ICES Journal of Marine Science, 63: 128–139 (2006)
doi:10.1016/j.icesjms.2005.06.010

Activity patterns, home-range size, and habitat utilization of *Sarpa salpa* (Teleostei: Sparidae) in the Mediterranean Sea

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Jadot, C., Donnay, A., Acolas, M. L., Cornet, Y., and Bégout Anras, M. L. 2006. Activity patterns, home-range size, and habitat utilization of *Sarpa salpa* in the Mediterranean. – ICES Journal of Marine Science, 63: 128–139.

Acoustic telemetry was used to record diel movement and habitat utilization of the salema (*Sarpa salpa*) (Teleostei: Sparidae) during three consecutive summers from 2000 to 2002 in the Calvi and Achiarina bays of Corsica in the Mediterranean Sea. A total of 18 fish was equipped with acoustic transmitters inserted in the body cavity, 13 were tracked in the Bay of Calvi (275 mm ± 26.9 L_F), and 5 in Achiarina Bay (260 mm ± 33.6 L_F). Two different systems were used to track the fish. The one used in the Bay of Calvi was a manual receiver and a directional hydrophone. The second system, used in Achiarina Bay, was a radio-acoustic-positioning (RAP) system that continuously monitored the movements of the fish. Fish positions were put in a geographic information system (GIS) with information on the substratum and depth. Two patterns of behaviour could be identified in the three years. Either the fish had clearly defined daytime as opposed to night-time areas of residency, characterized by different depths and substrata or the fish persistently occupied the same sites during both day and night. In the Bay of Calvi, six fish were released 1 km from the capture site. All of them showed homing ability and returned to the site within 48 h.

Keywords: GIS, habitat utilization, home range, homing, manual tracking, *Sarpa salpa*, telemetry, VRAP.

Received 21 July 2003; accepted 28 June 2005.

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Introduction

The salema, *Sarpa salpa* (L.), is an eurytherm species widely distributed throughout the Mediterranean, the whole Atlantic coast of Africa, including the Azores and Canary Islands, and also round South Africa to south of Mozambique on the Indian Ocean coast (Bauchot and Hureau, 1990). In the last 15 years, this poorly studied species in the Mediterranean Sea has attracted research interest because of first, its role as macro-grazer of seagrass (Velimirov, 1984; Havelange *et al.*, 1997; Jadot *et al.*, 2000, 2002), second, its biology in order to develop a management strategy (Méndez-Villamil *et al.*, 2001, 2002), and finally, its toxicity. Indeed it can cause Ciguatera-like or Caulerpa poisoning when consumed (Spanier, 1988; Spanier *et al.*, 1989; Chevaldonne, 1990).

This species is a protandrous hermaphrodite (Lissia-Frau, 1966, 1968; Sellami and Buslé, 1975); males are predominantly between 150 mm and 300 mm in length and females from 310 mm to 450 mm. Common to many Sparidae, sex conversion takes place over a wide range of sizes (230–350 mm) (Méndez-Villamil *et al.*, 2002); and as no external dimorphism exists, sex determination based only on size remains difficult.

S. salpa is ecologically significant in the *Posidonia oceanica* seagrass meadows, endemic of the Mediterranean Sea. This species accounts for up to 75% of the total herbivorous consumption (Cebrian *et al.*, 1996) and represents a significant part of the fish fauna (40–70% in biomass) (Francour, 1997, 2000). Herbivores, and more specifically the salema, in such ecosystems are therefore an essential link to higher levels of the foodweb as consumers of primary production. In the temperate meadows, the herbivores are not greatly represented compared with the tropical ones. Generally, authors assumed that they are a minor factor in the control of *P. oceanica* since grazing accounts only for a small percentage of leaf production (2–15% of the leaf production: Velimirov, 1984; Cebrian *et al.*, 1996; Havelange *et al.*, 1997; Pergent *et al.*, 1994, 1997; Cebrian and Duarte, 2001). Nevertheless, this assumption has been discussed and recent literature suggests that the role of the herbivores in the temperate zones is more important than generally thought (Verlaque, 1990; Cebrian *et al.*, 1996, 1997; Ojeda and Munoz, 1999; Ruitton *et al.*, 2000).

With recent advances in biotelemetry methods, valuable information on home-range size, habitat selection, and the activity of free-swimming fish in the marine environment is now obtainable (Winter, 1996). The main objective of this study was to gain a better understanding of the ecological and ethological interactions between the salema and the Mediterranean *P. oceanica* meadow. Specific aims of this work were to determine space and substratum utilization and the daily activity patterns of this species, using two methods of acoustic telemetry: manual tracking with a portable receiver and automatic tracking with a radio-linked, acoustic-positioning system.

Material and methods

Study site

This research took place at two different sites in the Mediterranean Sea, on the Corsican coast. The first study was carried out near the marine research station STARESO (STAtion de REcherche océanographique et SOus-marine) in Calvi Bay (42°35′N 8°43′E) (Figure 1) between June 2000 and September 2002. The second took place on the Lavezzi Islands in Achiarina Bay (41°20′N 9°15′E) (Figure 1). The meteorological conditions were particularly bad during the tracking month (October 2002), with very strong westerly winds (Figure 1).

Habitat mapping

Calvi Bay

The substratum and depth information of the study site was collected by Sargian (1997) via aerial photography and scuba-diving observations. The coast near the station consists of granite rocks going down into the sea to depths ranging between 8 m in front of the station and 30 m at the end of the Punta Revellatta (Figure 2a). The rocky substratum is made of granite blocks of variable size (scale decimetric to decametric) more or less piled up depending on the area. A rich macroalgal biocenosis (epilithic algal) dominated by *Cystoseira* spp. covers the rocks. Over the rocky area, the *Posidonia oceanica* grows on a gently sloped bottom down to the 38-m isobath, where the meadow is replaced by a sandy-gravel bottom. All data were input to Arcview GIS (Ersi™, Inc., Redlands, California) to form a depth-substratum theme. A fifth area was mathematically added to the substratum map. It is a buffer zone between the meadow and the sandy area of the shallow water. This zone was calculated as 10 m on both sides of the boundary between the two areas.

