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Movements of black and white anglerfish (*Lophius budegassa* and *L. piscatorius*) in the northeast Atlantic

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ABSTRACT

Within the frame of an international tagging program which has been carried out since 1995, movements of black and white anglerfish (*Lophius budegassa* and *L. piscatorius*) in Southern European waters were studied. This is the first large-scale study on movements of tagged black anglerfish. A total of 877 black anglerfish (6–88 cm total length) and 1326 white anglerfish (15–137 cm total length) were tagged. Times at liberty ranged from 1 to 665 days, with recapture rates of 21 (2.4%) and 50 (3.8%), respectively. A description of our tagging procedures is presented, together with the influences of the gear used, fish length and area of tagging on recapture rates. The type of fishing gear was the main factor affecting recapture rates. Fish length was neither related to the displacement distance nor to the time at liberty while the displacement distance was related to the time at liberty. Recapture locations suggested that movements occurred both in- and offshore. The largest displacement recorded was 408 km of a black anglerfish from southern to northern Bay of Biscay. The movements of the anglerfish indicate a mixing between northern and southern populations which may have strong implications for the current geographical boundaries of the stocks from a management perspective. Here, movement of white anglerfish between the Le Danois Bank and the Cantabrian continental shelf is reported for the first time.

1. Introduction

Both black (*Lophius budegassa*) and white anglerfish (*L. piscatorius*) are bottom living species that occur from shallow, inshore waters to 800 m and deeper than 1000 m, respectively (Whitehead et al., 1986; Quero and Vayne, 1997). The black anglerfish is distributed far to the south (Mediterranean and Eastern North Atlantic from the British Isles, 60°N, to Senegal, 12°N) while the white anglerfish has a more northern distribution (Mediterranean, Black Sea and Eastern North Atlantic from Barents Sea, 75°N, to Mauritania, 20°N), although the occurrence of both species overlaps considerably (Whitehead et al., 1986; Quero and Vayne, 1997).

In Europe, anglerfish are a commercially valuable species, caught by trawl and gillnetting fleets. Recent catches by vessels, mainly from France, Spain, UK, Ireland and Portugal have reached values around 40,000 t of white anglerfish, and around 9000 t of black anglerfish a year.

In the Northeast Atlantic, ICES establishes three areas for the assessments of anglerfish populations (Fig. 1): the southern stock of the southern shelf (Divisions VIIIc and IXa), the northern stock of the southern shelf (Divisions VIIb–k and VIIIabd), and the stock on the northern shelf (Division IIIa, sub-areas IV and VI). These stocks of anglerfish were established by international agreements on boundaries and coordinates and not based on biological features. The current stock or population definition of European anglerfish is questionable since there is a lack of information concerning their biology, specially their movements and possible migratory patterns. This information is fundamental to reduce uncertainties regarding stock boundary, for an enhanced fisheries assessment and management and for the adoption of alternative management measures, as closed areas.

The first movements of tagged black anglerfish on the southern shelf were reported by Landa et al. (2001~~a~~) and further information on tag-recapture is also available for the white anglerfish. Pereda and Landa (1997) reported on two white anglerfish, released on the south Bay of Biscay (ICES Division VIIIc, southern stock) and recaptured north of the Bay of Biscay (ICES Division VIIIab, northern stock). Their study showed that white anglerfish is able to cover large distances and that interaction is likely to occur among stocks.

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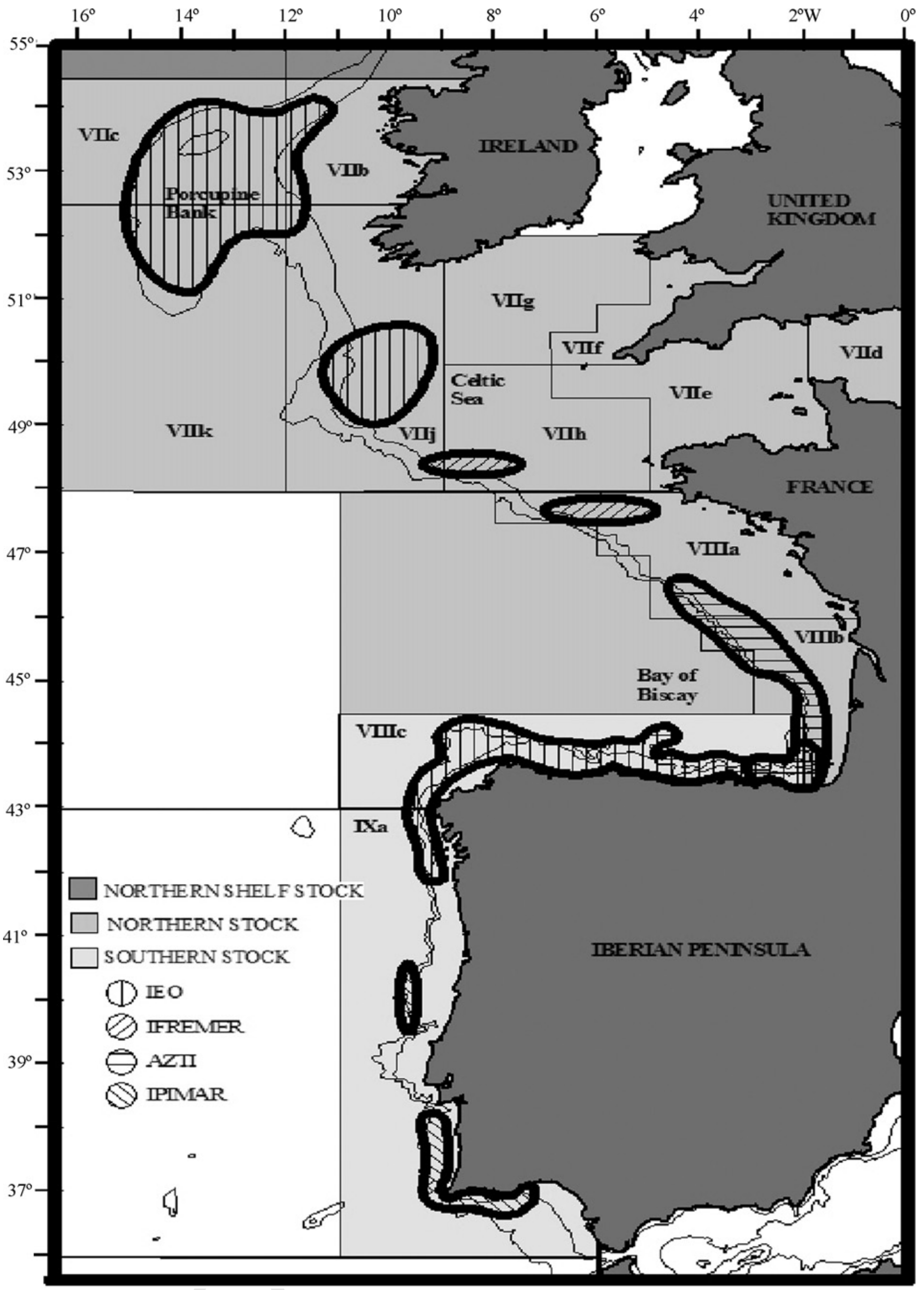

Fig. 1. Anglerfish stocks boundaries in the northeast Atlantic and locations of tagging areas covered by the institutions.

The longest distance, 876 km, travelled by a white anglerfish was recorded by Laurenson et al. (2005). They also showed new examples of movements among stocks, i.e. two fish tagged at the Shetland Islands (ICES Division IVa, northern shelf stock) were recaptured close to the Faroe Islands and Iceland, respectively (ICES Division IVa, Icelandic waters).

