# Movement patterns of the European squid *Loligo vulgaris* during the inshore spawning season

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**RUNNING HEAD: Movement patterns of *Loligo vulgaris***

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ABSTRACT:

The European squid *Loligo vulgaris* in the Western Mediterranean is exploited by both commercial and recreational fleets when it spawns at inshore waters. The inshore recreational fishery in the southern waters Mallorca (Balearic Islands) concentrates within a narrow, well-delineated area and takes place during a very specific period of the day (sunset). Another closely related species, *Loligo reynaudii*, displays a daily activity cycle during the spawning season ("feeding-at-night and spawning-in-the-day"). Here, the hypothesis that *L. vulgaris* could display a similar daily activity pattern has been tested using acoustic tracking telemetry. Two tracking experiments during May-July 2010 and December 2010-March 2011 were conducted, in which a total of 26 squid were tagged. The results obtained suggested that *L. vulgaris* movements differ between day and night. The squid seem to move within a small area during the daytime but it would cover a larger area from sunset to sunrise. The probability of detecting squid was greatest between a depth of 25 and 30 m. The abundance of egg clutches at this depth range also seemed to be greater. The distribution of the recreational fishing effort using line jigging, both in time (at sunset) and in space (at the 20-35-m depth range), also supports the "feeding-at-night and spawning-in-the-day" hypothesis.

KEYWORDS: Acoustic telemetry · Daily activity cycle · Recreational fishing effort · Egg clutch distribution

# INTRODUCTION

The European squid *Loligo vulgaris* Lamarck (1798) is targeted in the Mediterranean Sea by both commercial and recreational fishers (Guerra et al. 1994, González & Sánchez 2002, Morales-Nin et al. 2005). This species experiences large fishing pressure and has a high socio-economical value (Guerra et al. 1994, Ulaş & Aydin 2011).

Most of the life-history traits of this species are known (Guerra 1992, Guerra & Rocha 1994, Moreno et al. 2002, Šifner & Vrgoc 2004, Moreno et al. 2007). However, knowledge on the spatial and temporal pattern of habitat use by this species is still scarce and remains elusive, despite the relevance of such knowledge for assessing and managing fishery resources (Pecl et al. 2006, Botsford et al. 2009).

One of the movement patterns that has potential outcomes on fishing success is the in-offshore seasonally periodical movement. This type of movement has been repeatedly described and related to reproduction and feeding cycles in other cephalopods (Tinbergen & Verwey 1945, Worms 1983, Boyle et al. 1995), and it has been suggested that *L. vulgaris* would display this pattern (Sánchez & Guerra 1994, Šifner & Vrgoc 2004). Large mature or pre-mature individuals are abundant at shallow coastal waters, seemingly for mating and spawning; the new recruits seems to hatch near the coast and subsequently migrate towards deeper waters (Guerra 1992, Sánchez & Guerra 1994).

The outcome of such an abundance pattern is the development of a seasonal fishery for *L. vulgaris* when large squid are abundant close to shore. Nearshore spawning aggregations of other *Loligo* species are typically exploited using line jigging (Augustyn & Roel 1998, Hanlon 1998, Iwata et al. 2010, Postuma & Gasalla 2010). In inshore waters near Mallorca Island, other commercial gears, including seine and trammel nets, can sporadically capture squid as very valued bycatch (Cabanellas-Reboredo et al. 2011). However, the main gear used when targeting squid is line jigging, which is extensively used by both commercial (artisanal) and recreational fishers (Guerra et al. 1994; Cabanellas-Reboredo et al. 2011). The handline jigging method used by the artisanal fleet typically takes place at fishing grounds located between 20 and 35 m in depth, at night and with the use of lights. Recreational fishers use line jigging at the same fishing grounds but only at sunset (Cabanellas-Reboredo et al. 2011). The use of light is forbidden for the recreational fleet. However, recreational fishers also fish squid after sunset by trolling, but only in very shallow waters (Cabanellas-Reboredo et al. 2011) close to the illuminated shore of Palma city, between the shore and a depth of 10 m.

The specific goal of this study was to use acoustic tracking telemetry for 1) providing the first description of the movement of *L. vulgaris* during the inshore spawning period and 2) relating such a movement pattern with the spatiotemporal distribution of the fishing efforts.

Acoustic tracking telemetry has already been used for describing the movement patterns of other cephalopods (Stark et al. 2005, Payne & O'Dor 2006; Semmens et al. 2007, Dunstan et al. 2011) and for understanding the environmental cues of squid movements (Gilly et al. 2006). In addition, acoustic tracking has been used for describing the relationship between metabolic rate and behavior (O’Dor et al. 1994, O’Dor 2002, Aitken et al. 2005) and for improving fisheries management (Pecl et al. 2006). The movement patterns during spawning aggregations of *Loligo reynaudii* Orbigny (1845) and their relationship with environmental variability has been demonstrated using acoustic telemetry (Sauer et al. 1997, Downey et al. 2009).

## MATERIALS AND METHODS

### Experimental design

Two acoustic tracking experiments ($ATE_s$) were completed in the southern waters of Mallorca Island (Fig. 1; NW Mediterranean) during the two main spawning seasons of the species (winter and spring-early summer; Guerra & Rocha 1994, Šifner & Vrgoc 2004). A preliminary study covering a wide spatial range ($ATE_1$) was carried out between May and July 2010 (Fig. 1A) because no prior information on movement extent was available for *L. vulgaris*. In accordance with the results obtained in $ATE_1$, a second experiment ($ATE_2$) was completed between December 2010 and March 2011 (Fig. 1B).

