

Diel behaviour and habitat utilisation by the pearly razorfish during the spawning season

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ABSTRACT: Despite its small size, the pearly razorfish *Xyrichtys novacula* (Linnaeus, 1758) supports important targeted recreational and commercial fisheries. Here, we present the first data on the movements of this species obtained using acoustic telemetry in a temperate marine protected area (MPA). The results demonstrate that acoustic telemetry is well suited for behavioural studies, even in species of small size. The results confirmed previous speculations regarding the behaviour of this species, demonstrating a clear diel pattern with maximum rates of activity during the day and fewer detections at night, when the fish bury themselves in the soft bottom. *X. novacula* exhibited a sedentary lifestyle with limited movement. The fish occurred in an accumulated averaged area of $0.32 \pm 0.13 \text{ km}^2$ 95% of the time (95% kernel utilisation distribution [KUD]) and in a core area (50% KUD) of $0.07 \pm 0.02 \text{ km}^2$. These small areas of habitat utilisation existed independent of sex and diel behaviour. No daily migration pattern or specific resting locations were detected. The linearity index (as a proxy of site fidelity) demonstrated that the movement of *X. novacula* was random within a specific home range area (sedentary behaviour) rather than directional (nomadic behaviour). The observed diel pattern of behaviour confirms that this species is not vulnerable to nighttime fishing, and the small spatial scale of habitat utilisation suggests that small MPAs can be an effective management tool.

KEY WORDS: Acoustic telemetry · Continuous wavelet transform · Control tag · Home range · MPA · Protogynous hermaphrodite · *Xyrichtys novacula*

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INTRODUCTION

The pearly razorfish *Xyrichtys novacula* (Linnaeus, 1758) is one of the species most targeted by Mediterranean fishers, especially recreational fishers (Morales-Nin et al. 2005, 2010). This labrid exhibits a wide spatial distribution range including the Western Atlantic (from North Carolina [USA] to the north of the Gulf of Mexico and from the Caribbean to Brazil), Eastern Atlantic (from the southern coast of Spain to the south of Cape Lopez, Gabon), Mediterranean, Azores, Madeira, Canary Islands, Cape Verde and Sao Tome Island (Froese & Pauly 2005).

Xyrichtys novacula is a protogynous monandric hermaphrodite with marked sexual dimorphism (Marconato et al. 1995, Candi et al. 2004), a relatively short lifespan (8 yr; Froese & Pauly 2005) and a maximum total length of 320 mm (Froese & Pauly 2005). Sex inversion or transition typically occurs at 79% of the fish's maximum size (Linde & Palmer 2008), and spawning occurs in the warm season, with a peak in August (Cardinale et al. 1998). The preferred habitats of this species are coarse or very coarse unvegetated sandy bottoms (Katsanevakis 2005) or soft bottoms vegetated by *Cymodocea nodosa* meadows (Tuya et al. 2005), where it feeds on small benthic

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prey (Cardinale et al. 1997, Castriota et al. 2005a,b), occupying a mid-trophic level within the food web (Blanco et al. 2009, Box et al. 2010).

Some populations of this species have been subjected to overfishing, exhibiting clear decreases in abundance and their age and size distributions as well as the size at maturation, thereby decreasing the size at sex change and affecting reproductive output (Linde & Palmer 2008). In an effort to effectively manage this species, a number of management measures have been adopted, including seasonal closures, daily bag limits and minimum sizes of hooks (e.g. Morales-Nin et al. 2010).

However, the usefulness of MPAs depends on the scale of fish movement in relation to the size of the MPA (Kramer & Chapman 1999). Thus, effective MPAs must include appropriate habitats and be sufficiently large to encompass the regular movements of adult fish (i.e. their home ranges). Then, the spillover of early life stages (eggs and larvae) and the movement of adults into areas outside the MPA can only be successful (in terms of sustainability) if a stable adult population is able to persist within the protected area (Kaplan et al. 2006).

Unfortunately, most management measures continue to be based on the assumption that fish populations are spatially homogeneous (Botsford et al. 2009). However, catchability is clearly impacted by a species' underlying spatio-temporal behaviour, and knowledge of this behaviour is needed to improve decision-making processes (Botsford et al. 2003). This is the case for *Xyrichtys novacula*, for which little is known about its spatio-temporal movement patterns. In this context, acoustic telemetry is considered to represent an alternative to conventional tag-and-recapture studies for assessing individual fish movement, allowing us to improve existing knowledge of the spatial and temporal structure of fish species over various scales of space and time (Voegeli et al. 2001, Parsons & Egli 2005). The resulting improvements in experimental design (Heupel et al. 2006) and the development of new algorithms to support improved location of fish (Hedger et al. 2008) linked to the miniaturisation of acoustic tags make this methodology highly desirable for investigating spatial and temporal patterns in marine coastal fisheries. Thus, the main objective of the present study was to provide a first approach to identify the spatio-temporal behaviour of *X. novacula* using acoustic telemetry during the spawning season, specifically by assessing the home ranges and movement patterns of these fish during day versus nighttime hours. The implications of the results for management, such as de-

termining the size of an MPA to effectively protect this species, were also explored and directly linked to the sustainable development of the fishery of this species.

MATERIALS AND METHODS

Study site and acoustic receiver array

The MPA of Palma Bay is located to the south of Mallorca Island (NW Mediterranean; Fig. 1). Fishing activities in the MPA have been regulated since 1982 (Fisheries Department, Balearic Islands Government), and it contains 2 main areas with different degrees of protection: a no-take area (~2 km²) and a buffer area where both artisanal and recreational fishing are regulated (e.g. gear limitations or temporal closures) but not prohibited. The main habitat in the MPA is characterised by the endemic Mediterranean seagrass *Posidonia oceanica* (Fig. 1). However, the southern buffer area is dominated by fine sand (grain size from 0.125 to 0.250 mm) and coarse sand (grain size from 0.5 to 1 mm) bottoms, representing optimal habitat for *Xyrichtys novacula* (Katsanevakis 2005; Fig. 1).

In July 2011, a fixed array of 21 omni-directional acoustic receivers (model SUR-1, Sonotronics) was deployed in the southern area of the MPA, covering most of the soft bottom habitat (Fig. 1). Prior to deploying the receivers, the detection range of the tags to be used in the present study was assessed by mooring a number of tags at different distances from a receiver. The maximum detection range was >300 m (see details in Fig. 2). Thus, the receiver array, based on a 300 × 300 m grid, provided a high degree of detection overlap between receivers (see Fig. 1), allowing improved centre of activity estimations (Simpfendorfer et al. 2002).

