

## Original Article

# Foraging behaviour and prey consumption by grey seals (*Halichoerus grypus*)—spatial and trophic overlaps with fisheries in a marine protected area

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The roles of the marine national park of the Iroise Sea (France) are to maintain marine biodiversity, including the southernmost grey seal colony in the Eastern Atlantic, whilst managing sustainable human activities. This study compares the fish biomass taken by local seals and the landings by man in the Iroise Sea. Sixteen seals were satellite tracked from 1999 and 2003, providing location and behavioural (diving) data from which foraging locations were estimated. One individual spent a third of its foraging time in direct, long distance trips (200–350 km) across the English Channel, but most seals spent the majority (68.5%) of their foraging time in the Iroise Sea, making return trips within 30 km of their departure haulout sites. The energetic consumption of the seal colony, taking sex and age classes into account, was assessed and combined with seal abundance estimates and dietary data to assess the total prey consumption by seals, for each prey species. We estimated that during the study period, the grey seal colony in the Iroise Sea consumed around 115 tons of fish per year. The main source of uncertainty of this calculation came from the confidence intervals in total seal abundance estimates. This consumption comprised 13.6 tons of sea bass, 4.3 tons of pollack and 2.7 tons of sole, representing 16.4, 1.8, and 5.2% of landings in the same areas for these three fish species, respectively. Within the four ICES rectangles where grey seals foraged, overlap between seals and fisheries was greatest in rectangle 25E5 (72.7% of all foraging dives), where grey seals haul out, and less in rectangles 25E4 (11.7%), 26E5 (10.8%), and 26E4 (4.8%).

**Keywords:** fisheries interactions, Iroise Sea, management, Pinnipeds, prey intake, satellite telemetry.

## Introduction

Interactions between marine mammal populations and man are usually categorized as direct or indirect interactions, sometimes referred to as operational or ecological interactions respectively

(Baraff and Loughlin, 2000; Goldsworthy *et al.*, 2003). In the case of Pinnipeds, direct interactions include hunting (Leaper *et al.*, 2010), culling (Hamilton, 1983), bycatch in fishing gear (Björge *et al.*, 2002), or depredation from seals in fishing nets (Königson

*et al.*, 2007), while indirect interactions mainly relate to competition for shared resources by both seals and fishermen (Bowen, 1997). The latter—ecological interactions—are for the most part difficult to estimate, due to the difficult access to the different compartments of the ecosystem, but their general effects on seal populations and/or fisheries can be much more significant than operational interactions (Goldsworthy *et al.*, 2003). Situations concerning commercial fish stock collapses or conservation issues for seal populations have received most attention (e.g. Trzcinski *et al.*, 2006; Lowry *et al.*, 2011). Less acute situations however frequently arise and local conflicts with commercial or recreational fisheries are common where seals are present. These conflicts are undoubtedly exacerbated by the decrease in fishery resources over the last century (Christensen *et al.*, 2003).

In the 19th and early 20th centuries, many seal populations were heavily hunted in the North Atlantic. In the case of grey seals (*Halichoerus grypus*), this resulted in a sharp decline of the populations within most of the species range in the North-east Atlantic (Haug *et al.*, 2007). Protection was then afforded to the species, as early as in 1914 in the United Kingdom by the *Grey Seal Protection Act* (Summers, 1978), and in the second half of the twentieth century in most other European countries (Wilson *et al.*, 2001). Protection provided to the species allowed seal numbers to increase again. With the European Habitat Directive (92/43/EEC) introduced in 1992, more recent conservation efforts focused on the preservation of habitats. The Directive requires the designation of Special Areas of Conservation (SACs) in order to maintain or restore the natural habitats and/or populations of all species of Community interest (i.e. listed under Annex II of the Directive) to a favourable status, including grey seals.

In France, the grey seal is listed as a transient or resident species in 46 of such French marine SACs. More recently, marine national parks, often encompassing several existing SACs, were established with the objectives of providing favourable conservation status to marine biodiversity while maintaining sustainable human activities. Before creating the first French marine national park, the *Parc naturel marin d'Iroise* (set up in 2007 in western Brittany), it was therefore strongly advised that, next to protection of biodiversity, the marine park would allow the sustainable development of fishing activities, maritime and island tourism, in addition to the protection of biodiversity. Marine mammals, including bottlenose dolphins (*Tursiops truncatus*) and grey seals using the area year-round, were identified as flag species (Zacharias and Roff, 2001; Walpole and Leader-Williams, 2002), while their role in the local ecosystem remained poorly known. In this regard, during the decade preceding the official settlement of the marine park, stakeholders requested to investigate habitat and resource use by marine mammals and their interactions with human activities in the area.

Grey seals in the Iroise Sea are at the southern limit of the species range in the Eastern Atlantic (Härkönen *et al.*, 2007). Previous work combining regular censuses on haulout sites, photo ID and telemetry showed that many seals observed in the area use it alternatively with other haulout sites in the South-west British Isles during their annual cycle, although the seals tracked with satellite tags spent overall 66% of their time within the boundaries of the marine natural park (Vincent *et al.*, 2005). The colony size was estimated to be below a hundred seals in 1999–2000 (Gerondeau *et al.*, 2007) and seal counts increased by 7% per year during the preceding decade (Vincent *et al.*, 2005). Grey seal diet in the Iroise Sea was dominated by wrasse (Labridae), conger eel and sea bass (Ridoux *et al.*, 2007). Some prey species

identified in the grey seal diet in the area are also targeted by professional or recreational fisheries, but only three species have both high commercial value and represent a significant part of the seal diet: sea bass *Dicentrarchus labrax*, Pollack *Pollachius pollachius*, and common sole *Solea solea*.

The objectives of this article were to (i) assess seasonal and spatial foraging behaviour of grey seals in the Iroise Sea, (ii) estimate their prey consumption at the colony level, and (iii) compare their consumption of the aforementioned fish species to simultaneous fishery landings in the same areas. These comparisons required not only that the seals' diet and energy requirements were estimated, but also that the spatial distribution of their foraging activities were determined in order to overlay those with the fishery activities (Matthiopoulos *et al.*, 2008; Cronin *et al.*, 2012). Grey seal diet composition, prey energy contents and seal abundance were obtained from previously published work, while the foraging areas of the seals and comparisons with local fishery landings were assessed for the purpose of this article. Ultimately, the aim of this study was to provide an initial assessment of spatial and trophic overlaps with fisheries preceding the creation of the MPA, and thus allow further investigation on the effects of the MPA on interactions between seals and fisheries.

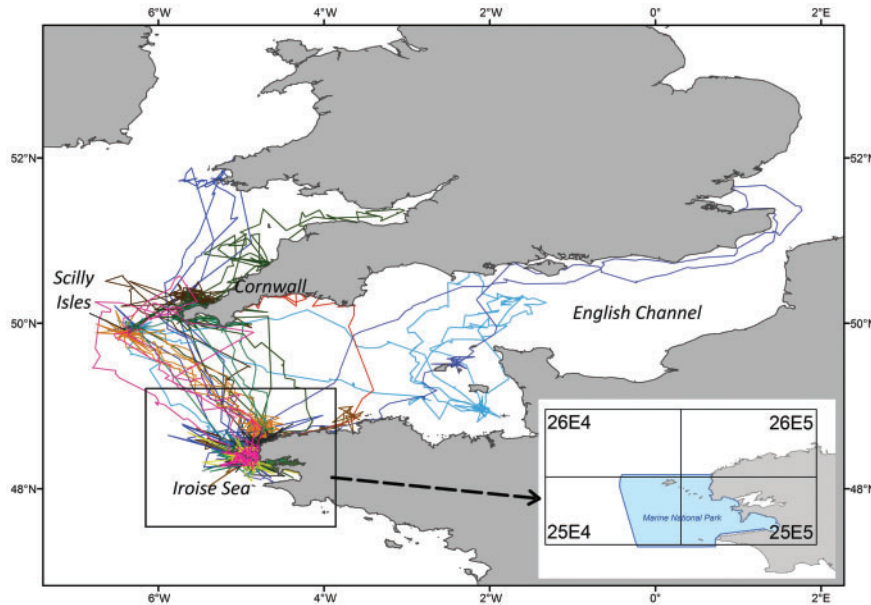
## Methods

### Study site

The Iroise Sea is located at the Western end of Brittany, France, at the confluence of the English Channel and the Bay of Biscay (Figure 1). The bathymetry remains relatively shallow as it stands on the continental shelf (110 m on average). Most grey seal haulout sites are located within the Molène archipelago, a shallow plateau (20 m deep) and 190 km<sup>2</sup> in extent, including a large number of small isolated islets. The area is characterized by complex hydrodynamic processes linked to the area's irregular topography, its strong tidal currents and its particular geographical location along the route of low-pressure atmospheric systems (Muller *et al.*, 2009). Physical processes in this frontal region and the variety of seabed substrates lead to high biodiversity. With over 300 algae species, 126 fish species and all of the large crustacean species recorded in France, the richness and variety of this ecosystem led to the labelling of the Iroise Sea as a 'Man and Biosphere Reserve' by UNESCO in 1988 (Hily and Glemarec, 1999). Fish species of commercial interest included monkfish (*Lophius* spp.), pollack (*P. pollachius*), rays, conger (*Conger conger*), flatfish (including sole, *S. solea*), pilchard (*Sardina pilchardus*), mackerel (*Scomber scomber*), as well as crustacean and shellfish species. In the late 1990s to early 2000s, commercial fishery activities in the Iroise Sea were estimated to support about 900 fishermen on 350 boats, mainly under 16 m. Other professional activities include seaweed harvesting and tourism (Alban and Boncoeur, 2004).

