 0.1; surgeonfish: 0.1, 0.25, and 0.5; jack: 0.1, 0.5, and 1.0). T_{21}, the rate of immigration into area 1 from area 2, given the type-specific value of T_{1s}, was as defined by Polacheck (1990, Equation 6).

A basic assumption of the model is that fishing does not affect fish distributions by altering habitat or by promoting density gradients between areas 1 and 2, i.e., dispersal is random and uniform throughout both areas and across their boundaries (Polacheck, 1990). This is realistic for fishes like jacks that range widely or that have very large home ranges. However, the assumption of uniform dispersal throughout both areas is debatable for fishes with home ranges that are small relative to the size of MFRs, particularly for strongly site-attached, territorial species like damselfishes whose ambits are trivial compared to the area of a reserve. Transfer rates that functionally approximate those based on an assumption of uniform, random dispersal might be tenable for home-ranging (or even territorial) organisms, if emigration out of MFRs into adjacent fished areas followed a "stepping stone" pattern with minimal time lags. Limited field data at present both support (Walsh, 1984) and counter (Wellington and Victor, 1988) such a model. The key factors here are the magnitude of time lags and the relative sizes of individual home ranges within particular MFRs.

An R_s value of 0.10 was used to represent the "standard-size" closure (Polacheck, 1990). Fishing mortality rates (F_c) were input over the range from 0.1 to $\geq 3M$, with special evaluation of $F_c = 0.5M$, M, and $2M$, based on the best estimate of natural mortality for each fish type. Total fishing effort (F_2) was homogeneously redistributed throughout the exploited area and fixed in magnitude (at a given F_c), regardless of the size of the closed area (Equation 7 in Polacheck, 1990).

SSB/R and *Y/R* are used as the primary bases of evaluation. Although measures of biomass are not usually applicable to species like the damselfish that are harvested on a numerical basis (see Ingles and Pauly [1984] for examples of consumptive exploitation of small-bodied fishes in artisanal fisheries), these measures were evaluated in the same way to maintain consistency.

First, the *SSB* and yield of a cohort were calculated, by using Polacheck's (1990) Equations 2 and 3 for the numerical standing stock and the numerical catch of each cohort comprising that stock:

$$\sum_{(t=1)}^{n} (N_{1,t+1} \cdot \bar{W}_{t+1} \cdot \%\text{mat}_{t+1}), \tag{3}$$

$$\sum_{(t=1)}^{n} (N_{2,t+1} \cdot \bar{W}_{t+1} \cdot \%\text{mat}_{t+1}), \text{ and} \tag{4}$$

$$\sum_{(t=1)}^{n} (C_{2,t} \cdot \bar{W}_t); \tag{5}$$

where $N_{1,t+1}$ and $N_{2,t+1}$ are the numbers of a cohort surviving in the respective area at time $(t+1)$; $C_{2,t}$ is the numerical catch of a cohort in area 2 at time t; $\bar{W}_t$ and $\bar{W}_{t+1}$ represent the mean weights of individual fish of the cohort at times t and $(t+1)$, respectively; and $\%\text{mat}_{t+1}$ is the percentage of the cohort that is sexually mature at time $(t+1)$.

SSB/R and *Y/R* were then calculated by standardizing the total spawning biomass and yield, respectively, of the cohort over its life span by the total number of recruits potentially (area 1) and directly (area 2) entering the fishery from that cohort (Gabriel et al., 1989). *SSB/R* was evaluated in terms of percentage of the virgin stock biomass possible if fishing was disallowed in both areas (Polacheck, 1990); 20% of virgin biomass was considered the threshold for recruitment overfishing (Beddington and Cooke, 1983).

Two series of simulations were run. One series treated the T_{12} and T_{21} values as fixed, assuming that, analogous to Polacheck's (1990) analyses for Georges Bank cod, transfer rates would remain constant and independent of relative fish densities in the two areas. Additional simulations, using the same initial T_{1s} values, were run for selected cases; in these runs, subsequent values of the transfer rates were treated as a density-dependent function of the changing, relative fish densities in the two areas. Subsequent values of T_{12} and T_{21} were adjusted as follows:

$$T_{12,t+1} = T_{12,t} \cdot \{ (N_{1,t}/N_1) / (N_{2,t}/N_2) \}^x, \text{ and} \tag{6}$$

$$T_{21,t+1} = T_{21,t} \cdot \{ (N_{2,t}/N_2) / (N_{1,t}/N_1) \}^x; \tag{7}$$

where N_1 is defined in Equation 2 and N_2 is the initial number of the cohort present in area 2; $N_{1,t}$ and $N_{2,t}$ are the numbers of fish surviving in the respective area at subsequent age t; and x is the power used to scale the ratio of fish densities. In Equations 6 and 7, the ratio of the numbers of fish surviving at time t was further adjusted by the ratio of initial densities in the two areas in order to scale for the propensity to emigrate at the onset. Two values of x were evaluated: 0.125 (eighth root) and 0.5 (square root). (Note: When x equals 0, the T_{12} and T_{21} are fixed; when x equals 1.0, these rates are continually readjusted by the changing ratio of relative densities.) Exponents of 0.125 and 0.5 were chosen because they bracketed rate changes of reasonable magnitude. In the surgeonfish, for example, an eighth-root adjustment would initially accelerate a median T_{1s} of 0.25 by about 20% for a median closure size of 25%, at an F_c of 1.0. The corresponding rate increase due to a square-root adjustment would be 60%.

