

CONFOUNDING EFFECTS OF THE EXPORT OF PRODUCTION AND THE DISPLACEMENT OF FISHING EFFORT FROM MARINE RESERVES

BENJAMIN S. HALPERN,^{1,2,4} STEVEN D. GAINES,³ AND ROBERT R. WARNER³

¹National Center for Ecological Analysis and Synthesis, 735 State Street, Santa Barbara, California 93101 USA

²Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95060 USA

³Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106 USA

Abstract. Marine reserves affect areas outside reserve boundaries via the displacement of fishing effort and the export of production. Here we focus on how these key factors interact to influence the results seen once reserves are created. For a settlement-limited fishery, export of increased production from within reserves can offset the effects of displaced fishing effort. We develop simple mathematical models that indicate net fisheries benefits can accrue at closures up to and perhaps beyond 50% of total stock area through the export of production, given documented average increases in biomass within reserves. However, reserve monitoring programs face problems identifying independent control sites because the spatial extent of export is unknown. Efforts to monitor reserve impacts on recruitment are further complicated by the fact that large reserve closures are likely necessary before significant changes in recruitment can be detected above normal interannual fluctuations. Resolving these limitations requires comprehensive monitoring data before reserves are implemented. Fortunately, studies of reserves that used Before–After, Control–Impact (BACI) experimental designs show that control and reserve sites were equivalent prior to protection, and that control sites improved after reserves were in place. Consequently, any bias in our current perception of reserve impacts likely underestimates their effect.

Key words: BACI experimental designs of marine reserves; export of fish production; fishing effort; marine protected areas; marine reserves; recruitment; reserve design; reserve monitoring.

INTRODUCTION

A major challenge in efforts to evaluate the effect of marine reserves on non-reserve areas stems from the fact that reserves are expected to affect areas beyond their borders by displacing fishing effort and exporting production. These two expectations lead to contradictory outcomes for biomass of populations outside the reserves and the consequent fisheries yields obtained from that biomass. The net result of establishing reserves could be a decrease, no change, or an increase in fish biomass outside the reserve, depending on which factor turns out to be more important.

In fact, much of the controversy around the creation of marine reserves and reserve networks stems from uncertainties about how or if reserves can compensate fishers for areas made unavailable to them as a result of implementation. Although marine reserves need not, and perhaps should not, be designed with fisheries management as a primary goal, it is important to explore how reserves will affect fisheries so that stocks outside reserve boundaries can be most effectively managed. The conventional wisdom is that little evidence exists for the export of production from reserves, and so the same number of fishers fishing in less area will cause

there to be fewer fish per fisher. This would be the case if marine reserves provided no benefit to populations of fish outside their boundaries.

However, a growing body of evidence suggests that reserves can affect areas outside their borders. Reserves can compensate for the loss in fishing area in two ways: through the spillover of adults across reserve boundaries and through the export of larvae from reserves to fished areas. Evidence shows that adult spillover can and does occur (e.g., Russ and Alcala 1996a, McClanahan and Mangi 2000, Roberts et al. 2001, Gell and Roberts 2002), but determining how many larvae reserves supply to non-reserve areas is a difficult task that has thus far relied primarily on theory (Man et al. 1995, Nowlis and Roberts 1999, Crowder et al. 2000, Botsford et al. 2001, Lipcius et al. 2001, Gaines et al. 2003) and a few correlative studies (Stoner and Ray 1996, Murawski et al. 2000, Valles et al. 2001). Estimates of average larval dispersal distances using a variety of indirect means (Kinlan and Gaines 2003, Shanks et al. 2003), however, suggest that the larvae of nearly all fish and most invertebrate species disperse much further than the typical sizes of marine reserves (Halpern 2003).

From a fisheries management perspective, the important questions are less about how many larvae are exported and more about the ability of this exported production to supply and sustain fisheries at current or

Manuscript received 5 May 2003; revised 28 October 2003; accepted 11 November 2003. Corresponding Editor: P. K. Dayton.

⁴ E-mail: halpern@nceas.ucsb.edu

TABLE 1. Relation between marine-reserve area (R) and changes in fishing pressure and larval production outside the reserve.

