



# Movement ecology of the white seabream *Diplodus sargus* across its life cycle: a review

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**Abstract** The white seabream *Diplodus sargus* (L., 1758) (Osteichthyes, Sparidae) is a littoral species living mainly in rocky habitats and distributed in the eastern Atlantic and the Mediterranean. This species is targeted by artisanal and recreational fisheries and presents a high commercial importance. Although classified by IUCN as a “least concern” species, it has been the object of marine ranching and restocking initiatives to counteract locally intense exploitation. Here, we review the current knowledge on the movement ecology of white seabream given the relevance of animal movement in ecological and behavioral studies and their potential application in management and conservation. The literature on this topic was analyzed in order to summarize the results of past research and to identify the gaps that still exist on the

matter. We reviewed a total of 27 papers focusing on the movement ecology of white seabream, where acoustic telemetry ( $n=12$ ), underwater visual observation and traditional tagging ( $n=6$ ), genetic analysis ( $n=6$ ), and otolith microchemistry ( $n=3$ ) were used. While the first three methods were applied to juveniles and adult fish, the last one was also used with larvae, which have been the object of experimental trials to ascertain their swimming abilities. The largest amount of information on activity rhythms (diurnal with a few exceptions), movement patterns (short distances), homing (ability to come back to the capture site), site fidelity (high), and home range ( $< 200$  ha on average and highly related with seabed morphology) were obtained through acoustic telemetry, whose main limitation is the minimum body size required for its application. The environmental variables found to affect movement patterns in this species are water temperature (which triggers spawning-based vertical movements), local sea conditions (which affect short-scale movements in juveniles), and the main seabed features (orientation and habitat type). The main gaps identified, which need more extensive research and some technological improvements, include the study of the effects of environmental variables on fish movements and further investigations on the movement patterns of juveniles.

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## Introduction

Animal movement plays a particularly important role towards understanding the behavioral ecology of marine and terrestrial organisms. Modern movement ecology integrates all forms and aspects of animal movement, thus providing a broader vision of a species activity across different life stages (Nathan et al. 2008). Studies on movement patterns encompassing different spatial and temporal scales can help to determine individual behavior, population dynamics, and community structure (Nathan et al. 2008). They can also elucidate activity patterns and habitat use (Di Lorenzo et al. 2016) and connectivity between habitats and habitat patches used by migratory species or by different life stages (Abecasis et al. 2009) and provide basic knowledge to establish the placement, extension, and zonation of protected areas in order to fit the home range of endangered species (Kramer & Chapman 1999; Gruss et al. 2010). Movement ecology is also considered a powerful tool for natural resources management and conservation (Abecasis et al. 2014; Allen and Singh 2016; Fraser et al. 2018).

A variety of techniques have been used to collect data on animal movement in the marine environment, mostly based on mark-and-recapture methods (Lucas and Baras 2000) and biotelemetry (Thorstad et al. 2013). The choice of the appropriate technique relies on the objective and scope of each study, life stage, body size, spatial and temporal scale, and the level of investigation (from individuals to population).

The fish genus *Diplodus* (Osteichthyes, Sparidae) includes twenty-three species distributed across the Mediterranean and Black Sea, both sides of the Atlantic Ocean, central and western Indian Ocean, and the Red Sea (Fricke et al. 2016). Among all species in this genus, the white seabream *Diplodus sargus* (L., 1758) is one of the most widely distributed, with a geographic range spanning across the Mediterranean, western Black Sea, and eastern Atlantic from Brittany to Canary Islands, Madeira, and northwestern Africa.

White seabreams usually occur in non-obligatory schools mainly on rocky and mixed habitats within 50 m depth, where they use crevices and holes as a nocturnal refuge or to hide from predators during diurnal activities (Harmelin 1987; Sala and Ballesteros 1997; Figueiredo et al. 2005).

The white seabream is a rudimentary hermaphrodite with partial digynic protandry and a spawning