In both of the experiments, an array of omni-directional acoustic receivers (Sonotronics© SUR-1) was deployed (Fig. 1). In $ATE_1$, a wide array distributed along the south of the island was designed to determine the broad scale of the movements (Fig. 1A). The distances between the receivers ranged from 2.6 to 8.9 km. The receivers were placed from 8 m depth (only one receiver) up to 30 m depth (Fig. 1A). A denser array covering only the main fishing grounds in Palma Bay was deployed during $ATE_2$ (Fig. 1B). The SURs were placed at the nodes of a 1000 x 1000 m grid. The receivers were placed at depths ranging between 8 to 38 m (Fig. 1B). The number of receivers used was 18 during $ATE_1$ and 17 during $ATE_2$. As probability of detection may be function not only of the distance between receiver and transmitter but also of depth (Claisse et al., 2011), the probability of detection at different distances was estimated at three different depths (10, 30 and 50 m depth) using control tags moored at prefixed distance from the receivers. Detection probability was assumed to follow a binomial distribution and data were fitted to a generalized linear model (GLM, *glm function* from the R package; depth was considered a categorical factor).

After the expected battery life of the tags had expired (see details below), we retrieved the receivers and downloaded the data.

## Acoustic Tagging

A total of 26 squid were tagged (Table 1) and released inside the receiver array, with 6 individuals during $ATE_1$ and 20 during $ATE_2$ (Fig. 1). Most of the individuals (n=23) were tagged using the miniature tag IBT-96-2 (Sonotronics$^{©}$). This transmitter measures 25 mm in length and 9.5 mm in diameter, weighs 2.5 g in water and has an expected lifespan of 60 d. Three individuals were tagged using the acoustic tag CT-82-1-E (Sonotronics$^{©}$; size: 38 × 15.6 mm; weight in water: 6 g; expected lifespan: 60 d). The transmitters were activated just before being implanted, and the acoustic tags never exceeded 1.57 % of the squid's body weight.

A specific sequence of beeps, with specific between-beep intervals and at a specific frequency allowed unambiguous squid identification (Table 1). A detection event was registered after a receiver detected a full sequence of beeps. Any detection event was labeled with an ID code, date (mm/dd/yyyy), hour (hh:mm:ss), frequency (kHz) and interval period (ms). A tolerance interval of 5 ms was selected for detecting and removing putative false detections, following the conservative criteria proposed by Sonotronics (see Sonotronics Unique Pinger ID Algorithm; http://www.sonotronics.com/) and adopted by other studies that used the same tracking equipment in the same area (March et al. 2010 - 2011, Alós et al. 2011).

The squid were caught at sunset using line jigging (Fig. 2A). The fishing and handling protocols that were adopted minimized the stress and damage to the squid (O'Dor et al. 1994, Gonçalves et al. 2009). The squid were immediately sexed, the dorsal mantle length (DML) was measured, and the squid were gently placed on a damp cloth where they were tagged (Fig. 2B and 2C, respectively). The sex was determined by observation of the hectocotylus (Ngoile 1987). Fertilized females were determined by the presence of spermatophores, a small white spot in the ventral buccal membrane (Ngoile 1987, Rasero & Portela 1998). Tag losses were minimized by gluing two hypodermic needles laterally to the tips of the tag (Fig. 2D). This procedure secures the tag inside of the squid's ventral mantle cavity (Downey et al. 2009). The tags were inserted at the middle-ventral mantle cavity, using a plastic pistol designed to avoid ripping the squid skin. Special care was taken to avoid piercing any organ with the hypodermic needles and to allow the correct seal of the mantle through the cartilages (O'Dor et al. 1994, Downey et al. 2009; Fig. 2F). Before sliding the tag inside a squid, a silicon washer was placed on the needles to protect the inner part of the mantle. The needles pierced the thickness of the mantle and were secured on the outside of the squid with a silicon washer and metal crimps (O'Dor et al. 1994; Fig. 2G). The full process of biological sampling and tagging lasted less than 2 min. After that, the tagged squid were placed into a 100-l seawater tank until the squid recovered the usual fin beating and swimming. Then, the squid were released at the same place where they were captured (Fig. 2H).

A number of preliminary trials were completed under controlled laboratory conditions 1) to improve the handling of squid and to reduce the tagging time, 2) to evaluate the viability of different tags in relation to the squid size and 3) to confirm that normal behavior (swimming and feeding) is recovered after tagging.

### Fishing effort and egg abundance

The spatial distributions of the fishing effort of the two recreational fishing methods, line jigging and trolling, were determined using visual censuses. Palma Bay was sampled 3 times a month during one year (2009). The GPS position, fishing mode and numbers of anglers per boat were recorded for any intercepted boat (unpublished data obtained by the CONFLICT research project CGL2008-958). The boat positions were mapped to explore the spatial distribution of recreational fishing.

Squid egg clutches were found on a relatively large number of receivers when the receivers were recovered. The egg clutches were placed at the knots of the rope, above and below the receiver (Fig. 2E). This unexpected finding allowed us to use the number of egg clutches as a proxy for the spatial distribution of spawning.

## Data analyses

The data of the receivers were downloaded from the SURs as text files, and an appropriate MS Access database was developed for managing this data. This database allowed for the removal of false detections and was used to obtain plots of the spatial and temporal distribution of the receptions (March et al. 2010). The number of detections per hour (chronograms) was plotted for each squid. The day-specific timing of the sunrise and sunset (US Naval Observatory; Astronomical Applications Department; http://aa.usno. navy.mil) were overlaid on the chronograms. Moreover, to test for differences between day and night in the number of detections (activity pattern), a generalized linear mixed model was applied (GLMM, Bates & Maechler 2010). The statistical unit chosen was the “visit event”. A visit event of a specific squid was defined as a set of consecutive detections registered by the same receiver (Stark et al. 2005). Two or more detections were considered “consecutive”, and thus, it was assumed that they belonged to the same visit event when there was less than 1 hour between them. When the time between two consecutive detections was greater than 1 hour, it was assumed that they belonged to two separate visit events. Similarly, when a squid was detected by two receivers, two independent visit events were assumed to occur. The visit events were categorized as either a “detection peak” (less than 4 hours between the first and last detection of the same visit event) or “detection cluster” (more than 4 hours between the first and last detection of the same visit event). Moreover, in accordance with the results of the experiment of detection range (see Results), only the visit events recorded from the receivers deployed at 25-30 m depth were included in the GLMM, attending to remove any effect of depth on the probability of detection. Anyway, those receivers accumulated most of the visit events (97.83%).