Reserve site, R (%)†	Increase in fishing effort outside reserve‡	Compensation factor§
1	1.01 ×	2.01
5	1.05 ×	2.05
10	1.11 ×	2.11
20	1.25 ×	2.25
30	1.43 ×	2.43
50	2.00 ×	3.00

† R = area set aside as reserve, as percentage of total habitat area.

‡ Multiplicative increase in fishing pressure, $(1/1 - R)$. For derivation of these values, see *The squeeze factor*.

§ Calculated as $(2 - R)/(1 - R)$. For derivation of compensation-factor values, see *The compensation factor*.

higher levels. What will be the stronger force structuring fish populations outside reserves—the displacement of fishing effort or the export of production? Put another way, how much export of production is necessary to offset the increase in fishing pressure from displaced fishers? One of the main goals of this paper is to evaluate and suggest answers to these questions.

Determination of the actual effects of reserves requires careful monitoring. However, a major challenge arises from difficulties in interpreting results from monitoring efforts. For example, a study may find that the biomass of fish inside a reserve is significantly higher than a comparable fished area nearby. Five possible scenarios exist to explain these results. After reserves were put into place, values could decrease in the reserve and decrease even more in the fished site, remain unchanged in the reserve and decrease in the fished site, or increase in the reserve while values in the fished site decreased, showed no change, or increased. These different responses clearly have different implications for how we interpret the impact of reserves, yet they all generate the same pattern—more biomass per unit area inside reserves than out. Well-designed before-after, control-impact (BACI) studies can resolve these possibilities, and we review the evidence from several such studies. As we discuss below, interpretation of results from monitoring programs of networks of multiple reserves is even more challenging than for single reserves.

One of the main goals for future monitoring programs of marine-reserve effects will be to determine the degree to which reserves supply larvae to areas outside reserve boundaries. A fair assessment of this potential impact requires that we have appropriate expectations. To help clarify and guide our expectations for the effects of reserves on areas outside their boundaries, we discuss three factors that should be kept in mind when designing reserves, developing monitoring programs, and interpreting results gained from such programs. First, we address the increase in fishing effort per unit area that would occur outside reserve

boundaries if fleet capacity and regulations were not changed. Second, for a settlement-limited fishery, we ask how much additional production reserves must export to compensate for the increases in fishing pressure due to this displaced fishing effort. Finally, we discuss how these two factors interact to affect the choice of appropriate and informative control sites for monitoring reserve performance. Previous models evaluating the effects of reserves on areas outside reserve boundaries (e.g., Attwood and Bennett 1995, Hastings and Botsford 1999, Nowlis and Roberts 1999, Botsford et al. 2001, Jennings 2001, Gaines et al. 2003) have not explicitly evaluated how displaced fishing effort may affect non-reserve fish populations, nor have they addressed whether increases in production from reserve populations can compensate for the change in fishing intensity outside reserve boundaries.

THE SQUEEZE FACTOR

Quantifying the effect of squeezing the same number of fishers into a smaller area is relatively straightforward. Consider the most conservative case with no response by fishers or management agencies, i.e., total fishing effort remains the same, albeit forced into a smaller area, and no new regulatory changes are imposed, such as stricter catch limits or fleet buy-back programs. If the fraction of total habitat area set aside in reserves is R , then the previous fishing effort is now concentrated in an area that is only $(1 - R)$ as large. As a result, the proportionate increase in fishing effort per unit area outside the reserves will be $1/(1 - R)$. For example, a 20% reserve closure ($R = 0.2$) would lead to a 25% increase in fishing pressure ($1/[1 - R] = 1.25$) to areas outside the reserve. The fishing pressure on populations outside the reserve accelerates as the fraction of area in reserves increases (see Table 1). At $R = 0.5$, fishing effort outside the reserves doubles. From the perspective of fish that are the targets of fishing, these increases in effort should translate into a comparable increase in risk of mortality in the short term.

These calculations assume that displaced fishing effort is distributed equally to areas outside the reserve boundaries. In more realistic scenarios, displaced fishers may relocate only a short distance, causing fishing intensity to remain relatively unchanged at locations far from the reserve but be greater than $1/(1 - R)$ at locations nearby the reserve. However, the potential for limited larval dispersal from within the reserve (Swearer et al. 1999, 2002) and the likelihood of at least some adult spillover (Attwood and Bennett 1994, McClanahan and Mangi 2000, Roberts et al. 2001) suggest that the benefits gained by fishers from reserves may parallel the spatial patterns of likely changes in fishing intensity. We deal with the possibility of reserves being able to compensate for changes in fishing intensity explicitly in the next section, but maintain the

assumption of uniform redistribution of displaced fishing effort here for the sake of simplicity.