Inclusion of a term for the density-dependent adjustment of transfer rates, as stocks are fished-down in the non-closed area, extends Polacheck's (1990) evaluation. This is perhaps an unnecessary refinement for stocks such as Georges Bank cod for which harvesting by trawl might reduce habitat quality in the non-closed area (Polacheck, 1990). However, non-destructive (e.g., hook and line) methods of artisanal fisheries on coral reefs do not reduce habitat quality. Furthermore, fishes may emigrate at an accelerated rate from a closure into the surrounding non-closed area where densities continue to decrease (tantamount to improving habitat quality). Compensatory emigration resulting from a density gradient is recognized as potentially important in the siting and design of nature reserves (Schonewald-Cox and Bayless, 1986).

Complementary simulations

In addition, the effects of varying M and the age-at-first capture (A_c) on total biomass per recruit (B/R) were simulated with the conventional Y/R model of Beverton-Holt (Sparre et al., 1989). Fishing mortality was evaluated at $0.5M$, M, and $1.5M$ or $2M$. A_c was examined with the most reasonable estimate of $A_c \pm 50\%$ for each of the three fish types (see footnote C of Table 2 for the type-specific values of A_c used in modeling closure effects). An age-at-recruitment to fishery habitat (A_r) value of 1.0 year was assumed for the surgeonfish and jack, and an A_r of 0.5 year for the damselfish.

Results

General

Results corroborate several of Polacheck's (1990) major results: SSB/R increased, while Y/R generally decreased, with increasing refuge size (Fig. 1). Even in cases where a closure positively affected yield, Y/R increased little. Y/R often was greater at higher levels of fishing effort (Fig. 1) and usually decreased at larger refuge sizes; the rate of decrease was less at higher fundamental transfer rates (Fig. 2, A–C). SSB/R was generally greater for closures of larger size at any particular transfer rate (Figs. 1 and 2). The positive effects of a closure of a given size on SSB/R were greater at lower rates of exploitation and diminished at higher transfer rates (Fig. 3). The rate of increase in SSB/R with refuge size was greater at lower transfer rates (Fig. 1, A–C). The progressive gain in SSB/R usually was greater than the progressive loss in Y/R for refuges of increasing size (Fig. 2).

Another general pattern was the relative importance of the interactive effect of natural and fishing mortality rates, compared to age at recruitment to the fishery. For most combinations of M and F_c, B/R was more strongly influenced by these two rates than by age at recruitment (Fig. 4, Table 3). Depending on fish type, B/R values ranged two- to five-fold as M and F_c values varied ±50% of their midpoint estimates, but ranged only twofold or less as A_c varied ±50% (Table 3).

By comparison, transfer rates had relatively little effect on SSB/R, compared with the effects of natural and fishing mortality rates. For a median-sized closure of 25%, changes in percentage of virgin SSB/R differed <10% within fish type for transfer rates that varied as much as two orders of magnitude (Fig. 3).

Another generality, not previously made explicit, is that ages at maturity and at first capture can more strongly influence spawning stock than can the presence and size of a refuge. The presence of a refuge will have a relatively weak effect on spawning biomass if the resource begins to be heavily exploited well before sexual maturity. In extreme cases, SSB/R might not be appreciably enhanced by large closures, despite relatively low transfer rates.

Fish types

Perhaps the most significant, specific result of the simulations was that fish types differed in how refuge size affected SSB/R levels. Large, apparent gains in percent virgin SSB/R of the damselfish occurred only at the expense of large losses in yield (Figs. 1A, 2A, 3A). Nontrivial (>5%) gains in percentage SSB/R of surgeonfish could occur at small (0.1) refuge sizes, although the overall rate of increase in SSB/R would be greater for larger closures (Figs. 1B, 3B). For the jack, however, gains in SSB/R of magnitude similar to those of the surgeonfish could be realized with increasing refuge size only for large ($R_1 > 0.3$) closures (Figs. 1C, 3C).

Simulation results appeared to vary among fish types in response to their differing growth rates and natural mortality and exploitation schedules. For example, in comparing the results for the high-mortality surgeonfish with those for the low-mortality jack, substantive gains in SSB/R of the jack (restricted to large closures) were further restricted to low ($F_c \le 0.4$) levels of fishing effort (Fig. 1C). SSB/R dropped below 20% of the virgin stock at $F_c = 0.3$, the fishing effort that was optimal for maximizing Y/R (Fig. 1C). For the surgeonfish, appreciable (≥10%) gains in SSB/R could occur under heavy ($F_c > 1$) exploitation rates for refuges as small as 10–20% (Fig. 3B), and ≥20% of virgin SSB/R can be sustained at $F_c \le 1.15$ (Fig. 1B).

