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Movement of blue shark, *Prionace glauca*, in the north-east Atlantic based on mark–recapture data

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A shark tagging programme along the Portuguese coast was initiated in 2001 in collaboration with the National Marine Fisheries Service. From a total of 168 blue sharks (*Prionace glauca*) tagged, 34 sharks were recaptured (20% return rate) providing important information on this species' movement patterns for the area. A total of 28 sharks travelled less than 1000 km while at liberty for time periods ranging from 22 to 1294 days. The remaining fish travelled long distances to north-west Africa, central Atlantic and the Bay of Biscay. Only one shark made a transatlantic migration, being recaptured 3187 km from the tagging site. North–south movements seem to be related to seasonal sea-surface temperature variation in the north-east Atlantic. Seasonal segregation of different life stages also occurs.

INTRODUCTION

The blue shark, *Prionace glauca* (Linnaeus, 1758), is probably the widest ranging chondrichthyian (Compagno, 1984) inhabiting oceanic and circumglobal waters both in temperate and tropical seas (Stevens, 1990). It is found over the entire mid-Atlantic, ranging from Newfoundland to Argentina in the west and from Norway to South Africa in the east (Compagno, 1984).

The study of sharks in their natural environment poses several difficulties due to their size, free-ranging behaviour, and the fact that they live in a relatively inaccessible and concealing environment (Sundström et al., 2001). Nonetheless, scientific tagging of sharks and other pelagic fish has been an area of considerable research. These studies have generally been hampered by a variety of factors, such as low tag returns, tagging induced mortality, incorrect recording of tag or recapture data (Kohler & Turner, 2001), dependence upon fishermen to return tags (Holden & Horrod, 1979), fishing pressure and tag shedding (Stevens, 1976; Graves et al., 2002). Furthermore, mark–recapture experiments provide no information concerning the extent and direction of movement during the intervening period at liberty (Bolle et al., 2005).

Despite their limitations, tagging programmes have provided valuable information on a wide variety of aspects of fish biology, including age validation and growth parameters (Pratt & Casey, 1983; Cailliet et al., 1992; Shackell et al., 1997; Hearn & Polacheck, 2003) as well as pelagic species' movements (Thorson, 1971; Holden & Horrod, 1979; Holland et al., 2001). Data gathered in such programmes can also be used to analyse the distribution of sizes and sex ratios, indices of relative abundance, multinational fisheries management and stock structure (Kohler et al., 2002). Blue shark tagging studies developed in the Atlantic Ocean have been successful in collecting information on short- and long-term movements and migrations, growth rate, reproductive behaviour and in identifying mating and nursery areas (Stevens, 1976; Casey, 1985).

The present study aims to describe the movement patterns of blue sharks tagged off the Portuguese coast and investigate the influence of bottom relief features and sea-surface temperature (SST) in these patterns and in the species' distribution in the north-east Atlantic.

MATERIALS AND METHODS

A shark tagging programme along the Portuguese coast was initiated in 2001 in cooperation with the National Marine Fisheries Service (NMFS). Blue sharks were caught on rod and line and marked by sport fishermen using charter boats, in three main areas of the Portuguese coast (Figure 1). Fishermen were trained for tagging according to the procedures of the NMFS Cooperative Shark Tagging Programme. Dart tags were implanted in the dorsal musculature near the base of the first dorsal fin. According to Casey (1985), this type of tag has the advantage of containing detailed return instructions, being visible and easily applied with simple and inexpensive equipment. Fishermen were asked to measure shark fork length (FL) (over-the-body) or, failing this, to estimate their length visually. Whenever shark FL was unavailable it was calculated from reported total length using the equations provided by Kohler et al. (1996).

All recaptures were made by commercial surface longline vessels targeting swordfish (*Xiphias gladius* Linnaeus,