THE COMPENSATION FACTOR

The estimates above assume no response by people to compensate for the displacement of fishing effort (i.e., total fishing effort remains constant). The estimates also assume that any responses by the animal and plant populations that receive protection from the reserve have no impact on populations outside the reserve. However, if protection within reserves leads to enhanced production of young or adults, and part of this production then spills over into areas beyond reserve boundaries, some of the increases in mortality outside the reserve due to the concentration of fishing effort could be offset by the export of biological benefits produced from the populations protected within reserves. How much additional production from the reserves would be needed to offset the added losses beyond reserve borders? Spillover of adults from the reserve to unprotected areas will contribute to this compensation (e.g., McClanahan and Mangi 2000, Roberts et al. 2001), but export of adults will likely be limited in spatial extent relative to the entire management area. The export of larvae, on the other hand, has the potential to service much larger regions and perhaps entire populations.

The potential for larval export from reserves to compensate for displaced fishing effort is conceptually easiest to address when fisheries are recruitment limited, so that future catch is determined primarily by the rate of successful settlement of larvae. For the rest of this paper we define "recruitment" as the settlement of larvae to the benthic phase of their life-cycle, and focus our attention on how recruitment changes in fished areas, acknowledging that populations within reserves may not be settlement limited as they grow larger. Most if not all over-fished populations are recruitment limited, and many other species, regardless of fishing intensity, have been shown to be recruitment limited (reviewed in Doherty [2002]). Consequently, the models we develop below should be broadly applicable.

To begin with, assume that (1) all larvae are released into a general larval pool and then settle equally to all areas, fished or not fished, (2) larval mortality is density independent, so that increases in production lead to equivalent increases in recruitment, and (3) adult fish are evenly distributed throughout their range, so that the amount of adult biomass initially protected by a reserve is proportional to the reserve size. Suppose the settlement rate of larvae per unit area of habitat = L . For reserves to compensate for the impact of increased fishing outside the reserve, this rate must increase in the face of increased fishing pressure to $L \times [1/(1 - R)]$. Since reserves are unlikely to have any direct effect on larval mortality, settlement rates in fished areas must be increased from an increase in production of larvae by adults in the reserve. If reserves enhance the pro-

duction of settlers per unit area to L_r , then the average settlement rate due to combined production from reserves and unprotected areas (which remains at L per unit area if full compensation occurs) will be

$$L \times (1 - R) + L_r \times R.$$

To offset the added losses outside the reserve, this settlement rate must equal or exceed

$$L \times \frac{1}{1 - R}.$$

Therefore,

$$L \times (1 - R) + L_r \times R = L \times \frac{1}{1 - R}.$$

Next solve for how large L_r must be to meet this criterion:

$$L_r = \frac{1}{R} L \left[\frac{1}{1 - R} - (1 - R) \right]$$

$$L_r = L \left[\frac{(2 - R)}{1 - R} \right].$$

Expressing this production rate in reserves relative to the production rate prior to reserve establishment, one obtains the critical compensation factor (CF) needed to offset the concentration of fishing effort:

$$CF = \frac{L_r}{L} = \frac{2 - R}{1 - R}.$$

Table 1 shows values of this compensation factor for a variety of reserve sizes and resulting squeeze factors, given our assumptions about displaced effort. Regardless of the size of a reserve, and no matter how few fishers are displaced by the reserve, production of future settlers needs to at least double inside the reserve to compensate for displaced fishing effort. However, production need only triple inside reserves to compensate for the displacement resulting from a 50% closure.

