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Meagre (*Argyrosomus regius)* move westward with favourable flows along the south coast of Portugal

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Abstract

Based on acoustic detections from a network of five stations along the south coast of Portugal, 25 transits of tagged meagre were identified between 2019 and 2020, mostly in summer. Comparisons with hourly current measurements from a moored Acoustic Doppler current Profiler and an High Frequency Radar system indicate that meagre move westward with favourable alongshore flows at a confidence level > 90% (while eastward transits observations were too few to be significant). Several similar transits of different individuals occurred within two days suggesting a species response to environmental changes. The analysis of surface seawater temperature from ERA5 shows that meagre always swam westward towards colder water, despite their warm water affinities. As such, they reached food-rich upwelling areas when the water temperature was higher than usual (due to the westward advection of warm water), probably optimizing their feeding ability. The demonstrated alongshore meagre movements in response to temperature variations induced by the mesoscale coastal circulation is particularly relevant for the management of this high economic value species in southern Portugal.

Keywords: Gulf of Cadiz; Coastal circulation; Acoustic telemetry; Fish behaviour; Fish movements

1) Introduction

Many fisheries management measures, such as closures or the design of Marine Protected Areas, require the understanding of fish movement patterns and how they relate to the surrounding environmental conditions (Allen and Singh, 2016). Although recent technological developments have allowed researchers to track and investigate the population dynamics of several marine species (Calò et al., 2013), their relationship with the mesoscale oceanic circulation remains largely unexplored.

The meagre *Argyrosomus regius* (Asso, 1801) is a large oceanodromous, benthopelagic teleost fish, reaching up to 1.80 m in total length, over 50 kg in body weight and with a maximum reported lifespan of 44 years (Gil et al., 2014; González-Quirós et al., 2011; Prista, 2013). It inhabits waters less than 200 m in depth (Lazo et al., 2010; Prista, 2013; Quero and Vayne, 1985) along the eastern Atlantic shelf (from southern Scandinavia to the Gulf of Guinea) and the Mediterranean Sea (González-Quirós et al., 2011; Parenti, 2020; Prista, 2011; Quero and Vayne, 1985). In winter, the species is found in relatively deep and cold water, where its behaviour is hardly described (Morales-Nin et al., 2012; Winkler et al., 2023). During summer, it moves to shallow and relatively warm coastal waters (typically, less than 30 m) for breeding in spawning aggregations (Hubans et al., 2017; Morales-Nin et al., 2012; Prista, 2013). Variations in local fisheries landings indicate that juveniles and adults migrate in schools along the coast (González-Quirós et al., 2011; Prista, 2013; Quero and Vayne, 1985), making them particularly vulnerable to fishing pressure owing to their high economic value and demand (Hubans et al., 2017; Monfort, 2010; Nousias et al., 2020; Poli et al., 2003).

To better understand the dynamics of meagre movements and their environmental triggers, this study evaluates the alongshore displacement of individuals (based on acoustic telemetry) together with the coastal circulation (from current measurements) along the South Portuguese coast. It is shown that meagre travel westward with favourable flows. This result is highly relevant for an efficient management of this important fishery resource. Changes in water temperature due to current advection are discussed as a potential driver of this behaviour.

2) Material and Methods

2.1. Study area

The study area encompasses the western bight of the northern inner shelf of the Gulf of Cádiz, which lies between Cape São Vicente (CSV) to the West and Cape Santa Maria (CSM) to the East along the south Portuguese coast (Figure 1a). The region, broadly oriented east-west, corresponds to the southern extremity of the Iberian upwelling system that develops in spring-summer along the western Iberian coast (Fiúza, 1983; García Lafuente and Ruiz, 2007; Relvas and Barton, 2002).