Achiarina Bay

The substratum and depth information was collected by De Vaugelas *et al.* (1995). The coast around the island is characterized by dense *P. oceanica* meadows with sandy area patches (Figure 2b).

In Calvi Bay, more than 150 scuba dives were made to observe habitat characteristics and fish behaviour from June 2000 to October 2002, 10% of the dives being made at night. In the Lavezzi Islands, due to bad weather conditions, we were able to dive only four times during the tracking period and only once at night.

Fish tagging

Fish tracked in Calvi Bay were captured with gillnets while scuba diving near STARESO in shallow waters (<15 m) (Figure 1). After capture, the fish were transferred straightaway to tanks containing water from the capture site in order to minimize perturbations. Fish from the Lavezzi Islands were captured using the same protocol but were placed in a cage prior to tagging (Figure 1).

The fish were anaesthetized using a 0.2-ml l^{-1} solution of 2-phenoxy-ethanol. When they were fully anaesthetized, showing no reaction to external stimuli, they were weighed to the nearest g and measured to the nearest mm (fork length, L_F) (Table 1). Then they were placed "ventral side up" into a V-shaped support adjusted to their morphology. The whole body except the ventral side stayed in the water, to avoid dehydration and to permit continuous oxygenation of the gills. After cleaning in *iso*-betadine, the transmitters (V8-1L, 38×8 mm^2 and V8-2L, 24×8 mm^2) were inserted into the peritoneal cavity and the wound closed using two sutures (Jadot, 2003). The transmitters did not exceed 2.6% of the body weight of the fish (Table 1). The procedure took less than 10 min. Following full recovery in a fresh seawater tank, the fish were released at their respective capture sites.

Manual tracking

Manual tracking was conducted from a boat equipped with a VH10 unidirectional hydrophone (VEMCO Ltd, Nova Scotia) and a VR60 receiver (VEMCO Ltd, Nova Scotia). The former was fastened to a small skiff to allow tracking by a single operator, permit rapid changes of direction, and to reduce the hydrodynamic and mechanical noise (Holland *et al.*, 1992).

At sea, the accuracy of the manual-tracking method depends on several factors. First, the depth of the transmitter and the presence or absence of a thermocline, which acts as an acoustic barrier. Second, vegetation, rocks, waves (in severe weather condition), and others obstacles can reduce the power of the signal. At the same study site, Jadot *et al.*

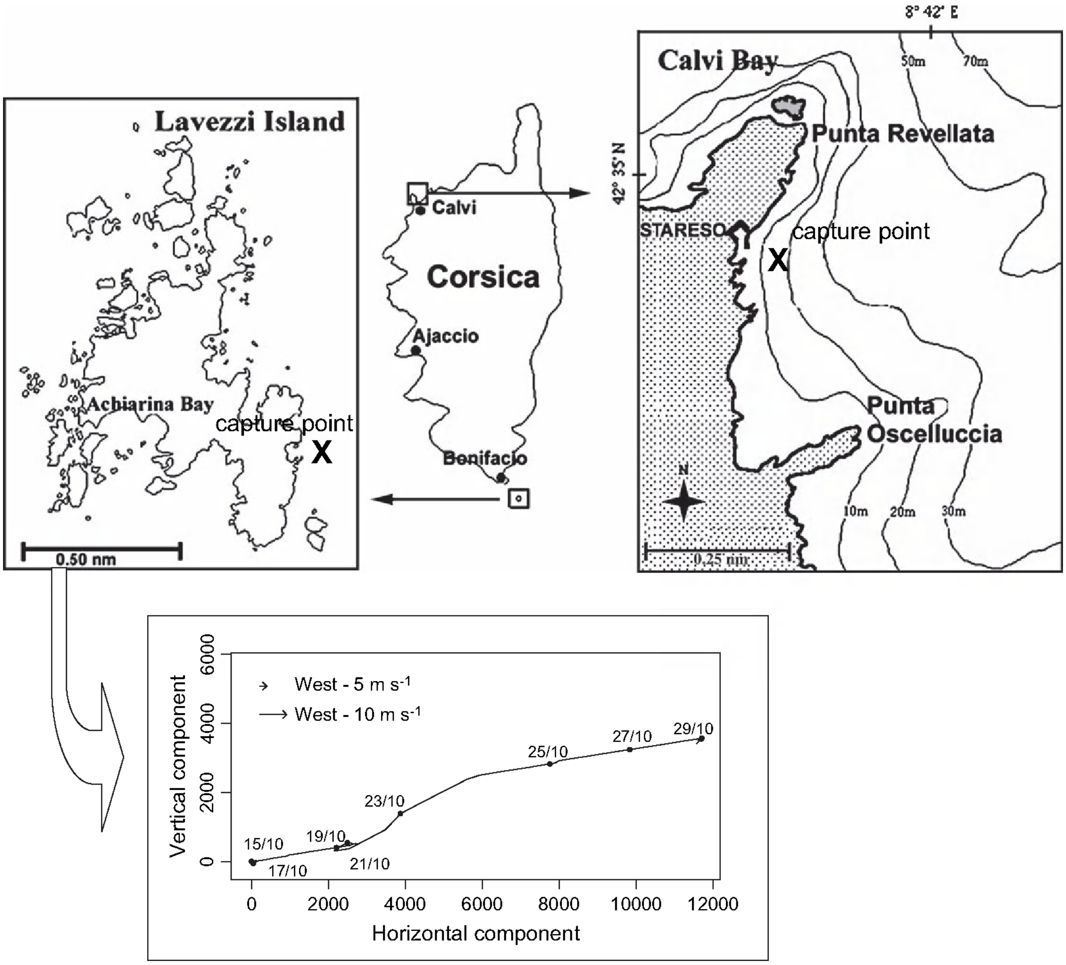

Figure 1. Map of Corsica showing the two study sites, Calvi Bay and the Lavezzi Islands. The capture sites are indicated for each study site. Bottom panel: wind at the Lavezzi Island site during the tracking period.

(2002) estimated that the accuracy of the fixes ranged from 10 m to 50 m.

