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Using movement data of Baltic grey seals to examine foraging-site fidelity: implications for seal–fishery conflict mitigation

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ABSTRACT: Knowledge of the intensity of spatial overlap between aquatic top predators and fisheries is required to efficiently alleviate the negative effects of marine mammal–fishery interactions. We used satellite telemetry to study the movements and habitat use of Baltic grey seals *Halichoerus grypus*, with special focus on the degree of site fidelity to foraging and haul-out areas and spatio-temporal overlap with coastal fisheries. Most of the tracked seals (14/16 individuals) were 'residents', which remained within 120 ± 62 km (mean ± SD) of their capture sites during the open-water season, whereas 2 'transient' seals occupied much larger areas, over 400 km from their capture sites. Residents used on average 4.3 ± 2.5 haul-out sites, indicating high haul-out site fidelity during the open-water season. Residents had active core areas (58 ± 35 km^2, 50% local nearest-neighbour convex hull [LoCoH], excluding haul-out locations) near river estuaries or at other shallow water areas, indicating foraging-site fidelity to these foraging grounds. They overlapped both spatially and temporally with trap-net fishing. The high site fidelity of grey seals indicates that foraging and haul-out areas should be taken into account in population management. Selective removal of seals overlapping with fishery could be a locally focused method to mitigate seal–fishery interactions. However, removal of individuals in foraging areas may also compromise the conservation needs of the population by targeting the same animals that are hauling out in seal sanctuaries.

KEY WORDS: Baltic Sea · GPS phone tag · Habitat preference · *Halichoerus grypus* · Home range · Seal–fishery overlap · Trap-net fishery

INTRODUCTION

Many large aquatic predators that move over extensive spatial scales restrict their movement to smaller specific areas during certain periods of time. Site fidelity, the tendency of an individual to return to a certain area over time, reflects areas important in satisfying different life-history priorities during the annual cycle of many species. Numerous marine species such as seabirds, large predatory fish, whales and seals show site fidelity to breeding and foraging grounds (Hamer et al. 2001, Bradshaw et al. 2004, Vincent et al. 2005, Foote et al. 2010, Kelly et al. 2010, Barnett et al. 2011, Russell et al. 2013, Augé et al. 2014). Foraging-site fidelity can cause intense spatial overlap between large aquatic predators and fisheries, and can lead to increased resource competition between the two (Hyrenbach & Dotson 2003, Hückstädt & Krautz 2004, Karpouzi et al. 2007, Pichegru et al. 2009, Augé et al. 2014). This conflict is complex as it includes both negative impacts on fisheries by the predators and increased predator mortality due to incidental by-catch and removal of individuals as a conflict mitigation strategy (Read 2008). In particular, there has been

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considerable debate globally over the interactions between many seal species and commercial fisheries (e.g. Linnell 2011, Bowen & Lidgard 2013). As a result, seals have been historically hunted worldwide to alleviate the conflict (Bowen & Lidgard 2013).

Studying foraging-site fidelity of pinnipeds in relation to the overlap with fisheries around the world can help to assess actions to mitigate both sides of the seal–fishery interaction. On the one hand, marine management areas have been found to be an effective measure in limiting interactions between aquatic predators and fisheries (Pichegru et al. 2010, Gormley et al. 2012). However, despite the fact that many pinniped species spend the majority of their time in the water, shaping protected areas to reduce the impacts of human activities has mainly been focused on terrestrial haul-out sites. Until recently, little attention has been paid to foraging areas, which are harder to identify (Cordes et al. 2011, Augé et al. 2014). For example, with the strong foraging-site fidelity of the New Zealand sea lion *Phocarctos hookeri*, protecting key foraging areas helps reduce the interactions with fisheries such as resource competition, by-catch mortality and reduction in habitat quality due to bottom trawling (Augé et al. 2014). On the other hand, to reduce the seal-induced damage to fisheries, spatial overlap between foraging areas of seals and fisheries indicates that selective removal of individuals in the fishing areas can be a more focused mitigation method than random hunting near haul-out sites (Graham et al. 2011). Selective removal is effective especially when individuals exhibit foraging-site fidelity and only a small fraction of the population is specialised and strongly overlaps with fisheries (Graham et al. 2011).

The Baltic grey seal *Halichoerus grypus* is a typical example of a seal species that strongly interacts with coastal fisheries. Although the present population (census size: 30 000 seals) is still less than half of its historical abundance at the beginning of the 20th century (Harding & Härkönen 1999, Kokko et al. 1999, Harding et al. 2007, FGFRI 2014), the conflict between seals and fisheries has aggravated substantially in the areas of high seal abundance (Jounela et al. 2006, Bruckmeier & Larsen 2008, Varjopuro 2011). In the main distribution area of the species, i.e. Finland and Sweden, grey seals are largely considered as game or even a pest species (Storm et al. 2007, Ministry of Agriculture and Forestry 2007). In contrast, in low-abundance areas of the southern Baltic Sea, i.e. Poland and Germany, the grey seal is considered to be a species that needs more focused conservation measures (Schwarz et al. 2003). In the main distribution area, the main policy instruments for conflict mitigation are hunting, compensation payments and financial support for the acquisition of seal-safe fishing gear (Ministry of Agriculture and Forestry 2007, Storm et al. 2007, Bruckmeier & Larsen 2008, Varjopuro 2011).

