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Snapper *Pagrus auratus* (Sparidae) home-range dynamics: acoustic tagging studies in a marine reserve

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ABSTRACT: The home-range size and location of reef-associated snapper *Pagrus auratus*: Sparidae were investigated by use of a radio acoustic-positioning telemetry (RAPT) system. Tags were surgically implanted in 5 snapper that were monitored every minute for a period of 5 mo, and then intermittently over a period of 1 yr. Site fidelity was high amongst these fish, with home ranges not exceeding 650 m in diameter or 139 600 m^2 in area. Eleven other snapper received tags by feeding and were tracked for periods of up to 2.5 d. Site fidelity was also high for these fish, with standardised estimates of home-range size not differing between the 2 groups. Home ranges overlapped considerably, indicating that the fish were not territorial. The location of the home ranges generally remained stable throughout the entire tracking period, although 1 fish relocated its home range by ~220 m. A new method of home-range estimation was developed, which matched the level of detail provided by the RAPT system, to directly estimate the time spent in an area. The relevance of this method and the residential behaviour of these fish are discussed, with reference to the general understanding of animal behaviour, previous investigations into snapper movement, and the selective capacity that may be imposed by marine reserves on fish behaviour.

KEY WORDS: *Pagrus auratus* · Snapper behaviour · Home range · Site fidelity · Residency · Utilisation distribution · New Zealand · Marine reserve

INTRODUCTION

The home-range parameters of animals interest biologists for 2 main reasons (Schoener 1981). First, home-range size can be related to feeding strategy, food density, resource use, metabolic demands, behaviour and efficiency of movement. Second, home-range characteristics can reflect both inter- and intraspecific interactions. Home range parameters interest conservationists and fisheries managers through their direct application to species management. For example, an understanding of fish home-range or behaviour is crucial to the effectiveness of marine reserve design (Roberts & Polunin 1991, Attwood & Bennett 1994, Holland et al. 1996, Zeller 1997, Allison et al. 1998, Woodroffe & Ginsberg 1998, Kramer & Chapman 1999, Willis et al.

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2000). Whether the reserve's goal is to increase fish abundance within the reserve (i.e. to protect brood stock) or to supplement the adjacent fishery through the emigration of fish or larval production from the reserve, both of these goals could be fulfilled by a spatial restriction on fishing. However, the size of the reserve relative to the mobility of the fish will influence the degree to which reserve population recovery is undermined by emigration to fished areas. Theoretically, a species with intermediate dispersal capabilities, relative to reserve size, should provide a balance between emigration to the fishery and accumulation of brood stock (DeMartini 1993). Species with higher mobility would not reside within the reserve long enough to receive significant protection, while highly resident species would recover the fastest but would have low emigration rates to fished areas.

In NE New Zealand, snapper *Pagrus auratus* (Sparidae) form the basis of the largest commercial and recreational fishery (Annala et al. 1999). Snapper are also the most abundant carnivorous fish within the inshore areas of northern New Zealand (Paul 1976), and are important at economic, cultural and ecological levels. For this reason marine reserve designs in NE New Zealand should optimise the effective protection of snapper. A well-designed reserve would maximise snapper biomass and therefore increase egg production (e.g. Willis et al. 2003), as well as have the potential to benefit the fishery through emigration of adults. If these goals are achieved, reserves may allow ecosystem 'recovery' by elevating snapper abundances to a level where exertion of top–down processes could regulate lower trophic levels, altering community structure and productivity to a state reflecting the absence of fishing (Babcock et al. 1999, Shears & Babcock 2002).

Despite their local importance, current knowledge of home-range and space-use characteristics of snapper is lacking. There is evidence suggesting that both resident and mobile behaviours are exhibited by snapper. For example in Shark Bay, Western Australia, tagged snapper from within the gulfs of Shark Bay were not recaptured more than 42 km from where they were tagged, whereas snapper from the open coast were recaptured up to 322 km from the tagging site (Moran 1987). In New Zealand similar results have been gathered from tagging studies. The majority of recaptures have been within 20 km of the tagging location, but some snapper were recaptured up to 418 km from the site of tagging (Paul 1967, Crossland 1976, Gilbert & McKenzie 1999).

Within the Cape Rodney to Okakari Point (CROP) Marine Reserve, the site of this study, the density of snapper above minimum legal size is 16 times greater than in adjacent fished areas (Willis et al. 2003). As the reserve only encompasses 5 km of coastline, the elevated densities alone suggest a degree of site fidelity. Berquist (1994) investigated this residency by acoustically tagging 2 snapper within the reserve. Both fish remained within an 800 m diameter for 2 and 5 d, respectively. Using individually coded elastomer tags, Willis et al. (2001) marked 117 snapper within the CROP Reserve. Forty-nine of these fish were resighted repeatedly over several months, and the greatest distance between relocations was only 500 m.

The aim of this study was to describe the movements of 'resident' snapper within the CROP Marine Reserve, using a radio-acoustic positioning and telemetry (RAPT) system to accurately track individuals over periods of a few months. The positional fixes provided by the RAPT system were often very frequent (every minute), but not provided at regular intervals. Due to this irregular sampling frequency, we present a new method of estimating home ranges where time is used as the contouring variable. Of further interest were (1) any changes in the home-range size and location over a period of months; and (2) differences between the home range parameters of snapper that were fed tags and those that had tags surgically implanted.

MATERIALS AND METHODS

Experimental area and procedure. This study was conducted in the CROP Marine Reserve primarily from January to June 2000, although further, less frequent observations were made through to January 2001. During this time snapper were continuously tracked via the use of a RAPT system (VEMCO). This system allowed accurate positioning (±1 to 2 m) (O'Dor et al. 1998) of individual fish, with a temporal resolution of minutes. Each monitored snapper contained a transmitter (pinger) that broadcast on a frequency unique to that individual. The ultrasonic signal transmitted from each fish was then received by 3 moored sono-buoys that relayed data to a land-based computer by radio signal. The computer then triangulated the position of the fish based on differences in arrival time of the signals. The sono-buoys were placed in a triangular configuration, approximately 300 m apart, within Goat Island Bay (Fig. 1). This area was chosen for its high abundance of snapper, shelter and the presence of shallow reef-habitat.

This study used V16 and V8 transmitters, also made by VEMCO. Five snapper (Table 1) received surgically implanted V16 transmitters. These V16 transmitters, ~16 mm diameter and 7.5 cm length, had a battery life conservatively estimated at 120 d (but were found to last much longer in water temperatures of 16 to 20°C). This allowed long-term detailed monitoring of snapper movements. The V8 transmitters (~8 mm diameter and

45 mm length) were small enough for snapper to swallow *in situ* , encased in bait, without any handling of the fish. The transmitter would be retained for ca. 2 d before passing through the body, at which time the transmitter could be relocated and retrieved using a diver-operated receiver (VUR96, VEMCO). The transmitter could then be fed to another fish. A total of 11 snapper from ca. 250 to 450 mm fork length (FL) were monitored for ca. 2 d each, by use of V8 transmitters (Table 1).

