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IMPACTS OF

MARINE RESERVES ON FISHERIES

A report and review of the literature

by

Robert J. Rowley

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Published by
Head Office,
Department of Conservation,
PO Box 10-420,
Wellington,
New Zealand

ISSN 0113-3713
ISBN 0-478-01432-5

This publication originated from work done under
Department of Conservation contract No.850
and was approved for publication by the
Director, Science and Research Division,
Department of Conservation, Wellington.

National Library of New Zealand
Cataloguing-in-Publication data

Rowley, Robert J.
Impacts of marine reserves on fisheries : a report and review of the literature / by Robert J. Rowley. Wellington, N.Z. : Head Office, Dept. of Conservation, c1992.
1v. (Science & research series, 0113-3713 ; no. 51)
Includes bibliographical references.
ISBN 0-478-01432-5
1. Fisheries–Environmental aspects. 2. Marine parks and reserves–Management. 3. Marine resources conservation. 4. Fishery management. I. New Zealand Dept. of Conservation. II. Title. III. Series: Science & research series ; no. 51.
333.952 (338.3727)

Keywords: fisheries management, harvest refuge, larval export, marine protected area, protective management, spillover, bibliography

CONTENTS

IMPACTS OF MARINE RESERVES ON FISHERIES
A report and review of the literature

by

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ABSTRACT

Marine reserves have the potential to increase fishery catches in two ways: through emigration of large fish across the border of a reserve and into local fishing areas (“spillover”); and through the export of larvae from a reserve, which may enhance recruitment into regional fishery stocks. There are also a variety of potential benefits of reserves that are important, but will not directly affect catches. These include: helping to maintain species genetic diversity and population size structure; providing a buffer against recruitment failure; and providing unharvested "baselines" from which to measure the effects of fishing.

The evidence regarding spillover from reserves is limited, but supports the conclusion that spillover will occur and may substantially augment local catches. The strongest response to spillover reserves is expected from species that have been heavily overfished reach potentially large sizes or ages, and whose movement range is limited. New Zealand species that may benefit include rock lobster, paua, groper, red moki, and blue cod.

Larval export reserves have the potential to substantially enhance fisheries over large regions, but this potential is entirely untested. New Zealand species that may benefit from larval export reserves include rock lobster, paua, and orange roughy.

Research needed to better design and manage marine reserves includes: description of the daily, ontogenic, feeding, spawning, and migratory movements of species of interest; and understanding of the transport of planktonic larvae by currents.

1. BACKGROUND AND LITERATURE REVIEW

This report was contracted to review and summarise the international scientific literature on the uses of marine reserves for fisheries management, and to recommend a research agenda to collect the information needed to effectively use marine reserves for fisheries management in New Zealand.

Marine reserves have been conceived in different ways by different groups of people:

- As areas where the natural communities of our coasts can be preserved free from all exploitation

- As regions available for non-commercial fishing

- As settings in which scientific research can be conducted on unexploited communities

- As underwater parks for snorkelers and divers to enjoy coming face-to-face with marine animals, and

- As fishery management areas which may help to sustain the long-term manageability of coastal fisheries.

All these are valid possibilities for marine reserves, and decisions regarding how (or if) reserves are to be established will require consideration of many divergent points of view. In this report I will leave most of these concepts for others to analyse, and focus solely on the potential role marine reserves may play in fisheries management.

In preparing this report I have reviewed over 300 publications. Most of these were not directly relevant, but this was often impossible to determine without reading them. Because much of the literature reviewed was not particularly relevant, I have presented the references in two parts. The References are a list of the publications cited in this report. It is organized so that citations that deal with marine reserves explicitly have their titles printed in **bold** typeface, and those that deal with fisheries or provide background information are in plain typeface. The second list (Bibliography) lists the remainder of the publications reviewed in preparation of this report. All bibliographic material is also available as a database with keywords and comments on Pro-Cite (MacIntosh format).

The fisheries information is the most current I could find, but a great deal of not-yet-published information is being analysed by New Zealand fisheries scientists. These scientists should be consulted for the most recent knowledge and for needed analyses.

2. INTRODUCTION

Marine reserves are being established worldwide at a rapid rate (Clark *et al.* 1989; Davis 1989; Plan Development Team (aka Bohnsack) 1990; Polunin 1990) and interest has recently focused on using these reserves in a fisheries management role (Wallis 1971; Davis and Dodrill1980; Davis 1981, 1989; Plan Development Team 1990; Roberts and Polunin 1991).

The establishment of marine reserves enjoys considerable public interest, which is broadly directed at protecting habitat from exploitation. This public enthusiasm for reserves may help supply the political motivation needed to overcome the social, economic and political complications involved in attempting to establish reserves that may (among other functions) be useful for fisheries management. While reserves established in this way will not be specifically designed to help manage fisheries, consideration of possible fisheries functions during the design and planning may greatly increase a reserve's potential benefit to local or regional fisheries.

This report will:

- Summarise the existing studies on the effects of reserves on local and regional fisheries

- Discuss possible (but largely unproven) effects of reserves

- Consider aspects of reserve design which may increase their benefit to fisheries

- Discuss the types of research needed to design and monitor reserves for fisheries management, and

- Include an annotated bibliography of the literature reviewed.

Many analyses of marine reserves have appeared recently or are in press. A bibliography for managers and scientists interested in fisheries applications of marine reserves should include: Davis 1989; Plan Development Team 1990; Polacheck 1990; Carr and Reed, in press; Roberts and Polunin 1991.

3. POTENTIAL BENEFITS OF MARINE RESERVES FOR FISHERY MANAGEMENT

3.1 "Spillover"

(Enhancement of local fisheries by emigration of adults and large juveniles from a reserve.)

The basic idea is that a protected population within a reserve may reach higher densities and larger sizes than are found outside the reserve. Movement of individuals across reserve boundaries will bring them within reach of local fisheries, and this "spillover" may increase local catches.

3.1.1 Existing data regarding spillover

There are two separate questions that need to be answered:

(a) Do protected species reach larger sizes and greater densities within reserves?

(b) Do individuals move across reserve boundaries and enhance local fisheries?

Many recent papers contain data relevant to these questions, and more papers are appearing almost daily.

(a) Responses to protection A common pattern emerges from comparison of studies on fish populations in reserves: for heavily fished species, reserves tend to support higher densities of larger individuals. Some of the differences in population densities are dramatic. Russ (1985) reported that fishes of the family Serranidae (basses) within the reserve at Sumilon Island, Philippines, were from 3 to 25 times denser than at two sites outside the reserve. In the Leigh Reserve (Cape Rodney to Okakari Point Marine Reserve, Leigh, New Zealand), lobster densities have, on average, increased to eight times the densities outside the reserve (MacDiarmid, ms), and density appears to still be increasing after nearly 15 years of protection (P. Breen, pers. comm.).

Studies that have examined the response of species protected within reserves are listed in Table 1.

Particularly relevant are those studies conducted within New Zealand waters or in temperate environments. These are summarised below.

Examples 1-5

1. Several studies have examined the response to protection of species in the 5 km long Leigh Reserve. McCormick and Choat (1987) compared the central region of the reserve to an adjacent strip of unprotected coast and found that red moki (*Cheilodactylus spectabilis*) were larger and over twice as dense within the reserve. These results were expanded on by Cole et al. (1990) who censused 15 species of fish, as well as sea urchin (*Evechinus chloroticus*) and rock lobster (*Jasus edwardsii*) at 5 sites within the reserve, compared with 3 unprotected sites, and found higher densities of red moki and rock lobster, and larger snapper (*Chrysophrys auratus*) within the reserve. MacDiarmid, in an unpublished manuscript, reports on a comparison of rock lobster populations in the reserve at Leigh and in 5 unprotected areas and concludes that the reserve supports higher densities of larger lobsters and produces much greater numbers of lobster larvae than the unprotected areas.

2. Bell (1983) censused 35 species of rocky-reef fishes (of which 13 were labrids and 9 were sparids) in a 5 km longshore X 2 km offshore reserve in the Mediterranean in

Table 1 A summary of studies, taxa, and results regarding the response of species to protection within marine reserves.

Reference	Taxa	Effect
Alcala & Russ 1990	15 families (80 species) of coral-reef fishes	several families decreased, 1 family increased, in density after protection ceased
Bell* 1983	35 species of rocky-reef fishes	11 of 18 species vulnerable to spearfishing showed higher densities within reserve
Bennett & Attwood* 1991	10 species of rocky-reef and surf fishes targetted by line fishing	6 of 10 species showed higher CPUE within reserve following protection
Bohnsack 1982	>100 species of coral-reef fishes	spear-fishing reduced densities of large predators, some smaller species increased within reserve
Buxton and Smale* 1989	3 species of rocky-reef sparids vulnerable to line fishing	2 of 3 species showed higher densities, 1 of 3 had larger average size, and all 3 showed largest maximum size within reserve
Castilla & Duran* 1985	"loco" (*Concholepas concholepas*) a gastropod collected intertidally	higher densities and larger sizes of loco within reserve, with dramatic changes in the intertidal community
Castilla & Bustamante 1989	Bull kelp (*Durvillaea antarctica*) collected intertidally for food	Higher densities and larger sizes of bull kelp within reserve
Cole et al * 1990	Spiny lobster (*Jasus edwardsii*), red moki (*Cheilodactylus spectabilis*), snapper (*Chrysophrys auratus*), 13 other spp	Red moki and spiny lo9bster denser, snapper larger within reserve
Craik 1991	Coral trout (*Plectropomus leopardus*)	Coral trout larger and denser on coral reefs closed to fishing
Lane et al. 1991	Queen conch (*Strombus gigas*), a large gastropod	Conch larger and more numerous within reserves
MacDiarmid* unpublished ms	Spiny lobster	Lobsters larger, much denser, estimated egg production much higher within reserve
McClanahan & Shafir 1990	Sea urchins and coral-reef fishes (including important urchin predators)	Fishes averaged 4x as dense within reserves, urchins 100x as dense outside reserves
McCormick & Choat* 1987	Red moki	Red moki larger and denser within reserve
Moreno et al. 1984, Oliva & Castilla 1986	"loco" (gastropod)	Size of loco, but not their density, increased within reserve following protection

(Continued on next page)

* References particularly relevant for New Zealand. They are summarized further in the text.