The tidal regime in the region is dominantly semidiurnal and mesotidal, with tidal currents oriented principally cross-shore (i.e., broadly north-south; Garel et al., 2016). The net (or subtidal) coastal circulation, corresponding to the flow averaged over one or several tidal cycles, is mainly alongshore with maximum velocities up to approximately 0.5 $m.s^{-1}$ (de Oliveira Júnior et al., 2022; Garel et al., 2016). At a seasonal time scale, the direction of these flows is balanced near CSV, but eastward flows progressively dominate, up to 80%, towards CSM (de Oliveira Júnior et al., 2022). Eastward flows result from upwelling jets produced locally or remotely along the western Portuguese coast (de Oliveira Júnior et al., 2022; Fiúza et al., 1982; Relvas and Barton, 2002; Relvas and Barton, 2005). Westward flows develop when upwelling favourable winds (i.e., from the western quadrant) relax or reverse (de Oliveira Júnior et al., 2021; Garel et al., 2016; Relvas and Barton, 2002; Sánchez et al., 2006; Teles-Machado et al., 2007). For details about the shelf circulation and its drivers, the readers are referred to de Oliveira Júnior et al. (2022).

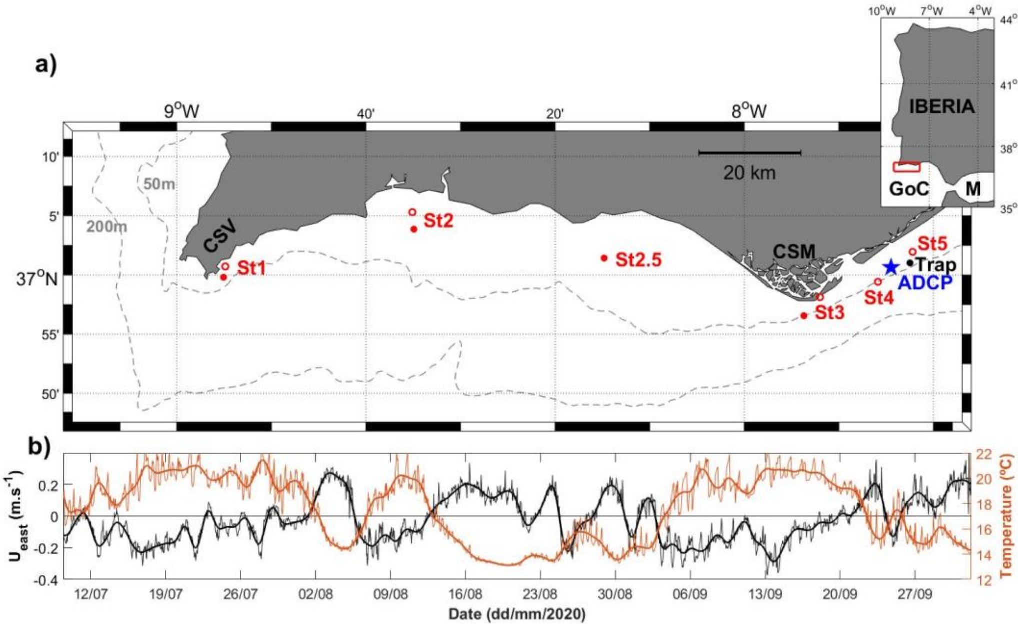


Figure 1. a) Location of the study area, between Cape San Vicente (CSV) and Cape Santa Maria (CSM) in Southwest Iberia (for general location, see inset; GoC: Gulf of Cadiz, M: Mediterranean Sea). The acoustic receiver stations 1 to 5 and nearby HFR nodes are indicated as non-filled and filled red circles, respectively (St2.5 corresponds to a HFR node, only). The locations of the ADCP mooring and tuna trap are indicated as a blue star and black dot, respectively. The 50 m and 200 m isobaths are reported as grey dashed lines. b) Depth-averaged eastward velocity (black lines, left axis, in m.s^{-1}) and near-bed water temperature (red lines, right axis, in °C) recorded by the ADCP (blue star in a) in July-September 2020; thin lines are raw data, thick lines are low-pass filtered data (as described in Section 2.3) to remove semidiurnal tidal oscillations.

Of special interest for this study, eastward flows advect cold water from the West coast and CSV, where the upwelling activity is strongest (Fiúza, 1983; Relvas and Barton, 2002; Relvas and Barton, 2005; Sánchez and Relvas, 2003; Vargas et al., 2003). In contrast, westward flows advect a tongue of warm water leaning along the coast, proceeding from Cádiz area located further East (Fiúza, 1983; García-Lafuente et al., 2006; Relvas and Barton, 2002). As a result, the coastal circulation in South Portugal is associated with sharp spatial and temporal water temperature variations in summer (Garel et al., 2016; Relvas and Barton, 2002). Changes at a given location frequently exceed 1°C per day for several consecutive days. An example is provided in Figure 1b, where the near bed temperature at an ADCP mooring (blue star in Figure 1a) oscillated between 14°C and 22°C with the zonal flow direction during the 2020 summer. Over several years (2014-2022), the summer records at this station ranged between 12.8°C (equivalent to the lowest value in winter) and 24.7°C (unpublished data). Although not specifically addressed by previous studies, such a regime strongly suggests sharp changes in the water properties near the coast.