It is clear that determining the effects of reserves on areas outside reserve boundaries depends critically on estimates of reserve production. Although the change in production within reserves has not been directly measured, many studies have examined changes in adult size. If gamete production increases linearly with biomass, a conservative assumption for most species (Wootton 1990), one can estimate CF using existing empirical studies of changes in biomass. Halpern's (2003) synthesis of studies of more than 80 reserves worldwide provides a broad, general picture of how reserves can affect biomass. On average, biomass tripled within reserves. This suggests that the expected increase in production within reserves could compensate on average for the displacement of fishing effort up to a 50% closure, if the fishery is settlement limited. If the fishery is not settlement limited, then increased production within a reserve will have smaller effects

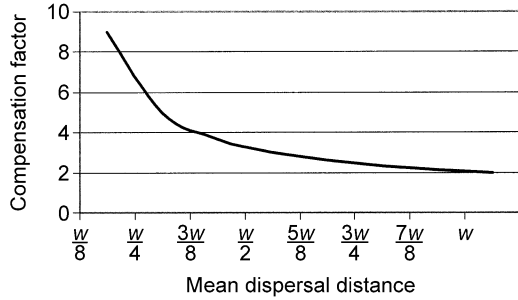


FIG. 1. The compensation factor (CF) value given varying average dispersal distances as a function of the width (w) of individual reserves. If reserve size is less than or equal to the mean dispersal distance, $CF = 2$ (i.e., larval production within reserves must be twice as high as in fished areas). Assuming that biomass triples within reserves (Halpern 2003), then species with average dispersal distances greater than half the width of the reserve should ultimately compensate for the displacement of fishers.

on yield in areas outside the reserve, although reserves could still have an effect via the spillover of adults to non-reserve areas. Given that no existing reserves or reserve networks enclose anything remotely close to 50% of the range of any marine species, these simple calculations predict that the impact of existing reserves on areas beyond their boundaries should commonly be beneficial despite the concentration of fishing effort.

One critical assumption in the above estimates is that larvae produced within the reserve disperse, on average, well beyond the boundaries of the reserve. For most species of fish and invertebrates this may be a reasonable starting assumption (e.g., see Kinlan and Gaines 2003, Shanks et al. 2003) given the size distribution of existing marine reserves (Halpern 2003). With this dispersal scenario, the fraction of larvae that ultimately settle back into a reserve is R . For some species, however, dispersal of young is much more limited. In addition, even with the potential for long-distance dispersal, realized larval dispersal may be much more limited in some oceanographic settings (e.g., Jones et al. 1999, Swearer et al. 1999). If larvae have restricted larval dispersal, can reserves still compensate for the displacement of fishers? Clearly, if larvae do not disperse at all, none of the higher production generated within the reserve benefits the fishery, because it is not exported to fished areas; there will be no compensation for the “squeeze” in fishing intensity.

To explore the case of limited dispersal, we focus on individual reserves rather than the overall fraction of habitat protected. Imagine a coastline with reserves of width w separated from each other such that the region s defines the size (w) of a reserve plus the distance to the next reserve. Suppose that larvae are dispersed away from their parents with a mean dispersal distance, d , a maximum dispersal distance, m , and probability distribution of dispersal distances, $f(x)$. Consider a conservative case of restricted dispersal where the

reserve size is large relative to the maximum dispersal distance. In this situation, the offspring of a female fish who spawns at the center of the reserve will all be retained within the reserve. A female spawning at the edge of a reserve, however, will export half of her offspring to the adjacent fished area. As spawning sites move from the edge of a reserve toward the center, the fraction of larvae exported declines. For any given location that is a distance b from the edge ($b \leq m$), the fraction of larvae exported is $1/2$ (because only larvae dispersing in one direction are exported) times the probability that larvae disperse a distance greater than b , i.e., the area of the tail of the dispersal probability distribution, $f(x)$, that lies beyond b :

$$\text{Fraction exported} = \frac{1}{2} \left[\int_b^m f(x) \, dx \right].$$

To estimate the total reserve contribution to the fished area, integrate over the contributions from all locations within a distance m of the edge of individual reserves. For any dispersal probability distribution, $f(x)$, this total contribution is

$$\frac{1}{2} \int_0^m x f(x) \, dx = \frac{1}{2} d$$

which is $1/2$ of the average larval dispersal distance, d . An equivalent contribution to each fished area comes from neighboring reserves on the right of the fished areas through export of larvae dispersed to the left from the reserves. Similarly, the fished area contributes an equivalent cumulative fraction of larvae to each of its neighboring reserves.

