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Migration and diving behavior of *Centrophorus squamosus* in the NE Atlantic. Combining electronic tagging and Argo hydrography to infer deep ocean trajectories

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ABSTRACT

A total of nine leafscale gulper sharks *Centrophorus squamosus* (Bonnaterre, 1788), were tagged with pop-up, satellite, archival, transmitting tags (PSAT) in the Marine Protected Area (MPA) of El Cachucho (Le Danois Bank) located in waters to the north of Spain, (NE Atlantic). Tags provided data on time, pressure and temperature that were used to examine movement patterns and diving behavior. Data collected from Argo floats in the study area have been used to devise a simple geolocation algorithm to infer the probable routes followed by this species. Tag release points revealed that *C. squamosus* moved both to the west (Galician waters) and to the north (Porcupine Bank) from the tagging area, suggesting well defined preferred pathways. The inferred trajectories indicated that sharks alternate periods constrained to specific geographical regions with quick and prompt movements covering large distances. Two sharks made conspicuous diurnal vertical migrations being at shallower depths around midnight and at maximum depths at midday, while other sharks did not make vertical migrations. Vertical movements were done smoothly and independently of the fish swimming long-distances or resting in the area. Overall results confirm that this species is highly migratory, supporting speeds of 20 nautical miles.day^{-1} and well capable to swim and make vertical migrations well above the abyssal plain.

1. Introduction

Knowledge of the movements and depth and temperature preferences of fish throughout their life cycle is crucial not only for understanding more about their biology and ecology, but also for conservation or management purposes. In general deep-water sharks are considered highly vulnerable species due to their life-history characteristics, (slow growth, late maturity and few off-spring), therefore obtaining more knowledge about their use of habitat and behaviors could help to preserve these deep-living species.

Particularly, the leafscale gulper shark, *Centrophorus squamosus* (Bonaterre, 1788) and Portuguese dogfish, *Centroscymnus coelolepis* (Barbosa du Bocage & Brito Capello, 1864) have been exploited commercially for many years (Clarke et al., 2002, 2005; Correia et al., 2003; Gordon et al., 2003; Pajuelo et al., 2010). Due to their population dynamical characteristics and the severe decline of catches, since 2010 several management measures have been adopted by EU countries to protect them and other deep-water shark populations in the NE Atlantic. In 2012 the EU TACs for deep-water sharks have been set at zero, and no bycatch has been permitted since (Council regulation (EU) 104/2015). A recently studied based on scientific deep-water trawl surveys carried out in Rockall Trough (NE Atlantic) do not suggest there has been a recovery of this species (Neat et al., 2015). Due to this decreasing trend in the population biomass and the apparent long lifespan and generation time of this species (Clarke et al., 2002), the leafscale gulper shark is currently included in the category *Endangered* on the IUCN Red List (Guallart et al., 2015).

Even though there is increased concern about the status of deep-water sharks, for most of the species there is rather limited information on their general ecology and life cycles, in particular little is known of the extent of their large-scale migrations and habitat preferences. Understanding these patterns of behavior is vital to assess the effect of marine protected areas (MPAs), individually or designed as networks, on their protection. Besides, determining whether changes in their behavior are the result of foraging opportunities, predator/competitor avoidance, or

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bioenergetic advantages is important for determining what effect these individuals have on ecological communities and how susceptible they may be to anthropogenic pressures or environmental perturbations such as habitat loss or climate change (Andrews et al., 2009).

The leafscale gulper shark, *Centrophorus squamosus* (Bonaterre, 1788), is a deepwater shark widely distributed in the northeast Atlantic, from Iceland south to Senegal, including Madeira, Azores and the Canary Islands (Hareide et al., 2001), and it lives also in the western Indian and western Pacific oceans. It is usually found on continental and insular slopes between 300 and 1500 m (Compagno, 1984; Clarke et al., 2001a, b). A large-scale distribution study based on sex, maturity and environment data collected from different areas indicates segregation patterns according to sex and maturity that might be associated with large-scale migrations (Moura et al., 2014). Genetic studies also suggest habitat partitioning but confirm the hypothesis of a single genetic stock (Verissimo et al., 2012).

In the northeast Atlantic pregnant females of *C. squamosus* are rarely caught (Girard et al., 1999; Clarke et al., 2001; Crozier, 2001; Figueiredo et al., 2008). Thus, limited information on some aspects of its reproduction exists. *C. squamosus* is an aplacental viviparous species (lecithotrophic viviparity). The ovarian fecundity, estimated counting ripe ova in mature specimens, is 7–15 follicles per mature female (Bañón et al., 2006; Clarke et al., 2001; Girard et al., 1999; Figueiredo et al., 2008), whereas uterine fecundity estimates are 2–10 embryos per gravid female (Bañon et al., 2006; Severino et al., 2009). Several studies indicate that females reach a greater size (124–128 cm) at first maturity than males (98–101 cm) (Bañón et al., 2006; Casas et al., 2001; Clarke et al., 2001; Girard et al., 1999; Figueiredo et al., 2008). There is no apparent seasonal reproductive cycle and size at birth is estimated at 35–43 cm. The low reproductive output along with the age estimates for this species (Clarke et al., 2002) indicate that leafscale gulper shark is high vulnerable to exploitation.

Recent studies of *C. squamosus* have revealed that it can be tagged with electronic tags, and the results demonstrate that it makes large-scale movements (Rodríguez-Cabello and Sánchez, et al., 2014). That study also provided prior information on the depth and temperature preferences of this deep-water shark. However, one of the main drawbacks of the pop-up satellite archival transmitting tags (PSAT) used for this species was the infeasibility of obtaining geolocation estimates and, therefore, of reconstructing the tracks followed by the sharks. Geolocation estimates from PSAT tags are primarily based on recorded light levels (Hill et al., 2001; Musyl et al., 2001; Ekstrom, 2004). Since there is almost no daylight at great depths, where the sharks we study live, it is not possible to estimate tag trajectories based on dawn and dusk times. Alternative approaches are currently based on acoustic telemetry, which has progressively become more used with the development and miniaturization of acoustic tags for examining the home ranges and essential habitats of marine species (Hussey et al., 2015) and in particular elasmobranchs (Sundström et al., 2001; Simpfendorfer et al., 2004). However, it has the drawback that the sharks must remain in the receiver array (acoustic monitoring) or be tracked for short periods (acoustic tracking). Thus, if the study area is small or the sharks make short displacements, it is an excellent tool, particularly in studies focused on the design of marine protected areas (MPA) or closed areas for management purposes. Nevertheless, in the case of sharks that make large-scale migrations, or for studies in extensive areas, this approach is rather limited.

In this paper we explore the feasibility of constraining the movements of deep-water species, in particular the leafscale gulper shark, based on combining temperature-depth records obtained from electronic tags with regional ocean hydrography provided by the Argo floats array. This approach is currently the only option for deep dwelling large migratory species.

Besides geographical displacements, the development of electronic tags has allowed study of the cyclical behavior patterns of a number of marine species, in particular diurnal vertical migrations. Many shark species display diel patterns of activity, generally occupying deeper waters during day and shallow waters at night (West et al., 2001; Nakano et al., 2003; Stokesbury et al., 2005; Graham et al., 2006; Shepard et al., 2006; Andrews et al., 2009; Daley et al., 2014 among others), whereas in other studies sharks have not shown diel patterns in their overall activity (Carey et al., 1995; Plekova et al., 2014). Besides the potential of leafscale gulper shark to make diel vertical migrations, it was observed long ago that deep-sea benthic fish exhibit rhythmic activity related to tidal cycles (Guennegan et al., 1979). In the case that *C. squamosus* has a tendency to move up or down the slope along with tidal currents, a signature at tidal frequencies should emerge in their tag's pressure records.

Therefore, the aim of this study was to provide more information about the diving behavior of *C. squamosus* and the tracks it follows in order to find out the main possible routes and the mechanisms it uses to orient spatially and to move long distances. Thus, based on the available datasets the objectives of the present contribution were: (1) to constrain as fully as possible the deep ocean trajectory of the shark based on the pressure-temperature records and the known hydrography of the region, and (2) to determine whether the sharks have cyclical behaviors (diurnal, tidal, etc). Related to the first item, it would be important to gain insights on whether or not sharks detach from the continental slope and swim at mid-depth above the abyssal plain.

2. Data set

2.1. Study area

Tagging was conducted in the El Cachucho (MPA), also known as Le Danois Bank (Le Danois, 1948). It is located in the Cantabrian Sea (NE Atlantic) 30 miles from the coast at 5°W (Fig. 1). The Bank has an elongated E-W disposition, with depths on the plateau summit ranging between 450 and 600 m. The northern face shows a pronounced slope which goes from 500 m at the top to more than 4000 m on the abyssal plain, which lies only 5 miles to the north (Sánchez et al., 2008).

2.2. Gear

Deep water sharks were caught using a bottom longline. The main gear characteristics were described in Rodriguez-Cabello and Sánchez (2014). Fishing was carried out at depths between 900 and 1100 m, with soaking time being restricted to 3h maximum and the haul speed was 0.4–0.5 $\mathrm{m\,s^{-1}}$. All sharks captured were carefully removed from the hooks by the crew.

2.3. Electronic tags

Leafscale gulper sharks were tagged using “Mini PAT” pop-up satellite archival transmitting tags (PSAT). Tags were programmed to release to the surface (pop-up) after 90–120 days from set up (Table 1). These tags record pressure, temperature and light intensity, and were programmed to store data each 300 s. Data are recorded continuously at the prescribed rate but, due to the satellite communications design, only portions of the record are successfully transmitted. Moreover, depth and temperature time-series messages are transmitted separately, thus in some cases only depth time-series messages or only temperature time-series

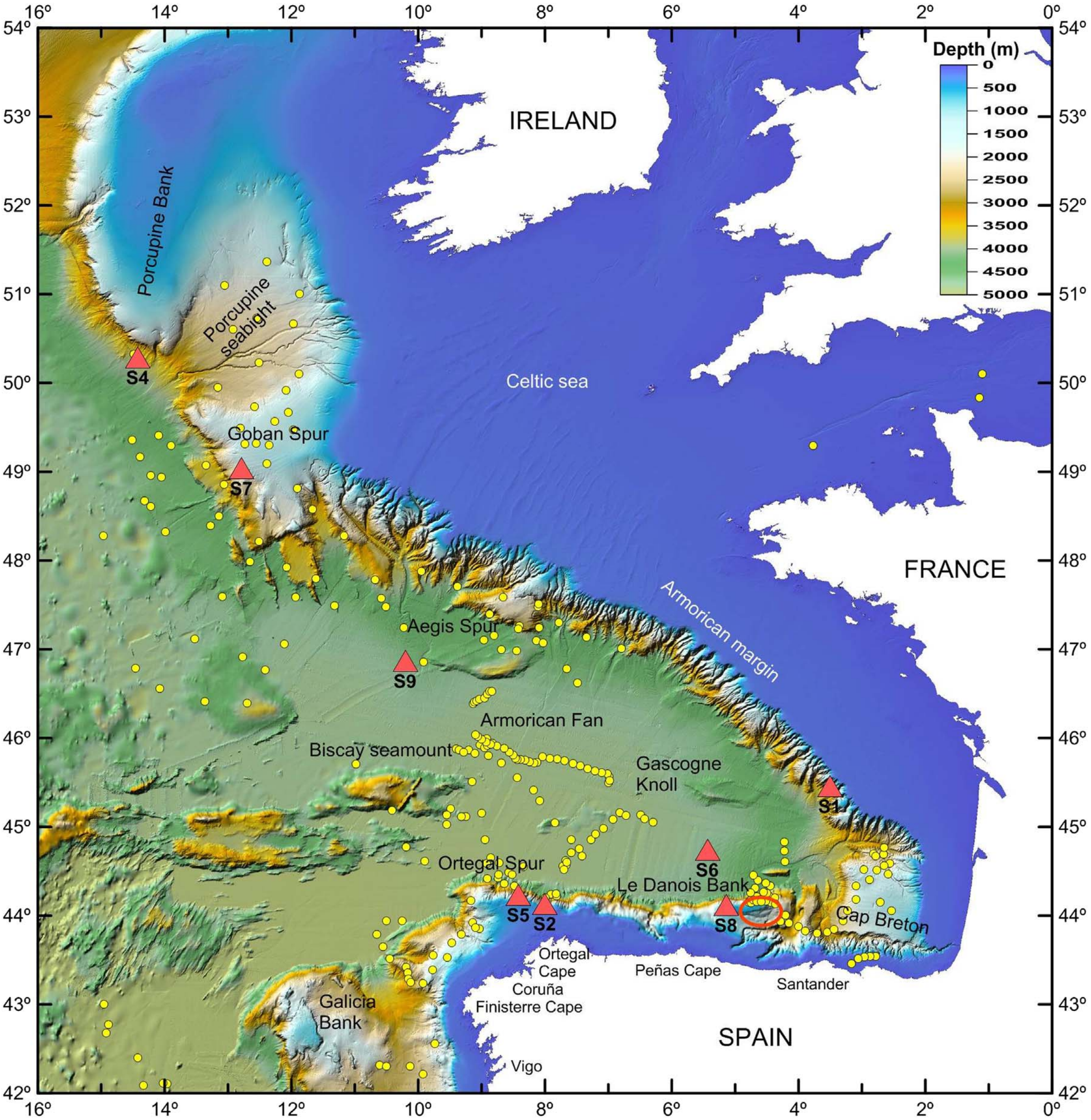

Fig. 1. The study area showing the continental shelf, the slope and some bathymetrical features. The red circle represents the tagging area in El Cachucho marine protected area (MPA). The red triangles show the detachment and surfacing locations of eight pop-up tags (PSATs) from sharks S1 to S9 (S3 never detached). Yellow circles indicate the position of Argos floats used in this study.(For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

messages are received. These characteristics of the records received impose a handicap when attempting to interpret the overall results (Table 2). The total number of messages received never exceeded the 70% of the data recorded, resulting in many gaps (Table 2). The resolution of the depth sensor in PAT tags is 0.5 m. The accuracy is ± 1% of the reading, ± 2 resolutions. Preliminary data analysis was done using Data Analysis Programs (WC-DAP) available from Wildlife Computers. As previously pointed out, due to the darkness or very limited light below 500 m, no data on light levels were recorded and consequently geo-locations could not be estimated from them. Only data on time, depth and temperature are available.