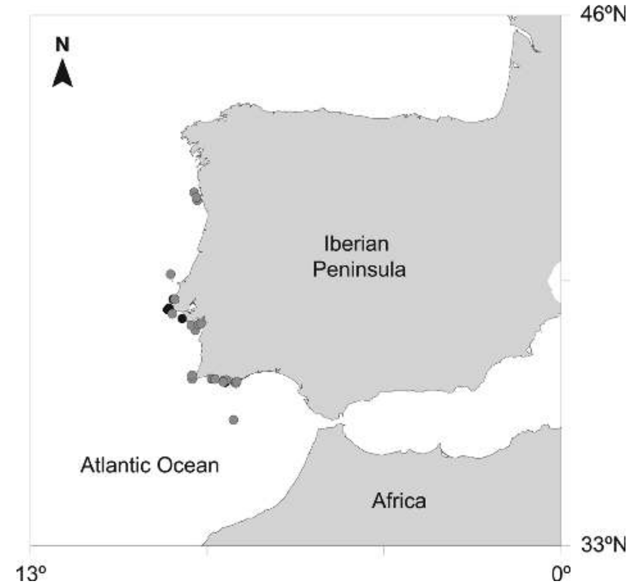

Figure 1. Locations of tagged sharks off the Portuguese coast; black circles are male positions and grey circles are female positions.

1758). Because size at recapture, when available, was always estimated roughly (in many cases it was only an estimate of dressed weight), FL at recapture was computed using the growth curves provided by Skomal & Natanson (2003) and time at liberty.

Capture and recapture locations were plotted on bottom topography and SST images with locations geo-referenced using the GRASS Geographical Information System (GRASS Development Team, 2005). Bathymetry data were obtained using the 2-min gridded global relief database (http://www.ngdc.noaa.gov/) from the Geophysical Data System (GEODAS) National Geophysical Data Center (NGDC). Minimum distance between capture and recapture sites was calculated avoiding land using the GRASS GIS shortest-path module (v.net.path), thus providing a better estimate of the travelled distance.

Sea-surface temperature (MODIS/Terra) data were obtained through the online PO.DAAC Ocean ESIP Tool (POET) (http://poet.jpl.nasa.gov/) at the Physical Oceanography Distributed Active Archive Center (PO.DAAC), NASA Jet Propulsion Laboratory. Seasons were defined as winter (December to February), spring

Table 1. *Release and recapture details for tagged blue sharks.*

Capture					Recapture					
Lat. N	Long. W	Date	Sex	FL (cm)	Lat. N	Long. W	Date	FL (cm)	DL	TD (Km)
36°53′	08°10′	03-Apr-01	F	147*	37°02′	07°30′	24-May-01	150*	51	62
36°55′	08°08′	20-Apr-01	F	110	37°00′	09°06′	24-May-01	112	34	89
36°58′	08°43′	26-Jun-01	F	116	36°56′	08°29′	20-Jul-01	118	24	12
36°58′	08°43′	28-Jun-01	M	120	36°56′	08°29′	20-Jul-01	122	22	12
36°57′	08°26′	07-Jun-01	M	125	39°30′	10°20′	26-Oct-01	136	141	360
37°09′	09°10′	07-May-01	M	105	38°17′	09°60′	18-Sep-01	117	134	146
36°58′	08°43′	30-Aug-01	F	134	37°10′	12°30′	31-Oct-01	138	62	349
36°58′	08°43′	05-Aug-01	F	98	41°30′	09°40′	06-Sep-01	100	32	553
36°54′	08°11′	17-Apr-01	F	120	43°52′	03°35′	01-Sep-01	129	137	1256
36°58′	08°43′	25-Jun-01	F	110	38°15′	08°53′	05-Nov-01	119	133	187
37°09′	09°10′	23-May-01	M	108	38°22′	08°56′	05-Nov-01	122	166	182
36°58′	08°43′	17-Jul-01	F	118	37°40′	10°20′	20-Nov-01	126	126	180
36°58′	08°43′	01-Sep-01	M	99	36°40′	08°01′	26-Nov-01	106	86	63
37°01′	08°34′	27-Jul-01	F	110	34°00′	07°53′	15-Jan-02	122	172	341
37°01′	08°34′	24-Jul-01	F	67	39°20′	14°00′	20-Jan-02	82	180	551
37°00′	08°35′	31-Jul-01	F	61	37°05′	09°06′	10-Apr-02	83	253	57
36°58′	08°43′	02-Nov-01	F	86	39°00′	18°00′	25-May-02	102	204	847
35°56′	08°09′	30-Apr-01	F	108	47°40′	08°15′	26-Jul-02	138	452	1344
36°54′	08°10′	24-Apr-01	F	108	46°50′	03°10′	23-Aug-02	140	486	1407
36°54′	08°25′	06-May-02	M	110	35°59′	08°34′	08-Aug-02	118	94	103
36°58′	08°43′	24-Oct-01	M	85	43°10′	09°45′	20-Aug-02	112	300	727
36°54′	08°25′	12-Jun-02	M	130	36°35′	11°40′	27-Jan-03	146	229	292
36°54′	08°25′	22-Jun-02	M	125	36°40′	14°15′	27-Jan-03	141	219	521
36°58′	08°43′	16-Aug-01	F	80	42°45′	17°24′	15-Dec-02	117	486	991
36°58′	08°43′	04-Aug-01	M	67	39°00′	45°00′	01-May-03	125	635	3187
38°23′	09°03′	14-Jun-03	F	93	42°10′	15°50′	27-Aug-03	99	74	717
36°53′	08°13′	03-Oct-03	M	100	36°30′	11°20′	28-Apr-04	118	208	281
36°58′	08°43′	04-Sep-02	F	120	40°30′	22°30′	04-Jun-04	159	639	1261
38°43′	09°44′	17-Oct-03	M	82	41°28′	11°00′	20-Aug-04	110	308	329
36°54′	08°25′	06-Jan-02	M	135	32°24′	9°40′	01-Sep-04	191**	969	514
36°54′	08°25′	10-Jul-02	F	130	22°11′	21°12′	12-Sep-04	175*	795	2049
36°54′	08°25′	13-Oct-02	F	96	35°30′	11°30′	10-Aug-04	142	667	318
36°54′	08°04′	11-Apr-01	F	113	36°45′	14°10′	26-Oct-04	186**	1294	544
36°57′	08°26′	12-Jun-01	F	110	30°15′	13°20′	13-Jan-04	167*	945	873