The goal was to differentiate between highly active movement (detection peak; the squid quickly crossed near a receiver) and slower movement (detection cluster; the squid spent more time within the detection range of the same receiver). A binomial logistic model was assumed; the response variable was zero when the visit event was a detection peak and was 1 otherwise. The putative explanatory variable was daytime vs. nighttime (categorical variable; nighttime included sunrise and sunset). The identity of the squid was treated as a random factor to account for variation at the individual level and to avoid pseudoreplication. This generalized linear mixed model (GLMM) was fitted using the *lme4* library from the R data analysis software package (http://www.r-project.org/). A p-value of 0.05 was chosen a priori as the critical level for a rejection of the null hypothesis.

The number of detections and the number of egg clutches corresponding to different bathymetric depth intervals were compared using boxplots. The number of intervals considered and their limits were selected to ensure that all of the intervals included a large enough number of receivers. The squid tracks were also plotted; the maps were produced using R package and improved using ArcGIS.

## RESULTS

### Detections

The results of the preliminary experiment aimed to explore the effects of depth and distance to receiver showed significant differences of the probability detection among depths (the probability increase with depth; GLM $p < 0.001$, Fig. 3). This result was similar to those reported by Claisse et al. (2011). However, the distance at which probability of detection is 0.5 was similar, especially when comparing the results obtained at 10 and 30 m depth (97 m and 100 m; the same figure for 50 m depth is 120 m; Fig. 3). This result strongly support that in spite of the existence of some depth effects, the detection probability is virtually the same at low and intermediate depth. Additionally, in the view of these results, the simultaneous reception of the same acoustic signal by more than one receiver was highly improbable.

A total of 8,835 true detections from 15 squid, out of the 26 tagged squid, were downloaded. The number of detections of each squid ranged between a minimum of 15 detections (squid 11) and a maximum of 2,378 for the squid 46 (Table 1). The total period (TP, in days) over which a squid was detected, defined as the number of days from the tagging day to the last day a squid was detected, ranged from 2 (squid 77) to 31 (squid 111). The mean TP (± SD) was 11.53 ± 7.73 d. The number of days that a squid was detected (DD) varied from 1 (squid 11) to 13 (squid 111 and 46). The mean DD (±SD) was 6.13 ± 3.88 d. The average number of receivers that detected the same squid was 2.06 ± 0.88 and ranged from 1 (squid 110, 11, 77) to 4 (squid 112 and 47). The specific data for the squid are detailed in Table 1.

### Temporal pattern

A preliminary inspection of the time series of the number of detections per time unit does not reveal any clear pattern. However, the definition of the two types of visit event, detection peaks and detection clusters, demonstrates the existence of significant differences between day and night (GLMM $p < 0.001$, Fig. 4). During the daytime, the squid tended to remain undetected, and very few visit events took place. However, in those cases, the detections tended to form a detection cluster. In some cases, a detection cluster even lasted most of the day (see examples in Fig. 4). Conversely, such long detection clusters of the same squid on the same receiver were nearly absent between sunset and sunrise. During the nighttime, the visit events tended to be shorter (detection peaks instead of detection clusters; see some examples in Fig. 4). Moreover, new appearances, when a specific squid was detected by two different receivers within the same day, took place more frequently during the nighttime (squid 112 and 47; see the stars in Fig. 4).

## Space use

The number of detections was higher between 25 and 30 m of depth (Fig. 5 & 6). The existence of some effects of depth on detection probability make that this results must be interpreted with some caution. However, some patterns clearly emerge and they seem robust against the small effects of depth: All of the squid were detected whitin the 25-30 m depth range (see some examples of the squid tracks in Fig. 5). Almost all (99.9%) of the detections during the $ATE_1$ experiment were made at this depth range, although it is important to note that 61% of the receivers were deployed at this depth range. Similarly, most of the detections (5,935, 99.26%) corresponded to the 25-30 m depth interval during $ATE_2$. Squid 110, 11 and 77 were detected by only one receiver that was placed at the depth range of 25-30 m. Most of the rest of the squid (80%) were also detected in this depth range. Nearly half of the squid moved between two closely positioned receivers, but in those cases, they remained within the 25-30 m depth area (53.33%; e.g., squid 4 and 7 in the Fig. 5A). Longer travels were performed by squid 108-10 and 112. The squid 108-10 toured 22.85 km during the 22 d of tracking. In the same way, the squid 112 traveled 22.2 km during the 14 d of tracking. These longer travels were also monitored by receivers deployed in the 25-30-m depth range (Fig. 5B).

During $ATE_2$, squid were also detected by both deeper (at 31-38 m of depth) and shallow receivers (at 16-24 m of depth). However, the prevalence of detections outside the 25-30 m range was very low (0.14% and 0.60% for deep and shallow receivers, respectively). Squid 47, a male, exemplified such a pattern. It reached receiver 19 at 16 m of depth from receiver 15 at 27 m of depth during the night but left this shallow water before sunrise, and it appeared again in deeper waters at sunset (receiver 4 at 37 m depth; see the grey star in the Fig. 4 and the movement track in the Fig. 5 C).

No squid were detected by the receivers placed in shallower waters (0-15 m depth), in spite of the fact that some of the squid were tagged and released there. For example, squid 46, a female, was fished, tagged and released in shallower waters without being detected by receivers deployed in this shallow area. However, this squid was detected one day later at 25 m of depth, and it spent some days in that area. After that period, this squid left that area at sunset to reach deeper waters at sunrise (receiver 2 at 35 m depth; Fig. 5C).