2.4. Argo floats

Argo is a global array of more than 3000 free-drifting profiling floats that measure the temperature and salinity of the upper 2000 m of the ocean (http://www.argo.ucsd.edu). They are currently a major component of the ocean observing system. The Argo array provides global ocean coverage at average 3-degree spacing, but buoy density in any specific region varies depending on specific deployment missions and regional circulation. Floats typically cycle from 2000 m to the surface every 10 days, with 4–5 year lifetimes for individual instruments. Vertical resolution varies from a few decibars in upper levels to 10–25 decibars deeper. All data collected by Argo floats are publically available in near real-time via the Global Data Assembly Centers (GDACs). Based on Argo profiles and other sources a number of gridded fields (climatologies) have been constructed.

3. Methods

3.1. Trajectory inference

Known regional temperature fields in the deep ocean can be used to constrain the possible location of a shark within a specific time frame. Fig. 2 provides the climatological temperature field

Table 1.
Summary of tag and recapture data obtained from the nine electronic tags attached to *Centrophorus squamosus* in the Cantabrian Sea (North of Spain), ordered by tagging date. Numbers of days initially programmed (Prog.) and fulfilled (Real). Weight* was estimated from the length-weight relationship (Casas et al., 2001).

Shark	Mini PAT Tag no	Length (cm)	Weight* (g)		Tagging data				Days		Recapture Data			Tag Released Area	Distance (nmi) Direct
				Sex	Date	Latitude	Longitude	Depth	Progr.	Real	Date	Latitude	Longitude		
1	PT 119,541	104	4744	M	12/10/2012	43°56.40' N	4°52.94' W	1041	120	45	1/23/2013	45°27.47' N	3°30.31' W	Armorican slope	104.8
2	PT 119,537	93	3152	M	12/10/2012	43°56.93' N	4°52.53' W	1041	120	116	4/5/2013	44°08.00' N	8°00.00' W	Cape Ortegal	143.1
3	PT 119,540	107	5264	M	12/10/2012	43°56.30' N	4°52.29' W	1078	130	0	Not released			–	–
4	PT 122,977	118	7492	M	6/13/2013	43°59.89' N	4°42.74' W	1098	90	90	9/12/2013	50°17.22' N	14°25.33' W	Porcupine Seabight	548.1
5	PT 119,539	99	3943	F	6/13/2013	43°59.91' N	4°42.08' W	1094	120	120	10/12/2013	44°14.03' N	8°25.09' W	Cape Ortegal	168.0
6	PT 122,978	122	8463	F	7/1/2013	44°04.72' N	4°30.64' W	1150	90	90	10/1/2013	44°44.53' N	5°26.18' W	North Le Danois Bank	56.4
7	PT 122,979	108	5420	M	9/20/2013	43.57'352 N	4.50'391 W	980	80	80	12/10/2013	49º02.30' N	12º47.20' W	Goban Spur	545.9
8	PT 122,980	107	5239	M	9/20/2013	43.57'113 N	4.50'020 W	1000	90	90	12/19/2013	44°07' 13' N	5°08' 55"W	Le Danois Bank	20.6
9	PT 119,538	110	5796	M	9/20/2013	43.57'113 N	4.50'020 W	1000	120	120	1/19/2014	46º52.02' N	10º12.18' N	Biscay abissal plain	366.5

Table 2.
Summary of valid data transmitted from electronic tags used in this study ordered by tag number. P refers to pressure and P&T refers to simultaneous pressure and temperature. In brackets it is shown the percentage of data coverage respect to the total operating period. For sharks S2, S5 and S8 (*) only the period in which the shark were alive or in continuous movement was considered.

Shark	Mini PAT	Type of data	Pressure	Press & Temp no records (%)
	Tag no		No records (%)	
1	PT 119,541	P	6316 (50.3%)	0
2*	PT 119,537	P	1295 (29.3%)	0
3	PT 119,540	–	–	–
4	PT 122,977	P & T	14,927 (57.2%)	4838 (18.5%)
5*	PT 119,539	P	1359 (60.0%)	0
6	PT 122,978	P & T	18,588 (71.3%)	4968 (19.0%)
7	PT 122,979	P & T	13,314 (57.6%)	4896 (21.2%)
8*	PT 122,980	P & T	7428 (43.8%)	1776 (10.7%)
9	PT 119,538	P & T	6768 (19.5%)	3888 (11.2%)

around the Bay of Biscay at two fixed depth levels during the Argo era. A shark pressure-temperature record would locate it somewhere along the corresponding isotherm within the error associated with the intrinsic variability of hydrographical fields.

Tagged sharks oscillated most of the time within a depth range from 800 to 1200 m with excursions up to 500 m and down to about 1500 m, thus portions of the local temperature profile are recorded by the shark depending on their vertical movements. The vertical structure of the temperature field varies regionally (Fig. 2), exhibiting stronger gradients toward the north as the Mediterranean Water core located at around 1000 m weakens (Iorga et al., 1999; Van Aken, 2000). The larger the vertical movements of the shark, the better we can constrain its most compatible location. Figs. 3(b) and (c) show the raw pressure and temperature records from shark S4. On Fig. 3(a) pressure and temperature profiles are superimposed on Argo profiles obtained around Le Danois and Porcupine Bight regions. It is clear that the hydrography is consistent with those of both the tagging area at the beginning of the series and the release area at the end. As complementary information, Fig. 3(d) shows how the temperature at a given depth drops with time, indicating northward displacement.

As an attempt to gain insights about the possible tracking of the sharks, we have devised a simple geolocation algorithm comparing, for a given time frame, each single shark pressure-temperature record against all available pressure-temperature profiles in the domain. Fig. 4(b) illustrates how the geolocation algorithm works for shark S4 during the second fortnight of June 2013. Eleven Argo profiles were available across the domain within that period (Fig. 4(a)). The number of available shark records within the fortnight was 1325 (about 40% of time). A root mean square (RMS) of the profile temperature minus shark temperature is taken as a measure of the degree of matching of each of the 11 available profiles (Fig. 4: b,c).

As expected, there are fluctuations, so the lowest RMS value is not assigned to the same Argo profile for every single PSAT record. The statistical approach requires choosing a timeframe as a compromise between having sufficient numbers of profiles and shark records while not allowing the shark to make improbably large displacements. The 15-day period provides up to hundreds of single shark records, while every Argo float across the domain should generate at least one profile.

As reference hydrography for comparisons, it is possible to consider gridded climatologies instead of raw Argo profiles. Though gridded products provide full coverage, the caveat is that spatial temperature fields are not static, fluctuating at several time-scales due to internal waves and internal tides, mesoscale processes (e.g. eddies), seasonality and interannual variability.

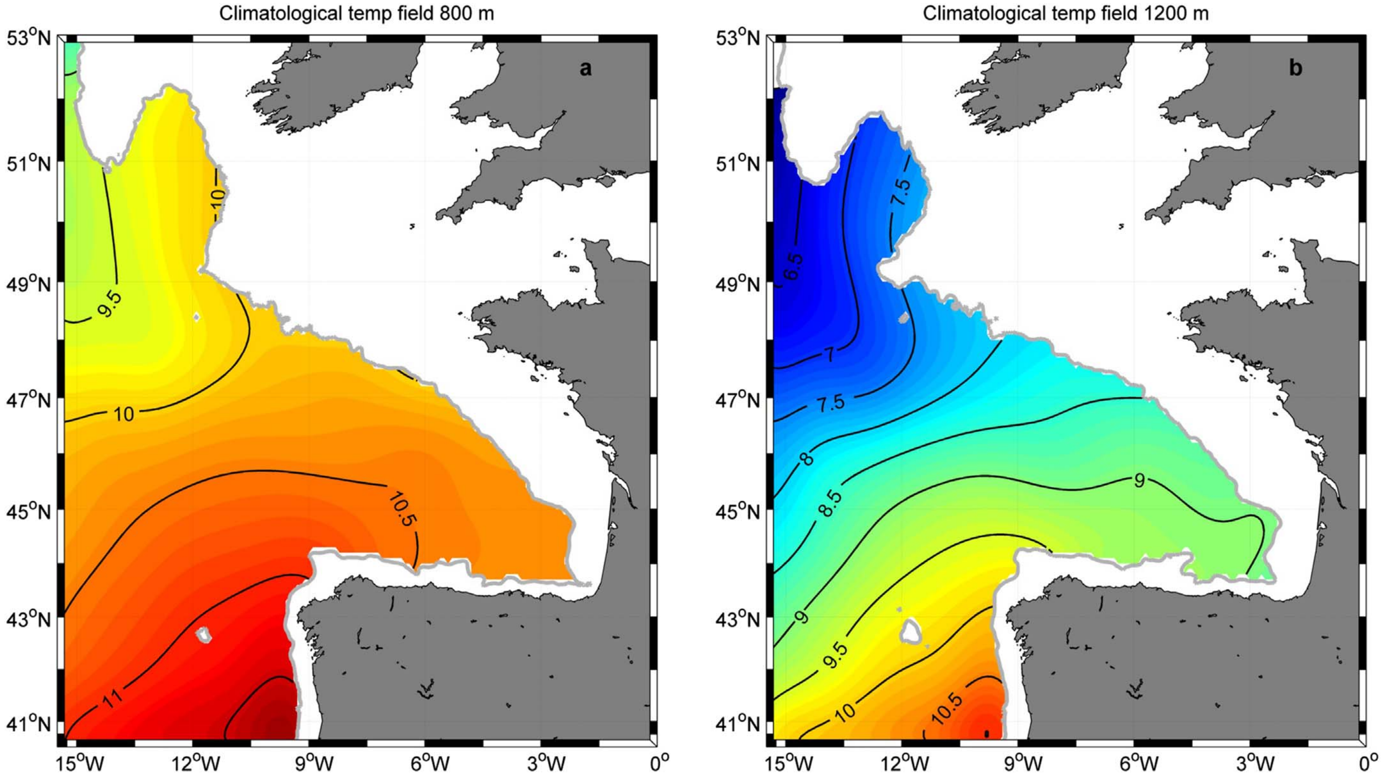

Fig. 2. Temperature field at 800 m (a) and 1200 m (b) around the study area based on the Roemmich-Gilson Argo climatology (Roemmich and Gilson, 2009, http://sio-argo.ucsd.edu/RG_Climatology.html).

Therefore, climatologic values (background mean fields) can be far from actual conditions in a given place and time, up to the order of several tenths of degree and equivalent to hundreds of kilometers in horizontal scale. Raw Argo profiles provide actual and unbiased local conditions, and their vertical resolution is higher, but the spatio-temporal coverage is limited. We have attempted to track the sharks using Roemmich-Gilson climatology (Roemmich et al., 2009) and EN4 (Good et al., 2013) gridded products. Many geolocations yielded by the gridded hydrography were close to those obtained from raw Argo (as is the case for the fortnight used in the previous example). Specific cases where the gridded hydrography-based geolocation is very close in time and space to an actual Argo float profile, or to the final release of the tag, were keys to appraise the performance of the climatology-based approach. Based on these specific cases, Argo profiles seem to perform better as hydrographic reference.