Considering the conflicting interests of seal conservation and fisheries management, information on the spatial ecology of Baltic grey seals is crucial for planning conservation and management strategies (Ministry of Agriculture and Forestry 2007). Telemetry studies have shown that juvenile grey seals move in large areas (Sjöberg et al. 1995), whereas adults concentrate their activities near haul-outs and show habitat preference in relation to bathymetry (Sjöberg & Ball 2000). In general, research on the movements of Baltic grey seals has mainly concentrated on young individuals (Sjöberg et al. 1995, Sjöberg & Ball 2000). More information on the spatial ecology of adults and their overlap with fisheries is needed, as studies on diet indicate that older grey seals, in particular, feed on large and economically important fish species (Lundström et al. 2010, Kauhala et al. 2011). Seasonal and inter-annual haul-out site fidelity has been shown for Baltic grey seals (Karlsson et al. 2005). However, there is little knowledge on foraging-site fidelity and potential overlap with coastal fisheries.

Studying the spatial ecology of free-ranging seals allows the level of interaction between seals and commercial coastal fisheries to be estimated, which is essential for effective seal and fishery management measures. The magnitude of the interactions depends partly on the degree of spatial and temporal resource overlap between seals and the fisheries (Matthiopoulos et al. 2008). In addition, an improved understanding of spatial ecology is critical in determining the ecological factors affecting the conservation needs of seal populations. Therefore, in this study, we examined the movements and habitat use of Baltic grey seals with special focus on the degree of foraging and haul-out site fidelity. In addition, we studied the spatial and temporal overlap of grey seals and coastal fisheries on several spatial scales.

MATERIALS AND METHODS

Animal handling and data recording

From 2008 to 2011, grey seals were captured with commercial pontoon traps (Hemmingsson et al. 2008) in the Bothnian Sea and the Gulf of Finland, which are both important areas for commercial coastal fisheries (see Fig. 1, see Table 1). The pontoon traps (3–4 traps annually) were equipped with 'non-return' gates attached in front of the fish chamber between June and November (see details in Lehtonen & Suuronen 2010). An alarm system sent a GSM (mobile phone) message when a seal was caught, guaranteeing a quick removal. After capture, the seals were guided to swim into a shuttle attached to the pontoon trap by sinking the fish chamber under the water. The seals were then transported to land in the shuttle and sedated using medetomidine (0.02–0.04 mg kg^{-1}, Zalopine®) and butorphanol (0.08 mg kg^{-1}, Butador®) by a veterinarian. The sedation was reversed with atipamezole (0.2 mg kg^{-1}, Antisedan®). A different anaesthetising protocol, medetomidine and butorphanol combined with midazolam (Dormicum®) or ketamine (Ketalar®), had been used at the beginning of the study, but this protocol was abandoned due to the death of 2 individuals.

GPS phone tags (Sea Mammal Research Unit, University of St. Andrews, UK) were attached to the dorsal fur above the scapulas with 2-component epoxy glue (Super Epoxy, 15 min). The phone tags were programmed to attempt to determine the GPS location 2–3 times per hour (see Table 1). To ensure later identification, a uniquely numbered plastic ID-tag (Jumbo tag, Dalton) was attached to the hind flipper and a plastic 'hat' (Kuggom Metal, Finland) was glued to the fur on the top of the head. Individuals that were small (≤70 kg) or in poor condition were equipped with only a plastic ID-tag and released without sedation. Sex and body weight were recorded for all captured seals. All captured seals were males and they were classified as adults or juveniles according to body weight on the basis of age–weight data (database of grey seals, Finnish Game and Fisheries Research Institute). Males with body weight <90 kg were categorised as juveniles (estimated age: <5 yr) and others (with body weight ≥90 kg) as adults. The research was permitted by the local game authorities (permit no. 2011/00087) and the Animal Experiment Board of Finland (permit nos. ESLH-2008-04828/YM-23 and ESAVI-2010-05432/Ym-23).

Temporal and behavioural classification of movement data

Grey seals are known to avoid areas with fast ice (Hook & Johnels 1972), and this phenomenon is likely to create differences in habitat usage and preference between open-water and ice-cover seasons. Also, coastal fishing with passive gear occurs mostly during the open-water season (highest effort between May and October; FGFRI 2009, 2010, 2011, 2012). Therefore, tracking data were divided into open-water and ice-cover seasons. The open-water season designation started when the tags were deployed (see Table 1) and ended with the seals' transition period (usually in mid-December). The transition period started when the seals left their open-water home ranges without permanently returning to this area during the study period and ended when the locations were again clustered in late December–early January. The transition period was left out of the spatial analyses, as migrations are not typically included in home range estimates (Kenward 2001). The ice-cover season started after the transition and ended when the tags stopped transmitting (see Table 1). Four studied seals did not make a transition, and the data were divided into open-water and ice-cover seasons by the average date of the beginning of transition obtained from other individuals (20 December). This coincided well with the average date (22 December) when the first ice-cover appeared in satellite pictures of the study areas (FMI 2014).

Location data on the seals were first filtered according to McConnell et al. (1992) and then divided into 2 behavioural classes: haul-out and active. A haul-out event began when the tag was continuously dry for 10 min and ended when wet for 40 s. Active locations (i.e. movements) were categorised as all locations when a seal was outside a 1 km threshold, based on the Euclidean distance from the haul-out site (Cronin et al. 2012).

Identification of home ranges and core areas

Individual total home ranges (for the whole tracking period) and seasonal home ranges (for open-water and ice-cover seasons) were estimated for seals with a tracking of over 30 d using the 95% minimum convex polygon (MCP; Worton 1987) and 95% adaptive local nearest-neighbour convex hull (a-LoCoH; Getz et al. 2007) methods. Main foraging areas for individuals were determined by constructing active core areas (50% LoCoH of the active locations). In a-LoCoH, the parameter *a* was set by taking the maximum distance between any 2 locations in the individual data set (Getz et al. 2007). The discovery curves from the 95% MCP and 100% LoCoH incremental analysis (Kenward 2001) were visually examined to ensure that the location data was sufficient for home range analysis.