The present study is the first large scale tagging study on movements of black anglerfish and large scale tagging study for white anglerfish in Southern European waters. A selection of suitable commercial gear for anglerfish tagging and recapture is described. We also analyse the relationships between fish length at tagging, gear used, location of tagging and recapture rates. Further, we assess the relationship between the size of the fish, their displacement distance and time at liberty. The movements of the recaptures are described, and possible interactions among stocks and their relationships with the geographical distributions of the commercial catches are discussed.

2. Methods

A tag-recapture program was carried out during the period 1995–2004 by four marine Institutions (IEO[1], IFREMER[2], AZTI[3] and IPIMAR[4]). In 1995 IFREMER initiated tagging experiments on anglerfish in the northern Bay of Biscay (ICES Divisions VIIIab)

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Table 1
Characteristics of fishing gear used to capture anglerfish for tagging

Area	Mesh size (tow duration in hours or setting time in days)			
	Scientific trawl	Commercial trawl	Trammel net	Gillnet "rasco"
VIIchjk	20 mm (30 min)	80 mm (4–5 h)	–	–
VIIIabd	35 mm (30 min)	70–80 mm (3–4 h)	500–600 mm/90–110 mm (1 days)	280 mm (2–3 days)
VIIIc-east	20 mm (30 min)	60–69 mm (3–4 h)	500–600 mm/90–110 mm (1 days)	280 mm (4–8 days)
VIIIc-west	–	–	–	280 mm (2–7 days)
IXa-north	–	–	–/– (2–5 days)	–
IXa-south	20 mm (30 min)	–	–	–

External net/internal net.

Table 2
Number of black (b) and white (w) anglerfish tagged per year

Institution	Sp.	1995–1998	1999	2000	2001	2002	2003	2004	Total
AZTI	b	6	133	75	6				220
	w	9	21	202	4	24			260
IEO	b	34		67	270	49	18	4	442
	w	175		54	390	215	97	35	966
IFREMER	b	83							83
	w	92							92
IPIMAR	b		23	56	34	19			132
	w		1	6	1				8
Total	b	123	156	198	310	68	18	4	877
	w	276	22	262	395	239	97	35	1326

(Dupouy, 2006), while IEO worked in the southern Bay of Biscay (ICES Division VIIIc) (Pereda and Landa, 1997). During 1996 and 1997 tagging continued under the framework of the EU Study project *BIOSDEF*[5]. The first recaptures of tagged anglerfish allowed considering that the tagging-recapture technique was adequate for anglerfish. Tagging studies of anglerfish later expanded to other areas of the Northeast Atlantic (ICES Divisions VIIj and IXa-north). In 1998 AZTI began to tag anglerfish in the Bay of Biscay (Divisions VIIIabd and VIIIc), and in 1999 IPIMAR tagged fish in Portuguese waters (Division IXa-south). The basis for developing a large scale continuous tagging program was agreed upon under the EU Study project *DEMASSESS*[6]. Surveys, commercial fleets and gears catching anglerfish were studied and the most appropriate gears for the tagging objectives of the project in each geographical study area selected. Selection was made following prior qualitative survival observations (*DEMASSESS*; Lucio et al., 2000). The acceptable recapture rates and the movements observed initially allowed a wider geographical tagging design covering also the Atlantic waters in South-western Europe. This approach was developed under the EU Study project GESSAN[7].

2.1. Fleets and gears for tagging

In the Porcupine Bank (ICES Division VIIbck) tagging was conducted during the annual Spanish bottom trawl survey. Anglerfish for tagging were caught in southern Ireland waters (ICES Division VIIjh) and in the northern Bay of Biscay (ICES Division VIIIabd) by commercial bottom trawls, French trawl surveys, commercial trammel nets and gillnets (mainly by a specialised gillnet called "rasco" which captures large anglerfish, Pereda et al., 1998; Bruno et al., 2001). In northern Spanish waters (ICES Divisions VIIIc and IXa-north), anglerfish were caught by commercial "rasco" gillnets, bottom trawls, trammel nets and during Spanish bottom trawl surveys. In Portuguese waters (ICES Division IXa-south) anglerfish were only caught during Portuguese bottom trawl surveys.

Gear characteristics (mesh size, tow duration or setting time) varied in some areas (Table 1). The Spanish and Portuguese scientific trawling had tow duration of half an hour and a mesh size of 20 mm, while the French gear, designed to catch anglerfish and flatfish, had a mesh size aperture of 35 mm. The commercial trawlers used a mesh size between 60 and 80 mm, while the tow duration ranged from 3 to 5 h. The trammel nets, with an internal mesh size of ca. 110 mm were set from 1 to 5 days. The "rasco" gillnets, with a larger mesh size (280 mm), were set between 2 and 8 days.

2.2. Tagging and recaptures

Upon retrieval of the fishing gear, all anglerfish suitable for tagging (non-damaged and with a lively appearance) were immediately measured and tagged. A spaghetti T-bar anchor type (Floy Tag®) tag was inserted using a tagging gun supplied with a 2 cm needle. The insertion area was the mid-dorsal part of the tail muscle, between the first and the second dorsal fins, apparently a less invasive area for fish. Tags were either yellow or red, 4 cm in length, individually numbered and printed with return and reward information. Immediately after tagging, the anglerfish were released back to the sea. For each fish, information on length, tag code number, release location and depth was recorded.

The locations of the tagging areas covered by the institutions participating in the program are presented in Fig. 1. Informative posters about the tag-recapture experiments, rewards for recaptures and the necessary information about the recapture were distributed to the fishing associations and ports of Portugal, Spain, France and Ireland.

The recapture data and the tag (sometimes also the fish) were reported. Most of the recoveries were directly notified by the fishermen or their associations to the marine institutions.

[5] *BIOSDEF*. Biological studies of demersal fish, 1998. Final Report to the Commission of European Communities, DG XIV, EU Study Contract 95/038, 890 pp.

[6] *DEMASSESS*. New assessment and biology of the main commercial fish species: hake and anglerfish of the southern shelf demersal stocks in the south western Europe. 2000. Final Report to the European Commission, DG XIV Fisheries, Study Contract 97/015.

[7] *GESSAN*. Genetic characterization and stock structure of the two species of anglerfish (*Lophius piscatorius* and *L. budegassa*) of the northeast Atlantic, 2002. Final Report to the European Commission, DG XIV Fisheries, Study Contract 99/013, Part I, 249 pp.

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Table 3
Number of black (b) and white (w) anglerfish tagged and the recapture rates (%) by area and fishing gear used for tagging

	Sp.	Area	Fishing gear				
			Scientific trawl	Commercial trawl	Trammel net	Gillnet "rasco"	Total
Tagged (n)	b	VIIchjk	44	153	0	0	197
		VIIIabd	75	186	1	42	304
		VIIIc-east	11	12	2	164	189
		VIIIc-west	0	6	0	29	35
		IXa-north	7	0	12	1	20
		IXa-south	129	0	3	0	132
		Total	266	357	18	236	877
	w	VIIchjk	318	130	0	0	448
		VIIIabd	89	15	186	86	376
		VIIIc-east	114	17	37	197	365
		VIIIc-west	2	1	0	126	129
		IXa-south	8	0	0	0	8
		Total	531	163	223	409	1326
Recapture rate (%)	b	VIIchjk	2.3	0.0	–	–	0.5
		VIIIabd	2.7	1.1	–	11.9	3.0
		VIIIc-east	0.0	0.0	–	5.5	4.8
		VIIIc-west	–	–	–	6.9	5.7
		IXa-north	–	–	0.0	–	0.0
		IXa-south	0.0	–	–	–	0.0
		Total	1.1	0.6	0.0	6.8	2.4
	w	VIIchjk	0.6	0.8	–	–	0.7
		VIIIabd	2.2	0.0	3.2	10.5	4.5
		VIIIc-east	1.8	0.0	0.0	9.1	5.5
		VIIIc-west	–	–	–	7.9	7.8
		IXa-south	–	–	–	–	–
		Total	1.1	0.6	2.7	9.0	3.8

2.3. Data analysis

2.3.1. Areas and fishing gears

The *G*-test (Sokal and Rohlf, 1995) was employed to determine if the gear used to capture the fish for tagging, or the geographical area where the fish were tagged, were related to the chance of recapturing the fish.