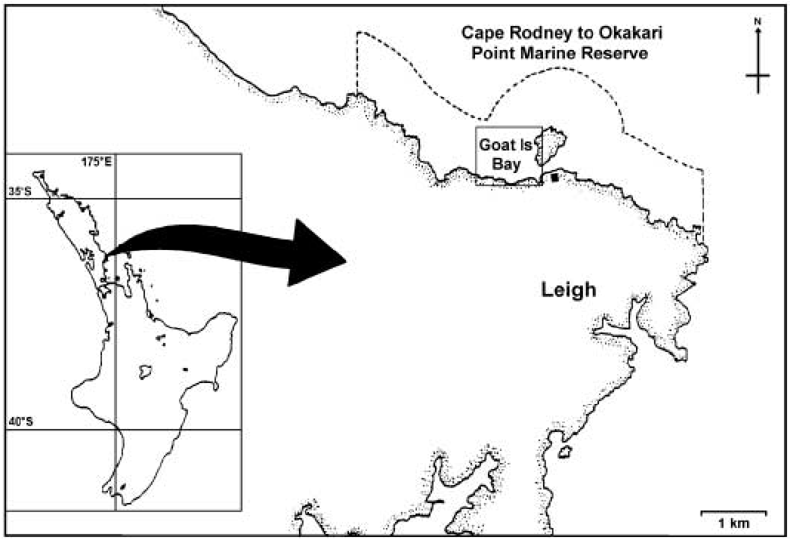

Fig. 1. Location map of North Island, New Zealand, and study area

Fish capture, handling and surgery. Snapper were caught from the CROP Reserve on hook and line, using modified barbless hooks (see Willis & Millar 2001) to reduce injury and the probability of 'gut hooking'. Surgical procedures followed the methods described by Zeller (1997). After capture, each fish was retained in an aquarium tank for 24 h to reduce stress levels before surgical insertion of ultrasonic transmitters. Fish were anaesthetised with clove oil at 0.27 ml l^{-1} (Munday & Wilson 1997). After the fish had become immobile it was placed in a sponge cradle and the incision area was de-scaled and then sterilised with Tamodine (Vetark products). An incision approximately 2 cm long was made 1 cm from the mid-line of the fish and 2 to 3 cm anterior of the anus. The transmitter was then inserted into the gut cavity. The wound was sealed with nylon sutures and each fish received an injection of tetracycline antibiotic (50 mg kg^{-1} of fish). During surgery the gills were irrigated with alternate doses of pure seawater and diluted anaesthetic to ensure the fish was ventilated but remained unconscious. Each fish was then left to recover for at least 24 h in an aquarium tank before release at the site of capture. No mortality occurred during this process.

Table 1. *Pagrus auratus.* Summary details of fish receiving V8 tags (via feeding; fish no. beginning with F) and V16 tags (implanted; fish no. beginning with S). FL: fork length

Fish no.	Fish size (mm FL)	Date released (dd/mm/yy)	Days monitored
F1	325	09/03/00	2.3
F2	400	15/03/00	2.5
F3	450	20/03/00	1.0
F4	400	20/03/00	0.8
F5	300	22/03/00	1.2
F6	300	24/03/00	1.9
F7	400	27/03/00	0.3
F8	375	28/03/00	0.2
F9	350	13/04/00	1.6
F10	400	16/05/00	2.0
F11	250	19/05/00	0.8
S4	426	24/01/00	130
S2	415	24/01/00	141
S3	532	24/01/00	141
S1	400	30/01/00	141
S5	515	04/02/00	135

After release, manual relocations of tagged fish were made using a hand-held directional hydrophone (VR60) and a diver-operated hand-held receiver (VUR96). These were also used to record additional fish locations after the RAPT system had been removed from Goat Island Bay. All snapper were also tagged with individually coded fluorescent elastomer tags implanted in the caudal fin membranes (Willis & Babcock 1998) to allow *in situ* visual identification.

Data processing. Using the programming software *Octave*, Version 2.0 (Eaton & Rawlings 1995), the locations of each fish were recalculated from the 'R-files' generated by the RAPT system. This procedure was required because the software provided by VEMCO only recorded the average of each series of positions ('D-files'). This meant that data would have been lost through an unquantified averaging process. After all raw positions had been calculated, the data were smoothed by the following set of criteria: (1) If a location was calculated more than 1000 m from the centre of the buoy array it was deleted. VEMCO specify that the RAPT system can detect pingers up to 1 km from the buoy array (O'Dor et al. 1998), however accuracy decreases rapidly beyond this distance. (2) While the tracking system was receiving data, certain files were noted to contain obviously erroneous buoy positions, due to spurious signals during rough weather (>20 knots wind speed). Data received during these noted periods were also deleted. (3) Spurious points were removed by the following algorithm: Between each triplet of consecutive fixes, the 2 speeds (Point 1 to Point 2 and Point 2 to Point 3) were calculated. If the minimum of these 2 speeds exceeded a certain maximum swimming speed, the middle point was deleted; typically, Points 1 and 3 were within a metre or so of one another, and Point 2 was hundreds of metres away. This process was applied recursively until no 2 consecutive fixes were separated by a speed exceeding the maximum swimming speed. The precise value of the maximum swimming speed was not critical; using values between 1 and 10 m s^{-1}, we applied this algorithm to positions obtained from an acoustic tag secured in a known location. This resulted in only slightly differing smoothed datasets. Because maximum swimming speeds for snapper (or indeed other sparids) are not known, a conservative value of 4 m s^{-1} was used. This value is consistent with the work of Blaxter & Dickson (1959), who specified a maximum swimming speed of ~2 to 3 m s^{-1} for Atlantic mackerel *Scomber scombrus*. In addition, measurement of snapper swimming speeds observed here did not exceed 0.5 m s^{-1}.

Home range estimation. To estimate home ranges from smoothed data, the tracking area was divided into a grid composed of 20 × 20 m bins. The amount of time individual fish were detected in each of these bins was then calculated using software written in Matlab™ (MathWorks 1998). This required 2 assumptions to be made: (1) The fish swam in a straight line between consecutive positional fixes as long as these fixes were not more than 30 min apart. Although the RAPT system attempted to locate a fish every minute, if the fish's acoustic signal was obscured by sea-floor structures or wave-generated noise, a fix would not be achieved. Therefore, a time lapse of greater than 30 min between fixes could occur. (2) The speed at which the fish swam between these 2 points was constant and equal to the distance divided by the time elapsed between 2 consecutive positional fixes. This allowed the location of the fish to be estimated between fixes as long as the tracking system located the fish every 30 min or less. In this way, an estimate of the amount of time a fish spent within each bin of the tracking area was obtained. These bin times were then contoured in ArcView, Version 3.2 (ESRI 1999), using the default values set for proximity assignment. Each of these contours represented the percentage of time that an individual fish resided within that area. For example, the 95% contour represented the area within which a fish spent 95% of its time. We follow Anderson (1982) in using this value to define an animal's home range. Within the home range, discrete core areas were defined as areas of >50% usage that were >40 m in diameter. For fish that received pingers by feeding, the entire period of tracking was represented in 1 home-range estimate. For fish that received pingers surgically, a longer time-series of data was available. To monitor the consistency of movements, separate home-range estimates were calculated for each of these fish over 4 time periods. These were chosen in order to represent the time between new moons, as a precaution to eliminate any unknown lunar effect on snapper behaviour, and were: (1) 6 February to 6 March; (2) 6 March to 5 April; (3) 5 April to 4 May; (4) 4 May to 3 June.

