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## Responses to marine reserves: Decreased dispersion of the sparid *Pagrus auratus* (snapper)

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### ABSTRACT

Quantifying the movement of exploited species inside marine reserves is a popular research topic, yet few studies have quantified movement inside and outside of reserves. If individuals inside reserves behave differently to those outside, this information should be incorporated into reserve design and in management efforts to avoid the selective removal of certain behaviors. We used acoustic telemetry to monitor the movements of the sparid *Pagrus auratus* (snapper) inside and outside a marine reserve (the Leigh Marine Reserve, north-eastern New Zealand). We tagged 39 snapper within an array of acoustic receivers that encompassed reserve and fished areas. Nineteen snapper were resident over a 5-month period; the remainder either left the array or died. Residential fish expressed two home range types. One group had uni-modal home ranges that on average encompassed c.900 m linear distance. All nine residential snapper from the reserve displayed this behavior, as well as five of ten residential fish from the non-reserve area. The second group (five fish, all from the non-reserve area) had home ranges with two separate modes (bi-modal home ranges), which on average encompassed c.2 100 m linear distance. We suggest that some aspect of the marine reserve environment encourages extreme residency by either the modification of individual behaviors or through the removal of selective exploitation. If true this suggests that reserves and populations of exploited animals may become dependent on the life history characteristics of the individuals they encourage or select for.

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### 1. Introduction

Understanding the movement dynamics of exploited species is important for the design and justification of marine reserves. Accordingly, many animal movement studies have focused on marine reserves (Attwood and Bennett, 1994; Meyer et al., 2000; Eristhee and Oxenford, 2001; Kelly and MacDiarmid, 2003; Lowe et al., 2003; Parsons et al., 2003; Starr et al., 2004; Edgar et al., 2004; Egli and Babcock, 2004), while other studies have attempted to justify reserves as a conservation tool by investigating the potential for movement from marine reserves into adjacent areas (spill-over) (Russ and Alcala, 1996; Kramer and Chapman, 1999; McClanahan and Mangi, 2000; Roberts et al., 2001; Zeller et al., 2003; Russ et al., 2004; Abesamis and Russ, 2005). Few studies, however, have concurrently tagged fish inside and adjacent to marine reserves, and as a result we have a poor understanding of how factors unique to the marine reserve environment may influence the movement dynamics of individual fish. Some factors that are known to differ inside reserves which may be potentially

important include highly elevated con-specific densities (Willis et al., 2003), habitat differences resulting from trophic cascades (Shears and Babcock, 2002), reduced human disturbance (Eggleston and Parsons, 2008) and the removal (or reduction) of fisheries-induced selection (Biro and Post, 2008). If the behavior of individuals or the behavioral composition of populations is influenced by the above factors then this may be an important consideration for conservation managers designing reserves.

The few studies that have concurrently tagged animals inside and adjacent to marine reserves produced inconsistent results. Attwood and Cowley (2005) found a higher frequency of long distance movements of dart tagged galjoen (*Dichistius capensis*) from a fished site, in contrast to galjoen tagged inside a marine reserve. Conversely, Cole et al. (2000) obtained fewer re-sightings of blue cod (*Parapercis colias*) tagged inside a marine reserve, consistent with larger scale dispersal of blue cod from the marine reserve. Through the tagging of lobsters (*Jasus edwardsii*) inside and outside of a reserve Linnane et al. (2005) observed greater movements of lobsters tagged inside a marine reserve. Finally, Zeller and Russ (1998) observed greater movements of freeze branded coral trout (*Plectropomus leopardus*) inside a marine reserve, but found no difference in the mean distance moved per day (inside vs. outside), when the same comparison was made with acoustic telemetry.

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If managers are to make informed decisions regarding the design of marine reserves then the expected response to protection, which is dependent on animal behavior, needs to be known. The studies listed above and the likely environmental changes expected within reserves both suggest that behavioral responses to marine reserves are not well understood and that either increased or decreased mobility may be expected. If an increase in mobility occurs, this has the potential to reduce the recovery of exploited species but increase supplementation to adjacent fisheries. In this instance managers may therefore wish to scale reserves to ensure that some central portion of the reserve provides complete protection in spite of the higher mobility of the species concerned. Alternatively, a decrease in mobility may suggest that exploited species recovery can be expected in even the smallest reserves. In this situation managers may see benefit in implementing more but smaller reserves. Behavioral responses to reserve implementation may also be opposite for different species or even interact with the habitat in which a reserve is emplaced. Managers may therefore need to prioritize the species for which the reserve is designed or adjust reserve design according to the habitat where the reserve will be located.

In the current study, we examined the movement dynamics of snapper *Pagrus auratus* inside, and adjacent to, the Cape Rodney to Okakari Point (CROP) Marine Reserve, near Leigh in north-eastern New Zealand. Populations of legal sized snapper (>27 cm Fork Length (FL) for recreational and >25 cm FL for commercial fishers) are estimated to be 14 times greater within the reserve than in adjacent fished areas (Willis et al., 2003). The snapper fishery is open to both commercial and recreational fishers throughout the year, although recreational fishing effort has a seasonal pattern, peaking over the austral summer (Hartill, Fishery Scientist, NIWA, unpublished data). Recreational fishers concentrate most of their effort in coastal areas and as such the majority of the snapper catch from the areas around the reserve boundaries is recreational. While accurate estimates of the catch from around the reserve are not available it is likely in the order of multiple tons annually (Hartill pers. comm.). The effect of this exploitation also impacts on lower trophic levels. Algal abundance on exploited reefs is thought to be suppressed by high abundances of herbivorous urchins, *Evechinus chloroticus* that are free of dominant reef carnivores such as snapper and spiny rocky lobster (*Jasus edwardsii*) (Shears and Babcock, 2002).