Tagging procedures

After the receiver arrays were deployed, 12 *Xyrichtys novacula* individuals were acoustically tagged using Pico-tags (model PT-2, Sonotronics). The miniaturised tags measured 19 mm in length and 7.1 mm in diameter, weighed 1 g in water and did not exceed 2% of the fish's body weight (Table 1). The tags had a manufacturer's expected lifespan of 12 d. However, the true lifespan of the acoustic tags was considerably longer (see 'Results'). Each tag emitted a specific sequence of pulses at a given frequency (70

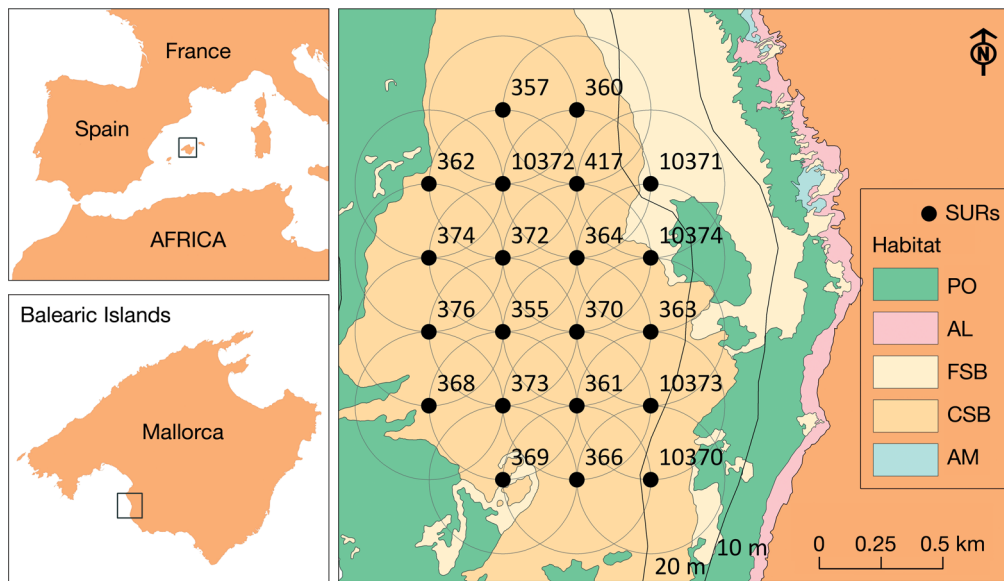


Fig. 1. Study site located in the marine protected area of Palma Bay, Mallorca Island (NW Mediterranean). The figure shows the omni-directional acoustic receivers (SUR-1) array detailing the ID receiver as well as a buffer area (detection range) of 300 m of radius. Habitat types are named as *Posidonia oceanica* seagrasses (PO), rocky bottoms with photophilous algae (AL), fine sand bottoms (FSB), coarse sand bottoms (CSB), and a mixture of algae and seagrasses (AM)

to 82 kHz), allowing individual fish to be identified (Table 1). The tags were programmed to emit signals every 1200 ms. When a receiver detected a signal, it was recorded as a single detection, which was labelled with a detection number and the date, hour, frequency (kHz) and interval period (ms).

All individuals were caught inside the fixed array by anglers at depths ranging from 22 to 25 m using conventional hook-and-line gear and small live shrimps as bait. Performing the tag-and-release of all individuals on the same day optimised the modelling procedures, allowing us to include the daily variation in the detection pattern in the model (see 'Data analysis'). Angling sessions were optimised to reduce the incidence of deep hooking and barotrauma effects, following published recommendations (Alós 2008, Alós et al. 2008, 2009). The tagging was performed in the spawning season (Cardinale et al. 1998), 7 males and 5 females were tagged to test sex-related differences in temporal and spatial patterns (Table 1).

The fish were measured (total length to the nearest mm), weighed (to the nearest g) and placed in a 150 l onboard aerated fish holding tank. Then, they were anaesthetised by immersion in 10 l of filtered sterile seawater containing 100 mg l^{-1} of tricaine methane-sulfonate (MS222). Each acoustic tag was surgically implanted into the peritoneal cavity through a dorso-ventral incision and sutured using non-absorbable sutures (Mersilk, 4-0, Ethicon), maximising sterile

conditions. The entire surgical process took <5 min. The fish was then placed in the onboard tank to recover until normal behaviour was observed (i.e. the effects of the MS222 disappeared). The fish were subsequently released from the boat at the same position where they had been captured and visually monitored until they reached the soft bottom, avoid-

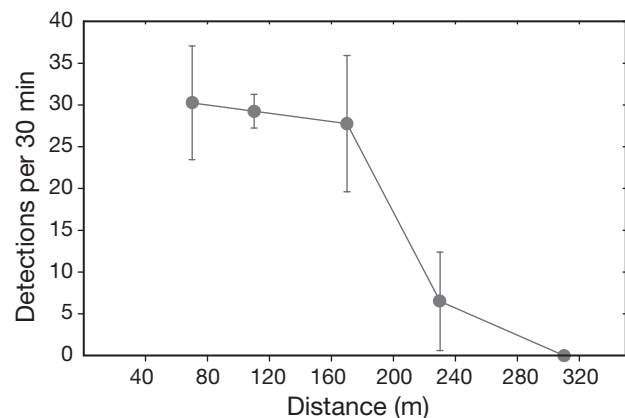


Fig. 2. Detection range test. Means \pm 95% CI of the detections per 30 min ($n = 4$) against the distance (m) obtained in the test. Variation of the depth (m) in the study area was <10 m, and the range tests were done at the average depth (~23 to 24 m). The test was carried out by mooring 5 different receivers (with the same configuration used in the tracking experiment) at different distances from an acoustic tag (the same used to tag individuals of *Xyrichtys novacula*). Results showed a strong decrease at 200 m and a maximum detection range of 300 m

Table 1. *Xyrichtys novacula*. Characteristics of the implanted acoustic tags (frequency) and individuals of *X. novacula* tagged (total length, weight and sex). ID: identification number. Release: day when the fish was tagged and released. Detections: total count of the detections downloaded from the array. Receivers: number of receivers that detected a specific fish. TP_i : period between the release date and the last detection for fish i ; DD_i : total number of days detected; RI_i : residence index

Fish ID	Total length (mm)	Weight (g)	Sex	Frequency (kHz)	Release (dd/mm)	Detections	Receivers	TP_i (d)	DD_i (d)	RI_i
1	190	75	Male	70	26/07	1648	15	22	14	0.6
2	187	72	Male	71	26/07	37 106	14	23	23	1
3	202	85	Male	72	26/07	4791	16	8	8	1
4	209	93	Male	73	26/07	50 327	16	22	22	1
5	189	74	Male	74	26/07	22 537	17	23	23	1
6	159	51	Female	75	26/07	15 269	7	17	17	1
7	185	70	Male	76	26/07	30 074	18	22	22	1
8	158	50	Female	77	26/07	67 171	12	23	23	1
9	158	54	Female	78	26/07	13 189	13	22	22	1
10	153	54	Female	79	26/07	25 929	17	22	22	1
11	159	53	Female	80	26/07	60 147	13	23	23	1
13	192	75	Male	82	26/07	69 652	17	23	23	1
Control tag	–	–	–	81	28/07	103 279	13	21	21	1

ing post-release predation. As recommended by Payne et al. (2010), a control tag (the same model as that used for the fishes; Table 1) was moored in the receiver array during the tracking period to help rule out environmental effects on the detection patterns (Table 1). The position, depth (m), day and hour were recorded for each tagged fish prior to its release.