Table 1 *(Continued)*

Reference	Taxa	Effect
Polunin & Roberts unpublished report	A large number of coral reef fishes from 2 Caribbean sites and 1 Egyptian Red Sea site	Complex results with most targeted (and some untargeted) species larger and denser within reserves, but with a few species (both targeted and untargeted) denser outside the reserves
Rice et al. 1989	'quahog' clams (*Mercenaria mercenaria*)	Clams larger, older and denser within reserves
Russ & Alcala 1989	102 species of coral reef fishes	Targeted species decreased in density , and wide community changes occurred within reserve during lapse of protection
Weil & Laughlin 1984	Queen conch (gastropod)	Conch larger and denser within reserve
White 1988	126 species of coral reef fishes	Targeted species denser, number of species greater within reserves

* References particularly relevant for New Zealand. They are summarized further in the text.

which spearfishing had been banned for years (gill netting and line fishing had been banned less than 6 months before the study). He surveyed 1 reserve site and 1 similar non-reserve site, and found higher densities of 11 targeted fish species at the reserve site. Many of these species had higher modal sizes within the reserve as well.

3. Bennett and Attwood (1991) monitored catch-per-unit-effort (CPUE) for 10 species targeted by line fishing at one site within a 46 km longshore X 5 km offshore reserve on the South African coast (the researchers were allowed to fish within the reserve). Six of the dominant 10 species caught showed higher after establishment of the reserve.

4. Buxton and Smale (1989) compared 3 rocky reef sites within a 60 km longshore X 5 km offshore reserve in South Africa to one heavily fished unprotected site. They compared numbers and size of three species of sparids that were targeted by a line-fishery. Two of the 3 species were significantly denser, and 1 of them was larger within the reserve.

5. Castilla and Duran (1985) and Moreno *et al*. (1986) monitored populations of "loco" gastropods in two small reserves along the Pacific coast of Chile. Castilla and Duran documented an increase in density of locos, and both studies recorded increases in size of locos within the reserves following protection, as well as dramatic community-level changes in habitat as the predatory snails reduced the density of herbivorous gastropods, allowing rich stands of algae to develop. These studies are interesting examples of secondary effects of protection. The thick stands of algae have transformed the intertidal reserves into very different communities; it is not clear from the studies whether the algal-dominated reserves will continue to support large populations of locos. Further study may show that changes due to protection have resulted in an environment that will not support large populations of the species being protected.

A scientific proof of the effect of a reserve on protected species would require multiple experimental sites within the reserve; multiple control sites outside the reserve; and all sites would need to be sampled both before and after closure of the reserve (Stewart-Oaten 1986; Stewart-Oaten *et* al. 1986). However, as pointed out by Ballantine (1991) scientific proofs are often impossibly burdensome for management decisions. While none of the studies yet published are complete enough to provide the level of scientific proof described above, in aggregate the existing research (Table 1) provides considerable support for the conclusion that, for heavily fished resident species (as opposed to migrants or widely ranging species), marine reserves tend to support denser populations of larger individuals than are found outside reserves.

(b) Enhancement of local catches by spillover There are very few studies that provide data that are directly relevant to this question.

Examples 6-8

6. The only direct test of this idea comes from a study of a coral reef fishery at Sumilon Island in the Philippines by Alcala and Russ (1990). Sumilon was the site of a coral reef reserve for ten years before a breakdown in protection in 1984 resulted in unrestricted fishing within the reserve. While reserve protection was still in effect, catch-per-unit-effort (CPUE) for boats fishing around the island was recorded over a one year period (1983-1984). Similar data were collected over a one year period beginning 18 months after protection failed (1985-1986). The total fishing was very similar during the two periods. **Following the breakdown of the reserve, CPUE declined significantly by 57% for hook and line, 58% for gill net, and 33% for trap fishing.** This decrease occurred despite the larger area available for fishing after the reserve protection collapsed (non-reserve plus the unprotected reserve). Thus, in this single well-studied case the marine reserve was exporting fish to surrounding areas and clearly supported a higher CPUE for local fisheries than was possible without the reserve.

7. Studies have followed tagged animals and clearly demonstrated net movement of animals from reserves into local fisheries (pink shrimp – Klima *et* al. 1986; 1986) (spiny lobsters -Davis and Dodrill 1980, 1989) with strong indications that the reserve-protected recruits substantially supported surrounding fisheries.

8. Craik (1991 ms) reports that trawlers operating in the Great Barrier Reef Marine Park have begun to support closures and to concentrate their fishing along the edges of protected areas. Similarly, W. Ballantine (pers. comm.) reports that the perimeter of the Leigh Reserve is often festooned with the buoys of long-lines and lobster pots - apparently placed to catch spillover from the reserve. A. MacDiarmid (pers. comm) has had spiny lobsters he tagged within the Leigh reserve caught by fishermen outside the reserve. These anecdotal reports suggest that spillover is occurring, but should be considered very tentative observations pending further study.

Whether protected individuals move across reserve boundaries and contribute significantly to local fisheries is even harder to prove than the within-reserve changes discussed above under **(a) Responses to protection.** To prove scientifically that a reserve significantly contributed to local fisheries requires the same experimental design described above, with sites inside and outside a reserve sampled before and after protection, but with the added difficulty of measuring catch per unit effort (CPUE) in fisheries that may show considerable variability related to establishment of the reserve. An alternative would be to tag animals both within and outside a reserve; estimate the net movement of fishable animals across the reserve borders; and quantify the net contribution of the reserve to local fisheries. Neither type of study has been done satisfactorily.

In summary, there are limited data to use in evaluating the hypothesis that species protected within a reserve will move across the reserve borders and enter local fisheries. What data do exist support the hypothesis. Despite the small amount of available data, there are good reasons, based on what is known of fish movement and behaviour, to expect that spillover will occur. However, accurate prediction of the amount of spillover expected for a particular species from a particular reserve is, at present, impossible.

3.1.2 Advantages and limitations of spillover The spillover of fishes from a reserve (if it occurs) will be a localised effect; vessels fishing along reserve boundaries may see increased catches. This could aid the local economy and encourage local public support for the reserve. Since major objections to establishment of reserves may be raised by the fishing communities whose fishing area will be reduced, the potential for increased catches through spillover may increase local support for reserves. Johannes (1978, 1982) pointed out that successful enforcement of a reserve depends upon support among local fishermen. Increased local catches due to spillover may provide a strong incentive to the local fishing community to help with enforcement of the reserve.

Spillover from a reserve will probably not demonstrably increase catches other than very near the reserve boundaries. This is because the amount of spillover from a reserve is limited and will be a function of (non-larval) production within the reserve (Polacheck 1990). Such production is ultimately limited by the size of the reserve and if the limited production of a reserve is spread over too large an area (by individuals emigrating large distances) it is unlikely to be significant. These ideas are developed further in Polacheck (1990) and Carr and Reed (in press) (summarised in Examples 10 and 17 below). An exception to this rule is juvenile emigration from recruitment or nursery habitat protected by a reserve. Large numbers of juveniles may emigrate from a "nursery" reserve, and their eventual contribution to regional fisheries will not be limited by production within the reserve (Davis and Dodrill 1980; 1989, and Gitschlag 1986)

3.1.3 Design considerations for spillover reserves

(a) Size A reserve must be large enough to retain a large proportion of the protected individuals within it for long enough for the effects of protection (increased size, density, or fecundity) to be realised (Polacheck 1990). While nearly any reserve may provide some level of such protection, the effectiveness of such a reserve can be greatly increased if we know the movement patterns of species targeted for protection.

> **Example 9**
> 9. In a study of the Key Reserve in Florida, Hunt (1991) found that spiny lobsters left the small (0.5 km^2) core area of the reserve where they were completely protected and each night foraged out over a much larger surrounding area where they were captured by divers and traps. Even those lobsters that consistently sheltered within the reserve by day received minimal protection because the reserve did not include the nighttime foraging range of the lobsters.

Pelagic or migratory species may be difficult to protect in small coastal reserves but may benefit from protection within very large offshore "open water" reserves. In contrast to pelagic species, many reef fish and shellfish have limited home ranges or movement patterns and could easily gain protection in coastal marine reserves, although even for reef fishes the range of movement varies greatly for different species (Plan Development Team 1990). The size of reserve needed to protect a species will depend on individual movement rates (daily, seasonal, migratory) and fishing pressure outside the reserve (Polacheck 1990). In addition, movement across reserve boundaries is likely to change following protection as densities and individual size of protected species increase within the reserve. Higher densities within the reserve may well result in higher than predicted rates of movement as crowding and competition for food lead many individuals to emigrate or travel further afield in search of food. Estimates of individual movement based on studies outside reserves (or prior to protection) should be considered conservative in terms of planning reserve size.

