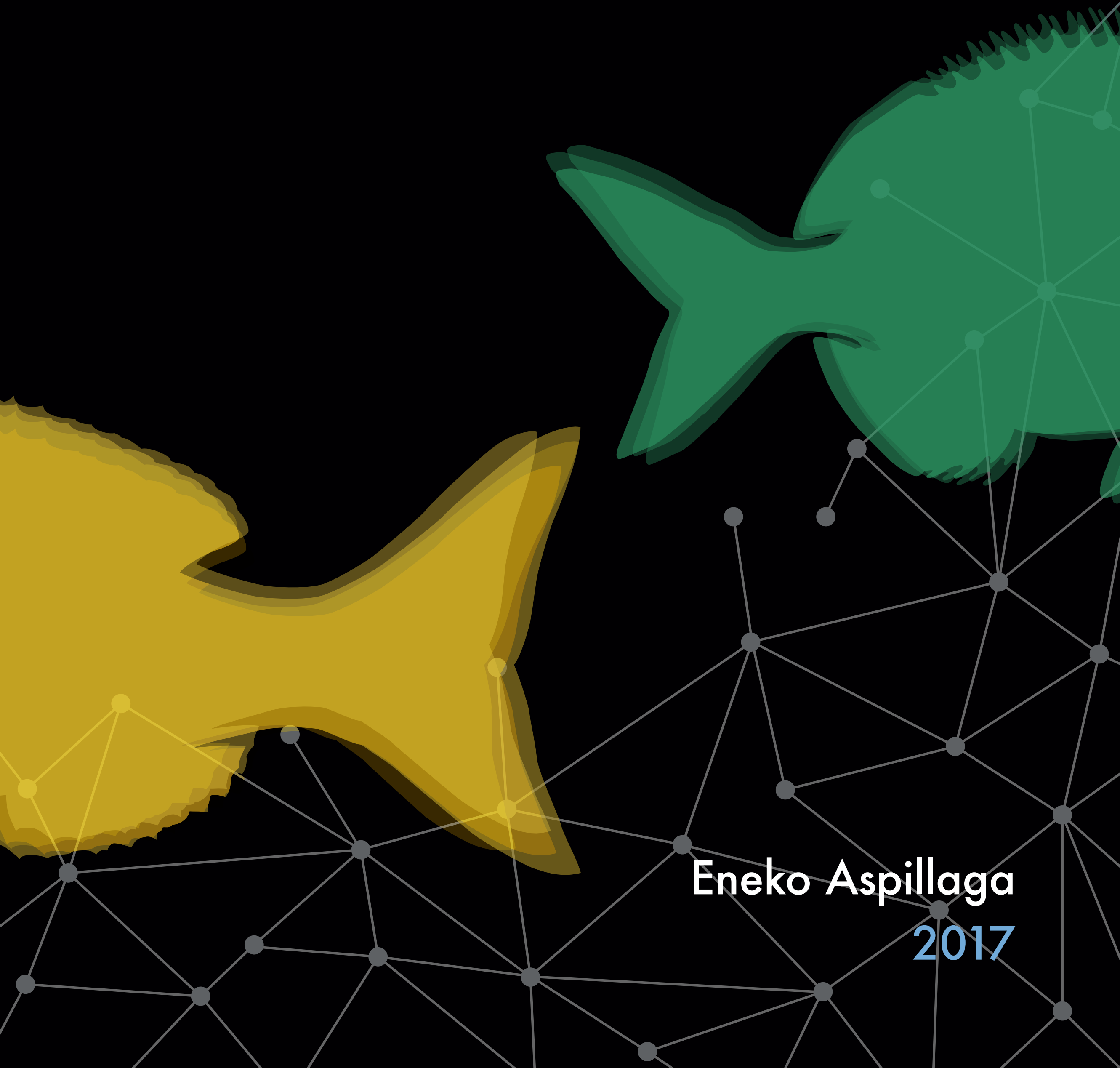
Movement ecology of coastal fishes in a marine protected area:

implications for management and conservation



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Movement ecology of coastal fishes in a marine protected area: implications for management and conservation

Memòria presentada per Eneko Aspillaga Cuevas per optar al grau de doctor per la Universitat de Barcelona

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Nire familiari,
itsasoa miresten irakasteagatik

A les Illes Medes

Esker onak

Qui m'hagués dit, no fa gaires anys, que acabaria escrivint aquestes línies així. No em refereixo a fer-ho a corre-cuita al tren, de camí a la impremta, cosa que sí era força esperable de mi, sinó a escriure-les en aquesta llengua. Però és que així és la vida, un misteri impredictible, sempre en constant moviment pels aclaparadors solcs de l'atzar. De vegades, penso, m'hagués agradat poder capturar-la, anestesiar-la i marcar-la amb algun dispositiu de telemetria, com he fet amb tots els neros, sargs, déntols, dorades i esclops que han passat per les meves anys durant els darrers anys, i que espero que segueixin pul·lulant sans i estalvis per aigües mediterrànies. Potser tindria una visió molt més clara de la meva trajectòria (o *track*) durant els gairebé set anys que porto per Catalunya. Tot així, no crec que quedés del tot reflectit el moltíssim que he gaudit durant la travessia de fer aquesta tesi. Em sento molt afortunat per haver pogut treballar en paratges impressionants, participant en molts projectes per intentar esbrinar els secrets dels ecosistemes marins. També m'ha permès passar hores submergit en mons menys terrenals, de scripts de `R`, anàlisis estadístics varis i supercomputació en paral·lel, on he descobert un nou univers altament satisfactori per la seva eficàcia, senzillesa i versatilitat. Però hi ha una cosa que sí quedaria clara: cap segment d'aquest *track* hagués estat possible sense tota la gent amb la que he tingut la sort de creuar-me pel meu camí. A tots vosaltres, us vull dedicar aquestes paraules d'agraïment. Em trobo, però, en una difícil situació, ja que heu estat molta gent els que m'heu aportat tantíssimes coses en un o més aspectes de la tesi, la vida i tot plegat. Tant és així, que formeu un espai multidimensional dins del meu cor (figuradament, realment esteu al meu cervell), que ara he d'escalar a una simple i única dimensió de lletres, paraules i noms encadenats. Espero fer-ho el millor possible, i amb valors d'estrès dins de l'acceptable (< 0.010), perquè vosaltres ho mereixeu!

Primer de tot, he d'agrair als meus mentors, Bernat i Fede, per haver-me donat l'oportunitat de realitzar aquesta feina, i per tota la confiança que sempre han dipositat en mi. Al Bernat li agraeixo especialment el seu suport incondicional contra tramuntana i marea, el haver comptat amb mi per a tantes campanyes al més pur 'estilo alpino', i per la seva companyia durant centenars d'hores d'immersió, on possiblement he après més, com a ecòleg i com a persona, que en cap altre lloc. En Fede també ha estat un element indispensable, aportant la vessant més teòrica i holística a aquesta tesi, i introduint-me a les arts arcanes de la computació. A més, sempre ha tret temps d'on no hi havia, ja fos per a una conversa estimulant, o per donar-me una espurna d'optimisme i seny cada cop que m'he trobat bloquejat. Tots dos us heu complementat d'una manera immillorable, potser sovint sense adonar-vos-en, guiant els meus passos des del principi fins a fer-me arribat a aquest bon port. A partir d'ara, només espero seguir gaudint d'estones enriquidores amb vosaltres, ja sigui a sobre o sota el mar, al clúster de computació o, perquè no, davant d'una bona cervesa.

Al llarg d'aquests anys he tingut la sort de poder treballar en el sí d'un petit gran grup d'investigació, anomenat MedRecover, format per grans professionals d'investigació, i sobre tot, per grans amics. Estic en especial deute amb na Cristina, perquè gràcies a ella va començar tot, amb aquell primer contracte que em va portat a treballar a un lloc tant impressionant com les illes Columbretes. A més, ha estat una mena de directora adoptiva, donant-me un suport addicional, però indispensable, amb la tesi sempre que ho he necessitat. Al David, li agraeixo haver-me donat l'oportunitat d'aplicar els meus incipients coneixements de telemetria acústica a Cabrera, durant les que possiblement han estat les campanyes més divertides en les que he participat, i sense dubte, en les que millor hem menjat. També vull donar les gràcies a en Rick i a l'Àngel, que juntament amb totes les persones anomenades fins ara, vàreu començar els experiments de telemetria acústica a les illes Medes, i m'heu ajudat en l'elaboració de la majoria de manuscrits d'aquesta tesi. No sabeu fins a quin punt les trajectòries de sargs i déntols que vàreu agafar fa gairebé 10 anys, que formen el nucli al voltant del qual gira aquesta tesi, han marcat la meva pròpia trajectòria. En Mikel i en Toni han estat uns pous de saviesa dels quals sempre he procurat aprendre, escoltant atentament els seus coneixements i anècdotes. Al Mikel li estaré sempre agraït pel bon record de vàries setmanes de pràctiques a l'Estartit, on vaig gaudir i aprendre tant cóm si fos un alumne més. Amb en Toni he tingut el plaer de compartir el despatx aquests últims mesos, durant els quals ha estat una gran font d'inspiració per a l'escriptura d'aquesta tesi (i difícilment oblidaré aquella increïble sarsuela de marisc a la que em va convidar a casa seva!). Tots dos, juntament amb en Bernat, em van instruir en l'art de contar peixos, donant-me l'oportunitat d'aportat el meu granet de sorra a la seva sèrie de dades històrica, i al coneixement general dels sistemes biològics de les Illes Medes. D'altre banda, en Quim ha estat un cap del grup sempre a l'altura de les circumstàncies. En Quim i en Josep Pascual (a qui encara no he tingut el plaer de conèixer personalment), van contribuir amb diverses sèries de dades de temperatura i altres variables ambientals, recollides al llarg dels anys amb tota la cura del món, i que han estat un element clau per a contestar moltes de les preguntes plantejades en aquesta tesi.

La resta de membres més joves de l'equip es mereixen una menció a part, per tots els bons moments de campanyes, riures i diversos canvis de despatx que hem gaudit junts durant aquest anys. Especialment al Pol, perquè sense ell aquest camí no hagués estat el mateix. Ha estat un company incansable en el que he pogut posar tota la meva confiança tant a dins com a fora de l'aigua, ja fos per a fer descompressions inacabables sota tempestes imponents (que altres patien), tenir converses/discussions existencials, sovint estadístiques, fins a altes hores de la nit, o anar a veure innumerables pel·lícules (de molt dolentes, però algunes de bones) al *Phenomena*. Per sort, encara ens quedem moltes hores d'aigua, feina i cine junts! A la Clara i a la Laura, amb les que vaig donar els meus primers passos en aquell cubícle sense finestra, encara que els seus les han acabat portant per altres indrets. A tots els que heu anat arribant després, Ignasi, Alba, Marta i Dani, per tots els llargs dies de mostrejos que sempre han estat degudament recompensats amb un bon banquet al Tucán, i per tots els *lab meetings* que ens han anat quedant pendents.

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Estos años, mi *home range* en Barcelona ha estado solapado con el de muchísima gente, que me han aportado muchas alegrías en lo profesional, pero sobre todo en lo personal. Me refiero a toda la invalorable gente que tuve la suerte de conocer durante el máster, y que han sido, desde entonces, una especie de familia con la que descubrir Barcelona: Clara y Stefano, María y Marcos, Julia, Manu, Marta, Gema, Yolanda y Oscar, siempre aportando el punto de mala influencia que tanto necesito, por muy desperdigados que estemos por el mundo. I en especial a l'Aurora, per tantes i tantes hores de discussions (més profitoses del que semblaven), per les impuntualitats que es paguen amb cerveses, i sobre tot, per la teva gran capacitat d'aguantar la meva cabuderia (encara que tu també vas ben servida!). I am also very thankful to my friend and flatmate David, with whom I was lucky to share home in Carrer de l'Equador during all these nice years. I finalment a l'Elena, per tots els moments de sol i mar.

Pixka bat atzerago joanda, asko eskertu behar dizuet nire biologo sena sustatu zenuten adiskide guztiei. Han egon zinetelako nago orain hemen. Bereziki Urtziri, berarekin batera eman bait nion hasiera Bartzelonako abentura honi. Asko bota izan ditut faltan azkeneko urte hauetan unibertsoko sekretuei buruzko eztabaidak, pisuko orduak trikitixarekin alaitzen zenituen modua, eta edozein kontu absurdoekin barre egin ahal izatea. Eta Euskalnaturaren parte diren eta izan diren guztiei: Ibon, Asier, Antton, Ostaizka, Mikel, Maialen, Axi, Lide, Iñaki, Maite, Aitor, eta batez ere gaur egun ekimen hau bizirik mantentzen ari zareten koadrila guztiari: aupa zuek!

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I a tu, que segurament no t'he anomenat, però que ara agafes aquesta tesi, potser fins i tot amb la intenció d'anar més enllà d'aquestes pàgines. En ella trobaràs el resultat final d'aquesta trajectòria, però sobre tot, el punt del qual parteixen tots els possibles camins d'un futur apassionant.

Trajecte de tren Blanes-Barcelona
Juny de 2017

Advisors' report

Dr. Bernat Hereu, professor at the Department of Evolutionary Biology, Ecology, and Environmental Sciences of the University of Barcelona, and Dr. Frederic Bartumeus, research professor at the Center for Advanced Studies of Blanes, advisors of the PhD thesis entitled **'Movement ecology of coastal fishes within a marine protected area: implications for management and conservation'**,

INFORM, that the research studies developed by Eneko Aspillaga for his Doctoral Thesis have been organized in four chapters, which correspond to four scientific papers listed below: two already published and two manuscripts to be submitted in the next months;

and CERTIFY, that the work has been carried out by Eneko Aspillaga in its totality, participating actively in all the task: setting the objectives, conceiving and performing acoustic telemetry experiments, analyzing the data, and writing the manuscripts.

Finally, we certify that the co-authors of the publications listed below and that conform this doctoral thesis, will not use this manuscripts in another PhD thesis.

Barcelona, 12 June 2017

Dr. Bernat Hereu　　　　Dr. Frederic Bartumeus

List and publication status of the chapters of this thesis:

CHAPTER 2: Aspillaga, E.[1], F. Bartumeus[2,3,4], C. Linares[1], R. M. Starr[5], À. López-Sanz[6], D. Díaz[7], M. Zabala[1], and B. Hereu[1]. 2016. Ordinary and extraordinary movement behaviour of small resident fish within a Mediterranean marine protected area. *PLoS ONE*, **11**: e0159813. 5-year impact factor (2015): 3.535

CHAPTER 3: Aspillaga, E.[1], F. Bartumeus[2,3,4], R. M. Starr[5], À. López-Sanz[6], C. Linares[1], D. Díaz[7], J. Garrabou[6,8], M. Zabala[1], and B. Hereu[1] (2017). Thermal stratification drives movement of a coastal apex predator. Scientific Reports, **7**: 526. 5-year impact factor (2015): 5.525

CHAPTER 4: Aspillaga, E.[1], F. Bartumeus[2,3,4], R. M. Starr[5], C. Linares[1], À. López-Sanz[6], D. Díaz[7], M. Zabala[1], and B. Hereu[1]. Space use, habitat selection, and spawning activity of a coastal apex predator: implications for MPA design. To be submitted to Biological Conservation. 5-year impact factor (2015): 4.748

CHAPTER 5: Aspillaga, E.[1], K. Safi[9,10], B. Hereu[1], and F. Bartumeus[2,3,4]. Modelling the 3D utilization distribution from Eulerian telemetry data. To be submitted to Methods in Ecology and Evolution. 5-year impact factor (2015): 8.121

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Abstract

Animal movement is a key biological process for the maintenance of ecosystem services, and a major concern for the conservation of biodiversity. The aim of movement ecology is to understand the causes and consequences of animal movement, including the effect of internal and external factors and its ecological implications. This research field has grown rapidly in the last decades fostered by recent technological and analytical developments, and is making substantial contributions to conservation biology, such as allowing the incorporation of the spatial and temporal scales of movement into management policies to enhance their scope and efficiency.

Marine protected areas (MPAs) are the most used tools to face the effects of anthropogenic impacts on marine ecosystems. They play a major role in restoring and conserving overfished fish populations, and also by potentially enhancing fisheries yield in adjacent areas through the direct spillover of juvenile and adult individuals. However, in order to be effective and generate such benefits, MPAs must be designed according to the movement attributes of targeted species, but this information is still rarely available, especially in temperate regions. In the last decades, passive acoustic telemetry techniques have demonstrated to be a valuable tool to study the movements and behavior of fishes covering large spatial and temporal scales, although the acoustic nature of the signals and the large amounts of data that they provide entail a series of challenges for their analysis and interpretation.

The main objective of this thesis is to characterize the movement ecology of coastal fishes in relation to MPAs. This constitutes a basic infor-

mation on the biology of species, which is required to understand changes in populations and ecosystems driven by natural or human induced impacts, as well as to correctly evaluate the outcomes of management actions. Specifically, the movements of two species, the white seabream (*Diplodus sargus*) and the common dentex (*Dentex dentex*), were monitored using acoustic telemetry in the Medes Islands MPA (Catalonia, NW Mediterranean Sea). Both species play important ecological and economical roles, shaping the structure and functioning of biological communities through top-down controls and being an important resource for local artisanal and recreational fisheries. Nevertheless, they present a contrasting biology (omnivorous vs. predator), and therefore, different conservation needs.

Firstly, we characterized the general movement attributes of the two species, including their space use, habitat preferences, and activity patterns, within zones with different protection levels of the MPA. Secondly, we studied the behavioral responses of the two species to environmental fluctuations by adding environmental information (seawater temperature and wave height) to movement analysis. These behavioral responses provide essential information on the ecology of the species, such as their resistance to perturbations. Thirdly, we characterized the movement behavior during the spawning season, describing, for the first time, the formation of spawning aggregations for both species. Finally, this thesis also has an important computational and numerical component. A special effort has been done to adapt and develop new methods to visualize and analyze acoustic telemetry data, especially to improve the space use estimations by incorporating the vertical dimension, in order to provide a more comprehensive view of complex movement patterns.

By studying the movement ecology of these species, we provide general mechanistic insights to understand the effects of protection on coastal fish species, as well as to predict future changes in their populations derived from climate change. The incorporation of information on the movement ecology of large number of species is key to propose integrative and more efficient management actions in the future.

Contents

CHAPTER 1

Introduction and objectives

1.1 General introduction

Coupling movement ecology and wildlife management

Movement, here understood as the change in the spatial location of a whole individual over time, is one of the main characteristics of life, and an important component in any ecological and evolutionary process (Nathan et al., 2008). It is a ubiquitous biological phenomenon: all organisms, from microorganisms to plants, and specially animals, have to move at some point of their life cycle. In many cases, movement is a response to short-term goals, such as searching for resources (e.g. food, suitable substrate), survival (e.g. escaping from predators, avoiding adverse environmental conditions), or reproduction (Bowler and Benton, 2005), but it might also be conditioned by its long-term implications on fitness (Winkler et al., 2014). Movement plays a major role in determining the fate of individuals, and thus, has profound effects on the structure and dynamics of populations, communities, and ecosystems (Nathan et al., 2008; Morales et al., 2010; van Moorter et al., 2013).

The main goal of movement ecology is to understand the effects of movement, including why, when or where organisms move, the influence of internal and external factors on this process, and its ecological implications. This research field has grown rapidly during the last decade, especially with regard to animal movement, fostered by recent advances in tracking technologies and computational methods. The current miniaturization of tracking devices (e.g. radio and acoustic transmitters, global positioning systems) is opening up the possibility of monitoring a growing number of species, overcoming the size restrictions of the past, and increasing our capacity to obtain high-resolution movement data (Cagnacci et al., 2010; Tomkiewicz et al., 2010). Moreover, biological sensors attached to tracking devices provide real time measures of the animals' internal state (Wilson et al., 2015). Simultaneously, advances in remote-sensing technology and the expansion of its coverage (e.g. Light Detection and Ranging – LiDAR, multibeam echosounders), are continuously providing environmental information and habitat characterizations (Wedding et al., 2011; Rogers et al., 2012), increasing our potential to contextualize, interpret, and extract relevant ecological conclusions from animal movement data (Scales et al., 2014; Demšar et al., 2015; Rose et al., 2015). Our increasing ability to collect vast amounts of tracking and environmental data presents new challenges that require revolutionary improvements in data management, processing, and analytical techniques (e.g. Patterson et al., 2008; Kranstauber et al., 2012). In this context, major conceptual advances have been made in recent years towards a cohesive framework to unify movement ecology research by working interdisciplinary and using more holistic approaches (Nathan et al., 2008), and to incorporate movement into biodiversity research (Jeltsch et al., 2013) and conservation (Allen and Singh, 2016).

Animal movement is critical for the maintenance of ecosystems services and biodiversity, and therefore, is related to major environmental problems. The field of movement ecology is making substantial contributions to improve management strategies, such as identifying the essential habitats for organisms or delimiting the pathways that are traversed by migratory species, which determine where and when conservation efforts must be intensified. Management actions that match the spatial and temporal scale of species movements are much more efficient than those that do not take into account movement (Thirgood et al., 2004; Moffitt et al., 2009).

A conceptual framework has been recently proposed to illustrate how animal movement knowledge can be used to improve management decisions

(Figure 1.1; Allen and Singh, 2016). First, it is important to identify the types of movements present in a population (e.g. sedentary, nomadic, or migratory; Mueller and Fagan, 2008) and their characteristics, such as shape and size of home ranges, timing and distances of movements, or location of migratory pathways. This information is crucial to determine the type and scale of management required, and for planning, designing and implementing specific actions. In addition, animal movement of keystone species provides important processes for the overall functioning of ecosystem, for example, providing interaction networks (e.g. predator-prey, plant pollinator; Kremen et al., 2007), or acting as a link between different ecosystems (Jeltsch et al., 2013; Pagès et al., 2013). Considering these ecological consequences of the movement permits to focus on conservation strategies that ensure multiple ecosystem services (Mitchell et al., 2013). Finally, the framework also contemplates an adaptive management component of evaluation to address the effectiveness of management actions, which is used to avoid implementing actions that do not achieve conservation goals (Ferraro and Pattanayak, 2006) and to guide the management objectives of future actions. Importantly, new insights into animal movement are calling into question the efficiency of traditional conservation approaches such as static protected areas, as they might be inadequate in terms of the spatial scale of the movements of targeted species. Linking management planning with movement ecology allows targeting conservation efforts where threats are located, prioritizing the most effective management decisions, and implementing novel management actions that are flexible in time and space (Allen and Singh, 2016).

In summary, technical, analytical and conceptual developments in movement ecology have revolutionized our perception about individuals, populations and ecosystems. These developments have increased the scope and the scale of the questions that we can address about the causes and consequences of movement, and have redefined the way we manage the environment.

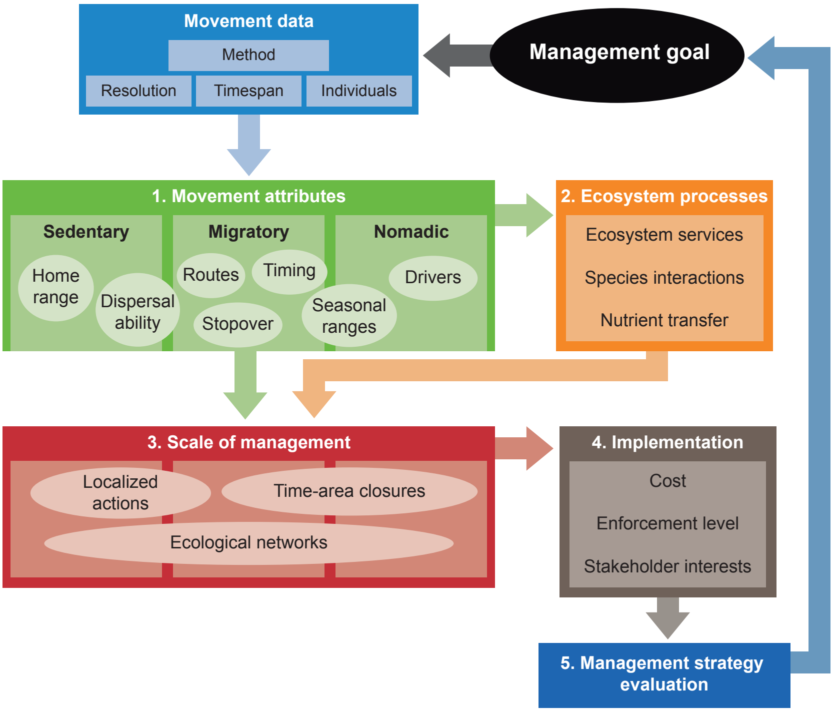

Figure 1.1: Movement-management framework to incorporate movement ecology into decision-making processes proposed by Allen and Singh (2016). Adequate movement data is used to understand the types and attributes of movements occurring in the study system and the ecosystem processes resulting from them. This information is used in the decision-making process to identify the potential management actions, which might be flexible in time and space, and guide their implementation. The final step evaluates the effectiveness of management creating an adaptive management cycle. Adapted from Allen and Singh (2016).

The efficiency of marine protected areas

Human induced global change, which includes intense exploitation of the sea, habitat destruction, pollution, introduced species, and climate change, has greatly altered marine ecosystems all around the world, especially in coastal areas (Halpern et al., 2008). Overfishing is the most prominent disturbances among anthropogenic impacts (Jackson et al., 2001), as it has deeply modified fish communities by selectively reducing the abundance of species in top levels of the trophic web (Pauly et al., 1998). The "ecological extinction" of these species, which are too scarce in order to assume their ecological role, has generated undesired top-down cascade effects that have triggered profound changes in the functioning and stability of whole ecosystems (Sala and Zabala, 1996; Baum and Worm, 2009; Estes et al., 2011).

Marine protected areas (MPAs) are being increasingly used as management tools to face the detrimental effects of anthropogenic impacts. By restricting fishing and other extractive activities, MPAs play a major role in protecting fish populations from overfishing, and therefore, in restoring the biodiversity and resilience of marine ecosystems (Halpern, 2003; Lester et al., 2009). Beside the primary conservation objectives, potential socio-economic benefits have also motivated the establishment of many MPAs. These expected benefits rely in the capacity of MPAs to enhance fisheries yield in adjacent areas through two main density-dependent mechanisms: an export of pelagic eggs and larvae that will increase recruitment (Christie et al., 2010; Harrison et al., 2012), and the spillover of juvenile and adult individuals (Gell and Roberts, 2003; Russ et al., 2004).

Despite the number of MPAs is rapidly increasing with the years, their capacity to generate socio-economic benefits is still under debate (Gell and Roberts, 2003). Many MPAs have failed to achieve the conservation objectives for which they were designed, presenting a poor performance in terms of recovery of fish biomass (Sala et al., 2012; Edgar et al., 2014). Several biological and socio-economic factors influence the low response of species to protection (Edgar et al., 2014). For instance, the high harvesting levels that are allowed in many MPAs and their low enforcement level, are often inconsistent with conservation goals (Guidetti et al., 2008). Some other MPA features, such as the size and location, might not match with the biological traits of targeted species, especially regarding movement behavior. First, in order to effectively protect a fish population, the protected area must be big enough to cover the regular movements of a significant part of individuals (Claudet et al., 2008). Second, the distribution of favorable habitats within the MPA, and their degree of continuity with habitats in non-protected areas, facilitate or restrict the movement of individuals across MPA boundaries (Forcada et al., 2008), lowering or enhancing the effect of protection. Therefore, understanding the scales and patterns of fish movements is necessary to understand the consequences of protection, as well as to design and apply efficient management actions from the scope of the movement ecology framework (Sale et al., 2005; Allen and Singh, 2016).

Fish movement in marine ecosystems

Fishes present a huge range of movements, which can be broadly divided into three types depending on their spatial and temporal scale: sedentary, nomadic, or migratory (Mueller and Fagan, 2008; Grüss et al., 2011). Animals moving in a sedentary range use to have stable home ranges (i.e., area required to carry out all their biological demands, such as feeding or resting; Mace et al., 1983), which are relatively small compared to the total distribution of the population. The home range of sedentary species ranges between several meters to tens of kilometers, and usually are placed in coastal areas such as rocky habitats or coral reefs. Nomadism consists on extent and random movements across the landscape through routes that do not repeat in time (Mueller and Fagan, 2008). This type of movement usually occurs in relatively homogeneous habitats, over distances ranging from a few hundreds of meters to hundreds of kilometers. Migrations are directed movements between specific areas, usually motivated by foraging or spawning needs or changes in environmental variables. Migratory movements can have an extent ranging from some hundreds of meters to thousands of kilometers, and unlike nomadism, occur through predictable and repeated routes. Ontogenetic migrations are a particular type of migrations, in which animals change their habitat preference and home range as they grow.

Distinct adult and juvenile movements can simultaneously occur within the same population (Grüss et al., 2011), making it difficult to unveil the underlying mechanisms associated to the observed movements (Sánchez-Lizaso et al., 2000; Goñi et al., 2010). On the one hand, species that are considered sedentary can eventually migrate to specific spawning grounds and then return to their original home range within some hours or days (Starr et al., 2007). On the other hand, behavioral polymorphism have been observed for many species, where a part of the population shows sedentary movements within home ranges, while the rest exhibits nomadic movements (e.g. Starr et al., 2004).

The different types of movements and their extent greatly affect the conservation outcomes of management actions (Figure 1.2). Sedentary species that move within small home ranges are thought to be the most benefited by the establishment of a protected area, because their movement extent is easily covered even by small MPAs (Claudet et al., 2008). Highly mobile migratory or nomadic species, by contrast, spend more time outside protected areas, where they are susceptible of being fished (Williams et al., 2009). It is also generally accepted that fish mobility increases with body size: species with large body sizes require exploiting resources over larger areas than small species, and it is also much less costly for them to travel over large distances (Kramer and Chapman, 1999; Sale et al., 2005). Highly mobile species use to be, in turn, long-lived, slow-growing, late-maturing and belonging to high trophic levels (Sale et al., 2005; Grüss et al., 2011), hence highly vulnerable to fishing and with augmented management complexity.

Technological advances to study the movement of marine animals

The greatness, complexity, and opacity of marine environments have been major impediments to study and understand their ecological functioning, especially regarding the animal movement and behavior. The first historical measures of abundances and movements of aquatic animals were based on predictable patterns of where and when valuable species could be captured (e.g. salmons, coastal whales), which usually formed part of traditional knowledge. During the past century, mark-recapture methods used in fisheries management provided the first systematic approach to study the

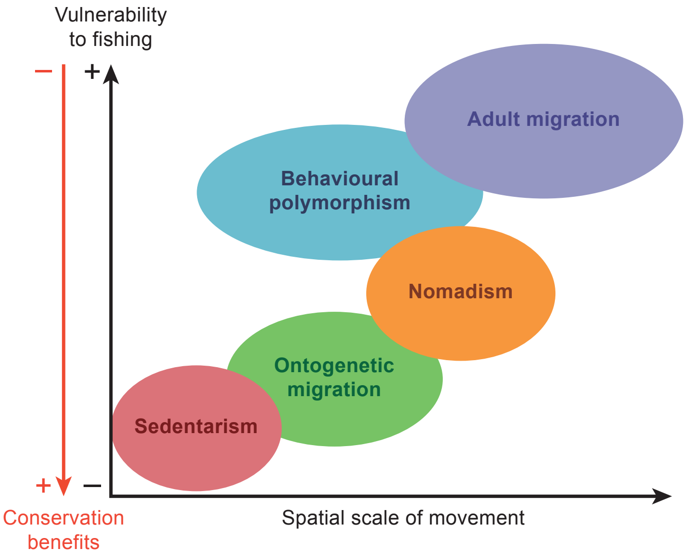

Figure 1.2: Relative scales of different fish movement types (x axis) and their impact on vulnerability to fishing and conservation benefits (y axis). Adapted from Grüss et al. (2011).

dynamics and distribution patterns of fish populations (Pradel, 1996). However, the spatial and temporal resolution of this method was low, restricted to the location and timing of tag and recapture events. It has been in the last two decades, when the development of aquatic telemetry systems has radically transformed our capacity to observe and monitor the movements of animals in their environment, allowing us to cover a wide range of spatial and temporal scales.

Aquatic telemetry involves placing electronic devices on animals, which then transmit data to remote logging or receiving stations. Most aquatic telemetry is based in two principal approaches: acoustic telemetry and satellite telemetry (Hazen et al., 2012; Donaldson et al., 2014; Hussey et al., 2015). In satellite telemetry, observations are transmitted to land-based receivers through orbiting satellites, while in acoustic telemetry signals are detected and logged by fixed or mobile receivers operating in the study site. Satellite telemetry allows to record fine-scale time series of data over vast spatial scales, including open oceans, but due to the size of the devices and the data transmission mechanism, its usage is restricted to large animals or to animals that regularly surface (Hussey et al., 2015). Tags used in acoustic telemetry are much smaller, and allow monitoring the movements of a wide range of species (Figure 1.3). For this reason, acoustic telemetry has become a widely-used method to study the movements of fish species and has focused most of the research on coastal, estuarine, and freshwater ecosystems (Hussey et al., 2015).

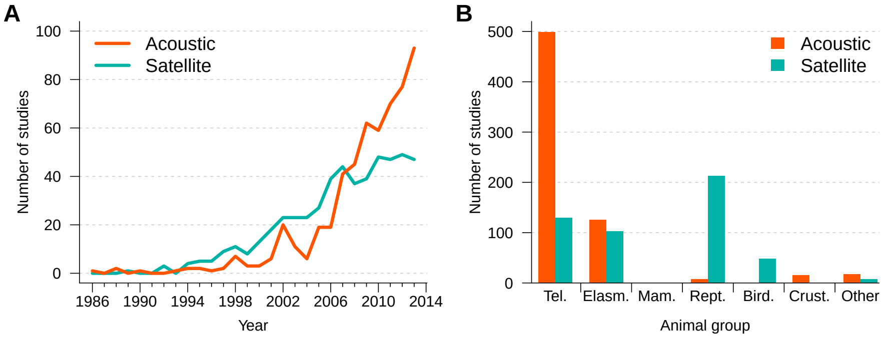

Figure 1.3: Distribution of acoustic and satellite telemetry studies per year between 1986-2013 (A) and by major aquatic animal groups (B). Tel.: teleost; Elasm.: elasmobranch; Mam.: marine mammals; Crust.: crustaceans, Bird.: marine flightless birds. Adapted from Hussey et al. (2015).

Acoustic telemetry techniques

In acoustic telemetry, animals are marked with electronic tags that emit acoustic signals (Figure 1.4), which are detected by receivers equipped with hydrophones. Two types of acoustic telemetry can be differentiated, active and passive, depending on the way in which receivers are operated. Acoustic tags used in active tracking emit single signals or pings at short and regular intervals of time (1-2 seconds) and at a given frequency (usually between 50 and 84 kHz), and movements of individuals are monitored from a boat using a handheld directional receiver (Holland et al., 1985). This technique allows a fine-scale positioning of the animal, but it is costly in terms of time and resources, because only one animal can be tracked at a time (Figure 1.5). In passive telemetry, by contrast, acoustic signals are detected and stored by submerged omnidirectional receivers placed at fixed positions in the study site, which must be regularly recovered in order to retrieve the data (Figure 1.6; Heupel et al., 2006). Passive telemetry tags emit coded acoustic signals, containing the identifier of the animal, at one unique given frequency (e.g., 69 or 180 kHz), so that multiple individuals and different species can be monitored at once. Therefore, passive telemetry is less labor intensive, as data collection operates autonomously once animals are tagged and the receiver array is established. It allows large areas to be efficiently covered and to monitor movements over long periods of time, ranging from few days to several years. Moreover, with the addition of sensors (e.g. depth, temperature, acceleration), acoustic tags can also document the environmental conditions surrounding an organism and measure their behavioral or physiological internal states, providing essential data to understand the characteristics and causes of the observed movement patterns.

Passive acoustic telemetry provides a valuable tool to study the movement ecology and behavior of aquatic animals. However, the acoustic nature of signals entail a series of concerns that must be considered. For instance, acoustic signals rapidly loss their power when traveling through water due to energy absorption. Therefore, the probability of detecting an individual decreases as it moves away from the receiver. This acoustic range at which signals are effectively detected has to be correctly quantified in order to properly design the acoustic telemetry experiment (e.g. number and placement of receivers, distance between them; Kessel et al., 2013). Moreover, acoustic range of telemetry signals might be affected by several physical and biological factors that vary during the study, such as habitat characteristics, hydrodynamics (currents, waves), or noise produced by biological or human activities (Payne et al., 2010; Welsh et al., 2012). Determining and monitoring the efficiency of the acoustic array, by placing control tags or by previously testing the acoustic range, is extremely important to interpret telemetry data and to reach to meaningful conclusions about fish behavior (Payne et al., 2010).

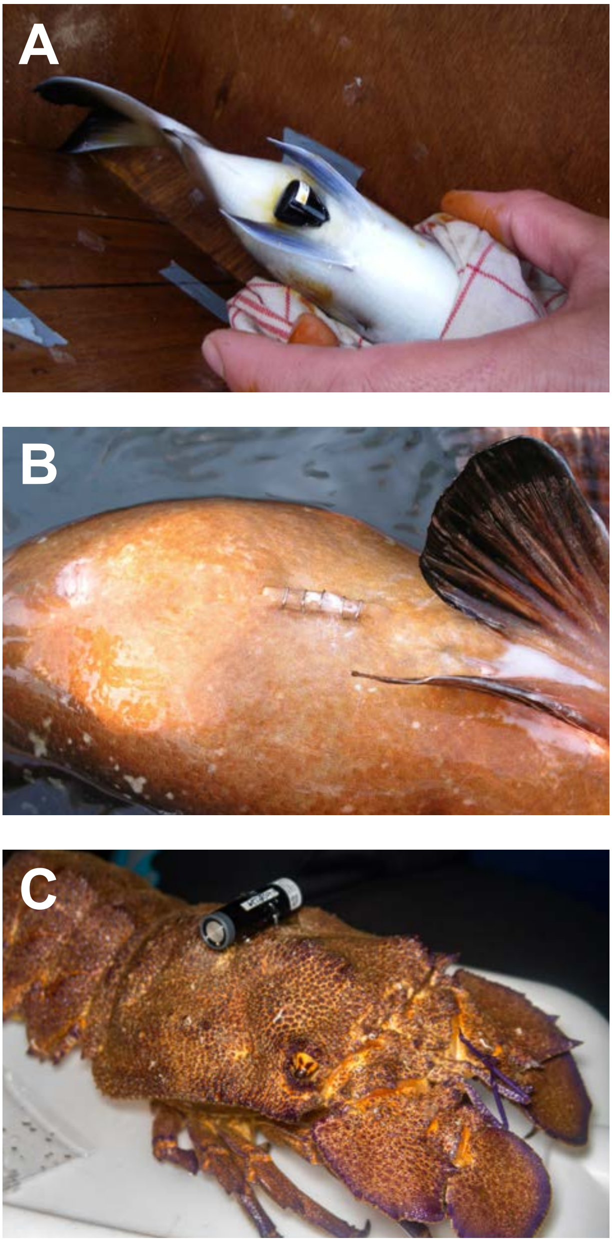

Figure 1.4: Marking marine animals with acoustic tags. A: an acoustic tag is introduced in the peritoneal cavity of a white seabream individual (*Diplodus sargus*) through an incision in the ventral area. B: the incision is sutured with surgical staples after placing a tag in a dusky grouper (*Epinephelus marginatus*). C: an acoustic tag externally attached with glue to a Mediterranean slipper lobster (*Scyllarides latus*). Photo credit: B. Hereu (A, B) and from the author (C).

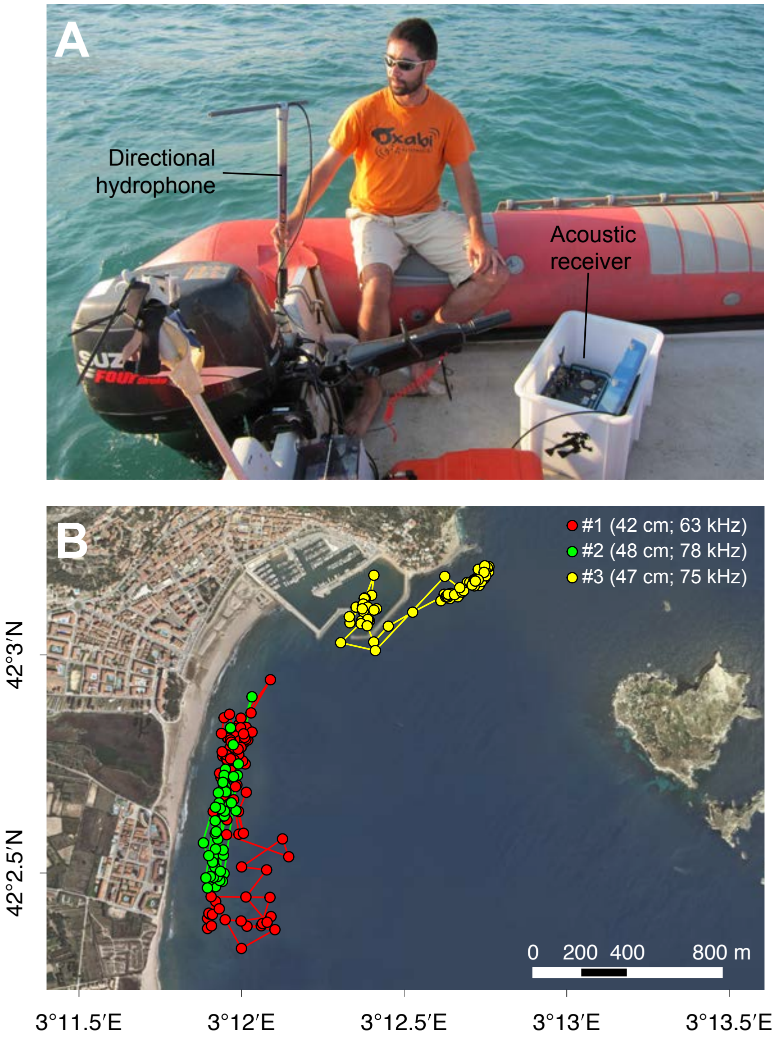

Figure 1.5: Active acoustic telemetry. A: Movement of individuals is followed from a boat with a portable acoustic receiver and a directional hydrophone. B: Movement paths of three gilthead seabream individuals (*Sparus aurata*) that were tracked during 24 h periods, taking one position every 15 minutes. Photo credit: B. Hereu.

Analyzing passive acoustic telemetry data

Passive acoustic telemetry can operate over a wide spectrum of spatial and temporal scales and generate vast amounts of data. The nature of the technique, however, poses several challenges for its analysis. Firstly, the possible locations of the animals are restricted to a discrete set of coordinates (i.e. position of the receivers), and thus, movement is perceivers as a Eulerian process where presences and absences alternate between those

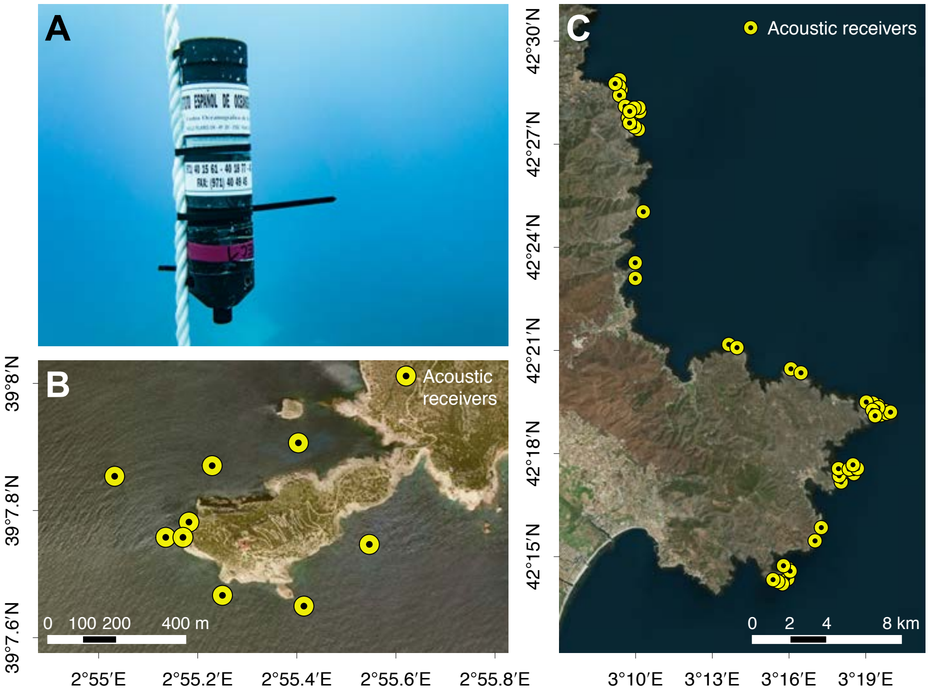

Figure 1.6: Passive acoustic telemetry. A) Signals from tagged animals are detected by acoustic receivers placed in fixed positions. B) Acoustic receiver array covering a relatively small area to monitor the movements of slipper lobsters (*Scyllarides latus*) in the Cabrera Archipelago National Park (Balearic Islands) (SCYTRACK project, Spanish Oceanographic Institute). C) Extensive acoustic telemetry array to study the movements of dusky groupers (*Epinephelus marginatus*) and white seabreams (*Diplodus sargus*) between the Cap de Creus natural park (Catalonia) and the natural reserve of Cerbère-Banyuls (France) (eCATE project, University of Perpignan and University of Barcelona). Photo credit: from the author.

locations. Secondly, due to the relatively large acoustic ranges (100-1000 m) at which signals might be detected, there is a big uncertainty related to each location, which must be incorporated when estimating the space use probabilities of individuals. Because of these limitations, classical analysis techniques are often not adequate to answer certain questions on the ecology of species using passive telemetry data. For instance, quantifying habitat use or detecting interactions between individuals (e.g. predator-prey, spawning behaviors), require accurate space use estimations that should also incorporate the vertical dimension of aquatic environments. However, space use is usually calculated using kernel density estimators that do not take into account the spatial and temporal correlation between locations (Worton, 1989; Simpfendorfer et al., 2002), while depth data, when available, is usually analyzed separately from the horizontal location data. In recent years, a number of tools have emerged for movement analysis that have a great potential to be applied to passive acoustic telemetry, such as movement-based space use estimators (Horne et al., 2007; Kranstauber et al., 2012), state-space movement models (Patterson et al., 2008), or network analysis (Jacoby and Freeman, 2016). Scientific publications applying these techniques to acoustic telemetry are being recently published (e.g. movement-based estimators: Papastamatiou et al., 2013; Pagès et al., 2013; state-space models: Alós et al., 2016; network analysis: Haulsee et al., 2016; Lea et al., 2016). However, there are still some challenges to be solved, such as the incorporation of the depth and physical habitat into movement analysis. We are now just exploring the possibilities of new methodologies, but there is still a lot of work to do to develop and adapt them to suit the peculiarities of acoustic telemetry data.

1.2 Objectives

The general objective of this thesis is to characterize the movement ecology of coastal fishes within Mediterranean marine protected areas (MPAs). This constitutes basic yet often unknown information about the biology of the species, which is required to understand changes in populations and ecosystems driven by natural or human induced impacts, and in turn is also essential to correctly evaluate the outcomes of management actions such as the establishment of MPAs.

This thesis also has an important computational and numerical component. All the chapters presented below have their core in movement data provided by passive acoustic telemetry. This technique generates large amounts of valuable data, but also several challenges for its interpretation. Because of this reason, a special effort was done during the course of this thesis to adapt and develop analytical and visualization methods for acoustic telemetry data. This has resulted in computational code and a number of methods that provide a more comprehensive view of the movement ecology of aquatic animals, and thus have a great applicability in future studies.

Two necto-benthic fish species were selected for these studies: the white seabream, *Diplodus sargus* (L., 1758), and the common dentex, *Dentex dentex* (L., 1758) (Figure 1.7). Despite of being from the same family (Sparidae), these two species greatly differ in their biology and behavior. The white seabream is a small- to medium-sized omnivorous fish, widely distributed and relatively abundant in Mediterranean coasts. The common dentex, by contrast, is a larger predator in the top of the trophic web of actual Mediterranean coastal ecosystems. Both species have an important

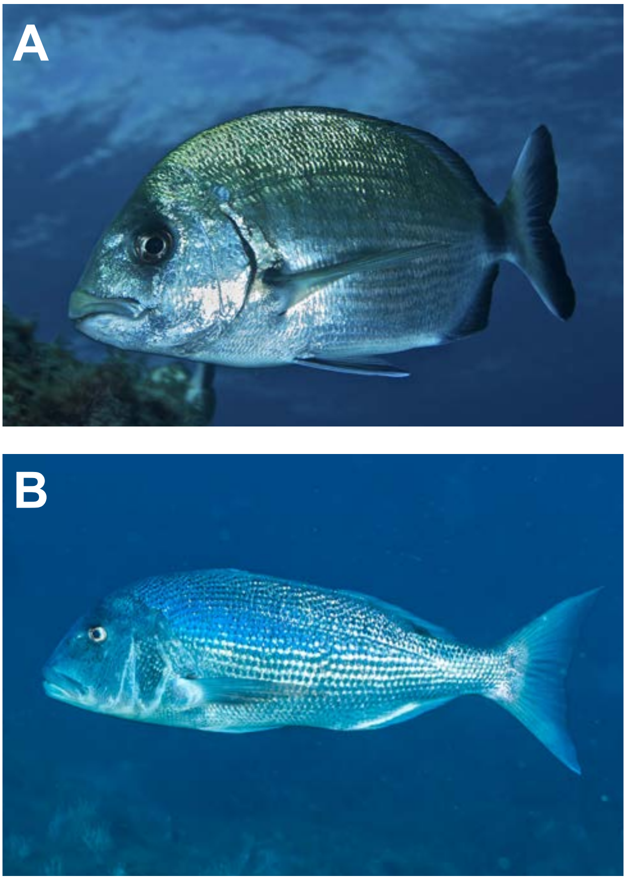

Figure 1.7: Pictures of the species studied in this thesis: the white seabream, *Diplodus sargus* (A), and the common dentex, *Dentex dentex* (B). Photo credit: B. Hereu (A) and from the author (B).

role in shaping marine ecosystems through top-down controls; on the herbivorous populations (e.g. sea urchins) in the case of the white seabream, and on populations of fish species in lower trophic levels in the case of the common dentex. Both species are also an important economical resource for local and recreational fisheries. However, the common dentex is a much more appreciated catch, and therefore suffers an intense fishing pressure that has decreased their populations in most Mediterranean coasts.

All the fieldwork has been carried out in the Medes Islands MPA (Catalonia, NW Mediterranean Sea, Figure 1.8). Despite its small size (93 ha), is one of the most successful Mediterranean MPAs, where one of the largest increases in fish diversity and biomass has been observed. Nevertheless, one of the most special features of the Medes Islands is the large amount of monitoring and research programs that have been performed in this area along several generations of scientists in the course of the almost 40 years elapsed since the establishment of the reserve. All this research effort provides a valuable and unique baseline information on the physical and biological processes happening in the MPA, which constitutes an excellent framework to propose and interpret new studies.

Specific objectives

To characterize the general movement patterns of coastal fish species (CHAPTER 2 and 4). We used passive acoustic telemetry to monitor the movement patterns of the white seabream and the common dentex. We aimed to quantify the space use (home range sizes), the habitat preference, and the most characteristic spatial and temporal activity patterns for each species.

To unveil behavioral movement responses of coastal fishes to environmental fluctuations (CHAPTER 2 and 3). We analyzed the horizontal and vertical movements of the two species together with physical environmental variables (wave height and seawater temperature). Behavioral responses provide insights into the ecology of the species, essential to understand their movement and distribution, predict future trends in population dynamics, and detect events that could threaten their conservation.

To describe the spawning behavior of coastal fishes (CHAPTER 2 and 4). Our objective was to detect and characterize special behaviors, such as the formation of aggregations, during the spawning season of each of the studied species. Spawning behaviors are generally unknown for most fish species, especially in temperate regions, despite of being a basic biological information with great implications for management.