The observed differences among fish types in the potential for MFRs to increase SSB/R also were strongly influenced by the ages at sexual maturity and recruitment to the fishery. Ages at first maturity and at first capture were attributes that differed greatly among the three fish types (damselfish: age 1; surgeonfish: age 2; jack: age 4; Table 2). Median B/R (equal to SSB/R for all except the damselfish at A_c = 0.5 year) varied by 30% for the damselfish, 100% for surgeonfish, and 35% for the jack among ages at first capture that varied ±50% of their respective midpoints (Table 3). Compared with age at first catch, transfer rates had less effect; SSB/R consistently varied ≤10% for the damselfish (with twofold variation in very low transfer rates; Fig. 3A), for the surgeonfish (with fivefold variation in moderate transfer rates; Fig. 3B), and for the jack (with tenfold variation in rapid transfer rates; Fig. 3C). At a reference F_c of 1.0 and a median closure size of 25%, SSB/R varied from <6 to 35% of virgin stock biomass, depending on fish type (Fig. 1, A–C).

Compensatory transfer rates

Even small (eighth root of density ratio) compensatory increases in transfer rates could have negated potential increases in SSB/R that might result from the presence of a closure. A larger adjustment with the square root of the density ratio, of course, can have an

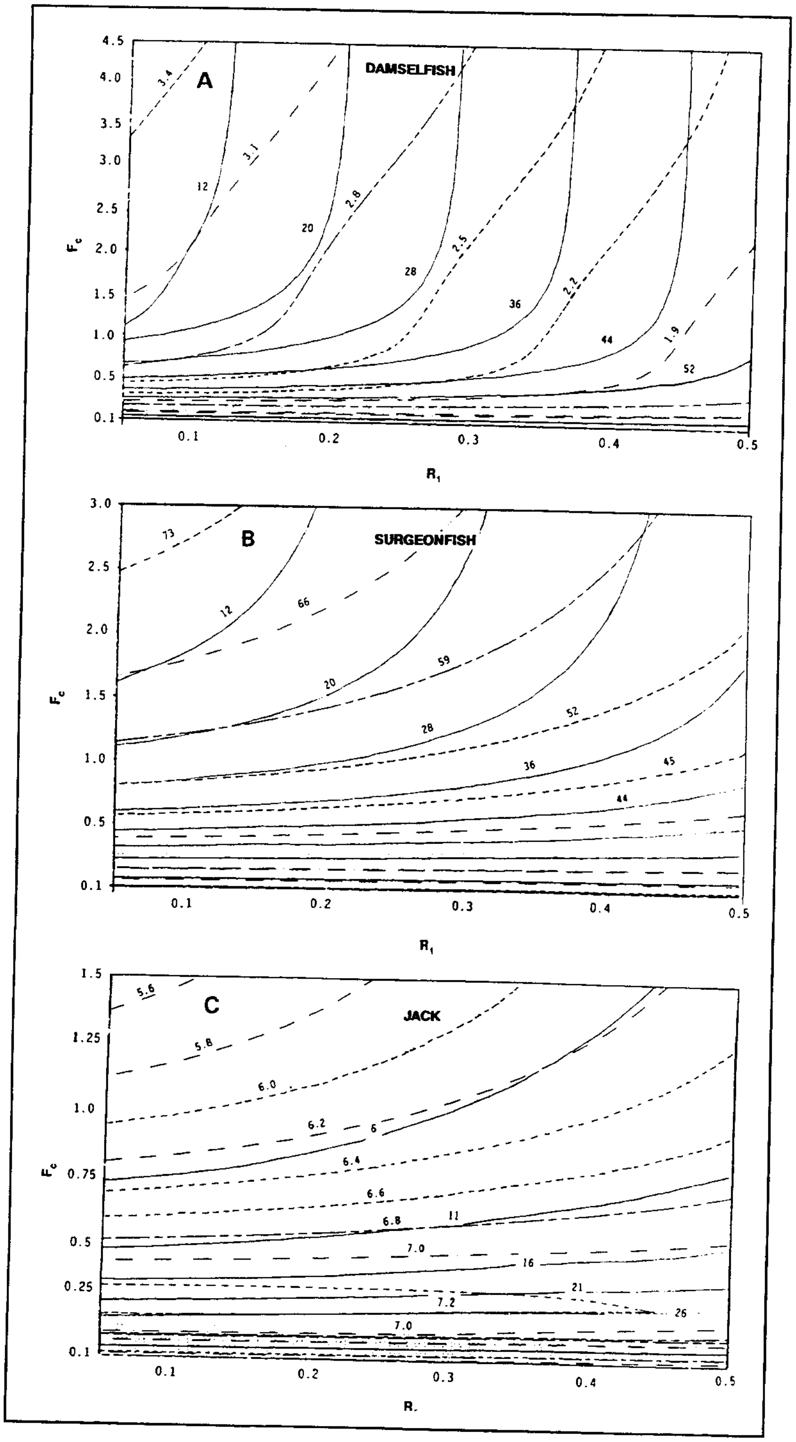

Figure 1
Overlay of a yield-per-recruit surface (various dashed lines) on a percentage spawning stock biomass-per-recruit surface (solid lines) as a function of refuge size (R_i) and fishing mortality rate (F_c) when transfer rate (T_{1x}) is constant: (**A**) damselfish (T_{1x} = 0.01); (**B**) surgeonfish (T_{1x} = 0.25); and (**C**) the jack (T_{1x} = 0.5). Spawning biomass values are expressed as a percentage of virgin biomass that would accrue if no fishing were allowed in areas 1 and 2.