Multiple tagging studies have been conducted on snapper within the CROP reserve. These studies have confirmed that snapper within the reserve are capable of restricting their movements to small areas of rocky reef (at a scale of hundreds of meters), explaining the higher abundance compared to the adjacent fished waters (Willis et al., 2001; Parsons et al., 2003; Egli and Babcock, 2004). Conversely, movement studies outside the marine reserve have been restricted to broad spatial scale mark-recapture experiments (but see Hartill et al., 2003), focused on snapper from deeper, soft sediment dominated environments (Paul, 1967; Crossland, 1976; Gilbert and McKenzie, 1999). These later studies provided only modest movement information, with poor associated spatial resolution, but did show that snapper can move over areas of many tens of kilometers. Therefore, we made direct comparisons of snapper movement inside vs. outside a marine reserve, by deploying an acoustic tracking array over both a portion of the CROP reserve, and the adjacent coastline, and tagged and released snapper in each. We then assessed the potential for differential movement dynamics between the two areas. Results suggest that reserves do have the potential to alter the behavior or the behavioral make up of individuals or populations, with likely consequences for the design of reserves and the maintenance of biodiversity within exploited populations.

## 2. Materials and methods

### 2.1. Study area and receiver set up

This study was conducted inside and adjacent to the CROP Marine Reserve (Fig. 1) from November 2007 to April 2008. We specifically chose the eastern end of the reserve and the immediately adjacent fished coastline to compare snapper movements, as both of these sections of coast are formed from the same rock type, and have similar topographic relief, bathymetry and exposure to the prevailing wind and swell (predominantly on a SW by NE axis). An array of 30 omni-directional hydrophones (Vemco VR2 W and VR2 receivers, VEMCO, Nova Scotia, Canada) was deployed across the eastern boundary of the reserve, encompassing a similar reserve and non-reserve spatial extent. The array was formed by placing receivers in a grid, forming equilateral triangles with a dimension of 400 m. This spacing was chosen as preliminary acoustic tag range testing showed a decline in tag reception beyond 200 m (Parsons unpublished data). Given this range threshold, we placed the most inshore row of receiver's c. 200 m from land. Receivers were kept in place using a mooring system consisting of a 40 kg steel weight attached by 8 mm polypropylene rope to a 20 cm diameter surface float. Four meters below the surface float, a 15 cm diameter sub-surface float was attached, and 75 cm below this the VR2 receiver was attached using cable ties. This system enabled us to retrieve the VR2 receivers for data down-loads during low tide periods, without having to retrieve the whole system. Receivers were downloaded over one to two consecutive low tides each month, for the 5 month duration of the study.

### 2.2. Tagging procedure

One reserve and one non-reserve area were chosen for the capture and tagging of snapper (Fig. 1). Both areas were of similar spatial extent and were chosen so that fish were tagged near the middle of the reserve and non-reserve sections of the array respectively.

Snapper were tagged over the week of the 16th to the 22nd November 2007 using methods that complied with New Zealand's Animal Welfare Act 1999 and approved by the NIWA Animal Ethics Committee (Application No. 93). Snapper were captured for tagging using hook and line. On capture, each snapper was initially held in a 250 l tank of seawater, and then transferred to an anesthetic bath of 0.3 ml l<sup>-1</sup> 2-phenoxyethanol (Munday and Wilson, 1997). After a fish was immobilized, it was inverted and placed in a sponge cradle, and the incision area de-scaled and sterilized with Tamodine (Vetark products). An incision approximately 2 cm long was made 1 cm from the mid-line of the fish, and 2–3 cm anterior of the anus. The transmitter (V13, 13 mm diameter × 45 mm length, Vemco, Nova Scotia, Canada) was then inserted into the gut cavity. The wound was sealed with absorbable sutures and each fish received an injection of tetracycline antibiotic (50 mg kg<sup>-1</sup> of fish). During surgery, the gills were irrigated with alternate doses of pure seawater and diluted anesthetic to ensure the fish was ventilated, but remained unconscious. Each fish was then transferred back to the 250 l holding tank until it had recovered primary orientation, and was capable of swimming around the tank (usually around 20 min), at which time it was released. All snapper also received an individually coded external dart tag with a 5 cm plastic streamer, to allow identification if later recaptured by fishermen. A total of 19 and 20 snapper were tagged inside and outside of the reserve respectively. An additional tag was retained for testing the detection capacity of the receiver array. Fish size was restricted between 29 and 45 cm FL across both reserve and non-reserve sites, so that any potential