Lat., latitude; Long., longitude; FL, fork length; DL, days at liberty; TD, travelled distance. FL at recapture was computed using the growth curves provided by Skomal & Natanson (2003) and time at liberty; *, sub-adult females; **, adult sharks.

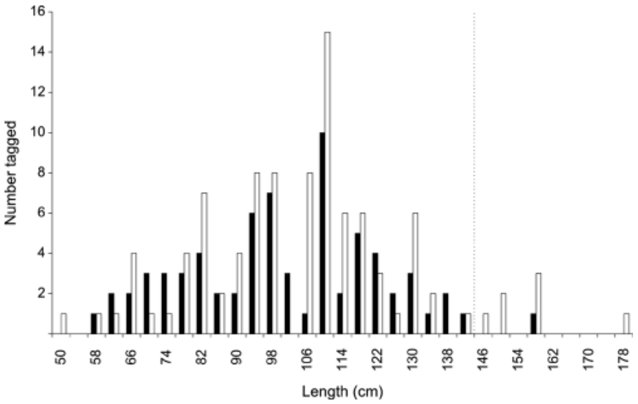

Figure 2. Length-frequency distributions of tagged blue sharks; black bars are males and white bars are females. Size at which females reach a sub-adult stage is depicted by a dotted line.

(March to May), summer (June to August) and autumn (September to November). Seasonal SST plots were calculated as 4-y seasonal averages comprising data from December 2000 to November 2004.

A χ^2-test was used to compare length distribution of recaptured fish (at tagging) and length distribution of all captured fish, in order to identify any bias in the recaptures. Pearson's correlation coefficients were estimated between distance travelled and time at liberty or size of fish (at recapture). A *t*-test was used to test for differences in average travelled distance between sexes.

RESULTS

Between April 2001 and September 2004, a total of 168 blue sharks was tagged off the Portuguese coast. The length-frequency distribution of captured sharks is shown in Figure 2. The average FL was 105 cm with a mode at approximately 110 cm. About 58% (N=98) of the tagged sharks were females, ranging in size from 51 to 180 cm FL. Males (N=70) were on average smaller, ranging from about 60 to 160 cm FL. Of the tagged sharks, all males and 93% of the females were immature, while 7% were passing through a sub-adult phase as defined by Pratt (1979).

During this study, 34 tags (20%) had been recovered. Details of shark length, position and date of capture and recapture are given in Table 1. Length distribution of recaptured fish (at tagging) was not statistically different from length distribution of all captured sharks (χ^2=21.849, df=26, P=0.696) suggesting that recapture was not conditioned by size at tagging.

Minimum travelled distance is depicted in Figure 3. Time at liberty and travelled distance were positively correlated, although this correlation was small (r=0.469, P=0.005). Of the 34 recaptured sharks, 28 travelled less than 1000 km, and were caught either in the same year or up to three and half years later. Of the remaining individuals, five females travelled long distances (between 1256 and 2049 km) and were caught off north-west Africa, in the central Atlantic and in the Bay of Biscay. Time at liberty for these fish ranged between 137 and 795 d.