Individual home range sizes between open-water and ice-cover seasons were compared using the Wilcoxon signed rank test in SigmaPlot for Windows 12.3 (Systat Software). The spatial overlap percent between seasonal home ranges was calculated according to Bernstein et al. (2007). In addition to individual home ranges, active group home ranges (all active locations) during the open-water season were estimated for all seals using 95% a-LoCoH. All home ranges were constructed using the package adehabitatHR (Calenge 2006) in R 2.15.3 (R Development Core Team 2013). Land areas were subtracted from the MCP home range estimates.

Overlap with fisheries

Habitat preference of grey seals was investigated during the open-water season, when the greatest overlap with coastal fisheries is expected. Manly's selection ratios (± Bonferroni adjusted confidence limits) were calculated according to Manly et al. (2002) using the adehabitatHS package (Calenge 2006) in R. Selection ratios were calculated for each seal by relating areas used (i.e. 95% LoCoH home range) to the available study area in 7 water-depth classes (0–10, 10–20, 20–30, 30–40, 40–50, 50–100, 100–200 m) defined from bathymetric raster maps (grid size: 250 × 250 m, Helsinki Commission HELCOM). The study area was defined separately for the Bothnian Sea and the Gulf of Finland by creating MCPs (95%) around all the locations of the seals captured in each area. Manly's selection ratios ($\hat{W}_{ij}$) indicate preference when $\hat{W}_{ij} > 1$ and avoidance when $\hat{W}_{ij} < 1$. Preference for specific habitat (depth class) was considered statistically significant when the confidence interval for the selection ratios was >1 and avoidance when the value was <1 (Manly et al. 2002).

We used 2 different fishery data sets to examine the spatial and temporal overlap between fisheries and tracked seals. First, catch report data based on EU fishing logbooks and coastal fishery forms from Finnish marine waters during 2008–2011 (FGFRI 2009, 2010, 2011, 2012) were used to examine the overlap between grey-seal tracking data, trap-net fishing effort and seal-induced damages. The data represent monthly trap-net fishing effort, overall catch and seal-induced catch losses of commercial fisheries in ICES statistical rectangles (50 × 50 km grids; ICES 2014). Second, a spatially limited, but more fine-scaled data set of trap-nets (location, type and fishing season of each trap-net) was used to examine spatial overlap of tracked grey seals and trap-nets on a weekly basis during 2010 and 2011. The trap-net location data were collected by interviewing commercial fishermen from areas overlapping with tracked seals in the Gulf of Finland. The trap-net location data set was limited to Finnish marine waters in the east and south, while the western limit was set at longitude 25° 35′ E (in the WGS84 coordinate system) (see Fig. 3B). In order to quantify the fine-scaled spatio-temporal overlap between tracked seals and trap-net fisheries, the percent of tracking days when each seal was within close proximity (<250 m) to trap-nets was calculated.

RESULTS

Grey-seal movements

All 28 grey seals captured with modified pontoon traps were males and most of them were adults (82%). The mean weight of the captured seals was 133 ± 36 kg (mean ± SD; range: 70–193 kg). All captured seals were marked with plastic ID tags and 21 of them were equipped with GPS phone tags. Four of the marked seals (3 with a GPS phone tag and 1 with an ID tag) were recaptured 1–3 times after initial release later in the year (Table 1). Overall, 16 tags provided data for at least 20 d (on average for 136 ± 69 d) and >50 locations, and these data sets were included in the analyses (Table 1). The average number of locations per day was 13 ± 9 per individual. The mean number of received locations per individual differed between study areas (1126 ± 1045 in the Bothnian Sea and 2779 ± 2236 in the Gulf of Finland). The results of the 95% MCP and 100% LoCoH incremental analysis reflected the small sample sizes in the Bothnian Sea, as the discovery curves for 4 individuals (AA08, SA09, CH09, KU09) did not reach the slow increase phase. In addition, this could be partly due to the less concentrated movements of juveniles (CH09 and KU09).

The total home range estimates varied considerably between individuals (33 675 ± 38 936 km^2 with MCP and 6858 ± 7936 with LoCoH; Table 2). Most of the studied seals (14/16 individuals) were categorised as 'residents', i.e. they remained within a distance of 120 ± 62 km from the capture site during the open-water season (Figs. 1 & 2). The mean size of the individual home range of residents during the open-water season was 4443 ± 6941 km^2 with the MCP estimator and 886 ± 764 km^2 with the LoCoH estimator (Table 2). Two seals (HE09 and VO11) were 'tran-

Table 1. Details of male Baltic grey seals *Halichoerus grypus* equipped with GPS phone tags. Parentheses: number of recaptures (in addition, 1 flipper-tagged male without a GPS phone tag was recaptured 2 times). Dates are dd/mm/yy. BS: Bothnian Sea, GF: Gulf of Finland, nd: no data available