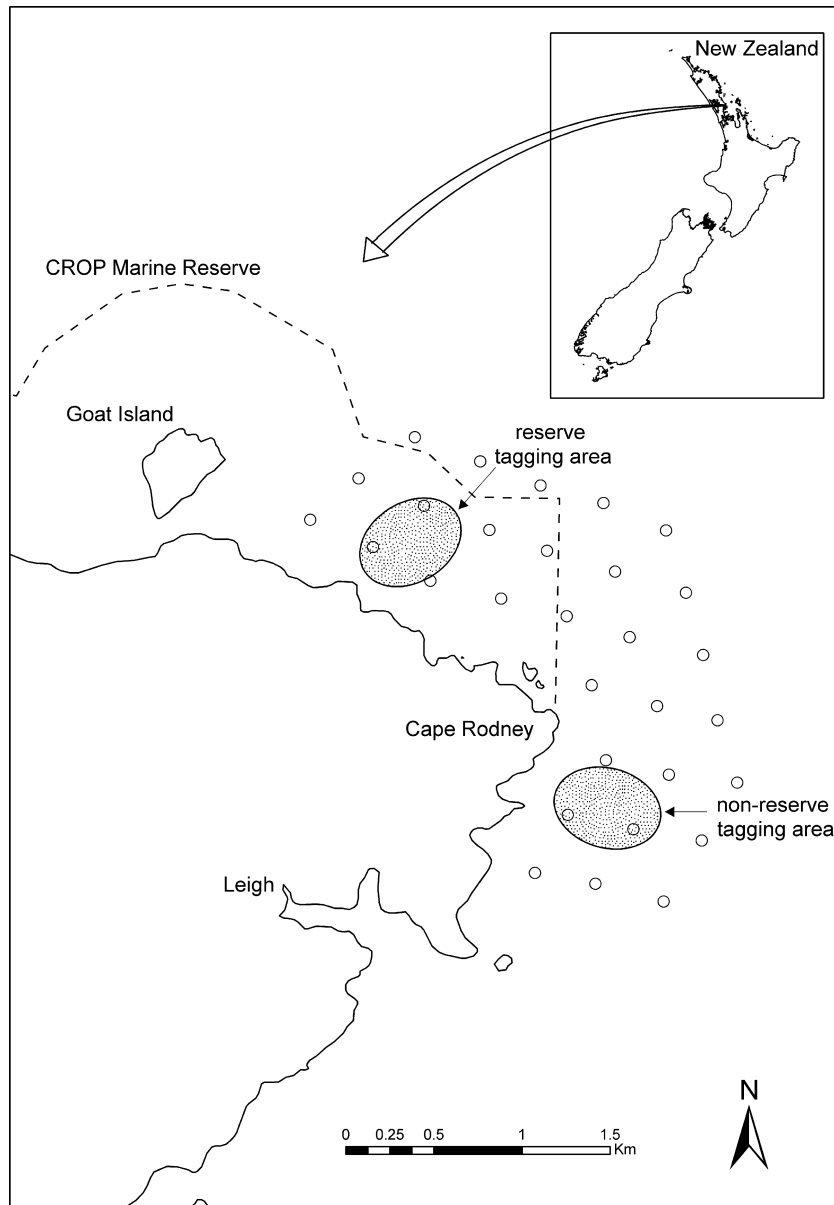


Fig. 1. Map of the study area with New Zealand (inset). Empty circles represent the location of VR2 W and VR2 receivers.

bias towards tagging larger snapper in the marine reserve was avoided. The average size of snapper tagged in each of the two areas was 34 cm. While others (Egli and Babcock, 2004) have randomized the fish chosen for tagging, such a process was not possible in non-reserve areas where a catch rate of only c. three fish of suitable size per day was possible. Therefore to maintain consistency outside vs. inside of the reserve we tagged all snapper caught that were of appropriate size.

### 2.3. Position estimation and testing of the array

We followed the methods of Simpfendorfer et al. (2002) to estimate short-term centers of activity for tagged snapper. This method suggests that the best estimate of a tagged fish's position is the average of the receiver locations (arithmetic mean used here), over some period of time, weighted by the number of receptions at each receiver during that time period (Simpfendorfer et al., 2002). This required that we determine: (1) if there was a linear decay in the

number of signals detected from a tag as it became more distant from a receiver, and (2) an appropriate time interval ( $\Delta t$ ) to perform the position averaging process over. To test for a linear decay in tag detection with increasing distance we attached a tag 2 m from the bottom of a buoyed drop-line, and deployed the tag at 25 random locations within the receiver array, for a 30 min time period at each. For each random location, we measured the distance to the nearest receiver, and compared that distance with the number of detections received during the 30 min time period. All data from the 25 deployments were collated and assessed. A negative linear relationship between the number of signal receptions per minute and the distance from the receiver was observed ( $r^2 = 0.9$ , data not presented). We set  $\Delta t$  to 30 min, long enough to accumulate multiple detections of individual tags (tags transmitted every 2 min on average), but short enough to minimize the potential for longer distance movements to be confounded with residential behavior (through averaging). Previous studies suggest that setting  $\Delta t$  over too long a period would not be an issue in the

current study, as the majority of snapper movements occur within an area less than the current study's 400 m receiver spacing (Parsons et al., 2003).

A potential concern with the mean-position algorithm of *Simpfendorfer et al. (2002)* is that acoustic receivers (or the location that they are in), may have consistently differing performances which could affect the calculation of positions. *Simpfendorfer et al. (2008)* addressed this by assessing performance metrics of individual receiver's, and how they varied through space and time. For the current study we calculated each receiver's code detection efficiency (CDE) on the days when the test tag was used. The CDE provides an estimate of the efficiency of a given receiver (but see *Simpfendorfer et al. (2008)* for a full description) so we used it to modify weightings in the position estimation of the test tag. Both the unadjusted and corrected mean-position estimates were then compared to the true location of the test tag in each random deployment. Correction using receiver CDE produced position estimates that were further from the test tag than unadjusted position estimates (112.7 vs. 88.5 m). We therefore used the standard mean-position algorithm for all position estimates of tagged fish. We are unsure as to why correction for receiver efficiency made position estimation worse, other than to suggest that certain receivers must have been over weighted by the corrections that were made.

#### 2.4. Home range estimation

The half hourly centre of activity positions for all tagged fish were imported into a geographic information system. Only fish that were resident within the receiver array (see Section 3), however, provided enough information to perform meaningful home range analysis. During the final months of the study some receivers were lost due to storm events or propeller strikes. Receivers were replaced when they were discovered to be missing, but holes in receiver coverage were present after 13 January 2008. Missing receivers would likely introduce a significant bias in estimating fish position by any quantitative method. Therefore, home range analysis was restricted to the c. eight week tracking period from mid-November 2007 (when fish were released) until the 13 January 2008, and a qualitative description of fish presence is given for the remainder of the tracking period. The first 24 h of movement data after release was excluded to avoid any behavior related to post-tagging trauma.