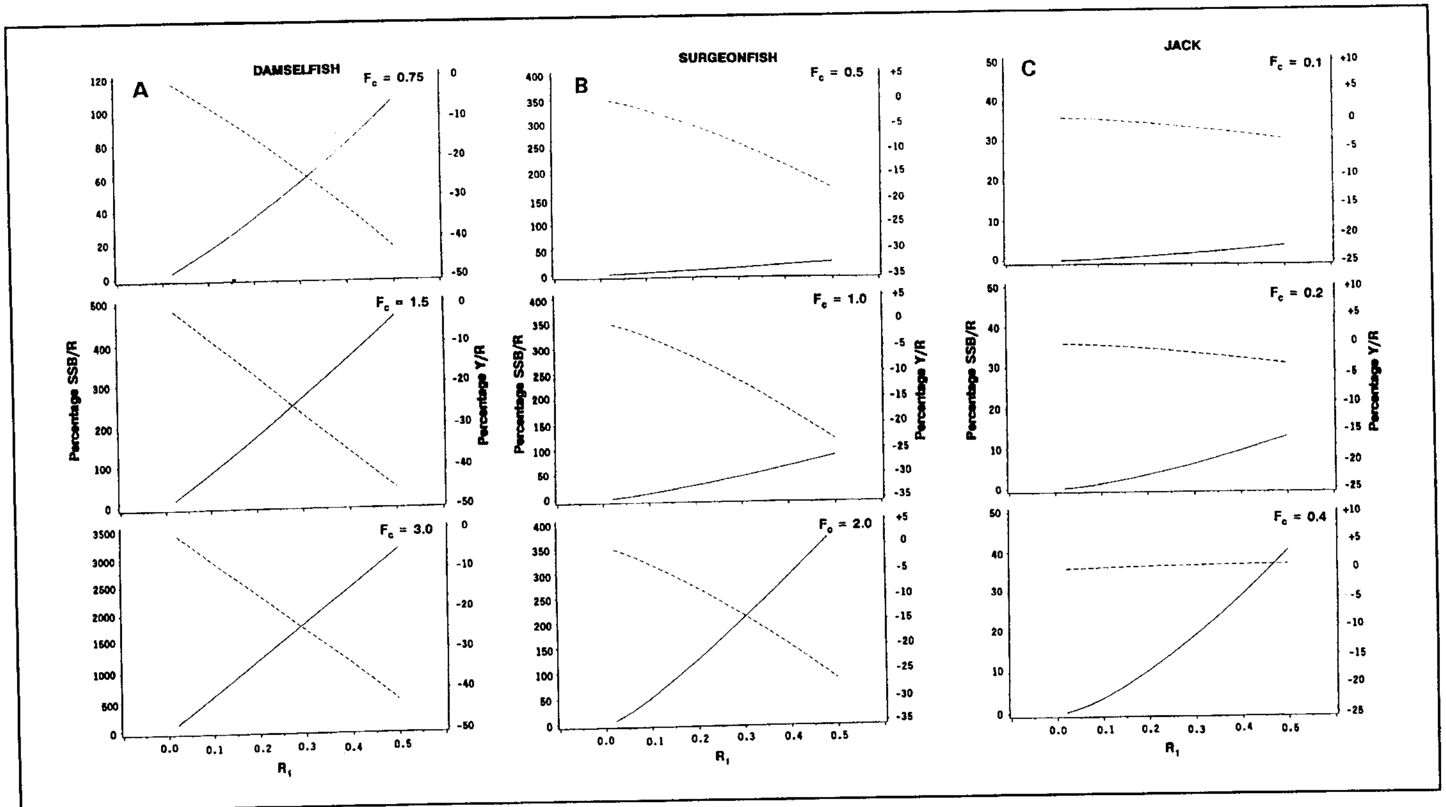

Figure 2

Percentage changes in spawning stock biomass per recruit (SSB/R; solid line) and yield per recruit (Y/R; dashed line) as a function of refuge size (R_1), when transfer rate (T_{1s}) is constant, for different fishing mortality rates (F_c): **(A)** damselfish (T_{1s} = 0.01); **(B)** surgeonfish (T_{1s} = 0.25), and **(C)** the jack (T_{1s} = 0.5). Spawning biomass and yield values are standardized by the biomass and yield that would accrue if there were no closure (i.e., both areas 1 and 2 open).