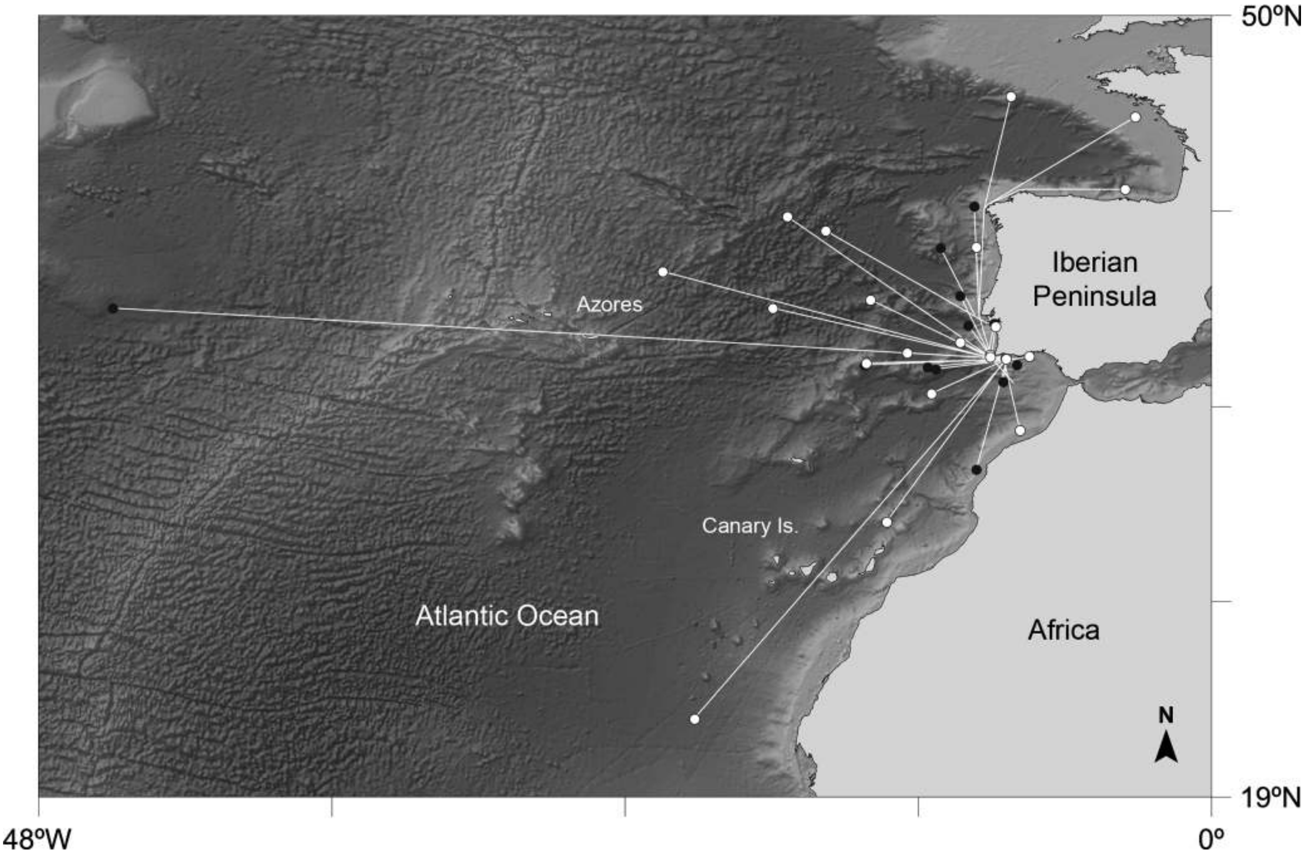

Figure 3. Travel paths and recapture positions for blue sharks; black circles are male recapture positions and white circles are female recapture positions.

