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## BRIEF COMMUNICATION

# Sex differentiation in seasonal distribution of the starry smooth-hound *Mustelus asterias*

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## Abstract

This mark-recapture study of starry smooth-hound *Mustelus asterias* tagged during the summer months near the Dutch coast demonstrates a large-scale spatial sex differentiation in their circannual migration patterns and small-scale spatial sex differentiation during summer. Overwintering occurs in the North Sea, English Channel and Bay of Biscay, with significantly more males in the Northern North Sea and more females in the Bay of Biscay. During summer, sheltered sea arms off the Dutch coast were almost exclusively used by adult females. In subsequent summers post-release, both sexes were mostly confined to the Southern North Sea, suggesting philopatry.

## KEYWORDS

elasmobranchs, Greater North Sea, mark-recapture programme, seasonal migration, sharks

Elasmobranch species play important roles in marine food webs, but are also especially vulnerable to human intervention, such as fisheries, because of their K-selected life history strategies, characterized by late attainment of sexual maturity, low fecundity and slow growth (Musick *et al.*, 2000; Myers *et al.*, 2007; Stevens *et al.*, 2000). However, effective management aimed at sustainable exploitation and conservation of these species is often not in place or hampered by a lack of relevant biological knowledge (Farrell *et al.*, 2010a; Dulvy *et al.*, 2014). The starry smooth-hound *Mustelus asterias* Cloquet 1819 is one such species, although its reproductive biology and life history has recently been described in some detail (Farrell *et al.*, 2010a,b, 2014; McCully Phillips and Ellis, 2015), its movement ecology, which is relevant for effective management, is still poorly understood. *M. asterias* is a medium-sized (up to 140 cm total length,  $L_T$ ) demersal, viviparous shark (Compagno, 1984), which is widespread in the Mediterranean and the north-east Atlantic where the species populates waters of the continental shelf in ICES Subareas 4, 6–8 (Burt *et al.*, 2013; ICES, 2019).

*M. asterias* expresses larger length at 50% maturity in the Irish and Celtic Seas (78 and 87 cm for males and females, respectively; Farrell *et al.*, 2010a) than in the Greater North Sea (70.4 and 81.9 cm; McCully Phillips and Ellis, 2015). The latter values were used in the present study, as specimens were captured and tagged in this area. Parturition occurred in February in the western English Channel and during June to July in the eastern English Channel and Southern North Sea. This could be an indication of protracted spawning, asynchronous parturition of the stock (McCully Phillips and Ellis, 2015), or the presence of different stocks (Brevé *et al.*, 2016). However, in the absence of more detailed studies, the Working Group on Elasmobranch Fishes (WGEF) considers there to be a single biological stock unit (ICES, 2019).

At present, there is no species or stock-specific management for *M. asterias*, even though there has been an unregulated rapid rise in bycatches (Silva and Ellis, 2019) and a population collapse of closely related *Mustelus* species in the Mediterranean (Colloca *et al.*, 2017, 2020). As a result, in 2015 the status of *M. asterias* was upgraded from “Least Concern” to “Near Threatened” (Nieto *et al.*, 2015). This justifies the prioritization of studies on behaviour, habitat use and movement patterns (Williamson *et al.*, 2019). Brevé *et al.* (2016), using a mark-recapture programme, showed indications of seasonal migration