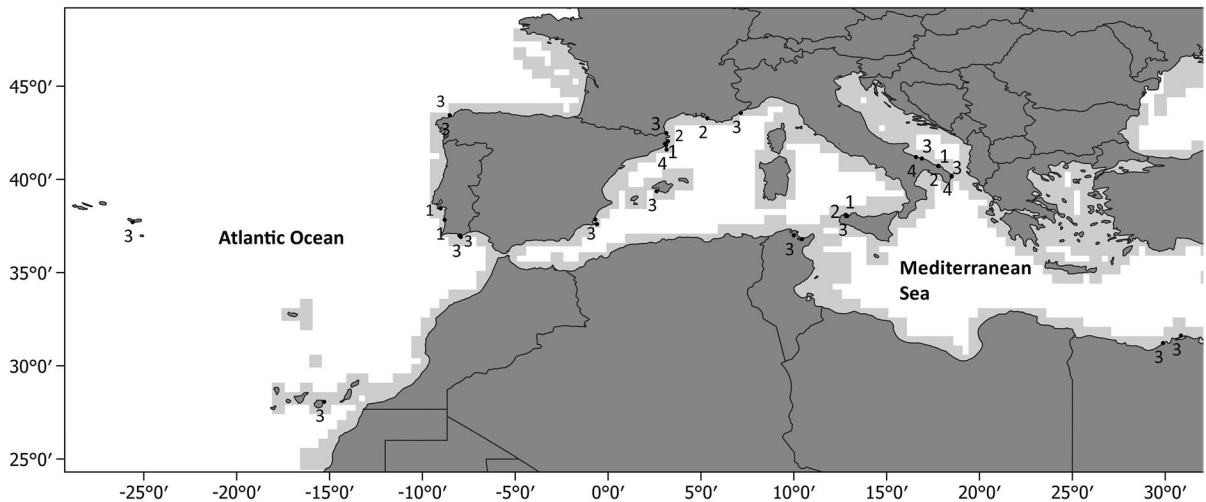
season spanning from winter to early summer at the Mediterranean and Azores latitude (Micale and Perdicchi 1994; Morato et al. 2003; Mouine et al. 2007; Giacalone et al. 2018). Sex reversal, which takes place at a median size of 23.5 cm (total length, TL) in the southwestern Mediterranean (Boufekane et al. 2021), is considered an evolutionary advantage irrespective of the sex change direction (Warner 1988), and higher effective population size has been suggested for *D. sargus* and other protandric fish when compared to fixed-sex species (Benvenuto et al. 2017; Waples et al. 2018). The mean relative fecundity ranges between  $254 \pm 152$  and  $573 \pm 63$  oocytes/g body weight (Martinez Pastor and Villegas Cuadros 1996; Boufekane et al. 2021). Somatic growth is especially fast during the first year of life (Martinez Pastor and Villegas Cuadros 1996) with highly variable estimates of the growth performance index ( $2.29 < \Phi < 6.06$ ; Benchalel and Kara 2013; Balik and Emre 2016).

The white seabream, classified as a “least concern” species by IUCN (Pollard et al. 2014), occupies a prominent position in commercial and recreational coastal fisheries (Harmelin-Vivien et al. 1995; Veiga et al. 2010), with reported Mediterranean landings of about 3500 tons/year for the period 2010–2018<sup>1</sup> (which do not include unreported catches from artisanal fisheries: see Pauly et al. 2014). This species has also been the object of marine ranching and restocking initiatives through the use of juveniles and sub-adults provided by local aquaculture facilities (D’Anna et al. 2004, 2012; Santos et al. 2006).

Several aspects of white seabream biology and ecology have been investigated such as feeding habits (Leitao et al. 2007), role as a keystone species in trophic cascades (Figueiredo et al. 2005), age and growth (Gordoa and Moli 1997; Abecasis et al. 2008), reproduction (Morato et al. 2003) and the potential for population recovery after fishing exclusion in marine reserves (Abecasis et al. 2015).

Studies on the movements of white seabream throughout its different life stages have been carried out across most of its distribution range (Fig. 1). This paper aims at reviewing and summarizing the main findings reported in the literature regarding the

<sup>1</sup> GFCM capture fisheries statistics: <http://www.fao.org/gfcm/data/capture-production/en/> (accessed: 15/09/2021).



**Fig. 1** Map showing the geographic distribution of the study areas as from the reviewed papers. Light-gray pixels indicate areas of likely occurrence of white seabream based on suitability of habitat. Black dots refer to individual study sites. 1,

acoustic telemetry studies; 2, underwater visual observation and traditional tagging studies; 3, genetic analysis studies; 4, otolith microchemistry studies. Source: AquaMaps (through [www.fishbase.org](http://www.fishbase.org)) (modified)

movement ecology of white seabream. Moreover, it discusses some of the technical aspects inherent to the methodologies used and addresses the gaps still existing in the knowledge of the movement ecology of this species.

### Paper selection and description of methods used in movement ecology studies

Relevant scientific literature was searched online through the Web of Science (Clarivate™) platform using various combinations of the following keywords: *Diplodus sargus*, movemen\*, home range, homing, activity patter\*, habitat use, distribution, and dispersal. We retrieved a total of 27 literature items and summarized the main findings regarding white seabream movement ecology, considering the investigation methodology used, information on fish size, habitat, and other features (see Fig. 1 for the geographic distribution of the reviewed studies). Four main methodologies were considered:

1) Acoustic telemetry (12 papers reviewed). Based on internally or externally attached electronic tags (=transmitters). The acoustic signal emitted by such transmitters is detected by acoustic receivers appropriately positioned throughout the

study area. Besides fish presence, data can also include biotic (heart rate, stomach pH, acceleration, etc.) and environmental (water temperature, depth, etc.) variables, depending on the type of tag used (Heylen and Nachtsheim 2018). This methodology allows for simultaneous tracking of multiple animals in different marine environments (Heupel et al. 2006) with the most recent technological developments allowing the tagging of fish as small as 9.5 cm (Rechisky et al. 2020) and some tags reaching a 10-year lifetime.