Seal ID	Capture site	Body weight (kg)	GPS attempts h^{-1}	No. of locations	Tracking period duration (d) Open-water season	Ice-cover season	Total	Start	End
BR08	BS	193	2	907	73	45	119	07/10/08	03/02/09
AA08	BS	98	2	201	33	60	94	16/11/08	18/02/09
PA08	BS	177	2	6	nd	nd	76	11/11/08	26/01/09
AR09	BS	147	2	1346	105	nd	105	03/09/09	17/12/09
SA09 (3)	BS	171	2	167	37	nd	37	11/09/09	18/10/09
HE09	BS	121	2	2757	93	139	230	20/09/09	08/05/10
RA09	BS	124	2	2607	81	123	211	01/10/09	30/04/10
VA09 (1)	BS	147	2	104	17	nd	17	02/10/09	19/10/09
MI09	BS	188	2	92	13	nd	13	26/10/09	08/11/09
KU09	BS	77[a]	2	796	57	43	101	06/11/09	15/02/10
CH09	BS	76[a]	3	229	30	42	80	24/11/09	12/02/10
LA09	BS	111	3	0	nd	nd	0	02/12/09	02/12/09
KA10	GF	125	3	2391	124	nd	124	01/07/10	02/11/10
CR10 (2)	GF	88[a]	3	4223	51	84	140	25/10/10	14/03/11
OT10	GF	123	3	5683	39	118	162	13/11/10	24/04/11
ST11	GF	133	3	99	7	nd	7	05/06/11	12/06/11
AH11	GF	113	3	6030	172	125	301	22/06/11	18/04/12
AR11	GF	156	3	781	81	nd	81	07/08/11	27/10/11
TY11	GF	173	3	479	51	nd	51	24/08/11	14/10/11
BE11	GF	121	3	979	99	51	158	30/08/11	04/02/12
VO11	GF	128	3	1662	94	81	176	16/09/11	10/03/12

[a]Juvenile according to weight

sients' and were mainly located outside Finnish coastal waters, within a distance of 402 and 818 km from the capture site, respectively. They occupied MCP home ranges of 50 142 km^2 and 132 761 km^2 and LoCoH home ranges of 1284 km^2 and 15 847 km^2, respectively (Table 2). During the open-water season, most of the residents (11/14 individuals) had active core areas (58 ± 35 km^2) near river estuaries at a mean distance of 17 ± 9 km from their capture sites (Fig. 1C,D). For 3 residents (adult AA08 and juveniles CH09 and KU09), the active core areas could not be reliably estimated with the given set of locations and lack of concentrated movements.

In general, home ranges for the open-water and ice-cover periods (LoCoH 95%) did not differ in size (Wilcoxon signed rank test, $Z = 3.54 \times 10^{-316}$, p = 1.00). Most resident seals that were tracked during both seasons (7/9 individuals) had separate open-water and ice-cover home ranges (overlap between home ranges: 0–1%; Table 2). These seals made a clear transition to ice-cover home ranges between 10 December and 4 January. The mean duration of the transition was 5 ± 2 d and the length varied from 107–492 km. However, the 2 residents (BR09, AA08) that did not make a transition occupied approximately the same areas during the whole study period (overlap ca. 20%; Table 2). The transients did not have a clear transition period. One transient seal (HE09) mainly occupied the same area in the eastern Baltic Proper as during the open-water season. The other transient (VO11) continued to move in large areas. Home ranges during the ice-cover period were mostly situated in the northern and eastern Baltic Proper or in the Gulf of Riga.

Resident seals made successive trips from active core areas to haul-out sites during the open-water season (Figs. 1 & 2). On average, residents from the Gulf of Finland and the Bothnian Sea used haul-out sites 64 ± 33 km from their capture sites (Fig. 2). Residents used on average 4.3 ± 2.5 haul-out sites during the open-water season. In the Gulf of Finland, 39% of the total (299 recorded events) haul-out events of residents were located in a seal sanctuary (5/7 individuals used this haul-out site) and 56% in the haul-out site (Hallikarti; easternmost haul-out in Fig. 1D) on the border area between Finland and Russia (4/7 individuals used this site) during the open-water season. Only a small fraction (5%) of haul-out events occurred at other haul-out sites. In the Bothnian Sea, 8% of haul-out events of residents were located in a seal sanctuary (4/7 individuals) and 31% in known haul-out sites in the southern Bothnian Sea (6/7 indi-

Error found in Table 2 after publication: 6 entries in each of two rows are displaced one column to the left. See corrected table at www.int-res.com/articles/meps2015/536/m536p282.pdf

Table 2. Estimated sizes (km^2) for total and seasonal home ranges (95 %) and active core areas (50 %) of Baltic grey seals *Halichoerus grypus*, distances from the capture site to core areas, and overlap between seasonal home ranges. Parentheses: number of core areas if >1. Residents: occupied areas near the capture site during open-water season; transients: left the capture area; MCP: minimum convex polygon; LoCoH: local nearest-neighbour convex hull; na: not applicable, as the LoCoH 50 % could not be reliably estimated with the combination of the chosen *a*-parameter and given amount of locations; nd: no data available

Seal ID	Open-water season				Ice-cover season				Total tracking period		Overlap (%)
	MCP (95 %)	LoCoH (95 %)	LoCoH (50 %)	Distance (km)	MCP (95 %)	LoCoH (95 %)	LoCoH (50 %)	Distance (km)	MCP (95 %)	LoCoH (95 %)	
Residents											
BR08	2040	1296	56	26	849	378	16	28	2039	1340	21
AA08	2470	605	na	nd	388	205	47	23	2031	605	19
AR09	26878	3012	65	5	nd	nd	nd	nd	26878	3012	nd
SA09	2760	629	99	12	nd	nd	nd	nd	2760	629	nd
RA09	2600	161	4	10	42737	10203	2503 (3)	346	61476	10349	0
KU09	8264	1195	na	nd	1454	733	151 (2)	213	18679	3291	0
CH09	8567	1806	na	nd	13662	3897	536	336	33076	7632	0
KA10	1026	556	95 (2)	28	nd	nd	nd	nd	1026	556	nd
CR10	1148	639	64	29	17663	8000	2328 (3)	420	50718	13433	0
OT10	1795	686	106 (3)	25	40360	12010	3167 (6)	370	75414	19455	0
AH11	798	271	13 (2)	10	48152	12414	1079 (3)	178	43943	9861	1
AR11	2620	936	72	4	nd	nd	nd	nd	2620	936	nd
TY11	811	432	36	24	nd	nd	nd	nd	811	432	nd
BE11	425	187	27	18	328	172	57 (2)	345	14052	759	0
Mean	4443	886	58	17	18399	5335	1098	251	23966	5164	4
SD	6941	764	35	9	20090	5318	1326	149	25292	6030	9
Median	2255	634	64	18	13662	3897	536	336	16365	2176	0
Transients											
HE09	50142	1284	na	nd	22568	6698	535 (2)	416	57668	10050	3
VO11	132761	15847	5269 (2)	679	73736	9861	1021 (2)	106	145606	27391	3
Mean	91452	8566		48152	8279	778	261	101637	18720		
SD	58420	10298		36181	2237	344	219	62182	12262		
Total											
Mean	15319	1846	492	72	23809	5870	1040	253	33675	6858	4
SD	33949	3802	1505	191	24467	4954	1124	150	38936	7936	8
Median	2535	662	64	21	17663	6698	536	336	22779	3152	0