2.2. Acoustic telemetry

Between September 2018 and October 2020, a total of 28 adult meagre, above 10 kg in weight and ranging between 1.12 and 1.43 m in total length, were passively captured in a tuna trap (Figure 1a) and released at the same location after surgical implementation of an acoustic transmitter. For surgery, fish were placed in a stretcher with running seawater through the gills for oxygenation and their eyes were covered with a wet cloth to reduce stress. The transmitter (V16-5x InnovaSea, with length of 98 mm, diameter of 16 mm and a weight in the air of 37 g) was inserted into the peritoneal cavity through a small incision in the ventral midline, which was closed with three separate stitches using an absorbable monofilament (Novosyn from Bbraun). The acoustic transmitters had a random emission signal between 60 and 120 seconds and an expected lifetime of 1,292 days.

To detect tagged fish presence, a network of acoustic receivers was installed from July 2018 (ongoing) along the study area in 10-30 m water depths. Owing to their detection range of approximately 1 km, receivers less than 2.2 km apart were considered as a single station, referred to as St1-5 from West to East (for location, see Figure 1a). St1 comprised 30 receivers, St5 two receivers, and St2, 3, 4 a single receiver. The present study considers fish detections until November 2021.

2.3. Current data acquisition and processing

Coastal current velocity records concomitant with fish detections (e.g., between March 2019 and November 2021) were obtained from a High Frequency Radar (HFR) system and Acoustic Doppler Current Profiler (ADCP) seabed moorings.

A pair of HFR antennas has been providing, since 2016, hourly surface velocities with a spatial resolution of about 1.5 km from the innershelf up to 60 km off the studied coast (CMEMS, 2017). The records on the innershelf were validated against in-situ current measurements from ADCPs bottom-mounted at about 20 m water depth along the coast (de Oliveira Júnior et al., 2022). The HFR time-series were extracted at the node nearest (i.e., < 4 km) to St1, St2 and St3 (Figure 1a, filled red circles). For St4 and St5, the closest HFR node was more than 12 km away and was not considered (for details about the HFR coverage area, see de Oliveira Júnior et al., 2022). The HFR velocities were also obtained at an intermediate location (without acoustic receiver nearby) between St2 and St3, referred to as St2.5. Gaps of up to 12 h in the velocity time series at each station were relatively rare (< 9%) and were interpolated linearly. Larger gaps occurred mainly at the western stations (St1, St2 and St2.5) during May 2019 and July 2020. A low-pass Butterworth filter with a cut-off period of 40 h was applied to the time series to remove the main tidal (and other high frequencies) oscillations.

An ADCP was installed on the seabed in 23 m water depth, between St4 and St5 (Figure 1a, blue star), for four periods of time: 29 Nov. 2018 – 11 Jun. 2019; 24 Jul. – 19 Nov. 2019; 23 Jan. – 25 Jun. 2020; and 09 Jul. – 02 Oct. 2020. For each deployment, the instrument (either a Workhorse 600 kHz or a Sentinel V 500 kHz from TRDI) provided hourly velocities with standard deviations less than 0.015 $m.s^{-1}$ every 0.5 or 1 meter along the water column. The velocity profiles were depth-averaged, discarding 15% of the records immediately below the lowest water surface (21 m at spring tide) to avoid signal contamination at the boundary. The depth-averaged velocities were lowpass-filtered as for the HFR records (e.g., Figure 1b) and used as a proxy for velocities at St4 and St5.

2.4. Data analysis

Fish displacements along the coast (hereafter referred to as transits) were identified based on pairs of acoustic detections of the same individual at distinct stations within a reasonable time lapse considering the distance travelled alongshore. For the longest (> 65 km) travels (i.e., between western stations St1-2 and eastern stations St3-5), transits lasting less than 100 h were considered (the discarded ones lasted more than one week); for short (< 17 km) transits, between the eastern stations, the limit was 10 h. These thresholds - that include most of the detection pairs from the dataset - are compatible with direct (rather than back-and-forth or multi-stage) displacements as they correspond to realistic swimming velocities and to the time scale of the alongshore current variability (about 3 days; Garel et al., 2016).