- 2) Underwater visual observation and traditional tagging (6 papers reviewed). Observations are performed by specifically trained scuba divers that employ visual census or video recording. This method may involve external tagging with number- or color-coded tags attached to fish body (Armannsson et al. 2007; Lucas and Baras 2000), which are useful also to collect information from recaptures by recreational or professional fishermen. Unlike acoustic telemetry, visual observations and tag-and-recapture methods provide time-limited data and therefore a poorly detailed picture of the overall movement pattern.
- 3) Genetics (6 papers reviewed). Genetic analyses have been used to investigate the connectivity pattern and dispersal distances in adults, juveniles, and larvae (Calò et al. 2013). DNA par-

entage analysis in particular has been used to measure larval dispersal distances based on the identification of the location of an individual's parents using highly polymorphic genetic markers and probability-based assignment techniques (Hansen et al. 2001; Planes et al. 2009; Abdul-Muneer 2014);

- 4) Otolith microchemistry (3 papers reviewed). This method is based on the capacity of otoliths to incorporate chemical signatures of the water mass frequented by fish since their embryonic stage. The chemical information acquired locally can be used to derive profiles of the movement history of individuals at a number of life history stages (Campana 1999; Green et al. 2009).

## Results

### Larvae

White seabream eggs hatch 3 days after spawning (Di Franco and Guidetti 2011), and the larvae spend up to 4 weeks in the water column before settling in a favorable environment (Vigliola 1999). The duration of a planktonic larval stage is considered a proxy of the dispersal potential of fishes (Macpherson and Raventós 2006), and the movements occurring at this stage are crucial for successful recruitment in coastal habitats (Baptista et al. 2019).

Knowledge of the larval dispersal patterns has proven useful to explain the connectivity dynamics in white seabream. Di Franco et al. (2012b) and Pujolar et al. (2013) have used a multidisciplinary approach to investigate the potential for propagules production and the connectivity patterns in a Mediterranean marine protected area (MPA) and estimated a potential larval dispersal of at least 200 km. Di Franco et al. (2012a) assessed the patterns of larval and post-settlement dispersal of white seabream at different spatial scales in the same MPA using otolith microchemistry and confirmed the dispersal pattern suggested by Pujolar et al. (2013). Individual variability in larval dispersal was related to differences in regional and local oceanographic features and hydrological parameters (Di Franco et al. 2012b; Baptista et al. 2020a).

The above-mentioned approaches consider larvae as passive particles but do not contemplate the

changes occurring from pre-metamorphic to post-flexion stages. Studies based on experimental trials have shown that white seabream larvae approaching the settlement stage have swimming abilities that can be used to orientate migration from the egg hatching area to the settlement habitats (Rossi et al. 2019). Studying the swimming performance of flexion and post-flexion larvae of white seabream, Baptista et al. (2019) supported the hypothesis that larvae are able to influence their own transport and distribution in coastal areas by means of their own swimming capabilities. These authors found experimental evidence that swimming speed and distance covered increased significantly across larval life. Their findings from lab tests showed that white seabream larvae are able to swim for up to 86.5 km over 10 straight days, starting about 45 days after hatching. Field confirmation of active movement in white seabream larvae was provided by Baptista et al. (2020b), who observed their successful movement from the spawning areas to the nearby lagoon that serves as a nursery area. On the other hand, the orientation capacity of the larvae towards a favorable settling habitat is subject to a high level of inter-individual variability that may have consequences on the dispersion and settlement processes (Baptista et al. 2020a).

### Juveniles

Habitat use and activity patterns of post-larval and early juvenile white seabream were studied by means of direct underwater observation in the northwestern Mediterranean (Garcia Rubies and Macpherson 1995; Harmelin-Vivien et al. 1995; Macpherson 1998). Settlers of 1–1.5-cm TL colonize very shallow, sheltered coastal areas at <2 m depth between late spring and early summer. Temporal partitioning has been suggested as a mechanism for avoiding competition with other *Diplodus* species sharing the same habitat (Garcia Rubies and Macpherson 1995; Harmelin-Vivien et al. 1995).

The selected microhabitats may vary according to the habitat patches present in the different localities, with a preference for pebbles and crannies along the rocky shores adjacent to sandy bottoms. An ontogenetic shift in habitat preference has been observed, with growing fish switching to several different substrates according to their availability in the area (Macpherson 1998). In late summer, when fish reach

6–7.5 cm TL, they tend to disperse over deeper areas characterized by rocky substrates covered with macroalgae to join the shoals of larger conspecifics. In a coastal lagoon of southern Portugal, it has been noted that late juveniles tend to occupy seagrass meadows in shallow waters, which serve as nursery and are left during the winter when they join the adult population outside the lagoon (Abecasis et al. 2009).

Like adults (D'Anna et al. 2011), juvenile seabream are attracted by artificial habitats. Young-of-the-year hatchery-reared seabream released over an offshore artificial reef area in NW Sicily moved soon towards the shore, selecting breakwaters and harbors richer in refuges and food as a preferential habitat (D'Anna et al. 2004).

Hatchery-reared juveniles were also used to test their dispersal along the shore. In this case, a conditioning to shelter and predators realized in rearing tanks proved an essential aid in the search of areas in the wild rich in suitable refuges, causing shorter distances run by fish after release (D'Anna et al. 2012).