RESULTS

LONG-TERM RESIDENCY

All 5 surgically tagged snapper remained attached to areas within the detection range of the tracking system (ca. 1000 m), from the time of release (January or February 2000) until the cessation of this study (June 2000). After continuous tracking ceased, 4 of these snapper were relocated 50 wk after they were originally released, using a diver-operated receiver. All relocations were within the same home ranges previously occupied by the fish. By mid-February 2001 no fish could be detected, which was probably due to the expiration of pinger batteries. By this time the pinger batteries were >200 d past their previously estimated capacity.

Home range and utilisation distribution

Surgically tagged fish

The home-range area of the 5 surgically tagged snapper varied between 13 960 and 230 000 m^2, whereas the area contained within the 50% contour varied from 1700 to 14 800 m^2 (Table 2, Figs. 2 to 7). The largest average home range of an individual was 3.5 times greater than the smallest (i.e. 99 500 m^2 for Fish S1 vs 28 400 m^2 for Fish S5). Perhaps the best illustration of this individual variation was the contrasting movements of Fish S2 and S4. For the second monitoring period, Fish S2 spent 30.4% of its time within one 20 × 20 m bin, while for the third monitoring period the highest per-bin usage for Fish S4 was only 1.3%. There was no evidence of territoriality, as home ranges and core areas overlapped considerably (Figs. 2 to 7).

The size of individual home ranges changed with time, but not consistently. Between the first and last monitoring periods 3 fish increased and 2 fish decreased their home-range areas. For example, Fish S2 (Fig. 3) increased its home-range area by 24% between February and June. The size of the 50% contour did not always remain in constant proportion to the

Table 2. *Pagrus auratus.* Home-range summary statistics for surgically tagged snapper. Each monitoring period represents a full lunar cycle

Fish no.	Monitoring period	Area within 95% contour (m^2)	Area within 50% contour (m^2)	Most intensive usage per 20 m bin (%)	50:95 % ratio (%)	No. of core areas	Movement of each core area (m)
S1	1	80 600	10 300	6.5	12.78	1	
	2	139 600	9 900	6.4	7.09	1	32.2
	3	90 700	14 800	3.8	16.32	1	9.8
	4	87 100	13 600	5.4	15.61	3	9.4
	Average ± SE	99 500 ± 13 500	12 200 ± 1200	5.5 ± 0.63	12.95 ± 2.10	1.5 ± 0.5	17.1 ± 6.52
S2	1	43 800	2100	21.2	4.79	1	
	2	29 400	1200	30.4	4.08	1	5
	3	43 600	2400	14.9	5.50	2	3
	4	35 400	1800	23.7	5.08	1	3.6
	Average ± SE	38 000 ± 3500	1900 ± 300	22.6 ± 3.2	4.87 ± 0.30	1.3 ± 0.25	3.9 ± 0.51
S3	1	54 400	7700	9	14.15	2	
	2	46 200	6000	11.9	12.99	2	1.0 and 37.0
	3	52 400	5800	12.3	11.07	2	8.1 and 17.5
	4	69 600	7700	12	11.06	2	12.4 and 34.0
	Average ± SE	55 600 ± 5000	6800 ± 500	11.3 ± 0.77	12.32 ± 0.76	2	7.2 ± 2.88 and 29.5 ± 6.49
S4	1	46 700	1700	5.4	3.60	1	
	2	61 200	7200	1.4	11.76	4	219.1
	3	56 200	5400	1.3	9.61	2	10.4 and 57.8
	4	60 300	5300	1.6	8.79	2	10.0 and 94.6
	Average ± SE	56 100 ± 3300	4900 ± 1200	2.4 ± 1	8.45 ± 1.72	2.3 ± 0.63	79.8 ± 60.30 and 76.2 ± 13
S5	1	35 800	1900	4.1	5.31	2	
	2	23 000	2500	3.9	10.87	2	5.4 and 5.4
	3	24 800	2300	4.2	9.27	1	16.8
	4	30 000	2700	3.7	9.00	1	9.9
	Average ± SE	28 400 ± 2900	2300 ± 200	4.0 ± 0.11	8.61 ± 1.17	1.5 ± 0.29	10.7 ± 2.44
Overall average ± SE		55 500 ± 6200	5600 ± 900	9.2 ± 1.80	9.44 ± 0.87	1.7 ± 0.18	32.1 ± 10.71

size of the overall home range. However, the 50% contour was always between 3.6 and 16.3% of the size of the overall home range. Individual variation of this ratio provided a good indication of the level of residency within the home range. In general, as home-range size increased, so did the area contained within the 50% contour. For example, Fish S1 had both the largest average value for its home range and also the largest average area within the 50% contour (12 200 m^2) (Table 2), producing an average 50:95% ratio of 12.95%. This was the highest 50:95% ratio observed here, indicating that this fish used the space within its home range more evenly than the other fish tagged in this study.

All 5 fish had more than 1 core area for at least 1 of the monitoring periods. For all fish, except Fish S4, the core areas were relatively stable in location, moving no more than 37 m between monitoring periods. By visually following the shape of an individual fish's home range over the 4 monitoring periods, it was possible to confirm that the shape of the home range and the location of the most intensively used areas remained relatively constant (Figs. 2 to 7). Core areas appeared (Fig. 2d) and disappeared (Fig. 3c,d), but home ranges generally appeared to have been oriented around a consistent core area. This 'main' core area was not necessarily at the centre of the home range.

The exception, Fish S4, shifted its home range between 6 March and 5 April by ~220 m (Fig. 5a,b). During the second monitoring period (Fig. 5b), a series of core areas from west to east was exhibited. This presumably represented the different areas this fish resided in as it was shifting home range over the period of 1 mo. In the last 2 monitoring periods the eastern-most part of these core areas became stable. The completeness of this home-range shift is further emphasised by the fact that after April the fish did not return to its previous core area.