To provide new methods and improve available ones to analyze and get more accurate estimates of space use (chapter 2, 4, and especially 5). We explored new methodologies with the objective to improve the space use estimations from passive acoustic telemetry data. This includes the development of a new numerical method to estimate the three-dimensional space use of individuals taking into account the local topography. We also aimed to develop new visualization methods to efficiently display large amounts of telemetry data.

To provide insights and movement-based tools for the management of coastal species (chapter 2, 3, 4). The final aim of the thesis is to relate the movement ecology of the studied species with their response to the protection provided by the Medes Islands MPA. This will allow us to identify specific conservations needs and provide baseline information to improve the design of new MPAs in the future.

Figure 1.8: Study site. The Medes Islands seen from the beach of l'Estartit. Photo credit: from the author.

CHAPTER 2

Ordinary and extraordinary movement behaviour of small resident fish within a Mediterranean marine protected area

Abstract

It is important to account for the movement behaviour of fishes when designing effective marine protected areas (MPAs). Fish movements occur across different spatial and temporal scales and understanding the variety of movements is essential to make correct management decisions. This study describes in detail the movement patterns of an economically and commercially important species, *Diplodus sargus*, within a well-enforced Mediterranean MPA. We monitored horizontal and vertical movements of 41 adult individuals using passive acoustic telemetry for up to one year. We applied novel analysis and visualization techniques to get a comprehensive view of a wide range of movements. *D. sargus* individuals were highly territorial, moving within small home ranges (< 1 km^2), inside which they displayed repetitive diel activity patterns. Extraordinary movements beyond the ordinary home range where observed under two specific conditions. First, during stormy events *D. sargus* presented a sheltering behaviour, moving to more protected places to avoid the disturbance. Second, during the spawning season they made excursions to deep areas (> 50 m), where they aggregated to spawn. This study advances our understanding about the functioning of an established MPA and provides important insights into the biology and management of a small sedentary species, suggesting the relevance of rare but important fish behaviours.

2.1 Introduction

Understanding the movement ecology of fishes is crucial for the management of marine ecosystems. The efficacy of a marine protected area (MPA) to protect and restore overexploited fish populations within its boundaries and to enhance sustainable fishing activities in adjacent areas depends greatly upon the relationship between the size of the MPA and the scale of the movements of targeted fish species (Kramer and Chapman, 1999; Botsford et al., 2009). However, movements of juvenile and adult fishes can occur over several spatial and temporal scales, providing a challenge when designing effective MPAs (Grüss et al., 2011). Therefore, having good baseline information on space-use patterns of different fish species is essential for making effective spatial management decisions, such as the design of an MPA or the configuration of a reserve network (McLeod et al., 2009; Green et al., 2015).

Home range (HR) is the area in which an individual spends the majority of its time and undertakes most of its routine activities, such as foraging and resting (Kramer and Chapman, 1999; Botsford et al., 2009). Very sedentary or territorial species have small HRs, and are more likely to benefit from the establishment of spatial protection (Moffitt et al., 2009; Williams et al., 2009) than highly mobile or migratory species that, by expending more time in open areas, become vulnerable to being fished (Chapman and Kramer, 2000; Gaines et al., 2010).

In addition to regular or routine movements, many sedentary species undergo sporadic movements involving larger spatial scales, responding to special needs raised by physical and biological factors. For example, many species undertake migrations to specific breeding areas during the spawning season (Domeier and Colin, 1997; Claydon, 2004). In coral reefs, these migrations often result in fish spawning aggregations (FSAs) (Sadovy de Mitcheson and Colin, 2012), which are highly predictable both in time and in space, and therefore render those species particularly susceptible to being overfished (Sala et al., 2001; Sadovy and Domeier, 2005). While about 200 tropical fish species are known to form FSAs (Sadovy de Mitcheson and Colin, 2012), very little is known about spawning behaviours of fish species in temperate seas. For instance, in the Mediterranean Sea there is only one species, the dusky groper (*Epinephelus marginatus*), which has been confirmed to form FSAs (Zabala et al., 1997; Hereu et al., 2006).

An understanding of the variety of fish movement patterns, from HR-level ordinary movements to sporadic (or extraordinary) migrations, is needed to correctly assess the effectiveness of MPAs. Acoustic telemetry techniques have proven to be powerful tools to serve this purpose, allowing long-term monitoring of fish movements over a wide range of spatial scales (Hussey et al., 2015). During the last two decades, these techniques have been successfully applied around the world to study the movements of a broad variety of marine species (Hussey et al., 2015; Grothues, 2009).

Here, we focus on the white seabream *Diplodus sargus* (L., 1758), using acoustic telemetry to study the movements of a common necto-benthic species within different protection levels of a Mediterranean MPA. *D. sargus* is one of the most abundant species of the infralittoral zone in the Mediterranean Sea, with a high ecological relevance as a grazer and prey species that helps shape rocky marine ecosystems (Sala and Zabala, 1996; Guidetti and Sala, 2007; Hereu et al., 2008). It is also of great importance in artisanal and recreational fisheries (FAO, 2014; Lloret et al., 2008). *D. sargus* is a well-studied species, and many aspects of its biology have been widely described (Harmelin-Vivien et al., 1995; Macpherson et al., 1997;

Sala and Ballesteros, 1997). Several telemetry studies have been published that describe the movements of *D. sargus* in different environments, such as coastal lagoons (Abecasis et al., 2009) and artificial reefs (Lino et al., 2009; D'Anna et al., 2011; Koeck et al., 2013; Abecasis et al., 2013). More recently, three studies focused on the movements of this species in relation to MPAs (Di Lorenzo et al., 2014; Abecasis et al., 2015; Di Lorenzo et al., 2016). All these studies describe the high sedentariness of *D. sargus*, reporting small HRs and high site fidelity. Some of the studies also describe daily movement cycles for this species (Lino et al., 2009; Abecasis et al., 2013; Di Lorenzo et al., 2014; Abecasis et al., 2015; Di Lorenzo et al., 2016), but little is known about how daily movement behaviour is affected during extreme environmental conditions or in the spawning period, the latter known to occur from March to June.

In this study we performed one of the longest telemetry experiments conducted to date with *D. sargus* in natural environments. Our high resolution and fine scale spatial data provide a comprehensive and up-to-date view of the movement ecology of this species, one that describes diel movement patterns and movement behaviour during severe climatic events and spawning periods. Information gathered from the wide spectra of movement scales and ecological conditions studied provide novel insights for the conservation of the species, and more generally, for the management of benthic fishes in Mediterranean MPAs.

2.2 Material and Methods

Study area

The study was carried out in the Medes Islands MPA (Catalonia, NW Mediterranean Sea), which comprises three zones with different protection levels (Figure 2.1). The fully protected marine reserve or no-take zone (NT) is placed in the small archipelago of the Medes Islands, and was established in 1983. A partially protected buffer zone or partial reserve (PR) encompasses a section of the nearby coast of the Montgrí massif. In this

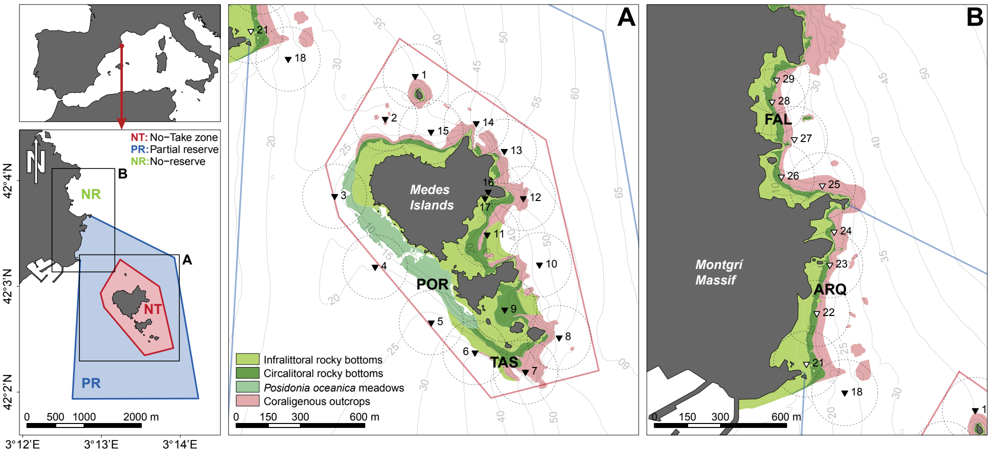

Figure 2.1: Study area and the acoustic receiver array. Black triangles correspond to acoustic receivers placed in May 2007 and white triangles to the receivers placed in September 2008. Dotted circles represent the average detection range (150 m). Red bold letters stand for the *Diplodus sargus* capture locations: TAS, Tascons; POR, Portitxol; ARQ: Arquets; FAL: Falaguer. The topographic base map (1:5.000) and the sea bottom bionomic map (Hereu et al., 2012) are freely accessible through the Institut Cartogràfic i Geològic de Catalunya (`www.icgc.cat`) under Creative Commons Attribution License (CC BY 4.0).

zone, limited traditional artisanal fishing (longline and trammel net gear) and recreational angling are allowed with restrictions. The rest of the coast is not subject to any specific regulation; all type of activities, including spearfishing, are allowed, and hence is considered a no-reserve zone (NR).

The Medes Islands and the Montgrí coast are areas of high ecological value because of the high diversity of marine habitats they encompass (Hereu et al., 2012). The shallow zones closest to the land contain heterogeneous rocky habitats, which are followed by coralligenous outcrops in deeper zones. In waters deeper than about 50 m, hard bottoms are succeeded by soft sandy bottoms, which form a band of soft sediments about 800 m wide between the rocky habitats of the Medes islands and the Montgrí massif on the coast. Since the establishment of the Medes Islands MPA, several studies have reported higher abundance and biomass of *D. sargus* and other vulnerable species, such as the dusky grouper *Epinephelus marginatus* and the common dentex *Dentex dentex*, inside the NT zone than in the PR and NR zones (Hereu et al., 2005; García-Rubies et al., 2013).

In this area of the coast, winter storms that arrive from the north and east are frequent (Pascual et al., 2012). One exceptionally severe easterly storm arrived off the Catalan coast on 26–27 December 2008. The storm produced winds surpassing 85 km/h and waves up to 14.4 m in maximum height. This storm, known as the St. Steve's Day Storm, greatly affected the study area, causing profound impacts on benthic communities at depths of up to 20 m (Sanchez-Vidal et al., 2012).

Acoustic monitoring system

A network comprised of 27 moored acoustic receivers (VR2 and VR2W, VEMCO, Nova Scotia, Canada) was installed in the study area (Figure 2.1). Moorings included anchors, chain, line, and subsurface floats. Receivers were placed 8 m below the surface. The installation of the receivers was performed in two stages. A first set of 17 receivers was placed within the NT zone, covering the entire perimeter of the Medes Islands, in June 2007 (Figure 2.1.A). A second set of 10 receivers was installed in the Montgrí coast in September 2008, 5 of them in the PR zone and 5 in the NR zone (Figure 2.1.B). All moorings and receivers were removed in July 2009, with the exception of #8, which was lost in the beginning of the experiment due to adverse sea conditions and was not replaced. During the extreme storm of 2008, receiver #22 was lost and then replaced by the receiver in position #23 in January 2009.

Signal range-tests were performed in the study site by placing multiple receivers at different distances from a transmitter of the same model used to tag fish. These tests revealed that the probability of detecting a signal was > 90 % out to a range of 150 m, after which the probability of reception dropped below 50 % (Figure 5.1). No test-transmitters were used during the study to detect possible changes in the reception efficiency. It has been described that the detection probabilities can be highly variable in coastal waters due to environmental noise caused by wave action, physical impediments and biological activity (Payne et al., 2010). We considered this impediment when interpreting our data, and hence we have avoided drawing biological conclusions from temporal patterns in the number of receptions.

Fish tagging

Ethics statement. The tagging protocol was approved by the Committee on the Ethics of Animal Experimentation of the University of Barcelona. The Department of Environment of the Catalan Government granted permissions for fishing, operating and releasing the animals in the Medes Islands Marine Reserve. All surgery was performed under 2-phenoxyethanol anaesthesia, and all efforts were made to minimize suffering.

Individuals of *D. sargus* where caught and tagged with V13P-1H acoustic tags (dimensions: 48 x 13 mm, power output: 153 dB, weight in water: 6.5 g; VEMCO, Nova Scotia, Canada), programmed to produce signals at random delay times between 80 and 180 s. A traditional angling technique was used to catch the individuals from the shoreline, and barbless hooks were used to minimize injuries. Fish were anesthetized by dipping them in a 0.2 $ml \cdot l^{-1}$ 2-phenoxyethanol solution. Tags were surgically introduced in the peritoneal cavity through an incision of 2 cm in the ventral area, which was then closed with sterile surgical staples. Before being released, fish were placed in recovery tanks filled with clean seawater until a full recovery of their normal activity was observed (usually between 10-20 min). The tagging procedure was conducted under aseptic conditions, and all efforts were made to minimize animal stress and suffering. The tagging methodology used is a standard procedure that has been used on *D. sargus* and other species in previous studies (Lino et al., 2009; Jadot et al., 2002; Pagès et al., 2013). The procedure has been demonstrated to have no long-term, adverse effects on fish behaviour and survival (Koeck et al., 2013).

A total of 41 individuals of *D. sargus* between 25 and 35 cm length were successfully tagged and released in four different locations (Figure 2.1). Two groups of 11 and 9 individuals, respectively, were caught in May 2007 in two locations separated by about 300 m within the NT zone (TAS and POR). In September and October 2008, two additional groups of 14 and 7 individuals were tagged in the ARQ (PR zone) and FAL (NR zone) locations. In order to assess the homing ability of this species, seven of the individuals captured in the ARQ location within the PR zone in the Montgrí coast were released in the TAS location within the Medes islands NT zone. The rest of the animals were released in the same location as they were captured.

Data analysis

Data from the VR2 receivers were regularly downloaded to VUE software (VEMCO, Nova Scotia, Canada) and directly imported to R (v.3.2.1) (R Core Team, 2015), where all the pre-processing and data analyses were performed. Sole receptions in a single receiver within a 24 h time interval were considered spurious and were therefore deleted.

Residence index

A residence index (RI) was calculated for each fish by dividing the total number of days the fish was detected (DD) by the number of days in the entire tracking period (TP) (Afonso et al., 2008). The time interval during which receiver #22 was missing (see above) was not used to calculate the RI of the fish from the ARQ location.

Home range size

The Brownian Bridge Movement Model (BBMM, Horne et al., 2007) was used to compute the utilization distribution (UD), i.e. the probability distribution defining the animal's use of space (Van Winkle, 1975), of each fish for the whole tracking period. The BBMM has advantages over the classical kernel UD estimator. While the kernel UD estimator only takes into account the spatial distribution of the locations, the BBMM also considers their time dependence, assuming a conditional random walk movement model between pairs of locations. Furthermore, the BBMM incorporates the location error in an implicit way during the calculation. Those two advantages make the BBMM especially suitable to analyse data from passive acoustic telemetry, where the position of the reception is fixed and the location error is as large as the signal detection range. BBMMs have been already applied to acoustic telemetry experiments (Pagès et al., 2013; Papastamatiou et al., 2013). BBMM were applied using the BBMM package (v.3.0) for R (Nielson et al., 2013).

HR and core area sizes were calculated as the minimum areas encompassing the 95% and 50% of the UD estimate volumes, respectively. We measured the space use sharing between each pair of *D. sargus* individuals using the Utilization Distribution Overlapping Index (UDOI) suggested by Fieberg and Kochanny (2005). The UDOI, being a function of the UD and its uniformity, equals zero when two UDs do not overlap, equals 1 when the UDs are completely overlapped and are uniformly distributed, and >1 when two UDs which are not uniformly distributed show a high degree of overlap (Fieberg and Kochanny, 2005). HR and core area sizes and the UDOI were calculated with the adehabitatHR package (v.0.4.14) for R (Calenge, 2006).

Diel patterns

In order to study the circadian behaviour of *D. sargus*, receptions were classified into day and night time periods as defined by local sunset and sunrise time from the US Naval Observatory (`http://aa.usno.navy.mil/data/index.php`, data accessed in 2013/09/12 for the coordinates of the Medes Islands 42°03'N 3°13'E). The presence of diel patterns was assessed for each individual following two different approaches. First, we created spatial chronogram plots, which were visually inspected. Spatial chronogram plots represent the receivers with the largest number of receptions in 30 min intervals in each day of the tracking period, and are an effective way to visualize, on a fine temporal scale, presences and absences of an individual among different zones of the receiver array. In a second approach, diel changes in the position of the fish were inferred from the mean depth and hourly reception number data (i.e. total number of receptions received during a single phase divided by its duration). We defined a phase-transition value (PT) for each day to night transition (D-N) as follows:

$$PT_{D-N} = D_t - N_t \ ,$$

where D_t is the corresponding value of a given variable for a day phase and N_t is the value of the same variable for the consecutive night phase. The distribution of the $PT_{\text{D-N}}$ values gives us a comprehensive view of the repeatability and cyclical nature of the diel movements. For example, significantly negative $PT_{\text{D-N}}$ values calculated with the mean depth indicate repeated movements to deeper waters at the nightfall, significantly positive values indicate movements to shallower waters, and values that do not differ from 0 indicate that there is no a consistent pattern in the change of the fish depth. $PT_{\text{D-N}}$ values for the hourly reception number provides information about diel movements between zones that differ in their acoustic performance. In order to ensure the cyclical nature of these movements, we also analysed the distribution of the PT values computed for pairs of consecutive day phases (D-D):

$$PT_{D-D} = D_t - D_{t+1}$$

Extraordinary movements

Sporadic extraordinary movements where inferred from the daily percentages of fish that were detected at given depths and distances from the edge of the HR (95% boundary). We generated depth classes using 1 m depth-intervals and distance-to-HR classes in categories of 200 m. Then, we computed on a daily basis the percentage of fish that were observed in each depth and distance-to-HR class. These percentages were then used to separate the daily observations into two categories: ordinary days, that is, days with ordinary movement behaviour, and extraordinary days, that is, days with extraordinary movement behaviour representing clear statistical outliers of the spatial and temporal metrics used. The two categories were grounded on a hierarchical clustering analysis and visualized with a metric multidimensional scaling, based on Bray-Curtis dissimilarities, and performed with the vegan package (v.2.3-2) for R (Oksanen et al., 2013). Finally, the occurrence of extraordinary movements was visually compared to in situ seawater temperature data (hourly measures for the Medes Islands, provided by the T-MedNet network, `http://www.t-mednet.org/`) and local wave height data (daily measures gently provided by J. Pascual, `http://meteolestartit.cat`).

2.3 Results

Summary of receptions

A total amount of 816,520 valid receptions were recorded by the receiver array during the whole monitoring period (Table 2.1). Long tracking periods were registered for almost all individuals, 329 ± 65 d (mean ± SD) for fish caught in the NT zone (TAS and POR locations) and 219 ± 88 d for those caught in the PR and NT zones (ARQ and FAL locations) (Figure 2.2). Three fish (#21, #51 and #98) disappeared within the first 15 monitoring days and were not detected again throughout the experiment, so they were not considered in the following analysis. Two fish (#55 and #76) did not return to their HR after the extreme storm of 2008.

None of the seven translocated fish remained in the released location. Two individuals (#94 and #96) returned to their original location after time intervals of 12 h and 6 d, respectively, and remained there until the end of the experiment (Figure 2.2). Three individuals (#53, #59 and #97) were detected for 7 d in the NT zone, but then departed from the area covered by the receptors and were never detected again in either the PR nor NR zones (Figure 2.2). The two remaining translocated fish (#52 and #95) were considered dead, as they were detected in the NT zone over long periods (31 and 257 d, respectively) by a single receiver and at a constant depth.

Table 2.1: Summary of the monitoring information of tagged *Diplodus sargus*. L: Total length; DD: Detection Days; TP: total Tracking Period (d); RI: Residence Index, CA: Core Area (50% UD); HR: Home Range (95% UD).

Fish ID	**L (cm)**	**Capt. loc.**	**Capt. date**	**Recep. no.**	**DD**	**TP**	**Depth-range (m)**	**RI (NT)**	**RI (PR)**	**RI (NR)**	**CA (km^2)**	**HR (km^2)**
13	22	TAS	2007-05-23	21767	353	361	0.7–8.6	0.98	0	0	0.08	0.41
14	32	TAS	2007-05-23	93053	363	364	3.2–12.9	1	0	0	0.16	0.67
16	21	TAS	2007-05-23	9605	193	200	0.2–10.4	0.96	0	0	0.08	0.40
17	29	TAS	2007-05-24	28459	353	363	4.0–13-0	0.97	0	0	0.14	0.61
19	26	TAS	2007-05-24	48800	357	364	0–15.0	0.98	0	0	0.16	0.67
20	33	TAS	2007-05-24	13348	329	356	1.6–17.3	0.92	0	0	0.18	0.76
22	26	TAS	2007-05-24	16582	197	199	0–9.1	0.99	0	0	0.19	0.86
48	23	TAS	2007-05-24	30983	344	364	0.2–10.1	0.95	0	0	0.18	0.74
49	23	TAS	2007-05-24	14388	201	212	0–4.0	0.95	0	0	0.18	0.83
21*	21	TAS	2007-05-24	850	13	13	–	–	–	–	–	–
51*	28	TAS	2007-05-24	1835	13	13	–	–	–	–	–	–
15	29	POR	2007-05-25	56314	363	364	0.4–9.5	1	0	0	0.14	0.81
23	30	POR	2007-05-25	10423	229	239	0–14.2	0.96	0	0	0.08	0.46
24	24	POR	2007-05-25	50621	364	366	0.1–9.3	0.99	0	0	0.10	0.57
25	26	POR	2007-05-25	46071	361	369	0.4–6.6	0.98	0	0	0.24	1.01
26	29	POR	2007-05-25	61909	364	366	0.2–13.6	0.99	0	0	0.11	0.68
28	33	POR	2007-05-25	19962	342	356	0.4–6.4	0.96	0	0	0.11	0.51
29	32	POR	2007-05-29	23692	356	360	0–7.3	0.99	0	0	0.18	0.74
30	26	POR	2007-05-29	32047	356	361	0.3–9.4	0.99	0	0	0.12	0.73
31	29	POR	2007-05-29	22679	343	357	0.7–9.9	0.96	0	0	0.25	1.01
54	29	ARQ	2008-09-25	3772	45	45	0–14.6	0	1	0	0.05	0.22
55	26	ARQ	2008-09-25	2020	47	48	0–5.5	0	0.98	0	0.06	0.27
56	35	ARQ	2008-09-25	9859	211	237	0–5.1	0	0.89	0	0.05	0.24
57	29	ARQ	2008-09-25	12768	230	235	0.4–9.8	0	0.97	0.04	0.05	0.26
58	35	ARQ	2008-09-25	8595	202	235	0.4–15.0	0	0.86	0.02	0.06	0.30
74	29	ARQ	2008-09-25	14961	220	228	0–7.3	0	0.96	0.04	0.06	0.28
99	29	ARQ	2008-10-17	9003	165	213	0–8.2	0	0.76	0.04	0.06	0.32
94^{T}	26	ARQ	2008-10-16	7972	165	216	0.4–11.7	0	0.76	0	0.09	0.35
96^{T}	23	ARQ	2008-10-17	5521	196	215	0.4–9.3	0.03	0.85	0.07	0.06	0.32
52^{T†}	32	ARQ	2008-09-26	10197	31	31	–	–	–	–	–	–
53^{T*}	28	ARQ	2008-09-26	297	7	7	–	–	–	–	–	–
59^{T*}	25	ARQ	2008-09-26	74	2	2	–	–	–	–	–	–
95^{T†}	23	ARQ	2008-10-17	48957	256	280	–	–	–	–	–	–
97^{T*}	26	ARQ	2008-10-17	42	2	2	–	–	–	–	–	–
40	23	FAL	2008-09-24	14054	244	293	0.6–11.4	0	0	0.83	0.05	0.20
60	32	FAL	2008-10-21	16194	267	276	0–9.6	0	0	0.97	0.04	0.18
61	21	FAL	2008-10-21	9938	211	219	0–8.9	0	0	0.96	0.04	0.17
72	21	FAL	2008-09-24	20098	295	303	0.6–10.6	0	0	0.97	0.05	0.21
75	24	FAL	2008-09-24	14720	278	301	0.7–14.9	0.01	0.01	0.92	0.06	0.24
76	23	FAL	2008-09-24	4013	93	94	1.3–12.8	0	0	0.99	0.04	0.16
98	35	FAL	2008-09-26	77	3	4	–	–	–	–	–	–

Letter ^{T} *accounts for translocated fish that were released in TAS. Fish marked with a* * *disappeared from the study site, and those marked with a* † *were considered dead.*

Site fidelity and home range sizes

All fish were full-time residents, presenting high RI values within their zones (Mean ± SD = 0.95 ± 0.06) (Table 2.1), with no significant differences among fish from different locations (Kruskal-Wallis test, $p > 0.05$). No relationship was detected between RI and fish size or tracking period length (Kruskal-Wallis test, $p > 0.05$). Fish were detected within narrow bathymetric ranges; the 95% of all receptions were registered between 0.4 and 11 m depth (Table 2.1).

All fish resided in core areas close to their capture location (Figure 2.3). HR sizes ranged between 0.16 and 1.01 km^2 and core area sizes ranged between 0.04 and 0.25 km^2 (Table 2.1). HR sizes were significantly smaller in fish from PR and NR zones compared to fish from the NT zone (one-way ANOVA, $p < 0.01$) (Figure 2.3), presumably due to a difference in the spatial arrangement of the receivers. No effect of fish length or tracking period on the HR size was observed (one-way ANOVA, $p > 0.05$). The

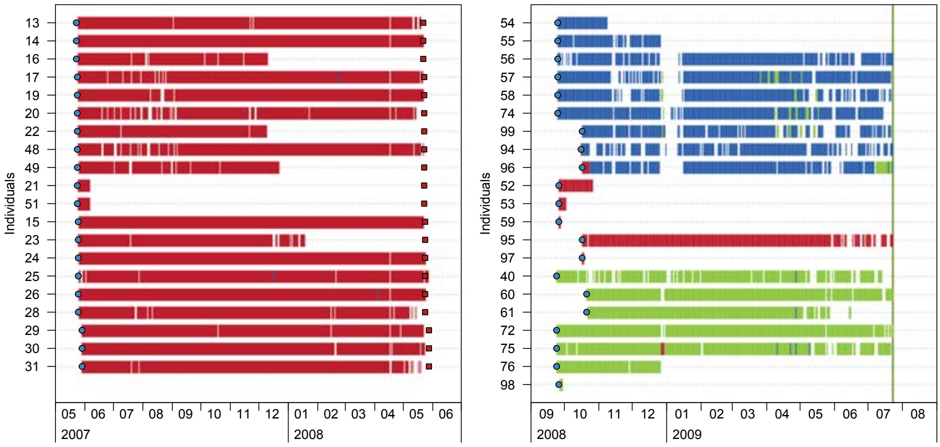

Figure 2.2: Daily presence-absence plot of tagged *Diplodus sargus* within the monitored area. Colours represent the different protection zones of the MPA; Red: no-take zone (NT), Blue: partial reserve (PR), Green: no-reserve (NR). Fish tag and release dates (blue circles), expected transmitter battery dead dates (red squares) and the final withdrawal of the receiver array (vertical green line) are shown.

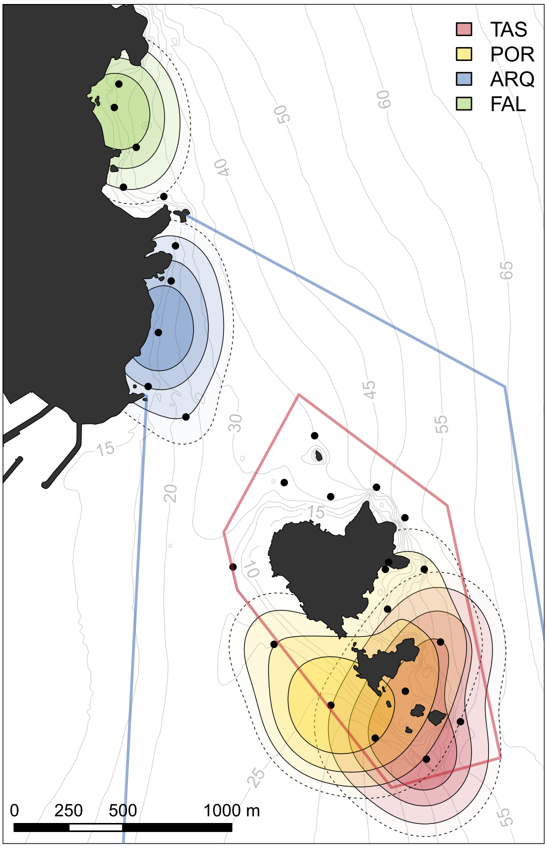

Figure 2.3: Mean spatial Utilization Distribution estimates of *Diplodus sargus*, for each capture location. The concentric polygons represent, from inside out, the areas covering the 50% (core area), 75%, 90%, and 95% (home range) of the volume of the Utilization Distribution computed by the Brownian Bridge Movement Model. The topographic base map (1:5.000) is freely accessible through the Institut Cartogràfic I Geològic de Catalunya (`www.icgc.cat`) under Creative Commons Attribution License (CC BY 4.0).

UDOI values denoted a very high degree of HR overlap between individuals from the same location (UDOI > 1) (Figure 2.4). The UDOI was lower (< 0.7) when comparing individuals from the two locations within the NT zone (TAS and POR). There was no HR overlap (UDOI $= 0$) when comparing individuals that came from different zones of the reserve.

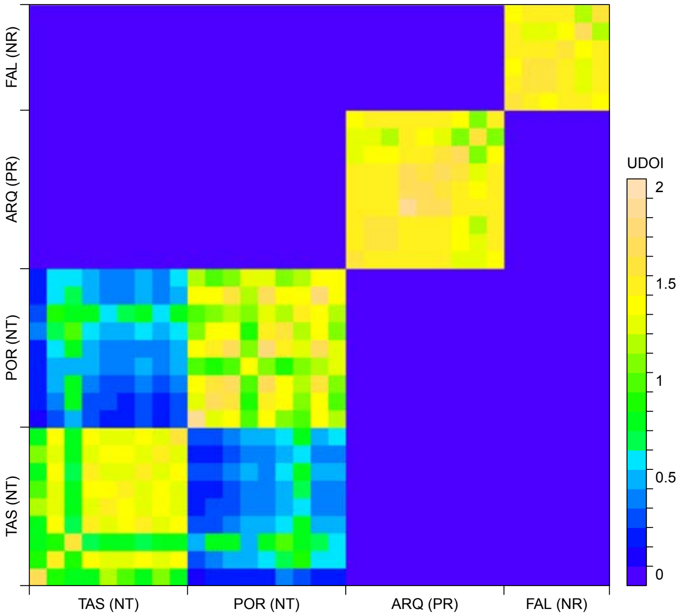

Figure 2.4: Utilization Distribution Overlap Index (UDOI) calculated for each pair of *Diplodus sargus* individuals. Yellow blocks represent high UDOIs observed when comparing individuals captured in the same location. Green and blue blocks represent lower degrees of overlap and the purple areas represent no-overlapping HRs.

Diel patterns

Visual inspection of spatial chronogram plots revealed clear diel patterns in 70% of tagged individuals (n = 23). These patterns were characterized by different colours either representing changes in the detecting receivers or reception gaps (white areas). An example of a spatial chronogram plot showing a clear daily pattern can be seen in Figure 2.5 for individual #14. This individual was observed at receivers 5, 6 and 7 during the day (green areas) and moved to receivers 9 and 10 during the night. Some punctual excursions to receivers 12, 13 and 14 are visible in December, March and April. See Figure 2.1 for the placement of the receivers.

The phase-transition values calculated for the mean depth between day and night phases ($PT_{D\text{-}N}$) revealed diel movements in depth in 70% of tagged individuals (n = 23), for which the median of the values was

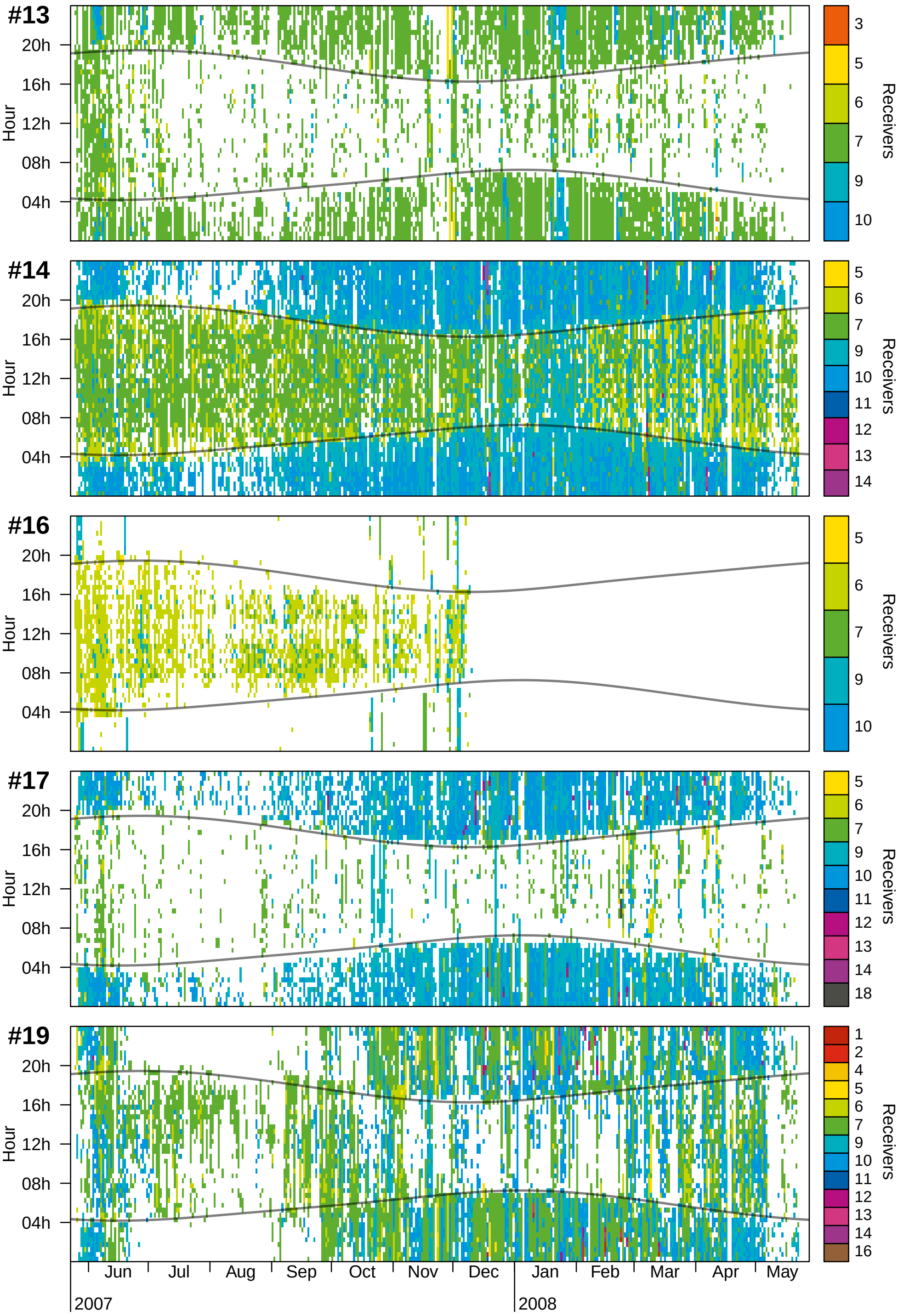

Figure 2.5: Spatial chronogram plots for all the tagged *Diplodus sargus* individuals. See the map in Figure 2.1 for the position of receivers. Black lines represent the local sunset and sunrise time.

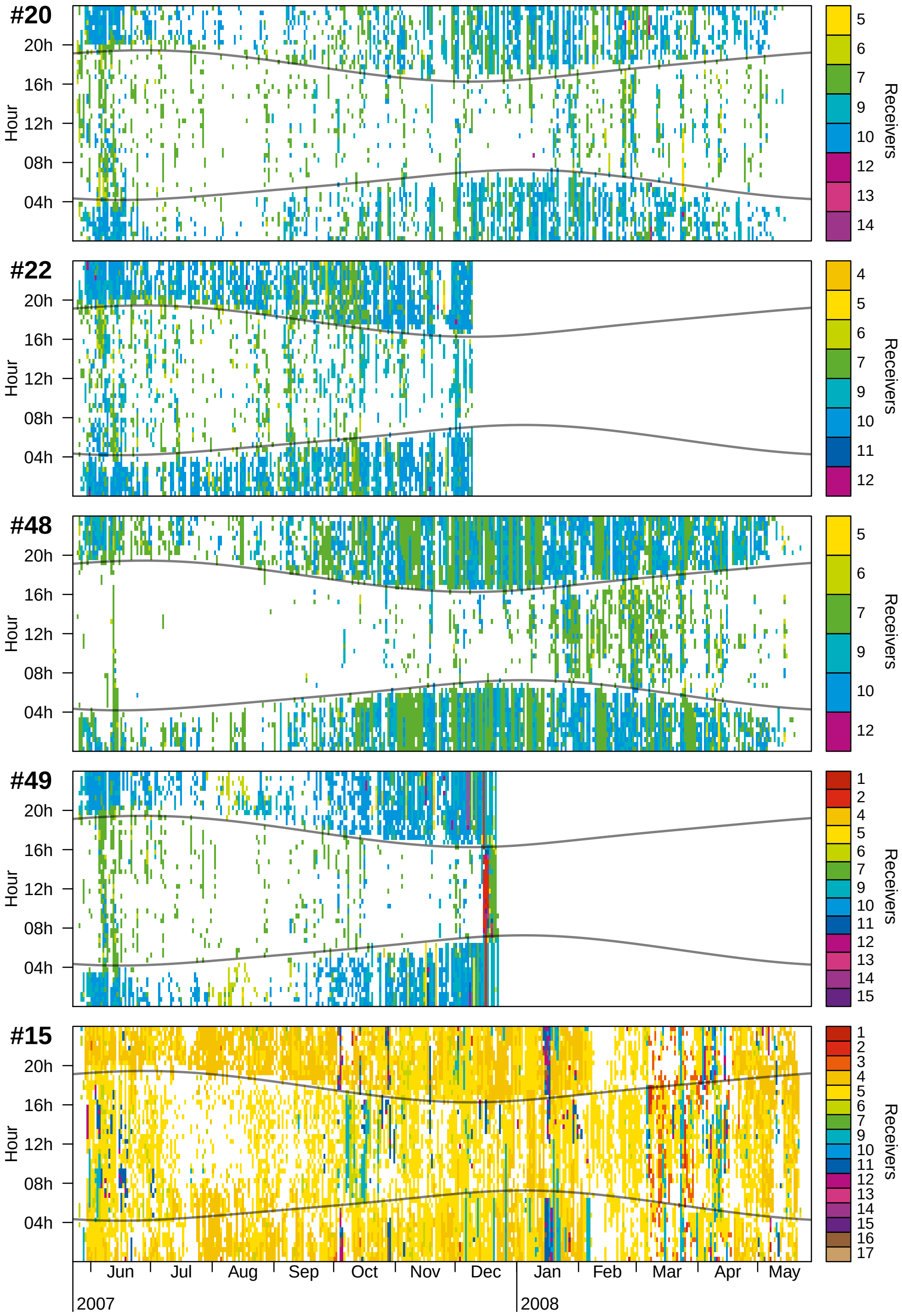

Figure 2.5: *(cont.)* Spatial chronogram plots for each tagged *Diplodus sargus* individual.

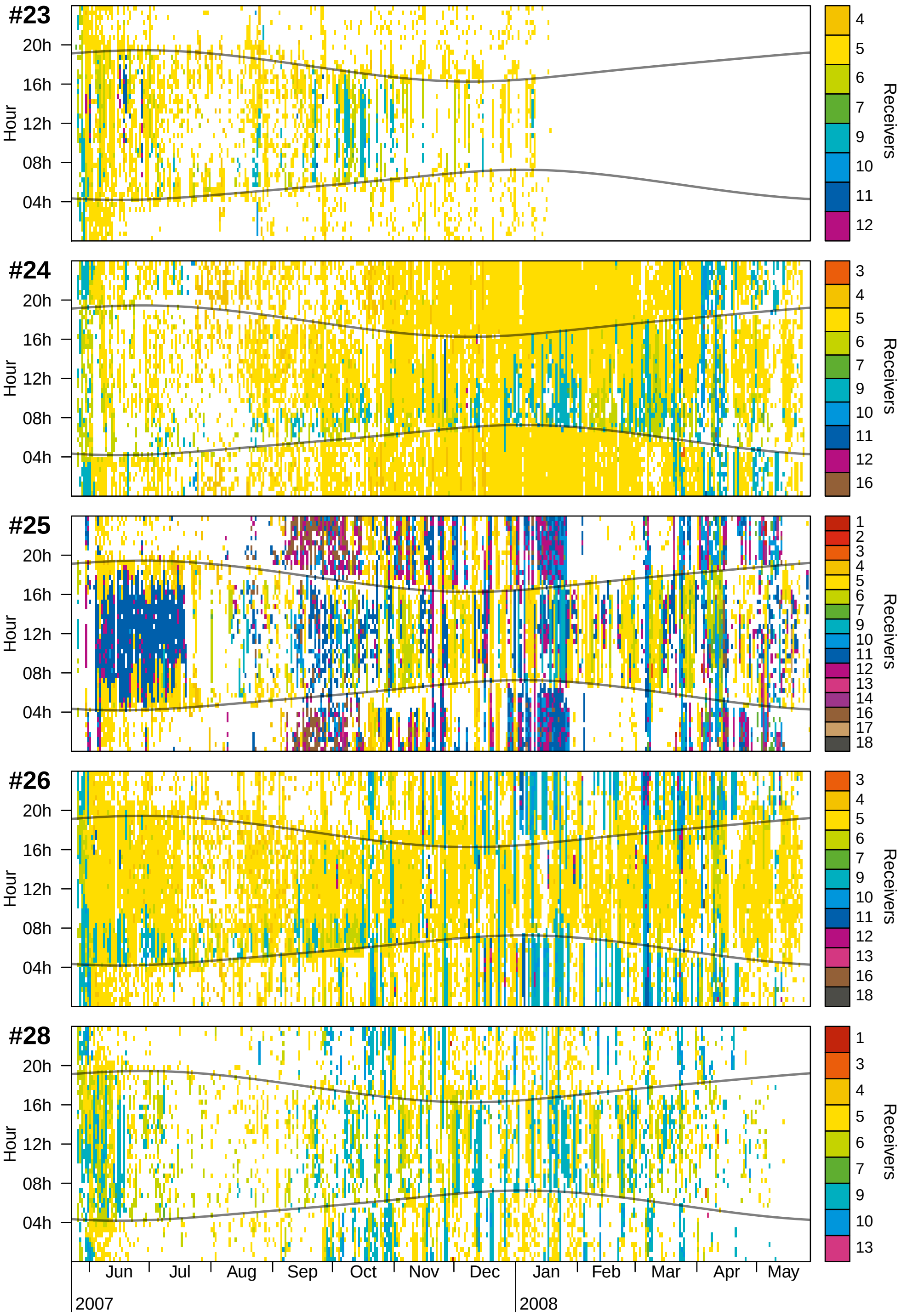

Figure 2.5: *(cont.)* Spatial chronogram plots for each tagged *Diplodus sargus* individual.

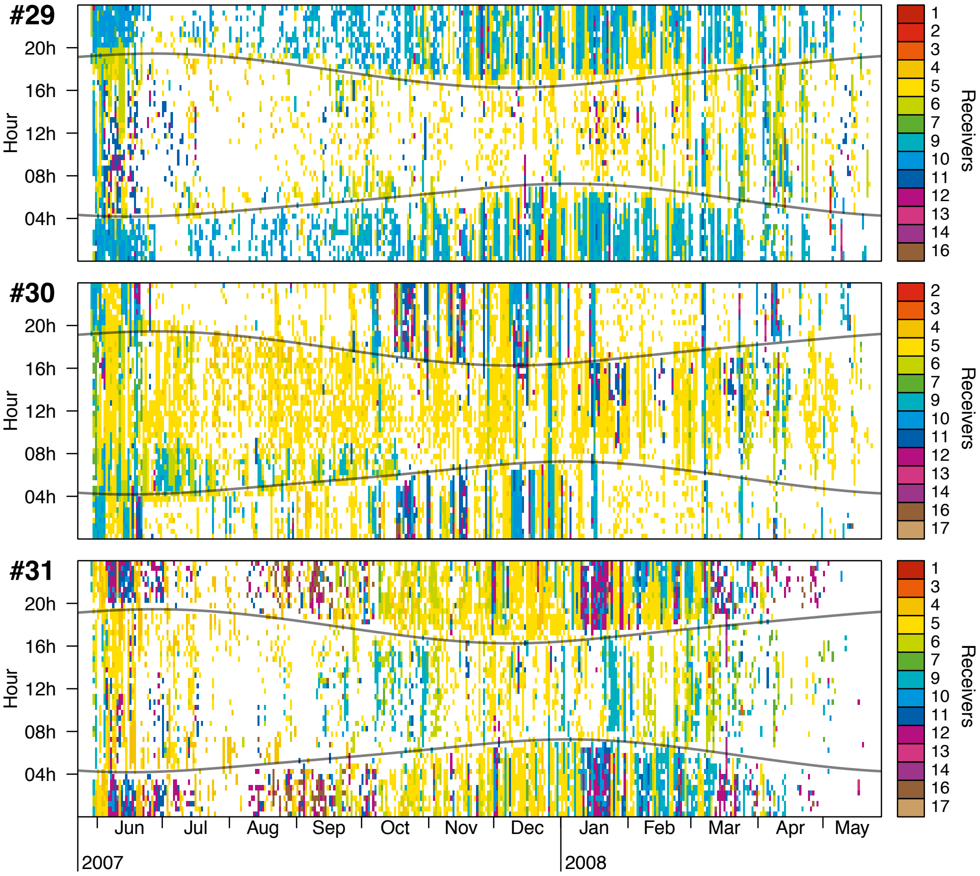

Figure 2.5: *(cont.)* Spatial chronogram plots for each tagged *Diplodus sargus* individual.

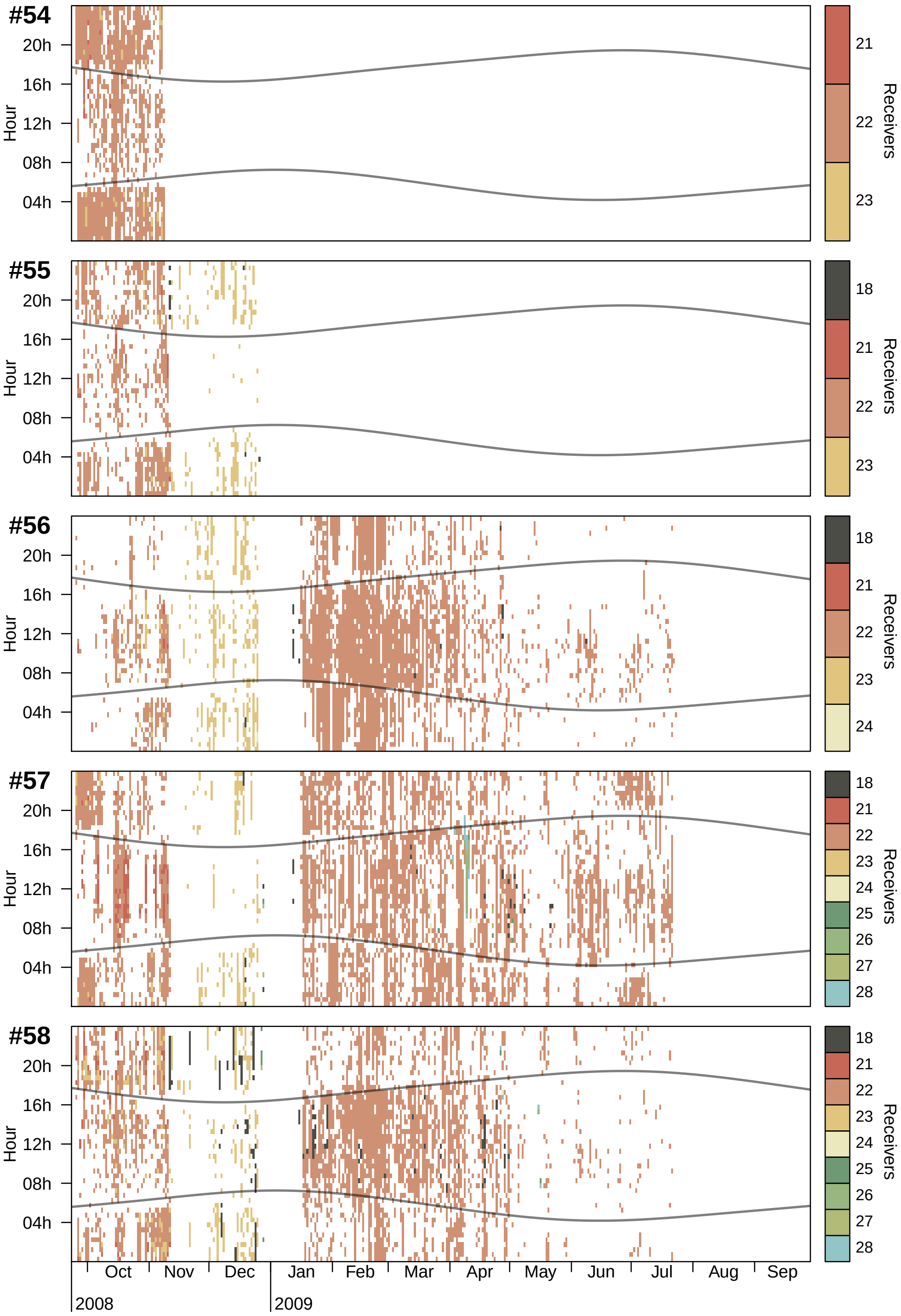

Figure 2.5: *(cont.)* Spatial chronogram plots for each tagged *Diplodus sargus* individual.