In relation to the spatial distribution of the fishing effort, the recreational fishers and part of the commercial fleet concentrated at sunset and in specific areas located between 20-35 m of depth. After sunset, the commercial fishers continued to fish at the same fishing ground but using lights. While that, after sunset, the recreational fishers continued to fish for some time by trolling and focusing almost all of their effort from the shoreline to 10 m of depth, just at the illuminated strip near the city lights (Fig. 7). The presence of egg clutches was recorded from shallower waters (1 egg clutch at receiver 17, at 9 m of depth) to deeper waters (3 egg clutches at receiver 9, at 38 m of depth) (Figs. 6 & 7). The number of egg clutches was small (0.25 ± 0.5; $ATE_2$ only) on the receivers placed in shallower waters (0-15 m). The receivers deployed at a depth interval between 16 and 24 m had mean values of 0.67 ± 0.58 and 0.5 ± 0.71 egg clutches per receiver for $ATE_1$ and $ATE_2$, respectively. All of the receivers that were deployed between 25 and 30 m had at least one egg clutch. The mean number of egg clutches per receiver was clearly higher between 25 and 30 m (2.18 ± 1.40 and 2.40 ± 0.55 for $ATE_1$ and $ATE_2$, respectively). Finally, the receivers that were placed at a depth between 31 and 38 m (only deployed during $ATE_2$) had 1.17 ± 1.17 egg clutches attached to their structures (Figs. 6 & 7).

## DISCUSSION

The present study provides the first description of the movement patterns of the European squid *L. vulgaris* during inshore spawning aggregations. The conceptual model of movement proposed here is characterized by two well-differentiated movement states. The typical daytime movement is characterized by a reduced mobility within a narrow area, hereafter referred as day-ground. The squid tend to remain for a long time (most of the daytime of a specific day) at a specific day-ground. However, the location of the day-ground may change between consecutive days. This location may be randomly selected within a larger area. The larger area is delimited by the Palma Bay grounds at 25-30 m of depth. The typical nighttime movement is characterized by increased mobility, i.e., a specific squid would spend only a short time at any given location, and will range over a wider area. Such a night-ground possibly covers most of the Palma Bay. This diel pattern might be due to periodic daily shifts between reproduction behavior during the day and feeding at night. The empirical evidence supporting this conceptual model emerges from 1) the existence of day-night differences in the detection pattern using acoustic tracking, 2) the spatiotemporal distribution of the fishing effort and 3) the spatial distribution of egg clutches.

The strongest evidence is from the day-night differences in the detection pattern. Squid, when detected during the daytime, tended to remain near the detection range of only one receiver in a detection cluster, supporting the hypothesis that the day-ground size is small. However, a specific squid was usually not detected in two consecutive days by the same receiver, suggesting that the day-ground location may change every day. Almost all of the daytime detection clusters occurred within the 25-30-m depth area of Palma Bay. We propose that the squid may be reproducing during the daytime within a well-defined area. Evidence supporting this specific hypothesis emerges from 1) the spatial distribution of egg clutches in Palma Bay and 2) the fact that the same pattern (i.e., daytime reproduction) has been repeatedly described for other cephalopods.

Concerning the spatial distribution of eggs, other studies suggest that even though egg clutches of *L. vulgaris* have been observed at depths from 2 m to 35 m, the clutches were more frequent between 20-30 m (Villa et al. 1997), very close to the 25-30-m depth area reported here. Concerning the daytime reproduction pattern, previous studies demonstrated that during the daytime, *L. reynaudii* remains at the spawning grounds (Sauer et al. 1997, Downey et al. 2009), where it performs a wide range of reproduction behaviors, such as fighting, guarding, sneaking, mating and egg laying (Hanlon et al. 2002). The same activity pattern has been proposed for the Southern Calamari Squid (*Sepioteuthis australis* Quoy & Gaimard, 1832), which arrives at sunrise at the vicinity of the spawning grounds and spawns there throughout the daytime (Pecl et al. 2006). Similarly, loliginid squid also showed reproductive activity during the daytime (Sauer et al. 1997, Jantzen & Havenhand 2003, Forsythe et al. 2004). A plausible and biologically sound explanation is that reproductive behaviors in cephalopods are strongly mediated by visual cues (Hanlon & Messenger 1996). Specifically, visually detectable body patterning plays an important courtship role during reproduction (Hanlon et al. 1994, Hanlon & Messenger 1996, Hanlon et al. 1999, Hanlon et al. 2002). In fact, intraspecific signaling in squid is known to occur mainly during daylight hours (Hanlon & Messenger 1996).

During the nighttime, the squid were more mobile. The main empirical evidence supporting this statement is that the squid, when detected at night, tend to remain for a short time near a specific receiver, creating detection peaks instead of detection clusters. We propose that *L. vulgaris* may be feeding during the nighttime. Increased activity linked to feeding at night (beginning at dusk) has been described in other squid

(O'Sullivan & Cullen 1983, Hanlon & Messenger 1996). Specifically, nocturnal predation has been proposed from the results obtained during other acoustic tracking experiments (Sauer et al. 1997, Stark et al. 2005, Downey et al. 2009). The stomach contents of *L. reynaudii* squid caught on the spawning grounds at night have more food than those caught during the daytime (Sauer & Lipiński 1991), supporting an increased predation activity during the nighttime like other loliginids.

Additional support for the conceptual model proposed here emerges from the spatiotemporal distribution of the recreational fishing effort. The spatial aggregation of the fishing effort has been adduced as indirect evidence for the spatial distribution of squid (Boyle & Rodhouse 2005, Pecl et al. 2006, Olyott et al. 2007). In our case, recreational fishing effort using line jigging concentrates between 20-35 m of depth during the sunset. We propose that recreational line jigging concentrates within this very narrow spatiotemporal window because squid catchability is higher. This hypothesis is founded on the following: 1) squid concentrate during the daytime at 25-30-m depth region to form spawning aggregations, and these aggregations probably break down at sunset due to a shift from reproduction to a feeding state (Downey et al. 2009), 2) squid probably feed during the nighttime, thus showing an increased interest for lures, 3) squid display a higher mobility during the nighttime, thus increasing the probability of encountering a lure and 4) at sunset, there is still enough light that favors the detection of the lures used in line jigging. Commercial (artisanal) fishers do not stop line jigging after dusk because they can use lights. Recreational fishers may continue to fish after dusk, but only by trolling. The trolling method in shallower waters (from shore to 10 m of depth) is performed by most of the anglers after fishing by line jigging. In accordance with our conceptual model, squid after dusk enlarge their space use from the 25-30-m depth area to a wider area that includes the trolling grounds. This pattern is exemplified by squid 47 (see Fig. 4 & 5C). We hypothesize that this squid would remained at the 25-30 m area during daytime but would became vulnerable to line jigging only at sunset. This squid would be also vulnerable to trolling after dusk, when it was detected at 16 m of depth, close to the trolling zone.