A modelling analysis of reserve size, movement rate and fishing pressure by Polacheck (1990) provides the best guidelines to date on the effect of movement rate on protection provided by a reserve.

Example 10
10. Polacheck (1990) uses a Beverton and Holt (1957) model with two components -a reserve population and a fished population outside the reserve, and calculates yield per recruit and spawning stock biomass per recruit as functions of reserve size and movement in and out of the reserve. His results are a first step toward estimates of the size of reserve needed to achieve a desired level of protection, and of the amount of reduction in fishing mortality we might expect from such a reserve. He shows that very substantial increases in egg production (measured as spawning stock biomass) can occur in a reserve if movement is low (i.e., little spillover) and fishing mortality outside is high. The results are extremely sensitive to movement rate (spillover), and he stresses the need for greater knowledge of fish movements. He concludes that small increases in catch (measured as yield-per-recruit) from a fishery can occur despite the closure of a portion of the fishable area in a reserve, but that this will only occur in specific circumstances, and that the main benefit of reserves will be to increase egg production (spawning stock biomass).

(b) Shape A high perimeter : area ratio will increase spillover across the reserve border (Buechner 1987) (Figure la). However, protection is lessened by spillover (if many fish leave the reserve and are caught), so designs to enhance spillover must be subordinate to, or balanced against, making the reserve large enough to protect the stock.

Recruitment of larvae to a reserve will depend on many aspects of the habitat and hydrography of the area protected. However, for reserves of the same total area, recruitment from the plankton will tend to be a function of the dimension of the reserve that intersects the prevailing currents (Figure lb). If a reserve protects settlement or recruitment habitat (for example, a reserve protecting the bryozoan "coral" beds described as a nursery to several species of fish; Jones 1992), then orienting the reserve so that it intersects the most current possible should tend to increase recruitment. An alternative design might include corridors or fingers of settlement habitat that extend out from the body of a reserve perpendicular to the prevailing current, which would serve as "collectors" of recruits for the main reserve (Figure lc & d). If, for example, a goal of a particular reserve were to increase recruitment of species that settle in floating algae (Carr 1989; Kingsford and Choat 1985) the "collector" area might be modified to include a series of surface buoys to entangle drifting algae (Figure 1d).

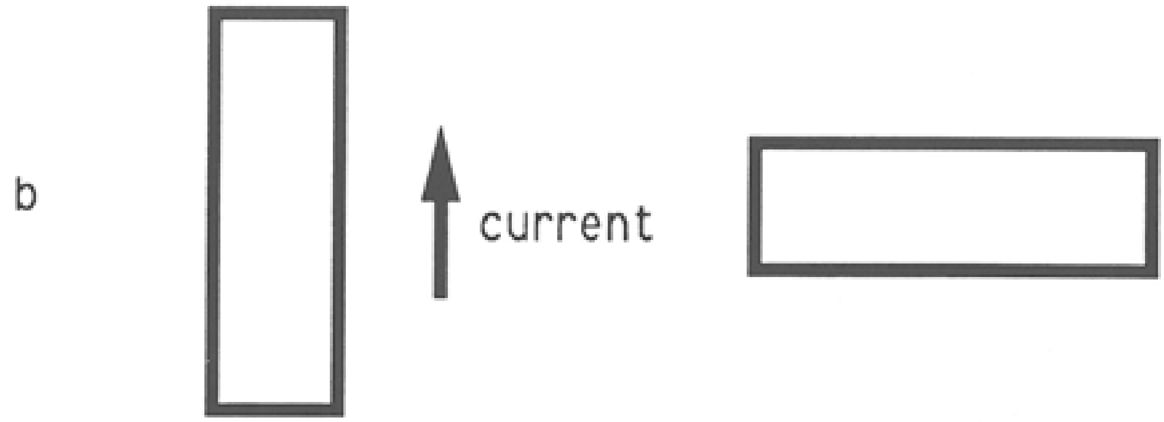
To be effective, a reserve must extend into deep enough water to protect a species that seasonally (or with greater size or age if those sizes are vulnerable to fishing) migrates from shallow to deep water, in which case the reserve must protect the stock until it is beyond the reach of existing (or projected) fisheries. The Plan Development Team (1990), in planning marine reserves for the U.S. southern Atlantic fisheries, have suggested sites that extend offshore to the 150 fathom depth contour to protect deep-living species.

(c) Location To enhance local fishing, a reserve should:

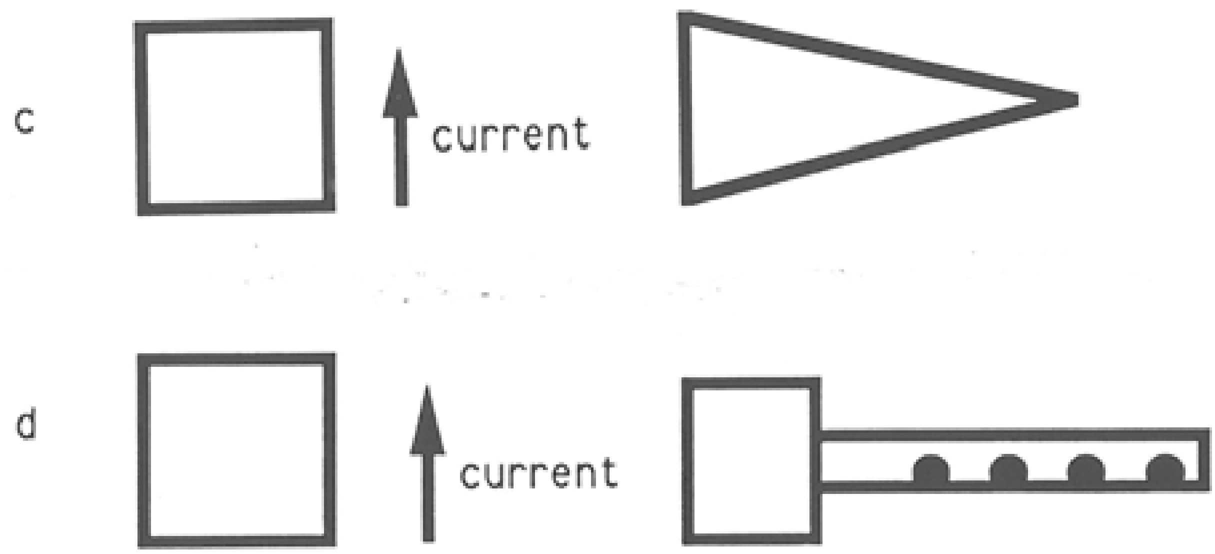
- Be within reach of fisheries

- Include recruitment habitat or substrate (nursery grounds), or be close enough to receive recruits from nursery grounds (which may require protection as well)

a The left figure has a lower perimeter : area ratio, and will tend to result in less spillover. (This is independent of current direction).



b The left figure will tend to collect fewer planktonic larvae, since its dimension intersecting the current is less than that of the right figure.



c and **d** These figures combine the ideas of **a** and **b**. The right figures have extensions of settlement habitat that intersect the prevailing current, and would tend to have greater recruitment from the plankton than the left figure. The dots in **d** are the surface buoys discussed in the text.

Figure 1 Examples of reserve shapes. All figures represent reserves that enclose similar habitat and have the same total areas.

- Have juveniles in many size/age classes which indicates a recent history of good recruitment (Grange 1990) or with a fishery history of consistent production, and

- Be subject to long-term regional control to protect the reserve, its nursery areas, and the routes of migration from nursery to reserve.

External threats to a reserve may include changes in the immediate coastal watershed (pollution, siltation), coastal development altering longshore drift of sediments, and dredging of sea-bottom destroying nursery grounds or migration routes from nursery to reserve.

3.1.4 Species considerations for spillover reserves The species that are most likely to show dramatic responses to protection in a reserve are those that have limited ranges of movement and whose age and size distributions have been strongly reduced by fishing pressure. These species will usually have relatively long lifespans and the maximum historical size is probably much larger than what is commonly caught today. New Zealand examples might include paua (*Haliotis iris*), blue cod (*Parapercis colias*), red moki (*Cheilodactylus spectabilis*) and groper (*Polyprion oxygeneios*). Rock lobsters (*Jasus edwardsii*) have long lifespans and were caught at much larger sizes historically, but it is not clear how their movement patterns might affect protection. Rock lobsters were expected to show minimal protection from the reserve at Leigh because they migrate through that area and were not expected to take up residence (W. Ballantine, pers. comm. 1992). However, it appears that many large lobsters have become residents of the reserve (MacDiarmid ms), so predictions of how rock lobsters might respond in other potential reserves are premature.

Daily movement studies of reef fish are quite limited and no relevant New Zealand examples were found. Longer term tagging studies have generally found that many reef fish species show high fidelity to particular reefs or sites. Most individuals show little or no movement, with a small percentage of individuals moving long distances (Plan Development Team 1990; Crossland 1982a,b).

A number of fishery species are known to undergo migrations associated with spawning. Hoki (*Macruronus novaezelandiae;* Murdoch, in press) and orange roughy (Hoplostethus atlanticus; Robertson *et al.* 1984) both migrate to (or aggregate at) specific spawning sites where they are heavily fished. For species like these the pattern of fishing pressure must be considered. Will protecting a portion of the spawning area provide adequate protection, or would stocks be heavily fished when dispersed or migrating outside the reserve? To protect these stocks would a reserve need to be large enough to include spawning, non-spawning, and migration habitats?

Many shallow water species move to deeper water as they get older, or to spawn (Davis and 1980; Miller and Giebel 1973). These species might be relatively easily protected by extending reserve protection offshore into deep enough water to include such movements.