### Grey seal foraging behaviour

Sixteen grey seals were captured in the Iroise Sea and fitted with Satellite Relay Data Loggers [SRDLs (<http://www.smru.st-and.ac.uk/Instrumentation/Downloads/>) (SRDL overview)], Sea Mammal Research Unit, UK) from 1999 to 2003 (Table 1). Data obtained from the tags included Argos locations, haulout records and diving data (Photopoulou *et al.*, 2015a). A sample of individual dive records were transmitted with the following parameters (Myers *et al.*, 2006): maximum depth, dive duration, post-dive surface duration, the 'percent area' allowing the calculation of the



**Figure 1.** Map of all seals' satellite tracking included in this study and delimitation of the marine national park of the Iroise Sea where the seals were caught. The four ICES rectangles are also shown in the detailed map.

**Table 1.** Details of grey seals fitted with SRDLs from 1999 to 2003 in the Iroise Sea, and total tracking duration. Total body length is measured nose to tail

| Seal | Capture date  | Sex | Body mass (kg) | Total body length (cm) | Total tracking duration (days) |
|------|---------------|-----|----------------|------------------------|--------------------------------|
| B01  | 30 April 1999 | M   | 99             | 147                    | 180                            |
| B02  | 2 May 1999    | M   | 101            | 148                    | 13                             |
| B03  | 2 May 1999    | M   | 114            | 159                    | 56                             |
| B04  | 6 May 1999    | M   | 42             | 117                    | 107                            |
| B05  | 7 May 1999    | F   | 58             | 119                    | 54                             |
| B06  | 9 May 1999    | F   | 37             | 112                    | 52                             |
| B07  | 3 July 2002   | F   | 76             | 144                    | 141                            |
| B08  | 4 July 2002   | M   | 155            | 156                    | 66                             |
| B09  | 4 July 2002   | M   | 67             | 137                    | 158                            |
| B10  | 5 July 2002   | F   | 139            | 176                    | 144                            |
| B11  | 7 July 2002   | M   | 75             | 145                    | 128                            |
| B12  | 8 July 2002   | M   | 151            | 185                    | 69                             |
| B13  | 09 July 2002  | M   | 101            | 157                    | 120                            |
| B14  | 13 July 2002  | M   | 206            | 200                    | 125                            |
| B15  | 29 July 2003  | F   | 61             | 143                    | 101                            |
| B16  | 2 August 2003 | F   | 114            | 161                    | 154                            |

Time At Depth index (TAD; cf Fedak *et al.*, 2001), and the time and depth of the three main inflexion points of the dive (Photopoulou *et al.*, 2015b). This data was used to check descent rates of individual dives, discriminating between sleeping and foraging behaviours in square dives (see below). Argos locations were processed with a speed-filter algorithm allowing rejection of locations that would require an unrealistic rate of travel to achieve (McConnell *et al.*, 1992).

A trip at sea was defined as time spent in the water between two consecutive haulouts. We defined two categories of trips (e.g. McConnell *et al.*, 1999; Cunningham *et al.*, 2009): return trips (when seals came back to haulout at the same area after their trip at sea) and travel trips (when the seals moved to a different haulout area). Haulout areas were considered to be

distinct when they were separated by at least 20 km. Argos locations located within the vicinity of haulout sites are often discarded in analyses because of the difficulty of interpreting behaviour near a haulout site. Given the relatively low accuracy of Argos locations' estimates (Vincent *et al.*, 2002), a buffer zone of 2–10 km around the haulout sites is usually chosen (McConnell *et al.*, 1999; Breed *et al.*, 2011) within which locations are not associated with the identification of foraging behaviour. In our study however, when selecting locations outside such buffer zones around the grey seals haulout sites, we found out that this discarded a very large proportion of locations, reaching 100% for several individuals, even when they were tracked during several months. It seemed likely that many seals tracked in this study were foraging very close to their haulout sites. Thus distance from a haulout site was not used as a criterion; instead foraging was inferred from dive shape.

Grey seals are usually benthic foragers, it is assumed that they perform “U-shape” (or square) dives close to the bottom when foraging (e.g. Thompson *et al.*, 1991; Beck *et al.*, 2003a,b; Bowen *et al.*, 2006). We used the TAD index in order to detect U-shape dives (Fedak *et al.*, 2001). This index uses an estimated Minimum Cost of Transport Speed (MCTS) for descent and ascent rates to create a dimensionless, index that provides a depth and duration independent measure of where the seals concentrate their activity during a dive. It usually varies from 0 (when most of the diving activity occurs at the shallowest depths of the dive) to 1 (when most of the diving activity is concentrated at the maximum depth). Some TAD values can exceed 1 when the seal's vertical speed exceeds this MCTS and all the remaining ‘available’ diving time is spent at maximum depth.

$$\text{TAD} = \frac{\frac{\text{Percent\_Area}}{100} * \text{DiveDur} * \text{MaxDepth} - \frac{\text{MaxDepth}^2}{S}}{\text{MaxDepth} * \text{DiveDur} - 2 * \frac{\text{MaxDepth}^2}{S}}$$

where

MaxDepth = Maximum depth of the dive  
 DiveDur = Dive duration  
 Percent Area = Percentage of the maximum dive trapezoid covered by the dive  
 S = Vertical travel speed, estimated MCTS

In order to calculate the TAD, the dive has to be deeper than the chosen minimum depth threshold, so only dives deeper than 6 m were kept in the analysis. The choice of individual MCTS values is crucial for the calculation of the TAD index. We calculated the TAD values for a series of increasing S values, ranging from 1.0 to 3.0 m.s<sup>-1</sup>. As suggested by Fedak *et al.* (2001), we checked the number of TAD values obtained between 0.5 and 1.0. When plotted according to the S value, this number reaches an asymptote. The best S value was selected for each seal when the second derivative of the number of 0.5 < TAD < 1.0 came to zero (or changed from a negative to a positive value). The second derivative was preferred to the first derivative because it allows the detection of possible inflection point, identified as reaching a threshold on the graph. The index was then calculated using the chosen S for each seal. Foraging dives were assumed to be U-shape dives, identified from TAD values higher than an arbitrary threshold of 0.8. Within square dives (TAD > 0.8), the threshold of 0.2 m.s<sup>-1</sup> was used to distinguish slow (potentially sleep) dives from faster (potentially foraging) dives (Vincent, unpublished data).

Foraging areas of the grey seals in the Iroise Sea were described for each quarter of the year, pooling the 4 years of tracking together. Little data were available for quarter one though, as this corresponds to the annual moult (when the tag detaches), so it was assumed that the foraging behaviour of the seals during this season was similar to that in the previous quarter (seals spending less time at sea during both the moulting and breeding season, i.e. during the first and last quarters of the year, respectively).

### Prey and energy consumption

Total prey consumption of grey seals in the Iroise Sea was calculated seasonally by combining the estimated total number of seals, the sex/age structure of the population, the diet of the grey seals in the Iroise Sea as well as the energy content of the prey, and the estimated energy consumption (EC) of grey seals of different sex/age categories. Most parameters, unless stated otherwise, were available for quarter 1 (Q1: January–February–March), quarter 2 (Q2: April–May–June), quarter 3 (Q3: July–August–September), and quarter 4 (Q4: October–November–December) separately. In the Iroise Sea, Q1 corresponds to the grey seal moulting period, Q2 to the post-moult period, Q3 to the pre-breeding period and Q4 to the breeding season.

