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Area utilisation and activity patterns of roman *Chrysoblephus laticeps* (Sparidae) in a small marine protected area

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Information on the movement of fish is vital to determine the effectiveness of marine protected areas (MPAs) for fish conservation and fisheries management. This study investigates area utilisation and activity patterns of 13 adult roman *Chrysoblephus laticeps* (Sparidae) using telemetry and underwater observations. Acoustic transmitters implanted into *C. laticeps* in tanks had no apparent effects on growth and mobility. Natural behaviour of the treated fish in the field was verified by SCUBA divers. Manual boat- and diver-based tracking was carried out inside the Castle Rock MPA, False Bay, South Africa, over a 17-month period. A radio acoustic positioning system (VRAP, VEMCO Ltd) was used to record automatically fish positions over two 1-month periods during and after the spawning season of roman. Manually recorded fish positions and VRAP positions inside the triangle of buoys within the system were accurate within 10m; deviations increased with increased distance of the fish from the centre of the system and during unfavourable sea conditions. Analysis of movement data using a 95% fixed kernel algorithm suggests that roman occupy small home ranges of between 1 000m^2 and 3 000m^2, which shows that this species is well suited for protection in small MPAs. Interestingly, the home range size did not seem to be related to fish size or habitat quality. Swimming activity decreased at night. During periods of cold-water upwelling, fish retreated into caves. During the spawning season, females extended their home ranges, which result in a 'spill over' effect of adult fish into fishing areas.

Keywords: *Chrysoblephus laticeps*, fish movement, home range, marine protected areas, roman, South Africa, spill over, telemetry

Introduction

It has become widely accepted that marine protected areas (MPAs) play an important role in sustainable management of fishery resources (Zeller 1997, Guénette *et al.* 1998, Parsons *et al.* 2003). Fishery enhancement is based on the protection of fish inside MPAs and the resulting increase in fish abundance outside MPAs because of the export of larvae and post-recruit fish (Roberts *et al.* 2003).

It has been shown that fish are successfully protected in MPAs (e.g. Gell and Roberts 2003, Gell *et al.* 2005). In South Africa, Bennett and Attwood (1991) reported a recovery of surf-zone fish species following the establishment of the De Hoop MPA on the southern coast. Buxton (1993) and Götz (2005) found higher fish densities and larger size-classes in areas closed to fishing compared with fished sites. However, these examples are from large MPAs (>40km^2).

The degree of protection offered by an MPA ultimately depends on how much of the area that a fish utilises is protected from fishing. The size of this area depends on a variety of factors relating to the life history of the species (e.g. maturity, size, sex) and to the environment (e.g. distribution of suitable habitat, food availability, seasonal and oceanographic conditions). Whereas large-scale movements (migrations, ranging and nomadism) are best studied with mark-and-recapture techniques, questions related to small-scale movements and home-range behaviour cannot be adequately resolved using that technique, which typically provides only two positions during the life history of the fish. Acoustic telemetry offers a better alternative for studying small-scale movements of marine fish because it allows continuous tracking of fish over extended time periods.

In this study, a combination of manual tracking and remote positioning was used in conjunction with underwater observations to investigate area utilisation by adult roman *Chrysoblephus laticeps* (Sparidae) and to determine the effects of biological (sex, size, spawning) and abiotic factors (habitat, season, time-of-day, temperature) on their movement behaviour. Because this is the first telemetry study of its kind on a South African marine teleost in a high-energy inshore environment, emphasis was also placed here on the description of the method and experimental design to provide guidelines for similar studies in the future. Long-term effects of the transmitter implantation procedure on growth and

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survival of roman were investigated in a tank experiment, range and accuracy of the position recordings were verified in test trials, and a data-cleaning routine was developed to remove outliers from the remote positioning data.

The study was carried out inside the Castle Rock MPA in False Bay on South Africa's south coast, a small reserve that is bordered by areas that are heavily utilised by commercial linefishers, shore-anglers and spearfishers (Lechanteur 1999), where even movements of a few hundred metres would make the population of roman inside the reserve vulnerable to fishing. Mark-and-recapture studies and anecdotal re-sightings of recognisable individuals indicate that roman are mostly resident during the greater part of their adult life (Penrith 1972, Buxton and Allen 1989, Griffiths and Wilke 2002, Bullen and Mann 2004). However, the extent of the area that roman utilise during resident periods remains uncertain.

Material and Methods

Study site

The Castle Rock MPA in False Bay (Figure 1) extends 3km alongshore from Bakoven Rock to Bobbejaanklip (34.23°S, 18.47°E–34.25°S, 18.47°E) and is approx. 6km^2 in extent. Its subtidal reef habitat is characterised by granite boulder fields and large sand flats, with dense kelp beds mainly along the coastline in water shallower than 15m. The reserve contains numerous exposed and submerged rocks. The seabed slopes gently to a maximum depth of 45m at the seaward boundary. Castle Rock MPA was originally proclaimed as a no-take zone, but since 1988 commercial fishing for snoek *Thyrsites atun*, a nomadic pelagic species, has been allowed inside the reserve.

Transmitter implantation trial

A total of eight roman was caught with rod and line in False Bay, east of Seal Island. Their swimbladders were deflated with a hypodermic needle. The fish were then anaesthetised in an 80l container filled with a 2-phenoxy-ethanol and a dummy transmitter (nylon cylinder with dimensions equal to a V8 transmitter, VEMCO Ltd, Halifax, Canada) was implanted into their peritoneal cavity following the methods described by Kerwath *et al*. (2005). After receiving an oxytetracycline injection (0.1ml 1 000g body weight^{-1}), the fish were released into a 2 000l holding tank with open seawater circulation. Another five fish were caught and kept as controls. On the following day, all fish were transferred to the Marine and Coastal Management (MCM) Research Aquarium, Sea Point, Cape Town. They were weighed (to the nearest g) and measured (to the nearest mm fork length) before being released into a 7 500l observation tank (diameter 2m, height 1.2m) with open circulating seawater supply.

The fish were fed to satiation 2–3 times a week with sardine *Sardinops sagax*, squid *Loligo vulgaris reynauldii* and white mussel *Donax serra*. Abnormal behaviour, signs of infections and any abnormal response to tag implants were noted. The fish were re-assessed after 40 days and 198 days. Weight, fork length, fish condition and the state of the incision scar were noted during these assessments. Digital photos of each individual fish and their incision scars were taken to facilitate individual recognition. After the second assessment, the fish were sacrificed and dissected.