There is almost no information available on activity patterns in white seabream juveniles. This might be due to the difficulties in making underwater observations of small individuals over sufficiently long time periods and to the impossibility of using an approach based on acoustic telemetry with small fish with the available technology. The only data available were recorded by Macpherson (1998), who did not observe any variation in aggregation or habitat use in settlers with different time of the day and turbidity, although higher aggregation and movement to slightly deeper waters was noticed in presence of rough waters, maybe to avoid the violent impact of waves.

## Adults

### *Residency*

Adult white seabream is highly residential regardless of study location or habitat monitored (Abecasis et al. 2009, 2013, 2015a, b; D'Anna et al. 2011; Koeck et al. 2013; Di Lorenzo et al. 2014; Aspillaga et al. 2016; Belo et al. 2016). Studies using acoustic telemetry reported an average residency index, i.e., an estimate of fish presence within the monitored area (Afonso et al. 2008), around 75% indicating that most of the time is spent within that area. These

findings corroborate a previous study conducted with visual census and external tagging that suggested the existence of high territoriality in white seabream (Macpherson 1998).

A high residency index is often related with homing ability, site fidelity, or territoriality. Homing, intended as the ability of an individual to move back to a known location (refuge, reproduction area, capture site, etc.) navigating through unfamiliar areas (Boles and Lohmann 2003; Yahner 2012) was documented for white seabream (Aspillaga et al. 2016; Di Lorenzo et al. 2016). This homing ability, and more generally the capacity of an individual to orientate through different habitats, allows the use of portions of its home range when environmental conditions or physiological needs change over time. Aspillaga et al. (2016) reported a high territoriality in fishes with a different degree of homing capability, probably related to discontinuity of the habitat they encountered in their post-release movements. Di Lorenzo et al. (2014) showed that 17 out of 20 white seabreams returned to the capture site 3 days after being released about 350 m away.

### *Home range*

The extension of home range, that is the area that an animal usually uses throughout its life, is affected by its movement patterns (Burt 1943). It is well known that an individual's home range can be strongly affected by environmental features such as habitat complexity and heterogeneity, availability and distribution of feeding, resting or reproductive grounds (Kramer and Chapman 1999) as well as duration and season of the monitoring period (Koeck et al. 2013; Abecasis et al. 2015). Home range extension in a variety of habitats (natural and artificial reefs, coastal lagoons) and bottom profiles (vertical, flat and mixed) has been estimated through acoustic telemetry using different metrics in terms of surfaces/contours (e.g., Abecasis et al. 2009; Lino et al. 2009; D'Anna et al. 2011; Giacalone et al. 2018b). The main (75% of studies) home range estimator adopted was the KUD95 (kernel utilization distribution). This algorithm, based on a density estimate of positions, provides the probability to find a fish within a certain area, which can be graphically represented and measured (Worton 1989). The remaining studies adopted the

**Table 1** Home range (HR) data provided by eight papers reviewed. *NR* natural reef, *AR* artificial reef

Author	Year	Environment	Bottom profile	HR type	HR surface (ha)		
					Min	Max	Mean ± s.d
Giacalone et al	2018	NR	Vertical	KUD95/50	0.5	1.2	0.8 ± 0.3
Aspillaga et al	2016	NR	Mixed	KUD95/50	16.0	101.0	49.1 ± 26.3
Abecasis et al	2015a	NR	Flat	KUD95/50	43.0	156.0	76.6 ± 39.2
Di Lorenzo et al	2014	NR	Flat	KUD95/50	2.9	40.1	20.6 ± 10.0
Abecasis et al	2013	NR + AR	Flat	KUD95/50	65.0	393.0	187.9 ± 112.7
D’Anna et al	2011	AR	Flat	KUD95/50	1.0	17.0	10.7 ± 8.5
Lino et al	2009	NR + AR	Flat	MCP	57.1	255.7	133.0 ± 87.1
Abecasis et al	2009	Lagoon	Flat	MCP	14.8	52.6	33.7 ± 26.7

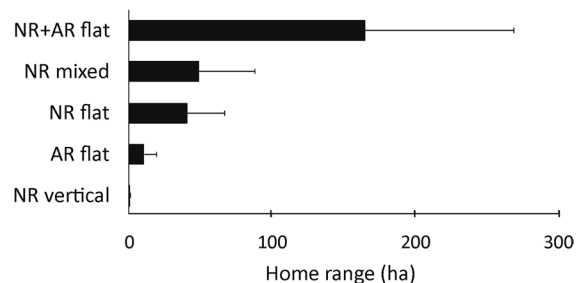
MCP (minimum convex polygon) algorithm, which quantifies the area of the minimum polygon that includes all known fish positions (Kernohan et al. 2001).

Home range extensions as reported in the literature are highly variable, ranging between 0.5 and 393 ha (Table 1). In most of the reviewed studies, fish size and study season are largely comparable (TL between 22 and 30 cm in 80% of tagged fish), whereas bottom habitat and depth profile were different. Thus, this large variation in home range size can probably be attributed to differences in habitat morphology and structure. It is also important to underline that home range areas were not always calculated based on fish position estimates but also considering the position of receivers with the highest number of detections recorded (presence/absence data), a condition that could have affected the real home range extension leading to an overestimation (Aspillaga et al. 2016).

