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## Socio-ecological approach of the recreational squid fishery

*Ph.D. Thesis*

A Thesis submitted for the degree of Doctor in Biology  
University of the Balearic Island

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*Socio-ecological approach of the recreational squid fishery* is a PhD thesis submitted  
for the degree of Doctor in Biology by Miguel Cabanellas Reboredo



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# Abstract

The social relevance of recreational fisheries and their impact on the exploited resources and on the ecosystems have been widely recognized. However, the impact of recreational fishing is still rarely accounted for when assessing the population dynamics of targeted species.

The European squid *Loligo vulgaris* is a paradigmatic case-study. In the Balearic Islands (NW Mediterranean), this species is targeted by both the commercial and the recreational fishing sectors. The commercial squid fishery is relatively well known but the effect of the recreational sector on the population dynamics of *L. vulgaris* is currently unknown although potentially relevant. The assessment and management of recreational fisheries is particularly challenging due to the difficulties in estimating both, catches and fishing effort. Accordingly, the main objective of this Ph.D. Thesis is to estimate the recreational squid harvest. To face this challenge requires a socio-ecological approach, by which the ecological characteristics of the squid, the social characteristics of the angler and the interactions between them have been tackled.

The first section of the Ph.D. Thesis provides new insights linking some features of the squid life-history with the recreational fishing effort patterns. First, it is demonstrated that during the cold season (winter-spring) squid expand their spawning area to inshore waters, probably searching for the environmental conditions that maximize spawning success (e.g., sea temperature). This pattern is in accordance with the hypothesis that squid undergoes inshore spawning migrations. Accordingly, recreational fishers (anglers) exploit squid when they approach to the coast for spawning. Second, squid moves more actively at nighttime than during the day. This pattern was revealed using acoustic tracking telemetry and it is in accordance with the hypothesis of “feeding at night and spawning during the day”. Accordingly, anglers exploit squid at sunset (using line jigging), when squid has already shift to the feeding state and lures are still visible.

Once solved the life-history patterns of *L. vulgaris*, the next step involved the un-

derstanding of the fishery dynamics. All boats fishing squid were recorded (on-boat censuses) in order to disentangle the drivers of angler’s site (and day) choices. Both, catch-related (expected harvest) and non-catch related variables (e.g., sea condition and distance to the nearest homeport) play a relevant role. This Ph.D. Thesis provides fine-scale ( $1 \text{ km}^2 \text{ day}^{-1}$ ) estimates of the recreational fishing effort.

Harvest not only depends on effort but on catch. To assess the effect of the environment on squid catchability, a set of experimental fishing sessions were performed. The combination of variables such as low windspeed, low atmospheric pressure and days close to the new moon maximized catch rates, although the main variable involved in catch fluctuations was sea temperature. Catches are higher during the cold season, which is again in accordance with the hypothesis that squid undergoes inshore spawning migrations. Moreover, the 30 minutes period around sunset is the more efficient than any other 30 minutes period before or after sunset for capturing squid. This second pattern is again in accordance with the “feeding at night and spawning during the day” hypothesis.

During the above-mentioned experimental fishing sessions, a potential indirect effect of jigging was detected: some squid escape by losing one or both tentacles. The possible indirect effect of tentacle loss was tested through tank experiments. The results showed that losing tentacles significantly decreased the predation efficiency, which in turn may affect long-term survival and fitness. We suggest that such a (possible) ghost fishing should be considered.

Finally, this Ph.D. Thesis proposes a new framework for estimating harvest by integrating the above-mentioned information. This framework combines model-based estimates of effort (varying in space and time) with model-based estimates of catches per unit effort (varying in time and on the angler type). In order to account for the angler heterogeneity, anglers were classified into three types according with the answers to a short interview. The questionnaire was designed for revealing angler’s skill and experience. By including heterogeneity of anglers, the estimated harvest gained in precision. The recreational squid harvest in Palma Bay was estimated in 20.5 tonnes during 2010. This means that recreational harvest represents 34% of the total squid landings by the entire commercial fleet of Mallorca Island during the same year (59.5 tonnes). Although to explicitly model the population dynamics of squid is outside the scope of this Ph.D. Thesis, this is the first empirical data quantifying the importance of the recreational fishing of *L. vulgaris*. The knowledge provided certainly should constitute a baseline for a long-term monitoring program, and it demonstrates that stock assessment should incorporate the role of the recreational fishery.

# Resumen

La importancia social y el impacto de la pesca recreativa ha sido ampliamente reconocido, no sólo sobre los recursos explotados sino también sobre el ecosistema. Sin embargo, dicho impacto sigue siendo un aspecto que en raras ocasiones es considerado cuando se evalúa la dinámica poblacional de las especies objetivo.

El calamar Europeo *Loligo vulgaris* es un caso paradigmático. En las Islas Baleares (Mediterráneo Occidental), esta especie es explotada tanto por el sector comercial como el recreativo. La pesca comercial de esta especie es una actividad relativamente bien conocida, pero el efecto de la pesca recreativa sobre la dinámica poblacional de esta especie es por el momento una incógnita, a pesar de ser potencialmente relevante. La evaluación y la gestión de la pesca recreativa es ciertamente compleja debido a las dificultades que entraña la estimación de sus capturas y de su esfuerzo pesquero. De acuerdo con esto, el principal objetivo de esta Tesis es estimar la recolección de calamar por parte de la pesca recreativa. Para hacer frente a este desafío, ciertos aspectos de la ecología del calamar, aspectos sociales del pescador y las interacciones entre ambos han sido abordados desde una perspectiva socio-ecológica.

La primera sección de esta Tesis proporciona nuevos conocimientos que relacionan aspectos del ciclo vital del calamar con el patrón de esfuerzo pesquero realizado por la flota recreativa. En primer lugar se demostró que durante la estación fría (invierno-primavera) *L. vulgaris* expande sus áreas de desove a cotas más someras, probablemente buscando condiciones ambientales que maximicen el éxito de su puesta (por ejemplo, la temperatura del mar). Este patrón concuerda con la hipótesis de que el calamar realiza migraciones a costa para desovar. Este momento es aprovechado por los pescadores recreativos para explotar el calamar. En segundo lugar se demostró que, durante este periodo de desove en costa, el calamar presenta un patrón de movimiento diferencial entre el día y la noche. El calamar es mucho más activo durante la noche que durante el día. Este patrón fue revelado utilizando la telemetría acústica, y se ajusta a la hipótesis de “alimentación de noche y desove durante el día”. De acuerdo con esto, la

pesca recreativa centra sus esfuerzos (al atardecer) durante el momento más vulnerable para la especie, puesto que el calamar ya ha cambiado al estado de alimentación y los señuelos son todavía visibles.

Una vez resuelto los patrones del ciclo vital del calamar estrechamente vinculados a su explotación, el paso siguiente fue entender la dinámica de la pesca recreativa. La localización de todas las barcas que pescaban calamar fue registrada (mediante censos visuales desde embarcación) con el objetivo de entender las variables que modulan la distribución espacio-temporal de los pescadores recreativos. Estimamos que tanto las variables relacionadas (recolección esperada) como las no relacionadas (por ejemplo, las condiciones del mar y la distancia al puerto más cercano) juegan un papel fundamental. Esta Tesis proporciona unas estimas a una precisa escala ( $1 \text{ km}^2 \text{ day}^{-1}$ ) del patrón espacio-temporal del esfuerzo pesquero de la flota de recreo.

Las recolección no sólo depende del esfuerzo, sino también de las capturas. Para evaluar los efectos de los factores ambientales sobre la capturabilidad del calamar se realizaron pescas experimentales. La combinación de variables tales como vientos débiles y baja presión atmosférica en días cercanos a la luna nueva maximizaron las capturas. Sin embargo, la principal variable involucrada en la fluctuación de las capturas de calamar fue la temperatura del mar. Las capturas son mayores durante los meses fríos. Este resultado concuerda con la ya mencionada hipótesis de las migraciones a costa que realiza el calamar para desovar. Además, las pescas experimentales revelaron que los 30 minutos en torno a la puesta del sol es el periodo donde la pesca recreativa captura más calamares. Este patrón diario casa con la hipótesis de “alimentación de noche y desove durante el día”.

Durante las ya mencionadas pescas experimentales se detectó un potencial efecto indirecto causado por la pesca con poteras: algunos calamares escapaban por la sección de uno o ambos tentáculos. Los posibles efectos indirectos causados por la pérdida de los tentáculos fueron testados mediante experimentación en cautividad. Los resultados mostraron que la pérdida de tentáculos provocaba una significativa pérdida de la eficacia de depredación y, que a su vez, podría afectar a supervivencia y al *fitness* de los calamares a largo plazo. Esto sugiere la posibilidad de una pesca fantasma que debiera tenerse en cuenta.

Finalmente, esta Tesis propone un nuevo marco para la estimación de la recolecta recreativa, integrando la información proporcionada anteriormente. Este enfoque combina las estimaciones basadas en el modelo de esfuerzo (que varía en espacio y tiempo) con estimaciones basadas en modelos de capturas por unidad de esfuerzo (que varían en tiempo y según la tipología del pescador). Con el fin de considerar la heterogeneidad



de los pescadores, estos fueron clasificados en tres tipos en base a sus respuestas a una entrevista. Esta entrevista fue diseñada para revelar la experiencia y capacidad del pescador. Mediante la inclusión de la heterogeneidad de los pescadores, las estimaciones de la recolecta fueron más precisas. Se estimó que la recolecta de calamar, por parte de la pesca recreativa en la Bahía de Palma, fue de 20.5 toneladas durante el 2010. Esto significa que la recolecta recreativa representa el 34% del total de desembarques realizados por toda la flota comercial de Mallorca durante el mismo año (59.5 toneladas). Aunque modelar de forma explícita la dinámica poblacional del calamar está fuera del alcance de esta Tesis, estos son los primeros datos empíricos que cuantifican la importancia de la pesca recreativa en *L. vulgaris*. El conocimiento aportado, sin duda, debe constituir la base sobre la que pivote un programa de monitoreo a largo plazo. A su vez, esta Tesis demuestra que la evaluación de los stocks deberían incorporar el papel potencial que la pesca recreativa ejerce sobre la dinámica poblacional de los recursos que explota.



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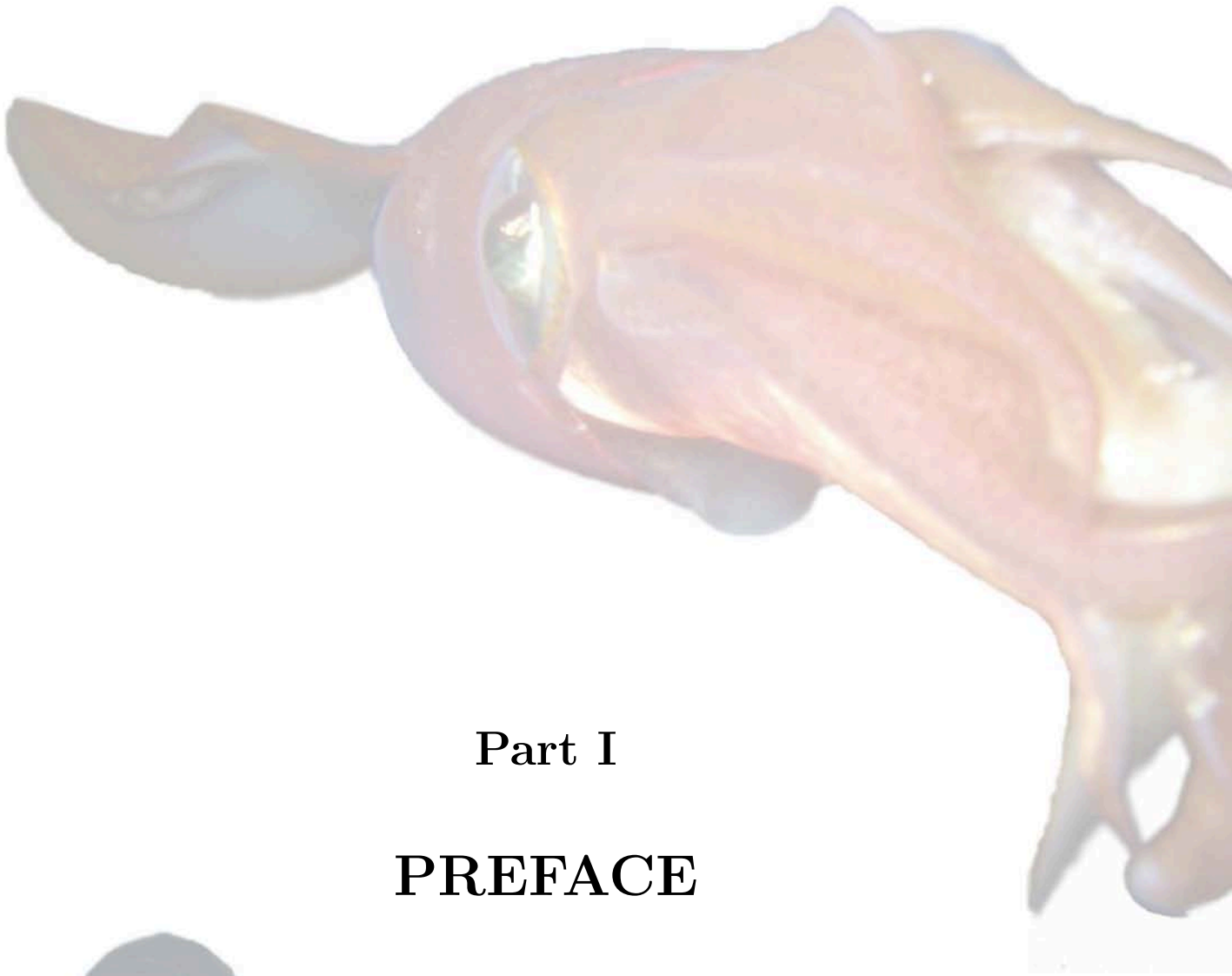
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Part I

# PREFACE





# Chapter 1

## Introduction

### 1.1 Socio-ecological system: an overview

The natural systems exploited by humans are characterized by the interdependence between a “ecological subsystem” and a “social subsystem” (Folke, 2006; Schlüter et al., 2012). The dynamics and complexity of these social-ecological systems (SEs) are driven by the feedbacks and interactions between natural resources and humans (Schlüter et al., 2012).

Fisheries overexploitation is an excellent example for introducing some of the singularities of SEs. Overexploitation by the commercial fleets seems to be one of the major causes of some stock collapse (Pauly et al., 1998, 2002). A fishery is said to collapse when fish population dynamics experience a regime shift and abundance does not recover even when apparently proper management rules are enforced (Costello et al., 2008; Worm et al., 2006). The consequence is that the stock becomes economically non profitable which, in turn, can cause the collapse of the industry supported by this specific resource (Gordon, 1991). However, the human-altered system are able to evolve and other species may became more abundant (e.g., jellyfish; Dong et al., 2010).

Another relevant example is fisheries-induced evolution (Allendorf and Hard, 2009; Jørgensen et al., 2007; Law, 2000). Harvesting has been demonstrated to be a primary selective driver for the target species. Artificial selection drives the evolution of the exploited species to some specific combination of life-history traits, which may cause population responses in unintended directions (King and McFarlane, 2003; Kuparinen and Hutchings, 2012; Rodhouse et al., 1998). Several studies reported relevant changes in life-history traits plausibly caused by fishing: changes in growth (Alós et al., In press; Ricker, 1981; Rijnsdorp and Van Leeuwen, 1992), fecundity (Horwood et al., 1986; Kelly

and Stevenson, 1985) or age-at-maturity (Dunlop et al., 2009; Pérez-Rodríguez et al., 2013). The general trend seems to be a shift towards a higher reproductive investment and smaller adult size (Alós, 2013).

These two examples highlight some of the features of SEs: complexity, capability to evolve and to adapt, potential for experiencing important regime shifts (and, in general, for experiencing non-linear dynamic), and capability for self-organization and for setting up across-scale interactions (Folke, 2006; Levin, 1998).

An obvious consequence of these features is that proper management of fisheries is not trivial at all, but demands sophisticated approaches and implies a detailed knowledge of all the pieces of the system and their interactions (Hilborn, 2007; Hilborn and Walters, 1992). Specifically, optimal management of fisheries should consider not only the biological and ecological characteristics of the target species but also the social characteristics of the stakeholders interested in the resource, and the interdependence between the ecological and the social dynamics (Carpenter et al., 2009; Horan et al., 2011). However, different stakeholders may interact with the resource in different ways and at different scales (Folke, 2006; Levin, 1998; Schlüter et al., 2012). For example, fishermen directly exploit the resource but managers act indirectly through controlling exploitation.

The recreational fisheries are an specially interesting case of SEs. Nowadays, the social relevance of recreational fisheries (RFs) and their impact not only on the exploited resources but on the ecosystem have been widely recognized. The number of recreational fishers (for simplifying, thereafter in this PhD, recreational fishers will be referred as *anglers*) has been estimated between 220 million (Bank, 2010) and 700 million people (Cooke and Cowx, 2004). Consequently, RFs may exert an important influence on stocks declines (Coleman et al., 2004b). The worldwide RF harvest would represent 12% of the global fish harvest (Cooke and Cowx, 2004). Given the number of anglers and their potential effects, there is a growing recognition of the economic, socio-cultural and ecological importance of recreational fishing worldwide (Bank, 2010; Welcomme et al., 2010).

Unlike commercial fisheries, RFs are characterized by the fact that the utility function that determines fishermen activity is not economic profit. The primary driver of angler motivation seems to be catch expectation, but other motivations are important too (Arlinghaus, 2006). Recreational fishing constitutes a multifaceted outdoor experience in which anglers seek multiple benefits in addition to catches (Driver and Knopf, 1976; Fedler and Ditton, 1994; Hendee, 1974). Alternative motivations may be to break the routine or to stay at a natural environment (Fedler and Ditton, 1994). Accordingly,

anglers may decide “When” and “Where” they go fishing based not only on expected catches (Hunt, 2005; Hunt et al., 2011; Lynch, 2006; Parnell et al., 2010; Post and Parkinson, 2012). Obviously, fishing regulations also affect the spatio-temporal pattern of fishing effort (Johnston et al., 2010, 2011) which emphasizes the mentioned above relevance of the role of stakeholders different from the anglers themselves. Managers are key stakeholders (Arlinghaus et al., 2013; van Poorten et al., 2011) and managing decisions should be based on proper monitoring of both the social subsystem and the ecological subsystem (Arlinghaus et al., 2013).

In summary, RF represents a relevant study case of SEs because:

- i) It has economical, socio-cultural and ecological importance.
- ii) RF integrates the biological and ecological characteristics of the target species, the social characteristics of the stakeholders interested in the resource, and the interdependence between the ecological and the social dynamic.
- iii) To understand the outcomes of recreational fishing is especially challenging due to the heterogeneity of anglers and their motivations (Arlinghaus et al., 2008b, 2013; Hunt et al., 2013; Larkin, 1978; Post, 2013).
- iv) RF and the populations of the target species are expected to change, evolve, adapt and reorganize through time (Arlinghaus et al., 2013).
- v) To maximize the resilience of the system and to achieve sustainability would ultimately depend on how the resources are managed which, in turns, should (ideally) depends on our understanding on the system dynamics (Arlinghaus et al., 2013).

## 1.2 Socio-ecological system case study: the recreational squid fishery

Typically, population dynamics and spatio-temporal distribution patterns of short lived species are more affected by environmental fluctuations than long lived species (Pierce et al., 2008). Most of the squid species seem to respond quickly to environmental cues (Pierce et al., 2008). Therefore, between-year variability in abundance and within-year patchiness are remarkable (Boyle and Rodhouse, 2005; Pierce and Guerra, 1994). These patterns ultimately can affect the spatio-temporal pattern of fishing effort (Boyle and Rodhouse, 2005; Pierce et al., 1998). Squid are exploited by different commercial fleets (from large trawlers to small-scale boats; Boyle and Rodhouse, 2005). Each fleet concentrates fishing effort at a specific stage of the life-history when squid are more vulnerable. For example, small-scale boats typically concentrate the effort when squid is forming near-shore spawning aggregations (Iwata et al., 2010; Postuma and Gasalla, 2010; Roberts and Sauer, 1994; Schön et al., 2002).

This seems to be the case of the European squid *Loligo vulgaris* (Lamarck, 1798) which is one of the most exploited cephalopod in the European waters (Moreno et al., 2013a; Pierce et al., 2010). *L. vulgaris* is a commercially valuable species. It is mainly captured by trawl fisheries (Chen et al., 2006a; González and Sánchez, 2002; Pierce et al., 2010; Royer et al., 2002; Vila et al., 2010; Young et al., 2006). Moreover, *L. vulgaris* is targeted by small-scale fisheries, specially in Spain and Portugal (Guerra et al., 1994). In the Mediterranean Sea, small-scale boats use two types of gears (or *métiers*): seines and hand-line jigging combined with attraction lights (Guerra et al., 1994; Lefkadltou et al., 1998; Ulaş and Aydin, 2011).

The European squid is also exploited by RF (Moreno et al., 2013a; Pierce et al., 2010). The effect of the RF on the population dynamics of *L. vulgaris* is currently unknown but it is plausibly relevant (Guerra et al., 1994). At the Balearic Islands, squid is one of the most important target species of the RF (Morales-Nin et al., 2005) and recreational squid fishing is one of the modalities implying more economic revenues (Morales-Nin et al., Submitted). This fishery takes place all year around but concentrates at the coldest months (winter and spring). Concerning the day temporal scale, recreational squid fishing is limited to a few hours around sunset. At the appropriate season, hundreds of RF boats cluster at specific near-shore fishing grounds. Anglers use line jigging (by hand or by rod-and-reel). In this fishing modality, anglers excites artificial jigs moving them up and down.

In summary, squid RF represents a relevant study case because:

- i) RF harvest on squid is largely unknown but plausibly relevant.
- ii) Squid is one of the most important target species for RF.
- iii) The clear-cut spatio-temporal pattern of fishing effort at both day and season scale is plausibly related with some specific event of the life-history of the squid. This is particularly relevant because any hypothesis on the process producing such a pattern provides a testable framework that would bridge the biological and ecological characteristics of the target species with the social characteristics of the stakeholders interested in the resource.

Therefore, understanding the recreational squid fishing system requires to address both the anglers' and squid features (Fig. 1.1).

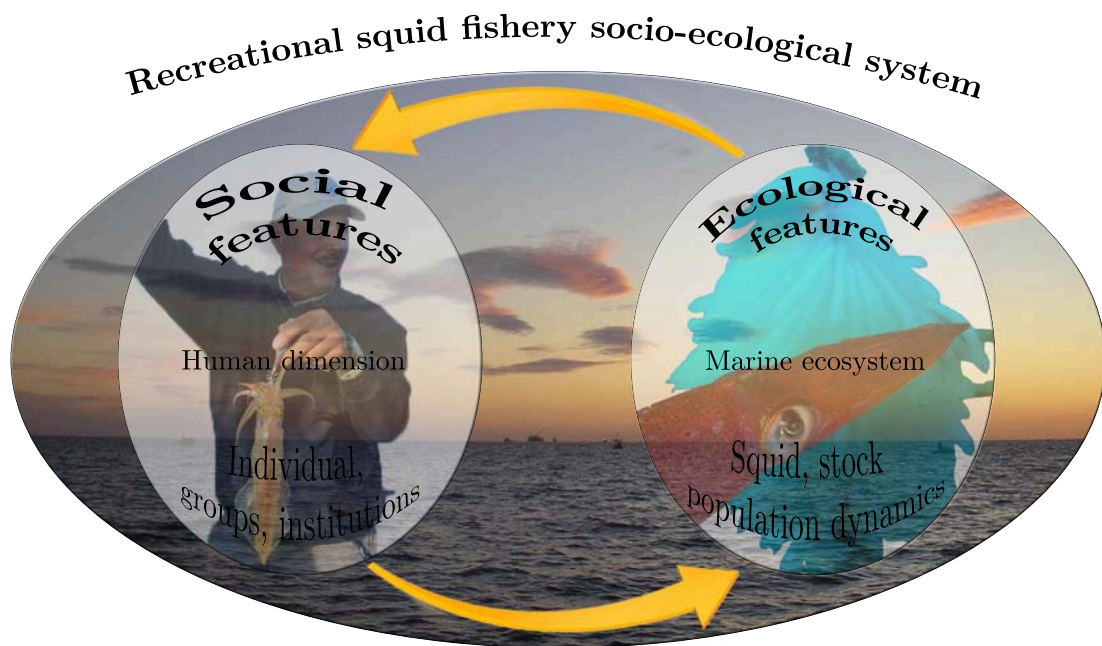


Figure 1.1: A conceptual sketch of a social-ecological framework for the recreational squid fishery adapted from Arlinghaus et al. (2013).

### 1.3 Objective and Structure of the Ph.D. Thesis

The main objective of this PhD is to estimate the squid harvest attributable to RF and to highlight the role of RF on the population dynamics of *L. vulgaris*.

To achieve this main goal, several sub-objectives were raised, and subsequently, were addressed based on the following working hypothesis (Fig. 1.2 & Fig. 1.3): squid migrate to inshore waters at the coldest season searching for the environmental conditions that maximize spawning success (e.g, optimal sea temperature for larval development; Villanueva et al., 2003). At mentioned above, this hypothesis provides a testable framework that would bridge the biological and ecological features of the target species with the angler's features.

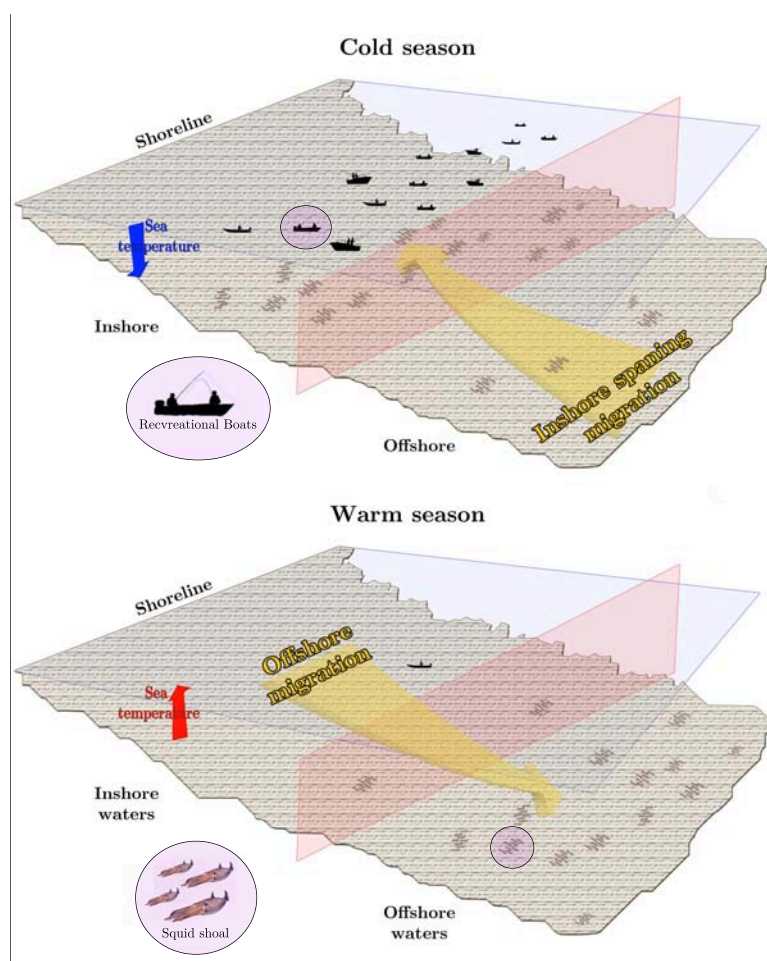


Figure 1.2: Work hypothesis of the Ph.D. Thesis: Palma Bay during sunset at different seasons (cold vs. warm season).



With this background, Section II focuses in some unknown biological and ecological issues that have a key relevance for linking squid behaviour and the two *a priori* qualitatively known patterns of RF effort (i.e., the seasonal pattern and the daily pattern). In this sense, Chapter 2 describes the preferential spawning areas and the environmental conditions affecting the spawning of the European squid. A number of artificial structures were deployed at different habitats and under different environmental conditions. These structures were used by squid for attaching eggs clutches. The results obtained support the hypothesis of the existence of inshore spawning aggregations. Chapter 3 addressed the problem of understanding the narrow temporal window (around sunset) during which squid seems vulnerable to RF. A number of squids were marked with acoustic transmitters in order to compare the movement pattern at daytime and nighttime.

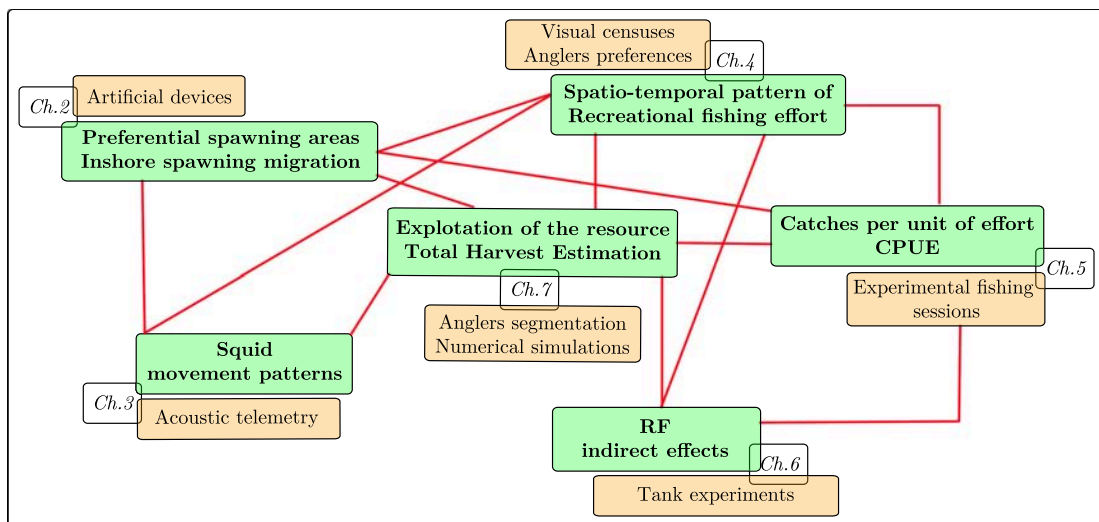


Figure 1.3: General framework and sub-objectives addressed in the present Ph.D. Thesis. Green boxes contain sub-objectives. Orange boxes show the main methodological procedures developed to address the objectives. Lines show the interactions among them.

Section III focuses on the anglers and their harvest. This Section is aimed to provide a quantitative description of the spatio-temporal pattern of fishing effort and to disentangle the potential drivers of this pattern (i.e., squid catches *vs.* catch-unrelated variables). Therefore, Chapter 4 deals with the spatio-temporal pattern of fishing effort. A number of surveys (visual censuses of recreational fishing boats) were completed in order to accurately describe the spatio-temporal pattern of fishing effort. Chapter 5 described the seasonal pattern of variability on squid catches and relates this pattern with a number of potential environmental drivers (e.g., sea temperature). The method

used was to emulate RF by means of standardized fishing sessions. Chapter 6 addressed a problem specific of the squid jigging fishery. It was previously known that jigging may cause the loss of squid tentacles. The injured squid escapes but squid survival was unknown. The existence of “ghost fishing” may bias the harvest estimations. For that reason, this Chapter copy with the potential effects related with tentacle losses through tank experiments. To conclude this Section, Chapter 7 integrates the results of all the previous Chapters with the final goal of estimating the harvest of the recreational fishing of *L. vulgaris* at Palma Bay. The harvest estimate combines the fishing effort (Chapter 4), the catch variability related with seasonal environment variables (Chapter 5) and the catch variability related with angler skills, which was estimated based on the data obtained from both an off-site survey and creel survey.

Finally, Section IV provides the general conclusions as well as future researches lines emerging from this Ph.D. Thesis (Chapter 8).

The background of the page features a close-up photograph of a squid. The upper portion shows the mantle, which is a pale, yellowish-tan color with distinct vertical ridges and a small, dark, circular spot. The lower portion shows the head, which is a darker, reddish-brown color with a large, prominent eye. The text is overlaid on this image.

**Part II**

**ECOLOGICAL ASPECTS**



## Chapter 2

# Identification of preferential spawning areas for the European squid

### 2.1 Abstract

Sustainable management of exploited stocks demands, among others issues, to identify the spawning spatio-temporal patterns and eventually to protect the spawning grounds of the target species. Squid seems to aggregate at this crucial period of the life-history, which implies increasing vulnerability to fishing. Unlike those of other Loliginid species, the spawning preferences of the European squid are largely unknown because finding egg clutches of this species in the wild is challenging. Validated records from research programs are virtually inexistent but unsystematic records from, for example fisherman, suggest that squid spawns regularly on artificial structures. In this Chapter, we report for first time a description of the spatio-temporal pattern of squid spawning on artificial devices (ADs). Thirty ADs were deployed over one year at a marine reserve (Cabrera National Park). ADs were distributed covering the three main types of benthic habitat, and ranging from 5 to 50 m depth. ADs were sampled monthly. Three main patterns have been evidenced: i) squid would prefer sandy bottoms for spawning, ii) spawning would peak in spring, and iii) squid would expand their spawning areas to shallower waters during the coldest months. It is debatable to extrapolate these patterns to those actually takes place in natural conditions. However, given the heavy fishing effort exerted on squid (Chapters 4 & 7) and data scarcity, the precautionary approach supports to take data from ADs as a starting point for advising sustain-

able management. Assuming that spawning at ADs and at the wild are correlated, the first pattern may be related to the faster marine currents that prevail on sandy bottoms and/or the lower abundance of potential predators in these habitats. The second pattern may be related to the typical phytoplankton-zooplankton cascade that, in the Western Mediterranean, takes place just preceding spring. The third pattern is in accordance with the hypothesis that squid may undergo a spawning migration.

KEY WORDS: Marine Protected Area, *Loligo vulgaris*, Egg Clutches, Essential Fish Habitats, Spawning Migrations.

## 2.2 Introduction

Habitat degradation and overfishing may cause severe decline in some exploited living marine resources (Worm et al., 2006). Cephalopods are important target species for fisheries worldwide (Boyle and Rodhouse, 2005), thus stocks are potentially susceptible to overfishing (Pierce and Guerra, 1994). As in the cases of other short-lived species, squid abundance experiences important between-year variability and depends on environmental variability (e.g., temperature; Pierce et al., 2008), which complicates management (Pierce and Guerra, 1994).

In an effort to promote sustainable fisheries, different management strategies have been implemented to reduce fishing mortality, mainly through fishing limitations. Conventional regulations consist in limiting days-at-sea, closing areas, closing seasons and implementing gear restrictions (Morales-Nin et al., 2010). However, in some cases, this conventional approach has been ineffective (Hutchings, 2000). Therefore, integrating species-specific fishing limitations with a broader management strategy has been proposed (Roberts et al., 2005). This new paradigm implies, for example, that the biology and ecology of the species to be protected should be considered to achieve a successful regulatory implementation. For example, the movement characteristics of a species should be known to determine the optimal extension of a marine protected area (Taylor and Mills, 2013; Walters, 2000). To address such integrated management strategy, previous research has indicated the importance of identifying and eventually protecting essential fish habitats (EFHs; Rosenberg et al., 2000). An EFH is the habitat identified as essential to the requirements of a species at any critical stage of the life history. EFHs would require special protection for improving stock status and ensuring long-term sustainability (Valavanis and Smith, 2007). Therefore, the protection of EFHs should be considered when managing fisheries (Benaka, 1999).

As an example that supports the potential usefulness of characterizing EFHs of cephalopods, sustainable development of the South African squid fishery was achieved after identifying and protecting some preferential spawning areas of the chokka squid, *L. reynaudii* Orbigny (1841) (Augustyn and Roel, 1998).

As highlighted in Chapters 4 & 7, the European squid, *L. vulgaris* experiences considerable fishing pressure. In addition to the commercial fishery, recreational fishing effort concentrates at specific grounds (inshore waters at 20-35 m depth; Chapter 4 & Cabanellas-Reboredo et al., 2014a) during the reproductive season of this species (winter-spring; Šifner and Vrgoč, 2004). Previous reports have suggested that the pattern depicted by the recreational fleet may be related to inshore-offshore spawning

migrations of this species (see Chapters 4 & 5; Cabanellas-Reboredo et al., 2012b, 2014a). Squid may undergo spawning migrations in an attempt to maximize spawning success (Cabanellas-Reboredo et al., 2012a; Villanueva et al., 2003) by optimizing embryonic development (e.g., seeking an optimal temperature range; Şen, 2005). In-shore spawning aggregations are more vulnerable to fishing (Boyle and Rodhouse, 2005). Therefore, fishing mortality is expected to intensify during a critical period in the squid life-history (Boyle and Rodhouse, 2005; Pierce and Guerra, 1994). The identification of spawning areas could play an important role in ensuring the stock sustainability as is the case of the above-mentioned *L. reynaudii* (Augustyn and Roel, 1998; Cochrane et al., 2014). Unfortunately, unlike other exploited Loliginid species (e.g., *L. reynaudii* or *L. opalescens*) whose spawning grounds have been well identified, delimited and characterized (Foote et al.; Sauer et al., 1993), data on explicit observations of the spatio-temporal spawning patterns of *L. vulgaris* are not available.

*L. vulgaris* females have been reported to lay eggs in clusters attached to different hard substrates or branched sessile organisms (Jereb and Roper, 2010). However, to find squid eggs at the wild seems to be very challenging. The study area considered in this Chapter is a National Park (Cabrera Archipelago National Park; CNP), thus a large number of systematic scientific sampling programs (scuba diving visual censuses) have been completed but reports of egg clutches are merely anecdotic (Vázquez-Luis et al., Submitted). Conversely, non validated or unsystematic reports of egg clutches attached to fishing gears and other artificial structures (e.g., ropes of acoustic tracking structures; Chapter 3 & Cabanellas-Reboredo et al., 2012a) are relatively frequent. When detecting natural egg clutches is difficult or impossible, the use of artificial substrates has been suggested as an alternative sampling methodology (e.g., in the case of *Perca fluviatilis*; Gillet et al., 2013) and they has been already used in the case of *L. vulgaris* (Villa et al., 1997).

This Chapter reported for first time a description of the spatio-temporal pattern of squid spawning on artificial devices (ADs). Three main patters have been evidenced: i) squid would prefer sandy bottoms for spawning, ii) spawning peak takes place in spring, and iii) squid would expand their spawning areas to shallower waters during the coldest months. At least the second and third pattern can be extrapolated from CNP to Palma Bay. In turn, it is important to note that the interpretation of the data obtained with ADs is not straightforward because the patterns observed may be biased in relation to the natural patterns. However, in the case of no data and applying a precautionary approach to a heavily exploited resource, the use of ADs may be a valuable starting point for implementing effective management measures.



## 2.3 Material & Methods

### 2.3.1 Study area

The study was conducted at CNP (Balearic Islands, NW Mediterranean; Fig. 2.1).

