Marine Ecological Research in New Zealand: Developing Predictive Models through the Study of No-Take Marine Reserves

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Abstract: *New Zealand established its first no-take marine reserve more than 25 years ago. Twenty no-take marine reserves have now been created, although few of these are considered comparable. We considered whether existing conceptual models of population and community structure based only on data from exploited systems lack the baseline information of natural states necessary to make accurate predictions for new reserves. Three of the oldest and best-studied reserves are situated on the northeastern coast of New Zealand. These reserves are considered broadly comparable replicates, and research has shown the recovery of previously exploited predator populations and the reestablishment of trophic controls over community structure and productivity. None of the major changes was predicted when the reserves were created. All the observations from and experimental tests of hypotheses in these three ecologically comparable reserves have provided predictive models for future reserves. Recent surveys in newly created reserves, however, suggest that these models are bioregion and habitat specific. In these new reserves the recovery of previously exploited predators was predicted but did not always occur. Where trends were correctly predicted, the speed and amplitude of the changes were not accurately predicted. Research in New Zealand suggests that it is not yet possible to predict explicit outcomes for newly created reserves and less possible to predict detailed results for systems of reserves. Results from a representative system of reserves, including all major habitats within all bioregions and broadly comparable reserves, are needed. Such a system will enable the range and variety of natural ecosystem dynamics to be investigated and provide the controls necessary to measure the effects of exploitation.*

Key Words: ecosystem change, effects of fishing, trophic cascade

Investigación Ecológica Marina en Nueva Zelanda: Desarrollo de Modelos Predictivos a través del Estudio de Reservas Marinas sin Captura

Resumen: *Nueva Zelanda estableció su primera reserve marina sin captura hace más de 25 años. A la fecha se han creado 21 reservas marinas sin captura, aunque algunas cuantas son consideradas comparables. Consideramos si los actuales modelos conceptuales de la estructura de poblaciones y comunidades basados sólo en datos de sistemas explotados carecen de la información básica de sistemas naturales necesaria para hacer predicciones precisas para reservas nuevas. Tres de las reservas más antiguas y mejor estudiadas están situadas en la costa nororiental de Nueva Zelanda. Estas reservas son consideradas réplicas ampliamente comparables, e investigaciones han mostrado la recuperación de poblaciones de depredadores explotadas previamente y el restablecimiento de controles tróficos sobre la estructura y productividad de la comunidad. Ninguno de los cambios mayores fue pronosticado cuando las reservas fueron creadas. Todas las pruebas experimentales de hipótesis en estas tres reservas ecológicamente comparables han proporcionado modelos predictivos para reservas futuras. Sin embargo, muestreos recientes en reservas nuevas sugieren que estos modelos son específicos para una bioregión y un hábitat. En estas reservas nuevas, la recuperación de depredadores explotados previamente fue pronosticada pero no ocurrió siempre. Cuando las tendencias fueron pronosticadas correctamente,*

la velocidad y amplitud de los cambios no fueron pronosticadas correctamente. La investigación en Nueva Zelanda sugiere que aún no es posible pronosticar resultados explícitos para reservas recién creadas y es menos posible pronosticar resultados detallados para sistemas de reservas. Se requieren resultados de un sistema representativo de reservas que incluya a todos los hábitats principales en todas las bioregiones, incluyendo las reservas ampliamente comparables. Tal sistema permitirá que el alcance y variedad de dinámicas de los ecosistemas naturales sean investigados y proporcionará los controles necesarios para medir los efectos de la explotación.

Palabras Clave: cambio en el ecosistema, cascada trófica, efectos de la pesca

Introduction

Terrestrial conservation in New Zealand has successfully created a range of highly protected reserves. Approximately 30% of the main islands' land area (Fig. 1) is in reserves, which are representative of the all the major terrestrial habitats (Towns & Ballantine 1993; Taylor & Smith 1997). Twenty no-take marine reserves now exist but represent <0.1% of the territorial waters of New Zealand (Babcock 2003). By comparing the scale maps showing reserves in terrestrial (Fig. 1) and marine (Fig. 2) habitats this disparity can be appreciated.