The mean energy content per unit weight,  $\bar{E}$ , is given by:

$$\bar{E} = \sum (E_i * p_i)$$

Where  $E_i$  is the energy content by weight for species  $i$  and  $p_i$  is the proportion of biomass of species  $i$  in the seal diet.

The total EC of grey seals in the Iroise Sea was then calculated for each quarter of the year and each sex/age category of seals:

$$EC_{s,q} : DEC_{s,q} * d_q * N_q * P_q$$

Where  $DEC_{s,q}$  is the Daily Energy Consumption (DEC) per sex/age category ( $s$ ) during quarter  $q$ , in J/day,  $d_q$  the number of days in quarter  $q$ ,  $N_q$  the total seal abundance during quarter  $q$  and  $P_q$  the proportion of seals belonging to each sex/age category during quarter  $q$ .

Lastly, the total prey Consumption ( $C$ ) by seals was calculated as follows, for each prey species and each quarter:

$$C_{i,q} = p_i * EC_{s,q} / \bar{E}$$

Sex/age categories are: adult male, adult female, sub-adult male, sub-adult female, and pups.

The total number of seals in the Iroise Sea was obtained from Gerondeau *et al.* (2007) who conducted capture-mark-recapture (CMR) analysis of the photo-identification data collected on haulout sites from March 1998 to August 2000. This provided an estimated total abundance of 73 seals during Quarter 1, 58 seals during Quarter 2, and 78 seals (averaged over 3 estimates) during Quarter 3 (Gerondeau *et al.*, 2007). Abundance estimates from CMR were available for all quarters except quarter 4: for this season, estimates were based on haulout counts (close to absolute abundance during the breeding season when breeding grey seals spend most of their time hauled out), i.e. 54 seals during Quarter 4.

The sex and age structure of the population was described for each quarter of the year from counts on the haulout sites. Male and female grey seals can be distinguished thanks to their pelage pattern (Vincent *et al.*, 2001), at least when seals are at least a few years old. Figures presented in Vincent *et al.* (2005) were re-analysed in order to obtain the following categories: adult males, sub-adult males (including juveniles more than a year old), adult females, sub-adult females, and pups (less than a year old, with no sex identification). In sub-adult and adult seals, when the sex could not be identified in the field, we assumed for this work that the sex ratio of the 'unknown' seal category was the same as for sexed seals. The distinction between sub-adult and adult seals was based on body and head size. Proportions of seals belonging to each category were calculated for each quarter of the year (Table 2).

Grey seal diet in the Iroise Sea was inferred by Ridoux *et al.* (2007) from 145 scats collected on haulout sites in the Molène archipelago from 1998 to 2000. We used the percentage of reconstituted biomass per prey species (or taxon). In the absence of data on seasonal variations of the seals' diet in the area, this data was used for all quarters, though estimated to be from mostly adult males during the moulting season.

DEC (Table 2) was calculated based on the daily energy expenditure values presented in Sparling (2003) and Sparling and Smout (2003). DEC was calculated by:

- (i) Taking into account the fact that grey seals are capital breeders and that they separate the activities of energy expenditure during breeding and energy acquisition for breeding, we assumed that the energy used during reproduction in the fourth quarter (when seals were using previously stored energy) had been collected during the previous quarters. Therefore we reallocated this portion of EC to the previous quarters based on the pattern of seasonal blubber mass gain from Fedak and Anderson (1987). Consumption in the

**Table 2.** Proportion of seals belonging to each of the 5 sex/age categories (%n = percentage of all seals counted), as assessed from regular censuses at haul-out sites from 1998 to 2000 (modified from Vincent *et al.*, 2005), and DEC (in kJ/d, per seal category, see text for more details) for each quarter of the year.

| Season               | Adult females |        | Sub-adult females |       | Adult males |        | Sub-adult males |        | Pups |        |
|----------------------|---------------|--------|-------------------|-------|-------------|--------|-----------------|--------|------|--------|
|                      | %n            | DEC    | %n                | DEC   | %n          | DEC    | %n              | DEC    | %n   | DEC    |
| Quarter 1 (Jan–Mar)  | 8%            | 53 667 | 14%               | 15646 | 39%         | 43 851 | 36%             | 16 616 | 3%   | 8688   |
| Quarter 2 (Apr–Jun)  | 17%           | 51 442 | 20%               | 16050 | 25%         | 53 684 | 31%             | 17 184 | 7%   | 11 082 |
| Quarter 3 (Jul–Sept) | 25%           | 32 675 | 20%               | 16007 | 15%         | 50 271 | 28%             | 17 163 | 12%  | 11 674 |
| Quarter 4 (Oct–Dec)  | 9%            | 23 997 | 27%               | 16964 | 21%         | 45 572 | 31%             | 18 297 | 10%  | 11 716 |

fourth quarter is therefore simply a reflection of the proportion of time spent outside of breeding and the metabolic cost of these activities.

- (ii) Incorporation of age and sex specific values for the efficiency of energy conversion.

Energy densities of the identified prey species were taken from Spitz *et al.* (2010) where 78 forage species in the Bay of Biscay from 2002 to 2008 have been analysed by adiabatic bomb-calorimetry. The average daily prey consumption per seal category and per quarter was calculated from the DEC, taking into account the percentage of reconstituted biomass per prey species and the average energy content of each of these prey species. These results were then multiplied by the total number of seals per sex/age category and per quarter with a lower and an upper estimate corresponding to the lower and upper bounds of the quarterly abundance estimates.

### Consequences of uncertainties in the consumption estimate

A number of potential uncertainties were identified in the calculation of the total prey consumption of the seals at the colony level. The main uncertainties identified here include the estimate of the total seal abundance, the assessment of the sex and age classes of these seals, the description of the seals' diet from faecal analyses and the choice of the energetic model. We quantified separately the consequences of each of these potential biases in the total estimate of prey consumption, by re-running the calculation with new numbers (usually extreme values). We used confidence intervals provided by CMR analyses for the estimation of the total seal abundance (Gerondeau *et al.*, 2007), ranging from 49 to 107 seals in Quarter 1, 48–71 seals in Quarter 2, 65–105 seals in Quarter 3 (there was no estimate therefore no confidence interval for Quarter 4). For the uncertainty related to the sex and age class of the seals, we considered all seals from the “unknown” category to be in one of the existing categories, and re-ran the calculation in all possible cases. Simulations for the percentages by reconstituted biomass in the diet of grey seals were generated for each prey species by 1000 bootstrap simulations of sampling errors on the initial dataset providing the 95% confidence intervals of the mean energy content  $\bar{E}$ . The consequences of the choice of the energetic model were assessed by estimating the lower and upper bounds of daily energetic consumption as respectively two times BMR (Basal Metabolic Rate) and three times BMR (Speakman, 2000).

### Comparison with fisheries

Comparison with fisheries was conducted within four ICES rectangles (26E4, 26E5, 25E4, and 25E5); fisheries landings were available for the years 1996–2002 in these ICES rectangles from an analysis by Ifremer of logbook data (DPMA/SIH Ifremer—CRTS La Rochelle) (<http://sih.ifremer.fr/>). Assuming the tracked seals were representative of the whole colony, we calculated the percentage of foraging effort (number of square dives performed by the tracked seals) in each of these four rectangles, and multiplied it by the estimated total prey consumption for all seals. We then compared for each quarter of the year the estimated prey consumption by seals to fisheries landings for the main prey species of commercial value, i.e. sea bass, pollack and common sole. A finer description of the spatial distribution of the seals' foraging behaviour and the fishery takes was conducted within rectangle 25E5, for which eight sub-areas were documented.