Nonetheless, even if the amount of available data does not allow a robust analysis, a simple ordination of home range values suggests a possible link between home range size and habitat type (Fig. 2). The smallest value was recorded in a natural reef area with a very steep bottom profile (Giacalone et al. 2018b), while the largest value was reported from a very heterogeneous habitat with artificial and natural reefs close to each other and distributed over large and mostly flat areas (Abecasis et al. 2013). Intermediate values were reported from natural reef habitats with flat or mixed bottom profiles (Abecasis et al. 2009, 2015; D’Anna et al. 2011; Di Lorenzo et al. 2014; Aspillaga et al. 2016).

*Diel activity*

Activity patterns in adult white seabream have been investigated mainly through acoustic telemetry and seem clearly based on the circadian cycle. Feeding is a strong driver for diel activity rhythm in this fish. Figueiredo et al. (2005) documented a very clear feeding cycle with a start at sunrise and a peak between midday and early afternoon, followed by a gradual decrease until sunset. This pattern is considered typical for a size-selective, visual predator (Eggers 1977). In general, the night time is characterized by lower levels of activity, which have been associated with a resting or sheltering phase (Harmelin 1987; Abecasis et al. 2013; Aspillaga et al. 2016; Belo et al. 2016). Food search has also been related with the diel activity patterns observed in artificial reefs and surrounding natural habitats. Abecasis et al. (2013) found diurnal activity peaks in artificial and sandy substrata that



**Fig. 2** Mean home range extension in the different habitats frequented by white seabream. NR, natural reef; AR, artificial reef. Flat, vertical, and mixed indicate the prevalent orientation of the seabed profile. Error bars indicate standard deviation (+s.d.)

were associated with feeding, while an inverse relation (night feeding on sand and day sheltering in the artificial reef) was described by D'Anna et al. (2011) and Koeck et al. (2013).

Aspillaga et al. (2016) noted a clear diel pattern in the preferred depth, although such pattern was distributed with individual-based heterogeneity rather than homogeneously across the population: 30% of observed individuals stayed deeper at night, while 39% preferred higher depths during the day. Diel vertical movements during the reproductive period were also observed, with spawning-related larger vertical movements occurring during the day (Aspillaga et al. 2016; Giacalone et al. 2018b). Evidence of vertical movement related with sea conditions was observed in the Medes Islands (western Mediterranean) where, during extreme weather events, white seabream left their preferred shallow habitat, highly exposed to wave action, and moved to deeper areas where the hydrodynamic conditions were less intense (Aspillaga et al. 2016).

### *Habitat use*

Studies on habitat use were mainly based on underwater visual observations and on acoustic telemetry. The results obtained suggest that adult white seabream may use different habitat types according to the geomorphological features of the site and hence to the habitats actually available, selecting what offers better resources in terms of food supply and/or refuges. In the Ria Formosa coastal lagoon (southern Portugal), characterized by sandy, muddy, and seagrass habitats, younger white seabream tend to occupy the seagrass areas, arguably because they provide more food and shelter than bare soft bottoms (Abecasis et al. 2009). Di Lorenzo et al. (2016) described habitat use in the no-take zone of a Mediterranean MPA hosting a high density of white seabream, where six different habitat types were available. Fishes used three habitat types (sand, rock, and *Posidonia oceanica* dead matte) with the same intensity irrespective of their size or sex, and the high residency exhibited excluded the occurrence of random or erratic movements. According to the same authors, the use of different habitat types would allow better resource partitioning in a densely populated area.

In the absence of anthropogenic disturbance and in presence of extensive rocky areas with different

morphological and hydrodynamical characteristics, white seabream tends to select specific rocky areas for different uses. In the no-take zone of an MPA located in southwestern Portugal, fish used three different main areas for different purposes: refuge, feeding, and as passageways (Belo et al. 2016). In particular, the highly complex bottoms close to an islet and subject to more intense hydrodynamics were considered suitable as feeding areas, especially during rising or high tide.

A particular pattern in habitat use was observed in artificial reef areas surrounded by mixed natural habitats. Sub-adult and adult hatchery-reared white seabream tagged (with either traditional tags or acoustic transmitters) and released on artificial reefs in pilot restocking experiments presented a naive behavior most probably influenced by their previous rearing environment. They did not show specific habitat use, exhibiting initial incapacity in the use of artificial substrata for sheltering and feeding (D'Anna et al. 2004; Santos et al. 2006; Lino et al. 2009). In southern Portugal, the home range of adult white seabream included all available habitats: natural reefs close to artificial habitats were used as the core area and thus considered their preferred habitat, but artificial reefs and sandy areas were also visited, particularly during day hours suggesting that they could be feeding grounds (Abecasis et al. 2013). An opposite habitat use was observed in northwestern Sicily and along the French Catalan coast, where white seabream stayed hidden in the artificial reef during the day and moved to the seagrass meadow located on nearby sandy bottoms at night to feed (D'Anna et al. 2011; Koeck et al. 2013). This behavior was interpreted as an anti-predator strategy based on the presence of shelters in the artificial reef and of a larger food supply on the vegetated sandy bottom.