2.3.2. Fish length and fishing gears

As the chance of recapture might be influenced not only by the gear but also by the fish size at tagging, the length distribution of all tagged fish were compared to that of tagged fish that were recaptured, using the Kruskal–Wallis non-parametric test. Previously, a comparison (using the Kruskal–Wallis analysis) of the length distribution of tagged anglerfish captured ($n > 10$) among different areas by a same fishing gear, allowed to group similar length distributions from different areas for a same kind of gear.

G-tests were used to test the effect of the fish size captured by gear on the recapture rate.

2.3.3. Time at liberty, displacement distance and variation in depth

The Tau-b Kendall coefficient was used to determine if the fish length at tagging was related to the distance of displacement, the time at liberty, and to the difference in depth between release and recapture. A linear regression analysis was used to explore the relationship between displacement distance and time at liberty.

To analyze the seasonal movements, the anglerfish between a week and 7 months at liberty were studied. In fish with more time at liberty, the outward journey could be masked by those of return, or vice versa, hence introducing bias in the analyses, so these fish were not considered.

To analyse seasonal variations in the movement of anglerfish, their mean displacements and variation in depth during the time at liberty were studied.

3. Results

A total of 877 black anglerfish and 1326 white anglerfish were tagged and released during the period 1995–2004. Table 2 shows the number of fish tagged by each of the participating institutes and year. Most of the tagging took place during 2000–2002.

Most of the anglerfish were tagged in Divisions VIIchjk, VIIIabd and VIIIc-east, with more than 500 anglerfish belonging to each of these areas (Table 3). More than 600 anglerfish were tagged in scientific and commercial trawlers, and in "rasco" gillnetters.

A total of 21 and 50 individuals of black and white anglerfish, respectively, were recaptured, with overall recapture rates of 2.4 and 3.8%, respectively. Recapture rates were estimated by area and fishing gear when the number of tagged anglerfish was higher than 10 (Table 3). Recapture rates varied depending on the location of release and the gear used to catch them, with similarities between both species. The highest rates (5–12%) were obtained for fish tagged with "rasco" gillnet, mainly in the southern Bay of Biscay (Divisions VIIIc and VIIIb); rates of around 3% were obtained for fish tagged in trammel net; up to 3% in scientific trawl, and up to 1% in commercial trawl (Table 3).

The sizes of the tagged anglerfish represented most of the length ranges of the populations, i.e. between 6 and 88 cm (50 cm of mean length) for the black anglerfish, and between 15 and 137 cm (52 cm of mean length) for the white anglerfish. Most of the recaptures were adults, their length range being 40–72 cm (58 cm of mean length) and 23–103 cm (72 cm of mean length) for black and white anglerfish respectively (Fig. 2).

3.1. Areas and fishing gears

There were significant differences in recapture rates among geographical areas in black ($G = 12.27$, $P < 0.001$) and in white anglerfish, ($G = 23.82$, $P < 0.001$) when data from all fishing gears were analysed together (Table 4a). However, when data from each gear type was

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Table 4
Result of *G*-tests comparing recapture rates of black (b) and white (w) anglerfish ((a) among geographical areas by capture gear, (b) among capture gear by geographical area. Scientific trawl (ST); commercial trawl (CT); trammel net (T); gillnet "rasco" (GR)); *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ns: not significantly different

Sp.	Gears	Areas compared	
(a)			
b	All gears	VIIchjk–VIIIabd–VIIIc-east–VIIIc-west–IXa-south	***
	Scientific trawl	VIIchjk–VIIIabd–VIIIc-east–IXa-south	*
	Commercial trawl	VIIchjk–VIIIabd–VIIIc-east	n.s.
	Gillnet rasco	VIIIabd–VIIIc-west–VIIIc-east	n.s.
w	All gears	VIIchjk–VIIIabd–VIIIc-east–VIIIc-west	***
	Scientific trawl	VIIchjk–VIIIabd–VIIIc-east	n.s.
	Commercial trawl	VIIchjk–VIIIabd–VIIIc-east	n.s.
	Trammel net	VIIIabd–VIIIc-east	n.s.
	Gillnet rasco	VIIIabd–VIIIc-west–VIIIc-east	n.s.
Sp.	**Areas**	**Gears compared**	
(b)			
b	All areas	ST–CT–GR	***
	All areas	ST–CT	n.s.
	VIIchjk	ST–CT	n.s.
	VIIIabd	ST–CT–GR	**
	VIIIc-east	ST–CT–GR	n.s.
w	All areas	ST–CT–T–GR	***
	All areas	ST–CT–T	n.s.
	VIII	ST–CT	n.s.
	VIIIabd	ST–CT–T–GR	**
	VIIIc-east	ST–CT–T–GR	***

analysed separately the only significant difference between areas was for scientific trawling in white anglerfish ($P < 0.05$). Therefore, the differences in the recapture rates are primarily influenced by the different gear used rather than by the area where the fish were tagged.

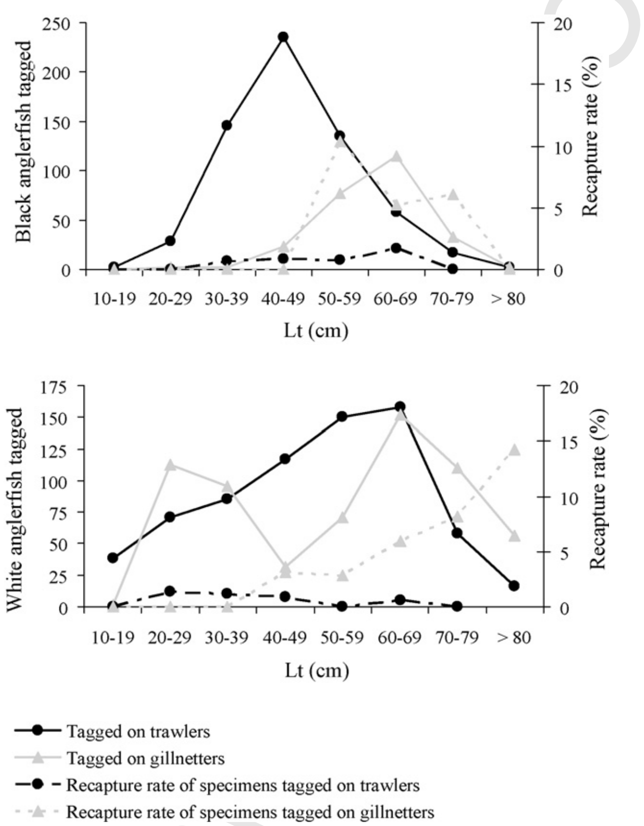

Fig. 2. Number of tagged black (upper figure) and white anglerfish (bottom) by length range (Lt, cm) that were caught by trawl and gillnet, and their respective recapture rates.