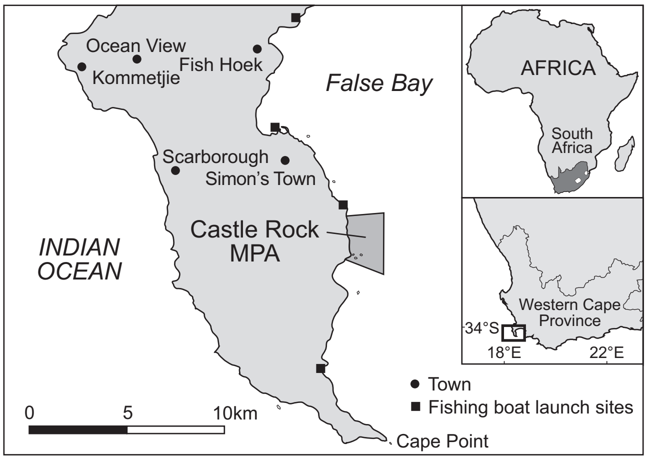

Figure 1: The Castle Rock marine protected area in False Bay, Western Cape, South Africa

Growth data analysis

To allow comparisons between growth rates of fish of different initial sizes, relative length increments (RLI) were calculated:

$$\mathrm{RLI} = \frac{\Delta L}{L_{inf} - L_i} \qquad (1)$$

where ΔL is the absolute length increment, L_{inf} the theoretical maximum length for roman (Götz 2005) and L_i the initial length. Weight increments were compared as absolute values. After testing for normality and homogeneity of variance (F-test), differences between the treatments were tested using t-tests.

Field study

Overview

In all, 13 roman were tracked during the period September 2002–March 2004. It was not possible to implement a strict tracking protocol, because tracking time per individual was dependent on battery life of the tag transmitter, sea conditions and availability of personnel and equipment. Three types of transmitters, manufactured by VEMCO Ltd, Halifax, Canada, with different battery lifespans, were used (Table 1). Details on the study animals' capture and release, tracking methods and individual tracking times are summarised in Table 2.

Three tracking methods were used: boat-based manual tracking, manual underwater tracking using SCUBA gear, and remote positioning with a radio acoustic positioning system (VRAP, VEMCO Ltd). Boat-based manual tracking was conducted mainly during five 2-week periods and opportunistically during day trips from September 2002–March 2004. The VRAP system was deployed in November 2003

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Table 1: Specifications of transmitters used in the field study

Transmitter type	Expected battery life (d)	Dimensions (diameter/length, mm)	Weight in water (g)
V16-4L	365	16/65	12
V13-1H	37	13/36	6
V8-SC-2H	25	9/30	3.1
V8-SC-2L	102	9/28	2.8

Table 2: Experimental details of roman tracking and remote positioning experiment

Fish number	Fork length (mm)	Functional sex	Gonad stage at catch	Transmitter type	Frequency (khz)	Capture method	Release method	Tracking method (m = manual, r = remote)	Release-date	End-date	Tracking period (d)
1	393	Male		V16-4L	60	SCUBA-angling	By diver	m	18 Sep 2002	7 Nov 2003	415
2	385	Male		V16-4L	54	Boat-angling	By diver	m	25 Sep 2002	27 Sep 2002	3
3	400	Male		V16-4L	54	SCUBA-angling	Surface	m	28 Sep 2002	29 Sep 2002	2
4	285	Female		V8SC-2L	84	Boat-angling	By diver	m	19 Feb 2003	6 Nov 2003	261
5	248	Female		V8SC-2H	78	Boat-angling	Surface	m	13 Jul 2003	18 Jul 2003	6
6	397	Male		V8SC-2H	63	Boat-angling	Surface	r, m	28 Oct 2003	1 Dec 2003	35
7	273	Female	Ripe	V8SC-2H	72	Boat-angling	Surface	r, m	29 Oct 2003	1 Dec 2003	34
8	354	?		V8SC-2H	66	Boat-angling	Surface	r, m	29 Oct 2003	1 Dec 2003	34
9	264	Female	Running	V8SC-2H	75	Boat-angling	Surface	r, m	31 Oct 2003	1 Dec 2003	32
10	227	Female		V13-1H	84	Boat-angling	Surface	r, m	3 Mar 2004	4 Mar 2004	2
11	282	Female		V13-1H	57	Boat-angling	Surface	r, m	4 Mar 2004	24 Mar 2004	21
12	335	?		V8SC-2H	54	Boat-angling	Surface	r, m	3 Mar 2004	24 Mar 2004	22
13	338	Male		V8SC-2H	69	Boat-angling	Surface	r, m	4 Mar 2004	24 Mar 2004	21

and March 2004, the respective periods during and after the spawning season of roman. SCUBA tracking was carried out opportunistically during the entire study period, depending on weather and oceanographic conditions.

Capture and surgery

Fish were caught either with rod and line from an anchored skiboat or by SCUBA divers using small fishing rods with 50cm of fixed line. The fish were brought to the surface slowly and handed over to the surgery team onboard. Circle hooks (1/0–5/0) were used to minimise gut- and gill-hooking.

After removing the hook, the fish were measured (to the nearest mm) on a wet plastic stretcher and the swimbladder was deflated with a hypodermic needle. The fish were then anaesthetised and transmitters were surgically implanted in a similar manner as described for the tank experiment. The fish were placed in a 80l container with oxygenated seawater immediately after the surgery. Once they resumed swimming, they were either released directly from the skiboat or put in a plastic bag filled with seawater and returned to the place of capture on the reef by a diver.

Manual boat-based tracking

A directional hydrophone (VEMCO; V10), attached to a 2m aluminium pole, was mounted amidships on the gunwale of a 5.5m skiboat, allowing 360° rotation. When lowered in tracking position, the pole extended below the hull of the boat. The hydrophone was connected to a VEMCO VR60 receiver. A position was recorded only when the signal was equally strong in all directions when the receiver was set to the lowest possible gain. Geographic coordinates (GP1850WDF GPS receiver; Furuno, USA), time, water depth and comments on the signal strength (weak vs strong) and regularity (regular vs irregular) were noted. Habitat was classified as ‘rock’, ‘sand’ or ‘mix’ as determined from the display on the echo-sounder. The accuracy of these classifications was verified during SCUBA dives. Temperature profiles throughout the water column were obtained using a bathythermograph deployed at a fixed GPS position on every outing.

In the first few hours after the fish was released, positions were typically recorded every 15min, depending on the activity of the fish. Once the fish had settled, positions were taken at hourly intervals. If a fish could not be located, a search in the form of an outward spiral from the last known position was undertaken. If the signal could not be detected within 1km from the last known position, that search was abandoned. When time permitted, all reefs in the entire study area were scanned for lost fish.