viduals) (Fig. 1C). However, 54 % of haul-out events were near (within 20 km) the active core areas.

Spatial and temporal overlap with fisheries

In the study area, both trap-net fisheries and resident seals preferred coastal waters during the open-water season (Fig. 3). Trap-net fishing effort was mainly situated in shallow water areas, and the mean depth of trap-net locations in the Gulf of Finland was 8.5 ± 7.6 m (Fig. 3). Resident seals also showed habitat preference for shallow water in their home ranges (Fig. 4). Manly's selection ratios showed that residents generally preferred areas with depths < 30 m and avoided areas > 50 m deep, although for the Bothnian Sea the selection for the 10–20 m depth class was not statistically significant. In contrast, transients did not show as clear a preference for shallow waters (Fig. 4).

The active core areas of residents overlapped with trap-net fishing areas where fishing effort was higher than the median (1710 trap-net days; Fig. 3A). They also overlapped with the greatest annual seal-induced catch losses (>6.5 tons, i.e. >50 % of the maximum value) during the open-water season (Fig. 3A). The resident seals in the Gulf of Finland (n = 7) visited within close proximity of trap-nets (≤250 m) on average 30 ± 20 % of all tracking days during open-water season. All of the most important prey categories of grey seals, Baltic herring *Clupea harengus membras*, whitefish *Coregonus lavaretus*, *Salmo* sp. and cyprinids (Lundström et al. 2010, Kauhala et al. 2011, Suuronen & Lehtonen 2012), were present in the catches of overlapping fishing areas.

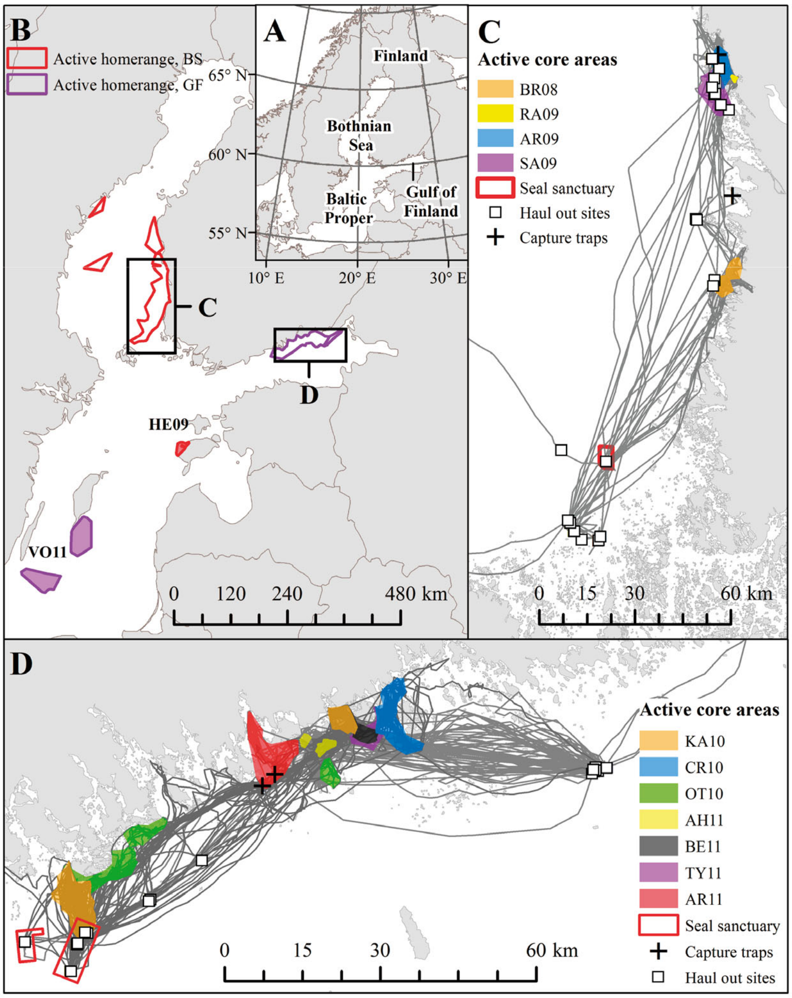

Fig. 1. (A) Baltic Sea study area. (B) Active group home ranges (95 % adaptive local nearest-neighbour convex hull [a-LoCoH]) of grey seals *Halichoerus grypus* captured in the Bothnian Sea (BS; n = 8) and Gulf of Finland (GF; n = 8) during the open-water season. The parts of the home ranges occupied by transient seals (n = 2) are indicated with fill colour and seal ID. (C,D) Individual active core areas of residents (50 % a-LoCoH) and tracks (grey lines) in the Bothnian Sea (n = 4) and the Gulf of Finland (n = 7). Core areas of 3 individuals (AA08, KU09, CH09) could not be reliably estimated

Seal tracking and trap-net fishing effort also overlapped temporally during the open-water season. However, fishing effort in the overlapping statistical rectangles was highest in June (mean: 6037 ± 3336 trap-net days), declining towards autumn, whereas the grey seals were mostly captured between October and November (75 % of individuals). The overall fisheries catches in the overlapping statistical rectangles had 2 peaks, one in May–June and the other in September–October. Residents usually left their open-water season foraging area in December (range between 10 December and 2 January), while trap-net fishing effort in the overlapping statistical rectangles declined after October to <20 % of the maximum effort in June (1077 ± 489 trap-net days), and remained at this level for the winter months (until April, range: 378–1286 trap-net days).