The first marine reserve in New Zealand was created more than 27 years ago as a place where scientific research could be conducted with minimal interference (Marine Reserves Act 1971). Recent reviews, however, suggest that no-take marine reserves should be established to achieve particular management aims. Many authors suggest aims for fisheries (e.g., Murray et al. 1999; Gell & Roberts 2003; Sale et al. 2005) and others for biodiversity conservation (e.g., Allison et al. 1998; Sala et al. 2002). Several reviews also suggest that once established, reserves should be assessed to gauge whether they are meeting their particular goals (e.g., Halpern & Warner 2002, 2003).

Underwood (1995) discussed how the "lack of overt debate and commentary by the research community about the roles of ecological research in issues of conservation, management, and sustained exploitation" has led to confusion between management and ecology. The resulting misunderstanding with managers can result in ecologists being compelled to make predictions about ecological processes and outcomes that either are not well understood (Underwood 1995) or have a high level of uncertainty (Ludwig et al. 1993). Predictive power is thought to be a major criterion for the evaluation of contemporary ecological theory (Peters 1991). Peters (1991), however, also lamented the confusion in the ecological literature "derived from process-oriented investigations which are studied for themselves because they cannot be related to any observable phenomena outside the experimental system." The missing link between observation and process was also highlighted by Underwood et al. (2000), who discussed the importance of testing the generality of ecological patterns before hypothesizing and investigating what processes might cause them.

Because of the complex nature of investigating patterns in marine communities, large-scale and long-term studies are needed to avoid problems associated with small-scale manipulations (Thrush et al. 2000). By testing the generality of patterns across several similar locations such as comparable marine reserves, observational studies can suggest models of processes for further investigation (Underwood et al. 2000; Willis et al. 2003*b*). Unlike a before/after control/impact (BACI) study, a problem in examining single, established marine reserves is that patterns correlated with reserve status, such as relationships between predator and prey densities, cannot be tested to eliminate other potential models for the distribution of organisms (Hurlbert 1984; Underwood et al. 2000; Russ 2002). For example, results might be confounded by other factors (e.g., wave action, sedimentation, or food availability) that structure the community (Shears & Babcock 2004).

No-take marine reserves can be considered large-scale manipulations of human predation and disturbance (Castilla & Duran 1985). In New Zealand, where the first humans arrived only about 1000 years ago, human exploitation of marine resources is relatively recent (Lalas & Bradshaw 2001). Marine reserves provide a situation in which a more natural community structure may recover (Ballantine 1991). A number of reviews have found that marine population structure and trophic relationships in the world's ocean and coastal systems have been altered drastically by historical overfishing (Pauly et al. 1998; Tegner & Dayton 2000; e.g., Jackson et al. 2001). If communities within marine reserves recover from the effects of harvesting it is likely that they will experience trophic interactions not previously observed by modern ecology (Jackson & Sala 2001). Research in New Zealand's marine reserves has been reviewed thoroughly (Babcock 2003; Shears & Babcock 2004). The major point we explore here is that predictive models of population and community change based only on data from exploited systems lack the baseline information of natural states necessary to make accurate predictions.
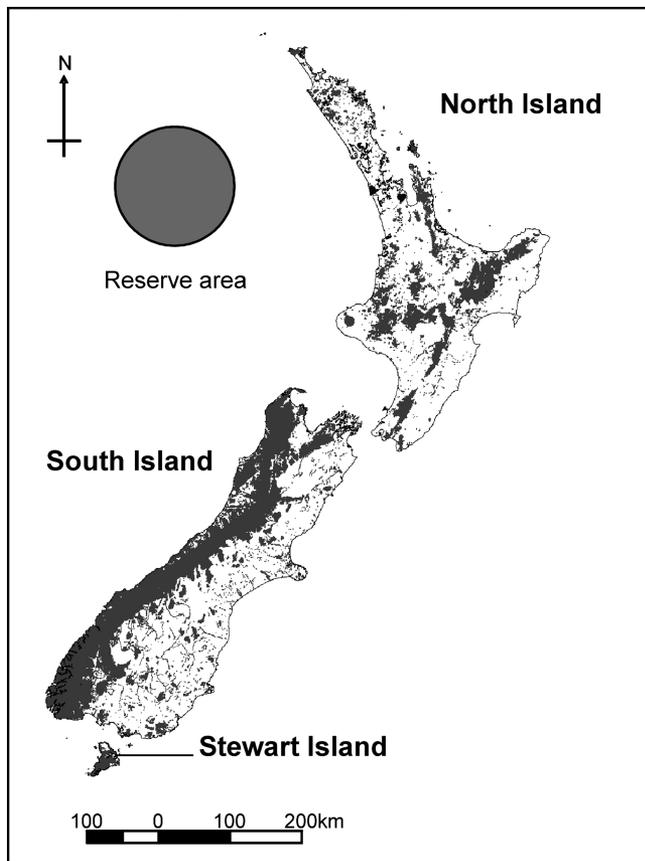
Figure 1. Terrestrial no-take reserves on the main islands of New Zealand. Reserves are shaded grey and are drawn to scale. The total area of all mainland terrestrial reserves is shown to scale as a circle.