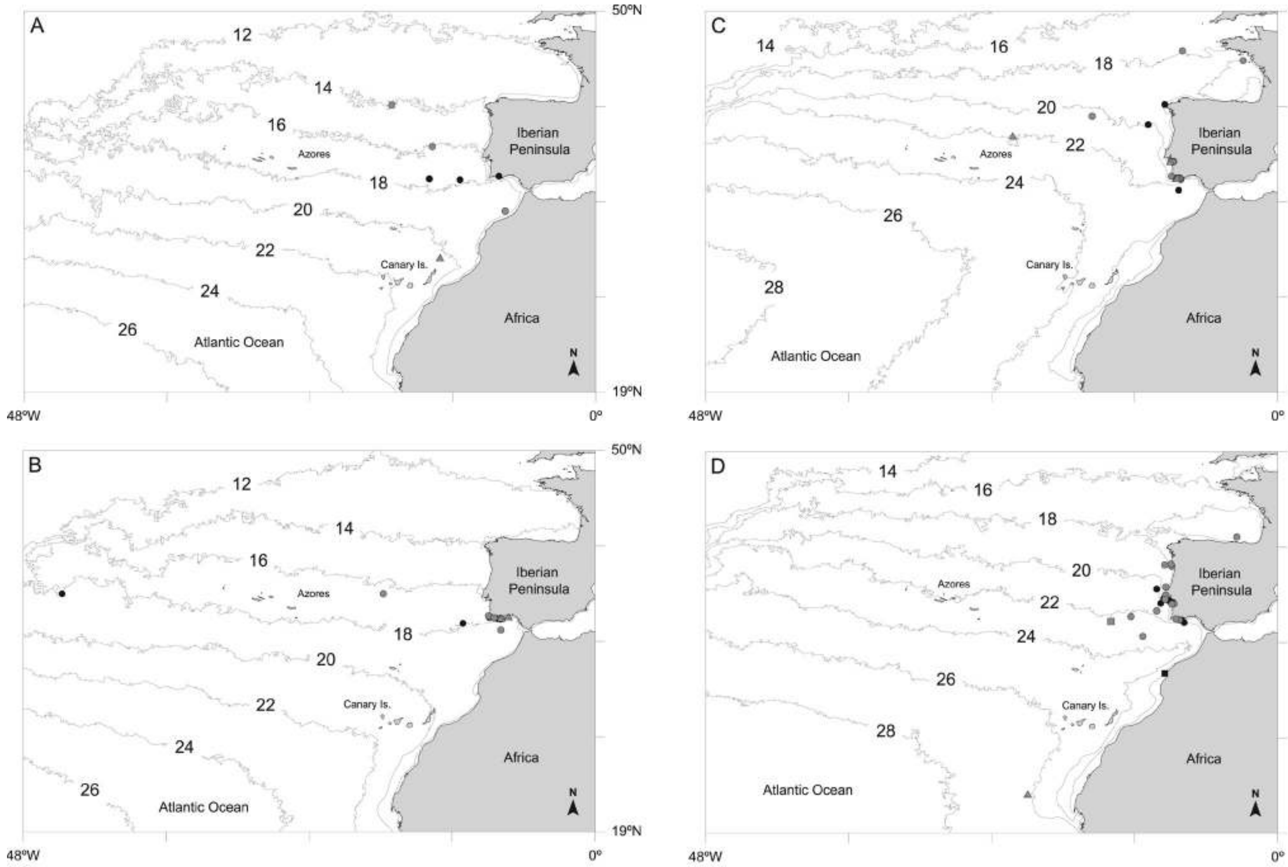

Figure 4. Positions of captured/recaptured blue sharks in relation to sea-surface temperature (SST) features. Plots represent 4-year seasonal averages, from December 2000 to November 2004. (A) Winter (December–February); (B) spring (March–May); (C) summer (June–August); (D) autumn (September–November). Black symbols are male capture/recapture positions; grey symbols are female capture/recapture positions; ○, immature sharks; △, sub-adult females; □, adult sharks.

According to the classification provided by Casey (1985), one male shark (67 cm FL at tagging) made a transatlantic migration travelling 3187 km in 635 d, an average of 5.02 km d^{-1}.

No correlation was found between size (FL at recapture) and travelled distance (r=0.250, P=0.154). Average travelled distance was not statistically significant between sexes (t=0.267, df=21, P=0.792). The rate of movement ranged from 0.23 to 17.29 km d^{-1}, with an average of 2.76 km d^{-1}.

Overall, 32 sharks were recaptured in the vicinity of areas with high bottom relief, such as seamounts, canyons or the continental shelf slope (Figure 3). There were two exceptions, one shark recaptured south of the Canary Islands (22°11′N 21°12′W) and another in the Bay of Biscay, west of Les Sables-d'Olonne (46°50′N 03°10′W).