The results of the comparisons of the recapture rates among gears for all areas showed significant differences in black ($G = 21.34$, $P < 0.001$) and in white anglerfish ($G = 41.77$, $P < 0.001$) (Table 4b). The "rasco" gillnet had the highest recapture rates of all gears (Table 3). When this gear was excluded from the statistical analyses, no significant differences ($P > 0.05$) were found among the rest of the fishing equipments (Table 4b). These results confirm that the differences in the recapture rates among gear observed in Table 3, are mainly due to the highest rate of the "rasco" gillnet.

3.2. Fish lengths and fishing gears

The length of the anglerfish was different depending on the gear used, fish being larger in gillnet compared to trawl (Table 5, Fig. 2). The mean length of captured black anglerfish by scientific and commercial trawl was 47 and 46 cm, respectively; and 62 cm by "rasco" gillnet. The mean length of captured white anglerfish by scientific and commercial trawl was 51 and 48 cm, respectively; 30 cm by trammel net and 68 cm by "rasco" gillnet.

The results of the comparisons among the length distributions of anglerfish captured by the same kind of gear in different areas showed no significant differences for the black anglerfish captured by "rasco" gillnet among the studied areas ($\chi^2 = 5.29$, $P > 0.05$), neither for those captured by commercial trawl among areas ($\chi^2 = 1.35$, $P > 0.05$), nor for white anglerfish captured by trammel net among areas ($\chi^2 = 1.67$, $P > 0.05$) (Table 5). Therefore, the length distributions of the tagged anglerfish without significant differences in the areas mentioned could be treated, respectively, as a whole in the following comparison.

To test if fish size affected the rate of recapture a comparison of length distribution of all tagged fish and that of tagged fish that were recaptured, was made. No significant differences were found ($\chi^2 = 0.00$, $P > 0.05$) between the lengths of all black anglerfish tagged in "rasco" gillnetters and the lengths at tagging of those recaptured. Neither significant differences were found between the lengths of all white anglerfish tagged in "rasco" gillnetters in VIIIc ($\chi^2 = 2.76$, $P > 0.05$), nor in VIIIabd ($\chi^2 = 1.21$, $P > 0.05$), nor for trammel net in VIIIabd–VIIIc-east ($\chi^2 = 0.59$, $P > 0.05$). The comparison

Table 5
Result of Kruskal–Wallis test comparing length distributions of tagged black (b) and white (w) anglerfish among geographical areas by each type of gear (*$P<0.05$; **$P<0.01$; ***$P<0.001$; ns: not significantly different), and the mean length (cm) by type of gear

Sp.	Gears	Areas compared	Difference	Mean length (cm)
b	All gears	VIIchjk–VIIIabd–VIIIc-east–VIIIc-west–IXa-north–IXa-south	***	50
	Scientific	VIIchjk–VIIIabd–VIIIc-east–IXa-south	**	46
	trawl	VIIchjk–VIIIabd–IXa-south	n.s.	46
		VIIIc-east	36	
	Commercial trawl	VIIchjk–VIIIabd–VIIIc-east	n.s.	47
	Gillnet rasco	VIIIabd–VIIIc-east–VIIIc-west	n.s.	62
w	All gears	VIIchjk–VIIIabd–VIIIc-east–VIIIc-west	***	52
	Scientific	VIIchjk–VIIIabd–VIIIc-east	***	
	trawl	VIIchjk–VIIIabd	n.s.	56
		VIIIc-east		29
	Commercial	VIIchjk–VIIIabd–VIIIc-east	***	48
	trawl	VIIIabd–VIIIc-east	n.s.	55
		VIIchjk		46
	Trammel net	VIIIabd–VIIIc-east	n.s.	30
	Gillnet	VIIIabd–VIIIc-east–VIIIc-west	***	68
	rasco	VIIIc-east–VIIIc-west	n.s.	70
		VIIIabd		58

was not possible to be performed for trawlers neither for black, nor for white anglerfish, due to the few recoveries.

To test if the recapture rate was more influenced by the gear used for tagging than by fish size, the recapture rate of a same length range (50–69 cm) with more than 100 black anglerfish was selected and compared between both types of gear. This resulted in higher recapture rates for gillnets (7.4%) than for trawls (1.4%) ($G=7.12$, $P<0.01$). In the case of white anglerfish (20–79 cm), the

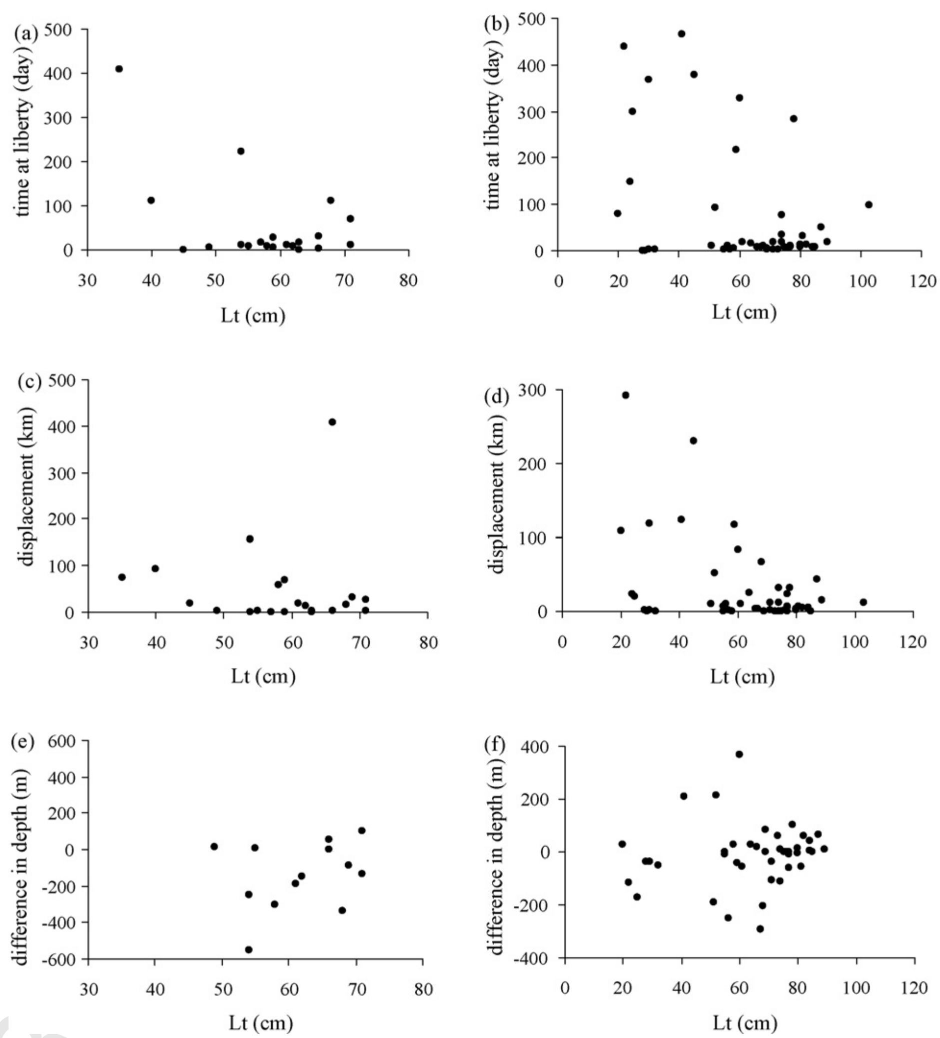

Fig. 3. Relationship between the length at tagging (Lt, cm) for black (left) and white anglerfish (right) and the time at liberty (a and b), displacement distance (c and d) and variation in depth between tagging and recapture (e and f).

recapture rates were also higher in gillnets (3.7%) than in trawls (0.7%) (G = 12.22, P < 0.001). Therefore, the use of the gillnet gear to capture the fish for tagging results significantly in higher recapture rates, probably due to the better chances of survival of fish that were less injured at capture.