To determine the accuracy of manual tracking positions, a preliminary trial was carried out. A SCUBA diver carrying a transmitter was deployed at a known geographic position. The boat then retreated beyond the detection range of the transmitter. The tracker, who was unaware of the position of the diver, had to detect the signal and direct the skipper to obtain a position for the diver. The geographic positions were then compared. This procedure was repeated three times, with approaches from different directions.

Manual underwater tracking

Underwater tracking was done by SCUBA divers with an underwater, hand-held unit (DPL-275 underwater pinger

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receiver; Datasonics, USA). Underwater tracking sessions were used to assess the condition of the fish with implants and to record their behaviour. Behavioural observations of the fish under study and their conspecifics were made during 23 SCUBA dives. Observations were recorded on underwater slates and on digital video.

Remote positioning

Position data were automatically calculated with the VRAP system. The system consisted of an array of three surface buoys, a base station and a computer. The signals from the transmitters were radioed to the base station ashore. When all three buoys received pulses, the computer software calculated the position of the transmitter by comparing the respective arrival times of signals at each hydrophone. The system was set up to cycle through the frequencies of the different transmitters. Depending on how many transmitters were deployed, each frequency was scanned at least every 8min. The scanning time per tag was set to one minute. Data were uploaded to the base station every 12s. The automatic calibration of the buoy positions was repeated every 4h to maximise the position accuracy.

Moorings

The mooring system was strengthened in order to withstand rough sea conditions at the study area. Each buoy was moored with three anchors, a main anchor that consisted of a steel-cable attached to five lengths of railway line (weight 60kg, length 80cm) and two side anchors, each made from polypropylene rope attached to two lengths of railway line. The side anchors were positioned to face the direction of oncoming waves. On each side anchor rope, a surface buoy was attached at a distance of about 2m from the VRAP buoy to prevent it from touching the hydrophone during rough seas (Figure 2).

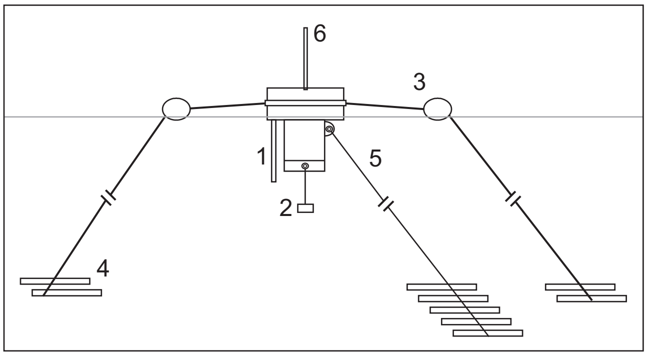

Figure 2: Schematic diagram of the enhanced mooring setup of one VRAP-buoy: 1 = hydrophone, 2 = counter-weight, 3 = side anchor rope with surface buoy, 4 = railway bars, 5 = main anchor (steel cable) and 6 = antenna

Accuracy and maximum range of the remote positioning

Erroneous position estimates may have resulted from background noise, signal reflection and turbulence. The maximum range of the system was determined during regular manual tracking of fish whose tag transmissions were not received by all three hydrophones and whose positions were therefore not plotted by the system. Two test transmitters were deployed to determine the accuracy of the position recordings. One was placed in the centre of the triangle of buoys (hereafter referred to as the triangle), the other one in a shallow area with high profile reef, outside the triangle about 40m north of the north-eastern buoy. The latter position was selected to determine the maximum deviation, because a position outside the triangle in the proximity of one buoy was expected to be most unfavourable for calculating accurate positions. Also, the shallow reef would likely cause high noise levels and signal shadowing, increasing the probability of outliers.

Data analysis

The 'position-average' algorithm from the VRAP5 software (Version 5.1.2; VEMCO Ltd) was selected to calculate all positions. All data points were transferred to a Microsoft Access database. A data-cleaning routine in Microsoft Visual Basic was developed to remove spurious position estimates. First, any positions that were more than 150m from the centre of the triangle were deemed unrealistic because they exceeded the maximum range of the system. Second, a data point was considered an outlier if the speed necessary to cover the distance between consecutive positions exceeded the plausible maximum swimming speed of roman. This speed was determined from data within the triangle during five days of favourable sea conditions, which were considered to be reliable recordings. The speed was calculated as the maximum velocity between consecutive points, assuming the fish travelled in a straight line. Third, after tests runs with different distances, any position resulting from a movement greater than 10 times the distance between the previous and the following positions in a time interval of <30min was considered an outlier and was removed from the dataset.

Minimum convex polygon (MCP) and fixed kernel home ranges were calculated in ArcView (Version 3.2, Environmental Systems Research Institute Inc., Redlands, California) GIS software with the Animal Movement extension (Hooge *et al.* 2001). The smoothing factor (h) was determined using the least-square cross-validation method available in the program.

Results

Transmitter implantation trial

Implanting the transmitters proved to be difficult onboard the skiboat on account of its rolling motion, which resulted in prolonged surgery times (i.e. the time the fish left the anaesthetic bath to its released into the holding tank) of 8–12min. Three fish died during surgery or immediately after release into the holding tank. The remaining five recovered within 10min of being released into the holding tank and their behaviour did not differ from that of the control fish. All fish started feeding after two days of being transferred to the holding tank in the aquarium.

After 40 days, all fish appeared to be in a healthy condition, the sutures had dissolved completely and the scales had grown back so that the incision scar was barely visible.

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There was no significant difference in weight increment between treated fish and the control group (t-test; F = 3.84, p = 0.22). Length increments were not analysed after 40 days because the error of length measurements was of similar magnitude as the growth during such a short interval. At the final assessment after 198 days, all fish were healthy and could be individually identified with the aid of digital photographs. There was no significant difference in growth rate between fish with implanted dummy transmitters and controls (t-test; F = 1.96, p = 0.52 [relative length increments]; and F = 1.02, p = 0.98 [weight increments]). No infections or haemorrhaging were observed and the dummy transmitters were embedded in mesenterial tissue.

Field study

Range and accuracy of manual tracking

The three trials resulted in deviations of 7m, 9m and 12m between the positional fix of the tracker and the GPS position of the diver. The signal was first received by the tracker at a distance of 180m, 150m and 200m respectively from the diver's position. However, during cold-water events (upwelling), the detection range frequently decreased to <50m. During such events, the signal became irregular and determination of the exact location was difficult. However, SCUBA tracking verified the accuracy of the surface tracking. In most instances, divers were able to locate the fish immediately by descending at the positions identified by surface tracking. Differences in signal appearance also gave clues to the whereabouts of the fish. If the signal suddenly became weak and irregular, the divers confirmed that the tracked fish had withdrawn into a crevice.