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TABLES

Table 1. Summary of the tagged squid and tags used. DML: dorsal mantle length; TP: the period between the release date and last detection in days; DD: the total number of days detected. The tagged squid without detections during the experiments are shown in grey, and nd indicates the absence of data for these squid. All of the females have copulated. The asterisk indicates a squid that was not considered because it presented an almost constant number of detections during the 60 d of tracking. Thus, we assume that this squid died near receiver 6 just after it was released.

| | **Squid Code** | **DML (mm)** | **Sex** | **Tag model** | **Tag frequency (Khz)** | **Tag interval (ms)** | **Tag & Release date (dd/mm/yyyy)** | **Total detections** | **No. of receivers** | **TP (d)** | **DD (d)** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **$ATE_1$** | 107 | 276 | Male | IBT-96-2 | 70 | 900 | 29/04/2010 | nd | nd | nd | nd |
| | 108-10 | 222 | Female | IBT-96-2 | 71 | 910 | 26/05/2010 | 409 | 2 | 22 | 8 |
| | 109-10 | 277 | Male | IBT-96-2 | 72 | 920 | 06/05/2010 | nd | nd | nd | nd |
| | 110 | 330 | Male | IBT-96-2 | 73 | 930 | 03/06/2010 | 1104 | 1 | 10 | 6 |
| | 111 | 276 | Male | IBT-96-2 | 74 | 940 | 27/04/2010 | 1204 | 2 | 31 | 13 |
| | 112 | 293 | Male | CT-82-1-E | 70 | 1040 | 20/05/2010 | 139 | 4 | 14 | 6 |
| **$ATE_2$** | 2 | 217 | Female | IBT-96-2 | 70 | 860 | 04/01/2011 | nd | nd | nd | nd |
| | 3 | 205 | Female | IBT-96-2 | 71 | 890 | 14/01/2011 | nd | nd | nd | nd |
| | 4 | 223 | Female | IBT-96-2 | 72 | 880 | 04/01/2011 | 1319 | 2 | 14 | 12 |
| | 5 | 205 | Female | IBT-96-2 | 73 | 910 | 18/01/2011 | nd | nd | nd | nd |
| | 7 | 193 | Male | IBT-96-2 | 75 | 930 | 24/01/2011 | 16 | 2 | 5 | 4 |
| | 8 | 215 | Female | IBT-96-2 | 76 | 920 | 05/02/2011 | 232 | 2 | 13 | 6 |
| | 9 | 240 | Female | IBT-96-2 | 77 | 950 | 19/01/2011 | nd | nd | nd | nd |
| | 10 | 205 | Female | IBT-96-2 | 78 | 940 | 24/01/2011 | 630 | 2 | 9 | 4 |
| | 11 | 230 | Male | IBT-96-2 | 79 | 970 | 19/01/2011 | 15 | 1 | 7 | 1 |
| | 16 | 250 | Male | CT-82-1-E | 69 | 1030 | 10/01/2011 | nd | nd | nd | nd |
| | 46 | 250 | Female | CT-82-1-E | 69 | 970 | 18/01/2011 | 2378 | 2 | 14 | 13 |
| | 47 | 175 | Male | IBT-96-2 | 70 | 980 | 04/01/2011 | 378 | 4 | 17 | 6 |
| | 48 | 230 | Female | IBT-96-2 | 71 | 990 | 07/01/2011 | nd | nd | nd | nd |
| | 77 | 230 | Female | IBT-96-2 | 70 | 920 | 11/01/2011 | 491 | 1 | 2 | 2 |
| | 78 | 209 | Male | IBT-96-2 | 71 | 930 | 04/01/2011 | nd | nd | nd | nd |
| | *79 | 220 | Male | IBT-96-2 | 72 | 940 | 07/01/2011 | 57813 | 1 | 60 | 59 |
| | 107 | 193 | Female | IBT-96-2 | 70 | 900 | 13/01/2011 | 66 | 2 | 7 | 6 |
| | 108-11 | 191 | Female | IBT-96-2 | 71 | 910 | 11/01/2011 | 66 | 2 | 4 | 2 |
| | 109-11 | 246 | Male | IBT-96-2 | 72 | 920 | 10/01/2011 | nd | nd | nd | nd |
| | 139 | 175 | Female | IBT-96-2 | 72 | 860 | 12/01/2011 | 388 | 2 | 4 | 3 |

# FIGURES

Fig. 1. Map of the receivers array deployed in 2010 (ATE$_1$, panel A) and 2011 (ATE$_2$, panel B). The individual black points denote the receiver's location. The damaged receivers have been represented by a cross (receivers 9 and 11). The isobaths each represent 10 m.