Data analysis

An MS Access database was used to store and manage all of the obtained detection data. Additionally, data from the US Naval Observatory (<http://aa.usno.navy.mil/>) were used to develop temporal categories of day and night based on local sunrise and sunset data. In terms of temporal patterns, the number of days on which a specific tagged fish (i) was detected (DD_i) was divided by the period between the release and the last detection date (TP_i) to calculate a residence index (RI_i) within the receiver array (March et al. 2010, Alós et al. 2011). The temporal pattern of detections was then examined by visually examining chronograms of the hourly detections of each individual and the hourly means plot of the detections.

A continuous wavelet transform (CWT) was then used to detect any periodicity in the detection pattern at different time scales. The mathematical robustness and predictive ability of CWT make it one of the most promising tools for use in multi-scale movement ecology, which couples the study of animal behaviour and environmental properties (Gaucherel 2011). The

CWT allows a time-series to be broken down into time-frequency space, providing an alternative to Fourier analysis or other time-frequency decomposition methods (Percival & Walden 2000) to identify temporal patterns in movement data (Gaucherel 2011) or in data obtained from acoustic tracking experiments (March et al. 2010, Alós et al. 2011). The *sowas* library in R package (www.r-project.org/) was used to compute the 2-dimensional wavelet spectrum and to perform a point-wise test at a 95% significance level for each tagged fish and for the control tag (Maraun et al. 2007). Wavelet coefficient values were normalised such that the highest spectral power was equal to 1 (March et al. 2010).

The spatial analysis was based on the Nadaraya-Watson kernel estimator (*sm* library in R; Bowman & Azzalini 1997), which was used to calculate the centre of activity positions (COAs) for the tracked fish i in 60 min time steps. Thus, estimation of the XY_i positions for Fish i was based on the positions of the receivers that detected the fish during a specific time-step period and weighted by the number of detections (Simpfendorfer et al. 2002). Then, 2 measures of the home range (HR) were estimated for each fish: (1) the minimum convex polygon based on 100% of the obtained positions (100% MCP $_i$) and (2) the cumulative and daily HR (based on the diel phases) as the bivariate fixed-kernel utilisation distributions (95 and 50% KUD $_i$). These HR estimates were based on the COAs estimated for each fish over a grid with a 50 × 50 m resolution using the *adehabitat* library in the R package (Calenge 2006).

KUDs are more robust than MCP to identify outlier COAs because they include a kernel bandwidth (KB) that allows consideration of the error estimations for the COAs (March et al. 2010, Alós et al. 2011). In contrast to previous studies that used a KB equal to the detection range (e.g. March et al. 2010), we obtained a direct measure of the positioning error based on the estimated COAs and the true position of the control tag. KB was considered to be equal to the mean of the positioning error of our control tag (see 'Results'). Thus, the COAs of the control tag were estimated and then compared with the known true position to directly estimate position error (~90 m, see 'Results'). Using this KB value, the obtained KUD estimates were more accurate but remained conservative due to the error in positioning obtained through acoustic telemetry.

The HR area is expected to increase over time and to eventually arrive at an asymptotic value when a fish has explored most of its true home range (Börger et al. 2008). Thus, temporal changes in the daily cumulative HR size were examined visually using HR curves. We assumed that the asymptotic HR (based on the 95% KUD) was reached when the percentage of difference between 2 consecutive days for the accumulated HR was <5% (Rechisky & Wetherbee 2003). Changes in HR size related to diel behaviour were also investigated using the index of reuse (IOR; Rechisky & Wetherbee 2003). The daily IOR_i was estimated for each fish i as $IOR_i = [OV_i(A_1, A_2)] \div (A_1 + A_2)$, where A_1 and A_2 are the activity spaces, and $OV_i(A_1, A_2)$ is the area of overlap between the 2 activity spaces (i.e. the daily accumulated 50% or 95% KUD areas for each diel phase; (Rechisky & Wetherbee 2003). Values of IOR_i close to 1 indicate a large overlap between the activity spaces and imply high site fidelity and an absence of diel differences in spatial utilisation. In contrast, values of IOR_i close to 0 indicate that the diel activity spaces are different, suggesting the occurrence of some type of daily migration (e.g. Hitt et al. 2011). Finally, the linearity index (LI_i) was estimated as an indicator of the direction of the fishes' movements (random vs. directional movement) and site fidelity. The index was calculated according to Alós et al. (2011).

Modelling spatio-temporal patterns

Significant temporal and spatial patterns were checked via generalised linear mixed models (GLMM; Zuur et al. 2009). The total daily detections pooled per diel phase (standardised based on the dif-

ferent duration of each phase) and the daily HR utilisation (based on the 95% KUD) structured by diel phases (day and night) for each fish were considered as dependent variables (y) in 2 different GLMM. In both cases, the diel phase (day vs. night) and sex as well as their interaction effects were considered as independent variables and treated as fixed factors.

Because the data were composed of repeated measures within individuals and within different tracking days, we considered the fish identity (ID) as a random factor and grouped the data based on the tracking date. The 2 different models (spatial and temporal) were fitted using the *glmm.admb* function of the *glmmADMB* library in the R package. In both cases, the data did not exhibit a Gaussian distribution (even after efforts at transformation). However, using a Poisson distribution without zero inflation, the residual distribution was normal (family = Poisson in the *glmmADMB* library). The normality of the residuals and model performance were examined by visual inspection of the residual distributions, plotting the residuals against the fitted values and using quantile-quantile (QQ) plots.

RESULTS

General results

A total of 501 119 detections (with a mean and standard deviation [SD] of $38\,548 \pm 29\,941.2$ detections per fish) were obtained during the study period (Table 1). The maximum number of detections was for the control tag (103 279 detections; Table 1). Tagged fish were detected by 15 receivers on average (SD = 3.1 receivers), whereas the control tag was detected by 13 different receivers (Table 1). In terms of the TP_i , the fish were tracked for a period of 3 wk (mean \pm SD = 21 ± 4.36 d), and the control tag was detected for 23 d, notably exceeding the expected life span (12 d) of the tags provided by Sonotronics (Table 1).

The DD_i were equal to the TP_i in almost all cases, obtaining the maximum values for the residency index (LI_i ; Table 1). Fish 1 and 3 had the lowest numbers of detections, and the temporal chronograms for these fish suggested possible mortality or tag loss, e.g. if the sutures did not hold (Table 1). Similarly, after 11 d of tracking, Fish 8 either died or lost its tag, exhibiting a nearly constant detection pattern (see 'Temporal patterns' and Fig. 3). Thus, Fish 1 and 3 and the period after 6 August for Fish 8 were not considered in the data analysis.

