

Ultrasonic tracking reveals multiple behavioural modes of snapper (*Pagrus auratus*) in a temperate no-take marine reserve

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Interactions between marine reserve populations and non-reserve populations of exploited fishes have generally been modelled using simplistic assumptions about behaviour. Consequently, there is a recognized need for better information on fish movement behaviour at the appropriate spatial scales to generate more realistic interaction models. Automated ultrasonic tracking of marine fish, applied in this study, offers the potential to continuously track individuals for periods of up to several years within the study area. Snapper (*Pagrus auratus*) (FL: 33–68 cm) were surgically implanted with individually coded ultrasonic transmitters to monitor their movement within the Cape Rodney to Okakari Point Marine Reserve in northeast New Zealand from October 2001 to September 2002. The range of movement patterns observed includes some fish resident for the entire tracking period, while others were more mobile. Of the latter group, some fish left the array permanently while others returned after up to 83 days of continuous absence. Nearly all fish showed some level of site fidelity for varying periods of the time they were tracked. Fish activity peaked in the summer, when highest densities are known to occur. Results suggest that snapper behaviour is variable, and that patterns of habitat utilization vary between fish and also seasonally. Such a complex range of behaviours may be a key component for achieving desirable outcomes for both conservation and fisheries in marine reserves.

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Introduction

A potential benefit of marine reserves is the net emigration of fished species to areas adjacent to reserves. This may occur under conditions of growth overfishing: if individuals occupy a home range exceeding the size of the protected area; have a smaller home range but located near the boundary; or if part of the life cycle (e.g. reproduction) involves migration beyond the reserve area. If present, net emigration would justify the use of marine reserves as not only conservation tools but also as fisheries enhancement tools (Alcala and Russ, 1990; Attwood and Bennett, 1994; Allison *et al.*, 1998; Kramer and Chapman, 1999). While these so-called “spillover” effects have rarely been shown conclusively (e.g. Alcala and Russ, 1990; Hilborn, 2002), cross-boundary movement of individuals has been reported for several species (Attwood and Bennett, 1994; Munro, 2000; Eristhee and Oxenford, 2001).

Virtually all of the benefits of marine reserves are highly dependent on the rate and scale of movement of particular species in relation to reserve size (Kramer and Chapman, 1999), which will determine the amount of time that individuals will spend in protected areas. While the understanding of movement patterns is absolutely central to the effectiveness of marine reserves, information relating to such movements is sparse (see Attwood and Bennett, 1994; Holland *et al.*, 1996; Zeller, 1997; Cole *et al.*, 2000; Willis *et al.*, 2001), particularly at scales relevant to (often small) marine reserves.

Choosing the size and spatial configuration of marine reserves to ensure the protection of important recreational and commercial target species can optimize their effectiveness. Information on movement patterns, activity, and home range size of the species concerned is considered very important to reserve design (Roberts and Polunin, 1991; Attwood and Bennett, 1994; Holland *et al.*, 1996; Zeller,

1997; Allison *et al.*, 1998; Woodroffe and Ginsberg, 1998; Kramer and Chapman, 1999; Willis *et al.*, 2000). Traditionally, such information has been obtained through mark and recapture studies. This has a major shortcoming, since it is usually restricted to one recapture locality for each fish (Zeller, 1999). Furthermore, the vast majority of mark–recapture studies conducted around the world have been part of fisheries stock assessments primarily aimed at determining stock size, and such data usually only resolve movements at large scales. Consequently, with conventional tags, detailed movement and activity patterns and home range size can only be the subject of speculation.

The New Zealand snapper (*Pagrus auratus*: Sparidae [Bloch and Schneider 1801]) is one of the most valuable recreational and commercial fish species in New Zealand (Annala *et al.*, 2002). Yet, considering its importance, a surprisingly small amount of research has been conducted on the movement patterns of snapper. Snapper are believed to follow a seasonal migration from deeper into shallow coastal waters during summer (Crossland, 1976); commonly referred to as the ‘schooling snapper theory’. These seasonal movements are believed to be related to changes in water temperature or the formation of spawning aggregations (Paul, 1976). This theory is at odds with the observed build-up of snapper abundance and spatial distribution in the Cape Rodney to Okakari Point (CROP) reserve (Willis *et al.*, 2000, 2003), and is more consistent with an alternative theory of polymorphic snapper behaviour, where a proportion of *P. auratus* are year round residents on reefs (Willis *et al.*, 2001; Egli and Babcock, 2002; Parsons *et al.*, 2003). Work by Attwood and Bennett (1994) on the South African sparid galjoen (*Coracinus capensis*) has shown that within a fish species more than one dispersion pattern is possible and may be common. The importance of such information to sustainable fisheries management has been realized in Shark Bay, Western Australia, where snapper exhibit both resident and mobile behaviour in a small geographic region, resulting in separate management of two stocks at scales of less than 200 km (Moran *et al.*, 1999).