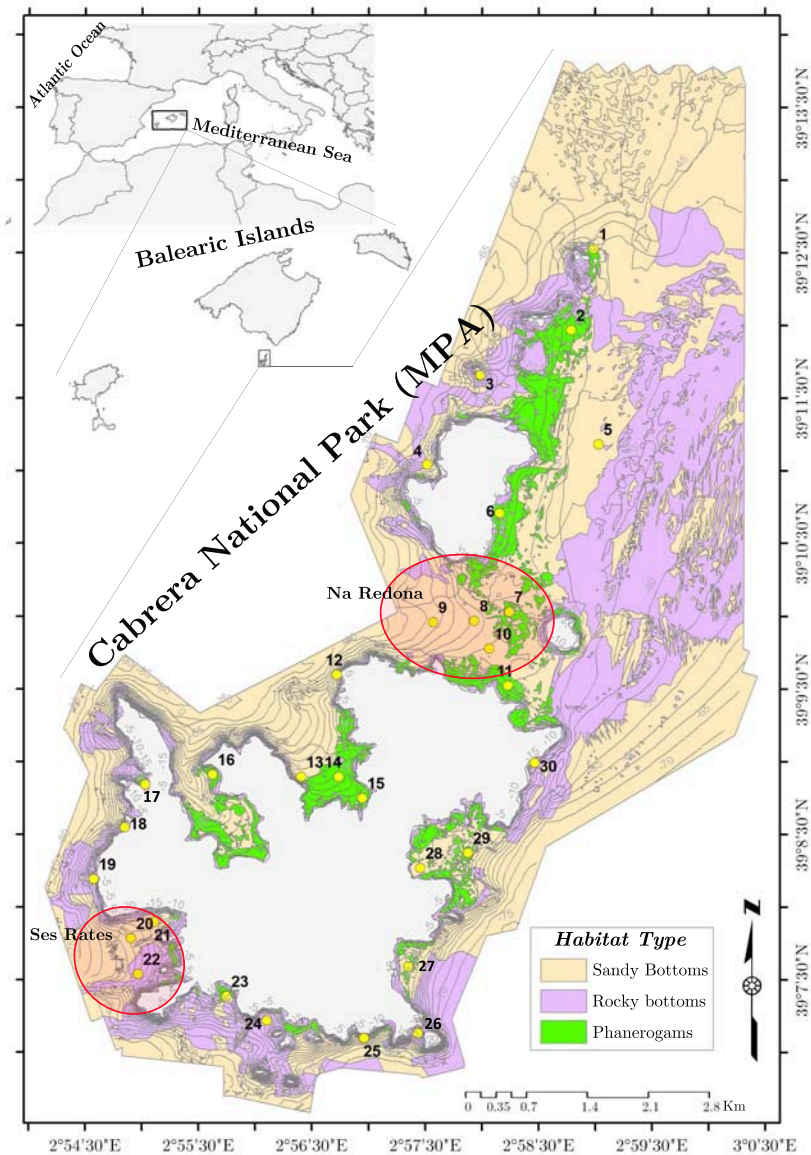


Figure 2.1: Location of the study area and distribution of artificial devices (ADs) on the three main benthic habitats around Cabrera National Park. Na Redona and Ses Rates locations are highlighted by red circles. Isobaths are designated at 5 m intervals.

CNP is a combination of nineteen small islands that form one of the largest marine reserves in the Mediterranean, with a coastline of 54 km and 87 km<sup>2</sup> of marine protected area (MPA). Fishing started very early at Cabrera, with archeological evidence of fish salting during Roman times (Frontera et al., 1993). Fishing activity in the 1960s was partially high due to the rising importance of recreational fishing (Massutí, 1991). After the enforcement of the marine reserve in 1991, a total of 80 small-scale boats were registered to fish in CNP waters (Coll et al., 1999). However, the current fishing effort is unknown, although most likely smaller, because these boats also operate outside CNP. The main activity of these small-scale boats is trammel net fishing, but they may also fish for squid using hand-line-jigging with attraction lights. Trawling and recreational fishing are banned within CNP.

### 2.3.2 Sampling strategy

Thirty ADs (Fig. 2.2A) were randomly deployed in the three main benthic habitat types present at CNP (phanerogams, sandy bottoms and rocky bottoms) and covering a depth range from 5 to 50 m (Fig. 2.1). ADs were recovered monthly, and the egg clutches attached to the structures were collected and counted (Fig. 2.2B & C). The sampling frequency was based on the embryonic development of *L. vulgaris*, which lasts approximately one month (Şen, 2005). Samples were collected from June 2012 to June 2013, with the exception of February due to rough weather. The smooth gooseneck barnacle, *Lepas anatifera* Linnaeus (1758), was found on a relatively large number of ADs buoys (Fig. 2.2D). The presence/absence of this barnacle was also recorded. The egg clutches were removed to avoid over-counting in the subsequent sampling period, and ADs were replaced in the same position after sampling.

### 2.3.3 Data analysis

The goal of the analysis was to identify the environmental variables affecting the number of egg clutches on an AD and use these variables to predict the expected number of eggs clutches on an AD located at any point of the MPA and at any time of the year. Raw data for all of the potential explanatory variables were obtained from diverse sources and are provided at different spatial scales. Therefore, the input data for the analyses were first prepared (*raster* library of the R package and ArcGIS 9.2 ESRI) to fit them to a common statistical unit (AD-Month). Then, a Zero-Inflated Poisson (ZIP) model was used to model the response variable (number of egg clutches by AD and per month) as a linear combination of the potential explanatory variables (Habitat Type, Depth

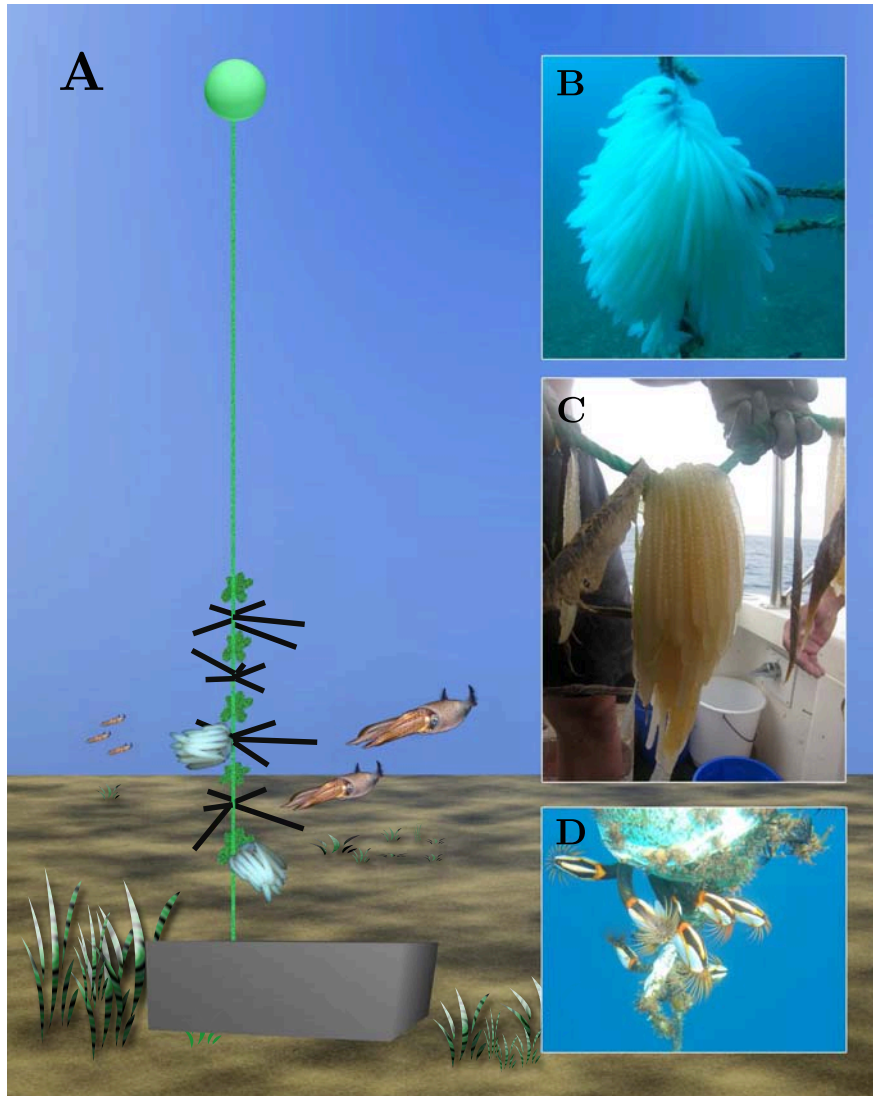


Figure 2.2: Artificial devices (ADs) for *L. vulgaris*: (A) Structure of the AD formed by a rope ( $\varnothing$  1.2 cm), a buoy to keep the rope extended and a weight on the bottom to fix the structure in place. The first two meters of rope from the bottom contain 5 knots and plastic flanges (16) placed among these knots (to increase the attachment surface). (B) Egg clutches attached to the rope or flanges. (C) Detail of the egg clutches recovered on board. (D) Recruitment of several individuals of *Lepas anatifera* on an AD buoy.

and Sea Surface Temperature; see below).

### 2.3.3.1 Predictive variables

Habitat Type (*HT*) and Depth (*D*) were obtained from the LIFE project (Posidonia-LIFE map, Government of Balearic Islands; <http://lifeposidonia.caib.es/user/>

home.htm), which provided information at a fine scale (5 m<sup>2</sup>). The 24 types of benthic habitats characterized by the LIFE project were grouped into three main types: i) sandy bottoms (*HTS*), ii) rocky bottoms (*HTR*) and iii) bottoms covered by phanerogams (*HTP*) (Table 2.1).

Daily Sea Surface Temperature (*SST*; in °C) was obtained from the MyOcean website (<http://www.myocean.eu>) with a spatial resolution of 1 km<sup>2</sup>.

Table 2.1: Reclassification of the Habitat types from the LIFE project characterization.

Habitat type	LIFE Project habitat classification
Sandy bottoms ( <i>HTS</i> )	Fine sand, Coarse sand, Poorly calibrated sand, Coralligenous, Dispersed coralligenous, Coastal dendritic, Precoralligenous, Dispersed precoralligenous.
Rocky bottoms ( <i>HTR</i> )	Dispersed sciaphilous community, Littoral rock sciaphilous community, Infralittoral rock photophilic community, Dispersed photophilic community, Peyssonnelia coastal detrital, Vidalia coastal detrital, Pebbles coastal detrital, Precoralligenous on hard bottom.
Phanerogams ( <i>HTP</i> )	Dense Cymodocea, Dispersed Cymodocea, Isolated phanerogams, Phanerogams with batches, Continuous phanerogams, Degraded phanerogams, Rocky phanerogams, Cymodocea-Caulerpa grassland.

### 2.3.3.2 Zero-Inflated Poisson Model

A preliminary inspection of the response variable ( $EggClutches_{ij}$ ; number of egg clutches at the  $i^{th}$  AD and in the  $j^{th}$  sampling period) corroborates the non-normal distribution of the data. The apparent excess of zero values suggests that actual counts may result from the mixing of a Poisson distribution and a binomial distribution. Such a binomial distribution determines the probability of obtaining a false zero (i.e., spawners are present at the area around a specific AD at the time of sampling, but the AD does not record the spawning activity of these squid; Martin et al., 2005). This type of data can be analyzed using a ZIP model (Zuur et al., 2012). The fact that all ADs are sampled at the same day implies an additional analytical complexity, because samples from the same day can not be considered independent. Therefore, the explanatory variables of *Habitat Type* (sandy *HBT*, rocky *HTR* and phanerogams *HTF*), *Depth* ( $D$ ) and *Sea Surface Temperature* (*SST*) were considered fixed variables, but the sampling period (*Month*) was added as a random effect. The binomial portion of the mixed ZIP

model was simply:

$$W_{ij} \sim \text{Bionomial}(\pi),$$

where  $W_{ij}$  can be either 0 or 1. The symbol “ $\sim$ ” should be read “distributed as”.

The Poisson portion was:

$$\mu_{eff_{ij}} = W_{ij} * \mu_{ij}$$

$$ObEC_{ij} \sim \text{Poisson}(\mu_{eff_{ij}})$$

$$\log(\mu_{ij}) = \beta_0 + \beta_1 HTS_i + \beta_2 HTR_i + \beta_3 D_i + \beta_4 SST_{ij} + \beta_5 D_i * SST_{ij} + \text{MonthEffect}_j$$

$$\text{MonthEffect}_i \sim \text{Normal}(0, \sigma),$$

where  $i$  denotes the 30 ADs,  $j$  the number of sampling dates (11) and  $ObEC_{ij}$  the observed number of egg clutches. It is important to note that when  $W_{ij}$  is zero, the effective mean of the Poisson process ( $\mu_{eff_{ij}}$ ) is zero as well; thus, the actual observed number of egg clutches ( $ObEC_{ij}$ ) is zero (i.e., a false zero). Otherwise ( $W_{ij} = 1$ ),  $\mu_{eff_{ij}}$  depends on the linear combination of the explanatory variables.

Currently, no closed statistical package allows fitting a ZIP model when including random effects. Therefore, this model was fitted using the Bayesian machinery as implemented in JAGS (<http://mcmc-jags.sourceforge.net>) and using the *R2jags* library (<http://cran.r-project.org/web/packages/R2jags/index.html>) from the R package (<http://www.r-project.org/v2.15-2>), with the following priors (mean and tolerance are indicated in brackets):

$$\beta_0 \text{ to } \beta_5 \sim \text{Normal}(0, 10^{-6})$$

$$\text{logit}(\pi) \sim \text{Normal}(0, 10^{-6})$$

$$\sigma_{\text{MonthEffect}} \sim \text{Gamma}(0.01, 0.001),$$

where  $\pi$  (the prevalence of false zero values) is within the interval between 0 and 1. The conventional tools for assessing proper mixing of the Monte Carlo Markov chains (MCMC), convergence and lack of autocorrelation (burning interval = 500; number of chains = 3; sample size per chain = 1000), were used.

After model fitting, the model residuals were inspected to check over-dispersion (Zuur et al., 2012). The occurrence of an identifiable effect of any putative explanatory variable was evaluated based on 95% Bayesian credibility intervals (CI) for  $\beta$ s (and whether these intervals included zero). Moreover, to improve the interpretations of

the results, the fitted ZIP parameters were used to predict the expected number of egg clutches around the entire spatial scenario (Cabrera National Park) at any time period. A spatial framework was defined by a grid of 381 cells of 500×500 m. The Eastern part of Cabrera National Park was not included in the predictions to avoid extrapolation at areas with scarce or no observations. One thousand simulations were run to estimate the expected numbers of egg clutches and its variability (95% credibility intervals). Then, the mean of the expected values for each cell were mapped.

### **2.3.3.3 Complementary variables**

To improve the interpretation of the results, some complementary variables were examined. These variables were not included in the ZIP model because they were not available for the entire spatial scenario or are available at coarse temporal scale, and thus could not be used with predictive purposes, and/or they are highly correlated with the variables included in the model (thus, avoiding potential collinearity problems). These complementary variables were presence/absence of *L. anatifera* on the AD buoys and *Sea Surface Chlorophyll*. The presence/absence of a filter-feeder species (*L. anatifera*) was used as a proxy (bioindicator) of zones where marine currents ensured food availability, which may improve the recruitment success of filter-feeder species (Inatsuchi et al., 2010). The effects of *Habitat Type* and *Depth* on the presence/absence of this barnacle were tested using a Generalized Linear Model (GLM) as implemented in the *lme4* library of the R package (<http://cran.r-project.org/web/packages/lme4/index.html>). The presence/absence of this barnacle on each AD was cumulated along the entire study period. The other complementary variable that was considered was *Sea Surface Chlorophyll* (*SSC*; mg m<sup>-3</sup>). To explore any type of relationship between squid spawning and primary production, the monthly average values of this variable were downloaded from the MyOcean website with a spatial resolution of 1 km<sup>2</sup>.

## 2.4 Results

Some egg clutches were recorded at some ADs throughout the entire year, but egg count reached a maximum peak in spring (May) with a gradual decrease afterwards (Fig. 2.3). The lowest number of egg clutches was recorded between October-January. Therefore, the spawning activity of *L. vulgaris* seems to extend all year-round.

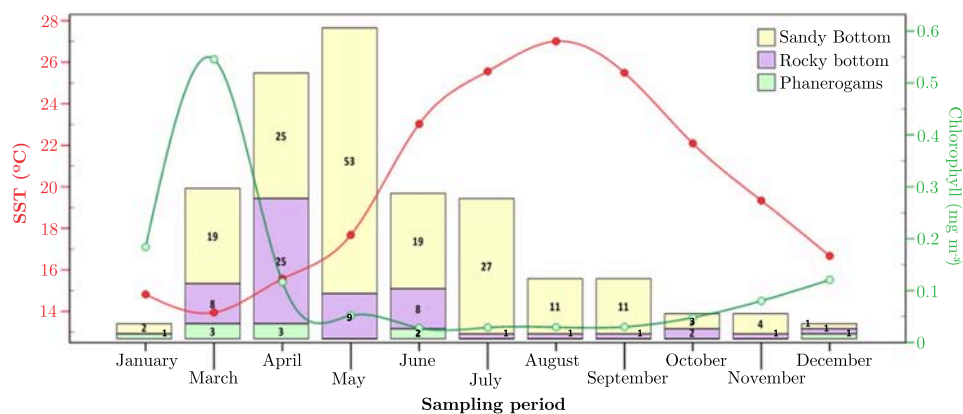


Figure 2.3: *L. vulgaris* spawning activity (cumulated number of egg clutches per month) related to benthic habitat (colours of the bars), sea surface temperature (*SST*, red line) and sea surface chlorophyll (*SSC*, green line). Note the absence of February due to logistical problems during the sampling process.

A total of 242 egg clutches were recorded, of which 72.3% were attached to ADs located on sandy bottoms (Fig. 2.3 & 2.4). ADs located on rocky bottoms recorded 23.5% of the total egg clutches. The eggs attached to ADs deployed on phanerogams accounted 4.2% only. Moreover, egg clutches were only recorded between depths of 18 to 50 m, indicating an avoidance of the shallowest waters (from 5 to 17 m depth). AD#27 (Fig. 2.1) was the shallowest AD (18 m depth) with egg clutches (Fig. 2.4).

The estimated values for the ZIP model parameters are summarized in Table 2.2.

Table 2.2: Summary statistics for the posterior distributions of fixed and random effects. Relevant fixed effects are highlighted in green.

	Parameters	Description	Mean	SD	Credibility Intervals		
					2.5%	Median	97.5%
	$\pi$	False zero parameters	0.281	0.078	0.135	0.278	0.434
Fixed factors	$\beta_0$	Grand mean	-2.445	0.609	-3.800	-2.390	-1.355
	<i>HTS</i>	Habitat type sandy	1.772	0.388	1.056	1.747	2.605
	<i>HTR</i>	Habitat type rocky	1.016	0.403	0.271	0.989	1.883
	<i>D</i>	Depth	-0.076	0.008	-0.093	-0.076	-0.060
	<i>SST</i>	Sea Surface Temperature	-0.126	0.099	-0.321	-0.126	0.056
	<i>D*SST</i>	Interaction Depth*Sea Surface Temperature	-0.007	0.002	-0.011	-0.007	-0.004
Random	$\sigma_\gamma$	Month effect	1.331	0.475	0.739	1.242	2.445

These results demonstrated an effect of habitat type on the spawning preferences of *L. vulgaris*. More egg clutches tend to be found on ADs located on the sandy bottom and, to a lesser extent, on rocky bottoms (Table 2.2). The expected number of egg clutches on phanerogam bottoms was smaller (note that this effect was included in the grand mean  $\beta_0$  in Table 2.2).

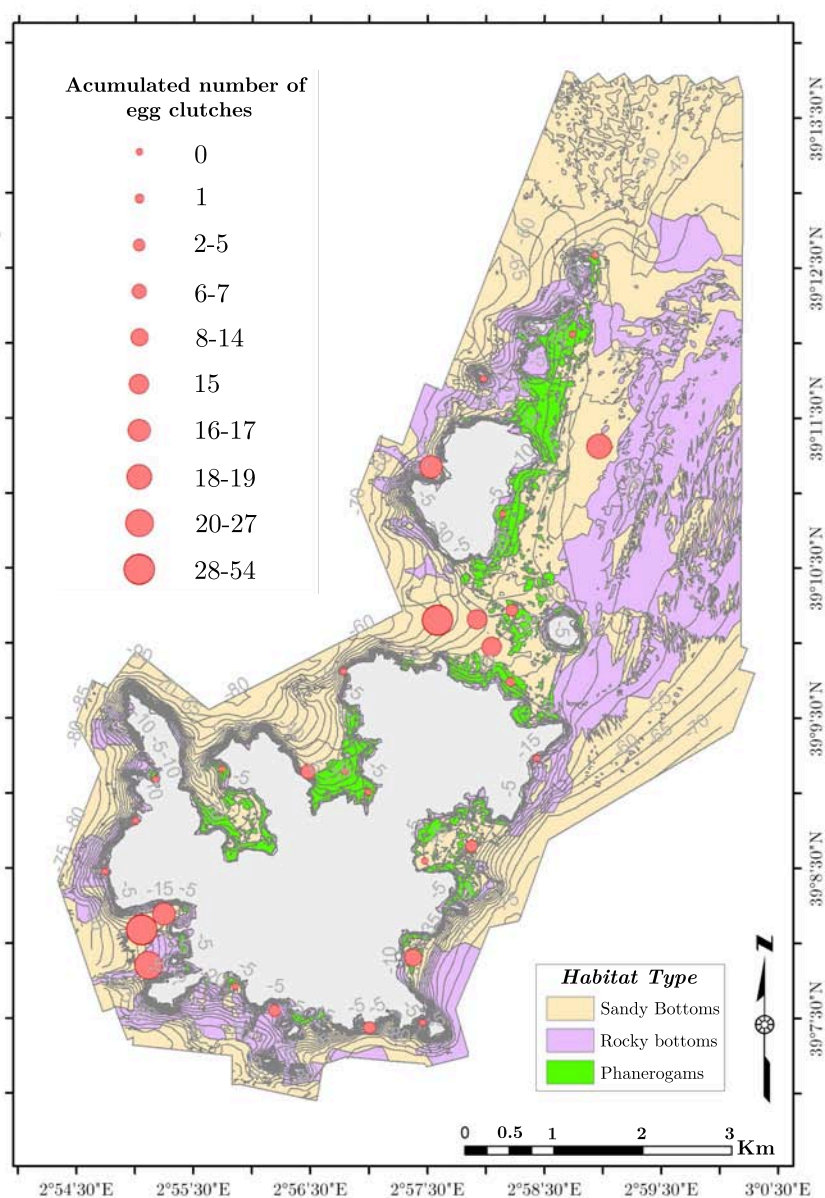


Figure 2.4: Spatial distribution of the accumulated number of egg clutches by an artificial device (AD).



Concerning *Depth*, the number of expected egg clutches increased at deeper ADs. *SST* alone had not a relevant effect on squid spawning preferences (95% CI included zero; Table 2.2). However, the interaction between *SST* and *Depth* suggested a relevant effect (Table 2.22 & Fig. 2.5): During warm months (e.g., September), egg clutches only appeared on ADs deployed in deeper waters (40-50 m depth; Fig. 2.5). Conversely, during cold months (e.g., February), egg clutches also appeared in shallower waters (18-39 m depth; Fig. 2.5).

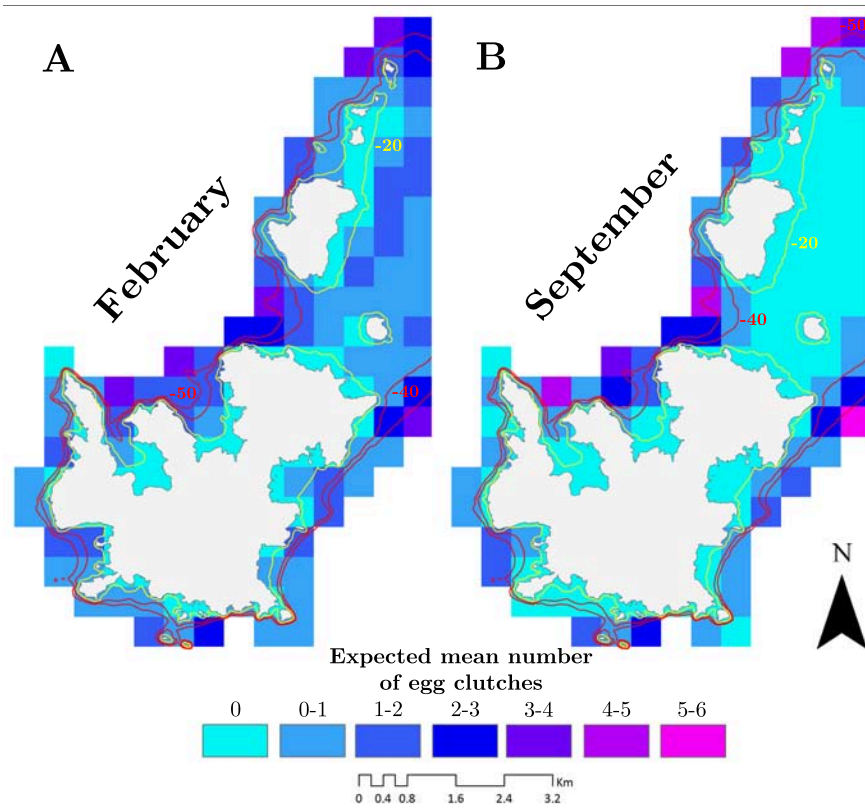


Figure 2.5: Maps predicting the expected mean number of egg clutches of *L. vulgaris* in a: (A) cold month and (B) warm month. Isobaths at 40 and 50 m depth are represented by red lines. The isobath at 20 m depth is represented by a yellow line.

In regards to the complementary variables, we found a significant relationship between the presence/absence of *L. anatifera* and *Depth* and *Habitat Type* variables. *L. anatifera* tend to be present at deeper ADs and at ADs located on sandy bottoms (GLM results  $p < 0.05$ ). The temporal pattern of the *SSC* showed a clear peak at the end of winter (maximum values in March) but remained at low levels during the rest of the year (Fig. 2.3).

## 2.5 Discussion

This Chapter reported for first time a description of the spatio-temporal pattern of squid spawning on artificial devices. Three main patterns have been evidenced: i) squid would prefer sandy bottoms for spawning, ii) spawning would peak in spring, and iii) squid would expand their spawning areas to shallower waters during the coldest months. However, the interpretation of the data obtained with ADs is not straightforward because the patterns observed may be biased in relation to the natural patterns. A number of hypotheses are possible. First, the chance of spawning on an AD is similar than on a natural substrate but clutches are cryptic and, therefore, not easily recorded by scuba divers. Second, the eggs clutches that should be laid in a large area around an AD are all attached to the AD (sink effect). Third, the strength of the sink effect depends on habitat or season, thus inducing bias. Fourth, squid are induced to spawn by the mere presence of an AD even at inadequate habitat or season.

The available evidences are weak and all concern fish. First, eggs counted by scuba divers on natural substrates and on artificial structures are different but correlated in *P. fluviatilis* (Gillet et al., 2013), which would be against the third and fourth hypotheses. Second, depending on the site, fish may shift to spawn from natural to nearby located artificial substrates after AD deployment (sink effect) or egg number may remain similar (Hickford and Schiel, 2013).

Note that both the first and the second hypothesis do not invalidate the patterns found because egg abundance on AD would be relative estimates of the egg abundance at natural conditions, and therefore natural and AD abundance would remain well correlated. Nevertheless, the interpretation of the patterns found should be done with caution until the third and fourth hypotheses were not rejected. In the meantime, given that squid is a heavily exploited resource (Chapters 4 & 7), and provided that virtually no data are available in spite that a large number of scuba diving visual censuses have been completed, a precautionary approach could be adopted and the spatio-temporal pattern depicted by ADs may be considered as a valuable starting point for identifying and characterizing the possible spawning EFHs and preferred spawning seasons of the European squid, *L. vulgaris*.

The first pattern found in this study showed that the European squid preferentially choose ADs located on sandy bottoms for spawning. This pattern may be the result of biased strength of the sink effect mentioned above. It is well known that most Loliginid species frequently attach eggs on ropes, nets, traps and other fishing gears when these artificial structures are available (Hanlon and Messenger, 1996; Jereb and

Roper, 2010). Few natural substrates would be available in sandy bottoms, thus ADs may be more effective to collect eggs. Conversely, rocky bottoms and phanerogams offer more potential natural substrates for egg attachment, thus ADs may be less effective.

Alternatively to the existence of a biased sink effect, squid preference for ADs located on sandy bottoms may reflect genuine habitat selection. In that case, this pattern might arise because the potential predator *Ehinuphelus marginatus* is very abundant in the CNP but is mainly restricted to rocky bottoms (Reñones et al., 1997, 1999). It has been reported that predator presence may induce disruptions of egg deposition and cause the absence of chokka squid (*L. reynaudii*) from *a priori* adequate spawning grounds (Lipiński and Soule, 2007; Smale et al., 2001). It is also possible that the presence of predators was not the only factor that triggered a positive selection for the sandy bottoms as preferential spawning habitat. The positive relationship between sandy bottom and the presence of the filter-feeder *L. anatifera* (GLM results; Section 2.4) suggests that sandy areas may have more favorable environmental conditions (food availability and currents; Inatsuchi et al., 2010), which in turn, may enhance survival of squid paralarvae (Martins et al., 2013; Roberts, 2005; Roberts and van den Berg, 2002).

The preferred spawning habitats of other squid seem to be species-specific. At one hand, it has been reported that other related Loliginid species (*L. opalescens* and *L. reynaudii*) spawn on sandy bottoms (McGowan, 1954; Sauer et al., 1993). Moreover, in the same geographic region (Central and NW Mediterranean sea), sandy and muddy bottom substrates have also been suggested as potential spawning areas for *L. vulgaris* (Sánchez et al., 2008; Valavanis et al., 2002). Conversely, gravel and rocky bottoms are preferred to spawn by another related species, *L. forbesi* (Smith et al., 2013).

Regarding to the second pattern found, *L. vulgaris* maximum spawning activity at ADs (May) occurred two months after the chlorophyll peak (March; Fig. 2.3). An increase in the number of egg clutches of *L. vulgaris* has previously been reported during periods of higher zooplankton abundance (Villa et al., 1997). At Cabrera National Park, after the primary production peak in March, the mesozooplankton biomass reaches maximum concentrations in May (Álvarez et al., 2012), suggesting that the spawning peak of squid (May) could be adjusted to maximize food availability (mesozooplankton) for paralarvae (Fig. 2.3). It has been suggested that the European squid is able to modulate the seasonal timing of reproductive effort (Arkhipkin, 1995; Guerra and Rocha, 1994; Moreno et al., 1994; Šifner and Vrgoč, 2004) according to the specific environmental conditions of different geographical areas (Boavida-Portugal et al., 2005; Moreno et al., 2002).

The European squid seems to show some spawning activity all-year-round (Šifner and Vrgoč, 2004) but temperature has been repeatedly related with the strength of the spawning activity (Pierce et al., 2008; Roberts, 1998; Sauer et al., 1991). However, *SST* alone had not a relevant effect on the temporal spawning pattern of *L. vulgaris* at Cabrera National Park. Conversely, the interaction between *SST* and *Depth* was clearly relevant. The relevant effect of this interaction is compatible with the existence of an offshore to inshore spawning migration during the coldest months. The outcome of such a migration would produce a spatial pattern similar to the one suggested by the model predictions (Fig. 2.5). *L. vulgaris* may spawn at deep waters throughout the year, but at cold months (when inshore waters reach lower temperature values), squid spawn in inshore waters. The hypothesis of inshore-offshore spawning migrations for the same species has been previously suggested by other studies in the Mediterranean Sea (Cabanellas-Reboredo et al., 2012b; Sánchez and Guerra, 1994; Tinbergen and Verwey, 1945; Valavanis et al., 2002). Additional but indirect evidence for the hypothesis of spawning migration emerges from the spatio-temporal pattern of fishing effort of the recreational squid jigging fishery (Chapters 4 & 5). Recreational squid fishing concentrates at inshore waters (20-35 m depth), but only during the cold season (Cabanellas-Reboredo et al., 2014a). Accordingly (Chapters 3 & 5), it has been suggested that the European squid seek spatio-temporal windows within which the sea temperature optimizes spawning success (Cabanellas-Reboredo et al., 2012a,b). Reproductive success seems to be maximized within a relatively narrow range of sea temperatures, which is 12 to 17°C for *L. vulgaris* (Villanueva et al., 2003), and such a narrow temperature range maximizes hatching success (Şen, 2005; Rosa et al., 2012). Therefore, depending on the sea temperature, squid may move from deeper waters to inshore waters. The existence of spawning migrations has been proposed for other Loliginid species; for example, *L. reynaudii* in South Africa, where the temperature is one of the main environmental variables involved in the inshore spawning migration of this species (Roberts, 1998; Sauer et al., 1991).

The second and third pattern described in this Chapter can be extrapolated to Palma Bay. This assumption is supported by the geographic proximity between two sampling areas (Palma Bay *vs.* CNP; around 45 Km).

Resource management of cephalopods has been performed with different measures such as a minimum legal size, the establishment of closed seasons, catch quotas and fishing power limitation (Augustyn and Roel, 1998; Boyle and Rodhouse, 2005; Otero et al., 2005; Pierce and Guerra, 1994; Rodhouse, 2001). However, perhaps due to their specific biological characteristics (very short life cycle, single lifetime breeding, and high

turnover rate of annual biomass; Boyle and Rodhouse, 2005), conventional management techniques have not worked appropriately with cephalopods (Pierce and Guerra, 1994), nor have been effective in preventing the acute decrease of some stocks in Galicia and elsewhere (Guerra et al., 2010). Another possible protection measure is to limit access to the resource by means of marine protected areas (MPAs). However, MPAs seem to be ineffective when protecting highly mobile species (Abecasis et al., 2013; Afonso et al., 2009; Claudet et al., 2010; Gerber et al., 2003; Kramer and Chapman, 1999; Nowlis and Roberts, 1999), which seems to be the case of *L. vulgaris* (Chapter 3; Cabanellas-Reboredo et al., 2012a). MPAs may still play a role in protecting the reproductive output of *L. vulgaris*, provided that they encompass appropriate spawning grounds. Recently, the protection of preferential reproductive EFHs for another cephalopod, *Octopus vulgaris*, was proposed as a management measure (Guerra et al., Submitted; Moreno et al., 2013b). In agreement with the results reported here, relatively small areas (e.g., those bounded by red circles in Fig. 2.1) could be especially favorable for spawning. Therefore, identifying and protecting these areas could enhance squid stock in places where it was necessary. However, as expected, most of the fishing effort is concentrated in these areas as well (Frontera et al., 1993) because fishermen are taking advantage of higher abundance and catches at EFHs. A compromise solution could be to protect EFHs only during the peak spawning in spring (spatio-temporal closure), but the trade-off between the short-term decrease in profit and long-term enhancement of the stock should be solved prior to suggest any specific measure.

The placement of artificial surfaces for cuttlefish spawning has been suggested to avoid egg loss (Blanc and Daguzan, 1998). However, ADs could promote egg laying at inappropriate sites. Therefore, after demonstrating that the availability of adequate substratum may be a limiting factor for squid spawning and that egg clutches laid on artificial structures are at least as successful as those laid at natural substrates, the usefulness of placing ADs at sandy bottoms could be explored as a complementary management measure, as it has already been implemented to improve spawning at degraded habitats (Hickford and Schiel, 2013).



## Chapter 3

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

### 3.1 Abstract

In the Western Mediterranean, the European squid *L. vulgaris* is exploited by both commercial and recreational fleet when it spawns in inshore waters. The inshore recreational fishery in the southern waters of Mallorca (Balearic Islands) concentrates within a narrow, well-delineated area (Chapter 4) and takes place during a very specific period of the day (sunset; Chapter 5). Another closely related species, *L. reynaudii*, displays a daily activity cycle during the spawning season (feeding at night and spawning in the day). In this Chapter, we tested the hypothesis that *L. vulgaris* could display a similar daily activity pattern using acoustic tracking telemetry. We conducted 2 acoustic tracking experiments during May to July 2010 and December 2010 to March 2011, in which a total of 26 squid were tagged. Our results suggested that *L. vulgaris* movements differ between day and night. The squid moved within a small area during the daytime but covered a larger area from sunset to sunrise. The probability of detecting squid was greatest at depths between 25 and 30 m. The abundance of egg clutches at this depth range was also greater than at other sampled depth. These patterns are in accordance with the “feeding at night and spawning in the day” hypothesis. This hypothesis also

explains the distribution of the recreational fishing effort using line jigging, both in time (at sunset) and in space (in the 20 to 35 m depth range).

KEY WORDS: Acoustic telemetry, Cephalopod, Daily activity cycle, Recreational fishing effort, Egg clutch distribution.



## 3.2 Introduction

Given the high socio-economical value of the squid *L. vulgaris* (Guerra et al., 1994; Moreno et al., 2013a; Ulaş and Aydin, 2011), most of the life-history traits of this species have been described in order to provide information for ensuring the sustainability of this resource (Guerra, 1992; Guerra and Rocha, 1994; Moreno et al., 2002, 2007; Šifner and Vrgoč, 2004). However, knowledge on the spatial and temporal patterns of habitat use by *L. vulgaris* is still scarce and remains elusive, despite the relevance of such knowledge for assessing and managing fishery resources (Botsford et al., 2009; Pecl et al., 2006).

One of the movement patterns that has potential outcomes on fishing success is the inshore-offshore seasonally periodical movement. This type of movement has been repeatedly described and related to reproduction and feeding cycles in other cephalopods (Boyle et al., 1995), and it has been suggested that *L. vulgaris* would display this pattern (Chapter 2; Cabanellas-Reboredo et al., 2014b; Sánchez and Guerra, 1994; Tinbergen and Verwey, 1945; Worms, 1983). Large individuals are abundant in shallow coastal waters, likely for mating and spawning; the new recruits appear to hatch near the coast and subsequently migrate towards deeper waters (Guerra, 1992; Sánchez and Guerra, 1994).

The outcome of such pattern is the development of a seasonal fishery for *L. vulgaris* when squid are abundant close to shore (Chapter 4 & Cabanellas-Reboredo et al., 2014a). Nearshore spawning aggregations of other Loliginid species are typically exploited using line jigging (Augustyn and Roel, 1998; Hanlon, 1998; Iwata et al., 2010; Postuma and Gasalla, 2010). In the case of *L. vulgaris*, in Mallorca (Balearic Islands) inshore aggregations of this species are mainly exploited using line jigging. This gear is extensively used by both commercial fleet and anglers (Cabanellas-Reboredo et al., 2011, 2014a; Guerra et al., 1994). Concerning the commercial fleet, squid are also sporadically captured using seines and trammel nets. In this two cases, squid is by-catch and not the targeted species itself (Cabanellas-Reboredo et al., 2011).

Commercial hand-line jigging typically takes place at fishing grounds located between 20 and 35 m in depth, at night, and with the use of lights. Anglers use line jigging at the same fishing grounds but only at sunset (Cabanellas-Reboredo et al., 2011, 2012b). The use of light is banned for the recreational fleet. However, anglers also fish for squid after sunset by trolling, between the shore and a depth of 10 m (Cabanellas-Reboredo et al., 2011, 2012b) close to the illuminated shore (by city lights) of Palma de Mallorca.

Acoustic tracking telemetry has been used to describe the movement patterns of other cephalopod species (Dunstan et al., 2011; Payne and O'Dor, 2006; Semmens et al., 2007; Stark et al., 2005) and to investigate the environmental cues of squid movements (Gilly et al., 2006). In addition, acoustic tracking has been used to describe the relationship between metabolic rate and behavior (Aitken et al., 2005; O'Dor, 2002; O'Dor et al., 1995) and to improve fisheries management (Pecl et al., 2006). The movement patterns during spawning aggregations of *L. reynaudii* and their relationship with environmental variability have been demonstrated by means of acoustic telemetry too (Downey et al., 2010; Sauer et al., 1997).