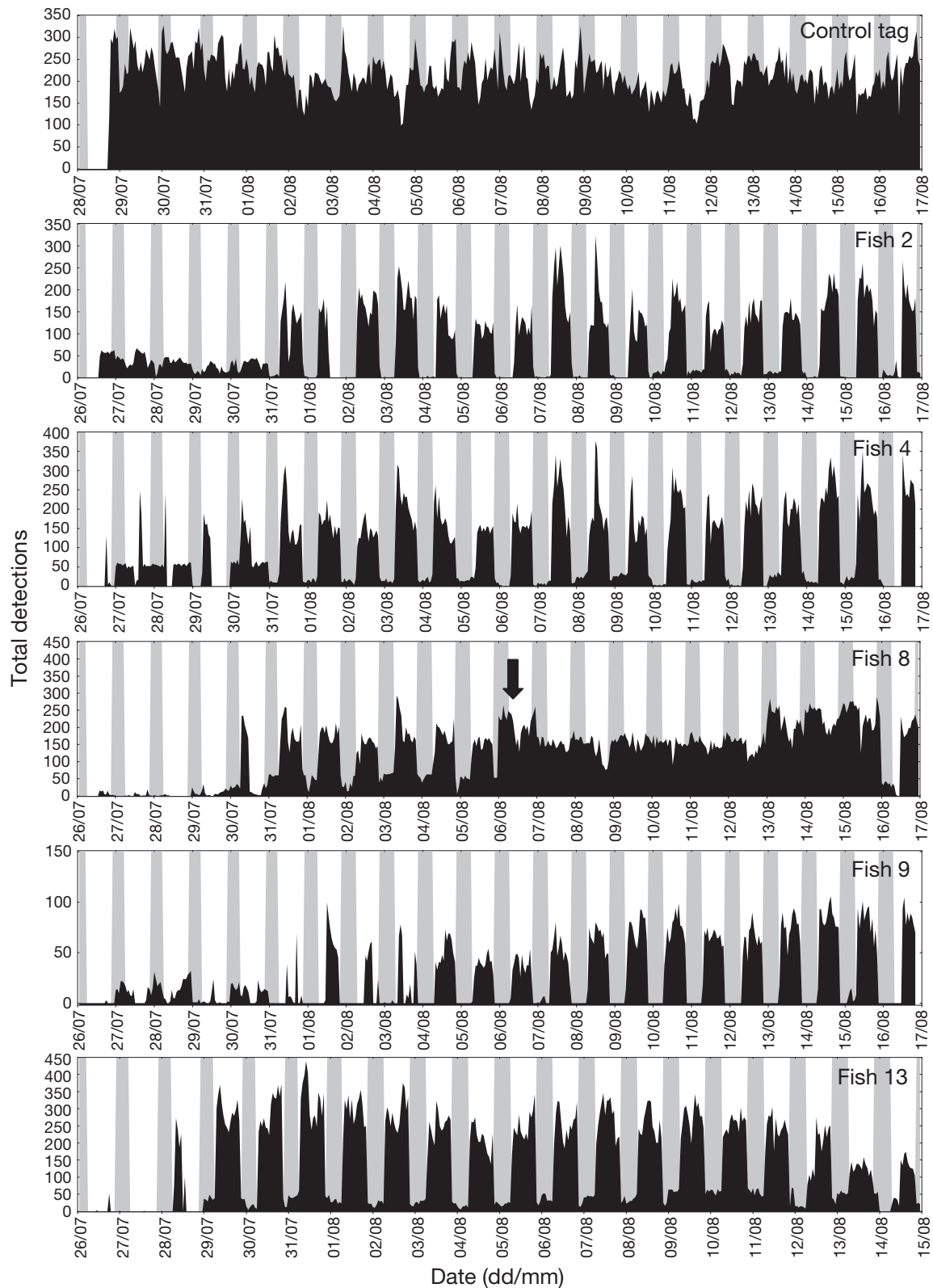


Fig. 3. *Xyrichtys novacula*. Hourly detections over the tracking period for the control tag and tagged Fish 2, 4, 8, 9 and 13. Vertical stripes indicate day (white) or night (grey) related to the local sunrise and sunset time. Note the higher number of detections during the day and the loss of a diel pattern after 12 d of tracking in Fish 8. No temporal pattern can be recognized in the control tag plot

Temporal patterns

Chronograms of hourly detections showed a clear temporal pattern (diel based) characterised by a strong decrease in the number of detections during the night (Fig. 3). During the first several days after the fish were tagged, the detection pattern was irregular, characterised by few detections, suggesting abnormal behaviour during a short period after capture and implantation (Fig. 3). These patterns were not observed in the chronogram of the control tag, indicating that this was not an environmental effect (Fig. 3).

The means plot also showed a diel pattern of greater numbers and variability of detections in daylight hours (Fig. 4), which was not seen with the control tag. The analysis performed using the CWT clearly confirmed this diel behaviour, with a significant periodicity (marked by the 95% significance level) detected at the 24 h scale in most cases (see examples for 4 different fish in Fig. 5). The abnormal behaviour during a short period after capture and implantation was also confirmed by the CWTs (Fig. 5). The CWT performed for the control tag did not show any temporal periodicity, and no other significant temporal behaviour was detected at any temporal scale for the tagged fishes (Fig. 5).

These temporal behaviours were significant, with a significant increase in detections occurring during daylight hours ($p < 0.001$; Table 2), and no significant difference between sexes was observed ($p = 0.37$; Table 2). However, the interaction effects between the diel phase and sex were significant, with males exhibiting lower mean detection rates during the night ($p < 0.001$; Table 2).

Spatial patterns

A total of 456 ± 57.6 (mean \pm SD) COAs were estimated for the tagged fish (Table 3). For the control tag, a total of 471 COAs were estimated and compared with the true TAG position (Table 3). The COA estimation error varied by 87.8 ± 38.4 m (mean \pm SD) over time, without any temporal pattern (Fig. 6). The positioning error estimated for the latitude and longitude is plotted in Fig. 6. The mean minimum convex polygon (MCP) estimated for all of the COAs for the tagged fish was 0.15 ± 0.12 km² (Table 3).

The mean accumulated bivariate fixed KUD_i estimated for the tagged fish were 0.32 ± 0.13 km² and 0.07 ± 0.02 km² for the 95% and 50% KUDs, respectively (Table 3). The variation in the daily cumulative 95% KUDs is represented in Fig. 7. The home range area (based on the 95% KUD) for all fishes reached an asymptote after 7.6 ± 4 d (mean \pm SD; Fig. 7, Table 3). Fig. 8 shows the spatial plot with the MCPs and 95% and 50% KUDs of Fishes 2, 4, 5, 6, 7, 9, 10, 11 and 13 for the purpose of visualising the general patterns of habitat utilisation. Spatial utilisation was similar for both night and day, with mean \pm SD for the 95% KUDs of 0.31 ± 0.13 km² for day and 0.29 ± 0.11 km² for night (Table 4). In the case of the 50% KUDs, these values were 0.06 ± 0.02 km² and 0.05 ± 0.01 km², respectively (Table 3). Spatial modelling did not show any significant effect for the diel phase, sex or their interaction (Table 2).