In the winter and spring months blue sharks were found in a SST range of 14–22°C and between 30°–43°N (Figure 4A,B). During summer and autumn, sharks were captured as far north as 48°N and the SST ranged from 16°C to 28°C (Figure 4C,D). Overall, 82% of the sharks were found in a SST range from 15.5°C to 20°C.

During winter and autumn months (Figure 4A,D), all immature males and females were found off the African and the Iberian Peninsula coasts. One mature female was found in offshore waters off the south-west coast of Portugal. One mature male and two sub-adult females were spotted off the African coast. In the spring and summer months no mature sharks were captured but sub-adult females were found both in southern and central Portugal and near the Azores archipelago.

DISCUSSION

The return rate of 20% obtained in this study is much higher than expected, since Stevens (1976) reported a return rate of 3.9% for sharks tagged in Portuguese waters and more than half of the 52 shark tagging studies reviewed by Kohler & Turner (2001) reported return rates of less than 5%. Some authors have suggested that small fish of modal length between 100 and 110 cm FL remain within a relatively confined area and do not take part in more extensive north–south migrations (Stevens, 1976; Kohler et al., 2002), thus increasing the probability of recapture. Although in the present study no positive correlation was found between size and travelled distance, 64% of the sharks that travelled less than 1000 km fall within the 100–110 cm FL size-range. The fact that in subsequent years blue sharks remain in or return to areas where they were tagged indicates that the Portuguese coast is a favoured area for this species in the north-east Atlantic.

Blue sharks tagged off Portugal between 1971 and 1981 (Stevens, 1976, 1990) were smaller than those observed in the present study, with reported sizes ranging from 35 to 134 cm FL with a mode of 84 cm FL (N=332). The high percentage of immature individuals observed in these studies (including the present data) suggests that the north-eastern Atlantic population consists primarily of immature males and immature and sub-adult females with the sex ratio favouring the females (Kohler et al., 2002). Data from an ongoing sampling programme (2003–2005) of commercial shark landings on the three main Portuguese docks confirms this, since 94% of captured male sharks were immature and 95% of females were immature or sub-adults.

Blue sharks are common off the Portuguese coast throughout the year and no seasonal pattern of movement is evident. On the other hand, results confirm that blue sharks undertake north–south migrations in the north-east Atlantic (Clarke & Stevens, 1974; Stevens, 1976; Casey, 1985; Stevens, 1990). One of the disadvantages of tagging programmes is the fact that most tag returns are made by commercial fishing vessels. Hence, the distribution of recaptures may reflect the commercial fleet's activity rather than the true extent of fish migration (Bolle et al., 2005). Nonetheless, the summer range expansion towards the north, previously described by Clarke & Stevens (1974) and Stevens (1976) for south-west England, seems not to be related to any seasonal changes in the distribution of longline fishing fleet, and thus biased by recapture methods. Data for swordfish catch per unit effort (e.g. Mejuto et al., 1992, 2003, 2004) show that in the north-east Atlantic fishing activity is rather constant throughout the year.

Although the number of recaptured individuals was small (N=34) no difference was found between sexes in the average distance travelled. The single transatlantic migration observed in this study supports the fact that juveniles are also involved in long-range movements (Casey, 1985).

Longlines are usually set in the vicinity of bottom topography features such as seamounts (unpublished data). Consequently, it is not surprising that 32 of the 34 recaptured blue sharks were caught near areas of high bottom relief. Seamounts support unusually large populations of fish (Wilson & Boehlert, 2004), including pelagic species (Sibert et al., 2000; Holland et al., 2001). Most likely, high-relief bottom structures serve as orientation points in the larger-scale movements of blue sharks, as is the case for other shark species (Klimley et al., 1988, 2002) and migratory pelagic fish (Holland et al., 1999; Sedberry & Loefer, 2001).

Water temperature is known to influence the movements of the blue shark (Nakano, 1994) as well as other fish (Laurs et al., 1977; Lutcavage et al., 2000; Sims et al., 2000; Skomal et al., 2004). The northward summer migration to British and Irish waters (Stevens, 1976; Henderson et al., 2001) seems to be influenced by an increase in SST north of the Iberian Peninsula (see Figure 4C,D). The results from the present work confirm that the blue shark has a wide thermal tolerance, but prefers a much narrower temperature range (Sciarrotta & Nelson, 1977; Carey & Scharold, 1990).

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