The length of a certain anglerfish captured for tagging with a specific gear could have influenced its possibilities of being recaptured. Black anglerfish captured by trawl in the length ranges 30–49 and 50–69 cm were studied. No significant differences in recapture rates (1.2% and 1.4%, respectively, G = 0.02, P > 0.05) were found between these length ranges. Similarly fish captured by gillnet, and in the 40–59 and 60–79 cm length ranges showed no significant differences in their recapture percentage: 8.2% and 5.4%, respectively (G = 0.74, P > 0.05). For white anglerfish captured by trawl, the length ranges of 10–29, 30–39, 40–49, 50–59 and 60–79 cm were compared resulting in similar recapture percentages, i.e. 1.0, 1.2, 1.0, 0.0 and 0.5%, respectively. No significant differences were found between those length ranges (G = 1.13, P > 0.05). Fig. 2 shows length distributions of tagged and recaptured specimens by gear, where two modal lengths of the capture by gillnet are showed, a smaller one corresponding to trammel net, and a larger one corresponding to captures by "rasco". For white anglerfish captured by trammel net, both length ranges compared (20–29 and 30–39 cm) showed recapture indices of 0.0%. For fish captured by "rasco" gillnet, the length ranges of 50–59, 60–69 and >70 cm were compared and the recapture indices were 2.8, 5.9 and 10.2%, respectively. Significant differences were found between those length ranges (G = 4.79, P < 0.05), with a clear increase of the recapture rate with the fish length. Therefore, not only the white anglerfish captured by "rasco" gillnet have more possibilities of being recaptured, but also larger fish of those tagged with "rasco" gillnet. These results show that although the comparison of length distribution of all tagged fish and that of tagged fish that were recaptured did not show significant differences for "rasco" gillnet, differences were observed when the analysis were performed in detail for several length ranges.

3.3. Time at liberty, displacement distance and variation in depth

The majority of recoveries of tagged black and white anglerfish, 71% and 68%, respectively, took place during the first month after release, most of them (52% and 60%) during the first 2 weeks. Only five black anglerfish were recaptured after 3 months at liberty; two of them after more than 1 year (between 408 and 665 days at liberty). Eleven white anglerfish exceeded 3 months at liberty; four of them were recaptured after more than 1 year (between 368 and 465 days).

The time at liberty of the recaptures was not significantly correlated to the length at tagging neither for black (n = 21, r = 0.08, P > 0.05) nor for white anglerfish (n = 50, r = 0.02, P > 0.05) (Fig. 3).

It is possible that anglerfish of different sizes can display different types of behaviour and, for instance, that the smaller fish would have more possibilities of being recaptured earlier. To test this possibility, the lengths at tagging of anglerfish recaptured during the first month at liberty were compared to those with more than 1 month at liberty. No significant differences being found (P > 0.05), neither for black, nor for white anglerfish.

The displacement distance was not significantly correlated to the length at tagging, neither for black (n = 18, r = −0.16, P > 0.05) nor for white anglerfish (n = 50, r = −0.14, P > 0.05) (Fig. 3). The five longest movements of white anglerfish were of juveniles between 20 and 45 cm in length.

The difference in depth between release and recapture was not significantly correlated to the length at tagging, neither for black anglerfish (n = 13, r = 0.22, P > 0.05) nor for white anglerfish (n = 44, r = 0.15, P > 0.05) (Fig. 3).

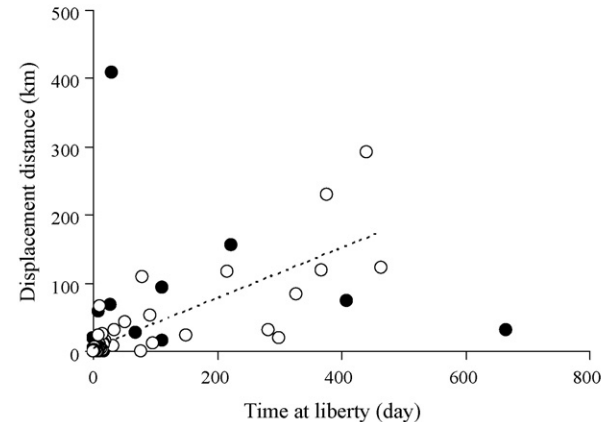

Fig. 4. Relationship between displacement distances and time at liberty of the recaptures of black (black spot) and white anglerfish (white spot and discontinuous line).

The displacement distance of recaptured black anglerfish was not significantly correlated to the time at liberty (n = 18, r = 0.35, P > 0.05). However, by ignoring the extreme movement of 408 km in 1 month, the correlation was significant (n = 17, r = 0.38, P < 0.05), but the ANOVA of the regression of both variables was not significant (P > 0.05). For white anglerfish, the displacement distance was significantly correlated with the time at liberty (n = 50, r = 0.68, P < 0.05) (Fig. 4), and the regression (r^2 = 0.72, P < 0.05) between both variables was: displacement (km) = 0.381 × time at liberty (days).

Based on the relationship between displacement distances and time at liberty of the anglerfish recaptured to date (Fig. 4), a mean displacement of 381 m per day was estimated for white anglerfish, with a maximum value of 6 km per day.

The mean displacement ~~(km × day)~~ data of the white anglerfish were analysed on a seasonal basis (Fig. 5). No significant differences were found (P > 0.05) when comparing the mean displacements from the fourth and first quarters with those of the second and third quarters.

The variation in depth between tagged and recaptured white anglerfish, showed that most of the movements to deeper bottoms were found from December to February (Fig. 5). There was a significant difference (P < 0.01) when comparing the depth variation of the fourth and first quarters with that of the second and third quarters. As for the trend of movements to deeper waters from December to February, there is no clear opposite trend during the rest of the year (Fig. 5). The scarce observations on depth variation for black anglerfish do not allow such a detailed analysis as that performed for white anglerfish.

3.4. Movements

Since most of the recaptures took place in a short period of time after releasing the tagged fish, most of the displacement distances were smaller than 20 km (all the distances were measured in a straight line) (Fig. 4). Displacement distances of six black and eight white anglerfish exceeded 50 km from the position of release. The highest movement of black anglerfish was 408 km after a month at liberty. The other five important movements ranged between 58 and 156 km, and took place within 14 months at liberty. The two longest movements of white anglerfish were 230 and 300 km after more than 1 year at liberty. Other four long movements ranged between 84 and 123 km, and took place from 2 months to more than a year.