With this background, the specific goal of this Chapter was to use acoustic tracking telemetry i) to provide the first description of the movement of *L. vulgaris* during the inshore aggregations, ii) to relate the formation of inshore aggregation with some event of the squid life history (i.e., spawning), and iii) to relate such a movement pattern to the spatio-temporal distribution of the fishing effort (Chapter 4).

### 3.3 Material & Methods

#### 3.3.1 Experimental design

We completed 2 acoustic tracking experiments (ATEs) in the southern waters of Mallorca (Northwest Mediterranean; Fig. 3.1) covering the peak of the spawning period of the species which has been previously described in Chapter 2 (Cabanelas-Reboredo et al., 2014b; Guerra and Rocha, 1994; Šifner and Vrgoč, 2004). A preliminary study covering a wide spatial range (ATE<sub>1</sub>) was carried out between May and July 2010 (Fig. 3.1A) because no prior information on the extend of the movement was available for *L. vulgaris*. In accordance with the results obtained in ATE<sub>1</sub>, a second experiment (ATE<sub>2</sub>) was completed between December 2010 and March 2011 (Fig. 3.1B).

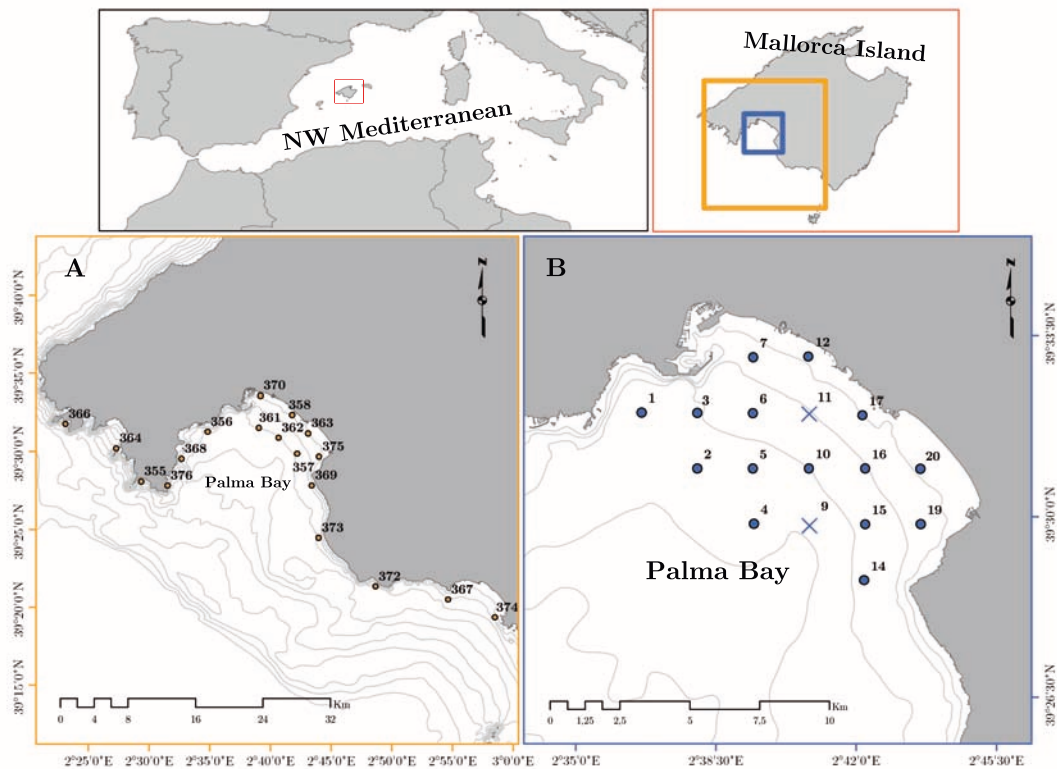


Figure 3.1: Receiver array deployed in (A) 2010 (acoustic tracking experiment 1, ATE<sub>1</sub>) and (B) 2011 (ATE<sub>2</sub>). ●, receiver locations; X, damaged receivers (no. 9 and 11). The isobaths each represent 10 m.

In both of experiments, an array of omni-directional acoustic receivers (Sonotronics<sup>©</sup> SUR-1) was deployed (Fig. 3.1). In ATE<sub>1</sub>, a widely distributed array along the South of the Island was designed to determine the broad scale of movements (Fig. 3.1A).

The distances between the receivers ranged from 2.6 to 8.9 km. The receivers were placed from 8 m depth (only 1 receiver) up to 30 m depth (Fig. 3.1A). A denser array covering only the main fishing grounds in Palma Bay was deployed during ATE<sub>2</sub> (Fig. 3.1B). The SURs were placed at the nodes of a 1 × Km grid and at depths ranging between 8 and 38 m (Fig. 3.1B). The number of receivers used was 18 during ATE<sub>1</sub> and 17 during ATE<sub>2</sub>. As the probability of detection may be a 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 3 different depths (10, 30, and 50 m) using control tags moored at prefixed distances from the receivers. Detection probability was assumed to follow a binomial distribution, and data were fitted to a generalized linear model (GLM, *glm* function in the R package). The three depth levels (10, 30, and 50 m) were considered as a categorical factors.

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

### 3.3.2 Acoustic tagging

In total, 26 squid were tagged (Table 3.1) and released inside the receiver array, with 6 individuals during ATE<sub>1</sub> and 20 during ATE<sub>2</sub> (Fig. 3.1). Most of the individuals ( $n = 23$ ) were tagged using the miniature tag IBT-96-2 (Sonotronics<sup>®</sup>; 25 mm in length; 9.5 mm in diameter; weight in water: 2.5 g; expected lifespan: 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 3.1). 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 (Alós et al., 2011; March et al., 2010, 2011).

The squid were caught at sunset using line jigging (Fig. 3.2A). Fishing and handling protocols (Gonçalves et al., 2009; O'Dor et al., 1995) minimized the stress and damage to the squid. The squid were immediately sexed, the dorsal mantle length (DML) was

Table 3.1: Tagged squid and tags used. ATE: acoustic tracking experiment. DML: dorsal mantle length. M: male; F: female. TP: period between the release date and last detection in days. DD: total number of days detected. All individuals were equipped with tag model IBT-96-2, except squid no. 112 (ATE<sub>1</sub>) and nos. 16 and 46 (ATE<sub>2</sub>). Tagged squid without detections during the experiments are shaded green (nd: no data for these squid). All of the females were fertilized.<sup>a</sup>This squid (highlighted in red) gave an almost constant number of detections during the 60 d of tracking. We assumed that it had died near receiver 6 just after it was released and did not consider it in the analysis.

	Squid code	DML (mm)	Sex	Tag frequency (Khz)	Tag interval (ms)	Tag & release date (dd/mm/yyyy)	Total detections	No. of receivers	TP (d)	DD (d)
ATE <sub>1</sub>	107	276	M	70	900	29/04/2010	nd	nd	nd	nd
	108-10	222	F	71	910	26/05/2010	409	2	22	8
	109-10	277	M	72	920	06/05/2010	nd	nd	nd	nd
	110	330	M	73	930	03/06/2010	1,104	1	10	6
	111	276	M	74	940	27/04/2010	1,204	2	31	13
	112	293	M	70	1040	20/05/2010	139	4	14	6
ATE <sub>2</sub>	2	217	F	70	860	04/01/2011	nd	nd	nd	nd
	3	205	F	71	890	14/01/2011	nd	nd	nd	nd
	4	223	F	72	880	04/01/2011	1,319	2	14	12
	5	205	F	73	910	18/01/2011	nd	nd	nd	nd
	7	193	M	75	930	24/01/2011	16	2	5	4
	8	215	F	76	920	05/02/2011	232	2	13	6
	9	240	F	77	950	19/01/2011	nd	nd	nd	nd
	10	205	F	78	940	24/01/2011	630	2	9	4
	11	230	M	79	970	19/01/2011	15	1	7	1
	16	250	M	69	1030	10/01/2011	nd	nd	nd	nd
	46	250	F	69	970	18/01/2011	2,378	2	14	13
	47	175	M	70	980	04/01/2011	378	4	17	6
	48	230	F	71	990	07/01/2011	nd	nd	nd	nd
	77	230	F	70	920	11/01/2011	491	1	2	2
	78	209	M	71	930	04/01/2011	nd	nd	nd	nd
	79 <sup>a</sup>	220	M	72	940	07/01/2011	5,7813	1	60	59
	107	193	F	70	900	13/01/2011	66	2	7	6
108-11	191	F	71	910	11/01/2011	66	2	4	2	
109-11	246	M	72	920	10/01/2011	nd	nd	nd	nd	
139	175	F	72	860	12/01/2011	388	2	4	3	

measured, and the squid were gently placed on a damp cloth where they were tagged (Fig. 3.2B & C). Sex was determined by observation of the hectocotylus (Ngoile, 1987). Fertilized females were identified by the presence of spermatophores, a small white spot in the ventral buccal membrane (Ngoile, 1987; Rasero and Portela, 1998). Tag losses were minimized by gluing 2 hypodermic needles laterally to the tips of the tag (Fig. 3.2D). This procedure secures the tag inside the squid's ventral mantle cavity (Downey et al., 2010). 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 (Downey et al., 2010; O'Dor et al., 1995; Fig. 3.2F). 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 thick part of the mantle and were secured on the outside of the squid with a silicon washer and metal crimps (O’Dor et al., 1995; Fig. 3.2G). The full process of biological sampling and tagging lasted <2 min. The tagged squid were placed into a 100 l seawater tank until they recovered and showed the typical fin beating and swimming. The squid were then released at the same location where they were captured (Fig. 3.2H).

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



Figure 3.2: Acoustic tracking logistics and methods. (A) Squid fished by line jigging. (B) Determination of squid sex and fertilization (in females). Inset details the presence of a spermatophore in the ventral buccal membrane (dashed oval). (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 tags. (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 loss of the transmitter. (H) Tagged squid in an open seawater tank on the boat. Inset shows the squid released in a tail-first direction favoring the output of air bubbles present in the mantle cavity.

### 3.3.3 Egg abundance

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. 3.2E). Squid uses to lay eggs on artificial devices (Chapter 2; Jereb and Roper, 2010). Therefore, the number of egg clutches were recorded and used as a proxy for the spatial distribution of spawning (i.e., for explaining the movement pattern found; see below)

This was an expected finding, given the demonstrated capability of similar structures to collect squid egg clutches (2). The number of egg clutches was used as a proxy of the spatial distribution of spawning. Nevertheless, the spatio-temporal spawning patterns were described in more detail at Chapter 2.

### 3.3.4 Data analyses

Data from the receivers were downloaded from the SURs as text files, and an appropriate MS Access database was developed to manage these 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  $h^{-1}$  (chronograms) was plotted for each squid. The day-specific timing of 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 (GLMM) was applied (Bates and 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, we assumed that they belonged to the same visit event when there was  $<1$  h between them. When the time between 2 consecutive detections was  $>1$  h, we assumed that they indicated 2 separate visit events. Similarly, when a squid was detected by 2 receivers, 2 independent visit events were assumed to occur. The visit events were categorized as either a detection peak ( $<4$  h between the first and last detection of the same visit event) or detection cluster ( $>4$  h 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 to 30 m depth were included in the GLMM, in an attempt to remove any effect of depth on the probability of detection. These receivers accumulated 97.83% of the visit events.

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 0 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 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 rejecting of the null hypothesis.

The number of detections and the number of egg clutches corresponding to different bathymetric depth intervals were compared using box plots. The number of depth 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 the R package and improved using ArcGIS.



## 3.4 Results

### 3.4.1 Detections

The results of the preliminary experiment aimed at exploring the effects of depth and distance to the receiver showed significant differences in the probability of detection among depths (probability increased with depth; GLM  $p < 0.001$ , Fig. 3.3).

This result was similar to those reported by Claisse et al. (2011). However, the distance at which probability of detection was 0.5 was similar when comparing the results obtained at 10 and 30 m depth (distance to receiver: 97 and 100 m, respectively; at 50 m depth, this distance increases to 120 m; Fig. 3.3). This result supported that despite some depth effects, the detection probability was virtually the same at low and intermediate depths. Additionally, given these results, the simultaneous reception of the same acoustic signal by more than 1 receiver was highly improbable.

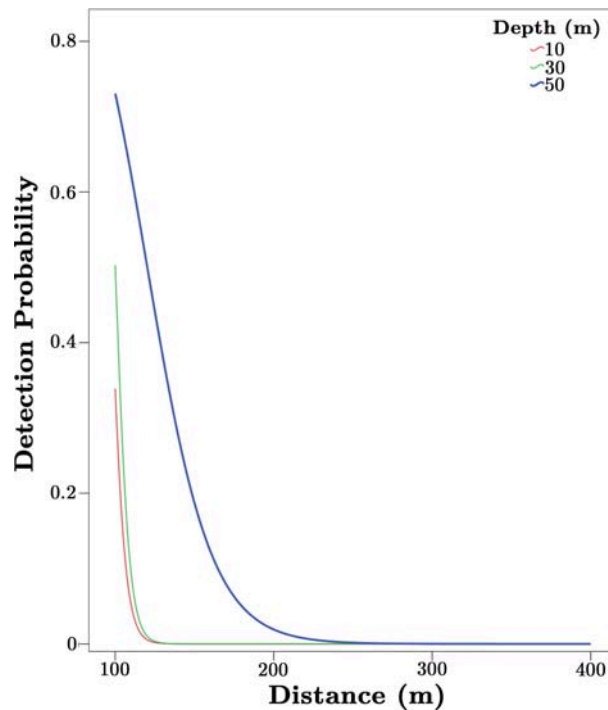


Figure 3.3: Detection probability against distance to the receiver at different depths obtained from the detection range test.

A total of 8,835 true detections from 15 squid, out of the 26 tagged individuals, were downloaded. The number of detections of each squid ranged between a minimum of 15 (squid 11) and a maximum of 2,378 for squid 46 (Table 3.1). The total period

(TP) 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 d (squid 111), mean  $\pm$  SD =  $11.53 \pm 7.73$  d. The number of days that a squid was detected (DD) varied from 1 (squid 11) to 13 d (squid 111 and 46), mean  $\pm$  SD =  $6.13 \pm 3.88$  d. The average number of receivers that detected the same squid was  $2.06 \pm 0.88$  and ranged from 1 (squid 110, 11, 77) to 4 (squid 112 and 47). Detailed data for all the squid are provided at Table 3.1.

### 3.4.2 Temporal pattern

A preliminary inspection of the time series of the number of detections per time unit did not reveal any clear pattern. However, the definition of the 2 types of visit event, detection peaks and detection clusters, demonstrates the existence of significant differences between day and night (GLMM  $p < 0.001$ , Fig. 3.4). 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. 3.4). 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 examples in Fig. 3.4). Moreover, new appearances, when a specific squid was detected by 2 different receivers within the same day, took place more frequently during the nighttime (squid 112 and 47; stars in Fig. 3.4).

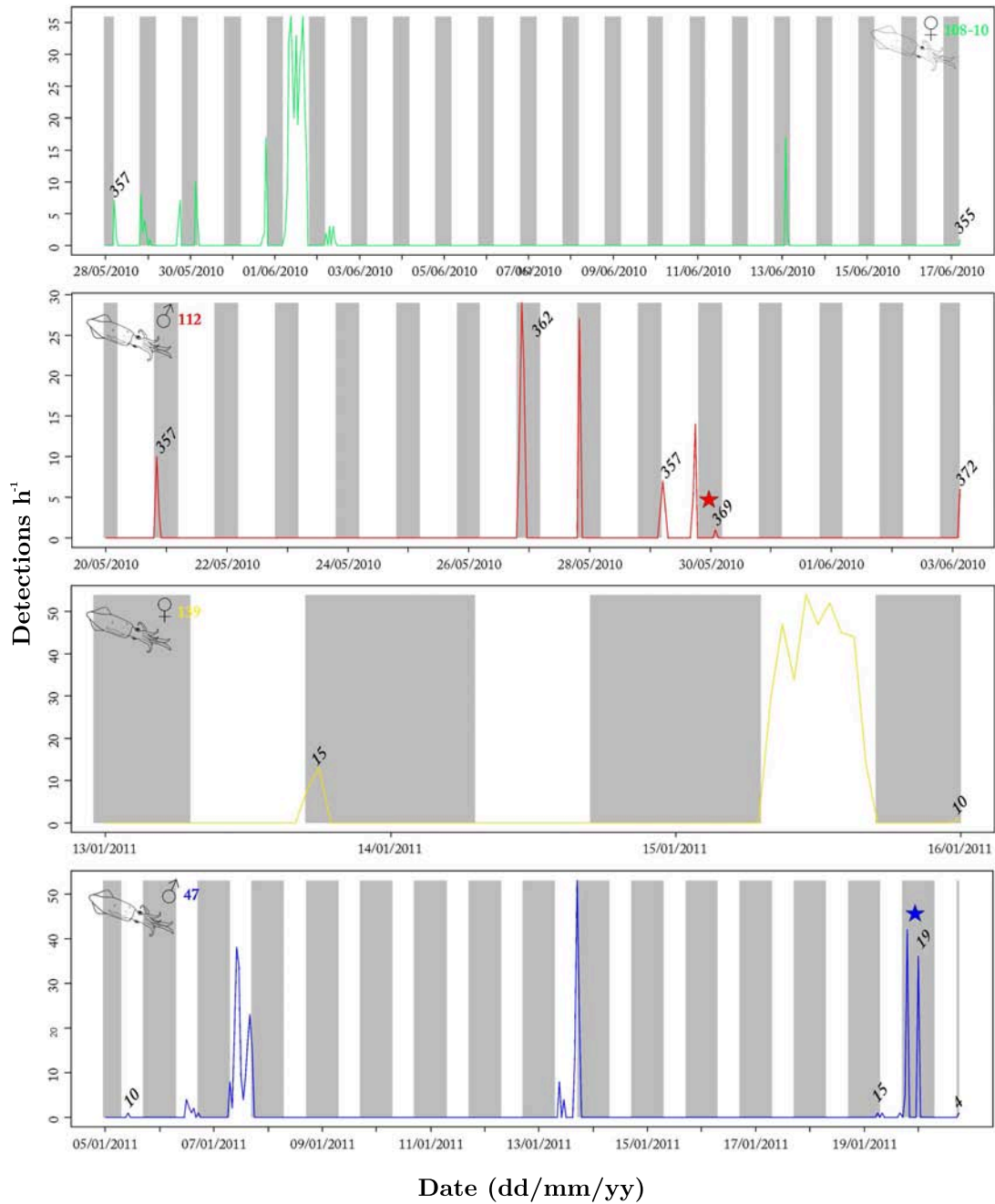


Figure 3.4: Full time series of the detections  $\text{h}^{-1}$  of 4 tagged squid from acoustic tracking experiment 1 (ATE<sub>1</sub>; squid 108-10 and 112) and ATE<sub>2</sub> (139 and 47). The vertical stripes represent day (white) and night (grey). On the x-axis, each mark indicates 00:00 h of each 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 2 different receivers within the same day.

### 3.4.3 Space use

As mentioned above, depth seems to affect the detection probabilities, thus our results must be interpreted with some caution. However, some patterns clearly emerge and seem robust against the effects of depth. The number of detections was higher between 25 and 30 m of depth (Figs. 3.5 & 3.6). All of the squid were detected at this depth range (some examples of squid tracks are shown in Fig. 3.5).

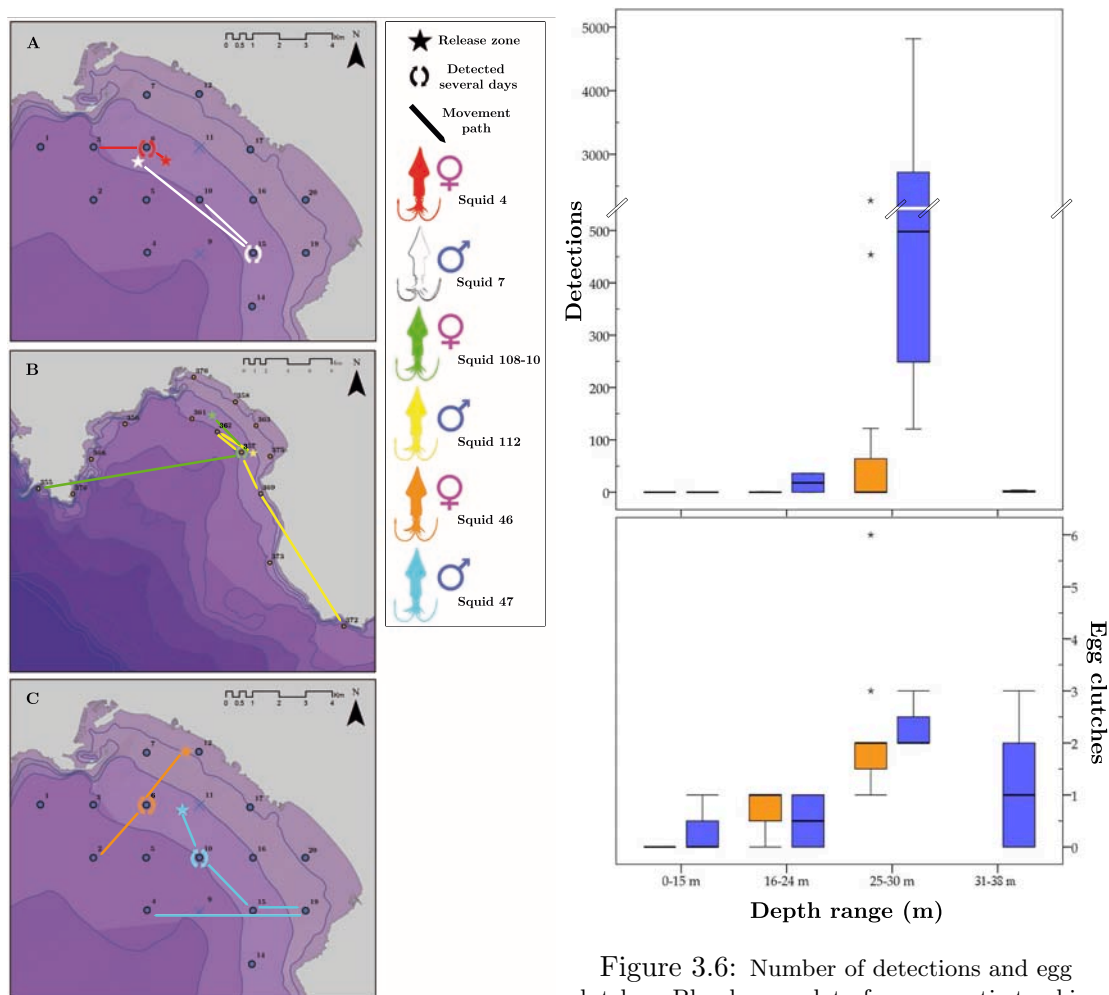


Figure 3.5: Squid tracks assuming the minimum distance traveled (Pecl et al., 2006). For symbols see Fig. 3.1 legend. (A) Squid nos. 4 and 7, (B) nos. 108-10 and 112, and (C) nos. 46 and 47.

Figure 3.6: Number of detections and egg clutches. Blue boxes: data from acoustic tracking experiment 1 (ATE<sub>1</sub>). Orange boxes: data from ATE<sub>2</sub>. No receivers were deployed in ATE<sub>1</sub> within the depth range of 31 to 38 m. Thick horizontal line = median, box = 25th to 75th percentile range, whiskers = 95% CI, asterisks = outliers.

Almost all (99.9%) of the detections during ATE<sub>1</sub> 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 to 30 m depth interval during ATE<sub>2</sub>. Squid 110, 11, and 77 were detected by only 1 receiver that was placed at a depth range of 25 to 30 m. Most of the remaining squid (80%) were also detected in this depth range. Nearly half of the squid moved between 2 closely located receivers, but in those cases, they remained within the 25 to 30 m depth area (53.33%; e.g., squid 4 and 7 in Fig. 3.5A). The longest travels were performed by squid 108-10 and 112. Squid 108-10 toured 22.85 km during 22 d. In the same way, squid 112 traveled 22.2 km during 14 d. These longer travels were also monitored by receivers deployed in the 25 to 30 m depth range (Fig. 3.5B). During ATE<sub>2</sub>, squid were also detected by both deeper (31 to 38 m) and shallower receivers (16 to 24 m). However, the prevalence of detections outside the 25 to 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 depth from receiver 15 at 27 m depth during the night but left shallow waters before sunrise, and it appeared again in deeper waters at sunset (receiver 4 at 37 m depth; see the grey star in Fig. 3.4 and the movement track in Fig. 3.5C).

No squid were detected by the receivers placed in shallower waters (0 to 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 caught, tagged, and released in shallower waters without being detected by the receivers deployed in this area. However, this squid was detected 1 d 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. 3.5C).

#### 3.4.4 Egg clutches

The presence of egg clutches was recorded from shallower waters (1 egg clutch at receiver 17, at 9 m depth) to deeper waters (3 egg clutches at receiver 9, at 38 m depth; Figs. 3.6). The number of egg clutches was small (mean  $\pm$  SD :  $0.25 \pm 0.5$ ; ATE<sub>2</sub> only) on the receivers placed in shallower waters (0 to 15 m). The receivers deployed at a depth interval between 16 and 24 m had mean values of  $0.67 \pm 0.58$  and  $0.5 \pm 0.71$  egg clutches per receiver for ATE<sub>1</sub> and ATE<sub>2</sub>, respectively. All of the receivers that were deployed between 25 and 30 m had at least 1 egg clutch. The mean number of egg clutches per receiver was clearly higher between 25 and 30 m ( $2.18 \pm 1.40$  and  $2.40 \pm 0.55$  for ATE<sub>1</sub> and ATE<sub>2</sub>, respectively). Finally, the receivers that were placed at a depth between 31 and 38 m (only deployed during ATE<sub>2</sub>) had  $1.17 \pm 1.17$  egg clutches attached to their

structures (Figs. 3.6).

### 3.5 Discussion

Our 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 2 well-differentiated movement states. The typical daytime movement is characterized by reduced mobility within a narrow area, hereafter referred as the day-ground. The squid tend to remain at a specific day-ground for a long time (most of the daytime of a specific day). 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 to 30 m of depth. The typical nighttime movement is characterized by increased mobility, i.e., a specific squid spends only a short time near any given receiver and moves over a wider area. Such a night-ground possibly covers most of Palma Bay. This diel pattern might be due to daily shifts between reproductive behavior during the day and feeding at night. The empirical evidence supporting this conceptual model emerges from i) the existence of day-night differences in the detection pattern using acoustic tracking, ii) the spatial distribution of egg clutches (present Chapter & Chapter 2), and iii) the spatio-temporal distribution of the fishing effort (Chapter 4).

The strongest evidence comes from the day-night differences in the detection pattern. When detected during the daytime, squid tended to remain near the detection range of only 1 receiver (detection cluster), supporting the hypothesis that the day-ground size is small. However, a specific squid was usually not detected on 2 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 to 30 m depth area of Palma Bay. According to these patterns, we suggest that the squid may be reproducing during the daytime. Evidence supporting this specific hypothesis also emerges from the fact that the same pattern (i.e., daytime reproduction) has been repeatedly described for other cephalopods. Previous studies demonstrated that during the daytime, *L. reynaudii* remains at the spawning grounds (Downey et al., 2010; Sauer et al., 1997), 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 (Forsythe et al., 2004; Jantzen and Havenhand, 2003; Sauer et al., 1997). A plausible and biologically sound expla-

nation is that reproductive behaviors in cephalopods are strongly mediated by visual cues (Hanlon and Messenger, 1996). Specifically, visually detectable body patterning plays an important courtship role during reproduction (Hanlon and Messenger, 1996; Hanlon et al., 1994, 1999, 2002). In fact, intraspecific signaling in squid is known to occur mainly during daylight hours (Hanlon and Messenger, 1996).

We also suggest that squid may be reproducing within a well-defined area. Evidence supporting this second hypothesis emerges from the spatial distribution of eggs clutches. In fact, other studies suggest that even though egg clutches of *L. vulgaris* have been observed at depths from 2 to 35 m, the clutches were more frequent between 20 and 30 m (Villa et al., 1997), very close to the 25 to 30 m depth area reported in this Chapter. This depth range is used by *L. vulgaris* for spawning during cold season (Chapter 2).

During the nighttime, the squid seems to be more mobile. The main empirical evidence supporting this statement is that when detected at night, the squid tended to remain for a short time near a specific receiver, producing 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 (Hanlon and Messenger, 1996; O'Sullivan and Cullen, 1983). Specifically, nocturnal feeding has been proposed from the results obtained by other acoustic tracking experiments (Downey et al., 2010; Sauer et al., 1997; Stark et al., 2005). The stomachs of *L. reynaudii* caught at night contained more food than those caught during the daytime (Sauer and Lipiński, 1991), supporting an increased predation activity during the nighttime.

Additional support for the conceptual model proposed here emerges from the spatio-temporal distribution of the recreational fishing effort (Fig. 3.7). The spatial aggregation of the fishing effort has been adduced as indirect evidence for the spatial distribution of squid (Boyle and Rodhouse, 2005; Olyott et al., 2007; Pecl et al., 2006). At the study site (Palma Bay), recreational fishing effort using line jigging concentrates between 20 and 35 m depth during the sunset (Chapter 4; Cabanellas-Reboredo et al., 2014a). We propose that recreational line jigging concentrates within this very narrow spatio-temporal window because squid catchability is higher (angler's catch-related motivation; Chapter 4). This hypothesis is based on: i) squid would concentrate during the daytime at 25 to 30 m depth to form spawning aggregations, and these aggregations probably break down at sunset due to a shift from a reproduction state to a feeding state (Downey et al., 2010), ii) squid probably feed during the nighttime, thus showing an increased interest for lures, iii) squid display a higher mobility during the nighttime, thus increasing the probability of encountering a lure, and iv) at sunset, sufficient light



enables the detection of the lures used in line jigging. Commercial (artisanal) fishers do not stop line jigging after dusk because they can use lights. Anglers may continue to fish after dusk, but only by trolling. The trolling method in shallower waters (from shore to 10 m depth) is performed by some anglers after finishing line jigging journey, but just at the illuminated strip near the city lights (Fig. 3.7). In accordance with our conceptual model, after dusk squid enlarge their space use from the 25 to 30 m depth area to a wider area that includes the trolling grounds. This pattern is exemplified by squid 47 (see Figs. 3.4 & 3.4C). We hypothesize that this squid remained in the 25 to 30 m area during the daytime but became vulnerable to line jigging only at sunset. This squid would also have been vulnerable to trolling after dusk, when it was detected at 16 m depth, close to the trolling zone.

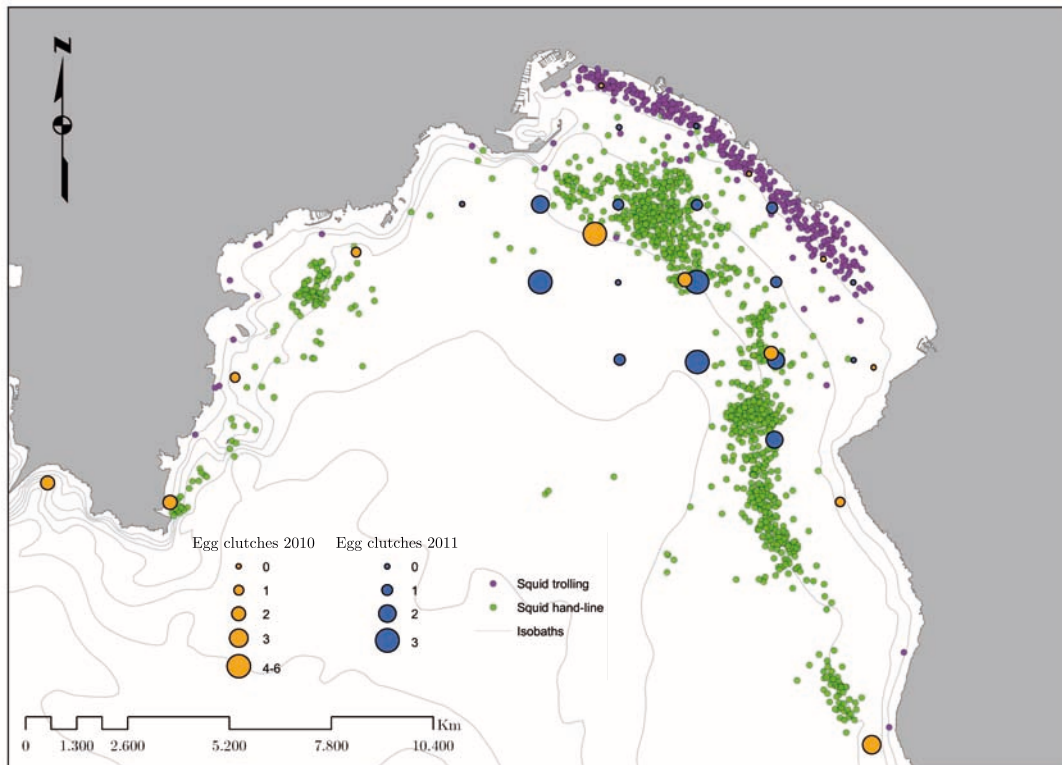
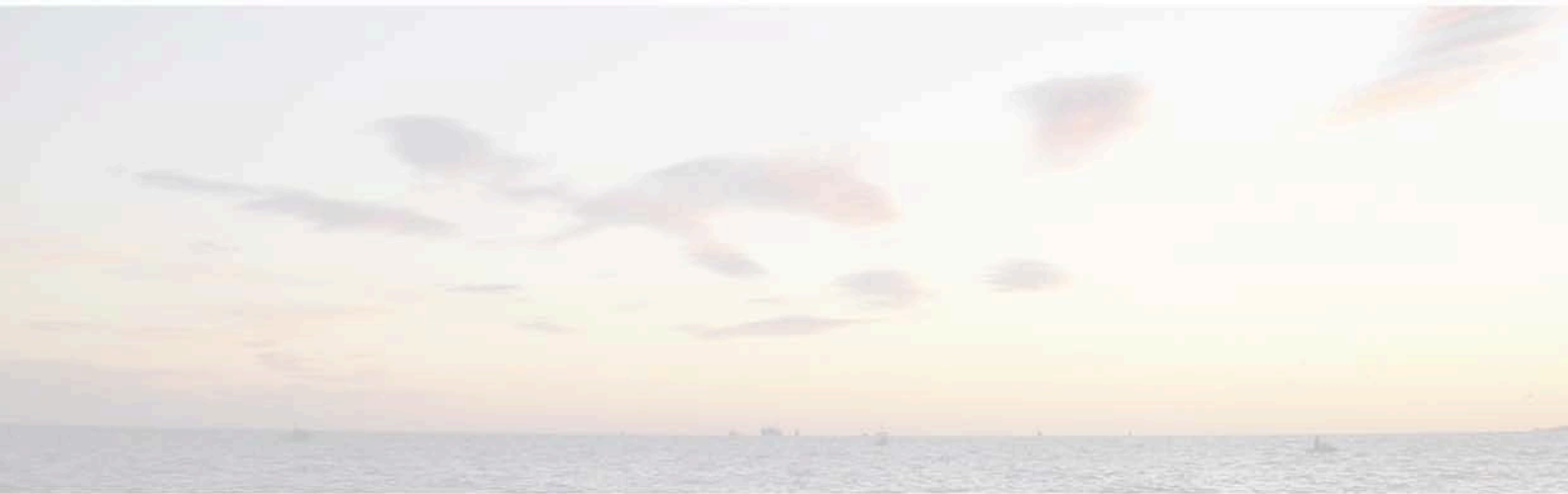


Figure 3.7: Spatial distribution of the recreational fishing effort (Chapter 4) and egg clutch abundance in Palma Bay, Mallorca. The isobaths each represent 10 m.



## Part III

# SOCIOLOGICAL ASPECTS





## Chapter 4

# Spatio-temporal distribution of recreational fishing effort

### 4.1 Abstract

Recreational fishing effort fluctuates in space and time. Therefore, one of the most relevant conceptual issues when managing recreational fishing is to understand the complexities associated with anglers' preferences in selecting site and day, and the way that these choices affect the catch. However, two practical pitfalls (data acquisition and statistical issues) are hampering progress towards the understanding of this problem. In this Chapter, we propose several strategic improvements and apply them to the recreational squid fishery in Palma Bay (Balearic Islands). The spatial scenario (20 km width) was surveyed 63 times (visual censuses) during two years. For each of the 173 grid cells (1 km<sup>2</sup>) into which Palma Bay was divided, the fishing effort (number of recreational boats targeting squid) was recorded. In addition, a number of variables intended to summarize any potential driver of anglers' choice were also recorded. The main drivers of squid recreational fishing in Palma Bay appeared to be the expected harvest and the distance to the nearest port, but the effect of these variables was clearly modulated by sea conditions. The fine-scale estimates of effort (daily predictions for each 1 km<sup>2</sup> cell) provided in this Chapter represent the first step towards understanding angler preferences, estimating total catches, and selecting the best management options for avoiding conflicts between stakeholders, thus ensuring resource sustainability.

KEY WORDS: Angler preferences, Fishing effort, Fishing quality, Hierarchical Bayesian model, *Loligo vulgaris*, Spatio-temporal analysis.

## 4.2 Introduction

The study of the for reasons for which anglers go fishing is fundamental for a better understanding of the heterogeneity of angler behaviour and the effects of this heterogeneity on catches. Accordingly, this topic has been extensively explored (Arlinghaus, 2006; Ditton, 2004). However, where and when anglers go fishing, i.e. the spatial and temporal distribution of recreational fishing effort, have received less attention (Hunt, 2005; Hunt et al., 2011), especially in the case of marine recreational fishing (Lynch, 2006; Parnell et al., 2010; Veiga et al., 2010). Nevertheless, this topic is relevant because understanding the spatial and temporal components of fishing effort has been widely demonstrated to improve the success of management decisions in the case of commercial fisheries (Lorenzen et al., 2010; Poos and Rijnsdorp, 2007). Recreational fisheries are rarely managed based on the same assessment methods used for commercial fisheries (Morales-Nin et al., 2010), but even when these methods are used in recreational fisheries management, management decisions are based on population dynamics models that may incorporate fishing effort but typically assume that both effort and fish abundance are spatially homogeneous (Lynch, 2006). However, although the spatial and temporal dimensions of the processes driving the spatial patterning of effort have been ignored, management measures often involve spatial and temporal restrictions (e.g., marine protected areas or seasonal closures; Morales-Nin et al. 2010). As a result, management measures can be inconsistent and can create conflicts between stakeholders (e.g., commercial fishers *vs.* anglers) because access to valued ecosystems, localities and stocks is prohibited or heavily curtailed (Coleman et al., 2004a; Cox et al., 2003; Granek et al., 2008; Salz and Loomis, 2005). Nevertheless, the complexities of anglers' preferences in selecting a site and a day for fishing continue to be poorly known and have been considered only rarely in analyses of marine recreational fishing (Parnell et al., 2010).

This gap is due to not only the complexities of anglers' preferences but also to the difficulties of obtaining, analysing and interpreting effort data for marine recreational fishing.

Data acquisition is more problematic for recreational than for commercial fishers. In the case of commercial fisheries, the mandatory use of tracking devices, such as vessel monitoring systems, has notably improved the knowledge of the spatial distribution of fishing effort (Bertrand et al., 2008; Gerritsen and Lordan, 2011; Mills et al., 2007). However, these systems have rarely been implemented in recreational fisheries. To solve this gap, alternative observational surveys, such as visual censuses, aerial counts

and interviews, have been developed (Fraidenburg and Bargmann, 1982; Smallwood and Beckley, 2012; Veiga et al., 2010). However, these alternative methods are expensive in terms of personnel and equipment and are especially difficult to apply in marine environments, where anglers can be distributed over tens of nautical miles. Despite several interesting attempts to minimize survey costs (e.g., monitoring fishing effort from the coast with photographic time-series; Parnell et al. 2010), the lack of an efficient, cost-effective and widely applicable method limits surveying marine recreational fishing effort (Parnell et al., 2010).