Range and accuracy of remote positioning

The mooring system kept the VRAP buoys steady, even during 70km h^{-1} winds and wave heights exceeding 2.5m. However, poor sea conditions resulted in a high number of outliers and in the loss of data owing to radio failure. On account of the high-energy environment and the high relief of the reefs in the study area, the receptive field of the VRAP system was smaller than anticipated. To achieve a satisfactory reception rate of positions, the distance between the buoys had to be reduced from 300m, as recommended from the VRAP hardware manual, to about 80m.

The accuracy of the positions in the centre of the triangle was high, even during unfavourable sea conditions. In all, 95% of the recordings of the test transmitter position fell within 2.2m. Accuracy and frequency of recordings deteriorated outside the triangle, especially around buoys and in high relief reef areas. Data from the second test transmitter from outside the triangle contained numerous outliers. Most of the deviations occurred along the axis from the centre of the triangle to the transmitter position (Figure 3). Assuming a bivariate normally distributed deviation, a Jenrich-Turner ellipsoid (bivariate normal method of Jenrich and Turner in Hooge *et al.* 2001) was used to describe the deviation. A subset of the data taken from the day with the worst deviations was chosen for the analysis to determine the maximum deviation. In all, 95% of the points along the main axis of deviation were within 33m of the centre, and along the short axis of the ellipsoid 95% of positions were within <5m.

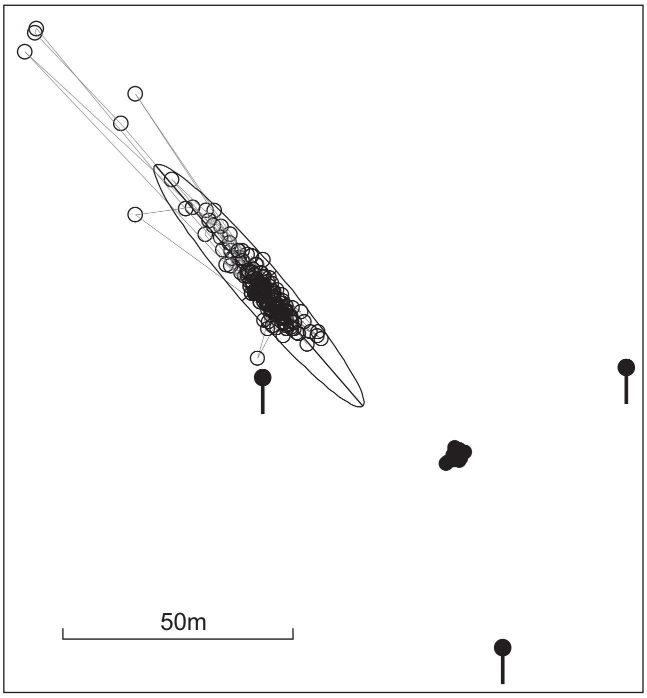

Figure 3: Plot of positional fixes of two stationary test transmitters (open circles and black dots) during a day with unfavourable sea conditions. The position of the VRAP array is indicated by the buoy symbols. The ellipsoid represents 95% of the points received from the transmitter outside the triangle, assuming a bivariate normal distribution of deviation

The maximum swimming speed of roman was estimated at 0.69m s^{-1}, equal to around three body lengths per second. The mean speed was 0.049m s^{-1} (SD 0.11m s^{-1}). The data-cleaning routine removed 10% of the records, resulting in a final dataset of 9 724 positions.

Capture, transmitter implantation and post-surgery effects

All fish, even those caught by divers, suffered from barotrauma and their swimbladders needed to be deflated prior to surgery. All 13 fish recovered from the surgical procedure and displayed normal swimming motion within 10min after surgery. The behaviour of 12 of the fish could be observed later during SCUBA tracking sessions.

Immediate post-release observations were made of the three fish that were returned to their capture location on the reef by SCUBA divers. Fish 1 retreated immediately into a large cave (Figure 4), where it was relocated by divers in the afternoon of the same day. Fish 2 slowly retreated from the divers, but remained in close proximity to the release spot. Fish 4 swam in a south-easterly direction to a position 100m from the original capture site (Figure 4); however, it returned to its original position in the afternoon, where it was seen foraging on reef invertebrates at a position within 10m of the original site of release. The fish under study appeared very active, moving continuously inside a small area, and acting aggressively towards roman of similar size while foraging.

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Whereas the majority of fish were not discernable from their untreated conspecifics by their behaviour, two fish (Fish 2 and Fish 3) displayed abnormal swimming motions. Fish 2 showed restricted mobility after one day. After two days, its condition deteriorated and it swam with its head up in an unnatural manner and was easily captured by a diver with a hand net. The fish was killed and later dissection showed that the tag had shifted forward between the liver and the stomach. Bruises of the peritoneal cavity lining and the liver lobe were evident. Fish 3 seemed less agile than other roman and swam with its head slightly elevated. This fish and Fish 10 disappeared one day after surgery and their signals could no longer be detected in the study area during several searches. Fish 10 disappeared from the receptive field of the VRAP system 3h after release and its condition could not be verified by underwater tracking.

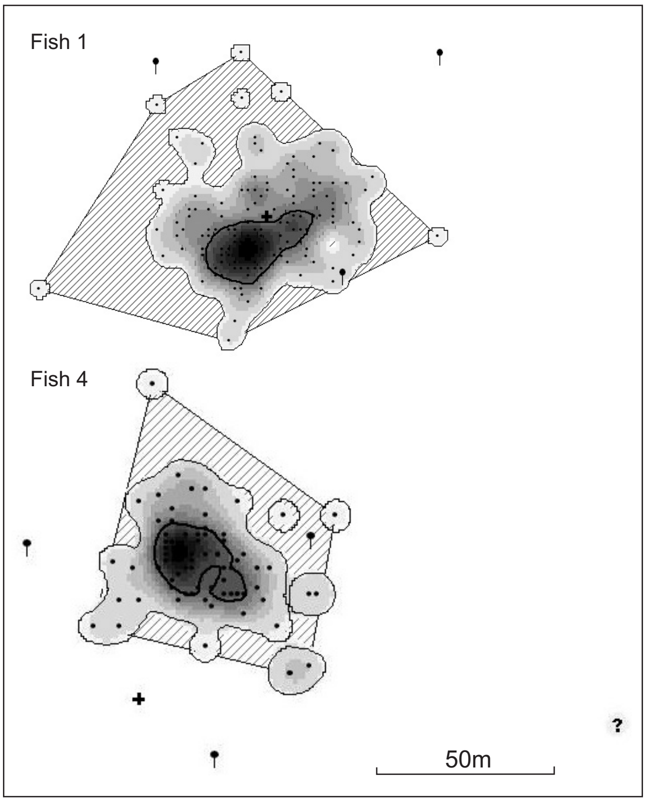

Figure 4: Minimum convex polygon (MCP) and kernel home range plot of Fish 1 and Fish 4 derived from manual tracking. Shading indicates the differences in utilisation density in 5% increments. The 95% and 50% kernel home ranges are emphasised with black lines, MCP home range areas are hatched. The position of the VRAP array is indicated by the buoy symbols. The cross marks the northern entrance of a cave utilised by Fish 1. The question mark indicates the first position of Fish 4 after the surgery. It was not included in the home range analysis