Interactions between individuals or species may limit the effect of a reserve. Particular species may not coexist (Diamond 1975) or may have conflicting habitat requirements (e.g., sea urchins that consume macroalgae are poor candidates to coexist with fishes that require macroalgae; Carr and Reed, in press). Large individuals may restrict recruitment into the reserve through protecting large territories or through cannibalism of juveniles. Alternatively, the presence of adults may enhance the recruitment of juveniles by modifying the habitat, providing refuge for recruits, or by acting as, or producing, a cue for larval settlement (Wilson 1968; Tegner and Dayton 1977; Highsmith 1982; Jensen and Morse 1984).

3.1.5 Research needed to design and manage spillover reserves

(a) Movement studies The primary research need is for studies of the daily, seasonal and ontogenic movements of individuals. The amount of protection that a reserve will provide decreases as the spillover of individuals' increases, and this is important regardless of the purpose of the reserve. How much spillover will occur depends strongly on the movement of individuals within the reserve as well as on reserve size and shape. There is very little information presently available on the daily movements of any fish, and for only a few species are ontogenic, seasonal, feeding, or spawning movements well described. Studies of daily movements and tagging studies (both long and short term), are crucial to gain an understanding of how to best design and use reserves for fisheries management.

(b) Recruitment/juvenile habitat requirements It is important that spillover reserves include any specific settlement or juvenile habitats that a desired species requires (or at least be close enough to nursery areas to receive recruits). Research to describe these requirements is needed. This is discussed further under **3.2.2 Species considerations for larval export**, below.

(c) Community ecology Protection of a highly fished species within a reserve may lead to community-level changes as the species becomes more common and its influence on the community increases (Castilla and Duran 1985; *et al.* 1986). These community level changes may result in a lower long-term production of the protected species (see Example 5 above). Inter-and intraspecific interactions may restrict the species that can coexist within a reserve, or may decrease (or enhance) the effect of a reserve as discussed under **3.1.4 Species considerations for spillover reserves**, above. Studies of both the autecology and the community ecology of those species which will be protected will help in the design and management of reserves. Specific topics of immediate interest include:

- Patterns of territoriality or space requirements (shelter holes, specific microhabitats) that may limit increases in density.

- Conflicts in resource requirements between species of interest such that a reserve managed for one species will be inhospitable to a second desired species.

3.2 "Larval export"

(The enhancement of regional fisheries by the export of larvae from a reserve.)

Another way in which marine reserves can be used for fisheries management is by being sources for the export of larvae to surrounding fishery stocks. Larval export from reserves has the potential to increase greatly the stability and sustainability of heavily impacted fisheries (Plan Development Team 1990; Carr and Reed, in press). However, the significance of this effect will be very dependent on the species involved, the fishing pressure they receive, the size of the reserve, and the local and regional current patterns. In addition, because of the difficulties in the research required, it will be difficult to determine whether the larvae produced within a reserve are substantially augmenting any particular fishery.

As in the discussion of spillover, the enhancement of regional fisheries by larval export has (at least) three separate aspects:

(a) Will the larvae produced within a reserve make a significant addition to the regional production of larvae?

(b) Will the larvae be transported to an area where they can recruit to a fishery of interest?

(c) Is larval settlement limiting for the fisheries of interest?

(a) Will the increase in larval production be substantial? The larger individuals and higher densities of protected species within a reserve can produce large, in some cases very large, numbers of planktonic larvae (Davis and 1980; Plan Development Team 1990). The fecundity of a female fish or shellfish often increases dramatically with increasing size. Since reserves tend to have both higher densities and larger individuals, the production of eggs from within a reserve has the potential to be very substantially greater than production from unprotected populations outside the reserve. MacDiarmid (ms.) estimates that the lobsters within the reserve at Leigh produce about 12 times as many eggs as are produced in a similar-sized area outside the reserve.

Examples 11-12

11. Plan Development Team (1990) present an example of the Atlantic red snapper. (*Lutjanus campechanus*). A fully grown female (61 cm long), such as would be common within a reserve, can produce 9,300,000 eggs. This is as many eggs as would be produced by 212 females 42 cm long!

12. A similar calculation for the New Zealand snapper (*Chrysophrys auratus*) suggests that from 15 to 74 females of 25 cm length would be needed to equal the egg production of one 50 cm female (based on data from 1977).

Whether the larvae produced within a reserve are a significant addition to the regional production of larvae depends (in part) on how strongly the species has been "recruitment overfished", that is, how much fishing pressure has reduced the production of eggs and larvae (spawning stock biomass). One measure of this comes from egg-per-recruit (EPR) fishery models (Annala and Breen 1989). EPR values present an estimate of egg production for a fished stock as a percentage of the egg production estimated for an unfished stock. EPR estimates for New Zealand fisheries are about 18% for paua (*Haliotis iris*; Schiel and Breen 1991) and as low as 1-2% for heavily fished rock lobster stocks (*Jasus edwardsii*; Annala and Breen 1989) Theoretical and empirical studies suggest that when estimates of "recruitment overfishing" (spawning stock biomass or EPR values) fall below 20% (Goodyear 1989) or 25% (Annala and Breen 1989) the fishery is in danger of collapse.

EPR values can also give a rough estimate of the increase in egg production that might be realized within a marine reserve. Based on the estimates above, it can be suggested that a reserve might be expected to produce 5 or 6 times as many paua larvae per area and up to 100 times as many lobster larvae per area as unprotected populations. In the extreme case of a fishery that has reduced the size of individuals to below the size of sexual maturity (the Karitane concession for rock lobster may be an example of this), there may be little or no reproduction occurring in the local stock and recruitment must rely on long-distance transport of larvae from stocks under less fishing pressure.

Recent research has also shown that the fertilization success of some (possibly many) invertebrates depends on how close together individuals are when they spawn (Pennington 1985; et al. 1991). Since fishing reduces density and thus tends to increase the distance between individuals, heavily fished invertebrate species may be reduced to densities at which little fertilization occurs. [This would be most likely to be important for species like paua (*Haliotis iris*) and urchin (Evechinus chloroticus), that do not aggregate to spawn, and less likely to be important for species like rock lobster (*Jasus edwardsii*) that pair for reproduction.]

When fishing pressure has greatly reduced the size or density of reproductive adults (spawning stock biomass), the larvae produced by the dense population of large individuals within a reserve may provide a very great increase in the regional production of larvae. These larvae will be transported by currents and may increase recruitment into regional populations outside the reserve.

I have found no information that specifically looks at spawning stock biomass for New Zealand species. In lieu of such specific measures, the recent history of recruitment to a fishery may give a useful look at whether the existing spawning stock is sufficient to support the fishery. If the numbers of small recruits is consistently high, or if several year classes are recognizable in size-frequency analyses, then it is less likely that spawning stock biomass is a limiting factor. If new recruits are uncommon and size-frequency analyses show few or no small size (age) modes, then it appears more likely that the increase in spawning stock biomass provided by a reserve may have a beneficial effect. [There are long-lived species for which recruitment may naturally occur rarely -for such species lack of recruits gives little evidence for recruitment limitation. The above discussion is a very simplistic look at recruitment limitation, and fisheries scientists should be consulted for proper analyses for species of interest.]

(b) Will the larvae be transported to a fishery of interest? Whether the larvae produced within a reserve recruit to any fisheries of interest will depend in part on where they are transported to by currents. The ultimate destination of planktonic larvae will depend on:

- The larval lifespan (see **3.2.2 Species considerations for larval export**, below),

- The direction and speed of currents transporting the larvae, including eddy events, short-term upwelling jets, and windrow formation (which are poorly understood for most New Zealand regions; R. Vennell pers. comm.), and

- On species-specific larval behaviour, which may influence speed and direction of travel through vertical migration (Boehlert and Mundy 1988) and orientation to internal waves and windrows (Zeldis and Jillett 1982; Shanks 1983; Jillett and Zeldis 1985; Kingsford and Choat 1985).

(c) Is larval settlement limiting the stock size of the species? This question is one aspect of the larger problem of stock-recruitment relationships. This problem has received a great deal of attention from fisheries scientists, but stock-recruitment relationships have proved very difficult to demonstrate (Beverton and Holt 1957; Cushing 1977). It is important to remember, though, that these studies do not indicate that stock-recruitment relationships do not exist, only that they are very difficult to demonstrate. There are good logical reasons to expect that stock-recruitment relation-ships do exist for most species at some level. A more useful question is: Is production of larvae correlated with recruitment in a tight-enough relationship to expect that the increase in larval production due to a reserve will be reflected in substantial increases in regional recruitment? Unfortunately, for most species this is not known. For the purposes of management, the number of recruits entering a fishery may give an initial estimate of whether a stock is recruitment limited (discussed above under **(a) Will the increase in production be substantial?).** Stock-recruitment problems have been reviewed by Rothschild (1986).

3.2.1 Existing data regarding larval export from reserves No studies were found that were designed to test the idea that larvae from a reserve recruited into regional fishery stocks outside the reserve. This is a difficult research problem, and it will be extremely difficult to prove that larvae produced within a reserve are substantially increasing recruitment into regional fisheries. Tracking the larvae produced within a reserve will be problematic (discussed below under **3.2.5 Research needed to design and manage larval export reserves**). Our ability to predict the transport of larvae by currents is very limited, and recruitment is known to be extremely variable for many species - making any cause-and-effect argument between increased recruitment and the existence of a reserve very tenuous.