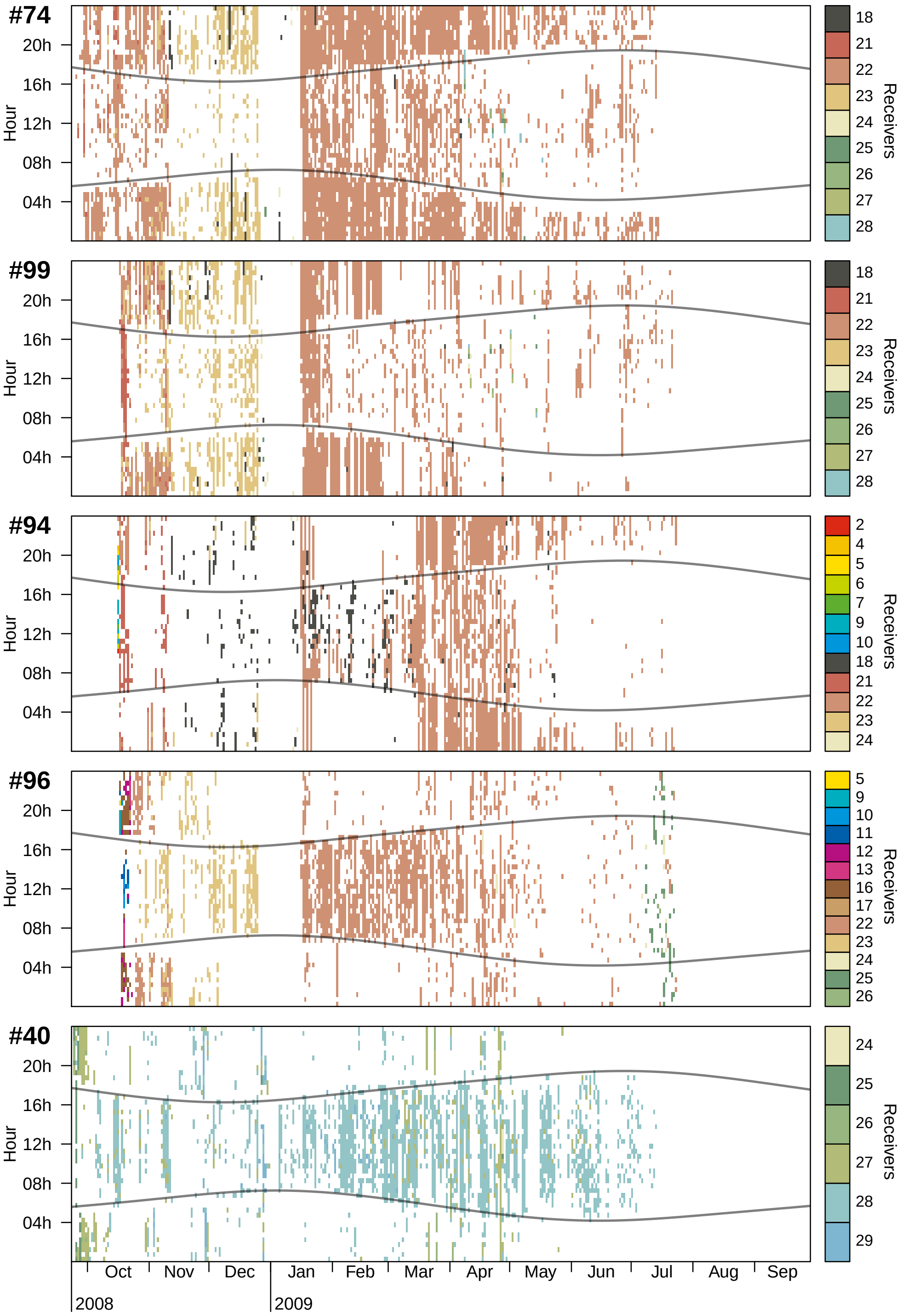

Figure 2.5: *(cont.)* Spatial chronogram plots for each tagged *Diplodus sargus* individual.

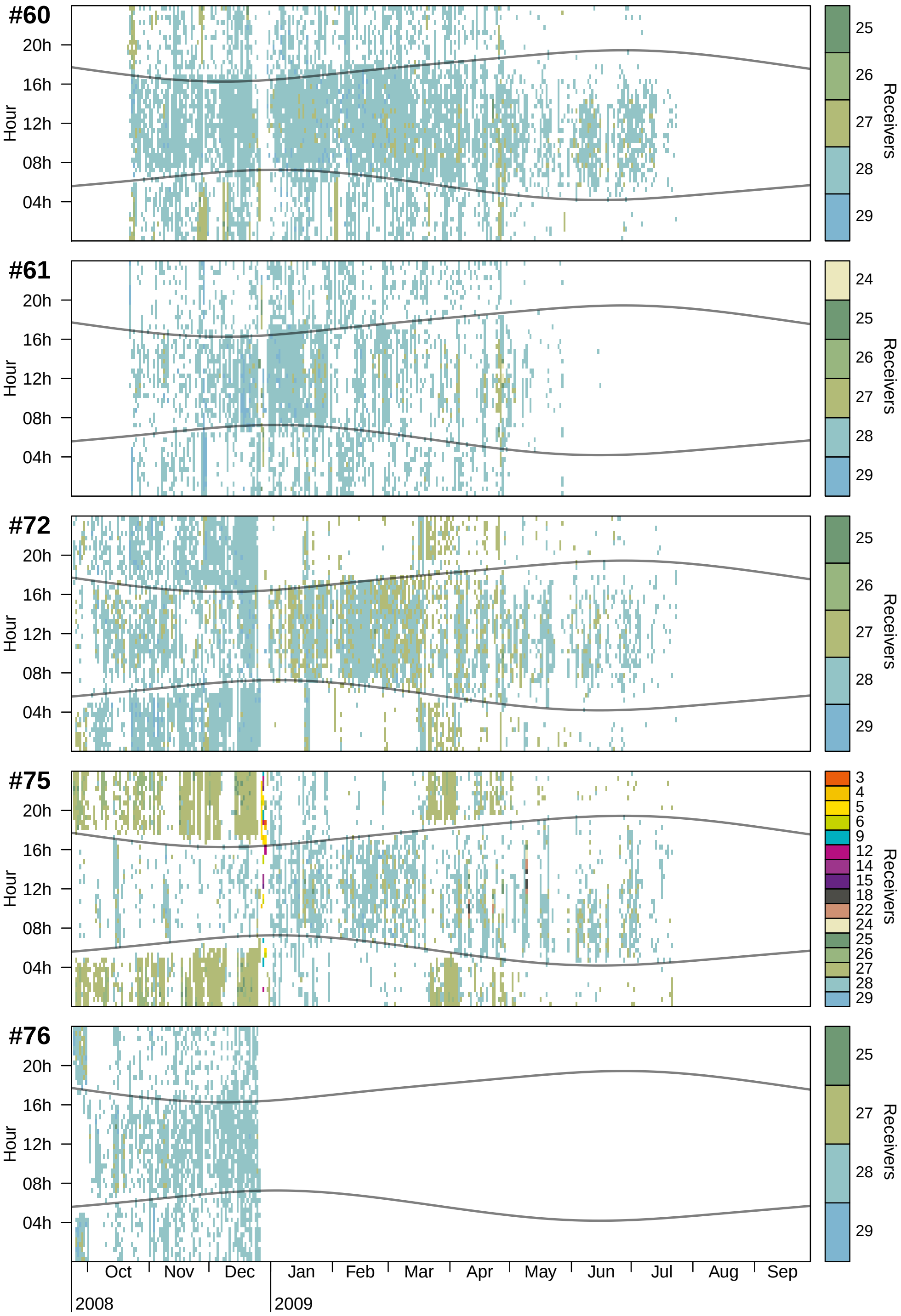

Figure 2.5: *(cont.)* Spatial chronogram plots for each tagged *Diplodus sargus* individual.

significantly different from zero (Wilcoxon signed-rank test, $p < 0.01$) (Figure 2.6A). In contrast, the medians of the phase-transition values between consecutive day phases ($PT_{D\text{-}D}$) did not significantly differ from zero in any fish (Wilcoxon signed-rank test, $p > 0.05$) – with the exception of the slight deviation observed in individual #13 (Wilcoxon signed-rank test, $p < 0.05$) – (Figure 2.6B), which means that each fish tends to be at a similar depth during day phases and confirms the cyclical nature of these movements. However, this analysis revealed large individual-level heterogeneity on depth daily-pattern behaviours: 30% of individuals ($n = 10$) were found at deeper areas during the night than during the day, while 39% of individuals ($n = 13$) showed the inverse pattern. Phase transition values for the hourly reception number showed the same heterogeneity (Figure 2.7). In this case, 48% of fish ($n = 16$) had significantly more receptions during the night and 42% individuals ($n = 14$) had more receptions during the day. Bringing all the results together, 100% of the monitored *D. sargus* individuals showed the signature of diel patterns based on at least one of the different metrics used: zone, depth and reception number.

Extraordinary movements

Based on the daily occurrence of *D. sargus* at different depths and distances from their individual HR (95% boundary), the cluster analysis (see section 2.2) was able to distinguish between two consistent day typologies: one for days with ordinary activity ($n = 551$, 94% of the analysed days) and another for days representing extraordinary behaviours ($n = 34$, 6% of the analysed days) (Figure 2.8 and 2.9). Extraordinary days were characterized mainly by the presence of an elevated percentage of individuals ($> 50\%$) at deeper than normal depths (usually below 20 m), and to a lesser degree, by the presence of individuals ($> 30\%$) at greater distances from the HR boundary. All the days with extraordinary behaviours occurred between November and December and March and April in the two study periods: 2007-2008 (corresponding to fish from the NT zone) and 2008-2009 (fish from the PR and NR zones).

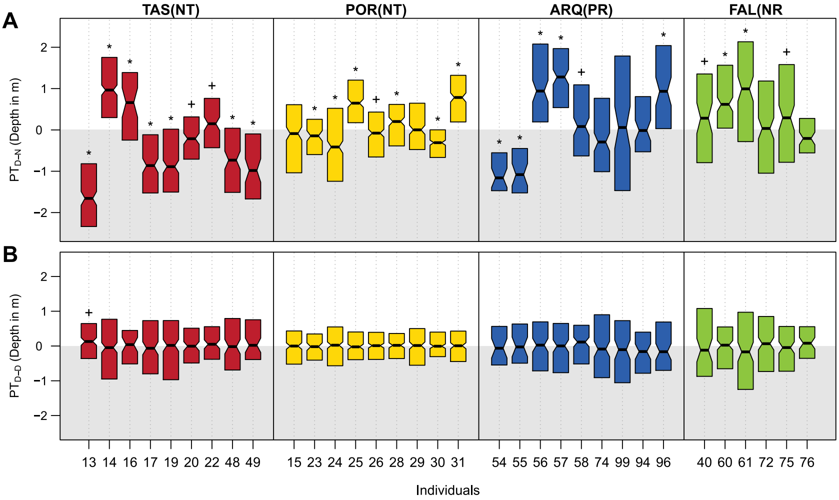

Figure 2.6: Distribution of phase-transition values (PT) calculated for the mean depth between consecutive day-night (A) and day-day (B) phases, for each *Diplodus sargus* individual. Lower and upper boundaries of the boxes represent the first and third quantiles of value distributions. Significant results of the Wilcoxon signed-rank tests against the null hypothesis of a median of zero are expressed by the symbols above the boxes; +: $p < 0.05$; *: $p < 0.01$.

Days with extraordinary movements happening from November to December coincided with (or were close to) periods with large (and highly variable) swell conditions (Figure 2.8). In contrast, extraordinary movements detected from March to April, could not be related to storm events but coincided with the spawning season for *D. sargus* (Morato et al., 2003; Mouine et al., 2007).

Storms caused a few individuals to move large distances from their HRs (but they were not necessarily observed at greater depths). The most extreme movement was performed by a single individual (#75) during the extreme storm of 2008, which travelled more than 2 km back and forth from its HR boundary (set in the NR zone), and was detected by several receivers from the NT zone (Figure 2.8; see the spatial chronogram plot for the individual #75 in Figure 2.5).

Extraordinary movements observed during the spawning period in-

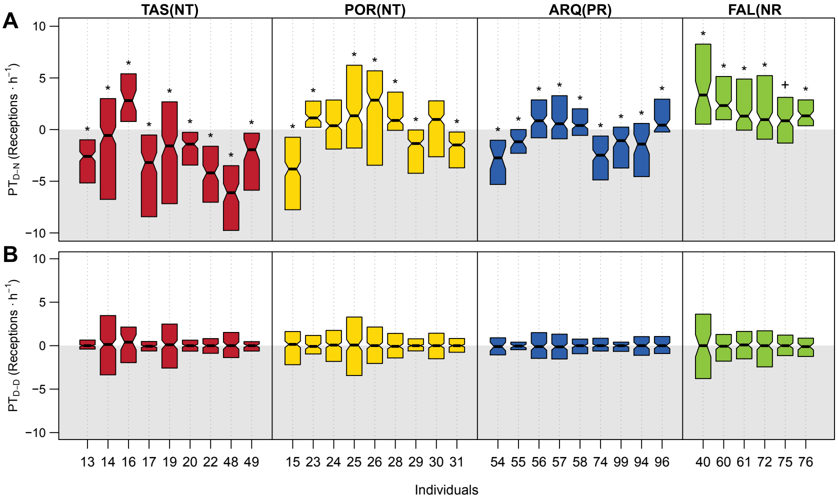

Figure 2.7: Distribution of phase-transition values (PT) calculated for the hourly reception number between consecutive day-night (A) and day-day (B) phases, for each *Diplodus sargus* individual. Lower and upper boundaries of the boxes represent the first and third quantiles of value distributions. Significant results of the Wilcoxon signed-rank tests against the null hypothesis of a median of zero are expressed by the symbols above the boxes; +: $p < 0.05$; *: $p < 0.01$.

volved large numbers of individuals moving to greater depths. During these days, 100% (n = 13) and 46% (n = 6) of the individuals tracked in the NT zone where observed deeper than 20 m and 50 m, respectively. For the same period, in the PR and NR zones vertical movements up to 20 m (not deeper most likely due to the position of the receivers, see Figure 2.1) were detected in 75% of individuals (n = 9). Likewise, fish were observed swimming large horizontal distances from their HR during the spawning period. In the NT zone, 50% of individuals (n = 7) were seen more than 400 m further from the edge of their HR, mainly traveling to the northern part of the Medes Islands (receivers #1, #2, #13 and #14) (e.g. see spatial chronogram plots for fish #14, #20 and #26 in Figure 2.5). In the PR and NR zones, 42% of individuals (n = 5) surpassed the distance of 400 m from their HR, crossing the reserve boundary between the PR and NR zones (e.g. see spatial chronogram plots for fish #57, #74, and #75 in Figure 2.5).

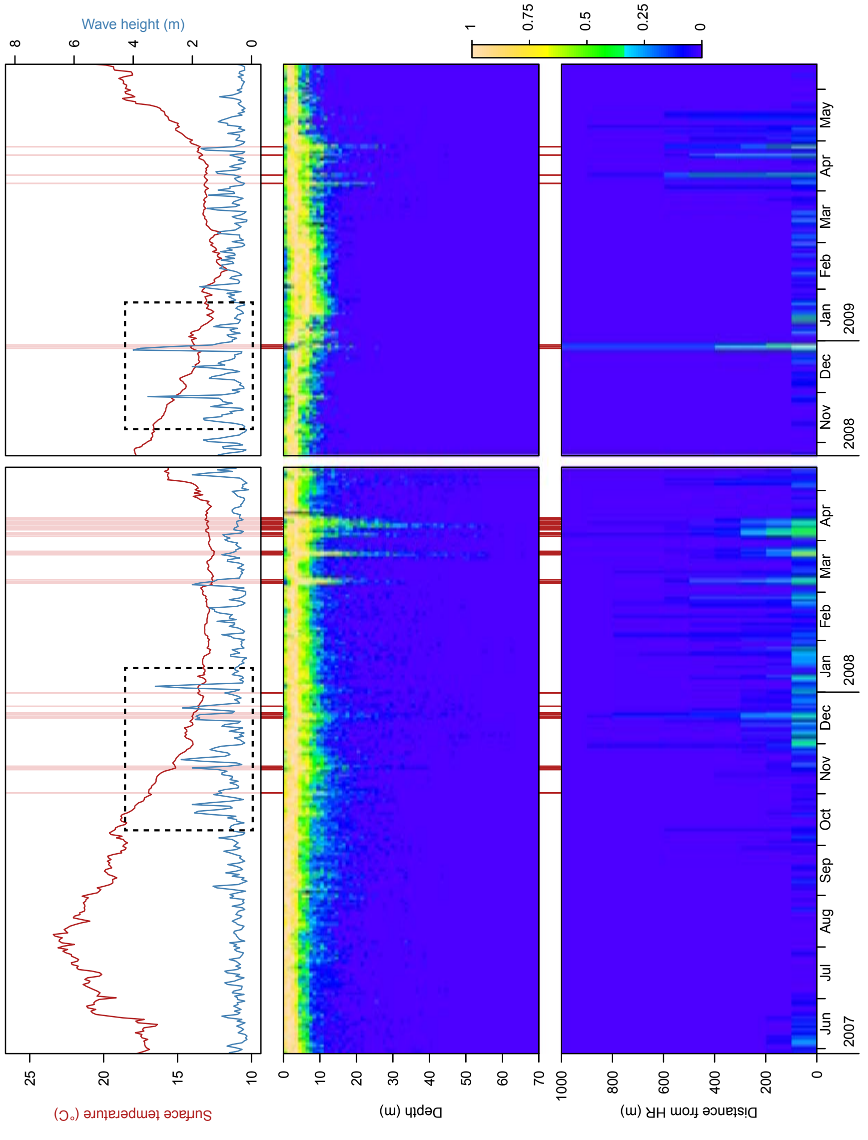

Figure 2.8: Daily mean sea surface temperature and wave height (A) and percentages of fish observed at different depths (B) and distances from their HR boundary (C). Red lines in the back point out days in which extraordinary activities were detected by the cluster analysis. Dotted black rectangles highlight periods with recurrent high wave conditions.

2.4 Discussion

Estimating sedentariness and HR sizes

Our study confirms the highly residential nature of *D. sargus*, and provides new evidence about the extent of this sedentary behaviour. Our estimate of mean HR (0.49 ± 0.26 km^2) falls within those reported by previous studies (between 0.03 and 4 km^2) (Lino et al., 2009; D'Anna et al., 2011; Koeck et al., 2013; Abecasis et al., 2013, 2015). Nevertheless, our findings suggest that this HR could be even smaller. For example, we found that the capture location of each individual was highly consistent with the placement of the HR; fish caught in the same location shared almost their entire estimated HR (UDOI values $>$ 1), while the overlap among fish from different locations was very low, even if the locations were separated for only 300 m. Moreover, the bathymetric distribution of the tagged fish was restricted to

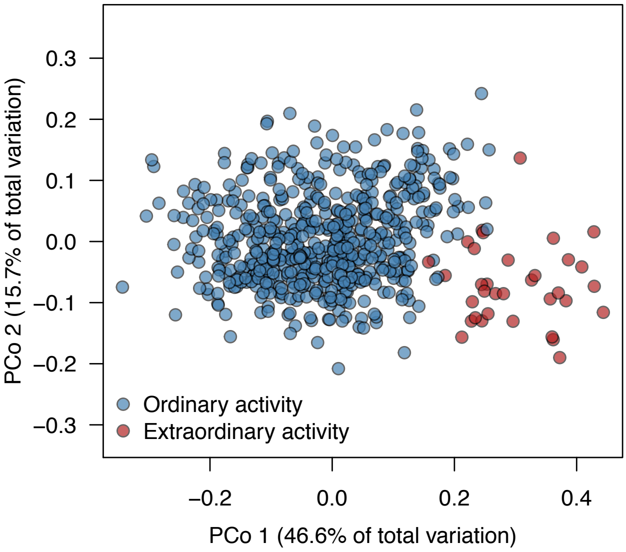

Figure 2.9: Metric multidimensional scaling analysis depicting similarities between days in fish occurrence at different depths and distances-to-HR. The two main groups of days detected by the cluster analysis (ordinary and extraordinary) are shown in different colours.

relatively shallow depths, rarely exceeding 15 m. This distribution coincides with descriptions of the diurnal behaviour of this species provided by Sala and Ballesteros (1997), who reported the highest densities of this species near the surge zone, where it feeds on algae and benthic invertebrates.

The narrow bathymetric range and the low degree of HR overlap between individuals that were captured in the two close locations within the NT zone, illustrate the high territoriality of this species, but also point out that the estimated size of the HR is, in all likeliness, overestimated. When contrasting the extension of the estimated HR of each individual, the bathymetry of the study site (Hereu et al., 2012), and the depth distribution of tagged individuals it became evident that a major part of the estimated HR falls in deep areas that are rarely or never frequented by the animals. In fact, in our study only 9-27% of the area of the HR is located in depths above 15 m. Thus, the real HR of this species must be dramatically smaller than the estimated one.

The overestimation of the HR is due to the large positional uncertainty of the passive acoustic telemetry incorporated in the estimation of the UD. This uncertainty depends on the detection radius of the acoustic transmitters and the characteristics of the study site and may range between tens and hundreds meters. When including this positional error as the kernel bandwidth in kernel density functions (Worton, 1989) or as the location error in the BBMM (Horne et al., 2007), the resulting utilization probabilities might spill to areas that are in fact not frequented by the animals. This HR overestimation is inherent to every acoustic telemetry study that applies error-scaled UD estimation methods, but it may only be apparent in steep study areas, presenting large depth variations within short distances, such as our study site. The development of new modelling techniques that take into account the depth information from the transmitters and the bathymetrical data of the study site would allow the acquisition of more accurate and non-overestimated utilization probabilities of the animals. Moreover, models incorporating benthic topography will better identify habitat selection behaviour and diel fine-scale movements of fishes, with clear implications for the management of the species at small spatial scales within the MPA.

Our data as well as several behavioural descriptions of *D. sargus* (Sala and Ballesteros, 1997; Figueiredo et al., 2005; Aguzzi et al., 2013) suggest that the small HR of this species is divided in two smaller areas or microhabitats: a feeding area during the day and a resting or sheltering area during the night, with two small migrations between them. The repetitive day-night patterns observed throughout the study period and the variability found between individuals suggest that day and night activity spots remained constant over the long-term and are specific for each individual.

Inferring nocturnal and diurnal activity patterns based on the number of receptions is highly problematic (Payne et al., 2010). Local abiotic and biotic factors can drastically reduce the reception performance of acoustic signals (Heupel et al., 2006; March et al., 2010; Welsh et al., 2012). Therefore, the specific placement of the day-time foraging and night-time resting territories in acoustically more or less favourable areas will generate different reception patterns, which might not be related to periods with different degrees of biological activity. Therefore, the strong territoriality of *D. sargus* has major implications for the interpretation of temporal patterns from acoustic telemetry data. For this reason, and due to the lack of test signals, we have avoided drawing behavioural conclusions from patterns in the number of receptions, and they are only presented as an additional confirmation of the patterns observed in both the spatial chronogram plots and the mean depth changes between day and night phases.

Our results demonstrate that even relatively small MPAs might be extensive enough to effectively protect *D. sargus* populations. Moreover, due to the high site fidelity of this species, parameters such as density, mean size and biomass of *D. sargus* populations could be used as meaningful indicators of local pressures and ecological status at each study site (Burger and Gochfeld, 2001). Therefore, we can expect that the management activities performed in each zone of the MPA, such as reducing the fishing pressure, will have a significant impact on those indicators. Several studies performed in the Medes Islands marine reserve have reported significantly higher biomasses, densities and mean sizes for *D. sargus* and other fished species in the NT zone, but not in the PR and NR zones (Hereu et al., 2005; García-Rubies et al., 2013). Taking into account that the movement behaviour of *D. sargus* does not change among zones, these results suggest that the restriction of fishing activities in the partial reserve has a limited benefit on fish populations and hence, the low efficiency of partially protected zones for the full recovery of fish populations (García-Rubies et al., 2013; Denny and Babcock, 2004; Sala et al., 2012).

Another consequence of the territoriality of the adult individuals of *D. sargus* is a very limited capacity to spillover. During the study period a very low number of cross-boundary movements were detected, mostly between the PR and NR zones, and they were linked to very specific ecological conditions (e.g. storms, spawning). Moreover, most of the individuals that were translocated failed to return from the NT zone to the PR. On continuous rocky habitats, *D. sargus* has shown large homing movements, and individuals traveling up to 600 and 900 m to their original capture zone have been reported (D'Anna et al., 2011; Di Lorenzo et al., 2014). Here, we hypothesize that the sand gap between the Medes Islands and the Montgrí massif rocky bottoms may be acting as an impediment to the movements of *D. sargus*. Indeed, habitat discontinuities have been noted to act as partial barriers for several coral reef species (Chapman and Kramer, 2000; Meyer et al., 2010). However, it is interesting to note that the sandy gap between the Medes islands and the nearby zone is not an obstacle for the movement of other species, such as the herbivorous fish *Sarpa salpa* (Pagès et al., 2013).

Extraordinary movements

Despite being strongly sedentary, *D. sargus* demonstrated the ability to undertake considerable movements to areas outside their ordinary depth-range and HR. Those movements, which were generally quick (lasting less than a day), were generated by specific physical (waves) and biological (spawning) factors. Extreme climatic events, such as severe storms, can act as mobilizing agents for benthic fish. During those extreme events *D. sargus* left its preferred shallow habitat, which was highly exposed to the wave action, and moved to areas where the hydrological conditions were less intense. In a parallel study, Pagès et al. (2013) described movements of *S. salpa* to deep sheltered areas during the extreme storm of 2008. The same escaping behaviour has been also described for several tropical fish species (Walsh, 1983; Letourneur et al., 1993). These movements allow fish populations to endure the disturbances without suffering significant population losses (Pagès et al., 2013). Moreover, severe storms can relocate the HR of some of the individuals into new zones (Walsh, 1983), and may be a mechanism by which sedentary species could generate adult spillover from an MPA to adjacent zones.

Our study also provides fundamental knowledge on the spawning behaviour of *D. sargus*. The spawning of this species is triggered by a change in the thermal regime, specifically related to the increase of the seawater temperature immediately after the winter minimum (Morato et al., 2003; Mouine et al., 2007). We observed that during this period, spawning movements happened in several pulses over a few days, in which *D. sargus* visited deep spawning areas. Most of those areas were located within the computed HR, but some individuals also travelled further distances up to 600 m away from the edge of their HR (1 km away from the centre of their core area). However, those movements seemed to have a limit, as none of the individual from the NT zone left the fully protected area, and none of the individuals from the PR and NR crossed to the NT zone. Similar spawning movements of the same magnitude (1-2 km) were reported for this species by Di Lorenzo et al. (2014).

As the observed spawning movements occurred synchronously and during short periods of time, we hypothesize that *D. sargus* forms FSAs. Two types of FSAs have been described depending on their frequency, length of time, site specificity, and the distance travelled by individuals (Domeier and Colin, 1997). In ‘resident’ FSAs, individuals move to the spawning sites from relatively small and local areas in short migrations of few hours or less.

They usually happen at a specific time over several days, and last for only few hours. ‘Transient’ FSAs, in contrast, are characterized by longer migrations from relatively larger areas, to specific spawning sites where the aggregation persists for longer periods of several days or weeks. The spawning movements that we have observed in *D. sargus* involved individuals moving small distances from their core HR areas to spawning sites. Therefore, we suggest *D. sargus* aggregations be considered as resident FSAs.

Aggregating behaviour of *D. sargus* during spawning has gone unnoticed until now, but it can be an important issue for the conservation of the species. To better understand the population dynamics, it is important to determine if the captures of *D. sargus*, by both artisanal and industrial fisheries, increase during the breeding season. Moreover, this fundamental gap of knowledge in such an abundant and widespread species raises new questions about the spawning behaviour of other, less common, species and highlights the need to further study the behavioural ecology of small Mediterranean fishes. Repetitive fishing activities on predictable FSAs can cause severe damage and the collapse of fish populations (Sala et al., 2001; Sadovy and Domeier, 2005). FSAs might be a common strategy among coastal fish species in the Mediterranean, therefore knowing whether the species generate FSAs, and their timing and location is essential when deciding the placement, size and shape, and protection-levels of MPAs.

CHAPTER 3

Thermal stratification drives movement of a coastal apex predator

Abstract

A characterization of the thermal ecology of fishes is needed to better understand changes in ecosystems and species distributions arising from global warming. The movement of wild animals during changing environmental conditions provides essential information to help predict the future thermal response of large marine predators. We used acoustic telemetry to monitor the vertical movement activity of the common dentex (*Dentex dentex*), a Mediterranean coastal predator, in relation to the oscillations of the seasonal thermocline during two summer periods in the Medes Islands marine reserve (NW Mediterranean Sea). During the summer stratification period, the common dentex presented a clear preference for the warm suprathermoclinal layer, and adjusted their vertical movements following the depth changes of the thermocline. The same preference was also observed during the night, when fish were less active. Due to this behaviour, we hypothesize that inter-annual thermal oscillations and the predicted lengthening of summer conditions will have a significant positive impact on the metabolic efficiency, activity levels, and population dynamics of this species, particularly in its northern limit of distribution. These changes in the dynamics of an ecosystem's keystone predator might cascade down to lower trophic levels, potentially re-defining the coastal fish communities of the future.

3.1 Introduction

Temperature is a key environmental factor that, through profound physiological effects, influences the fitness and survival of ectothermic organisms (Crawshaw, 1977; Magnuson et al., 1979; Brown et al., 2004). Ectothermic organisms are usually adapted to live within a limited range of temperatures, which includes a thermal optimum that maximizes their physiological performance (Martin and Huey, 2008). When conditions move away from this optimum, an organism experiences reduced growth, reproduction, foraging, or competitiveness (Huey and Kingsolver, 1989; Pörtner and Farrell, 2008). Temperature shifts from the preferred range will thus greatly affect the dynamics of a species, altering the relative abundances of a population and changing the horizontal and vertical distribution of individuals (Dulvy et al., 2008; Last et al., 2010; Montero-Serra et al., 2014; Freitas et al., 2015). In the case of ecosystem keystone species such as apex predators, community-changing herbivores, or structure-forming species, temperature-driven changes in abundance may cause ripple-effects in other levels of the food web, changing the structure and functioning of the ecosystem (Vergés et al., 2014; Kortsch et al., 2015). In the face of global climate change, a great deal of research effort is being expended to characterize the thermal ecology of marine organisms, as it is necessary to understand the trends in ecosystems arising from the warming of the global ocean (Pörtner and Farrell, 2008; Harley et al., 2006).

The ability to move makes fishes much more resistant to environmental change than less mobile or sessile benthic species (Pagès et al., 2013). As with many other mobile animals, marine fishes can readily exploit thermal gradients to regulate their body temperature and increase their metabolic efficiency (Holland et al., 1992; Pépino et al., 2015). Movement is thus a good behavioural response with which to infer the thermal ecology of a fish species. Controlled laboratory experiments have shown that fish move across thermal gradients to attain a preferred temperature (Sims et al., 2006; Cerqueira et al., 2016), and have allowed the researchers to investigate the response of an individual's internal temperature to a fluctuating environment (Pépino et al., 2015). However, laboratory experiments are not feasible for large marine predators, and hence studies in the wild using acoustic telemetry and bio-logging technologies are a much more practical approach to study the thermal preference of these animals (Freitas et al., 2015; Sims et al., 2006; Hussey et al., 2015).

Within the complexity of oceanographic conditions, the thermocline is a prominent structure. Thermoclines are hydrographical structures caused by large temperature gradients and that generate a significant segregation of resources. Thermoclines set up a heterogeneous thermal environment wherein mobile organisms have developed behavioural responses according to the trade-off between their physiological requirements and energy demands. For instance, many oceanic predators need to maintain warm body temperatures in order to sustain their foraging activity, but often their preys concentrate in cold deep waters. In order to exploit those food resources, several tuna species (Holland et al., 1992; Block et al., 1997; Kitagawa et al., 2000) as well as the ocean sunfish (Nakamura et al., 2015) rewarm during relatively long periods in the suprathermoclinal layer before performing short excursions below the thermocline to forage. Less attention has been paid to this kind of behaviours in coastal predators (Sims et al., 2006), despite their key roles in shaping coastal communities and their relevance as indicators of good ecosystem conservation status (Stevenson et al., 2007; Sala et al., 2012; García-Rubies et al., 2013).

In this study we focused on the common dentex, *Dentex dentex*

(L. 1758), one of the main coastal apex predators in the Mediterranean Sea and an important fishery resource for both artisanal and recreational fisheries (Morales-Nin and Moranta, 1997; Morales-Nin et al., 2005; Font and Lloret, 2011). The common dentex is present along the Atlantic and Mediterranean coasts, but its populations are more abundant in central and southern Mediterranean and rare in the Northern Mediterranean Sea (Bayle-Sempere et al., 1991; Marengo et al., 2014). A global decrease in fishery landings of common dentex has been reported by FAO during the last three decades (Marengo et al., 2014), reason why it is classified as 'vulnerable' by the International Union for the Conservation of Nature (IUCN) in the Red List of Threatened Species (Carpenter and Russell, 2014). However, in several Mediterranean sectors its abundance seems to be increasing, as shown by an increase in fishery landings in several Spanish ports (Orozco et al., 2011), and the fast recovery of its populations in marine protected areas (García-Rubies et al., 2013). The common dentex inhabits infra- and circa-littoral rocky bottoms and seagrass meadows, and is more abundant at depths between 15–30 m (Bauchot and Hureau, 1986; Ramos-Espla and Bayle-Sempere, 1991). The usual depth distribution of adult individuals coincides with the depth range at which the seasonal thermocline establishes between May and October in the NW Mediterranean Sea (Bensoussan et al., 2010). Summer conditions in the Mediterranean Sea are characterized by high water column stability and high temperatures, resulting in a strong stratification of the water column. However, this thermocline is known to display strong vertical oscillations in short time periods, such as a few hours or days, which are mainly driven by the wind and movement of water masses, and are also dependent on local hydrographic conditions caused by coastal orientation and bathymetry (Bensoussan et al., 2010).

We monitored the vertical movements of the common dentex using acoustic telemetry and characterized the thermal environment using in situ temperature loggers during two consecutive summers in the Medes Island marine protected area (NW Mediterranean Sea, Figure 3.1). Our objective was to describe the thermal preference of the common dentex by analysing its vertical movements and activity patterns during stratified and non-stratified hydrographical periods. Describing the thermal ecology of this iconic apex predator will help us to predict their population dynamics during future warm water periods and the probable cascade effects on coastal marine ecosystems.

3.2 Methods

Acoustic telemetry study

Information about movements from 12 *D. dentex* individuals was collected from an acoustic telemetry study carried out in the Medes Islands MPA (Catalonia, NW Mediterranean Sea) between 2007 and 2008 (Table 3.1). Fish were captured by jigging hook-and-line fishing gear from a boat and tagged with V13P-1H acoustic transmitters (VEMCO, Nova Scotia; dimensions: 48 × 13 mm; power output: 153 dB; weight in water: 6.5 g), which were implanted in the peritoneal cavity using a standard surgical procedure (Lino et al., 2009; Koeck et al., 2013). The tagging protocol followed the guidelines provided by the Ministry of Agriculture, Livestock, Fisheries and Food of the Catalan Government (decree 214/1997), and was approved by the Committee on the Ethics of Animal Experimentation of the University of Barcelona. The Department of Environment of the Catalan Government granted permissions for fishing, operating and releasing the animals in the Medes Islands Marine Reserve. All surgery was performed under 2-phenoxyethanol anaesthesia, and all efforts were made to minimize suffering. The sex of individuals could not be determined due to the lack of sexual dimorphism in this species. Transmitters were equipped with a pressure sensor and were programmed to emit signals with a random delay between 80 and 180 s. Movements of tagged individuals were monitored by a network of 17 acoustic receivers placed around the study area (Figure 3.1). Signal range-tests were performed in the area and revealed an average detection range of 150 m around the receivers (see chapter 2 and Aspillaga et al., 2016 for more details). Individuals were divided into two sets depending on their capture date (May–June 2007: n = 3; December 2007–January 2008:

n = 9). All the analyses were restricted to a different time period for each set (Jun/4 2007 to May/21 2008, and Jan/1 2008 to Nov/11 2008, respectively), corresponding to the period in which all the individuals in the set were simultaneously tracked.

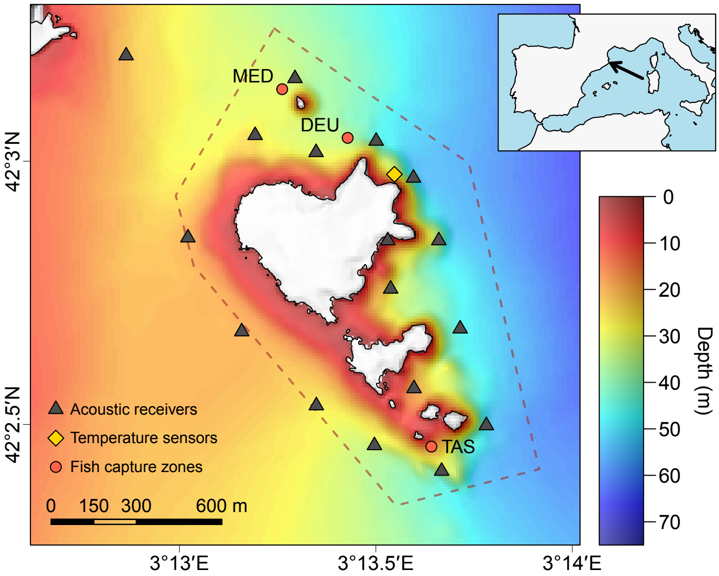

Figure 3.1: Bathymetric map of the study site and the location of acoustic receivers and temperature sensors. The approximate locations where the common dentex individuals were captured are also shown (see Table 3.1). In situ temperature sensors were placed every 5 m (between 5–40 m) in the marked location. The topographic base map (1:5.000), DEM and bathymetry are freely accessible through the Cartographic and Geologic Institute of Catalonia (`www.icgc.cat`) under Creative Commons Attribution License (CC BY 4.0).

Temperature data

Hourly measures of *in situ* temperature were provided by the T-MedNet network (`http://www.t-mednet.org`). Temperature was registered by autonomous sensors (HOBO Water Temp Pro v2) placed in rocky ledges at depth intervals of 5 m (from 5 to 40 m depth) at one location of the study site (Figure 3.1). Additional temperature data, corresponding to manually-operated sensors for one sampling station situated at 2.5 nautical miles offshore the eastern side of the islands, was provided by J. Pascual (`http://meteolestartit.cat`). At that station, temperature profiles were generated every 2–3 days using a CTD that recorded measures every meter, from the surface to a depth of 90 m.

Data analysis

The thermocline depth was calculated from hourly temperature profiles. A four parameter logistic regression was fitted to each profile, and the mean depth of the thermocline was then determined as the depth at which the first derivate of the model presented its maximum value (as in McKinzie et al., 2014). The upper and lower limits of the thermocline were also determined from the peaks in the second derivate of the model. The strength of the thermocline was then calculated as the temperature gradient (°C·m^{-1}) between its upper and lower limits. In order to calculate the depth of the thermocline when it was below the depth-range of the autonomous sensors (40 m), the in situ temperature profiles were complemented with an interpolation of the manual CTD casts taken between 40 and 80 m depth. Thermocline depth was only calculated for the profiles where the total temperature difference between the surface and the deepest measures was higher than 3°C.

Acoustic telemetry data was pooled in 5 min intervals and the mean depth was calculated for each common dentex individual, in order to remove duplicated detections in different receivers and to homogenize the data distribution along time. These intervals were then classified into consecutive day/night periods, defined by local sunset and sunrise time provided by the NOAA Solar Calculator (`www.esrl.noaa.gov/gmd/grad/solcalc/`) for the coordinates of the Medes Islands (42°03'N 3°13'E, WGS84), and the mean depths and variances were calculated for each period. Variance of the depth was used as an approximation to fish vertical activity, assuming that the range of vertical movements is bigger when fish are active (e.g. when foraging) than when they are resting. In order to detect diel and seasonal patterns of fish activity, a linear mixed-effects model was applied to the variance data after applying a logarithmic transformation, considering the day/night period and the season as fixed factors and the fish tag number as a random factor. To test the effect of the thermocline depth on the fish depth, only data corresponding to the summer was used, as it was the only season in which a well-developed thermocline was present. A non-linear mixed-effects model was applied to test this relationship, where the mean depth of the thermocline and day/night period were considered the primary and secondary covariates, respectively, and the fish tag number as a random factor. All the data was managed and analysed in R (R Core Team, 2016), and mixed effects models were fitted using the 'nlme' package (Pinheiro et al., 2016). Performances of the models were visually inspected in residual distribution and residual vs. fitted values plots.

3.3 Results

Thermal regime and depth of the thermocline

Surface temperatures ranged from a minimum of 12.4°C in winter (March 2008) to maximum temperatures of 23.9°C (August 2007) and 24.6°C (August 2008) in summer (Figure 3.2a,b). The stratification of the water column started in early May and became stronger as summer progressed, with the temperature gradient increasing in strength in July and August (Figure 3.3). The temperature gradient relaxed at the end of summer (September), becoming weaker and deeper, until a complete breakdown at the end of October. Shortly after that, the water column was well mixed with a temperature of about 17°C, before displaying a progressive cooling until the minimum winter temperature.

During the maximum stratification period, with surface temperatures above 19°C (between mid-June and mid-September), significant oscillations of the thermocline were observed in both 2007 and 2008, but there were clear differences between years (Figure 3.2). The summer of 2007 presented shallower thermocline positions than the summer of 2008 (Figure 3.3a). The

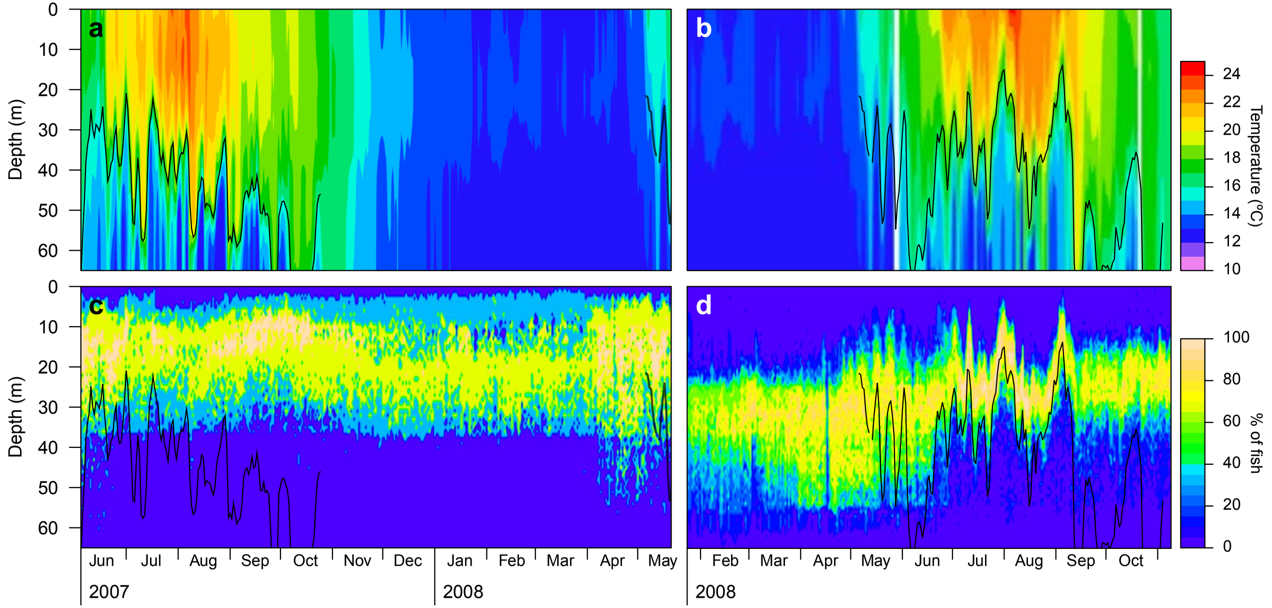

Figure 3.2: Daily temperature profiles (a,b) and vertical distributions of common dentex individuals (c,d). The panel in the left (c) corresponds to the set of individuals captured in May-June 2007 (n = 3), and the panel in right (d) to the set of individuals captured in December 2007-January 2008 (n = 9). Solid lines represent the daily mean depth of the thermocline.

shallowest thermocline depths in 2007 were recorded in July, during which thermocline depths shallower than 15 m occurred on only two days. By contrast, in 2008 shallow thermoclines were registered during the entire summer (July, August and September), and observations of the thermocline shallower than 15 m occurred in 14 different days. Moreover, the maximum temperature gradients observed in July and August 2008 were much more elevated than the gradients observed in the same period in 2007 (Figure 3.3b).

Vertical movement activity patterns

The total length of tagged individuals ranged between 42 and 65 cm (Table 3.1), with no differences in size between the first set of individuals (n = 3), tagged in May-June 2007, and the second set (n = 9), tagged in December 2007-January 2008 (Kruskal-Wallis test, $\chi^2 = 2.203$, df = 1, p = 0.138). However, the individuals from the first set utilized shallower depths (5–30 m) than the individuals from the second set (20–45 m) (Table 3.1 and Figure 3.2a). The linear mixed-effects model used to test the differences between vertical movements (depth fluctuations for each day/night period) revealed a significant day-night and seasonal effect (Table 3.2). Over-

Table 3.1: Summary of the information and detections of tagged common dentex individuals. Deep excursions refer to the percentage of detections happening below the lower thermocline limit during the summer period (see Methods section 3.2).

Fish Id.	Length (cm)	Capture site	Capture date	Depth (m)	Total detect.	Detections (in summer)		Deep excursions	
						Day	Night	Day	Night
18	63	TAS	2007-05-24	16.2 ± 4.8	64419	11035	5010	0.02	0.04
43	63	TAS	2007-06-03	8.7 ± 4.5	53049	9436	5017	0.01	0
44	59	MED	2007-06-03	23.7 ± 4.8	86551	12142	8840	0.27	0.06
32	55	TAS	2007-12-02	29.7 ± 8.7	51402	7901	6438	1.73	0.99
33	61	TAS	2007-12-01	29.1 ± 7.8	46308	6792	5138	3.99	1.52
34	47	TAS	2007-12-01	20.9 ± 5.9	16971	4159	3414	0.41	0.09
35	46	POR	2008-01-22	26.2 ± 7.6	48140	5700	5162	1.95	0.19
37	53	DEU	2007-12-02	30.5 ± 6.8	40478	2043	2360	1.47	0.85
39	42	POR	2008-01-22	25.6 ± 4.7	35693	4412	3167	2.04	0.47
42	62	TAS	2007-12-01	33.9 ± 9.8	53804	10365	7531	8.28	3.24
45	59	DEU	2007-12-01	37 ± 9.2	45218	6786	2315	8.38	2.51
50	65	TAS	2007-12-01	24 ± 4.5	62724	11661	5712	0.99	1.79

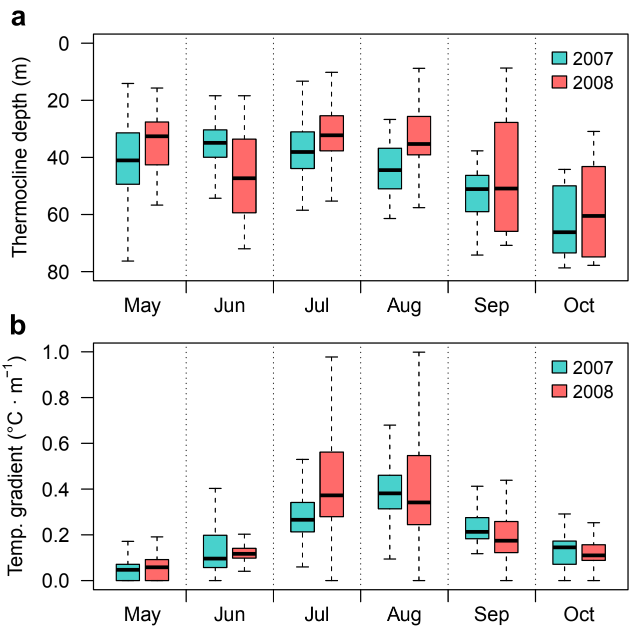

Figure 3.3: Hourly thermocline depth (a) and temperature gradient (b) values, separated by month and year. The black line near the middle and the lower and upper box boundaries represent the median and the first and third quartiles of values, respectively. Ends of the whiskers represent values at 1.5 times the interquartile range of the box.

all, the vertical movement activity was greater during the day than during the night, and the seasonal pattern was marked by a higher vertical movement activity in spring compared to the rest of the seasons, which did not differ (Figure 3.4).

Effect of the thermocline on fish depth

Tagged common dentex exhibited a characteristic pattern of vertical movements during the summer 2008, in which the depth of most of fish oscillated rapidly over periods of a few days (Figure 3.2d). This pattern was not directly observable from tagged fish in the summer 2007 (Figure 3.2c). A logistic mixed effects model explained the relationship between the observed depth patterns and the depth of the thermocline (Figure 3.5 and Table

3). This model demonstrated a non-linear relationship between the average depths of tagged fish and the thermocline depth. When the thermocline was shallower than the depth-range used by each fish (20–45 m), the depth of the thermocline correlated positively and linearly with the mean fish depth. This relationship broke down and became asymptotic when the thermocline sank below the preferred depth range. Indeed, the individual asymptote values estimated by the model fell within the depth-range that each fish inhabited outside the summer season (Figure 3.5). The effect of the day/night period was significant only in the estimation of one of the parameters of the model, the asymptote, but it had a relatively small effect (Table 3), thus indicating that individuals followed similar movement patterns above the thermocline indistinctively of the time of the day.

Despite this average relationship, several punctual excursions below the lower limit of the thermocline were observed during the summer period (Table 3.1). The amount of detections below the thermocline was low (<2%)

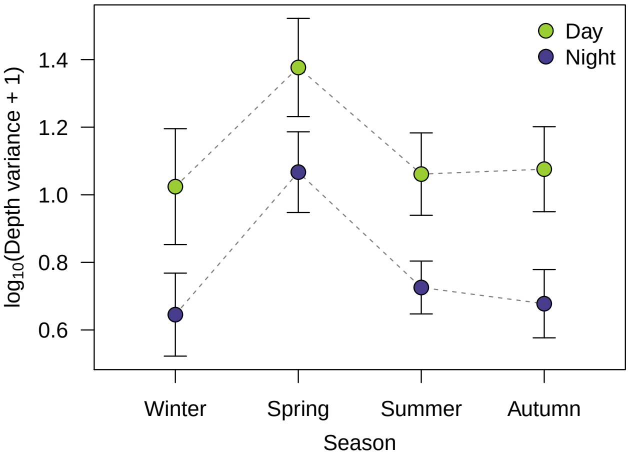

Figure 3.4: Effects of the day/night cycle and the season on the vertical movement activity of common dentex. Vertical movement activity is quantified as the variance of depth (after a logarithmic transformation). Filled circles and error bars represent the mean values predicted by the linear mixed effects model and the 95% confidence intervals, respectively.

for most of fishes, excepting for three individuals, #33, #42, and #45, which presented higher percentages. Overall, the percentage of detections below the thermocline was significantly higher during the daytime than during the night (paired samples t-test: t = 2.49; df = 11, p = 0.015).

3.4 Discussion

During the study period we observed the typical seasonal thermal cycle for the NW Mediterranean Sea, which is characterized by a mixed phase followed by a thermal stratification period (Bensoussan et al., 2010). Although this seasonal pattern repeats every year, there were inter-annual differences with respect to the maximum and minimum temperatures and the duration and magnitude of the stratification (Bensoussan et al., 2010; Pascual et al., 2012). During our study, the thermocline underwent several transient but recurring oscillations in the course of the stratification period. These oscillations included changes of up to 20 m in the depth of the thermocline and 10°C in the temperature at certain depths. Our observations were similar to those described by Bensoussan et al. (2010), who indicated that thermocline oscillations represent an important fraction of the annual thermal variability despite their proportionately low duration (2.1 ± 0.8 days on

Table 3.2: Results of the linear mixed effects model testing the effect of the day/night period and the season on vertical movement activity levels.