## Results

### Foraging behaviour

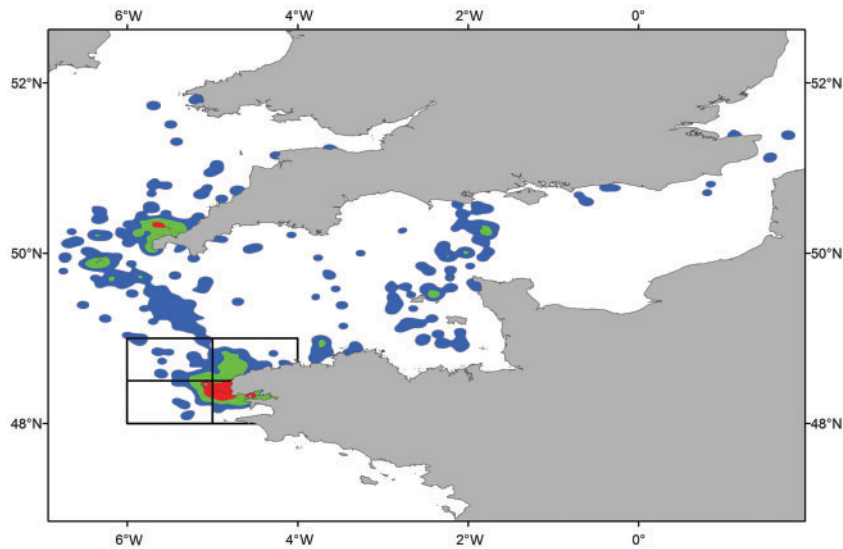
The average ( $\pm$  SD) seal tracking duration was  $104 \pm 47$  days. Overall, the seals spent 19% of their time hauled out, and 81% at sea. Most travel trips (movements at sea between two distinct haulout sites) were performed across the Channel, and lasted several days (Table 3). One seal (B03) did two extended return trips in the Channel (extending 160 and 190 km from the haulout site and lasting 232 and 244 hours respectively) but all other seals remained within 10 to 30 kilometres from their haulout sites during their return trips.

A sample of 50 930 individual dives deeper than 6 m were transmitted by the tags, among which 7388 dive records included detailed data allowing the calculation of the vertical speed. The TAD index was calculated for each seal testing a series of increasing S (vertical speed) values, from 1.0 to 3.0  $\text{m}\cdot\text{s}^{-1}$ , and the best value was selected for each of the individuals when the derivative of the number of TAD values obtained between 0.5 and 1.0 became null (Supplementary Figure S1). These seal-specific S values (Table 3) were then used to calculate the TAD index for each individual dive. We obtained 3156 dives selected as U-shape dives (TAD > 0.8) with a descent rate higher than 0.2  $\text{m}\cdot\text{s}^{-1}$ . Most seals showed similar percentages of U-shape dives in return trips and travel trips. There were individual variations in those results however. Some seals spent more time (56–67%) and performed more U dives (68–88%) in travel trips than in return trips (seals B05 and B06), while five seals spent virtually all (99–100%) their tracking time at sea in return trips (Table 3). Kernel densities were used to map the distribution of the seals' foraging effort over the whole tracking area (Figure 2). Most foraging activity

**Table 3.** Estimated vertical speed(S) for each seal, and statistics on the travel and return trips (mean duration  $\pm$  SD), percentage of time spent in return trips, maximum extent of return trips (maximum distance from the previous or next haulout site) and percentage of all foraging dives (with TAD > 0.8) performed during return trips. Seal B02 is excluded because of its short tracking duration

| Seal | S speed (m.s <sup>-1</sup> ) | Travel trips |                                    |                                       | Return trips |                   |                     |                  |           |
|------|------------------------------|--------------|------------------------------------|---------------------------------------|--------------|-------------------|---------------------|------------------|-----------|
|      |                              | Duration (h) | Mean U-Dive depth (m) <sup>a</sup> | Maximum U-dive depth (m) <sup>a</sup> | % time       | Mean duration (h) | Maximum extent (km) | U-Dive depth (m) | % U dives |
| B01  | 2.1                          | 124 $\pm$ 30 | 74 $\pm$ 39                        | 136                                   | 84%          | 48 $\pm$ 39       | 15 $\pm$ 13         | 13 $\pm$ 6       | 78%       |
| B03  | 2.2                          | 88 $\pm$ 22  | 74 $\pm$ 29                        | 136                                   | 66%          | 175 $\pm$ 102     | 35 $\pm$ 69         | 16 $\pm$ 8       | 78%       |
| B04  | 2.1                          | 204          | 80 $\pm$ 22                        | 107                                   | 81%          | 55 $\pm$ 35       | 27 $\pm$ 17         | 17 $\pm$ 6       | 91%       |
| B05  | 1.4                          | 105 $\pm$ 7  | –                                  | –                                     | 44%          | 15 $\pm$ 13       | 13 $\pm$ 16         | 13 $\pm$ 6       | 12%       |
| B06  | 2.1                          | 144 $\pm$ 90 | 33 $\pm$ 18                        | 99                                    | 33%          | 26 $\pm$ 16       | 13 $\pm$ 11         | 14 $\pm$ 5       | 32%       |
| B07  | 1.9                          | 35 $\pm$ 12  | –                                  | –                                     | 99%          | 21 $\pm$ 16       | 11 $\pm$ 9          | 19 $\pm$ 5       | 99%       |
| B08  | 1.8                          | –            | –                                  | –                                     | 100%         | 19 $\pm$ 9        | 11 $\pm$ 7          | 13 $\pm$ 2       | 99%       |
| B09  | 1.8                          | 96 $\pm$ 43  | 53 $\pm$ 27                        | 99                                    | 61%          | 30 $\pm$ 19       | 29 $\pm$ 18         | 15 $\pm$ 5       | 61%       |
| B10  | 1.4                          | –            | –                                  | –                                     | 100%         | 39 $\pm$ 22       | 17 $\pm$ 8          | 16 $\pm$ 4       | 100%      |
| B11  | 1.9                          | 30 $\pm$ 13  | –                                  | –                                     | 72%          | 15 $\pm$ 14       | 11 $\pm$ 9          | 16 $\pm$ 6       | 51%       |
| B12  | 1.6                          | 85 $\pm$ 32  | 80 $\pm$ 37                        | 115                                   | 48%          | 35 $\pm$ 25       | 14 $\pm$ 11         | 14 $\pm$ 4       | 59%       |
| B13  | 1.7                          | 68 $\pm$ 10  | 65 $\pm$ 31                        | 115                                   | 83%          | 16 $\pm$ 10       | 15 $\pm$ 11         | 16 $\pm$ 6       | 91%       |
| B14  | 1.3                          | –            | –                                  | –                                     | 100%         | 30 $\pm$ 21       | 17 $\pm$ 12         | 18 $\pm$ 5       | 100%      |
| B15  | 1.8                          | –            | –                                  | –                                     | 100%         | 24 $\pm$ 19       | 11 $\pm$ 8          | 13 $\pm$ 5       | 100%      |
| B16  | 1.6                          | 139 $\pm$ 39 | 91 $\pm$ 23                        | 115                                   | 91%          | 28 $\pm$ 20       | 8 $\pm$ 6           | 12 $\pm$ 2       | 97%       |

<sup>a</sup>mean and maximum U-dive depths (dives with TAD > 0.8) during travel trips are given for dive locations located outside the vicinity of haulout sites, i.e at a minimum distance of 15 km. Seals B05, B07 and B11 did short travel trips that fell within that distance from the nearest haulout sites so dive depth data is not provided for their travel trips.

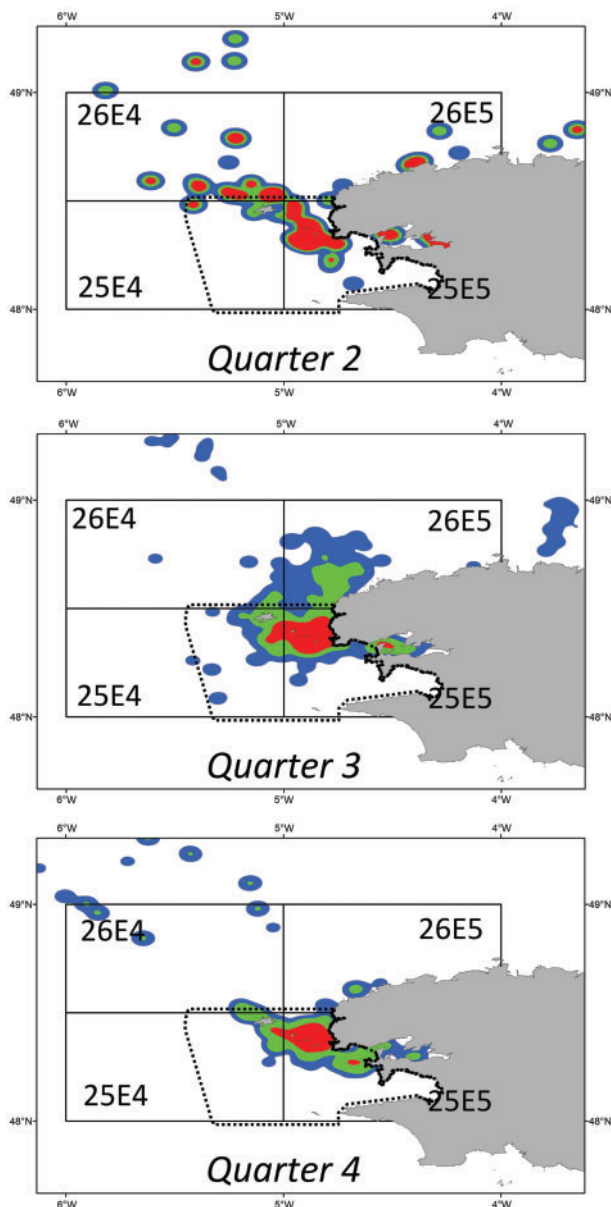


**Figure 2.** Grey seals' foraging areas as assessed from satellite telemetry. Core to extended foraging areas are presented from 50, 75, and 95% Kernel densities of all foraging dive locations, during travel and return trips (see text for definition). The four ICES rectangles for which fisheries landings are used here are also shown.