Data do exist, however, that demonstrate that fishing often reduces the reproductive output (spawning stock biomass) of exploited stocks (Plan Development Team 1990; and Goodyear 1989), and reserves do provide sites of high egg or larval production (Davis and Dodrill 1980, MacDiarmid, ms). Given these data, it appears that marine reserves may have very great potential for increasing recruitment into fisheries for which production of eggs or larvae is limiting.

One study inadvertently tested the hypothesis of larval export from a de-facto reserve for abalone (paua):

Example 13
13. Tegner (in press) transplanted over 4000 adult green abalone to a region of the California coast where they existed historically, but are now very scarce. All the transplants were placed in a localised area, creating a de facto reserve with natural

densities surrounded by large areas with extremely low densities. After four years, a survey of the surrounding areas up to about 8 km away discovered abalone recruits at higher than expected densities. While the study design does not rule out the possibility of unexpected natural recruitment to the area, it appears likely that larvae exported from the "reserve" did increase recruitment to regional populations outside the reserve.

In summary, the export of larvae from reserves to augment regional fisheries has great potential, and appears logically feasible, but is almost entirely unproven. It's only great benefit will be to fisheries that are settlement limited, and its success will depend on many difficult-to-predict factors that effect larval transport and recruitment. Despite these limitations, for certain fisheries larval export from reserves may have the potential to greatly augment recruitment over large regions.

3.2.2 Species considerations for larval export

(a) Specific requirements The species requirements described above (**3.1.4 Species considerations for spillover reserves**) are also very relevant to larval export reserves. In addition, larval export will be most effective for species with high fecundity and, if possible, a relatively short larval lifespan. A short larval lifespan limits the region over which an effect may occur, which increases the chances of the there being a substantial effect within that region. Species with long larval periods may be able to substantially augment recruitment over large areas if their fecundity is great enough: for less fecund species, it is probably preferable if their larval period is limited as well. New Zealand species that might benefit from larval export reserves are limited, but rock lobster (*Jasus edwardsii*), orange roughy (*Hoplostethus atlanticus*), and paua (*Haliotis iris*) are clear candidates for consideration. Rock lobsters have the complication that larval lifespan is extended (10-20 months) and this decreases, but does not disprove, the expectation that their larvae will recruit to fisheries of interest.

(b) Dispersal distance and direction The eventual destination of larvae exported from a reserve depends (in part) on how long they spend in the plankton, and where the currents carry them in that time. Larvae of New Zealand fisheries species have planktonic periods that range from a few days (paua; Tong et al. 1987) to from 10-20 months (rock lobster; Booth et al. 1990) with a wide range in between. The size, placement, and number of larval export reserves needed to support a fishery will be very dependent on the direction and distance of larval transport. These ideas are more thoroughly discussed in Carr and Reed (in press; summarized below in Example 15).

Larvae of many species have been collected far from the nearest source of adults, and may disperse over large distances (Scheltema and Williams 1983). This tends to reduce the likelihood of substantial numbers of larvae reaching a particular stock, but can have advantages for the design of larval export reserves, since for widely dispersing species reserves can be widely distributed (Hardwick et al. 1991; below).

Example 14

14. Hardwick *et al.* (1991) describe an investigation by the California Department of Fish and Game of the usefulness of marine reserves for larval export to increase the recruitment of rockfishes (Scorpaenidae: Sebastes) to nearshore reef areas. Rockfish are long-lived, and move between reefs very little as adults. They have been heavily fished and their spawning biomass appears to be low. After looking at voluminous data on the regional distribution of rockfish larvae, Cal. Dept. F. & G believes that

"spawning adults residing in a few, relatively small refugia may be able to supply young fish to a large area".

[This was extracted from a talk and abstract from the meeting of the American Fisheries Society in 1991. I have written to Dr Hardwick requesting more information or reprints, but have received no response. This study might be worth further follow-up.]

3.2.3 Design considerations for larval export reserves

(a) Size The size of reserve needed will depend on the larval production of the reserve relative to non-protected regions, the pattern and rates of movement of the species, the fishing pressure, and the size of the region over which larval export is expected to operate (the "replenishment area" of Carr and Reed, in press). These factors are included in modelling analyses of this problem by Polacheck (1990) (Example 10, above), and Carr and Reed (in press) (Example 15, below).

Example 15
Carr and Reed (in press) explore ideas about the size and design of larval export reserves. They use a conceptual model to predict the size of reserve needed to maintain a hypothetical fishery, and discuss strategies of reserve placement and number based on estimates of larval dispersal distances. The paper explores many of the concepts needed to develop larval export reserves. A second part of the paper describes different patterns of reproduction and larval-life-history found in reef fishes and they suggest different reserve designs to reflect these differences.

(b) Location The location of a reserve will be a crucial factor in determining its success at exporting larvae to regional fisheries. Many factors must be considered in determining the best location for a larval export reserve:

- Reserve location must be determined after consideration of larval lifespan, and transport directions and distances ("replenishment area"). Many possible sites for reserves will probably export larvae into areas or situations where successful recruitment is unlikely. For instance, a reserve located near one end of a species' geographic range may, depending on current direction, export larvae into, or out of the range of the species.

- A reserve located upstream of an upwelling jet or an offshore current associated with a headland may lose many of its larvae as they are swept offshore (Ebert and Russell 1988). Alternatively, this may be a normal occurrence for some longer-lived larvae, and they may possess the means of returning to nearshore areas to settle (Zeldis and Jillett 1982; Shanks 1983; Kingsford 1990).

- A reserve within a bay or sound may export larvae mainly to nearby locations due to retention of water masses within the enclosed area (Levin1983).

- A reserve located upstream of a pollution source may have many of its exported larvae killed or damaged by the pollution (Kingsford 1992; Raimondi and Schmitt, in press; both in Examples below).

Examples 16-17
16. A recent paper by and Schmitt (in press) has shown that abalone larvae suffered elevated mortality when suspended within a plume of "produced water" which was

being dumped into the ocean from an oil facility. In addition, the percentage of the survivors that successfully metamorphosed when later challenged with suitable settlement substrates was significantly less than for control groups.

17. In a study of fish larvae, Kingsford (1991) has found greater numbers of larvae with deformities in samples collected within a plume of urban sewage pollution than in control samples taken outside the pollution plume.

Many invertebrate larvae settle in response to very specific chemical cues (reviewed in Crisp 1974; Morse 1990). If pollution disrupts their ability to properly respond to those cues, then the larvae either will not settle, or may settle in habitats or environments where they cannot survive. Thus a pollution source, even one which causes little or no direct larval mortality, may be affecting the larvae in ways that greatly reduce their chances of successfully recruiting. In these ways pollution sources that impact (or are downstream of) a marine reserve may greatly reduce the success of larval export from the reserve.

If a network, or series, of reserves is planned, they should be located such that each reserve can supply larvae to the next reserve, that is, each reserve should be within the "replenishment area" of other reserves. This will tend to buffer the entire system against recruitment failure.

3.2.4 Advantages and limitations of larval export reserves The main advantage of this type of reserve is that, for species and situations in which it works, it could have a very substantial effect over a large region. Other benefits are discussed below under **3.3 Maintenance of genetic diversity...**, and **3.6 Buffer against recruitment failure.**

There are many limitations for larval export reserves:
(a) Specific requirements For larval export from a reserve to substantially augment regional recruitment will require a species for which settlement is limiting, a recruitment relationship exists (even though it may be undetectable), and spawning stock biomass is greatly reduced (presumably by fishing pressure). New Zealand examples of species that fill these criteria may be limited (see above under **3.1.4** and **3.2.2 Species considerations** . . ., for several possibilities).

(b) Limited local effect A reserve designed to export larvae may have little or no local effect (except spillover, discussed above), since the larvae produced within the reserve will be transported some distance away by the prevailing currents and will probably recruit (if anywhere) to populations distant from the reserve. Thus justification of this type of reserve may require a regional, or even international perspective and it may be difficult to gain local support.

(c) Dependent on recruitment habitat or substrate outside the reserve Many important fishery species require specific habitats or substrates for larval settlement and/or juvenile "nursery grounds" (Fairweather 1991). Recruits of certain species of flatfish are almost exclusively found within estuaries (Roper 1979; Roper and Jillett 1981). Bryozoan "coral" beds have been identified as nursery grounds for tarakihi (*Cheilodactylus marcopterus*), snapper (*Chrysophrys auratus),* and John Dory (*Zeus* *faber*) (Vooren 1975; Bradstock and Gordon 1983). Macroalgae is required as settlement and juvenile habitat for both *Pseudolabrus celidotus* in New Zealand (Jones 1984a, b) and Sebastes rockfish in California (Carr 1989).

These studies point out the potential importance of recruitment habitat or nursery grounds. The larvae exported from a reserve will have little effect if the settlement substrates or juvenile nurseries they require have been destroyed, for example by trawling (Jones 1992), siltation (Samoilys 1988), pollution (Examples 16 and 17; above) or reclamation of estuaries. Reserves to protect adults and export larvae could become empty monuments to our limited vision if recruitment needs are not protected as well.

(d) Subject to all the vagaries of natural recruitment Recruitment of planktonically dispersed marine organisms is notoriously variable both over time (Sissenwine 1984) and space (Gaines and Roughgarden 1985; Sutherland 1990). The variability reflects poorly understood complexities of larval behaviour and both local and regional hydrography. Larval responses to surface slicks and internal waves (Shanks 1983; Kingsford and Choat 1985; Kingsford *et al* 1991), vertical migrations (Boehlert and Mundy 1988) and larval association with flotsam (Kingsford and Choat 1985), can be adaptive responses that, at least occasionally, deliver larvae to the habitats they require, but our understanding of these factors and their variability is very limited. Large-scale hydrography such as the Tasman Current, gyres, upwelling jets, and tidal currents vary in occurrence, speed, and position (Heath 1985; R. Vennell, pers. comm.), and we rarely understand either the causes or consequences of such variability.