The values (mean \pm SD) for the IOR_i ranged from 0.48 ± 0.1 to 0.96 ± 0.06 and from 0.18 ± 0.09 to 0.91 ± 0.12 for the 95% and 50% KUDs, respectively, and in most cases, were >0.5 , suggesting a high degree of overlap between day and night activity spaces

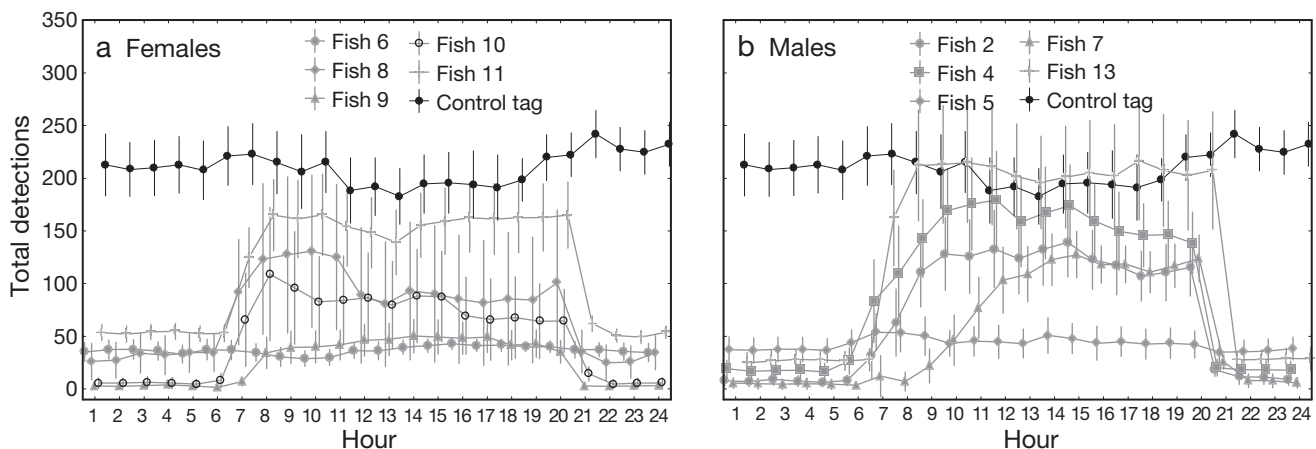


Fig. 4. *Xyrichtys novacula*. Detections per hour (mean \pm CI) during a daily period. Control tag and (a) females and (b) males

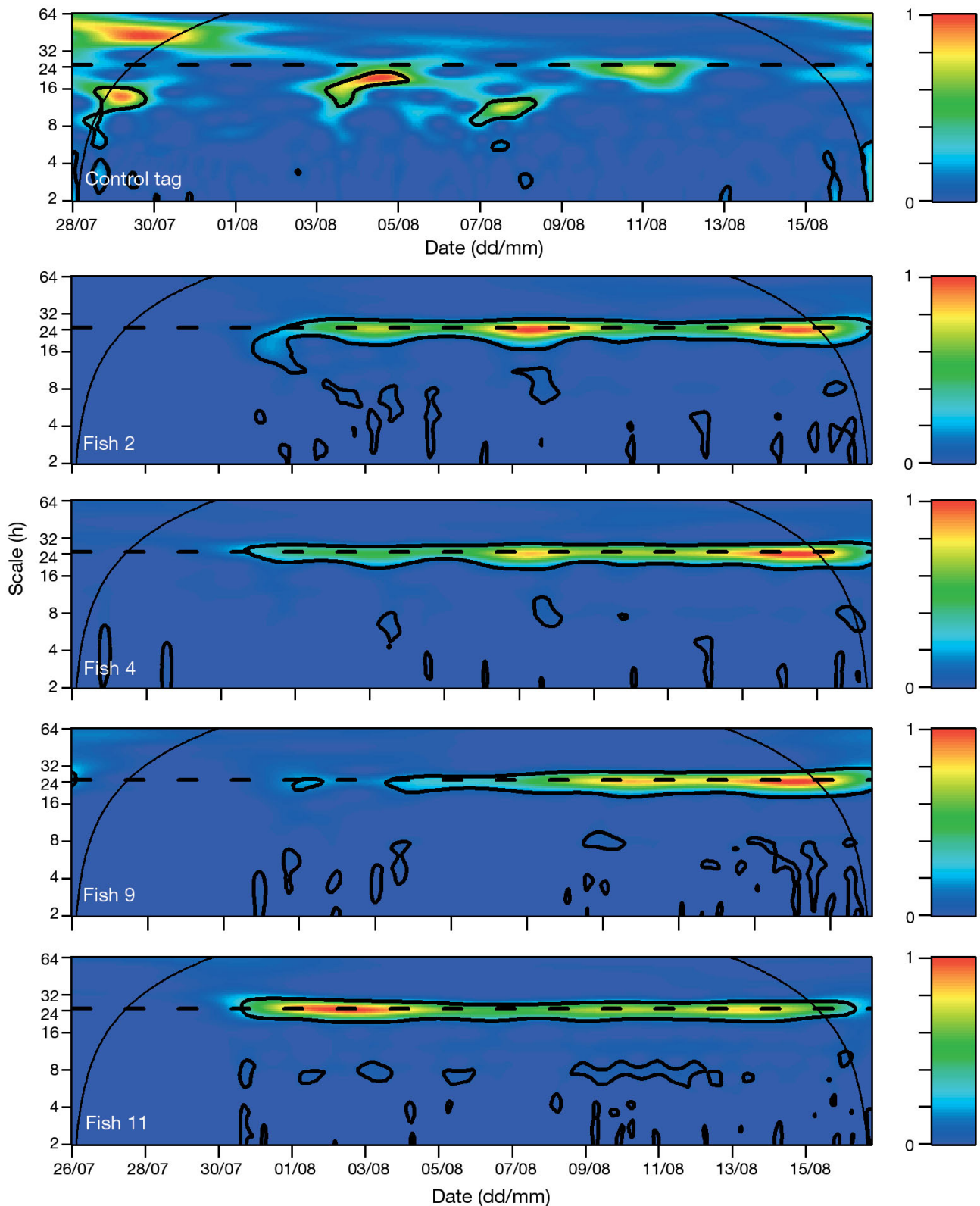


Fig. 5. *Xyrichtys novacula*. Wavelet sample spectra fitted for the control tag and Fish 2, 4, 9 and 11. Continuous thin lines represent the cone of influence (COI), and values outside the COI should not be interpreted due to edge effects. Thick contours represent the 95% confidence level, and significant periodicities were detected in all cases on a 24 h scale (indicated as a horizontal dashed line). No periodicity in the detection pattern was detected in the control tag

Table 2. *Xyrichtys novacula*. Estimate, standard error, z-values and p-values obtained in generalised linear mixed models fitted to test (a) temporal (mean detections per diel phase) and (b) spatial (mean home range per diel phase) patterns. In both cases, the independent variables (fixed factors) were the diel phase (day vs. night), sex (male vs. female) and their interaction. *** very highly significant