It has been recognized that species within marine reserves may be affected by protection in at least four ways (Shears & Babcock 2004). These effects can be grouped into first-order direct effects, such as recovery of previously exploited populations, and indirect effects, including second-order declines in prey or competitor populations; third-order changes in habitats resulting from tri-level trophic cascades; and fourth-order changes in faunal distribution and diversity associated with habitat change.

Northeastern New Zealand

Northeastern New Zealand contains eight reserves (Table 1, Fig. 1); three of the longest established (Cape Rodney-Okakari Point Marine Reserve [Leigh], Te Whanganui a Hei Marine Reserve [Hahei], and Tawharanui Marine Park [Tawharanui]) are considered broadly comparable replicates. These reserves have the longest history of research, and several experimental investigations (Kelly et al. 2000; Willis et al. 2003a; Langlois et al. 2005) have used the three locations as replicates to test the generality of effects of marine reserve status. The majority of our analysis is limited to these reserves; however, we use some examples from new reserves in other bioregions. We used the range of population and community changes within these reserves to examine three questions: What predictions, if any, were made of the observed changes? Can precise predictions be made now? How should the existing framework of reserves be extended to improve prediction?
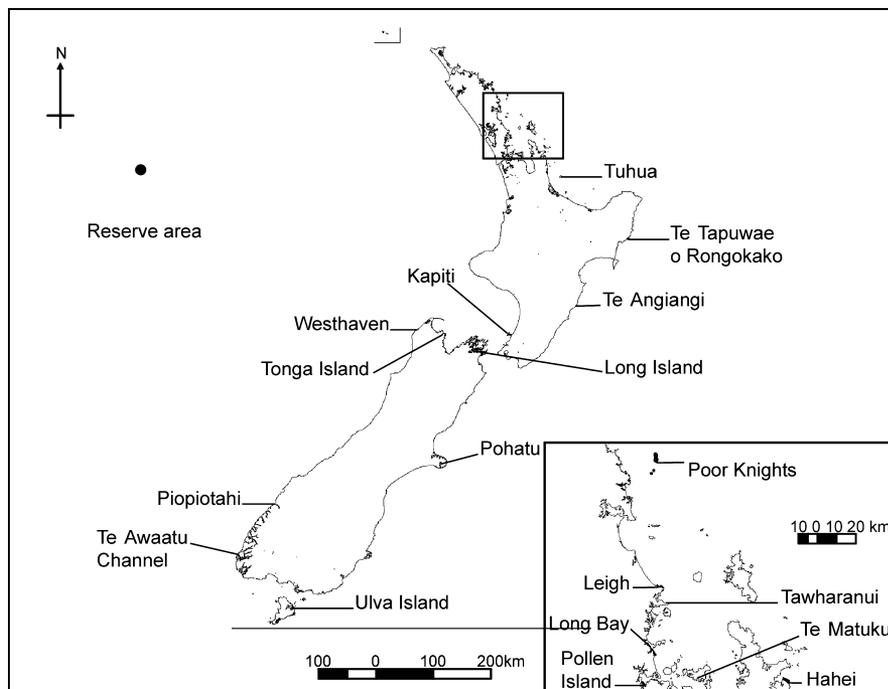

