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Evidence for long-term site fidelity of snapper (*Pagrus auratus*) within a marine reserve

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Abstract Increases in the density of exploited species on unfished reefs logically implies that some individuals are at least temporarily resident, or show fidelity to a particular area. We tagged snapper (*Pagrus auratus* (Bloch & Schneider 1801)) in the Leigh Marine Reserve, New Zealand using visible implant fluorescent elastomer tags, recoverable by diver visual sightings without the need to recapture the fish. Batch tagging of snapper (n = 907) was done during an angling survey in June and December 1996, and individually coded tags were implanted by divers (n = 117) in January 1999. Snapper tagged during both programmes were recovered on irregular intervals from 1997 to 2000. There were 71 recoveries of batch tags within 500 m of their tagging sites, and these recoveries were still being made >3 years after tagging. Of individually coded fish, 49 (42%) were seen, sometimes repeatedly over several months, close to their respective tagging sites. These observations included snapper as small as 23 cm fork length, contradicting the commonly held impression that only large snapper take up long-term residency on reefs. This preliminary evidence suggests that some snapper exhibit site fidelity to areas only a few hundred metres wide, and in the absence of fishing may occupy the same area for years.

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INTRODUCTION

The snapper (*Pagrus auratus* (Bloch & Schneider 1801): Sparidae) is a wide-ranging demersal predatory fish that is heavily exploited by both commercial and recreational fishers in northern New Zealand. The SNA 1 (north-eastern New Zealand) stock produces 69.3% of the total commercial catch (Annala et al. 2000), but is currently below the theoretical biomass at maximum sustainable yield and requires rebuilding to reduce the risk of collapse (Davies et al. 1999). It has been widely suggested that such risk might be lowered by the implementation of marine reserves (areas closed to all forms of fishing or disturbance) by preserving a portion of the spawning stock (e.g., Roberts & Polunin 1991; Rowley 1994; Allison et al. 1998; Horwood et al. 1998; Guénette & Pitcher 1999). Retention of an unfished population should result in proportionally greater numbers of large individuals (Willis et al. 2000), with consequent increases in gamete production (Zeldis & Francis 1998) per unit area, assuming that fish form resident spawning aggregations within reserves.

Previous attempts to determine movement patterns of snapper have been conducted at large spatial scales, used spaghetti or dart tags, and relied on tag returns from commercial and recreational fishers. Paul (1967) found that although some fish moved large distances, most returns of snapper tagged in shallow areas of the Hauraki Gulf had moved little distance from their release site. Crossland (1976) also found that a few tagged fish travelled more than 50 n mile within 1 year of tagging, but that c. 80% of returns were caught within 20 n mile of the tagging site. Tong (1978) obtained similar results and supported Crossland's (1976) contention that seasonal aggregations of "school fish" originate from shallow, inshore areas. In a later review, Crossland (1982) concluded that most snapper were resident "in a particular area" and movements were related to foraging or spawning. Most recently, Gilbert & McKenzie (1999) found that bias in mark-recapture estimates of snapper stock size may have been at least partly the result of a lack of mixing of tagged and untagged fish. They suggested that snapper might have consistent home ranges of 10–20 km diameter.

When the Cape Rodney to Okakari Point (Leigh) marine reserve was established (1975), it was generally considered that reserve establishment would have little effect on snapper density, because this species was thought to be highly mobile (W. J. Ballantine pers. comm.). Recent work at this marine reserve (36°16′S, 174°48′E) has shown that total snapper density inside the reserve is 11 times greater than in adjacent fished areas, and that the density of fish larger than minimum legal size (MLS) is in the order of 30 times greater (Millar & Willis 1999; Willis et al. 2000). The buildup of high densities of fish in a relatively small area (the reserve is c. 5 km long and extends 800 m offshore) logically implies that there must be some site fidelity exhibited by at least a portion of the snapper in the reserve. Hydroacoustic tagging of two snapper at Goat Island, for 2 and 5 days respectively, showed that those fish moved no further than 800 m for the duration of the study (Berquist 1994). There have been no further attempts to determine whether snapper exhibit site fidelity at small spatial scales.