Fish tagged by feeding

The home range size of snapper that were fed tags varied between 3900 and 50 329 m^2, and the area

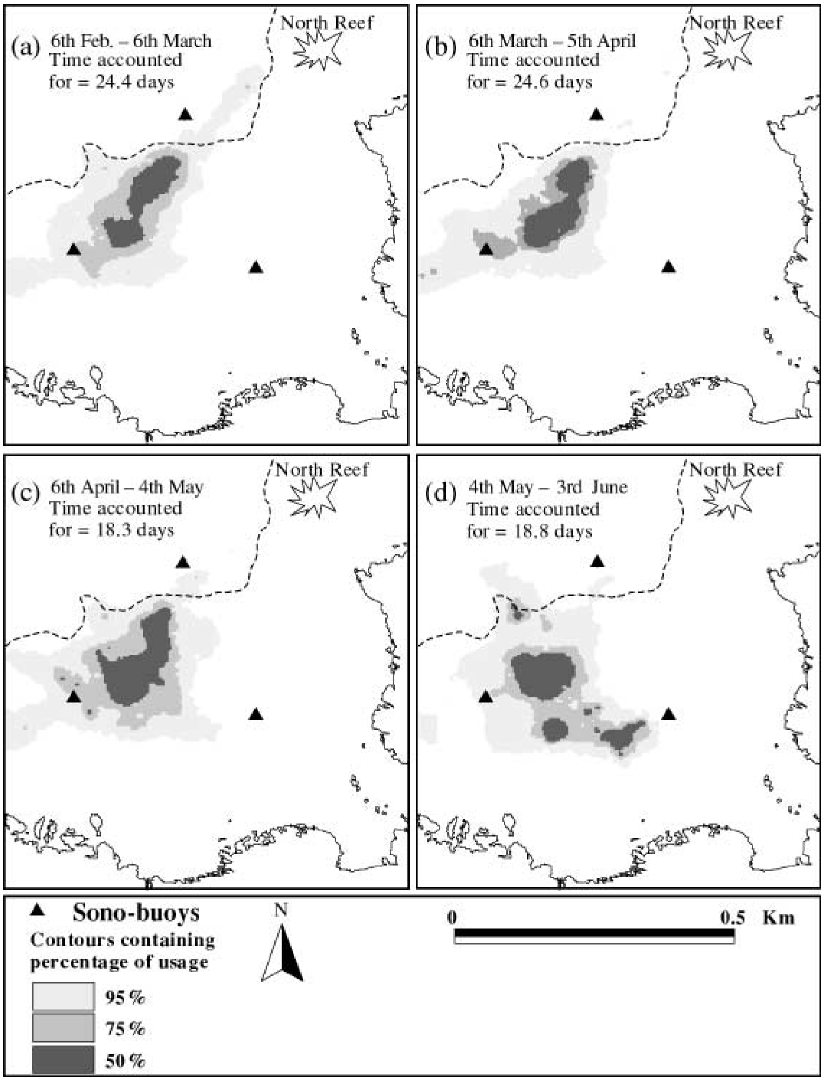

Fig. 2. *Pagrus auratus.* Home range and utilisation distributions of Fish S1 (400 mm fork length) for 4 lunar cycles between February and June 2000

within the 50% contour varied from 122 to 2901 m^2 (Table 3, Fig. 7). The highest per-bin usage intensity ranged from 12.2 to 43.6%, while the number of core areas was either 1 or 2.

The home-range sizes and areas of 50% usage for these fish were similar, but generally smaller than those of the snapper that received surgically inserted tags. Accordingly, the highest per-bin usage values were generally greater than those of the surgically tagged snapper. This was due to the short monitoring time, 0.1 to 2.3 d, relative to surgically tagged (minimum of 6.7 d) snapper. To account for these differences, 11 portions of data were selected, each with a length equal to one of the monitoring periods of fish tagged by feeding. Home ranges were then estimated for these randomly selected portions of data. Paired comparisons of these randomly selected home ranges and the home ranges of fish tagged by feeding revealed no significant difference (Wilcoxon signed rank sum, $p > 0.05$). This indicated that both tagging methods produced similar range estimates, but also that shorter monitoring periods underestimated the true extent of a fish's movements. The relationship between home-range size and the duration of the calculation period was

Table 3. *Pagrus auratus.* Home-range summary statistics of snapper that received tags by feeding

Fish no.	Area within 95% contour (m^2)	Area within 50% contour (m^2)	Most intensive usage per 20 m bin (%)	50:95% ratio (%)	No. of activity centres
F1	26 235	1965	16.1	7.49	1
F2	18 290	433	17.6	2.37	1
F3	17 097	1355	12.2	7.93	2
F4	12 297	813	13.3	6.61	1
F5	10 345	1138	31.2	11.00	1
F6	23 998	1342	14.6	5.59	2
F7	50 329	2901	12.7	5.76	2
F8	3 877	325	40.7	8.38	1
F9	13 666	1084	17.0	7.93	1
F10	11 226	976	31.2	8.69	1
F11	11 117	122	43.6	1.10	1
Average ± SE	18 648 ± 3757	1114 ± 238	23.9 ± 3.53	6.62 ± 0.86	1.3 ± 0.14

further investigated. Home ranges were estimated for randomly selected portions of data with lengths between 1 and 30 d. While there was large variance, most probably due to differences between individual fish, it appeared that home range size stabilised when ≥7 d of monitoring were used in the calculation (Fig. 8).

Response to human activity

While using the diver-operated receiver, numerous attempts were made to visually re-sight each of the surgically tagged snapper. On every occasion, the tagged fish would allow divers to approach to a close distance, as indicated by the signal strength on the receiver, but would not come within the diver's visual range, regardless of water clarity. These surgically tagged snapper maintained this behaviour for the duration of the study (>5 mo). In marked contrast, snapper that received tags via feeding were not as cautious, and the pinger signal led to visual relocation on every attempt.