These studies suggest that white seabream may also select artificial reefs as their preferred habitat (Koeck et al. 2013). In this case, a certain number among the monitored fish were permanently resident in the artificial reefs during the study period, while a larger number of fish preferred the natural rocky bottom, and a smaller percentage had an erratic behavior with no clear habitat preference. The reasons behind the different use of artificial structures might be related with the complexity of the artificial reef design, with more complex structures offering more

refuge and sheltering opportunities (Abecasis et al 2013).

The white seabream is known to use crevices and holes as a nocturnal refuge (or to escape from a predator during the day) and open grounds with algae or seagrass for foraging. Because of this behavior, the strict connection existing between feeding and resting/hiding areas could be the key to explain the differences between the home range values reported by different authors. In this sense, where the habitat offers a high complexity, an individual does not need to cover a large area in search of food or a safe place, which can all be found in a limited space. On the other hand, in patchy environments such as rocky platforms or artificial reefs mixed with sandy bottoms or seagrass meadows, the individuals are forced to cover larger areas in search of prey or to find a suitable/safe resting ground.

### *Reproduction*

The spawning period of white seabream is strongly mediated by seawater temperature and takes place, in the Mediterranean, between late winter and early spring with a peak in March and April (Mouine et al. 2007; Giacalone et al. 2018a). Evidence of a change in the movement patterns of white seabream during the spawning season was provided by Divanach (1985), Harmelin-Vivien et al. (1995), and Pastor (2008), who documented a temporary migration to deeper waters (>40–50 m) based on visual census and fishing data.

Studies conducted with acoustic telemetry over habitats characterized by vast flat areas recorded a home range expansion during the spawning period with extended forays to areas outside the regular home range (Di Lorenzo et al. 2014; Abecasis et al. 2015). In contrast, in studies carried out in predominantly vertical environments, there was no evidence of a change in home range extension related to the reproductive phase; instead, it was observed that vertical movements took place in pulses over a few days, during which white seabream visited deeper areas located within their home range (Aspillaga et al. 2016; Giacalone et al. 2018b). These reproductive movements occurred between late night and mid-afternoon and were characterized by a mean duration of 6 to 10 h and a maximum depth of 39 to 81 m (Giacalone et al. 2018b). Movements of such

type suggest that white seabream make resident spawning aggregations, in which individuals move to the spawning site from relatively small and local areas in short migrations of a few hours or less (de Mitcheson and Colin 2012).

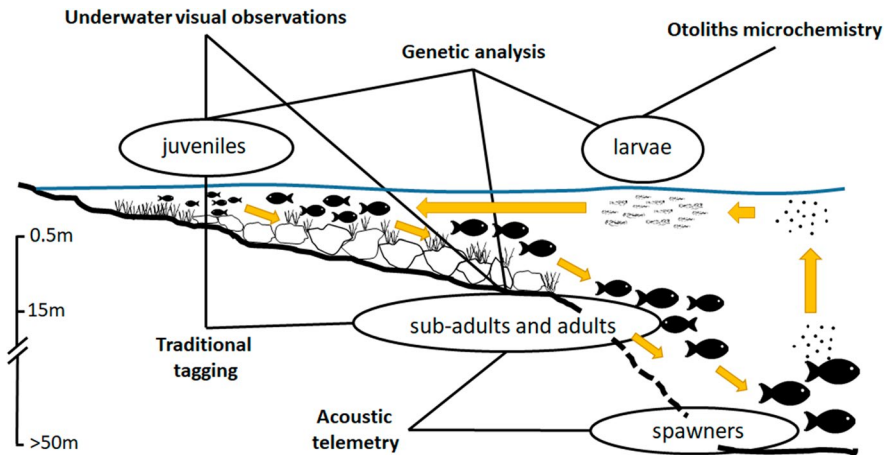
### *Populations*

At the population level, dispersal seems to occur at a spatial scale of 100 km as inferred by Lenfant and Planes (1996) using genetic differentiation and is largely mediated by larval dispersal. González-Wangüemert et al. (2004, 2007), examining the genetic structure of white seabream populations from five southwestern Mediterranean localities, found spatial and temporal genetic differences related mainly to geographic distance and local oceanographic factors. Investigating the genetic structure and connectivity between continental and insular populations of white seabream from north-eastern Atlantic and the Mediterranean, González-Wangüemert et al. (2010) attributed the breakdown of effective genetic exchange in the Azorean population to hydrographic and hydrodynamic factors acting as barriers to the free dispersal of fishes, while no such breakdown was detected between Mediterranean populations characterized by much shorter distance between islands and mainland. The existence of no significant genetic differentiation between four sites located along 100 km of Egyptian coast (southeastern Mediterranean) has been explained by a high level of inbreeding caused by the free movement of adults among sites (Megahed et al. 2020).