Movement patterns of exploited fishes have important implications for the potential of marine reserves to be used as fishery management tools (Holland et al. 1993; Zeller & Russ 1998; Sladek Nowlis & Roberts 1999). Kramer & Chapman (1999) predicted that recovery within reserves would likely be most pronounced by those species with very limited movement. However, a high degree of site fidelity is likely to minimise any effect of fishery enhancement adjacent to a reserve, as adult emigration rates might be very low unless density dependence displaces individuals from the reserve to fished habitat (Zeller & Russ 1998; Kramer & Chapman 1999). Beverton & Holt (1957) considered that increases in fishery yield-per-recruit may occur through random diffusion of fish from closed areas, rather than relying on specific biological processes. At present, there is little evidence of fishery enhancement from marine reserves (but see Russ & Alcala 1996). Knowledge of general movement patterns of exploited species will allow the estimation of the minimum size of reserve required to protect viable populations of exploited species.

Here, we present evidence for small-scale site fidelity of snapper within the Leigh Marine Reserve, based on repeated visual recovery of snapper tagged with visible implant fluorescent elastomer tags (Willis & Babcock 1998) over a 4-year period.

MATERIALS AND METHODS

Tagging

Snapper were tagged using visible implant fluorescent elastomer (VIFE) microtags (Northwest Marine Technology Inc., Shaw Island, Washington, United States). VIFE tags have been shown to have a high (93%) retention rate in snapper, do not cause wound infections or the difficulties with fouling (Barrett 1995) common with dart or spaghetti tags, and can be recovered visually on multiple occasions without having to recapture the fish (Willis & Babcock 1998). Fish are identified by making multiple implants combining different tag colours and locations (Frederick 1997) which, depending on tag colour, are identifiable by divers 2–4 m from the tagged fish (Willis & Babcock 1998). Implants were placed in the translucent membrane between caudal fin rays of snapper using a 22-gauge needle, and were c. 15 mm long × 1 mm wide.

Long-term study—1996 batch tagging

Snapper were captured on 15 June, 29 June, 7 December, and 15 December 1996 by rod-and-line angling, as part of a survey to estimate their density in and around the Leigh Marine Reserve (Millar & Willis 1999; Willis et al. 2000). The survey area was divided into 10 similarly sized areas (six reserve and four non-reserve, Fig. 1), and fish caught were measured (to nearest cm below fork length (FL)), and given a single tag with a colour (red, orange, green, yellow, or blue) and location (dorsal or ventral caudal fin lobe) unique to that survey area (Table 1). If previously tagged fish were recaptured during the angling survey, a second tag was added coded for the second capture area. Tagged snapper were released immediately after tagging (generally within 1 min of capture) at the capture site.

Resights of tagged fish were obtained irregularly throughout 1997–2000 by the authors and other divers working at various sites throughout the reserve and environs. Additional tag returns were obtained from snapper caught in comparative hook trials conducted (using angling gear) in the reserve