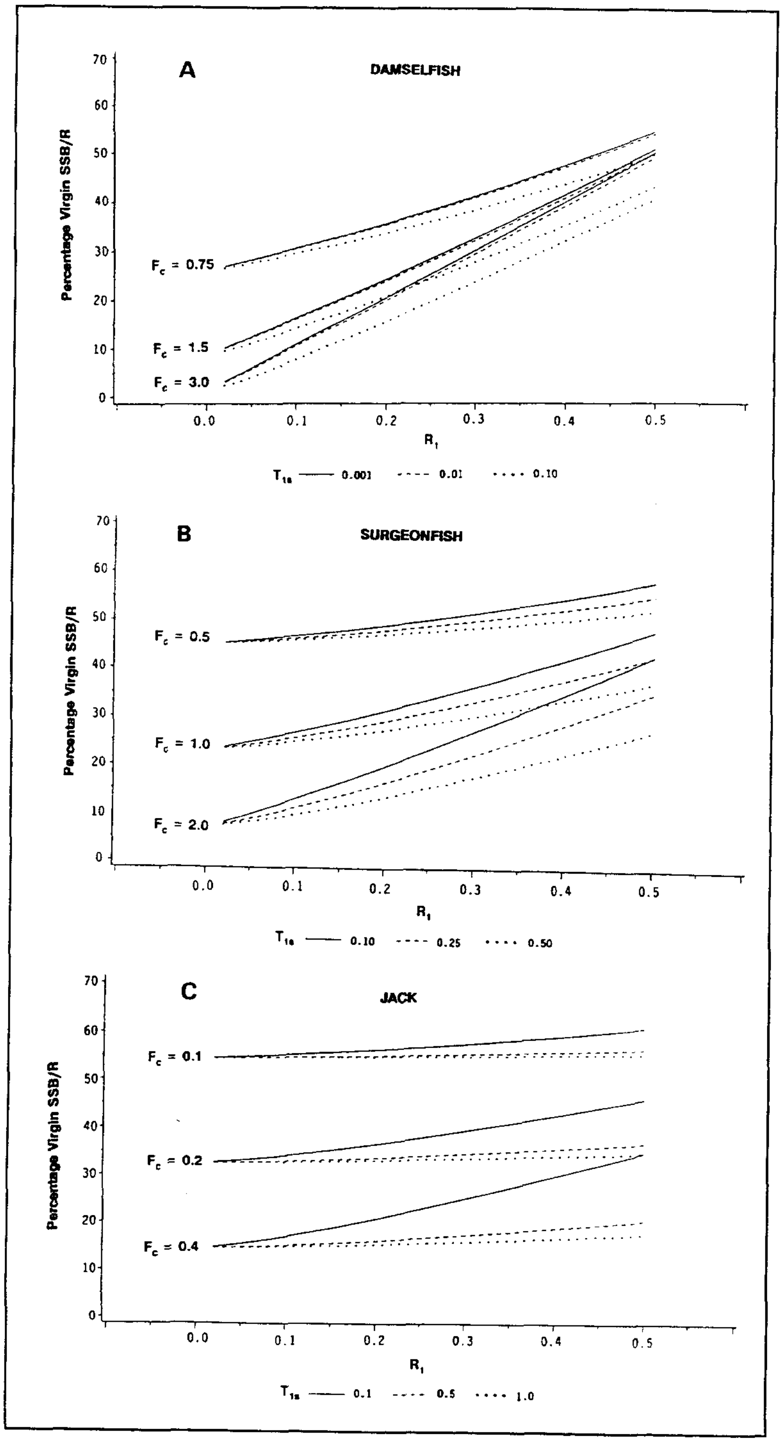

Figure 3

Relative changes in spawning stock biomass per recruit (*SSB/R*) as a function of refuge size (R_1) compared at fishing mortality rates (F_c) equal to natural mortality rates (M) of $0.5M$, M, and $2M$, among a range of possible fundamental transfer rates (T_{1s}) for (**A**) damselfish (in grams), (**B**) surgeonfish (in grams), and (**C**) the jack (in kilograms). *SSB/R* values are standardized by the respective virgin biomass value that would accrue if no fishing were allowed in areas 1 and 2.