DISCUSSION

Our study confirms that, while grey seals are capable of travelling long distances (Sjöberg et al. 1995, McConnell et al. 1999), they also often concentrate their movements in relatively small areas near haul-out sites for extended periods (McConnell et al. 1999, Sjöberg & Ball 2000, Austin et al. 2004). In our study, most of the tracked seals were residents (88 %), staying near their capture sites on relatively small home ranges during the open-water season. Only 2 seals left the area of capture during the open-water season and were therefore categorised as transients. The open-water home ranges of resident seals (4443 km^2) were similar to summer home ranges previously reported in the Baltic Sea (6293 km^2; Sjöberg & Ball 2000) and in the western Atlantic (8900 km^2; Harvey et al. 2008). Transients had larger MCP home ranges (>50 000 km^2). On average, all home ranges for the total tracking period were large (33 675 km^2; 95 % MCP). All our study seals were males, and this could have had an effect on this result, as males often move over larger areas than females (Austin et al. 2004, Breed et al. 2009). Home-range estimates also typically increase with increasing tracking period and sample size (Kenward 2001). Although residents remained on small home ranges during the open-water season, most of them also made a 100–500 km long transition to the wintering areas in the Baltic Proper or the Gulf of Riga, which include drift-ice breeding areas. Most seals also visited the land breeding areas in the southern Archipelago Sea of Finland and coastal areas of Saaremaa in Estonia (Jüssi et al. 2008). In addition to the long tracking period, we used GPS phone tags that often provide larger sample sizes compared to the Argos system (Vincent et al. 2010). Although a few individuals of our data set had relatively few locations, the

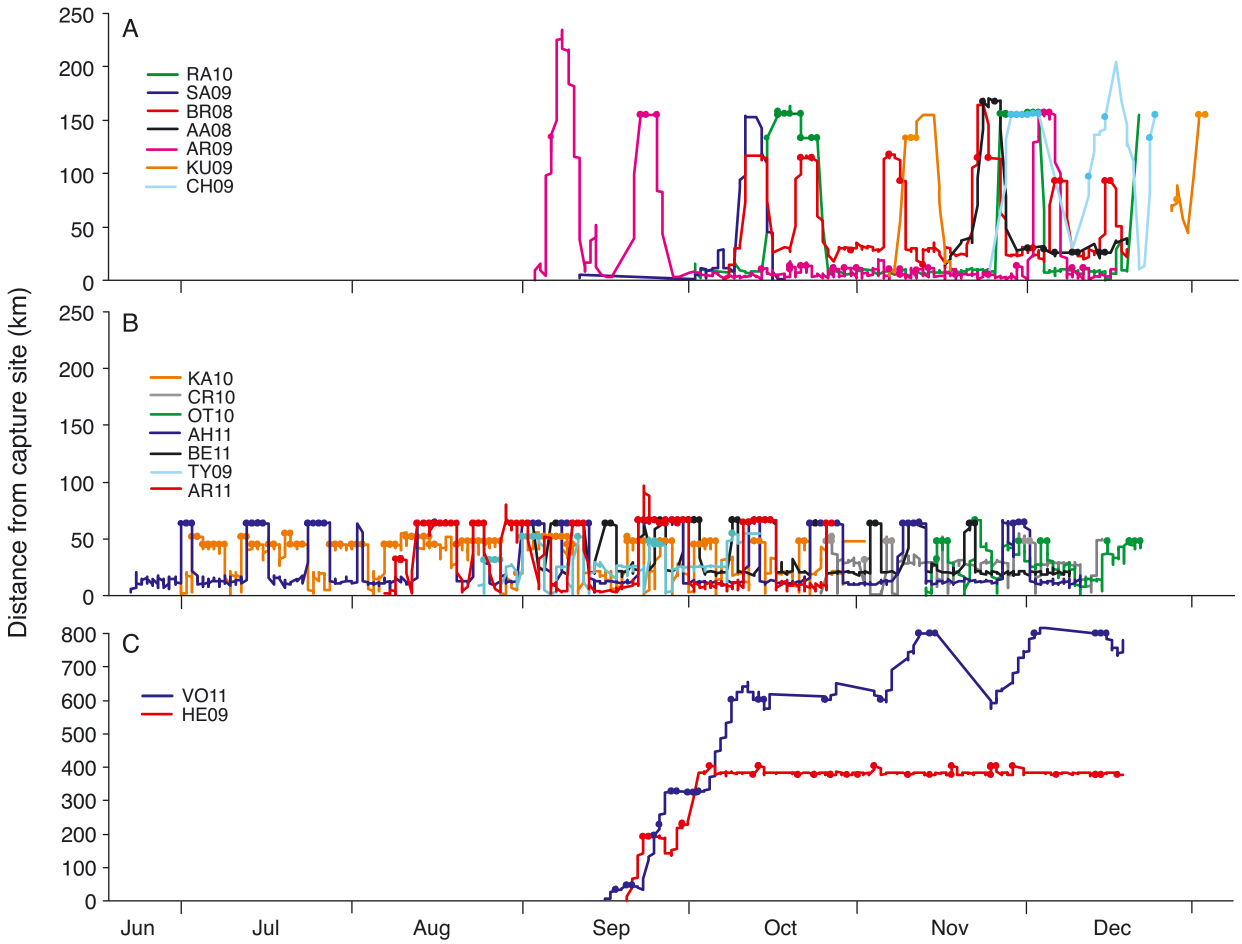

Fig. 2. Distances between capture sites and GPS locations of Baltic grey seals *Halichoerus grypus* during the open-water season, for resident seals occupying (A) the Bothnian Sea and (B) Gulf of Finland, and (C) transient seals occupying other areas (note different scale or the *y*-axis). Solid lines: distance to active locations, dots: distance to haul-out locations