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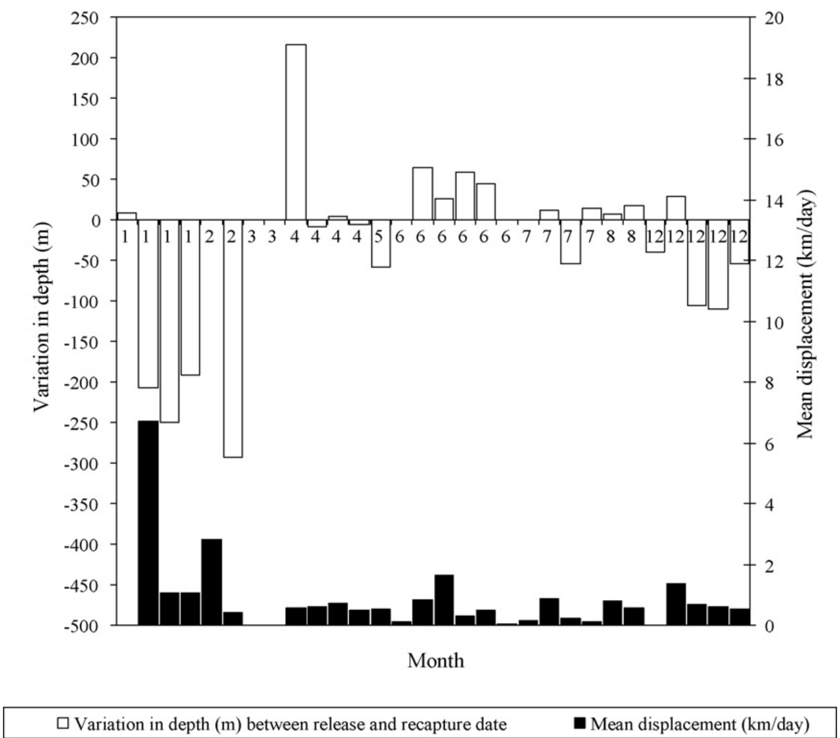

Fig. 5. Variation in depth (m) of each recaptured white anglerfish between the release and recapture dates ordered by the middle month when at liberty. Mean displacement (km × day) of the same fish.

Most of the areas where both black and white tagged anglerfish were recaptured were located in the Bay of Biscay with a considerable amount in its southeastern parts (Divisions VIIIc-east and VIIIb-south) (Figs. 6 and 7).

The black anglerfish with the longest movement was tagged south of the Division VIIIb, close to the boundary between the northern and southern stocks, and was recaptured in the Division VIIIa (northern stock) (Fig. 6). Another noticeable long movement was a recapture 7 months after tagging in Division VIIIb (northern stock), 156 km east of the tagging location in Division VIIIc (southern stock)) (Fig. 6). Other three significant movements, between 69 and 94 km, were observed around Brittany (northern Bay of Biscay), where two black anglerfish were recaptured after a few months in shallow waters at similar latitude in Division VIIIa (Fig. 6).

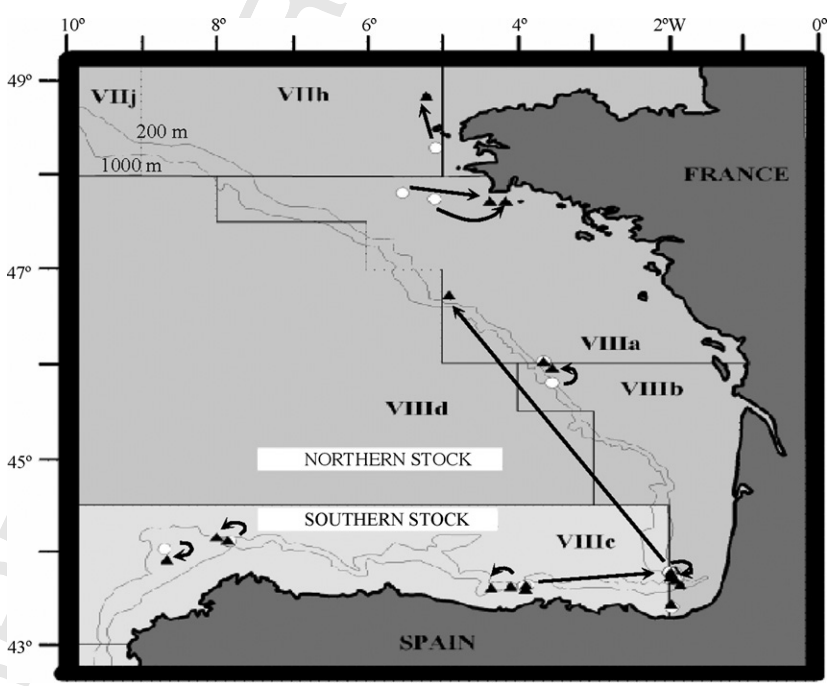

Fig. 6. Locations of the tagged (circle) and recaptured (triangle) black anglerfish.

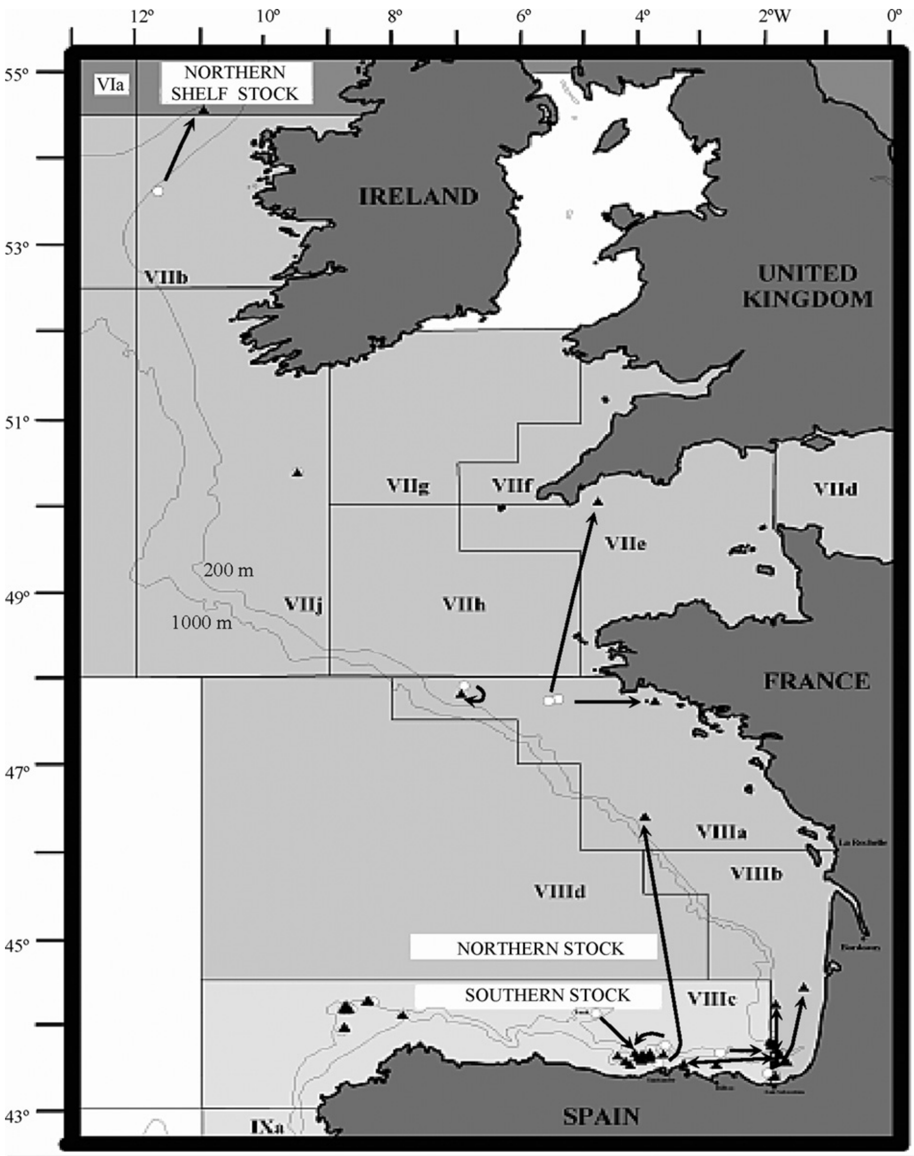

Fig. 7. Locations of the tagged (circle) and recaptured (triangle) white anglerfish.