After locating the fish on each survey day, bearings were taken on three landmarks, and the fish position was noted in a logbook. To minimize the possibility of losing the fish, positional fixes were taken every 30 min from dawn to dusk at the beginning of the study. In time, a pattern of movements and habitat utilization became evident and positional fixes were taken every 2 h, except during the 24-h cycles were the fixes were taken every 4 h (Table 2).

VRAP

A radio-linked, acoustic-positioning array (VRAP, VEMCO Ltd, Nova Scotia) was moored in October 2002 in Achiarina Bay. The system comprised three buoys aligned in a triangular array. Each RAP buoy had a unidirectional hydrophone and receiver for detecting ultrasonic signals, and a VHF modem and antenna for simultaneous communication to the base station. The base station, installed onshore, decodes the signals from each RAP buoy and plots in real-time the detailed position information from underwater transmitters on a computer monitor before saving the data on a hard disk. This system is more expensive than the manual-tracking method and requires more logistical support, e.g. a boat big enough to transport the buoys, divers to moor them, and a home base for reception of the transmitted signals. However, the advantages of the VRAP system are twofold. First, it remotely triangulates an accurate position of each fish. Several studies have tested the position accuracy of the VRAP system and they estimated an accuracy of between 1 m and 3 m, with positions farther from the array being less accurate (Bégout Anras *et al.*, 1999; Klimley *et al.*, 2001; Zamora and Moreno-Amich, 2002). Second, the system operates autonomously, and is thus able to record the positions of the fish over a longer period than the labour-intensive,

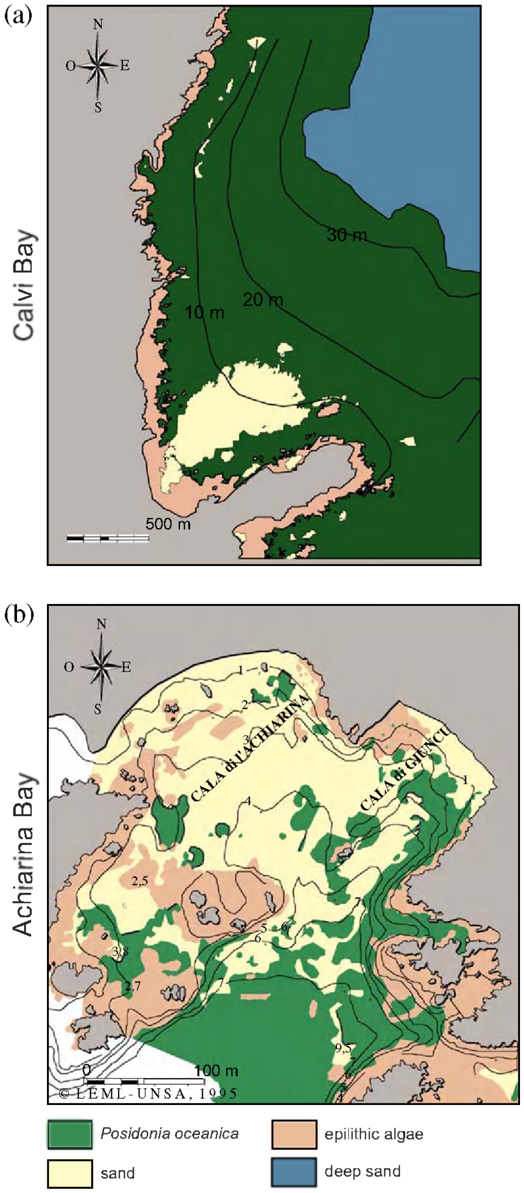

Figure 2. Different substrata types in (a) Calvi Bay, and (b) Achiarina Bay.

manpower-demanding, manual tracking aboard a boat; and this over 24 h per day (Klimley *et al.*, 2001).

The array was anchored on the western side of the Lavezzi Islands to protect the sonobuoys from the violent currents and waves very frequent at that time of the year in the area. The location of the array was also influenced by prior detection of the tagged fish via the manual-tracking system. The base station on the island communicated with each buoy individually, tuning automatically to listen to a prescribed frequency every 20 s. The data were subsequently converted to 1-min intervals.

Displacement experiment

Scuba-diving observations of fish released immediately after tagging suggested that the fish returned to the point of capture. To investigate the ability of this species to return to a specific location we conducted a displacement experiment. Three *S. salpa* were released at locations 625 m from the capture point and three at 850 m (namely Punta Revellata and Punta Oscelluccia, Figure 1). Seven fish were released at the capture site as a control group. The return of these displaced tagged fish to the point of capture was observed by the same tracking techniques used for the other fish, positional fixes having been taken directly following release.

Integrating telemetry data with GIS

Each position, manually or automatically taken, was recorded with date, time, and fish ID. The data files produced by the automated tracking system gave fish-position data tables using an arbitrary coordinate system. Those coordinates were transformed to geodetic coordinates (Lambert 2) and interpreted as a theme in the Arcview® GIS environment (Ersi™, Inc., Redlands, California).

Data treatments

A series of descriptive statistics of fish movement was calculated using Animal Movement Analyst Extension (AMAE) of Arcview® (Hooge *et al.*, 1997) to represent basic behaviour. The overall track distance is the sum of distances between consecutive points (m). The maximum speed is the maximum distance travelled per day (m day^{-1}). The Core area corresponds to the 50% Kernel home range (m^2). The dispersion of the data (r^2) is the mean-squared distance (MSD) from the centre of activity (m^2). The eccentricity is the ratio between the minor and the major axis length of range. This programme also calculated a fixed-kernel, home-range (KHR) utilization distribution as a grid coverage using *ad hoc* calculation of a smoothing parameter (H) by the least-squares cross-validation. The KHR is calculated for a probability of 95%, 75%, and 50% to find the fish. The 95% contour is usually considered as the area the animal actually uses (the home range) and the 50% contour as the core area of activity (Hooge *et al.*, 1997). As the KHR function does not recognize land as opposed to water substratum, the KHR was calculated for each fish using the AMAE extension, i.e. all land areas being clipped out using ArcView geoprocessing tools, then the area of the KHR contours was recalculated. This step was not realized in Jadot *et al.* (2002) and explains the differences observed for fish 1–6. Paired t-tests were run to compare differences between the sizes of day and night home ranges of all subjects. All statistical analyses were performed with Stat View 5.0.1® (SAS Institute Inc., Cary, North Carolina). The data could not be analysed for fish 14, 15, 16, and 18 because of the small number of positional fixes obtained.