The second handicap, data analysis, is technical and related to the inherent non-independence of the data. For example, the number of anglers at neighbouring sites tend to be more similar than expected (i.e., spatial autocorrelation; Dormann et al. 2007). A variety of statistical methods have been developed to correct for the effects of non-independence but they apply only to relatively simple cases and if a number of implicit assumptions are met. In the case of fishing effort, in addition to spatial structure, the response variable is expressed as counts (number of anglers) with large numbers of zeros. Such zero-inflation (Zuur et al., 2009) typically emerges if the response variable is affected by hierarchical processes. In our case, the expected number of anglers in a site may be relatively large according to, e.g. fishing quality, but no anglers may be found because of bad weather. Hierarchical Bayesian models are especially suitable for addressing such type of processes (Viana et al., 2013).

However, angler behaviour itself is the core problem. An angler's decision is not only motivated by complex combinations of variables but also involves a substantial stochastic component (Arlinghaus et al., 2013). As a result, the predictive capability of oversimplified models may be limited. One of the possible alternatives available for improving model performance is to apply analytical strategies borrowed from animal ecology. Specifically, the ideal free distribution (IFD, a distribution that matches resources and foragers; Fretwell and Lucas Jr. 1970) could provide a suitable framework for describing how anglers should be distributed in space to harmonize the between-patch catch rate with the spatial pattern of prey abundance (Gillis and vanderLee, 2012). However, empirical data from commercial fisheries strongly suggest that the spatial distribution of fishers does not fit an IFD (Gillis and Peterman, 1998; Matsumura et al., 2010; Poos and Rijnsdorp, 2007). This departure is plausibly related to the effects of other concomitant variables not directly related to catch, such as cost, imperfect information on prey distributions, or interference among fishers (Matsumura et al., 2010; Poos and Rijnsdorp, 2007). The inadequacy of the ideal free distribution is also arguable in the case of recreational fisheries because many factors in addition to

catch expectation affect anglers' choice (Hunt et al., 2011).

Recently, the possible drivers affecting the choice of a site and a day by anglers have been revised and classified in terms of six broad types or attributes: i) *Fishing quality*, ii) *Costs*, iii) *Facility development*, iv) *Environmental quality*, v) *Interactions among anglers*, and vi) *Regulations* (Hunt, 2005). Therefore, we propose to use a correlational approach based on the conceptual framework proposed by Hunt (2005) as an alternative strategy for identifying the main drivers of the number of anglers in a given time and area unit. This correlational approach was applied to the recreational squid fishery at the Palma Bay. The approach we propose divides Palma Bay into a grid of 173 cells (each 1 km<sup>2</sup>). The fine-scale estimates (daily predictions of effort for each 1-km<sup>2</sup> cell) provided by the model constitute the first step towards estimating not only total (annual) catches but also for understanding their spatio-temporal patterns. In addition to offering new insights into the conceptual relationship between effort and its potential drivers (thus, understanding angler preferences), the modelling approach adopted in this Chapter has immediate usefulness for managers. This information may be used for selecting the best management options, avoiding conflicts between stakeholders (especially between commercial fishers and recreational anglers; Morales-Nin et al. 2010) and ensuring resource sustainability.



## 4.3 Material & Methods

### 4.3.1 Sampling recreational fishing effort

This study was conducted at Palma Bay (Fig. 4.1).

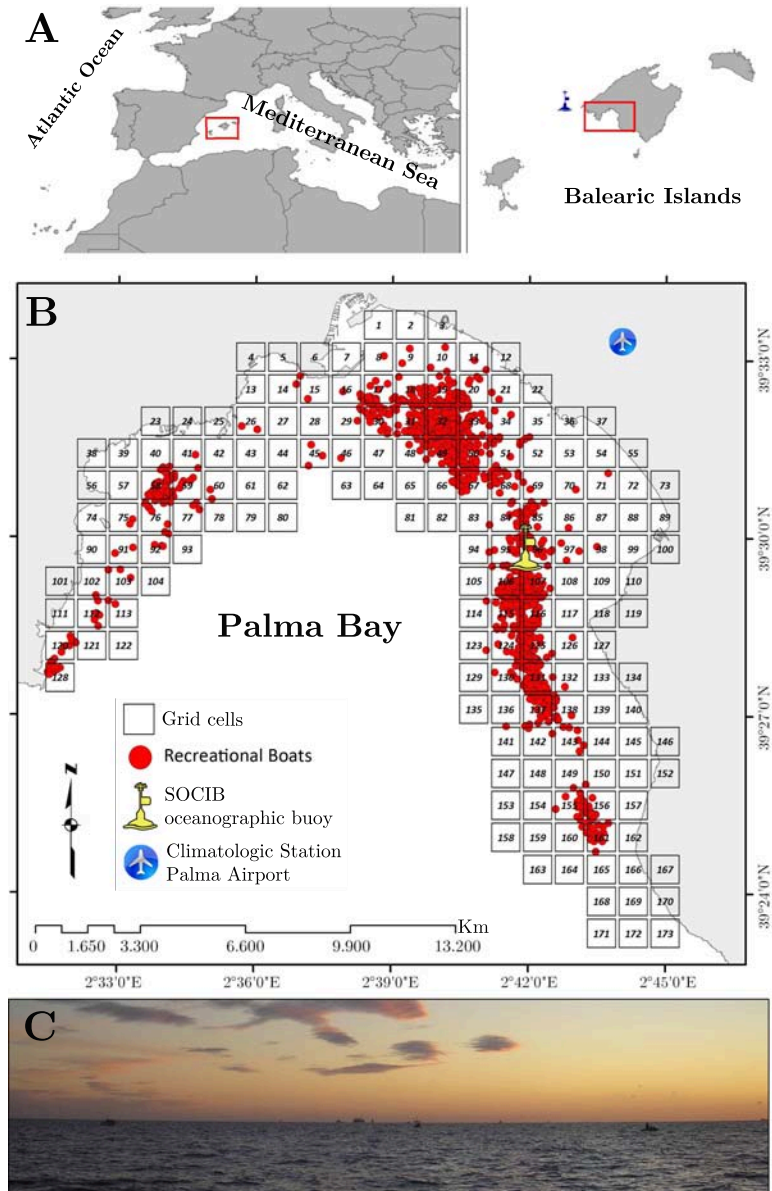


Figure 4.1: Study area: (A) location of the study area. Blue icon represents the location of the oceanographic buoy supported by the Spanish government (Puertos del Estado; Dragonera Bouy). (B) Grid of  $173 \times 1 \text{ km}^2$  cells into which the geographic area was divided for the study. The red points (1271) are the boat positions pooled across 63 visual censuses. (C) Example of the recreational boats observed during a visual census.

A total of 63 visual censuses of Palma Bay were completed. The entire study area was surveyed from a research boat, and the geographic coordinates of any recreational boat targeting squid were recorded with a Garmin 72<sup>®</sup> GPS. The spatial extent of the survey was defined based on previous knowledge of the general distribution of the recreational fleet (Fig. 4.1B). Visual censuses were completed between January 2009 and December 2010 (1-3 censuses per month) on randomly chosen days (except that days were stratified by business and non-business days; McCluskey and Lewison 2008). On average, a new census was completed every 11 days. Therefore, censuses were assumed to be temporally independent.

The typical fishing journey is relatively short (2-3 hours), starting 1-2 h before sunset and continuing until 1 h after sunset (Chapter 5; Cabanellas-Reboredo et al. 2012b). Each visual census required 1.5 h to be completed. The censuses started 1 h before sunset, thus they covered the period of maximum fishing activity. This strategy minimized the probability that some boats remained uncounted or were counted more than once.

The spatial framework was defined in terms of a grid of 173 cells of 1 km<sup>2</sup> (Fig. 4.1B). The cell size for this scenario was selected based on a trade-off between obtaining the highest spatial resolution, ensuring within-cell homogeneity and minimizing spatial autocorrelation (Section 4.3.3.2). The response variable for the following analyses was the number of recreational boats in a cell ( $Boats_{ij}$ , where  $i$  ranged from 1-173 cells and  $j$  ranged from 1-63 days).

Despite this Chapter focuses only on the recreational line jigging modality, the spatial distribution of boats using another recreational modality (trolling; Chapter 1) was determined using the same sampling strategy (15 visual census but at nighttime). The spatial distributions of the fishing effort of the 2 recreational fishing methods, line jigging and trolling, were mapped.

### 4.3.2 Predictors of recreational fishing effort

For each statistical unit (cell-day), a number of potential predictor variables were collected or estimated as surrogates of the six attributes described by Hunt (2005): *Fishing quality*, *Costs*, *Facility development*, *Environmental quality*, *Interactions among anglers*, and *Regulations*. Note, however, that in certain cases the variable that was actually measured may be related to more than one attribute.

Because the direct measurement of *Fishing quality* is difficult, several proxies have been proposed (Hunt, 2005). In our case, data on squid abundance are not available

at the spatio-temporal scale needed. However, the Catch Per Unit of Effort (CPUE) of recreational squid anglers has a clear seasonal pattern because it is correlated with sea temperature (Chapter 5; Cabanellas-Reboredo et al. 2012b). Moreover, the movement pattern of squid (as revealed by acoustic tracking; Chapter 3 & Cabanellas-Reboredo et al. 2012a) maximizes the probability of encounter with anglers at 25-30 m depth. Therefore, we used the combination of *Depth* and *Sea-bottom temperature* as an indirect proxy for *Fishing quality*. In terms of *Costs*, we used the distance to the nearest harbour (*Port distance*) as a surrogate for travel cost. Regarding *Facility development*, this attribute is represented, for example by the number of port, marina services, boat launches or campground facilities (Hunt, 2005). However, the geography of Palma Bay and the large number of ports and marinas implies that the effect of the availability of these services partially matches with the distance to the nearest port. Therefore, *Costs* and *Facility development* may be confounded in Palma Bay. A completely different approach is to consider the availability of free time as a surrogate of *Facility development*. Therefore, the variable *Holidays* (business *vs.* non-business days) was selected because non-business days offer more logistical facilities to the anglers for fishing; therefore, holidays may be preferred for fishing (McCluskey and Lewison, 2008).

In freshwater ecosystems, *Environmental quality* has been approximated, for example, by water quality (Hunt, 2005). In our case, *Benthic habitat* (presence *vs.* absence of *Posidonia oceanica* meadows) was selected because the presence of this seagrass is a recognized index of good environmental quality and ecosystem health (Montefalcone, 2009). The attribute *Interaction among anglers* was indirectly considered when dealing with to spatial autocorrelation (see below Section 4.3.3.2). The rationale for this selection is that the number of boats observed in a cell when the spatial distribution is contagious, is greater than expected if the number of boats in the neighbouring cells is high. In terms of *Regulations* attribute, we selected the variable *Reserve* (fishing within *vs.* outside the limits of a marine protected area, MPA). In our study area, an MPA extending from the coastline to a depth of 30 m has been enforced since 1982, and recreational fishing is allowed in the MPA under certain restrictions (seasonal and daily closures, species, fishing modalities and fishing gear sizes). Although recreational squid fishing using jigging is allowed (Morales-Nin et al., 2010), this variable was included since ignorance of the regulations could play an important role in anglers' behaviour (Johnston et al., 2010, 2011).

Finally, Hunt (2005) emphasizes the potential effects of weather and, more generally, environmental pressure on anglers' decisions about when and where to fish. Consequently, *Sea condition* (wave height) was included as a potential explanatory variable

for anglers' decisions.

### 4.3.3 Data analyses

The data were modelled with both inferential (i.e., to determine which of the explanatory variables listed above are correlated with the observed number of boats) and predictive purposes (i.e., to estimate the expected number of boats in some relevant scenarios). Note that, as mentioned above, the effects of sea condition operates at a different level than the effects of the other variables (i.e., the expected number of boats may be high but all boats would remain at port because of bad weather). The Bayesian approach is especially suitable for analysing this type of complex hierarchical model (Viana et al., 2013). In addition, the sampling design imposes an additional modelling complexity. Logistical constraints demand that all cells of the scenario should be sampled on the same day. Therefore, these observations may all be affected in the same way by some unknown circumstance not included in the model. Cells sampled on the same day are not independent observations, and non-independence of observations may severely affect inference. Non-independence may be circumvented by grouping all cells sampled on the same day and estimating a common random effect. In our case, non-independence of the statistical units (cell-day) was circumvented by including three different random effects that account for: i) between-census heterogeneity, ii) between-cell heterogeneity, and iii) spatial autocorrelation.

#### 4.3.3.1 Predictive variables

Raw data for the predictive variables were obtained from diverse sources and are at different spatial scales. Therefore, the input data for the analyses were first prepared with R package (*raster* library; Hijmans and van Etten 2012) and ArcGIS 9.2 (ESRI) to fit the raw data to a common statistical unit (cell-day).

For fixed explanatory variables, *Sea-bottom temperature* (*SBT*; Fig. 4.2A) was obtained from a Regional Ocean Modelling System (ROMS) applied over the western sector of the Mediterranean Sea with a horizontal resolution of 2 km<sup>2</sup> (Tintoré et al., 2012). The model output was found to be highly correlated ( $r^2 = 0.94$ ) with empirical data from the Balearic Islands Coastal Observing and Forecasting System (SOCIB) oceanographic buoy located within the study area (Fig. 4.1b).

For *Depth* (*D*), a multilevel B-spline interpolation algorithm (library *MBA* from R package; Lee et al. 1997) was applied to point-data sounding from nautical charts (Marine Institute of Hydrography, 1:25 000) to obtain the digitized bathymetry of the

study area (Fig. 4.2B).

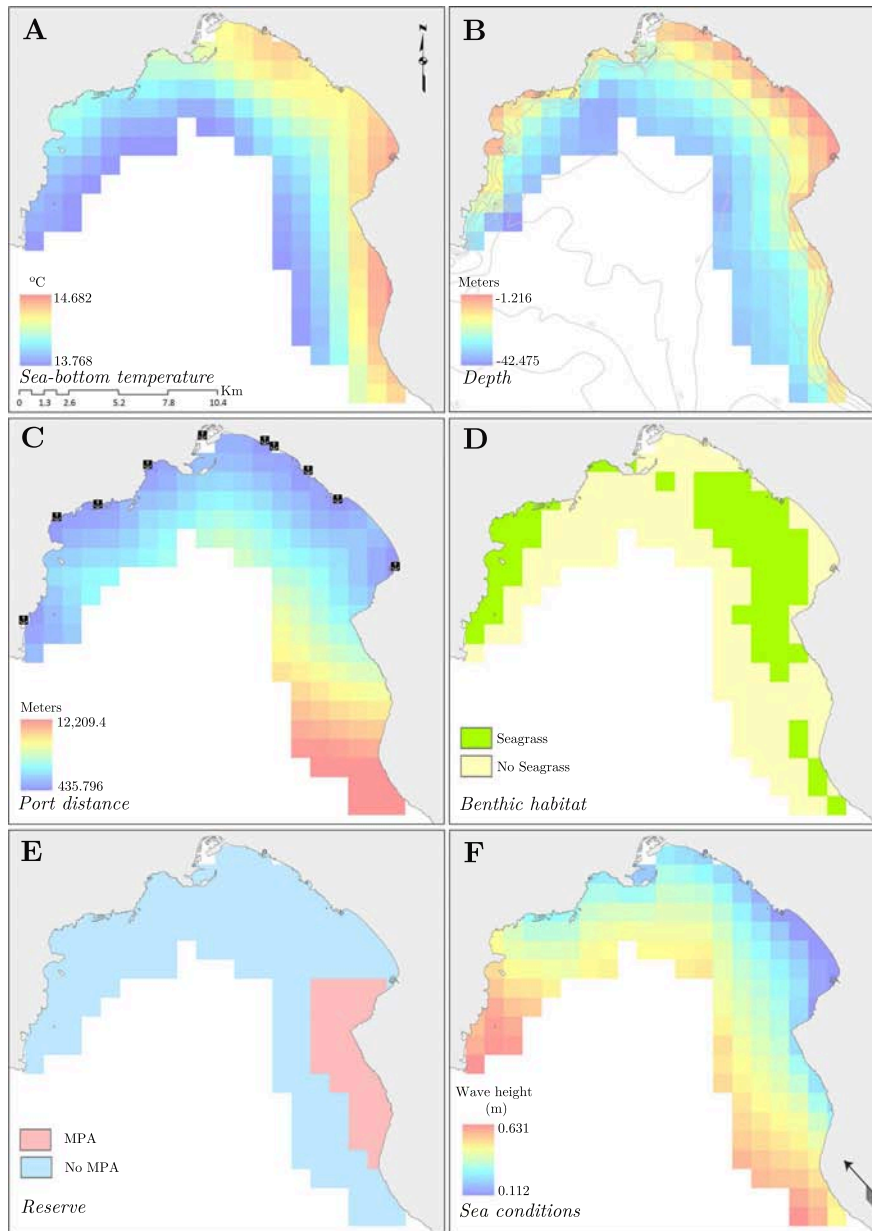


Figure 4.2: Potentially explanatory variables considered: (A) *Sea-bottom temperature* of a specific sampling day (31 March 2010). (B) *Depth* (10-m isobaths). (C) *Port distance* (harbours indicated by an anchor symbol). (D) *Benthic habitat*. (E) *Reserve*. (F) an example of *Sea condition* for a given day (wave height; the arrow indicates the wind direction).

The distance (*Port distance, PD*) from the midpoint of each cell to the nearest port was calculated using the Spatial Analyst extension of ArcGIS 9.2 (ESRI) (Fig. 4.2C).

Cell-day units were categorized as business *vs.* non-business to obtain the categorical variable *Holidays* ( $H$ ).

To obtain *Benthic habitat* ( $BH$ ; Fig. 4.2D), we combined a recently available seagrass map produced with a drop-camera system (March et al., 2013) with a benthic map of the MPA (Posidonia-LIFE map; <http://lifeposidonia.caib.es>). The combined map was used to define the most widespread bottom type (seagrass *vs.* no seagrass) in each of the cells considered.

The categorical variable *Reserve* ( $R$ ; Fig. 4.2E) simply defines whether a cell is inside or outside the MPA and was constructed using the Spatial Analyst extension of ArcGIS 9.2 (ESRI).

For *Sea condition* ( $SC$ ), the daily average wave height, with a spatial resolution of 1 km<sup>2</sup>, was obtained (Fig. 4.2F) using the following approach. First, the spatio-temporal variability of wave height was characterized with a principal component analysis (PCA) of the output from an operational wave model (<http://www.socib.es/?seccion=modellering&facility=sapo>). The two first modes explained 98% of the variance. These data were only available from September 2011 to March 2012 and did not fully cover the sampling period. So, for the sampling period the temporal amplitude of those modes were obtained through a multiple linear regression with local winds measured at the Palma airport (Fig. 4.1B) and wave height outside the bay, at the Dragonera buoy (Fig. 4.1A). This model was validated with observations inside the bay (SOCIB Buoy; Fig. 4.1B), resulting in a correlation of 0.79 and a root-mean square error (RMSE) of 0.2 m. Details of this model are provided at Appendix A.

#### 4.3.3.2 Hierarchical Bayesian model

Modelling count data (i.e., number of boats in a cell-day) is usually performed assuming a Poisson distribution, but this assumption is rarely met because i) the mean and variance must be the same, which rarely occurs in practice due to the omnipresence of overdispersion (Neyens et al., 2012), and ii) observations in adjacent cells are assumed to be independent, which can be unrealistic. Different modelling approaches have been proposed to circumvent these problems (Neyens et al., 2012). From these approaches, we selected a Conditional AutoRegressive (CAR) convolution model (Lawson et al., 2000), with certain modifications due to the specific characteristics of the case study (Fig. 4.3).

The number of boats observed in the  $i^{th}$  cell of the  $j^{th}$  census ( $Boats_{ij}$ ) was assumed

to be Poisson distributed:

$$Boats_{ij} \sim \text{Poisson}(\mu_{eff_{ij}}),$$

where the expected effective mean number of boats ( $\mu_{eff_{ij}}$ ) is the product of two components (Fig. 4.3): the probability that a boat goes fishing given specific *Sea conditions* ( $p_{ij}$ ) and the expected mean number of boats given the weather-independent variables ( $\mu_{ij}$ ). We modelled  $p_{ij}$  as a logit function of *Sea conditions* ( $SC$ ):

$$\text{Logit}(p_{ij}) = \alpha_{SC} + \beta_{SC} SC_{ij}.$$

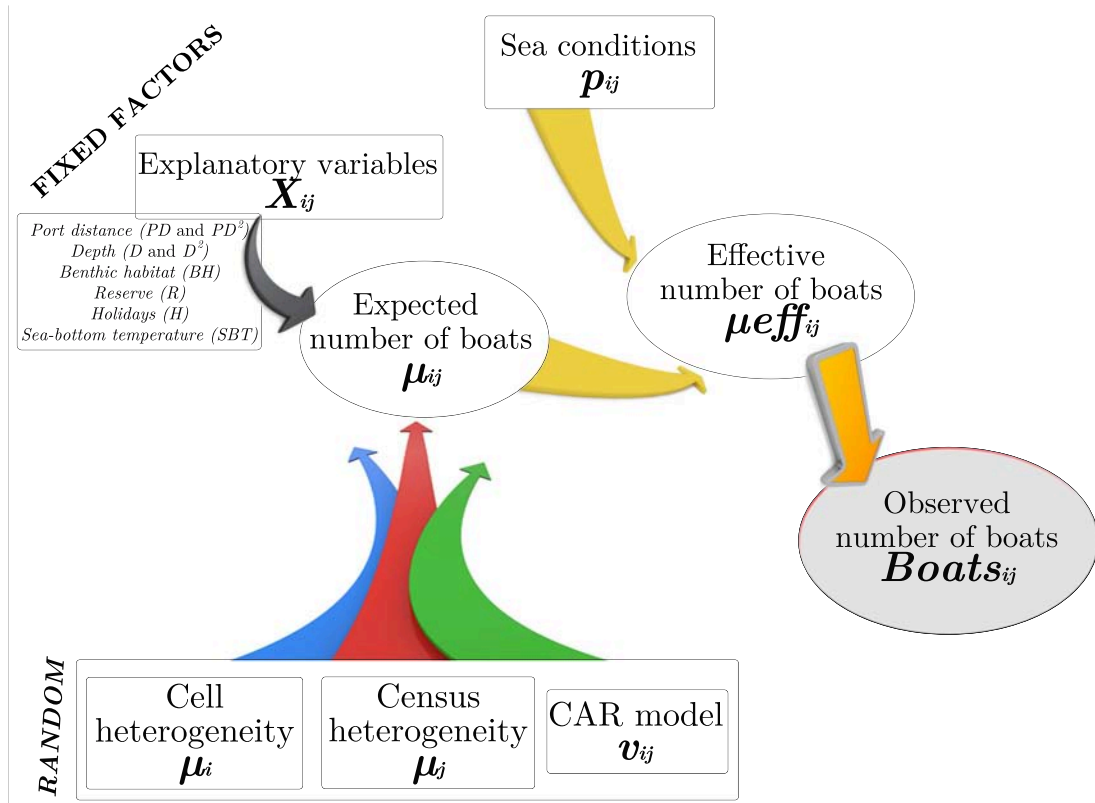


Figure 4.3: Directed acyclic graph of the hierarchical Bayesian model implemented. The subindices  $i$  and  $j$  indicate cell and day, respectively.

The expected mean number of boats ( $\mu_{ij}$ ) was given by:

$$\log(\mu_{ij}) = \alpha_0 + X_{ij}^t \beta + u_i^{cell} + u_j^{census} + v_{ij},$$

where  $\alpha_0$  represents the grand mean and the second term is a linear combination of the fixed factors:

$$X_{ij}^t \beta = \beta_1 PD + \beta_2 PD^2 + \beta_3 D + \beta_4 D^2 + \beta_5 BH + \beta_6 R + \beta_7 H + \beta_8 SBT.$$

Note that, based on previous inspection of the raw data, two quadratic terms have been added to accommodate possible non-linear (i.e., unimodal) effects of distance to the nearest port ( $PD$ ) and  $Depth$  ( $D$ ) that would be related to the existence of an optimal value around which the number of expected boats would decrease. The remaining variables were *Benthic habitat* ( $BH$ ), *Reserve* ( $R$ ), *Holidays* ( $H$ ), and *Sea-bottom temperature* ( $SBT$ ).

Two unstructured random effects were considered to accommodate the overdispersion related to cell ( $u^{cell}$ ) and census ( $u^{census}$ ) specificities. Cell heterogeneity refers to specificities of the  $i^{th}$  cell across all censuses that are not modelled by the fixed variables listed above. Similarly, census heterogeneity refers to a random effect affecting all cells of the same census. In both cases, these random effects were assumed to be normally distributed, with zero mean and variance  $\sigma_{cell}$  and  $\sigma_{census}$ , respectively:

$$u \sim Normal(0, \sigma).$$

Finally,  $v_{ij}$  represents the spatially correlated heterogeneity, which is assumed to follow a CAR model (Besag and Kooperberg, 1995):

$$v_{ijk} | v_{jk, i \neq jk} \sim Normal(\bar{v}_{ij}, \sigma_{ij})$$

$$\bar{v}_{ij} = \frac{\sum_{k=1}^N w_{ik} v_{ijk}}{\sum_{k=1}^N w_{ik}},$$

where the element of the weight adjacency matrix ( $w$ ) was set to 1 only for the four cells sharing a common side with cell  $i$ , and to zero otherwise. Note that this term only includes the observations within the same day. The magnitude of the variance associated with this term was also used for indirectly assessing the magnitude of the *Interactions among anglers*, but it was used at the between-cell spatial scale only because interactions at smaller scales cannot be considered with this analytical approach.

The parameters of this model were estimated using a Bayesian approach, which is especially suitable for hierarchical models (Clark, 2007).

The occurrence of an identifiable effect of any putative explanatory variable was evaluated based on 95% Bayesian credibility intervals (CI) for  $\beta$  (and whether these



intervals included zero). The model was fitted using the Bayesian machinery as implemented in WinBugs (<http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.Q5shtmlv1.4>) and using the *R2WinBUGS* library v2.1-18 (Sturtz et al., 2005) from the R package (<http://www.r-project.org/v2.15-2>). Uninformative, virtually flat priors were used in all cases. In the case of the random effect for spatial autocorrelation, the built-in *car.normal* distribution was used. Conventional tools were used to assess the proper mixing of the Markov chains Monte Carlo (MCMC) run in each analysis, the convergence of the algorithm and the lack of autocorrelation by adjusting the burning interval, the thinning interval, the number of chains and the valid sample size.

Note that the rawdata consisted of 63 censuses 173 cells, or 10,899 rows. Therefore, a single run of this model may require several days. Therefore, no attempts at variable selection or cross-validation were made. However, the estimated and observed values were compared in order to identify any bias. The model parameters were used to simulate 100 sets of expected numbers of recreational boats, and the means of these simulated numbers were compared with the observed numbers. Temporal bias was assessed by pooling the expected values of all cells in a census (63 censuses), and spatial bias was assessed by polling the expected values of all censuses for a given cell (173 cells). In addition, the residuals (observed-expected values) after spatial pooling were mapped to discard any spatially structured trend.

To better visualize the relevance of variables for which an identifiable effect was demonstrated, partial effects were estimated using Monte Carlo simulations. The specific effects of each one of these variables were simulated in turn while the remaining variables in the model were kept constant. The constant values selected for simulating the expected number of boats were as follows: outside the MPA ( $R$ ), on a seagrass meadow ( $BH$ ), in a business day ( $H$ ), at the average depth (26.5 m), at the average distance to the nearest port (3.1 km) and at the average temperature (12.8°C). To facilitate between-variable comparisons, simulations were performed assuming calm conditions (the wave height was set to 0.0 m).

## 4.4 Results

A total of 1,271 recreational boats fishing squid were counted over two years (63 censuses). At least one boat was detected in 78% of the censuses, and the average number of boats per census was  $20.2 \pm 27.4$  (mean  $\pm$  SD). No boats were observed in nearly one-half of the cells (51%). The average number of boats per cell (pooled across all 63 censuses) was  $7.4 \pm 17.6$  boats. No boats were observed in 95.4% of the cell-day units.

The model predictions showed neither temporal nor spatial systematic bias, as demonstrated by plotting the expected against the observed number of boats (Fig. 4.4A-C). The spatial residuals showed certain spatial trends (larger residuals in cells with a greater expected number of boats), but the relative values of these residuals were small (a maximum of 2.2% of the observed number of boats; Fig. 4.4D).

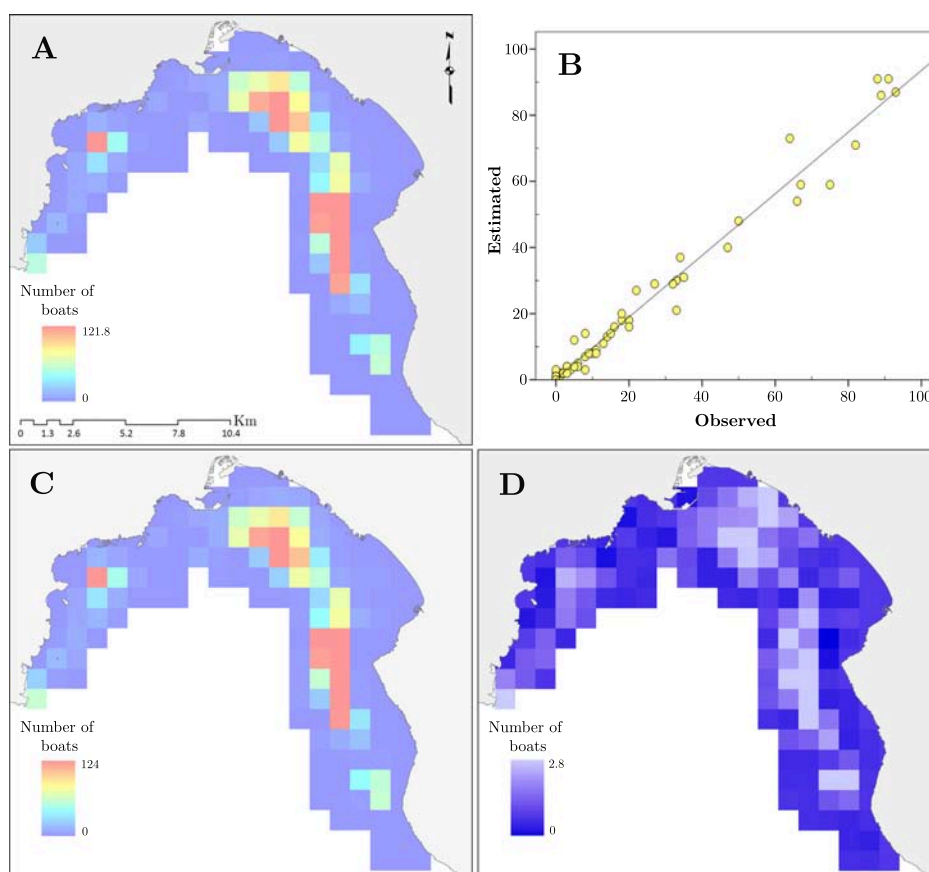


Figure 4.4: Model validation: (A) expected number of boats per cell (i.e., pooling values for each cell across censuses). (B) expected *vs.* observed number of boats per census. (C) observed number of boats per cell (i.e., pooling values for each cell across censuses). (D) residuals (map A-map C).

The fitted values for the model parameters are summarized in Table 4.1. *Sea-bottom temperature* showed a negative effect on the number of boats (i.e., a larger number of boats at a lower temperature; Fig. 2.5A). *Depth* and *Depth*<sup>2</sup> showed a negative effect too, which suggest the existence of an optimal depth (26.5 m) at which the expected number of boats reached a maximum (Fig. 2.5B). These variables are assumed to be proxies of *Fishing quality* (see Section 4.5).

Similar to the result for *Depth*, *Port Distance*<sup>2</sup> showed a negative effect, suggesting an optimal distance (3,092.7 m) at which the number of boats per cell reached a maximum (Fig. 2.5C). In contrast, the holiday-related characteristic of the day (holiday or non-holiday) appeared to be irrelevant (the 95% CI included zero; Table 4.1). The distribution of the anglers was positively correlated with the presence of seagrass (Fig. 2.5D).

The presence of an MPA did not affect the distribution of the anglers (the 95% CI included zero; Table 4.1 & Fig. 2.5E), who tended to cluster near the vicinity of the border of the MPA.

*Sea conditions* played an important role in site and day choice. Poor sea conditions caused a marked decrease in the number of recreational boats. Despite the presence of substantial unexplained variability, the probability that a boat departed from port decreased, on average, to 0.5 at a wave height of 0.8 m. The probability that a boat would go fishing was always negligible if the wave height was > 1.5 m (Fig. 2.5F).

Table 4.1: Summary statistics for the posterior distributions of fixed and random effects. Relevant fixed effects are highlighted in green. Note that random effects are expressed as tolerance (variance<sup>-1</sup>); thus, the variance related to autocorrelation (CAR) is virtually zero, and the between-census variance is (approximately) twice as large as the between-cell variance.

	Parameters	Description	Mean	SD	Credibility Intervals		
					2.5%	Median	97.5%
	$\pi$	False zero parameters	0.281	0.078	0.135	0.278	0.434
Fixed factors	<i>SC</i>	Sea conditions	-6.257	1.014	-8.419	-6.203	-4.405
	$\alpha$	Grand mean	-1.106	0.488	-1.932	-1.147	0.012
	<i>SBT</i>	Sea-bottom temperature	-0.381	0.141	-0.670	-0.382	-0.103
	<i>D</i>	Depth	-1.297	0.386	-2.049	-1.300	-0.541
	<i>D</i> <sup>2</sup>	Depth <sup>2</sup>	-2.183	0.382	-2.915	-2.166	-1.490
	<i>PD</i>	Port distance	-0.180	0.300	-0.754	-0.185	0.342
	<i>PD</i> <sup>2</sup>	Port distance <sup>2</sup>	-0.598	0.246	-1.080	-0.573	-0.142
	<i>H</i>	Holidays	-0.271	0.206	-0.755	-0.254	0.070
	<i>BH</i>	Benthic habitat	1.435	0.374	0.687	1.434	2.170
	<i>R</i>	Reserve	-1.007	0.564	-2.182	-1.010	0.178
Random	<i>CAR</i>	Spatial autocorrelation	1,920.145	709.966	606.722	1,821	3,139.1
	<i>VC</i>	Visual census	0.127	0.035	0.067	0.124	0.203
	<i>C</i>	Cell	0.305	0.060	0.205	0.299	0.433

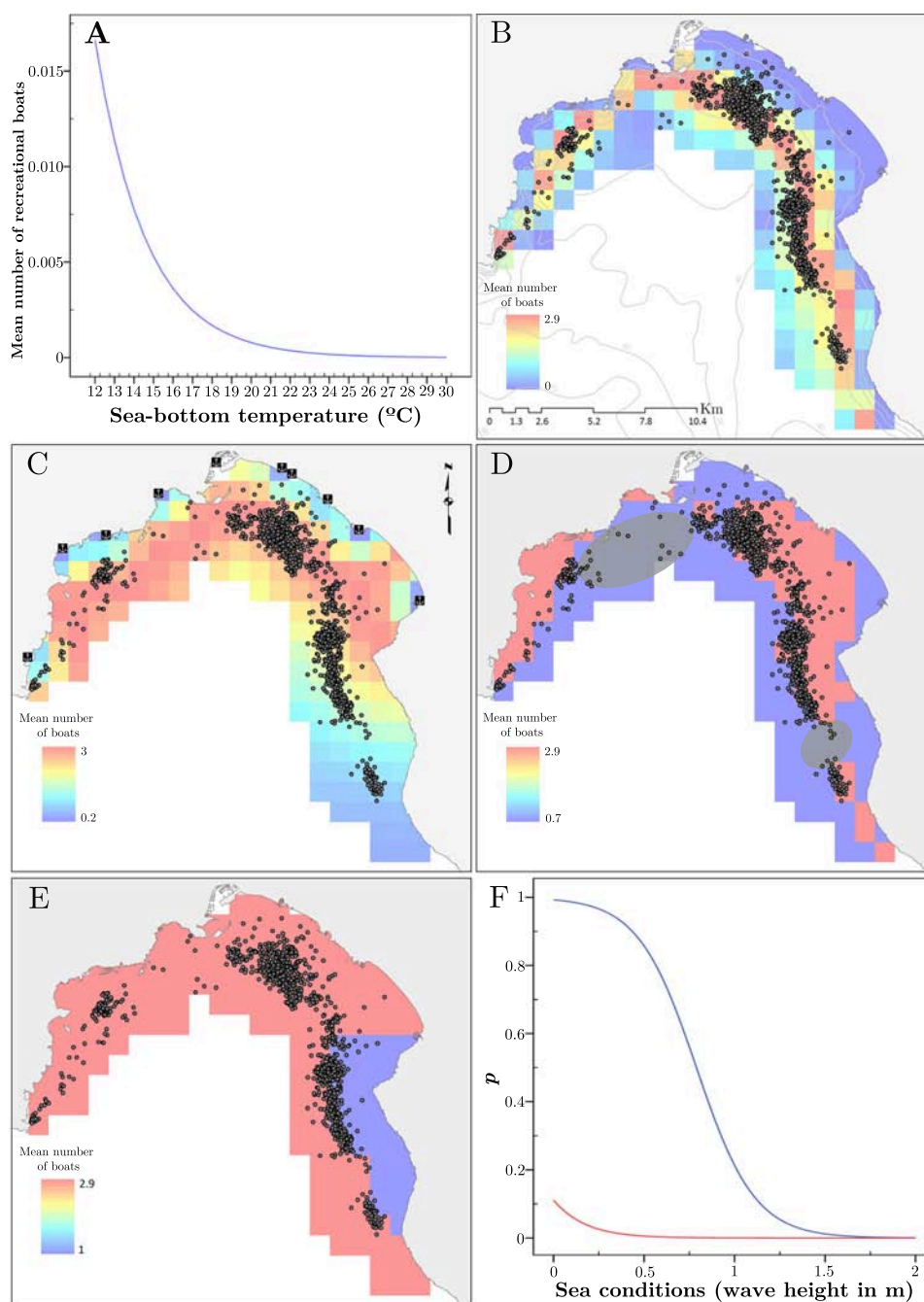


Figure 4.5: Partial effects (mean number of recreational boats after 100 simulations) of (A) *Sea-bottom temperature* (no map is shown because temperature is virtually constant at a given day and no interactions with other variables were considered); (B) *Depth*; (C) *Port distance*; (D) *Benthic habitat* (grey ellipses indicate the two principal gaps in the seagrass meadow of Palma Bay); (E) *Reserve*. (F) *Sea conditions*, where lines represent the 95% upper (blue) and lower (red) probabilities that a boat will leave port given different Sea conditions.

Regarding the trolling modality, a total of 356 boats were recorded. These boats tend to perform their activity at shallow waters (from shore to 10 m depth). Most of the anglers performed this modality near the city lights (Fig. 3.7 in Chapter 3).