From the five recaptures of white anglerfish with long movements, four of them were tagged in Division VIIIc (southern stock) during the fourth and the first quarters, and were recovered in Divisions VIIIab (northern stock) between 10 days and 15 months later, having covered from 52 to 292 km Fig. 7). The remaining recaptures moved in the opposite direction, from the tagging grounds in Division VIIIb (northern stock) to the recapture areas in Division VIIIc (southern stock), covering a distance of 123 km during 15 months at liberty.

Another significant movement of white anglerfish took place in the Cantabrian Sea (Division VIIIc-center), from Le Danois Bank ("El Cachucho") to the continental shelf, 84 km after 11 months (Fig. 8).

The four recaptures with small movements (between 20 and 43 km) in Division VIIIc were recaptured after short times at liberty (<2 months). They were tagged during the first or second quarters and recaptured to the west of the positions of release (Fig. 8).

Two white anglerfish tagged west of Brittany (Division VIIIa-north), were recaptured 12 months after tagging and had movements of 118 km and 230 km to the east and northeast, respectively, into shallower waters than those at which they had been tagged (Fig. 7).

From the white anglerfish tagged in western Ireland, one of them was recaptured in Division VIa (northern shelf stock), 117 km north of where it was tagged (Division VIIb, northern stock) (Fig. 7).

Because of the low number of samples we were unable to obtain reliable results on seasonal movements. However one can deduce from the data that white anglerfish in the southern Bay of Biscay (Division VIIIc-east) had a seasonal trend moving towards south-west and shallower waters between April and August. The only two movements during the first quarter were of white anglerfish towards the northeast from the southern Bay of Biscay. The only movement of black anglerfish during the first quarter was towards the north from the southern Bay of Biscay.

4. Discussion

4.1. Tagging-recapture

Anglerfish do not have a gas bladder (Rojo, 1988) and are resilient to being brought up to the surface. This study corroborates the usefulness of the tagging technique in black anglerfish as Landa et al. (2001a) had shown. The convenience of tagging white angler-

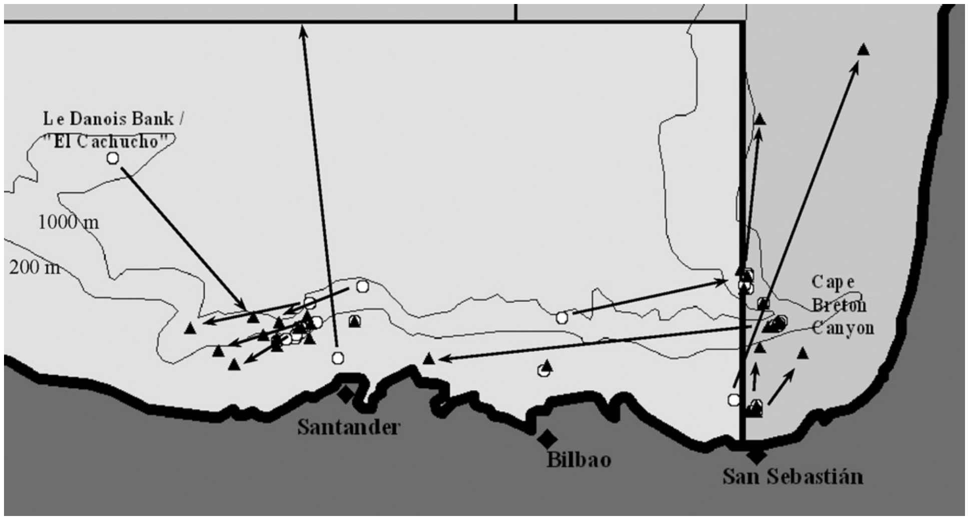

Fig. 8. Locations of the tagged (circle) and recaptured (triangle) white anglerfish in southern Bay of Biscay.

fish had already been corroborated by Pereda and Landa (1997) and Laurenson et al. (2005). Moreover, the daily activity pattern and vertical migration behaviour of the northwest Atlantic anglerfish, *L. americanus*, have been reported, based on data storage tags (Rountree et al., 2006).

The overall recapture rates obtained in the present study were lower than those estimated for white anglerfish tagged in northern European waters (4.5%) (Laurenson et al., 2005), and for *L. litulon* tagged in Japanese waters (5.6%) (Kitazawa and Yamamoto, 2002). However, the recapture rates of those studies are within the range of values estimated for different gear types and areas (Table 2). For both species, our results indicate that the differences in recapture rates between areas are more related to the fishing gear used than to other factors (geographical areas or differences between both species). Overall, the recapture rates of between 2 and 6% found for the genus *Lophius* are in the range of the rates estimated for other fish in which tagging results have been considered successful (de Pontual et al., 2003; Sigurdsson et al., 2006).

Qualitative observations indicated that the duration of the tows had effects on fish survival and therefore, on the possibility of successful tagging. Fishing tows of most bottom trawlers in Iberian waters (Spanish in ICES Divisions VIIIc and IXa-north, and Portuguese in Division IXa-south) were considered unsuitable for tagging due to their long duration. Furthermore, the anglerfish catches in many tows of these fleets were poor since they were not the targeted species. On the other hand, the tows of the trawlers in Divisions VIIIabd had shorter durations and therefore this fleet was regarded more suitable for tagging (Lucio et al., 2000).

The procedures used in capturing and handling the anglerfish may also have had an influence on the condition for tagging. Trawl gear seems to be more damaging than gillnet and therefore affecting survival rates to a higher degree. Although no significant differences were found in recapture rates between scientific and commercial trawls, the higher rates in the former could have been due to the shorter duration of the tows. Other factors, such as the duration of the trip, may also have had an influence on the recapture rates. In areas where the fleet has long trips (Spanish trawlers in Divisions VIIchjk longer than 2 weeks), the fishermen may be less interest in retaining and reporting the recaptures than in shorter trips. "Rasco" gillnet had higher recapture rates than trammel net or trawl for both species of anglerfish and it seems to be the most suitable gear for tagging experiments.

In accordance to Laurenson et al. (2005), we did not find any relationship between fish length at release and the chance of recapture for black anglerfish captured by trawl or gillnet. Neither did we find any relationship of the kind when trawl was used for capturing white anglerfish. However, for white anglerfish caught by "rasco" gillnet the recapture rate increased with increasing size of fish, probably due to their higher endurance under tagging.

Although the size of the anglerfish had no apparent influence on the displacement distance, as was also observed by Laurenson et al. (2005), the five longest displacements of white anglerfish were undertaken by juveniles. Fish size had no influence either on the period at liberty, although the displacement distance was related to the period at liberty. These facts may indicate that the displacements can occur throughout the life span of both species.

4.2. Movements

The morphology of the anglerfish suggests that it is a weak swimmer (Wheeler, 1969) which is in contrast to the long displacements observed in the current study. Since ca 70% of tagged anglerfish were recovered within a month after release, the information provided would be more useful if the time interval at liberty had been longer. Given the short time elapsed, most of the displacement distances were shorter than 25 km.