The alongshore current directions at the acoustic stations were determined based on the east-component of the subtidal velocities (HFR for St1-3 and ADCP for St4-5). For each transit, the current velocity was obtained at the exact time of meagre's detections, i.e., at both the start and end stations. The mean HFR velocity during the transit was also computed at intermediate stations, if any (as it was not known when the fish overshooted the station). In addition, the mean current velocity near CSM was also reported, as it is generally representative of the direction of coastal currents along the studied coast, especially for relatively strong (> 0.1 m.s^{-1}) currents (de Oliveira Júnior et al., 2022). The mean current was computed using records from the ADCP or from the HFR node near St3 (when ADCP data were not available). Details about gaps in the ADCP and HFR time-series and corrective measures are provided for each identified transit in Section 3 "Results" (see Table 1).

The directions (eastward or westward) of fish transits and of the concurrent alongshore subtidal flow were gathered in a 2x2 contingency table. The significance of the association between transit and current directions was determined using a Fisher's exact test, which indicates whether an association is random (0) or not (1) for a given confidence level (Fisher, 1922; Upton, 1992).

3) Results

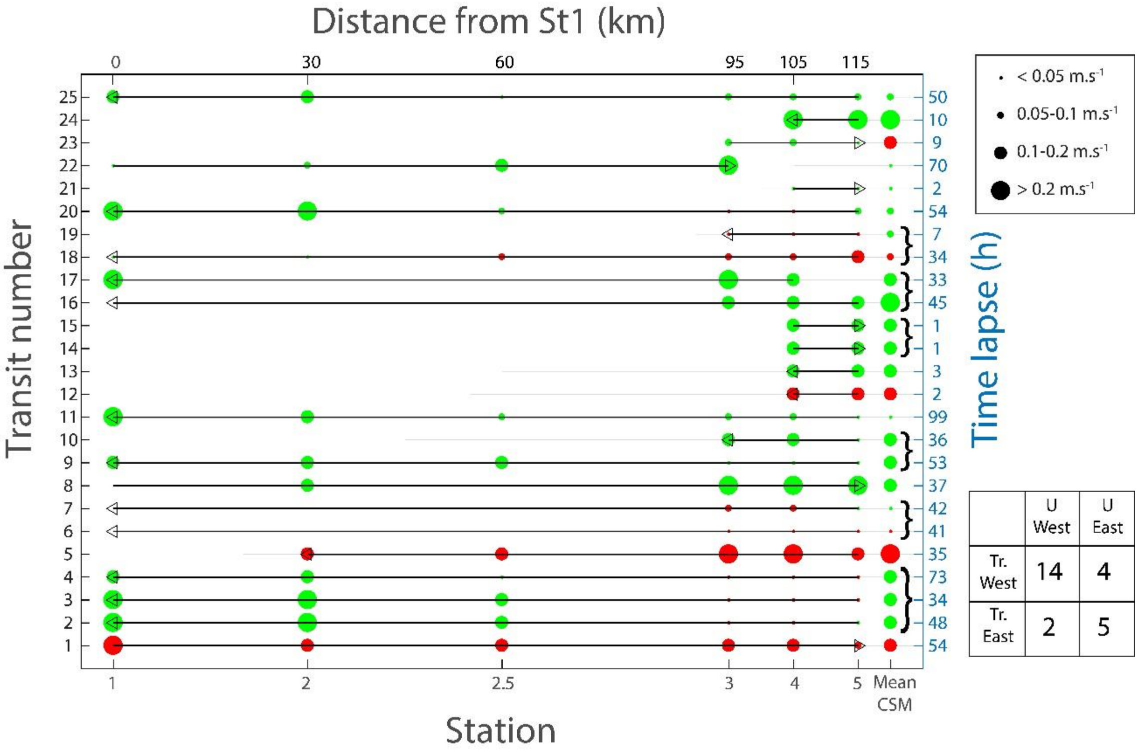
Acoustic detections occurred throughout the year but were more frequent between March and September, when 25 transits were identified (Table 1). Six of these transits are constituted by detections at two consecutive pairs of stations (e.g., St1 and St3, then St3 and St5), with a short time (< 2.5 h) between fish arrival (first detection) and leaving (second detection) at the middle station (e.g., St3). Because fish were tagged near CSM, at the eastern limit of the monitoring array (see tuna trap location in Figure 1), most of the transits (18 events, 72%) were westward.