Genetic studies have shown that white seabream population structure and connectivity appear to be largely mediated by larval dispersal with adult connectivity having a minor role except on a shorter spatial scale (Lenfant and Planes 1996; González-Wangüemert et al. 2004, 2007, 2010; Megahed et al. 2020). This finding is supported by several studies on the dispersal capabilities of larval, juvenile, and adult individuals using methods such as otolith microchemistry and tagging that show a decrease in dispersal capability across life span (Abecasis et al. 2009; Di Franco et al 2012b; Abecasis et al 2015; Belo et al 2016; Giacalone et al. 2018b).



**Fig. 3** Picture resuming the ontogenetic shift in habitat and depth of white seabream, with the main methods adopted to assess the movement ecology at different life stages. Modified from Harmelin-Vivien et al. (1995)



## Discussion

In this review, we have summarized the main aspects of the movement ecology of white seabream in different environments and regions. We have focused particularly on home range, activity patterns, and habitat use throughout white seabream's life history. This review provides a state of the art of the acquired knowledge as well as of the scientific and methodological gaps dealing with the movement ecology of this species at different life stages.

Information on the movement ecology of each life stage has been obtained from the application of one or more methodologies, as summarized in Fig. 3. The main reason for that is the specificity of the study hypothesis as well as the adequacy of the methods to the kind of information desired in terms of applicability, quality of data provided, research budget, etc. For example, otolith microchemistry cannot be applied to home range estimates of a group of individuals, and acoustic transmitters cannot be implanted on a larva or a small juvenile. As a consequence, there is a lack of information regarding some aspects of the movement ecology of white seabream at particular life stages or, in some cases, an absence of standard sampling protocols as in the case of acoustic telemetry studies.

The estimate of dispersal distances for early life stages of marine organisms remains one of the greatest challenges in ecology. Dispersal patterns of white seabream larvae have been assessed using different approaches including biophysical models, genetics, and otolith microchemistry that allowed to estimate

a potential larval dispersal of ca. 200 km. However, these methods often differ in the spatial and temporal scales of applicability and show strengths and weaknesses. In particular, biophysical models allow to track larvae over longer spatial and temporal scales, but they require biological and physical parameter assessment and validation with empirical data (Assis et al. 2021). Otolith microchemistry has proven to be an effective method to describe the movement history of white seabream larvae but at short scales. These results show the difficulty to track planktonic individuals at sea (Andrello et al. 2013) and highlight the need to implement more effective techniques to describe larval dispersal patterns.

Baptista et al. (2019), Baptista et al. (2020b) found that white seabream larvae are able to orientate their movements towards a favorable settling habitat. These findings highlight the importance of the behavioral and skill changes occurring during the larval phase. Moreover, the hypothesis that white seabream larvae are able to influence their own transport and distribution in coastal areas requires further studies to investigate physical and biological features that could affect their movements, especially in a context of ongoing climate change. New knowledge about larval dispersal patterns could also contribute to explain the inter-individual variability that influences the dispersion and settlement processes of white seabream (Baptista et al. 2020a) and the connectivity dynamics among populations (Pujolar et al. 2013).

Regarding juveniles, movement ecology information focused mainly on habitat selection, assessed through direct underwater observation (Garcia-Rubies

and Macpherson 1995; Harmelin-Vivien et al. 1995; Macpherson 1998). There is some evidence that different microhabitats may be chosen according to the general seabed morphology of the area and to fish size. This variability suggests that further research is needed to assess the type of habitat required by such a widely diffused species, with surveys covering many different submerged landscapes from rocky shores to seagrass beds to breakwaters, which can all be used by white seabream during the first months of life (Macpherson 1998). Coastal lagoons have been shown to act as nursery areas in southern Portugal (Abecasis et al. 2009; Baptista et al. 2020a, b). Lagoons and more generally transitional waters differ from open coastal areas in terms of environmental conditions and available microhabitats (Kennish and Paerl 2010), and their role as fish nurseries in the Mediterranean has been highlighted (Maci and Basset 2009; Verdiell-Cubedo et al. 2013).

Unlike habitat selection, there are still knowledge gaps concerning home range and activity patterns of juvenile white seabream. A better knowledge of how microhabitats are used in space and time as a source of food and shelter could shed light on the movements involved in settlement and local distribution and help to explain the successful presence of this species in so many different coastal habitats (Garcia-Rubies and Macpherson 1995; Harmelin-Vivien et al. 1995). The use of video tools, avoiding the disturbing presence of divers, could aid in the collection of data on short-scale movements of juveniles across a diel cycle and help to ascertain when and how fish move to exploit the available resources (Delcourt et al. 2013; Brancioni et al. 2019; Espadero et al. 2020).

The studies that used acoustic telemetry on adults revealed the most complete and abundant information in terms of home range, habitat use, and spawning-related activity patterns and movements. The results of this review highlight the existence of strong territorialism and diurnal activity in white seabream. Importantly, habitat structure and sea bottom topography seem to affect the home range extent but also the activity pattern, with a clear switch from diurnal to nocturnal foraging activity when the risk of potential predation increases.