Home range patterns

The 10 remaining fish were resident within small home ranges during their individual tracking periods (Table 3). For Fish 1 and Fish 4, those with the longest observation times, all positions were within 55m of the original capture location during their respective tracking periods of 14 months and 8 months. (The first position of Fish 4 was attributed to post-capture stress and therefore not included in home range calculations). These fish were found during every tracking attempt, close to the position of original capture, even after periods of up to 3 months between tracking events.

Fish 4 was incidentally caught 8 months after its release, at a position <100m from its original capture site. It appeared in good condition, with a length increase of 8mm since its release. It had ripe ovaries with no visible testicular tissue. The internal organs appeared healthy. The tag was embedded in mesenterial tissue and there was no haemorrhaging of the surrounding tissues.

A similar home range extent was found from the remote positioning of Fish 6 during the spawning season and Fish 11–13 after the spawning season (Figures 5, 6). Some 95% of recorded positions were within a distance of <50m from the release site. All four fish were logged by the system every day of the tracking period. Fish 5 was only observed over a period of 6 days and unfavourable sea conditions precluded frequent position recording. However, the fish was resident in a small home range during this period and it was found in a crevice close to its capture spot during two underwater tracking sessions.

Table 3: Home range sizes of roman in the Castle Rock MPA

Fish number	Tracking method	Greatest distance between two positions (m)	Minimum convex polygon area (m²)	50% kernel home range (m²)	95% kernel home range (m²)
1	Manual	95	9 612	362	2 760
2		–	–	–	–
3		–	–	–	–
4		145	3 524	447	2 783
5		52	883	227	1 278
6	Remote/manual	204	9 218	250	1 087
7	(spawning season)	317	19 167	2 864	11 561
8		336	36 134	1 052	7 927
9		328	24 280	2 225	10 631
10		–	–	–	–
11	Remote/manual	150	9 612	195	924
12	(after spawning season)	154	11 924	169	1 304
13		142	12 594	243	1 562

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Spawning-related behaviour

Three fish that were tracked during their spawning season each showed similar activity patterns, but which were dissimilar to the other fish. Fish 7 and Fish 9, two female fish with ripe ovaries, and Fish 8, whose sex could not be visually determined, appeared to be more active, covering larger distances within short periods (Figure 5). Although they frequented the VRAP triangle during most of the study period, the system repeatedly failed to calculate their positions for periods of several hours or even days. However, the signal was received by at least one of the buoys, indicating the presence of the fish in the area, just outside the receptive field of one of the buoys. Manual tracking showed that the fish had moved inshore during those periods, into areas of dense kelp. The same locations were frequented a number of times during these outings, and the fish were always found at those preferred locations with all manual tracking positions within a 30m diameter. No temporal pattern was evident in the movement of fish between locations within the triangle and the kelp areas. Few positions were recorded on the sandy areas between the triangle and the kelp, indicating fast movement of individuals between those areas.

SCUBA tracking during two dives, one on the afternoon of 6 November in the kelp and in the triangle and the other in the triangle in the afternoon of the following day, allowed spawning-related behaviour to be observed. At both localities, fish swam parallel to each other in close proximity, then one fish tilted away from the other to expose its white abdominal area. If the other fish did not withdraw, it was attacked. Only female fish with an estimated fork length of between 200mm and 300mm, including the two under study (females), exhibited this behaviour. Large fish (males) did not engage in aggressive displays. Fish 6 (a male) was observed during the same dives, but did it not exhibit any of the behaviour described above.

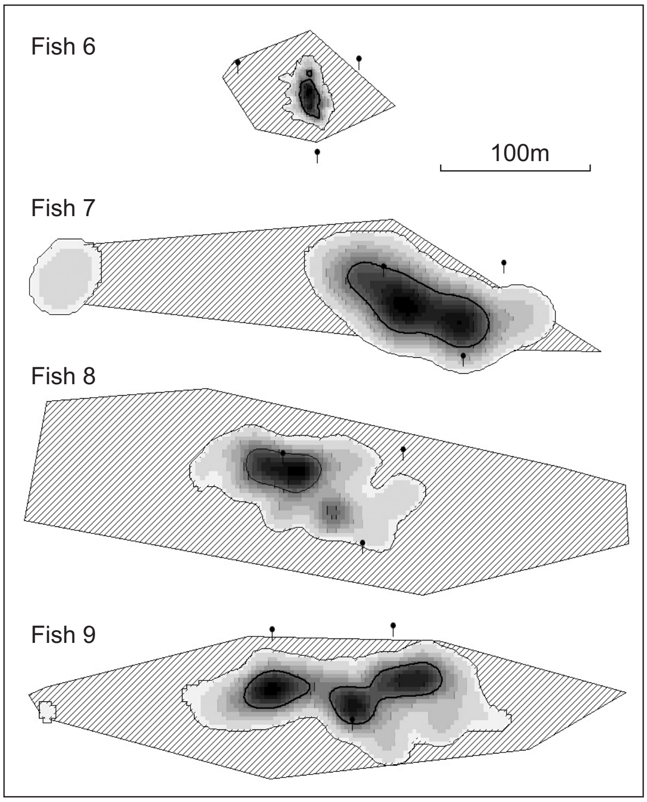

Figure 5: Minimum convex polygon (MCP) and kernel home range plot of fish during the spawning season. Manual tracking and remote positioning data were combined for the home range calculations. Shading indicates the differences in utilisation density in 5% increments. The 95% and 50% kernel home ranges are emphasised with black lines, MCP home range areas are hatched. The position of the VRAP array is indicated by the buoy symbols