We used Hawth's analysis tools for ArcGIS ([www.spatial ecology.com/htools](http://www.spatial ecology.com/htools)) to estimate the 95% and 50% kernel utilization density distribution (UD) as an estimate of each fishes home range. The 95% UD contour is often used to represent the home range of an animal (*Anderson, 1982; Parsons et al., 2003; Jadot et al., 2006; Katajisto and Moilanen, 2006*) and we use the terms synonymously here. Temporal autocorrelation was not a concern in the current study, as data were regularly spaced in time due to the mean-position algorithm. To calculate UD contours, we set  $h_s$  (the space ker-

nel) for each fish as the average value of  $h_{opt}$  from all individuals ( $h_{opt}$  represents an effective method of producing a reference value for  $h_s$  (*Worton, 1989*) and in the current study was equal to 64.25).

### 3. Results

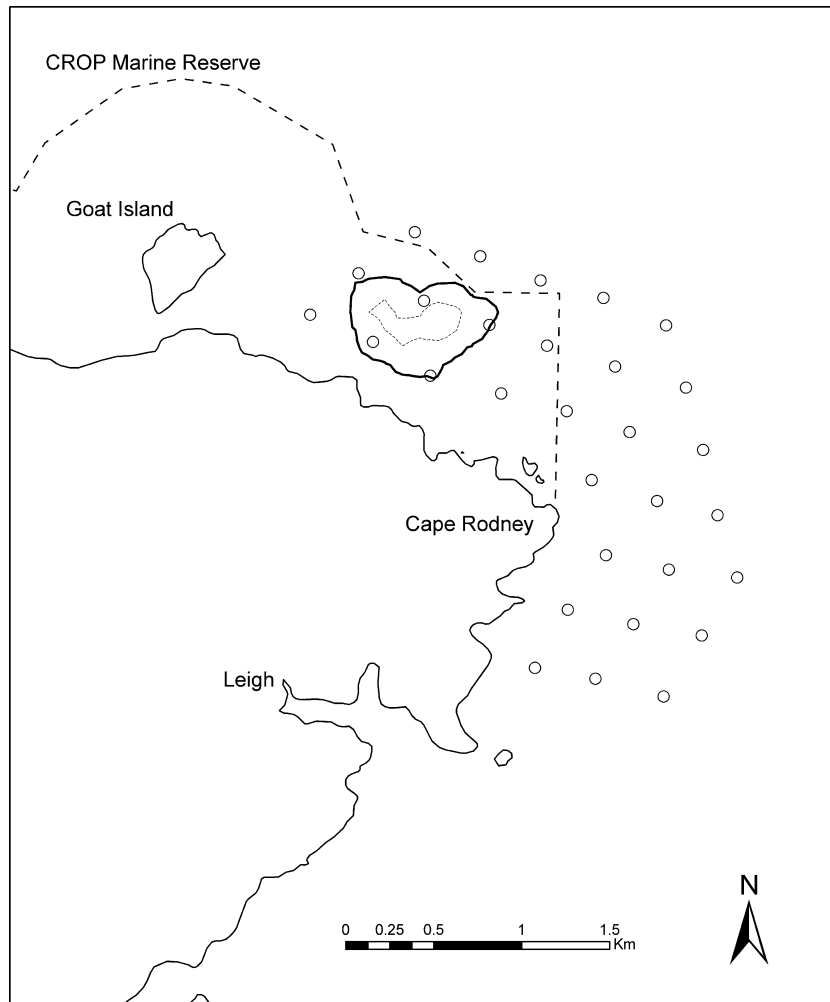
Thirty-nine snapper were tagged inside and adjacent to the CROP Marine Reserve in November 2007. The movements of these fish were monitored by an array of acoustic receivers for 5 months, although only the first 2 months of tracking were completed with a full array of receivers. Individual movement behavior of tagged snapper varied, but fell into three distinct categories. The first category was fish detected frequently throughout the tracking period (present for >65% of available half hour time bins). We defined these fish as residents. The second category of tagged snapper were those detected only very infrequently (present for <5% of available half hour time bins), preventing any meaningful interpretation of their behavior. Their behavior was defined as unknown. Some of these fish were only detected for the first few days after tagging and they probably moved and/or died outside the array detection range. Others were detected more than 15 days after tagging, and were more likely to have been transiently present in the tracking array. Holding tank experiments suggest that mortality from invasive trauma in snapper is minimal after 15 days (*McKenzie, Fishery Scientist, NIWA, unpublished data*). The third category of tagged snapper expressed very restricted movement with associated depth ranges (tags contained pressure sensors), which were exactly synchronized with the oscillations and amplitude of local tides. These fish were determined to have died.

These three behavioral categories were found in similar proportions in both the reserve and non-reserve tagging areas. This suggested that comparable numbers of resident vs. transient snapper were tagged in each area, and that a similar number of snapper from each appeared to have died from tagging related stress (*Table 1*).

Home ranges of resident snapper (defined as those detected frequently throughout the monitoring period) could be split into two further categories. The first spent most of their time utilizing one area. The home ranges of these fish encompassed one main 95% UD area (in some cases a second separate, but small, 95% UD contour was also present) that fully contained one 50% UD (*Fig. 2*). The second category of resident snapper spread the area they utilized over a distance of 1.5 km or more, which in 4/5 cases created the appearance of two centers of activity. Their home ranges took the form of either two separate 95% UD's of similar size, each containing separate 50% UD's (four fish, *Fig. 3a*); or a 95% UD that was elongated over a distance of >1.5 km (one fish) (*Fig. 3b*). This group of fish were defined as bi-modal residents, whereas the former group of fish were defined as uni-modal residents. While the term bi-modal does not strictly apply to all fish in this group, in terms of the size of marine reserve required to encompass a fish's home range all fish in the bi-modal group were functionally very similar. All bi-modal residents located one of their two main areas of use,

**Table 1**  
Summary statistics for tagged snapper, including home range statistics for resident snapper. Numbers expressed as averages  $\pm 1$  standard error (except for sample size column). Behavior categories are defined in the Results section. Home range length is the distance between the furthest extremities of the 95% UD contour. Percentage detected is the percentage of available 30 min time bins each snapper was detected by at least one receiver.