Table 1- Detected fish transits along the study area. Grey areas indicate transits of several individuals in the same direction within two days.

Transit number	Start	End	Time start	Transit duration (h)	Fish ID	Missing data
1	St1	St5	29/03/2019 10:08	54	3	
2	St5	St1	30/05/2019 15:23	48	6	
3	St5	St1	31/05/2019 12:09	34	3	
4	St5	St1	01/06/2019 18:43	73	2	
5	St5	St2	02/07/2019 10:49	35	1	No ADCP record at Armona: mean velocity computed from HFR data near St3
6	St5	St1	23/07/2019 18:06	41	5	ADCP records started 15 h after detection: mean velocity computed from HFR data near St3 No HFR record at St1, St2 and St2.5
7	St5	St1	24/07/2019 13:31	42	9	No HFR record at St1, St2 and St2.5
8	St1	St5	26/07/2019 12:04	37	5	HFR records started 5 h (St1 and St2) and 1 h (St2.5) after detection: the mean velocity at St2 and St2.5 was computed, only (i.e., no velocity at St1)
9	St5	St1	23/08/2019 07:49	53	10	
10	St5	St3	25/08/2019 21:47	36	15	
11	St5	St1	31/08/2019 12:36	99	8	
12	St5	St4	27/09/2019 15:48	2	21	
13	St5	St4	12/10/2019 04:06	3	17	
14	St4	St5	15/11/2019 04:48	1	9	
15	St4	St5	15/11/2019 04:51	1	2	
16	St5	St1	27/05/2020 09:20	45	7	No HFR record at St1, St2 and St2.5

17	St4	St1	28/05/2020 09:20	33	3	No HFR record at St2 and St2.5
18	St5	St1	08/07/2020 13:00	34	10	ADCP records starting 21 h after detection: mean velocity computed from HFR data near St3
19	St5	St3	09/07/2020 21:36	7	13	
20	St5	St1	12/07/2020 19:51	54	18	
21	St4	St5	23/08/2020 00:04	2	6	
22	St1	St3	29/08/2020 10:43	70	3	
23	St3	St5	03/09/2020 16:33	9	3	
24	St5	St4	13/09/2020 19:44	10	5	
25	St5	St1	20/10/2020 11:22	50	27	No ADCP record at Armona: mean velocity computed from HFR data near St3

Nine transits in the CSM area (i.e., between St3 and St5) were shorter than 10 h, except transit #10 that lasted 36 h. The 16 longer transits between the western (St1-2) and eastern (St3-5) stations lasted between 33 h and 99 h, the majority (13) lasting less than 55 h. The corresponding fish average swimming speed was between 0.1 m.s^{-1} and 1.2 m.s^{-1}, with the majority (16 transits) between 0.5 m.s^{-1} and 1 m.s^{-1}. It is noted that for about half of the transits (13 events, 52%), two to three fish travelled in the same direction within two days (Table 1, grey rows; see also the brackets at the right of the mean CSM velocities in Figure 2).



	U West	U East
Tr. West	14	4
Tr. East	2	5

Figure 2. Fish transits (left y-axis) and eastward subtidal current direction at stations St1-5 and CSM (lower x-axis; the distance eastward from St1 is reported on the upper x-axis, in km). The transit direction is indicated by the arrow on each horizontal line. The size of the circle at each station indicates the current magnitude (no data if no circle on the line). The circle colours indicate whether the transit was with favourable (green) or opposed (red) currents. Brackets (near the right y-axis) indicate distinct fish transits in the same direction within 2 days. The correspondence between transit (Tr) and current (U) directions are summarized in a contingency table (bottom right).