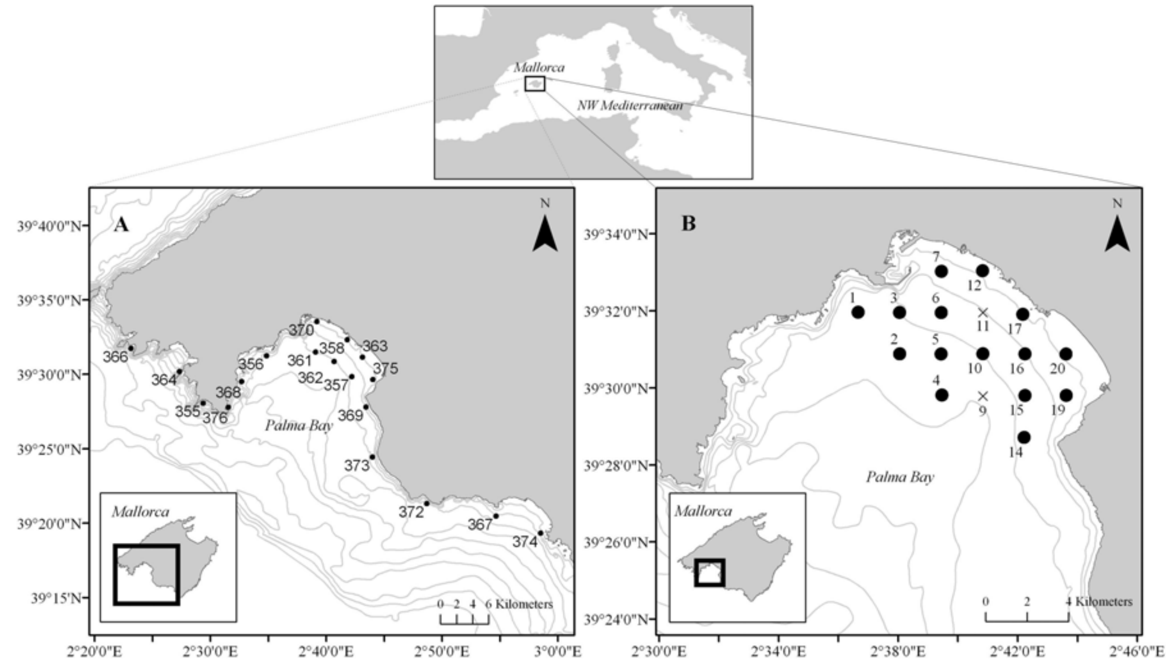

Fig. 2. Acoustic tracking logistics and methods. (A) Squid fished by line jigging. (B) Squid sex and fertilization (females) determination. The image defined by the white dashed line details the presence of a spermatophore in the ventral buccal membrane. (C) Dorsal mantle length measurement to the nearest 5 mm. (D) Acoustic tags used in the experiments with sterile hypodermic needles attached laterally to the tag. (E) An egg clutch attached to a receiver rope. (F) Location of the acoustic transmitter. (G) Silicon washers, which were pushed onto the ends of the hypodermic needles and slipped over each needle. The metal cylinder was crimped using pliers to avoid the loss of transmitter. (H) The tagged squid in an open seawater tank on the boat. The image highlighted by the white dashed line shows the squid release in a tail-first direction favoring the output of the air bubbles present in the mantle cavity.

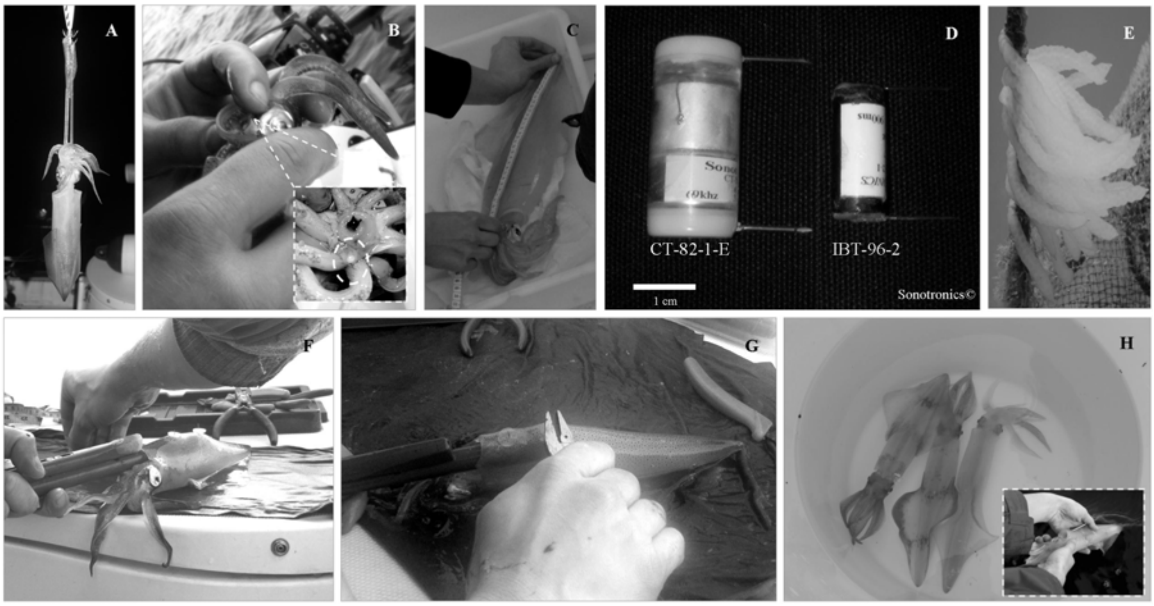

Fig. 3. Curves of detection probability against the distance at different depths obtained from the detection range test.