Table 1. Characteristics of the tagged *Sarpa salpa*. TW and TBWR are "transmitter weight in air" and "transmitter to body weight ratio" in air. L is the loss of the fish, D is the death of the fish, T is the end of the transmitter battery life, and E is the end of the tracking period. Fish 13–18 were tracked with the automatic system.

Fish code	Fork length (mm)	Weight (g)	TW (g)	TBWR (%)	Date of release	Time tracked (days)	Total number of position fixes	Data source	Study site
1	289	536	2.7	0.5	08 June 2000	3	85	Jadot *et al.*, 2002	STARESO
2	288	490	3.5	0.7	13 June 2000	5	12	Jadot *et al.*, 2002	STARESO
3	283	376	3.5	0.9	21 June 2000	12	41	Jadot *et al.*, 2002	STARESO
4	317	633	2.7	0.4	05 July 2000	11	38	Jadot *et al.*, 2002	STARESO
5	149	313	3.5	1.1	02 Sept 2000	22	59	Jadot *et al.*, 2002	STARESO
6	284	447	3.5	0.7	02 Sept 2000	18	48	Jadot *et al.*, 2002	STARESO
7	235	260	3.3	1.3	23 July 2001	38	48	This study	STARESO
8	250	306	4.7	1.5	23 Aug 2001	49	40	This study	STARESO
9	239	226	4.7	2.1	23 Aug 2001	49	38	This study	STARESO
10	319	425	1.1	2.6	23 Aug 2001	15	10	This study	STARESO
11	269	307	4.7	1.5	23 Aug 2001	36	30	This study	STARESO
12	286	360	4.7	1.3	18 Sept 2002	16	13	This study	STARESO
13	268	270	4.7	1.7	18 Sept 2002	11	99	This study	STARESO
14	225	220	3.3	1.5	16 Oct 2002	1	11	This study	Lavezzi
15	229	260	4.7	1.8	16 Oct 2002	1	15	This study	Lavezzi
16	219	180	4.7	2.6	16 Oct 2002	1	5	This study	Lavezzi
17	211	182	3.3	1.8	16 Oct 2002	6	91	This study	Lavezzi
18	223	180	4.7	2.6	16 Oct 2002	1	6	This study	Lavezzi

The dawn period was established as 1 h before sunrise given by the French IMCCE (Institut de Mécanique Céleste et de Calcul d'Éphémérides, http://www.imcce.fr), and the dusk as 1 h before sunset. These periods were adjusted to every fish in relation to the months, June–October, of the tracking exercise.

The activity patterns were measured by the mean distance moved between consecutive fixes taken at fixed intervals. We used a non-parametric Friedman test to test the null hypothesis that salema utilize each habitat category in identical proportion. After the null hypothesis was rejected, an adjustment of the α-level was realized by a Bonferroni correction to allow multiple comparisons. The different substrata were then tested against each other to detect preference or avoidance of individual habitat (Wilcoxon Signed Rank test). The Spearman correlation test was used to analyse the relationship between the size of the fish and the core area of the home range (level of decision used $r = 0.09$, $p > 0.05$). The Kruskal–Wallis test was applied to compare the size of the home range of the different fish (d.f. = 4, $p > 0.05$). The non-parametric paired t-test was used to compare the size of the day and night home range of all the fish at 50%, 75%, and 95% contour levels (d.f. = 12, $p < 0.01$).

Table 2. Frequency of manual tracking in Calvi Bay.

Year	Positioning
2000	Every 30 min
2001	Every 2 h
2002	Every 2 h 24 h cycles: every 4 h

Results

The Bay of Calvi

A total of 13 *Sarpa salpa* was successfully tagged and tracked between 08 June 2000 and 18 September 2002. A total of 285 individual fish-tracking days was conducted and 721 dawn, 2151 daytime, 742 dusk and 378 night-time position fixes were acquired. These data are summarized for each fish in Table 1. The number of days tracked per fish was variable, ranging from 3 to 49 days, with a mean of 21.9 days. Likewise, the number of position fixes per fish was also highly variable, ranging from 85 to 594 with a mean of 307 positions. The low number of tracking days and position fixes for fish 1 and 2 (respectively: 3 and 5 days of tracking; 85 and 121 position fixes) was due to the loss of fish 1 and death of fish 2. The latter was found cut in two on the bottom of the bay. Natural predation cannot be ruled out but is considered unlikely.

Activity patterns

As shown by Jadot *et al.* (2002) for fish 1–6, the same pattern of activities was found in this instance for the seven other fish studied. *Sarpa salpa* exhibited a distinct diurnal activity pattern, remaining inactive by night and then moving during daytime. Diurnal activities usually started within an hour after sunrise and ended within 30–60 min of before sunset. During the observational dives, the fish were observed actively grazing during the day and resting during the night. The twilight periods were transitional periods where intermediary behaviours of the fish were observed. *S. salpa* grazed less and were more mobile during dawn and dusk (mean distance moved, respectively, 1.9 ± 0.6 m s^{-1} and 1.4 ± 0.7 m s^{-1}) than during the day or the night (mean distance moved, respectively, 0.8 ± 0.2 m s^{-1} and 0.7 ± 0.3 m s^{-1}) (Figure 3).

The fish stayed in a restricted area during the day, and then they moved to a resting area. This was either the same as the day area or an area situated a maximum of 1 km from the day site (Figure 4). All fish but numbers 1 and 4 used those two types of area for the "night" home range. No correlation with weather condition, tides, or external influences was found to explain the shift in the two zones of night areas. Moreover, fish tracked simultaneously were moving from a resting site to another one independently.

The overall track distance was highly variable from one fish to another, ranking from 4752.5 m to 55 260.8 m. The maximum speed observed ranged from 9.3 m day^{-1} to 992 m day^{-1}, with the maximum observed for fish 8 (Table 3).