overall sampling frequency (13 locations per day) was higher than in several earlier grey-seal studies using the Argos system (2.1 locations per day in Sjöberg & Ball 2000, 3.9 locations in Austin et al. 2004 and 6.6 locations in Vincent et al. 2005).

Most adult grey seals showed strong foraging and haul-out site fidelity during the open-water season, as has also been shown in earlier studies (Karlsson et al. 2005, Vincent et al. 2005, Russell et al. 2013). We determined the foraging areas with active location points (locations at or near haul-out sites were excluded), although these locations contained seal behaviour other than foraging (i.e. transits, socialising and resting). However, foraging constitutes about 50% of the total time budget of seals (McClintock et al. 2013) and it is likely to dominate at-sea behaviour. We therefore assumed that the active core areas reflect the important foraging grounds. Resident seals preferred the vicinity of river estuaries and other shallow-water areas for foraging. They also made repeated trips between the inshore foraging areas and off-shore haul-out sites, which were small islets approximately 15–50 km from the mainland. Haul-out site fidelity of residents was to the general area rather than 1 specific haul-out site, as has been observed before in the Baltic Sea (Karlsson et al. 2005). The typical foraging areas found in our study were similar to those seen with several other seal species, which generally make foraging trips to relatively shallow areas on the continental shelves that are often associated with sediment type or slope (McConnell et al. 1999, Breed et al. 2006, Aarts et al. 2008, Heerah et al. 2013, Muelbert et al. 2013) or proximity to river estuaries, for example (Wright et al. 2010, Graham et al. 2011, Bajzak et al. 2013).

Resident grey seals showed a preference for shallow (<30 m deep) coastal areas and avoided deeper (>50 m) areas during the open-water season, which is relatively similar to the earlier findings for Baltic grey seals (Sjöberg & Ball 2000). The preference for

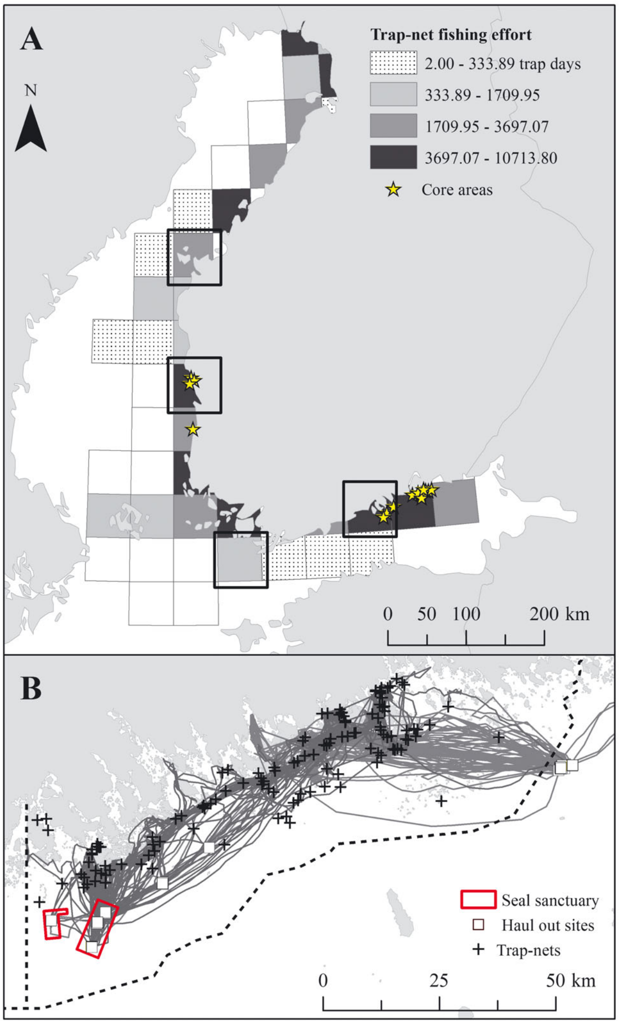

Fig. 3. (A) Spatial distribution of the active core areas of resident seals *Halichoerus grypus* (n = 11), the mean trap-net fishing effort and the most seal-induced damage (black rectangles, >6.5 tons) along the Finnish coast in 2008–2011. (B) Movements (n = 7) of the resident seals and trap-net locations in 2010–2011 during the open-water season. The extent of trap-net location data is indicated with a dashed line

shallow water areas leads to an inevitable overlap with coastal fisheries. However, scale is a critical factor in determining spatial overlap between top predators and fisheries, and results may differ when a different scale is chosen (Reid et al. 2004, Pichegru et al. 2009). The residents of our study overlapped both temporally and spatially with commercial trap-net fisheries on many spatial scales. On a relatively coarse spatial scale (50 × 50 km), resident seals showed foraging-site fidelity to their capture areas that had a high fishing effort with trap-nets and high seal-induced damage. Also, on a finer scale (accuracy likely <200 m), residents visited the vicinity (≤250 m) of trap-nets on 30% of tracking days, indicating strong spatial overlap. Although the coexistence of seals with fisheries does not necessarily indicate depredation, the seals whose foraging areas overlap with coastal fishing areas might share the same resources as the fisheries, causing both direct and indirect impacts to the fisheries. The seals and fisheries potentially use the same resources since the most important prey species of grey seals (Baltic herring, whitefish, *Salmo* sp. and cyprinids; Lundström et al. 2010, Kauhala et al. 2011, Suuronen & Lehtonen 2012) were also present in fisheries catches in overlapping areas.