Smith and Francis (1991) have reported that snapper recruitment success around the North Island of New Zealand reflects El Nino-Southern Oscillation patterns. Francis (in press) has found a similar correlation between recruitment and El Nino patterns for sub-tropical and tropical reef fishes. Many New Zealand species may show similarly variable recruitment in response to variations in both small and large-scale hydrography, but recruitment of few species has been studied sufficiently to recognize any such response. This variability does not suggest that larval export will not work, since despite such overwhelming complexity, most species manage to recruit often enough to maintain their populations in spite of intense fishing pressure. It does, however, suggest that the contribution of larvae from any particular reserve will vary over time in ways that are, unpredictable.

3.2.5 Research needed to design and manage larval export reserves The studies described above under **3.1.5 Research needed to . . . spillover reserves**, are also very relevant for larval export reserves. Studies of individual movement are needed, since little increase in larval production will occur if a reserve is too small and the normal movements of individuals take them outside the reserve and expose them to fishing. Settlement and recruitment or nursery requirements must be understood because the larval production from a reserve will be wasted if required settlement substrates and recruitment or nursery habitats are not available in the area to which larvae are exported.

In addition to the research already described, a number of research questions or topics are particularly relevant to larval export reserves:

(a) Is larval production limiting? The design of larval export reserves will benefit from any studies that help to answer the question posed earlier: "Is production of larvae correlated with recruitment in a tight-enough relationship to expect that the increase in larval production due to a reserve will be reflected in substantial increases in regional recruitment?" Since the problem of stock-recruitment relationships has confounded fisheries researchers for decades, it might be wise to focus efforts on determining whether populations are limited by the number of settlers or small recruits. This research could reduce the number of species being considered for management through larval export reserves. For example, if the number of settlers or new recruits appears to be predictably high, then the species is less likely to show a substantial response to an increase in larval production. Efforts to answer the broader question of stock-recruitment relationships could then be focused on species more likely to benefit from larval export reserves, i.e., species for which the numbers of settlers or small recruits appears to be limiting population numbers.

(b) Larval transport studies The location, size and number of larval export reserves needed to support a fishery will be very dependent on the direction and distance of larval transport in the plankton. Types of research that will help predict the location and size of the "replenishment area" to which larvae will be exported from a reserve include those described below.

Current/ hydrography studies Larval transport can be studied using current drogues (Lobel and Robinson 1986; McShane *et al* 1988) or, less expensively, small, passive driftcards or drift bottles. New Zealand and the southern oceans have a long history of drift card and bottle studies (Brodie 1960; Jenks *et al.* 1982). These can be very informative if used to answer specific questions regarding larval transport. To imitate more accurately the larval transport of certain larvae, current drogues have been developed that are programmable to vertically migrate in a pattern similar to the pattern shown by the larvae (Wolcott 1989).

> **Example 18**
> 18. Tegner and Butler (1985) used drift cards released near an island population of green abalone (*Haliotis fulgens*) to determine whether larvae released by that population were likely to be able to repopulate regions of the mainland coast. Based on return times from cards collected on the mainland coast, they concluded that transport time from island to coast was greater than the time between spawning and the end of the larval "competent period". Based, in part, on this study Tegner transplanted a population of green abalone to the coast (described in Example 13, above).

Studies of regional oceanography and hydrography (Heath 1985) add to our understanding of transport mechanisms, especially if attempts are made to link large-scale processes to smaller-scale events and short-lived phenomena that may be crucial to larval transport (Zeldis and Jillett 1982; Jillett and Zeldis 1985; Murdoch 1989; Murdoch et al. 1990). More recent efforts to produce detailed descriptions of large-scale current patterns from analyses of satellite imagery (R. Vennell, pers. comm.) may facilitate descriptions of the linkages between regional and local processes.

Modelling of current transport processes Mathematical modelling of current processes can be used to generate predictions regarding larval transport (James, et al., in press). These estimates of larval transport can be used to predict both effective locations for larval export reserves, and the likely "replenishment areas" of those reserves (James *et al.*, in press). These methods are being used extensively in management of the Great Barrier Reef (Craik 1991). While these models have generated clear predictions, and those predictions are being used in management decisions, it is not yet clear how accurate the predictions are.

Larval marking and tracking Studies that could follow the larvae produced at a potential reserve site through planktonic transport to settlement, or recognize recruits that had been spawned from a particular site could add significantly to our knowledge of larval transport patterns. Several techniques have been developed recently that may allow such tracking of marked larvae or recognition of recruits. A method of permanently marking large numbers of larvae (Rowley 1992) and the creation of large numbers of fluorescent molecular markers (e.g., Molecular Probes Inc., Eugene, Oregon, USA), few of which have ever been tested for field use, suggest that there are untested techniques that may allow us to tag, and possibly follow, larvae in the field. Genetic tags (Smith *et al.* 1981; Burton and Swisher 1984; Grosberg 1987), discussed in a review by Levin (1990) are another rapidly developing field that may allow recognition of recruits spawned at particular sites. These methods may allow detailed studies of small-and large-scale larval transport processes.

Research that improves our ability to understand or predict larval transport will improve our ability to design and manage larval export reserves.

(c) Autecology and community ecology of species of interest There are many ways in which the effectiveness of larval export reserves may be diminished by intra-or inter-specific interactions within them:

- Is the population structure within the reserve likely to develop in a direction that limits reproduction, e.g., excess males or "post-reproductive" individuals?

- Are egg-laying or spawning sites limited in number or through competition with other species (Breitburg 1987).

- Will established adults severely limit recruitment through aggression or cannibalism?

These are a few examples of ways in which autecology or community ecology may influence the effectiveness of larval export. Any studies that increase our understanding of a species of interest are likely to improve our ability to design or manage reserves.

3.3 Maintenance of genetic diversity and population size/age structure

There are several ways in which marine reserves may help to prevent the degradation of fishery stocks genetic resources:

- **Help to maintain rare alleles** Depletion of stocks does not necessarily greatly reduce a species genetic resources; a small number of individuals can retain over ¾ of a species genetic variance (Polunin 1990). Those alleles that are naturally rare, however, are quickly lost when populations decline, and these may be the very alleles that are helpful during unusual conditions (epidemics, climate change?). Smith *et al.* (1991) demonstrated loss of genetic diversity over a six year period in heavily fished orange roughy stocks. Reserves will help to maintain the full complement of a stocks' genetic resources by maintaining populations under natural conditions of size and density (Polunin 1990).

- **Moderation of fishing pressure selection effects** Reserves will moderate selection for early reproduction/small size caused by fishing pressure. Fishing mortality can be a major selective force on heavily fished stocks, and the direction of selection is expected to be toward earlier reproduction and smaller size (Plan Development Team 1990; Law 1991). For many reasons, a genetic response to fishing pressure is very difficult to demonstrate, yet; despite the difficulties, studies have implicated fishery-caused selection in reductions in the age at maturity of Atlantic Salmon (*Salmo salar*), and decreases in average size of chinook (*Oncorhynchus tshawytscha*) and pink salmon (*O. gorbusha*) (Plan Development Team 1990). Reserves, by allowing protected stocks to develop to full size and age, will reduce the effects of this sort of directional selection.

- **Selection for reduced movement of vulnerable animals** An alternate form of directional selection may develop if reserves protect the major reproductive populations for a stock. Since individual movement (daily, seasonal or ontogenic) may take an individual across the reserve border and expose it to fishing, protection within reserves may select for reduced movement of vulnerable-sized individuals in the stocks they protect. This should only develop in species or stocks in which the majority of reproduction occurs within reserves.

3.4 Providing unharvested baselines to measure harvesting effects

Some fisheries questions can best be answered through research conducted, in part, in marine reserves (for more examples see Ballantine 1991):

- Many fisheries remove top-or mid-level carnivores. What is the effect of this removal on the reef community?

- Fishery species often suffer mortality or injury as by-catch to other fisheries or when undersized. How does this level or type of injury compare to "natural" injury?

- How does the fecundity of an "average" sized fish compare to the fecundity of a very large individual?

These are all questions which can be best answered by comparing fished stocks to unfished stocks. This has often been done by treating as "unfished" those stocks that enjoy de-facto protection by being far from port or otherwise inaccessible. The development of more efficient fishing methods and larger boats has greatly reduced this protection. In order to evaluate the effects of fishing, it is crucial to have an unfished stock for comparison. Marine reserves may provide the only unfished stocks available to provide baseline data against which to measure the effects of fishing.

3.5 Possible trophy fisheries

The full-grown fish protected within a reserve will occasionally wander over the borders of the reserve. This was discussed above under **3.1 Spillover.** A second possible use for this spillover is the development of "trophy" fisheries (Plan Development Team 1990). How many New Zealand fishermen would like a chance to catch a groper of the size seen only in old photographs? How many divers would like a chance to catch a rock lobster that's too big to fit into a goody bag? These sorts of fisheries will never reach a large volume, but may develop into high visibility, very popular recreational activities centred around the perimeters of reserves.

3.6 Buffer against recruitment failure

An unexpected recruitment failure that strikes a heavily exploited fishery may threaten the sustainability of that fishery. Marine reserves will help protect the recruitment supply by maintaining a population of reproductive individuals safe from fishing mortality (Plan Development Team 1990).