Advances in technology have allowed more detailed behavioural studies to take place (e.g. Zeller and Russ, 1998; Eristhee and Oxenford, 2001; Simpfendorfer *et al.*, 2002). With the advent of automated ultrasonic telemetry, individual fish can be continuously tracked within the array’s range for extended periods of time on spatial scales ranging from metres to kilometres (Voegeli *et al.*, 2001). Based on visual tagging and radio-acoustic positioning telemetry (RAPT) in the Cape Rodney to Okakari Point Marine Reserve, there is no direct evidence that snapper on coastal reefs ever move further than a few hundred metres (Willis *et al.*, 2001; Parsons *et al.*, 2003), yet seasonal censuses of snapper numbers on coastal reefs suggest otherwise. The number of snapper on coastal reefs is roughly twice as high during summer as it is in winter

(Willis *et al.*, 2003), implying that many snapper stay on coastal reefs over summer and then undertake large-scale movements (Crossland, 1976; Paul, 1976), presumably to offshore grounds. These contrasting sets of observations are consistent with a polymorphic behaviour pattern in snapper.

Previous attempts to examine snapper movements applied visual tagging techniques using large numbers of fish with relatively low spatial resolution (Willis *et al.*, 2001). Additionally, advanced ultrasonic tracking with high accuracy was used, but limited by high costs to few individuals (Parsons *et al.*, 2003). The present study was initiated to fill critical gaps in our knowledge of snapper movement patterns by using acoustic tracking methods that allow us to operate on spatial scales intermediate to those used previously. Our goal was to examine presence and absence of individual snapper inside the marine reserve and to examine variability in their movement patterns over longer time periods. This is particularly important to the understanding of snapper ecology and the establishment of effective marine reserves, since fish movements examined by the present study are of the order required for a fish to leave (or enter) a marine reserve.

Material and methods

Study site

This study was conducted at the Cape Rodney to Okakari Point (CROP) Marine Reserve located on the northeastern coast of New Zealand (36° 49′ S 147° 47′ E) (Figure 1). This ‘no-take’ marine reserve established in 1977 encompasses an area of 518 ha and is New Zealand’s oldest marine reserve. The reserve contains high densities of commercially and recreationally exploited fish species, including snapper (*P. auratus*), New Zealand’s most valuable coastal finfish industry (Annala *et al.*, 2002).

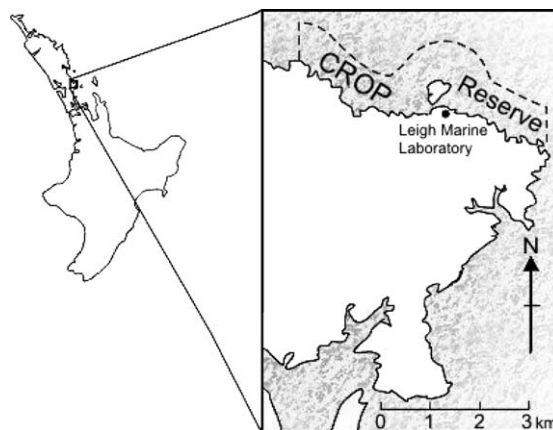


Figure 1. Map of the CROP Marine Reserve in northeast New Zealand.

Automated ultrasonic tracking

During austral summer 2001/2002 an array of seven VEMCO VR2 (Vemco Ltd., Shad Bay, Canada) omnidirectional hydrophones were deployed in 20–30-m depth around the centre of the marine reserve, with a signal range covering 5.4 km² (extending approximately 3 km in length and 1.5 km in width; Figure 2). All hydrophones were placed in open sand areas to minimize acoustic shadows that might occur in structurally complex areas near the shore. These monitoring stations were complemented with two additional receivers at either end of the reserve in 2002. A functional range of ≤500 m was found in range trials conducted with fixed transmitters deployed at set distances from the hydrophone over a 1-week period (D. Egli, unpublished data). The geometry of the hydrophone array was selected to maximize coverage in critical parts of the study area and provide information on the movements of animals entering, exiting, and moving across the main study area.