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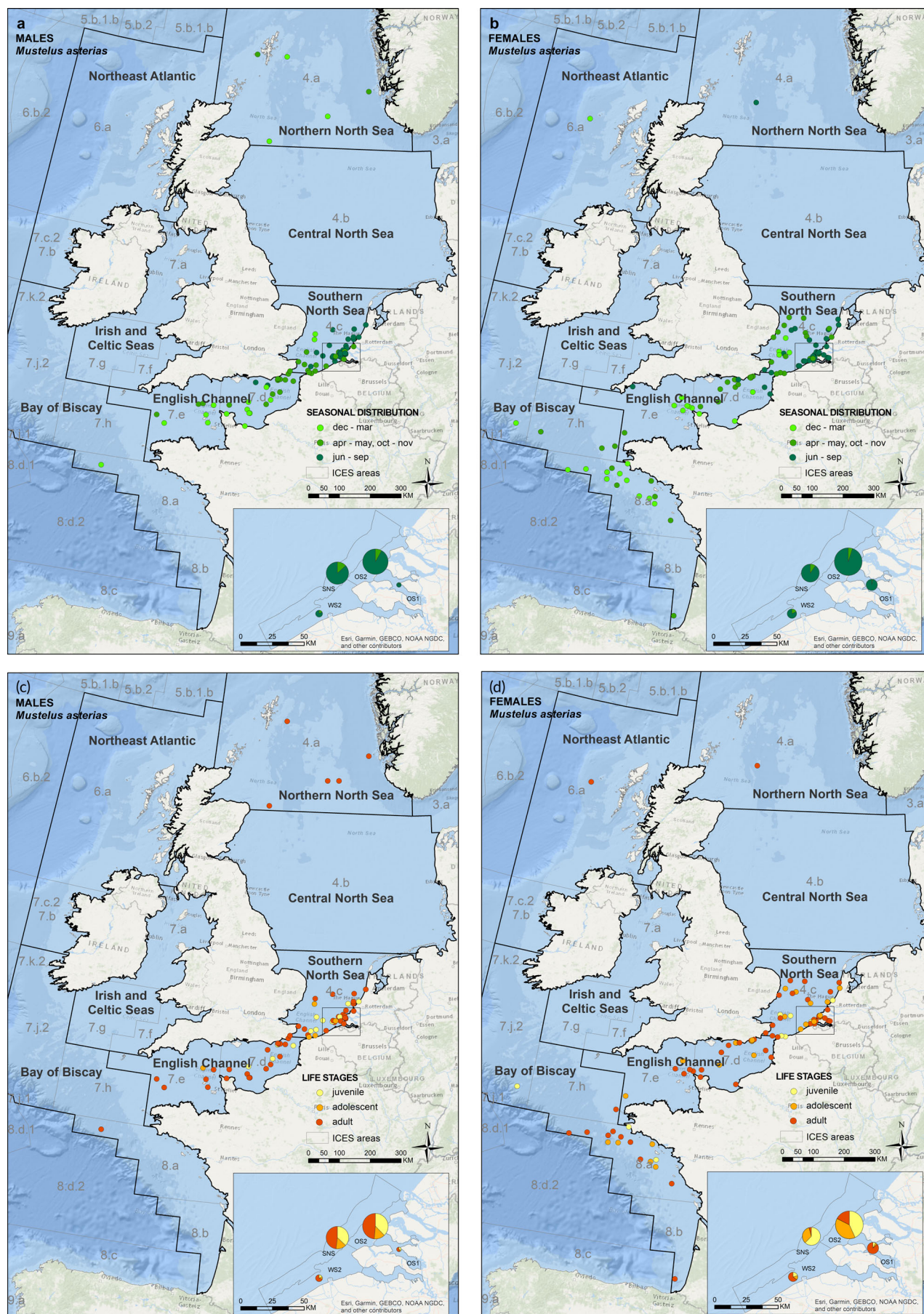


FIGURE 1 Legend on next page.



patterns of *M. asterias* and of nonmixing between *M. asterias* from the North Sea and Celtic Sea during summer. The present study is based on a continuation of the mark-recapture programme for four more years and aimed to further determine seasonal distributions of *M. asterias* to support sustainable and meaningful management of the species.

Between June 2011 and August 2019, a total of 4495 individuals of *M. asterias* were captured during a long-term angler-led tagging programme. Of these, in total 3699 individuals ( $> 40$  cm  $L_T$ ) were ID-tagged with plastic rototags attached to the base of the first dorsal fin, as described in Brevé *et al.* (2016). Sharks were caught by a group of licensed taggers that included 28 recreational anglers and one electric pulse trawler. Fishing occurred in ICES area 4.c., that is, in the river Scheldt outer estuary (Westerschelde) and the adjacent sea arm in the Netherlands (Oosterschelde). During the whole study period 99.9% of all *M. asterias* individuals were caught between May and October, even though fishing continued throughout the year. Areas are subdivided into the regions OS1 (inner part of Oosterschelde sea arm), OS2 (seaside "mouth" of the Oosterschelde sea arm), WS2 (seaside "mouth" of the Westerschelde estuary) and SNS (Dutch coastal zone in the Southern North Sea; Figure 1, small inset panels). All tagging activities were under licence of the Dutch Animal Welfare Act, project reference 2013170.a.