All available profiles from Argo floats for the life period of the tags were downloaded from Coriolis Data Center (http://www.coriolis.eu.org). Particularly, all profiles from June 1, 2013 to March 20, 2014 have been recovered for those floats entering the box: $42^\circ-52^\circ$N/$15^\circ-01^\circ$W. A total of 11 floats had been around the area during the period, profiling on a once per 10-days basis. Therefore, all profiles available in specific fortnights have been considered. Unfortunately there was no Argo profile in the southeastern Bay of Biscay from Jul-16 to Jul 31, so this fortnight has to be interpreted carefully.

3.2. *Pressure cycles and vertical movements*

Information regarding vertical movements of the sharks is embedded in the pressure record (assimilated as depth). As previously noted, due to tag operation and transmission constraints, the pressure record is an irregularly spaced time series. For unevenly sampled series it is not possible to apply the classical Fourier analysis for identifying cyclical components, and the adequate procedure is the Lomb-Scargle normalized periodogram (e.g. Thomson et al., 2014). We have applied the Lomb-Scargle algorithm as described in Press et al., 1992 for those sharks with a reasonable lengthy pressure records (see Table 2). The influence of each periodic component is indicated by the magnitude of the corresponding spectral peak in a periodogram.

A first inspection of the raw pressure record indicated that there was a dominant low-frequency component in the signals; the sharks moved to shallower or deeper areas on a time-scale of days to weeks (Fig. 3). In order to isolate correctly the cyclic behavior associated with diurnal or tidal rhythms, it was necessary to remove this background slow-varying trend before computing spectra (Thomson et al., 2014). To do so, we pre-treated the raw pressure series with a high-pass symmetrical Butterworth filter (cut-off period of 10 days).

4. Results

4.1. *Migration or horizontal movements*

According to the messages received by the Argos satellite, the tags were released to the sea surface at different positions within the Bay of Biscay (Fig. 1). The first tag (S1) detached to the northeast (on the French slope) at 104.8 nmi from the release location (direct trajectory) after 45 days. Two tags (S2 and S5) detached approximately 150 nmi straight to the west of the tagging area after 4 months. Another two tags (S6 and S7) detached close to the tagging area after 3 months, whereas two sharks (S4 and S7) moved to the north to the Porcupine Bight area, a distance of 548 and 545 nmi (direct trajectory) after 90 and 80 days respectively (Table 1). Finally, the PSAT from the last shark tagged (S9), detached after 4 months, in the middle of the Bay of Biscay over the abyssal plain and far away from the continental slope, about 366 nmi to the northwest from release (direct trajectory). No

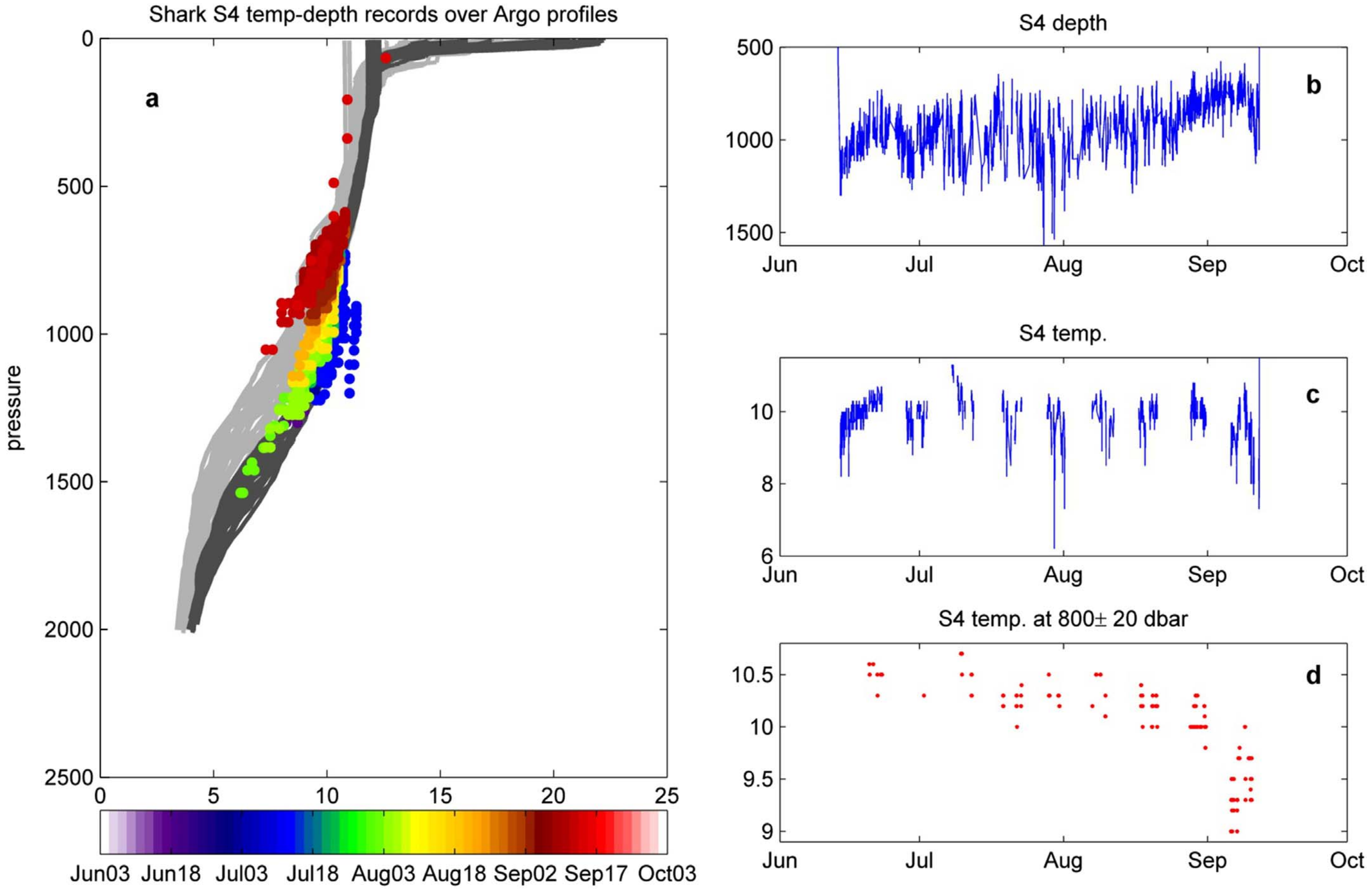

Fig. 3. a) Pressure-Temperature records of shark S4 superimposed on all historical Argo profiles around Le Danois (43–46°N;004–006°W, dark gray) and Celtic Sea (46–50°N;010–014°W, light gray) regions. The color of shark records evolves along with calendar date, as indicated in the color scale. b) Raw pressure record. C) Raw temperature record. D) Temperature records at depths of 800 ± 20 m.(For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

information from tag S3 was ever received.

The tracking estimates based on known regional hydrography are only possible for tags that provided pressure and temperature records, i.e. S4, S6, S7 and S9 (see Table 2). Next we describe the probable tracks of these 4 sharks. In general terms, the records suggest that the sharks remain confined to specific regions for long periods and exhibit relatively quick movements across different regions. Thus, there is no smooth or continuous transit from tagging area towards the final detachment area.

Shark S4 (Fig. 5), 3 months at liberty, (from June 13 to September 12), provided first and second matches with profiles in the southeastern Bay of Biscay (an Argo float was over the NE sector of Le Danois Bank in that period). The second fortnight estimate (June 16 to July 1) corresponded to the example of the algorithm function shown in Fig. 4. Indeed, for this specific fortnight the matching of the profile in the SE Bay of Biscay was close in pressure-temperature space to a profile located NW of Finisterre, so the shark may well be somewhere in between these regions. For the next timeframe (first fortnight of July, after one month) the closest matching is NW off the Galician coast. This also happened in the second fortnight of July, but unfortunately there is no profile in the Bay of Biscay to match with the S4 time-series. In the first fortnight of August the closest matching is again around Le Danois Bank, and then S4 moved quickly toward Goban Spur in the Porcupine Bight region, where it stayed until the end of the record.

Given the information obtained, the shark S4 seems to have moved first to the west across the southern reach of the Bay of Biscay toward the Ortegal region or even farther, staying around the area until at least the second fortnight of July. The first fortnight of August the shark seems to have been again in the SE Bay of Biscay, (could equally be around Le Danois or somewhere else along the French continental slope). In the second fortnight of August the shark's hydrography unequivocally corresponds to latitudes far to the north. Therefore, the long trip made by the shark was accomplished within less than one month around mid-August (note: there are profiles about midway at the Armorican slope that do not provide matching). Nevertheless, it is not possible to tell whether the shark followed the continental shelf or swan at mid-depth above the abyssal plain.

For shark S7 (Fig. 6), 80 days carrying the PSAT, we see roughly the same pattern. The first match happened NW of Ortegal, instead of right at Le Danois, suggesting also an initial westward movement. The next three fortnights were in the south-eastern most Bay of Biscay (Santander-Cap Breton). Then the shark moved quickly (in less than one month) to the Goban Spur-Porcupine area (again there are profiles over the Armorican slope that do not provide good matching). However, the final location before the tag detached, in the Goban Spur area, was at the Armorican slope, suggesting that the shark moved southward again. We should keep in mind that we can only assign the shark to a relatively broad region, so it is only clear that the shark was moving around the Armorican slope to Goban-Spur region.

Shark S9 (Fig. 7), that carried its PSAT four months, stayed in the SE Bay of Biscay the first four fortnights (two months), and then it apparently moved westwards toward Galician waters or even farther. In the first fortnight of November there is a good

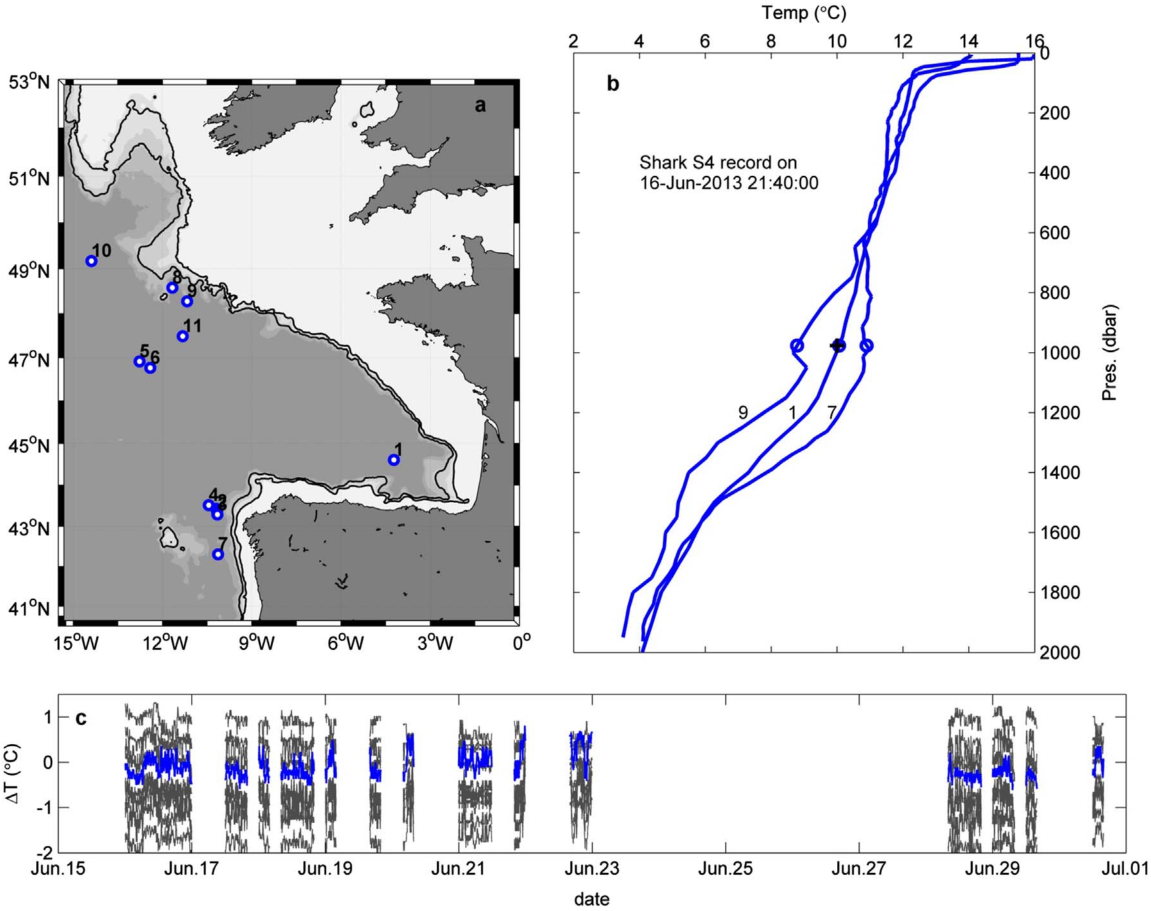

Fig. 4. (a) Argo float profiles available in the domain of interest for the second fortnight of June 2013. After analysis these are ranked from more to less consistent with the shark record. Isobaths of 600 and 1400 m are shown. (b) Record for shark S4 (black cross) comparison with three independent Argo profiles (blue circles, see subfig a for locations). (c) Time series of Argo profile minus shark temperature records; blue highlights the time series with the lowest RMS difference (designated #1 in subfigs a and b). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

match with a float profile SW of the Galician Bank. Given that few depth-temperature records were available for this period, and that the temperature at the target depth 800–1200 is similar to that off Ortegal (see Fig. 2), it is likely that the shark was around Ortegal in this period with the Galician Bank profile being a spurious matching. Then, the shark appears to move towards the Iberian Abyssal Plain offshore from the Armorican slope. Interestingly, the position of detachment of this tag was above the abyssal plain far from the continental slope, suggesting that the shark may have moved there at midwater depths well above the very deep seafloor.