## 4.5 Discussion

The spatio-temporal pattern of recreational squid fishing effort in Palma Bay appears to be the result of the combined effects of bottom temperature, depth, distance to port, habitat type and weather conditions. The spatial component (i.e., “Where”) is defined by a clear trend for boats to tend to cluster where the depth is between 25 and 30 m, just at the lowest limit of *P. oceanica* meadows and  $\approx 3000$  m from the nearest port. The temporal component (i.e., “When”) was defined by a clear seasonality, peaking during the coldest months, whereas the occurrence of squid fishing during late summer and autumn was merely anecdotal. However, the weather conditions determined the actual decision by the anglers if all other variables were favourable.

In this study, we addressed the three problems that are commonly associated in determining spatio-temporal patterns of recreational fishing effort, namely, data acquisition, statistical technicalities, and the complexity of the anglers’ preferences. In terms of data acquisition, visual censuses of boats provides high-quality data (McCluskey and Lewison, 2008) in comparison with interview based surveys, which are prone to bias due to inaccurate answers (Sharp et al., 2005). However, visual censuses involve higher costs, especially in marine fisheries (Fraidenburg and Bargmann, 1982). In our case, the tendency of squid anglers to be spatially (near the coastline) and temporally aggregated (around sunset; Chapter 5 & Cabanellas-Reboredo et al., 2012b) reduced the survey cost. Thus, visual censuses may be an alternative for relatively small, closed bays where anglers move near the coast (e.g., Lynch, 2006). In this type of scenario, visual censuses can even be replaced by photographic time-series taken from the coast, thus minimizing cost but maintaining acceptable precision in determining the position of the boats (Parnell et al., 2010). Related to this type of photographic survey, satellite remote sensing has been used to quantify fishing by the commercial squid fishery by estimating the light intensity of the devices used to aggregate squids near the boat (Maxwell et al., 2004; Waluda et al., 2004). In our case, anglers are prohibited from using light to attract squid. Therefore, in the case of the recreational squid fishery, visual censuses represent an optimal trade-off between cost and data quality.

After the problem of data acquisition has been successfully addressed, the next problem is how to analyse the data. The typical problems of this type of data are that i) the raw data are zero-inflated counts (number of boats per cell); ii) because the observations are spatially and temporally structured, specific solutions must be adopted to circumvent the lack of independence between the statistical units considered; and iii) fixed effects are hierarchically structured, as e.g., the effect of weather

conditions mentioned above. These technical problems are well known, and appropriate solutions for each individual problem have previously been proposed. For example, various approaches have been shown to provide unbiased solutions for the problem of spatial autocorrelation of normally distributed and independently sampled data (Dormann et al., 2007). However, the difficulties are exacerbated if all three problems occur simultaneously. Fortunately, Bayesian hierarchical modelling allows modular solutions for each of the above-mentioned problems to be combined in a relatively straightforward and intuitive way. In this study, we adopted a Bayesian CAR convolution model (Lawson et al., 2000). One of the strengths of the Bayesian approach is precisely its plasticity and ability to fit the specific characteristics of complex problems (Clark, 2007). Nevertheless, the Bayesian approach is a computation-intensive method, and the time needed for convergence depends on both the model and the data. Specifically, the model implemented in this Chapter may require several days to converge. In practice, this constraint limits the possibility of validating the model predictions via a leave-one-out or other similar Monte Carlo strategy (Lockwood and Schervish, 2005). However, in our case, after pooling the data by census (all cells of a given census) and by cell (all censuses of a given cell), the predictions appear to be precise and unbiased (Fig. 4.4). Therefore, Bayesian hierarchical modelling represents an optimal trade-off between the possibility of implementing complex models and the results obtained.

The third and most important problem successfully addressed here is to understand anglers' preferences in selecting a site and a day. In our case, the anglers' decisions appear to be the result of a combination of different attributes proposed by Hunt (2005). Note that Hunt's attributes are abstract and complex concepts, thus, to conclude that a specific attribute has some effect of fishing effort depends in part on the metric chosen for measuring it. The proxies we have chosen seem *a priori* reasonable for identifying the general factors affecting fishing effort, but certainly other alternative proxies can be designed in order to focus on different aspects of the same attribute. For example, depending on the specific fishery, fishing quality may be more related to number of captures, size, diversity or preferred species. In our case, no direct measurement of *Fishing quality* was available, but this attribute certainly plays a significant role. This attribute has been recognized as one of the most important determinants of the preferences and satisfaction of anglers in a variety of situations (Arlinghaus, 2006), particularly in consumption-oriented contexts (Kyle et al., 2007). In most cases, *Fishing quality* determines the pattern of the spatial distribution of anglers (Hunt, 2005), because anglers select fishing sites where the fish size and/or catch rate are presumed to be high (Aas et al., 2000; Schuhmann and Schwabe, 2004). In other cases, a site

is chosen according to the characteristics of the water body, because anglers assume that certain sites potentially hold target species (Montgomery and Needelman, 1997). This example suggests that the different attributes proposed by Hunt (2005) are not always mutually exclusive, because better *Fishing quality* is expected from water bodies of higher *Environmental quality*, another attribute identified by Hunt (2005). In our case, *Fishing quality* was assumed represented by the combination of temperature and depth. The assumed relationship between temperature and squid abundance is based on the empirical evidence provided by experimental fishing sessions (Chapter 5; Cabanellas-Reboredo et al., 2012b). The suggested biological process underlying this relationship is that squid migrate inshore (and thus become vulnerable to recreational fishing) during the cold season (winter-spring) to search for the environmental conditions that maximize spawning success (Chapter 2 & 5; Cabanellas-Reboredo et al., 2012b). In relation to *Depth*, empirical evidence for the preference of squid for depths of ~25-30 m during the spawning season is provided by acoustic tracking (Chapter 3; Cabanellas-Reboredo et al., 2012a). Temperature is well correlated with the seasonal pattern depicted by fishing effort, which reaches its maximum in winter-spring, specifically during the inshore spawning season (Chapter 2). Similarly, fishing effort clusters at a depth of ~25-30 m. Therefore, we interpret the combination of these two patterns to be a response of fishing effort to an increased abundance of squid. A similar spatio-temporal correlation between fishing effort and catches has been described for other species and explained by an increased vulnerability to recreational fishing during spawning aggregations (Coleman et al., 1996; Erisman et al., 2011).

The positive correlation between squid abundance and fishing effort could suggest that the spatio-temporal patterns of effort may follow an ideal free distribution (Gillis and vanderLee, 2012). However, Costs can also affect choices by anglers (Hunt, 2005; Post and Parkinson, 2012). Specifically, travel cost is inversely correlated with recreational effort for rainbow trout (*Oncorhynchus mykiss*) and walleye (*Sander vitreus*) (Hunt et al., 2011; Post and Parkinson, 2012; Post et al., 2008). In the current study, *Costs* are represented by the distance to the nearest port. Boats tend to cluster  $\approx 3000$  m from the nearest port. Note that, as in the case of *Depth*, sites too close to the coast are not preferred. Therefore, the observed pattern could emerge from a combination of multiple factors, e.g. it is probable that this pattern reflects the balance between fuel expenses and expected harvest (Hunt, 2005; Lynch, 2006). In addition, the security granted by the proximity to a port might represent a complementary factor (Kaoru et al., 1995). However, the hot spots where the highest effort is concentrated based on depth and on the distance to the nearest port are similar but not exactly the same



(Fig. 4.5B & C), and the statistical model confirms that both effects (*Port distance* and *Depth*) are relevant and complementary.

Another attribute proposed by Hunt to affect effort distribution is *Facility development*. Better facilities (port and marina services, number of boat launches or campground facilities) positively influence anglers' site choice (Kaoru et al., 1995; Morey et al., 2002). Alternatively, we used the variable *Holidays* as a measure of the facilities available to anglers in a given day. Whatever the classification of this variable, differences in fishing effort between holidays and working days have been reported (Bucher, 2006; Parnell et al., 2010). Interestingly, fishing effort does not differ between weekend and working days in our case. This result may be related to two characteristics of the squid fishery in Palma Bay: i) fishing journeys are short (~2-3 h) and are performed around sunset (Chapter 5; Cabanellas-Reboredo et al., 2012b), and ii) fishing grounds are close to port. Therefore, the time needed for a fishing journey is fully compatible with the usual working time. This result facilitates future monitoring of the recreational fishing effort for squid, because there is no need to stratify sampling (holiday-working day), as suggested by McCluskey and Lewison (2008).

Another variable unrelated to catch that determines the distribution of recreational effort is *Environmental quality* (the fourth attribute proposed by Hunt). This attribute aims to measure the water quality or aesthetic aspects of the fishing site, and it appears that anglers' choice is positively affected by these characteristics (Hunt, 2005; Quinn, 1992; Spencer and Spangler, 1992). Nevertheless, *Environmental quality* is difficult to separate from *Fishing quality* because anglers may, in fact, select a site based on the expected harvest (Schramm et al., 2003), which, in turn, is expected to be better at sites with good *Environmental quality*. In our study, *Environmental quality* was represented by the occurrence of *P. oceanica*, because it is an ecosystem-welfare indicator species (Montefalcone, 2009). It has been reported that fishing effort on another related squid species (*Sepioteuthis australis*) is associated with sites where there are seagrass meadows (Lynch, 2006). It is especially interesting that the absence of *P. oceanica* explains a noticeable gap where no boats are found, despite it seems optimal in relation to *Depth* (grey circles in Fig. 4.5D). In any case, the process responsible for this pattern remains elusive.

The fifth attribute proposed by Hunt (2005) is *Interaction among anglers*, which may have a relevant effect on the degree of aggregation observed in other recreational fisheries. However, empirical data on this attribute are scarce and contradictory, suggesting that angler (i.e., experience; Bryan, 1977) and fishery specificities (e.g., rivers vs. lakes; Beville and Kerr, 2009) may even produce opposite patterns. This attribute

was considered only indirectly in this Chapter to model spatial autocorrelation. Note that the main purpose of adopting the CAR modelling strategy is not the analysis of autocorrelation itself but the robust estimation of the values of the fixed effects (e.g., *Depth*). However, the strength of autocorrelation may be indirectly inferred by the amount of variance attributed to this source of variability. Following this rationale, spatial autocorrelation at the 1 km<sup>2</sup> scale should be considered virtually negligible (Table 4.1). Therefore, the number of boats in a cell is virtually independent of the number of boats in the neighbouring cells. Note, however, that this result does not invalidate the possibility of autocorrelation at a smaller scale (within cells). The possibility that a type of magnet effect occurs at very short distances (i.e., the presence of a boat increases the probability that other boats will arrive) is very appealing and would explain the underestimation of the number of boats by our model when the expected value is very high (Fig. 4.4D). However, the cell size adopted here prevents exploration of this possibility.

The last catch-unrelated variable considered by Hunt (2005) to affect anglers' site choice is *Regulations*. The implementation of fishing regulations is considered to represent one of the most important factors affecting the spatial and temporal distribution of fishing effort in both commercial (Horta e Costa et al., 2013; Salas and Gaertner, 2004) and recreational fisheries (Aas et al., 2000; Hunt, 2005; Scrogin et al., 2004). In the specific case of marine protected areas, anglers typically redistribute effort after the implementation of an MPA (De Freitas et al., 2013; Fujitani et al., 2012). Ignorance of the regulations, not the regulations themselves, is one of the primary reasons that anglers avoid MPAs (Johnston et al., 2010, 2011). Accordingly, *Regulations* was approximated in this study by the putative effects of fishing within or outside an MPA, but no differences in effort were found in our case (i.e., the so-called reserve effect was not relevant). In contrast, hook-and-line fishing effort (i.e., targeting fish, not squid) at the same MPA is smaller than at nearby non-protected sites, although catch rate and fish size (i.e., *Fishing quality*) are higher inside the protected area (Alós and Arlinghaus, 2013). We suggest that in our case, the optimal squid fishing ground (~25-30 m; Fig. 4.5B) is at the very limit of the MPA (Fig. 4.5E). Thus, squid anglers always behave as if they were outside the MPA.

Finally, (Hunt, 2005) also emphasized that the combined effect of the six attributes on recreational fishing effort could be markedly modulated by environmental factors. In this study, this effect was found for *Sea conditions*. The hierarchical structure of the Bayesian model allowed the effects of weather to be tested prior to the other variables in the hierarchy. The expected number of boats in a cell-day unit was multiplied by the

probability that those boats go fishing, which in turn was modelled by *Sea conditions*. As a result, in late summer, when the expected number of boats was nearly zero, the predicted number of boats was also zero. This result was virtually independent of the weather. In contrast, in winter, when the expected number of boats was high in accordance with the variables that were unrelated to the immediate weather conditions, the effective predicted number of boats was high in calm weather but zero in stormy weather.

Overall, although several currently measurable variables can be associated with more than one attribute proposed by (Hunt, 2005), a correlational approach between the number of boats and a broad range of variables potentially related to these attributes has successfully addressed the questions of “When” and “Where” squid anglers go to fish at Palma Bay. This approach offers a good starting point for integrating anglers’ behaviour in an effort to understand the social dimension of the recreational fishery, which is one of the most challenging topics in the field (Arlinghaus et al., 2013). In contrast to the general belief, the catches of anglers are not merely anecdotal information (Chapter 7; Post et al., 2002), and the combined effects of commercial and recreational fisheries can cause overfishing and stock collapse. Typically, however, only catches from the commercial fishery are assessed. Squid is an example of a stock that is heavily exploited by both recreational and commercial fisheries (Chapter 5; Cabanellas-Reboredo et al., 2011, 2014a). Thus, ignoring certain stakeholders, may not only generate conflicts between stakeholders but may also be useless. Results such as those obtained here can be used to solve specific management problems in two ways. First, the fine-scale estimates of effort (daily predictions for each 1 km<sup>2</sup> cell) provided in this Chapter may constitute the first step towards estimating the total harvest by the recreational fleet (Chapter 7). We propose that, given the number of anglers and the averaged catches per fishing trip, the total squid catches could be approximated and incorporated into population dynamics models, which, in turn, should inform management decisions. Second, this approach allows a better understanding of anglers’ preferences. This knowledge can be used to select the management option that maximizes the resource sustainably while minimizing potential conflicts with anglers. For example, it can be used for selecting the best location for an MPA. Therefore, incorporating the spatial and temporal dimensions of effort when designing management strategies should facilitate the process by which anglers better internalize specific management rules and should create a favourable climate for further advances in the context of an adaptive management strategy, which may be more effective for ensuring resource sustainability.

The spatio-temporal pattern of the trolling modality (conducted at shallow waters

during nighttime) may be related to the foraging behaviour displayed by squid during nighttime. After dusk, the squid enlarge their space use, and consequently, can reach trolling fishing grounds (Chapter 3). In addition, the advantage of these shallow areas *vs.* line jigging fishing grounds (~25-30 m depth) seems to be related to the illumination of the city lights. This indirect illumination could facilitate the detection of the artificial lures used by trolling (Chapter 3)

## Chapter 5

# Environmental effects on recreational squid jigging fishery catches

### 5.1 Abstract

Experimental fishing sessions simulating the operating procedures of the recreational fishery for the European squid that operates at inshore Palma Bay were conducted to investigate the effects of environmental variables on squid catches. The catch per unit of effort (CPUE) of line jigging sessions showed a seasonal pattern (higher CPUE during colder months). Two alternative hypotheses can explain such a pattern. First, squid could migrate inshore during colder months to seek spatio-temporal windows within which the sea temperature maximize spawning success (Chapter 2). Second, the timing of the seasonal reproductive peak and the growth rate of any given cohort would result in a higher percentage of squid whose body size is greater than the gear-specific vulnerability threshold during the colder months. The combination of environmental variables that maximized CPUE was a low sea surface temperature, a low windspeed, low atmospheric pressure, and days close to the new moon. A specific period of the day, narrowly around sunset, favoured the catches. Within this narrow period, the sunlight is still sufficient to allow the recreational fishing lures to be effective, and the squid have already shifted to a more active pattern of movement characteristic of the night-time period (Chapter 3).

KEY WORDS: CPUE, Generalized linear mixed model, Sea surface temperature.

## 5.2 Introduction

Most cephalopods are able to avoid negative environmental conditions through short-term adjustments to environmental variations (Pecl and Jackson, 2008; Pierce et al., 2008). One noticeable example of this capability is that cephalopods typically perform migrations that are related to environmental changes. These migrations cause substantial changes in spatial distribution (Roberts and Sauer, 1994; Sauer et al., 1991). The primary drivers of migration appear to be the need to search for better feeding conditions (Martins and Perez, 2007; Martins et al., 2006) or for particular areas where environmental conditions optimize spawning success (Roberts and Sauer, 1994; Sauer et al., 1991).

The vulnerability of squid to fishing changes as a consequence of these migrations (Pierce et al., 1998). For example, certain artisanal fisheries for Loliginid squids operate only when these species migrate inshore in response to favourable environmental cues (Iwata et al., 2010; Postuma and Gasalla, 2010; Schön et al., 2002). For this reason, a better understanding of the relationship between cephalopod vulnerability and environmental changes is essential for managing cephalopod fisheries (Boyle and Rodhouse, 2005; Pierce et al., 2008; Schön et al., 2002).

Previous studies focusing on commercial fisheries have shown that many environmental factors, such as moon phase, period of the day, windspeed, wind direction, rainfall, sea temperature, turbidity, and sea conditions, could play a role in the vulnerability and catch per unit of effort (CPUE) of squid (Chen et al., 2006b; Lefkadltou et al., 1998; Mercer and Bucy, 1983; Nowara and Walker, 1998; Postuma and Gasalla, 2010; Schön et al., 2002; Ulaş and Aydin, 2011). As it has been mentioned in previous Chapters, due to the high socio-economic importance of *L. vulgaris* in the Mediterranean, this cephalopod experiences a high level of exploitation by professional fisheries, either as target or bycatch (González and Sánchez, 2002; Guerra et al., 1994; Worms, 1983).

In the Balearic Islands, in addition to commercial fishing, the European squid is also targeted by recreational fleet (Chapter 4; Cabanellas-Reboredo et al., 2014a; Morales-Nin et al., 2005). However, the specific influence of environmental factors on the vulnerability of squid to recreational fishing remains unknown. In fact, the effects of environmental factors on recreational fishing catches have been addressed only for a few freshwater or large game-fish species (Kuparinen et al., 2010; Ortega-Garcia et al., 2008).

At Palma Bay, tens to hundreds of recreational boats may concentrate at specific grounds (inshore; Chapter 4 & Cabanellas-Reboredo et al., 2014a) and during the

spawning season of this species (Chapter 2 & 3; Cabanellas-Reboredo et al., 2012a, 2014b). This pattern of fishing effort suggests a possible spatio-temporal relationship between vulnerability to fishing and environmental conditions. In addition, recreational fishing activity occurs primarily at sunset (Chapter 4; Cabanellas-Reboredo et al., 2014a). This temporal clustering suggests a possible additional relationship between environment and vulnerability occurring on a within-day temporal scale (Chapter 3; Cabanellas-Reboredo et al., 2012a).

With this background, the specific objective of this Chapter was to analyse the effects of environmental factors on the recreational catches of *L. vulgaris* at two different temporal scales: i) seasonally, and ii) daily. In addition, the spatial pattern of recreational fishing effort suggests the existence of three differentiated areas (Fig. 4.1; Chapter 4). Therefore, Palma Bay was divided into three areas in order to test between-area differences in CPUE that could be related with some area-specific environmental characteristic.

## 5.3 Material & Methods

### 5.3.1 Sampling

Based on the spatial distribution of the recreational squid fleet (Chapter 4), Palma Bay was divided into three areas (Fig. 5.1).

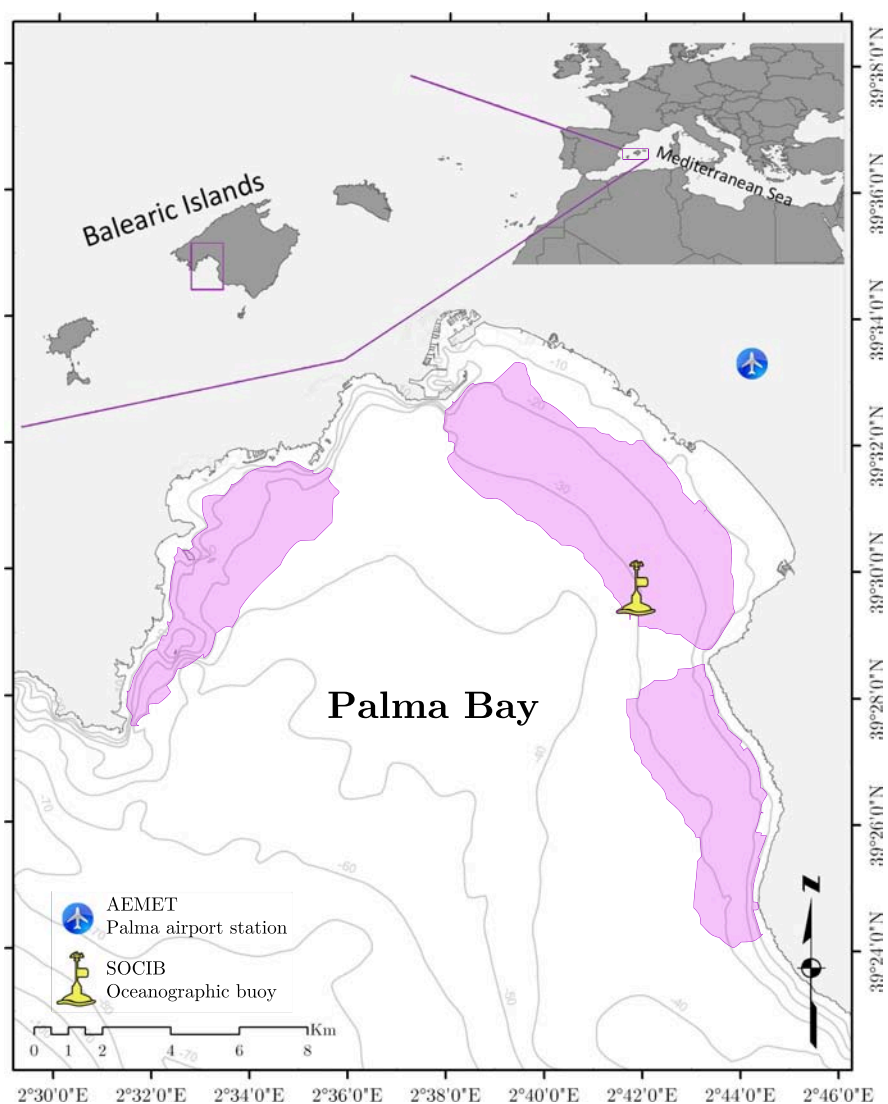


Figure 5.1: Sampling area. The colored areas divide the Palma Bay into three main fishing areas. The isobaths represent 10 m intervals.

From July 2009 to February 2011 a total of 55 experimental fishing sessions of 1.5 h duration were performed (2-4 sessions per month). Each fishing session was conducted at a randomly chosen area. To simulate the method by squid anglers (Chapter 4),



experimental fishing sessions were conducted within a narrow depth range (25-30 m) and around sunset because anglers concentrate on this spatio-temporal range (Chapter 3 & 4). We used line jigging with artificial lures (squid jigs; Boyle and Rodhouse, 2005). Each experimental fishing session was divided into three 30 minute periods (*day period*: “before”, “during”, and “after” sunset, with actual sunset in the middle of the “during” period). CPUE was measured as the number of squid captured per time unit (in the case of CPUE<sub>Total</sub> the time unit was 1.5 hours, whereas for CPUE<sub>Partial</sub> the time unit was 30 minutes; we standardized to account for the number of anglers on board; see below Section 5.3.3.3).

The dorsal mantle length (DML) was measured to the nearest mm for most (71%) of the captured squid.

### 5.3.2 Environmental data

Several environmental variables were recorded for each experimental fishing session. Air temperature (°C, mean of the sampling day), rainfall (l m<sup>-2</sup>, total of the sampling day), windspeed (m s<sup>-1</sup>, mean of the sampling day), atmospheric pressure (hPa, mean of the sampling day) and hours of sunshine (h day<sup>-1</sup>) were obtained from the Governmental Meteorology Agency (AEMET; Fig. 5.1). The sea condition during the sampling session was categorized using the Douglas Sea scale, a scale which measures the height of the waves and also measures the swell of the sea. In addition, the sea surface temperature (*SST*) was monitored at sunset with an oceanographic buoy maintained by SOCIB (Fig. 5.1). The daily moon phase data were obtained from the US Naval Observatory (<http://aa.usno.navy.mil/data/docs/MoonFraction.html>). We used the fraction of the moon that was illuminated on a given day as a quantitative representation of the lunar phase. The raw data (moonlight percentages; deBruyn and Meeuwig, 2001; Kuparinen et al., 2010) were sine-transformed. As a result, the moon phase was described by values ranging between 1 (full moon) and -1 (new moon). Tidal effects were not considered because the tides in the Mediterranean Sea vary only a few cm (Arabelos et al., 2011).

### 5.3.3 Statistical analyses

Four statistical analyses have been performed addressing the following goals: i) a *t*-test to explore seasonal differences in squid length frequencies, ii) a principal components analysis (PCA) to check correlation among environmental variables and avoid collinearity in the generalized linear model (GLM), iii) a GLM to test the effect of environmental

variables on daily CPUE and, iv) a generalized linear mixed model (GLMM) to test CPUE variability at the within day scale (among *day period*; i.e., before, after and during sunset).

### 5.3.3.1 Squid length

The seasonal [warm (June-October) *vs.* cold months (November-May)] differences in squid length were analysed with a conventional *t*-test of log-transformed data. The variances were found to be homogeneous (Levene test) after logarithmic transformation, and the residuals were found to be normally distributed (Shapiro-Wilk test).

### 5.3.3.2 Preliminary screening of environmental variables

A PCA on all the environmental variables considered was conducted to reveal correlation patterns and to avoid collinearity among variables. The PCA results suggested that there were several groups of highly correlated environmental variables (Fig. 5.2). If two or more variables showed a high correlation (positive or negative), we selected only one variable per group. The selected variable was the one for which effects on CPUE or on biologically relevant traits had previously been reported (Lefkadltou et al., 1998; Mercer and Bucy, 1983; Pierce et al., 2008; Sauer et al., 1991; Schön et al., 2002). After this preliminary screening, *SST*, *windspeed*, *atmospheric pressure*, *hours of sunshine*, and *moon phase* were selected to test their effects on squid CPUE. The PCA was conducted with CANOCO 4.5.

### 5.3.3.3 Generalized linear model

The number of squid caught per experimental fishing session ( $CPUE_{Total}$ ; number of squid after pooling the captures of the three *day periods* of the same fishing session) was modelled using a GLM. The pooling procedure was applied to avoid pseudoreplication, which could result because the model included environmental variables that could potentially affect the three periods in the same way (e.g., *SST*). Moreover, because the CPUE data were expressed as counts, a Poisson distribution was selected to model the CPUE as follows:

$$CPUE_i \sim Poisson(\mu_i)$$

$$\log(\mu_i) = \beta X_{i,j},$$

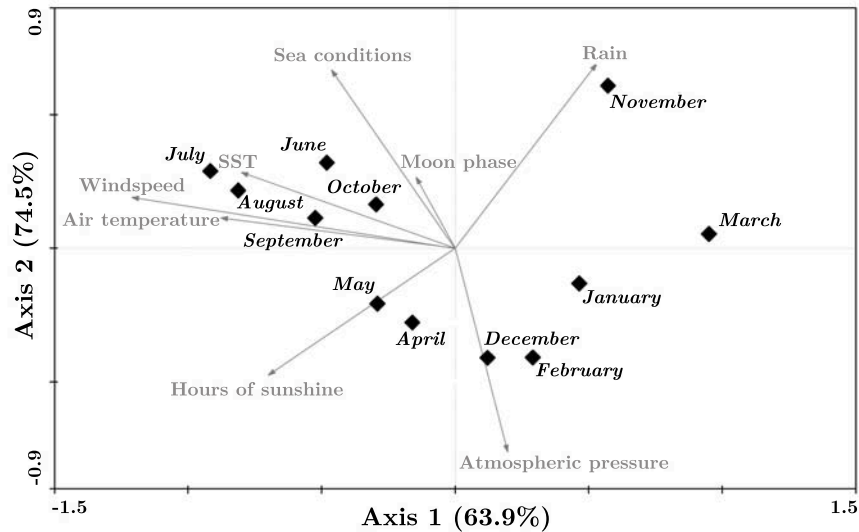


Figure 5.2: Plot of the PCA results. Values in brackets are the cumulative percentage of variance based on the two first components. Months have been added to the plot (as the average position of all the sampling days in a month) in order to facilitate the interpretation.

where  $i = 1$  to 55 experimental fishing sessions, and  $X$  represents the matrix of  $j = 1$  to  $n$  environmental variables. The model was fitted with the *glm* function of the R package (<http://www.rproject.org>). The experimental fishing sessions were conducted by (the same) two anglers, except in a few cases, where one or three anglers carried out the fishing session. Therefore,  $CPUE_{Total}$  was standardized by the number of anglers onboard, as represented by the value of the *offset* argument. The initial model included all the environmental variables selected after the PCA (*SST*, *windspeed*, *atmospheric pressure*, *hours of sunshine*, and *moon phase*), as well as the fishing *area* (Fig. 5.1). An AIC-based backward model simplification procedure was applied (*step* function of the R package). The existence of collinearity among the variables included in the final model was evaluated by estimating the variance inflation factor (VIF; Heiberger and Holland, 2004).

The response variable (CPUE) may be not only affected by a number of variables but also by how distant in time were two consecutive experimental fishing sessions (i.e., temporal autocorrelation). Since fishing sessions were irregularly spaced, standard time series approaches (e.g., an arima model) are not appropriate. Instead, a variogram analysis that is extensively utilized in geostatistics to evaluate spatial correlation can also be used for evaluating temporal autocorrelation (Luo et al., 2006). A

temporal variogram compares the variances of groups of samples located at different time intervals. The rationale is that in a scenario without temporal autocorrelation, samples from the same time interval should have the same variability than samples corresponding to a very distant dates. Temporal variograms of the models' residuals were estimated using the *variog* function. Then, the *variog.mc.env* function was used for generating 95% confidence intervals by non-parametric bootstrapping (1,000 iterations). When observed variances were within such confidence intervals, absence of autocorrelation can be concluded.

### 5.3.3.4 Generalized linear mixed model

To assess the effects of the *day period* on CPUE (CPUE<sub>Partial</sub>; before, during and after sunset), a GLMM (Bates and Maechler, 2010) was completed, given that the three 30-min periods sampled in a single day were not independent samples. A Poisson distribution was assumed because the CPUE<sub>Partial</sub> was expressed as count data:

$$\begin{aligned} CPUE_{ij} &\sim \text{Poisson}(\mu_{ij}) \\ \log(\mu_{ij}) &= \beta_0 + \beta \text{ day period}_{ij} + \text{day effect}_i, \\ \text{day effect}_i &\sim \text{Normal}(0, \sigma^2), \end{aligned}$$

where  $i = 1$  to 55 experimental fishing sessions, and  $j = 1$  to 3 (*day period*). Hence, the number of squid captured during each of the three *day periods* was the response variable (i.e.,  $55 \times 3 = 165$  observations of CPUE<sub>Partial</sub>), *day period* was incorporated as the only fixed factor and fishing day (*day effect*) was considered a random factor to incorporate the structure of the sampling design. As above, CPUE<sub>Partial</sub> was standardized by the number of anglers onboard with the *offset* argument. The model was fitted with the *lmer* function implemented in the library *lme4* from the R package.

To visualize the effects of the different *day period*, the expected CPUE<sub>Partial</sub> of a single angler was estimated with a parametric bootstrap procedure. The parameters of the model were used to obtain the expected point estimate CPUE before, after and during sunset. A total of 1,000 fishing sessions were simulated, based on a Poisson distribution.

## 5.4 Results

Despite some within-season variability, CPUE values showed a seasonal pattern: the catches during warm months (summer and early autumn) were smaller than those during cold months (late autumn, winter and spring; Fig. 5.3).

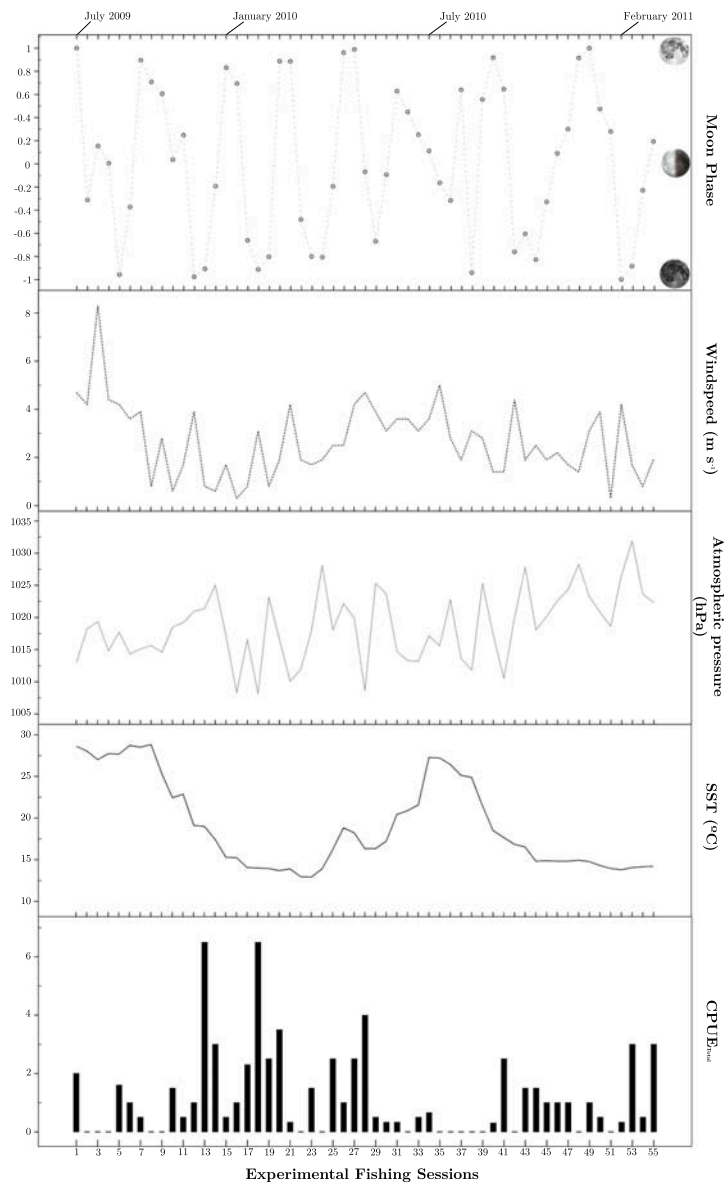


Figure 5.3: Daily values for all experimental fishing sessions of  $CPUE_{Total}$ ,  $SST$ , *atmospheric pressure*, *windspeed* and *moon phase*. In the plot of the moon phase, the grey and black circles represent the full and new moon, respectively. The sphere with grey and black shadows symbolizes the first and third quarter moon phases.

The mean size of the squid captured was 20.73 cm  $\pm$  4.50 (SD). The differences in mean size between the warm (June to October) and cold months were not significant ( $t = -0.918$ ,  $d.f. = 95$ ,  $p > 0.05$ ).

Concerning the effects on CPUE of the environmental variables selected after PCA (*SST*, *windspeed*, *atmospheric pressure*, *hours of sunshine* and *moon phase*), the results obtained by the final GLM (details on the backward model selection procedure are provided in Table 5.1) are summarized in Table 5.2.

Table 5.1: AIC values and degrees of freedom for each GLM tested during model selection. Poisson distribution of the data was selected and  $f$  is the number of experimental anglers. The final model selected is highlighted with green colour.

	MODELS	d.f.	AIC
GLM	<sup>1</sup> CPUE <sub>Total+offset(f)+fishing area+SST+windspeed+hours of sunshine+atmospheric pressure+moon phase</sub>	8	276.751
	<sup>2</sup> CPUE <sub>Total+offset(f)+fishing area+SST+windspeed+atmospheric pressure+moon phase</sub>	7	275.371
	<sup>3</sup> CPUE <sub>Total+offset(f)+SST+windspeed+atmospheric pressure+moon phase</sub>	5	272.925

Table 5.2: Results of the statistical analyses;  $p < 0.001^{***}$ ,  $p < 0.01^{**}$ ,  $p < 0.05^*$ . Variables have been mean-centered in the case of GLMM.

		Estimate	Standard Error	z values	Pr(> z )
GLM	(Intercept)	57.385	15.802	3.632	
	SST	-0.059	0.019	-3.003	**
	Windspeed	-0.171	0.071	-2.442	*
	Atmospheric pressure	-0.055	0.016	-3.537	***
	Moon phase	-0.463	0.138	-3.341	***
GLMM	(Intercept)	-2.076	0.253	-8.068	
	After sunset	0.673	0.251	2.681	**
	During sunset	0.940	0.241	3.903	***

The variables included in the final GLM were not collinear (VIFs values were 1.3 or smaller; the suggested threshold for avoiding collinearity problems is 5; Heiberger and Holland, 2004). Moreover, concerning temporal autocorrelation, none of the empirical variances estimated at different time intervals were outside the 95% confidence intervals. Thus experimental fishing sessions (sampling dates) were fully independent. The GLM results indicated that *SST* had a significant negative effect on CPUE (Fig. 5.3). Moreover, CPUE was also significantly affected by *windspeed*, *atmospheric pressure* and *moon phase*. CPUE increased at low windspeeds, at low atmospheric pressure and on days close to the new moon (Table 5.2 & Fig. 5.3). In contrast, the spatial distribution (fishing are; Fig. 5.1) of the experimental fishing sessions did not affect CPUE.

The GLMM results indicated that the *day period* significantly affected CPUE (Table 5.2). CPUE was lower before sunset, higher during sunset, and intermediately after

sunset. The results of the parametric bootstrap are shown in Fig. 5.4.

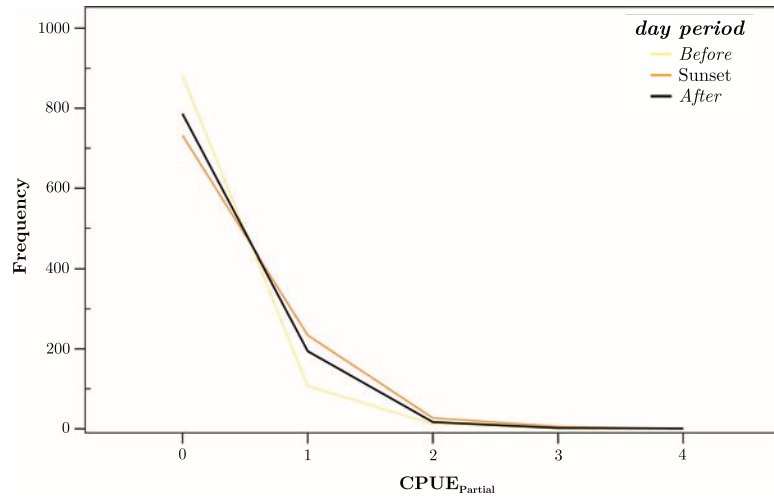


Figure 5.4: Distribution of the expected  $CPUE_{\text{Partial}}$  for 1,000 simulated experimental fishing sessions corresponding to different *day period* (before, after and during sunset).

## 5.5 Discussion

The results presented in this Chapter have demonstrated that the CPUE of recreational jigging of the European squid is significantly correlated with environmental variation. The most relevant environmental variable affecting CPUE was *SST*. The combination of environmental variables that maximized CPUE was low *SST*, low windspeed, low atmospheric pressure and days close to new moon.