was concentrated around haulout sites, especially in the Iroise Sea (and from Cornwall and the Scilly Isles to a lesser extent, Figure 1), but many foraging dives were also identified in the Channel either during long return trips (B03) or during travel trips between French and UK colonies. All return trips performed by the seals in the Iroise Sea lay within the four ICES rectangles detailed in this article. Most foraging activity was concentrated in ICES rectangle 25E5 (Figure 3). Overall, 68.5% of the seals' foraging dives were located in the Iroise Sea, and 55% were located within the perimeter of the marine national park of the Iroise Sea.

### Prey consumption

Total seasonal consumption was estimated, for each prey species, according to the percentage of reconstituted biomass of these prey species in the grey seal diet in the Iroise Sea and the EC of each sex/age categories of the seals (Table 4). We estimated that adult grey seals eat on average 380–850 kg of fish per quarter, while sub-adult seals and pups consume 250–290 kg and 140–185 kg per quarter and per seal respectively, depending on the quarters (Table 4). Multiplied by the number of seals (per sex/age category), these results allow a global estimate of prey consumption at the colony scale. We estimated a total prey consumption



**Figure 3.** Grey seals' foraging areas in and around the marine national park of Iroise (dashed line), as assessed from the diving behaviour of the seals during return trips. Quarters 2 (April–June), 3 (July–September), and 4 (October–December) are presented while Quarter 1 (January–March) is not available (no satellite tracking available during the grey seals' moulting period). Core to extended foraging areas are presented from 50, 75, and 95% Kernel densities of foraging dive locations. The four ICES rectangles for which fisheries landings are used here are also shown.

of around 115 tons of fish over the year for the whole grey seal colony of the Iroise Sea.

Uncertainties on total seal numbers proved to be the main parameter influencing the confidence intervals in the estimate of total prey consumption (Figure 4): due to minimum and maximum estimates of total seal abundance available for this study, the total prey consumption by the seal colony varied from 93.1 to 147.9 tons of fish per year, respectively. The choice of the

energetic model also had a strong impact on the calculation, with an estimate of 83.7–124.2 tons of fish consumed per year using a generic model (based on BMR) to estimate the seals' EC. The population structure (knowledge of sex and age category of the seals) and sampling errors in diet composition as assessed from faecal analysis had much weaker consequences on the overall estimate (estimates ranging from 109.9 to 120.6 tons and 110.7 to 118.5 tons, respectively; Figure 4).

### Comparison with fisheries

Only three species represented a significant proportion in both seal consumption and local human take within the Iroise Sea. Annually, we estimated that seals took 13.6 tons of sea bass, 4.3 tons of pollack and 2.7 tons of sole (Table 5). The annual commercial fishery landings for these species in the area from 1996 to 2002 were on average 52.0 tons of sole, 245.6 tons of pollack and 82.8 tons of sea bass. Fisheries landings for these species were available for each ICES rectangle and for each quarter of the year, allowing a fine scale comparison with the seals' estimated intake. The distribution of the seals' foraging effort among ICES rectangles was estimated from the percentage of foraging dives performed in each rectangle (Figure 3): this seal-foraging effort is mainly located in rectangle 25E5 (72.7% of all foraging dives), and to a lesser extent in rectangles 25E4 (11.7%), 26E5 (10.8%) and 26E4 (4.8%). The highest degree of overlap therefore appeared in rectangle 25E5 for the three fish species. In this area, the estimated annual fish consumption by the seals equalled 7.7% of the average annual sole biomass landed by fishermen, 4.6% for Pollack and 19.4% for sea bass. This last species representing the largest percentage of seals' intake compared with the fisheries, we described the spatial overlap between seal foraging effort and fishery takes of sea bass at a finer spatial scale within rectangle 25E5 (Figure 5). In sub-areas 25E510 and 25E520, where most of the seals' haulout sites are located, the estimated sea bass consumption by grey seals was much greater than the amount of fish taken by fishermen in these sub-areas. The highest overlap in terms of tons of fish taken was in sub-areas 25E530 and 25E540, where fishermen took on average 13.2 and 9.8 tons of sea bass per year, and the seals' consumption was estimated to be 50 and 49% of these biomasses, respectively. In all other sub-areas, the estimated seal consumption was negligible (Figure 5).

### Discussion

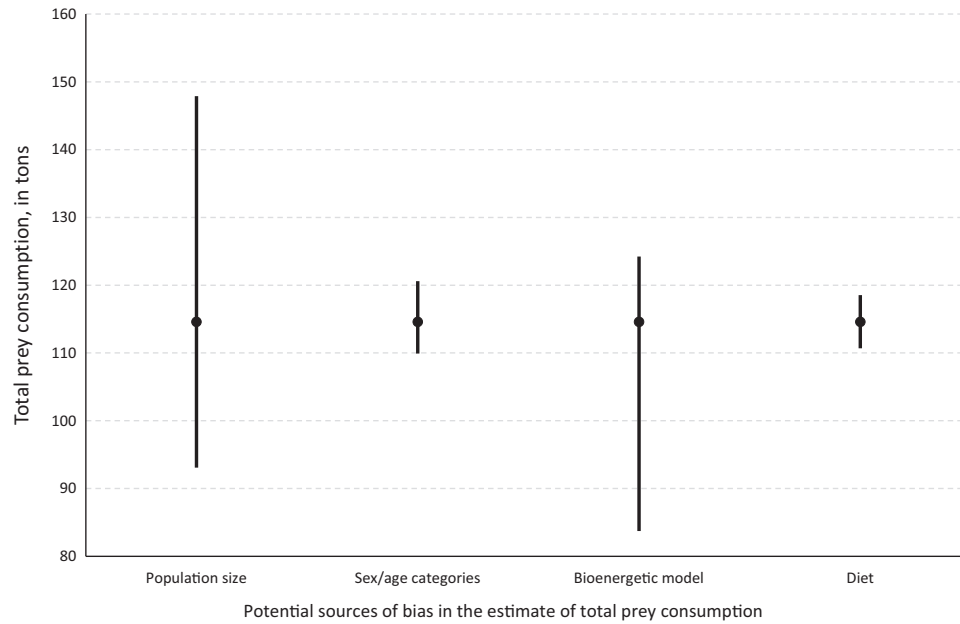
This is the first study of grey seals foraging behaviour at the southern limit of the species' range in the North-east Atlantic. We also provide a unique and comprehensive estimate for the comparison of spatial distribution of the seals' foraging effort, total and detailed prey consumption at the colony level, and fisheries landings for the same prey species, during the same period and at the same geographical scale. One individual spent a third of its foraging time in direct, long distance trips across the English Channel, but most seals spent the majority (68.5%) of their foraging time in the Iroise Sea (55% within the perimeter of the marine national park of the Iroise Sea), making return trips within 30 km of their departure haulout sites. We estimated that during the study period, the grey seal colony in the Iroise Sea consumed 114.6 tons of fish per year. This comprised 13.6 tons of sea bass, 4.3 tons of pollack and 2.7 tons of sole, representing 16.4, 1.8, and 5.2% of average annual landings in the same areas for these three fish species, respectively.