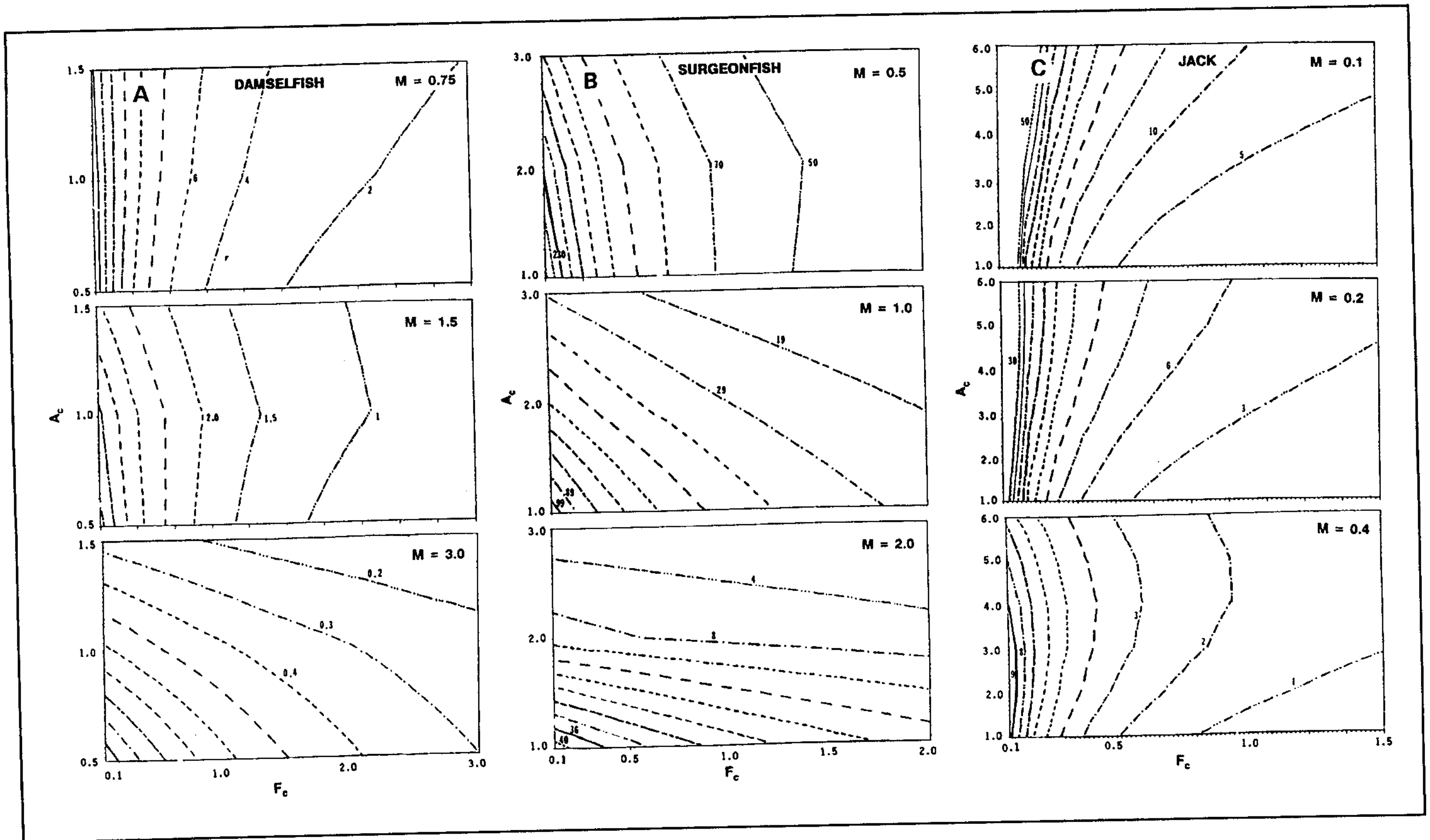

Figure 4

Stock biomass per recruit (B/R) surfaces as a function of fishing mortality rates (F_c) and age-at-recruitment to the fishery (A_c) for (**A**) damselfish (in grams), (**B**) surgeonfish (in grams), and (**C**) the jack (in kilograms).

Table 3

Equilibrium B/R (total biomass per recruit) values without any refuge at select combinations of A_c (age-at-first-capture), M (natural mortality rate), and F_c (fishing mortality rate) for each of the three fish types. See text Methods, Table 1, and footnotes to Table 2 for basis of chosen A_c and M values. F_c was evaluated at values equal to $0.5M$, M, and $1.5M$. B/R at the most reasonable (midpoint) values of A_c and M are emphasized in bold and underlined type, respectively, and the relative influences of A_c, M, and F_c on B/R are noted. A_r = 0.5 year (damselfish) and 1.0 year (surgeonfish and jack).

Damselfish B/R (g)

	A_c = 0.5			**A_c = 1.0**			A_c = 1.5		
At M =	0.75	1.5	2.25	0.75	1.5	2.25	0.75	1.5	2.25
If F_c = 0.75	5.4	2.1	1.1	**6.7**	**2.3**	**1.0**	7.4	1.9	0.6
1.50	2.1	1.1	0.7	**3.3**	**1.4**	**0.7**	4.0	1.2	0.4
2.25	1.1	0.7	0.5	**2.0**	**1.0**	**0.5**	2.6	0.9	0.3

$M = F_c >> A_c$

Surgeonfish B/R (g)

	A_c = 1.0			**A_c = 2.0**			A_c = 3.0		
At M =	0.5	1.0	1.5	0.5	1.0	1.5	0.5	1.0	1.5
If F_c = 0.50	119.9	66.8	44.8	**110.0**	**40.5**	**17.4**	85.4	19.9	5.3
1.00	66.8	44.8	33.2	**66.7**	**28.7**	**13.4**	54.0	14.4	4.2
1.50	44.8	33.2	26.2	**47.3**	**22.1**	**10.9**	39.2	11.3	3.4

$M > F_c = A_c$

Jack B/R (kg)

	A_c = 2.0			**A_c = 4.0**			A_c = 6.0		
At M =	0.1	0.2	0.3	0.1	0.2	0.3	0.1	0.2	0.3
If F_c = 0.1	96.4	36.6	17.6	**112.3**	**40.3**	**18.0**	123.0	39.8	15.6
0.2	40.4	19.4	10.8	**54.5**	**24.3**	**12.2**	65.6	25.8	11.3
0.3	21.5	11.9	7.3	**32.8**	**16.5**	**9.0**	42.5	18.6	8.7

$M > F_c > A_c$

even larger countering effect (Fig. 5). The effect of compensatory rate adjustments apparently varied with fish type in a manner not directly related to fundamental transfer rate. When the surgeonfish and jack were each evaluated using T_{1s} = 0.1 as the fundamental rate, compensatory dampening in the rate of SSB/R gain at larger refuge sizes was less for the surgeonfish (Fig. 5A) than for the jack (Fig. 5B).