This study has demonstrated that CPUE increases at low *SST* values. Two alternative hypotheses could explain such a pattern. First, squid could migrate inshore during colder months to seek spatio-temporal windows within which the sea temperature optimizes spawning success (Chapter 2). The catches from different commercial fleets are known to depend on sea temperature. For a closely related species, this relationship is well explained by migration (*L. forbesi* Steenstrup, 1856; Sims et al., 2001). Spawning appears to be one of the specific drivers of *L. vulgaris* movements (Sánchez and Guerra, 1994; Worms, 1983). Reproductive success seems to be maximized within a relatively narrow range of sea temperatures, which is 12 to 17°C for *L. vulgaris* (Villanueva et al., 2003). Such a narrow temperature range maximizes hatching success (Şen, 2005). *L. vulgaris* appears capable of spawning throughout the year (Chapter 2; Cabanellas-Reboredo et al., 2014b; Guerra and Rocha, 1994; Šifner and Vrgoč, 2004, but the inshore summer temperature in the northwest Mediterranean frequently falls outside such an optimal temperature range (Nykjaer, 2009). The *SST* in the study area reflected the typical conditions of the western Mediterranean, with minimum temperatures of approximately 14°C, a well-mixed water column during the late winter, and maximum temperatures in late August (Álvarez et al., 2012). Therefore, according to the spawning migration hypothesis (Fig. 1.2 in Chapter 1), squid would remain offshore during summer but would move inshore for spawning during winter and spring (i.e., the main reproductive season of *L. vulgaris*: Chapter 2; Šifner and Vrgoč, 2004).

Inshore migrations of other squid have important consequences on inshore fishing because these migrations make squid accessible to the coastal small-scale hand-line jigging fisheries (Augustyn and Roel, 1998; Boyle and Rodhouse, 2005; Iwata et al., 2010; Rodrigues and Gasalla, 2008). Furthermore, the captures of chokka squid, *L. reynaudii*, performed by the South African jigging fishery are related to the formation of inshore spawning aggregations (Roberts and Sauer, 1994; Schön et al., 2002). Consequently, the negative relationship between CPUE and temperature reported here could be explained by a seasonal migration to inshore spawning grounds (Chapter 2). Alternatively, food availability has been also proposed as another possible driver of inshore



migration (Martins and Perez, 2007; Martins et al., 2006).

The second hypothesis compatible with the seasonal pattern found (a higher CPUE during the colder months) is that this pattern could result from the size selectivity of the squid jigs. *L. vulgaris* paralarvae may hatch and recruit to more extensive fishing grounds than those exploited by the recreational fleet. The juveniles would grow and develop until they reached a specific size at which squid become vulnerable to jigging (Tokai and Ueta, 1999). Consequently, the catches of the anglers would only be significant after most of the squid stock attained that size threshold. Therefore, local depletion after these optimal months (caused either by post-spawning mortality or by fishing mortality, or both) may be a case of hyperdepletion (the appearance that stock size has declined much more than it actually has; Hilborn and Walters, 1992).

Unfortunately, neither of these two competing hypotheses can be rejected based on independent data (i.e., landings by the commercial fleet) because no data on the specific fishing areas used by this fleet are available. Moreover, it is well known that the commercial fleet frequently changes its fishing grounds in an attempt to maximize catches. This procedure results in a very noisy temporal series of squid catches, with no clear seasonal trend (Fig. 7.6 in Chapter 7). In addition, the growth rate (Natsukari and Komine, 1992) and the size at sexual maturation (160 and 125 mm for females and males, respectively; Šifner and Vrgoč, 2004) are such that the observed mean size (20.7 cm) of our catches is consistent with both hypotheses.

The negative correlation between atmospheric pressure and catch rates is also difficult to explain. All fishing sessions occurred with relatively good weather conditions and within a narrow range of typically anticyclonic values of atmospheric pressure (1008.2-1031.9 hPa). Therefore, it cannot be concluded that CPUE increases during adverse weather or sea conditions. Conversely, low values of atmospheric pressure within this narrow range may affect some aspect of squid physiology or behaviour, although the specific process involved requires further investigation. Our findings also suggest that mild winds represent the optimal weather condition for maximizing jigging success. In this context, it appears evident that rolling motion and excessive drift caused by strong winds disturb the optimal performance of the recreational fishing gear and reduce catches (Mercer and Bucy, 1983; Schön et al., 2002).

Our results showed that CPUE increased significantly on days close to the new moon phase. Experimental fishing sessions simulating commercial tactics (Mercer and Bucy, 1983) and studies based on commercial landings (Chen, 1998; Chen et al., 2006b) of different oceanic squids reported the same pattern. Schön et al. (2002) reported an increase in chokka squid (*L. reynaudi*) catches near the new moon. However, the process

relating moon phase and CPUE remains unclear. For example, conflicting data are reported even for the same species (*Ommastrephes bartrami* LeSueur, 1821), for which maximum CPUE values have been associated with both the full moon (Nakamura and Siriraksophon, 1992) and the new moon (Chen et al., 2006b). Commercial catch rates of other Loliginid squid (including *L. vulgaris*) have been reported to increase during full moon (Postuma and Gasalla, 2010; Ulaş and Aydin, 2011; Young et al., 2006). Overall, it is not possible to compare these results because gears and fishing tactics differ (e.g., lights may or may not be used to attract the squid). However, because the moon phase has no tidal effect in the Mediterranean Sea (Arabelos et al., 2011), physiological and behavioural changes related to lunar rhythms, comparable to those described for other cephalopods (Cobb et al., 1995; Denton and Gilpin-Brown, 1961; Spratt, 1979) may explain the relationship between moon phase and CPUE, although this topic requires further studies (Naylor, 2001).

Our results for the *day period* showed that CPUE was highest during the sunset period (30 minutes during dusk). This result may be due to the combination of the activity pattern of the squid (feeding at night and spawning during the day) and the visibility conditions favouring squid predation. A day-night difference in activity patterns has been demonstrated for *L. reynaudii* (Downey et al., 2010) and *L. vulgaris* (Chapter 3; Cabanellas-Reboredo et al., 2012a). Squid show a more active type of movement from sunset to sunrise (night-time). The increase in the level of nocturnal activity appears to be related to squid foraging (Downey et al., 2010; Nowara and Walker, 1998; Sauer and Lipiński, 1991). At sunrise, squid behaviour would shift from feeding to reproduction (mating and spawning behaviour; Cabanellas-Reboredo et al., 2012a; Downey et al., 2010; Hanlon et al., 2002; Sauer et al., 1997) and would remain in that state throughout the day. Therefore, a low CPUE before sunset could occur because most squid were still in a reproductive behavioural state (Chapter 3; Cabanellas-Reboredo et al., 2012a; Downey et al., 2010). A low CPUE after sunset could be related to low visibility, which would prevent squid from detecting artificial jigs (Postuma and Gasalla, 2010; Ulaş and Aydin, 2011) even if the squid were already in the feeding behavioural state. Vision is the principal sense involved in predation by neritic squid (Hanlon and Messenger, 1996). Because the use of lights to attract squid is prohibited for the recreational fleet in the Balearic Islands (BOE, 2011), the anglers concentrate their fishing efforts near sunset (Chapter 4; Cabanellas-Reboredo et al., 2014a). During this period, catchability is maximized because optimal visibility is present and the squid are especially inclined to feed (enhanced voracity and activity; Chapter 3 & Cabanellas-Reboredo et al., 2012a).

The seasonal variability in CPUE reported in this Chapter suggests that a temporal closure of the inshore grounds could enhance the stock by protecting potential spawners and increasing the reproductive potential of the population. In fact, this management tool has been applied in other cases (South African chokka squid fishery; Augustyn and Roel, 1998. Two cases of temporal closure (for fish) have been successfully implemented in the Balearic Islands (*Xyrichtys novacula* Linnaeus (1758) and *Seriola durmerili* Risso (1810)) (Morales-Nin et al., 2005). However, the case of squid at Palma Bay is not comparable. The status of the stock is unknown because no study of population dynamics that includes all fleets that exploit squid (trawling, small-scale and recreational fleets) has ever been conducted. Note that, as suggested above, partial analyses can produce a misleading conclusion because in the case of hyperdepletion, abundance indices would incorrectly indicate depletion. Therefore, a number of basic and key life history questions need to be addressed prior to the adoption of any specific management measure, e.g. whether squid migrate inshore for spawning, such that the spawners avoid mortality by fishing by commercial trawlers, or alternatively, whether the stock is evenly spread inshore and offshore and trawlers exploit the stock all year round while the recreational fishery only exploits squid (seasonally) when they reach a size vulnerable to the lures. This is particularly important because in this case the socio-economic importance of the three fleets could generate severe conflicts that could ultimately have harmful effects on the sustainability of the squid catches.



## Chapter 6

# Indirect line jigging effects on the European squid *Loligo vulgaris*

### 6.1 Abstract

The European squid *L. vulgaris* is an important target species of commercial and recreational fisheries in the NW Mediterranean. The largest proportion of catches comes from trawlers (Chapter 7). However, the most usual fishing gear used by the small-scale commercial fishery and recreational fishery is line jigging. Squid are trapped when they try to seize the lure with their tentacles. An unknown but possibly significant number of squid are able to escape by losing one or both of their tentacles (drop off rate). Between April and July 2010, two sets of experiments under controlled laboratory conditions were carried out to test ( $n = 15$  squid) the indirect effects of tentacle loss on predation success and predation behaviour. The first set of experiments consisted of estimating the number of attacks and time spent until a squid with no ( $n = 5$ ), one ( $n = 5$ ) or two tentacles ( $n = 5$ ) successfully caught a prey item. Independent trials were carried out with two prey types with very different swimming capabilities (fish and shrimp). The second set of experiments consisted of prey-selectivity trials to determine whether squid prefer fish or shrimp when both are available. The results obtained clearly demonstrate not only that squid missing tentacles have a reduced predation performance but also that they can change predation preferences and predation behaviour. These changes might negatively affect the condition and the reduced fitness of injured squid. Therefore, the consequences that squid lose their tentacles deserve more attention. This indirect effect of line jigging may imply unreported fishing mortality (ghost fishing) that should be considered when adopting management decisions.

KEY WORDS: Line jigging, Drop off rate, Tentacle removal, Captivity experiments.

## 6.2 Introduction

Detailed knowledge of the effects of fishing on a fishery resource is necessary to determine the maximum sustainable yield, and thereby prevent overfishing (Coll et al., 2008; Jackson et al., 2001; Pauly et al., 2002). The direct effects of fishing, such as changes in abundance or age/size distribution, are one of the principal objectives of study in exploited cephalopod stocks (Boyle and Rodhouse, 2005); however, indirect effects have received less attention. As it has been repetitively mentioned along this PhD Thesis, *L. vulgaris* is targeted by commercial and recreational fisheries in the Mediterranean (Cabanellas-Reboredo et al., 2014a; González and Sánchez, 2002; Guerra et al., 1994; Morales-Nin et al., 2005; Turk et al., 1986), and has a high commercial value (Ulaş and Aydin, 2011). Taking the year 2009 as example, the annual catch of the commercial (trawling and small-scale ) fleet was 119.5 tons, representing  $1.5 \times 10^6$  € (<http://www.wwww.agriculturaipesca.caib.es>). The largest percentage of the catch is taken by the trawl fleet (unpublished data from D.G. Pesca, Govern de les Illes Balears: Department of Fisheries, Balearic Islands Government 2009). Although the landings of the small-scale fleet (hand-line jigging with lights attraction, seine fishing and a few sporadic catches by trammel net) are smaller than those of the trawl fleet, the squid harvested by this fleet are of better quality and have a higher economic value on the market (unpublished data from D.G. Pesca and personal observations).

The recreational fishery also targets squid (Chapter 4; Cabanellas-Reboredo et al., 2014a). Recreational fishing is one of the main leisure activities in the Balearic Islands, and *L. vulgaris* is one of the most important target species of this fishery (Cabanellas-Reboredo et al., 2012b, 2014a; Morales-Nin et al., 2005). Squid are caught using line jigging (Cabanellas-Reboredo et al., 2014a; Moreno et al., 2013a; Pierce et al., 2010). In Mallorca, anglers use vertical jigging (by hand or by rod-and-reel) and trolling (Chapter 4).

Therefore, conflicts can arise due to the fact that it being exploited by both the commercial and recreational fisheries. In addition, the most valued squid are exploited by the small-scale fishery and the recreational fishery using the same gear (line jigging). Squid are trapped when they try to catch the lure with their tentacles. However, an unknown but possibly substantial number of squid are able to escape but one or both of their tentacles are amputated (Fig. 6.1).

The rate of tentacle drop off is unknown for *L. vulgaris*, but interviews with anglers and fishermen (unpublished data obtained in the CONFLICT research project CGL2008-958) as well as the data obtained during experimental fishing sessions (Chap-



Figure 6.1: Some examples of broken tentacles caused by fishing with jigs.

ter 5) suggest that it occurs frequently in the Balearic Islands. This phenomenon (tentacle drop off) has already been reported for other squid (Chen et al., 2008; Chen, 1996; Kurosaka et al., 2012), but in studies aimed at improving fishing technology (Kurosaka et al., 2012; Sun and Chen, 1996). We expect that tentacle drop off has some negative outcomes for the condition and survival of the injured squid because squid would lose predation capability (Hanlon and Messenger, 1996; Hurley, 1976). Therefore, tentacle drop off may lead to an unreported fishing mortality (ghost fishing; Matsuoka et al., 2005) and/or a reduction in fitness. Both processes deserve more attention in order to improve the management of this fishery. In this Chapter we compare the predation capability and behaviour of injured *vs.* uninjured squid under controlled laboratory conditions and discuss the outcomes on the squid fishery assessment.

## 6.3 Material & Methods

Experiments in controlled laboratory conditions with squid were conducted at the Aquaculture Station of LIMIA (Balearic Government, Andratx, Spain) between April and July 2010. Experimentation with captive squid has been used to describe different life history traits of squid (Hanlon, 1978; Hanlon and Messenger, 1996; O'Dor et al., 1977, 1995), including behavioural features (Hanlon and Messenger, 1996; Porteiro et al., 1990). It is difficult to keep squid in captivity in good condition (Gonçalves et al., 2009; Hanlon and Messenger, 1996). Fortunately, most of the specificities of *L. vulgaris* are known (Lipiński, 1987; Turk et al., 1986; Vidal et al., 2005; Villanueva, 2000).

### 6.3.1 Collection and transport

Adults of the European squid *L. vulgaris* were caught during experimental angling sessions at sunset because catch rate reaches at the maximum during this period (Chapter 3 & 5; Cabanellas-Reboredo et al., 2012a,b). Angling sessions were done using line jigging (Fig. 6.2A) because this method minimises stress and damage (Gonçalves et al., 2009; O'Dor et al., 1995; Porteiro et al., 1990). Squid were placed into a 100 l tank as soon as they were caught (Fig. 6.2B & C). A bilge pump renewing 750 l of seawater per hour ensured that the oxygen and temperature levels were safe and prevented ink from accumulating (Chabala et al., 1986). Once at port, squid were transported by car in the same tank to the laboratory. An air pump maintained the optimal oxygen level during the journey, which lasted no more than 5-7 min. The squid were placed in the experimental tanks immediately on arrival (Fig. 6.2D-F). Extreme care was taken during handling not to damage the gladius and the skin, which are very fragile (Hanlon, 1990).

### 6.3.2 Experimental settings

The LIMIA facilities have an open circulation system that collects water directly from the sea. This water is stored in a well where it is maintained at similar conditions throughout the year. Temperature ( $20.53 \pm 0.08$  °C), pH ( $7.69 \pm 0.01$ ), salinity ( $37.29 \pm 0.49\%$ ), some metals (Fe  $< 0.001$  mg l<sup>-1</sup> & Mn  $0.21 \pm 0.02$  mg l<sup>-1</sup>) and nitrogen levels were monitored twice a month and remained constant during the experiment. Ammonia, nitrite and nitrate all remained at undetectable level, below 0.001 mg l<sup>-1</sup>.

The experiments were carried out in identical 300 l rectangular tanks (1.03 m long,



0.73 m wide and 0.56 m high; Fig. 6.2D-F). The seawater renewal rate was  $144.78 \pm 15.67$  l h<sup>-1</sup>. Following the suggestion made by Gonçalves et al. (2009) for *L. forbesi*, all experiments were illuminated indirectly to simulate the conditions experienced by wild squid (Guerra, 1992). Tanks were covered by an opaque lid and received diffuse light from a small window with an 8:00-20:00 daily photoperiod. Fluorescent lights provided a dim indirect light the rest of the time. The tanks remained uncovered during the experiments. After each trial, the tanks were cleaned. The stress suffered by the squid was minimised.

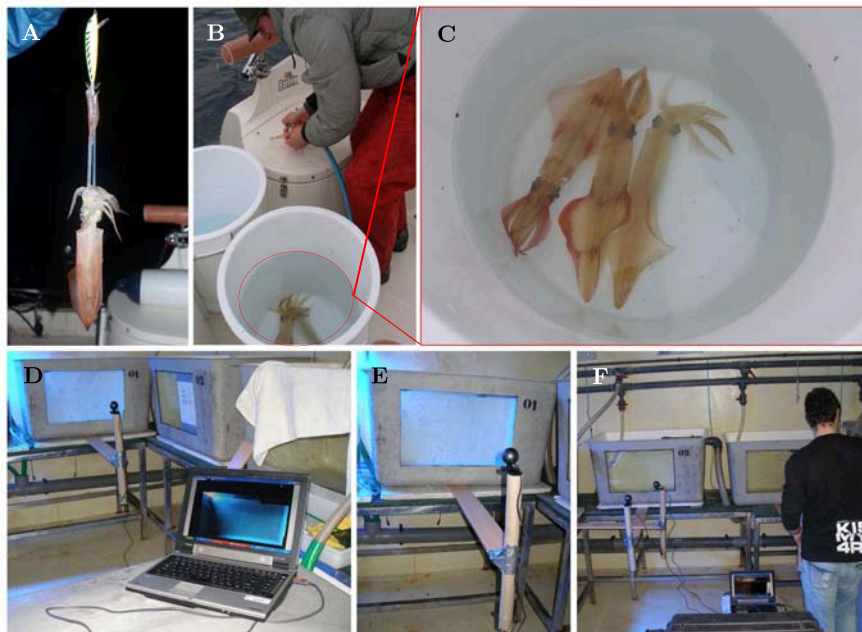


Figure 6.2: Sampling logistics: (A) Adult of *L. vulgaris* captured by line jigging. (B) Squid placed into a 100 l tank (D) Detail of squid confined. (D-F) Infrastructure developed for the experiments in captivity.

A Logitech QuickCam E3500 was deployed above the experimental tanks. The signal from the camera was recorded and allowed us to measure all the variables of interest (e.g., number of attacks; see below Sections 6.3.3 & 6.3.4) without disturbing the behaviour of the squid.

Two prey with different degrees of mobility and thus needing different predation tactics, the sea bass *Dicentrarchus labrax* Linnaeus (1758) and the common prawn *Palaemon serratus* Pennant (1777), were chosen to represent the two main types of potential prey of squid (Pierce et al., 1994; Rocha et al., 1994; Fig. 6.3). Live prey of the same size were provided throughout the experiments. The mean fish length ( $\pm$

SD) (*D. labrax*) was  $10.07 \pm 1.43$  total length (cm) and mean weight was  $12.23 \pm 2.25$  (g) ( $n = 100$ ). *P. serratus* had a mean carapace length of  $0.98 \pm 0.05$  (cm) and weight of  $0.70 \pm 0.11$  (g) ( $n = 100$ ).



Figure 6.3: The two types of preys selected to conduct the experiments. At left, the common prawn *P. serratus*. At right, the sea bass *D. labrax*.

All squid, once they had been placed in the experimental tanks, were acclimatised to the new conditions during 3 days (including the catch day) without feeding. It is assumed that after this period the starvation level had been standardised (Fiorito and Gherardi, 1999; Hanlon and Messenger, 1996). Preliminary trials confirmed that after 3 days all squid showed similar behaviour (i.e., the squid attacked the two prey types with a hungry attitude).

A total of 15 squid were used in the two sets of experiments. They were submitted to exactly the same handling in order to standardise the trials. All the experiments were conducted during the day, generally between 08:00 and 13:00. Two kinds of experiments were carried out: individual tests and prey-selectivity tests. At the end of the experiments the squid were euthanized by rapid decapitation (Boyle, 1991; Moltschanivskyj et al., 2007), and the dorsal mantle length (DML), body weight (BW), sex and sexual maturity stage (scale described in Boyle and Ngoile, 1993) were recorded. The squid showed some variability in DML ( $18.18 \pm 2.35$  cm), BW ( $161.14 \pm 55.41$  g) and maturity stage (stages II-III maturing or IV mature), and therefore they were randomly assigned to the different experiments and treatments to avoid any bias related to size, maturity stage or sex. All squid survived for the time needed to complete the trials.

### 6.3.3 Individual experiments

The individual experiments consisted of monitoring the number of attacks and the time taken to successfully catch a prey item. Predation time was not calculated from when the prey was released but from when the squid adopted hunting morphology and behaviour (Fig. 6.4). That is, the squid changed from transparent to red due to hunting excitation. The tips of the tentacles also turn red (Hurley, 1976). Similarly, the number of attacks was defined as the number of times the squid shot out its tentacles in an attempt to seize the prey. For the squid without tentacles, the number of attacks was considered to be the number of times the squid rushed quickly towards the prey.

Independent experiments were carried out using the two prey types (fish and shrimp). A before-after (BA) design was adopted (Fig. 6.5). In a first step (*before*; day 4 of the experiment), all squid were allowed to hunt with both tentacles. After this first step, one or two tentacles were cut off (one-tentacle treatment or no-tentacle treatment) to simulate how tentacles drop off due to fishing. The squid in the control treatment were subjected to similar handling as if their tentacles had been cut off. The squid had an extra acclimatisation day in order to assimilate the damage and stress due to the amputation and to standardise the hunger level again. In a second step (*after*; day 6 of the ex-

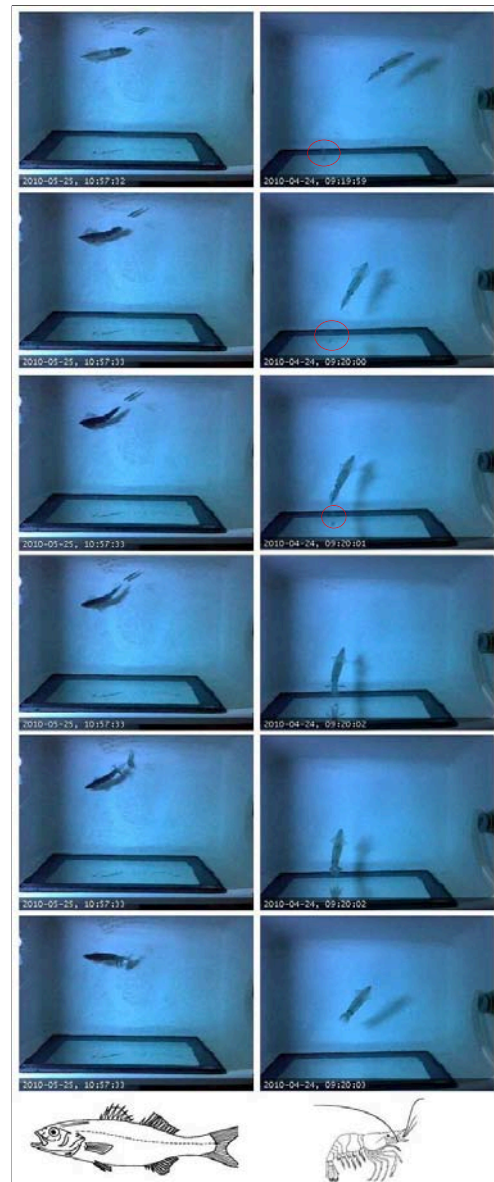


Figure 6.4: Sequence of squid attack on fish (left sequence) and shrimp (right sequence) captured by a Logitech QuickCam E3500 deployed above the experimental tanks.

periment), the squid were allowed to hunt with both tentacles (control squid), with 1 tentacle (one-tentacle squid) or without tentacles (no-tentacle squid).

### 6.3.4 Prey-selectivity test

The prey-selectivity experiment was carried out on day 7 of the experiment (Fig. 6.5). This experiment consisted in offering one fish and one shrimp simultaneously to the squid and recording which prey was caught first. Assuming that the two kinds of prey were equally available, the prey that a predator attacked first was considered “preferred” (Staudinger and Juanes, 2010).

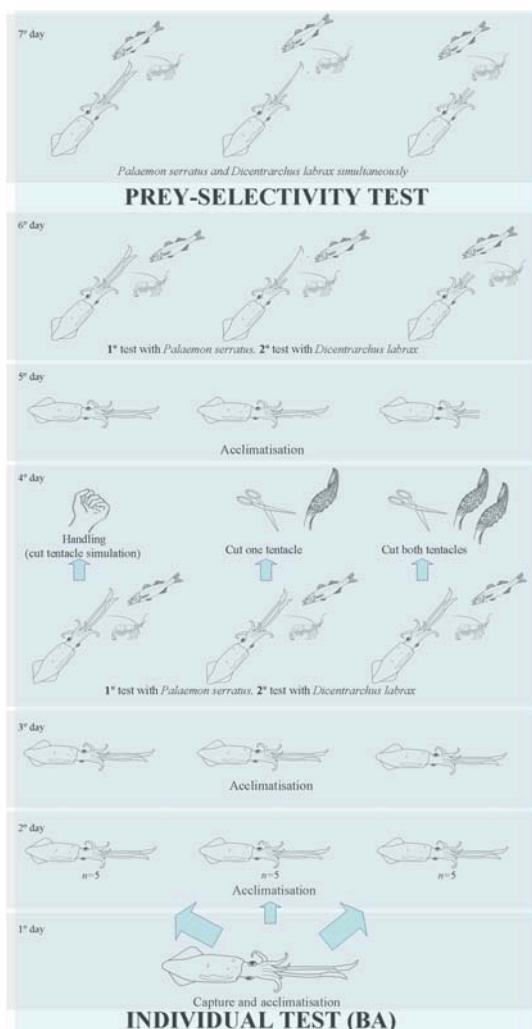


Figure 6.5: Scheme of the experimental design.

### 6.3.5 Statistical analysis

A generalised linear mixed model (GLMM; Pinheiro and Bates, 2000) was used to analyse the differences in predation time and attack number between the different treatments (control squid, one-tentacle squid and no-tentacle squid). The specific model used was:

$$Y_{ijk} = T_i + (T * BA)_{ij} + I_k + e_{ijk},$$

where  $Y$  is the dependent variable (predation time or attack number). Treatment ( $T$ ;  $i = 1 - 3$ ) and before-after ( $BA$ ;  $j = 1 - 2$ ) were considered as fixed factors, as well as their interaction.  $T_{i=1,2,3}$  denotes the treatment (control, one-tentacle and no-tentacle squid). This model takes into account that a squid in good condition will be able to catch the prey quicker than the mean, not only before but also after amputation. The individual effects ( $I_{k=1-15squid}$ ) are assumed to be a normally distributed variable with zero mean and variance  $\sigma_{ind}^2$ :

$$I \sim Normal(0, \sigma_{ind}^2).$$

Finally,  $e_{ijk}$  is a normally distributed error with zero mean and variance  $\sigma^2$ :

$$e \sim Normal(0, \sigma^2).$$

The only effect of interest is the interaction  $T*BA$ . Differences between treatments ( $T$ ) can be related to a non-random distribution of squid among treatments. Similarly, before-after differences can be related to unknown effects of the experimental design. For example, all squid could improve their reaction time if the acclimatisation time was increased. However, the interaction between these two sources of variability can only be attributed to the effects of losing a tentacle. The variable predation time was analysed assuming normally distributed residuals. Therefore, normality was tested and the raw data were transformed using log or Box-Cox transformation (depending on fish or shrimp experiments; see Section 6.4). The number of attacks was assumed to follow a Poisson distribution. The parameters of the model were estimated using the *lmer* function from the *lme4* library (Bates and Maechler, 2010). *Lme4* is an R package library (<http://www.r-project.org>). The significance of the interaction  $T*BA$  was assessed by comparing the full model (including the interaction) with the additive model (only including  $T$  and  $BA$ ). The models were compared using the Akaike

Information Criterion (AIC). The confidence intervals of the fixed effects were estimated using a Monte Carlo Markov Chain (MCMC) iterative procedure as implemented in the function *pvals.fnc* of the *lme4* library. The MCMC sampling was used to sample (fixed) parameters from their expected distributions conditional on distribution of (typically) subsets of related samples (random factors). Thus, the variances and covariances of the random effects are properly reflected on the variation of the fixed parameter (Baayen, 2008). This function was used to estimate the variance and confidence intervals of the different treatments (fixed effects).

A two-step analysis was carried out for the prey-selectivity data. First, a  $\chi^2$ -test was performed to determine differences among treatments in the proportion of squid that preferred fish. As no significant differences were found (see Section 6.4), all squid were pooled and the probability of obtaining the observed proportion of squid that preferred fish was calculated assuming (null hypothesis) no preference for a prey type (binomial distribution with  $p = q = 0.5$ ).

## 6.4 Results

In summary, the results showed that all squid clearly preferred feeding on fish, but the disabled squid presented a decrease in depredation effectiveness on this fast moving prey. However, the depredation efficiency for slow moving preys (e.g., shrimps) was not reduced (Fig. 6.6).

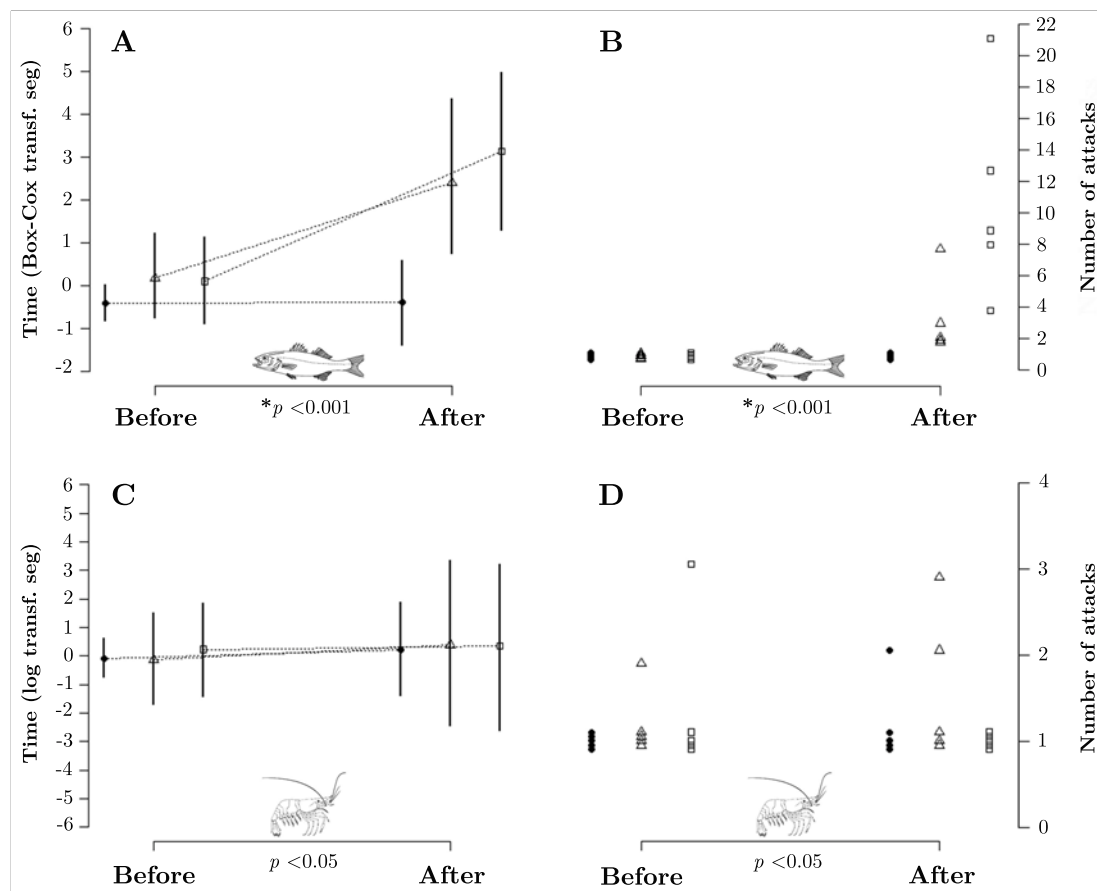


Figure 6.6: Results of the individual tests ( $n = 15$  squid: 5 control, 5 one-tentacle and 5 no-tentacle squid): (A) predation time in seconds (Box-Cox transformed values) on Sea Bass *D. labrax*; (B) number of attacks on *D. labrax*; (C) predation time in seconds (logarithms transformed values) on common Prawn *P. serratus*; (D) number of attacks on *P. serratus*. Symbols represent: ●, control squid; Δ, one-tentacle squid; and □, no-tentacle squid.

The individual tests demonstrated that for predation time on fish, the interaction  $T^*BA$  was significant (Likelihood ratio test:  $p < 0.001$ ; The AIC value of the model with the interaction term is 45.4 while the corresponding AIC of the model without the interaction term is 70.7), which strongly suggests that tentacle drop off has an effect on predation time. The results for the number of attacks are the same (Likelihood ratio

test:  $p < 0.05$ ; The AIC value of the model with the interaction term is 26.8 while the corresponding AIC of the model without the interaction term is 28.9). Before amputation all the squid had a similar predation time. The estimated values for the fixed effects after back transformation the Box-Cox transformation are 0.73 s for controls, 1.11 s for one-tentacle squid and 1.21 s for no-tentacle squid. All squid executed the same number of attacks before amputation (1 attack in all cases). After amputation, only the control squid showed similar values to those before amputation (1 attack and 0.66 s). The disabled squid (one-tentacle and no-tentacle) had a significantly higher predation time and number of attacks (48.97 s and 3.4 attacks, 352.17 s and 11.0 attacks respectively; Fig. 6.6A & B). In the individual tests on shrimp as prey, the interaction  $T^*BA$  showed no significant differences in the number of attacks (Likelihood ratio test:  $p > 0.05$ ; The AIC value of the model with the interaction term is 15.15 while the corresponding AIC of the model without the interaction term is 18.33), or predation time (Likelihood ratio test:  $p > 0.05$ ; The AIC value of the model with the interaction term is 94.7 while the corresponding AIC of the model without the interaction term is 91.1). The predicted (fixed effects) predation time was similar for control (before: 0.86 s; after: 1.34 s), one-tentacle (before: 1.23 s; after: 1.21 s) and no-tentacle squid (before: 1.13 s; after: 1.13 s; Fig. 6.6C & D).



## 6.5 Discussion

The laboratory controlled experiments demonstrate that squid that are missing one or both tentacles show reduced predation effectiveness on fast moving prey (i.e., fish) in comparison with control two-tentacle squid. The tentacles (the main predation tools that permit the squid to seize their prey) combined with the arms (tools to secure their prey and bring their food to their mouth) are an efficient predation system (Guerra, 1992; Hanlon and Messenger, 1996; Hurley, 1976; see Fig. 6.4 & Fig. 6.7). Consequently, it was expected that the loss of one or both tentacles would lead to an increase in the number of failed attacks and predation time, and therefore a higher energy expenditure (O'Dor and Webber, 1991; Webber et al., 2000). However, there were no differences between the predation effectiveness of the injured and control squid on slow moving prey (i.e., shrimp). For this prey, the predation tactics of the injured squid are based on using their arms only and coming in closer to the prey before launching the attack (see predation sequence performed by squid on this type of prey; Fig. 6.4). This strategy is only efficient for slow moving prey (Guerao and Ribera, 1996). The tactic of using the arms rather than the tentacles to catch small and slow prey has been reported for other squid species (Hanlon and Messenger, 1996; Hurley, 1976). However, for catching fast moving prey (Claireaux et al., 2006), using the tentacles is clearly more efficient.

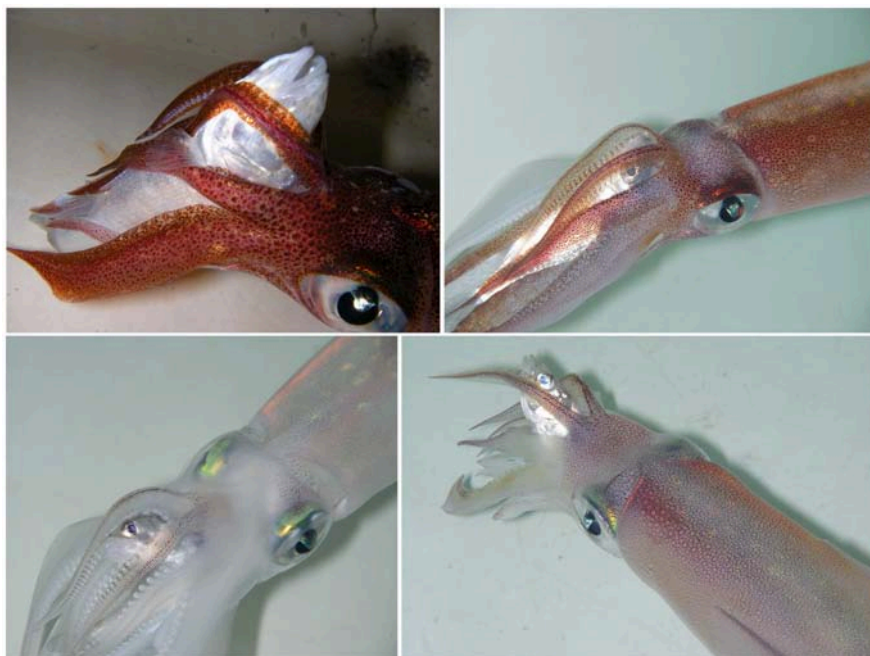


Figure 6.7: Detail of the immobilized fish by squid arms during the experiments.

Nevertheless, the prey-selectivity tests demonstrated a general preference for fish irrespective of the treatment. Fish seem to be the main component of the diet of *L. vulgaris* (between 70 and 90%; Coelho et al., 1997; Guerra, 1992; Pierce et al., 1994; Rocha et al., 1994). Squid invest large amounts of energy in movement (O'Dor, 1988b; O'Dor and Webber, 1991; Trueman, 1980), and thus have a high metabolic rate and a high energy expenditure (Boucher-Rodoni and Mangold, 1989; O'Dor, 1988a; O'Dor et al., 1995). Therefore, the preference for fish could be related to a better feeding-biomass/energetic-effort trade-off (attacks number or predation time) regardless of the disadvantages in terms of the difficulty of hunting. Our results suggest that disabled squid in the wild might change their diet to include a larger proportion of slow moving prey, such as shrimp. This conclusion is based on four arguments: i) the predation effectiveness of the injured squid decreases when they hunt fast moving prey, but injured and uninjured squid have a similar effectiveness in the case of slow moving prey; ii) the shoaling behaviour of squid probably implies some intraspecific competition for food (Hanlon and Messenger, 1996); therefore, a change in diet could facilitate the survival of the injured squid in the wild; iii) Shrimp and crabs are also part of the diet of the European squid (Coelho et al., 1997; Guerra, 1992; Pierce et al., 1994; Rocha et al., 1994); thus, we are not proposing that injured squid prey on new items but rather

change the proportion of slow *vs.* fast moving prey; iv) Squid display high behavioural plasticity (Hanlon and Messenger, 1996), and thus injured individuals might adapt to a new situation by changing their diet (González and Guerra, 2008).