**Table 4.** Grey seal diet, prey energy content and estimated seasonal prey consumption for the Iroise Sea

| Grey seals' prey species in Iroise | %M    | Average energetic value (KJ/g) | Average prey consumption (in kg) by grey seal pups, per quarter |       |       |       | Average prey consumption (in kg) by sub-adult grey seal females, per quarter |       |       |       | Average prey consumption (in kg) by sub-adult grey seal males, per quarter |       |       |       | Average daily consumption (in kg) by adult grey seal females, per quarter |       |       |       | Average prey consumption (in kg) by adult grey seal males, per quarter |       |       |       |       |       |       |
|------------------------------------|-------|--------------------------------|---|-------|-------|-------|--|-------|-------|-------|--|-------|-------|-------|---|-------|-------|-------|--|-------|-------|-------|-------|-------|-------|
|                                    |       |                                | Q1  | Q2    | Q3    | Q4    | Q1   | Q2    | Q3    | Q4    | Q1   | Q2    | Q3    | Q4    | Q1  | Q2    | Q3    | Q4    | Q1   | Q2    | Q3    | Q4    |       |       |       |
| Undetermined gobiidae              | 0.0   | 5.6                            | 0.0   | 0.0   | 0.0   | 0.0   | 0.0  | 0.0   | 0.0   | 0.0   | 0.0  | 0.0   | 0.0   | 0.1   | 0.1   | 0.1   | 0.1   | 0.0   | 0.1  | 0.1   | 0.1   | 0.1   | 0.1   | 0.1   |       |
| <i>Alloteuthis</i> sp              | 0.0   | 3.9                            | 0.1   | 0.1   | 0.1   | 0.1   | 0.1  | 0.1   | 0.1   | 0.1   | 0.1  | 0.1   | 0.1   | 0.1   | 0.1   | 0.1   | 0.1   | 0.1   | 0.3  | 0.3   | 0.3   | 0.3   | 0.3   | 0.3   | 0.3   |
| <i>Callionymus</i> sp              | 0.1   | 5.2                            | 0.1   | 0.1   | 0.1   | 0.2   | 0.2  | 0.2   | 0.2   | 0.2   | 0.2  | 0.2   | 0.2   | 0.2   | 0.2   | 0.2   | 0.2   | 0.2   | 0.7  | 0.7   | 0.7   | 0.4   | 0.3   | 0.6   | 0.7   |
| <i>Taurulus bubalis</i>            | 0.3   | 4.2                            | 0.4   | 0.5   | 0.5   | 0.7   | 0.7  | 0.7   | 0.8   | 0.7   | 0.8  | 0.8   | 0.8   | 0.8   | 0.8   | 0.8   | 0.8   | 2.4   | 2.3  | 1.4   | 1.1   | 1.9   | 2.4   | 2.2   | 2.0   |
| <i>Atherina presbyter</i>          | 0.3   | 7.3                            | 0.4   | 0.5   | 0.5   | 0.7   | 0.7  | 0.7   | 0.8   | 0.8   | 0.8  | 0.8   | 0.8   | 0.8   | 0.8   | 0.8   | 2.5   | 2.4   | 1.5  | 1.1   | 2.0   | 2.5   | 2.3   | 2.1   | 2.1   |
| Undetermined cottidae              | 0.3   | 4.2                            | 0.4   | 0.6   | 0.6   | 0.8   | 0.8  | 0.8   | 0.9   | 0.9   | 0.9  | 0.9   | 0.9   | 0.9   | 0.9   | 0.9   | 2.8   | 2.7   | 1.7  | 1.2   | 2.3   | 2.8   | 2.6   | 2.3   | 2.3   |
| <i>Pleuronectes platessa</i>       | 0.5   | 5.8                            | 0.7   | 0.9   | 0.9   | 1.3   | 1.3  | 1.3   | 1.4   | 1.3   | 1.4  | 1.4   | 1.5   | 1.6   | 1.6   | 1.6   | 4.3   | 4.1   | 2.6  | 1.9   | 3.5   | 4.3   | 4.1   | 3.7   | 4.2   |
| Undetermined ammocetidae           | 0.6   | 5.3                            | 0.8   | 1.0   | 1.1   | 1.1   | 1.1  | 1.5   | 1.5   | 1.5   | 1.5  | 1.6   | 1.7   | 1.7   | 1.7   | 5.0   | 4.8   | 3.0   | 2.2  | 4.1   | 5.0   | 4.7   | 4.1   | 3.7   | 4.2   |
| Undetermined mugilidae             | 0.7   | 6.5                            | 1.0   | 1.3   | 1.3   | 1.8   | 1.8  | 1.8   | 1.8   | 1.9   | 1.9  | 2.0   | 2.0   | 2.0   | 2.1   | 6.1   | 5.9   | 3.7   | 2.7  | 5.0   | 6.1   | 5.8   | 5.2   | 5.2   | 5.2   |
| <i>Trachurus trachurus</i>         | 0.8   | 6.0                            | 1.1   | 1.4   | 1.5   | 1.5   | 1.9  | 2.0   | 2.0   | 2.1   | 2.1  | 2.1   | 2.1   | 2.1   | 2.1   | 6.7   | 6.4   | 4.1   | 3.0  | 5.4   | 6.7   | 6.2   | 5.7   | 5.7   | 5.7   |
| <i>S. scombrus</i>                 | 0.9   | 7.9                            | 1.2   | 1.6   | 1.6   | 2.2   | 2.3  | 2.2   | 2.4   | 2.3   | 2.4  | 2.4   | 2.4   | 2.4   | 2.4   | 7.5   | 7.2   | 4.6   | 3.4  | 6.2   | 7.5   | 7.1   | 6.4   | 6.4   | 6.4   |
| <i>Trisopterus</i> spp             | 1.0   | 4.9                            | 1.4   | 1.8   | 1.9   | 1.9   | 2.6  | 2.7   | 2.6   | 2.8   | 2.7  | 2.8   | 2.8   | 2.8   | 2.8   | 8.9   | 8.5   | 5.4   | 4.0  | 7.2   | 8.9   | 8.3   | 7.5   | 7.5   | 7.5   |
| <i>Belone belone</i>               | 1.1   | 6.2                            | 1.6   | 2.0   | 2.1   | 2.1   | 2.8  | 2.9   | 2.9   | 3.0   | 3.0  | 3.0   | 3.0   | 3.1   | 3.1   | 9.6   | 9.2   | 5.8   | 4.3  | 7.8   | 9.6   | 9.0   | 8.1   | 8.1   | 8.1   |
| <i>Loligo</i> spp                  | 1.4   | 4.7                            | 2.0   | 2.5   | 2.7   | 2.7   | 3.6  | 3.7   | 3.7   | 3.9   | 3.8  | 3.9   | 3.9   | 4.2   | 4.2   | 12.2  | 11.7  | 7.5   | 5.5  | 10.0  | 12.2  | 11.5  | 10.4  | 10.4  | 10.4  |
| <i>S. solea</i>                    | 2.3   | 5.0                            | 3.2   | 4.1   | 4.3   | 4.3   | 5.7  | 5.9   | 5.9   | 6.2   | 6.1  | 6.3   | 6.3   | 6.7   | 6.7   | 19.7  | 18.9  | 12.0  | 8.8  | 16.1  | 19.7  | 18.4  | 16.7  | 16.7  | 16.7  |
| Rockling                           | 2.6   | 5.5                            | 3.6   | 4.6   | 4.9   | 4.9   | 6.5  | 6.7   | 6.7   | 7.1   | 6.9  | 7.2   | 7.2   | 7.6   | 7.6   | 22.4  | 21.5  | 13.6  | 10.0   | 18.3  | 22.4  | 21.0  | 19.0  | 19.0  | 19.0  |
| <i>Pollachius</i> spp              | 3.7   | 4.2                            | 5.1   | 5.5   | 6.9   | 6.9   | 9.2  | 9.5   | 9.4   | 10.0  | 9.8  | 10.1  | 10.1  | 10.8  | 10.8  | 31.7  | 30.3  | 19.3  | 14.2   | 25.9  | 31.7  | 29.6  | 26.9  | 26.9  | 26.9  |
| <i>D. labrax</i>                   | 11.9  | 6.0                            | 16.4  | 20.9  | 22.0  | 22.1  | 29.5   | 30.2  | 30.2  | 32.0  | 31.3   | 32.4  | 32.3  | 34.5  | 34.5  | 101.1 | 96.9  | 61.6  | 45.2   | 82.6  | 101.2 | 94.7  | 85.9  | 85.9  | 85.9  |
| <i>Conger conger</i>               | 20.7  | 6.9                            | 28.5  | 36.3  | 38.3  | 38.4  | 51.3   | 52.6  | 52.5  | 55.6  | 54.5   | 56.3  | 56.3  | 60.0  | 60.0  | 175.9 | 168.6 | 107.1 | 78.7   | 143.8 | 176.0 | 164.8 | 149.4 | 149.4 | 149.4 |
| Labridae                           | 50.6  | 5.4                            | 69.7  | 88.9  | 93.7  | 94.0  | 125.6  | 128.8 | 128.5 | 136.1 | 133.3  | 137.9 | 137.7 | 146.8 | 146.8   | 430.7 | 412.8 | 262.2 | 192.6  | 351.9 | 430.8 | 403.4 | 365.7 | 365.7 | 365.7 |
| Total                              | 100.0 |                                | 137.7   | 175.6 | 185.0 | 185.7 | 248.0  | 254.4 | 253.7 | 268.9 | 263.3  | 272.3 | 272.0 | 290.0 | 290.0   | 850.5 | 815.2 | 517.8 | 380.3  | 695.0 | 850.8 | 796.7 | 722.2 | 722.2 | 722.2 |

The proportion of each prey species in the grey seal diet is expressed as a percentage of the reconstituted biomass from scat content analysis (%M, from Ridoux et al., 2007). Average energetic values of prey species (in kJ/g) were taken from Spitz et al. (2010). Average prey consumption (in kg per seal and per quarter of the year, Q1–Q4) were obtained from Sparling (2003) and Sparling and Smout (2003).