Of the six fish displaced from the point of capture, by 625 m or 850 m, 100% returned to the point of capture within 2 days. The seven "control" fish released at the capture site remained there.

Direct qualitative observations by scuba divers have shown that the path used by the fish as they moved from one activity area to another was always the same, following the coast to join this or that site.

Home range

Although individuals exhibited considerable variation in the size of their home range on successive days, the general areas occupied remained fairly consistent throughout the tracking period. Except for fish 8 which had an unusually large core area, high maximum speed, and dispersion factor (respectively, 25 222 m^2, 995 m day^{-1}, and 285 305 m^2), the dispersion factors (r^2) varied from 5104 m^2 to 61 639 m^2 and the eccentricity varied from 1.36 to 3.12 (Table 3).

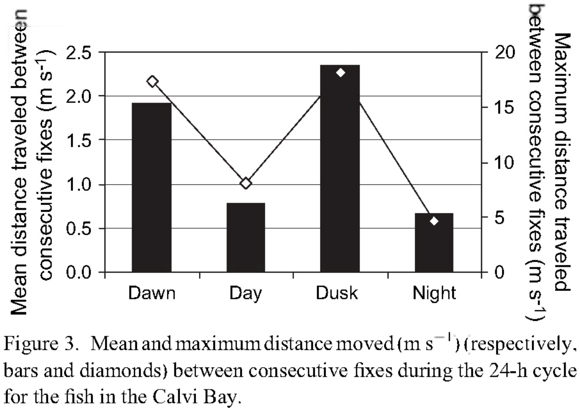

Figure 3. Mean and maximum distance moved (m s^{-1}) (respectively, bars and diamonds) between consecutive fixes during the 24-h cycle for the fish in the Calvi Bay.

The night sites, for the three measures of home range examined (95%, 75%, and 50%), were significantly larger than the day sites (paired t-test, d.f. = 12, $p < 0.01$). The night and day areas, for all subjects during the entire tracking periods, were plotted on all substrata (Figure 5). The night and day sites of fish 7, 8, and 13 are illustrative of the two different locations for the day and night sites (Figure 6). The activity core is characterized by a small single spot for the day and two spots during the night (Figure 6). All but fish 1 and 4 displayed those types of space-use patterns. Fish 1 was tracked on only two nights and then it was lost, so the results of the night-activity core analysis was a single spot. Fish 4 stayed in the vicinity of the STARESO harbour even during the night.

Tracked fish concentrated their daytime activity in core areas rather than utilizing all parts of their home range with equal intensity. Mean core areas for all the fish except fish 8 were between 255 m^2 and 11 768 m^2 and usually encompassed 18.5 ± 7.2% of the home-range area. Fish 8 had an unusually large home range of 278 714 m^2, 44 868 m^2, and 25 222 m^2, viz. 95%, 75%, and 50% contour levels, nevertheless. The core area in this case was similar to the other tagged fish and encompassed 9.05% of the daily home range.

Habitat utilization

The fish tracked in the Bay of Calvi were substratum-specific, utilizing *Posidonia* meadow and epilithic algae during the day, represented by 51% and 41% of the fixes, respectively (Figure 7). During the night, the fish were resting either in an area similar to the day-activity core, or in a particular area, situated at the limit of the *Posidonia* meadow and a sandy patch. The location of fish 5 and 7 during the day and the night on the different substrata is shown in Figure 4. During the night-time, 28% of the fixes were located on the limit zone and 41% and 31% on the *Posidonia* or the algae, respectively. Statistical analyses indicated that there were no significant differences in the use of the substratum *Posidonia* or algae during the 24-h cycle (Table 4). Furthermore, there was no significant difference in the use of the limit zone, the *Posidonia*, or algae during the night. The sand with a percentage of utilization close to 0 was significantly less used than the three other areas.

The Lavezzi Islands

Five *Sarpa salpa* were caught, tagged, and released in the west bay of the Lavezzi Islands (Table 1). The high loss rate of the fish tagged on 16 October 2002 (fish 14, 15, 16, and 18) was due most probably to the bad weather conditions forcing the fish to move away from the area surveyed by the buoys. Manual tracking failed to relocate them.