Fish capture and tagging

Between October 2001 and May 2002, snapper were caught at various locations evenly distributed within 100–300 m to the west, north, and east of Goat Island in the CROP Marine Reserve, using barbless hooks and lines. Captured fish were selected for tagging based on a randomization process to avoid biasing the captures towards resident, dominant fish. The first two fish captured were immediately released and randomly assigned fish were kept subsequently. Snapper were retained at ambient water temperature and natural light cycles in 2000-l holding tanks at the Leigh Marine Laboratory for a minimum of 24 h (average

of 6 days) prior to and 24 h (average of 6 days) after surgery. They were then released at the capture location.

Eighteen snapper (FL: 33–68 cm) were fitted with Vemco ultrasonic V16 (90 mm) and V8SC (30 mm) RCODED transmitters between 23 October 2001 and 30 May 2002. For all fish the transmitter weight in water never exceeded 1.1% of the body weight. Fish were anaesthetized with clove oil (Parsons *et al.*, 2003) and placed in holding tanks to recover after surgery. The transmitters were surgically implanted into the peritoneal cavity (Zeller, 1997) and the 3-cm-long incision sutured with three stitches of synthetic absorbable surgical suture. There was no postoperative mortality. The signal from the transmitters was expected to last for approximately 200–700 days depending on the type of transmitter.

Movement data analysis

The automated VR2 tracking system used is not a real time tracking system such as RAPT, but it does provide continuous data on the presence and position of fish at scales > 0.1 km through an array of hydrophone buoys. The maximum scale of tracking is dependent on the number of hydrophones deployed. Using the receiver array described above (Figure 2), short-term activity centres were estimated as described by *Simpfendorfer et al.* (2002). To estimate the snappers' likely activity centre, all valid detections were summarized for each receiver over 1-h periods. The estimated position of the fish was then calculated as the mean of the receiver position weighted by the number of detections. The overlapping reception range created by the proximity of the receivers provided

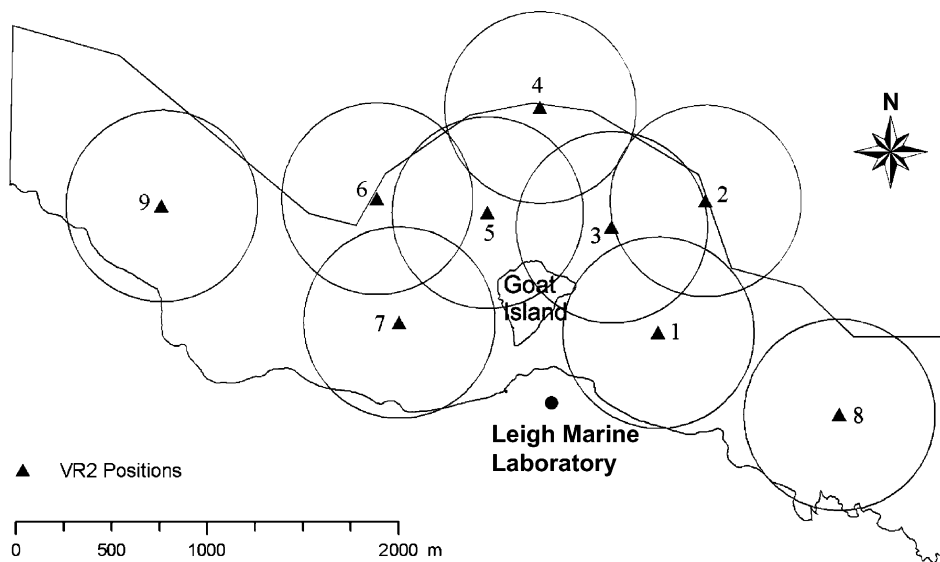


Figure 2. Map of the CROP Marine Reserve with the locations of the hydrophones. Note: Hydrophones 1–7 deployed in 2001, hydrophones 8 and 9 deployed in 2002.

additional accuracy to augment the presence–absence information available from single receivers.