**Figure 4.** Confidence intervals around the prey consumption estimate, according to the source of uncertainty in the calculation. In each case, only one parameter is changed to assess the minimum and maximum consumption estimates, all other parameters remaining constant.

**Table 5.** Estimated total biomasses of prey consumed by grey seals in the Iroise Sea, per year quarter

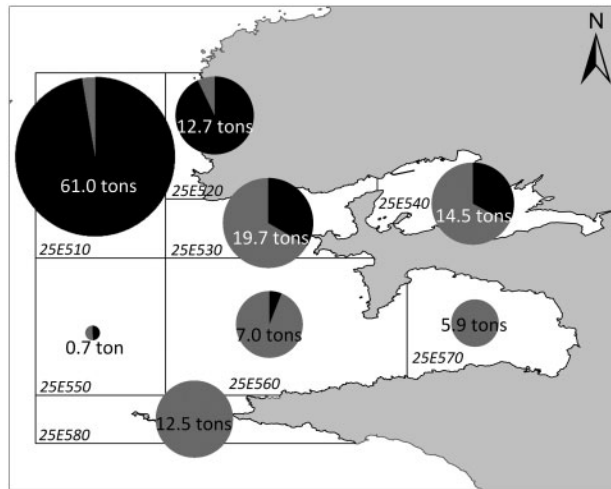
| Total prey consumption (seals) and landings (fisheries), in tons | Quarter 1 (Jan–Mar) | Quarter 2 (Apr–Jun) | Quarter 3 (Jul–Sept) | Quarter 4 (Oct–Dec) | Whole year   |
|--|---------------------|---------------------|----------------------|---------------------|--------------|
| Total prey consumption by seals                                  | 34.5                | 28.9                | 31.1                 | 20.1                | 114.6        |
| Total sea bass consumption by seals                              | 4.1                 | 3.4                 | 3.7                  | 2.4                 | 13.6         |
| Total landings of sea bass                                       | 26.4 ± 12.7         | 24.1 ± 12.0         | 19.1 ± 18.7          | 13.2 ± 7.6          | 82.8 ± 46.0  |
| Total pollack consumption by seals                               | 1.3                 | 1.1                 | 1.2                  | 0.7                 | 4.3          |
| Total landings of pollack  | 91.3 ± 44.4         | 68.9 ± 26.9         | 49.6 ± 19.3          | 35.8 ± 13.7         | 245.6 ± 91.1 |
| Total sole consumption by seals                                  | 0.8                 | 0.7                 | 0.7                  | 0.5                 | 2.7          |
| Total landings of sole   | 20.6 ± 9.2          | 10.3 ± 8.6          | 12.3 ± 4.1           | 8.9 ± 3.0           | 52.0 ± 19.5  |

Detailed seal consumption is given for the three main species targeted by fishermen and seals: sea bass, sole and pollack, for which average quarterly fishery landings are also reported (for the same years, 1999–2003).

### Grey seal foraging behaviour

Grey seal behaviour was inferred from dive shape, with square dives indicating foraging (Thompson *et al.*, 1991; Sjöberg and Ball, 2000; Goulet *et al.*, 2001; Austin *et al.*, 2006; Bowen *et al.*, 2006). U-shape dives, identified from the TAD index, were described as typical of this benthic forager, but they can also correspond to sleeping dives (Thompson *et al.*, 1991; Sjöberg *et al.*, 2000). The only way to distinguish the two, in our study where most dives were performed in the close vicinity of haulout sites and with poor location accuracy, was to check the swimming speed of the seal. Slow square dives would correspond to sleeping dives while faster dives would correspond to foraging (Thompson *et al.*, 1991; Lesage *et al.*, 1999; Sjöberg *et al.*, 2000). Our results showed that seals performed such U-shape dives not only during return trips from their haulout sites, but also during extended, linear travel trips across the Channel. Ratios of maximum dive depth over available bathymetry were not detailed in this article, due to the lack of accuracy of both Argos locations and the resolution of the available bathymetry data in the middle of the Channel. Many of these square dives however reached or exceeded 100 m, which corresponds to the know bottom depth in

this area. Thus it is likely that most of these square dives were indeed benthic dives. Grey seals dive continuously when they travel at sea, but their dive shape is usually thought to change from V-shape (for travelling) to U-shape (for foraging). It is therefore highly probable that at least some seals do forage during these travel trips between consecutive haulout sites. If this feeding behaviour might be opportunistic for some seals (Thompson *et al.*, 1991) and represent a small proportion of their foraging effort, we suggest that for other seals (like seal B03 in this study, spending most of its time hauled out the rest of the time) foraging along long distance travel trips might represent a significant foraging strategy. Most tracked seals however mainly foraged during return trips at a short distance from their haulout sites. The average maximum extent of these return trips was shorter than 30 km for all seals, and shorter than 15 km for ten of them (Table 3). This is particularly true in the Iroise Sea, where the 16 seals performed 68.5% of their overall foraging effort (as assessed from the percentage of foraging dives over the whole tracking time). Most studies on the species report longer distances for return trips between haulout and foraging areas, ranging 25–50 or 75 km on average (Hammond *et al.*, 1993; Sjöberg *et al.*, 1995;



**Figure 5.** Spatial and quantitative overlap between seal foraging effort and fisheries activities, within eight subareas included in ICES rectangle 25E5. For each sub-area, the total fish consumption is given in tons, representing the estimated seals' consumption added to the fisheries landings, while the graphs show the proportion of fish taken by the seals (in black) or the fishermen (in grey).

McConnell *et al.*, 1999; Sjöberg *et al.*, 2000; Harvey *et al.*, 2008). The shorter distance for the grey seals in the Iroise Sea might be due (i) to the low number of seals (reduced competition), (ii) the supposedly high prey availability in the area (Hily and Glemarec, 1999), (iii) the individual specialization of seals on different prey species in the area, likely due to the high diversity of prey (Hily and Glemarec, 1999; Ridoux *et al.*, 2007) or a combination of these hypotheses.

### Limitations in prey consumption estimate

This study combined a number of methods, each of them implying sources of bias and uncertainties in the overall estimate of the spatially explicit prey consumption of the seal colony. The main one, i.e. having the strongest impact on this calculation, came from the estimation of the total number of seals using the area seasonally. Similarly, Smith *et al.*, (2015) showed from sensitivity analyses that abundance estimates (of the predators) were the most influential parameter when estimating cetaceans annual consumption. A finer description of the prey consumption of the seal colony would therefore require a reduction of confidence intervals in the estimate of the total abundance.

The assumptions made in converting seasonal estimates of energy expenditure to seasonal EC may have introduced a degree of error in seasonal estimates of prey consumption given the uncertainty around the exact pattern of food intake throughout the year. However it is likely that expenditure and consumption are balanced at the scale of a year and therefore annual consumption estimates calculated in this way are both a reasonable reflection of overall consumption and a more precise estimation than generic energetic models classically used in such approaches.