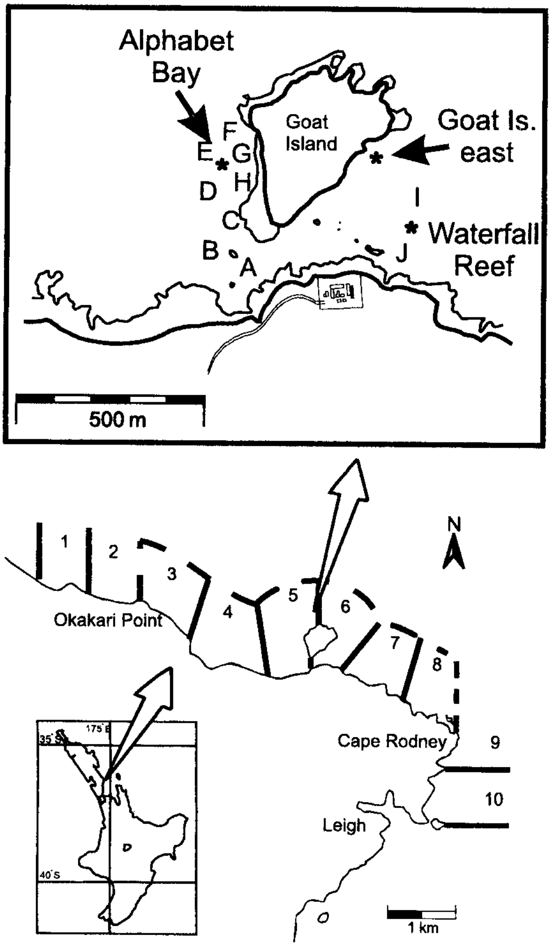

Fig. 1 Maps showing the Cape Rodney to Okakari Point marine reserve, New Zealand, with survey areas used for the angling (batch-tagging) survey, with a close up of the Goat Island area. Locations of the three tagging sites for individually coded tags are indicated by *. Sites marked A–H were regular tag observation sites during 1999, and Sites I–J were additional observation sites during early 2000.

during January 1997 (Willis 2000). We also publicised the programme with local commercial and recreational fishers, and asked them to check catches for tagged snapper.

We could not make quantitative assessments of recovery rates of tags, because the observation effort expended was inconsistent through time (most of the diving effort, and hence most of the resights, were made during summer). Also, since many of the resights were obtained by divers engaged upon other tasks, there was little between-diver consistency in the amount of effort made to detect tags.

Short-term study—1999 individual tagging

Between 6 January and 5 February 1999, we tagged 117 snapper at three locations: in Alphabet Bay, on the west side of Goat Island (n = 97); on the east side of Goat Island (n = 7); and at Waterfall Reef (n = 13) (Fig. 1). Fish were caught underwater by divers using a short handline with a barbless hook, and immobilised in knotless nylon netting to allow tagging (Willis & Babcock 1998). Each fish was given an individual tag code, based on the five available tag colours and four positions in the caudal fin: two in the dorsal lobe and two in the ventral lobe (tags were read dorsally to ventrally, e.g., RYGY = red yellow green yellow). Tagged snapper were measured to ±1 mm FL using a measuring board. Where fish caught already possessed a single tag from the 1996 angling study, it was incorporated into the new four-colour tag combination. Underwater tagging removes much of the physiological stress and handling damage caused by removal from the water (Pankhurst & Kime 1991; Willis & Babcock 1998).

Tagged fish were visually recovered by diver surveys of the area at irregular intervals from 1 February 1999 to 21 May 2000. Resights were gathered in two ways: opportunistic resights recorded by ourselves and colleagues while diving for other purposes, and structured observations at particular sites. We exploited the diver-positive behaviour exhibited by snapper around Goat Island (Cole 1994) to obtain resights. We found that snapper would approach a stationary diver more closely than a moving diver. The diver would therefore swim to a series of predetermined sites (marked A–H on Fig. 1) and remain stationary for 5 min, during which he would examine all snapper that approached to within 2–4 m for tags. We also recorded tagged snapper that could not be individually identified. These records were from fish that either did not approach closely enough for the tag to be identified with certainty, or from fish with ambiguous tag codes caused by loss of one or more of the four implants.

Since quantitative analysis of tag return rates was precluded by several sources of bias (caused by a combination of fish behaviour and the manner in which resights were obtained—see Discussion), interpretation of results was limited to observational evidence for site fidelity.

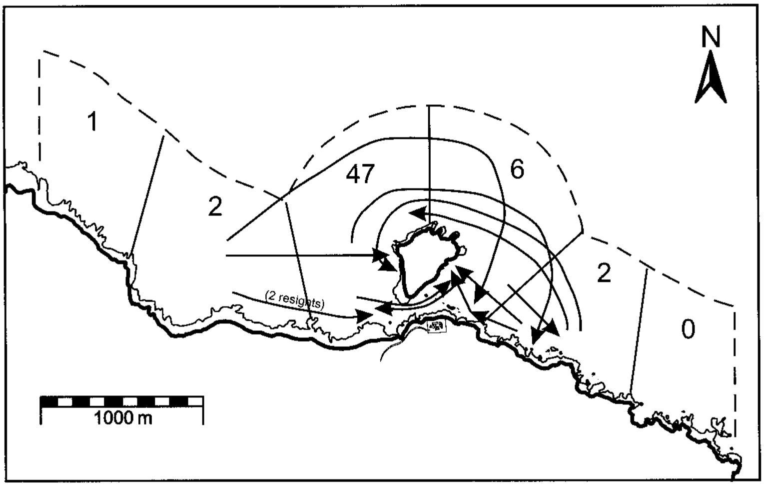

Fig. 2 Map of the Cape Rodney to Okakari Point marine reserve, New Zealand, with movements of batch-tagged snapper (*Pagrus auratus*) inferred from resights. Numbers are the number of resights within each survey area of tags implanted in that area.