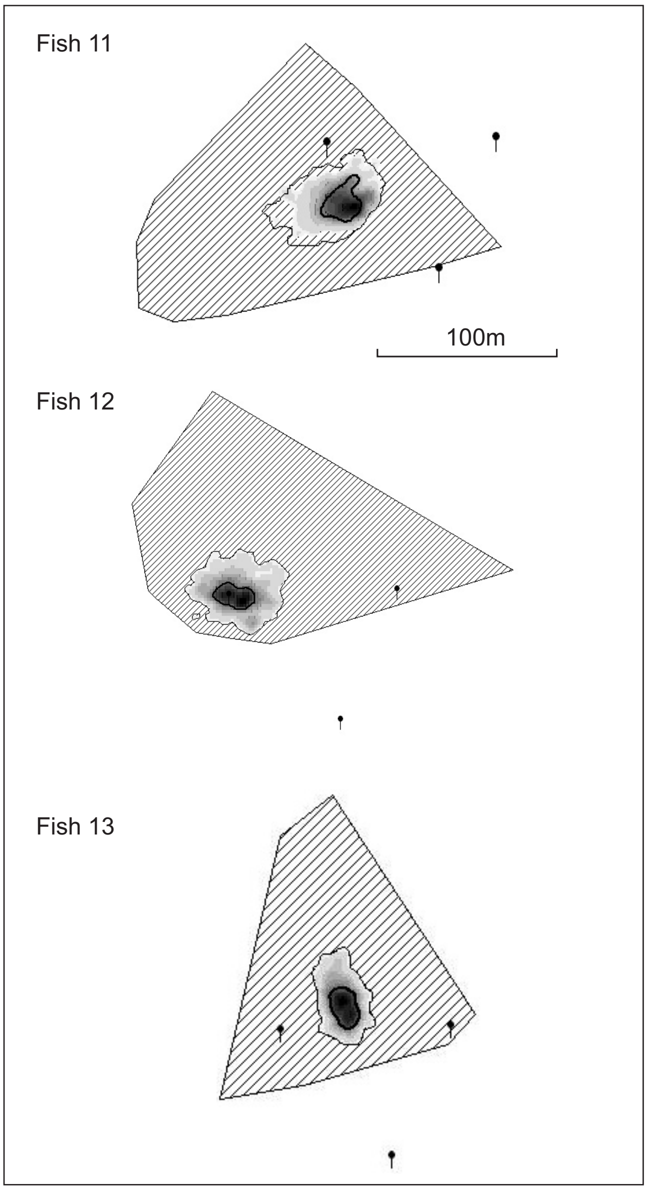

Figure 6: Minimum convex polygon (MCP) and kernel home range plot of fish after the end of the spawning season. Manual tracking and remote positioning data were combined for the home range calculations. Shading indicates the differences in utilisation density in 5% increments. The 95% and 50% kernel home ranges are emphasised with black lines, MCP home range areas are hatched. The position of the VRAP array is indicated by the buoy symbols

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Habitat utilisation

A clear habitat preference was distinguished from the echo-sounder recordings during manual tracking. In all, 98% of the recorded positions were over clearly discernable rocky substrata or over areas of rock/sand interface. Only 2% of the positions were taken over sand. During SCUBA tracking, the animals were never encountered in sandy areas, although the remotely recorded positions of Fish 7–9 indicated that they crossed sandy areas between two reef complexes during the spawning season.

Although the fish were strongly reef-associated, there was a clear difference between habitats occupied by individual fish. Fish 1 resided in a high-relief reef area with diverse invertebrate communities, which was dominated by large boulders with numerous caves and crevices. The frequent withdrawal of the fish into a large cave resulted in a weak and irregular signal on the surface VR60 receiver on the boat, where pulses were received only from certain directions close to the actual position of the cave. Some 97% of the manual tracking positions were taken over rock and none over sand. In contrast, the area occupied by Fish 4 was dominated by low-relief reef surrounded by sand with strong siltation at the edges of the gently sloping rocky areas. This was reflected in its position recordings, with 74% noted as ‘mix’ and 6% as ‘sand’.

Activity patterns

The average swimming speed of the remotely tracked fish ranged between 0.11m s^{-1} and 0.16m s^{-1} (Table 4). Fish 6 was selected to investigate changes in activity patterns, because its home range was inside the triangle and its positioning was therefore frequent and accurate. Average swimming speeds differed significantly between different periods of the day (Kruskal-Wallis test, H = 35.44, p = 0.000). The fish swam slowest between 0:00 and 4:00 and was most agile between 12:00 and 16:00 (Table 4).

At night between 20:00 and 4:00, no positions were logged by the VRAP system for Fish 7, Fish 9 and Fish 11. However, the first and the last recorded positions in the morning and evening were well within the detection range of the system and there was no track indicating movement out of the receptive field.

Fish 1 was manually tracked during three nights (Figure 7). Whereas positions were easily obtained until dusk, the signal became weak and irregular after dark for positions around the location of the cave, which was marked by a surface reference buoy. Fish 4 was tracked during one night, when all the positions were within 30m of each other. The signal on the surface receiver unit was clear during that night, indicating that the fish was not in a cave.

Table 4: Average swimming speed of Fish 6 at different times of the day

Time period (h)	Average swimming speed (m s^{-1}) (SD)
0:00–4:00	0.058 (0.10)
4:00–8:00	0.111 (0.15)
8:00–12:00	0.128 (0.18)
12:00–16:00	0.139 (0.17)
16:00–20:00	0.125 (0.16)
20:00–0:00	0.089 (0.14)
Total	0.113 (0.16)

Fish 1 was tracked during a cold-water event between 11 and 13 December 2002 (Figure 8). The signal received from the surface receiver unit became weak and irregular in the same manner as described for nocturnal periods for all positions around the cave area. Diver-tracking confirmed that the fish had retreated into the cave. During 11 December, bottom temperatures decreased to 10.3°C, the lowest temperature recorded thus far during the study. Divers reported that no fish were found in the open and the signal was difficult to detect with the hand-held underwater unit. The divers found Fish 1 in a small crevice at the back of the cave together with other roman of similar size. The divers tracked the fish to the same location inside the cave on the following day.