Figure 2. Marine no-take reserves around the main islands of New Zealand. Reserves are shaded grey and are drawn to scale. The two largest marine reserves (Auckland and Kermadec islands) are around offshore islands in the New Zealand Exclusive Economic Zone but not pictured on this map. The inset shows the Hauraki Gulf and environs with the location of seven additional marine reserves. The total area of all coastal marine reserve is shown to scale as a circle.

Table 1. New Zealand's marine reserves, including their size and year of gazetting.

Marine reserve title (name used)	Size (km²)	Date established
Coastal		
Cape Rodney to Okakari Point (Leigh)	5.2	1975
Tawharanui Marine Park (Tawharanui)	3.5	1981
Te Whanganui a Hei (Hahei)	8.4	1992
Kapiti	21.7	1992
Tuhua–Mayor Island	10.6	1992
Long Island–Kokomohua	6.2	1993
Piopiotahi	6.9	1993
Te Awaatu Channel–The Gut	0.9	1993
Tonga Island	18.4	1993
Westhaven–Te Tai Tapu	5.4	1994
Long Bay–Okura	9.8	1995
Pollen Island–Motu Manawa	5.0	1995
Te Angiangi	4.5	1997
Poor Knights Islands	18.9	1998
Pohatu Marine Reserve	2.2	1999
Te Tapuwae o Rongokako	24.5	1999
Te Matuku Bay	3.2	2003
Ulva Island–Te Wharawhara	10.8	2004
Offshore islands		
Kermadec Islands	7,482.7	1990
Auckland Islands	4,840.0	2003

Results from Three Comparable Marine Reserves

First-Order Changes (Exploited Species)

Two important commercially and recreationally fished species have been intensively studied within the three comparable reserves in northeastern New Zealand: the snapper (*Pagrus auratus*) and rock lobster (*Jasus edwardsii*). Existing knowledge before the creation of reserves suggested that mobile species such as the snapper (Paul 1976) and rock lobster (McKoy 1983) would not respond to protection within reserves as small as Leigh, Tawharanui, or Hahei. There was no initial expectation of change in these previously exploited species (Ballantine 1989). The abundance and biomass of these species increased within these reserves, however, after protection from fishing. Greater than legal-sized snappers (>270 mm fork length) are about 14 times more abundant inside the reserves than outside (Willis et al. 2003*a*). Legal-sized rock lobsters (>100 mm carapace length) are estimated to be 3.7 times more abundant inside these reserves (Kelly et al. 2000). Behavioral studies of snappers and rock lobsters within these reserves demonstrated that, although these species can be highly mobile, they also display complex small-scale movement patterns (e.g., periods of home ranging, MacDiarmid 1991; Kelly et al. 1999; Willis et al. 2001; Parsons et al. 2003). Such movement patterns have allowed their populations to recover from fishing within relatively small reserves. Parsons and Egli (2005) discuss

the progression of research using marine reserves that has led to new information on snapper movement and novel insights into teleost behavior.