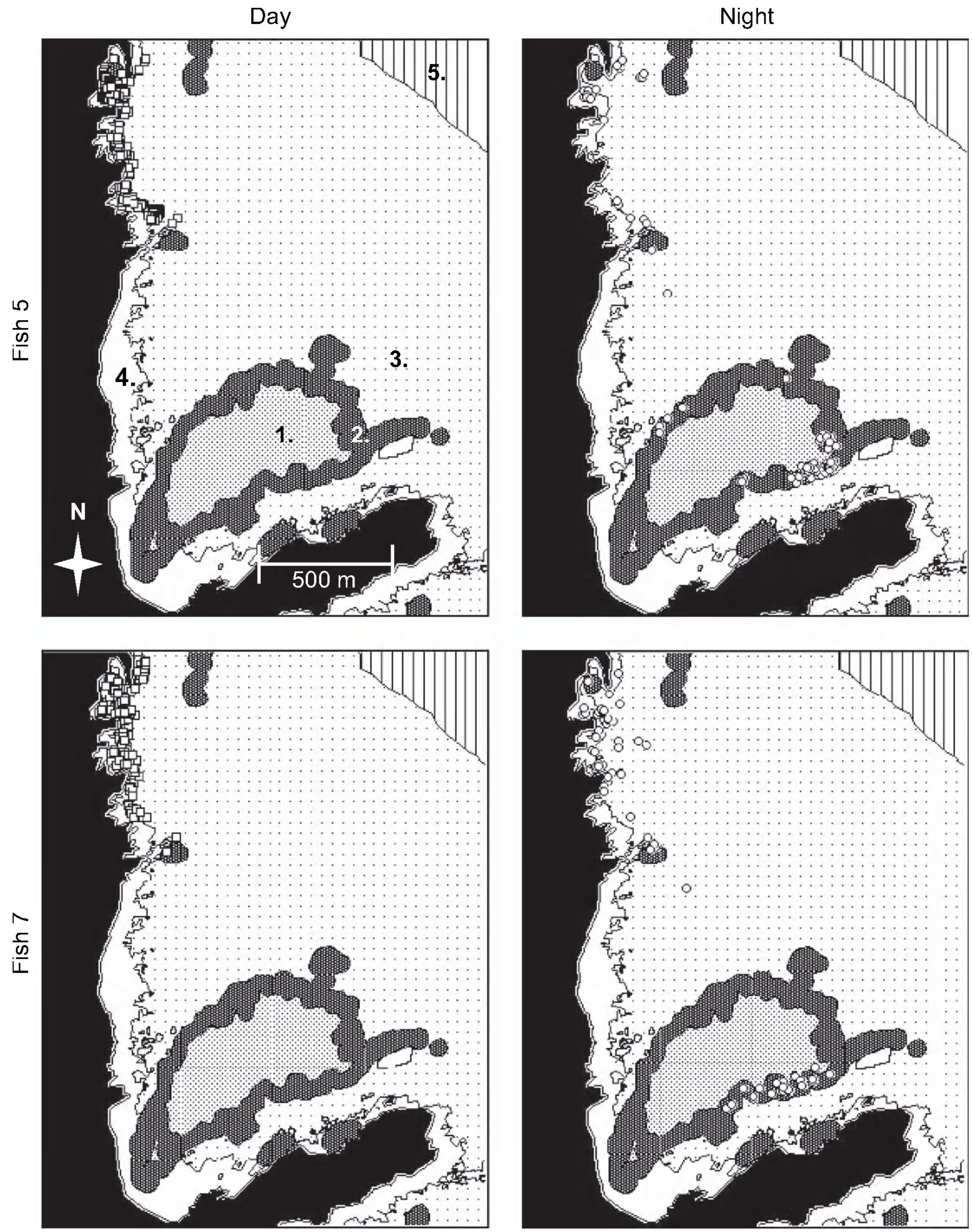

Figure 4. Night and day positional fixes for fish 5 and 7 in Calvi Bay on the different substrata. 1. is sand; 2. is the limit zone between the sand and the meadow; 3. is the meadow of *Posidonia oceanica*; 4. is the epilithic algae; and 5. is the deep sand. Land is shown in black.

No fish were found by the buoyed array at the capture site within 2 days. After locating fish 17 in Achiarina Bay by manual tracking, the buoyed array was taken there and re-established. Fish 17 was then tracked for 4 consecutive days (Figure 8). The signal was found at dusk and during the night but disappeared from the acoustic-buoyed array at dawn. Indeed, the buoys array was located in the night area of the fish and was able to estimate the

Table 3. Measures of *Sarpa salpa* movement in Calvi Bay and off the Lavezzi Islands.

Fish	Overall track distance (m)	Maximum speed (m day^{-1})	Core area (m^2)	KHR 95%	r^2 (m^2)	Eccentricity
1	1 093.9	9.3	255	1 596	10 359	3.12
2	4 752.5	584.1	5 723	22 067	11 258	1.37
3	10 598.2	633.7	5 563	19 655	28 249	2.14
4	5 132.4	225.7	2 519	7 612	6 598	2.58
5	19 354.2	640.4	3 964	31 817	40 206	2.53
6	7 802.2	455.6	1 328	7 116	5 104	1.36
7	22 014.1	440.6	3 645	24 800	25 012	2.29
8	55 260.8	995.2	25 222	278 711	285 305	3.15
9	7 076.7	338.9	524	2 430	6 953	1.45
10	5 615.5	292.3	2 685	17 659	16 841	1.63
11	32 456.2	462.7	11 654	104 290	61 639	1.75
12	10 389.8	10.4	11 768	101 177	7 841	1.88
13	7 470.9	104.9	9 768	71 829	54 632	1.99
17	7 423.9	84.3	265	1 991	1 163	1.08

night-activity core. The nocturnal home range for the tracked fish was very restricted at 1991 m^2, 854 m^2, and 266 m^2 for the 95%, 75%, and 50% contour levels, respectively. The substratum of the area visited by fish 17 during twilight and night periods was a boundary zone between the *P. oceanica* meadow and a sandy area, or a sandy area (Figure 2b). The activity pattern of fish 17 was similar to the 13 other salema tracked in Calvi Bay. The distances between two positional fixes were very small (average 7 ± 9.1 m) and the swimming speed almost zero, confirming the resting activity of the fish.

Discussion

By combining manual-tracking, automated-monitoring, and direct-diving observations, we were able to gather qualitative and quantitative information on the home range, the habitat utilization, and the movement patterns of *S. salpa*.

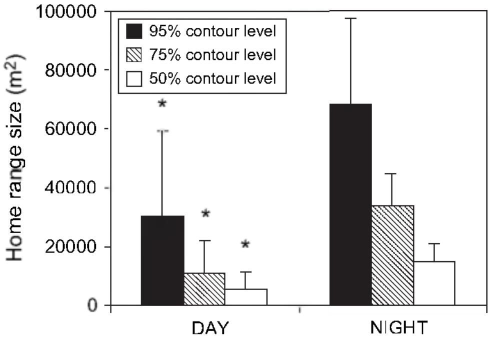

Figure 5. Temporal changes in the size of the home-range areas of *Sarpa salpa* in Calvi Bay. The mean sizes of 95%, 75%, and 50% contour levels are shown for day and night observations (±s.d.).

Home range and movement patterns

The home range of *Sarpa salpa* varied significantly between day and night. Day direct observations indicated extended periods of grazing on two main types of substrata: the *Posidonia* meadow or the epilithic algae. Night home-range activity areas were characterized by two core areas. The first was situated at the same site as the day-activity area. The second was situated in a very specific zone: the border between the *Posidonia* meadow and sandy area. This particular zone is often a unique patch where a lot of fish gathered. Other fish species exhibit a similar strategy, undergoing diel migration between feeding grounds and sheltered areas (Hobson, 1972; Gladfelter, 1979; Lowry and Suthers, 1998). Furthermore, in many diurnal fish, the onset and cessation of daily activity coincides closely with the rising and the setting of the sun (Hobson, 1972; Clark and Green, 1990).