Discussion

Methodology

The application of telemetry in a high-energy, inshore environment such as the Castle Rock MPA posed a number of challenges. The high relief of the reefs in the study area caused frequent shadowing and reflection of the acoustic pulse, which resulted in reduced reception range of the VRAP system as well as irregular signals during manual tracking. Kelp cover, however, did not seem to have an influence on the signal strength. Matthews *et al.* (1990)

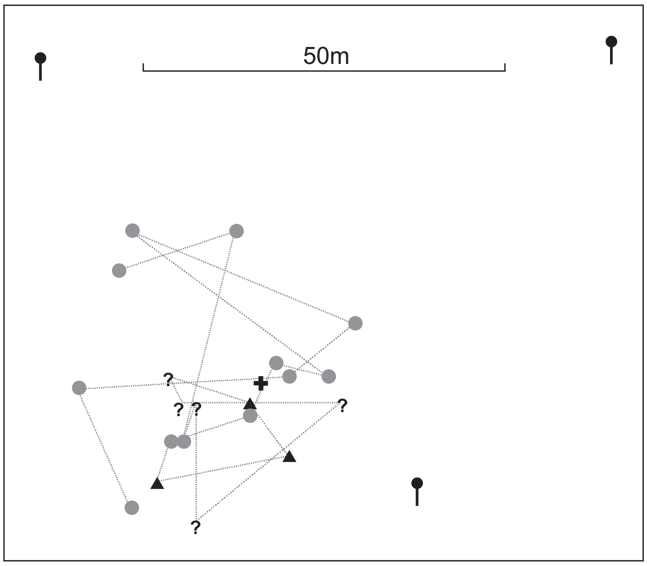

Figure 7: Example of manual-tracking positions of Fish 1 during the night. Positions are plotted from the morning of 25 September to the evening of 26 of September 2002. Grey circles indicate daytime positions, night positions are indicated by black triangles. Question marks represent positions with weak and irregular signal during the night. The position of the VRAP array is indicated by the buoy symbols, the cross demarcates the northern entrance of the cave that was used by the fish for shelter

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reported similar findings in a tracking experiment on quillback rockfish *Sebastes maligner* on shallow rocky reefs in Washington State, although their maximum detection range of 1km was much higher than that of the current study. Because roman are generally resident and do not display rapid movements, the lower detection range did not pose a serious problem in this study.

Knowledge of the accuracy of the recorded positions is important for studying highly resident species. Erroneous positions can affect the size of the calculated home ranges, therefore, manual tracking methods are favoured because they preclude false recordings. The accuracy of the remotely recorded positions, however, depends on a number of factors, including sea condition, distance of the fish from the centre of the system, position over the reef in relation to the system and topography of the area. Therefore, *de facto* outliers cannot be discerned from real positions and removal of outliers according to strict mathematical rules based on position in relation to the triangle was not possible. However, the data-cleaning routine presented here is an improvement to the procedure used by Parsons *et al.* (2003), because it included the plausible maximum swimming speed of the species under study.

Capture, transmitter implantation and post-surgery effects

In fish tracking experiments, it is important to know how quickly the fish resume their natural behaviour after release. Hooking, capture, handling and exposure to air have a negative effect on the condition of fish in catch-and-release experiments (Thorstad *et al.* 2001b). Most ‘tagging-induced’ mortalities occur within the first 24h after release (Finstad *et al.* 2003). In the current study, the high mortality rate during and immediately after the surgery in preparation for the tank experiment can be attributed to the unfavourable sea conditions, which resulted in difficulties during surgery, long handling times and rough handling on an unsteady vessel. During the field study, when the surgery was carried out in calm conditions on a skiboat, no mortalities occurred during or immediately after the surgery. The fact that two fish in the field study experienced severe side effects after release highlights the importance of verifying the condition of the fish by underwater tracking (i.e. Matthews *et al.* 1990, Bolden 2002), because surface tracking did not indicate any abnormal behaviour (long stationary periods or increased movement). Fish 4 displayed increased swimming activity immediately after release. This could have been a flight reaction after being released by the diver, or the result of capture-stress, an effect that has been observed in other studies (e.g. Connolly *et al.* 2002).

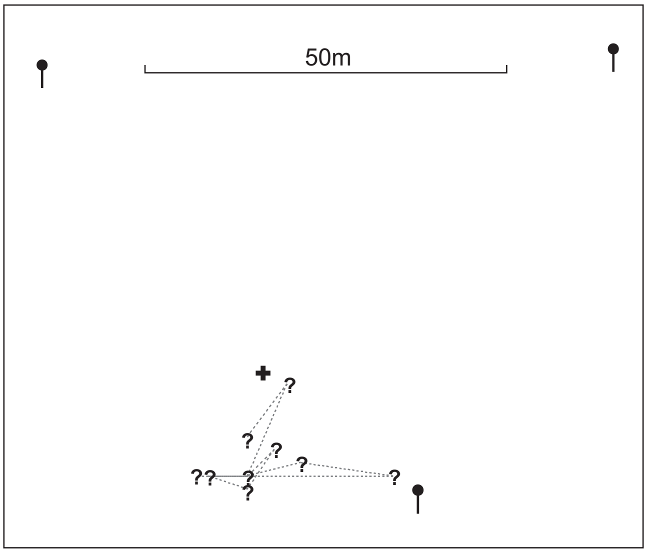

Figure 8: Manual-tracking positions of Fish 1 from the morning of 11 December to the evening of 13 December 2002. Question marks represent positions with weak and irregular signal. The position of the VRAP array is indicated by the buoy symbols and the cross demarcates the northern entrance of the cave

An additional factor that negatively affected the fish under study was the rupture of the swimbladder, caused by rapidly expanding gas when the fish was pulled to the surface. Over-inflation of the swimbladder could be caused by handling (Keniry *et al.* 1996), which was unavoidable when capturing fish using SCUBA gear to bring them slowly to the surface. This type of barotrauma can result in impaired buoyancy control and increases the chance of predation. It is possible that this may have been the cause of the disappearance of Fish 3 and Fish 10.

The long-term effects of transmitter implantation are highly variable (*inter alia* Martinelli *et al.* 1998, Thorstad *et al.* 2000, 2001b, Jadot 2003). Methods similar to the one described here were successfully applied on other sparids (Parsons *et al.* 2003, Jadot 2003, Kerwath 2006). The tank experiment showed no long-term effects as a direct result of the implant procedure. The healthy condition and the normal gonad development of Fish 4 some eight months after release supported these findings.

Home range patterns

This study confirms that adult roman utilise confined areas for prolonged periods and it provides the first estimates of its home range size. Previously, evidence of resident behaviour of roman was from mark-and-recapture studies (Buxton and Allen 1989, Griffiths and Wilke 2002), and from anecdotal diver observations on individuals with characteristic markings that were repeatedly sighted at the same location. Although long-distance movements in the order of several km have been reported occasionally for roman (Griffiths and Wilke 2002, Bullen and Mann 2004), they are not considered here because they can be more effectively studied with mark-and-recapture techniques (Kerwath *et al*. 2007).