Second-Order Changes (Mostly in Prey)

Marked decreases in the abundance and dominance of urchins have been recorded in reserves at Leigh and Tawharanui (Cole & Keuskamp 1998; Shears & Babcock 2003). Tethering experiments by Shears and Babcock (2002) confirmed the chances of predation were seven times higher inside reserves relative to outside and that at least 45% of sea urchin mortality was attributable to predation by rock lobsters. Reductions in kelp-associated cryptic fishes have been recorded at Leigh and may be due to the effects of predation or competition (Willis & Anderson 2003). In sandy habitats adjacent to rocky reefs in the three comparable reserves, reduced densities of large infaunal bivalves near reefs have been found (Langlois et al. 2005*a*). In subsequent caging studies (Langlois et al. 2005*b*) at multiple sites there were significant levels of predation at reserve sites but not in fished areas. Results of this study suggested that predation by large rock lobsters can regulate the abundance and size structure of infaunal bivalve populations.

Third-Order Changes

In the early 1960s Dromgoole (1964) commented (without data) that at several localities in northeastern New Zealand formerly thick beds of the kelp *Ecklonia radiata* had disappeared in the shallow sublittoral zone. Dromgoole suggested they gradually declined over the previous 10–15 years and were replaced by coralline-encrusted surfaces grazed by the sea urchin *Evechinus chloroticus*. Early researchers considered this "urchin barrens" habitat a typical part of the depth-related zonation of northeastern New Zealand (Ayling 1978). Ayling (1981) and Andrew and Choat (1982) suggested grazing by *E. chloroticus* maintains the barrens habitat. When the permanent quadrats of Ayling (1978) were revisited in 1994, a major decrease in the area of barrens dominated by *E. chloroticus* was documented (Babcock et al. 1999). Babcock et al. described a shift from sea urchin-dominated barrens to kelp and mixed macroalgal stands at Leigh and Tawharanui over the 20-year period since the reserve was created. They suggested that the greater sizes and densities of the main sea-urchin predators within the reserves—snappers and rock lobsters—reduced populations of *E. chloroticus* and allowed the shallow macroalgal beds reported by Dromgoole (1964) to recover. Because both commercial and recreational fishers heavily target snappers and rock lobsters, Babcock et al. (1999) suggested this fishery reduced the impact of a natural trophic cascade, causing a large-scale reduction in the extent of macroalgal habitats and benthic primary productivity.

The significant time lag in the recovery of trophic cascade effects after reserve creation is most likely a consequence of the time needed for predator populations to build up and urchin populations to fall below the minimum density necessary to maintain barrens habitats (~1 m^2, Babcock 2003). Decreases in urchin density and habitat transitions from barrens to macroalgae were still being recorded in the Leigh reserve as recently as 2000 (Shears & Babcock 2003).

Fourth-Order Changes

Ayling (1981) reported the community associated with the barrens habitat to be of low diversity. The replacement of this habitat with macroalgal beds is likely to produce increases in biodiversity. Results of previous studies of kelp and algal turf habitats show that these algal habitats are characterized by rich faunal associations (e.g., in associated algal turfs, Taylor 1998*b*, and in the kelp holdfasts, Goodsell & Connell 2002). Therefore changes in algal distributions will result in increases in faunal diversity and also in productivity. For example, Taylor (1998*a*), working in the shallow subtidal habitats within the Leigh reserve, found the contribution of kelp and turf epifauna to secondary production to be 78% of the reef productivity. Shears and Babcock (2003) also reported differences in the abundance of the limpet *Cellana stellifera* and the turbinid gastropod *Cookia sulcata* between reserve and nonreserve sites. This may have been related to the high cover of coralline turf observed at reserve sites with lower densities of grazing urchins. Shears and Babcock (2003) suggest this could be an example of a further indirect effect where predation of urchins results in habitat facilitation (sensu Menge 1995) that leads to increased populations of *C. sulcata*.

Comparison with Other Reserves

Differences in First-Order Effects

The three comparable reserves in northeastern New Zealand enabled the investigation of processes resulting in the recovery of previously exploited predators (MacDiarmid & Breen 1993; Parsons et al. 2003). Based on recovery of these species, it was expected that snappers and rock lobsters would recover in a similar fashion within newly created reserves in the northeastern bioregion.