Because this method can only show a shift in the centre of activity over a 1-h period, it could not be used to estimate swimming speed; however, fish movement patterns were expected to be correlated with distances between successive activity centre estimates.

The positional accuracy of this method was measured by comparing averaged DGPS locations of stationary and towed transmitters with activity centres estimated using acoustic receivers. The estimated activity centre was found to be within a radius of 95.2 m (± 18.5 m) of the actual position.

Presence–absence analysis

Presence–absence during hourly bins over the whole time at liberty was used to examine long-term site fidelity of snapper. The time between release of the tagged fish until the end of the observation period or the disappearance of the signal (duration of monitoring period) was regarded as the time at liberty. There was no case where the disappearance could be linked to migration or natural or fishing mortality. If the transmitter was recorded on at least one receiver during a 60-min period it was assumed to be present for that hour. The ratio of presence to absence was thought to be an indicator of potential exposure to fishing mortality beyond the receiver range (and hence marine reserve boundary). We considered this to be a conservative estimate, as the range of the receivers near the boundary reaches beyond the reserve boundary. Fish were only rarely recorded on outer receivers and therefore absence of the fish from the array would indicate that the fish was beyond the protected area.

Results

Eighteen snapper (33–68 cm fork length [FL]) were monitored from 11 to 343 days between October 2001 and September 2002. Fourteen of these fish were recorded during more than 120 days (Table 1). Of the remaining fish, two were monitored between 50 and 100 days, while two fish disappeared after less than 1 month.

Presence–absence analysis

The proportion of time present within the array by any one of the monitored snapper varied widely, ranging from 25.1 to 100%, with an average of 63.4 s.e. $\pm 6.4\%$ (Table 1). Seven snapper were absent for more than 50% of the duration of the monitoring period. Logit transformed percent presence of snapper within the receiver array was not significantly correlated with duration of individual monitoring periods ($F_{[1,16]} = 3.956$, $r^2 = 0.198$, $p = 0.064$) or with fork length ($F_{[1,16]} = 2.657$, $r^2 = 0.142$, $p = 0.123$).

The lowest proportional presence within the array was recorded for fish 30 (25.1%). In contrast to the others, fish 30 spent most of its time near the channel between Goat Island and the mainland (between receivers 1 and 7; Figure 2). This area was near the inner edge of the coverage area, and acoustic shadows in this shallow rocky environment may have reduced the detectability of the transmitter. In contrast, the majority of absence periods from other fish followed detections on the outer receivers or near the edge of the array.

Only fish 8 was recorded every day since the date of release (Table 1). All other fish displayed varying periods of absence from the study site. Over the duration of the study, three fish were absent from the study area for over 70 consecutive days. The highest number of individual absent periods of fish was observed in August, when water temperatures are coldest (Leigh Marine Laboratory climate records).

A frequency histogram suggests that there might be two distinct groups of fish (Figure 3). Seven fish were present over 80% of the monitoring period. The remaining fish, despite not only being recorded on the outer receivers, appear to be distributed around much lower presence levels.

Fish movement patterns

The mean distance between consecutive position estimates was calculated as the linear distance between the activity centre estimates, and therefore restricted to periods where at least two successive data points were available. Only fish present during three seasons were examined to enable seasonal and between-fish comparisons. Movement rates averaged over all seasons were 117.0 m h^{-1} (s.e. $\pm 12.0 \text{ m h}^{-1}$), ranging widely from 22.3 m h^{-1} (s.e. $\pm 5.3 \text{ m h}^{-1}$) to 290.0 m h^{-1} (s.e. $\pm 11.9 \text{ m h}^{-1}$) for individual fish and seasonal periods. Average seasonal

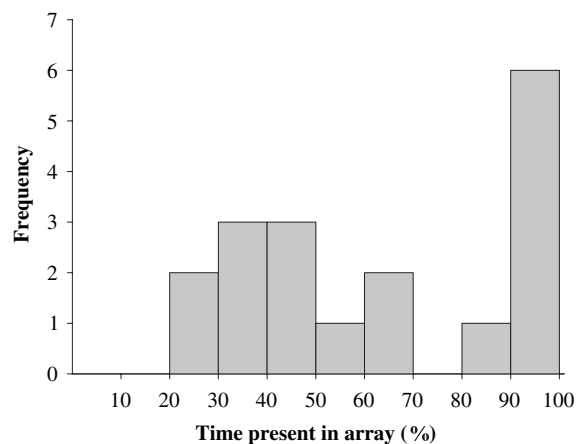


Figure 3. Frequency of fish by per cent presence in the array over the total time at liberty.