This species displayed increased activity during the day while feeding, yet the night-time resting period has a larger home range. This particular type of behaviour can be linked to an optimal feeding strategy, i.e. high familiarity of fixed sites to increase feeding efficiency. Resting sites were not as site specific. No correlation with weather condition, tides, or external influences (predators) was found to explain the difference between the two types of resting areas. Furthermore, fish tracked simultaneously were located in either resting site, independently.

Interestingly, direct observations using scuba divers showed that the path used by the fish from one activity area to another was always the same. This particular pattern of behaviour is also evident in terrestrial species, where animals make trips between non-contiguous home-range areas using corridors (Jaremovic and Croft, 1987). Night-resting site fidelity, which involves fish returning to the same resting location on successive nights, is also well known and has been demonstrated in several fish species (Hobson,

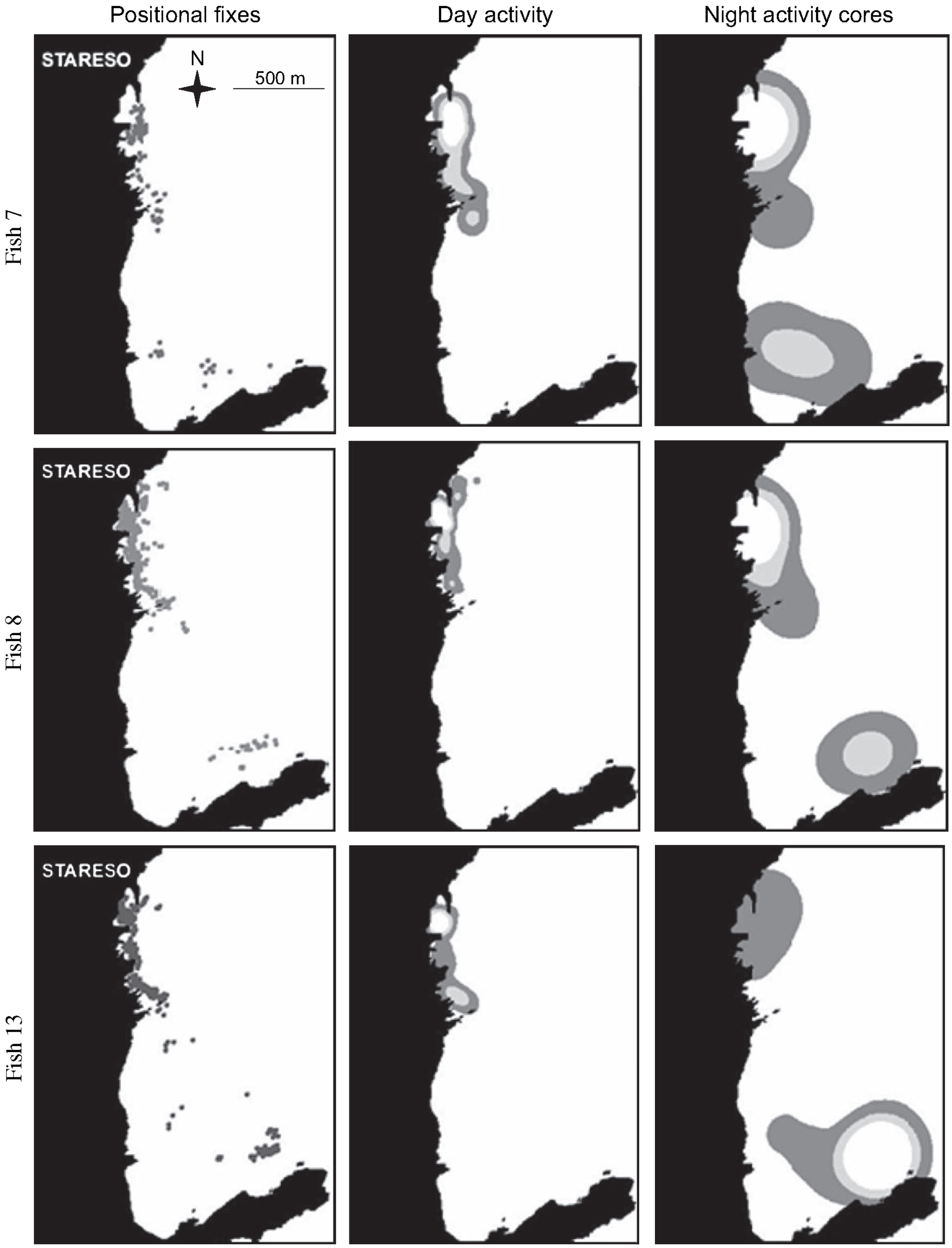

Figure 6. Day- and night-activity cores (for 95%, 75%, and 50% contour levels) for salema 7, 8, and 13 in Calvi Bay.

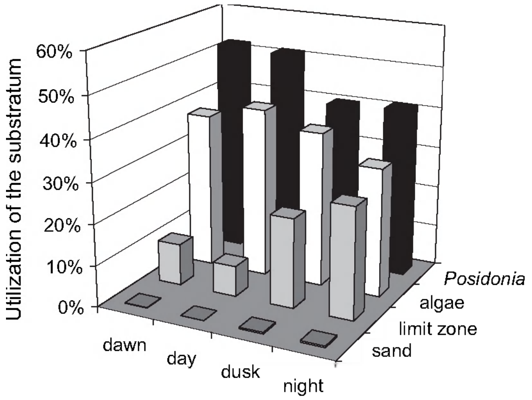

Figure 7. Substratum used by the tagged *Sarpa salpa* at the Calvi site as a function of the four periods of time studied over the 24-h cycle. Limit zone was a transition zone between sand and *Posidonia* meadow. The dawn and dusk periods were determined as, respectively, 1 h before sunrise or sunset.

1972; Ehrlich *et al.*, 1977; Clark and Green, 1990). The size of the night home range of the individual tracked in the Lavezzi Islands showed an approximate tenfold decrease, showing the ability of this species to adjust its behaviour when the environmental conditions force it to do so. Nevertheless, these findings are supported only by the observation of one fish and further investigations are needed.