RESULTS

1996 batch tagging

Most resights of angler-tagged snapper were made in survey Areas 5 and 6 (Fig. 2). Of the 71 resights obtained, 58 (82%) were made in the same area as the fish were tagged. It is likely that several of the resights (particularly in Area 5) were repeated sightings of a few fish, but as we could not discriminate individuals, we could not be sure how many of the sightings were repeats. Based on size estimates made by divers, we estimate that the 71 resights were obtained from at least 30 different fish. There was no pattern to the inferred direction of movement of the few individuals which were detected outside their original tagging area (Fig. 2).

Two fish were retagged during the angling survey. One (330 mm FL) was caught in Area 3 in June 1996, retagged in the same area on 7 December 1996, but was not subsequently resighted. The other (344 mm FL) was first captured in Area 4 in June 1996, retagged in Area 5 on 7 December 1996, and has been since (16 December 1996–6 March 2000) resighted 8 times in Area 5, in the vicinity of Alphabet Bay. Two further tagged snapper were recaptured by angling on 23 January 1997. One, caught for the second time in Area 7 (310 mm FL) was resighted 10 weeks later at the Goat Island east tagging site (Area 6). The other was caught for the second time in Area 4, but has not been resighted.

No tag returns were received from fishers, and no tagged snapper were seen on dives outside of the marine reserve.

Table 1 Total number and size range (mm fork length (FL)) of *Pagrus auratus* batch tagged in each survey area, with tag code, during angling surveys of Leigh Marine Reserve, New Zealand, and environs in June and December 1996.

Area	No. tagged	Size range (mm FL)	Tag colour	Tag position (caudal lobe)
1	1	370	Blue	Dorsal
2	3	196–341	Yellow	Dorsal
3	72	210–590	Yellow	Ventral
4	118	212–600	Orange	Dorsal
5	215	245–800	Orange	Ventral
6	197	199–1000	Green	Dorsal
7	174	210–850	Green	Ventral
8	86	175–470	Red	Dorsal
9	34	160–415	Red	Ventral
10	7	220–250	Blue	Ventral

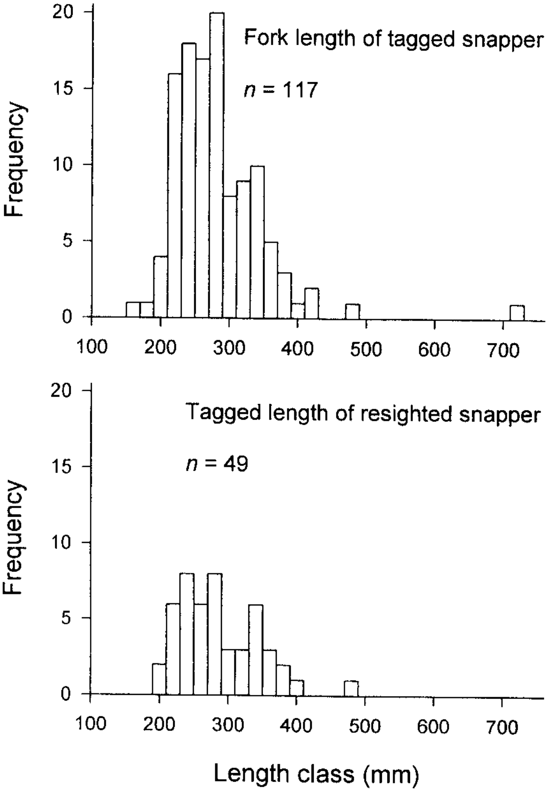

Fig. 3 Length distributions of individually tagged snapper (*Pagrus auratus*), and lengths at tagging of resighted snapper (excludes tagged fish not positively identified, n = sample size).