Level	Estimate	SE	DF	t-value	p-value
(Intercept)	1.061	0.087	6,518	12.179	<0.001**
Day/Night period					
Night	-0.410	0.041	6,518	-10.023	<0.001**
Season					
Spring	0.354	0.064	6,518	5.553	<0.001**
Summer	0.025	0.043	6,518	0.585	0.558
Autumn	0.032	0.043	6,518	0.734	0.463
Day/Night period x Season					
Night:Spring	0.073	0.022	6,518	3.400	0.001**
Night:Summer	0.046	0.021	6,518	2-183	0.020*
Night:Autumn	-0.015	0.024	6,518	-0.657	0.511

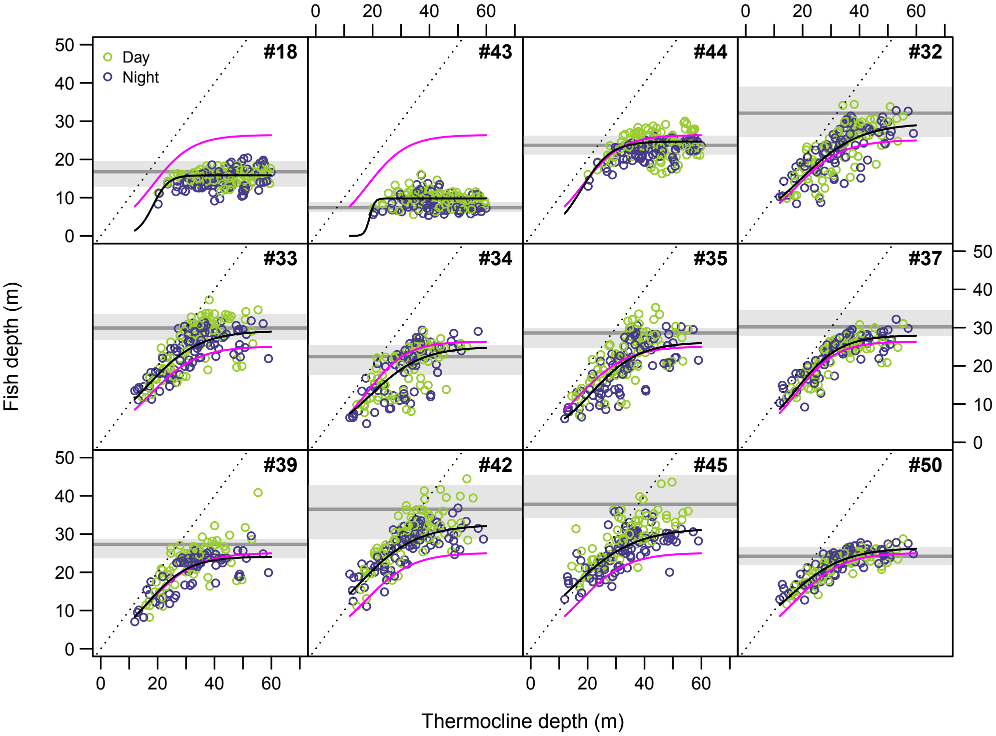

Figure 3.5: Relationship between mean fish depths and mean thermocline depths during the summer season, factorized by day/night periods, for each tagged fish (n = 12). Solid black lines represent the logistic models adjusted for each individual, and the magenta line is the mean prediction for the population. Black dotted lines highlight pure linear (1:1) relationships. Grey line and box in the bottom represent the median and the first and third quartiles, respectively, of the depths measured for each fish outside the summer period.

average). Bensoussan et al. (2010) also reported that the relative variability of the temperature in summer in the study area increases with depth, reaching a maximum variability at depths between 25 and 40 m. At those depths, benthic communities are exposed to an average daily temperature variation of around 2°C (with maximum values around 10°C), and a weekly variation of around 7°C (with maximum values of 11.5°C). The swimming depth of the common dentex was strongly influenced by the temperature variations caused by the thermal structure of the water column, as shown by the relationship between the depth of the thermocline and the depths of tagged

Table 3.3: Results of the non-linear mixed effects models testing the effect of the depth of the thermocline and the day/night period on mean fish depths. The fitted values for each parameter defining the logistic curve and their significance are shown: Asym = maximum value of the curve; x_0 = x-value of the inflexion point; k = steepness of the curve.

Parameter	**Estimate**	**S.E.**	**D.F.**	**t-value**	**p-value**
Asym					
(Intercept)	26.39	2.10	2,042	12.55	<0.001**
Night	-1.28	0.65	2,042	-1.98	0.048*
x_0					
(Intercept)	18.18	0.50	2,042	36.02	<0.001**
Night	-0.73	0.69	2,042	-1.07	0.287
k					
(Intercept)	6.99	0.97	2,042	7.18	<0.001**
Night	1.31	0.69	2,042	1.9	0.057

fish (Figure 3.5). Transient thermocline rising events were related to upward displacements of individuals from the specific depths that they utilized outside the stratification period or during deeper thermocline events. Thus, common dentex demonstrated a clear preference for the suprathermoclinal warm water over the colder water below the thermocline.

Our main hypothesis is that a physiological optimization strategy was behind the observed behaviour of the common dentex. Temperature strongly affects the basal metabolic rate in fishes, restricting or enhancing physiological and behavioural processes(Magnuson et al., 1979). Some studies on the effect of thermal gradients on fish have found that individuals spend most of their time (~75%) within ±2°C of their preferred temperature, which coincides with the optimal physiological temperature that maximizes growth (Magnuson and Destasio, 1997). It has been also described that fish swimming speed or endurance is enhanced to a peak by an optimum temperature and is reduced when the temperature decreases or increases towards the tolerance limits (Randall and Brauner, 1991; Lee et al., 2003; Claireaux et al., 2006). The maximum swimming speed is a limiting factor for the foraging activity, and for this reason many oceanic predators must warm their body temperature in order to be able to hunt in cold deep waters (Holland et al., 1992; Furukawa et al., 2014). Thus, we hypothesize that the common dentex selects its thermal niche, presumably to approach the optimal temperature for growth and/or foraging in order to increase an individual's net energy gain.

An alternative hypothesis would be that the observed movement behaviour of the common dentex was driven by indirect effects such as food distribution. The common dentex is a diurnal predator (Aguzzi et al., 2013), which primarily forages on other fishes (about 74% of prey items), and to a lesser degree on cephalopods and crustaceans (Morales-Nin and Moranta, 1997; Chemmam-Abdelkader et al., 2004). Consequently, foraging events were the most likely cause of the high vertical activity levels that we observed during the day (Figure 3.4), while low activities during the night might be related to resting behaviour. Similar diel activity patterns have been observed in other coastal species (Aguzzi et al., 2013; Aspillaga et al., 2016), including other predators (Sims et al., 2006). Regarding the relationship between the thermocline depth and the vertical distribution of individuals, our model indicated that the diel cycle had a negligible effect. This implies that a presumable concentration of prey items in the suprathermoclinal layer during the summer is not enough to explain the vertical movements of the common dentex. If that were the case, we would expect to observe a relaxation of the depth restriction imposed by the thermocline during the night, with individuals returning to their preferred depths to rest, similar to what has been described for the dogfish by Sims et al. (2006). On the contrary, most of the excursions below the thermocline were observed during the day, and were very probably related to punctual foraging events. Therefore, our results indicate that the observed vertical distributions of individuals during summer were more probably caused by a direct selection of the preferred temperature-range, rather than by an irregular distribution of preys items above and below the thermocline.

Our approach to estimate activity patterns could discern between day and night activity periods, but it was not adequate to resolve seasonal activity patterns. The common dentex resided within the study site throughout the year, facing two different thermal conditions (summer and winter) that we would expect to have a significant effect on fish physiology and activity. Cabled video observatories have already described a seasonal activity rhythm for the common dentex, which showed higher occurrences between August and October, indicating a change in its horizontal activity pattern coinciding with high water temperatures (Aguzzi et al., 2015). Similarly, (Abdelkader and Ktari, 1985) described an increase in the food intake of common dentex between April and May, coinciding with the timing of the spawning, and a decrease in consumption from September to February. These movement and feeding patterns are thought to be related to seasonal variations on the abundance of their prey items, mainly coastal fishes such as sparids, labrids and picarels (*Spicara maena*) (Morales-Nin and Moranta, 1997), which tipically are more abundant in summer than in winter. Interestingly, the common dentex has shown an unsual ability to withstand long periods without food, which seems to be an adaptation to cope with unfavourable periods (Pérez-Jiménez et al., 2012), such as the low prey availability and low temperatures during winter. However, our analysis did not show significant differences between the vertical activities of summer and winter. Nevertheless, it was able to detect an increase of the activity during spring, very probably related to the spawning, which has been described to occur between April and May (Morales-Nin and Moranta, 1997). During this period, the common dentex is thought to perform excursions to deep rocky outcrops, where it aggregates to spawn (Morales-Nin and Moranta, 1997; Marengo et al., 2014). Characterizing spawning movements and periods is key for designing effective conservation measures for emblematic fish species (Sala et al., 2001; Sadovy de Mitcheson and Colin, 2012), and thus they should be studied more carefully in the future.

Changes in the distribution of individuals associated with seasonal and inter-annual environmental fluctuations provide insights into how populations may shift under global climate change. The current global change is driving not only a steady increase of global water temperatures, but also a lengthening of the summer period (Coma et al., 2009). For instance, the thermal stratification has increased in the NW Mediterranean Sea during the last three decades, which has already lengthened the duration of yearly summer conditions by a ∼40% (Coma et al., 2009). Consequently, warm water fish species are being positively affected, leveraging the higher presence of favourable conditions that enhance both their metabolic and foraging efficiency, thus improving their survival rate and reproductive success (Walther et al., 2002; Rijnsdorp et al., 2009). These kinds of environmental fluctuations are proposed as the cause of the inter-annual fluctuations in the capture rates of many important demersal fishery resources (Massutí et al., 2008), including the common dentex (Marengo et al., 2014; Ramos-Espla and Bayle-Sempere, 1991). The redistribution of preferred temperature ranges is generating changes in both the horizontal and vertical distributions of coastal fish assemblages (Dulvy et al., 2008; Last et al., 2010). For instance, recent local data suggest that the common dentex might be expanding in the northern Mediterranean (García-Rubies et al., 2013; Orozco et al., 2011). Our results, by confirming the preference of this species for warm water, provides valuable information on the ecology of the species and a mechanistic understanding to the mentioned population fluctuations and expansion.

In this study, we used acoustic telemetry to provide some valuable insights on the thermal ecology of the common dentex and the possible future trends of its populations. The common dentex and other apex predators are keystone species in marine food webs, and are often used as indicators of the structure and functioning of ecosystems (Stevenson et al., 2007; Sala et al., 2012). Also, the abundances of species occupying high trophic levels shape biological communities through top-down trophic effects (Myers et al., 2007; Heithaus et al., 2008), although the extent of the impact is still under debate (Roff et al., 2016). Climate change will differentially affect different species, depending on their physiological and behavioural traits (Pörtner and Farrell, 2008; Kortsch et al., 2015), and as a result generate unpredictable effects that will interact with other perturbations such as overfishing. To make reliable predictions of future biological assemblages and main ecological trends, it is necessary to understand the mechanisms underpinning the responses of different species to climate change.

CHAPTER 4

Space use, habitat selection, and spawning activity of a coastal apex predator: implications for MPA design

Abstract

Marine protected areas (MPAs) play a major role in protecting apex predator fish species from overfishing. In order to be effective, MPAs must be designed in accordance with the biological and behavioural characteristics of targeted species, but this information is rarely available. We used acoustic telemetry and novel quantitative analysis and visualization techniques to study the long-term movement patterns of *Dentex dentex*, an iconic coastal apex predator and an important fishery resource in the Mediterranean Sea, in order to help understand the effects of protection on this species. *D. dentex* within the Medes Islands MPA (NW Mediterranean Sea) showed relatively small home ranges (0.79 ± 0.22 km^2) and high site fidelity (RI $= 0.97 \pm 0.06$), although they did display complex diel and seasonal movement patterns, often involving diurnal excursions within and outside the fully protected zone. During the spawning season (April-June), *D. dentex* individuals moved to specific areas and performed synchronous movements to deep rocky reefs ($>$50 m), suggesting the formation of spawning aggregations. The movement ecology of *D. dentex* demonstrates that the conservation of coastal predator species might be improved by small MPAs that encompass the adequate extension of favourable habitats, including spawning areas, as well as the potential of such species to enhance sustainable fisheries in adjacent non-protected areas through adult spillover.

4.1 Introduction

Marine protected areas (MPAs) are widely-used management tools to confront the impacts of overfishing, but require quantitative and accurate ecological baseline information to be effectively designed and managed. For instance, the efficacy of MPAs to protect and restore overfished populations depends on the coverage that the reserve gives to the regular movements of individuals (Kramer and Chapman, 1999); and therefore, knowledge on the extent of the movements and habitat use of targeted species is especially important when deciding the MPA size and placement (Grüss et al., 2011; Allen and Singh, 2016; Lea et al., 2016). However, such information is rarely available, leading often to erroneous managing decisions and less effective MPAs (Moffitt et al., 2009; Edgar et al., 2014). In the last decades, acoustic telemetry techniques have been successfully used to monitor the movements of marine species over large spatial and temporal scales (Hussey et al., 2015), and together with the development of new analysis techniques incorporating habitat and environmental variables (chapter 2 and 3; Aspillaga et al., 2016, 2017, have provided essential information on species' spatial ecology that has been used to improve management and conservation strategies (e.g. Lea et al., 2016).

Apex predators have been intensely targeted by fisheries over the centuries. It is estimated that large predatory fish populations have been reduced by 90% worldwide due to overfishing (Jennings and Blanchard, 2004; Myers and Worm, 2005). The decline of apex predators has entailed a loss of their key role maintaining the diversity and stability of marine ecosystems through strong top-down control mechanisms (Baum and Worm, 2009; Britten et al., 2014), generating undesirable cascade effects that have augmented the ecological impacts of overfishing (Heithaus et al., 2008; Ferretti et al., 2010; McCauley et al., 2015). The high vulnerability of large predators to fishing pressure is partly explained by their biological traits, such as a great longevity, low growth rates, late sexual maturity and slow population dynamics, which confer, in turn, a low recovery capacity to their populations (Myers and Worm, 2005). They also have broader home range sizes than species in lower trophic levels (Grüss et al., 2011), as well as complex movement patterns (e.g. diel, seasonal or spawning migrations), that might limit the value of special conservation measures such as MPAs (Kramer and Chapman, 1999; Starr et al., 2007).

The common dentex, *Dentex dentex* (L., 1758), is an iconic predator of Mediterranean coastal ecosystems, and an important fishery resource heavily exploited by professional and recreational fisheries (Morales-Nin and Moranta, 1997; Font and Lloret, 2011; Marengo et al., 2015). It is a long-lived species, with a lifespan exceeding 20 years and a maximum growth length of around 100 cm (Ramos-Espla and Bayle-Sempere, 1991; Morales-Nin and Moranta, 1997; Marengo et al., 2014). FAO has reported a steady decline of *D. dentex* captures by fisheries in the Mediterranean Sea since the 1990s (Abdul Malak et al., 2011; Marengo et al., 2014), and is the reason why this species has been classified as 'vulnerable' in the Red List of Threatened Species by the IUCN (Carpenter and Russell, 2014). It is considered rare in the North-Western Mediterranean Sea, but large populations occur within several MPAs (Gómez et al., 2006; García-Rubies et al., 2013; Marengo et al., 2015). Despite its ecological and economical importance and the need for improved management of this species, information on the biology and ecology of *D. dentex* in natural environments is still scarce.

In this study, we used passive acoustic telemetry to monitor the movements of *D. dentex* over long periods of time (up to 1 year) in the Medes Islands MPA (Catalonia, NW Mediterranean). We applied novel analytical techniques, adapted to acoustic telemetry data, to describe the main movement patterns, such as home range, site fidelity, habitat use, and the presence of diel, seasonal, and spawning behaviours. By describing the movement ecology of this species, we provide essential information to assess the effectiveness of MPAs to protect coastal predator species, as well as insights to improve management strategies that might combine conservation and economical exploitation.

4.2 Methods

Study area

The study was carried out in the Medes Islands MPA (Catalonia, NW Mediterranean Sea; Figure 4.1). The MPA has its core in the fully protected or no-take zone (NT), which was established around the archipelago of Medes islands in 1983, and where all fishing activities are prohibited. A partially protected reserve zone (PR) was established surrounding the NT zone in 1990, also encompassing a section of the nearby mainland coast. In the PR zone, traditional artisanal fishing (longline and trammel net gear) and recreational fishing (angling) are allowed with restrictions. In the areas outside the MPA (no reserve zone, NR), all type of fishing activities, including spearfishing, are allowed.

The seafloor of the Medes Islands MPA is characterized by a highly heterogeneous and diverse set of habitats (Hereu et al., 2012). The east side of the archipelago presents a steep topography, with rocky habitats and coralligenous outcrops extending down to around 50 m depth (Figure 4.1; Hereu et al., 2012). The west side of the archipelago, by contrast, presents a flatter topography with abundant soft sandy bottoms and a *Posidonia oceanica* seagrass meadow. Monitoring studies have been performed in the marine reserve since the establishment of the protection, and have reported a remarkable recovery of main predator species, such as the dusky grouper (*Epinephelus marginatus*), the common dentex (*Dentex dentex*), the European seabass (*Dicentrarchus labrax*) and the brown meagre (*Sciaena umbra*),

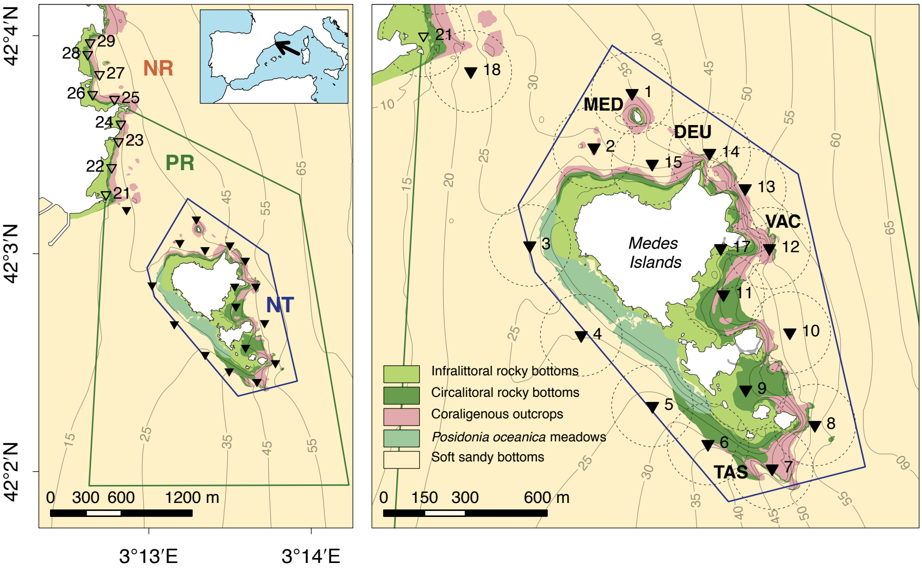

Figure 4.1: Map of the study area and design of the acoustic receiver array. Filled triangles represent acoustic receivers placed in the beginning of the experiment (May 2007), and the empty ones represent the additional set placed in September 2008. Dotted circles correspond to the average signal detection range (150 m). Black bold letters stand for the capture locations of *D. dentex* individuals (see Table 4.1). NT: no-take zone; PR: partial reserve; NR: no-reserve zone. The topographic base map (1:5.000) and the sea bottom bionomic map (Hereu et al. 2012) are freely accessible through the Cartographic and Geologic Institute of Catalonia (`www.icgc.cat`) under Creative Commons Attribution License (CC BY 4.0).

within the NT zone (García-Rubies et al., 2013). This recovery has not been observed in the PR zone, where those species are virtually absent or present low biomasses that do not differ from the ones in the NR zone and other open areas outside the MPA.

Acoustic receiver array

A network of 17 acoustic receivers (VR2 and VR2W, VEMCO Ltd., Nova Scotia, Canada) was installed in the study site to monitor the movements of *D. dentex* and other fish species simultaneously (chapter 2; Aspillaga et al., 2016; Pagès et al., 2013). 16 receivers were placed covering the entire perimeter of the NT zone, and one receiver (#18) was put in a location close to the mainland coast to detect possible movements towards the PR zone (Figure 4.1). Receivers were placed at about 8 m below the surface in moorings with anchors, chain, line, and subsurface floats. An additional set of 10 receivers was installed in the mainland coast in September 2008 (5 receivers in each of the PR and NR zones). Signal range tests were performed in the field by placing multiple receivers at different distances from a transmitter, and revealed an average detection range of 150 m (see chapter 2 and Aspillaga et al., 2016 for more details). No test-transmitters were used to detect changes in the reception efficiency due to environmental noise (wave action, physical impediments or biological activity; Welsh et al., 2012). One of the receivers (#8) was lost in the beginning of the experiment due to adverse sea conditions and was not replaced. Data from receivers were regularly downloaded through VUE software (VEMCO Ltd., Nova Scotia, Canada) and directly imported to R v. 3.2.2 (R Core Team, 2016), where data management and all the statistical analysis were performed. Sole receptions in the acoustic array within 24 h intervals were considered spurious and removed from the database.

Fish tagging

A total of 20 *D. dentex* adult individuals were caught and tagged with V13P-1H acoustic transmitters equipped with a pressure sensor (dimensions: 48 x 13 mm, weight in water: 6.5 g; power output: 153 dB, signal delay: 80-180 s; VEMCO, Nova Scotia, Canada). Individuals were captured from a boat, by jigging hook-and-line fishing gear with barbless hooks to minimize injuries, at different locations within the NT zone during May, June and December 2007 (Figure 4.1, Table 4.1). The sex of individuals could not be determined due to the lack of sexual dimorphism in this species. Transmitters were implanted in the peritoneal cavity of animals using a standard surgical procedure (Lino et al., 2009; Koeck et al., 2013), under 2-phenoxyethanol anaesthesia (0.2 ml·l^{-1} solution). The tagging protocol followed the guidelines provided by the Ministry of Agriculture, Livestock, Fisheries and Food of the Catalan Government (decree 214/1997), and was approved by the

Committee on the Ethics of Animal Experimentation of the University of Barcelona. The Department of Environment of the Catalan Government granted permissions for fishing, operating and releasing the animals in the Medes Islands Marine Reserve.

Residence index and home range size

In order to estimate the amount of time that each fish expended within the NT zone, a residence index was calculated dividing the number of days in which the individual was detected by the total number of days in the tracking period (i.e., period between the release date and the date of the last detection) (Afonso et al., 2008).

The utilization distribution (UD) and home range (HR) of each individual were estimated using the dynamic Brownian bridge movement model (dBBMM; Kranstauber et al., 2012), an extension of the Brownian bridge movement model (BBMM, Horne et al., 2007), which has already demonstrated to be especially adequate for acoustic telemetry data (e.g. Papastamatiou et al., 2013; Pagès et al., 2013; Aspillaga et al., 2016. The dBBMM adds the advantage of adjusting behavioural variability across the animal's trajectory, rather than assuming a fixed overall variability associated to movement behaviour, thus providing more accurate quantifications of the UD (Kranstauber et al., 2012). Detections were previously thinned to 10-min intervals to avoid possible artefacts derived from irregular temporal sampling. The UD estimation was burst into consecutive day and night periods, determined by local sunset and sunrise times provided by the NOAA Solar Calculator (`www.esrl.noaa.gov/gmd/grad/solcalc/`) for the coordinates of the Medes Islands (42°03'N 3°13'E, WGS84).

Daily movement extent and core area sizes were calculated as the areas encompassing the 95% and 50%, respectively, of the daily UD volumes estimated for each individual and consecutive day and night period. The total UD for each individual (calculated by summing all the separate day/night UDs) was used to estimate the home range extent (HR) and core area sizes (i.e., areas encompassing the 95% and 50% of the total UD volume, respectively). The dBBMM was applied using the 'brownian.bridge.dyn' function in the R package 'move' v.2.1.0 (Kranstauber and Smolla, 2016).

Horizontal movement patterns

Two different approaches, based on the location data (horizontal) and depth data (vertical), were used to infer diel and seasonal movement patterns. Horizontal movement patterns were first analysed by visually inspecting spatial chronogram plots, which represent the receivers at which an individual was detected in every 30 min interval of the tracking period (chapter 2; Aspillaga et al., 2016). The effect of the diel period (day/night) on the daily movement extent and core area size was tested applying a linear mixed effects model, considering the fish ID as a random effect.

Additionally, we computed the similarity between all the pairs of daily UDs (among all individuals and day/night periods) to detect differences between individuals and test the effect of the diel period and the season (winter/spring/summer/autumn) in space use patterns. Similarities between pairs of UDs were calculated using the earth mover's distance (EMD, Kranstauber et al., 2016), a recent adaptation to movement ecology of a commonly used image retrieval method, which measures similarity as the effort that takes to shape one UD into the other. The EMD, unlike previous methods to compute spatial overlaps, does not exclusively rely on the exact spatial overlay between UDs, but takes into account the proximity in space use in terms also of relative intensity. A permutational analysis, applied to the matrix with all the EMDs, was used to test the general effect of the fish ID, the diel period and the season. A fuzzy clustering analysis (Kaufman and Rousseeuw, 1990) was also performed on the EMD matrix to classify all the UDs in 6 different groups or clusters. The fuzzy clustering algorithm assigns to each observation the probability of belonging to each of the groups. The grouping probabilities of each UD were then used to visualize the space use patterns of different individuals under a common classification, and allowed us to detect co-occurrence of individuals in specific zones and times. EMD and the permutational analysis were applied using the 'emd' and 'adonis' function in the R packages 'move' v.2.1.0 (Kranstauber and Smolla, 2016) and 'vegan' v.2.4-1 (Oksanen et al., 2013), respectively. The fuzzy clustering was performed with the 'fanny' function in the R package 'cluster' v.2.0.5 (Maechler et al., 2017).

Habitat use

In order to estimate the habitat preferences of tagged individuals, the distribution of depth values provided by acoustic transmitters was directly compared with the bathymetric distribution of seabed habitats within the coverage of the acoustic array. Vertical distribution of habitats was characterized based on the bathymetry and bionomical cartography available for the study area (Hereu et al., 2012), by extracting the depth value for each 1 x 1 m raster cell associated to an habitat.

Vertical activity patterns

The average absolute deviation (AAD) of fish depth values (i.e., mean absolute difference between values and their mean) was used as a proxy of the vertical movement activity. AADs were calculated for each individual and consecutive dawn, day, dusk, and night period. In this case, dawn and dusk periods were determined as the periods before and after the night in which solar position was between $-18°$ (astronomical twilight) and $18°$ over the horizon, using the NOAA solar calculator. AAD values were then log-transformed to achieve normality, and a linear mixed effects model was applied to test the effect of the diel period and the week (fixed effects), considering the fish ID as a random factor. The fits of linear mixed effects models were visually inspected in terms of the residual distribution and residual vs. fitted values plots. Linear mixed effects models were applied using the package 'nlme' v.3.1-128 for R (Pinheiro et al., 2016).

4.3 Results

Summary of detections

A total of 2097277 valid detections were recorded by the receiver array. Most of fishes presented long tracking periods (Table 4.1, Figure 4.2), being tracked during practically all the estimated battery life of each acoustic tag (between 342 and 366 days). Only two fishes disappeared shortly after the release date (#40 and #38, 1 and 3 days after release, respectively). Several causes might cause the disappearance of an individual from the acoustic array (e.g. departure from the array, death, or transmitter malfunction), but it is usually impossible to distinguish between them. However, we could confirm the deaths of two of the tagged individuals (#38 and #41), as they were detected at constant depths and by a single receiver during the last days of their tracking period (3 and 242 days after release, respectively). Two individuals were captured by local fishermen in the surroundings of the NT zone: #40 was captured 145 days after disappearing from the acoustic array; and #37 was captured more than three years after the last detection (in May 2012), with a length increment of 11 cm (from 53 to 64 cm). Individuals with extremely short tracking periods (<3 days, #38 and #40) were excluded from further analyses, and only fish with tracking periods of >90 days (n = 16) were taken into account for diel and seasonal movement pattern analysis.

All the individuals presented a high residence index within the NT zone (mean ± SD = 0.97 ± 0.06; Table 4.1, Figure 4.2). 72% of individuals (n = 13) were detected within the NT zone in every day of their tracking period (RI = 1), while the remaining 28% (n = 5) expended some days in acoustically uncovered areas, probably outside the NT zone. Two individuals (#37 and #46) underwent transient excursions of less than a day to the PR zone, as they were detected by receiver #18 in different 17 and 46 days, respectively, usually during the daytime (91% of detections in receiver #18). The second set of receivers, although it was installed at the end of the *D. dentex* monitoring experiment (during the last 120 days) and only received a few receptions in 14 different days, allowed us to detect sporadic excursions to the PR and NR zones of 4 of the 9 individuals that were still being monitored at that time (Figure 4.2). The majority of those detections (98%) also happened during the daytime, usually in days in which those fishes were also detected in the NT zone.

Home range size and horizontal movement patterns

Home range (HR) sizes ranged between 0.38 and 1.13 km^2 (mean ± SD = 0.79 ± 0.22 km^2), and core areas between 0.08 and 0.31 km^2 (mean ± SD = 0.16 ± 0.06) (Table 4.1). The permutational analysis detected significant differences between individual UDs (F = 1752.60, permutations = 999, p = 0.001), which accounted for most of the variability observed in the EMDs ($R^2 = 0.73$), and indicated a differential use of the areas within the NT zone (Figure 4.3).

Table 4.1: Summary of acoustic monitoring information of tagged *Dentex dentex* individuals. L: total length; DD: detection days; TP: total tracking period; RI: residence index; CA: core area (50% UD); HR: home range (%95 UD).

Fish ID	L (cm)	Release date	Capture zone	Total detections	DD (d)	TP (d)	RI (d)	RI (h)	CA (km^2)	HR (km^2)
12	68	2007-05-23	TAS	30296	89	91	0.98	0.79	0.13	0.6
18	63	2007-05-24	TAS	127061	364	365	1	0.92	0.31	1.13
27	60	2007-05-26	TAS	27261	45	45	1	0.95	0.14	0.81
43	63	2007-06-03	TAS	88917	356	356	1	0.91	0.2	0.92
44	59	2007-06-03	MED	184521	356	356	1	0.99	0.08	0.38
50	65	2007-12-01	TAS	170251	345	345	1	0.98	0.24	1.06
41*	47	2007-12-01	TAS	130318	241	242	1	0.98	0.13	0.59
33	61	2007-12-01	TAS	102725	344	345	1	0.94	0.15	0.73
34	47	2007-12-01	TAS	39603	285	346	0.82	0.52	0.17	1.13
45	59	2007-12-01	DEU	150775	345	345	1	0.92	0.18	0.71
46	48	2007-12-01	VAC	137544	216	216	1	0.94	0.1	0.55
47	65	2007-12-01	VAC	116407	217	246	0.88	0.86	0.21	0.89
42	62	2007-12-01	TAS	121111	365	366	1	0.97	0.1	0.71
40	60	2007-12-02	TAS	102	1	1	-	-	-	-
32	55	2007-12-02	TAS	115840	344	345	1	0.92	0.13	0.69
36	63	2007-12-02	DEU	205307	248	248	1	0.96	0.15	0.63
37	53	2007-12-02	DEU	134088	346	365	0.94	0.76	0.18	1.17
35	46	2008-01-22	TAS	122314	337	338	1	0.85	0.14	0.83
39	42	2008-01-22	TAS	91757	285	342	0.83	0.67	0.12	0.74
38*	78	2008-01-22	TAS	1079	3	4	-	-	-	-

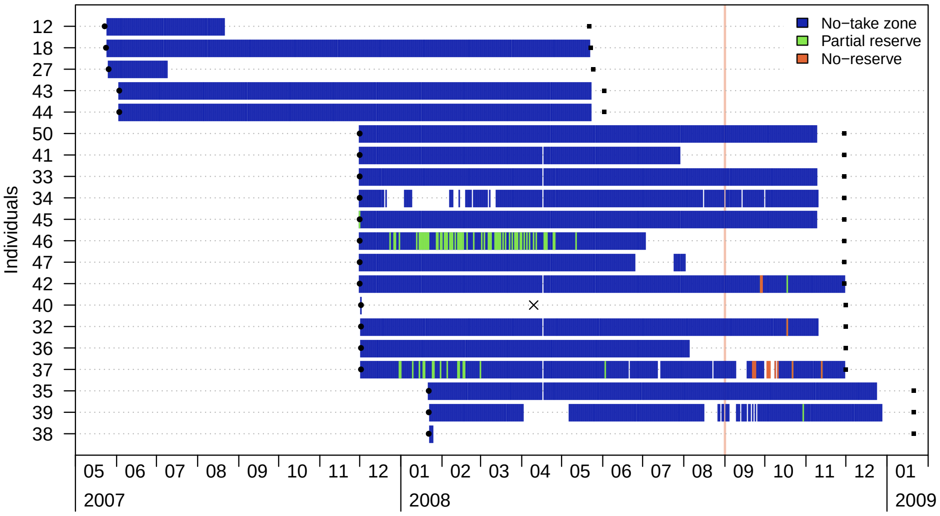

Figure 4.2: Daily presence-absence of tagged *Dentex dentex* within the acoustic monitoring array. Colours indicate the different zones of the MPA. Circles and squares represent capture dates and the estimated battery dead date (1 yr), respectively. The vertical red line in the background represent the date on which the second set of receivers was placed. The cross in individual #40 stands for the date on which that individual was captured by a local fisherman.

Further permutational analyses performed within the EMD distances of each tagged individual revealed the existence of significant diel and seasonal space-use patterns (Table 4.2). The day/night period had a significant effect ($p < 0.01$) in 81% of individuals ($n = 13$), and explained movement variability with an average R^2 of 0.18 ± 0.14. Those patterns were also directly observable in plots showing the home range movement extent and core area by diel period (Figure 4.4), and also in spatial chronogram plots (Figure 4.5). The permutational analysis on EMDs also reported a significant effect of the season in all the analysed individuals ($n = 16$), explaining movement variability with an average R^2 of 0.13 ± 0.08 (Table 4.2). The interaction diel cycle/season was also significant in 98% of individuals ($n = 15$), but explained a small part of the variance (average $R^2 = 0.05 \pm 0.03$) (Table 4.2). Daily core areas and movement extents were significantly larger

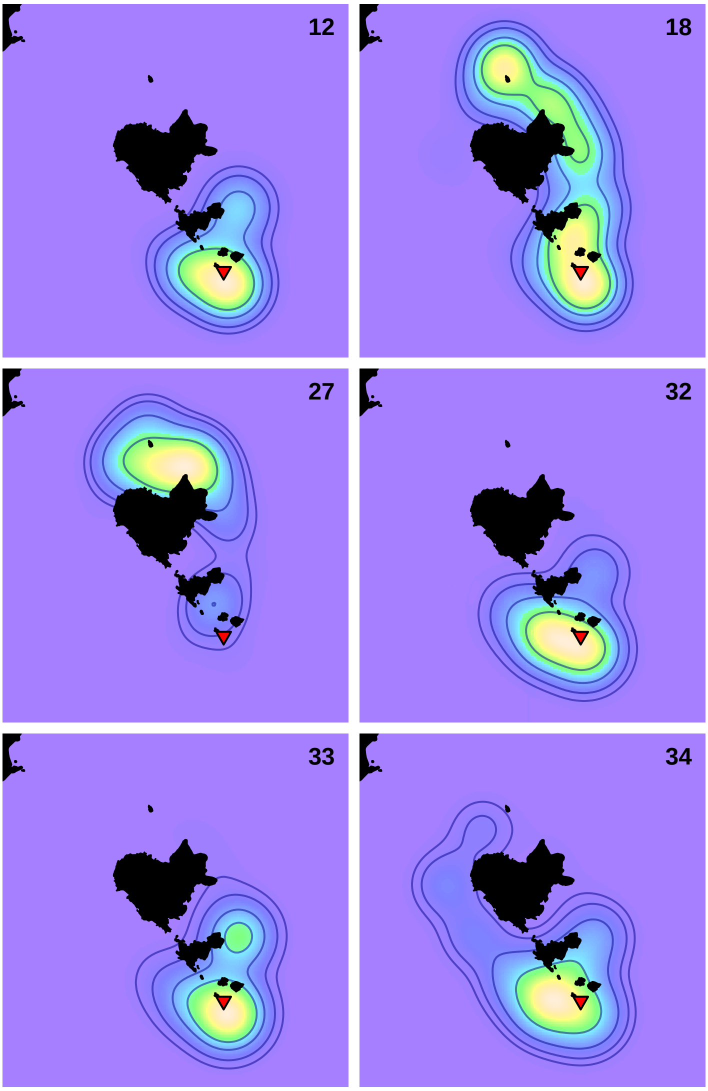

Figure 4.3: Estimates of the spatial utilization distribution (UD) of *Dentex dentex* individuals, calculated with dBBMM. Yellow colours indicate the highest utilization probabilities, and purple colours probabilities close to 0. Concentric polygons represent, from inside out, the areas covering the 95% (home range), 90%, 75% and 50% (core area) of UD volumes. The inverted red triangle points the approximate location at which the fish was captured.

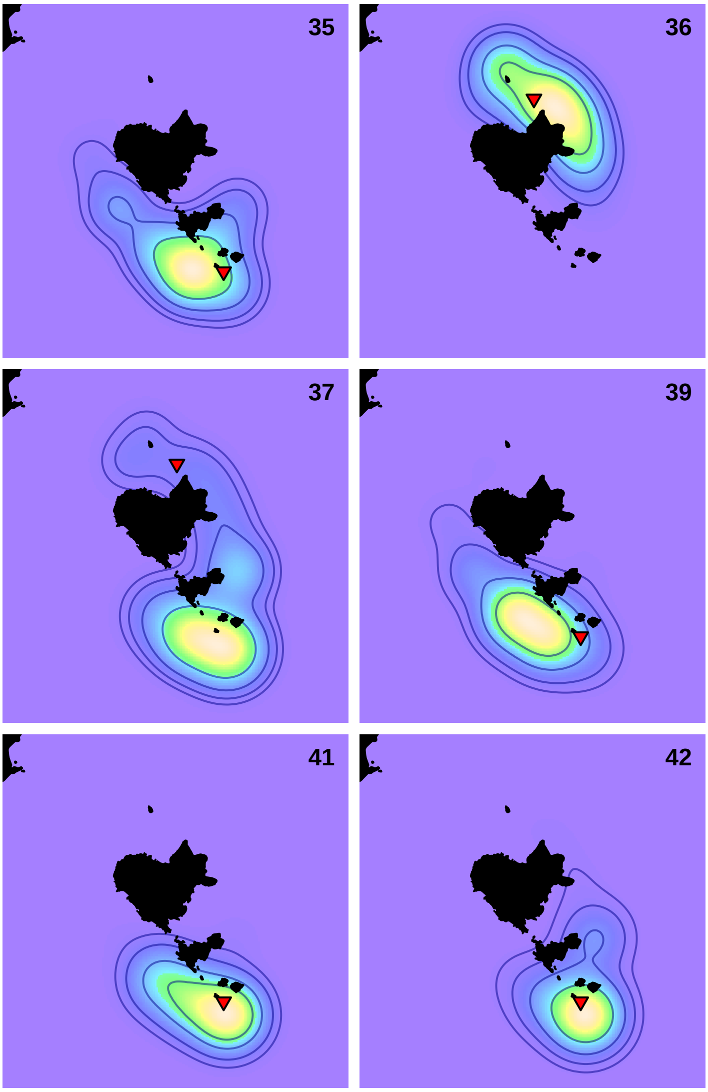

Figure 4.3: *(cont.)* Estimates of the spatial utilization distribution (UD) of *Dentex dentex* individuals, calculated with dBBMM.

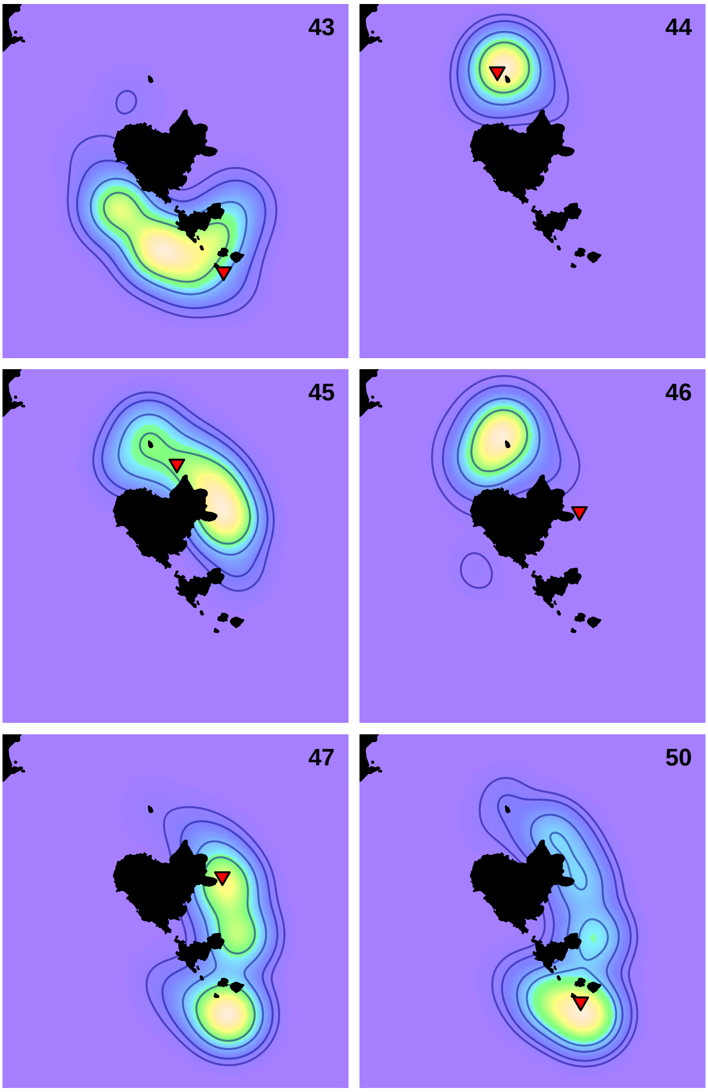

Figure 4.3: *(cont.)* Estimates of the spatial utilization distribution (UD) of *Dentex dentex* individuals, calculated with dBBMM.

during the day than during the night (linear mixed effects model on log-transformed extent sizes; core area: t-value = -2.626; df = 9631; $p < 0.01$; movement extent: t-value = -3.009; df = 9631; $p < 0.01$).

Vertical distribution and activity patterns

D. dentex individuals were detected in a wide range of depths (between 3.5 and 60 m), but depths between 20 and 40 m where preferentially used (Figure 4.6). This depth range coincided with the bathymetric distribution of circalittoral hard bottoms, mostly consisting on rocky bottoms and coralligenous outcrops. Only two individuals used shallower depths (#18 and #43), overlapping with the distribution of infralittoral algae bottoms and Posidonia oceanica meadows (Figure 4.6). During the spawning period (April-June), individuals were observed making rapid and synchronous excursions to deep areas ($\tilde{5}0$ m)(Figure 4.7), presumably to the lower limit of circalittoral hard bottoms, which mainly happened between dawn and the first hours of the day.

Dentex dentex presented higher vertical activities during the day, dusk and dawn than during the night (linear mixed effects model: F = 64.001; df = 15,325; $p < 0.01$) (Figure 4.8A). The mixed effects model also revealed some seasonal patterns, mainly consisting on an increase of the activity levels during some weeks between April and June (linear mixed effects model: F = 78.753; df = 15,325; $p < 0.01$) (Figure 4.8A), related to the rapid excursions to deep rocky areas previously described (Figure 4.7). This seasonal increase of vertical activity levels was more intense during dawn, day, and night periods, but had no effect during dusk.

By applying a fuzzy clustering analysis on EMD distances previously calculated (see Methods section), we were able to identify 6 main activity areas within the NT zone, underneath the complex diel/seasonal patterns shown at the individual level (Figure 4.9). By analysing the occurrence of individuals in each of the clusters, we could detect several transient increases of the proportion of individuals co-occurring in one of the activity areas

Table 4.2: Results of the permutational analysis of variance performed on the EMD distances between the UDs of consecutive day/night periods. One analysis was performed per each tagged *Dentex dentex* individual, testing the effect of the day/night period, the season (winter, spring, summer, and autumn) and their interaction.

Fish Id.	**Day/Night**					**Season**					**Day/Night x Season**				
	D.F.	**SS**	**F-Model**	**R^2**	**p**	**D.F.**	**SS**	**F-Model**	**R^2**	**p**	**D.F.**	**SS**	**F-Model**	**R^2**	**p**
18	1	4.37E+07	313.61	0.25	0.001	3	2.14E+07	51.24	0.12	0.001	3	8.71E+06	20.84	0.05	0.001
32	1	8.34E+04	3.26	0	0.049	3	1.48E+06	19.31	0.08	0.001	3	7.36E+05	9.6	0.04	0.001
33	1	5.73E+05	15.92	0.02	0.001	3	5.77E+06	53.45	0.17	0.001	3	2.58E+06	23.93	0.08	0.001
34	1	2.11E+05	2.19	0	0.113	3	3.44E+06	11.9	0.07	0.001	3	1.40E+05	0.48	0	0.773
35	1	2.23E+06	49.29	0.06	0.001	3	4.30E+06	31.63	0.11	0.001	3	2.22E+06	16.33	0.06	0.001
36	1	6.60E+06	359.51	0.36	0.001	3	1.96E+06	35.52	0.11	0.001	3	8.44E+05	15.32	0.05	0.001
37	1	1.36E+07	144.24	0.18	0.001	3	1.98E+06	6.98	0.03	0.001	3	2.67E+06	9.41	0.03	0.001
39	1	8.74E+05	25.09	0.04	0.001	3	3.25E+06	31.07	0.14	0.001	3	1.73E+06	16.53	0.07	0.001
41	1	8.27E+04	5.26	0.01	0.019	3	4.48E+06	95.18	0.36	0.001	3	4.49E+05	9.53	0.04	0.001
42	1	4.17E+05	13.18	0.01	0.001	3	3.66E+06	38.58	0.12	0.001	3	3.46E+06	36.47	0.11	0.001
43	1	1.27E+07	458.16	0.33	0.001	3	6.09E+06	73.47	0.16	0.001	3	6.69E+05	8.07	0.02	0.001
44	1	1.21E+05	70.79	0.09	0.001	3	9.07E+04	17.76	0.06	0.001	3	1.61E+04	3.16	0.01	0.002
45	1	1.98E+07	666.05	0.44	0.001	3	3.34E+06	37.44	0.07	0.001	3	2.39E+06	26.77	0.05	0.001
46	1	9.30E+05	48.99	0.1	0.001	3	4.00E+05	7.03	0.04	0.003	3	4.83E+05	8.48	0.05	0.002
47	1	1.34E+07	235.11	0.28	0.001	3	1.03E+07	60.51	0.21	0.001	3	9.33E+05	5.46	0.02	0.001
50	1	1.65E+07	151.32	0.17	0.001	3	6.91E+06	21.1	0.07	0.001	3	2.36E+06	7.2	0.02	0.001

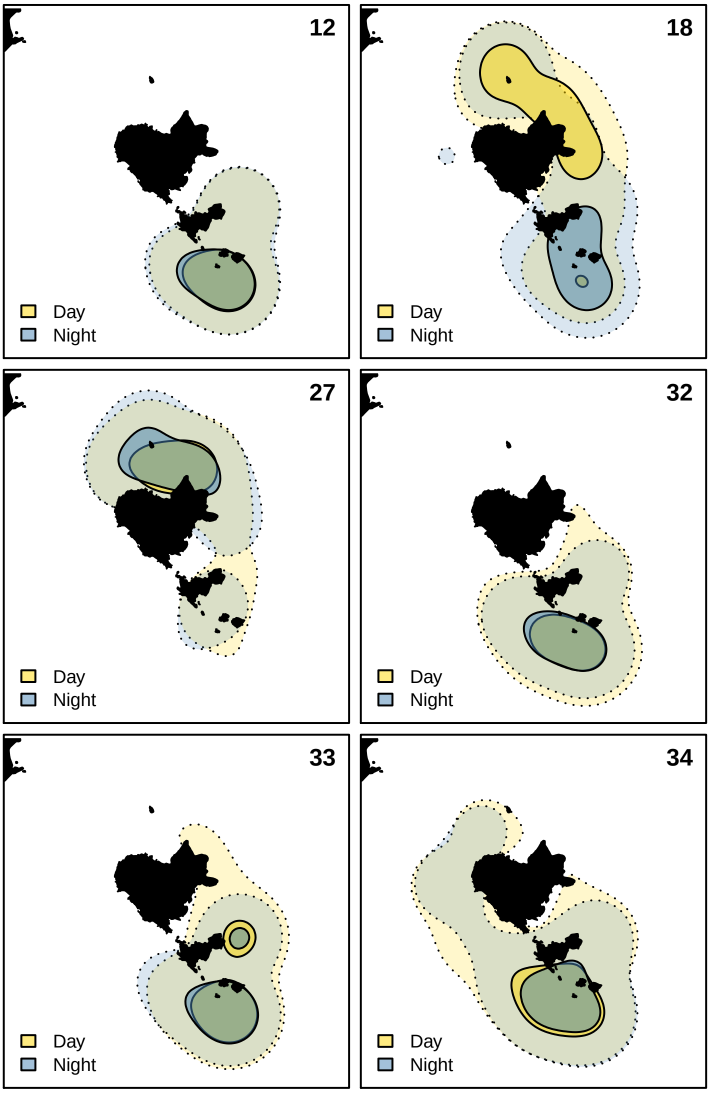

Figure 4.4: Differences between the movement extent and core areas by day/night periods in all the tagged *Dentex dentex* individuals. Light dashed polygons represent movement extents (95% of the UD volume) and the dark solid polygons core areas (50% of the UD volume).

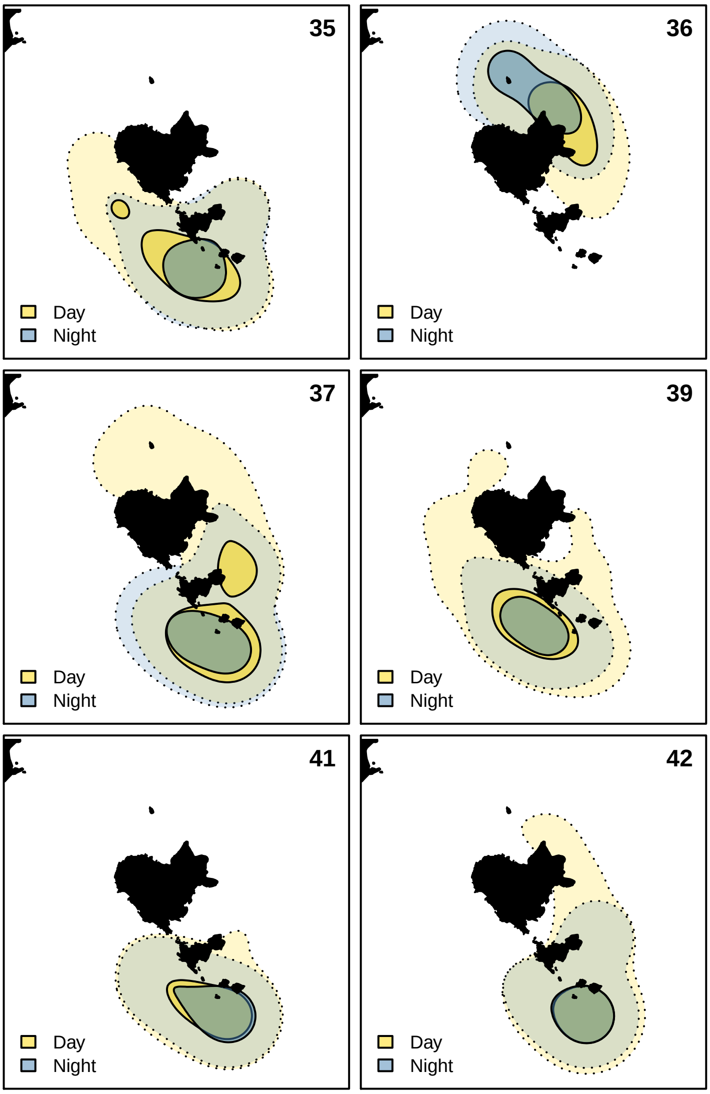

Figure 4.4: *(cont.)* Differences between the movement extent and core areas by day/night periods in all the tagged *Dentex dentex* individuals.