Tagging area	Behavior category	Sample size	Fork length (cm)	Home range area (m <sup>2</sup> )	Home range length (m)	Percentage detected
NR	Uni-modal residents	5	34.1 $\pm$ 0.2	264 934 $\pm$ 35 009	687 $\pm$ 102	89.0 $\pm$ 6.8
	Bi-modal residents	5	36.3 $\pm$ 0.3	454 327 $\pm$ 75 475	2 127 $\pm$ 77	99.2 $\pm$ 0.2
	Unknown	7	32.0 $\pm$ 0.1			1.5 $\pm$ 0.5
	Dead	3	34.5 $\pm$ 0.2			45.0 $\pm$ 20.9
R	Uni-modal residents	9	35.9 $\pm$ 0.2	278 893 $\pm$ 35 745	903 $\pm$ 156	85.2 $\pm$ 7.7
	Unknown	6	32.9 $\pm$ 0.1			1.4 $\pm$ 0.7
	Dead	4	31.4 $\pm$ 0.1			63.4 $\pm$ 14.9



**Fig. 2.** Example of a typical uni-modal home range, in this case for a fish tagged inside the reserve tagging area. Solid line represents the 95% UD contour, dashed line represents the 50% UD contour.

or elongated their home range, to the north of where they were tagged, just inside the marine reserve boundary near Cape Rodney. All of these bi-modal residents moved to the northern most part of their home range within a few days of being tagged, and remained there for time periods ranging from 3 days to 1 month, before returning to the location of original tagging in the non-reserve area. Three out of five of these bi-modal residents then made multiple trips back and forth between the northern and southern parts of their home ranges. These movements were not necessarily on consecutive days. On average bi-modal residents spent 71.6% (standard error = 6.9%) of the time they were detected in the southern part of their home range close to their original tagging location.

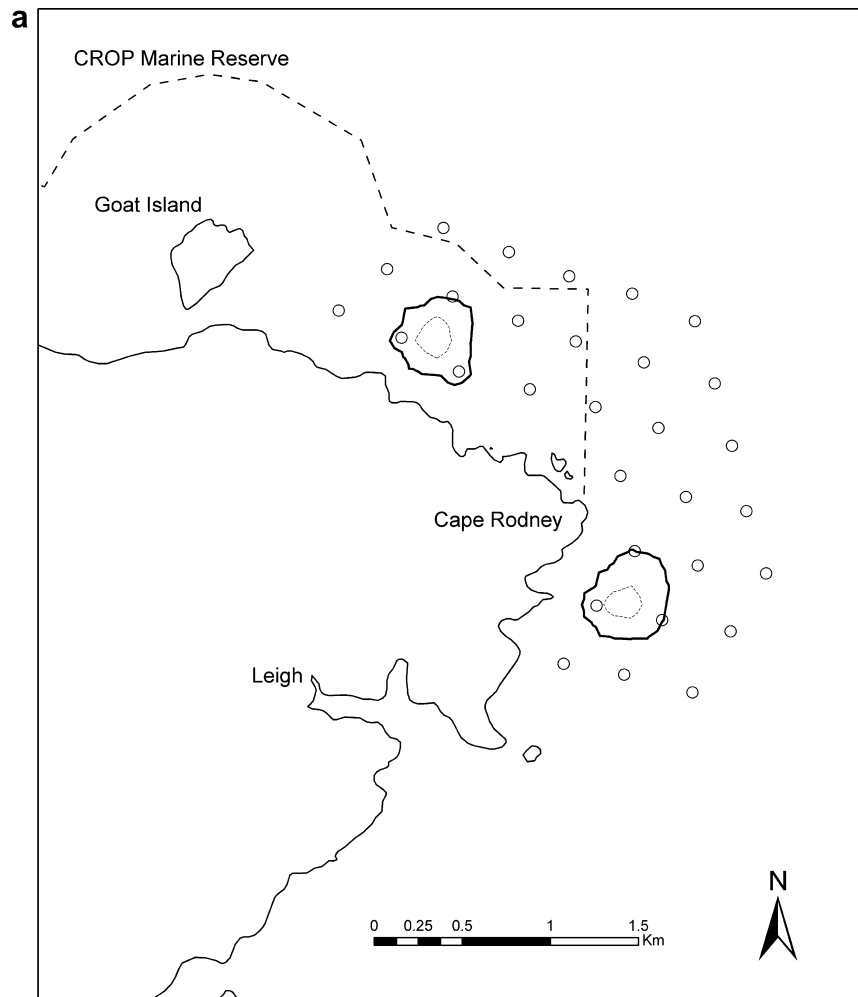
The ratio of tagged snapper expressing uni-modal vs. bi-modal home ranges differed between the reserve and non-reserve tagging areas (Table 1). This dissimilarity was significantly unlikely to occur by chance (Fisher's exact test;  $p = 0.03$ ). An examination of two parameters of home ranges, namely maximum straight line distance between the furthest extremities of the 95% UD contours (referred to as home range length in Table 1), and of the total area encompassed by the 95% UD, was compared across three levels of the factor behavior. These were bi-modal residents, uni-modal residents from the reserve and uni-modal residents from the non-reserve. Assumptions of heterogeneity of variance and normality were assessed and where required data were log transformed for these tests. Straight line distance was significantly greater for bi-

modal residents relative to uni-modal residents from the reserve and non-reserve (1-way ANOVA;  $df = 2$ ,  $F = 11.03$ ,  $p < 0.01$ ); while significant differences in home range area were also found (1-way ANOVA;  $df = 2$ ,  $F = 4.19$ ,  $p < 0.04$ ) between bi-modal residents from the non-reserve tagging area and uni-modal residents from the non-reserve tagging area, but not compared to uni-modal residents from the reserve tagging area.