To estimate the critical compensation for the squeezed fishery, we focus on a single fished area between two reserves. Prior to the establishment of the reserve, the region s generated $L \times s$ settlers. Without reserves, contributions to and from adjacent fished areas through larval dispersal would be equivalent. Thus, the pattern of dispersal can be ignored. With reserves, the smaller fished area only generates $L \times (s - w)$ recruits. Some of these larvae are exported to the adjacent two reserves ($L \times 2 \times [1/2d]$). In addition, some recruits arrive from the adjacent reserves ($L_r \times 2 \times [1/2d]$). Therefore, to compensate for the enhanced fishing pressure, this total production to the fished area must equal $L \times s$:

$$L \times s = L \times (s - w - d) + L_r \times d.$$

The resulting CF is

$$CF = \frac{L_r}{L} = \frac{w + d}{d}.$$

If we express average dispersal distance in terms of reserve size, w , and a nominal scaling parameter, k , e.g., if $d = w/k$, then CF equals $k + 1$ (Fig. 1). As with dispersal into a common larval pool, the CF converges to a minimum value of 2 as d approaches w . Shorter

dispersal distances require a higher CF to offset the effects of displaced fishing. Therefore, fished species may respond differently to the same reserves. Using the biomass estimates of Halpern (2003) to project an average CF of 3, species with average dispersal distances greater than half the width of the reserve should ultimately compensate for the displacement of fishers. On the other hand, species with shorter average dispersal distances would receive insufficient export of production from the reserves to compensate for the squeezed fishery. Although estimates of dispersal distances are only available for a tiny fraction of marine species, it is likely that the great majority of fished species disperse farther than the average reserve size, given the distribution of existing reserve sizes (Halpern 2003). Some harvested species, however, such as abalone (McShane et al. 1988) or kelp (Reed et al. 1992), may rarely satisfy these compensation criteria, since their average dispersal distance can be quite limited. In addition, since the total fraction of habitat protected by a network of reserves can be increased both by increasing reserve size and by decreasing reserve spacing, scaling individual reserve size to the average dispersal distance of key fished species provides a simple mechanism for compensating for displaced fishing even for networks covering large cumulative areas.

Another implicit assumption in our calculations is that species are relatively sedentary and site attached. Because they have limited ranges of movement, these species can benefit from reserve protection and grow to produce a greater number of offspring. Generally, these species comprise a majority of a community. The conclusions from our work likely do not apply to more highly mobile species. However, because of their mobility these species are both unlikely to benefit from reserve protection nor be harmed by displaced fishing effort. They will simply be caught in different locations. In short, reserves provide little benefit but create little cost for highly mobile species, and would therefore have little effect on fishers who target these species, aside from constraints imposed by being forced to fish in different locations (e.g., with different travel costs).

Even sedentary species can make directed movements that may alter the way in which production is exported from reserves. In particular, many species are known to migrate to spawning aggregation sites. If these aggregation sites fall within reserve boundaries, then their effect on larval production depends on how much the reserves reduce mortality on the spawning females. If fishing mortality largely occurs prior to aggregation, then reserves that protect aggregation sites may have little impact on production. If substantial fishing mortality would otherwise occur when fish are aggregated to spawn (e.g., because they are much easier to catch while aggregated), then reserves should enhance larval production directly in proportion to the reduction in mortality they provide. For example, if

two-thirds of spawning females were, on average, caught prior to spawning while at the aggregation site, then a reserve protecting the spawning site would effectively triple larval production. This would be equivalent to the value of $3R$ assumed above. If aggregation sites fall outside reserve boundaries and are targeted by fisheries, then some of the benefits of the accumulated adult biomass within reserves would be lost when females migrate to spawn. In these circumstances, the simple model above would overestimate the benefits of reserves to the fishery.

Even though biological compensation appears to be large enough to offset fisher displacement from large reserves, this biological compensation does not occur immediately. Fishers can move in a day, changing the intensity of fishing effort outside reserves literally overnight. The accumulation of biomass within reserves (the source of compensatory production) will certainly take longer. Evidence suggests that community-wide average biomass responds rapidly to reserve protection, within one to three years after reserve creation (Halpern and Warner 2002), although there is also evidence that many species, particularly those with slow growth rates or late ages at maturation, will build up biomass within reserves much more slowly (e.g., Gell and Roberts 2002, Russ 2002). The spillover of adults from reserves should happen more quickly and therefore help offset some of the losses to fishers from fishing grounds becoming protected by reserves, but the interim years between reserve creation and the realization of production compensation will likely require alternative policy measures for fisheries on slowly growing species. However, our analyses suggest that fishers will often benefit in the long run with reserves in place.