The Poor Knights Marine Reserve (fully established in 1998) was the first no-take area created in New Zealand where a BACI sampling design was used to investigate changes in previously exploited species. These offshore islands are influenced by the warmer waters of the East Auckland Current (EAC, Francis et al. 1999). Snappers increased rapidly over 4 years to levels 7.4 times higher than the prereserve survey, and total snapper biomass also increased by 818% (Denny et al. 2004). This increase in snapper abundance was surprisingly rapid because a time lag is expected when fish populations are recovering from previous heavy fishing pressure (Polunin & Roberts 1993). Denny et al. (2004) suggested that the flow of the EAC could be the reason for the rapid increase in juvenile snapper numbers, but adult numbers are most likely the result of stronger than expected seasonal onshore migrations (Willis et al. 2003*a*). No increase in rock lobsters has been observed at the Poor Knights (Booth et al. 2000), and the EAC is thought to play a role in limiting the supply of rock lobster larvae (Chiswell 2003).

On the southeastern coast of the North Island (Fig. 1), two reserves have been recently created at Te Angiangi and Te Tapuwae o Rongokako (Table 1). Densities of rock lobsters within the reserves are much higher than densities in adjacent fished areas, but no changes in fish populations have been observed (D. Freeman, unpublished data). The increase in density of rock lobsters occurred particularly in reef areas deeper than any areas present at Leigh, Tawharanui, or Hahei.

Differences in Known Trophic Cascades

The predator-urchin-kelp trophic cascade described by Shears and Babcock (2002) has thus far been observed only within the reserves at Leigh and Tawharanui. This ecological model needs to be tested across various environmental gradients and examined over longer time periods. For example, die-back events have been observed to alter the demographics of kelp stands (Schiel 1988; Haggit & Babcock 2003). Urchin barrens habitat dominates the shallow subtidal in the northeastern bioregion but is rare or absent along the majority of the New Zealand coastline (Shears 2003). Reserves in other bioregions are likely to respond in a different manner (Shears & Babcock 2004).

Conclusions and Recommendations

Problems of Prediction

For at least 10 years after the first New Zealand reserve was created, the idea of predicting changes was not considered explicitly. Most research and effort was directed toward producing maps of habitats and developing the methodologies for this (Ayling 1978; Ayling et al. 1981). Changes in abundance (stratified by habitat) and distribution of habitats could be considered only after a baseline had been established. The predictions that developed from subsequent observation and investigation of process were essentially new for marine ecology in the context of marine reserves. More recent research in newly created reserves and surveys of the New Zealand coastline suggest that these new models of population and community dynamics are highly specific to habitat and bioregion.

Accurate and detailed predictions of changes because of protection will be difficult or impossible to make because of the complexities of trophic interactions and population dynamics. Changes within reserves involve many species at various trophic levels (Shears & Babcock 2002), are likely to vary across environmental gradients (Shears & Babcock 2004), and may involve time lags (Babcock 2003). Results from New Zealand suggest that the current level of knowledge is insufficient for ecologists to predict the detailed outcomes of creating new marine reserves in other habitats and bioregions.

Improving prediction is likely to be complicated by several factors. For example, although the recovery of snapper populations has been well studied in several reserves, detailed predictive models are likely to be habitat specific (Parsons et al. 2003) and controlled by seasonal migration (Willis et al. 2003*a*), small-scale movement patterns, (Parsons & Egli 2005) and coastal currents (Francis et al. 1999).

Jones et al. (1992) predicted that changes in the food webs would involve changes to habitat structure and thus profoundly affect nearly all organisms occupying rocky reefs. However, only one trophic cascade has so far been detected and was observed only within two reserves. Another complication can arise through historical changes in megafauna (Jackson & Sala 2001). The present density of snapper and rock lobster in the Leigh Reserve may be higher than in prehuman times. Larger predators such as sharks, seals, and whales were once common along the northeastern coast but were quickly fished to low levels (Baker et al. 1999; Lalas & Bradshaw 2001; Baker & Clapham 2004). Anecdotal accounts, however, suggest populations of rock lobsters and snappers at Leigh were far higher in the late 1800s than those currently observed in the reserve. Their recovery to "natural" levels could result in further unpredicted trophic cascades.