Finally, the tag on shark S6 (Fig. 8) detached after 3 months, close to its release site at Le Danois Bank. Luckily, there was an Argo float around that area for almost the whole period and all the best matches to the S6 record were provided by that float, however in the second fortnight of July there was no profile from this Argo float and thus the best matching is located west of Galicia. It is most likely that this shark did not migrate west, but stayed in the waters surrounding the MPA.

4.2. Swimming behavior or vertical movements

Fig. 9 provides the Lomb periodogram for the sharks with reasonably lengthy pressure records as indicated in the methods section (i.e. sharks S1, S4, S6, S7, S8 and S9, see Table 2). References for relevant frequencies are: daily cycle (d), inertial frequency at 46°N (f), semi-diurnal tidal component (M2) and semidiurnal tidal overtone (M4).°

According to the analysis, sharks S1, S7 and S9 did not exhibit any cyclical pattern. Sharks S7 and more markedly S9 showed a quite smooth red-noise spectrum (preference for slowly varying motions without strong peaks of vertical movement) while the S1 spectrum accumulated some energy in between inertial and diurnal frequencies. Note that S1 and S9 are the two shortest records among the six valid for analysis, with data equivalent to 21.9 and 22.5 full days respectively. Shark S7 on the other hand had data equivalent to 46.2 full days. A diurnal peak emerged for shark S6, clearly above background frequencies but, while clearly discernible, it cannot be considered a strong signal. Finally, sharks S4 and specially S8 did show strong diurnal cycles dominating the record. In general, there were no evident cycles in pressure at tidal frequencies; only a weak signal close to semidiurnal M2 frequency appeared in sharks S4 and S6, but those signals are too weak to attempt drawing any conclusions.

Since sharks S4 and S8 showed robust preference for diurnal movements it was possible to make a harmonic analysis of the pressure record for the diurnal component only for these two sharks. That was done to characterize the movement's amplitude and phase. Fig. 10(a),(c) shows the harmonic fit, together with a few days sample of the raw record in which the migratory behavior is apparent. Both sharks made diurnal excursions in which the shallower depth was reached around midnight (500–800 m) and maximum depth was attained at midday (900–1200 m). The amplitude of cycles for the selected time frames were about 400 m for both sharks, but the migratory pattern is intermittent so the computed harmonic amplitudes (which take into account portions

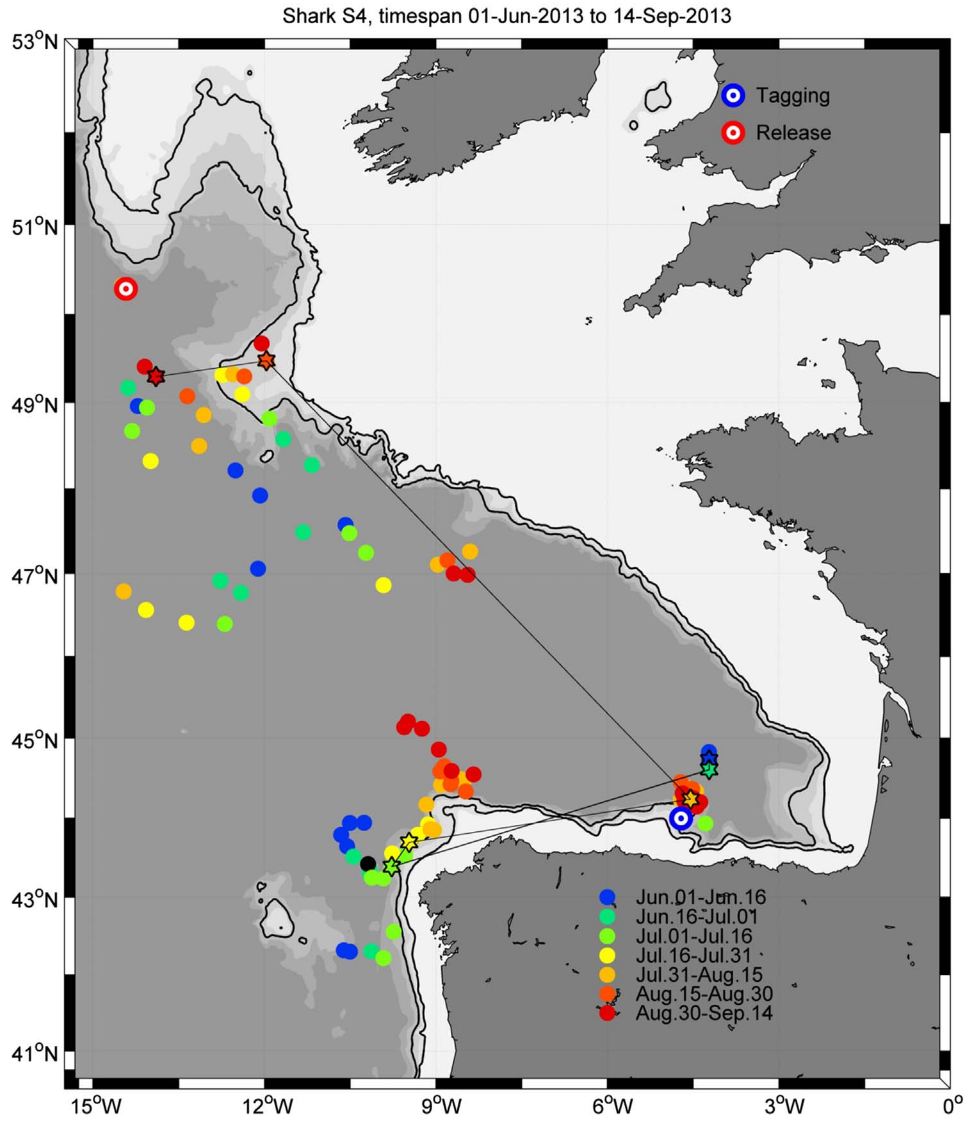

Fig. 5. Shark S4 sequence of best Argo-profiles to shark-record matching within fortnights. All available profiles are shown as dots with color evolving along with calendar date from blue to red. Star symbols indicate best-matches. Circled dots indicate tag releases and detachments. Black dots indicate invalid Argo profiles (too shallow, truncated, etc). Isobaths at 600 and 1400 m are shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of the record where there is no vertical movement) are around 100–200 m. Shark S8 is the only one that made vertical migrations most of the time, and it also made two isolated dives down to more than 1500 m.

Finally, for sharks S4 and S8 that performed diurnal migrations, a preference appeared in their records for upward velocities around evening and downward movements before dawn. Fig. 10 (c),(d) show raw averages of vertical velocities by hours. The signal is fairly clean for shark S8 with maximum downward velocity at 4 UTC and upward velocity at 17 UTC. Shark S4's signal is noisier, but the pattern is also consistent. Average vertical velocities were well below 1 m per minute, so the migration is very slow. Raw pressure records confirm that, when actively migrating, the vertical movements are slow lasting several hours.

5. Discussion

Although pop-up tags were not initially designed to be used for deep-water species, the need to obtain better information on some vulnerable or endangered species for which a lack of information exists (Aarestrup et al., 2009; Béguer-Pon et al., 2012; Graham et al., 2006; Sims et al., 2003) has persuaded us to use the tags to study them. Besides, the development and improvement of this type of tags (greater depth range, more storage capacity, miniaturization) has allowed extension of their application to many species (Musyl et al., 2011), in particular to non-commercial species for which PSAT tags can provide data independently of the fishery.

As mentioned before, geolocation estimates from pop-up tags have been primarily based on light levels recorded from PSAT tags (Hill et al., 2001; Musyl et al., 2001; Ekstrom, 2004). The light-based calculations produce rather raw estimates of geolocation, thus several studies have used other variables in conjunction with light levels, such as sea-surface temperature (SST) recorded or obtained from satellite imagery, bathymetry and tidal data, to improve these estimates (Beck et al., 2002; Hunter et al., 2003; Teo et al., 2004; Nielsen et al., 2006; Skomal et al., 2009). Despite great advances in methods providing latitude and longitude estimates, the accuracy is still rather low: ±0.2 to ±0.9° in longitude and ±0.6 to ±4.4° in latitude (Musyl et al., 2001; Welch et al., 2001). Profiling floats data have an enormous range of applications, and

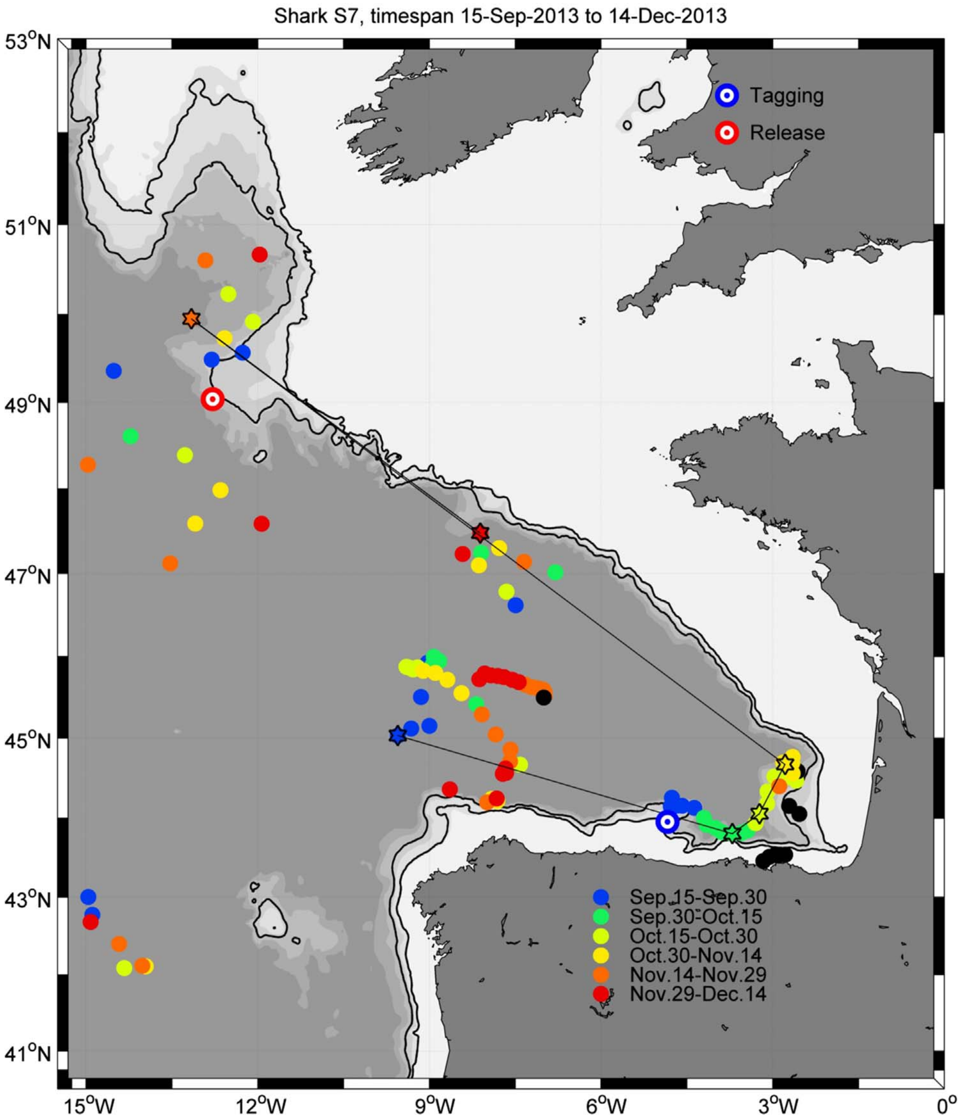

Fig. 6. Shark S7 sequence of best Argo-profiles to shark-record matching within fortnights. All available profiles are shown as dots with color evolving along with calendar date from blue to red. Star symbols indicate best-matches. Circled dots indicate tag releases and detachments. Black dots indicate invalid Argo profiles (too shallow, truncated, etc). Isobaths at 600 and 1400 m are shown.(For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

we have shown that in combination with electronic tags they can help to elucidate migratory routes based on comparison of temperature profiles. Even though accuracy is again rather low, tag profile to float profile comparisons can be as effective as previous methods. They have the advantage of being the only alternative to date that can be used for deep-water species.