The temporal scope of our movement data is mainly within the open-water season when the passive gear effort is also the highest. Although the trap-nets for capturing seals were set out in June, most of the seals were captured in autumn (from September onwards). Our results coincided with previous findings that seal-induced damages tend to increase during autumn in the Baltic Sea (Fjälling 2005, Fjälling et al. 2006). In our study, most trap-net fishing ceased after October due to harsh weather conditions, while the grey seals left the area in December. This could suggest that the seals continue foraging even after the trap-net fishing season is over. Many residents foraged close to half of the year without substantially overlapping with the same fishing areas as during the open-water season, due to the low overlap between seasonal home ranges and the decline of trap-net fishing after October. However, the degree of overlap between grey seals and coastal fisheries during the winter may increase due to climate change (Meier et al. 2004). Grey seals generally prefer open-water areas as they do not keep breathing holes in the ice (Hook & Johnels 1972). Therefore, grey seals can be expected to stay closer to the coasts if the period and extent of fast-ice declines.

The grey seals captured with pontoon traps were all males and most of them were adults. This, combined with foraging-site fidelity and spatio-temporal overlap with trap-net fisheries, indicates a high level of interaction between grey-seal males and fisheries. Previous studies also suggest that males might cause more direct catch losses to the fishery than females, as males visit inside the pontoon traps more often (Lehtonen & Suuronen 2010, Königson et al. 2013), and the sex ratio of seals shot near fishing gear is biased towards males (K. Kauhala et al. unpubl.). In addition, while Baltic herring is the most important prey species for both sexes and all age groups, sex-related differences in diet have been reported. In particular, adult males also feed on bigger fish, such

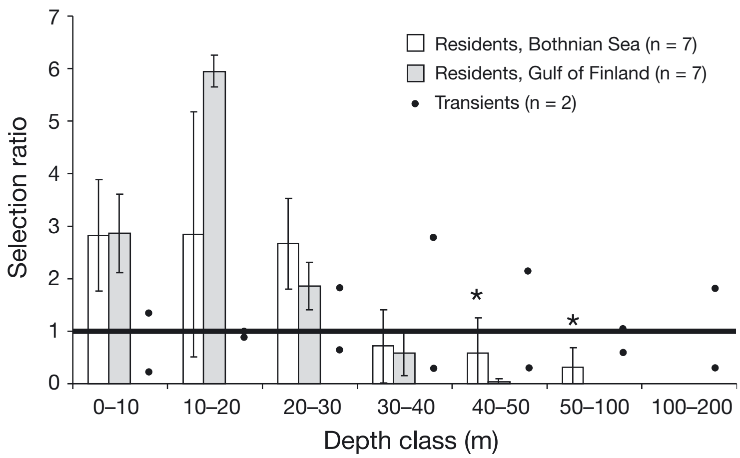

Fig. 4. Habitat preference for depth classes of Baltic grey seals *Halichoerus grypus* during the open-water season. Selection ratios and Bonferroni corrected confidence intervals (Manly at al. 2002) indicate preference when >1 (statistically significant when confidence interval [CI] > 1) and avoidance when <1 (statistically significant when CI < 1). *An impossible negative confidence limit was replaced by 0.0

as *Salmo* sp. (Lundström et al. 2010, Kauhala et al. 2011, Suuronen & Lehtonen 2012). These results give an indication that some males might be so-called problem individuals (sensu Linnell et al. 1999), which are responsible for a disproportional impact on trap-net fisheries. Hunting (annual quota: approx. 1730 seals) has become a key policy instrument for the mitigation of seal-induced losses to coastal fisheries in the northern Baltic Sea (Ministry of Agriculture and Forestry 2007, Bruckmeier & Larsen 2008, Varjopuro 2011, Kauhala et al. 2012, Naturvårdsverket 2013). However, most of the hunting takes place on spring ice (Kauhala et al. 2012) and is not targeted at individuals that strongly overlap with fisheries. Selective removal of individuals occurring near the fishing gear could be a more locally focused conflict mitigation method. In the future, comparative telemetry data from potential problem seals and non-problem seals would further our understanding on the seal–fishery conflict. Also, more fine-scaled analyses on foraging behaviour and habitat preference during foraging, based on diving behaviour, for example, are encouraged.

Haul-out site fidelity (Karlsson et al. 2005, Vincent et al. 2005, present study) combined with foraging-site fidelity (Russell et al. 2013, present study) illustrates the connectivity between these 2 areas in the context of conservation needs. In our study, 64 % of resident seals used seal sanctuaries for hauling out but the same individuals also strongly overlapped with coastal fisheries, which is likely to increase their mortality risk (by mitigation actions or incidental by-catch). Our study, therefore, confirms the importance for the recognition of foraging areas when planning conservation measures, which has also been previously suggested (Augé et al. 2014). Additionally, detailed knowledge on seasonal movement patterns is important in planning conservation measures. For example, in our study, due to extensive movements of grey seals especially after the open-water season, local mitigation actions may actually target some individuals that breed in the southern Baltic Sea where the local abundance of grey seals is low. This in turn may compromise conservation goals in these areas (Schwarz et al. 2003). The conflicting interests of several stakeholders necessitates that these factors must be taken into account when setting management policy.

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