Discussion

MFRs and enhanced Y/R

Simulations to date suggest that MFRs have the potential to augment SSB/R, but enhance Y/R little, if at all, in adjacent non-closed areas (Polacheck, 1990; the present study). The only empirical study to date was inconclusive: Alcala and Russ's (1990) observations of an effect on reef fish catches adjacent to the Sumilon Island reserve were from a series of years in which the reserve operated and from only one year of reduced catches that began 18 months after the reserve's protected status ended. Catches were dominated by one taxon (fusiliers, family Caesionidae; 65% of total) that used the reef for nocturnal shelter but whose zooplankton prey may have been unrelated to reef area (Alcala and Russ, 1990). Brief changes in yield, rather than Y/R, particularly on a small (0.5 km^2) spatial scale, may represent nonequilibrium phenomena (e.g., lagged effects on adult abundance resulting from a localized change in recruitment). Alcala and Russ's (1990) observations therefore are not necessarily inconsistent with simulation results (see Russ et al., in press).

Clearly, additional empirical measures are needed for Y/R as well as SSB/R of fishery resources in exploited regions adjacent to MFRs. For the present discussion, however, this paper will focus on simulated SSB/R results.

Relative influences of input parameters

Growth rate is a major influence of biomass accrual within refuges (Polacheck, 1990), as fast-growing fish can elaborate more surplus production (yield) per unit time and unit area of refuge than can slow-growing fish. And since growth and mortality rates are linked, it is not surprising that mortality rate is important, as fishes with a higher natural mortality can support fisheries in which they are harvested more heavily and earlier in life than can fishes with a lower mortality rate.

In the basic yield model, the effects of natural mortality and level of exploitation overwhelm those of age at first capture. Proportional changes in rates obviously have larger effects than equal-sized changes in the time period over which the rates apply. Of greater interest here are the relative magnitudes of the effects

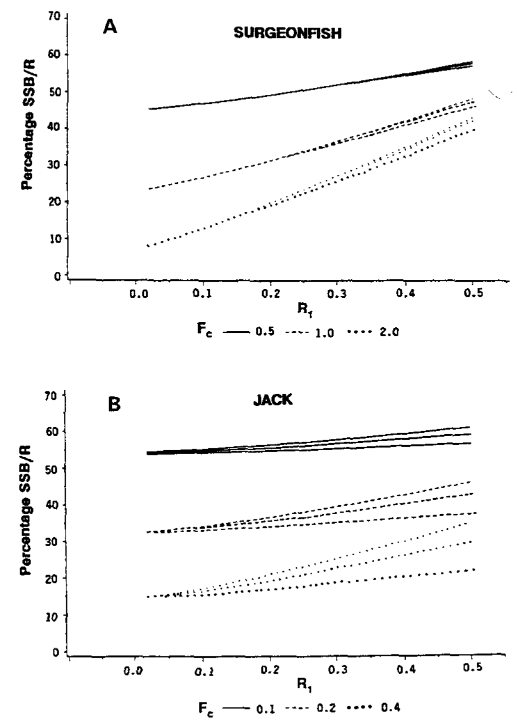

Figure 5

Percentage changes in spawning stock biomass per recruit (SSB/R) as a function of refuge size (R_1), fundamental transfer rate (T_{1s}), and two levels of density-dependent, compensatory adjustment of this fundamental rate: **(A)** surgeonfish (T_{1s} = 0.1); **(B)** jack (T_{1s} = 0.1). Within each triplet of lines, the upper, middle, and lower line depicts the unadjusted, adjusted 0.125-power, and adjusted 0.5-power rate, respectively.

of ages at sexual maturity and first capture, versus those of refuge size and transfer rates. I suggest that the former can have large influences for relatively short-lived, fast-growing species like the surgeonfish for which changes in age at first capture of only ±1 year represent a large fraction of its life span.

Circumstantial evidence suggests that the relative ages at sexual maturity and first capture can be important. Prior evaluations of the potential for MFRs to conserve the SSB of overfished commercial stocks (e.g., red snapper, *Lutjanus campechanus*) have concurrently considered other management safeguards, such as size limits in the non-closed area (Plan Development Team, 1990). However, nearshore reef fishes subject to recreational harvest are often fished at sizes and ages considerably less than those at sexual maturity, even on moderately populated islands (e.g., the island of Hawaii; Hayes et al., 1982). For reef fishes near densely populated areas where exploitation is likely to be intense on pre-reproductive fish, the potential for MFRs to enhance SSB/R may be severely compromised, even at closure sizes that are as large as is practical (e.g., 25%).

Compensatory emigration

Density-dependent increases in the fundamental transfer rate can in essence depress potential gains in SSB/R in a manner analogous to that of a higher but constant fundamental transfer rate. The observation that gains in SSB/R at increasingly large refuge sizes were strongly offset by compensatory movements in the jack, but not in the surgeonfish, perhaps reflects the jack's slower growth rate, greater longevity, and lower mortality rate. Longevity, per se, may be important, because the model that was used to describe compensatory emigration is dependent upon time as well as age.