5.1. *Migration or horizontal movements*

The new trajectories inferred by the comparison of archival electronic tag data with Argo profiles reveal the capacity of the leafscale gulper shark to make long migratory journeys. This capacity is even greater than has been previously estimated (Rodríguez-Cabello and Sánchez, et al., 2014). According to the projected trajectories, the sharks seem to alternate relatively stationary periods with quick migrations within the study area. The swimming speed of *C. squamosus* is also much faster than was expected, since the longest distances were covered in 15–30 days. For example shark S4 and shark S7 moved from the south of the Bay of Biscay to the Porcupine Bight (approximately 550 nmi) in 30 days or less, a speed of more than 15 nautical miles.day^{-1}.

The facts that some of the positions where the tags detached and that the estimated trajectories inferred by comparing tag data with Argo profiles were located over depths >4000 m support the theory that this species can swim in mid-water without strictly following the continental slope or shelf. Though this behavior has not been previously demonstrated, it is in agreement with some catches of this species over abyssal plains (Compagno et al., 1998; Priede et al., 2006).

According to the results, two of the sharks (S2 and S5) moved to Cape Ortegal (offshore of the northern Galician coast) where the tags detached. Although both sharks apparently died after one month, and for unknown reasons the tags did not detach and remained on the bottom for nearly three months (Rodriguez-Cabello and Sánchez, 2014), it is surprising that both sharks followed the same route. On the other hand, the trajectories inferred from two of the four tags analyzed (S4 and S9) showed that those sharks moved to the Galician coast or surrounding waters and then moved back to the east side of the Bay of Biscay. This fact brings up the question whether there is just random movement, or is a directional or well defined westward route taken before a return to the east and finally migration north, as most of the estimated

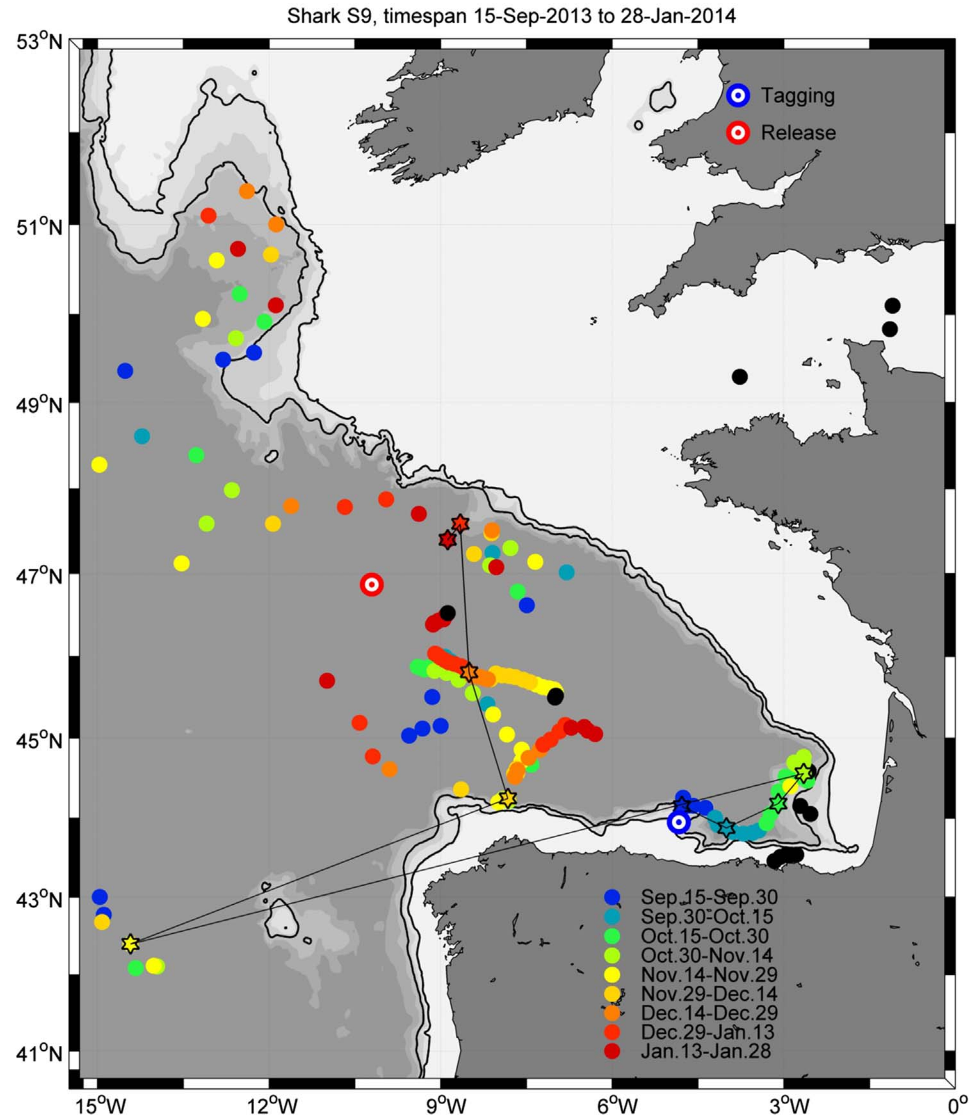

Fig. 7. Shark S9 sequence of best Argo-profiles to shark-record matching within fortnights. All available profiles are shown as dots with color evolving along with calendar date from blue to red. Star symbols indicate best-matches. Circled dots indicate tag releases and detachments. Black dots indicate invalid Argo profiles (too shallow, truncated, etc). Isobaths at 600 and 1400 m are shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

trajectories suggest.

No previous studies regarding migrations of *Centrophorus squamosus* exist, apart from Rodriguez-Cabello and Sánchez, (2014). If you changed this reference before now should be Rodríguez-Cabello et al., (2014) However, studies based on geographical distribution, population structure, biological parameters and reproductive strategies support that this species could make large-scale migrations (Clarke et al., 2001; Figueiredo et al., 2008; Girard et al., 1999, 2001; Moura et al., 2014; Severino et al., 2009). The presence of certain size classes or reproductive phases of *C. squamosus* in areas of the continental slope, and their total absence from others, allowed some authors to suggest a migration pattern linked to reproductive activity (Clarke et al., 2002). According to Moura et al., 2014 pregnant females were only recorded off Iceland, in Portuguese waters (Figueiredo et al., 2008) and from the Madeira Archipelago (Severino et al., 2009; Pajuelo et al., 2010). Those authors suggested a possible cyclical migration encompassing the Mid-Atlantic Ridge and the continental slopes of Europe (Girard et al., 1999). Our results and the lack of pregnant females also in this area are consistent with this hypothesis.

Taking into account the length at maturity (L_{50}) estimated for this species (Casas et al., 2001; Clarke et al., 2002; Girard et al., 1999), which is close to 98–101 cm for males and 124–128 cm for females, the specimens tagged, 6 males and 2 females (Table 1) were mature with the exceptions of one male, shark 2 (TL=93 cm) and the two females, sharks 5 and 6 (TL=99 cm and TL=122 cm respectively) (Table 1). Based on the inferred trajectories, the major differences observed regarding size and sex are that one of the females (shark 6) did not move up to the north and remained in the Bay of Biscay. However, the few data available do not allow a full analysis regarding size, sex or seasonal patterns. The two sharks 4 and 7 which moved to the north, close to the Porcupine Bight waters, were tagged in June and September and the tag detached in September and December, respectively (Table 1). In addition, sharks 2 and 5, whose tags detached in Galician waters, were also tagged in different periods (December and June respectively). Thus, there is no seasonal migration pattern apparent in our records; more data will be needed to test that.

Whereas the leafscale gulper shark migration pattern is linked to reproductive activity, feeding strategy or seasonal behavior, we cannot conclude at present. However, it appears that sharks do not move randomly but follow specific routes. Direct movements of

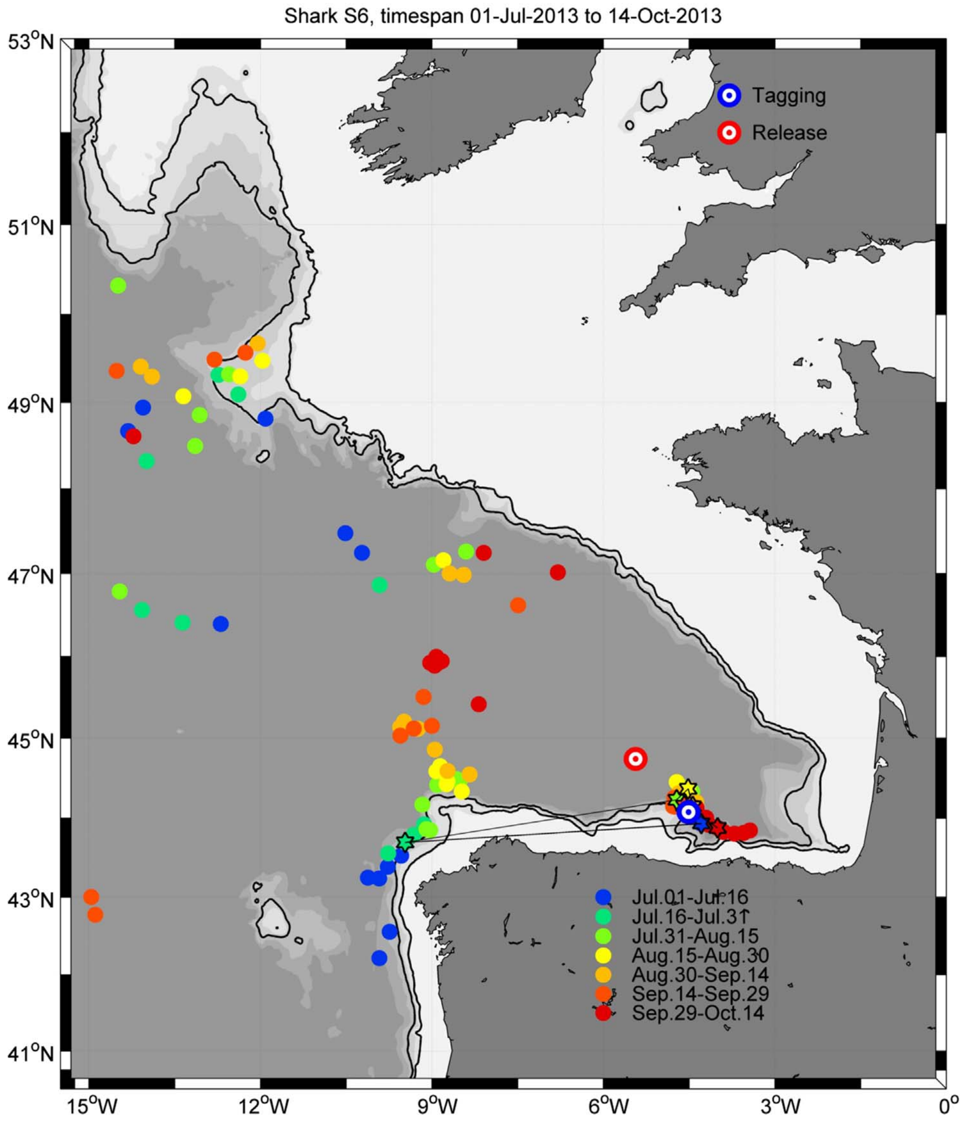

Fig. 8. Shark S6 sequence of best Argo-profiles to shark-record matching within fortnights. All available profiles are shown as dots with color evolving along with calendar date from blue to red. Star symbols indicate best-matches. Circled dots indicate tag releases and detachments. Black dots indicate invalid Argo profiles (too shallow, truncated, etc). Isobaths at 600 and 1400 m are shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

sharks through the open ocean have mostly been attributed to geomagnetic orientation (Klimley, 1993; Montgomery et al., 2001). However, multiple sensory mechanisms can be integrated and used as navigational cues (vision, olfaction, lateral line, memory, etc.). Field observations and sampling around the globe suggest that sharks and other pelagic species, such as tuna or billfishes may be attracted to seamounts for feeding, mating or orientation (Klimley, 1993; Holland et al., 1999). As these authors pointed out, seamounts may represent navigational waypoints, however this hypothesis has been poorly tested. More precise tracking would be needed to check whether this theory is valid for deep-sea shark migrations.