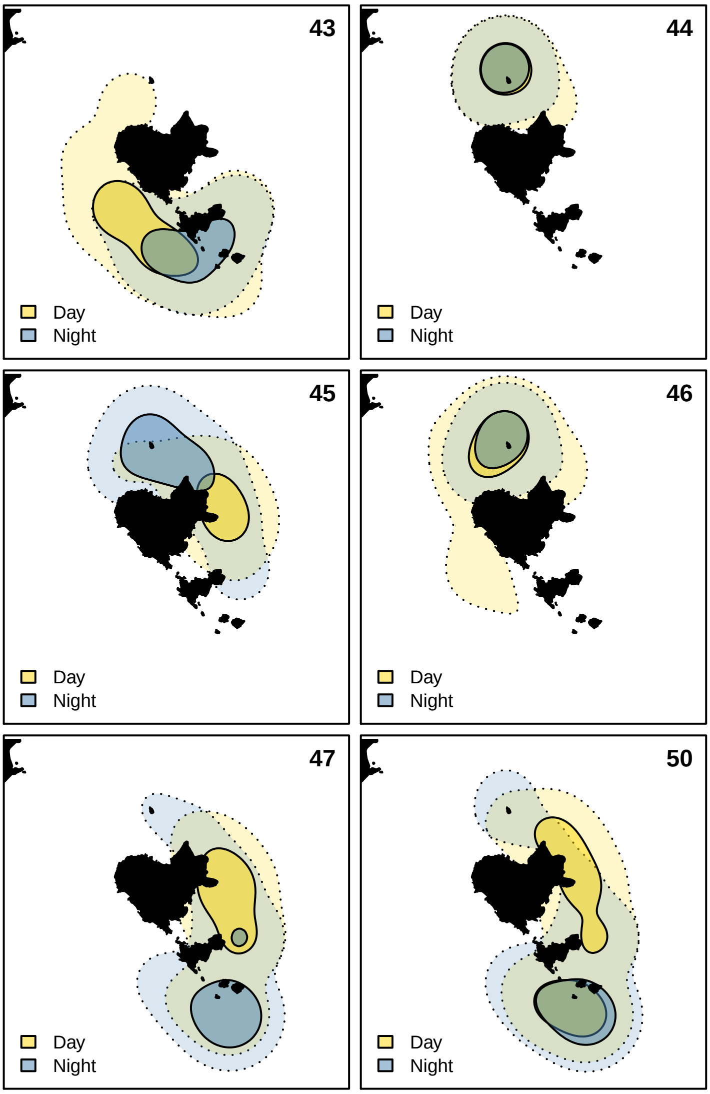

Figure 4.4: *(cont.)* Differences between the movement extent and core areas by day/night periods in all the tagged *Dentex dentex* individuals.

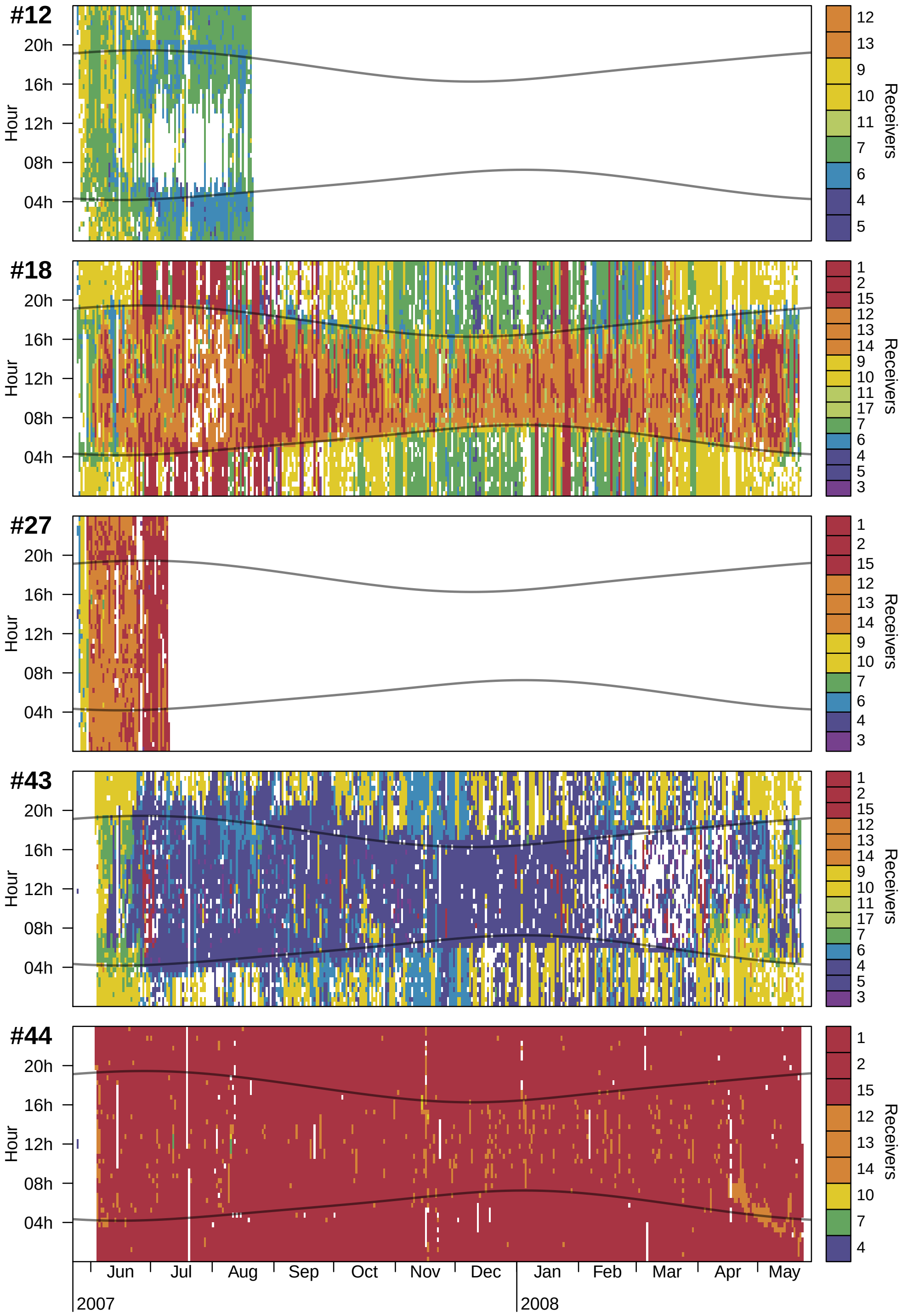

Figure 4.5: Spatial chronogram plots for all the tagged *Dentex dentex* individuals. Receivers are grouped under the same colour depending on their proximity, in order to facilitate the interpretation of the figure. See the map in Figure 4.1 for the position of receivers. Black lines represent the local sunset and sunrise time.

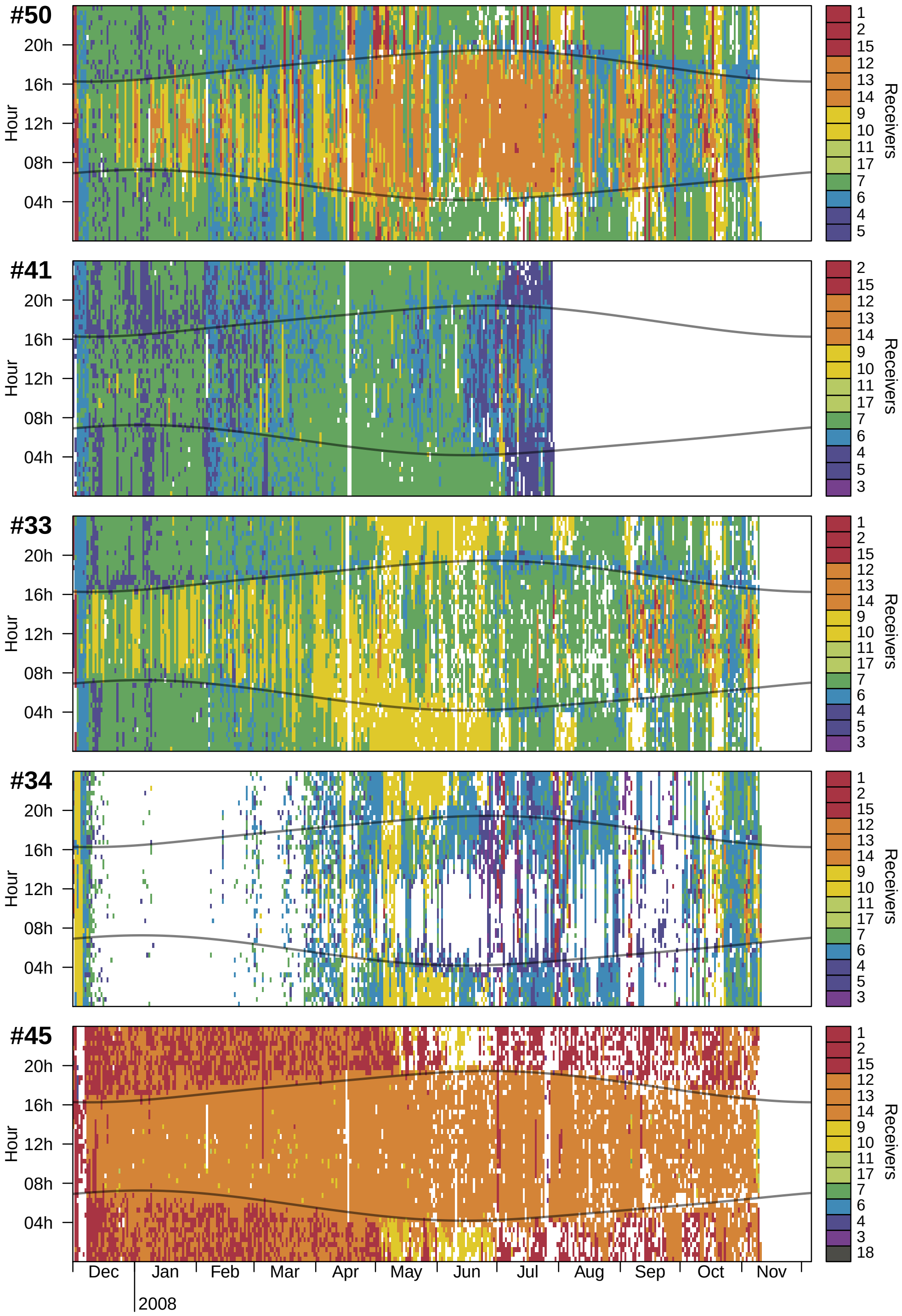

Figure 4.5: *(cont.)* Spatial chronogram plots for all the tagged *Dentex dentex* individuals.

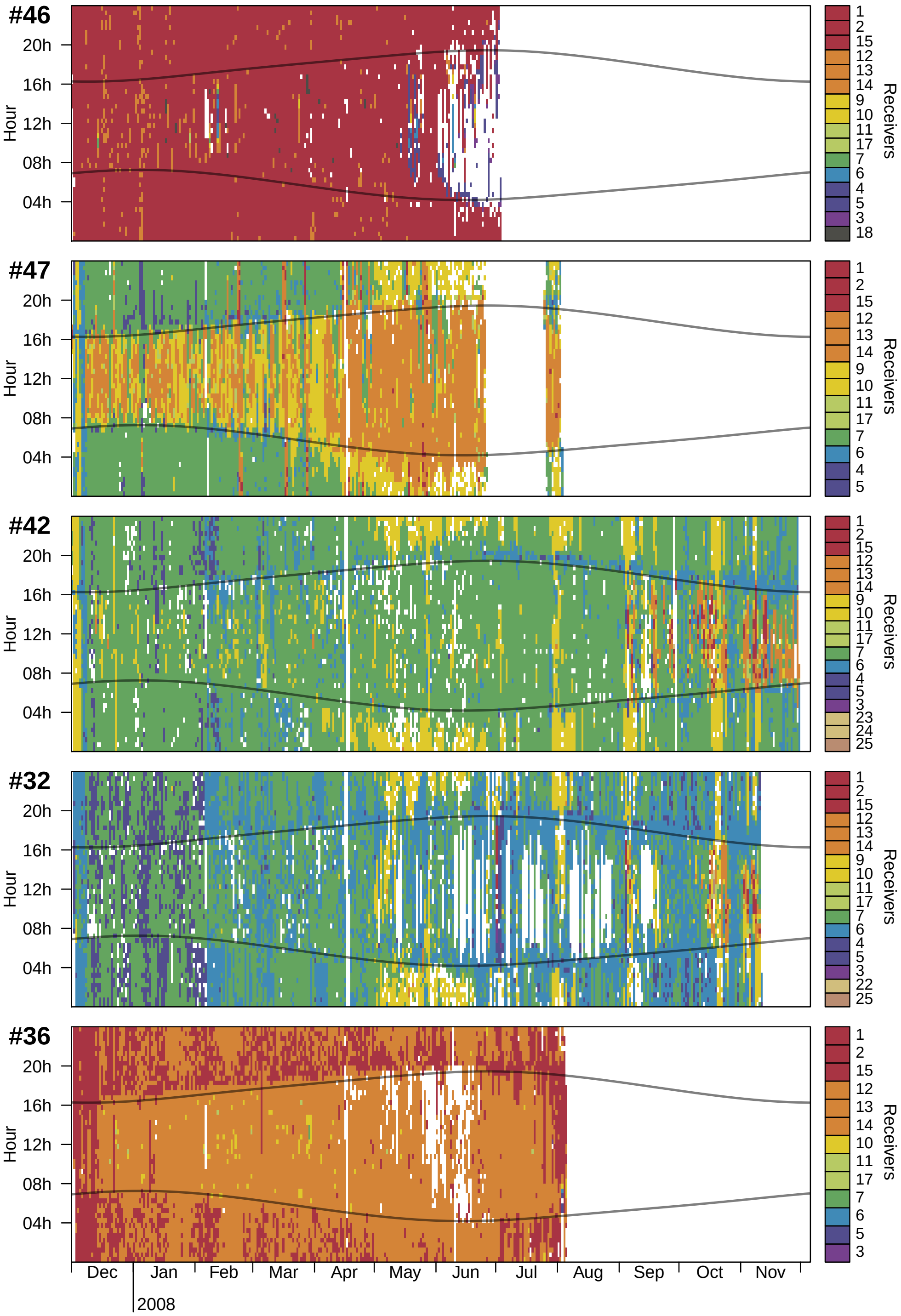

Figure 4.5: *(cont.)* Spatial chronogram plots for all the tagged *Dentex dentex* individuals.

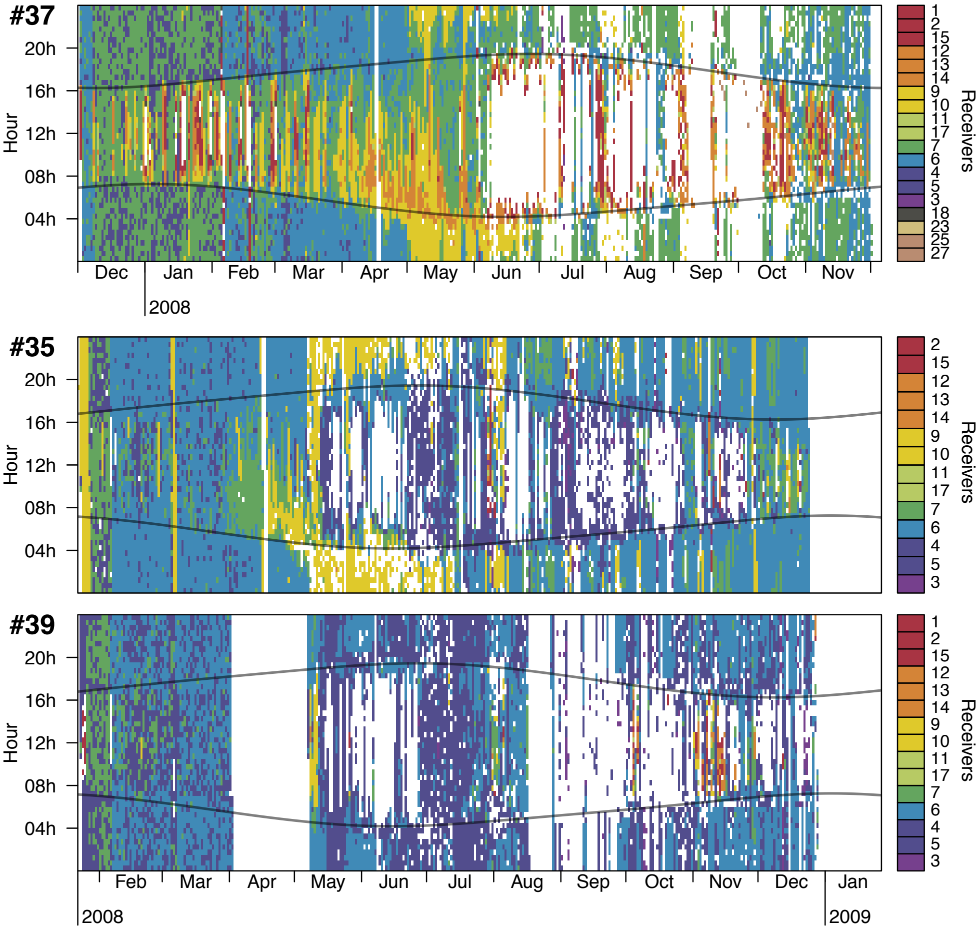

Figure 4.5: *(cont.)* Spatial chronogram plots for all the tagged *Dentex dentex* individuals.

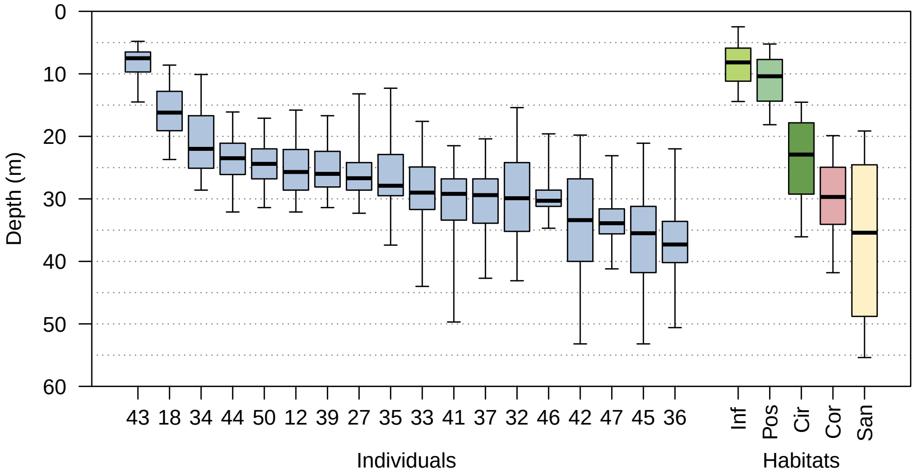

Figure 4.6: Vertical distribution of the acoustic signals detected for each *Dentex dentex* individual (in blue), and of the main seafloor habitats within the reception range (Inf: infrallitoral rocky bottoms, Pos: *Posidonia oceanica* meadows, Cir: circallitoral rocky bottoms, Cor: coralligenous outcrops, San: soft sandy bottoms). Habitat distribution was estimated from the bionomic map of the Medes Islands (Hereu et al., 2012).

(cluster #3) during the night (Figure 4.8B and 4.9). The most prominent increase happened between April and June, coinciding with the spawning season and the characteristic vertical patterns previously described. Some other punctual increases were also observed in July and August, very probably related to decreases of water temperature due to thermocline oscillations (Figure 4.8B and C).

4.4 Discussion

The limited home range and the high site fidelity shown by *D. dentex* evidence that small protected areas allow the restoration and conservation of overfished coastal fish populations. This result is concomitant with the recovery patterns observed for the *D. dentex* populations at the study site. Despite its small size (94 ha), the no-take (NT) zone from the Medes Islands MPA is a very successful protected area where most of the vulnerable fish

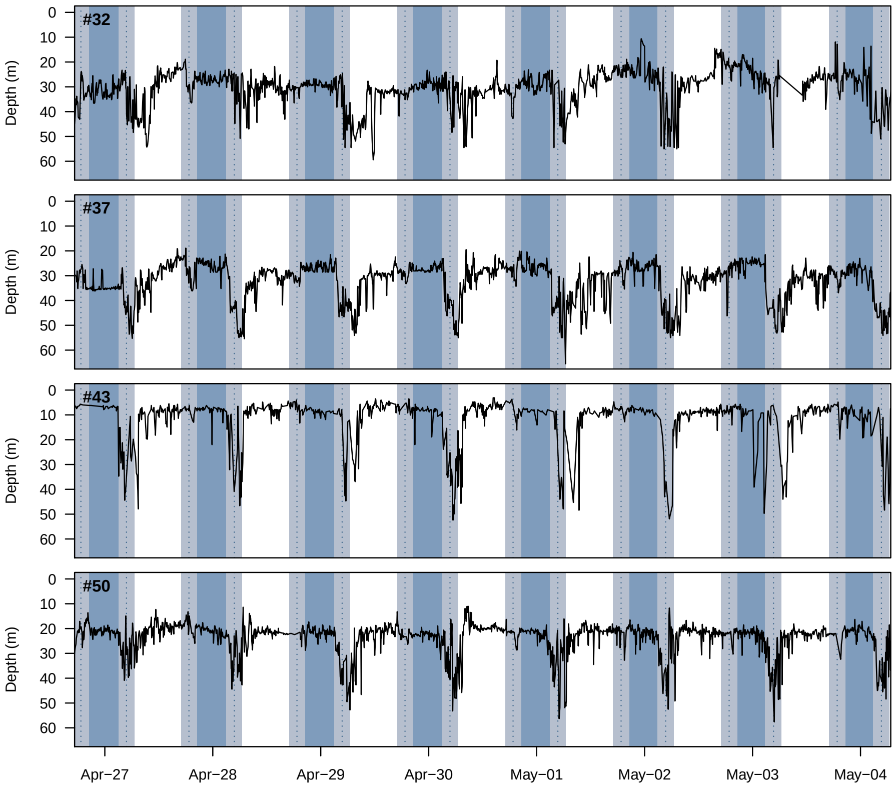

Figure 4.7: Vertical movement of four *Dentex dentex* individuals within the spawning season. Day and night periods are indicated by white and dark-blue areas. Lighter areas before and after nights represent dusk and dawn periods, as considered in the analysis of vertical movements (solar positions over the horizon between −18° and 18°).

populations have shown an increment since the establishment of the reserve (García-Rubies et al. 2013), reaching one of the highest fish biomasses in the Mediterranean Sea (Sala et al., 2012). *D. dentex* is among the most favoured species in the reserve; its population has undergone a fourfold increase of biomass during the past two decades and still keeps growing, indicating that the population of the Medes islands has not achieved the carrying capacity yet (García-Rubies et al., 2013). The exceptional recovery of *D. dentex* within the NT zone, might have been fostered by the steady increase of sea-

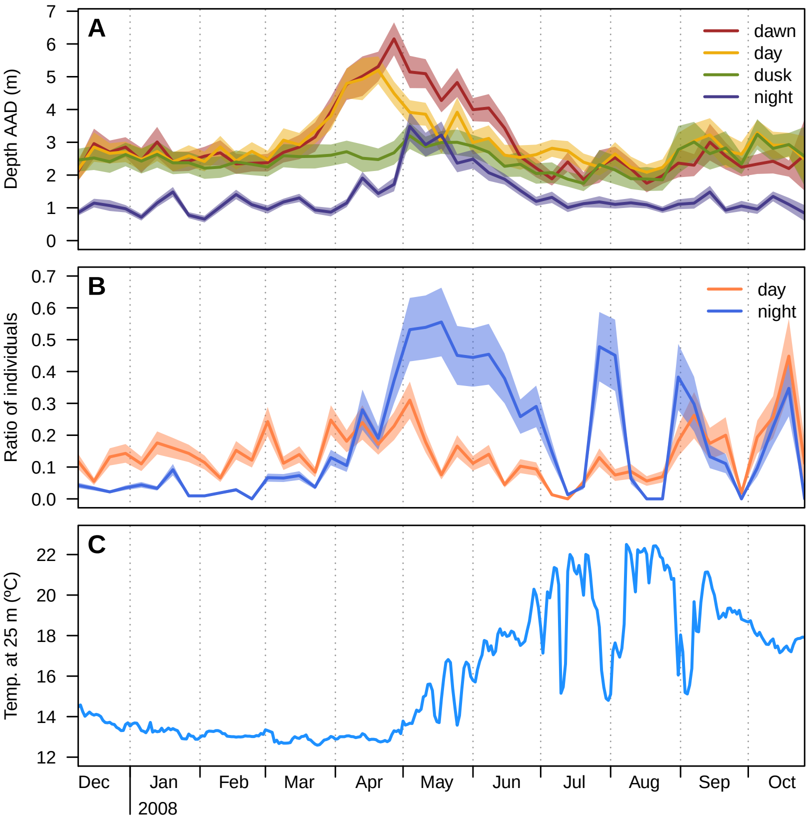

Figure 4.8: Weekly averages of the vertical activity of *Dentex dentex* individuals (A), of the proportion of individuals assigned to the cluster #3 by the clustering analysis (B) (see Figure 4.9), and daily average temperatures registered by an in situ sensor at 25 m depth (C). Shaded polygons in A and B indicate the standard error of weekly mean values (lines). Temperature data was provided by the TMedNet network (`www.t-mednet.org`).

water temperature related to global warming (García-Rubies et al., 2013), together with the thermophilic nature of this species (chapter 3;Aspillaga et al., 2017). Our highly-resolved movement analyses demonstrate the effectiveness of the Medes Islands MPA and emphasizes the potential of NW Mediterranean region to embrace large *D. dentex* populations.

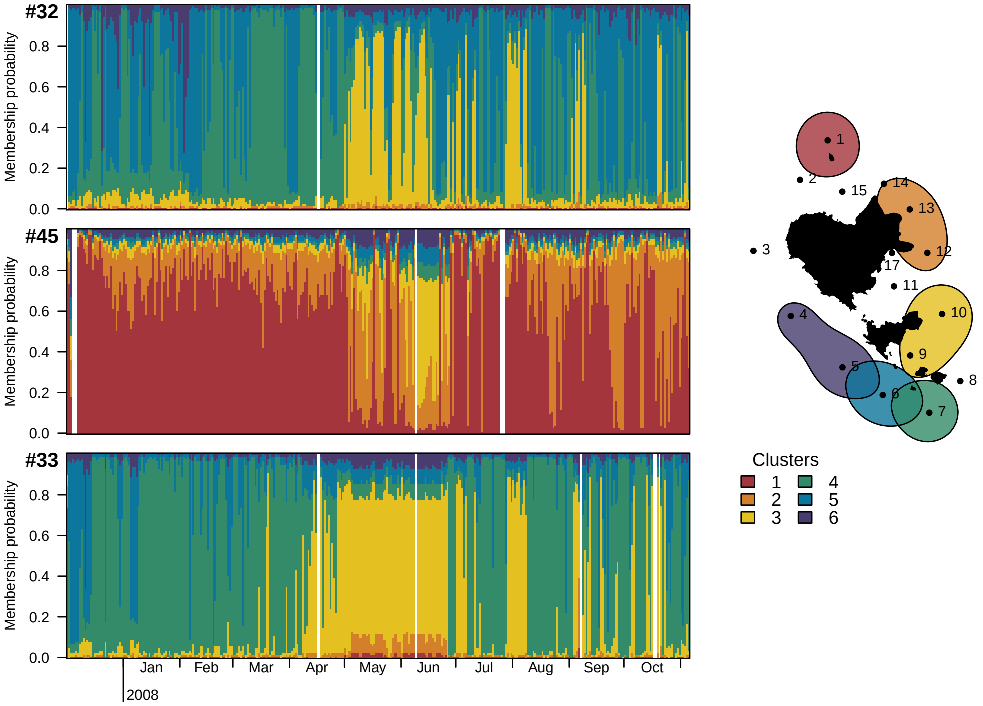

Figure 4.9: Grouping probabilities of daily UDs at night of three *Dentex dentex* individuals into six different clusters. An increase of the probabilities of cluster #3 can be observed in all the individuals between May and June. The map in the left shows the core areas of characteristic UDs that were assigned to each cluster.

Spillover capacity

Despite its limited home range and high site fidelity, *D. dentex* presented complex diel and seasonal movement patterns with considerable implications for the conservation of the species. The higher vertical activities and broader movement ranges observed during the daytime were very likely related to the diurnal nature of *D. dentex* (chapter 3; Aguzzi et al., 2013; Aspillaga et al., 2017), which is known to be a visual predator that forages on fish, crustaceans and cephalopods (Morales-Nin and Moranta, 1997). Our results also prove that those daytime foraging events often entail recursive displacements over significant distances, both within the NT zone (1 km, e.g.

individuals #18, #47 and #50 in Figure 4.5), or even to the partial reserve (PR) and no-reserve (NR) zones (more than 3 km, e.g. individuals #32, #37, and #42 in Figure 4.5). At a seasonal scale, we observed space use small-scale redistributions, probably caused by biotic or abiotic factors such as prey distribution or changes in environmental conditions. For example, in chapter 3 (Aspillaga et al., 2017), we proved that the vertical distribution of *D. dentex* is greatly affected by temperature in summer, when individuals move to shallower depths to avoid cold water during thermocline uprising events. Here, we demonstrate that changes in temperature also entail changes in the horizontal distribution of individuals (Figure 4.8). Similar seasonal activity changes have been also observed through cabled video observatories (Aguzzi et al., 2015), which have reported higher occurrences of *D. dentex* during summer, coinciding with higher water temperatures.

Species with relatively small home ranges, but complex movement patterns, such as *D. dentex*, have been proposed as optimal to reconcile the conservational and economic objective of MPAs (Moffitt et al., 2009). Moderate levels of mobility allow spillover (i.e. biomass export by juvenile and adult individuals) towards open non-protected areas, while still giving an effective protection to a significant part of the population within the MPA (Botsford et al., 2003; Gerber et al., 2003). Increases of *D. dentex* captures have been already reported in adjacent areas of several Mediterranean MPAs (Gómez et al., 2006; Forcada et al., 2009; Marengo et al., 2015). This spillover of adult individuals, if correctly managed, might be exploited to develop a sustainable local fishery activity in the MPA surroundings (Gell and Roberts, 2003).

Spawning behaviour

Our results also account for the first description of the spawning behaviour of *D. dentex*, which has been unknown until now, despite its relevance for the conservation of the species. Studies on the gonadal cycle have demonstrated that the spawning takes place between April and June (Morales-Nin and Moranta, 1997; Grau et al., 2016), and that the egg release happens along several days in the spawning season (Glamuzina et al., 1989). Tagged *D. dentex* individuals presented complex movement patterns coinciding with the spawning season, during which individuals grouped in certain areas (Figure 4.8 and Figure 4.9) and the vertical movement activity increased due to rapid excursions to deep zones (> 50 m) (Figure 4.7). Moreover, those movements happened synchronically between night and the first hours of the day, suggesting the formation of a fish spawning aggregation (Domeier and Colin, 1997), taking place around the placement of cluster #3 (Figure 4.9). The beginning of this behavioural pattern coincided with the increase of water temperatures in spring after the winter minimum, indicating a probable thermal triggering and synchronising mechanism.

Fish spawning aggregations are a common phenomenon among coastal fish species that have been widely studied in tropical ecosystems (Sadovy de Mitcheson and Colin, 2012). However, this behaviour is still largely unknown in temperate fish species. In the Mediterranean Sea only one species, the dusky grouper (*Epinephelus marginatus*, Serranidae), has been confirmed in the field to form spawning aggregations (Zabala et al., 1997; Hereu et al., 2006), but there exist indirect evidences of this reproductive behaviour in other species. For instance, other acoustic telemetry study in the Medes Islands MPA, showed that the white seabream (*Diplodus sargus*, Sparidae) increases its movement range and performs synchronous excursions to deep rocky habitats during its spawning season (March-April) (chapter 2; Aspillaga et al., 2016), presenting a similar spawning behaviour as the one here reported for *D. dentex*. Aggregations in deep rocky habitats might be a common spawning behaviour among the Sparidae, as was pointed by Harmelin-Vivien et al. (1995).

Spawning aggregations, being predictable in time and space, can be easily targeted by intensive fishing, which might suppose a great threat for the conservation of the species. For instance, (Marengo et al., 2016) reported a sharp increase of *D. dentex* captures around Corsica during the spawning season. A heavy fishing pressure on a fish spawning aggregation removes high portions of adult individuals from the adult stock, severely damaging source populations, and even causing their complete collapse (Sala et al., 2001; Sadovy and Domeier, 2005). Therefore, it is important to identify zones where spawning aggregations occur, and to consider them a conservation priority applying specific management actions such as their inclusion in no-take areas or the application of seasonal closures during spawning (Marengo et al., 2016).

Insights for the management of the species

The abundance of favourable habitats and their degree of isolation have been identified as features that enhance the success of a MPA (Coll et al., 2013; Edgar et al., 2014). The habitats most frequented by *D. dentex*, circalittoral rocky bottoms and coralligenous outcrops, are well represented in the Medes Islands NT zone (Hereu et al., 2012). Both habitats, but specially coralligenous outcrops, are essential habitats harbouring great biodiversity (Ballesteros, 2006). Moreover, they present a high structural complexity and steep slopes, which are two characteristics that increase the capacity of ecosystems to sustain high fish biomasses (Coll et al., 2013). In addition, the sand gap between the rocky bottoms from the NT zone and the PR zone might be acting as a soft barrier hindering the movements of *D. dentex* and other species to non-protected areas in the mainland coast, augmenting the protection effect on the species (Chapman and Kramer, 2000; Meyer et al., 2010). Coastal predators might present larger movement extents in continuous rocky coasts than in isolated ones, and should be further studied in order to decide the optimum MPA size in any given geographical area. These results also highlight the importance of mapping marine habitats in order to focus conservation efforts in the most favourable landscape configurations.

The occasional presence of *D. dentex* individuals from the NT zone in both the PR and no-reserve zones, indicates that essential habitats or resources occur in such areas. However, the PR zone of the Medes Islands MPA has shown a little capacity to rebuild vulnerable fish populations within its boundaries, and the presence of *D. dentex* is always in low numbers

(García-Rubies et al., 2013). We hypothesize that there are two main factors lowering the efficiency of the PR zone. First, the PR zone is too small or does not cover enough of the preferred habitats of *D. dentex*, specially taking into account that it is established in a continuous coast. Second, the pressure exerted by fishing activities in the PR zone and adjacent areas prevents the recovery of *D. dentex* populations. Coastal apex predators are vulnerable even to low fishing pressures (Ferretti et al., 2010), and especially to the spearfishing pressure (Lloret et al., 2008), which is allowed in the surroundings of the PR zone. The utility of partially protected areas is being subject to discussion (Denny and Babcock, 2004), and a good reinforcement seems to be key for the success of an MPA (Sala et al., 2012; Edgar et al., 2014).

Conclusions

Our study contributes with the first detailed description of the movement patterns of *D. dentex*, a species with an important role on coastal food webs and as a highly-appreciated fishery resource. In this study, we evidenced the mechanism through which *D. dentex* is benefited by small MPAs or MPA networks, as well as the great potential of the species to enhance sustainable fishery activities through spillover. However, it is necessary to better identify the essential habitats and the areas were spawning occur, especially outside the MPAs, where both research and management efforts should be intensified. Ideally, the knowledge on movement patterns should be extended to other species in the MPA, in order to propose integrated and flexible MPA management strategies.

CHAPTER 5

Modelling the 3D utilization distribution from Eulerian telemetry data

Abstract

Depth is an essential dimension along which many processes happen in aquatic environments. Passive acoustic telemetry provides the opportunity to monitor and contextualize the movements of diverse aquatic animals. The Eulerian structure of the data (movements perceived from fixed locations), however, and the consequences of sound propagation in water pose some challenges, hindering the incorporation of the vertical dimension into the space use analysis. Here we propose a new data-driven numerical tool to estimate 3D space use from telemetry networks. The method is based on simulating large numbers of random realizations of the trajectories, according to the determined detection probability around receivers, integrating depth information from transmitters, and the local topography. The method is explained in detail and tested with acoustic telemetry data from the common dentex (*Dentex dentex*) within a Mediterranean marine protected area. We present 3D space use estimations for all the tagged individuals, and compare them with 2D representations of space use calculated with a probabilistic method (dynamic Brownian bridge movement model). 3D space use estimations provided a more comprehensive view on the movement ecology of the common dentex, much of which is missed by 2D representations. As an example, we can have more realistic representations of the actual spatial co-occurrence of individuals, including the identification of relevant spawning aggregations.

5.1 Introduction

Understanding the patterns and the processes that influence animal movement is one of the goals of movement ecology (Nathan et al., 2008), and often requires rigorous estimations of the space use. Animal movement has been traditionally studied in a two-dimensional (2D) domain (x and y coordinates), often obviating the vertical dimension (z), which is essential for the activity of many types of organisms (e.g. aquatic, flying, arboreal, or burrowing; Belant et al., 2012). The relevance of the vertical dimension is especially conspicuous in aquatic environments, where almost every environmental variable (light, temperature, or hydrodynamics, among others) predictably varies with depth, generating sharp ecological gradients that affect species distribution and community dynamics (Garrabou et al., 2002). The movement behaviour of mobile organisms is also affected by such gradients, which might act as more or less strong barriers limiting their potential space use (Kitagawa et al., 2000; Aspillaga et al., 2017, chapter 3). Moreover, interactions among individuals (e.g. aggregation, avoidance) are often reflected in a differential use of the space, resulting in a vertical stratification (Simpfendorfer et al., 2012; Bestley et al., 2015; Vivancos et al., 2016). Therefore, analyses that are limited to a 2D space provide a partial if not unrealistic view of the underpinning biological processes, and 3D approaches are mandatory to obtain relevant ecological and behavioural conclusions (Belant et al., 2012).

Acoustic telemetry is the most widely used technique to monitor movement of aquatic animals (Heupel et al., 2006; Hussey et al., 2015), and is commonly used to estimate space use probabilities (e.g., chapter 2 and 4; Simpfendorfer et al., 2002; Lowe et al., 2003; Aspillaga et al., 2016). In passive acoustic telemetry, animals tagged with acoustic transmitters are monitored by a network of receivers placed at fixed locations in the study area (Heupel et al., 2006), and thus, movement is perceived in a Eulerian mode as presences, absences, or transitions between discrete locations. The uncertainty regarding the position of tagged animals tends to be large (hundreds of meters), as it depends on the distance at which acoustic signals are detectable (i.e. within detection range), which must then be properly evaluated to include the effect of topographic and environmental factors that affect sound propagation (Simpfendorfer et al., 2008; Welsh et al., 2012; Kessel et al., 2013). Precise localization of animals is only possible when receivers are placed on a grid relatively close to each other, allowing the calculation of short centres of activity (Simpfendorfer et al., 2002) or the application of more sophisticated triangulation methods (e.g. VEMCO Positioning System, VEMCO, Nova Scotia, Canada) (Roy et al., 2014; Steel et al., 2014). Typical coast-lined configurations are problematic given that non-mesh architectures prevent triangulation techniques and highly resolved spatial locations.

Most often, accurate depth data is provided by acoustic transmitters attached to animals (Veilleux et al., 2016), but rarely taken into account when estimating space use probabilities and home range sizes. In the recent years, several probabilistic approaches have been proposed to estimate volumetric space use, by incorporating the vertical dimension into the classical kernel density estimation method (Worton, 1989; Simpfendorfer et al., 2012), or into movement-based methods such as the Brownian bridge movement model and its dynamic extension (Horne et al., 2007; Kranstauber et al., 2012; Tracey et al., 2014). Although existing 3D space use estimation methods are not yet widely used, they have demonstrated a huge potential to provide more realistic insights into ecology and behaviour of aquatic organisms enabling intuitive visualizations of 3D space use volumes in a geographical context (Simpfendorfer et al., 2012; Tracey et al., 2014; Udyawer et al., 2015), and increasing the accuracy of measures of spatial and temporal overlap (Udyawer et al., 2015; Vivancos et al., 2016).

Another challenge in movement analysis is the incorporation of topographical characteristics affecting space use estimations. Prominent types of landforms, such as mountains or rivers in terrestrial ecosystems, or emerged landmasses in aquatic ones, can pose insurmountable barriers to the movement of animals, and should bias the estimation of the space yet are rarely included in the analysis (Benhamou and Cornélis, 2010; Barry and McIntyre, 2011). In addition, due to the expansion of remote sensing surveys (e.g. Light Detection and Ranging, LiDAR, multibeam echosounders), fine-scale characterizations of animal habitats are becoming more widely available (Wedding et al., 2011; Rogers et al., 2012), and together with the increase of the computational capacity available to researchers, unique opportunities to contextualize and interpret the complexity of animal movement patterns are emerging (Demšar et al., 2015).

Here, we propose a new computational method to estimate 3D space use probabilities from passive acoustic telemetry data. It is an empirically-driven numerical method, which integrates the location uncertainty of non-highly resolved acoustic telemetry data by simulating large numbers of possible trajectories according to the empirically determined detection probabilities around receivers (detection range and presence of acoustic shadows) and the observed movement transitions among receivers. During the path generation process, the 3D random trajectories can be restricted by a topographical model of the study site, preventing the use of volumes shallower than the depth at which the animal was detected, and avoiding hard boundaries such as emerging land. Compared to recent 3D space use approximations (Simpfendorfer et al., 2012; Tracey et al., 2014), our method makes minimal modelling assumptions and accounts for movement barriers in a natural way, but is limited in that it requires a good physical characterization of the study site, which implies the use of context data beyond the one provided by the acoustic array. We present a general overview of our method, and in particular the R functions to estimate 3D utilization distributions for Eulerian position information such as provided by acoustic telemetry. In addition, we apply the method to estimate space use from telemetry data from the common dentex (*Dentex dentex*), one of the main coastal predator fish species in the Mediterranean Sea, and discuss the future potential of the method.

5.2 Methods

The method to estimate 3D space use probabilities has been completely developed in the R programming environment (R Core Team, 2016), and is divided in three steps to be executed sequentially: (1) empirical characterization of detection probabilities, (2) generation of random trajectories, and (3) assemblage of 3D volumes. The main features of each of the steps are sketched below, but a vignette with a detailed explanation and the R code to run the method is provided in the supplementary material together with example datasets Appendix A. The code for some intermediate steps that have been summarized in R functions which are also supplied within the dataset.

The application of the method is illustrated with data from an acoustic telemetry experiment performed in the Medes Islands MPA (NW Mediterranean Sea) (for more details, see chapter 2 and 4). 17 acoustic receivers were placed in line along the coast, at around 5 m depth in moorings with lines and subsurface floats. The bathymetric raster map of the study area was freely obtained from the Cartographic and Geologic Institute of Catalonia (`www.icgc.cat`) under Creative Commons Attribution License (CC BY 4.0), and adjusted to a resolution of 10 x 10 m.

Empirical characterization of detection probabilities

Two main factors modulate the probability of being detected by an acoustic receiver: the distance between the transmitter and the receiver, and the presence of physical impediments for the transmission of acoustic signals. There are many other environmental variables that might also affect the acoustic performance, such as the swell, currents, water stratification, or noise from biological or human activities (Heupel et al., 2006; Huveneers et al., 2016), but they are omitted due to the difficulty that entails characterizing them.

Modelling the acoustic range (i.e. the probability for a transmitter to be detected depending on the distance to the receiver) is an important step prior to establishing a telemetry experiment, as it determines basic aspects of the design of the acoustic array, such as the number of receivers and their separation distance (Welsh et al., 2012; Kessel et al., 2013). Acoustic range tests are usually done by placing several receivers and one or more transmitters at increasing distances between them, to then determine the percentage of emitted signals that are detected at each distance. In order to be used in this method, the decrease in detection probability with distance is characterized for all the receivers by adjusting a logistic regression model to one acoustic range test (Figure 5.1).

It is impossible for acoustic signals to pass through solid objects that interpose in their way to the receiver. Therefore, the presence of heterogeneous rocky bottoms or emerged landmasses might generate acoustic shadow areas within the potential range of the receiver array, from which the tagged animals will not be detected. In this method, we use a viewshed analysis to identify the acoustic shadow areas generated by emerged landmasses, in order to incorporate the effect of such zones during the simulation of random trajectories. Viewshed is a commonly used terrain analysis technique that recognizes the geographical area that is visible from a specific location (Haverkort et al., 2009), which is also applicable to sound propagation. The viewshed analysis is applied to the topographic base map of the study area through the GRASS GIS software (GRASS Development Team, 2017) (Figure 5.2).

Generation of random path realizations

In the next step, a large number (e.g. 100) of random trajectories are simulated from the original telemetry data. Performing each path realization is a computationally slow sequential procedure, and its duration depends on the number of detections to be processed. Therefore, a prior thinning is highly recommendable for large data sets with a high temporal resolution (e.g. detection intervals of less than 15 or 30 minutes). In order to reduce the amount of data while maintaining its original variability, we propose a random thinning method that pools telemetry data into specific time intervals (e.g. 30 minutes), generating a unique combination of data before starting each simulation. The thinning method commits a receiver to each time interval, randomly sampled according to the proportion of signals detected by each receiver in that interval, and assigns a depth value that is selected from the probability distribution of the measured depths for the same interval.

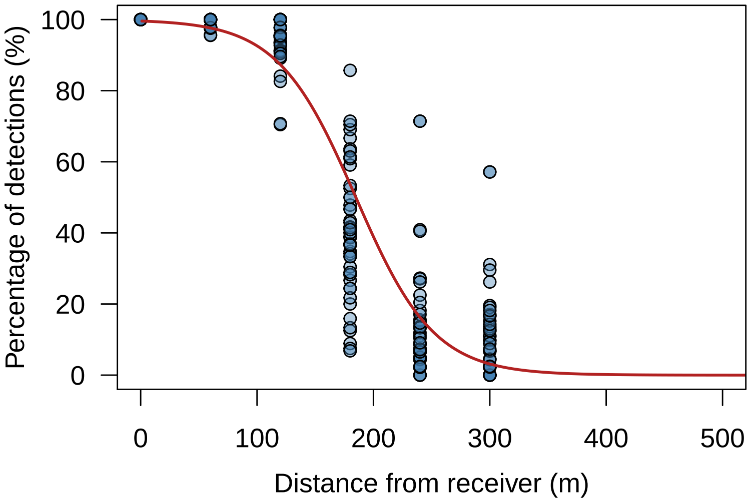

Figure 5.1: Results from an acoustic range test performed in the study site. Points represent the percentage of signals detected during one-hour intervals. The red line corresponds to the logistic regression model adjusted to the data.

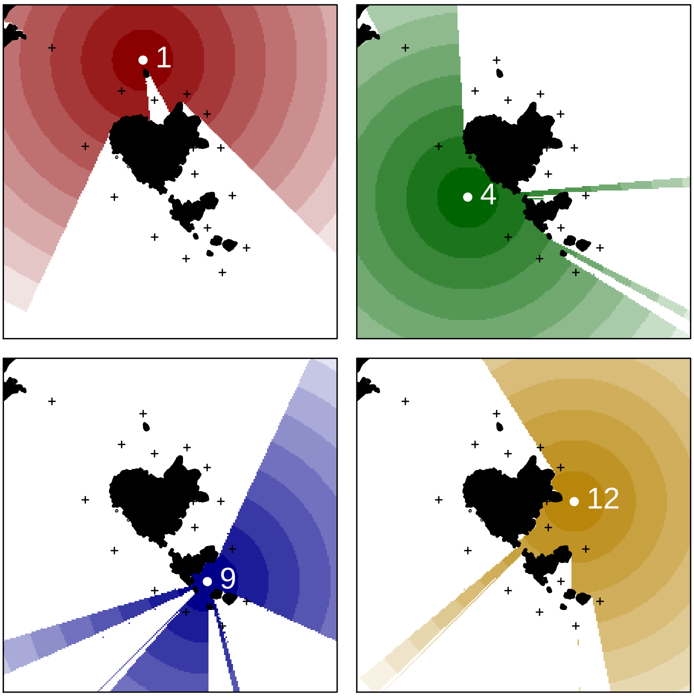

Figure 5.2: Viewshed analysis for four receivers (#1, #4, #9, and #12) placed in the study site. Black areas in the map represent emerged landmasses. Distance from receivers is indicated in intervals of 100 m by bands of different colour intensity.

Random paths are then constructed by sampling a pair of geographical coordinates for each observation (original detections or thinned time intervals), taking into account the characterization of the acoustic performance, the depth values, and the local topography (bathymetry). The coordinate sampling of each observation is based on a probability raster, obtained by applying the acoustic range model (Figure 5.1) to the three-dimensional distances between the given receiver and the raster cells at the depth of the observation. Raster cells in acoustic shadow areas or at depths shallower than the observation are excluded from the sampling. In addition, the distance to the previous location is considered by also excluding the cells that are beyond a maximum distance that the animal might have reached in the time elapsed from the previous observation, assuming a fixed maximum speed (e.g. 1 m·s^{-1}). This allows to avoid unlikely movements between distant locations in short periods of time, which might happen when the individual is placed halfway between two receivers and detections alternate rapidly between them.

During the sampling process, consecutive pairs of coordinates are joined together using a least-cost path approach, which finds the shortest route between both locations but take into account the topography to avoid crossing unsuitable areas such as emerged landmasses. As a final result, a three-dimensional trajectory is obtained from each iteration (Figure 5.3).

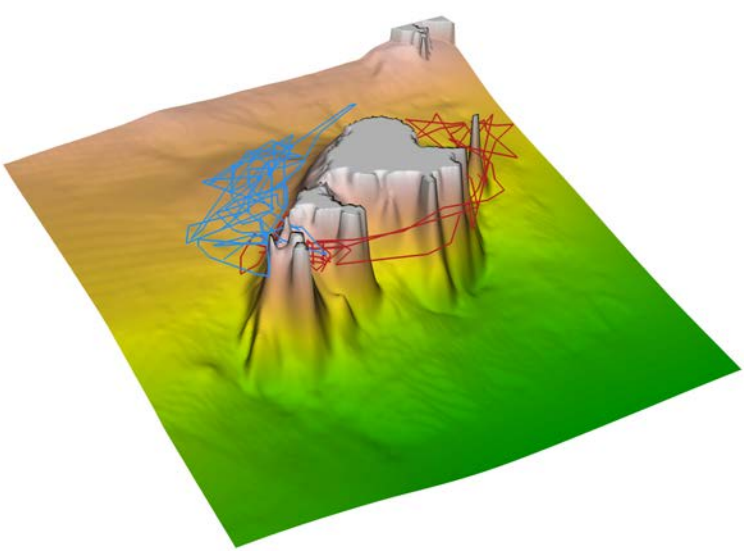

Figure 5.3: Example of simulated random trajectories for two different individuals (different colours). The vertical axis has been 10 times magnified compared to horizontal axes.

Assemblage of utilization distribution volumes

Three-dimensional utilization distributions (3D-UDs) are estimated from the average spatial occurrence of all the random path realizations. To calculate the average spatial occurrence, the study site is divided into a three-dimensional grid of voxels of a given horizontal and vertical resolution (e.g. 10 x 10 x 1 m), and the percentage of segments crossing each voxel is calculated for each random path. Then, all the path realizations are merged together to calculate the average percentage of segments crossing each voxel. These average values are finally smoothed by applying a three-dimensional kernel estimation, to generate the definitive 3D-UDs, which are stored in raster stacks where each layer corresponds to a given depth-range. 3D-UDs can be used to calculate the volume sizes and spatial overlaps for different probability contours, or be exported to external software (e.g. Paraview) for visualization.

Testing the method

We used data from a previous acoustic telemetry study with the common dentex (*Dentex dentex*) to apply the method and test its performance. Data corresponded to the movements of 10 individuals (ranging from 47 to 65 cm in length), tagged with V13P acoustic tags (signal delay: 80-180; VEMCO, Nova Scotia, Canada) and simultaneously monitored by the already described acoustic array (Figure 5.2), between Dec-12 2007 and May-31 2008. More details on the original results of the study can be found on chapter 4.

We used the method to compute the 3D-UD of each individual, considering all the tracking period and using 100 simulations. The total space-use volume was estimated as the product of the number of voxels within a certain probability contour of the UD (50% and 95%) and the volume of each individual voxel (10 x 10 x 1 m^3). Overlap indices were calculated between pairs of 3D-UDs, for 50% and 95% UD probability contours, by dividing the volume of the overlapped space by the size of the 3D-UD volume contours. 3D-UD volumes were exported and visualized in Paraview (Ahrens et al., 2005).