The several recaptures showing long geographical movements of white anglerfish in this study confirm the travelled behaviour showed previously by Pereda and Landa (1997) that showed displacement distances up to 292 km in the Bay of Biscay, and Laurenson et al. (2005) that recorded movement of an immature female 876 km from the Shetland Island towards the south coast of Iceland. Juveniles of white anglerfish have a pelagic behaviour which may promote wider dispersal and expansion of their natural habitat (Arkhipov and Mylnikov, 2002). Near-surface captures of post-juveniles recorded in the northeast Atlantic suggest the ability of young anglerfish to undertake short migrations (Hislop et al., 2000). The vertical migrations found in the northwestern congener, *L. americanus* (Rountree et al., 2006) also confirm the active behaviour of these related species.

Black anglerfish also travelled considerable distances. The record of 408 km within a month of release contrasts to all other fish surveyed, i.e. a mean displacement distance of around 13 km per day, compared to the overall average of 149 m per day. Similarly, (Kitazawa and Yamamoto, 2002) recorded a large displacement of

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L. litulon in Japanese waters amounting to 239 km in 26 days, with an average distance of 9 km per day.

An interesting movement of a white anglerfish was from Le Danois Bank ("El Cachucho"), a white anglerfish fishing area in which the main gear type used is the "rasco" gillnet. The bank is an ecological relevant marginal shelf in the Cantabrian Sea (Division VIIIc), composed of an almost flat surface located at a depth of 450–600 m, 25 km off the continental shelf and separated by a deeper internal basin (850 m) (Serrano et al., 2005). In 2008 Le Danois Bank was declared the first offshore Marine Protected Area in Spain and therefore information on the behaviour of the main commercial bottom species inhabiting it is of interest. Differences in ecological indices have been found between Le Danois Bank and the Cantabrian continental shelf (Serrano et al., 2005), and the bank may act as an isolated area for populations of some species. However, the white anglerfish tagged in Le Danois Bank and recaptured at the continental shelf shows the first evidence of movements between these two areas.

Information derived from commercial catches in the recapture areas is useful to understand anglerfish movements. Catches of gillnet targeting anglerfish in the southeast Bay of Biscay (Division VIIIc-east) took place at an average depth of 400 m (Pereda et al., 1998). These capture increase progressively from east to west and show relative high yields between December and February for black anglerfish, and between January and April for white anglerfish (Pereda et al., 1998). Tagging data combined with the temporal variation in commercial catches suggest that adult white anglerfish can move to deeper waters during the first quarter of the year, from the southeast towards the northeast Bay of Biscay, turning towards southwest and shallower depths during the second quarter.

Migrations from feeding to spawning areas are common among many commercial fish, and the displacements of anglerfish could be spawning related. Onshore~~–~~ offshore movements have been reported for *L. americanus* and *L. litulon* in response to thermal conditions, prey availability or spawning (Steimle et al., 1999; Yoneda et al., 2002). Duarte et al. (2001) suggested that white anglerfish undertakes a spawning migration to depths not accessible for the fishery fleet in Iberian Atlantic waters, and Hislop et al. ~~(2000)~~ also suggested that the spawning grounds around Britain are in relatively deep waters (150–900 m). The spawning season of white anglerfish in most of the North East Atlantic takes place mainly between January and May (Duarte et al., 2001; ICES, 2007~~a~~). Therefore, our observations concerning the displacement of the adult white anglerfish to deeper waters in the southeast Bay of Biscay could be related to reproductive activities.

The spawning season of black anglerfish occurs between November and February in the north of Spain (Duarte et al., 2001). Despite the scarce observations on seasonal variations in depth distribution in the present study for this species, the movements to deeper waters during the fourth and first quarter together with the highest yield indices in the deep catches by "rasco" gillnet, may indicate a comparable behaviour to white anglerfish and also related to spawning.

Oceanographic features may play a significant role in the movements of anglerfish. In the south Bay of Biscay a poleward current flows in winter eastward, in the upper 250 m, and, turning northward in French waters following the continental slope, at velocities up to 15 cm s^{-1}. There is evidence of a weaker countercurrent flowing westward in winter, in deeper (250–600 m) and offshore waters, where the bottom depths are higher than 1000 m (Pingree and Le Cann, 1990; Gil and Gomis, in press). During summer, the flow over the continental slope in the south Bay of Biscay is westward, and weaker than the poleward current (van Aken, 2002; Gil, ~~in press)~~. Most of the recaptures of white anglerfish indicating displacements during the fourth and first quarter, and that large displacement (408 km) of a black anglerfish during the first quarter were in the same north-easterly direction as the poleward current, therefore, this current could have an effect on those seasonal displacements.

4.3. Interactions between stocks

The recapture of two black anglerfish, one released in the distribution area of the southern stock and recaptured in the northern stock location, and another released at the boundaries between these stocks and found in the northern stock area, is probably linked to movements between populations. This is a first evidence of interactions between black anglerfish stocks.

Individual movements of white anglerfish between stocks were shown by Pereda and Landa (1997). In the present study we provide further evidence of these movements in both directions, i.e. from the north to the south stock and vice versa. The white anglerfish tagged in western Ireland (northern stock) and recaptured toward the North, in the distribution area of the northern shelf stock, represents the first evidence of anglerfish movements between these two stocks. The results of the present study together with the findings of Laurenson et al. (2005) on movements between the northern shelf stock and Icelandic waters, indicate movements of anglerfish among the areas of distribution of the three stocks considered in the northeast Atlantic.

Populations of anglerfish from the western and southern European Atlantic waters have been considered to be two different stocks, the so-called northern and southern stocks. This definition has not been based on biological features but rather on political agreements on boundaries, considering the Cape Breton Canyon, a geographical barrier. Fariña et al. (2004) showed that more than 98% of the total genetic variation was within these stocks and a relatively small proportion between stocks, indicating that the current geographic separation between the northern and the southern stock lacks genetic evidence and is poorly sustained. The results of the present study support the results of Fariña et al. (2004) and cast doubt on the biological basis of the current definition of these stocks. Furthermore, the movements between stocks may explain the limited genetic isolation observed for both European anglerfish stocks (Crozier, 1987; Charrier et al., 2006), as has been found for other Lophius species (Leslie and Grant, 1990; Chikarmane et al., 2000). On the other hand, the lack of genetic differences between both stocks could mean that there is no true separation between them. Information on fish life history parameters as the recent evidence of the real growth of the anglerfish obtained from tagging-recapture experiments in these stocks (Laurenson et al., 2005; Landa et al., 2008), are also useful to achieve a accurate definition of the stocks studied (Begg, 2005).

The reported displacement of anglerfish between the northern and the southern Bay of Biscay is likely not to be an exceptional event confined to some few individuals, but more like a general occurrence, as indicated by the seasonal variations found in the geographical distribution of commercial captures.

Since stock definitions are essential for fishery management, the present results point out the need for revising the assessment and management of anglerfish in the Bay of Biscay and the Celtic Sea. A failure in discriminating population structures could lead to over-fishing and finally to a possible erosion of genetic diversity at the species level (Stephenson, 1999). Stock definitions have tended not to be revisited in fisheries management. Stock structure can often create more uncertainty in fisheries management, particularly when it contradicts historically established stock and management boundaries, however, ignoring such information can contribute to an erroneous and ineffective fisheries management (Begg and Waldman, 1999).

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Q4 ## ~~Uncited references~~

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