MONITORING RESERVE IMPACTS

To be politically feasible, reserves must achieve the goals established for them. However, accurately assessing reserve performance will be difficult for several reasons.

Lack of independent controls

Most notably, it is nearly impossible to identify a truly independent control site for monitoring the effects of reserve networks (systems of reserves that collectively span a wide area). Supposedly, reserves affect nearby areas both negatively, via displaced fishing effort, and positively, via export of production. In fact, one of the criteria used to design reserve networks is that individual reserves within a network are connected to each other, usually through larval dispersal. This implies that all areas between the reserves will also likely receive export. Thus areas both inside and outside of reserves should be subject to reserve effects, and contemporary sites used to take measurements inside (reserve effect) and outside (control) a reserve network cannot be truly independent. Consequently,

monitoring programs may need to sample at many sites across a gradient of distances from the reserve boundary, both outside and within the reserve, to characterize the effects of reserves and the spatial extent of those effects. No particular area outside a reserve can be reliably identified as a control until we have a much better understanding of the dispersal distances of pelagic larvae.

Intrinsic variation in recruitment

Increases in the production of larvae within reserves may not result in detectable increases in recruitment outside the reserve unless substantial portions of the sea are set aside. Assuming that larval production triples within reserves (Halpern 2003) and that this production is dispersed equally across all areas (an assumption that approximates reality if the average dispersal distance of target species is much larger than the size of individual reserves, which is likely the case for most existing reserves since the reserves are relatively small), then the total productivity is the production contributed from the reserves ($3R$) plus the production from non-reserve areas ($1 - R$), adjusted by the change in survival outside the reserve due to the displacement of fishing effort ($1/[1/(1 - R)]$), or simply $1 - R$). Thus, overall larval production is

$$3R + [(1 - R) \times (1 - R)] = 1 + R + R^2$$

and the fraction of this total production that recruits back into reserves is equal to the fraction of the total area devoted to reserves (R). If increases in production of larvae are directly related to overall increases in subsequent recruitment, then closing 10% of waters would lead to an 11% overall increase in recruitment, a 30% closure to a 39% increase, and a 60% closure to a doubling of recruitment.

The calculation described above assumes that larvae disperse quite broadly. If dispersal distances are much shorter (on the order of the size of individual reserves), some of the increase in production within reserves will be retained inside the reserve, causing settlement rates to vary spatially as a function of distance from the reserve boundary. Far from the reserve, settlement rates should be unaffected by contributions from the reserve. If dispersal distances are smaller than the reserve size, settlement increases should match the increases in production in the center of the reserve, while at the reserve boundary settlement rates should be at the midpoint between these two extremes. Again, using the biomass patterns in Halpern (2003) to forecast a tripling of larval production within the reserve, settlement rates near the reserve boundary should be twice as high as average rates far from the reserve. The rate of average settlement should decline as a function of distance from the reserve boundary, with the rate of decline set by the shape of the probability distribution of dispersal distances.

These two scenarios present the two possible extremes for larval dispersal: larvae disperse a great distance relative to reserve size or they disperse a distance shorter than the width of the reserves. In either case changes in recruitment in fished areas after reserves are put in place will not be large ($>30\%$) unless total reserve size is relatively large (wide dispersal) or one is measuring recruitment immediately next to the reserve boundary (limited dispersal). In a perfect world with adequate sample size, even a 10% increase in recruitment might be detectable. However, given the inherent variability in annual recruitment for most species (e.g., Caffey 1985, Roughgarden et al. 1988, Siegel et al. 2003), the effects of reserve networks on population-wide recruitment may not be detectable unless sizable areas are set aside or many years of data from monitoring programs are available. This is essentially a signal-to-noise problem. A synthesis of the recruitment dynamics of 82 invertebrate species of all life-history types (Eckert 2003) can give a sense of how much noise, i.e., normal variation, there is in recruitment. Short dispersers (species with planktonic, non-feeding development) had an average coefficient of variation (cv) value of about 155, i.e., the average 1 SD was half again as large as the mean, while long dispersers (species with planktonic, feeding development) had an average cv value of 145 (Eckert 2003).