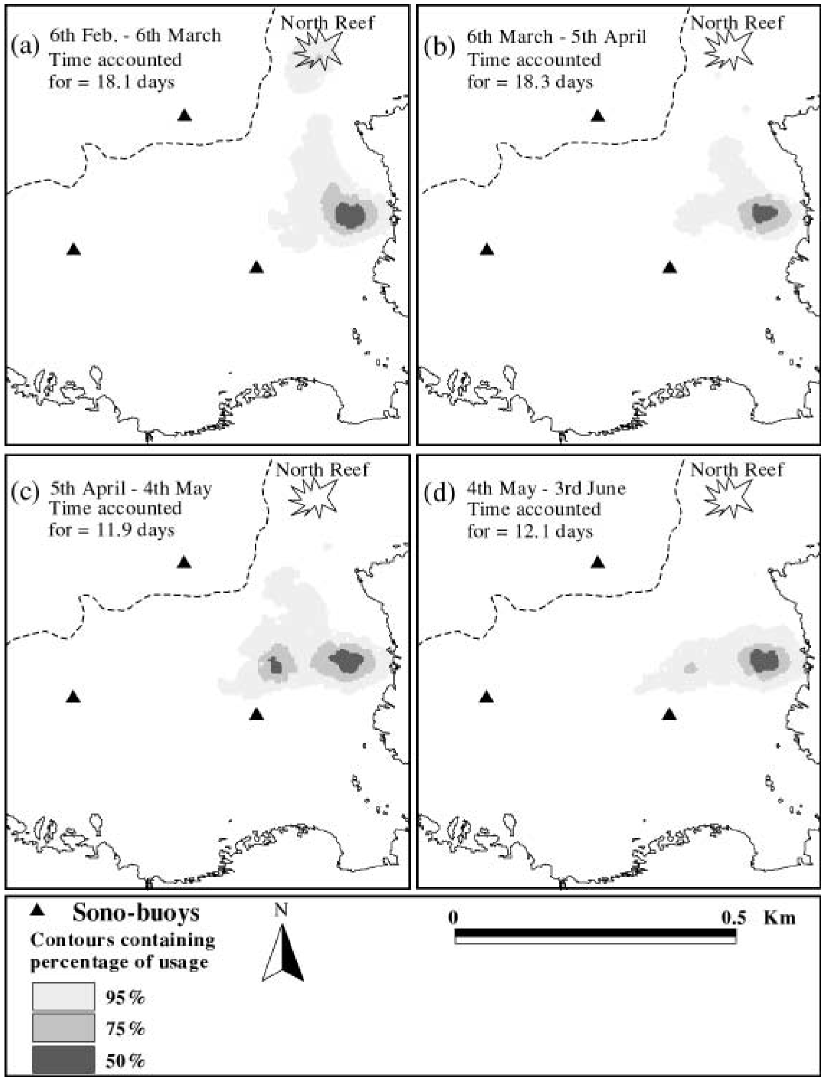

Fig. 3. *Pagrus auratus.* Home range and utilisation distributions of Fish S2 (415 mm fork length) for 4 lunar cycles between February and June 2000

Unaccountable time

The amount of time an individual snapper was unaccountable during a lunar tracking period varied from as little as 4.4 to as much as 22.8 d (Figs. 2 to 7). There are 4 possible reasons why the RAPT system could not account for snapper positions: (1) tagged snapper were moving to areas outside the detection range of the system; (2) tagged snapper were moving to areas where the system was obstructed; (3) extreme sea conditions reduced the amount of time that fish could be detected; and (4) the system was shut down intermittently. The first of these possibilities only appeared to make a major contribution to the home range estimate of Fish S1 (Fig. 2). Here, part of the home range was excluded from analysis by discarding locations outside its western border. For Fish S2 and S4 (Figs. 3 & 5, respectively), a combination of explanations (2) and (3) is most likely. The habitats these fish occupied were shallow and complex. Therefore, when storm conditions occurred, the fish were most likely to have their signals obstructed, as their habitats are areas most prone to turbulence. Indeed, the frequency of storm conditions (wave surge > 2 m) was greatest in the last 2 monitoring periods (Table 4), which could explain why these fish had the lowest percentage of time accounted for during these periods. The 3rd and 4th possibilities are likely to explain the majority of the remaining unaccounted time. When storm conditions occurred, the tracking system often produced spurious buoy and fish positions (hundreds of metres from where they should have been). Data files containing such positions were deleted to avoid incorporating errors into home-range estimates. Storm conditions also made it difficult to replace the sono-buoy batteries, resulting in the system being frequently shut down. Finally, during the last 2 monitoring periods, the system was used to con-

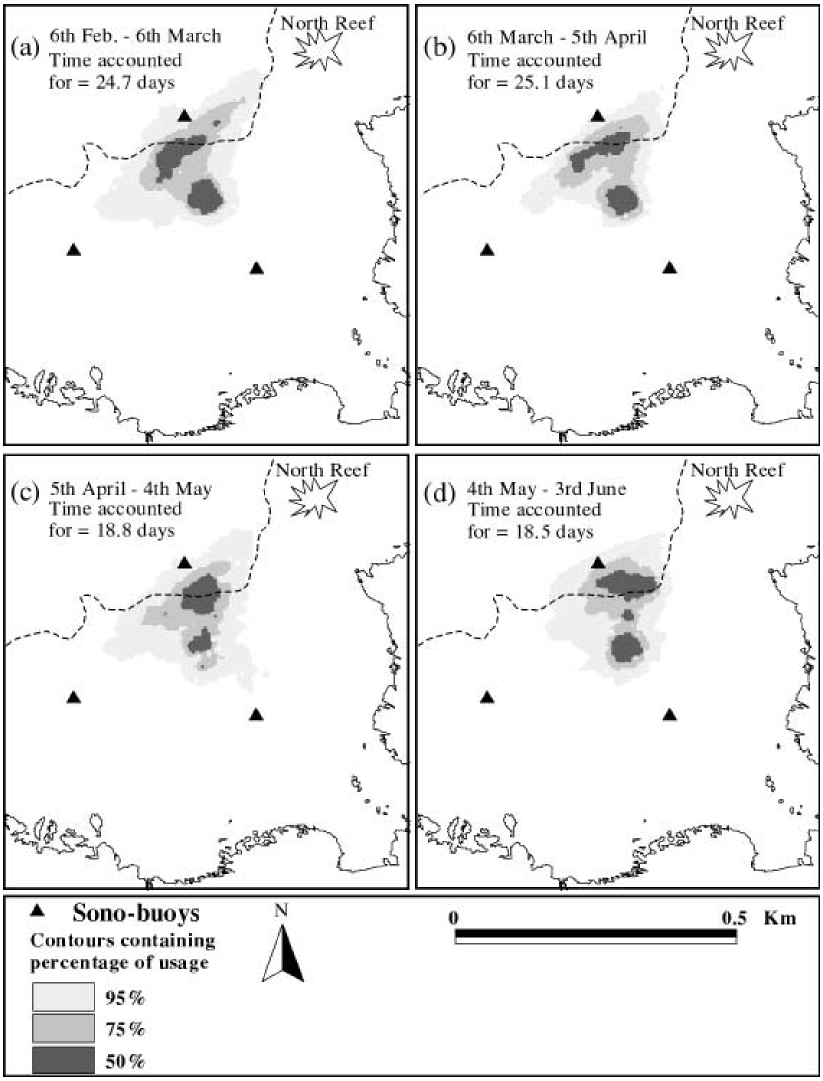

Fig. 4. *Pagrus auratus.* Home range and utilisation distributions of Fish S3 (532 mm fork length) for 4 lunar cycles between February and June 2000

struct a habitat map (Parsons et al. submitted). This resulted in extended lengths of time when the system was not searching for fish. When these periods of missing data were totalled (Table 5), a large proportion of these data could be accounted for, especially in the last 2 monitoring periods when bad weather and alternate use of the system were most frequent. Therefore, differences in the time accounted for were most probably related to the complications discussed above, not differences in fish behaviour. Despite the lower amount of accountable time, home-range estimates from the last 2 monitoring periods were similar, if not larger, than those produced from the earlier periods of tracking (Table 2). This suggested that when snapper could not be detected, they were still utilising space in a similar manner as when they could be detected.