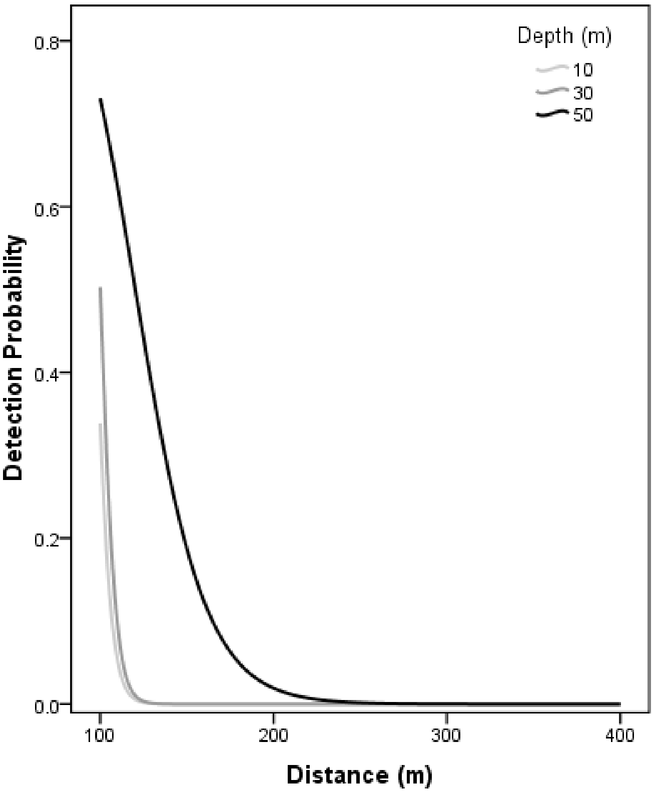

Fig. 4. Full time series of the detection numbers per hour of 4 tagged squid from ATE$_1$ (108-10 and 112) and ATE$_2$ (139 and 47). The vertical stripes represent day (white) and night (grey). On the x-axis, each mark indicates the 00:00 hours of each day. When a squid was detected by another receiver, the new receiver ID is indicated at the first detection. The stars represent the new appearances, when a specific squid was detected by two different receivers within the same day.

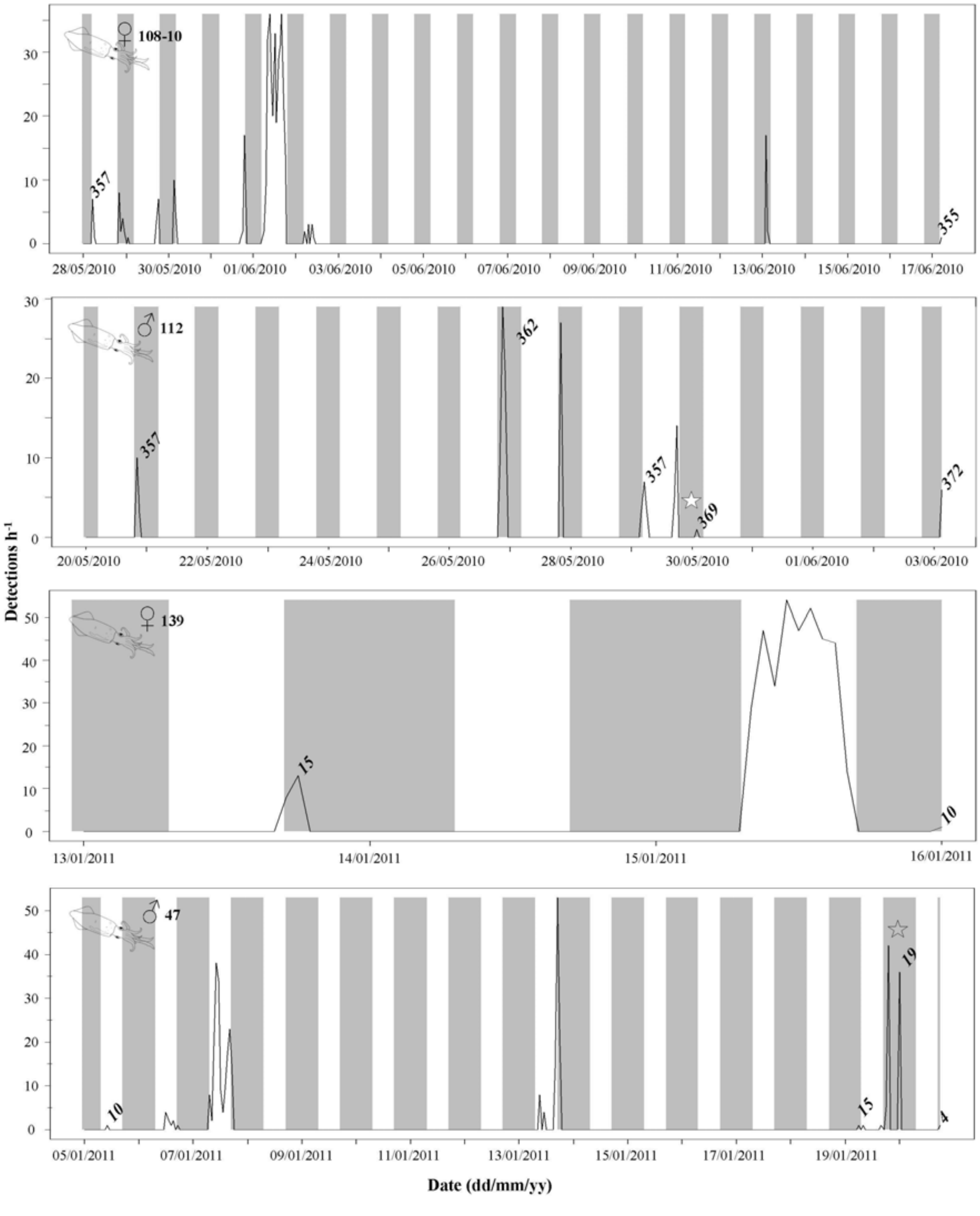

Fig. 5. Squid tracks assuming the minimum distance traveled (Pecl et al. 2006).