> [Plan Development Team (1990) discuss a wide variety of possible social, enforcement, and management benefits of marine reserves.]

4. GENERAL CONSIDERATIONS

4.1 Single-versus multi-species

There is a perception that marine reserves will provide effective protection to all resident species with little need for detailed knowledge of the species and without direct management of populations within the reserve. This is, in many cases, wishful thinking. To protect targeted species effectively, reserves will have to 1) be well designed for the species' needs (at least food, shelter, habitat), which are often poorly known, 2) retain the desired environment despite great changes in the density and size of the protected species that are likely to follow protection. The studies of loco described above (Castilla and Duran 1985; Morenp *et al.* 1986; Example 5) demonstrate this point. Another example is the well-documented overgrazing of algal communities by sea urchins (Ebeling et al; 1985; Andrew and Choat 1982; Scheibling 1984). If a reserve protects both sea urchins and fishes that require macroalgae, how is management to respond if urchins begin overgrazing the algae and threaten to turn the entire reserve into a coralline algae community that supports few fishes and only stunted urchins? There are probably many undescribed examples of sets of species that cannot co-occur in protected situations where one or more species can increase greatly in density.

> [In practice it may be wise to establish a hierarchy of priority for resident species that will be used for management decisions in a particular reserve.]

4.2 Active management and the need for flexible regulation

The problems discussed above point out the desirability of active management of reserves. Management may need to include a variety of options, including allowing selective fishing. If reserves are established under regulations that prevent management of the populations within, we may find ourselves with a reserve designed to protect paua in which paua are scarce and sea urchins have taken over, or a reserve in which a strong recruitment of a long-lived predator has eradicated a desired species.

The need to allow active management creates a difficult problem for the design of reserve regulations. It may be difficult to allow management the flexibility to manage populations while insulating them against the considerable public pressure to manage in a particular manner (i.e., allowing selective fishing). If it is not politically or socially realistic to both allow active management and to prevent public pressure from adversely influencing its use, then it may be advisable to "close" reserves entirely, thereby assuring at least some aspects of protection.

4.3 Terrestrial threats to marine reserves

There are considerable threats to coastal reserves that come not from the sea, but from the adjacent land. Siltation from rivers has damaged protected reefs in Kenya (Samoilys 1988), sewage has damaged reefs in Hawaii (Maragos *et al.* 1985) and organisms along localised areas of the New Zealand coast show high levels of heavy metal accumulation, probably as a result of runoff from terrestrial pollution (P. Mladenov pers. comm.). In addition, coastal pollution can adversely affect marine larvae as described above

(Examples 16 and 17). In many ways, coastal and river runoff can threaten the habitat protected within a reserve.

Interruption or modification of longshore drift can have serious consequences for "downstream" habitats and in this way coastal development "upstream" of a reserve may degrade protected reserve habitats.

While it may be desirable for protection of the reserve to restrict uses of rivers or watersheds that empty into or near a reserve, traditional use and private ownership of coastal land may make such regulations difficult or impossible to establish. Siting proposed reserves offshore of protected terrestrial habitats, or extending terrestrial park areas to include reserves offers an excellent alternative way of protecting reserves from these threats (Batisse 1990; Grange 1990).

4.4 A possible hazard to fisheries

There is potential for reserves to be incorrectly perceived by both the public and by management as solving the problems of overfishing for a particular species. Evaluating how effectively a reserve is augmenting a regional fishery will be very difficult. If, in the absence of conclusive data on performance, a reserve is perceived as being effective, social and political pressure may lead to increased quotas or relaxing of the regulations protecting the fishery. Incorrect assumptions as to a reserves' effectiveness could lead to very severe overfishing of stocks supposedly protected by a reserve (Carr and Reed, in press; for a similar argument applied to fish hatcheries, see Maccall 1989).

5. CONCLUSIONS

There is good evidence that marine reserves are likely to contain higher densities and larger sizes of heavily fished species than are found outside reserves. Many New Zealand fisheries show evidence of "growth overfishing" and will probably respond in this way.

Spillover will probably occur from these reserves and may augment local catches. There are good reasons to expect such spillover, but there is little direct evidence for it, and the magnitude of a possible increase in local catches is impossible to predict. In the one published test of these ideas the reserve at Sumilon Island in the Philippines substantially increased local catches and more than made up for the reduction in fishable area caused by the establishment of the reserve.

Larval export from reserves has the potential to greatly increase recruitment to heavily exploited regional fisheries. There is little proof that this works, but there are good reasons to expect it to work, and plans for these sorts of reserves are progressing worldwide. A substantial effect is probably limited to species which are heavily recruitment overfished, potentially long-lived, and show a strong increase in fecundity with increasing size or age. New Zealand species that fit these requirements appear to be relatively limited, but rock lobster (Jasus edwardsii), orange roughy (*Hoplostethus atlanticus*), and paua (*Haliotis iris*) are clear candidates for consideration. The only published test of these ideas provided reasonably strong evidence that a de facto reserve for green abalone (paua) exported larvae and increased recruitment to nearby areas outside the reserve.

A clear priority for needed research is study of the individual movements and habitat requirements of species of interest. These studies should include daily ambits, migrations and seasonal movements, larval settlement and juvenile habitat requirements. This information is needed to improve the design of reserves whether they are intended to protect stocks, provide spillover, or export larvae.

To design or test larval export reserves we need better knowledge of the local and regional hydrography including currents, gyres, eddies, upwelling jets, and tidal currents, and studies of larval transport through these hydrographic features. These studies should include: satellite imaging of current flow, drift-card and drogue studies, larval behaviour and the length of pre-competent and competent periods, larval settlement requirements, larval marking and tracking, and genetic tag studies.

To estimate the expected spillover from a reserve to nearby fisheries we need better information on the (non-larval) productivity of the species of interest. This may, however, be difficult to measure until a region is protected due to the complicating effects of fishing. After protection, tagging studies that follow the movements of individuals into or out of reserves can provide an estimate of spillover.

6. ACKNOWLEDGEMENTS

I would like to thank the following people for their assistance:
Sue Watson, Marine Science, University of Otago, for making a good start on this project and for conducting some of the original library research.

Philip Mladenov and John Jillett, Department of Marine Science, University of Otago, for commenting on earlier versions of the manuscript.

The staff of the interloan desk, Science Library, University of Otago, for rapidly tracking down a lot of obscure references.

The many scientists I talked with at MAF Fisheries and NZOI for their knowledgeable help.

Andrew Jeffs, Department of Conservation, for his enthusiasm and for his comments on an earlier draft.

7. LITERATURE

In preparing this report I have reviewed over 300 publications. Most of these were not directly relevant, but this was often impossible to determine without reading them. Because much of the literature reviewed was not particularly relevant, I have presented the references in two parts. The first list is **8. References** which is a listing of the publications cited in this report. It is organized so that citations which deal with marine reserves explicitly have their titles printed in **bold** typeface, and those that deal with fisheries or provide background information are in plain typeface. The second list is **9. Bibliography** which lists the remainder of the publications reviewed in the preparation of this report. All bibliographic material is also available as a database with keywords and comments on Pro-Cite MacIntosh format).

8. REFERENCES

Alcala, A.C. and G.R. Russ. 1990. A direct test of the effects of protective management on abundance and yield of tropical marine resources. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* (International Council for the Exploration of the Sea) 46: 40-47. [A.C. Marine Laboratory, University, Dumaguete City, Negros 6200, Phillipines]
Reasonably strong evidence from Sumilon Island reserve that protection increased fish densities within the reserve and that spillover augmented fisheries in local area.

Andrew, N.L. and J.H. Choat. 1982. The influence of predation and conspecific adults on the abundance of juvenile Evechinus chloroticus. *Oecologica* 54: 80-87.

Annala J.H and Breen P.A. 1989. Yield-and egg-per-recruit analyses for the New Zealand rock lobster, *Jasus edwardsii*. *New Zealand Journal of Marine and Freshwater Research* 23: 93-105

Ballantine, W.J. 1991. **Marine Reserves for New Zealand**. University of Auckland, New Zealand: The Friends of the Leigh Laboratory. [University of Auckland, Leigh Laboratory Bulletin No. 25]

Batisse, M. 1990. **Development and implementation of the biosphere reserve concept and its applicability to coastal regions.** *Environmental Conservation* 17: 111-116

Biosphere reserve as applied to coastal zones -argues for combined marine-terrestrial reserves.

Bell, J.D. 1983. Effects of depth and marine reserve fishing on the structure of a rocky reef fish assemblage in the North-Western Mediterranean Sea. *Journal of Applied Ecology* 20: 357-369.

Documents increased size and density of spear-fishing-vulnerable species within a no-spear-fishing reserve (1974-1980). Line and gill-netting allowed until (1979) - 1yr before study.

Bennett, B.A. and C.G. Attwood. 1991. **Evidence for recovery of a surf-zone fish assemblage following the establishment of a marine reserve on the southern coast of South Africa.** *Marine Ecology Progress Series* 75: 173-181.

Size and density effects within reserve. Before/after data. Also some data on fish movements relative to protection effectiveness.

Beverton, R.J.H. and S.J. Attwood. 1957. On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food: Fishery Investigations, Series II Volume XIX. London, Her Majesty's Stationery Office. [Quote from frontispiece "From (this work) a solution can be found to any problem of fishery regulation in the world..."]

The portion of their model relevant to marine reserves is Section 10: Spatial variation in the values of parameters; movement of fish within the exploited area.

Bochlert, G.W. and B.C. Mundy. 1988. Roles of behavioural and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Symposium* 3: 51-67.