DISCUSSION

Home-range size

This study presents the first estimates of snapper home range. While some previous studies have been successful in obtaining repetitive locations of individual snapper, the duration of sampling was either too short (Berquist 1994) or the number of locations too few (Willis et al. 2001) to assess snapper home-range size. The estimates of home-range size obtained here varied between 23 000 and 139 600 m^2, with corresponding maximum diameters of 190 and 620 m, respectively. These results are consistent with those of Willis et al. (2001), where residency was demonstrated over a scale of hundreds of metres in a larger sample-size of snapper (49 resighted out of 117 tagged) and a period of >3 yr. While the logistics and cost of acoustic telemetry limited our sample size, the additional detail we provide show that the 5 fish tagged in this study were resident within the reserve for the 5 mo of monitoring. In addition, 4 of these 5 fish were located within the same individual home ranges 1 yr after release. Speculation may suggest that the reason these snapper remained resident within the CROP Reserve was due to the fish feeding activities of tourists. However, the fish tagged in this study spent either none, or a very small, proportion of their time in areas where feeding occurred. In addition, snapper that received tags surgically

Table 4. Wave surge conditions for each monitoring period

Monitoring period (dd/mm/yy)	Days with surge > 2 m	Accountable missing time (d)
06/02/00–06/03/00	4	0.06
06/03/00–05/04/00	4	2.21
05/04/00–04/05/00	6	6.83
04/06/00–03/06/00	9	9.54

Number of days with accountable missing data. Explanations include: System being shut down due to low voltage; alternate use of the system; and deletion of data files containing spurious positions

Table 5. Number of days with accountable missing data. Explanations include: (1) System being shut down due to low voltage; (3) alternate use of the system; and (2) deletion of data files containing spurious positions

Monitoring period (dd/mm/yy)	Accountable missing time (d)
06/02/00–06/03/00	0.06
06/03/00–05/04/00	2.21
05/04/00–04/05/00	6.83
04/06/00–03/06/00	9.54

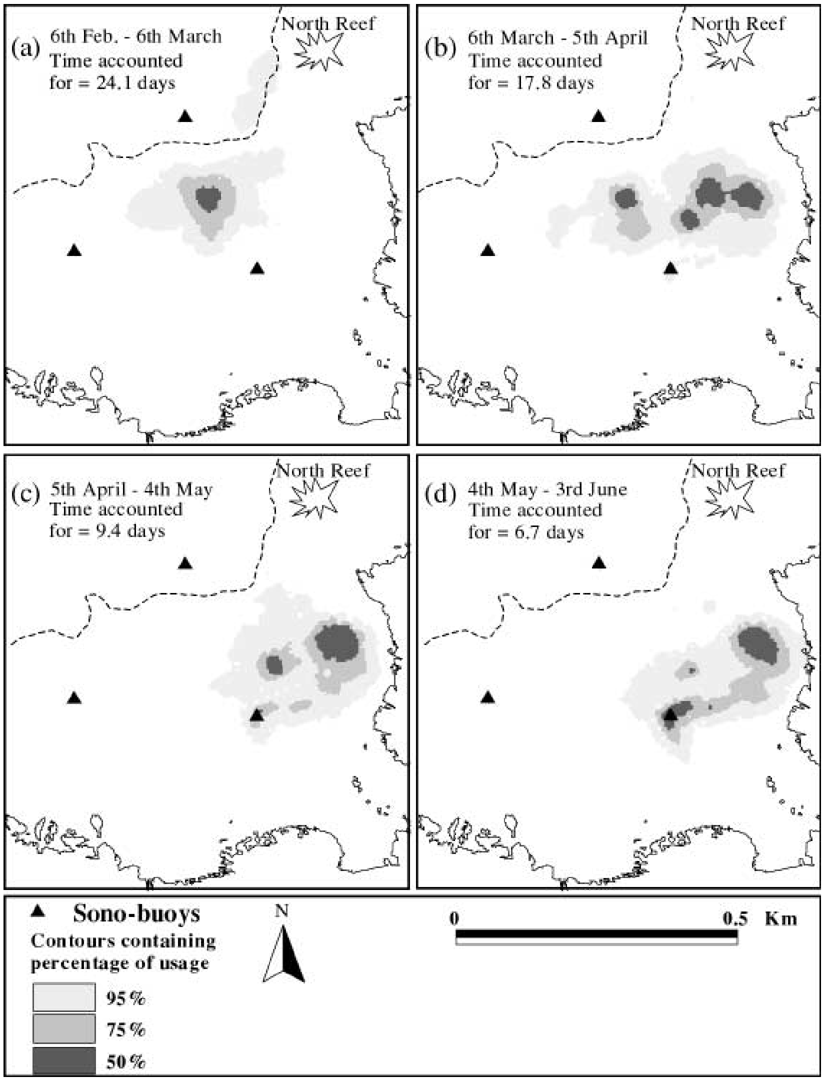

Fig. 5. *Pagrus auratus.* Home range and utilisation distributions of Fish S4 (426 mm fork length) for 4 lunar cycles between February and June 2000

would not allow divers to visually locate them. While human-derived sustenance may be important to some reserve-dwelling fish, it seems unlikely to be important here.

The home-range estimates presented here were based on the monthly monitoring periods of 5 snapper that received tags surgically. The decision to estimate home ranges over a lunar month was arbitrary; however, it did allow for observation of any changes in behaviour throughout the entire tracking period (5 mo). This decision appeared to be reasonable due to the individual consistency of home-range size (<24% change over 4 mo), and stasis of home-range location throughout the entire 5 mo tracking period (<37 m movement of core areas for all fish except S4). Snapper that received tags by feeding were not included in this estimate due to differences in the length of the monitoring period. Because home range is a function of time as well as space, the period over which home ranges are estimated must be taken into consideration in order to make estimates comparable (White & Garrott 1990). Further investigation of this issue revealed that the area used by an individual snapper did not appear to increase when ≥7 d of monitoring were incorporated in the estimate. Therefore, home-range estimates based on periods of monitoring up to 2.3 d are not directly comparable to home ranges estimated over a month, and we recommend that at least 7 d of monitoring be used in future calculations of snapper home range. For this reason, the monitoring of snapper tagged by feeding served 2 important purposes: (1) It demonstrated that the range of movements that these fish exhibited was not dissimilar to the movements of the surgically tagged fish. This lends confidence to the idea that the surgical procedure did not drastically alter the space-use characteristics of snapper; and (2) the 11 snapper fed acoustic tags also increased the sample size of fish that expressed small-scale residency.