Between 2011 and 2019, the total number of reported recaptures was 220 (4.9%; Table 1): 114 females (50–124 cm  $L_T$ ), 102 males (47–105 cm  $L_T$ ) and four nonsexed (56–100 cm  $L_T$ ). For the statistical analysis, nonsexed fish were excluded, and juveniles and adolescents were pooled as immature fish. Time at liberty and minimum distance travelled (*i.e.*, the distance between their places of tagging and recapture, measured in a straight line) between release and recapture ranged between 1–2476 days and 1–1541 km in females, and 1–1795 days and 1–999 in males, respectively.

At a smaller spatial scale, patterns in the distribution of female and male *M. asterias* in the capture data during summer (June–September) show that in the more sheltered areas adult females dominated the catches (82.4% in OS1 and 43.8% in WS2), with fewer adult males (6.9% and 24.3%) and immature fish present (10.7% and 32.0%). In contrast, relatively more adult males and immature fish were caught in more exposed sea areas, including SNS (27.2% males and 71.1% immatures) and OS2 (21.5% and 66.2%) (Figure 1c,d; Chi-squared test:  $\chi^2(6) = 1106$ ,  $P < 0.001$ ). This small-scale spatial sex differentiation in distribution in summer is most likely related to the use of OS1 and WS2 as pupping areas. Of all 66 pups ( $< 33$  cm  $L_T$ ), 65 were caught during the warmest summer months (July and August) and one in September in these areas. This pattern is similar to that in many

coastal sharks that use warm, sheltered, shallow waters to avoid predation of their pups (Speed *et al.*, 2010).

At a larger spatial scale, seasonal patterns in recaptures of female and male *M. asterias* were visualized in maps using ArcGIS® software. Seasons were defined as spring (April and May), summer (June–September), autumn (October–November) and winter (December–March), with areas Northern North Sea, Central North Sea, Southern North Sea, English Channel, Bay of Biscay, Irish and Celtic Seas and North-east Atlantic. There are also apparent differences in large-scale spatial migration patterns between males and females across seasons (Figure 1). The distributions of female and male *M. asterias* differed significantly between areas in spring (Chi-squared test:  $\chi^2(3) = 12.4$ ,  $P = 0.006$ ) and winter ( $\chi^2(3) = 9.22$ ,  $P = 0.027$ ), with relatively more males in the Northern North Sea and more females in the Bay of Biscay. This sex differentiation was not apparent in summer ( $\chi^2(2) = 1.32$ ,  $P = 0.516$ ), or autumn ( $\chi^2(2) = 1.75$ ,  $P = 0.418$ ). Sexual differentiation in the circannual migration pattern was also apparent from the minimum distance travelled of individual sharks. An ANOVA was performed on Box-Cox transformed minimum distances travelled to ensure normal and homoscedastic distribution of residuals. Minimum distance travelled was significantly affected by season ( $F_{(3,177)} = 48.7$ ,  $P < 0.001$ ,  $\omega = 0.66$ ), with greater distances travelled in winter and spring, and by sex ( $F_{(1,177)} = 8.60$ ,  $P = 0.009$ ,  $\omega = 0.14$ ), with females generally migrating farther (Table 1).

The analysis of captures and recaptures clearly shows sex-differentiated migration patterns for *M. asterias* at several spatial scales. During summer, small-scale spatial sex differentiation was observed, where sheltered sea arms were almost exclusively used by adult females. During winter and spring, large-scale spatial sex differentiation was observed. Adult females migrated almost exclusively south to the English Channel and into the Bay of Biscay, while adult males partially migrated south to the English Channel and to the Northern North Sea, but rarely into the Bay of Biscay. Equal ratios of male and female *M. asterias* were observed in the English Channel. The short distances between the tagging locations and recaptures during subsequent summer months after tagging suggests a degree of philopatry. No recaptures occurred in the Irish and Celtic Seas, which implies the presence of separate subpopulations which use the Irish and Celtic Seas and the Southern North Sea for feeding and pupping.