For the period 14 January–April 2008 we were not able to use the mean-position algorithm method to estimate fish position due to missing receivers. A qualitative assessment of the receiver detections from this period, however, suggested that for the majority of snapper, movements were similar to those during the first 8 weeks of the tracking period. Overall, 8/10 resident snapper from the non-reserve and 8/9 resident snapper from the reserve were detected right till the end of the tracking period; the remaining three resident snapper were not detected for the last 2–4 weeks of tracking. In addition, 2/5 resident snapper with bi-modal home ranges constrained their movements to one mode for the later half of the tracking period.

#### 4. Discussion

This study is one of the first to explicitly compare the movement behavior of an animal inside and adjacent to a marine reserve



**Fig. 3.** Examples of typical bi-modal home ranges for fish tagged in the non-reserve tagging area. (a) Four resident snapper exhibited a bi-modal home range with two discrete areas of use. (b) One resident snapper exhibited an elongated bi-modal home range with connected areas of use. Solid line represents the 95% UD contour, dashed line represents the 50% UD contour.

concurrently. Our results show that some tagged snapper from non-reserve areas utilized space in a different manner from that of snapper tagged in the marine reserve. Specifically, of the resident snapper tagged in the non-reserve area, half had home ranges with more than one main area of use, and as a result their home ranges spanned a linear distance of  $\sim 2127$  m on average. In contrast, of the resident snapper tagged in the reserve, all had home ranges with one main area of use, resulting in home ranges that spanned a linear distance of  $\sim 903$  m on average. This suggests that studies where tagging is only conducted inside reserves may be ignoring important differences in animal behavior associated with the reserves themselves. As a result, incorrect conclusions regarding the design of marine reserves and the recovery of exploited species within them may occur.

In the introduction we listed four studies where tagging had been conducted concurrently inside and outside of reserves. While some of these studies suggested that increased density of individuals within reserves may have promoted increased mobility (Linnane et al., 2005) others suggested that residential individuals were likely to be more abundant inside of reserves through reduced exposure to fishing pressure (Attwood and Cowley, 2005). The inconsistency of these results may be due to their reliance on mark recapture methods. Mark recapture provides little information about the movements of individual animals and results can be biased by the spatial distribution of recapture effort (which was

unknown in many of these studies). The application of acoustic tracking methods allowed us to distinguish small scale differences in residential behavior that would not have been possible through mark recapture. The weakness of acoustic tracking, however, is the restricted spatial range and often small sample size that can be achieved (both discussed below). What our results suggest to managers contemplating reserve design or attempting to interpret monitoring data is that recovery may be expected even in small reserves. Recovery in small reserves, however, may only come about through protection of a behavioral subset of the entire population. The generality of our results is not known and behavioral responses to the reserve environment may need to be assessed on a case by case basis for managers to make prudent decisions.

Home ranges with more than one main, or core, area of use have been previously documented (Eristhee and Oxenford, 2001; Jorgensen et al., 2006; Topping et al., 2006). Explanations for these multiple areas of use include the location of important habitat components (e.g. Jorgensen et al., 2006) and spawning aggregations (e.g. Zeller, 1998). The use of multiple core areas has also been previously observed for snapper (Parsons et al., 2003). These multiple core areas, however, occurred at a different scale to the bi-modal home ranges of the current study (100 m vs. 1–2 km separation) and would not have been detectable with the less accurate positioning of the VR2 receivers used in the current study. Parsons et al. (2003) also documented larger movements ( $\sim 500$  m) which