Home range size

In this study, four different measures of the extent of the home range were provided, each for the entire observational period of the individual fish: maximum distance between two positions, minimum convex polygon (MCP) and 50% and 95% fixed kernel home ranges. Each method has its own merits and limitations (e.g. Anderson 1982, Worton 1989, Seaman and Powell 1996, Hooge *et al.* 2001). The maximum distance between recorded positions does not

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provide information on home range area, because it is confined to one dimension such as that provided by the mark-and-recapture method. Calculating a home range area with this distance as diameter would produce an overestimate, because home ranges are never completely circular. Furthermore, this method as well as the MCP is prone to sample size effects and errors caused by outliers. Kernel estimators describe home ranges in a probabilistic sense. They estimate the distribution of an animal's position (utilisation distribution) in a nonparametric manner. Seaman and Powell (1996) found that the cross-validated fixed kernel estimator provided the best area estimates in simulations; however, the area estimate depends on sample size and data structure.

The differences between home range sizes estimated by the different methods for the same dataset are clearly illustrated in this study. For example, the 95% kernel home range for Fish 6 was four times the size of the 50% kernel home range and the MCP was nine times the size of the 95% kernel. These discrepancies have to be taken into account when comparing estimates from different studies and when home range size is used to determine the size of MPAs. The present results lead to the conclusion that, to offer 100% protection to an individual post-recruit roman, without taking the possibility of occasional home range relocation into account, an area of c. 40 000m^2 would have to be closed to fishing. To ensure a 95% protection of its utilised area, only a quarter of this area has to be closed. This area could be further reduced to 3 000m^2 for most of the year, if it is combined with a general closed season during the spawning season.

Kramer and Chapman (1999) suggested that home range size is a function of fish size. However, home range size depends on other factors such as competition, availability of suitable habitat, food environment, shelter or access to reproduction. Positive correlations have been found for bluehead wrasse *Thalassoma bifasciatum* (Tecumseh *et al.* 1990) and lemon sharks *Negaprion brevirostris* (Morrissey *et al.* 1993), but a negative correlation has been suggested for saithe *Pollachius virens* (Sarno *et al.* 1994) and no relationship was found for coral trout *Plectropomus leopardus* Zeller (1997). Data for the six roman that had reliable home range estimates for outside the spawning season did not indicate a correlation with fish size, neither for 50% kernels nor for 95% kernels. However, our dataset was small and could not be tested statistically. Mark-and-recapture studies on roman also found no relation between size and movement distance (Griffiths and Wilke 2002, Bullen and Mann 2004, Kerwath 2006).

Spawning-related behaviour

Although not conclusive, on account of the small sample size and the failure to determine the sex of all the fish under study, the observations here, however, provide the first evidence for a gender-specific change in home range area size for roman. The area utilised by the two reproductively active females was 2–5 times greater than the area for roman at other times. Within this extended range, these fish moved between several core areas, where they remained stationary for prolonged periods, engaging in courtship behaviour. Buxton (1987) reported on rushing (one animal chasing the other) and lateral display for roman of all sizes, whereas in this study, observations of this behaviour were limited to small fish (females), large males in the vicinity remaining inactive. Roman are serial spawners, so the pattern observed here might be an evolutionary adaptation to increase mating and spawning success, in which males remain site-attached and females compete to pair with different males over a wider reef area. This would result in a selective process for stronger females because they would be able to mate more often with different males. This behaviour also has implications for the functionality of small MPAs, because females during the spawning season might extend their home range beyond the MPA boundaries and therefore become vulnerable to fishing.

Activity patterns

Outside the spawning season, all the fish under study had a focal point within their home ranges that was disproportionately utilised, marked by the 50% kernel area. This pattern is commonly found in reef-associated fish (Zeller 1997). From the manual tracking results and the underwater observations of Fish 1, it was evident that the location of the focal point was associated with a shelter site. The use of shelters may be an adaptation to decrease predation. During a sudden drop in temperature at the study site, as a result of upwelling, Fish 1 remained inside or within 10m of its shelter for three days. In poilikothermic animals, blood oxygen affinity, haemoglobin oxygen saturation and digestive enzymes only perform optimally within a narrow temperature range (Moyle and Cech 2000), and rapid temperature drops can result in the fish becoming lethargic (Smith and Heemstra 1986). Withdrawal into crevices might protect them from predators such white sharks *Carcharodon carcharias* and Cape fur seals *Arctocephalus pusillus pusillus,* which are not affected by such temperature changes. There was evidence that roman exhibit a diurnal activity pattern, with decreased swimming speeds and the use of shelter sites during parts of the nocturnal period, a behaviour that is common in temperate species (Ebeling and Bray 1976, Sarno *et al.* 1994). Contrary to anecdotal diver observations (Penrith 1972, Lechanteur 1999), there was no indication in this study that large roman are generally territorial with regard to their shelter. A territory is an area that is defended against intruders (Dingle 1996). An animal defends an area to sequester resources therein, which may be food, shelter, favourable nesting or spawning sites or a combination of all (Wootton 1999). All the home ranges of the fish tracked in this study overlapped and fish of all sizes are frequently found within a small area during underwater assessments (Götz 2005, SEK pers. obs.). Several large males were frequently observed inside the cave inhabited by Fish 1, and during the cold-water period described above, two large fish were found side by side in the same crevice.

Territorial behaviour can change in relation to the presence of conspecifics and the availability of food (Dill 1983, in Wootton 1999). In this study, Fish 4 showed aggression towards other roman during foraging. Because that fish inhabited an area of low-relief reef, the food availability

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might be limited so the benefits from defending a food source might outweigh the costs. Territorial behaviour among roman has also been observed in tank experiments, where the availability of food was spatially limited (SEK pers. obs.). No aggression was found when food supply was saturated. Similar behaviour has been found in Japanese rice fish *Oryzias latipes* (Magnuson 1962, cited in Wootton 1999).

Conclusions

Despite the limitations of telemetry when applied in a high-energy inshore environment, this technique is suitable for studying temperate reef fish. Whereas previous mark-and-recapture studies on roman only provide an indication of the linear extent of fish movement, the use of telemetry in this study made it possible (for the first time) to estimate the area utilised by individual adult roman. Accepting the 95% fixed kernel as the most reliable estimate, the size of this area is in the order of 1 000–3 000m^2, independent of habitat and fish size. Because it utilises a small area, roman could be successfully protected inside even small MPAs. However, more detailed studies on the reproductive behaviour of this species are necessary in order to determine the extent of the movement of females during their spawning season. This might have important implications in regards to the functionality of small MPAs if fish are likely to ‘spill over’ into fished areas.

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