However, technical details about the methodology adopted by the different studies have to be considered, especially those dealing with the home range estimation. The starting point of any home range

measurement is the actual geographical position of an individual (Gregory 2017). The home range can be estimated using different position-based methods: (1) assuming the receiver's position as the fish location, (2) inferring a "fish activity center" position based on triangulation of detected signals at several acoustic receivers in fixed time intervals (Simpfendorfer et al. 2002), and (3) using more recent positioning methods such as the YAPS software (Yet Another Positioning Solver: Baktoft et al. 2017). The position error associated with each method ranges from hundreds of meters, when using the receiver location, to few tens of meters when using the fish activity center (Giacalone et al. 2005), to less than 10 m using YAPS. Thus, the type of fish positions used can strongly affect the precision of home range estimates.

Another important aspect of home range calculation is the algorithm used. Different methods are available: grid cells (Haugen 1942), minimum convex polygon or MCP (Hayne 1949), kernel utilization distribution or KUD (Worton 1989), and local convex hull or LoCoH (Getz et al. 2007), to name a few. In each of these methods, some parameters can be arbitrarily decided by the researcher such as grid dimension, percentage of positions included in the calculation, and smoothing factor (*h value*), all having a direct effect on the final result in terms of home range shape and extent. In five out of eight studies providing home range estimates, KUD was used on fishes' center of activity, while in the remaining studies, the calculation of the home range (applying KUD and MCP) was based on the receivers' position, which resulted in a very likely overestimation (as suggested by Aspillaga et al. 2016).

In order to compare different home range estimates from different studies or locations, it is recommended to use the same calculation method, but also the same or similar number of positions and methods used to obtain those locations (Gregory 2017). For this reason, the adoption of a common guideline or a shared data acquisition and analysis protocol should be encouraged by the acoustic telemetry researchers' community.

As far as activity patterns are concerned, a crucial point is the choice of the variable used as a proxy of activity. In most cases, the hourly bin of detections (a simple binary code applied to detections recorded each hour in a day) was used, based on the assumption that white seabreams prefer to stay hidden when

resting (detections=0) while they swim or feed in open spaces when active (detections>0). The variation of the raw number of detections per hour was never adopted as a response variable as it can vary between different days (depending on the sea conditions) or between day and night. It has been noted that the sounds produced by benthic animals living in rocky environments increase over night and may influence the ultrasonic sound detection (Payne et al. 2010). In order to detect a variation between day and night patterns, range testing (i.e., the characterization of the receivers' detection range) and the use of reference tags helping the interpretation of acoustic data have been increasingly recommended in recent years. Unfortunately, among the reviewed papers, only five of them (Koeck et al. 2013; Di Lorenzo et al. 2014; Di Lorenzo et al. 2016; Abecasis et al. 2015; Giacalone et al. 2018b) have reported information about range testing, while only one paper adopted reference tags and applied a corrective coefficient for the standardization of acoustic detections (Koeck et al. 2013).

The use of accelerometers, which can gather data regarding body movement in three dimensions, is another option for investigating individual activity making it easier to discriminate what a tagged individual is actually doing. None of the reviewed studies adopted accelerometer sensors, probably because of the high size ratio between tags and fish. However, in two occasions, ultrasonic tags were equipped with pressure sensors providing important information about the depth profile of the detected movements (Aspillaga et al. 2016; Giacalone et al. 2018b).

Finally, the relationship between tag size and body size represented a limit to the application of acoustic telemetry on white seabream, since the smallest individual tagged with an acoustic transmitter was 18 cm TL (D'Anna et al. 2011). Since this species undergoes an ontogenetic shift in habitat usage and gregariousness, it would be interesting to look at the home range and habitat use of settlers using the recently developed smaller acoustic tags.

At the population level, information on connectivity and dispersal patterns comes mainly from the application of genetics. Studies on the genetic structure of white seabream populations showed that the segregation of different populations occurs at a spatial scale of 100 km (Lenfant & Planes 1996). Large-scale larval dispersal (> 200 km, Di Franco et al. 2012b), as well as indications of a potential large migration

of sub-adult individuals (Abecasis et al. 2009; Belo et al. 2016) corroborate this finding. Genetic differences among populations are mainly related to geographic distance and local oceanographic factors that act as barriers to the free dispersal of fish (González-Wangüemert et al. 2004, 2007, 2010). However, many aspects dealing with the relationships between oceanographic fronts and genetic structure are still poorly understood. Further studies are needed for a better understanding of the spatial structure and connectivity among white seabream populations and to plan effective management tools for the sustainable management of this important species.

## Conclusions

The knowledge of movement patterns, home range, and dispersal from the individual up to the population level remains the most powerful tool to protect and manage white seabream and more generally the wild populations of most species. This review summarizes the most relevant findings about the movement ecology of white seabream. The studies made have shed light on important behavioral and ecological aspects such as the change in movement patterns as an adaptation to different habitat structures. Despite the specificity of the different methodologies and the amount of information available in the literature, more efforts should be made to (i) elaborate and adopt common research protocols, especially in the case of acoustic telemetry studies, (ii) investigate the role of environmental variables as drivers of larval movements, and (iii) develop new technologies for assessing the movement patterns in juveniles.

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## Declarations

**Ethics approval** No approval of research ethics committees was required to accomplish the goals of this study because the results presented are based on a literature research and did not directly involve any living organism.

**Conflict of interest** The authors declare no competing interests.

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