1999 individual tagging

Of 117 snapper tagged with individual implant combinations, 49 (42%) were subsequently resighted and positively identified within the study area. This is a conservative estimate of the proportion of tagged fish that remained resident (within 400 m of the tagging site), because on almost all dives, some tagged fish were seen that could not be individually identified and hence were not included in analyses. Most of the tagging and resighting effort was made at Alphabet Bay, where we resighted 46 of the 97 snapper tagged (47%). The length-frequency distribution of resighted snapper was not significantly different from that of tagged fish (Kolmogorov-Smirnov test, D = 0.09, $P > 0.05$, Fig. 3), indicating that there was no size-related bias in the probability of resighting tags. There was also no effect of fish size on the frequency of multiple resights (Fig. 4).

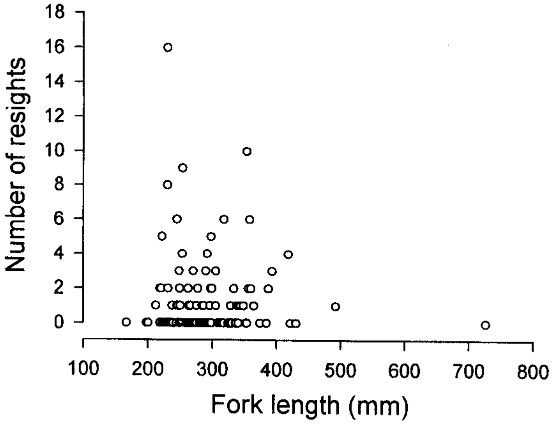

Fig. 4 Number of resights of individually tagged snapper (*Pagrus auratus*) plotted against fork length at tagging (excludes tagged fish not positively identified).

The positions of resightings of representative snapper are shown in Fig. 5–7. The most frequently resighted snapper (RRYY, 16 records, Fig. 5) was 230 mm FL at tagging, and the second most-sighted fish (10 records, Fig. 6) was 353 mm FL at tagging. No resighted snapper were more than 500 m from their tagging site, and although we cannot speculate on movements made between these observations, consistency in the specific locations of individuals indicate that they have fidelity to relatively small home ranges (e.g., Fig. 6). We could make fewer observations during winter because of poor weather conditions, but we did detect nine (identifiable) tagged snapper in May 1999 (Table 2), two of which were detected (along with eight others) in the same area in September 1999. Unless snapper are capable of homing to very specific locations following larger movements, such fish might be resident on specific reefs all year.

The longest period of site fidelity we have established for snapper in this study is from a 328 mm fish last sighted on 29 March 2000 (Fig. 7). If we conservatively assume that it received its first tag on 15 December 1996, this fish has been occupying (or returning to) the same area for over 3 years. We had no resights of this fish in the intervening period, so cannot speculate on its movements between sightings. This example of long-term site fidelity is not unique. There were at least two other snapper tagged during the 1996 angling survey (but not subsequently given individual tags) resighted in Area 5 during 2000. One was double tagged (described in the previous