Dayton et al. (2000) commented on the difficulty of studying trophic relationships in marine communities when present communities and ecosystems have been highly altered by fishing activity, and Jackson et al. (2001) detailed how these changes have been occurring for a very long time in most regions. The changes produced by no-take reserves are likely to be affected by a large range of factors. These include not only the region and habitat but also the size and shape of the area (e.g., edge effects, Neigel 2003), the spatial arrangement of the area (e.g., relation to currents, Denny et al. 2004), novel forms of behavior due to new population structures (Parsons & Egli 2005), and the total amount of reserve area. The amount of reserve area may become the most important factor once systems of reserves exceed 5–10% of the total area within bioregions (see Jackson & Sala 2001), although no empirical evidence exists because of the small relative area of most no-take reserves. For all these reasons, reliable predictive models are likely to be possible only after a fully representative range of reserves (e.g., of different sizes and habitat types) has been studied and provide the

data on which to base such theories (Underwood et al. 2000).

The history of research in New Zealand's reserves has produced some valuable lessons for assessing ecosystem changes within reserves. Habitat maps and spatially explicit sampling, initiated by Ayling et al. (1981), were essential in demonstrating the extent of potential habitat changes within reserves (Babcock et al. 1999; Parsons et al. 2004). For example, in the reserve at Leigh, Andrew and Choat (1982) found strong evidence suggesting sea urchins controlled kelp density, but in small-scale caging studies larger predators (snapper and rock lobster) were incapable of controlling populations of sea urchins. Observations suggest that sea urchin populations were decreasing and that barrens habitats are replaced by kelp forest (Cole & Keuskamp 1998), but comparison through spatial mapping clarified this pattern (Parsons et al. 2004).

The Need for Representation and Replication

The establishment of marine reserves has been hailed as a large-scale experimental framework for the investigation of effects of harvesting (Dayton et al. 1995) and as controls for adaptive management (Agardy 2000). It is therefore logical to attempt to design marine reserve systems to achieve these objectives (Norse 2002). If systems of marine reserves are designed to achieve specific management aims, however, only particular habitats and community types may be selected. Any such restrictions would limit ecological research and the testing of models relating to different habitat types. Although it is scientifically interesting to propose and test models of the changes within marine reserves, this should not restrict the planning of future reserve systems. To optimize scientific opportunities it is necessary to represent all habitats within each bioregion and to have spatial replication of comparable reserves (e.g., Agardy 2000; Friedlander et al. 2003; Leslie et al. 2003). Management and science need a range of reserves rather than a precise allocation suggested by particular models. Such a system would provide a sound basis for experiments to test and improve ecological models (Hurlbert 1984; Underwood et al. 2000).

Recommendations

In New Zealand, long-term studies on a variety of topics have been made in a limited range of highly protected reserves. Results of these studies show many varied and complex ecological changes, some of which were major. Most of the changes, however, were not predicted in any useful way before they were observed. Recently created systems of reserves did not attempt detailed predictions in the Great Barrier Reef Marine Park (Fernandes et al. 2005 [this issue]), around the coast of Victoria (ECC 2000), and for the waters around the Californian Channel Islands (Davis 2005 [this issue]). These events show

that detailed management aims for the establishment of marine reserves are not necessary.

The aim of no-take marine reserves should be simply to minimize human disturbance and allow the recovery of as natural a situation as possible. Reserve systems might then begin to provide a "window to the past and a vision for the future" (Bohnsack 2003). Our conclusions from the history of ecological research in northeastern New Zealand's no-take areas support the principles for marine reserve systems proposed by the United Nations Expert Group on marine biodiversity (SCBD 2004).

Acknowledgments

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