Utilisation distribution

The use of space within the home ranges estimated here was not uniform. Each snapper spent 50% of its time within an area that was only 3.6 to 16.3% of the total home-range size. In general, the area within which snapper spent ≥50% of their time ranged between 1700 and 14 800 m^2, or 55 and 200 m in diameter. This implied that while they were observed rang-

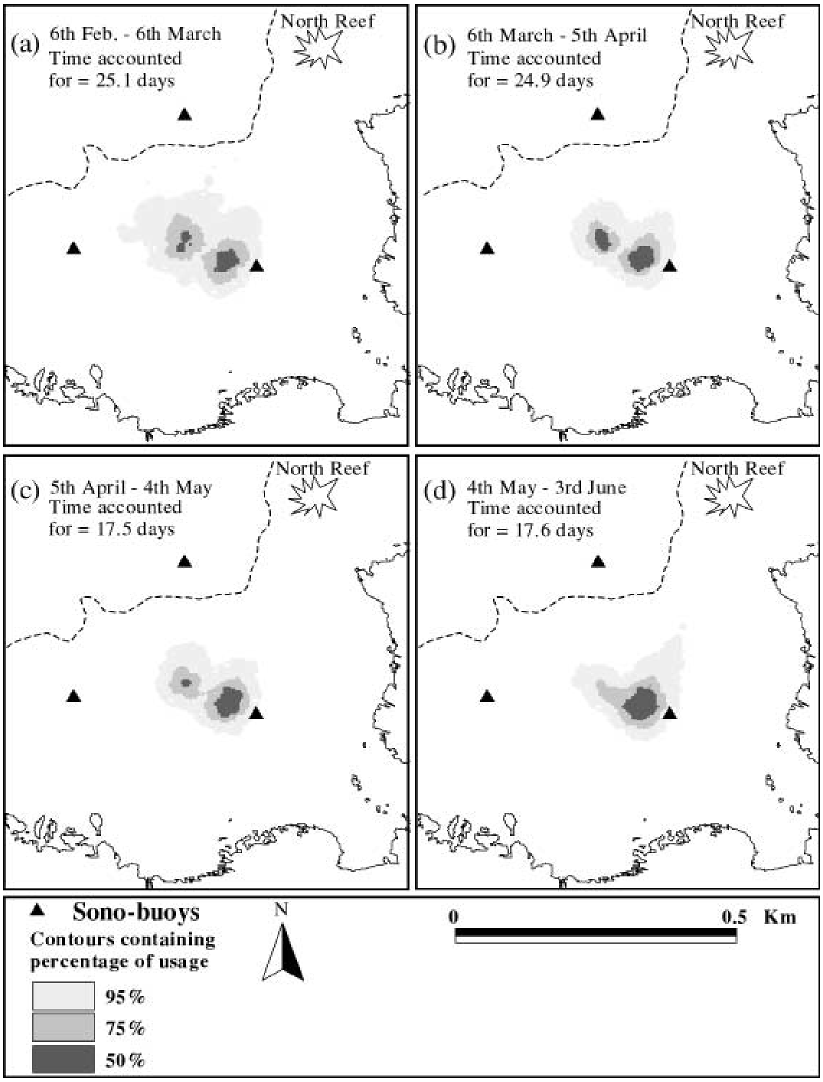

Fig. 6. *Pagrus auratus.* Home range and utilisation distributions of Fish S5 (515 mm fork length) for 4 lunar cycles between February and June 2000

ing over an area of up to 620 m diameter, most of the time they were within an area of only 200 m diameter. The most extreme example was Fish S4 (Fig. 5). During the first monitoring period, this fish spent 50% of its time in an area of only 1700 m^2, or 55 m diameter.

All surgically tagged fish had more than 1 core area in at least 1 of the monitoring periods, and these core areas were not always located at the centre of the home range. This is logical, as some areas could provide better shelter or food than others. It remains unknown whether these core areas are located where a fish resides when it is inactive (e.g. Løkkeborg et al. 2000) or whether a disproportionate amount of foraging and/or social interaction are occurring at these locations. Regardless of which resources are being utilised, they are unlikely to be distributed uniformly. Therefore, it was not unexpected that fish home ranges were irregular.

With respect to other marine fish species, only 5 studies have investigated the use of space within the home range. Four of these studies used manual tracking (Holland et al. 1993, 1996, Meyer et al. 2000, Eristhee & Oxenford 2001), while one used an automated system (Cote et al. 1998). The short duration of these studies (<62 d), the intermittent periods of tracking, and the low number of positional fixes (<1429) provided limited behavioural information below the level of home–range size estimation. When utilisation distributions were calculated in this study, time was used as the density variable, fish were continuously tracked for periods of up to 140 d, and the maximum number of fixes obtained for an individual was in excess of 475 000. Therefore, the current study presents the first accurate and long-term example of how a marine fish species occupies space on a sub-home-range level.

The behavioural variation inherent within this small sample of snapper suggested that individualised behavioural traits existed within 1 species. A further example of this variation was the daily movement of Fish S1, S2 and S4 (Figs. 2a, 4a & 6a) between their individual home ranges and 'North Reef'. These movements most commonly occurred between 10:00 and 13:00 h, and ceased to occur altogether after March (D. M. P. unpubl. data). The characteristics of these movements were consistent with the daily and seasonal patterns that snapper exhibit while spawning (Scott et al. 1993). While it is not possible to discern the reason for these movements from this analysis, it is possible that: (1) North Reef was the site of a localised spawning aggregation within the reserve; and (2) structures such as North Reef could be used as a geographic marker for historic spawning aggregations.

Home range stability

Four of the surgically tagged fish maintained home ranges with a consistent shape and location (<37 m movement between monitoring periods). Such stability was not expressed by Fish S4. Between the second and third monitoring periods, this fish increased the number of core areas it was using from 1 to 4 (Fig. 4b). These core areas led from west to east across Goat Island Bay. Illustration of this movement using 5 d portions of time (not presented) revealed that core-area shifting was a gradual process. New core areas were established by gradually increasing the use of an alternate area, while the use of the original core area was maintained. Similarly, core areas were abandoned by gradually decreasing the use of them. This fish maintained 3 core areas at one time. By the 4th monitoring period it had established, and then rejected, or was evicted from, 2 core areas before settling in the eastern-most core area. This suggested that some time between 6 March and 5 April, this fish relocated its home range by ca. 220 m. During the last monitoring period, the core area of the first monitoring period was not revisited. Therefore any resources available within the original core area were obtained from its new home range or not required at all. Kramer & Chapman (1999) speculated that relocations were most likely to occur after several sampling trips from the established home range. This probably was the case here.