	Estimate \pm SE	z	Pr ($>$ t)
a) Temporal patterns (log-daily detections)			
(Intercept)	6.61 \pm 0.48	13.65	<0.001***
Diel phase (night)	-2.03 \pm 0.05	-37.15	<0.001***
Sex (male)	0.29 \pm 0.32	0.90	0.37
Diel phase (night) \times Sex (male)	-0.26 \pm 0.06	-4.58	<0.001***
b) Spatial patterns (log-spatial utilisation)			
(Intercept)	-1.77 \pm 0.25	-7.08	<0.001***
Diel phase (night)	-0.05 \pm 0.36	-0.14	0.89
Sex (male)	0.07 \pm 0.33	0.21	0.84
Diel phase (night) \times Sex (male)	0.00 \pm 0.48	0.01	0.99

(Table 4). Finally, all of the values of the LI_i were close to 0, with a mean \pm SD of 0.04 ± 0.02 , showing a high degree of site fidelity, thus rejecting the hypothesis of nomadic movement in favour of the hypothesis of random movements (Table 4).

DISCUSSION

The pearly razorfish *Xyrichtys novacula* is a small labrid that is widely targeted by the professional and recreational fisheries in the Mediterranean. Due to this intense exploitation, some of its populations have been overexploited, and various spatio-temporal management strategies have been adopted for this species. In the present study, we provide the first attempt to determine habitat use by this species by employing acoustic telemetry in a temperate MPA. This species exhibited clear diel behaviour affecting their vulnerability to fishing, as they bury themselves in the sand at night.

In terms of spatial patterns, *X. novacula* individuals exhibited small HR of $<0.5 \text{ km}^2$ and high site fidelity, indicating that small MPAs represent a promising management tool for this species. In this first acoustic telemetry study of *X. novacula*, we

Table 3. *Xyrichtys novacula*. Number of centres of activity positions (COA), minimum convex polygons based on 100% of the positions (100% MCPs), the asymptote value (i.e. day on which the accumulated home range changed $<5\%$) and the accumulated and diel-based bivariate normal fixed kernel utilisation distributions (95 and 50% KUD) in km^2 estimates for each tagged fish i

Fish ID	Sex	COA _{<i>i</i>}	MCP _{<i>i</i>}	Asymptote (d)	KUD _{<i>i</i>} 95%			KUD _{<i>i</i>} 50%		
					Accumulated	Day	Night	Accumulated	Day	Night
2	Male	489	0.11	7	0.36	0.34	0.32	0.08	0.07	0.06
4	Male	493	0.17	7	0.35	0.33	0.33	0.09	0.08	0.05
5	Male	507	0.28	10	0.45	0.47	0.41	0.07	0.07	0.07
6	Female	391	0.01	1	0.16	0.16	0.15	0.04	0.04	0.04
7	Male	435	0.36	5	0.48	0.47	0.45	0.07	0.06	0.07
8	Female	500	0.04	4	0.21	0.21	0.20	0.04	0.04	0.04
9	Female	359	0.15	9	0.32	0.31	0.33	0.07	0.06	0.08
10	Female	392	0.25	13	0.51	0.51	0.43	0.11	0.11	0.07
11	Female	523	0.02	14	0.17	0.17	0.15	0.04	0.04	0.04
13	Male	471	0.09	6	0.21	0.20	0.17	0.05	0.05	0.04

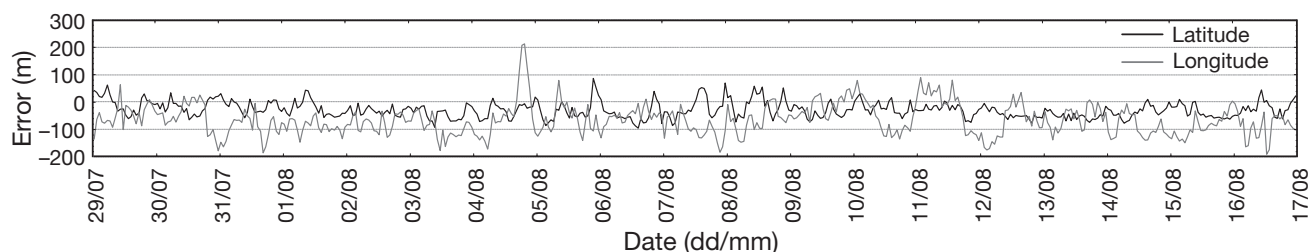


Fig. 6. Positioning error (m) of the hourly estimated centre of activity positions of the control tag. Latitude and longitude errors are individually represented

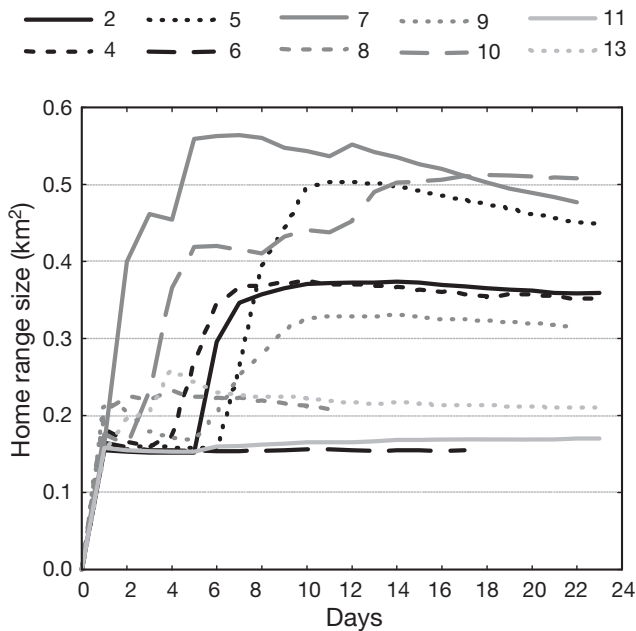


Fig. 7. *Xyrichtys novacula*. Daily cumulative home range estimates (km^2 ; based on 95% kernel utilisation distributions) of the tagged fish nos. 2, 4 to 11, and 13

were able to incorporate emerging techniques to improve the array's accuracy and to demonstrate the effectiveness of miniaturised acoustic tags for studying a small-bodied species.

Two main methodological improvements adopted here should be mentioned because they can be generalised to any type of acoustic telemetry experiment. (1) The applicability of control tags and their ability to track changes in detection due to environmental or biological causes has recently been noted (see details in Payne et al. 2010). Here, the use of a control tag allowed us not only to discard any environmental pattern in the detection pattern (the detection pattern was time-independent) but also to confirm that the decrease in nighttime detections was biological and most likely due to the 'burying' behaviour characteristic of this species (Katsanevakis 2005). (2) It is generally assumed that the behaviour of tagged fish is normal if proper surgical procedures and tag choices have been applied. However, in this study, several days post-release passed before the fish returned to normal behaviour (Fig. 3). The tagged fish in our study were less mobile and may have buried themselves during the first 3 to 4 d after tag implantation. Normal behaviour (mainly characterised by the diel pattern) subsequently returned for all of the tagged fish. Therefore, this result should be considered in further experiments in this species.