We analysed the performance of the method and compared 3D-UDs against two bi-dimensional space use estimations (2D-UDs). More specifically, we compared 2D-UDs calculated by using the dynamic Brownian bridge movement model (dBBMM, Kranstauber et al., 2012) to 2D-UDs obtained by vertically collapsing 3D-UD volumes, that is, by summing the UD values of all the depth layers. We also characterized the 3D volume estimation conditioned to the length of the tracks and the number of path realizations. We used different periods of days (i.e. 1, 7, 30, and 180) as a surrogate of path lengths, and increased the number of path realizations from 1 to 100. We analysed the efficiency of the method to incorporate and avoid geographical barriers by comparing the size and overlap of the original 3D-UDs with respect to 3D-UDs computed without including the topographic information.

Finally, we tested the efficacy of the method to quantify spatial co-occurrence. The movement behaviour of the common dentex is known to change during the spawning period (taking place between May and June), when individuals punctually migrate to deep rocky bottoms to breed (chapter 4). In order to explore whether 3D estimations of space use improve our knowledge about these collective movements, we computed the overlap indices between 3D-UD estimations for the monitored individuals in one week outside and another within the spawning period (February and May 2008, respectively). 3D-UDs were computed separately for day and night periods, determined by local sunset and sunrise times provided by the NOAA Solar Calculator (`www.esrl.noaa.gov/gmd/grad/solcalc/`).

5.3 Results and discussion

Optimization of the number of random path realizations

Generating each random path realization proved a time-consuming step, which might be optimized by adjusting the number of path realizations that are required to reach a stable 3D-UD solution, depending on the amount of telemetry data to be processed. Short tracking periods, usually consisting of fewer locations, require large amounts of random paths in order to reduce the variability of the resulting space use estimations (Figure 5.4). Long tracking periods, by contrast, contain much more data points that already capture most of the space use variability, hence robust space use volumes can be obtained with fewer path realizations. In our case, using a thinned dataset with a temporal resolution of 30 minutes, almost 70 path realizations were required to substantially reduce the variability of the resulting volume when processing a unique tracking day, but 30 or 40 realizations were enough when processing 30 or more tracking days (Figure 5.4).

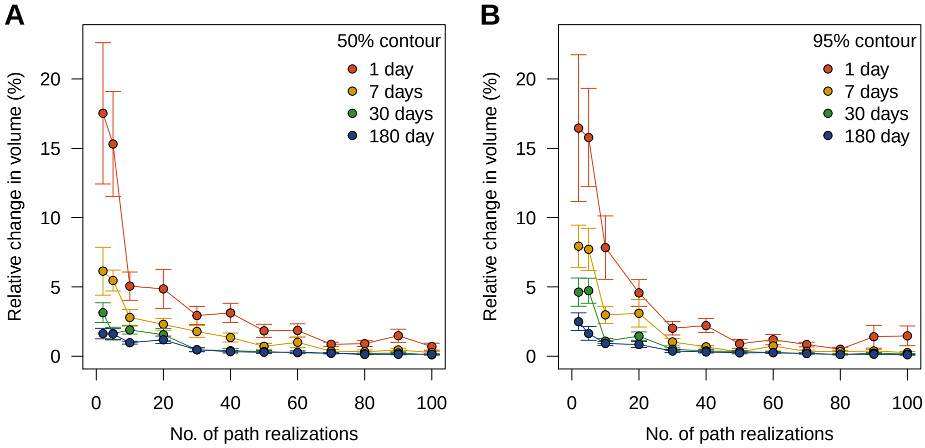

Figure 5.4: Relative change of 3D-UD volumes for 50% (A) and 95% (B) contour levels when increasing the number of processed random path realizations and using datasets of different lengths (number of days).

3D vs 2D space use estimations

Estimations of 3D space use probabilities were obtained for all the analysed common dentex individuals, which provided a spatially explicit view of the location of their home ranges (Figure 5.5). A clear vertical segregation could be observed between several individuals, which could not have been unveiled from 2D space use estimations.

When considering only the horizontal plane, both the 3D-UDs and 2D-UDs were highly consistent (Figure 5.6). This is so, despite the 3D version makes minimal assumptions on the underlying nature of the movement process whereas the 2D version, grounded on the dBBMM (Horne et al.,

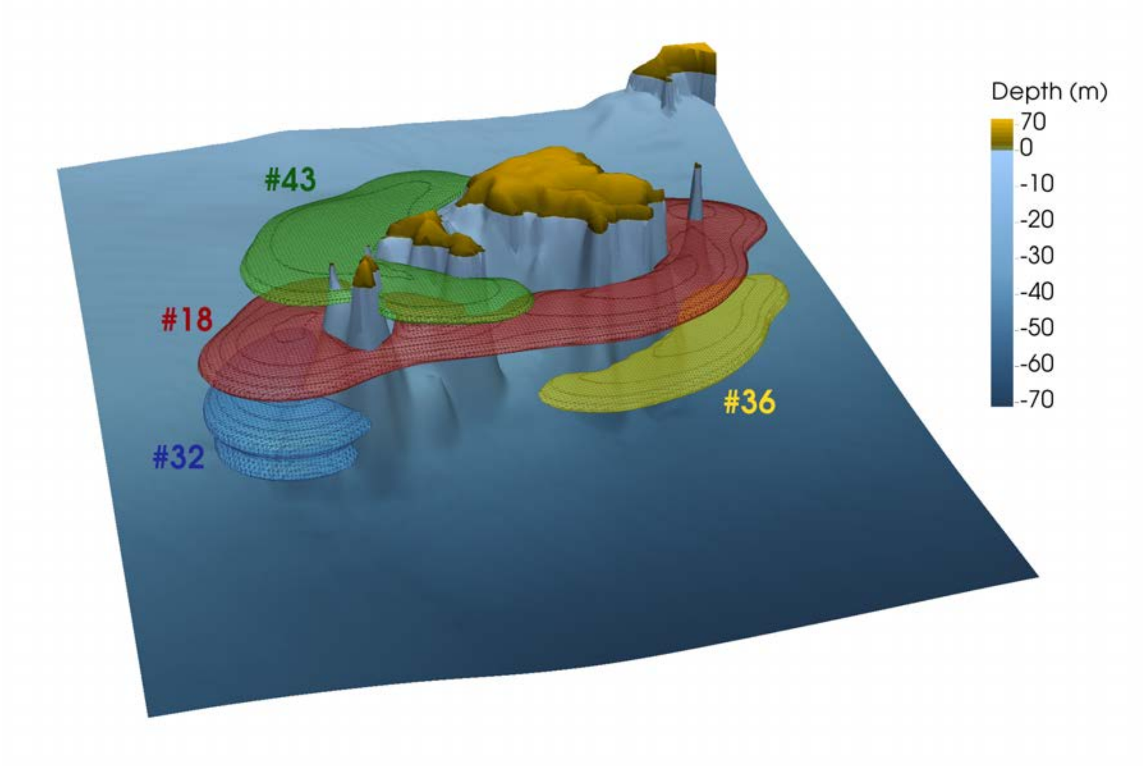

Figure 5.5: 3D-UD volumes (50% contour level) of four common dentex individuals (different colours and codes). The vertical axis has been 10 times magnified compared to horizontal axes.

2007; Kranstauber et al., 2012), assumes a Brownian movement between locations. The important difference, however, was that 3D-UD estimates, when taking into account the topography, effectively excluded unfrequented shallow areas and unsuitable emerged landmasses (Figure 5.6). This demonstrates the adequacy of the data-driven, numerical approach addressed in this work to handle and incorporate geographical barriers into space use characterizations, both for 2D and 3D estimations.

The inclusion of the vertical dimension gives a unique view of the space use patterns of individuals, especially when studying spatial overlap. Overlap indices of 3D-UDs were lower in average than the overlaps of 2D-UDs, but there was no particular pattern between them (Figure 5.7). 2D

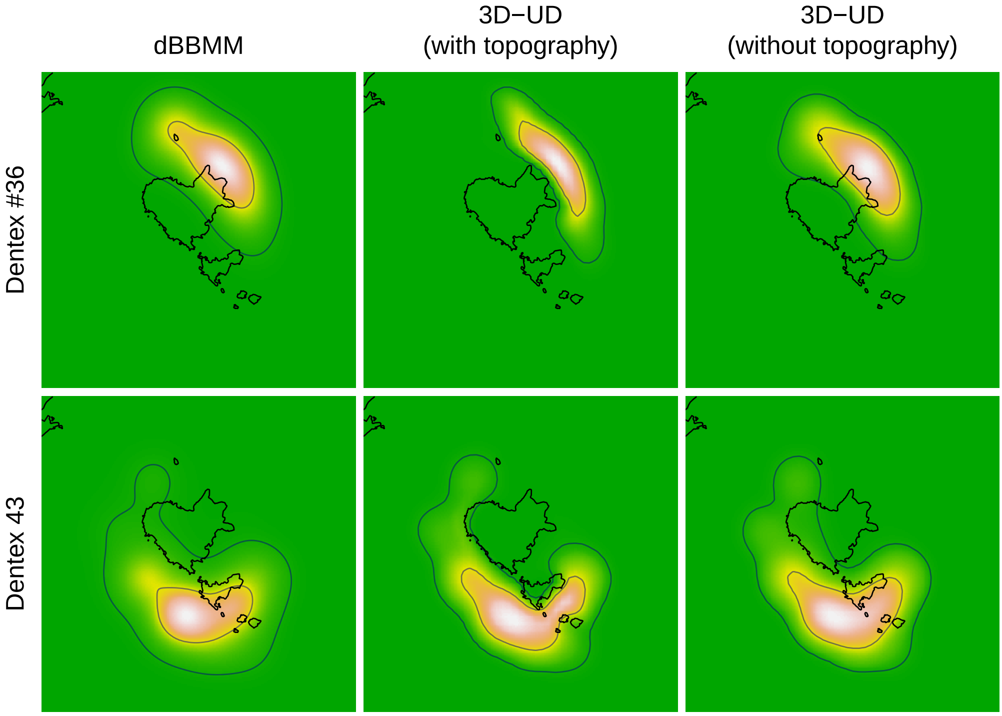

Figure 5.6: Bi-dimensional representations of utilization distributions of two common dentex individuals (rows) calculated with the dynamic Brownian bridge movement model (left), and by collapsing 3D-UD volumes that incorporate (middle) or do not incorporate the topography (right). Polygons indicate, from the inside out, the 50% and 95% contour levels.

estimations overestimated the spatial overlap because did not account for the segregation of individuals across depth, conditioned to being in the same plane, as was already described by Simpfendorfer et al. (2012). 2D-UD estimations, besides overestimating the spatial co-occurrence, provided a partial view of individual behavioural processes, and much of the ecological information would have been lost if depth was not taken into account. 3D-UD estimates, will in the future increase the definition with which we can study space use patterns and specific behaviours, such as temporal aggregations of individuals. For instance, the spawning behaviour of common dentex, described in chapter 4, becomes more evident when analysing the 3D overlaps. During the night period of the spawning season, 3D spatial overlap among individuals increases in comparison to diurnal or no-spawning periods, when there is almost no overlap between their 50% contour volumes (Figure 5.8). These differences are not apparent analysing only 2D-UD overlaps. By combining the horizontal and vertical data, 3D-UD estimations provide a valuable tool to detect and easily visualize susceptible areas where animals aggregate, and thus have important implications for species management.

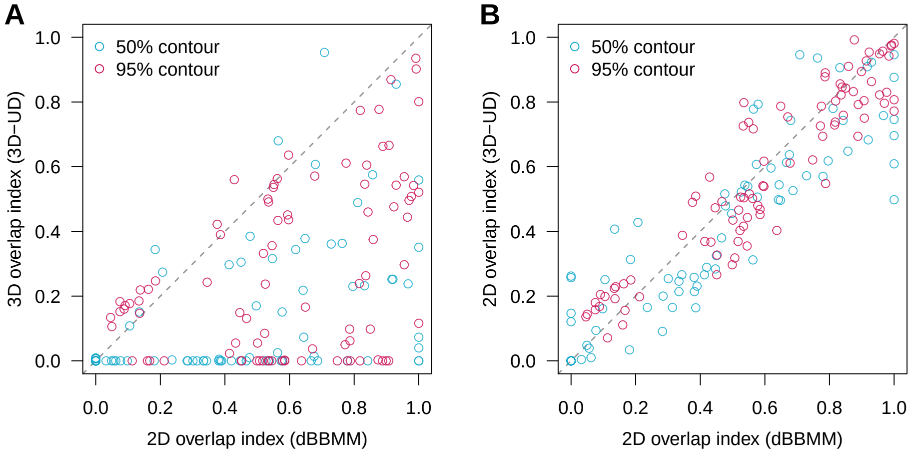

Figure 5.7: Comparison between overlap indices for bi-dimensional UDs (calculated with the dynamic Brownian bridge movement model) and overlap indices for volumetric (A) and collapsed (B) 3D-UDs, of common dentex individuals.

Future developments

A major advantage of this method is its high flexibility to accommodate additional data and further modifications. For instance, the acoustic range varies depending on the habitat in which the receiver is located (Welsh et al., 2012). Therefore, data from specific range tests could be applied to each receiver placed in acoustically differing areas within the same acoustic array. In addition, fixed control tags are often used to continuously monitor the acoustic performance of the receivers, and such information could be incorporated to dynamically adjust the acoustic range for each time period. Fine scale characterizations of the study site, such as high resolution cartographies or detailed in situ characterization of acoustic shadow areas, could also be used to improve 3D-UD estimations.

UD estimations through random trajectory generation also embraces a big potential to incorporate more information, or anticipating novel behavioural scenarios. By modelling the distribution of speed, behavioural modes, or other characteristics of the movement, more realistic path realizations could be obtained, which would also allow to incorporate behavioural changes in space use estimation. Continuous time movement or state-space models could be used for this purpose (Johnson et al., 2008; Alós et al.,

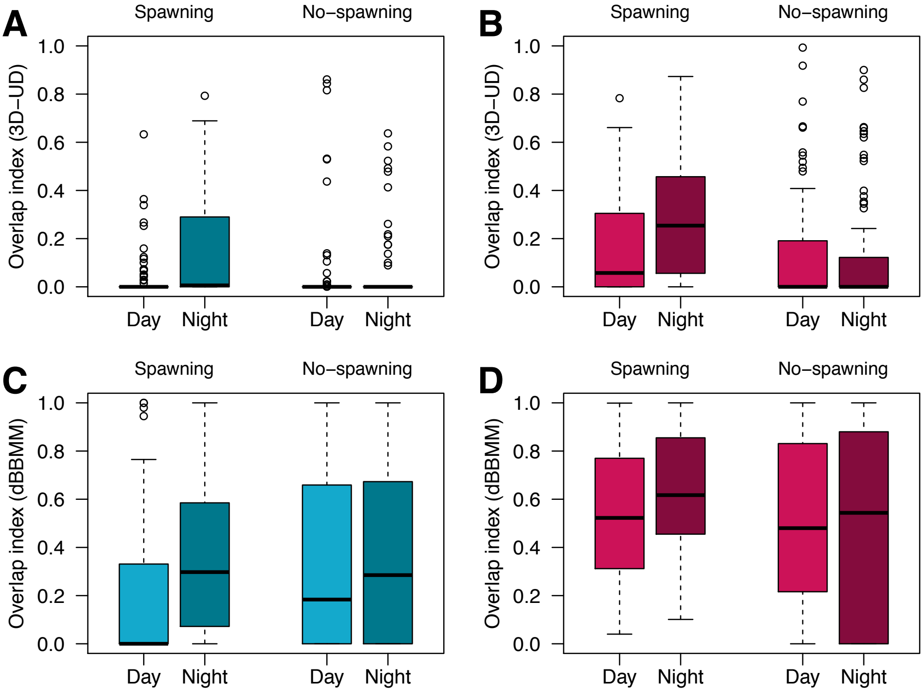

Figure 5.8: Overlap index between volumetric (3D-UD, A-B) and bidimensional (dBBMM, C-D) space use estimations of common dentex individuals during a week within and outside the spawning season. Panels (A) and (C) correspond to 50% UD contour levels, and panels (B) and (D) to 95% UD contour levels.

2016), but they should be previously adapted to incorporate topographical information.

5.4 Conclusions

The increasing number of passive acoustic telemetry studies are providing vast amounts of movement data with a great potential to unveil the ecology of many aquatic species, but the development of new analysis methods is necessary to get the most out of all the collected information. Here we present a flexible method to estimate 3D space use probabilities, which might be used with different configurations of acoustic receiver arrays, and could even be extended to other Eulerian-based dataset collections (e.g. camera traps). By incorporating the vertical dimension and the topographical data, this method provides a geographically and temporally explicit view of the space use of animals moving in a 3D environment.

CHAPTER 6

General discussion and conclusions

6.1 General discussion

Movement patterns of coastal fishes

Passive acoustic telemetry, together with new analytical and visualization methods, provide valuable data on the biology of fish species. In previous chapters, we have contributed new insights into the behavior and ecology of two Mediterranean species, the white seabream (*Diplodus sargus*) and the common dentex (*Dentex dentex*), and have discussed the implications for their conservation separately. Now, by considering the two species together, we can move towards a broader framework (Allen and Singh, 2016) that allow us to characterize key features of coastal fish movement ecology that are essential to promote coherent management measures (Figure 6.1).

Movement attributes

The white seabream and the common dentex are two sedentary species that move within a home range, but that present different movement attributes. Both species display diel space use and activity patterns, being more active during the day than during the night. The white seabream was found to be extremely territorial, moving between nearby foraging and resting areas within a relatively small home range (0.49 ± 0.26 km^2) (chapter 2). The common dentex, by contrast, effectively uses larger areas (0.79 ± 0.22 km^2), but with a high intraspecific variability, as some individuals are able to move between relatively distant areas (1-2 km) on a daily basis (chapter 4). Moreover, they also differ in their habitat use: the white seabream prefers infralittoral shallow seabeds (0-15 m), while the common dentex preferentially uses circalittoral rocky bottoms (20-40 m). Different movement attributes are very likely related to the different biology (omnivorous vs. predator) and size (small vs. large) of the two species, and have a direct effect on the design and outcomes of protection measures, as will be discussed below.

Influence of environmental factors

Fluctuations of environmental conditions cause changes in the space use patterns of coastal fish species. Changes in two physical variables, the water turbulence and the temperature, caused different types of responses in the studied species. Shallow infralittoral beds, inhabited by the white seabream, are greatly affected by the swell. It can be hypothesized that light to moderate wave conditions have a positive effect on this species, allowing white seabreams to forage in the surge zone, where food availability increases due to waves breaking and exposing the mediolittoral benthic invertebrates, which are a fundamental component of their diet (e.g. mussels and other bivalves, sea uchins; Sala and Ballesteros, 1997). Excessively strong waves, however, generate extreme turbulent conditions in shallow areas that white seabreams and other species (e.g. the salema, *Sarpa salpa*) avoid by moving to sheltered or deeper areas (chapter 2, Pagès et al., 2013). We could not verify the same patterns for the common dentex, as no individuals were tagged during the major storm that occurred in the Catalan coast in 2008 (Mateo and García-Rubies, 2012). However, the common dentex very likely also avoids the effects of an extreme perturbation by moving to deeper circalittoral areas, as no decrease in their populations was observed immediately after such exceptional storm (García-Rubies et al., 2012). On the other hand, the common dentex presented a high sensitivity to abrupt temperature changes during summer, changing their spatial distribution following the oscillations of the depth of thermocline (chapter 3). These changes were only observed in individuals inhabiting relatively deep areas (20-40 m), coinciding with the depth range at which temperature variations are most pronounced.

Besides temperature and turbulence, many other physical factors might also affect fish activity patterns, such as changes in currents, salinity, or water turbidity. Unfavorable conditions temporally displace individuals from their usual home range, but if such fluctuations are sufficiently strong or have a high persistence, they can generate structural damages on habitats (e.g. Garrabou et al., 2009; Sanchez-Vidal et al., 2012) and long-term changes in fish populations and whole communities (Walsh, 1983; Wernberg et al., 2016). Extreme events such as cyclonic storms have been reported to cause redistributions of individuals (Lassig, 1983), and therefore, this is possibly a mechanism contributing to landscape connectivity by favoring fish dispersal. The effects of environmental fluctuations might also have a direct impact on the conservation of species. When individuals move or aggregate in predictable zones, their catchability might increase making them more susceptible to be targeted by fisheries (Stoner, 2004).

Spawning behaviour

Despite several indirect evidences existed before, we provide the first direct observations on the spawning behavior of the white seabream and the common dentex. Both species show a similar behavior, punctually aggregating in deep areas during their corresponding spawning periods (March-April, and May-June, respectively; chapter 2 and chapter 4). Most of the previous evidences of such behaviors for these and other species are based on punctual increases in fisheries captures coinciding with the spawning period. Spawning periods and behaviors of many species, especially in temperate regions, are not always scientifically documented, but known by fishermen who use this knowledge to increase their fishing efficiency, as in the case of the white seabream and the common dentex. The formation of spawning aggregations often increases the catchability of species by increasing their abundance in specific areas (Sadovy de Mitcheson and Colin, 2012). In addition, spawning aggregations might occur in accessible areas allowing the fishermen to use highly effective fishing gears that are usually addressed to other pelagic or demersal species (e.g. purse-seine, bottom trawl). For instance, tons of white seabreams are captured by purse-seine fishing in the Atlantic Spanish coast between February and April. The same fishing art is used in the Mediterranean coast to capture large amounts of gilthead seabreams (*Sparus aurata*) during its spawning season around October. In this case, these massive captures are thought to be the main reason by which gilthead seabream populations have decreased within the Medes Islands MPA (García-Rubies et al., 2013). For the case of the common dentex, a local fisherman working in the surroundings of the Medes Islands MPA reported higher catches during May 2012 (including one of the individuals tagged for our study), using bottom longlines addressed to other demersal species with which he had never caught a common dentex before (Quim Llenes, pers. comm.). Similar patterns were also reported by Marengo et al. (2016), but using fish and spiny lobster nets in Corsica. However, beyond personal and punctual observations, available fisheries data are often deficient in that they do not properly specify the fishing effort, the capture zone, or the used gears, while anecdotal captures do not constitute solid evidence of reproductive behavior and spawning aggregations of many species.

More empirical research is needed in order to detect and characterize spawning aggregation behaviors in temperate regions. It is primordial to know which species produce such aggregations, and to describe their exact timing and triggering mechanisms, the specific areas or habitats where they occur, the number of individuals involved, and the distance travelled from their home ranges (Sadovy de Mitcheson and Colin, 2012). Acoustic telemetry techniques, together with three-dimensional fine-scale estimations of space use (chapter 5), provide a powerful tool to locate these aggregations in space and time, where other more specific methodologies might be applied later (e.g. underwater video surveys, visual censuses, echo-sounders).

Insights for management

By studying the movement ecology of the white seabream and the common dentex, we provide a mechanistic view of the effectiveness of small MPAs to protect and restore coastal fish populations. However, the studied species have different movement attributes (e.g. home range sizes) and therefore different conservation needs (Figure 6.1; Allen and Singh, 2016). These needs are clearly observable in the recovery patterns of both species in the zones with different protection levels within the Medes Islands MPA (i.e. no-take zone, partial reserve zone, and non-protected zone) (Hereu et al., 2016). The total prohibition of fishing activities in the no-take zone has resulted in a large recovery of the populations of all the species that are vulnerable to fishing, including the common dentex and the white seabream (Figure 6.2) (García-Rubies and Zabala, 1990; García-Rubies et al., 2013; Hereu et al., 2016). Nevertheless, both species have responded differently in the partial reserve zone, where traditional fishing and angling are allowed under restrictions. Despite the moderate protection, the common dentex is virtually absent in this zone, with abundances that do not differ from the non-protected zone (Figure 6.2). The white seabream, by contrast, shows some degree of recovery regarding its abundance and biomass within the partial reserve compared to the non-protected zone (Figure 6.2). Interestingly, abundances in the partial reserve are as high as in the no-take zone, but the overall biomass is lower. This points out that the main difference between the no-take zone and the partial reserve is the absence of large white seabream individuals (>40 cm) in the latter.

Reserve size, the continuity of habitats between zones, and the enforcement level are considered the main characteristics that define the effectiveness of a MPA (Edgar et al., 2014). Nevertheless, it is also crucial to consider how the movement patterns of different species condition the restoration of fish populations inside a MPA. For instance, a small partially protected zone might be adequate to protect highly territorial species such as the white seabream, but the size-structure of its population will be modulated by the allowed moderate fishing activity that selectively removes large individuals. On the contrary, the same zone and fishing intensity might be inadequate for more mobile predator species whose home range covers larger areas (Figure 6.1). In addition, the home range size might be favored by habitat continuities between protected and no-protected zones, especially for the more mobile species. In this context, protected areas must be de-

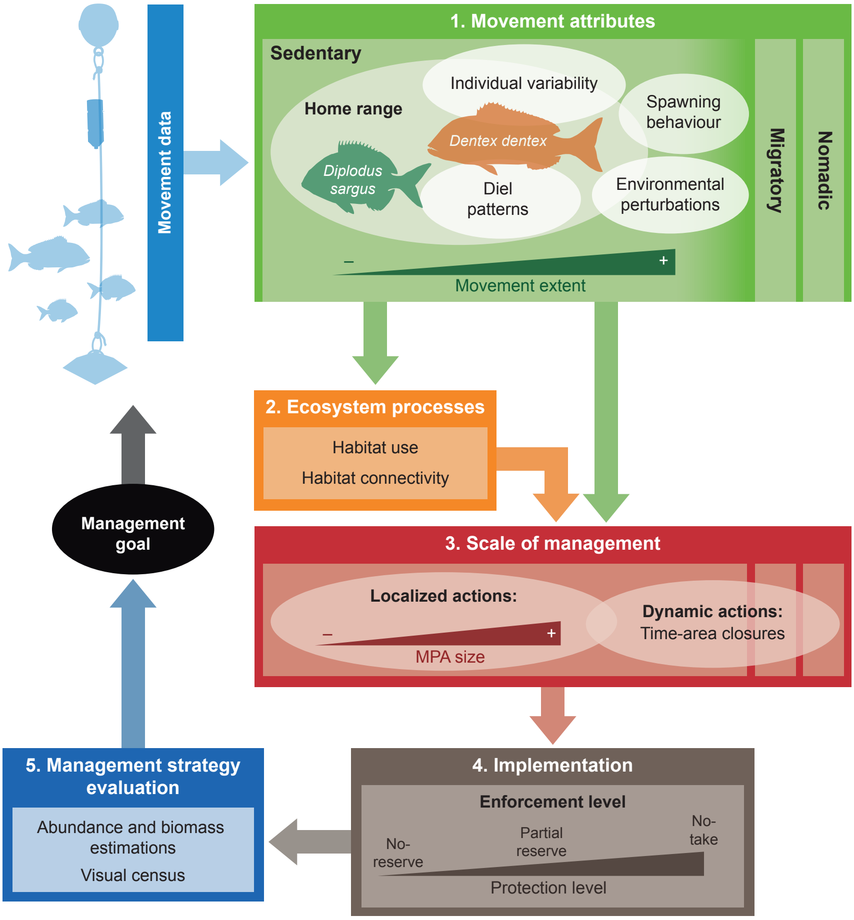

Figure 6.1: The movement-management framework introduced in chapter 1 (Figure 1.1) adapted to incorporate the main conclusions of the thesis. Coastal fish species, despite being sedentary within a home range, exhibit complex diel movement patterns and a relatively large inter-individual variability. Moreover, movements beyond the home range might happen due to the spawning behavior and the effect of environmental perturbations. These movement attributes define the scale of the required management actions. Localized actions, such as small marine protected areas, can effectively protect populations of coastal species, but subject to the presence of preferred habitats and their connectivity with non-protected areas. Extraordinary movements beyond the home range, by contrast, might require dynamic or flexible management actions such as time-area closures. The movement attributes of targeted species and the scale of management actions greatly determine the enforcement of the protection. More mobile species often require higher protection levels, especially in small MPAs. Finally, the effectiveness of such management strategies might be evaluated studying the response of fish populations by estimating a range of species densities and biomasses. The constant monitoring of population dynamics may also allow to identify new management goals, that in turn may require new goal-oriented acoustic telemetry setups and movement data.

signed to ensure the presence of favorable habitats for each species, but also placing its boundaries coinciding with natural habitat discontinuities, which have proven to be the most efficient managing decisions (Forcada et al., 2008).

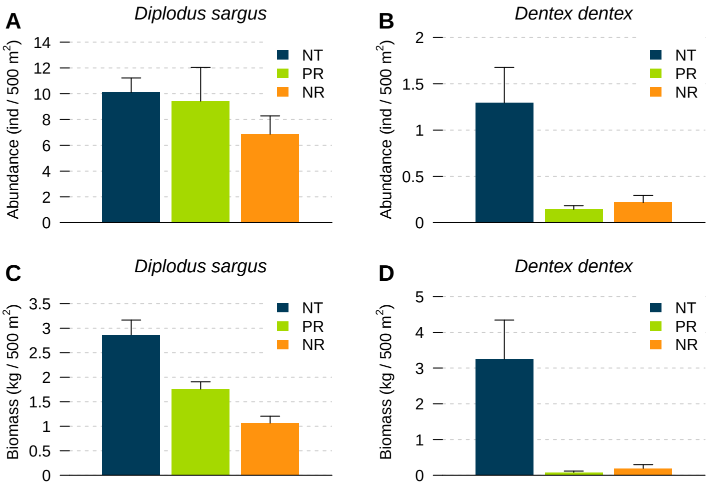

Figure 6.2: Average abundance and biomass of white seabream (A, C) and common dentex (B and D) in zones with different protection levels within the Medes Islands MPA. Data corresponds to underwater visual censuses conducted in August 2016 within the biological monitoring program of the reserve (Hereu et al., 2016). NT: no-take zone; PR: partial reserve zone; NR: non-reserve zone.

A good characterization of environmental and biological extraordinary events of maximum vulnerability, including their causes and spatiotemporal recurrence, is also key information with a great potential to promote a sustainable management of exploited species (Grüss et al., 2013). In particular, spawning behaviors or storm- and temperature-driven relocations, may affect the catchability of many species, as the ones targeted in this thesis, and are also of great concern for conservation (Fulton et al., 1999). The exploitation of spawning aggregations, where reproductive fish are highly vulnerable, not only depletes the stocks, but also reduces the spawning capacity of the species (Sala et al., 2001). Thus, if the areas and times where aggregations occur are identified, and their vulnerability to different fishing gears is assessed, we will be able to design and implement new dynamic management measures, such as time-area closures, which are crucial for the conservation of some species (Figure 6.1).

All the information obtained by studying the movement ecology of the two species, provides substantial insights that might be specifically applied to improve the effectiveness of the Medes Islands MPA. Despite the no-take zone has demonstrated to be highly effective, the partial reserve has not been successful in protecting the most mobile species such as the common dentex. Therefore, the size of this area should be extended to encompass larger areas of favorable habitats for this species (e.g. coralligenous outcrops). Moreover, the conservation of the common dentex and other species would be highly favored by the creation of additional small no-take zones along the mainland coast of the Montgrí Massif, which would also enhance the fisheries yield in partially protected zones through spillover. Finally, extraordinary movements during the spawning season or due to environmental perturbations should also be taken into account, especially if animals move to non-protected areas, and might require special measures such as temporal fishing closures in such zones.

Scaling up towards an ecosystem level movement approach

Animal movement is a complex behavioral response conditioned by physiological, biological, and environmental drivers. The study of the movement patterns of single individuals from a few species and during a limited period of time only provides a small part of our understanding of whole ecosystems. Getting a more comprehensive view of the ecosystem-level functioning, would require to monitor the movements of large number of species simultaneously and to analyze them together within the same environmental and scientific framework. For this purpose, improved space use estimation techniques incorporating three dimensions (chapter 5), together with recently developed analysis techniques, such as the Earth Mover's distance (Kranstauber et al., 2016) and unsupervised machine-learning classification techniques (e.g. t-stochastic neighbor embedding, t-SNE, Berman et al., 2013; Bartumeus et al., 2016), can be potentially used to generate joint behavioral landscapes of all the studied species, where to test the effects of intra- and inter-specific interactions and the influence of environmental factors. This would allow, for example, to identify the bottleneck conditions or perturbation thresholds affecting communities, and in turn, increase our ability to design integrative and efficient management actions.

In order to scale up individual movements to population or ecosystem levels, we need to face the challenge of properly addressing individual-level behavioral complexity. When population-level space use patterns are inferred from individual patterns, it is often assumed that the movements of the tracked individuals are representative of the population, and that the idea of an 'average' individual exists (Gutowsky et al., 2015). However, animals of the same species under the same environmental conditions frequently behave differently depending on their sex, age, social position or internal physiological state. This behavioral variability was visible, for example, in the differences between the space uses of the common dentex individuals studied in chapter 4. This behavioral variability should be quantified and incorporated to obtain better estimates of movement-related process, such as the effect of landscape or environmental features causing specific behaviors (Schick et al., 2008). On the other hand, miniaturized acoustic tags can be used to monitor the movement of individuals during different phases of their life cycle, including the juvenile phase, which is the main phase of dispersal for many species, and therefore essential to understand the structure of the populations and ecological connectivity between zones (Di Franco et al., 2015). Moreover, the wide range of biotelemetry sensors available today also provide the possibility of measuring internal conditions of fishes (e.g. heart rate, locomotor activity, body temperature, tissue biogeochemistry), which have a great potential to help understand the motivations underlying movement (Wilson et al., 2015). The usefulness of biological sensor tags has not been fully leveraged yet; the information that they provide could be used to measure direct reaction of species to anthropogenic activities (e.g. fishing, touristic frequentation), in order to identify the main stressors in space and time (Rose et al., 2015; Wilson et al., 2015).

Recent methodological and technological advances are making it possible to address ecological questions of increasing complexity. By linking the movements of an increasing number of species to physiology, behavioral plasticity, and environmental change, we can potentially obtain a holistic view of the ecosystem functioning, including the mechanistic causes of population changes and the resilience of communities. This information has a great potential to be used in predictive modelling to anticipate the future challenges derived from climate or global change, such as species distribution and community changes. At the very end, an ecosystem-level movement approach will improve the efficiency and the scope of conservation actions, for instance, by guiding the design of interconnected reserve networks covering large extensions.

6.2 Conclusions

General movement patterns of coastal fish species

- The white seabream (*Diplodus sargus*) is an extremely sedentary species with a high site fidelity (0.95 ± 0.06) and a small home range (0.49 ± 0.26 km^2). It preferentially uses infralittoral rocky habitats (0-15 m), and displays repetitive diel movements between closely located foraging and resting areas. However, the white seabream is able to perform extraordinary movements beyond its normal movement range, as a response to environmental factors or for spawning purposes (see below) (CHAPTER 2).
- The common dentex (*Dentex dentex*) is a sedentary species also showing a high site fidelity (0.97 ± 0.06) and a small home range (0.79 ± 0.22 km^2) within the Medes Islands MPA. It displays complex diel and seasonal patterns, often involving diurnal foraging excursions within and outside the protected zone, but with a high variability between individuals. The common dentex preferentially uses circalittoral rocky bottoms and coralligenous outcrops (CHAPTER 4).

Behavioral responses to environmental fluctuations

- The white seabream avoids strong perturbations such as severe storms by moving to sheltered or deeper areas outside its home range. This highlights the role of extreme climatic events as a mobilizing agent for infralittoral fishes, and thus, as a mechanism by which sedentary species might generate spillover or contribute to the connectivity between distant zones. Moreover, the punctual extraordinary movements performed by this species might cause spillover (CHAPTER 2).

- During the summer stratification period, the common dentex adjusted its vertical distribution depending on the temperature changes caused by the oscillations of the thermocline, showing a clear preference for the warm suprathermoclinal layer. We hypothesize that the common dentex is selecting its thermal niche, in order to approach the optimal physiological temperature for its activity rhythms. The confirmation of the thermophilic nature of this species provides a mechanistic understanding to the positive effects of climate change on common dentex populations (CHAPTER 3).

Spawning behavior

- The white seabream displayed a characteristic behavior during the spawning season (March-April), where individuals aggregated in deep rocky bottoms during several pulses over a few days. These movements seem to be related to the increase of water temperature immediately after the winter minimum. During the deep excursions, several individuals travelled along significant distances of up to 1 km from their home range, occasionally crossing reserve boundaries (CHAPTER 2).

- The common dentex also displayed a characteristic behavior during the spawning season (May-June), which also implied aggregating in deep rocky bottoms. During the spawning season, individuals aggregated in specific zones of the MPA and performed synchronous excursions to deep areas between the night and the first hours of the day (CHAPTER 4).

Insights for the management

- The no-take and partial reserve zones of the Medes Islands MPA provide an effective protection for white seabream populations, by effectively covering their movement extents. Due to the small home range of the white seabream, this species has a limited capacity to generate spillover (CHAPTER 2).

- The no-take zone of the Medes Islands MPA provides an effective protection for common dentex populations, by effectively covering most of their movement extent. However, the complex diel and seasonal patterns confer to this species a moderate mobility and the potential to generate spillover in adjacent areas, which might enhance local fisheries. The partial reserve zone of the Medes Islands has proven not to be effective for this species, because of its limited size, the habitat continuity with non-protected zones, and the moderate fishing pressure allowed there (CHAPTER 4).

Development of new methods to obtain better space use estimates

- The Spatial Chronogram Plots here developed are an efficient way to visualize large amounts of acoustic telemetry data from which to infer diel activity patterns (CHAPTER 2 and CHAPTER 4).

- The Brownian bridge movement model (BBMM) and its dynamic extension were used to estimate the space use of white seabream and common dentex individuals. However, space use was overestimated due to the large location uncertainties of acoustic telemetry data. By taking into account the spatial and temporal correlation of movement data and allowing the incorporation of the location error during the computation, these movement-based methods are more adequate and provide more accurate estimates of space use from acoustic telemetry data (CHAPTER 2 and CHAPTER 4).

- By applying the utilization distribution overlapping index between white seabream individuals captured in different locations of the reserve, we provide a new vision on the sedentariness of this species (CHAPTER 2).

- Estimates of the spatial co-occurrence of common dentex individuals where obtained by comparing and classifying the space use estimates of the dynamic BBMM with the Earth Mover's Distance approach. This allowed a better delimitation of the spawning area of this species (CHAPTER 4).

- A new numerical method was developed to estimate space use by integrating the vertical dimension and topographical barriers. The resulting 3D space use estimates where consistent with the utilization distributions provided by the dBBMM, but effectively avoided using unsuitable emerged or unfrequented shallow areas. Incorporating the vertical data provides a more detailed and geographically and temporally explicit view of the space use of aquatic animals and their spatial co-occurrence (CHAPTER 5).

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APPENDIX A

Modelling 3D utilization distributions in R

Modelling 3D utilization distributions in R

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Contents

Introduction

This document is a step-by-step guide to estimate 3D utilization distributions (3D-UDs) from passive acoustic telemetry data in `R`, following the new numerical method proposed in Chapter 5. The main novelty of this method is that it takes into account the detection probability around receivers, which is empirically determined, and integrates the depth information from transmitters and the local topography. The method simulates large numbers of random path realizations that are then assembled to estimate space use probabilities. All the procedure explained here is carried out with an openly available sample dataset.

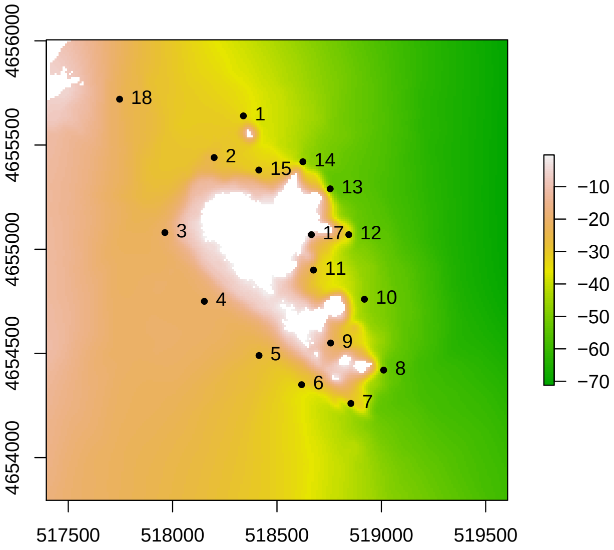
Sample dataset

The sample dataset, together with some own built `R` functions, can be downloaded at the following link:

https://figshare.com/s/a43e3f16c48209c8f7ee

Two directories, `"./R"` and `"./data"`, can be found in the compressed file. The `"./R"` directory contains the own built `R` functions that implement several key steps in the method. The `"./data"` directory contains the following data files:

- **`tracking` (`tracking_data.rda`):** Passive acoustic telemetry data from two common dentex (*Dentex dentex*) individuals ('dentex18' and 'dentex43') in the Medes Islands marine protected area (Catalonia, NW Mediterranean Sea). The tracking period takes place from 01/Oct/2007 to 31/Dec/2007. Movements were tracked with a fixed array of 16 acoustic receivers.
- **`receivers` (`receiver.rda`):** Geographical coordinates of the 16 acoustic receivers used in the acoustic telemetry study (see image below). Coordinates are in UTM, referred to the datum WGS84 zone 31N.
- **`bathymetry` (`bathy_medes.rda`):** Bathymetric raster map (class `RasterLayer`) of the study area (see image below). It has a resolution of 10x10 m and a total extension of 221x221 cells. Land areas are denoted by `NA` values. The coordinates are in UTM, referred to the datum WGS84 zone 31N.
- **`range.test` (`range_test.rda`):** Data from an acoustic range test performed in the study area. The data frame contains the hourly percentages of signals detected by receivers placed at different distances from one acoustic transmitter.



Some additional objects, which are created in some steps during the application of the method, are also provided in the `".\data"` directory. Despite we provide all the code, one may want to skip these steps when following this guide, as they are slow and memory consuming or require external software (like `GRASS`).

- **`viewshed` (`viewshed.rda`):** Raster map representing the pixels outside acoustic shadows and their horizontal distance to receivers. It is a `RasterStack` object with one layer for each receiver, and is generated using `GRASS` during the *Empirical characterization of detection probabilities* (Step 1.2).
- **`depth.cost.matrix` (`depths_cost_matrix.rda`):** A list of `TransitionLayer` objects indicating the cost of moving between adjacent raster cells. There is one `TransitionLayer` for each 1 m depth interval (from 0 to 70 m), which considers suitable only cells at depths equal to or greater than the assigned one, and excludes the cells at shallower depths.This object is generated with the `gdistance` package, and is used during the *Generation of random path realizations* (Step 2.2).
- **`simulations` (`sample_simulations.rda`):** A list containing 100 random path realizations for each of the two common dentex individuals in the sample telemetry data (`tracking` object). This object is created during the *Generation of random path realizations* (Step 2.2).

Finally, a number of `R` packages is also required to apply the method.

```
# Load required packages
library(lubridate)
library(plyr)
library(sp)
library(raster)
library(gdistance)
library(rgeos)
library(ks)
library(rgl)

# Set the working directory to the unzipped directory
setwd("/mydirectory/ud3d_sample/")

# Load the own built functions
functions <- list.files("./R", full.names = TRUE, pattern = ".R")
invisible(lapply(functions, source, .GlobalEnv))

# Load sample dataset
data <- list.files("./data", full.names = TRUE,
                   pattern = ".[R-r]da")
invisible(lapply(data, load, .GlobalEnv))
```

General overview of the method

The process to estimate 3D-UDs is divided in three sequential steps:

1. **Empirical characterization of detection probabilities:** Data from an acoustic range test and the local topography are used to characterize the spatial probability of being detected by each receiver.
2. **Generation of random path realizations:** A large number of random trajectories are simulated from the acoustic telemetry data, taking into account the characterization of the acoustic performance, the depth values, and the local topography.
3. **Assemblage of utilization distribution volumes:** 3D-UDs are estimated from the spatial occurrence of all the generated random path realizations within the 3D grid in which the study site is divided.

Step 1: Empirical characterization of detection probabilities

In this step, we are going to characterize the acoustic performance of the receiver array, by modelling the detection probability depending on the distance to the receiver, and detecting acoustic shadow areas using the viewshed analysis.

1.1. Modelling the acoustic range

Acoustic signals gradually lose their power when travelling through the water due to energy absorption. Therefore, the probability of detecting a signal decreases with increasing distance between transmitters and receivers, until reaching the critical distance, known as the detection range, at which most of the signals are no longer detected. Assessing the average detection range is highly important to design the receiver array and for the correct interpretation of the data. This range is often tested by placing receivers at increasing distances from a transmitter and then calculating the percentage of signals that arrives to each distance.

The `range.test` data frame contains data from one range test performed in the study area. The data frame represents the percentage of signals (`perc`) received during one hour intervals (identified by `hour.id`) by receivers at different distances (`dist`).

```r
head(range.test)
```

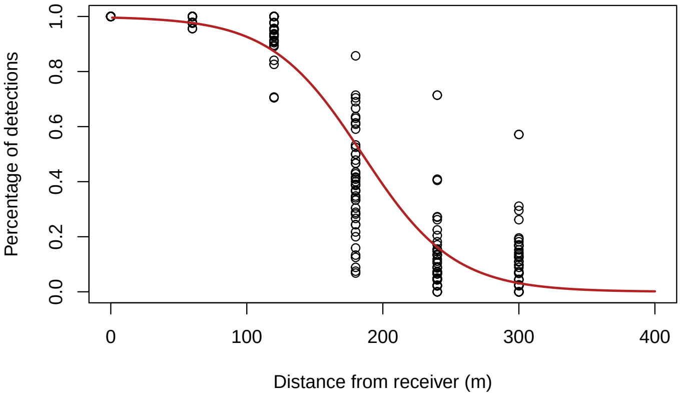
```
##   hour.id dist recep total perc
## 1       1    0    46    46    1
## 2       2    0    46    46    1
## 3       3    0    46    46    1
## 4       4    0    45    45    1
## 5       5    0    41    41    1
## 6       6    0    40    40    1
```

We adjust a logistic regression model to get the probability distribution of being detected as function of the distance.

```
det.range <- glm(perc ~ dist, data = range.test,
                 family = quasibinomial(logit))
```

We can plot the data to see how the function adjusts.

```
plot(perc ~ dist, data = range.test, xlim = c(0, 400),
     ylab = "Percentage of detections",
     xlab = "Distance from receiver (m)")

lines(1:400, predict(det.range, data.frame(dist = 1:400),
                     type = "response"),
      type = "l", col = "firebrick", lwd = 2)
```



1.2. Acoustic shadows

In this step, we are going to characterize the acoustic shadow areas within our study site. Acoustic shadows are due to the presence of prominent physical obstacles in the study area, which impede the signal transmision from the transmitter to the receiver. Here, we will identify the most evident acoustic shadow areas, which are areas hindered by emerged landmasses. This is done by applying the 'viewshed' analysis from the `GRASS` software to the bathymetry raster. This analysis determines the areas of the terrain that are visible from specific locations (in our case, the position of the receivers), which is also applicable to sound propagation in water. As we are interested in only eliminating the most evident acoustic shadow areas, we will exaggerate the height of the land cells and the height at which the receiver is placed when computing the 'viewshed'.

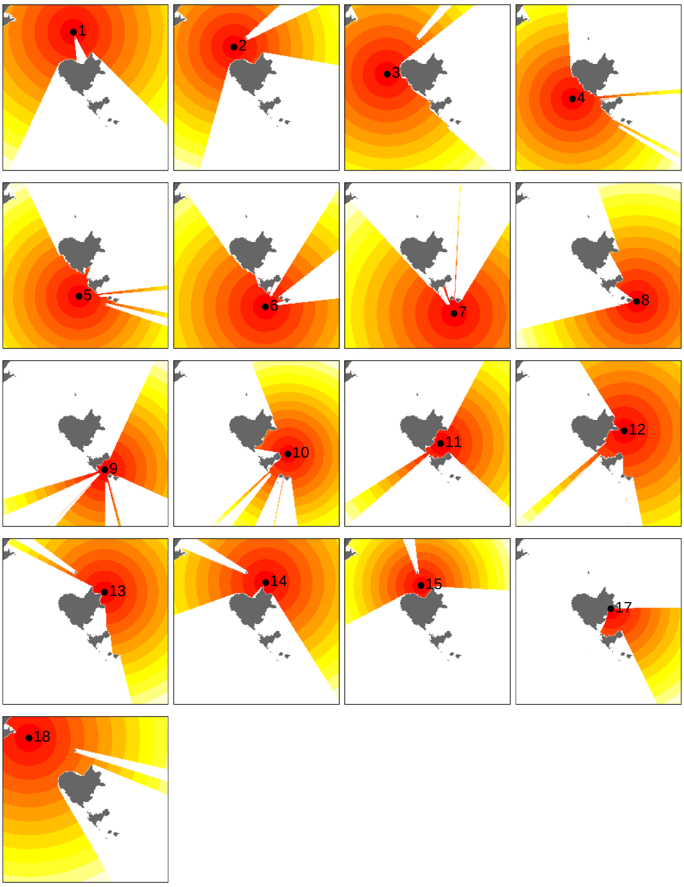
At the same time, we will calculate the lineal distance (in 2D) between each receiver and all the cells outside acoustic shadow areas. This distance will be used, after adding the vertical component (during the simulation of random paths, *Step 2.2*), together with the acoustic range model (*Step 1.1*) to obtain the spatial detection probabilities around each receiver and to sample pairs of coordinates around in the *Sampling and reconstruction of random path realizations* (Step 2.2).

NOTE: As using `GRASS` through `R` is not very straightforward, we recommend not running this part of the code if you are just following the guide with the example dataset. Instead, the result of this code is provided in the `viewshed` object, so it can be directly used in subsequent steps.

```
library(rgrass7)

# In the bathymetry raster, NA values correspond to emerged areas.
# We will exaggerate the height of these areas to make sure
# everything behind them is removed in the viewshed analysis
elevation <- bathymetry
elevation[is.na(elevation)] <- 1e+10
elevation <- as(elevation, "SpatialPixelsDataFrame")

# Initialize GRASS session
initGRASS("/Applications/GRASS-7.0.app/Contents/MacOS/",
          home = tempdir(), override = TRUE)

# Load the elevation raster in GRASS
writeRAST(x = elevation, vname = "elevation", overwrite = TRUE)

# Set the region for the analysis
execGRASS("g.region", parameters = list(raster = "elevation"))

# Loop for each receiver
viewshed <- lapply(receivers$id, function(i) {

  # Coordinates of the receivers
  coord <- as.numeric(receivers[receivers$id == i, 2:3])

  # Execute the 'viewshed' analysis
  #==================================
  execGRASS("r.viewshed", flags = c("overwrite", "b", "quiet"),
            parameters = list(input = "elevation",
                              output = "viewshed",
                              coordinates = coord,
                              target_elevation = 500))

  # Export raster from GRASS and assign NA values and a projection
  rast.tmp <- raster(readRAST("viewshed"))
  proj4string(rast.tmp) <- proj4string(elevation)
  rast.tmp[rast.tmp == 0 | is.na(bathymetry)] <- NA
```

```
  # Calculate lineal distances from receivers to each raster cell
  #================================================================
  distances <- sqrt((coordinates(rast.tmp)[, 1] - coord[1])^2 +
                      (coordinates(rast.tmp)[, 2] - coord[2])^2)
  rast.tmp[!is.na(rast.tmp)] <- distances[!is.na(values(rast.tmp))]

  return(rast.tmp)

})

names(viewshed) <- validNames(receivers$id)
viewshed <- stack(viewshed)
```

This is how it looks like for each receiver. The yellowish the colour, the greater the distance from the receiver. White parts of the plots represent acoustic shadows caused by emerged landmasses (in grey):



Step 2: Generation of random path realizations

2.1 Thin telemetry data

The provided object `tracking` contains acoustic telemetry data from two common dentex (*Dentex dentex*) individuals in the Medes Islands marine protected area. The object is a data frame where each row corresponds to one detection. The `receiver` column indicates the identifier of the receiver that detected the signal, and the `code` column the identifier of the detected fish (in this case, *dentex18* and *dentex43*). `date.time` and `depth` columns indicate the date and time (in UTC) and the depth, respectively, at which the detection occurred. In total, the data frame contains 61,528 detections that took place between October 1 and December 31 2007. In this case, transmitters were originally programmed to emit signals at random intervals between 80 and 180 seconds (to reduce the probability of collision between signals).

```
head(tracking)
```

```
##       code           date.time receiver depth
## 1 dentex18 2007-10-01 00:03:03        9  10.6
## 2 dentex18 2007-10-01 00:04:42        9  10.6
## 3 dentex18 2007-10-01 00:06:36        9  11.4
## 4 dentex18 2007-10-01 00:09:02        9  11.0
## 5 dentex18 2007-10-01 00:12:57        9  11.0
## 6 dentex18 2007-10-01 00:15:50       10  11.4
```

```
# We will split the data into a list to make it easier to apply the
# method to both individuals at the same time
tracking <- split(tracking, tracking$code)

# Names of the individuals:
names(tracking)
```

```
## [1] "dentex18" "dentex43"
```

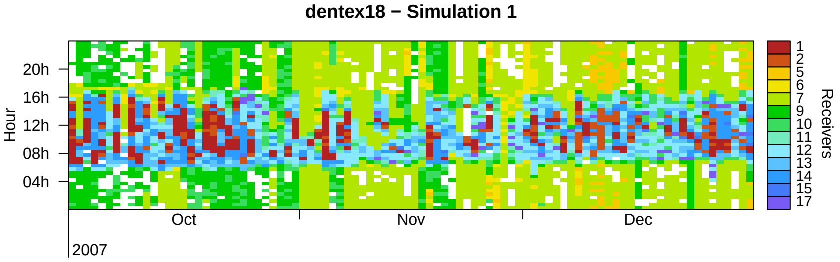
In this first step, we will thin acoustic telemetry data into 30-minute intervals, using our own `thinData` function, which assigns to each time-interval one receiver and a depth value. This allows to reduce the number of data to be processed, and hence the computation time, but maintaining the observed variability. The receiver is randomly sampled among all the receivers that detected the individual during the given time-interval, weighted with the amount of detections in each receiver. The depth value is sampled from a density distribution of all the depth values registered during the same given time-interval.