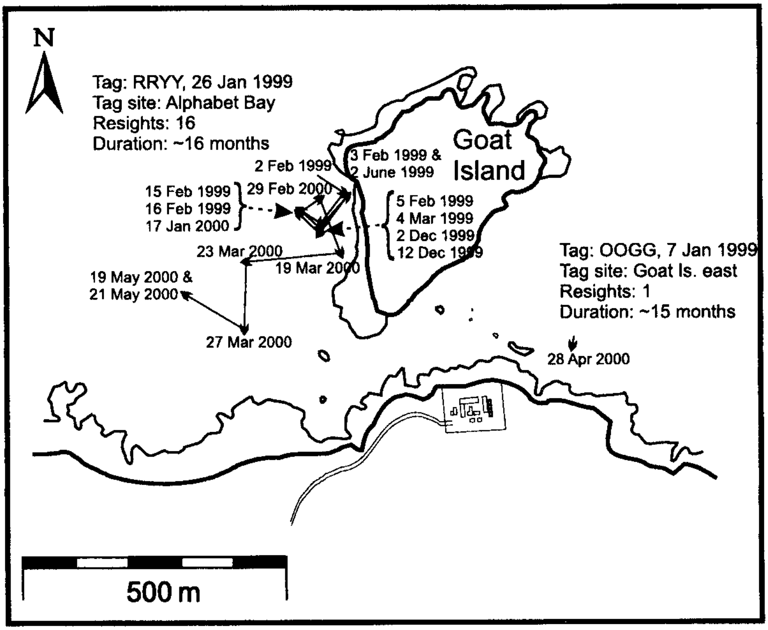

Fig. 5 Consecutive resight locations and dates of two snapper (*Pagrus auratus*) tagged at Alphabet Bay and Goat Island east, New Zealand. Lengths at tagging: RRYY = 230 mm fork length (FL), OOGG = 338 mm FL.

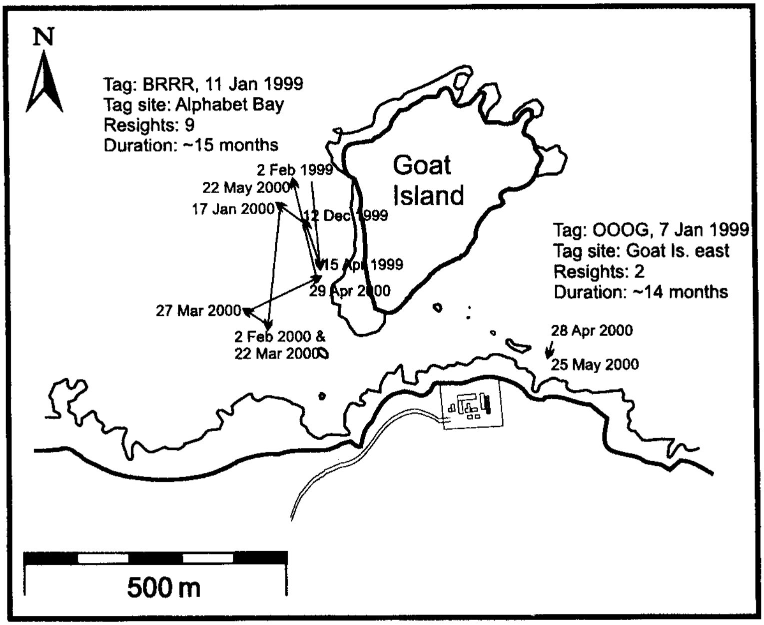

Fig. 6 Consecutive resight locations and dates of two snapper (*Pagrus auratus*) tagged at Alphabet Bay and Goat island east, New Zealand. Lengths at tagging: BRRR = 353 mm fork length (FL), OOOG = 387 mm FL.

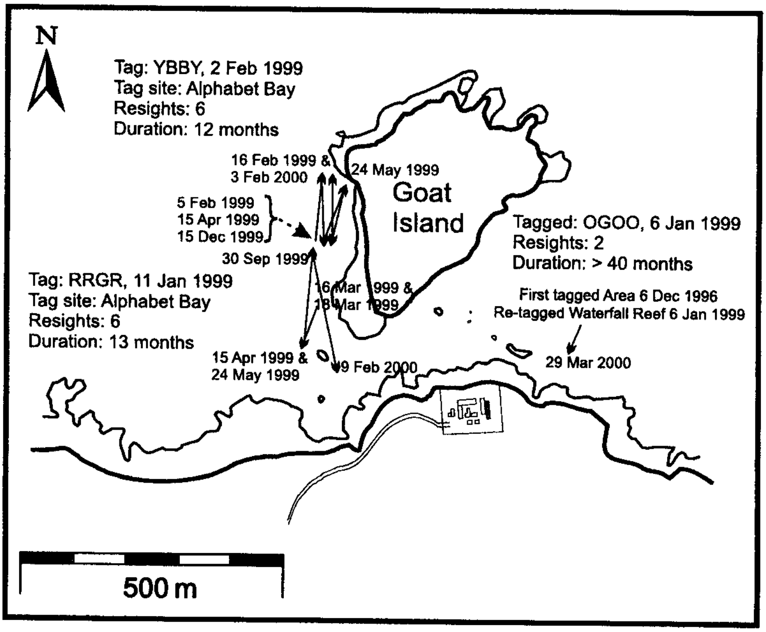

Fig. 7 Consecutive resight locations and dates of three snapper (*Pagrus auratus*) tagged at Alphabet Bay and Waterfall Reef, New Zealand. Lengths at tagging: YBBY = 245 mm fork length (FL), RRGR = 358 mm FL, OGOO = 328 mm FL.