Significant changes in diel behaviour have previously been reported for marine coastal species in the Mediterranean (Jadot et al. 2002, March et al. 2010, Alós et al. 2011). However, the ability to infer diel behaviour from detection patterns is a controversial issue, and different behaviours can generate the same diel detection pattern, including daily migrations (e.g. Hitt et al. 2011), hiding behaviour during the night (e.g. March et al. 2010) or fluctuations in environmental conditions (Payne et al. 2010). In some cases, the detection pattern changes because fish remain hidden during the night, and the decrease in detection is purely motivated by physical factors. This is the case for many species associated with a particular structure, such as many reef fish species (e.g. Topping et al. 2005) and even some species inhabiting seagrass meadows (March et al. 2010, Alós et al. 2011).

This also appears to be the case for *Xyrichtys novacula*. It is well known that this species exhibits feeding (Cardinale et al. 1997), mating (experiment performed in the spawning season; Marconato et al. 1995, Cardinale et al. 1998) and social behaviours (Marconato et al. 1995) during the day. It has also been previously reported that this fish may bury itself in the sand during the night to rest (Katsanevakis 2005). This diel behaviour pattern was supported by the detection pattern obtained in the present study, with significantly more detections during the day than the night. Moreover, use of the control tag (a tag set just 1 m from the bottom) indicated that it was fish behaviour rather than environmental fluctuations that caused the decrease in nighttime detections (Payne et al. 2010).

Wavelet analysis was helpful for analysing the periodicities in the tag detections and, thus, the diel behaviour of *Xyrichtys novacula*. Wavelet analysis has been used successfully to determine periodicities in other Mediterranean fishes and at other time scales (March et al. 2010, Alós et al. 2011), confirming the usefulness of this tool for detecting regime shifts in fish movement. The diel behaviour exhibited by *X. novacula* was independent of sex and, thus, not due to a factor affecting general detections, such as the thicker body wall in males (because males are bigger than females). However, the interaction between diel phase and sex was significant, with males detected less during nighttime. Two possible behavioural explanations for why the probability of detecting males is lower compared to females during the nighttime are that (1) males may bury themselves more completely or deeply than females and that (2) males may remain buried for a longer time period than females.

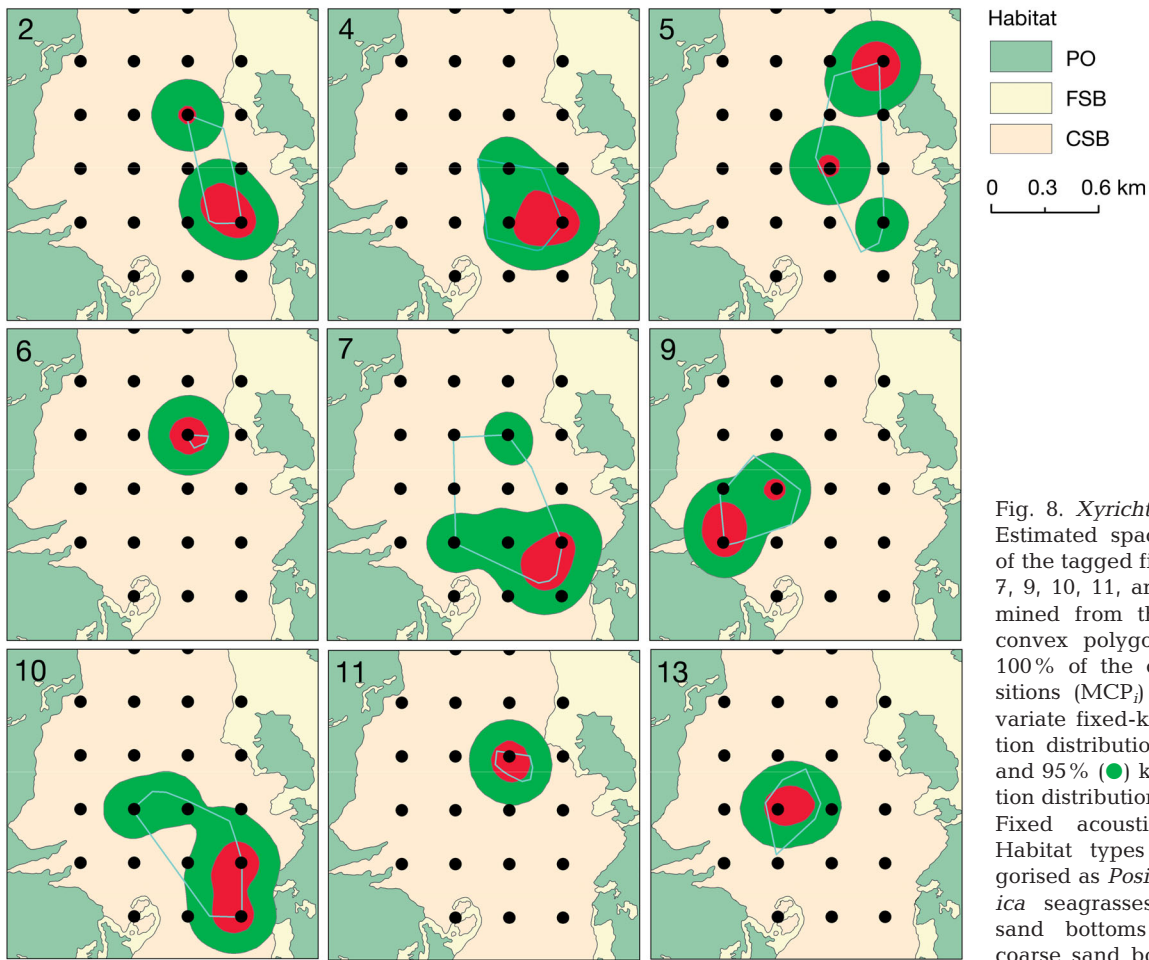


Fig. 8. *Xyrichtys novacula*. Estimated space utilisation of the tagged fish (2, 4, 5, 6, 7, 9, 10, 11, and 13) determined from the minimum convex polygon based on 100% of the obtained positions (MCP_i) and the bivariate fixed-kernel utilisation distributions, 50% (●) and 95% (●) kernel utilisation distributions (KUD_i). ●: Fixed acoustic receivers. Habitat types were categorised as *Posidonia oceanica* seagrasses (PO), fine sand bottoms (FSB) and coarse sand bottoms (CSB)

The results of the present study further support previous research indicating the preference of this species for soft bottom habitats. In fact, it has previously been reported that there is a relationship between the abundance of *Xyrichtys novacula* and micro-habitat

Table 4. *Xyrichtys novacula*. Individual mean \pm SD of the index of reuse (IOR_i) based on the 95 and 50% kernel utilization distributions [KUD] and the linearity index (LI_i)