Ogden and Lobel (1978) defined three foraging strategies for a diurnal herbivorous fish: territorial defence, group foraging or individual home ranges. *S. salpa* is a group-grazing fish within a well-defined home range. The strategy adopted is related to habitat type as much as to taxonomic status (Ogden and Lobel, 1978). Home-range behaviour develops where the food is neither limiting nor widely used by other species (Horn, 1989). Indeed, the Corsican *Posidonia* meadows are among the more productive ecosystems of the Mediterranean Sea (Boudouresque *et al.*, 1984), and *S. salpa* is the only fish grazer of this seaweed (Cebrian *et al.*, 1996). Consequently, competition for the resource is very limited and favours a home-range foraging strategy.

Individuals showed a clear preference for a very limited number of locations within the home range and this particular behaviour has been reported for many species of fish (Bradbury *et al.*, 1995; Eristhee and Oxenford, 2001). It has been suggested that evolutionary advantages arise from it, such as improved feeding efficiency and the reduced risk of predation, via the use within the home range of a restricted number of preferred sites and therefore a great familiarity with localized areas. However, predation on *S. salpa* is not well documented in Calvi Bay.

Substratum utilization

Our study showed that *S. salpa* was a substratum-specific species in the Mediterranean. During the day, they were found either on the *Posidonia* meadow or on the epilithic algae, while at night they sheltered either on the same site as daytime or on the border between the meadow and sandy patches. Moreover, Cebrian *et al.* (1996) showed that *S. salpa* selects productive meadows, and Verlaque (1990) revealed that salema adapted grazing activity to the abundance of the plant/algae, showing its ability to adapt its behaviour to the environment. Therefore, caution must be applied in extrapolating ecological data from a single zone to a large area. Hence, studies on different meadows throughout the year need to be done to avoid a false estimation of the herbivore's ecological role in such an ecosystem.

Homing

"Homing" is an animal's ability to return to the territory or original capture site after displacement (Wotton, 1990). Our displacement experiment demonstrated that the salema could return to the point of capture, with 100% of the displaced fish returning to the capture site within 2 days. The stimuli used to determine direction may include vision through the recognition of landmarks, olfactory stimulation, the use of a sun compass, the pattern of polarized light in the sky, and water currents (Hasler and Wisby, 1958; Wotton, 1990).

In the case of the Lavezzi site, the fish did not return to the capture site. This can be explained by the strong winds, and therefore currents and swell, in this area at the time of the tracking session. The fish probably moved to a more protected area, less exposed to wind, such as Achiarina Bay, where fish 17 was found together with occasional signals from the other fish, which is a semi-enclosed bay with the opening not open to the dominant winds, currents, or swell.

Table 4. Comparison of space occupation during the four periods of the 24-h cycle (dawn, day, dusk, and night). Occupation data for the different periods were tested against each other by Wilcoxon's test at a 0.05 level of significance. P. is the substratum *Posidonia*, A. is the substratum algae, L. is the boundary between the algae and the *Posidonia* substratum, and S. is the substratum sand. n.s. is non-significant, * is $p < 0.01$, and ** is $p < 0.001$.

Period of the day	P. vs. S.	P. vs. A.	P. vs. L.	A. vs. S.	A. vs. L.	S. vs. L.
Dawn	*	n.s.	*	*	*	*
Day	**	n.s.	**	**	*	**
Dusk	**	n.s.	*	**	n.s.	*
Night	**	n.s.	n.s.	*	n.s.	*

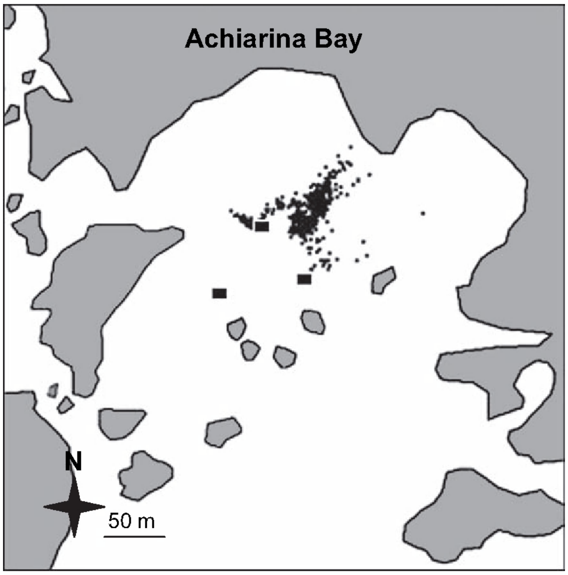

Figure 8. Positional fixes of the tagged fish in Achiarina Bay.

Homing behaviour is well documented in several marine tropical and temperate fish species (Crossman, 1977; Lowry and Suthers, 1998; Lembo *et al.*, 1999), but this is the first time that this particular behaviour has been demonstrated for *S. salpa*. Once established in areas of suitable substrata, fish could maintain their occupancy through the ability to return to the same location over time. Homing ability also sustains populations in one area, acting to stabilize spatial distribution; although functionally different, it has a similar purpose to the "territoriality" exhibited by other species (Green, 1971; Crossman, 1977).

Suggested further studies

Our study showed that the incorporation of fish-position data sets into GIS greatly enhanced their usefulness in examining spatial and temporal patterns of movement in relation to substratum (Eristhee and Oxenford, 2001). Nevertheless, further studies should be done to investigate the behaviour of this fish during winter, as *Sarpa salpa* are present in Calvi Bay during summer, and afterwards move away to deeper unknown sites at the end of autumn. Furthermore, as the bathymetric repartition and the foraging behaviour of the salema is size dependent (Verlaque, 1990), further studies should be done to investigate the habitat utilization and feeding habits of larger individuals. Greater knowledge of movement patterns, habitat utilization, and the home range of salema is needed for the eventual protection of the population.

Acknowledgements

We thank E. Guyot and D. Collard from the CEGEL, for assistance in the field in the Lavezzi Islands. Support for this paper was provided by a PhD research grant from FRIA (Fonds pour la Formation à la recherche dans l'Industrie et l'Agriculture) to the first author. The authors wish to thank the staff of the STARESO marine research station and the staff of the Réserve Naturelle des Bouches de Bonifacio. This article is a MARE publication.

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