Before the present mark-recapture study, sex-differentiated migration was unknown for *M. asterias*. It has, however, been described in a few other coastal shark species in the North-east Atlantic. For example, the cosmopolitan and highly mobile tope shark (*Galeorhinus galeus*) occurs in shallow coastal areas in the North-east Atlantic during the summer months (Compagno, 1984) and moves out

**FIGURE 1** Seasonal distribution of (a) male and (b) female *M. asterias*, and distribution of immature life stages (juveniles, adolescents) and adults for (c) males and (d) females. Fish were captured and tagged in the Netherlands between April and October in 2011–2019 (small inset panels). Total length data in centimetres was obtained from McCully Phillips and Ellis (2015) to identify life stages, with  $L^{50}$  for a division between pups ( $< 33$  cm), males: juveniles (33–65 cm), adolescents ( $65 \leq 70.4$  cm), adults ( $> 70.4$  cm), and females: juveniles (33–69 cm), adolescents ( $69 \leq 81.9$  cm) and adults  $> 81.9$  cm)

**TABLE 1** Number of tagged and recaptured starry smooth-hound (*M. asterias*) during 2011–2019 per area and the straight-line (minimum) distances travelled (km) since tagging

	Winter			Spring			Summer			Autumn			Grand total							
	Female	Male	Unsexed	Total	Female	Male	Unsexed	Total	Female	Male	Unsexed	Total	Female	Male	Unsexed	Total				
Number of tagged fish off the Dutch coast																				
OS1			0	2			2	212	21		4	237	0	214	21	4	239			
OS2			0	43		66	2	111	1011	748		1803	22	11	1076	825	48	1949		
SNS			0	50		101	2	153	480	654		1143	6	2	536	757	11	1304		
WS2			0	5		3		8	115	54		173	18	8	138	65	4	207		
Total	0	0	0	100	170	4	274	1818	1477	61	21	3356	46	21	1964	1668	67	3699		
Number of recaptures																				
North East Atlantic	1		1				0					0		1	0	0	1	1		
Northern North sea	4	1	5		2		2	1				1		0	1	6	1	8		
Southern North Sea	6	6	12	5	13	1	19	35	32		1	68	14	13	27	60	64	2	126	
English Channel	14	13	27	9	12		21	4	2			6	5	4	1	10	32	31	1	64
Bay of Biscay	11	1	12	7			7					0	2		2	20	1	0	21	
Total	32	24	1	57	21	27	49	40	34	1	17	75	21	17	1	114	102	4	220	
Minimum distances travelled by recaptured individuals (km)																				
Mean	566	442		497		245		105	58		198									
Range	94–1424	82–972		105–1326	1–999			1–830	1–290		4–811									
Standard deviation	333	250		366	255			177	65		193									
Median	459	410		295	215			40	39		143									
Number of observations	28	22		16	23			34	31		16									

to deeper offshore waters during winter, with some mature females ranging further south to the Mediterranean (Colloca *et al.*, 2019; Thorburn *et al.*, 2019). The underlying causes of sex-specific migration in shark species are still largely unknown but Wearmouth *et al.* (2009) and Speed *et al.* (2010) suggested several potential causes for spatial separation of the sexes in sharks, including females avoiding mating, resource competition, diet, reduction in pup mortality, sex-specific habitat requirements and the thermal niche hypothesis. This hypothesis predicts the migration of females to warmer southern waters where metabolic rate is increased, consequently increasing the growth and development of embryos (Hurst *et al.*, 1999). The temporal separation of certain adult female *M. asterias* that migrate to the Bay of Biscay during winter may be explained by their capacity to store sperm (Farrell *et al.*, 2010a) and may enable them to conserve energy by limiting multiple matings during a time when embryonic development requires more energy: a principle that is also suggested in the dogfish, *Scyliorhinus canicula* (Sims *et al.*, 2001). Another possibility is that in a cold-blooded viviparous species like *M. asterias*, pregnant females use wintering habitat with higher temperatures to increase embryonic development. In contrast, the occurrence of larger *M. asterias* males in the Northern North Sea may be related to the presence of important prey (McCully Phillips & Ellis, 2015). Remarkably, none of the 3699 tagged *M. asterias* individuals in this present study were recaptured in the Central North Sea (ICES area 4.b.), nor in the Irish and Celtic Seas, despite intensive demersal fisheries in both areas, which is in line with philopatry to summer feeding and pupping grounds in *M. asterias*.

The results indicate that management of *M. asterias* should integrate both large (from the Northern North Sea to the Bay of Biscay) and smaller spatial and temporal scales, taking into account year-round movement patterns as well as specific feeding and pupping habitats. Moreover, management should also consider the existence of several subpopulations potentially coexisting in the coastal waters of western Europe. To further investigate this, a combination of tracking individual movements with telemetry and using different genetic techniques is advised.

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## ETHICAL STATEMENT

The care and use of experimental animals complied with the Dutch Animal Welfare Act, guidelines and policies as approved by the Centrale Commissie Dierproeven (Dutch Central Committee Animal Experiments), project reference 2013170.a.

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