Fish no.	IOR _i (95% KUD) Mean \pm SD	IOR _i (50% KUD) Mean \pm SD	LI _i
2	0.62 \pm 0.21	0.36 \pm 0.34	0.03
4	0.50 \pm 0.19	0.19 \pm 0.29	0.04
5	0.87 \pm 0.20	0.82 \pm 0.23	0.07
6	0.96 \pm 0.06	0.91 \pm 0.12	0.06
7	0.61 \pm 0.17	0.32 \pm 0.28	0.04
8	0.77 \pm 0.14	0.59 \pm 0.23	0.01
9	0.67 \pm 0.20	0.48 \pm 0.28	0.04
10	0.67 \pm 0.20	0.47 \pm 0.32	0.08
11	0.74 \pm 0.13	0.54 \pm 0.22	0.01
13	0.48 \pm 0.10	0.18 \pm 0.09	0.01

characteristics in terms of grain size, with *X. novacula* preferring bottom habitats of a medium grain diameter (Katsanevakis 2005) and seagrass vegetation of *Cymodocea nodosa* (Tuya et al. 2005). In this preferred habitat, individuals feed mostly on benthic crustaceans and molluscs within the fine and well-sorted sand assemblages (Cardinale et al. 1997). Unfortunately, this kind of micro-habitat characterisation is not available for our study area as in the previous work by Katsanevakis (2005), and only 2 main habitats were available (fine and coarse sand bottoms). However, the abundance of *X. novacula* appeared to be higher in the receiver array (mainly dominated by coarse sand bottoms with grain size from 0.5 to 1 mm) than in the northern and northeastern areas of the study site, where fine sand bottom (grain size from 0.125 to 0.250 mm; see Fig. 1) is the main habitat (J. Alós pers. comm.). Thus, this type of bottom habitat would appear to represent an important consideration for future MPAs for this species.

The present study highlighted the importance of acoustic telemetry for the validation of visual obser-

vations, which are typically carried out over limited time periods and spaces. For example, although previous observations performed for periods of several hours suggested that this species was sedentary, with a habitat utilisation area of 400 to 800 m² (Marconato et al. 1995), our method allowed us to track individuals for up to 3 wk in most cases. In all cases, the tracking period was sufficiently long that habitat utilisation reached an asymptote, meaning that additional tracking time was not necessary to obtain the HR areas for both males and females (the average time to reach the asymptote value was >1 wk).

Our results indicate that this species uses a small HR. Numerous hermaphrodites in Mediterranean coastal areas exhibit relatively small HR areas (e.g. Palmer et al. 2011). In most cases, these results regarding small habitat utilisation areas are in accord with species with complex social structures, often hermaphroditic, similar to *Xyrichtys novacula*. Previous data on the mating behaviour of this species indicated that their behaviour is harem, and males patrol and defend females from other males (Marconato et al. 1995). As a consequence, relatively small habitat usage areas were expected for this species during the spawning season.

Although a clear diel pattern was observed in terms of the number of detections, the HR sizes were similar for day versus night. Therefore, although the fish remained buried during the night, they did not rest in the same place each night. Many marine fishes perform daily migrations (using different spaces on a daily basis) between foraging and resting areas (see the review by Krumme 2009 and some specific examples in Hitt et al. 2011). In fact, some Mediterranean species inhabiting *Posidonia oceanica* seagrasses perform daily migrations, using different areas for foraging versus resting (Jadot et al. 2002). However, other small species, such as species of the genus *Serranus*, that show increased activity during the day (hiding in meadows or rocks to prevent predation during the night) do not show a change in the cumulative size of their HR on a diel basis (March et al. 2010, Alós et al. 2011). This type of behaviour, where there is no site fidelity with respect to nighttime resting sites, appears to also be the case for *Xyrichtys novacula*. This trend was confirmed by the high degree of overlap between the day and night activity spaces used on a daily basis, rejecting the hypothesis of a specific site for resting.

There were also no sex-related differences in HR sizes. It has been observed that in some species of protogynous hermaphrodites, the larger individuals (males) exhibit smaller HR areas than the smaller (fe-

male) individuals (e.g. *Epinephelus lativa*; Kaunda-Arara & Rose 2004). In the specific case of *Xyrichtys novacula*, previous short-term SCUBA observations of mating behaviour suggested that females occupy small areas, while males patrol and defend larger areas, usually encompassing 4 to 6 areas occupied by females (Marconato et al. 1995). Based on the results obtained here, the HR area used by females and males is not different, thus rejecting the hypothesis that males use larger areas, at least over the studied time scale (3 wk). Finally, the small spatial usage indicating a sedentary life style was confirmed by the low values of the LI. LI values close to 0 suggest that the movements of *X. novacula* are more related to random movements within the HR than directed movement, characterising this species as sedentary in general, with a limited adult dispersal capability and higher activity during the day than at night.

The results obtained here have direct implications for conservation and can be directly linked to the management of this species. (1) The overall results showed that *Xyrichtys novacula* uses small HR areas and exhibits high site fidelity with respect to these areas, with most activity occurring during the day. This finding implies that catchability will be strongly affected by local fishing pressure and the diel phase (day or night fishing activity). The high site fidelity observed makes this species a good coastal bio-indicator of anthropogenic activity, such as fishing. (2) This species appears to have a strong affinity for a specific kind of habitat. The existing reports regarding habitat preferences of this species (Katsanevakis 2005, Tuya et al. 2005) and the results obtained here enhance the relevance of often unappreciated soft bottoms in the context of the protection of essential habitat for this species.

(3) A consequence of the sedentary pattern and small HR observed for *Xyrichtys novacula* is that relatively small protected areas could effectively protect this species during its spawning season. Similarly, relatively small MPAs could also reduce fishing mortality for fish located within the protected area. Consequently, greater numbers of older, larger individuals could be maintained inside the protected area, thereby producing a considerable increase in the reproductive potential of the population (due to the higher fecundity of older and larger fish). Thus, this pool of high-fecundity fish could be the key to maintaining sustainable population levels and preserving the naturally occurring genetic structure in the surrounding exploited areas through the movement of eggs and larvae (because spawning is pelagic; Marconato et al. 1995). Moreover, if the pop-

ulation is allowed to increase in biomass, more adult individuals are likely to be observed closer to the boundary of the MPA and are expected to encounter fishing mortality beyond the protected area (Kramer & Chapman 1999). All of this information should be useful for managers in designing MPAs, especially because the use of relatively small MPAs in the Mediterranean has increased recently (Francour et al. 2001). Finally, Katsanevakis (2005) reported that the habitat of *X. novacula* does not change outside the reproductive season, but different aspects of the behaviour of this species remain controversial (i.e. burying behaviour outside the reproductive season). Thus, further research should be performed in this vein, exploring all of the spatio-temporal patterns observed in the present study during the non-reproductive season. Then, all of these positive factors could be used to guide the exploitation of stocks of *X. novacula* in a direction favouring the sustainable development of this fishery.

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