For each transit, the mean (zonal) current velocity near CSM was between 0.03 and 0.23 m.s^{-1}, with most (16) being larger than 0.1 m.s^{-1} (Figure 2), indicative of a well-developed circulation. In agreement, the current direction was generally constant, both spatially and temporally, during the transits (i.e., the circles have generally the same colour for a given transit in Figure 2). Thus, the mean velocity near CSM was a suitable indicator of the main (or dominant) current direction along the coast during each transit. Exceptions occurred for a few transits characterized by weak (< 0.05 m.s^{-1}) coastal flows (e.g., transits #7, #19 and #23).

Considering the mean velocity direction near CSM, 19 out of 25 (76%) transits were performed with favourable currents (Figure 2, green circles), 14 of those westward and five eastward (see the transit direction indicated with arrows in Figure 2). Moreover, four out of six (67%) transits with opposed currents (Figure 2, red circles) were towards the West. The same results were obtained with unfiltered data as tidal flows are mainly cross-shore (the difference being occasional changes in the direction of weak flows).

The above results suggest a strong correspondence between alongshore currents and transit directions, particularly when fish were moving westward. For statistical confirmation, the Fisher's exact test was applied, considering a one-tailed hypothesis because of the large predominance of westward transits. The test indicates that the association between westward flows and transits is true (i.e., not random) at a 96% confidence level. The same result (at the same confidence level) was obtained discarding the nine transits (#6, #7, #11, #18-22 and #25) with the weakest (< 0.1 m.s^{-1}) mean flow at CSM, for which the dominant current direction was often ambiguous (i.e., with opposed directions at stations). Overall, the criterion selected to identify the coastal flow direction and the exclusion of events with an unclear dominant direction did not affect the high confidence level of the one-tailed Fisher's exact test, which remained larger than 90% in all cases.

4) Discussion

The Fisher's exact test is an alternative to the Chi-Square Test of Independence when one or more of the cells count in a 2×2 table is less than 5 (see Andres and Tejedor, 1995); it is therefore well-suited for the analysis of the present results (see the contingency table in Figure 2). The test is based on the hypothesis that the probability distribution is normal, meaning that the occurrence of eastward and westward flows is balanced along the studied coast. The analysis of long-term (2016-2020) HFR data has shown that this is the case near CSV, only, while eastward flows increasingly dominate (up to 80%) towards CSM (see Table 2 in de Oliveira Júnior et al., 2022). Similar results were obtained considering only the period of fish transit detections, between March and September of 2019 and 2020 (not shown). The non-normality induced by the dominance of eastward flows reinforces the statistical correspondence established by the Fisher's exact test between fish transits and westward flows (the latter being less frequent than eastward flows). Although based on scarce data, the results strongly support that meagre displace with favourable currents along the coast, at least in the westward direction.

Most meagre detections occurred between March and September, in agreement with their known preference for shallow waters during the summer months (Winkler et al., 2023). The detection of individuals performing similar and nearly concomitant transits further supports an observed tendency to travel in schools in response to environmental triggers (unpublished data). While water temperature is thought to be the most important factor determining the migration and reproduction of meagre (Duncan et al., 2013; Monfort, 2010), it is also well-known that coastal flows in summer are associated with large temperature variations in the study area (e.g., Figure 1b; Garel et al., 2016).

To discuss further potential relationship between transit direction and current-induced temperature variations, ERA5 hourly sea surface temperatures (SST) were extracted near CSV and CSM between March 2019 and November 2020 (Figure 3). The observed SST, between 15°C and 25°C, was within the range of temperatures favoured by meagre (Nousias et al., 2020; Winkler et al., 2023). In summer, the SST was significantly lower at CSV than at CSM due to the strong upwelling activity at this location (Fiúza, 1983; Vargas et al., 2003). Thus, meagre swimming eastward in summer reached relatively warmer water (see transits #8 and #22 in Figure 3), in agreement with their thermal preferences (Winkler et al., 2023). The latter is strongly linked to the optimum temperature at which the physiological functions of a fish are at maximum efficiency (Bernatzeder & Britz, 2007). For example, anecdotal reports suggest that meagre do not feed when the temperature is less than 15°C. Thus, eastward transits were probably triggered by relatively low temperatures at CSV (< 19°C in Figure 3). In contrast, all westward transits - except transit #25 that occurred in Autumn - started when the water temperature was sharply rising or peaking (Figure 3) owing to strong westward flow advection (e.g., Garel et al., 2016), as exemplified in Figure 1b. This includes transits with opposed (eastward) currents, supporting that temperature is a major environmental trigger for meagre travels. Meagre reached water near CSV that was 0.6°C to 3°C colder than when they left CSM (Figure 3), opposed to their warm water affinity. However, the water was also significantly warmer than usual at this upwelling area which might be otherwise less appealing due to cool water temperatures. Thus, it is hypothesized that meagre moved with warm westward flows to reach upwelling, food-rich grounds (near CSV) where their feeding capacity is increased by the (untypical) relatively warm water.