section), and the other (possessing a single orange ventral tag and 45 cm estimated length) was most recently seen on 3 February 2000 in northern Alphabet Bay. In addition, the fish shown to have moved from Area 6 to Area 7 in Fig. 2 was resighted on 7 December 1999, conservatively 36 months after tagging.

DISCUSSION

This study illustrates that snapper can exhibit long-term (>3 year) site fidelity, in the sense that individuals are repeatedly present at the same site.

Table 2 Numbers of tagged snapper (*Pagrus auratus*) seen at eight locations adjacent to Goat Island, New Zealand (Sites A–H, Fig. 1) throughout 1999. Snapper were tagged between 6 January and 5 February 1999.

Date of observations	No. of identified snapper	Cumulative no. new individuals	No. of unidentified snapper
16 Mar 1999	11	11	1
18 Mar 1999	9	18	0
15 Apr 1999	13	27	3
24 May 1999	9	27	2
30 Sep 1999	10	29	2
12 Dec 1999	6	31	1

It is unknown whether these fish remain continuously within the locality, or if they leave the area and return to the original reef at regular or irregular intervals. Given the large elevations in density of snapper within the marine reserve (Millar & Willis 1999; Willis et al. 2000), it is likely that the limited home range of these site-attached fish provides them complete protection within the confines of the reserve. It has been suggested that the feeding of fish in the vicinity of Goat Island by visitors might be responsible for maintaining high densities of resident snapper in the area. Although such activity may be a contributing factor, the presence of tagged snapper during winter (when visitor numbers are low) and the detection of resident fish at locations remote from feeding activities, leads us to conclude that site fidelity is a naturally occurring behaviour. Snapper probably attempt to establish residency on fished reefs as well, but the high level of recreational fishing effort within the Hauraki Gulf curtails these attempts.

Large-scale tagging studies on other sparid species in South Africa have indicated that sedentary behaviour is common in the Sparidae (Buxton & Allen 1989; Attwood & Bennett 1995). If resident snapper form spawning aggregations within marine reserves, where they are protected from fishing mortality, the case for use of marine reserves as a hedge against recruitment overfishing (e.g., Attwood & Bennett 1995; Sladek Nowlis & Roberts 1999) is strengthened. An additional beneficial effect of reserves might be protection of small, but reproductively active snapper from incidental capture. It has been shown that capture-related stress can affect ovulation in snapper (Carragher & Pankhurst 1991), implying that fishing activity might reduce gamete production even when fish are carefully handled and released.

Constraints on interpretation

Logistic limitations caused us to batch tag snapper by survey area in the angling survey, so we could not usually differentiate individual resighted fish. There could have been as few as 11 (if divers' size estimates were ignored) or as many as 71 (if each resighting was a separate individual). The actual number probably lies somewhere midway between these extremes (incorporating size estimates, our minimum estimate was 30). Even with the unlikely assumption that the higher number is correct, there were very few recoveries of angling-caught fish (8%), relative to the proportion of underwater-tagged snapper recovered. This may be because of higher mortality after release in angling caught fish, the stress of capture causing fish to leave the area, or tag loss. The retention rate of VIFE tags is known to be reliant on the skill of the person doing the tagging (Frederick 1997), and the large number of people involved in the angling programme might have resulted in tags of variable quality.

There were no resights of snapper tagged outside of Areas 4–7. These areas contributed 78% of the total number of fish tagged (which reflected snapper relative density), and were most frequently dived, so low return rates from elsewhere might not be surprising. Other explanations are that either fishing pressure on the reserve boundaries (or poaching) removed fish from these areas, or that only resident snapper habituated to divers (Cole 1994) would approach close enough to be identified (see below). Many of the fish tagged in the June 1996 angling survey might also have migrated to deeper water (i.e., left the reserve because of natural seasonal movements) after being tagged (Crossland 1976).