5.2. Swimming behavior or vertical movements

Diel vertical migration (DVM) is a well known issue driving the movement of pelagic and deep fish (Neilson and Perry, 1990; Afonso et al., 2014), including elasmobranchs (Hammerschlag et al., 2011; Shepard et al., 2006; Sims et al., 2003). In most cases these cyclic changes in the position of aquatic organisms in the water column are linked to a feeding behavior (Carey et al., 1990; Graham et al., 2006; Sims et al., 2003; Steven et al., 2010; Daley et al., 2014), whereas in other cases it is related to predator avoidance (Robinson, 2003) It is here the reference of Robinson, 2003 or bioenergetic efficiency via thermoregulation (Aarestrup et al., 2009; Sims et al., 2006). Furthermore some authors suggest that vertical oscillations could serve as guide to orient fish migration (Klimley, 1993; Westerberg et al., 2007).

Among the six sharks analyzed, only two, S4 and S8, showed a clear diel cycle, whereas shark S4 and S6 showed a very weak semi-diurnal signal. No evidence of any diel frequency was observed in the other 3 sharks. Therefore, the pattern is not consistent among individuals, and we cannot conclude whether this species has a regular cyclic diving behavior. Intraspecific plasticity in behavior is known from a range of oceanic fishes. A similar pattern was found by Plekova et al. (2014) who investigated the Artic skate's (*Amblyraja hyperborea*) movements with pop-up archival tags. They found a relationship between depth and the diel cycle in some individuals but not in others, so they concluded that DVM might not be a consistent behavior of Artic skates. They also did not find any clear cyclic or temporal patterns in the Greenland halibut, *Reinhardtius hippoglossoides* (Plekova et al., 2012).

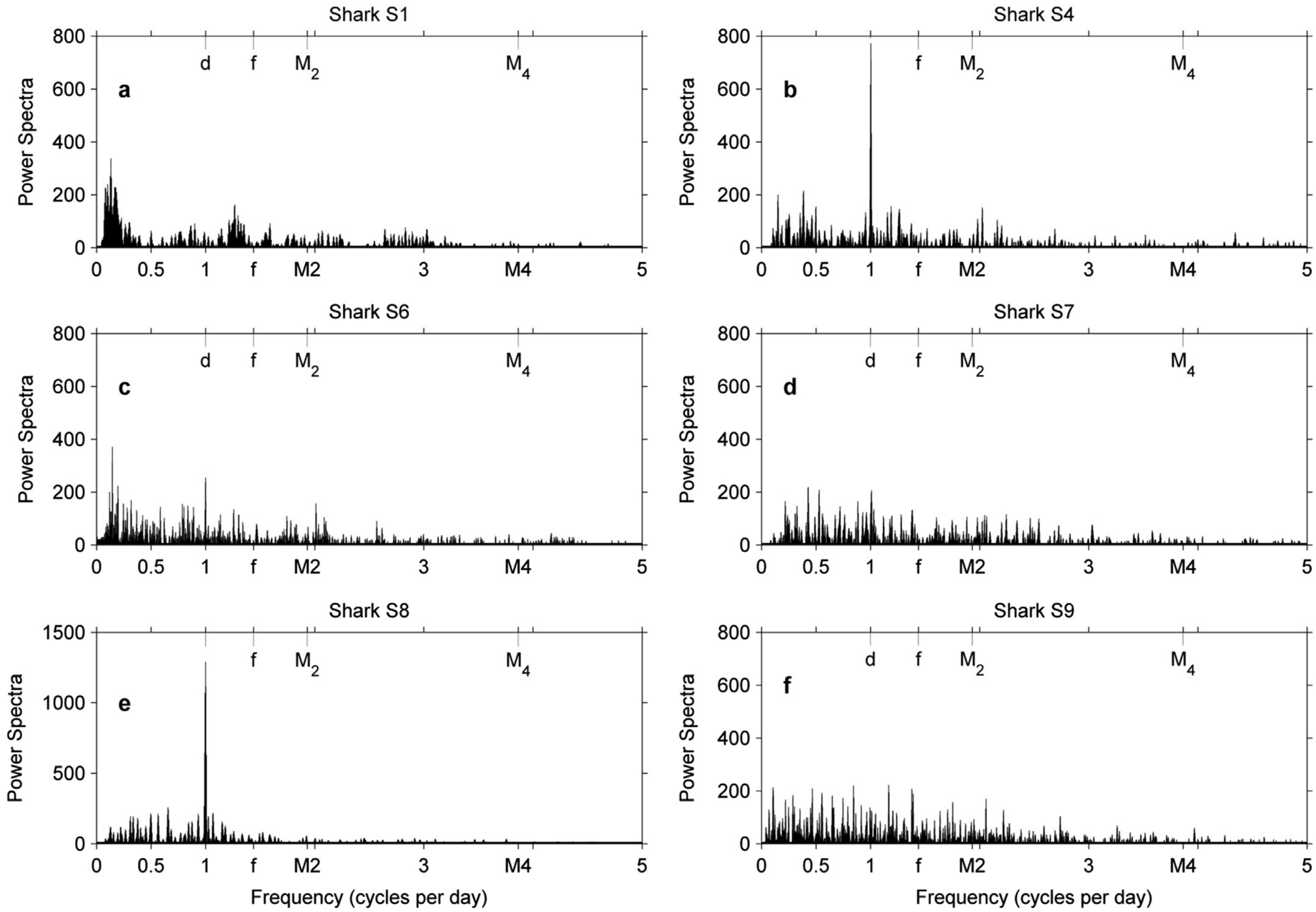

Fig. 9. Lomb-normalized periodogram of pressure record of sharks with a relatively lengthy PSAT records (equivalent to 22–65 full days, see Table 2). Raw pressure records were pre-treated with a high-pass filter (see text for details). Spectral peaks below 0.05 confidence level are not included.

However, quite a number of sharks, mainly pelagic sharks, show more complex diving behavior. For example, Graham et al., 2006 revealed diel and lunar periodicity in the vertical movements of whale sharks, *Rhincodon typus,* whereas Shepard et al., 2006 reported predominant diel periodicities in vertical migration of basking shark, *Cetorhinus maximus* and a tidal pattern related to the shark's zooplankton prey. However, again, not all of the basking sharks analyzed showed the same pattern. Analogous diel, tidal and seasonal activity patterns were reported for the sixgill shark, *Hexanchus griseus,* being the foraging hypothesis the most consistent to explain those cycles (Andrews et al., 2009). Other studies do not show any diel pattern in shark activity (Plekova et al. 2014) or describe contradictory results from the same species of shark. The latter is the case of the greenland shark *Sommniosus microcephalus* (Campana et al., 2015; Stokesbury et al., 2005) and the sixgill shark *Hexanchus griseus* (Andrews et al., 2009). In most cases this is due to the limited number of individuals tagged or because the studies were confined to a certain area or season, making it difficult to draw any conclusion. In Australia, a passive acoustic tracking study carried out on a congeneric species, *Centrophorus zeehaani*, showed a pronounced diel vertical migration driven by lunar and seasonal cycles (Daley et al., 2014). Those authors suggest that its vertical migration is a feeding strategy to exploit deep-scattering layers of micronekton.

According to several studies and despite spatial differences, *C. squamosus* shows benthic feeding behavior. It preys mainly on benthic or demersal teleosts (Dunn et al., 2010; Wetherbee, 2000), on cephalopods, unidentified teleosts and crustaceans (Mauchline et al., 1983; Macpherson et al., 1987; Ebert et al., 1992;). DVM by zooplankton is a well known phenomenon that occurs in all the world's oceans. More recently, studies performed on other marine taxonomic groups such as myctophid fishes (Watanabe et al., 1999), cephalopods (Clarke, 2007) and crustaceans (Vestheim et al., 2009) have revealed DVM behavior that very likely is an adaptive response to their prey (Afonso et al., 2014), and thus could affect the diving behavior of their predators. That interpretation may be appropriate for the leafscale gulper shark that feeds on these preys. In this study only two sharks (S4 and S8) showed a diurnal vertical migration pattern, making it difficult to draw any strong conclusion. However upwards and downwards movements were done very slowly, less than 1 m.min^{-1} (Figs. 10 (c) and (d)). These movement rates do not suggest that foraging behavior is the principal cause of this activity.

Klimley, 1993 pointed out that one explanation for the oscillatory diving behavior observed in some sharks is that it guides migration. Remarkably, one of the sharks that showed this pattern (S4) migrated up to Porcupine area, whereas the other one (S8), apparently did not move from the tagging area. Thus, it is not possible to relate the few cases of DVM specifically with migrations or stationary periods. It is well known that elasmobranchs possess receptors, the Ampullae of Lorenzini that are sensitive to electric fields (Kalmijn, 1971, 2000; Molteno et al., 2009). According to several studies the intensity of local magnetic gradients varies with depth. Thus, as Klimley, 1993 pointed out, differences in geomagnetic intensity could help hammerheads and likely other sharks to orient geographically. Taking into account that

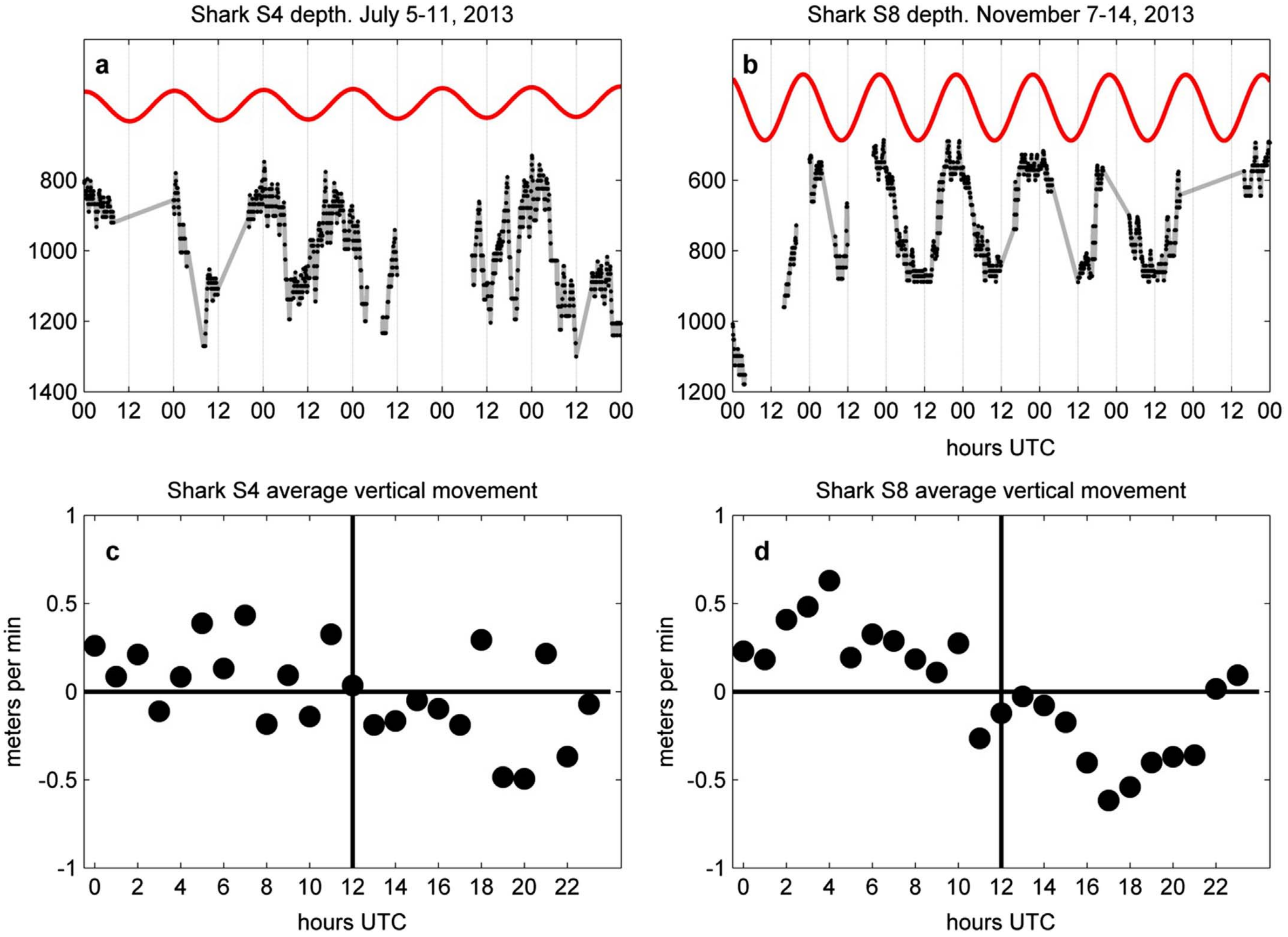

Fig. 10. Upper panels. One-week, raw pressure records from sharks S4 (left) and S8 (right), exhibiting a clear diel migration. Superimposed in red (phase-shifted) is the best-fitting pure harmonic signal of 24-hour period to the whole record. Lower panels: Vertical velocity of sharks computed only from consecutive records 5 min apart and averaged by hour of day for the whole record. Note that east of 7.5°W we stay in the Greenwich meridian time zone and west of this longitude we enter UTC-1 region. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