To overcome this formidable amount of natural variation, either recruitment must increase many-fold or it must be monitored for many years to create a larger sample size after reserve creation. Consequently, increases in recruitment from networks of small reserves or small single reserves are unlikely to be detectable across the range of a species, especially for species with broad dispersal distances. Production is being increased, but its signal will likely be diluted broadly and masked by large temporal variation. Even large reserves will need to be monitored for many years after reserve creation before an effect on recruitment may be detectable statistically. Species with limited dispersal distances relative to reserve size should provide the most statistically powerful tests of reserve effects on recruitment, because they should show larger effect sizes near the reserve boundary. Since nearly all existing protected areas can be classified as small reserves or small networks, it will be very difficult to determine the extent to which these reserves are affecting recruitment given current set-asides. Even though reserves are enhancing production on average three-fold within their boundaries, the cumulative export benefits may be difficult to detect against a background of fluctuating recruitment.

Evidence from BACI studies

The need for designing reserve-monitoring programs with adequate and appropriate controls has been discussed before (Guidetti 2002, Hilborn 2002, Russ 2002). One message from this work is that monitoring

TABLE 2. Data for changes in four biological measures from studies that made measurements before and after marine-reserve creation in control (fished) and impact (reserve) sites (BACI design).

Biological measure	N	Inside-before vs. outside-before						Outside-after vs. outside-before					
		Trends			Actual values			Trends			Actual values		
		No. better	No. ND	No. worse	Log ratio	t	P	No. better	No. ND	No. worse	Log ratio	t	P
Density	9	3	1	5	0.12 ± 0.47	0.75	0.47	7	1	1	0.25 ± 0.50	1.52	0.17
Biomass	3	1	1	1	0.08 ± 0.20	0.70	0.56	3	0	0	0.40 ± 0.41	1.71	0.23
Size	2	2	0	0	0.02 ± 0.007			1	0	1			
Diversity	3	2	0	1	0.05 ± 0.07	1.21	0.35	1	0	2	-0.05 ± 0.08	-1.20	0.37
Combined	17	8	2	7				12	1	4			

Notes: From the studies of marine reserves that were reviewed by Halpern (2003) and Gell and Roberts (2002), a total of nine reserves from seven different studies were evaluated using a BACI design. Data are presented for comparisons of reserve and non-reserve sites before reserve creation and of non-reserve sites before and after reserve creation. First, comparisons were classified as better, worse, or not different (ND) according to the value of the first comparator (inside-before or outside-after) relative to the second (outside-before in both cases) regardless of significance (ND indicates that values were identical); in most cases of difference, values differed by over 100%. Second, the actual values for each reserve were expressed as a ratio, and then log-transformed for statistical purposes. Log ratio values are presented as mean ± 1 SD. A two-tailed, one-sample *t* test was performed to compare the log-transformed ratio of the indicated comparisons to the null hypothesis of no difference (i.e., log ratio = 0). The *t* test was not performed for "size" because sample size ($N = 2$) was too small for statistical comparison.

programs need to take measurements both before and after reserve creation at sites inside and outside the reserve, and we have discussed how control sites at varying distances from reserve boundaries may be necessary to determine the extent to which reserves affect areas beyond their borders (see *lack of independent controls*, above). Few studies of individual-reserve effects have had such sampling programs. Without measurements made before reserve creation, it is difficult to assign causes to any differences seen between reserve and fished locations. In fact, it has been suggested (Hilborn 2002) that a bias may exist in the perceived effect of reserve protection because (1) reserves were likely placed in inherently more productive locations and (2) displaced fishing effort when reserves are created should lower values in the control site outside the reserve due to the higher fishing pressure.

Although the need for a proper sampling design has been identified, it remains unknown how a lack of such a design may have influenced the results of previous reserve-monitoring programs. Analyses of reserve studies that used a before-after, control-impact (BACI) experimental design can be used to evaluate if the potential biases outlined by Hilborn (2002) exist. If reserves were placed in more productive locations, then measurements comparing reserve and fished locations from before reserve creation should indicate higher values of density, biomass, etc., at the reserve location. Furthermore, if displaced fishing effort as a result of reserve protection subsequently lowered values of density, etc., outside the reserve, then control sites should show a decrease in density, etc., after reserves were established.