SLOSS effects on MFR function

Simberloff (1988) reviewed the SLOSS concept and the meager results to date regarding whether multiple, small reserves function the same as single reserves of equal total size. Historically the issue of SLOSS has been applied to the preservation of threatened and endangered species or the conservation of biotic diversity (Bell and Boecklen, 1990, but see Goeden, 1979). It is increasingly apparent that meaningful stewardship of the environment and its biota extends beyond these simple (although often difficult to implement) criteria. Overexploiting an ecosystem's productivity by overfishing (Russ, 1991) is just as detrimental as recruitment or growth overfishing.

Bohnsack (1991) recently applied the SLOSS concept in a review of the function of artificial reefs. Obviously MFRs also can be evaluated in terms of SLOSS—the question then may be, "Do several small reserves potentially enhance SSB/R to the same extent as one reserve of equivalent total size?" A realistic example may be the relative fishery enhancement potential of ten 1% closures versus one 10% closure. Establishing a MFR of 10% may be impossible on a heavily populated island (like Oahu, Hawaii) where shoreline development is near saturation. The siting of multiple, smaller refuges, each about 1% of the total area, may be feasible, however. But can a total closure of realistic size (10%) be beneficial, and can the potential of ten 1% closures approximate it?

The simulation results suggest that a total closure of 10% may enhance the spawning stock of a fast-growing, moderately vagile reef species such as surgeonfish: at a fishing mortality rate (F_c) of 1.0 (equal to M = 1.0), SSB/R can be increased by about 24% over the no-closure case for an MFR of 10%, if the lower bound of T_{1s} (0.10) is used as the fundamental emigration rate. By using the higher bound for T_{1s} (0.5) and an F_c still at 1.0, SSB/R is increased by 12% for the single 10% closure.

The overall contribution of multiple, small closures will be less, however, than that of one closure of equal total size, in inverse proportion to the increase in the total perimeter of (hence dispersal from) the multiple closures. (This follows from the general rule that smaller reserves have greater perimeter-to-area ratios than larger reserves of equivalent shape [Schonewald-Cox and Bayless, 1986].) In our example, the total perimeter of ten 1% closures is about three times ($\sqrt{10}$) that of one 10% closure. Hence, for a given fundamental transfer rate, the actual transfer rate will be appreciably greater, and the additive contribution of ten 1% closures to SSB/R will be several times less, than that of one 10% closure. Multiple 1% closures might translate to an actual emigration rate approaching 0.5 for a surgeonfish that is moderately vagile (T_{1s} = 0.1–0.25) relative to an MFR of 10%.

For the preceding arguments to hold, we must further assume that the multiple closures will not interact spatially. It seems reasonable though that for post-settlement stages of species with low fundamental transfer rates, ten 1% reserves may function independently if well-spaced, perhaps even on a relatively small (e.g., 100-km perimeter) island such as Oahu, Hawaii.

For simplicity, SLOSS arguments generally ignore the interactive effects of refuge shape and size. However, habitat geometry (shape as well as size) importantly influences dispersal into and from a habitat, regardless of whether an organism's movements are home-ranging or free-ranging (Stamps et al., 1987). Edge "permeability" (i.e., whether a reserve is sited within a larger area of homogeneous "soft-edged" habitat or is a functional island surrounded by discontinuous "hard-edged" habitat) also significantly affects dispersal (Buechner, 1987; Stamps et al., 1987). Small increases in edge permeability have disproportionately large effects on dispersal when boundaries are hard, whereas habitat shape exerts a controlling influence on dispersal when boundaries are soft (Buechner, 1987; Stamps et al., 1987). For shoreline-bounded reef closures, the shape of the MFR is clearly more important to residential reef fishes if the MFR is sited within a larger region of similar habitat than if different habitats (e.g., extensive sand channels) are used to provide its physical boundaries.

Future research

The overall net effect of the diverse compensatory and depensatory factors that may influence the movement patterns of fishes into and out of MFRs is beyond even semiquantitative appraisal at present. Major advances in our understanding of the function of MFRs await development of techniques that describe the fundamental transfer rates of fishes (Polacheck, 1990) and that further estimate the changes in movement rates that may occur as densities change over time. The results of my preliminary analyses suggest that future studies should focus on fast-growing, moderately vagile species such as many surgeonfishes, rather than reef transients or philopatriots. My preliminary conclusions should be reevaluated as more data become available for these and other types of reef fishes.

Management potential

MFRs have the potential to enhance the biomass and spawning stock of species with rapid growth and moderate, fundamental transfer rates (Polacheck, 1990; the present paper). Many factors, however, contribute to whether this potential is likely to be realized in practice: the age schedule of harvest and the magnitude of fishing effort in the non-closed area; whether one versus a few or many MFRs of a given total area are used, thereby promoting progressively larger increases in fundamental transfer rates; and whether compensatory emigration acts to further inflate vulnerability and deflate SSB/R. Decisions as to the number versus size of MFRs that can be sited, given the total shoreline extent of reef available, are social issues. Size limits and fishing effort (bag limits) also are subject to their own management politics, and MFRs will not make them obsolete. Although the fast growth and moderate movement rates of certain tropical reef fishes predispose them to benefit from refuges, it is unlikely that the establishment of MFRs alone, without complementary regulation of effort and the size composition of catch in non-closed areas, can augment the SSB/R of fishes on heavily exploited island reefs.

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