Although the feeding-biomass/energetic-effort rate is probably less efficient in a shrimp-based diet, this could be the only way to survive in a scenario in which injured squid must compete with uninjured squid. Survival after the loss of their tentacles has been reported for other Ommastrephid squid (Okiyama, 1993). Specifically, the loss of another important predation tool (the clubs) has been reported not to be fatal (Bolstad and O'Shea, 2004). However, in these cases (Bolstad and O'Shea, 2004; Okiyama, 1993) the drop off rate is unknown, and therefore how many injured squid achieve long-term survival is also unknown. Short-term survival could be very high because in our case 100% of the squid survived after they had lost one or both tentacles.

The shift from a fish-based to a shrimp-based diet might reduce the squid's biological condition (Dawe, 1988; Pecl, 2004), which in turn could lead to increased long-term mortality. Several catch-and-release studies report the relevance of post-release mortality (Alós et al., 2009), its implications for fish condition (Hall et al., 2009) and its relevance for fisheries management (Coggins Jr. et al., 2007; Cooke and Schramm, 2007). In the case of squid, line jigging may result in the loss of one or both tentacles which in turn causes a decrease in the squid's predation effectiveness on fast moving prey. Moreover, it might also increase long-term mortality. This indirect mortality and/or reduction in fitness should be considered as ghost fishing and should be added to the mortality estimates based on the catches reported by the professional and recreational fleets (Erzini et al., 2008; Matsuoka et al., 2005).



## Chapter 7

# Estimating total harvest of the recreational squid fishery at Palma Bay

### 7.1 Abstract

The harvested biomass extracted by recreational fishing is still widely ignored in many fisheries around the globe. One of the reasons may be that estimating the biomass harvested or fishing mortality in recreational fisheries is very challenging, and usually demands sophisticated social-ecological approaches. In fact, although the distribution of the fishing effort on time and space, and the large heterogeneity of the anglers skills have been largely recognized to affect total harvest estimations, these two key factors are usually not considered when estimating total harvest. In this Chapter, we propose a new framework to estimate total harvest in recreational fisheries. This approach combines detailed estimates of effort with estimates of catches per unit of effort (CPUEs) that are specific for each one of the types of anglers considered. We first modelled the spatial and temporal structure of fishing effort using a ZIP model to estimate the number of anglers per km<sup>2</sup> of the fishery using visual census data of the recreational boats (Chapter 4). Second, we categorized anglers into three types according to their experience and skills using an off-site interview survey. Anglers from a second survey (an on-site creel survey) were classified in the same three types and type-specific CPUE estimates were obtained from a GLM model including also some environmental co-variables (Chapter 5). Finally, we matched for every day of a given year (2010): i) the predictions of daily fishing effort; ii) the predicted catch

rates per angler type and; iii) the proportions of the three types of anglers, in order to estimate the daily harvest and its confidence interval (CI) which were estimated by bootstrapping. The results obtained for the recreational squid fishery at Palma Bay suggests that this activity harvested around 20.5 tonnes during 2010, which represented an impressive 34% of the total squid landings by the entire commercial fleet of Mallorca Island (59.5 tonnes). The precision of the total harvest biomass was notably improved when considering the different types of anglers. In fact, the harvest estimate was also reduced when considering the heterogeneity of angler's skills (20.5 tonnes, 95% CI: 19.5 to 21.7) or ignoring them (26.6 tonnes, wider 95% CI: 25.2 to 28.2) which highlighted the importance of incorporating the anglers heterogeneity in recreational fisheries management. Our modelling process is innovative; it is fully based on fishery-independent data, can be easily implemented to any other fishery and has a reasonable predictive ability. Therefore, we suggest that it could be useful for managers and fisheries scientists worldwide that deal with recreational fisheries.

KEY WORDS: Recreational fishery, *Loligo vulgaris*, Fishing effort, Angler typology, Catch rates, Total harvest.

## 7.2 Introduction

Fishing mortality and total harvest are key parameters for characterizing the population dynamics of exploited stocks (Anderson et al., 2008; Hilborn and Walters, 1992; Hsieh et al., 2006; Neubauer et al., 2013). Usually, harvest from the recreational fishing is neglected and only the harvest from the commercial fleets is accounted for (Lewin et al., 2006; Pawson et al., 2008). However, there is a growing evidence of the relevance of the recreational fisheries on the decline of some exploited fish stocks (Coleman et al., 2004b; Cooke and Cowx, 2004). To disregard this mortality component may give an overoptimistic image of the stock status and drive it to overfishing (Post et al., 2002). Moreover, as we introduced in Chapter 1, the effects of recreational fishing may go beyond a mere reduction of abundance (Coleman et al., 2004b; Cooke and Cowx, 2004). Recreational fishing gears are size selective, which may imply severe (non natural but human-driven) selection pressure on a number of life history traits (Allendorf and Hard, 2009; Sutter et al., 2012). The set of life history features favoured by recreational fishing is similar to the produced by most commercial gears: increased juvenile growth, reduced adult size, to move sexual maturity toward younger age (Alós, 2013; Sutter et al., 2012). This fishing-related syndrome may cause relevant shifts in population dynamics and on the reference points (e.g., on the Maximum Sustainable Yield; MSY) that would ensure stock sustainability (Conover and Munch, 2002; Enberg et al., 2009; Kuparinen and Hutchings, 2012; Matsumura et al., 2011).

Therefore, to provide precise and accurate estimates of harvest is a pivotal question when dealing with the management of recreational fishing (Hartill et al., 2012; Steffe et al., 2008). Harvest ( $H$ ) could be simply estimated by combining effort ( $E$ ) and catches per unit of effort ( $CPUE$ ):

$$H = E \times CPUE,$$

but ignoring the huge heterogeneity of both (effort and CPUE) produces naïve, severely biased estimates. To estimate the harvest attributable to the recreational fishing is specially challenging. The main problem to be concerned with is the large amount anglers in comparison with the relatively reduced number of commercial fishermen (Cooke and Cowx, 2004). In addition, commercial fisherman is usually subjected to mandatory surveys aimed to provide data on the spatial and the temporal distribution of effort. Moreover, the progressive implementation of tracking devices such as vessel monitoring systems (VMS) provides detailed information of the temporal and spatial distribution of the fishing effort (Bertrand et al., 2008; Gerritsen and Lordan, 2011; Mills et al.,

2007). Proper combination of these data and fisheries-independent surveys should improve the estimation of the reference points needed for stock management (Beare et al., 2005; Cotter and Pilling, 2007; Mesnil et al., 2009). Despite this possibility, the spatial and temporal variability in effort are usually ignored even for the commercial fisheries. In recreational fisheries, virtually no data are available and the spatial distribution of the fishing effort has been only considered very recently (e.g., Cabanellas-Reboredo et al., 2014a; Hunt et al., 2011; Post and Parkinson, 2012). However, some fishery collapses has been related to inappropriate assumptions on the spatial distribution of the fisheries (e.g., Lorenzen et al., 2010; Post et al., 2008).

Similarly to the case of effort, to report catches is mandatory for most of the commercial fleets but to obtain catch data for recreational fleets is even more elusive. Anglers are not only orders of magnitude larger in number than commercial fishermen but also less accessible and more heterogeneous (Arlinghaus et al., 2013). Accordingly, full censuses of all the anglers are almost always impossible (McCluskey and Lewison, 2008). In consequence, the conventional approach for estimating recreational harvest is based in designing proper sampling programs from which to upscale reliable estimates for all the population of anglers (Pollock et al., 1994). However, heterogeneity is huge (e.g., between days, access points, zones, type of fishing modality, angler expertise and motivations) which may imply large biases (Arlinghaus et al., 2013; Council, 2006; Hunt, 2005; McCluskey and Lewison, 2008; Pollock et al., 1994, 1997). Creel surveys (on-site surveys of anglers, usually at the access points; the angler is asked about the target species, catch, time spent fishing and any other relevant question) may provide reliable information about both, effort and catches, which may be combined to estimate harvest (Hartill et al., 2012; Pollock et al., 1994) but relatively complex, stratified sampling design is needed (Griffiths et al., 2013; Pollock et al., 1994, 1997; Rocklin et al., 2014) and proper error propagation (needed for estimating precision) requires sophisticated statistical methods (Lockwood, 1997; McCormick et al., 2013).

In this Chapter, an alternative approach is proposed based on the detailed knowledge available for the spatio-temporal distribution of the recreational squid (*L. vulgaris*) fishing effort (Chapter 4; Cabanellas-Reboredo et al., 2014a). Briefly, model-based estimates of effort (number of boats) have been obtained for each one of the  $173 \times 1$  km<sup>2</sup> cells of the spatial scenario considered (Palma Bay), and for each day of one year. The model (a Zero Inflated Poisson model) combines a range of explanatory variables, which are aimed to related effort with the main motivations of anglers (*Fishing quality, Costs, Facility development, Environmental quality, Interactions among anglers, and Regulations*; see Cabanellas-Reboredo et al., 2014a; Hunt, 2005). Given such de-



tailed estimates, harvest can be independently estimated for each cell and day, provided that reliable estimates of CPUE are available. In the case study (the squid fishery at the Palma Bay), model-based estimates of CPUE from four environmental variables (sea surface temperature, windspeed, atmospheric pressure, new moon phase) are also available (Chapter 5; Cabanellas-Reboredo et al., 2012b) but only for a given type of angler. Nevertheless, anglers, and thus CPUEs are largely heterogeneous (Johnston et al., 2010). Obviously, skill and expertise affects CPUE and influence harvest estimate (e.g., Fulton et al., 2011; Johnston et al., 2010, 2013). Therefore, to segment the recreational population into a relatively small number of angler types has been recommended to simplify the large heterogeneity of this complex sector (Ditton, 2004). Each group of anglers has his own motivations, satisfactions and preferences (Arlinghaus, 2006; Arlinghaus et al., 2008a; Connelly et al., 2001; Kyle et al., 2007; Spencer and Spangler, 1992). These features should be able to summarize angler skills, experience and, ultimately, CPUE (Fisher, 1997; Hunt et al., 2002; Johnston et al., 2010, 2013).

In the present Chapter, a method for segmenting the anglers into three groups (*less-skilled*, *medium-skilled*, *very-skilled*) is proposed based on an off-site interview. This method allows precise and accurate prediction of group membership for the anglers intercepted during an independent creel survey which consist in the same off-site interview plus and additional question on catches. These data allow to enlarge the CPUE model proposed in Chapter 5 from only one angler type to the three types of anglers considered. Overall, the proposed approach takes into account the main sources of variability in both effort and catches. Moreover, uncertainty was propagated using appropriate bootstrap method in order to derive not only point estimation for harvest but also a reliable confidence interval, the latter being even more relevant for advising management (Dortel et al., 2013).

## 7.3 Material & Methods

### 7.3.1 Study case

Detailed description of the jigging fishery of the European squid *L. vulgaris* at Palma Bay is provided in the previous Chapters (Chapter 1, 3, 4, 5 & 6). However, it is important to highlight here two relevant features of this fishery: i) the duration of a fishing journey is nearly constant (2 hours around sunset; Chapter 4). Squid are not vulnerable at day time because they plausibly are at reproductive behavioural state and ignore the lures. Around sunset squid shift to feeding behaviour state and then became vulnerable but only for a few hours because at nighttime squid would be unable to detect the lures (Chapter 3 & 5; Cabanellas-Reboredo et al., 2012a,b); ii) Squid anglers cluster at spatially very well-defined fishing spots (Fig. 7.1), which are well known by all the participants (Chapter 4).

Spatial differences in catches between and within these fishing spots seems to be non-significant (Chapter 5; Cabanellas-Reboredo et al., 2012b). This pattern is the expected outcome when anglers select *a priori* the optimal sites for maximizing catches. Based in these facts, only between-day and between angler variability has been considered for estimating CPUE (see below).

### 7.3.2 Harvest estimation

As mentioned above, Total harvest ( $H$ ) was estimated by the product of the effort ( $E$ ) and harvest rate ( $CPUE$ , or catches per unit of effort):

$$H = E \times CPUE.$$

Effort predictions for every day of the year ( $i$ ), and for each one of the  $j$  1 km<sup>2</sup> cells ( $j = 1$  to 173) of the considered spatial scenario (Fig. 7.1) are available from model-based predictions from a ZIP model (Chapter 4; Cabanellas-Reboredo et al., 2014a).  $CPUE$  are available for every day of the year ( $i = 1$  to 365) from model-based estimations from a Poisson model (Chapter 5; Cabanellas-Reboredo et al., 2012b). As mentioned above,  $CPUE$  seems to be spatially independent provided that an angler has chosen the proper fishing grounds. Thus, we considered:

$$H_{ij} = E_{ij} \times CPUE_j.$$

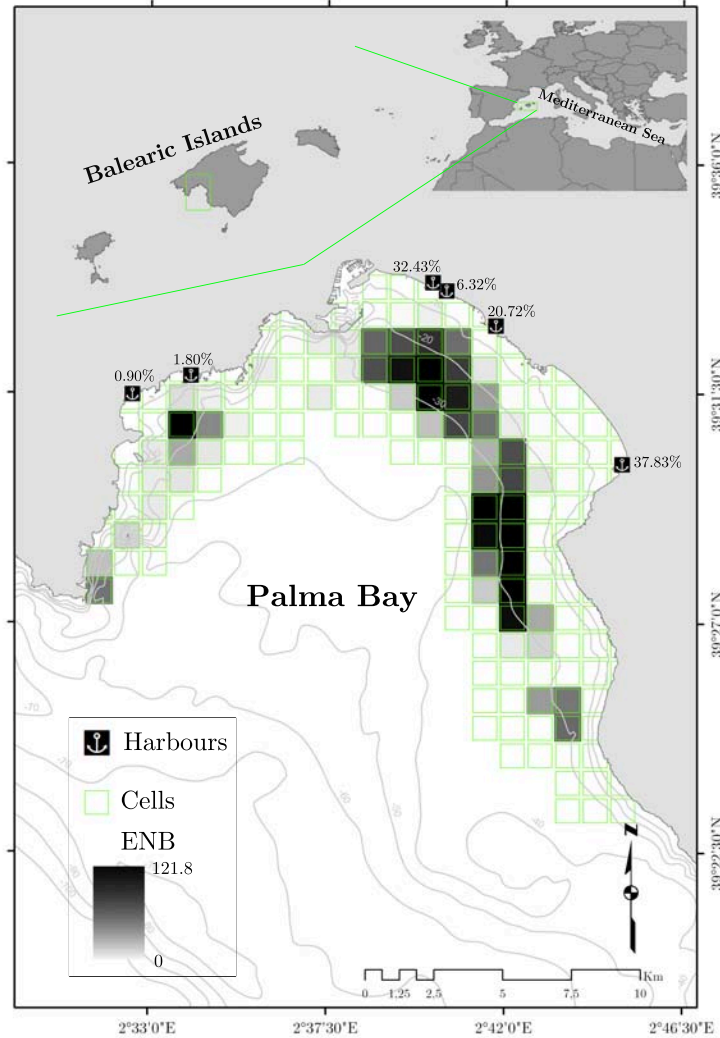


Figure 7.1: Study area. Each anchor symbol (harbours) shows the % of the total 110 on-site creel surveys performed. Green squares represent the grid of  $173 \times 1 \text{ km}^2$  cells into which the geographic area was divided for the study reported in Chapter 4 (Cabanelas-Reboredo et al., 2014a). ENB shows the expected number of recreational boats estimated by the model proposed in Chapter 4 (Cabanelas-Reboredo et al., 2014a).

In addition, we explicitly considered that CPUE may differ depending on the angler type  $k$  ( $k = 1$  to 3; see details of angler segmentation below in Section 7.3.6):

$$H_{ijk} = E_{ijk} \times CPUE_{jk}.$$

Therefore, the cumulated harvest for one year and for all the considered scenario will

be given by:

$$H = \sum_{i=1}^{365} \sum_{j=1}^{173} \sum_{k=1}^3 E_{ijk} CPUE_{jk}.$$

However, this equation can be rewritten as (Fig. 7.2)

$$H = \sum_{i=1}^{365} \sum_{j=1}^{173} \sum_{b=1}^{B_{ij}} \sum_{f=1}^{F_i} \sum_{k=1}^3 H_{ijb fk}.$$

The assumption made are:

- i) The effect in a given day and cell depends only on the environmental conditions of this day and cell (Chapter 4).
- ii) The harvest of a given type of angler depends only on the environmental conditions of the day and are independent of the cell, in the sense that a given angler would capture (in a given day) the same averaged number of squid at two different cells, provided that this two cells have the same environmental characteristics (Chapter 5).
- iii) The harvest of an angler in a given day and cell depends only on the angler type.
- iv) Harvest per angler in a given day is equivalent to  $CPUE_i$  provided that the duration of a fishing journey is always the same ( $\approx 2$  hours; Chapter 4 & 5).
- v) The percentage of anglers from each one of the three types is constant in the time and space (35-53-18% for the anglers *emphless-skilled*, *medium-skilled* and *very-skilled* respectively). This assumption is justified bellow at Section 7.3.4.

### 7.3.3 Fishing effort

Accordingly with the nearly constant (between seasons and between anglers) duration of a fishing journey (Chapter 5; Cabanellas-Reboredo et al., 2012b), total effort (i.e., number of anglers in the day  $i$  and cell  $j$  by now ignoring angler type but see below) was expressed as number of boats per day and estimated from:

$$E_{ij} = \sum_{b=1}^{B_{ij}} F_{ijb},$$

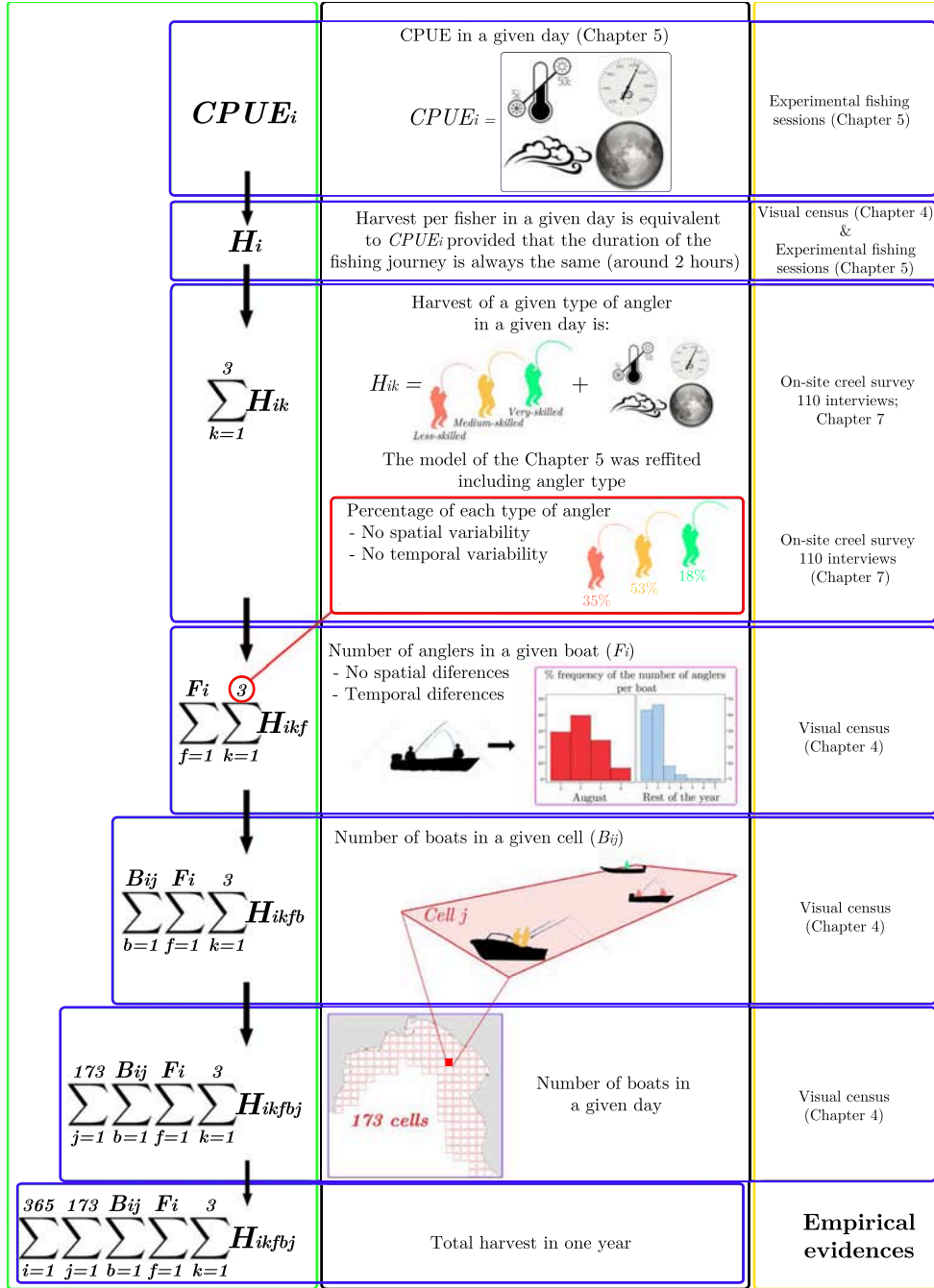


Figure 7.2: Overview of the analytical strategy.

where  $B_{ij}$  is the predicted number of boats in the day  $i$  and the cell  $j$  and  $F_j$  is the number of anglers per boat. Predicted  $B_{ij}$  values those obtained from the space- and time-explicit model in Chapter 4 (Cabanelas-Reboredo et al., 2014a). In order to

obtain not only point estimates but reliable confidence intervals of  $B_{ij}$ ,  $N$  ( $N = 1,000$ ) random bootstrap samples were produced taking into account, not only the uncertainty in the model parameters, but also the three levels of stochastic variation considered by the model (cell, day and unstructured, residual variation):

$$B_{ijn} = \bar{B}_{ijn} + \varepsilon_{day} + \varepsilon_{cell} + \varepsilon_{res},$$

where: i)  $N$  estimates of the number of boats,  $\bar{B}_{ijn}$ , (the subindex  $n$  denotes each one of the  $N$  bootstrap replicates) were obtained by combining the values of the explanatory variables for the day  $i$  and the cell  $j$  (Chapter 4; Table 4.1) and  $N$  random samples of the model parameters according to:

$$P_n \sim Normal(mean_p, \sigma_p),$$

where  $mean_p$  and  $\sigma_p$  are the mean and standard deviation of the posterior bayesian estimates of each one of the parameter of the model in Chapter 4 (Table 4.1); ii) Provided that estimates for non sampled days are needed,  $N$  random samples of  $\varepsilon_{day}$  and  $\varepsilon_{res}$  were obtained from:

$$\begin{aligned} \varepsilon_{dayin} &\sim Normal(0, \sigma_{day}) \\ \varepsilon_{resijn} &\sim Normal(0, \sigma_{res}) \end{aligned}$$

Conversely, all cells of the spatial scenario have been sampled, thus:

$$\varepsilon_{celljn} \sim Normal(\bar{\varepsilon}_{cellj}, \sigma_{\bar{\varepsilon}_{cellj}})$$

where  $\bar{\varepsilon}_{cellj}$  and  $\sigma_{\bar{\varepsilon}_{cellj}}$  are the mean and standard deviation of the posterior Bayesian estimates provided by the model (Table 4.1 in Chapter 4; Cabanellas-Reboredo et al., 2014a). Concerning the number of anglers per boat ( $F_i$ ), we first explored the existence of differences depending on week day (weekend *vs.* working day) and season (between month differences). Accordingly with the pattern detected (see Results 7.4; no differences between days and differences between August and the other months),  $N$  random samples from the empiric data corresponding to the day  $i$  (i.e., separate distribution depending if  $i$  was August or the rest of the year) was obtained by bootstrapping (function *sample* of the R package). Empirical data of the number of angler per boat comes from 1,271 actually surveyed boats from the 63 censuses described in Chapter 4 (Cabanellas-Reboredo et al., 2014a).

In summary, the output of the effort block was  $N$  random samples of the expected number of anglers ( $E_{ijn}$ ) in each cell for every day in one year.

### 7.3.4 Type of anglers in a boat

Anglers intercepted in an access point survey (APS; see details of the on-site creel survey in Appendix B) were classified into three groups (*less-skilled*, *medium-skilled*, *very-skilled*; the classification method is fully described below in Section 7.3.6). The existence of seasonal variations in the proportion of each type of angler were tested ( $\chi^2$ -test) and rejected (see Section 7.4 of results). Accordingly, the  $N$  random samples of the expected number of anglers ( $E_{ijn}$ ) in each cell for every day in one year were randomly assigned to one of the three types by bootstrapping (function *sample* of the R package) on the empirical distribution of the 110 anglers actually interviewed (on-site surveys; Section 7.3.7).

### 7.3.5 CPUE by angler type

CPUE may depend not only on the angler type but also on a number of environmental variables. In the study area, CPUE has been demonstrated to depend on sea temperature, wind speed, atmospheric pressure and moon phase (Chapter 5; Cabanellas-Reboredo et al., 2012b). Assuming the same conceptual relationship between catches and environmental variables, the total catches by angler and fishing journey obtained during the on-site survey (110 interviews; see details below in Section 7.3.7) has been refitted to the following model:

$$y = ENV + AnglerType$$
$$CPUE \sim Poisson(e^y),$$

where  $y$  is the average number of squid per journey and boat (at the *log* scale). *ENV* are the above-mentioned relevant environmental variables on squid catches (Chapter 5; Cabanellas-Reboredo et al., 2012b) and *AnglerType* is a categorical variable defining the type of angler (the classification method is fully described below in Section 7.3.6). The interaction model (i.e.,  $ENV^* AnglerType$ ) was also considered and rejected (see Results 7.4). This model was used to produce bootstrap-based estimates of CPUE for every angler type and for every day in one year. As mentioned above, at the study area, CPUE seems to be spatially homogeneous (i.e., there are not differences among the three areas which the Palma Bay was divided; Chapter 5; Cabanellas-Reboredo

et al., 2012b). The bootstrapping procedure was similar (but simpler given the model structure) to the described above for effort. The number of bootstrap-based estimates of CPUE in a give cell and day will be  $E_{ijkn}$  and point estimates and confidence intervals  $H$  was estimated from:

$$H_{ijn} = \sum_{m=1}^{E_{ijkn}} CPU E_{ijkn},$$

where  $E_{ijkn}$  is the number of anglers of each type, at an specific cell and day corresponding to the  $n$  bootstrap sample ( $N = 1,000$ ). Note that harvest ( $H$ ) and  $CPUE$  per fishing journey are equivalent because the demonstration of duration of the the fishing journey is always the same ( $\approx 2$  hours; Chapter 4 & 5).

### 7.3.6 Segmentation of recreational fleet

As it has been emphasizes before, segmentation is defined here as a method for classifying anglers within a few types given a number of angler features. These features should be able to summarize angler experience and skills and, ultimately, be able to predict potential harvest. Provided that interview-based data directly asking on harvest are especially prone to biases and uncertainty (Lyle et al., 2007; Vaske et al., 2003), we propose i) to delineate a few groups of anglers based on off-site interviews (off-site survey, OSS). Anglers are asked to answer a questionnaire that excludes any question for directly estimating harvest, ii) to build a classification tool for assigning anglers to an specific type based on the answers, iii) to test the ability of the classification tool for correctly assigning group membership. After it, a on-site creel survey (in our case, an access point survey; APS) of the same questioner have been completed and harvest have been recorded. The answers of this second interview are used for assigning each angler to a type. Then, between-type differences in harvest and any pattern of variation in the proportions of angler types can be formally tested.

In our case, 164 OSS and 110 APS questionnaires have been completed (details specified below in Section 7.3.7). Concerning OSS, between-questionnaire similarity has been determined using the Gower distance as implemented in the *daisy* function of the *cluster* library (Maechler et al., 2013) of the R package. Patterns of between-angler similarity were visualized by a Principal Coordinate Analysis (Borcard and Legendre, 2002). An increasing number of groups (between 2 and 10) have been delineated using *k-means* as implemented in the *pam* function of the *cluster* library. A classification tool (random forest; Liaw and Wiener, 2002) was parameterized using the group membership



delineated by *k-means*. Random forests were implemented using the function *randomForest* function of the *randomForest* library (Liaw and Wiener, 2002). The answers to the questionnaire were the predictor variables of the random forest. A leave-one-out cross-validation procedure was used to estimate the goodness of random forest predictions. The optimal number of groups in which can be efficiently divided the anglers by *k-means* was defined by the maximum cross-validated success rate. The existence of between-group differences in the proportions of the responses to each question were tested ( $\chi^2$ -test) and the questions showing significant departures from randomness were used to characterize the profile of each angler type.

Concerning on-site interviews (110 APS), group membership of each angler was estimated from the answers of the questionnaire. Note that APS interviews were completed when the boat comes back to the access point after a fishing journey and that they include an additional question on the catch obtained at this specific fishing journey. Catches (i.e., number of squid) were verified by the interview. Otherwise, the survey were not considered. Between-group differences in CPUE were tested (ANOVA). However, given that harvest experiences important variation depending on seasonality and other environmental variables (Chapter 5; Cabanellas-Reboredo et al., 2012b), we analyzed the difference between the harvest reported by an angler and the mean harvest expected for the day when the anglers was interviewed. Such expected harvest was estimated from the CPUE model described in Chapter 5 (Cabanellas-Reboredo et al., 2012b).

### 7.3.7 Angler surveys

CPUE are expected to vary not only due to the environmental variables affecting abundance and catchability but also depending on the anglers skills. The off-site survey (OSS) is aimed to delineate a few types of anglers according to their skills. A few preliminary interviews to some anglers with *a priori* well-differentiated skills was used for designing the OSS questionnaire, which consists in 10 questions (Appendix B).

Between October 2011 and September 2012, a total of 969 OSS interviews were completed off-site, at the Regional Government offices where anglers obtain the recreational fishing licence. It is expected that anglers intercepted constitute a random sample the recreational population. From all the interviews, only 164 went to fishing squid at least once during the last year and these questionnaires were used for defining the types of anglers (see above).

The on-site survey (access point survey; APS) are intended to estimate the actual

CPUE for the different types of anglers defined using OSS. A random sampling among different harbours was conducted (the percentage of anglers intercepted at the different harbours and Marinas are detailed at Fig. 7.1). The skipper of the boat was interviewed and only the skipper's catch was considered for the analysis (Section 7.3.5) after it was checked by the interviewer. A total of 110 surveys were completed between October 2011 and September 2012 (i.e., the same sampling period considered for OSS).

### 7.3.8 Comparing recreational and commercial harvest

Daily landings from the commercial fleet for the same period have been compared with the recreational harvest predicted in this Chapter. It is mandatory that fish sales from fisher to fishmongers must be done at a single central fish market (Palma wharf; OPMALLORCAMAR). From these mandatory records, daily squid landings from bottom trawl and small-scale fisheries (hand-line jigging, seine fishing and trammel net) were compared together. It is important to note that for the trawl fishery, the two sympatric species *L. vulgaris* and *L. forbesi* are commercialized in a pooled commercial category. As a consequence, the daily squid landings from trawl fishery included the two species. This is not a problem for small-scale fisheries since these *métiers* only capture *L. vulgaris*.

Note that recreational harvest is estimated here as number of squid day<sup>-1</sup> and commercial harvest are referred in kg day<sup>-1</sup>. To compare these figures, the mean weight and standard deviation of a sample of 340 squid captured by recreational fleet were estimated. After testing for normality, recreational harvest in weight was estimated by bootstrapping the weight distribution using the *rnorm* function of the R package. The number of random samples was the predicted number of squid of a given day and cell, and the harvest in weight was the sum of the random samples. This approach assumes that size (and proportionally weight) of squid captured by anglers remains constant along seasons, which was suggested in Chapter 5 (Cabanellas-Reboredo et al., 2012b).

## 7.4 Results

### 7.4.1 Harvest and Effort estimations

The number of fishing journeys at Palma Bay during 2010 was estimated in 15,767 (95% bootstrapped confidence interval: 15,014.65 to 16,625.60; Fig. 7.3A). The effort peaked at cold season (November-May). Harvest peaked also at the cold season. When angler skills were accounted for (i.e., considering three types of anglers), the estimated number of squids captured at Palma Bay during 2010 was 101,394.5 (95% bootstrapped CI: 96,203.0 to 107,032.6; Fig. 7.3B). The estimated number of squid captured at Palma Bay during 2010 when angler skill was ignored was 131,357 (95% bootstrapped CI: 124,304.7 to 139,093.0). The estimated catch in weight was 20.54 tonnes when angler skills were accounted for and 26.62 when angler skills were ignored (or 6.08 tonnes more).

Concerning CPUE, the effects of some environmental variables (e.g., sea surface temperature) was already demonstrated (Chapter 5; Cabanellas-Reboredo et al., 2012b). However, the new data set analysed in this Chapter demonstrated that the AIC value (622.17) of a model with those environmental variables only was significantly larger (likelihood ratio test:  $p < 0.001$ ) than the corresponding AIC value (533.42) when *AnglerType* is included in the model. Interestingly, the AIC value (539.48) of a model including the interaction between the above mentioned environmental variables and *AnglerType* is significantly larger (likelihood ratio test:  $p < 0.05$ ), suggesting that the effects of *AnglerType* are additive to those of the environmental variables.

Estimated CPUE for each type of angler during 2010 showed clear differences (Fig. 7.3C). Estimated CPUE were highest and more variable as the skills of the angler increase (*less-skilled* < *medium-skilled* < *very-skilled*; Fig. 7.3C). Therefore, the proportions of anglers of one or other type definitely affects the expected CPUE because larger harvest is expected for *very-skilled* anglers. However, these proportions seems to remain constant in time ( $\chi^2 = 0.6195$ , *d.f.* = 2,  $p = 0.734$ ; note that the sample size only allowed proper comparison at the season temporal scale). The most frequent angler type is *medium-skilled* (53%). The *less-skilled* anglers represented 35% and the anglers *very-skilled* represented 18% of the anglers fishing at a given moment.

Conversely, the number of anglers per boat differed significantly between months (see frequency of the number of anglers per boat in Fig. 7.2). In August, the number of anglers per boat ( $2.08 \pm 0.90$ ; mean  $\pm$  SD) is significantly higher in comparison with the number of anglers ( $1.71 \pm 0.76$ ) during the rest of the year (GLM; for August  $p < 0.05$ ).

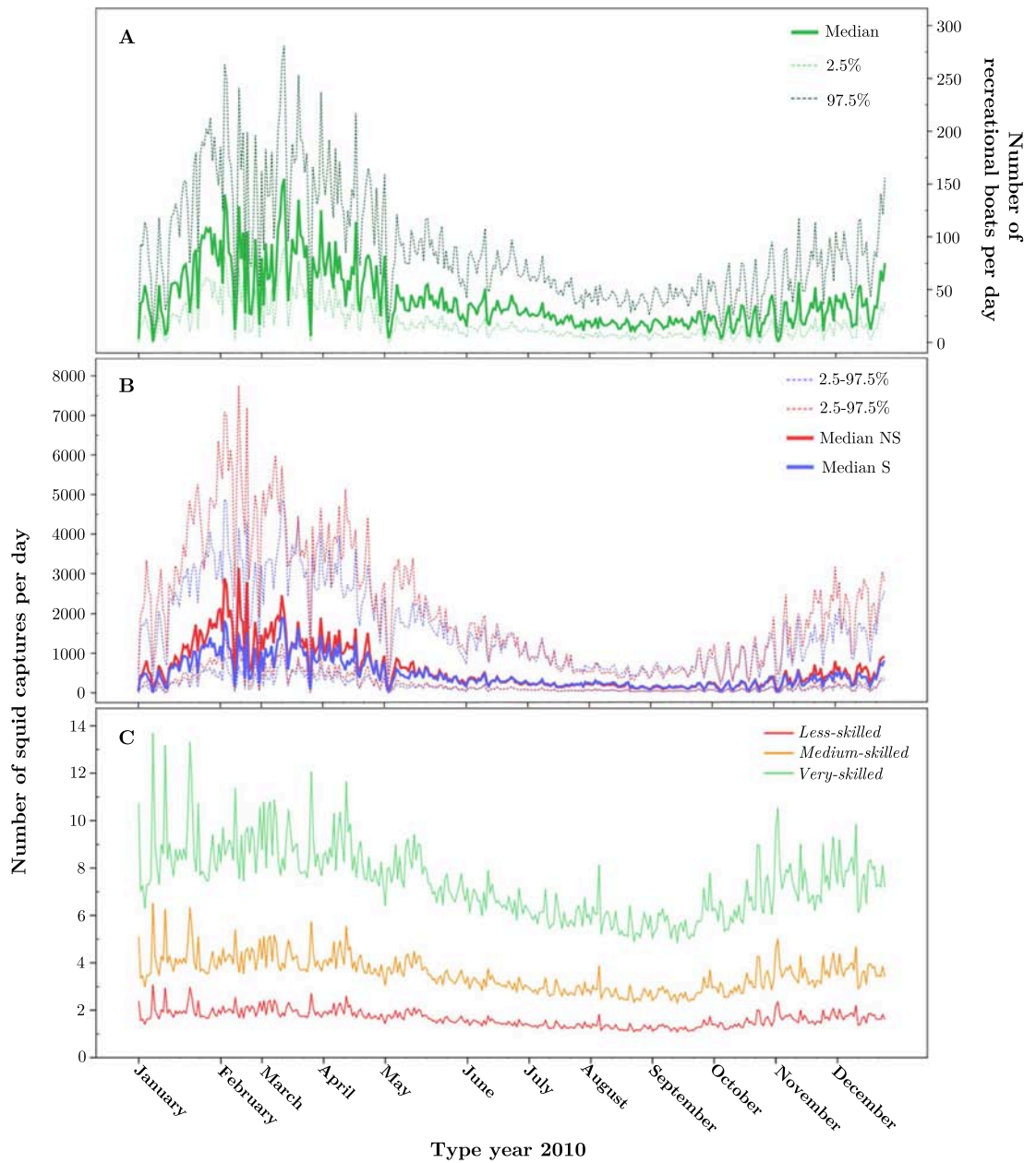


Figure 7.3: (A) Median number of recreational boats estimated throughout 2010. The intervals (2.5-97.5%) are represented by dotted lines. (B) Number of squid captured by recreational fleet taking into account the three types of angler (median catches represented by continuous blue line; 50%-S) and ignoring the type of angler (median catches represented by continuous red line; 50%-NS). Dotted lines represent confidence intervals (2.5-97.5%). (C) Median captures estimated per angler of each type during 2010.

## 7.4.2 Recreational squid fleet segmentation

The answers of the OSS questionnaire was used to determine between-angler differences. The main patterns depicted by these differences are shown in Fig. 7.4A (results of a Principal Correlation Analysis). The anglers were splitted in a progressive (from 2 to 10) number of groups using *k-means* as partitioning algorithm and a predictive classification tool (random forest) were implemented in each case. However, when this tools is applied using a leave-one-out crossvalidation, the success of prediction varied depending on the number of groups considered. The classification of squid anglers in 3 groups showed the highest percentage of correct assignments (97.5%; Fig. 7.4B). The confusion table corresponding to 3 groups shows only 4 cases of wrong prediction of group membership (Table 7.1). Provided this high success in predicting group-membership, the classification tool implemented with OSS questionnaires were used to predict group membership of the anglers interviewed in APS. Note that the actual harvest is not considered when segmenting anglers (OSS). Nevertheless, after predicting the group-membership to the anglers intercepted in the APS, between-type differences of catches were tested (Fig. 7.4C).