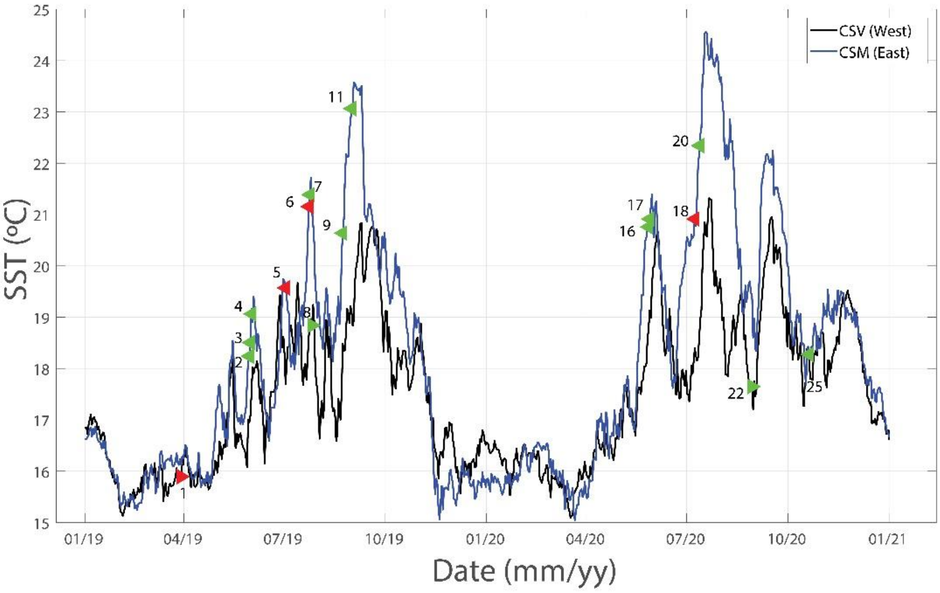


Figure 3. SST near Cabo Santa Maria (CSM) at East (blue line) and Cabo São Vicente (CSV) at West (back line) from March 2019 to November 2020 and indication of the start of the westward (>) and eastward (<) transits between St1-2 and St3-5 with favourable (opposed) currents in green (red). The position of the markers along the y-axis indicates the SST at the start of each transit. The transit number is indicated near each marker.

5) Conclusions

This research provides one of the few results on the association between fish movement and the mesoscale circulation in coastal areas. The analysis of concurrent acoustic detections and current measurements shows that, in summer, meagre move along the South coast of Portugal with favourable alongshore flows. The correspondence is particularly robust (i.e., not random at > 90% confidence level) for westward transits, which were largely dominant in the observations. Several individuals performed the same transit within two days suggesting a species behavioural response to environmental changes.

The correspondence between meagre movement and coastal current directions is related to drastic temperature variations induced by the advection of warm and cold water by westward and eastward flows, respectively. Few transit observations suggest that low temperatures at CSV trigger eastward movements towards warmer water, in agreement with their thermal preference. In contrast, meagre travel westward towards relatively colder water. This behaviour is explained by the concurrent westward flow advection that raises the temperature near CSV and thus probably increases the feeding abilities of meagre in a food-rich area with otherwise significantly cooler upwelled water.

Overall, this research contributes to the knowledge of meagre dynamics and support the species' warm water affinity. In South Portugal, meagre movements are associated with water temperature variations induced by the mesoscale circulation. This information is particularly relevant for the efficient management of such an economically important species. In particular, the possibility of apprehending and anticipating meagre movements based on coastal flow direction could lead to directed measures such as temporal fisheries closure. To gain further insight into the species behaviour, future studies should expand the times-series of acoustic detections coupled with current measurements, along with in-situ measurements of water quality parameters at both CSM and CSV areas.

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