A mark-recapture study based on visual recovery of tagged fish was only possible because snapper in some areas (especially Areas 5 and 6) of the Leigh Marine Reserve have become diver-positive in their behaviour (Cole 1994). This localised behaviour hampered other analyses, however. For example, we could not make population size estimates or make direct comparisons of tag return rates between areas within the reserve based on our resights because, first, the probability of resighting tagged (or any) snapper was inconsistent between areas. Second, the high percentage of individually tagged snapper subsequently resighted may be the result of the non-random selection of the initial tagged sample. The snapper most likely to be tagged were those that would approach divers, and hence we were more likely to tag resident fish. The angling survey was more likely to randomly sample fish from a population containing the complete suite of behaviours—from diver positive to diver negative. Third, many of the tag recoveries were collected opportunistically, and we had no way of determining how much relative effort was made by each observer to examine snapper for tags.

Implications for assessment of population dynamics and management

Snapper appear to conform to the "polymorphic behaviour" model of Attwood & Bennett (1994), in the sense that some individuals become resident on reefs, whereas others disperse over a wide area (Paul 1967; Crossland 1976, 1982; Tong 1978). Many models (especially fisheries models) of fish population dynamics tend to be oversimplified, with particular documented behaviours attributed to entire species (where behaviour is considered at all). With regard to the potential application of marine reserves to fishery management, Attwood & Bennett (1995) found that failure to account for variability in behaviour within species could result in underestimates of optimal reserve size. The *a priori* assumption of random mixing of individuals, and failure to account for individual variability in fish behaviour, has also resulted in the introduction of bias in snapper population estimates from tag-recapture studies (Gilbert & McKenzie 1999). The identification of this bias led Gilbert & McKenzie (1999) to suggest that snapper might have home ranges of 10–20 km. We suggest that reef-associated fish might have home ranges at least one order of magnitude smaller than this. If snapper biomass is concentrated over reefs relative to soft-sediment habitats (as suggested by commercial and recreational line-fishing patterns), an individual-based mechanistic approach to modelling (Persson et al. 1997) will be required to improve the accuracy of population size estimates.

An individual-based approach might be generally applicable to many exploited species in New Zealand and elsewhere. For example, Beentjes

& Francis (1999) showed some evidence for site fidelity in hapuku (*Polyprion oxygeneios*), but also that many individuals travelled great distances. Behavioural polymorphism might be affected by density-dependence (Attwood & Bennett 1995; Kramer & Chapman 1999) or other small-scale ecological effects such as predator-prey interactions or resource limitation. Large-scale seasonal movements of snapper have been described which might be related to spawning behaviour (Crossland 1976), but there is also seasonality in the distribution of non-spawning juveniles at some sites (Kingett & Choat 1981; Francis 1995). Snapper are probably the most studied marine fish species in New Zealand, but their behaviour and ecology at small spatial scales is still poorly known. If we are to attempt to design marine reserves for the express purpose of fishery management, or improve existing management strategies, detailed knowledge of major target species movements, home range size (where applicable), spatial patterns of resource use, and behaviour will be needed. One of the major difficulties with interpretation of mark-recapture data is the lack of knowledge of fish movements between captures or resightings. Such information could be obtained by the use of ultrasonic telemetry using hand-held hydrophones (e.g., Zeller 1999), or continuous automated tracking using fixed array radio-acoustic positioning systems (e.g., Løkkeborg & Fernö 1999).

Since this paper was accepted, two more tagged snapper have been recovered from anglers fishing illegally within the reserve. The first (342 mm FL) possessed a green ventral tag, and was taken from the vicinity of Tabletop Reef (Area 7, the same area it had been tagged) on 15 December 2000. This observation extends the minimum recorded length of residence for an individual fish to at least 4 years. An individually-tagged fish was recovered on 27 April 2001 from Goat Island Beach. It was tagged YYYR and had not been previously resighted. It was 296 mm FL at tagging on 26 January 1999, and 363 mm FL when recovered.

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