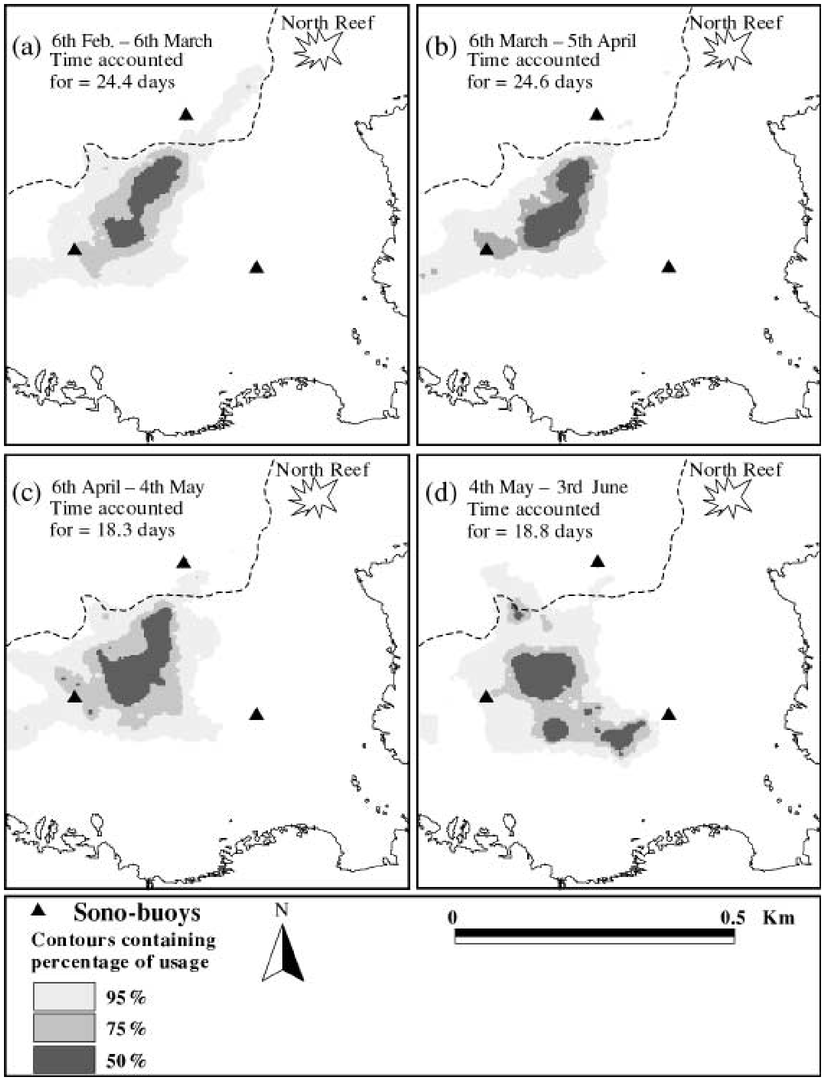

Fig. 7. *Pagrus auratus.* Home range and utilisation distributions of 4 of the fish that received acoustic tags. Fork lengths: F1 = 325 mm, F2 = 400 mm, F3 = 450 mm, F4 = 400 mm

Relocation events could be initiated by seasonal change of an environmental variable (e.g. wave exposure or the abundance of prey). At this time of year a proportion of the snapper population follow a seasonal off-reef migration (Crossland 1976, Willis et al. 2003), which might also have some influence on within-reef movements. Other factors that may effect home range shifts could include the interaction with other snapper. In the current study considerable home-range overlap was observed. In addition, the high density of snapper within Goat Island Bay (Willis et al. 2003) precludes the possibility that individual home ranges of this size could be occupied exclusively. This suggests 2 things: (1) the carrying capacity of a reserve, or any other area, cannot be calculated by dividing area by the average size of a snapper home range; and (2) movements between different areas are not restricted by the possibility of entering another snapper's home range.

While Willis et al. (2001) demonstrated that snapper were resident within the CROP Reserve, results presented in the current study indicate that these fish did not leave the reserve between times of re-sighting. In short, it was possible to quantify the size and permanency of snapper home ranges. Other studies of snapper movement have also suggested that snapper were resident, but at much larger scales. With respect to the scales investigated in this study, fish movement over scales of kilometres, as described by Paul (1967) and Crossland (1982), referred to the fish as mobile, not resident. Nevertheless, from the conclusions of these

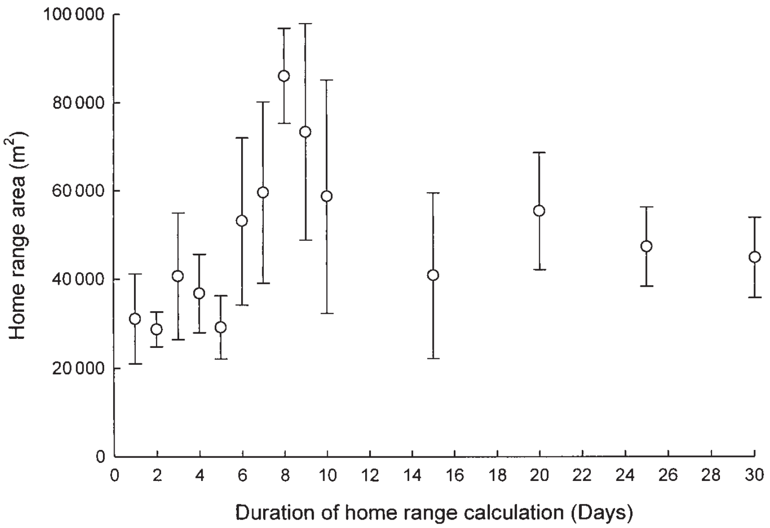

Fig. 8. *Pagrus auratus.* Relationship between home-range size and length of time used in the calculation. Values represent means ± SE (n = 3)

previous studies, and those presented here, it would appear that snapper are capable of exhibiting both vagile and residential behaviours. A similar pattern has been observed in the movement patterns of galjoen *Coracinus capensis* (Attwood & Bennett 1994). While most of the galjoen tagged were recaptured within 5 km of the release site, 17.8% were caught >25 km away, the greatest distance to recapture being 1040 km.

Within the CROP Reserve, indirect evidence suggests that some snapper are wider dispersing than those tagged in this study. Willis et al. (2003) monitored the density of snapper throughout 3 NE New Zealand marine reserves and their adjacent fished areas. Consistent seasonal fluctuations of snapper abundance, both inside and outside reserves, suggested that part of the inshore snapper population was not resident and left coastal areas sometime between April and October. The fact that similar fluctuations existed outside of reserves indicates that this pattern is probably not restricted to marine reserves.

If fisheries select for different traits through increased mortality (e.g. Hilborn & Walters 1992, Coleman et al. 1996, McGovern et al. 1998, Conover & Munch 2002, Hauser et al. 2002), then marine reserves may change this selection regime and exert their own selective pressure through decreased mortality. The observation that all snapper tagged in this study resided in areas 2 orders of magnitude smaller than previously documented (Paul 1967, Crossland 1982) may be due to the behavioural selections made by such a reserve. The explanation is as follows: Within the snapper population a continuum of mobility behaviour exists. Within reserves, the fish with the highest tendency to exhibit residential behaviour are favoured. This is due to the small size of established reserves (<9 km^2) and the heavy fishing pressure on their boundaries (T. J. W. pers. obs.). Any snapper of higher mobility would therefore spend at least some time outside of the reserve, increasing the chance of capture. If all snapper were uniformly as mobile as described by Paul (1967) and Crossland (1982), then it is likely that snapper abundances would not have responded as positively to protection within reserves of the current size (Willis et al. 2003). Those estimates reflect the average mobility of a population whose behavioural distribution may have been altered by exploitation, whereas the estimates presented in this study represent individual estimates from a population with behavioural traits that may have been affected by a lack of exploitation. This scenario illustrates 2 important points: (1) within a species, assumptions about homogeneous behaviour cannot always be made (Willis et al. 2001), and management decisions, rather than being based on such assumptions, are likely to have unexpected and possibly unfavourable consequences; and (2) a marine reserve's potential to replenish adjacent fisheries will be dependent on the reproductive and growth potential of the individuals it selects for.

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