leafscale gulper shark can swim either following the slope or in midwater over depths of more than 4000 m, and that some of the tracks and release points are close to singular bathymetrical features, the hypothesis that *C. squamosus* could also detect local magnetic gradients and use them to orientated might be possible. Nevertheless, as we mentioned above, if this were the case, DVM should have been observed in almost all the tagged sharks. Another argument that casts doubts on this hypothesis is that most of the seamounts located in the study area are very deep, and it is not clear how the leafscale gulper shark could perceive their induced differences in the geomagnetic fields.

Westerberg, 1984 suggested that fishes could obtain the information needed to maintain a directional course from discontinuous thermal gradients through the water column. The fact that the thermal gradient is rather weak in the mid-depth northeast Atlantic (about 1000 m) does not support this hypothesis in our case. As it has been reported, in some oceanic fishes and pelagic sharks such as hammerheads *Sphyrna lewini*, (Klimley, 1993), blue sharks, *Prionace glauca*, (Carey et al., 1990), makos, *Isurus oxyrhinchus,* or white sharks, *Carcharodon carcharias*, (Klimley et al., 2002), that vertical diving oscillations are not restricted to crossing the thermal gradient.

Despite the new data, the factors driving the movements of *Centrophorus squamosus* are still unknown, but they may be related to feeding or mating. More data are needed to examine these hypothesis.

5.3. Future actions

More leafscale gulper sharks should be tagged to obtain a broad picture of the possible routes followed by this deep-water shark. Besides the new approach of combining Argo data, the use of electromagnetic sensors, or conductivity sensors in conjunction with temperature vs. depth profiles could much improve the possibility to track the fish and consistently estimate their geolocations.

Once movement patterns are defined and depth and temperature preferences of a species are well known, then movements can be modeled and used for better decision making in conservation. That would include the design of marine protected areas and general resource management efforts. If some vulnerable deep-water species like the leafscale gulper shark are known to concentrate or move to certain areas (seamounts, canyons or other deep sea features) in certain periods, then the benefits of protecting those areas and avoiding fishing activities in them could greatly improve the survival and recovery of their populations.

6. Conclusions

This study has demonstrated that the use of pop-up tags for leafscale gulper shark studies can provide very interesting and useful information to define its possible migration routes, swimming behavior and habitat preferences. It also demonstrated that the use of Argo floats profiles in conjunction with electronic tag data can be extremely helpful for elucidating the routes followed by the sharks. The combination of technologies has been able to show that leafscale gulper shark is truly a highly migratory species, swimming much faster than previously though. Also, these sharks seem capable of travelling in mid-water over great depths, thus do not necessarily follow the slope. An interesting outcome is that sharks present individual peculiarities in behavior; neither large-scale horizontal migration patterns nor diurnal vertical movements are consistent among individuals nor univocally explained by any of the existing single theories. Therefore, this study is just a single step in our understanding of the ecology and behavioral patterns of deep-sea sharks, highlighting strong complexity and bringing out new uncertainties rather than settling current issues.

Acknowledgments

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References

Aarestrup, K., Økland, F., Hansen, M.M., Righton, D., Gargan, P., Castonguay, M., Bernatchez, L., Howey, P., Sparholt, H., Pedersen, M.L., McKinley, R.S., 2009. Oceanic spawning migration of the European eel (*Anguilla anguilla*). Science 325 (www.sciencemag.org).

Afonso, P., McGinty, N., Graça, G., Fontes, J., Inácio, M., Totland, A., Menezes, G., 2014. Vertical migrations of a deep-sea fish and its prey. PLoS One 9 (5), e97884. http://dx.doi.org/10.1371/journal.pone 0097884.

Andrews, K.S., Williams, G.D., Farrer, D., Tolimieri, N., Harvey, C.J., Bargmann, G., Levin, P.S., 2009. Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator. Anim. Behav. 78 (2), 525–536.

Barbosa du Bocage, J.V., de Brit Capello, F., 1864. Sur quelques espèces inédites de Squalidae de la tribu Acanthiana Gray, qui fréquentent les côtes du Portugal. Proc. Zool. Soc. London, 260–263.

Bañón, R., Piñeiro, C., Casas, M., 2006. Biological aspects of deep water sharks Centroscymnus coelolepis and Centrophorus squamosus in Galician waters (north-eastern Spain). J. Mar. Biol. Assoc. U.K 86, 843–846. http://dx.doi.org/10.1017/S0025315406013774.

Beck, C.A., McMillan, J.L., Bowen, W.D., 2002. An algorithm to improve geolocation positions using sea surface temperature and diving depth. Mar. Mamm. Sci. 18, 940–951.

Béguer-Pon, M., Benchetrit, J., Castonguay, M., Aarestrup, K., Campana, S.E., Stokesbury, M.J., Dodson, J., 2012. Shark predation on migrating adult american eels (*Anguilla rostrata*) in the gulf of St. Lawrence. PLoS One 7 (10), e46830. http://dx.doi.org/10.1371/journal.pone.0046830.

Bonnaterre, J.P., 1788. Ichthyologie.Tableau encyclopédique et méthodique des trois règnes de la nature. Paris, 215 (pl. A-B +1–100.

Campana, S.E., Fisk, A.T., Klimley, A.P., 2015. Movements of Arctic and northwest Atlantic Greenland sharks (*Somniosus microcephalus*) monitored with archival satellite pop-up tags suggest long-range migrations. Deep-Sea Res. Part II 115, 109–115. http://dx.doi.org/10.1016/j.dsr2.2013.11.001i.

Carey, F.G., Scharold, J.V., 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. Mar. Biol. 106, 329–342.

Carey, F.G., Clark, E., 1995. Depth telemetry from the sixgill shark, *Hexanchus griseus*, at Bermuda. Env. Biol. Fish. 42, 7–14.

Casas, J.M., Piñeiro, C., Bañón, R. Maturity and Other Biological Aspects of Main Deep-water Squaloid Sharks, in the North and Northwest of the Iberian Peninsula (ICES Divisions VIIIc, IXa and IXb). NAFO SCR Doc. 01/121, 2001 21.

Clarke, M.W., Conolly, P.L., Bracken, J.J., 2001a. Aspects of the reproduction of the deep water sharks *Centroscymnus coelolepis* and *Centrophorus squamosus* from west of Ireland and Scotland. J. Mar. Biol. Asses. UK 81, 1019–1029. http://dx.doi.org/10.1017/S0025315401005008.

Clarke, M. W., Conolly, P. L., Bracken, J. J., 2001b. Biology of exploited deep-water sharks West of Ireland and Scotland. NAFO Council Report Doc. 01/108, 18 pp. Available at archive.nafo.int/ open/sc/2001/scr01–108.

Clarke, M.W., Connolly, P.L., Bracken, J.J., 2002. Age estimation of the exploited deepwater shark *Centrophorus squamosus* from the continental slopes of the Rockall Trough and Porcupine Bank. J. Fish. Biol. 60, 501–514.

Clarke, M.W., Borges, L., Officer, R.A., 2005. Comparisons of trawl and longline catches of deep-water elasmobranchs west and north of Ireland. J. Northw. Atl. Fish. Sci. Fish. Sci. 35, 429–442.

Clarke, M., 2007. Chapter 11. Seamounts and cephalopods. In: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), Seamounts: Ecology, Fisheries & Conservation. Blackwell Publishing Ltd, Oxford, UKhttp://dx.doi.org/10.1002/9780470691953.ch11.

Compagno, L.J.V., 1984. FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. FAO Fish. Synop 125 Vol. 4 (Pt. 2), 251–655.

Compagno, L.J.V., Niem, V.H., 1998. Scyliorhinidae. Catsharks. In: Carpenter, K.E., Niem, V.H. (Eds.), FAO Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. FAO, Rome, pp. 1279–1292.

Correia, J.P.S., Smith, M.F.L., 2003. Elasmobranch landings for the Portuguese commercial fishery from 1986 to 2001. Mar. Fish. Rev. 65, 32–40.

Crozier, P., 2001. Distribution and reproductive biology of two deepwater sharks, Centroscymnus coelolepis (Portuguese dogfish) and *Centrophorus squamosus* (Leafscale gulper shark),in the Rockall Trough area of the North-east Atlantic. NAFOSCRDoc.01/105, SerialN4493, 5 pp.

Daley, R.K., Williams, A., Green, M., Barker, B., Brodie, P., 2014. Can marine reserves conserve vulnerable sharks in the deep sea? A case study of *Centrophorus zeehaani* (Centrophoridae), examined with acoustic telemetry. Deep-Sea Res. 115, 127–136. http://dx.doi.org/10.1016/j.dsr2.2014.05.017i.

Dunn, M.R., Szabo, A., Mc Veagh, M.S., Smith, P.J., 2010. The diet of deepwater sharks and the benefits of using DNA identification of prey. Deep-Sea Res. 57, 923–930.

Ebert, D.A., Compagno, L.J.V., Cowley, P.D., 1992. A preliminary investigation of the feeding ecology of squaloid sharks off the west coast of southern Africa. S. Afr. J. Mar. Sci. 12, 601–609.

Ekstrom, P.A., 2004. An advance in geolocation by light. Mem. Natl. Inst. Polar. Res. 58, 210–226.

Figueiredo, I., Moura, T., Neves, A., Gordo, L.S., 2008. Reproductive strategy of leafscale gulper shark, *Centrophorus squamosus*, and Portuguese dogfish, *Centroscymnus coelolepis*, on the Portuguese continental slope. J. Fish. Biol. 73, 206–225.

Girard, M., 2001. Distribution et reproduction de deux espèces de requins de grands fonds, les "sikis" *Centrophorus squamosus* et *Centroscymnus coelolepis* exploités dans l'Atantique nord-est. B. Soc. Zool. FR 126, 291–298.

Girard, M., Du Buit, M.H., 1999. Reproductive biology of two deep-water sharks from the British Isles *Centroscymnus coelolepis Centrophorus squamosus* (Chondrichthyes: Squalidae). J. Mar. Biol. Assoc. U.K. 79, 923–931.

Good, S.A., Martin, M.J., Rayner, N.A., 2013. EN4: quality controlled ocean temperature and salinity profiles and monthly objective analyses with uncertainty estimates. J. Geophys. Res. Oceans 118, 6704–6716. http://dx.doi.org/10.1002/2013JC009067.

Gordon, J.D.M., Bergstad, O.A., Figueiredo, I., Menezes, G., 2003. Deep-water fisheries of the Northeast Atlantic: I description and current trends. J. Northw. Atl. Fish. Sci. 31, 137–150.

Graham, R.T., Roberts, C.M., Smart, J.C.R., 2006. Diving behaviour of whale sharks in relation to a predictable food pulse. J. R. Soc. Interface 3, 109–116. http://dx.doi.org/10.1098/rsif.2005.0082.

Guallart, J., Walls, R.H.L., White, W.T., 2015. *Centrophorus squamosus.* The IUCN Red List of Threatened Species 2015: e.T41871A48954989.

Guennegan, Y., Rannou, M., 1979. Semi-diurnal rhythmic activity in deep-sea benthic fishes in the Bay of Biscay. Sarsia 64 (1–2), 113–116.