Table 1. Summary data for acoustically monitored snapper in the CROP marine reserve from October 2001 to September 2002. Days monitored since release and maximum number of days of consecutive absent time. The percentage presence is calculated on an hourly presence-absence since release.

Fish no.	Date released	FL (cm)	FL monitored absent time		% Present overall
			Days monitored	Max. days absent	
1	23 Oct 2001	64.0	343	71	53.5
2	28 Mar 2002	54.5	187	6	94.6
3	11 Apr 2002	64.5	173	9	33.0
4	23 Oct 2001	63.8	91	25	38.3
6	21 Dec 2001	61.5	56	1	67.6
7	21 Dec 2001	68.0	284	83	35.5
8	27 Feb 2002	53.5	216	0	95.3
9	06 Feb 2002	52.5	237	78	27.6
11	28 Mar 2002	51.0	187	1	88.7
12	11 Apr 2002	56.0	173	20	49.9
13	30 Apr 2002	50.0	154	2	93.5
14	30 May 2002	52.0	124	3	96.0
30	06 Feb 2002	46.0	237	18	25.1
31	27 Feb 2002	45.0	216	3	51.9
32	08 Apr 2002	46.0	176	1	91.8
35	08 Apr 2002	38.0	11	0	100.0
40	30 Apr 2002	37.5	22	4	46.0
41	30 May 2002	33.0	124	3	60.9

movement rates appeared to show maximum average movement rates in summer with 142.0 m h^{-1} (s.e. $\pm 3.2 \text{ m h}^{-1}$) and lowest movement rate in winter with 104.5 m h^{-1} (s.e. $\pm 2.0 \text{ m h}^{-1}$).

Only fish 7 displayed a continuous decrease of activity throughout the year (Figure 4). The low values in winter and spring for fish 7 coincided with periods of low sample size of movement rates. Similarly, fish 8 displayed unexpectedly low activity levels in summer (Figure 4), but the summer sample size was nearly an order of magnitude lower than for the other seasons. Fish 31, which was recorded mainly on positions 5–7 (Figure 2) in the northwestern part of the monitoring array, was found to have the maximum activity level in winter. Again, the sample size for summer and spring was much lower. More even occurrences on an increased number of monitoring stations resulted in high movement rates observed for fish 11, indicating a change in behaviour. In addition, the sample size for spring is much lower. The different release dates result in some variance of sample sizes for different seasons but still show an overall seasonal trend in the movement rates.

Discussion

As part of any effective marine reserve design it is crucial to gain detailed knowledge of the mobility and habitat utilization of its inhabitants (Roberts and Polunin, 1991; Attwood and Bennett, 1994; Zeller, 1997), since improperly designed

reserves may provide a false sense of security for fisheries and conservation (Carr and Reed, 1993). Acquiring continuous individual-based movement data, combined with population density distribution and changes, as well as habitat information also allows new insights into teleost life history.

Previous research suggests that levels of site fidelity of snapper may be so high that emigration or spillover could be negligible (Parsons *et al.*, 2003). In contrast, this study

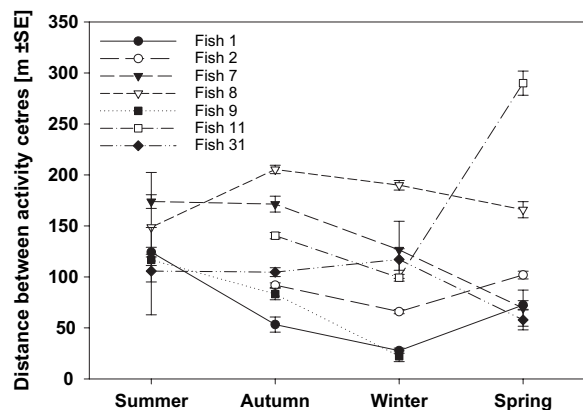


Figure 4. Mean distance in metres between hourly estimates of activity centres averaged over 3 month periods (Spring: October–December; Summer: January–March; Autumn: April–June; Winter: July–September). Only fish monitored for at least three periods were included.