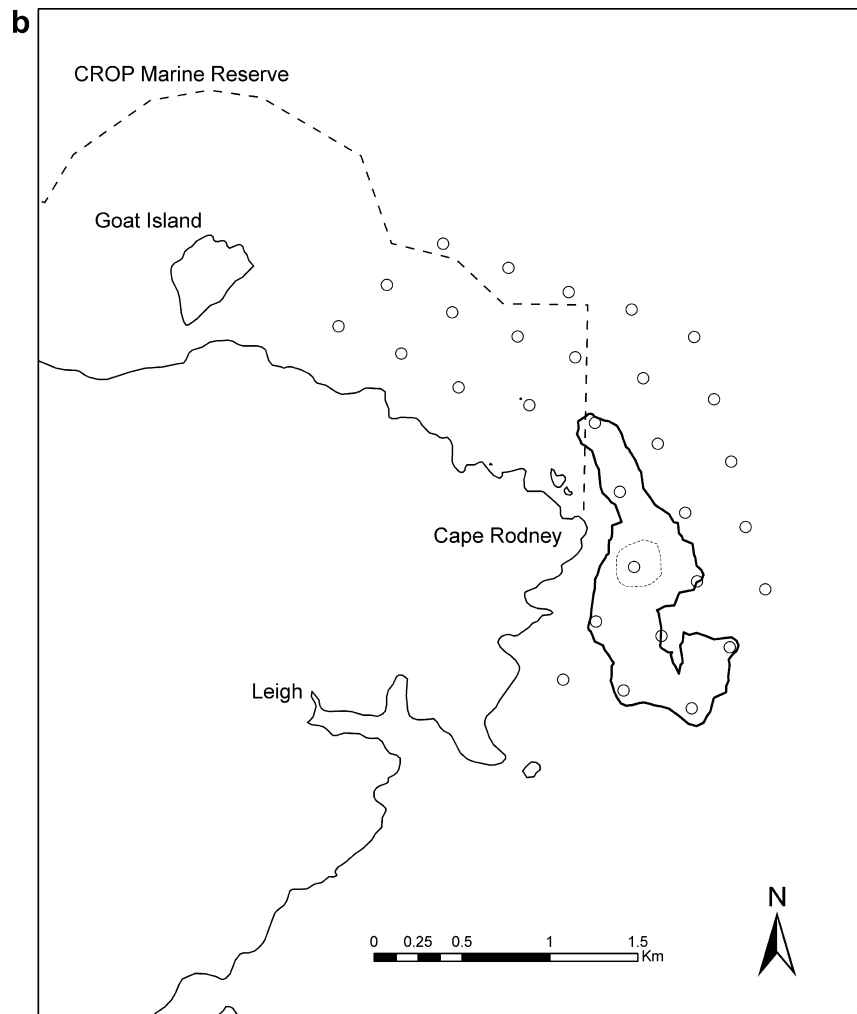


Fig. 3 (continued)

were attributed to be spawning events. While the current study took place when snapper are reproductively active, the bi-modal home ranges were not created by daily movements that were characteristic of the purported spawning events described by Parsons et al. (2003). We do not exclude the possibility that seasonal events such as spawning may alter the home range dynamics of resident snapper to some extent. For instance, qualitative assessment of snapper movements for the second half of the monitoring period suggested that some resident snapper altered their movement behavior during this period. If small scale alterations in home range dynamics did occur outside of the period for which we monitored snapper movements this does not undermine the differences (i.e. bi-modal vs. uni-modal home ranges) observed during the monitoring period. These differences still suggest that some aspect of the marine reserve environment is important to snapper behavior for at least part of the year.

Aside from small scale variation in movement dynamics it is important to note that snapper are capable of dispersion over much greater distances than described in the current study. Previous tagging studies have shown that snapper can move tens to hundreds of km (Paul, 1967; Crossland, 1982; Gilbert and McKenzie, 1999) and seasonal variation in abundance estimates (Willis et al., 2003) indirectly suggest that onshore vs. offshore migrations are likely to occur each year. The snapper we observed as resident within the tagging array may have made similar longer distance movements at a time of year when their movements were not

being monitored. If this occurred for resident fish from the marine reserve it may expose them to fishing pressure for part of the year. It is unlikely, however, that a significant proportion of reserve or non-reserve snapper from this area make annual offshore movements; dart tagging work conducted on these same reefs suggests that these fish are rarely caught away from the location of tagging (<10% recaptured away from the original reef of tagging, Parsons unpublished data). If some portion of the snapper population from these reefs did undertake longer distance movements it seems more likely that the fish described as 'unknown' would be the most likely candidates.

Previous studies where snapper received acoustic tags also contained significant proportions of tagged fish that were poorly detected, presumably through movements outside of receiver range (Hartill et al., 2003; Egli and Babcock, 2004). With this knowledge, it is indeed possible that some of the snapper classed as 'unknown' in the current study may have moved many km from their original capture location. If this were true, we have no evidence that different proportions of reserve vs. non-reserve fish with 'unknown' behaviors undertook long distance movements. The remaining sample size of resident fish was not large (9 reserve residents vs. 10 non-reserve residents), but was sufficient to provide significant evidence that among resident fish, those from the marine reserve were more likely to express levels of extreme residency (uni-modal home ranges) than resident fish from outside of the marine reserve. The suggestion that some level of mixing exists between res-

idental and more mobile snapper is not unexpected and does not preclude any effect of the reserve on the home range dynamics of the resident snapper. Furthermore, we would not expect any effect of the reserve on the more mobile snapper given the scale of the reserve relative to the movements of more mobile snapper.

The restricted nature of acoustic receiver arrays is a factor which limits our ability to explain the observations of the current study. For example, resident snapper tagged in the reserve may have also exhibited bi-modal home ranges, but with one portion of their home range unobserved and to the north of the receiver array. If this were true we would have expected extended periods of absence from the array and a high proportion of detections from the northern edge of the receiver array. Neither of these possibilities was evident in the data collected, and the great majority of time that these fish were at large is accounted for by detections (c. 85% of all available half hour time bins had detections). Alternatively, snapper that were not residents (categorized as 'unknown' in the Results section) may have exhibited bi-modal behavior, but completely outside of the receiver array. This possibility cannot be entirely ruled out, but if this were true we would have expected these fish with unknown behavior types to have returned to the area where they were originally caught (unless they had no degree of site attachment), and therefore to have been detected for periods greater than they were (c. 1.5% of available half hour time bins on average).

A potential criticism of our results is that snapper with bi-modal home ranges may not necessarily be 'non-reserve fish', as their home ranges encompassed areas both inside and outside of the reserve. By chance the same bi-modal fish may have been caught and tagged inside, as opposed to outside the reserve. If this were a likely event we would have expected a mixture of both bi-modal and uni-modal residents to have been tagged inside the reserve. This didn't occur, instead bi-modal residents were only tagged outside of the reserve and the odds of this occurring by chance were significantly unlikely. Furthermore, bi-modal residents spent a much higher proportion of time outside of the reserve (71.6%), close to their original tagging location, than inside the reserve at the northern portion of their home ranges.

Another concern is the proportion of tagged snapper that we classified as dead (7/39). Previous studies that surgically inserted tags into snapper did not experience any mortality, but also did not use tags with depth sensors. We were only able to confirm mortality when tag depth sensors produced oscillations that exactly matched those of local tides. This capacity was not possible in previous studies and suggests that some level of tagging related mortality may have been overlooked.