Bohnsack, J.A. 1982. **Effects of piscivorous predator removal on coral reef fish community structure**. Cailliet, G.M. and C.A. Simenstad (Eds.) Gutshop '81: Fish food habit studies. *Proceedings of the third Pacific* workshop, Asilomar *Conference Center, Pacific Grove, CA, 6-9 December 1981.*

Looe Key (when spearfishing was allowed) had fewer large piscivores than either of 2 "control" reefs. Also recorded some secondary increases in density of some smaller species on unprotected reef.

Bohnsack, J.A. 1990. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic. **[Referenced under Plan Development Team 1990]**

Booth, J.D., R.J. Street and P.J. Smith. 1990. Systematic status of the rock lobsters *Jasus edwardsii* from New Zealand and *J. novachollandiae* from Australia. *New Zealand Journal of Marine and Freshwater Research* 24: 239-249.

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Suggests perimeter : area ratio for shape considerations. This may be applicable to species becoming vulnerable to fishing during movement outside a reserve.

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Buxton, C.D. and M.J. Smale. 1989. Abundance and distribution patterns of three temperate marine reef fish (Teleostei: sparidae) in exploited and unexploited areas off the southern Cape coast. *Journal Ecology* 26: 441-451.
Evidence for increased density and size within reserve for spp vulnerable to spear-and line-fishing.

Carr, M.H. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *Journal of Experimental Biology and Ecology* 126: 59-76.
Demonstrates the importance of recruitment substrate for successful recruitment of reef fishes. [See also Jones 1984a & b *J. Ex.Biol.Ecol.* 75:257-303]

Carr, M.H. and D.C. Reed. (in press) **Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes.** *Canadian Journal of Fisheries and Aquatic Science.*
Discusses design of refuges for augmentation of larval recruitment to fished stocks. Very useful.

Castilla, J.C. and L.R. Duran. 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos* 45: 391-399.
Reserve increased the size density of locos, but locos are reducing their food (mussels). When the food is gone will the area be an effective loco reserve?

Castilla, J.C. and R.H. Bustamante. 1989. Human exclusion from rocky intertidal of Las Cruces, central Chile: effect on *Durvillaea antarctica* (Phaeophyta, Durvilleales). *Marine Ecology Progress Series* 50: 203-214.
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Overview of GBRMP reserves, 70% of bottom trawled yearly in some areas, anecdotal evidence for spillover of prawns, Plectropomus (coral trout): closed reefs adults denser & larger, juveniles less dense, but no variability or statistics.

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Davis, G.E. 1989. **Designated harvest refugia: the next stage of marine fishery management in California.** *CalCOFI Rep* 30:53-58
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Good discussion of consumptive uses.

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Davis, G.E. and J.W. 1989. **Recreational fishery and population dynamics of spiny lobsters, in Florida Bay, Everglades National Park, 1977-1980.** *Bulletin of Marine Science* 78-88.
Points out importance of nursery refuges, high fishing pressure regionally. Nearly all adults removed from population each year.

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Summary of Tortugas reserve pink shrimp studies.

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Conch more numerous and larger in protected areas, warns that "in the absence of intense ... protection refugia may become the illegal fishery of the unscrupulous".

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Semi-popular, unreferenced article on the selective pressures caused by fishing.

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Early reference to drift tube use to answer specific questions re larvae.

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Reference for larval marking & tracking studies

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Maccall, A.D. 1989. Against marine fish hatcheries: ironies of fishery politics in the technological era. *California Cooperative Oceanic Fisheries investigations Report* 30: 46-48

Excellent warning re using reserves to forestall management

MacDiarmid, A.B. (ms) **Comparison of spiny lobster (Decapoda: Palinuridae) poplations between reserve and fished areas in north-east New Zealand.** Fisheries Research Centre, Greta Point, PO Box 297, Wellington, New Zealand. (Unpublished ms.)

Lobsters larger, much denser, and estimated egg production much higher in reserve.

Maragos, J.E., C. Evans and P. Holthus 1985. Reef corals in Kaneohe Bay six years before and after termination of sewage discharges. *Proceedings of the 5th International Coral Reef Tahiti* 4: 189-194

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Good citation for within-refuge effects, broad changes hypothesized**.**

McCormick, M.I. and J.H. Choat 1987. **Estimating total abundance of a large temperate-reef fish using visual strip-transects.** *Marine Biology* 96: 469-478

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Moreno, C.A., K.M. Lunecke and M.I. Lepez 1986. **The response of an intertidal *Concholepas concholepas* (Gastropoda) population to protection from Man in southern Chile and the effects on benthic sessile assemblages.** *OIKOS* 46: 359-364

Good citation for dramatic, unexpected changes following establishment of reserve. Slow (several year) response of predator (loco), which gets larger, but not more dense, in reserve.

Moreno, C.A., J.P. Sutherland and H.F. Jara 1984. **Man as a predator in the intertidal zone of southern Chile.** *OIKOS* 42: 155-160

Human removal of *Fissurella* leads to higher algal biomass. Does protection eventually lead to reduced production due to overgrazing?

Morse, D.E. 1990. Recent progress in larval settlement and metamorphosis: closing the gaps between molecular biology and ecology. *Bulletin of Marine Science* 46(2): 465-483

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Fissurella larger and more common in accessible areas of reserve than outside.

Pennington, J.T. 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. *Biological Bulletin* 169: 417-430.

Plan Development Team 1990. **The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic.** *NOAA Technical Memorandum.* Dr. J. A. Bohnsack, National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, **33149, USA.**
Very useful technical report on reserves for fisheries management.

Polacheck, T. 1990**. Year around closed areas as a management tool.** *Natural Resource Modeling* **327-354.**
Very relevant. Model that investigates effects of fish movement, fishing pressure and refuge size on the effects of a reserve on catch and spawning stock biomass (larval export).

Polunin, N.V.C. 1990. **Marine regulated areas: an expanded approach for the tropics.** *Resource Management and Optimization* 7(1-4): 283-299
Suggests the replenishment zone idea needs testing.

Polunin, N.V.C. and C. Roberts 1992. **Responses of Reef Fisheries to Area Closure.** [Unpublished final report for funding grant.] [Copy supplied by first author]
Complex results from 2 Caribbean sites and Red Sea site with most targeted species denser and larger within reserves, but with a few species (both targeted and untargeted) denser outside reserves. Higher densities did not appear to be a recruitment response.

Raimondi, P.R. and R.J. Schmitt (in press) Effects of point source pollution on settlement of larvae. *Proceedings of International Produced Water Symposium*.
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Rice, M.A., C. Hickox and I. Zehra 1989. **Effects of intensive fishing effort on the population structure of quahogs, *Mercenaria mercenaria* (Linnaeus 1758), in Narragansett Bay.** *Journal of Shellfish Research* 8(2): 345-354
Two "reserves" closed because of bacterial contamination are compared to a heavily fished site. Reserves have higher densities, larger, older populations.

Roberts, C.M. and N.V.C. Polunin 1991. **Are marine reserves effective in management of reef fisheries?** *Reviews in Fish Biology and Fisheries* 1: 65-91.
Excellent discussion of reserves as fisheries management tools. Focuses on tropical reserves.

Robertson, D.A., P.J. Grimes and P.J. McMillan 1984. Orange roughy on Chatham Rise; results of a trawl survey. *Fisheries Division occasional publication 39.* 19 p. [Ministry of Agriculture and Fisheries, Wellington, New Zealand]

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Community-level response to breakdown in reserve enforcement.

Samoilys, M.A. 1988. **Abundance and species richness of coral reef fish on the Kenyan coast: the effects of protective management and fishing.** *Proceedings of the 6th International Coral Reef Symposium, Australia, 1988.*
Reserves not necessarily resulting in higher diversity, or density. Good example of a long-term, well-protected reserve damaged by river siltation.

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Schiel, D.R. and P.A. Breen 1991. Population structure, ageing, and fishing mortality of the New Zealand abalone *Haliotis iris. Fishery Bulletin U.S.* 89: 681-691.

Shanks, A.L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Marine Ecology Progress Series* 13: 311-315.
Initial reference to internal waves transporting larvae -but see Zeldis and Jillett 1982.

Sissenwine, M.P. 1984. Why do fish populations vary? In May, R.M. (Ed) *Exploitation of marine communities.* Berlin, Springer-Verlag.
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Smith, P.J. and M.P. Francis 1991. Snapper reseeding in Hauraki Gulf: Scientific considerations. *MAF Fisheries, Greta Point, Internal Report No. 172.*

Smith, P.J., R.I.C. Francis and M. McVeagh 1991. Loss of genetic diversity due to fishing pressure. *Fisheries Research 10:* 309-3 16.
Three sites sampled over a 6 year period during which virgin biomass was reduced 70%. All 3 sites showed significant reductions in heterozygosity. Selective fishing for older (thus more heterozygose) individuals suggested as significant.

Smith, P.J., G.J. Patchell and P.G. Benson 1981. Genetic tagsin New Zealand hoki *Macruronus novaezelandiae. Animal Blood Groups and Biochemical Genetics* 12: 37-45
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BACIP sampling design.

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BACIP design.

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Tong, L.J., G.A. Moss and J. Illingworth 1987. enhancement of a natural population of the abalone, *Haliotis iris,* using cultured larvae. *Aquaculture* 62: 67-72

Vooren. C.M. 1975. Nursery grounds of tarakihi(Teleostei: Cheilodactylidae) around New Zealand. *New Zealand Journal of Marine and Freshwater Research* 9(2): 121-158.

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