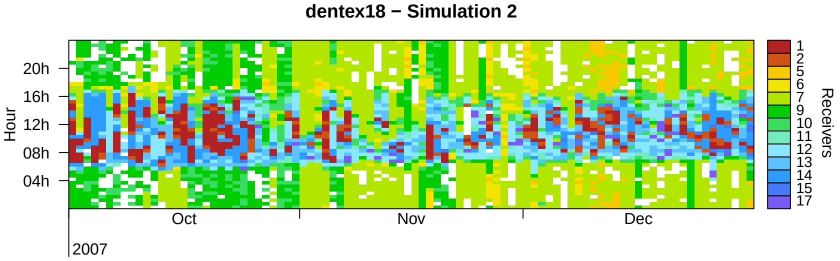
```
t30min <- lapply(tracking, thinData, time.int = "30min")

head(t30min[["dentex18"]])
```

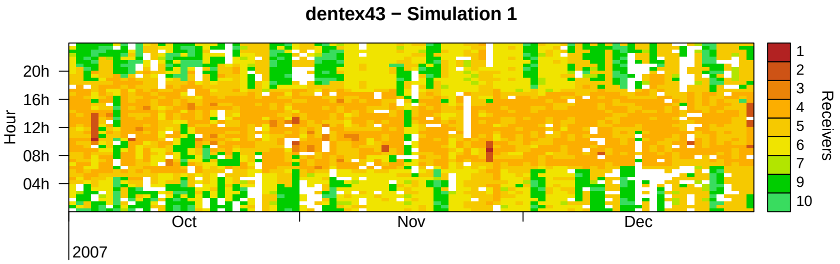
```
##       code           date.time receiver depth
## 1 dentex18 2007-10-01 00:00:00        9  11.1
## 2 dentex18 2007-10-01 00:30:00       10  11.4
## 3 dentex18 2007-10-01 01:00:00        9  12.4
## 4 dentex18 2007-10-01 01:30:00        9  11.2
## 5 dentex18 2007-10-01 02:00:00        9  12.7
## 6 dentex18 2007-10-01 02:30:00        9  12.4
```

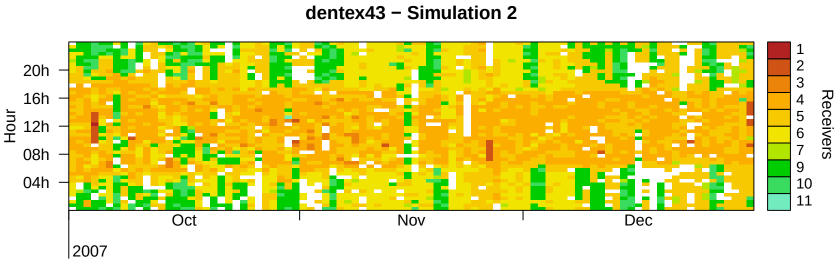
This step adds the variability observed in the original data to the resulting data frame. We can check it comparing two different thinned data frames:

```
# Generate other path realization to compare with the previous
t30min.2 <- lapply(tracking, thinData)

par(mfrow = c(2, 1), mar = c(3.1, 4.1, 3.1, 5.1))

for (i in names(tracking)) {

  t30.tmp <- list(t30min[[i]], t30min.2[[i]])

  for(x in 1:length(t30.tmp)) {

    spatChronoPlot(date.time = t30.tmp[[x]]$date.time,
                   receiver = factor(t30.tmp[[x]]$receiver,
                                     levels = receivers$id))
    title(main = paste(i, "- Simulation", x))
  }
}
```

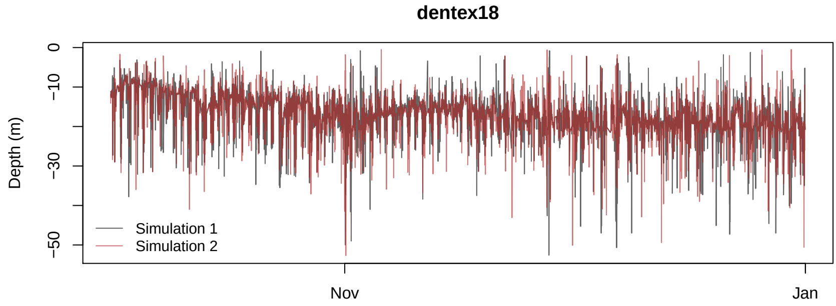


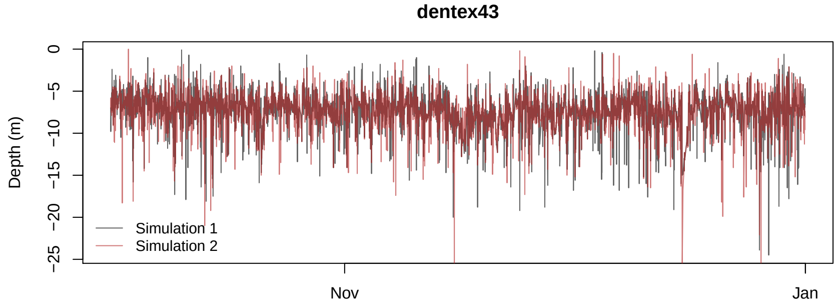






We can also see the comparison between depth values from two thinned data frames.





2.2. Sampling and reconstruction of random path realizations

The `reconstrPath` function samples the geographic coordinates for each receiver and depth value specified in the thinned acoustic telemetry data data (*Step 2.1*), taking into account the following things:

- **Distance from the receiver:** Given a receiver and a depth, calculates the three dimensional distance between the location of the receiver (5 m below the surface) and all the raster cells presenting depths equal or higher to the given one, by adding the depth difference to the horizontal distances already calculated in the `viewshed` object (*Step 1.2*). Then, it applies the acoustic-range logistic model (*Step 1.1*) to get the relative probability of being detected at each cell.
- **Distance from the previous detection:** The `max.vel` argument allows to limit the maximum speed (in m/s) that the fish is assumed to reach during the simulation, in order to avoid unlikely movements between distant locations in short periods of time. Depending on the specified `max.vel` value and the elapsed time from the previous detection, a maximum distance is determined. Then, the shortest distances from the previous location to the rest of raster cells (and avoiding landmasses) is calculated with the `gdistance` package. Finally, the probability of being detected in cells at greater distances than the calculated maximum distance is set to zero. This is especially useful when the fish is situated halfway between two receivers and detections rapidly alternate between them. Setting a maximum velocity avoids extremely rapid movements between the extremes of the acoustic ranges of the receivers and forces the position of the fish to be somewhere in between them.

After sampling two pairs of coordinates, the function finds the shortest path connecting them taking into account the topography. By default, the only restriction to compute the shortest path is not to cross land areas. However, if the `depth.cost` argument is provided, the paths will not cross cells shallower than the minimum depth of the points to join. The `depth.cost` must contain a list with one element for each 1 m depth interval (between 0 and 70 m, the maximum depth at the study area). Each element in that object is a transition matrix, generated with the `gdistance` package, but excluding cells at different depths. The `depth.cost.matrix` object can be created using the `leastCostMap` function as in the following code. As this is quite slow, the `depth.cost.matrix` object is already provided in the sample data set.

```r
# Select depth intervals to compute the matrix
depths <- 0:70

depth.cost.matrix <- lapply(depths, function(x) {
  leastCostMap(bathymetry, min.depth = x)
})

names(depth.cost.matrix) <- 0:70
```

Now we will check how the `recontrPath` function works with the first 50 positions of our thinned tracks:

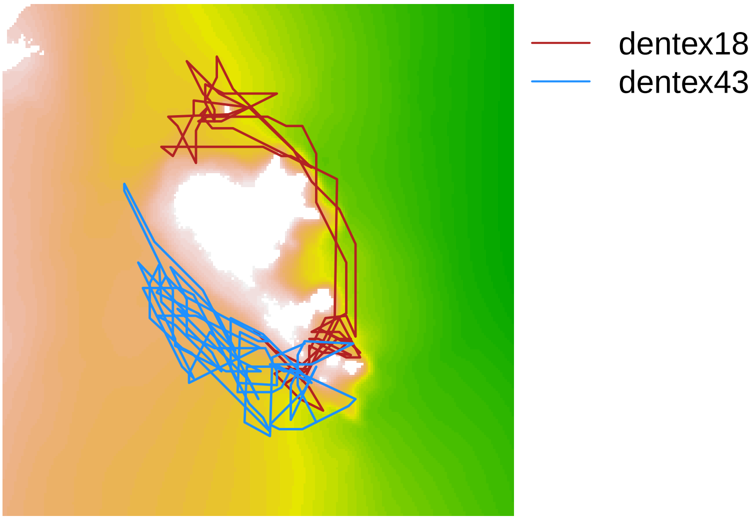
```
reconstr.path <- lapply(t30min, function(df) {

  # Remove receiver NAs and missing depths (if there are NAs).
  # We will run the example with only the first 50 positions
  df <- subset(df, !is.na(receiver) & !is.na(depth))

  path <- reconstrPath(data = df[1:50, ], bathy = bathymetry,
                       dist.shadow = viewshed,
                       det.range = det.range,
                       depth.cost = depth.cost,
                       max.vel = 3, check = TRUE)

})

head(reconstr.path[[1]])
```

```
##   loc receiver           date.time      x       y depth type
## 1   1        9 2007-10-01 00:00:00 518860 4654540  11.0    o
## 2   2        9 2007-10-01 00:30:00 518900 4654560  10.9    o
## 3   0     <NA> 2007-10-01 00:40:45 518850 4654560  10.4    p
## 4   3        9 2007-10-01 01:00:00 518770 4654600   9.6    o
## 5   4        9 2007-10-01 01:30:00 518880 4654540  11.7    o
## 6   0     <NA> 2007-10-01 01:34:47 518850 4654510  11.7    p
```

The resulting data.frame adds the `x` and `y` coordinates to the sampled radiotracking data. Moreover, it adds the additional coordinates that define the least cost paths around the land barriers. The 'original' locations from the sampled data are marked with an 'o' in the `type` column, while the estimated coordinates for the least cost paths are marked with a 'p' (from predicted).

Now we can take a look at the path in two and three dimensions:

```
# Plot in two dimensions
#========================
image(bathymetry, col = terrain.colors(50), asp = 1, ann = FALSE,
      axes = FALSE)
lines(reconstr.path[[1]][, c("x", "y")], col = "firebrick",
      lwd = 1.2)
lines(reconstr.path[[2]][, c("x", "y")], col = "dodgerblue",
      lwd = 1.2)
legend("topright", legend = names(reconstr.path), bty = "n",
       col = c("firebrick", "dodgerblue"), lty = 1)
```



```
# Plot in three dimensions (with the 'rgl' package)
#====================================================

# Create the matrix to plot the bathymetry
x <- unique(coordinates(bathymetry)[, 1])
y <- unique(coordinates(bathymetry)[, 2])
z <- matrix(values(bathymetry), ncol = length(x))
z[is.na(z)] <- 0

# Prepare the color scale for bathymetry
zlim <- range(z, na.rm = TRUE)
zlen <- round(zlim[2] - zlim[1] + 1)
col <- c(terrain.colors(zlen)[z - zlim[1] + 1])

# Set the display matrix (manually obtained to get the desired view)
mat <- matrix(c(0.48, 0.88, -0.06, 0.00, -0.30, 0.23, 0.93, 0.00,
                0.83, -0.42, 0.37, 0.00, 0.00, 0.00, 0.00, 1.00),
              nrow = 4, byrow = TRUE)

open3d(scale = c(1, 1, 10), windowRect = c(0, 0, 1200, 700))
rgl.viewpoint(userMatrix = mat, zoom = 0.65, fov = 30)
rgl.pop("lights")
light3d(specular="black")
surface3d(x, y, z, col = col)
lines3d(x = reconstr.path[[1]]$x, reconstr.path[[1]]$y,
        -reconstr.path[[1]]$depth, lwd = 2, col = "firebrick")
lines3d(x = reconstr.path[[2]]$x, reconstr.path[[2]]$y,
        -reconstr.path[[2]]$depth, lwd = 2, col = "dodgerblue")
rgl.snapshot("./fig/3d_traj.png", fmt = "png", top = TRUE)
```

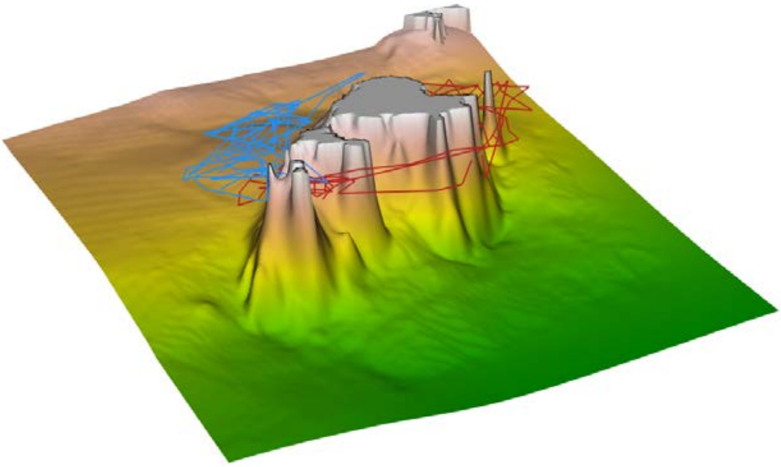


Figure 1: 3D path realizations

Arrived to this point, we are interested in generating a large number of simulations of our original track. We do this applying the `thinData` (*Step 2.1*) and the `reconstrPath` (*Step 2.2*) functions sequentially as many times as simulations we want. We can perform this process in parallel using the `llply` function from the `plyr` package.

NOTE: This process takes a lot of time, so I do not recommend to run this part of the code. The resulting list object is provided in the `simulations` object that can be used directly.

```
library(doMC)
doMC::registerDoMC(cores = 18) # Set number of cores to parallelize

simulations <- lapply(tracking, function(df) {

  id <- df$code[1]

  sim.ind <- llply(1:100, .parallel = TRUE, function(x) {

    # Print individual and current simulation number
    cat(id, "simulation no.", x, "\n")

    t30min <- thinData(df, depth.range = c(0, 69))
    t30min <- subset(t30min, !is.na(receiver) & !is.na(depth))

    reconstr.path <- reconstrPath(data = t30min, bathy = bathymetry,
```

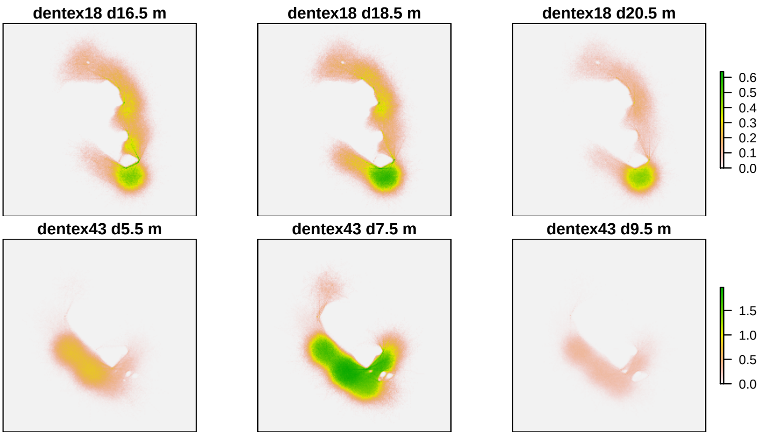
```
                                  dist.shadow = viewshed,
                                  det.range = det.range,
                                  depth.cost = depth.cost,
                                  max.vel = 1)
    return(reconstr.path)
  })
})
```

Step 3. Assemblage of utilization distribution volumes

In this step, we are going to calculate the average number of times that simulated trajectories cross each voxel in the study area, using the `voxelize` function. Voxels are defined with the same x and y resolution as the bathymetry raster (10 x 10 m), and a z resolution of 1 m. The `voxelize` function first interpolates each path in points every 2 minutes, in order to ensure that there are points that fall in all the voxels crossed by the different segments. Then, it evaluates the proportion of segments of a simulated trajectory that cross each voxel. Finally, it calculates the average values for all the simulations. The resulting object is a `RasterStack`, with each layer representing the average proportion of simulated paths crossing the voxels at a given depth range.

```
rast3d <- lapply(simulations, voxelize, depths = 0: 69,
                raster = bathymetry)
```

The next image shows the result for six different depth ranges:



In this last step, we are going to generate smooth UD contours applying a 3D kernel density estimation to the values calculated for each voxel in the previous step. First, we have to convert the 'RasterStack' object into a data frame with the x, y, and z coordinates and the average proportion of paths crossing each voxel.

Then we apply the `kde` function from the `ks` package to get the three-dimensional kernel density distribution. For now, we will let the `kde` function to set the kernel bandwidth values according to its optimization algorithms.

```r
kde <- llply(rast3d, function(r) {

  # Convert the RasterStack into a table
  depths <- as.numeric(substr(names(r), start = 2, stop = 6))

   table <- ldply(1:length(depths), function(d) {
    data.frame(coordinates(r),
               depth = -rep(depths[d], nrow(coordinates(r))),
               cont = values(r)[, d])
  })

  # Kernel Density estimation
  t <- table[which(table$cont > 0), ]
  kde.tmp <- kde(x = t[, 1:3], w = t$cont, compute.cont = FALSE)

  return(kde.tmp)
})
```

Finally, we can compute and plot the 3D-UD contours using the `rgl` package. This example shows the 50% and the 90% UD contours for the two individuals in the example dataset.

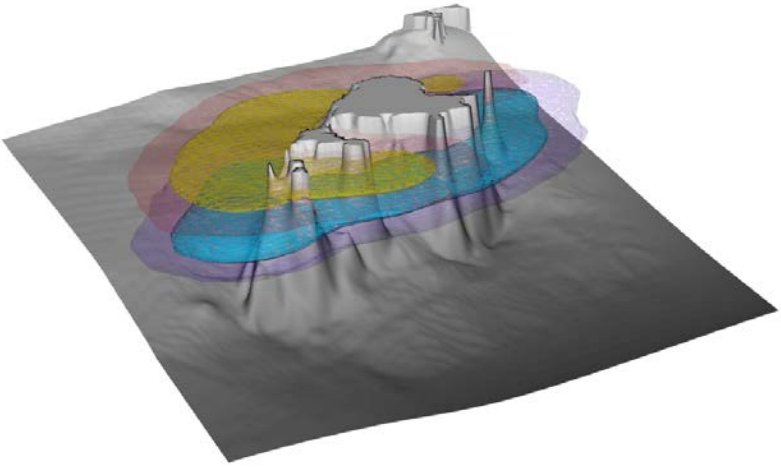


Figure 2: 50% and 90% contours (inner and outer volumes) for the two individuals (different color tonalities)

This last part of code applies the `volumeUD` function to compute the UD volumes from 3D-UD estimations.

```
# Compute UD volumes

ud.vol <- llply(1:length(kde), function(i) {

    rast.tmp <- predictKde(kde[[i]], bathymetry,
                           depths = -(0.5:69.5))
    rast.tmp <- volumeUD(rast.tmp)
    return(rast.tmp)

})

names(ud.vol) <- names(tracking)
```

Plotting and exploring those contours with the `rgl` package is quite slow. It is recomended to calculate the UD volumes from the kde object and to import them to another visualization software such as `Paraview`.

```
# Compute UD volumes

contour.table <- llply(ud.vol, function(r) {

  # Convert the RasterStack into a table
  depths <- as.numeric(substr(names(r), start = 3, stop = 6))

  tmp <- ldply(1:length(depths), function(d) {

    data.frame(coordinates(r),
               z =  -rep(depths[d], nrow(coordinates(r))),
               vol = values(r)[, d])

  })
  return(tmp)
})


# Save the tables to import in paraview
for (i in names(contour.table)) {
  write.csv(contour.table[[i]], row.names = FALSE,
            file = paste0("./data_paraview/", i, ".csv"))
}
```

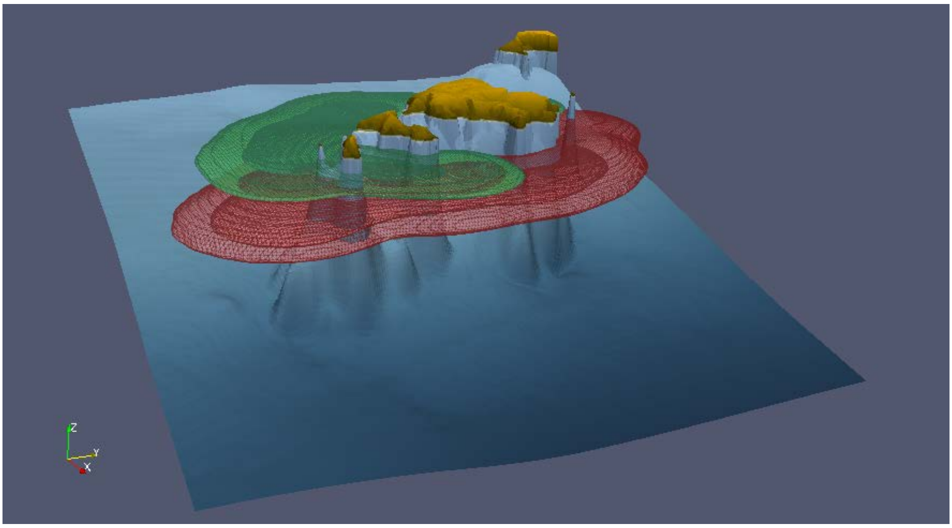


Figure 3: Paraview capture showing the same contours as the previous figure

Overlap between 3D-UD volumes

In this last step, we show how to calculate the overlap index between two UD-3D volumes with the `intersect3d` function. This function takes a list of 3D-UD volumes and calculates, for each pair of elements, the proportion of voxels that they have in common within a certain contour level. If the `symmetric` argument is `FALSE`, the proportion is calculated in relation to the total number of voxels of each UD volume.

```
overlap.50 <- intersect3d(ud.vol, level = 0.5, symmetric = FALSE)
overlap.95 <- intersect3d(ud.vol, level = 0.95, symmetric = FALSE)

# In this case, the volumes are not overlapped at the
# 50% contour level...
overlap.50
```

```
##          dentex18 dentex43
## dentex18        1        0
## dentex43        0        1
```

```
# But they slightly overlap at 95% contour level
overlap.95
```

```
##          dentex18 dentex43
## dentex18     1.00    0.029
## dentex43     0.08    1.000
```

APPENDIX B

Published work

PLOS ONE

RESEARCH ARTICLE

Ordinary and Extraordinary Movement Behaviour of Small Resident Fish within a Mediterranean Marine Protected Area

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Abstract

It is important to account for the movement behaviour of fishes when designing effective marine protected areas (MPAs). Fish movements occur across different spatial and temporal scales and understanding the variety of movements is essential to make correct management decisions. This study describes in detail the movement patterns of an economically and commercially important species, *Diplodus sargus*, within a well-enforced Mediterranean MPA. We monitored horizontal and vertical movements of 41 adult individuals using passive acoustic telemetry for up to one year. We applied novel analysis and visualization techniques to get a comprehensive view of a wide range of movements. *D*. *sargus* individuals were highly territorial, moving within small home ranges (< 1 km^2), inside which they displayed repetitive diel activity patterns. Extraordinary movements beyond the ordinary home range were observed under two specific conditions. First, during stormy events *D*. *sargus* presented a sheltering behaviour, moving to more protected places to avoid the disturbance. Second, during the spawning season they made excursions to deep areas (> 50 m), where they aggregated to spawn. This study advances our understanding about the functioning of an established MPA and provides important insights into the biology and management of a small sedentary species, suggesting the relevance of rare but important fish behaviours.

Introduction

Understanding the movement ecology of fishes is crucial for the management of marine ecosystems. The efficacy of a marine protected area (MPA) to protect and restore overexploited fish populations within its boundaries and to enhance sustainable fishing activities in adjacent areas depends greatly upon the relationship between the size of the MPA and the scale of the

Competing Interests: The authors have declared that no competing interests exist.

movements of targeted fish species [1,2]. However, movements of juvenile and adult fishes can occur over several spatial and temporal scales, providing a challenge when designing effective MPAs [3]. Therefore, having good baseline information on space-use patterns of different fish species is essential for making effective spatial management decisions, such as the design of an MPA or the configuration of a reserve network [4,5].

Home range (HR) is the area in which an individual spends the majority of its time and undertakes most of its routine activities, such as foraging and resting [1,2]. Very sedentary or territorial species have small HRs, and are more likely to benefit from the establishment of spatial protection [6,7] than highly mobile or migratory species that, by expending more time in open areas, become vulnerable to being fished [8,9].

In addition to regular or routine movements, many sedentary species undergo sporadic movements involving larger spatial scales, responding to special needs raised by physical and biological factors. For example, many species undertake migrations to specific breeding areas during the spawning season [10,11]. In coral reefs, these migrations often result in fish spawning aggregations (FSAs) [12], which are highly predictable both in time and in space, and therefore render those species particularly susceptible to being overfished [13,14]. While about 200 tropical fish species are known to form FSAs [12], very little is known about spawning behaviours of fish species in temperate seas. For instance, in the Mediterranean Sea there is only one species, the dusky groper (*Epinephelus marginatus*), which has been confirmed to form FSAs [15,16].

An understanding of the variety of fish movement patterns, from HR-level ordinary movements to sporadic (or extraordinary) migrations, is needed to correctly assess the effectiveness of MPAs. Acoustic telemetry techniques have proven to be powerful tools to serve this purpose, allowing long-term monitoring of fish movements over a wide range of spatial scales [17]. During the last two decades, these techniques have been successfully applied around the world to study the movements of a broad variety of marine species [17,18].

Here, we focus on the white seabream *Diplodus sargus* (L., 1758), using acoustic telemetry to study the movements of a common necto-benthic species within different protection levels of a Mediterranean MPA. *D. sargus* is one of the most abundant species of the infralittoral zone in the Mediterranean Sea, with a high ecological relevance as a grazer and prey species that helps shape rocky marine ecosystems [19–21]. It is also of great importance in artisanal and recreational fisheries [22,23]. *D. sargus* is a well-studied species, and many aspects of its biology have been widely described [24–26]. Several telemetry studies have been published that describe the movements of *D. sargus* in different environments, such as coastal lagoons [27] and artificial reefs [28–31]. More recently, three studies focused on the movements of this species in relation to MPAs [32–34]. All these studies describe the high sedentariness of *D. sargus*, reporting small HRs and high site fidelity. Some of the studies also describe daily movement cycles for this species [28–31,34], but little is known about how daily movement behaviour is affected during extreme environmental conditions or in the spawning period, the latter known to occur from March to June.

In this study we performed one of the longest telemetry experiments conducted to date with *D. sargus* in natural environments. Our high resolution and fine scale spatial data provide a comprehensive and up-to-date view of the movement ecology of this species, one that describes diel movement patterns and movement behaviour during severe climatic events and spawning periods. Information gathered from the wide spectra of movement scales and ecological conditions studied provide novel insights for the conservation of the species, and more generally, for the management of benthic fishes in Mediterranean MPAs.

Materials and Methods

Study area

The study was carried out in the Medes Islands MPA (Catalonia, NW Mediterranean Sea), which comprises three zones with different protection levels (Fig 1). The fully protected marine reserve or no-take zone (NT) is placed in the small archipelago of the Medes Islands, and was established in 1983. A partially protected buffer zone or partial reserve (PR) encompasses a section of the nearby coast of the Montgrí massif. In this zone, limited traditional artisanal fishing (longline and trammel net gear) and recreational angling are allowed with restrictions. The rest of the coast is not subject to any specific regulation; all type of activities, including spearfishing, are allowed, and hence is considered a no-reserve zone (NR).

The Medes Islands and the Montgrí coast are areas of high ecological value because of the high diversity of marine habitats they encompass [35]. The shallow zones closest to the land contain heterogeneous rocky habitats, which are followed by coralligenous outcrops in deeper zones. In waters deeper than about 50 m, hard bottoms are succeeded by soft sandy bottoms, which form a band of soft sediments about 800 m wide between the rocky habitats of the Medes islands and the Montgrí massif on the coast. Since the establishment of the Medes Islands MPA, several studies have reported higher abundance and biomass of *D. sargus* and other vulnerable species, such as the dusky grouper *Epinephelus marginatus* and the common dentex *Dentex dentex*, inside the NT zone than in the PR and NR zones [36,37].

In this area of the coast, winter storms that arrive from the north and east are frequent [38]. One exceptionally severe easterly storm arrived off the Catalan coast on 26–27 December 2008. The storm produced winds surpassing 85 km/h and waves up to 14.4 m in maximum height. This storm, known as the St. Steve's Day Storm, greatly affected the study area, causing profound impacts on benthic communities at depths of up to 20 m [39].

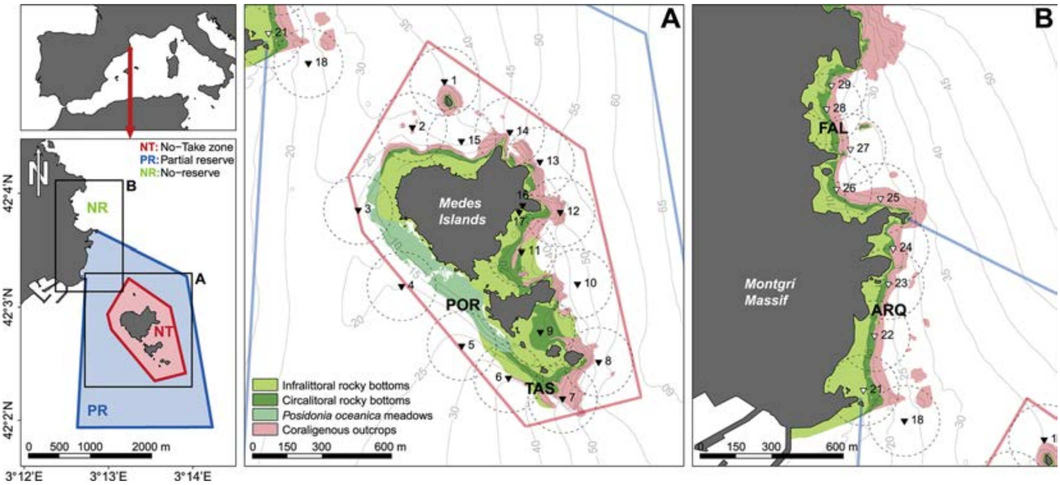

Fig 1. Study area and the acoustic receiver array. Black triangles correspond to acoustic receivers placed in May 2007 and white triangles to the receivers placed in September 2008. Dotted circles represent the average detection range (150 m). Red bold letters stand for the *Diplodus sargus* capture locations: TAS, Tascons; POR, Portitxol; ARQ: Arquets; FAL: Falaguer. The topographic base map (1:5.000) and the sea bottom bionomic map [35] are freely accessible through the Institut Cartogràfic i Geològic de Catalunya (www.icgc.cat) under Creative Commons Attribution License (CC BY 4.0).

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Acoustic monitoring system

A network comprised of 27 moored acoustic receivers (VR2 and VR2W, VEMCO, Nova Scotia, Canada) was installed in the study area (Fig 1). Moorings included anchors, chain, line, and subsurface floats. Receivers were placed 8 m below the surface. The installation of the receivers was performed in two stages. A first set of 17 receivers was placed within the NT zone, covering the entire perimeter of the Medes Islands, in June 2007 (Fig 1A). A second set of 10 receivers was installed in the Montgrí coast in September 2008, 5 of them in the PR zone and 5 in the NR zone (Fig 1B). All moorings and receivers were removed in July 2009, with the exception of #8, which was lost in the beginning of the experiment due to adverse sea conditions and was not replaced. During the extreme storm of 2008, receiver #22 was lost and then replaced by the receiver in position #23 in January 2009.

Signal range-tests were performed in the study site by placing multiple receivers at different distances from a transmitter of the same model used to tag fish. These tests revealed that the probability of detecting a signal was >90% out to a range of 150 m, after which the probability of reception dropped below 50% (S1 Fig). No test-transmitters were used during the study to detect possible changes in the reception efficiency. It has been described that the detection probabilities can be highly variable in coastal waters due to environmental noise caused by wave action, physical impediments and biological activity [40]. We considered this impediment when interpreting our data, and hence we have avoided drawing biological conclusions from temporal patterns in the number of receptions.

Fish tagging

Ethics statement. The tagging protocol was approved by the Committee on the Ethics of Animal Experimentation of the University of Barcelona. The Department of Environment of the Catalan Government granted permissions for fishing, operating and releasing the animals in the Medes Islands Marine Reserve. All surgery was performed under 2-phenoxyethanol anaesthesia, and all efforts were made to minimize suffering.

Individuals of *D. sargus* where caught and tagged with V13P-1H acoustic tags (dimensions: 48 x 13 mm, power output: 153 dB, weight in water: 6.5 g; VEMCO, Nova Scotia, Canada), programmed to produce signals at random delay times between 80 and 180 s. A traditional angling technique was used to catch the individuals from the shoreline, and barbless hooks were used to minimize injuries. Fish were anesthetized by dipping them in a 0.2 $ml \cdot l^{-1}$ 2-phenoxyethanol solution. Tags were surgically introduced in the peritoneal cavity through an incision of 2 cm in the ventral area, which was then closed with sterile surgical staples. Before being released, fish were placed in recovery tanks filled with clean seawater until a full recovery of their normal activity was observed (usually between 10–20 min). The tagging procedure was conducted under aseptic conditions, and all efforts were made to minimize animal stress and suffering. The tagging methodology used is a standard procedure that has been used on *D. sargus* and other species in previous studies [28,41,42]. The procedure has been demonstrated to have no long-term, adverse effects on fish behaviour and survival [43].

A total of 41 individuals of *D. sargus* between 25 and 35 cm length were successfully tagged and released in four different locations (Fig 1). Two groups of 11 and 9 individuals, respectively, were caught in May 2007 in two locations separated by about 300 m within the NT zone (TAS and POR). In September and October 2008, two additional groups of 14 and 7 individuals were tagged in the ARQ (PR zone) and FAL (NR zone) locations. In order to assess the homing ability of this species, seven of the individuals captured in the ARQ location within the PR zone in the Montgrí coast were released in the TAS location within the Medes islands NT zone. The rest of the animals were released in the same location as they were captured.

Data analysis

Data from the VR2 receivers were regularly downloaded to VUE software (VEMCO, Nova Scotia, Canada) and directly imported to R (v.3.2.1) [44], where all the pre-processing and data analyses were performed. Sole receptions in a single receiver within a 24 h time interval were considered spurious and were therefore deleted.

Residence index. A residence index (RI) was calculated for each fish by dividing the total number of days the fish was detected (DD) by the number of days in the entire tracking period (TP) [45]. The time interval during which receiver #22 was missing (see above) was not used to calculate the RI of the fish from the ARQ location.

Home range size. The Brownian Bridge Movement Model (BBMM) [46] was used to compute the utilization distribution (UD), i.e. the probability distribution defining the animal's use of space [47], of each fish for the whole tracking period. The BBMM has advantages over the classical kernel UD estimator. While the kernel UD estimator only takes into account the spatial distribution of the locations, the BBMM also considers their time dependence, assuming a conditional random walk movement model between pairs of locations. Furthermore, the BBMM incorporates the location error in an implicit way during the calculation. Those two advantages make the BBMM especially suitable to analyse data from passive acoustic telemetry, where the position of the reception is fixed and the location error is as large as the signal detection range. BBMMs have been already applied to acoustic telemetry experiments [42,48]. BBMM were applied using the BBMM package (v.3.0) for R [49].

HR and core area sizes were calculated as the minimum areas encompassing the 95% and 50% of the UD estimate volumes, respectively. We measured the space use sharing between each pair of *D. sargus* individuals using the Utilization Distribution Overlapping Index (UDOI) suggested by Fieberg & Kochanny [50]. The UDOI, being a function of the UD and its uniformity, equals zero when two UDs do not overlap, equals 1 when the UDs are completely overlapped and are uniformly distributed, and >1 when two UDs which are not uniformly distributed show a high degree of overlap [50]. HR and core area sizes and the UDOI were calculated with the adehabitatHR package (v.0.4.14) for R [51].

Diel patterns. In order to study the circadian behaviour of *D. sargus*, receptions were classified into day and night time periods as defined by local sunset and sunrise time from the US Naval Observatory (http://aa.usno.navy.mil/data/index.php, data accessed in 2013/09/12 for the coordinates of the Medes Islands 42°03'N 3°13'E). The presence of diel patterns was assessed for each individual following two different approaches. First, we created spatial chronogram plots, which were visually inspected. Spatial chronogram plots represent the receivers with the largest number of receptions in 30 min intervals in each day of the tracking period, and are an effective way to visualize, on a fine temporal scale, presences and absences of an individual among different zones of the receiver array. In a second approach, diel changes in the position of the fish were inferred from the mean depth and hourly reception number data (i.e. total number of receptions received during a single phase divided by its duration). We defined a phase-transition value (PT) for each day to night transition (D-N) as follows:

$$PT_{D-N} = D_t - N_t$$

where D_t is the corresponding value of a given variable for a day phase and N_t is the value of the same variable for the consecutive night phase. The distribution of the $PT_{D\text{-}N}$ values gives us a comprehensive view of the repeatability and cyclical nature of the diel movements. For example, significantly negative $PT_{D\text{-}N}$ values calculated with the mean depth indicate repeated movements to deeper waters at the nightfall, significantly positive values indicate movements to shallower waters, and values that do not differ from 0 indicate that there is no a consistent pattern in the change of the fish depth. $PT_{D\text{-}N}$ values for the hourly reception number provides information about diel movements between zones that differ in their acoustic performance. In order to ensure the cyclical nature of these movements, we also analysed the distribution of the PT values computed for pairs of consecutive day phases (D-D):

$$PT_{D-D} = D_t - D_{t+1}$$

where D_{t+1} is the value of the variable in the next consecutive day-phase.

Extraordinary movements. Sporadic extraordinary movements where inferred from the daily percentages of fish that were detected at given depths and distances from the edge of the HR (95% boundary). We generated depth classes using 1 m depth-intervals and distance-to-HR classes in categories of 200 m. Then, we computed on a daily basis the percentage of fish that were observed in each depth and distance-to-HR class. These percentages were then used to separate the daily observations into two categories: ordinary days, that is, days with ordinary movement behaviour, and extraordinary days, that is, days with extraordinary movement behaviour representing clear statistical outliers of the spatial and temporal metrics used. The two categories were grounded on a hierarchical clustering analysis and visualized with a metric multidimensional scaling, based on Bray-Curtis dissimilarities, and performed with the vegan package (v.2.3–2) for R [52]. Finally, the occurrence of extraordinary movements was visually compared to *in situ* seawater temperature data (hourly measures for the Medes Islands, provided by the T-MedNet network, http://www.t-mednet.org/) and local wave height data (daily measures gently provided by J. Pascual, http://meteolestartit.cat).

Results

Summary of receptions

A total amount of 816,520 valid receptions were recorded by the receiver array during the whole monitoring period (Table 1). Long tracking periods were registered for almost all individuals, 329 ± 65 d (mean ± SD) for fish caught in the NT zone (TAS and POR locations) and 219 ± 88 d for those caught in the PR and NT zones (ARQ and FAL locations) (Fig 2). Three fish (#21, #51 and #98) disappeared within the first 15 monitoring days and were not detected again throughout the experiment, so they were not considered in the following analysis. Two fish (#55 and #76) did not return to their HR after the extreme storm of 2008.

None of the seven translocated fish remained in the released location. Two individuals (#94 and #96) returned to their original location after time intervals of 12 h and 6 d, respectively, and remained there until the end of the experiment (Fig 2). Three individuals (#53, #59 and #97) were detected for 7 d in the NT zone, but then departed from the area covered by the receptors and were never detected again in either the PR nor NR zones (Fig 2). The two remaining translocated fish (#52 and #95) were considered dead, as they were detected in the NT zone over long periods (31 and 257 d, respectively) by a single receiver and at a constant depth.

Site fidelity and home range sizes

All fish were full-time residents, presenting high RI values within their zones (Mean ± SD = 0.95 ± 0.06) (Table 1), with no significant differences among fish from different locations (Kruskal-Wallis test, $p > 0.05$). No relationship was detected between RI and fish size or tracking period length (Kruskal-Wallis test, $p > 0.05$). Fish were detected within narrow bathymetric ranges; the 95% of all receptions were registered between 0.4 and 11 m depth (Table 1).

Table 1. Summary of the monitoring information of tagged *Diplodus sargus*. DD: Detection Days; TP: total Tracking Period (d); RI: Residence Index, CA: Core Area; HR: Home Range.

Fish ID	Length (cm)	Capture location	Capture date	Recep. No.	DD	TP	Depth Range (m)	RI NT	RI PR	RI NR	CA 50% (km²)	HR 95% (km²)
13	22	TAS	2007-05-23	21767	353	361	0.7–8.6	0.98	0	0	0.08	0.41
14	32	TAS	2007-05-23	93053	363	364	3.2–12.9	1	0	0	0.16	0.67
16	21	TAS	2007-05-23	9605	193	200	0.2–10.4	0.96	0	0	0.08	0.40
17	29	TAS	2007-05-24	28459	353	363	4.0–13–0	0.97	0	0	0.14	0.61
19	26	TAS	2007-05-24	48800	357	364	0–15.0	0.98	0	0	0.16	0.67
20	33	TAS	2007-05-24	13348	329	356	1.6–17.3	0.92	0	0	0.18	0.76
22	26	TAS	2007-05-24	16582	197	199	0–9.1	0.99	0	0	0.19	0.86
48	23	TAS	2007-05-24	30983	344	364	0.2–10.1	0.95	0	0	0.18	0.74
49	23	TAS	2007-05-24	14388	201	212	0–4.0	0.95	0	0	0.18	0.83
21*	21	TAS	2007-05-24	850	13	13	-	-	-	-	-	-
51*	28	TAS	2007-05-24	1835	13	13	-	-	-	-	-	-
15	29	POR	2007-05-25	56314	363	364	0.4–9.5	1	0	0	0.14	0.81
23	30	POR	2007-05-25	10423	229	239	0–14.2	0.96	0	0	0.08	0.46
24	24	POR	2007-05-25	50621	364	366	0.1–9.3	0.99	0	0	0.10	0.57
25	26	POR	2007-05-25	46071	361	369	0.4–6.6	0.98	0	0	0.24	1.01
26	29	POR	2007-05-25	61909	364	366	0.2–13.6	0.99	0	0	0.11	0.68
28	33	POR	2007-05-25	19962	342	356	0.4–6.4	0.96	0	0	0.11	0.51
29	32	POR	2007-05-29	23692	356	360	0–7.3	0.99	0	0	0.18	0.74
30	26	POR	2007-05-29	32047	356	361	0.3–9.4	0.99	0	0	0.12	0.73
31	29	POR	2007-05-29	22679	343	357	0.7–9.9	0.96	0	0	0.25	1.01
54	29	ARQ	2008-09-25	3772	45	45	0–14.6	0	1	0	0.05	0.22
55	26	ARQ	2008-09-25	2020	47	48	0–5.5	0	0.98	0	0.06	0.27
56	35	ARQ	2008-09-25	9859	211	237	0–5.1	0	0.89	0	0.05	0.24
57	29	ARQ	2008-09-25	12768	230	235	0.4–9.8	0	0.97	0.04	0.05	0.26
58	35	ARQ	2008-09-25	8595	202	235	0.4–15.0	0	0.86	0.02	0.06	0.30
74	29	ARQ	2008-09-25	14961	220	228	0–7.3	0	0.96	0.04	0.06	0.28
99	29	ARQ	2008-10-17	9003	165	213	0–8.2	0	0.76	0.04	0.06	0.32
94T	26	ARQ	2008-10-16	7972	165	216	0.4–11.7	0	0.76	0	0.09	0.35
96T	23	ARQ	2008-10-17	5521	196	215	0.4–9.3	0.03	0.85	0.07	0.06	0.32
52T†	32	ARQ	2008-09-26	10197	31	31	-	-	-	-	-	-
53T*	28	ARQ	2008-09-26	297	7	7	-	-	-	-	-	-
59T*	25	ARQ	2008-09-26	74	2	2	-	-	-	-	-	-
95T†	23	ARQ	2008-10-17	48957	256	280	-	-	-	-	-	-
97T*	26	ARQ	2008-10-17	42	2	2	-	-	-	-	-	-
40	23	FAL	2008-09-24	14054	244	293	0.6–11.4	0	0.00	0.83	0.05	0.20
60	32	FAL	2008-10-21	16194	267	276	0–9.6	0	0.00	0.97	0.04	0.18
61	21	FAL	2008-10-21	9938	211	219	0–8.9	0	0.00	0.96	0.04	0.17
72	21	FAL	2008-09-24	20098	295	303	0.6–10.6	0	0.00	0.97	0.05	0.21
75	24	FAL	2008-09-24	14720	278	301	0.7–14.9	0.01	0.01	0.92	0.06	0.24
76	23	FAL	2008-09-24	4013	93	94	1.3–12.8	0	0.00	0.99	0.04	0.16
98*	35	FAL	2008-09-26	77	3	4	-	-	-	-	-	-

Letter 'T' accounts for translocated fish that were released in TAS. Fish marked with a '' disappeared from the study site, and those marked with a '†' were considered dead.*

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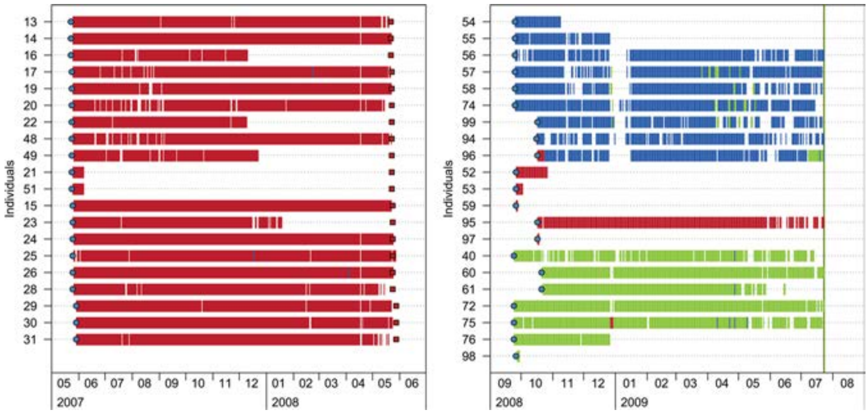

Fig 2. Daily presence-absence plot of tagged *Diplodus sargus* within the monitored area. Colours represent the different protection zones of the MPA; Red: no-take zone (NT), Blue: partial reserve (PR), Green: no-reserve (NR). Fish tag and release dates (blue circles), expected transmitter battery dead dates (red squares) and the final withdrawal of the receiver array (vertical green line) are shown.

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All fish resided in core areas close to their capture location (Fig 3). HR sizes ranged between 0.16 and 1.01 km^2 and core area sizes ranged between 0.04 and 0.25 km^2 (Table 1). HR sizes were significantly smaller in fish from PR and NR zones compared to fish from the NT zone (one-way ANOVA, $p < 0.01$) (Fig 3), presumably due to a difference in the spatial arrangement of the receivers. No effect of fish length or tracking period on the HR size was observed (one-way ANOVA, $p > 0.05$). The UDOI values denoted a very high degree of HR overlap between individuals from the same location (UDOI > 1) (Fig 4). The UDOI was lower (< 0.7) when comparing individuals from the two locations within the NT zone (TAS and POR). There was no HR overlap (UDOI = 0) when comparing individuals that came from different zones of the reserve.

Diel patterns

Visual inspection of spatial chronogram plots revealed clear diel patterns in 70% of tagged individuals (n = 23). These patterns were characterized by different colours either representing changes in the detecting receivers or reception gaps (white areas). An example of a spatial chronogram plot showing a clear daily pattern can be seen in Fig 5. Spatial chronogram plots for the rest of individuals are available as Supporting Information (S2 Fig).

The phase-transition values calculated for the mean depth between day and night phases ($PT_{D\text{-}N}$) revealed diel movements in depth in 70% of tagged individuals (n = 23), for which the median of the values was significantly different from zero (Wilcoxon signed-rank test, $p < 0.01$) (Fig 6A). In contrast, the medians of the phase-transition values between consecutive day phases ($PT_{D\text{-}D}$) did not significantly differ from zero in any fish (Wilcoxon signed-rank test, $p > 0.05$)–with the exception of the slight deviation observed in individual #13 (Wilcoxon signed-rank test, $p < 0.05$)–(Fig 6B), which means that each fish tends to be at a similar depth during day phases and confirms the cyclical nature of these movements. However, this analysis revealed large individual-level heterogeneity on depth daily-pattern behaviours: 30% of individuals (n = 10) were found at deeper areas during the night than during the day, while 39% of individuals (n = 13) showed the inverse pattern. Phase transition values for the hourly

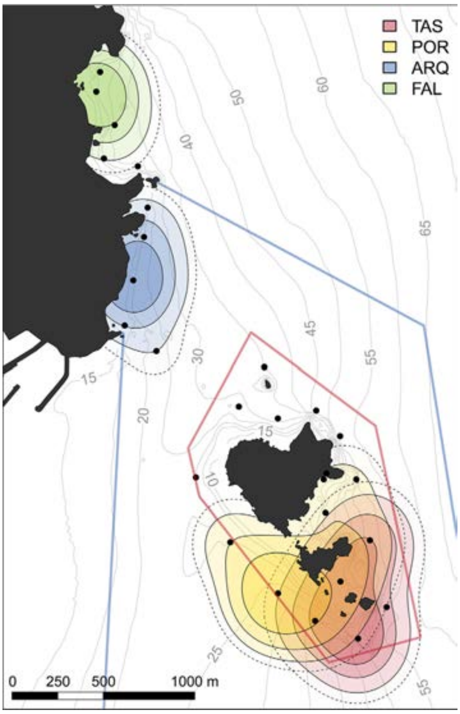

Fig 3. Mean spatial Utilization Distribution estimates of *Diplodus sargus*, for each capture location. The concentric polygons represent, from inside out, the areas covering the 50% (core area), 75%, 90%, and 95% (home range) of the volume of the Utilization Distribution computed by the Brownian Bridge Movement Model. The topographic base map (1:5.000) is freely accessible through the Institut Cartogràfic I Geològic de Catalunya (www.icgc.cat) under Creative Commons Attribution License (CC BY 4.0).