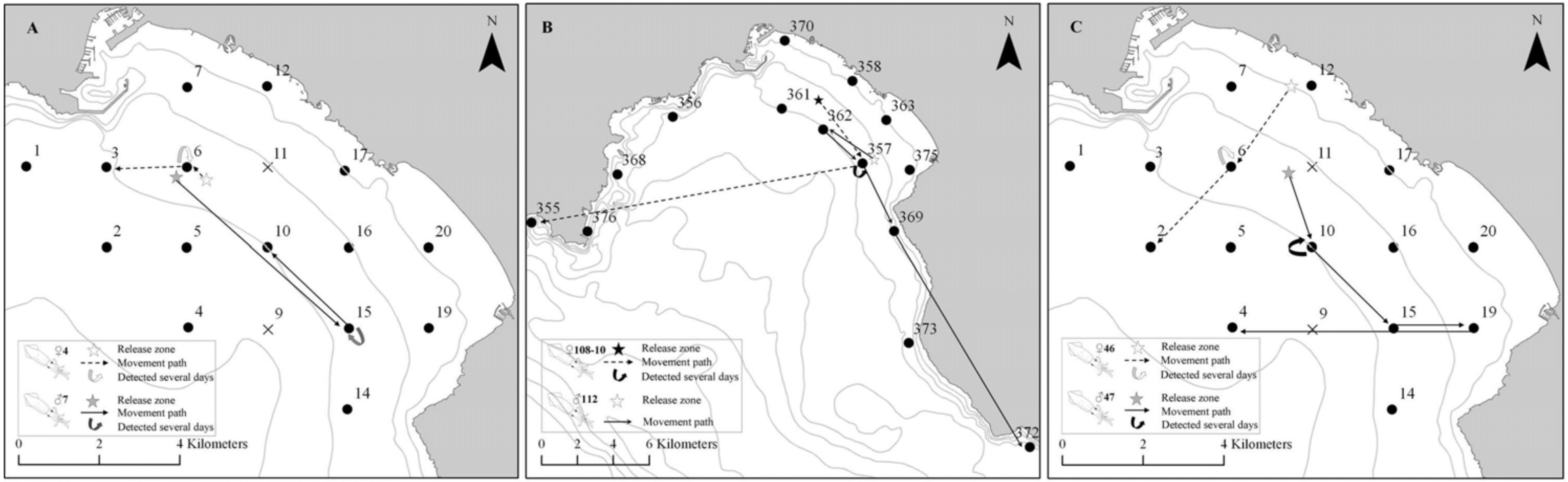

Fig. 6. Boxplot of the number of detections and egg clutches. The white boxes show the data from ATE$_1$, while the black boxes represent data from ATE$_2$. Receivers were not deployed in ATE$_1$ within the depth range of 31-38 m. Outliers have been represented with a star.

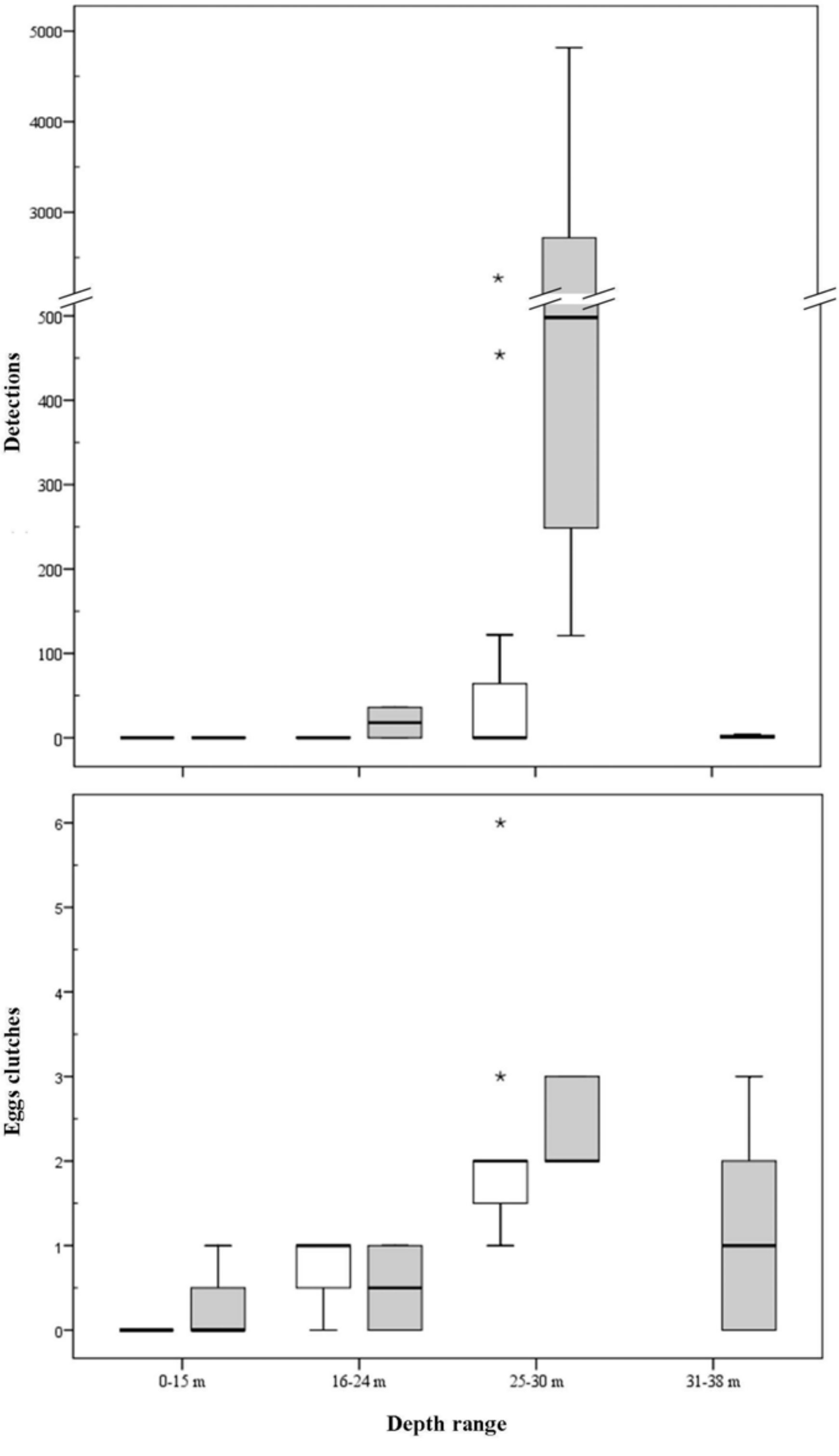

Fig. 7. Spatial distribution of the recreational fishing effort and egg clutch abundance in Palma Bay. The isobaths each represent 10 m.