While the current study did not explicitly investigate the mechanisms that may explain the differences in movement dynamics observed across reserve boundaries, the most likely explanations are linked to the contrasting levels of protection in the two tagging areas. One such explanation relates to the 14 times higher density of legal sized snapper inside compared to outside of the reserve (Willis et al., 2003). This difference in con-specific density may cause snapper within the reserve to restrict their movements to reduce the potential of agonistic interactions. A similar effect of con-specific density has been previously demonstrated on territory size (Norman and Jones, 1984). If differences in con-specific density contributed to the observations in the current study it is unclear exactly how that process would operate as snapper home ranges overlap, often with high densities occupying the same areas (Parsons et al., 2003, D. Parsons pers. obs.).

Another potential explanation relates to habitat differences between the two tagging areas. Within the CROP Reserve reduced abundance's of grazing herbivores exist due to the recovery of dominant carnivores following protection through reserve status.

As a result, reef areas inside the CROP Reserve have a greater abundance of macro-algae relative to adjacent fished reefs (Babcock et al., 1999; Shears and Babcock, 2002). Greater abundance of *Ecklonia radiata* (a large canopy forming brown kelp) and other macro-algae are likely to increase primary productivity and habitat complexity, potentially elevating the abundance of prey items inside the reserve. If snapper food resources per unit area were higher through this process, then snapper could forage over smaller spatial extents than in a non-reserve context, and hence might be expected to have smaller home ranges. Surveys of benthic invertebrates however, suggest that some potential food items of snapper (including the dominant urchin, *Evechinus chloroticus*, the limpet *Cellana stellifera* (Shears and Babcock, 2003) and the infaunal bivalves *Dosinia subrosea* and *Myadora striata* (Langlois et al., 2005)) are actually less abundant inside the reserve (although one gastropod, *Cookia sulcata*, is more abundant inside the CROP Reserve). Given the above observations, it seems unlikely that differences in the abundance of benthic prey items explain the observations of the current study. The differences in home range dynamics that were observed, however, may be a simple response to the increased shelter offered by the higher abundance of *Ecklonia radiata* inside the reserve.

The final explanation we present is that fish inside the reserve may be differentially exposed to fishery induced selection, dependent on their movement behavior. In this scenario, individuals with small home ranges that are centered within a reserve will not often cross over the reserve boundaries, and in turn will be much less likely to be removed by fishing. For individuals with home ranges outside of reserves no such selection pressure will exist as all individuals are exposed to the fishery all the time, regardless of movement behavior. Similar predictions have been made with respect to the recovery of mobile vs. resident species inside reserves (e.g. Kramer and Chapman, 1999); here we simply extend that premise to encompass within species variability. It is important to note that we are not implying that evolution of home range size is occurring within the reserve because there is no likely mechanism for the progeny of extreme residents to also recruit to reserves. What we are suggesting, as one explanation of our observations, is that contrasting fishing pressure across reserve boundaries and individual differences in movement dynamics may determine the likelihood of survival for animals with home ranges centered in reserves.

Theoretical modeling studies have suggested that selection can act on individual differences in dispersal (Travis and Dytham, 1998) and that reserves may impose selection that favors reduced dispersal (Baskett et al., 2007; Miethe et al., 2009). Less common, however, is empirical evidence supporting these theoretical studies. What has been empirically demonstrated is that individual behavior (in this case activity and boldness) can be selected against by exploitation (Biro and Post, 2008). Far more attention, however, has been devoted to documenting spill-over and the influence of con-specific density on fish movement (Russ and Alcala, 1996; Kramer and Chapman, 1999; McClanahan and Mangi, 2000; Roberts et al., 2001; Zeller et al., 2003; Russ et al., 2004; Abesamis and Russ, 2005). While a more general approach to the potential outcomes of marine reserves may be prudent, the increased residency observed in the current study in no way precludes spill-over from occurring. Spill-over is likely to occur through discrete home range relocation events (Abesamis and Russ, 2005), which are compatible or even complimentary with our results. For example, the lack of wider dispersing residents within the reserve may suggest that those wider dispersing fish had been caught during cross boundary movements.

The results presented in the current study have important conservation implications for marine reserves and the management of fish stocks and biodiversity in general. First, the unanticipated responses of animal behavior to marine protection emphasize the ex-



tent to which exploitation modifies the entire environment outside of reserves. This suggests that holistic conservation measures such as reserves are a useful addition to single species management. Second, we might expect that some mobile animals will unexpectedly respond to reserve protection through behavioral responses to the reserve environment or selection of the most residential individuals inside reserves. In addition, as reserve size increases relative to the movement range of an exploited species we would anticipate a different mix of behavior types to be contained within that reserve. This has important implications for the design of reserves, suggesting that extensive knowledge about animal behavior may be required if the full impact of reserves is to be anticipated. Third, the behavioral diversity demonstrated in the current study may complicate the way a population responds to exploitation. For example, an exploited population consisting of both resident and mobile individuals may be sustainably exploited overall, but contain pockets where residents have been removed. Such localized depletion may have severe consequences for the surrounding environment. For example, reduced abundance of resident snapper was likely a major factor contributing to reduced algae biomass and primary production in rocky reefs in north-eastern New Zealand (Babcock et al., 1999; Shears and Babcock, 2002). Ensuring that a full suite of behavioral repertoires exists within reserve populations may be an important consideration in the design of reserves. Furthermore, if the behavioral diversity expressed within a population is fixed then selective removal of those behaviors may lead to a reduction in biodiversity at the behavioral level. In a worst case scenario this may also lead to an overrepresentation of individuals with undesirable traits (Cooke et al., 2007). Marine reserves are likely to be the best approach of protecting against such losses in biodiversity, however identifying the behavioral diversity that exists is a prudent first step. Clearly we require a greater understanding of the response of animal behavior to reserves and exploitation. These responses may not always be anticipated but have the potential to determine the success of reserves and the management of exploited species.

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