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reception number showed the same heterogeneity (S3 Fig). In this case, 48% of fish (n = 16) had significantly more receptions during the night and 42% individuals (n = 14) had more receptions during the day. Bringing all the results together, 100% of the monitored *D. sargus* individuals showed the signature of diel patterns based on at least one of the different metrics used: zone, depth and reception number.

Extraordinary movements

Based on the daily occurrence of *D. sargus* at different depths and distances from their individual HR (95% boundary), the cluster analysis (see Methods section) was able to distinguish between two consistent day typologies: one for days with ordinary activity (n = 551, 94% of the analysed days) and another for days representing extraordinary behaviours (n = 34, 6% of the analysed days) (Figs 7 and 8). Extraordinary days were characterized mainly by the presence of an elevated percentage of individuals (> 50%) at deeper than normal depths (usually below 20 m), and to a lesser degree, by the presence of individuals (> 30%) at greater distances from the HR boundary. All the days with extraordinary behaviours occurred between November and December and March and April in the two study periods: 2007–2008 (corresponding to fish from the NT zone) and 2008–2009 (fish from the PR and NR zones).

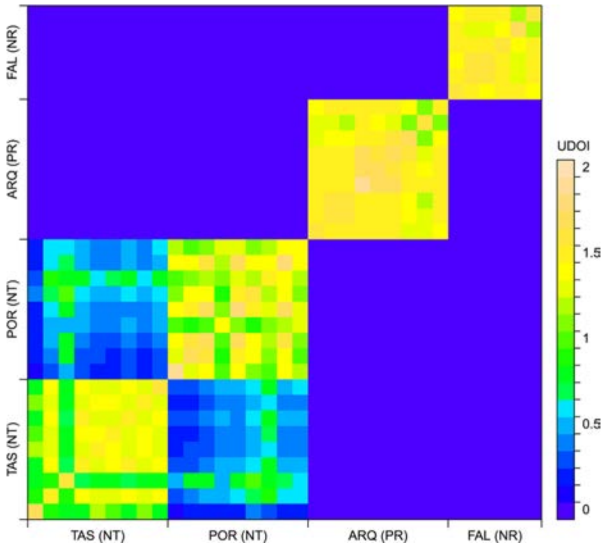

Fig 4. Utilization Distribution Overlap Index (UDOI) calculated for each pair of *Diplodus sargus* individuals. Yellow blocks represent high UDOIs observed when comparing individuals captured in the same location. Green and blue blocks represent lower degrees of overlap and the purple areas represent no-overlapping HRs.

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Days with extraordinary movements happening from November to December coincided with (or were close to) periods with large (and highly variable) swell conditions (Fig 7). In contrast, extraordinary movements detected from March to April, could not be related to storm events but coincided with the spawning season for *D. sargus* [53,54].

Storms caused a few individuals to move large distances from their HRs (but they were not necessarily observed at greater depths). The most extreme movement was performed by a

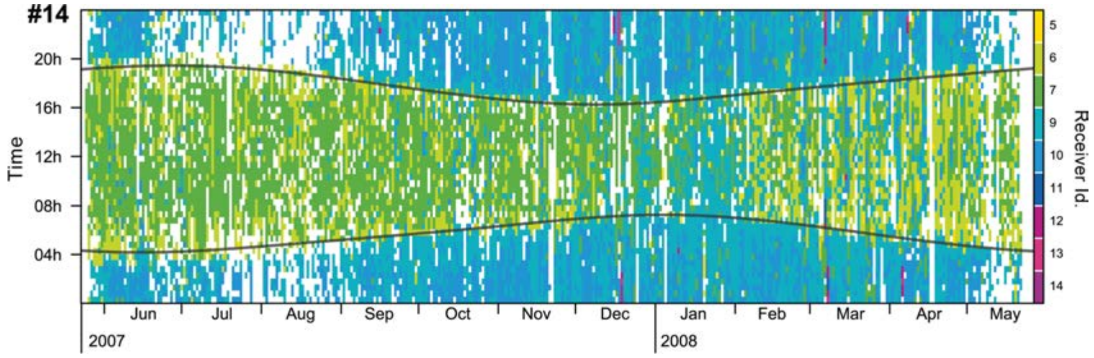

Fig 5. Spatial chronogram plot for one tagged *Diplodus sargus* individual (#14), showing a clear diel movement pattern. This individual was observed at receivers 5, 6 and 7 during the day (green areas) and moved to receivers 9 and 10 during the night. Some punctual excursions to receivers 12, 13 and 14 are visible in December, March and April. White areas represent 30 min intervals with no receptions. See Fig 1 for the placement of the receivers.

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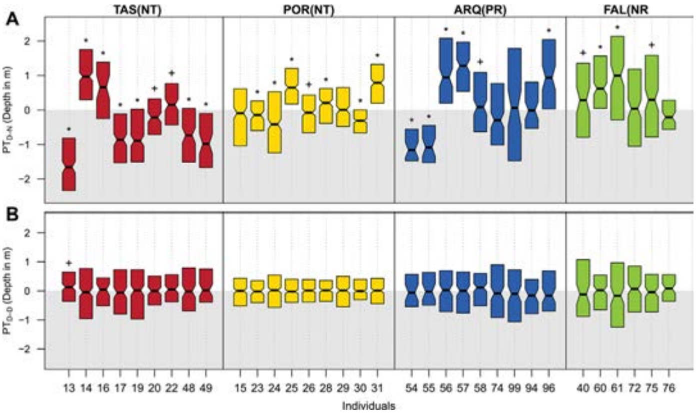

Fig 6. Distribution of phase-transition values (PT) calculated for the mean depth between consecutive day-night (A) and day-day (B) phases, for each *Diplodus sargus* individual. Lower and upper boundaries of the boxes represent the first and third quantiles of value distributions. Significant results of the Wilcoxon signed-rank tests against the null hypothesis of a median of zero are expressed by the symbols above the boxes; +: $p < 0.05$; *: $p < 0.01$.

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single individual (#75) during the extreme storm of 2008, which travelled more than 2 km back and forth from its HR boundary (set in the NR zone), and was detected by several receivers from the NT zone (Fig 7; see the spatial chronogram plot for the individual #75 in S2 Fig).

Extraordinary movements observed during the spawning period involved large numbers of individuals moving to greater depths. During these days, 100% (n = 13) and 46% (n = 6) of the individuals tracked in the NT zone where observed deeper than 20 m and 50 m, respectively. For the same period, in the PR and NR zones vertical movements up to 20 m (not deeper most likely due to the position of the receivers, see Fig 1) were detected in 75% of individuals (n = 9). Likewise, fish were observed swimming large horizontal distances from their HR during the spawning period. In the NT zone, 50% of individuals (n = 7) were seen more than 400 m further from the edge of their HR, mainly traveling to the northern part of the Medes Islands (receivers #1, #2, #13 and #14) (e.g. see spatial chronogram plots for fish #14, #20 and #26 in S2 Fig). In the PR and NR zones, 42% of individuals (n = 5) surpassed the distance of 400 m from their HR, crossing the reserve boundary between the PR and NR zones (e.g. see spatial chronogram plots for fish #57, #74, and #75 in S2 Fig).

Discussion

Estimating sedentariness and HR sizes

Our study confirms the highly residential nature of *D. sargus*, and provides new evidence about the extent of this sedentary behaviour. Our estimate of mean HR (0.49 ± 0.26 km^2) falls within those reported by previous studies (between 0.03 and 4 km^2) [28–31,33]. Nevertheless, our findings suggest that this HR could be even smaller. For example, we found that the capture location of each individual was highly consistent with the placement of the HR; fish caught in the same location shared almost their entire estimated HR (UDOI values > 1), while the overlap among fish from different locations was very low, even if the locations were separated for only 300 m. Moreover, the bathymetric distribution of the tagged fish was restricted to relatively shallow depths, rarely exceeding 15 m. This distribution coincides with descriptions of

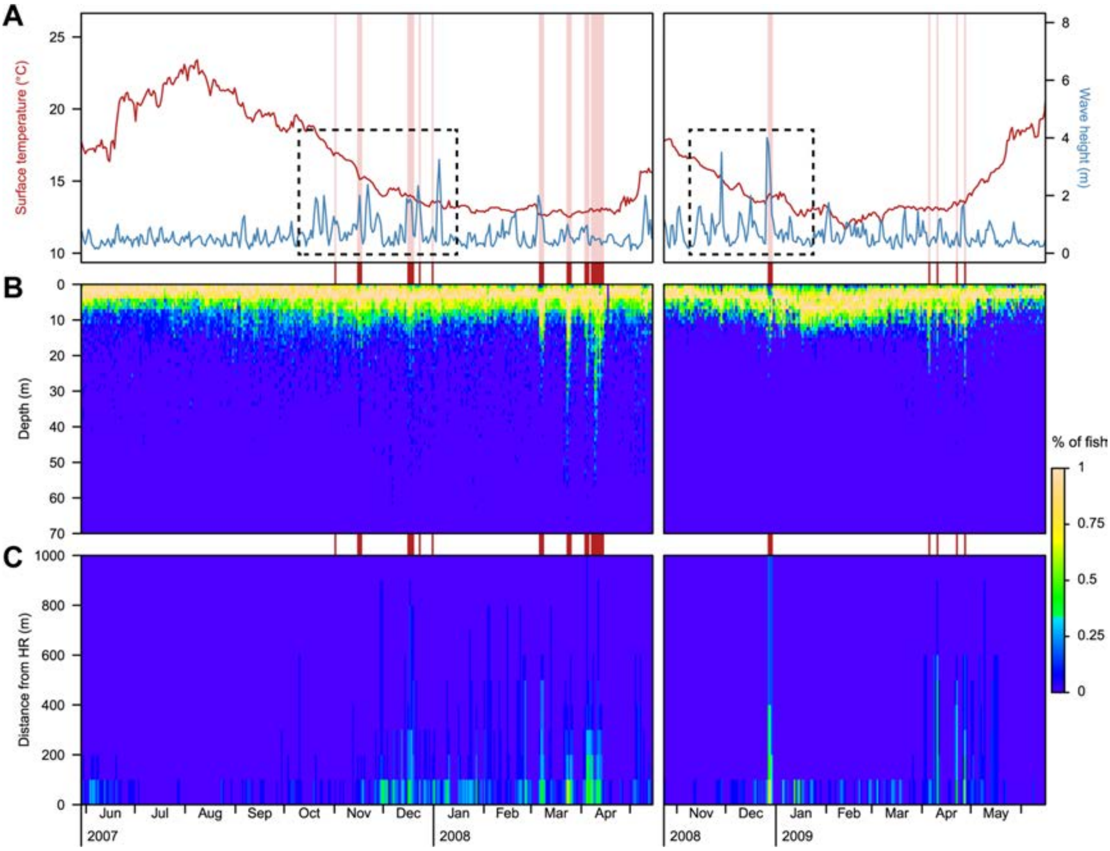

Fig 7. Daily mean sea surface temperature and wave height (A) and percentages of fish observed at different depths (B) and distances from their HR boundary (C). Red lines in the back point out days in which extraordinary activities were detected by the cluster analysis. Dotted black rectangles highlight periods with recurrent high wave conditions.

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the diurnal behaviour of this species provided by Sala & Ballesteros [26], who reported the highest densities of this species near the surge zone, where it feeds on algae and benthic invertebrates.

The narrow bathymetric range and the low degree of HR overlap between individuals that were captured in the two close locations within the NT zone, illustrate the high territoriality of this species, but also point out that the estimated size of the HR is, in all likeliness, overestimated. When contrasting the extension of the estimated HR of each individual, the bathymetry of the study site [35], and the depth distribution of tagged individuals it became evident that a major part of the estimated HR falls in deep areas that are rarely or never frequented by the animals. In fact, in our study only 9–27% of the area of the HR is located in depths above 15 m. Thus, the real HR of this species must be dramatically smaller than the estimated one.

The overestimation of the HR is due to the large positional uncertainty of the passive acoustic telemetry incorporated in the estimation of the UD. This uncertainty depends on the detection radius of the acoustic transmitters and the characteristics of the study site and may range

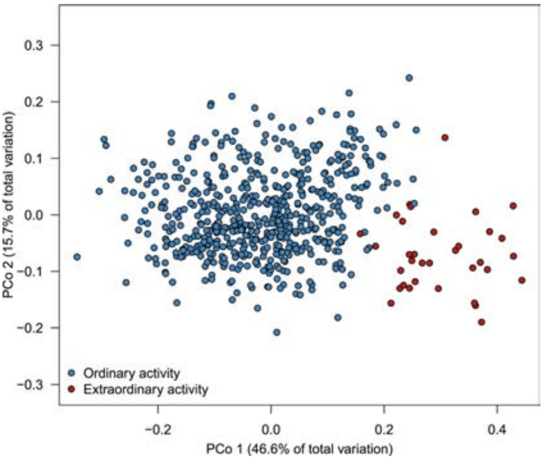

Fig 8. Metric multidimensional scaling analysis depicting similarities between days in fish occurrence at different depths and distances-to-HR. The two main groups of days detected by the cluster analysis (ordinary and extraordinary) are shown in different colours.

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between tens and hundreds meters. When including this positional error as the kernel bandwidth in kernel density functions [55] or as the location error in the BBMM [46], the resulting utilization probabilities might spill to areas that are in fact not frequented by the animals. This HR overestimation is inherent to every acoustic telemetry study that applies error-scaled UD estimation methods, but it may only be apparent in steep study areas, presenting large depth variations within short distances, such as our study site. The development of new modelling techniques that take into account the depth information from the transmitters and the bathymetrical data of the study site would allow the acquisition of more accurate and non-overestimated utilization probabilities of the animals. Moreover, models incorporating benthic topography will better identify habitat selection behaviour and diel fine-scale movements of fishes, with clear implications for the management of the species at small spatial scales within the MPA.

Our data as well as several behavioural descriptions of *D. sargus* [26,56,57] suggest that the small HR of this species is divided in two smaller areas or microhabitats: a feeding area during the day and a resting or sheltering area during the night, with two small migrations between them. The repetitive day-night patterns observed throughout the study period and the variability found between individuals suggest that day and night activity spots remained constant over the long-term and are specific for each individual.

Inferring nocturnal and diurnal activity patterns based on the number of receptions is highly problematic [40]. Local abiotic and biotic factors can drastically reduce the reception performance of acoustic signals [58–60]. Therefore, the specific placement of the day-time foraging and night-time resting territories in acoustically more or less favourable areas will generate different reception patterns, which might not be related to periods with different degrees of biological activity. Therefore, the strong territoriality of *D. sargus* has major implications for the interpretation of temporal patterns from acoustic telemetry data. For this reason, and due to the lack of test signals, we have avoided drawing behavioural conclusions from patterns in the number of receptions, and they are only presented as an additional confirmation of the patterns observed in both the spatial chronogram plots and the mean depth changes between day and night phases.

Our results demonstrate that even relatively small MPAs might be extensive enough to effectively protect *D. sargus* populations. Moreover, due to the high site fidelity of this species, parameters such as density, mean size and biomass of *D. sargus* populations could be used as meaningful indicators of local pressures and ecological status at each study site [61]. Therefore, we can expect that the management activities performed in each zone of the MPA, such as reducing the fishing pressure, will have a significant impact on those indicators. Several studies performed in the Medes Islands marine reserve have reported significantly higher biomasses, densities and mean sizes for *D. sargus* and other fished species in the NT zone, but not in the PR and NR zones [36,37]. Taking into account that the movement behaviour of *D. sargus* does not change among zones, these results suggest that the restriction of fishing activities in the partial reserve has a limited benefit on fish populations and hence, the low efficiency of partially protected zones for the full recovery of fish populations [37,62,63].

Another consequence of the territoriality of the adult individuals of *D. sargus* is a very limited capacity to spillover. During the study period a very low number of cross-boundary movements were detected, mostly between the PR and NR zones, and they were linked to very specific ecological conditions (e.g. storms, spawning). Moreover, most of the individuals that were translocated failed to return from the NT zone to the PR. On continuous rocky habitats, *D. sargus* has shown large homing movements, and individuals traveling up to 600 and 900 m to their original capture zone have been reported [29,32]. Here, we hypothesize that the sand gap between the Medes Islands and the Montgrí massif rocky bottoms may be acting as an impediment to the movements of *D. sargus*. Indeed, habitat discontinuities have been noted to act as partial barriers for several coral reef species [8,64]. However, it is interesting to note that the sandy gap between the Medes islands and the nearby zone is not an obstacle for the movement of other species, such as the herbivorous fish *Sarpa salpa* [42].

Extraordinary movements

Despite being strongly sedentary, *D. sargus* demonstrated the ability to undertake considerable movements to areas outside their ordinary depth-range and HR. Those movements, which were generally quick (lasting less than a day), were generated by specific physical (waves) and biological (spawning) factors. Extreme climatic events, such as severe storms, can act as mobilizing agents for benthic fish. During those extreme events *D. sargus* left its preferred shallow habitat, which was highly exposed to the wave action, and moved to areas where the hydrological conditions were less intense. In a parallel study, Pagès *et al.* [65] described movements of *S. salpa* to deep sheltered areas during the extreme storm of 2008. The same escaping behaviour has been also described for several tropical fish species [66,67]. These movements allow fish populations to endure the disturbances without suffering significant population losses [65]. Moreover, severe storms can relocate the HR of some of the individuals into new zones [66], and may be a mechanism by which sedentary species could generate adult spillover from an MPA to adjacent zones.

Our study also provides fundamental knowledge on the spawning behaviour of *D. sargus*. The spawning of this species is triggered by a change in the thermal regime, specifically related to the increase of the seawater temperature immediately after the winter minimum [53,54]. We observed that during this period, spawning movements happened in several pulses over a few days, in which *D. sargus* visited deep spawning areas. Most of those areas were located within the computed HR, but some individuals also travelled further distances up to 600 m away from the edge of their HR (1 km away from the centre of their core area). However, those movements seemed to have a limit, as none of the individual from the NT zone left the fully protected area, and none of the individuals from the PR and NR crossed to the NT zone. Similar spawning movements of the same magnitude (1–2 km) were reported for this species by Di Lorenzo *et al.* [32].

As the observed spawning movements occurred synchronously and during short periods of time, we hypothesize that *D. sargus* forms FSAs. Two types of FSAs have been described depending on their frequency, length of time, site specificity, and the distance travelled by individuals [10]. In 'resident' FSAs, individuals move to the spawning sites from relatively small and local areas in short migrations of few hours or less. They usually happen at a specific time over several days, and last for only few hours. 'Transient' FSAs, in contrast, are characterized by longer migrations from relatively larger areas, to specific spawning sites where the aggregation persists for longer periods of several days or weeks. The spawning movements that we have observed in *D. sargus* involved individuals moving small distances from their core HR areas to spawning sites. Therefore, we suggest *D. sargus* aggregations be considered as resident FSAs.

Aggregating behaviour of *D. sargus* during spawning has gone unnoticed until now, but it can be an important issue for the conservation of the species. To better understand the population dynamics, it is important to determine if the captures of *D. sargus*, by both artisanal and industrial fisheries, increase during the breeding season. Moreover, this fundamental gap of knowledge in such an abundant and widespread species raises new questions about the spawning behaviour of other, less common, species and highlights the need to further study the behavioural ecology of small Mediterranean fishes. Repetitive fishing activities on predictable FSAs can cause severe damage and the collapse of fish populations [13,14]. FSAs might be a common strategy among coastal fish species in the Mediterranean, therefore knowing whether the species generate FSAs, and their timing and location is essential when deciding the placement, size and shape, and protection-levels of MPAs.

Supporting Information

S1 Fig. Results of the signal range-tests performed in the study site. The dots represent the mean (±SE) probability of tag detection at increasing distances from acoustic receivers.
(PDF)

S2 Fig. Spatial chronogram plots for each tagged *Diplodus sargus* individual.
(PDF)

S3 Fig. Distribution of phase-transition values (PT) calculated for the hourly reception number between consecutive day-night (A) and day-day (B) phases, for each *Diplodus sargus* individual. Lower and upper boundaries of the boxes represent the first and third quantiles of value distributions. Significant results of the Wilcoxon signed-rank tests against the null hypothesis of a median of zero are expressed by the symbols above the boxes; +: $p < 0.05$; *: $p < 0.01$.
(PDF)

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Author Contributions

Conceived and designed the experiments: BH RMS CL MZ DD AL. Performed the experiments: BH RMS AL CL DD MZ. Analyzed the data: EA FB BH AL. Contributed reagents/materials/analysis tools: MZ BH EA FB RMS. Wrote the paper: EA FB BH CL RMS AL DD MZ.

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Thermal stratification drives movement of a coastal apex predator

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A characterization of the thermal ecology of fishes is needed to better understand changes in ecosystems and species distributions arising from global warming. The movement of wild animals during changing environmental conditions provides essential information to help predict the future thermal response of large marine predators. We used acoustic telemetry to monitor the vertical movement activity of the common dentex (*Dentex dentex*), a Mediterranean coastal predator, in relation to the oscillations of the seasonal thermocline during two summer periods in the Medes Islands marine reserve (NW Mediterranean Sea). During the summer stratification period, the common dentex presented a clear preference for the warm suprathermoclinal layer, and adjusted their vertical movements following the depth changes of the thermocline. The same preference was also observed during the night, when fish were less active. Due to this behaviour, we hypothesize that inter-annual thermal oscillations and the predicted lengthening of summer conditions will have a significant positive impact on the metabolic efficiency, activity levels, and population dynamics of this species, particularly in its northern limit of distribution. These changes in the dynamics of an ecosystem's keystone predator might cascade down to lower trophic levels, potentially re-defining the coastal fish communities of the future.

Temperature is a key environmental factor that, through profound physiological effects, influences the fitness and survival of ectothermic organisms[1–3]. Ectothermic organisms are usually adapted to live within a limited range of temperatures, which includes a thermal optimum that maximizes their physiological performance[4]. When conditions move away from this optimum, an organism experiences reduced growth, reproduction, foraging, or competitiveness[5,6]. Temperature shifts from the preferred range will thus greatly affect the dynamics of a species, altering the relative abundances of a population and changing the horizontal and vertical distribution of individuals[7–10]. In the case of ecosystem keystone species such as apex predators, community-changing herbivores, or structure-forming species, temperature-driven changes in abundance may cause ripple-effects in other levels of the food web, changing the structure and functioning of the ecosystem[11,12]. In the face of global climate change, a great deal of research effort is being expended to characterize the thermal ecology of marine organisms, as it is necessary to understand the trends in ecosystems arising from the warming of the global ocean[6,13].

The ability to move makes fishes much more resistant to environmental change than less mobile or sessile benthic species[14]. As with many other mobile animals, marine fishes can readily exploit thermal gradients to regulate their body temperature and increase their metabolic efficiency[15,16]. Movement is thus a good behavioural response with which to infer the thermal ecology of a fish species. Controlled laboratory experiments have shown that fish move across thermal gradients to attain a preferred temperature[17,18], and have allowed the researchers to investigate the response of an individual's internal temperature to a fluctuating environment[16]. However,

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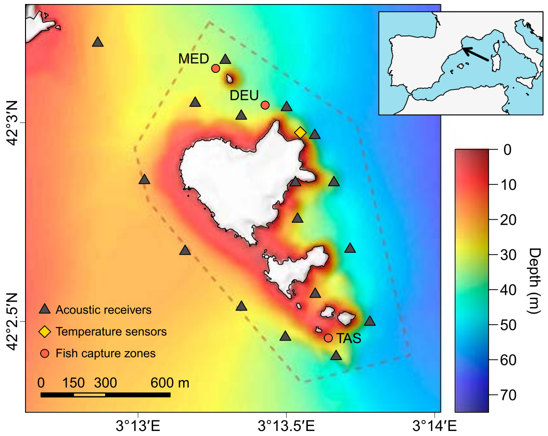

Figure 1. Bathymetric map of the study site and the location of acoustic receivers and temperature sensors. The approximate locations where the common dentex individuals were captured are also shown (see Table 1). *In situ* temperature sensors were placed every 5 m (between 5–40 m) in the marked location. Map was created using R[60] version 3.3.1 (https://cran.r-project.org). The topographic base map (1:5.000), DEM and bathymetry are freely accessible through the Cartographic and Geologic Institute of Catalonia (www.icgc.cat) under Creative Commons Attribution License (CC BY 4.0).

ID	Length (cm)	Capture site	Capture date	Mean depth ± SD (m)	Total detections	Detections during the summer period (No. of 5 min intervals)		Deep excursions (% of summer detections)	
						Day	Night	Day	Night
18	63	TAS	2007-05-24	16.2 ± 4.8	64,419	11,035	5,010	0.02	0.04
43	63	TAS	2007-06-03	8.7 ± 4.5	53,049	9,436	5,017	0.01	0.00
44	59	MED	2007-06-03	23.7 ± 4.8	86,551	12,142	8,840	0.27	0.06
32	55	TAS	2007-12-02	29.7 ± 8.7	51,402	7,901	6,438	1.73	0.99
33	61	TAS	2007-12-01	29.1 ± 7.8	46,308	6,792	5,138	3.99	1.52
34	47	TAS	2007-12-01	20.9 ± 5.9	16,971	4,159	3,414	0.41	0.09
35	46	TAS	2008-01-22	26.2 ± 7.6	48,140	5,700	5,162	1.95	0.19
37	53	DEU	2007-12-02	30.5 ± 6.8	40,478	2,043	2,360	1.47	0.85
39	42	TAS	2008-01-22	25.6 ± 4.7	35,693	4,412	3,167	2.04	0.47
42	62	TAS	2007-12-01	33.9 ± 9.8	53,804	10,365	7,531	8.28	3.24
45	59	DEU	2007-12-01	37.0 ± 9.2	45,218	6,786	2,315	8.38	2.51
50	65	TAS	2007-12-01	24.0 ± 4.5	62,724	11,661	5,712	0.99	1.79

Table 1. Summary of the information and detections of tagged common dentex individuals. Deep excursions refer to the percentage of detections happening below the lower thermocline limit during the summer period (see Methods section).

laboratory experiments are not feasible for large marine predators, and hence studies in the wild using acoustic telemetry and bio-logging technologies are a much more practical approach to study the thermal preference of these animals[10, 17, 19].

Within the complexity of oceanographic conditions, the thermocline is a prominent structure. Thermoclines are hydrographical structures caused by large temperature gradients and that generate a significant segregation of resources. Thermoclines set up a heterogeneous thermal environment wherein mobile organisms have developed behavioural responses according to the trade-off between their physiological requirements and energy demands. For instance, many oceanic predators need to maintain warm body temperatures in order to sustain their foraging activity, but often their preys concentrate in cold deep waters. In order to exploit those food resources, several tuna species[15, 20, 21] as well as the ocean sunfish[22] rewarm during relatively long periods in the suprathermoclinal layer before performing short excursions below the thermocline to forage. Less attention has been paid to this kind of behaviours in coastal predators[17], despite their key roles in shaping coastal communities and their relevance as indicators of good ecosystem conservation status[23–25].

In this study we focused on the common dentex, *Dentex dentex* (L. 1758), one of the main coastal apex predators in the Mediterranean Sea and an important fishery resource for both artisanal and recreational fisheries[26–28].

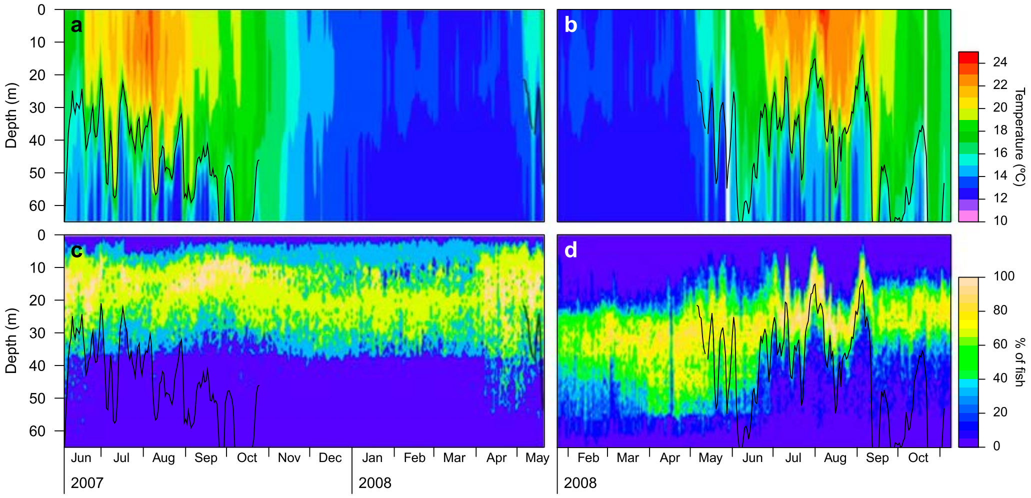

Figure 2. Daily temperature profiles (**a,b**) and vertical distributions of common dentex individuals (**c,d**). The panel in the left (**c**) corresponds to the set of individuals captured in May-June 2007 (n = 3), and the panel in right (**d**) to the set of individuals captured in December 2007-January 2008 (n = 9). Solid lines represent the daily mean depth of the thermocline.

The common dentex is present along the Atlantic and Mediterranean coasts, but its populations are more abundant in central and southern Mediterranean and rare in the Northern Mediterranean Sea[29, 30]. A global decrease in fishery landings of common dentex has been reported by FAO during the last three decades[30], reason why it is classified as 'vulnerable' by the International Union for the Conservation of Nature (IUCN) in the Red List of Threatened Species[31]. However, in several Mediterranean sectors its abundance seems to be increasing, as shown by an increase in fishery landings in several Spanish ports[32], and the fast recovery of its populations in marine protected areas[25]. The common dentex inhabits infra- and circa-littoral rocky bottoms and seagrass meadows, and is more abundant at depths between 15–30 m[33, 34]. The usual depth distribution of adult individuals coincides with the depth range at which the seasonal thermocline establishes between May and October in the NW Mediterranean Sea[35]. Summer conditions in the Mediterranean Sea are characterized by high water column stability and high temperatures, resulting in a strong stratification of the water column. However, this thermocline is known to display strong vertical oscillations in short time periods, such as a few hours or days, which are mainly driven by the wind and movement of water masses, and are also dependent on local hydrographic conditions caused by coastal orientation and bathymetry[35].

We monitored the vertical movements of the common dentex using acoustic telemetry and characterized the thermal environment using *in situ* temperature loggers during two consecutive summers in the Medes Island marine protected area (NW Mediterranean Sea, Fig. 1). Our objective was to describe the thermal preference of the common dentex by analysing its vertical movements and activity patterns during stratified and non-stratified hydrographical periods. Describing the thermal ecology of this iconic apex predator will help us to predict their population dynamics during future warm water periods and the probable cascade effects on coastal marine ecosystems.

Results

Thermal regime and depth of the thermocline.

Surface temperatures ranged from a minimum of 12.4 °C in winter (March 2008) to maximum temperatures of 23.9 °C (August 2007) and 24.6 °C (August 2008) in summer (Fig. 2a,b). The stratification of the water column started in early May and became stronger as summer progressed, with the temperature gradient increasing in strength in July and August (Fig. 3). The temperature gradient relaxed at the end of summer (September), becoming weaker and deeper, until a complete breakdown at the end of October. Shortly after that, the water column was well mixed with a temperature of about 17 °C, before displaying a progressive cooling until the minimum winter temperature.

During the maximum stratification period, with surface temperatures above 19 °C (between mid-June and mid-September), significant oscillations of the thermocline were observed in both 2007 and 2008, but there were clear differences between years (Fig. 2). The summer of 2007 presented shallower thermocline positions than the summer of 2008 (Fig. 3a). The shallowest thermocline depths in 2007 were recorded in July, during which thermocline depths shallower than 15 m occurred on only two days. By contrast, in 2008 shallow thermoclines were registered during the entire summer (July, August and September), and observations of the thermocline shallower than 15 m occurred in 14 different days. Moreover, the maximum temperature gradients observed in July and August 2008 were much more elevated than the gradients observed in the same period in 2007 (Fig. 3b).

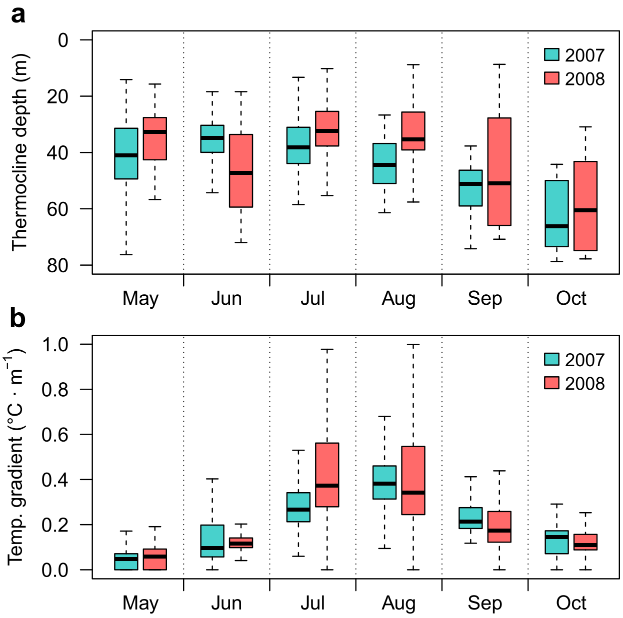

Figure 3. Hourly thermocline depth (**a**) and temperature gradient (**b**) values, separated by month and year. The black line near the middle and the lower and upper box boundaries represent the median and the first and third quartiles of values, respectively. Ends of the whiskers represent values at 1.5 times the interquartile range of the box.

Level	Estimate	SE	DF	t-value	p-value
(Intercept)	1.061	0.087	6,518	12.179	<0.001**
Day/Night period					
Night	−0.410	0.041	6,518	−10.023	<0.001**
Season					
Spring	0.354	0.064	6,518	5.553	<0.001**
Summer	0.025	0.043	6,518	0.585	0.558
Autumn	0.032	0.043	6,518	0.734	0.463
Day/Night period × Season					
Night:Spring	0.073	0.022	6,518	3.400	0.001**
Night:Summer	0.046	0.021	6,518	2.183	0.020*
Night:Autumn	−0.015	0.024	6,518	−0.657	0.511

Table 2. Results of the linear mixed effects model testing the effect of the day/night period and the season on vertical movement activity levels.

Vertical movement activity patterns. The total length of tagged individuals ranged between 42 and 65 cm (Table 1), with no differences in size between the first set of individuals (n = 3), tagged in May-June 2007, and the second set (n = 9), tagged in December 2007-January 2008 (Kruskal-Wallis test, $\chi^2 = 2.203$, df = 1, p = 0.138). However, the individuals from the first set utilized shallower depths (5–30 m) than the individuals from the second set (20–45 m) (Table 1 and Fig. 2a). The linear mixed-effects model used to test the differences between vertical movements (depth fluctuations for each day/night period) revealed a significant day-night and seasonal effect (Table 2). Overall, the vertical movement activity was greater during the day than during the night, and the seasonal pattern was marked by a higher vertical movement activity in spring compared to the rest of the seasons, which did not differ (Fig. 4).

Effect of the thermocline on fish depth. Tagged common dentex exhibited a characteristic pattern of vertical movements during the summer 2008, in which the depth of most of fish oscillated rapidly over periods of a few days (Fig. 2d). This pattern was not directly observable from tagged fish in the summer 2007 (Fig. 2c). A logistic mixed effects model explained the relationship between the observed depth patterns and the depth of the thermocline (Fig. 5 and Table 3). This model demonstrated a non-linear relationship between the average depths of tagged fish and the thermocline depth. When the thermocline was shallower than the depth-range used by

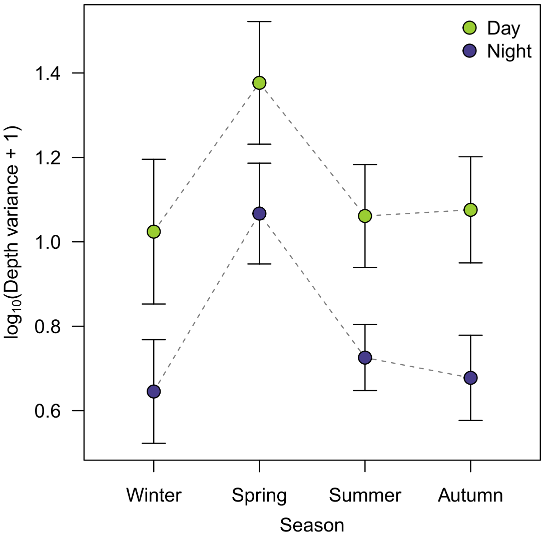

Figure 4. Effects of the day/night cycle and the season on the vertical movement activity of common dentex. Vertical movement activity is quantified as the variance of depth (after a logarithmic transformation). Filled circles and error bars represent the mean values predicted by the linear mixed effects model and the 95% confidence intervals, respectively.

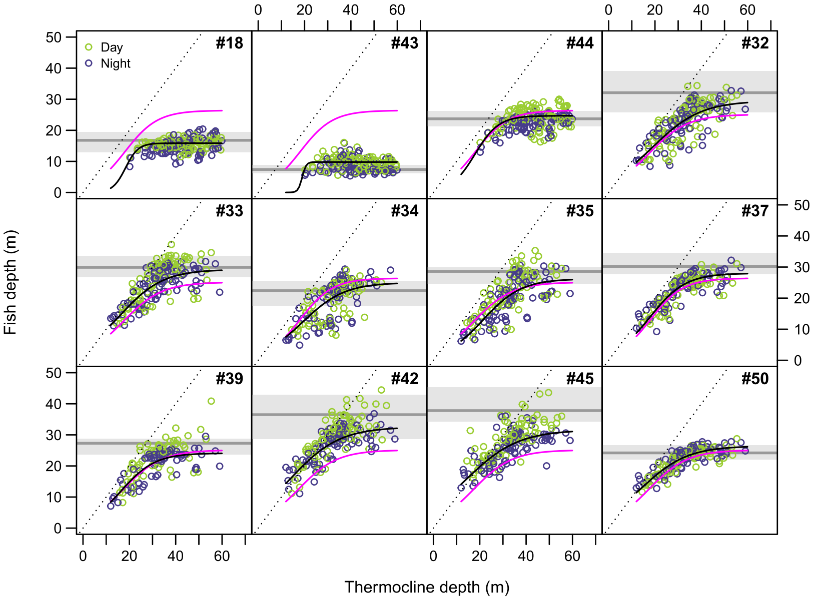

Figure 5. Relationship between mean fish depths and mean thermocline depths during the summer season, factorized by day/night periods, for each tagged fish (n = 12). Solid black lines represent the logistic models adjusted for each individual, and the magenta line is the mean prediction for the population. Black dotted lines highlight pure linear (1:1) relationships. Grey line and box in the bottom represent the median and the first and third quartiles, respectively, of the depths measured for each fish outside the summer period.

Parameter	Estimate	S.E.	D.F.	t-value	p-value
Asym					
(Intercept)	26.39	2.10	2042	12.55	<0.001**
Night	−1.28	0.65	2042	−1.98	0.048*
x_0					
(Intercept)	18.18	0.50	2042	36.02	<0.001**
Night	−0.73	0.69	2042	−1.07	0.287
k					
(Intercept)	6.99	0.97	2042	7.18	<0.001**
Night	1.31	0.69	2042	1.90	0.057

Table 3. Results of the non-linear mixed effects models testing the effect of the depth of the thermocline and the day/night period on mean fish depths. The fitted values for each parameter defining the logistic curve and their significance are shown: Asym = maximum value of the curve; x0 = x-value of the inflexion point; k = steepness of the curve.

each fish (20–45 m), the depth of the thermocline correlated positively and linearly with the mean fish depth. This relationship broke down and became asymptotic when the thermocline sank below the preferred depth range. Indeed, the individual asymptote values estimated by the model fell within the depth-range that each fish inhabited outside the summer season (Fig. 5). The effect of the day/night period was significant only in the estimation of one of the parameters of the model, the asymptote, but it had a relatively small effect (Table 3), thus indicating that individuals followed similar movement patterns above the thermocline indistinctively of the time of the day.

Despite this average relationship, several punctual excursions below the lower limit of the thermocline were observed during the summer period (Table 1). The amount of detections below the thermocline was low (<2%) for most of fishes, excepting for three individuals, #33, #42, and #45, which presented higher percentages. Overall, the percentage of detections below the thermocline was significantly higher during the daytime than during the night (paired samples t-test: t = 2.49; df = 11, p = 0.015).

Discussion

During the study period we observed the typical seasonal thermal cycle for the NW Mediterranean Sea, which is characterized by a mixed phase followed by a thermal stratification period[35]. Although this seasonal pattern repeats every year, there were inter-annual differences with respect to the maximum and minimum temperatures and the duration and magnitude of the stratification[35, 36]. During our study, the thermocline underwent several transient but recurring oscillations in the course of the stratification period. These oscillations included changes of up to 20 m in the depth of the thermocline and 10 °C in the temperature at certain depths. Our observations were similar to those described by Bensoussan *et al.*[35], who indicated that thermocline oscillations represent an important fraction of the annual thermal variability despite their proportionately low duration (2.1 ± 0.8 days on average). Bensoussan *et al.*[35] also reported that the relative variability of the temperature in summer in the study area increases with depth, reaching a maximum variability at depths between 25 and 40 m. At those depths, benthic communities are exposed to an average daily temperature variation of around 2 °C (with maximum values around 10 °C), and a weekly variation of around 7 °C (with maximum values of 11.5 °C). The swimming depth of the common dentex was strongly influenced by the temperature variations caused by the thermal structure of the water column, as shown by the relationship between the depth of the thermocline and the depths of tagged fish (Fig. 5). Transient thermocline rising events were related to upward displacements of individuals from the specific depths that they utilized outside the stratification period or during deeper thermocline events. Thus, common dentex demonstrated a clear preference for the suprathermoclinal warm water over the colder water below the thermocline.

Our main hypothesis is that a physiological optimization strategy was behind the observed behaviour of the common dentex. Temperature strongly affects the basal metabolic rate in fishes, restricting or enhancing physiological and behavioural processes[2]. Some studies on the effect of thermal gradients on fish have found that individuals spend most of their time (~75%) within ±2 °C of their preferred temperature, which coincides with the optimal physiological temperature that maximizes growth[37]. It has been also described that fish swimming speed or endurance is enhanced to a peak by an optimum temperature and is reduced when the temperature decreases or increases towards the tolerance limits[38–40]. The maximum swimming speed is a limiting factor for the foraging activity, and for this reason many oceanic predators must warm their body temperature in order to be able to hunt in cold deep waters[15, 41]. Thus, we hypothesize that the common dentex selects its thermal niche, presumably to approach the optimal temperature for growth and/or foraging in order to increase an individual's net energy gain.

An alternative hypothesis would be that the observed movement behaviour of the common dentex was driven by indirect effects such as food distribution. The common dentex is a diurnal predator[42], which primarily forages on other fishes (about 74% of prey items), and to a lesser degree on cephalopods and crustaceans[26, 43]. Consequently, foraging events were the most likely cause of the high vertical activity levels that we observed during the day (Fig. 4), while low activities during the night might be related to resting behaviour. Similar diel activity patterns have been observed in other coastal species[42, 44] including other predators[17]. Regarding the relationship between the thermocline depth and the vertical distribution of individuals, our model indicated that the diel cycle had a negligible effect. This implies that a presumable concentration of prey items in the suprathermoclinal layer during the summer is not enough to explain the vertical movements of the common dentex. If that were the case, we would expect to observe a relaxation of the depth restriction imposed by the thermocline during the night, with individuals returning to their preferred depths to rest, similar to what has been described for the dogfish by Sims *et al.*[17]. On the contrary, most of the excursions below the thermocline were observed during the day, and were very probably related to punctual foraging events. Therefore, our results indicate that the observed vertical distributions of individuals during summer were more probably caused by a direct selection of the preferred temperature-range, rather than by an irregular distribution of preys items above and below the thermocline.

Our approach to estimate activity patterns could discern between day and night activity periods, but it was not adequate to resolve seasonal activity patterns. The common dentex resided within the study site throughout the year, facing two different thermal conditions (summer and winter) that we would expect to have a significant effect on fish physiology and activity. Cabled video observatories have already described a seasonal activity rhythm for the common dentex, which showed higher occurrences between August and October, indicating a change in its horizontal activity pattern coinciding with high water temperatures[45]. Similarly, Abdelkader and Ktari[46] described an increase in the food intake of common dentex between April and May, coinciding with the timing of the spawning, and a decrease in consumption from September to February. These movement and feeding patterns are thought to be related to seasonal variations on the abundance of their prey items, mainly coastal fishes such as sparids, labrids and picarels (*Spicara maena*)[26], which tipically are more abundant in summer than in winter. Interestingly, the common dentex has shown an unsual ability to withstand long periods without food, which seems to be an adaptation to cope with unfavourable periods[47], such as the low prey availability and low temperatures during winter. However, our analysis did not show significant differences between the vertical activities of summer and winter. Nevertheless, it was able to detect an increase of the activity during spring, very probably related to the spawning, which has been described to occur between April and May[26]. During this period, the common dentex is thought to perform excursions to deep rocky outcrops, where it aggregates to spawn[26, 30]. Characterizing spawning movements and periods is key for designing effective conservation measures for emblematic fish species[48, 49], and thus they should be studied more carefully in the future.

Changes in the distribution of individuals associated with seasonal and inter-annual environmental fluctuations provide insights into how populations may shift under global climate change. The current global change is driving not only a steady increase of global water temperatures, but also a lengthening of the summer period[50]. For instance, the thermal stratification has increased in the NW Mediterranean Sea during the last three decades, which has already lengthened the duration of yearly summer conditions by a ~40%[50]. Consequently, warm water fish species are being positively affected, leveraging the higher presence of favourable conditions that enhance both their metabolic and foraging efficiency, thus improving their survival rate and reproductive success[51, 52]. These kinds of environmental fluctuations are proposed as the cause of the inter-annual fluctuations in the capture rates of many important demersal fishery resources[53], including the common dentex[30, 34]. The redistribution of preferred temperature ranges is generating changes in both the horizontal and vertical distributions of coastal fish assemblages[7, 8]. For instance, recent local data suggest that the common dentex might be expanding in the northern Mediterranean[25, 32]. Our results, by confirming the preference of this species for warm water, provides valuable information on the ecology of the species and a mechanistic understanding to the mentioned population fluctuations and expansion.

In this study, we used acoustic telemetry to provide some valuable insights on the thermal ecology of the common dentex and the possible future trends of its populations. The common dentex and other apex predators are keystone species in marine food webs, and are often used as indicators of the structure and functioning of ecosystems[23, 24]. Also, the abundances of species occupying high trophic levels shape biological communities through top-down trophic effects[54, 55], although the extent of the impact is still under debate[56]. Climate change will differentially affect different species, depending on their physiological and behavioural traits[6, 12], and as a result generate unpredictable effects that will interact with other perturbations such as overfishing. To make reliable predictions of future biological assemblages and main ecological trends, it is necessary to understand the mechanisms underpinning the responses of different species to climate change.

Methods

Acoustic telemetry study. Information about movements from 12 *D. dentex* individuals was collected from an acoustic telemetry study carried out in the Medes Islands MPA (Catalonia, NW Mediterranean Sea) between 2007 and 2008. Fish were captured by jigging hook-and-line fishing gear from a boat and tagged with V13P-1H acoustic transmitters (VEMCO, Nova Scotia; dimensions: 48 × 13 mm; power output: 153 dB; weight in water: 6.5 g), which were implanted in the peritoneal cavity using a standard surgical procedure[57, 58]. The tagging protocol followed the guidelines provided by the Ministry of Agriculture, Livestock, Fisheries and Food of the Catalan Government (decree 214/1997), and was approved by the Committee on the Ethics of Animal Experimentation of the University of Barcelona. The Department of Environment of the Catalan Government granted permissions for fishing, operating and releasing the animals in the Medes Islands Marine Reserve. All surgery was performed under 2-phenoxyethanol anaesthesia, and all efforts were made to minimize suffering. The sex of individuals could not be determined due to the lack of sexual dimorphism in this species. Transmitters were equipped with a pressure sensor and were programmed to emit signals with a random delay between 80 and 180 s. Movements of tagged individuals were monitored by a network of 17 acoustic receivers placed around the study area (Fig. 1). Signal range-tests were performed in the area and revealed an average detection range of 150 m around the receivers (see Aspillaga *et al.*[44] for more details). Individuals were divided into two sets depending on their capture date (May-June 2007: n = 3; December 2007-January 2008: n = 9). All the analyses were restricted to a different time period for each set (Jun/4 2007 to May/21 2008, and Jan/1 2008 to Nov/11 2008, respectively), corresponding to the period in which all the individuals in the set were simultaneously tracked.

Temperature data. Hourly measures of *in situ* temperature were provided by the T-MedNet network (http://www.t-mednet.org). Temperature was registered by autonomous sensors (HOBO Water Temp Pro v2) placed in rocky ledges at depth intervals of 5 m (from 5 to 40 m depth) at one location of the study site (Fig. 1). Additional temperature data, corresponding to manually-operated sensors for one sampling station situated at 2.5 nautical miles offshore the eastern side of the islands, was provided by J. Pascual (http://meteolestartit.cat). At that station, temperature profiles were generated every 2–3 days using a CTD that recorded measures every meter, from the surface to a depth of 90 m.

Data analysis. The thermocline depth was calculated from hourly temperature profiles. A four parameter logistic regression was fitted to each profile, and the mean depth of the thermocline was then determined as the depth at which the first derivate of the model presented its maximum value (as in McKinzie *et al.*[59]). The upper and lower limits of the thermocline were also determined from the peaks in the second derivate of the model. The strength of the thermocline was then calculated as the temperature gradient ($°C \cdot m^{-1}$) between its upper and lower limits. In order to calculate the depth of the thermocline when it was below the depth-range of the autonomous sensors (40 m), the *in situ* temperature profiles were complemented with an interpolation of the manual CTD casts taken between 40 and 80 m depth. Thermocline depth was only calculated for the profiles where the total temperature difference between the surface and the deepest measures was higher than 3 °C.

Acoustic telemetry data was pooled in 5 min intervals and the mean depth was calculated for each common dentex individual, in order to remove duplicated detections in different receivers and to homogenize the data distribution along time. These intervals were then classified into consecutive day/night periods, defined by local sunset and sunrise time provided by the NOAA Solar Calculator (www.esrl.noaa.gov/gmd/grad/solcalc/) for the coordinates of the Medes Islands (42°03′N 3°13′E, WGS84), and the mean depths and variances were calculated for each period. Variance of the depth was used as an approximation to fish vertical activity, assuming that the range of vertical movements is bigger when fish are active (e.g. when foraging) than when they are resting. In order to detect diel and seasonal patterns of fish activity, a linear mixed-effects model was applied to the variance data after applying a logarithmic transformation, considering the day/night period and the season as fixed factors and the fish tag number as a random factor. To test the effect of the thermocline depth on the fish depth, only data corresponding to the summer was used, as it was the only season in which a well-developed thermocline was present. A non-linear mixed-effects model was applied to test this relationship, where the mean depth of the thermocline and day/night period were considered the primary and secondary covariates, respectively, and the fish tag number as a random factor. All the data was managed and analysed in R[60], and mixed effects models were fitted using the 'nlme' package[61]. Performances of the models were visually inspected in residual distribution and residual vs. fitted values plots.

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Author Contributions

B.H., R.M.S., C.L., M.Z., D.D. and A.L. conceived the acoustic telemetry study and conducted the fieldwork. J.G. obtained and processed the *in situ* temperature data. E.A., F.B., J.G. and B.H. analysed the data. E.A. wrote the main manuscript text. All authors reviewed the manuscript.

Additional Information

Competing Interests: The authors declare that they have no competing interests.