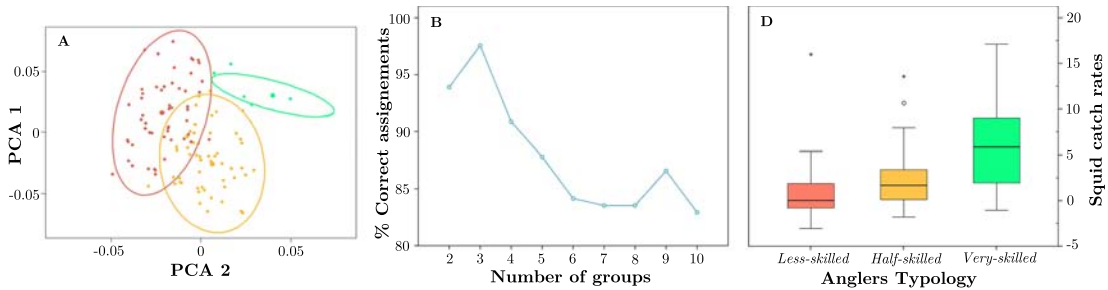


Figure 7.4: (A) Principal Coordinate Analysis (PCA) of the matrix of distances for the 3-groups segmentation. Red, orange and green colour represent anglers *less-skilled*, *medium-skilled* and *very-skilled* respectively. (B) Percentage of correct assignments when increasing the number of types of angler from 2 to 10. (D) Catch rates (number of squid per fishing journey) by angler typology.

Table 7.1: Confusion table that compares the assignments between 3-groups segmentation and the predictions of cross-validation (green values indicates the correct assignments).

		Segmentation		
		1	2	3
Cross-validation predictions	1	70	2	0
	2	2	65	0
	3	0	0	25

Anglers (OSS) answered significantly different to all of the questions depending on the type of angler. Therefore all the questions can be used to define each one of the three anglers profiles (Fig. 7.5):

**Less-skilled** (in red at Fig. 7.4).

Anglers of this type are well represented in the three age categories considered (>40, 40-60, >60 years old) . The traditional Llaüts and Motor-boats of different lengths (both large >6 m and small boats ≤6 m) are used by this type of anglers. They typically turn off the boat engine and prefer leaving the boat to drift with currents. They tend to uses only one hand-line jigging gear and selects fishing spot influenced by the presence of other boats in the zone. They usually do not know the allowed maximum quota and report to fish less than 16 squid at the best fishing journey.

**medium-skilled** (in orange at Fig. 7.4).

Anglers of this type are well represented in the three age categories considered but are more frequent those between 40 and 60 years old. Anglers seems to prefer larger motor boats (>6 m) and they do not show clear preferences for any specific fishing tactics (an-

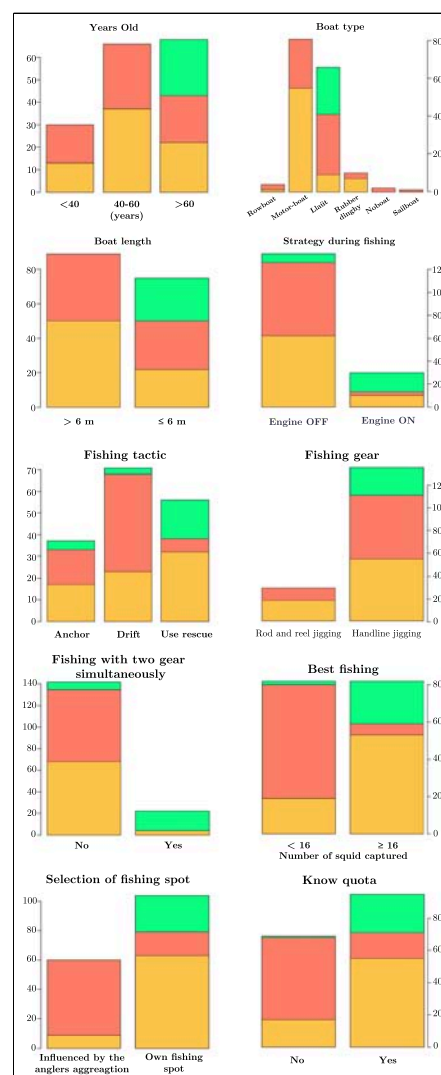


Figure 7.5: Number of responses of each type of angler for each significative variables involved on 3-groups segmentation. Red, orange and green colour represent anglers *less-skilled*, *medium-skilled* and *very-skilled* respectively.

chor, drift and use rescue are all used; see Appendix B). They prefer to use only one jigging gear, and prefer to go for fishing at their own, at pre-selected fishing spots. Most of them know the allowed maximum quota and report to fish  $\geq 16$  squid during the best fishing journey.

**Very-skilled** (in green at Fig. 7.4) They tend to be older ( $>60$  years old) and most of them own a traditional boat (Llaüt) of  $\leq 6$  m long. They prefer to use two hand-line jigging gears at the same time, to go for fishing at their own fishing spots, and keep up the engine running all the time. To prevent drift, this type of angler deploys a rescue device. Moreover, this type of angler knows the quota and reported to fish  $\geq 16$  squid at the best fishing journey.

### 7.4.3 Commercial vs. recreational harvest

Regarding the comparison between the recreational and the commercial fleets, during 2010 the annual harvest by the professional fleet at the Mallorca Islands (trawling and artisanal) was 59.5 tonnes. Therefore, the recreational harvest at Palma Bay (assuming the captures estimated after considering segmentation) represented 34% of the harvest from the commercial fleet (Fig. 7.6). During the peak of recreational fishing season (colder months; Chapter 4), the recreational harvest was comparable, and even, slightly exceeded the captures obtained by commercial fleet.

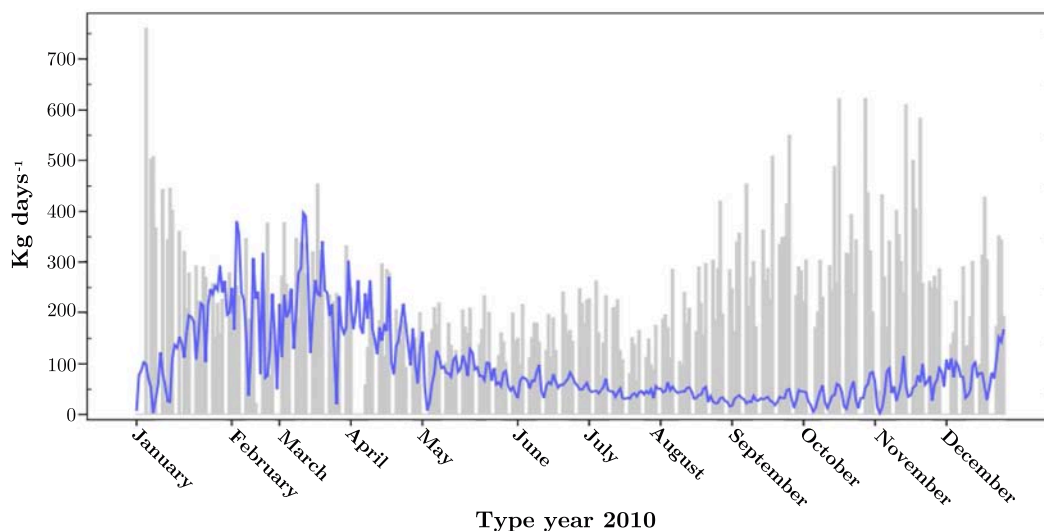


Figure 7.6: Daily squid catches from commercial (black bars) and recreational fishery (blue line) during 2010.

## 7.5 Discussion

In this Chapter, a new framework for estimating harvest attributable to recreational fisheries is proposed. Specifically, the spatio-temporal variability in effort, the temporal variability in catches, and the between-angler variability in catches are explicitly considered. Harvest was estimated by combining effort and CPUE. Effort is estimated from fishery-independent data (boat censuses; Chapter 4). Type-specific CPUE is estimated from a GLM model including, beside the effect of some environmental variables (Chapter 5), the angler typology (from a creel survey). Finally, harvest results from upscaling CPUE to the estimated number of anglers after taking into account the type of anglers (i.e., angler skills; Appendix B).

One of the major difficulties when estimating recreational harvest is the spatio-temporal variability of the distribution of the fishing effort (McCluskey and Lewison, 2008). By explicitly incorporating the spatial and temporal distribution of the fishing effort, the decision-making process of the anglers when choosing “Where” and “When” they go for fishing is indirectly integrated in the harvest estimation. This is a key aspect for recreational fisheries because the value of a given site is usually not only related with the expected catches but also with other attributes (e.g., distance to the nearest marina; Cabanellas-Reboredo et al., 2014a; Hunt, 2005). In Chapter 4, we provided a general framework to estimate the spatio-temporal distribution of the recreational fishery, considering both catch-related and catch-independent variables that may affect the preferences of anglers (Cabanellas-Reboredo et al., 2014a). Our approach was based in solving two major drawbacks when dealing with recreational fishing effort: data acquisition and modelling (Chapter 4). In the present Chapter, we used the effort estimated produced in Chapter 4 to copy with the spatial and temporal heterogeneity of harvest. Estimates the recreational squid fishing effort were obtained for any day of a given year and for any 1 km<sup>2</sup> cell of the spatial scenario considered. This capability highlights one of the advantages of the approach proposed here, since explicit consideration of the spatial distribution of the effort is advisable for designing an effective management approach (Post and Parkinson, 2012).

The second difficulty when estimating recreational harvest is angler heterogeneity. The fact that anglers are by far more diverse than commercial fishermen is well known. Catches will depend on squid abundance and vulnerability but also on angler skills (e.g., Johnston et al., 2013) and other motivations different from catches can be even more important than catches themselves (Arlinghaus, 2006). In consequence, the proposed approach takes into account angler variability by classifying anglers into three types. To



classify them into a reduced number of groups and ignoring within-group variability has been proposed for facing the anglers heterogeneity (Ditton, 2004; Ditton et al., 1992). Such simplification allowed to identify some correlated features of fishing behavior. For example, some highly specialized anglers were likely to cite resource-related motivation (e.g., trophy fish), to rely on skills to catch fish, and to favour more restrictive harvest regulations as well as to practise catch and release (Arlinghaus and Mehner, 2004; Chipman and Helfrich, 1988; Connelly et al., 2001; Nguyen et al., 2013; Salz and Loomis, 2005). It is expected that after knowing anglers motivations and preferences, CPUE estimates may be more precise. In our case, for example, *very-skilled* anglers are able to fish with two gears at the same time, which implies high experience to prevent tangling the two lines. By fishing in this way, the angler can take profit of the shoaling behaviour squids (Hanlon and Messenger, 1996). Consequently, CPUE of experienced anglers is higher (see Appendix B & Fig. 7.3C). Similar correlations have been also reported elsewhere (Johnston et al., 2010, 2013).

Therefore, classification (= segmentation) based on different features (e.g., experience, skills, motivations) may be used to improve the estimates of CPUEs. Conversely, CPUE estimated obtained from interview-based surveys and relying on questions directly related with catch are prone to bias (Lyle et al., 2007; Vaske et al., 2003). It is well known that the cognitive processes suggests that the quantity of the responses obtained by multiplication can be seriously biased (Vaske et al., 2003). Therefore, here we avoided any direct question on recent catches and only one generic question about the best fishing journey forever was included in the survey (Appendix B). It is assumed that this response was unbiased because anglers will remember this figure.

The application of the new framework proposed in this Chapter, allowed us to obtain a more precise estimation of the recreational harvest. Precision (in terms of smaller confidence intervals) was improved by 22.8% when the the angler skills were included. The estimated harvest was 20.54 tonnes when angler skills were accounted for and 26.62 when angler skills were ignored (or 6.08 tonnes more). Differences in catch and harvest depending on angler type have been also reported by Johnston et al. (2010).

The recreational harvest in Palma Bay (20.54 tonnes) was estimated to be the 34% of the total harvest of the commercial fleet for all the Mallorca Island. Note that the commercial fleet not only includes the artisanal fleet (hand-line jigging, seine fishing and sporadic captures with trammel net) but about thirty trawlers are included too. Therefore, despite that *L. vulgaris* suffers a relevant fishing pressure from the recreational fishery (Cabanellas-Reboredo et al., 2014a; Moreno et al., 2013a; Pierce

et al., 2010), the recreational harvest had never been addressed till now, when for the first time, we provided an estimate of the recreational catches.

Note that the figure of 37% may be even considered an underestimation because, although the Palma bay is the main recreational fishing zone of the Balearic Islands (Morales-Nin et al., 2005), it represents an small area compared to the Mallorca Island. Moreover, it is important to highlight that squid landings by the trawl fishery (*métier* that accumulate the 82% of the total commercial squid captures) was composed by two species (*L. vulgaris* and *L. forbesi*) that are pooled in a single commercial category. In addition, although this PhD addresses the most important modality of recreational fishing effort (line jigging during sunset; Cabanellas-Reboredo et al., 2011, 2012b, 2014a), an small but may be relevant number of anglers target squid by trolling at night and by line jigging at sunrise.

In any case, it is undisputable that recreational fishery play a relevant role on of the populations dynamics of squid. This role has been previously suggested (Guerra et al., 1994; Simón et al., 1996) but here, empirical data are provided for first time. Other studies also warned about the important role of the recreational fisheries may play in the decline of fish stocks (Coleman et al., 2004b; Cooke and Cowx, 2004; Post et al., 2002). In some specific cases, it has been suggested that the outcomes of recreational fishing may be larger that those from the commercial fisheries (Cooke and Cowx, 2006).

Most stocks worldwide are managed taking into account the harvest from the commercial fleets only (Cooke and Cowx, 2004). The figures on recreational harvest reported here suggests that squid management based on data and analysis of the commercial fishing may be insufficient to properly predict the population dynamics of *L. vulgaris*. This problem may exacerbate in the cases of species with short-life cycles (annually renewed in the case of squid; Boyle and Rodhouse, 2005). In these cases, environmental dependencies (Pierce et al., 2008) and fishing can lead to very important and unpredictable between-year variability (Pierce and Guerra, 1994). For that reason, we suggest to include recreational fishery as another relevant source of fishing mortality, as it has been suggested for other fisheries (Cooke and Cowx, 2006).

Part IV

**DISCUSSION &  
CONCLUSIONS**





## Chapter 8

# General discussion & conclusions

### 8.1 Discussion

The social relevance of RF and their impact not only on the exploited resources but on the ecosystem have been worldwide recognized (Coleman et al., 2004b; Cooke and Cowx, 2004). The recreational sector has become increasingly important over the past 50 years for many species (Coleman et al., 2004b; Cooke and Cowx, 2004; Post et al., 2002). The role of this sector on the decline of some stocks can be equivalent, and in some cases, higher than the role of their commercial counterparts (Coleman et al., 2004b; Cooke and Cowx, 2004; Pawson et al., 2008; Post et al., 2002). As a consequence, an effective management of the exploited stocks should integrate both, recreational and commercial fisheries (Cooke and Cowx, 2006), as it is already done in the case of some stocks exploited by anglers from industrialized countries such as USA, Canada or Australia (Coleman et al., 2004b; Lynch, 2006; Post et al., 2008). However, in southern EU the available information in relation to RF is still inadequate (Font and Lloret, 2014). Therefore the consequences of RF on the population dynamics of the exploited species remain largely unknown. This is especially apparent for the squid *L. vulgaris*, which is intensively exploited by the commercial and the recreational fleets (Cabanellas-Reboredo et al., 2014a; Moreno et al., 2013a; Pierce et al., 2010). For that reason, assessing the consequence of recreational exploitation in squid should be a major priority for managers and fisheries scientists. This Ph.D. Thesis provides some pieces of relevant information about the recreational exploitation of squid (*L. vulgaris*).

Although it is not frequent, the harvest of RF has been incorporated in the stock assessment of some fisheries. For example, Post et al. (2008) implemented a model to estimate the effect of RF on the population dynamics of rainbow trout, *Oncorhynchus*

*mykiss*. This example demonstrates that incorporating the RF effects when adopting management decisions can notably improve yield. However, cephalopods can not be properly assessed using simple assessment methods (Boyle and Rodhouse, 2005; Pauly, 1985; Pierce and Guerra, 1994). In the case of squid, standard assessment methods can fail because i) squid, as other short-lived species, are very vulnerable to environmental fluctuations which implies variable (and difficult to predict) population dynamics, and ii) squids experience important variations of the spatio-temporal distribution. Spawning migrations is a relevant example. Generally, Loliginid species (e.g., *L. reynaudii* or *L. forbesi*) undergo such type of migrations searching for suitable conditions that maximize spawning success (Boyle and Rodhouse, 2005; Roberts and Sauer, 1994; Sims et al., 2001). This highly variable spatio-temporal distribution determines the pattern of vulnerability of squid to fishing, which in turn determines, or at least modulates, the spatio-temporal distribution of the fishing effort (Cabanellas-Reboredo et al., 2014a; Pierce et al., 1998; Postuma and Gasalla, 2010; Schön et al., 2002).

Therefore, squid and squid anglers should be managed as a socio-ecological system, that is, taking into account not only the “ecological subsystem” but also the “social subsystem” and, specially, the interaction between the two subsystems.

Unfortunately, after working more than four year in this issue, it has been evidenced that the complexities outlined in the paragraphs below are only the tip of the iceberg. To achieve the paramount objective of modelling squid population dynamics and, therefore, to be able of predicting the outcomes of alternative management strategies, is still not possible. Nevertheless, this Ph.D. Thesis provides a relevant starting point. Each of the goals achieved has opened a new window and in this last Chapter the relevance of these goals, their limitations and the possible future research lines to progress forward are discussed.

This Ph.D. Thesis provides detailed data on the spawning preferences of *L. vulgaris* in the Mediterranean (Chapter 2). We demonstrated that, squid expands its spawning areas, from deep to shallow and nearshore areas during the cold season and that this pattern is in accordance with the hypothesis of a spawning migration. Certainly, many marine species undergo spawning migrations. For example, the migration pattern of the Bluefin Tuna (*Thunnus thynnus*) from the Atlantic to the Mediterranean it is well known (see e.g., Block et al., 2001). Spawning migrations are also described for other squid species (Boyle and Rodhouse, 2005; Roberts and Sauer, 1994; Sims et al., 2001) and they were even suggested for *L. vulgaris* (Sánchez and Guerra, 1994; Tinbergen and Verwey, 1945; Worms, 1983). It is plausible that, *L. vulgaris* performs seasonal migrations searching for the environmental conditions that maximize spawning success

(e.g., sea temperature; Villanueva et al., 2003). The data obtained from artificial devices (Chapter 2) supports the spawning migrations hypothesis. However, eggs clutches seems to be cryptic and, in spite of the effort invested, there is a need for further confirmation that the pattern depicted by artificial devices reflects the natural pattern. The fraction of the stock that would migrate is another relevant point. Are some squid remaining at deeper waters all the time? The data reported at Chapter 2 are restricted to relatively shallow waters ( $\geq 50$  m), thus the plausible spawning activity at deeper waters ( $> 50$  m depth) needs further confirmation. In the case of the related species *L. reynaudii*, most of the spawning activity is restricted to the range between 20 and 70 m depth but deeper spawning grounds (70-130 m depth) also play a secondary but still relevant role because these deep grounds seems to enhance the resilience of the stock (Roberts et al., 2012). The existence of such a deep spawning in the case of *L. vulgaris* is a relevant question since deep spawning grounds would be heavily exploited by the trawl fishery, which not only would affect spawners but also egg clutches (Jones, 1992). Conversely, in the case that most of the stock migrates inshore during spawning, it would be vulnerable to recreational and small-scale fishery during a sensible period of squid life cycle. These two alternative scenarios imply not only different modelling strategies (a single stock or two spatially diverse stocks) but also different management implications.

At Chapter 3, it is demonstrated that *L. vulgaris* displays a different movement pattern at night (more active) than at daytime (less active). Certainly, many marine species display some type of diel pattern. For example, the pearly razorfish *Xyrichtys novacula* is active at daytime only and at night seems to remain buried into the soft bottom (Alós et al., 2012). The fact that fish is moving, increase their vulnerability. This is a common pattern on fisheries: more active fish, more vulnerability (Alós et al., In press). Specifically, the pattern found for the squid is in accordance with the hypothesis “feeding at night and spawning at day”. This pattern is relevant because it defines a short temporal window within which squid is vulnerable to anglers: around sunset squid has already shift to the feeding state but lures are still visible.

Provided that expected catch is one of the most important motivation in consumption-oriented RF (which is the case of squid; Cabanellas-Reboredo et al., 2014a), the pattern of diel activity directly links squid life history with the temporal distribution of the effort in the sense that the duration of a fishing journey is limited to  $\approx 2$  hours around sunset. These factors affecting catches have been analyzed at two scales (Chapter 5). At the within-day scale, catch peaks just around sunset, which is in accordance with the “feeding at night and spawning at day” hypothesis (Chapter 3). At the seasonal

scale, catch peaks at the cold season which is in accordance with the spawning migration hypothesis (Chapter 2). This Ph.D. Thesis provides the first data on squid catch based on controlled sessions that emulates angling behaviour. The method used has been useful for delineating the environmental dependencies of catches but it has an important drawback: logistic constraints imposed that fishing sessions were performed by a limited number of voluntaries, which precluded an explicit evaluation of the effect of angler's skills. This bottleneck has been solved using on-site surveys but better methods should be developed in the future. One possible solution may be to substantially enlarge the number of anglers involved in the controlled fishing sessions, the number of on-site surveys or both.

Catch rates are, together with the fishing effort, the main aspects to estimate fishing mortality (Hilborn and Walters, 1992). In Chapter 4, we provide a novel framework for estimating fishing effort at a detailed spatial (1 km<sup>2</sup> unit) and temporal (day) scale. Sea condition plays a relevant role. However, as expected in a consumption-oriented fishery, variables related with catch expectations are also important predictors of fishing effort. It has been clearly evidenced that effort is highly heterogeneous in space and time, and ignoring such heterogeneity will imply severe biases. Effort estimates are based in on-boat censuses of all the boats fishing squid at Palma Bay. Provided that the fishing journey is relatively short ( $\approx 2$  hours) and that the censuses took place at sunset, it is expected that a few boats remain uncounted. However, more effort should be done for improving the method. For example, an useful methodology could be the use of photographic time-series Parnell et al. (2010). In the case of the razor fish (*X. novacula*), fishing grounds are close to the shore line and preliminary trials suggest that images from the coats provides boat positions with an accuracy below 100 m, which is fully adequate for the spatial detail required. Alternative approaches based on the recent development of drones should be explored too.

The data on effort and catch produced in the previous Chapters were combined at Chapter 7, which is the core of the Ph.D. Thesis. A number of problems have been successfully addressed and solved in order to combine effort and catches but special effort has been made to address the problem of angler's heterogeneity (Arlinghaus et al., 2008a; Johnston et al., 2010, 2013; Post and Parkinson, 2012). Anglers are classified into three types depending on the answers to a short interview. This interview has been designed for highlighting between-angler differences in skills and, ultimately, in catches. This strategy circumvents the need to directly answering on catches, which in general is not reliable (Lyle et al., 2007; Vaske et al., 2003). One of the most important differences between commercial fishers and anglers is that fishing effort and catches



are assumed to be known in the case of the commercial fleet. The squid harvested by RF for a given year (2010) has been estimated in 20,54 tonnes. This estimate is more precise in comparison of a similar estimate obtained when ignoring angler heterogeneity (26.62 tonnes). In the case of squid in Mallorca, RF supposes 25.6% of the total squid captured (Fig. 8.1). This figure highlights the relevance of RF.

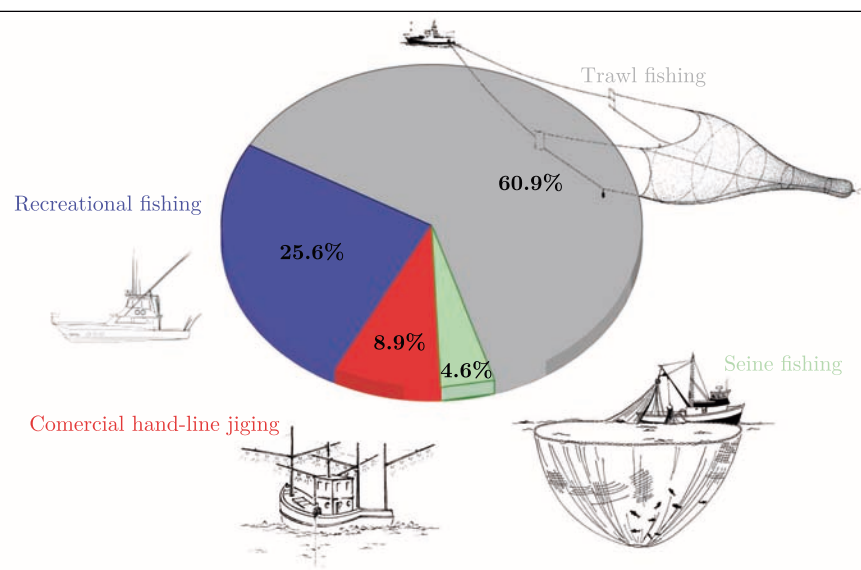


Figure 8.1: Percentage distribution of the 80.1 tonnes of squid captured by the commercial (all fleet from Mallorca) and recreation fishery (only Palma Bay) during 2010 (from data reported in Chapter 7).

This figure should be the basis of a long-term monitoring program that should furnish the data needed for modelling the long-term trend of the population dynamics. However, as mentioned above, to properly model squid population dynamics is still not possible and only after achieving this objective, the total (i.e., after polling recreational and commercial fishing) harvest would be qualified as sustainable or unsustainable. Some of the points that should be addressed for achieving this objective are:

- i) Concerning RF, it would be desirable to include harvest estimates from modalities other than sunset jigging (i.e., trolling during nighttime and line jigging during sunrise).
- ii) Concerning the commercial fishery, trawlers account around the 60.9% of the total squid landings (Fig. 8.1) but two species (*L. vulgaris* and *L. forbesi*) are polled in a common commercial category. Therefore, it is imperative to disentangle the fraction corresponding to each one of the two species.

- iii) Concerning line jigging fisheries (small-scale and recreational fishery) it would be desirable to quantify the impact of the unreported fishing mortality caused by the drop off rate from jigs (ghost fishing; Chapter 6).
- iv) The mentioned above problem of the possible existence of two stocks (inshore and off shore) should be solved.

Only when these problems are solved, it will be possible to predict the outcomes of alternative management strategies, or even if any management measure is necessary. In the meantime, some comments can be advanced. The most common management measures for commercial fishers are restrictions of the gear characteristics, minimum legal size (e.g., 100 mm ML in Spain and Portugal) and the number of licences (Moreno et al., 2013a). For RF, the main management measures are spatial and temporal restrictions and bag limit (Morales-Nin et al., 2010). Bag limits (in the Balearic Islands, 10 squid per angler and fishing trip) are useless, provided that anglers rarely attain the limit. Concerning MPAs, they are also not useful for protecting adults due to the high movement capability of squid (Chapter 3). Temporal closures of spawning grounds could be proposed (Chapter 2). In fact, the temporal closure of inshore spawning ground (exploited by commercial hand-line jigging fishery) has been one of the success measures to achieve a sustainable exploitation of *L. reynaudii* (Augustyn and Roel, 1998; Augustyn et al., 1992; Cochrane et al., 2014). Unfortunately, the current knowledge does not support that this measure can enhance the long-term yield (but certainly, it will decrease short-term profit). Similarly, current knowledge is not sufficient for promoting artificial devices where squid would attach more egg clutches (Chapter 2). Moreover, temporal closure during the *L. vulgaris* spawning season will be problematic because recreational effort only concentrates at this season. Nevertheless, temporal closure in the case of the razor fish (*X. novacula*) has been well accepted by the anglers, which highlight the importance of promoting management rules that are simple, have clear scientific support and produce verifiable results.

## 8.2 Conclusions

1. *L. vulgaris* spawns all the year but reaches a maximum peak in spring (May). This pattern seems to be related to phytoplankton-zooplankton cascade that takes place just preceding spring.
2. *L. vulgaris* spawns at deeper waters. However, this species expands its spawning areas to shallow waters during cold season supporting inshore spawning migrations hypothesis with implications for the vulnerability as squid remaining at deeper waters are not vulnerable to neither small-scale fishery nor recreational fishery.
3. During the inshore spawning season, *L. vulgaris* performs a well-differentiated movement pattern: the squid move within a small area during the daytime but cover a larger area from sunset to sunrise. This pattern supports the “feeding at night and spawning in the day” hypothesis. The timing of recreational fishing is strongly related with squid behaviour because angler focus their activity when squid catchability is higher.
4. The spatio-temporal fishing effort is linked to both, catch-related and non-catch-related variables. Effort peaks during inshore spawning aggregations (coldest months). Anglers tend to cluster between 25-30 m depth. However, the sea conditions determine the final decision to go or not to go fishing.
5. Catches of the recreational fleet are related with some environmental variables. The sea temperature is the variable with higher importance at the seasonal scale. Windspeed, moon phase and atmospheric pressure affect at daily-scale.
6. Sunset is the period of higher catchability probably due to two main traits: i) the sunlight is still enough to allow the recreational fishing lures to be effective, and ii) the squid have already shifted to a more active movement pattern characteristic of the night-time period (“feeding at night and spawning in the day” hypothesis).
7. Squid that have lost one or both tentacles by drop off from jigs may become part of an unreported fishing mortality with potential consequences on the population dynamic of this species. For that reason, this “ghost fishing” should be taken into account to ensure a sustainable management of this fishery.
8. The recreational squid fishery represents 34% of the total captures performed by commercial fleet. Therefore, RF plays a relevant role in the dynamic population

of *L. vulgaris*.

9. All of these conclusions represent a breakthrough in the understanding of this complex socio-ecological system, providing essential information to proper management of any marine resource exploited by recreational fishing.

## Appendix A

# Statistical development of Sea condition model

Regarding *Sea Condition (SC)*, daily-averaged wave height, with a spatial resolution of 1 km<sup>2</sup>, was required. However, wave height information in the Palma Bay is limited. Observations are only available from a single buoy (SOCIB buoy; Fig. 4.1B) and started in December 2009 (thus later than censuses began). As a complement, an operational wave forecasting system (<http://www.socib.es/?seccion=modellering&facility=sapo>) was implemented in the bay and provides 3-hourly wave height fields with a spatial resolution of 500 m. However, this system started in September 2011, also later than the survey period. Therefore, we have developed a semi-empirical model to produce the required wave height information for the survey period. The model is constructed as follows. First, the spatio-temporal variability of the wave height in the Palma Bay has been characterized through a principal components analysis (PCA) of the operational wave forecasts. The first two modes explained a 98% of the variance. Thus, the wave field (SWH) can be expressed as:

$$SWH(x, t) = \alpha_1(t)\psi_1(x) + \alpha_2(t)\psi_2(x),$$

where  $\psi_1$  and  $\psi_2$  represent the spatial modes and only depend on the location ( $x$ ), and  $\alpha_1$  and  $\alpha_2$  represent the corresponding temporal amplitudes and only depend on the time ( $t$ ). Then, the temporal amplitudes are approximated using a linear combination of local winds ( $U, V$ ) and large scale waves ( $SWH_{remote}$ ):

$$\tilde{\alpha}(t) = \gamma_U U + \gamma_V V + \gamma_{UV} [U^2 + V^2]^{1/2} + \gamma_{SWH} SWH_{remote} + \gamma_0,$$

where the  $\gamma$ 's are the regression factors obtained for the period when the operational forecasts were available. For the survey period (2009–2010), wind observations in the Palma Airport (Fig. 4.1B) and large scale waves observed at the Dragonera buoy (Fig. 4.1A) have been used to obtain the approximated temporal amplitudes and, subsequently, the semi-empirical wave field ( $SWH_{SE}$ ):

$$SWH_{SE}(x, t) = \tilde{\alpha}_1(t)\psi_1(x) + \tilde{\alpha}_2(t)\psi_2(x) = f^0(U, V, SWH_{remote}).$$

The modelled wave heights have been compared to the available SOCIB buoy measurements inside the bay (Fig. 4.1) for the period December 2009–December 2010. The correlation was 0.79 and the RMS error 0.2 m.

## Appendix B

# Segmentation survey

In order to address the recreational fleet segmentation, a survey was developed based on the experience and skills of one of the best recreational anglers of the sampling area. This angler combines the following features related to his skill and experience; this angler is older than 60 years. He has a small traditional boat (Llaüt <6 m). He has his own fishing spots based on his experience. During squid fishing, this angler uses simultaneously two hand-line jigging gears. This feature allows the angler to take advantage of the encounter with a squid shoal (Hanlon and Messenger, 1996), and consequently, maximize his captures. Since squid shift their behaviour from a passive movement during daytime to active movement from sunset to sunrise (Chapter 3; Cabanellas-Reboredo et al. 2012a), the angler is moved around his different fishing spots searching the squid shoals. For that reason, and for an active-effective movement of the boat, this angler keeps up the engine running to develop a strategy based on the probability of encounter. Moreover, this angler prevents drift by intense winds deploying a rescue (fishing tool involving a high level of handling). This strategy allows the angler to take advantage of the encounter with squid shoal during the days with intense winds (variable indirectly involved on squid CPUEs; Chapter 5 & Cabanellas-Reboredo et al. 2012b). This angler knows the quota since that, he normally reaches the bag-limit (10 squid per angler and fishing trip). His best fishing amounts to  $\geq 16$  squid.

As a result, each of the questions made to anglers for evaluating their experience and skill is explained bellow in Table B.1:

Table B.1: Segmentation survey including each question (**bold text**) and the reason of each one (normal text) to interpret the experience and skill of the anglers. *Italic text* indicates the input (possible answers) for the segmentation analysis. The common questions for both surveys (OSS and APS) are closed at white panels. While questions only for OSS or APS are enclosed in yellow and green panels, respectively (questions not included in segmentation analysis).

<p><b>During this last year, have you ever gone fishing squid?</b> After the positive response, the operator of the Licenses offered a survey to the angler</p>						
1	<b>Years old</b>					
	The age may be a degree of experience					
	<table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="text-align: center; width: 33%;"><i>&lt;40 years</i></td> <td style="text-align: center; width: 33%;"><i>40-60 years</i></td> <td style="text-align: center; width: 33%;"><i>&gt;60 years</i></td> </tr> </table>	<i>&lt;40 years</i>	<i>40-60 years</i>	<i>&gt;60 years</i>		
<i>&lt;40 years</i>	<i>40-60 years</i>	<i>&gt;60 years</i>				
2	<b>Boat type</b>					
	The use of certain boat determines different degrees of navigation skill					
	<table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="text-align: center; width: 16.6%;"><i>Rowboat</i></td> <td style="text-align: center; width: 16.6%;"><i>Motor-boat</i></td> <td style="text-align: center; width: 16.6%;"><i>Llaüt</i></td> <td style="text-align: center; width: 16.6%;"><i>Rubber dinghy</i></td> <td style="text-align: center; width: 16.6%;"><i>No-boat</i></td> <td style="text-align: center; width: 16.6%;"><i>Sailboat</i></td> </tr> </table>	<i>Rowboat</i>	<i>Motor-boat</i>	<i>Llaüt</i>	<i>Rubber dinghy</i>	<i>No-boat</i>
<i>Rowboat</i>	<i>Motor-boat</i>	<i>Llaüt</i>	<i>Rubber dinghy</i>	<i>No-boat</i>	<i>Sailboat</i>	
2	<b>Boat length</b>					
	Normally, experimented squid anglers use small boats					
	<table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="text-align: center; width: 50%;"><i>≤6 m</i></td> <td style="text-align: center; width: 50%;"><i>&gt;6 m</i></td> </tr> </table>	<i>≤6 m</i>	<i>&gt;6 m</i>			
<i>≤6 m</i>	<i>&gt;6 m</i>					
4	<b>Turn off the boat engine during squid jigging? (Strategy during fishing)</b>					
	The affirmative response indicates a low degree of experience, since the encounter probability with squid decreases. Experienced anglers search squid batches constantly, moving around their fishing spots					
	<table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="text-align: center; width: 50%;"><i>Yes-Off</i></td> <td style="text-align: center; width: 50%;"><i>No-On</i></td> </tr> </table>	<i>Yes-Off</i>	<i>No-On</i>			
<i>Yes-Off</i>	<i>No-On</i>					
5	<b>Behaviour during the fishing with intense wind (fishing tactic)</b>					
	The excessive drift, caused by intense winds, disturbs the optimal performance of squid jigging and, consequently reduces catches (the squid batches is wasted; Cabanellas-Reboredo et al. 2012b). However, the fact to anchor (typical of an inexperienced squid angler) highly reduces the probability to encounter squid batches. Therefore, a trade-off between the encounter probability and excessive drift must be applied. The use of rescue (parachute deployment) prevents excessive drift, but requires a high degree of experience. While, free rolling motion (drift) is typical of squid angler with medium experience					
	<table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="text-align: center; width: 33%;"><i>Anchor</i></td> <td style="text-align: center; width: 33%;"><i>Drift</i></td> <td style="text-align: center; width: 33%;"><i>Use rescue</i></td> </tr> </table>	<i>Anchor</i>	<i>Drift</i>	<i>Use rescue</i>		
<i>Anchor</i>	<i>Drift</i>	<i>Use rescue</i>				
6	<b>Fishing gear used</b>					
	Hand-line jigging gear requires more ability, since the fishing line should be placed neatly on the boat. Jigging with rod and reel facilitates the fishing to inexperienced anglers, avoiding the tangles of the line					
	<table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="text-align: center; width: 50%;"><i>Hand-jigging</i></td> <td style="text-align: center; width: 50%;"><i>Jigging with rod and reel</i></td> </tr> </table>	<i>Hand-jigging</i>	<i>Jigging with rod and reel</i>			
<i>Hand-jigging</i>	<i>Jigging with rod and reel</i>					
7	<b>Do you use 2 fishing gears (hand-jigging), simultaneously?)</b>					
	The affirmative response reveals a high degree of experience. Few squid anglers are able to fishing with two hands simultaneously					
	<table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="text-align: center; width: 50%;"><i>Yes-two gears</i></td> <td style="text-align: center; width: 50%;"><i>No-one gear</i></td> </tr> </table>	<i>Yes-two gears</i>	<i>No-one gear</i>			
<i>Yes-two gears</i>	<i>No-one gear</i>					
8	<b>How many squid have fished during the best fishing of his/her life?)</b>					
	Unlike other catch-dependent questions, this is a question that all anglers remember very well and without confusion. A high number of captures may represent a high degree of experience and skill					
	<table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="text-align: center; width: 50%;"><i>&lt;16 squid</i></td> <td style="text-align: center; width: 50%;"><i>≥16 squid</i></td> </tr> </table>	<i>&lt;16 squid</i>	<i>≥16 squid</i>			
<i>&lt;16 squid</i>	<i>≥16 squid</i>					
9	<b>Selection of fishing spot</b>					
	The selection of fishing zone by inexperienced angler is influenced by the presence of other boats. While, a experienced angler has his own fishing spots. These experienced anglers determine the aggregation of the inexperienced anglers					
	<table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="text-align: center; width: 50%;"><i>Influenced by anglers aggregation</i></td> <td style="text-align: center; width: 50%;"><i>Own fishing spot</i></td> </tr> </table>	<i>Influenced by anglers aggregation</i>	<i>Own fishing spot</i>			
<i>Influenced by anglers aggregation</i>	<i>Own fishing spot</i>					
10	<b>Do you know fishing bag limits? How many squid or Kg?)</b>					
	An inexperienced angler does not know the bag limits since he/she ever or hardly ever reaches the limit. The additional question (How many squid or Kg?) is a control question to attest the veracity of the angler response					
	<table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="text-align: center; width: 50%;"><i>Yes</i></td> <td style="text-align: center; width: 50%;"><i>No</i></td> </tr> </table>	<i>Yes</i>	<i>No</i>			
<i>Yes</i>	<i>No</i>					
<p><b>Squid catches for the present fishing session (checking captures)</b></p>						



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