Syntheses of results from the few reserve studies that used a BACI design (Castilla and Duran 1985, Castilla and Bustamante 1989, McClanahan and Kaunda-Arara 1996, Russ and Alcala 1996b, Edgar and Barrett 1999,

Roberts et al. 2001, Tawake et al. 2001) suggest that such potential biases do not exist. There is no significant difference between pre-reserve fished and reserve values, nor do values change significantly in fished areas after reserve creation (Table 2). If anything, changes in fished areas tended to be positive despite displaced fishing effort, suggesting a service function for marine reserves that would create a bias against seeing a reserve effect. This is exactly the challenge we describe above for finding a true control site; reserves appear to be affecting areas outside reserve boundaries, and so a single "control" site will be insufficient to determine the extent of this reserve effect.

Combining all the results from these limited analyses suggests that "control" sites tend to improve after reserve protection in most situations (Table 2), although the small sample size of these analyses require that caution be used when generalizing the results. This service function of reserves to fished areas occurred despite the increased fishing intensity that most of these "control" sites likely incurred as fishers displaced by the reserve moved to these nearby locations. Although we have focused on the potential for reserves to export larval production to fished areas in our analyses above (see *The compensation factor*), the service function provided by the reserves in these studies is probably due to the spillover of adult fish, as suggested by the authors of the studies used in these analyses. Regardless of the source of this service function, these results demonstrate that changes in fishing pressure outside reserves that may have occurred from displaced fishing effort did not negatively affect fish populations outside reserves, and highlight the challenges inherent in efforts to evaluate the actual effect of reserves on marine populations.

CONCLUSIONS

The appropriate design and monitoring of marine reserves require accurate expectations for the impacts

of within-reserve changes on populations of fish outside reserves. To date most expectations have been based on only one of the two factors we discuss here: either reserves will increase reproductive output and therefore benefit fisheries catch, or displaced fishing effort will decrease total catch. Here we combine these factors to develop simple expectations for how reserves affect areas outside reserve boundaries and highlight key issues that must be considered when developing and evaluating marine reserves and reserve networks. For settlement-limited fisheries, the increase of production within reserves (on average, a tripling) may compensate for greater fishing pressure outside the reserve, up to at least a 50% closure of habitat. However, if total reserve area is too small, then such compensation from reserves due to increases in overall recruitment may be difficult to detect within the normal fluctuations in recruitment, even when the increases are real.

Because reserves are expected to affect areas outside the reserve, it will be difficult to have independent control sites for monitoring reserve networks. Most studies to date that evaluated reserve effects probably did not have truly independent control sites, simply because export from reserves can affect areas outside the closure. Limited evidence suggests that biases for detecting a positive reserve effect are unlikely, however, in that reserves do not appear to have been placed in disproportionately productive areas, nor do areas outside of reserves decline in biological value after reserve establishment. In fact, a slight bias may exist against seeing a reserve effect, because areas outside the reserve actually tend to improve. This is encouraging evidence for the export function of reserves. These studies highlight the need for monitoring programs to include data from before reserve implementation if reserve effects are to be assessed accurately.

Attention to these issues does not ensure any particular result. Instead, it helps to set appropriate goals and expectations for the development and monitoring of marine reserves and reserve networks. Once developed, these goals and expectations can then allow for the proper design, and when necessary the redesign, of reserves and reserve networks.

ACKNOWLEDGMENTS

This paper benefited greatly from comments by Paul Dayton, Garry Russ, and one anonymous reviewer. This work was conducted as part of the working group entitled "Development of Tools for the Practical Design of Marine Reserves," supported by the National Center for Ecological Analysis and Synthesis, a Center funded by the U.S. National Science Foundation (Grant number DEB-94-21535), the University of California—Santa Barbara, the California Resources Agency, and the California Environmental Protection Agency. Support was also provided by the Partnership for the Interdisciplinary Study of Coastal Oceans (PISCO), funded by the David and Lucille Packard Foundation, the Andrew W. Mellon Foundation, and the Smith Program, funded by The Nature Conservancy.

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