found a range of different movement patterns, with the coastal snapper population sampled in the CROP reserve displaying a distinctly bimodal behaviour pattern. It is possible that the tagging of Parsons *et al.* (2003) was biased towards highly resident fish; a possibility that our randomized tagging protocol was designed to overcome. The most important finding of this study was the high proportion of time some fish spent outside the study area. Of the fish tracked, 95% spent some time outside the study area and 44% spent more than half the monitoring period outside the study area. Thus, while some fish will benefit from high levels of protection and are unlikely to be caught, others may be vulnerable to the fishery for varying periods of time. While we lack direct evidence, this most likely presents a scenario in which fish from the reserve may be captured by adjacent fisheries, such as suggested for some tropical fisheries (Alcala and Russ, 1990; Roberts *et al.*, 2001), and also demonstrated for the lobster fishery adjacent to the CROP Marine Reserve (Kelly *et al.*, 2002). The spatial pattern of snapper density within the CROP reserve is suggestive of fishery effects on the reserve population with lower relative densities of snapper towards the reserve boundaries (Willis *et al.*, 2003). The results presented in this study are also consistent with seasonal changes in snapper abundance on coastal reefs (Willis *et al.*, 2003), in which roughly 50% leave coastal reef systems over the winter.

Fish that disappeared from the tracking array returned after periods of hours to months. While a short period of absence could result from acoustic shadows produced in shallow, highly complex substrate, it is unlikely that snapper remain stationary in such areas for long periods. Using hourly detection intervals prevents a gross underestimation of presence–absence assessment. It is possible that they may also return to their previous activity centres (or home ranges) after longer seasonal periods of absence from the reef. Results from long-term spatial analysis may confirm this.

Most snapper showed relatively small individual variations between seasonal average movement rates. However, results indicate a much greater variability between individuals. This could not be attributed to size of fish (see also Willis *et al.*, 2001), but may be related to differences in habitat composition, and local differences in population densities (Matthews, 1990a, b; Barrett, 1995), or even acquired or genetic individual behavioural variability. Although no significant relationship has been found between fish length and movement rates, this might be biased by the lack of information during the extended excursions undertaken by larger fish. With the monitoring system applied in this study no information can be obtained beyond the reception range of the receivers. A combination of archival tags and coded acoustic transmitters might be able to provide more information for the time spent outside the array.

Ultimately, the measure of whether a reserve is protecting exploited fish will be seen as an increase in fish abundance and size within reserves. This has clearly been

demonstrated in reserves around northeastern New Zealand including the CROP Marine Reserve (Willis *et al.*, 2003). Nevertheless, this study indicates that there is a clear potential for cross-boundary migration, with fish moving on spatial scales that take them outside the protection of the reserve. It therefore seems likely that the abundance of snapper within the CROP Marine Reserve might be higher if the reserve were larger in size. The increased abundances recorded inside the reserve suggest that such emigration or spillover is happening at a rate that still allows recovery of snapper populations. Only large-scale mark–recapture studies, combined with intensive studies of catch and fishing effort around the reserve, will definitively answer the question of whether the reserve has resulted in fisheries yield enhancement. Such demonstration will require long-term research commitments.

In the medium term, the implications of the range of movement patterns we have recorded can also be explored for both conservation and fisheries using numerical models. For example, to achieve both conservation and fisheries management goals, marine reserves have to be of sufficient size to protect the target species. The proportion of cross-boundary movement or spillover is likely to decrease for less mobile species or, in larger reserves due to the smaller ratio of perimeter to area (Kramer and Chapman, 1999). This will also be affected by the shape of the reserve as well as topography and habitat suitability of the whole area. If populations are allowed to increase in density inside the reserve, more individuals are likely to be closer to the boundary and exposed to fishing mortality beyond the protected area. The present study suggests that because fish do not display uniform behaviour, even within a single species, using random diffusion models would not be appropriate to model cross-boundary movement. Ultimately, spatial distribution of fish movement patterns needs to be incorporated into models of protected fish populations such as those of snapper inside the CROP Marine Reserve. These models can then be validated by comparison of predicted effects with observed effects from various no-take marine reserves in northeastern New Zealand (Willis *et al.*, 2003).

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