Hammerschlag, N., Gallagher, A.J., Lazarre, D.M., 2011. A review of shark satellite tagging studies. J. Exp. Mar. Biol. Ecol. 398, 1–8.

Hareide, N.-R., Garnes, G., 2001. The distribution and catch rates of deep water 548 fish along the Mid-549 Atlantic Ridge from 43°N to 61°N. J. Fish. Res. 51, 297–310.

Hill, R.D., Braun, M.J., 2001. Geolocation by light-level, the next step: latitude. In: Sibert, J., Nielsen, J.L. (Eds.), Electronic tagging and tracking in marine fisheries. Kluwer Academic Publishers, Dordrecht, pp. 443–456.

Holland, K.N., Kleiber, P., Kajiura, S.M., 1999. Different residence times of yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*, found in mixed aggregations over a seamount. Fish. Bull. 97, 392–395.

Hunter, E., Aldridge, J.N., Metcalfe, J.D., Arnold, G.P., 2003. Geolocation of free-ranging fish on the European continental shelf as determined from environmental variables I. Tidal location method. Mar. Biol. 142, 601–609.

Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Kocik, J.F., Flemming, J.E.M., Whoriskey, F.G., 2015. Aquatic animal telemetry: a panoramic window into the underwater world. Science (6240), 348. http://dx.doi.org/10.1126/science.1255642.

Iorga, M.C., Lozier, M.S., 1999. Signatures of the Mediterranean outflow from a North Atlantic climatology: 2. diagnostic velocity fields. J. Geophys. Res. 104, 25985–26009, doi: 10.1029/1999JC900204. Issn: 0148–0227.

Kalmijn, A.J., 1971. The electric sense of sharks and rays. J. Exp. Biol. 55, 371–383.

Kalmijn, Ad.J., 2000. Detection and processing of electromagnetic and near-field acoustic signals in elasmobranch fishes. Philos. Trans. R. Soc. Lond. B 355, 1135–1141.

Klimley, A.P., 1993. Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. Mar. Biol. 117 (1), 1–22.

Klimley, A.P., Beavers, S.C., Curtis, T.H., Jorgensen, S.J., 2002. Movements and swimming behavior of 3 species of sharks in La Jolla Canyon, California. Environ. Biol. Fish. 63, 117–135.

Le Danois, Ed., 1948. Les Profondeurs de la Mer. Trente ans de recherches sur la faune sous-marine au large des côtes de France. Ed. Payot, Paris.

Mauchline, J., Gordon, J.D.M., 1983. Diets of the sharks and chimaeroids of the Rockall Trough, northeastern Atlantic Ocean. Mar. Biol. 75, 269–278.

Macpherson, E., Roel, B.A., 1987. Trophic relationships in demersal fish community off Namibia. S. Afr. J. Mar. Sci. 5, 585–596.

Molteno, T.C.A., Kennedy, W.L., 2009. Navigation by induction-based magneto reception in elasmobranch fishes. J. Biophys. 2009, 1–6. http://dx.doi.org/10.1155/2009/380976.

Montgomery, J.C., Walker, M.M., 2001. Orientation and navigation in elasmobranchs: which way forward? Environ. Biol. Fish. 60, 109–116.

Moura, T., Jones, E., Clarke, M.W., Cotton, C.F., Croziere, P., Daley, R.K., Diez, G., Dobby, H., Dyb, J.E., Fossen, I., Irvine, S.B., Jakobsdottir, K., López-Abellán, L.J., Lorance, P., Pascual-Alayón, P., Severino, R.B., Figueiredo, I., 2014. Large-scale distribution of three deep-water squaloid sharks: Integrating data on sex, maturity and environment. Fish. Res. 157, 47–61.

Musyl, M.K., Brill, R.W., Curran, D.S., Gunn, J.S., Hartog, J.R., Hill, R.D., Welch, D.W., Eveson, J.P., Boggs, C.H., Brainard, R.E., 2001. Ability of archival tags to provide estimates of geographical position based on light intensity. In: Sibert, J.R., Nielsen, J.L. (Eds.), Electronic tagging and tracking in marine fisheries Reviews: Methods and Technologies in Fish Biology and Fisheries. Kluwer Academic Press, Dordrecht, pp. 343–368.

Musyl, M.K., Domeier, M.L., Nasby-Lucas, N., Brill, R.W., McNaughton, L.M., Swimmer, J.Y., Lutcavage, M.S., Wilson, S.G., Galuardi, B., Liddle, J.B., 2011. Performance of pop-up satellite archival tags. Mar. Ecol. Prog. Ser. 433, 1–28.

Nakano, H., Matsunaga, H., Okamoto, H., Okazaki, M., 2003. Acoustic tracking of bigeye thresher shark *Alopias superciliosus* in the eastern Pacific Ocean. Mar. Ecol. Prog. Ser. 265, 255–261.

Neat, F.C., Burns, F., Jones, E., Blasdale, T., 2015. The diversity, distribution and status of deep-water elasmobranchs in the Rockall Trough, north-east Atlantic Ocean. J. Fish. Biol. 87, 1469–1488. http://dx.doi.org/10.1111/jfb.12822.

Nielsen, A., Bigelow, K.A., Musyl, M.K., Sibert, J.R., 2006. Improving light-based geolocation by including sea surface temperature. Fish. Oceanogr. 15, 314–325.

Pajuelo, J.G., González, J.A., Santana, J.L., 2010. Bycatch and incidental catch of the black scabbardfish (*Aphanopus carbo*) fishery off the Canary Islands. Fish. Res. 106, 448–453.

Peklova, I., Hussey, N.E., Hedges, K.J., Treble, M.A., Fisk, A.T., 2012. Depth and temperature preferences of the deepwater flatfish Greenland halibut *Reinhardtius hippoglossoides* in an Arctic marine ecosystem. Mar. Ecol. Prog. Ser. 467, 193–205. http://dx.doi.org/10.3354/meps09899.

Peklova, I., Hussey, N.E., Hedges, K.J., Treble, M.A., Fisk, A., 2014. Movement, depth and temperature preferences of an important by catch species, Arctic skate *Amblyraja hyperborea,* in Cumberland Sound, Canadian Arctic. Endanger. Res. Species 23, 229–240. http://dx.doi.org/10.3354/esr00563.

W. Press, S. Teukolsky, W. Vetterling, B. Flannery, Numerical Recipes in Fortran 77: The Art of Scientific Computing, 1992 933.

Priede, I.G., Froese, R., Bailey, D.M., Bergstad, O.A., Collins, M.A., Dyb, J.E., Henriques, C., Jones, E.G., King, N., 2006. Numerical Recipes in Fortran 77: The Art of Scientific Computing. P. Roy. Soc. Lond. B Biol. 273 (1592), 1435–1441.

Robison, B.H., 2003. What drives the diel vertical migrations of Antarctic midwater fish? J. Mar. Biol. Ass U.K. 83, 639–642.

Rodríguez-Cabello, C., Sánchez, F., 2014. Is *Centrophorus squamosus* a highly migratory deep-water shark? Deep-Sea Res. PT I 92, 1–10.

Roemmich, D., Gilson, J., 2009. The 20014–2008 mean and annual cycle of temperature, salinity, and steric height in the global ocean from the Argo Program. Progr. Oceanogr. 82, 81–100.

Sánchez, F., Serrano, A., Parra, S., Ballesteros, M., Cartes, J.E., 2008. Habitat characteristics as determinant of the structure and spatial distribution of epibenthic and demersal communities of Le Danois Bank (Cantabrian Sea, N. Spain). J. Mar. Syst. 72, 64–86.

Severino, R., Afonso-Dias, I., Delgado, J., Afonso-Dias, M., 2009. Aspects of the biology of the leaf-scale gulper shark *Centrophorus squamosus* (Bonnaterre, 1788) off Madeira archipelago. Arquipél. Life Mar. Sci. 26, 57–61.

Shepard, E.L.C., Ahmed, M.Z., Southall, E.J., Witt, M.J., Metcalfe, J.D., Sims, D.W., 2006. Diel and tidal rhythms in diving behavior of pelagic sharks identified by signal processing of archival tagging data. Mar. Ecol. Prog. Ser. 328, 205–213.

Simpfendorfer, C.A., Heupel, M.R., 2004. Assessing habitat use and movement (Chapter 19). Biology of Sharks and their Relatives 2004. CRC Press, pp. 553–572, ISBN: 978-0-8493-1514-5.

Sims, D.W., Southall, E.J., Richardson, A.J., Reid, P.C., Metcalfe, J.D., 2003. Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. Mar. Ecol. 248, 187–196.

Sims, D.W., Wearmouth, V.J., Southall, E.J., Hill, J.M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G.C., Righton, D., Metcalfe, J.D., Nash, J.P., Morritt, D., 2006. Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. J. Anim. Ecol. 75 (1), 176–190.

Skomal, G.B., Zeeman, S.I., Chisholm, J.H., Summers, E.L., Walsh, H.J., McMahon, K. W., Thorrold, S.R., 2009. Transequatorial migrations by basking sharks in the Western Atlantic Ocean. Curr. Biol. 19 (12), 1019–1022. http://dx.doi.org/10.1016/j.cub.2009.04.019.

Stevens, J.D., Bradford, R.W., West, G.J., 2010. Satellite tagging of blue sharks (*Prionace glauca*) and other pelagic sharks of eastern Australia: depth behaviour, temperature experience and movements. Mar. Biol. 157, 575–591. http://dx.doi.org/10.1007/s00227–009-1343–6.

Stokesbury, M.J.W., Harvey-Clark, C., Gallant, J., Block, B.A., Myers, R.A., 2005. Movement and environmental preferences of Greenland sharks (*Somniosus microcephalus*) electronically tagged in the St. Lawrence Estuary, Canada. Mar. Biol. 148, 159–165. http://dx.doi.org/10.1007/s00227–005-0061-y.

Sundström, L.F., Gruber, S.H., Clermont, S.M., Correia, J.P.S., de Marignac, J.R.C., Morrissey, J.F., Lowrance, C.R., Thomassen, L., Oliveira, M.T., 2001. Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. Environ. Biol. Fish. 60, 225–250.

Teo, S.L.H., Boustany, A., Blackwell, S., Walli, A., Weng, K.C., Block, B.A., 2004. Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. Mar. Ecol. Prog. Ser. 283, 81–98.

Thomson, R.E., Emery, W.J., 2014. Data analysis methods in physical oceanography, third ed Elsevier Sciences, Newnes, p. 728, ISBN: 9780123877833.

Van Aken, H.M., 2000. The hydrography of the mid-latitude Northeast Atlantic Ocean. I: The deep water masses. Deep-Sea Res. PT I 47, 757–788. http://dx.doi.org/10.1016/S0967–0637(99)00092–8.

Verissimo, A., McDowell, J.R., Graves, J.E., 2012. Genetic population structure and connectivity in a commercially exploited and wide-ranging deep water shark, the leafscale gulper shark (*Centrophorus squamosus*). Mar. Freshw. Res. 63, 505–512.

Vestheim, H., Kaartvedt, S., 2009. Vertical migration, feeding and colouration in the mesopelagic shrimp *Sergestes arcticus*. J. Plankton Res. 31 (11), 1427–1435. http://dx.doi.org/10.1093/plankt/fbp077.

Watanabe, H., Moku, M., Kawaguchi, K., Ishimaru, K., Ohno, A., 1999. Diel vertical migration of myctophid fishes (Family Myctophidae) in the transitional waters of the western North Pacific. Fish. Oceanogr. 8 (2), 115–127.

Welch, D.W., Eveson, J.P., 2001. Recent progress in estimating geoposition using daylight. In: Sibert, J.R., Nielsen, J.L. (Eds.), Electronic Tagging and Tracking in Marine Fisheries. Kluwer Academic Publisher, Dordrecht, pp. 369–383.

West, G.J., Stevens, J.D., 2001. Archival tagging of school shark, *Galeorhinus galeus*, in Australia: initial results. Environ. Biol. Fish. 60, 283–298.

Westerberg, H., 1984. The orientation of fish and the vertical stratification at fine- and micro-structure scales. In: McCleave, J.D., Arnold, G.P., Dodson, J.J., Neill, W. H. (Eds.), Mechanisms of Migration in Fishes. Plenum Press, New York, pp. 179–203.

Westerberg, H., Lagenfelt, I., Svedang, H., 2007. Silver eel migration behaviour in the Baltic. ICES J. Mar. Sci. 64 (7), 1457–1462.

Wetherbee, B.M., 2000. Assemblage of deep-sea sharks on Chatham Rise, New Zealand. Fish. Bull. 98, 189–198.