In addition to the well-known limitations of faecal analysis (e.g. Pierce and Boyle, 1991), grey seal diet can vary seasonally according to prey availability (Hammond *et al.*, 1994; Beck *et al.*, 2007; Brown *et al.*, 2012). Our work is here mainly based on grey seal diet during the moulting period, i.e. quarter 1, and could not

take into account the potential seasonal variations in prey composition due to the lack of availability of faecal samples outside this period (Ridoux *et al.* 2007). However, the main prey species are common fish species found year-round in the Iroise Sea and the foraging trips are located close to their haulout sites year-round. In addition, although fishery landings did vary over the seasons (and years), none of the three main prey species disappeared from these statistics during either quarter, suggesting that these fish species were available to fishermen as well as seals year-round.

Sex and age differences were also shown in grey seals' foraging behaviour (Beck *et al.*, 2003a,b; Harvey *et al.*, 2008). Such a difference was not taken into account in the present study, because seal catches were biased towards males and the sample size was too small to assess both sex and age influences on location of the seasonal foraging areas. Although it is only possible to infer from the few adult female's tracking data that their foraging areas are not strikingly different from that of males, our analysis showed that in terms of prey consumption, the uncertainty due to the sex/age structure of the population had a limited consequence on the overall estimate.

We had to assume that the foraging effort was uniformly distributed in space over all prey species, i.e. that all identified prey were homogeneously distributed and caught by the seals within the identified foraging areas. This is obviously not true, as prey distribution is heterogeneous, depending on habitat type and predation risks. Unfortunately, no published or unpublished data is available to document this prey distribution in the Iroise Sea. This is especially difficult for fish species that are not targeted by fishermen, but constitute a significant proportion of grey seal diet (like the wrasse). We assume that this undocumented source of variation remains acceptable given the very localized foraging areas of the seals around the haulout sites.

### Comparison with fisheries landings

We estimated that during the study period (1998–2001), grey seals consumed 114.6 tons of fish per year. Most of this is covered by the consumption of sea wrasse (Labridae), the main grey seal prey in the Iroise Sea, but it also includes commercially valued fish species. Among all grey seal prey, the main species also targeted by fishermen are the pollack, sole, and sea bass. These species account for 3.7, 2.3, and 11.9% (by mass) of the grey seal diet in the Iroise Sea respectively (Ridoux *et al.*, 2007). Assuming the diet shows little variation in the seasons, we estimated that grey seals consumed 13.6 tons of sea bass, 4.3 tons of pollack and 2.7 tons of sole annually. Within the four ICES rectangles where grey seals foraged (26E4, 26E5, 25E4, and 25E5), this seal consumption represented, at maximum, 5.2% of sole, 1.8% of pollack, and 16.4% of sea bass weight landed by fishermen during the same years. The overlap in species was therefore stronger for sole and sea bass, two species with a higher commercial value than pollack. Within the four ICES rectangles where grey seals foraged, overlap between seals and fisheries was greater in rectangle 25E5 (72.7% of all foraging dives), where grey seals haul out, and to a lesser extent in rectangles 25E4 (11.7%), 26E5 (10.8%), and 26E4 (4.8%). In ICES rectangle 25E5, seal predation on sea bass is estimated to reach 9.9 tons per year, i.e. 19.4% of the 50.9 tons per year landed by professional fishermen in the same area. A description of the overlap between seals' foraging behaviour and sea bass consumption and fisheries' take on the same species within

rectangle 25E5 showed that the main feeding grounds for grey seals were located around their haulout sites, in sub-areas that are not important fishing grounds for fishermen, but in sub-areas 25E530 and 25E540 where fishermen took on average 13 and 10 tons of sea bass annually, the estimated seals' consumption represented half of their take. French landings of sea bass were here certainly underestimated and particularly for small-scale inshore fisheries (ICES, 2014). Furthermore, recreational catches of sea bass accounted for a significant part of the overall catch in the study area (Rocklin *et al.*, 2014), hence the overlap estimated in the present study between seals and man was probably overestimated. In the Celtic seas, ICES advised nevertheless in 2013 that sea bass adult stock size was too low and fishing pressure was too high to ensure an optimal use in the long term. Sole adult stock size on the other hand was large enough to ensure an optimal use in the long term, while pollack adult stock size and fishing pressure were unknown (ICES, 2013). Further steps should focus on the impact of additional mortality seal predation on the sea bass stock dynamic in this area.

Although competition for prey between seals and fisheries has received much attention over the last decades (e.g. Harwood and Greenwood, 1985; NAMMCO, 1996; Chouinard *et al.*, 2005; Jounela *et al.*, 2006; Cronin *et al.*, 2012; Oksanen *et al.*, 2014), few studies have quantitatively and spatially assessed the comparison of prey consumption by both predators over the same maritime areas. Matthiopoulos *et al.* (2008) and Smout *et al.* (2014) modelled the prey consumption by grey seals at a large geographical scale, around the United Kingdom. They highlighted the ecological parameters influencing the predator-prey relationships and the consequences for the management of seal-fisheries interactions, including variations in predation related to prey availability, predators' population dynamics, spatial heterogeneity and multi-species interactions. At a smaller geographical scale, Børge *et al.* (2002) compared harbour seals' prey consumption (based on energy requirement and diet analysis) to fisheries landings in an area covering 100–150 km<sup>2</sup>. They estimated that harbour seals consumed 32.1 tons of fish in the area where fisheries occur, representing 157% and 79% of fish biomass landed by the fishermen. This estimate was conducted in a much smaller area than in our study (4100 km<sup>2</sup> per ICES rectangle) and was based on a different seal species, but it highlights the potentially high ecological interactions between seals and fisheries in coastal areas.

## Conclusions

This study is based on grey seals' foraging behaviour and fisheries data that date back from 1999–2003, at a time when the marine national park of the Iroise Sea was under settlement. Our aim is to describe the overlap between the two consumers before the implementation of management rules by the marine park, drawing a reference line for future assessment. The combination of telemetry (for the identification of foraging areas), censuses and photo ID (for the assessment of seal numbers and sex/age structure) as well as faecal analysis (for the assessment of diet) proved to be a powerful tool to inform local managers about ecological interactions between grey seals and fisheries.

In the context of increasing seal numbers in this MPA (Vincent *et al.*, 2005), revised quantitative estimation of prey consumption by the seal colony should be periodically assessed. This updated assessment should use more accurate location data, like Fastloc GPS (Dujon *et al.*, 2014) in order to identify foraging areas at a finer geographical scale, given the short distance of the

seals' return trips within the Iroise Sea. Seasonal variations in grey seal diet or distribution of prey availability also need to be identified, while new estimates of total seal abundance would greatly improve the accuracy of the estimate.

## Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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## Literature Cited

- Alban, F., and Boncoeur, J. 2004. An assessment of the potential interest of fishermen in boat-chartering in the context of a marine park: the case of the Iroise Sea, western Brittany, France. *In* Contesting the foreshore - Tourism, society, and politics on the coast. Ed. by J. Boissevain and T. Selwyn. Amsterdam University Press, Amsterdam, pp. 185–203.
- Austin, D., Bowen, D., McMillan, J., and Iverson, S. 2006. Linking movement, diving, and habitat to foraging success in a large marine predator. *Ecology*, 87: 3095–3108.
- Baraff, L., and Loughlin, T. 2000. Trends and potential interactions between Pinnipeds and fisheries of New England and the US west coast. *Marine Fisheries Review*, 62: 1–39.
- Beck, C., Bowen, D., McMillan, J., and Iverson, S. 2003. Sex differences in diving at multiple temporal scales in a size-dimorphic capital breeder. *Journal of Animal Ecology*, 72: 979–993.
- Beck, C., Bowen, W., McMillan, J., and Iverson, S. 2003. Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. *Animal Behavior*, 66: 777–789.
- Beck, C., Iverson, S., Bowen, D. W., and Blanchard, W. 2007. Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. *Journal of Animal Ecology*, 76: 490–502.
- Bjørge, A., Bekkby, T., Bakkestuen, V., and Framstad, E. 2002. Interactions between harbour seals, *Phoca vitulina*, and fisheries in complex coastal waters explored by combined Geographic Information System (GIS) and energetics modelling. *ICES Journal of Marine Science*, 59: 29–42.
- Bowen, W. 1997. Role of marine mammals in aquatic ecosystems. *Marine Ecological Progress Series*, 158: 267–274.
- Bowen, D.W., Beck, C.A., Iverson, S.J., Austin, D., McMillan, J.I. 2006. Linking predator foraging behaviour and diet with variability in continental shelf ecosystems: grey seals of eastern Canada. *In* Top predators in marine ecosystems Ed. By I.L. Boyd, S.

- Wanless, and C.J. Camphuysen. Cambridge University Press, Cambridge, pp. 63–81.
- Breed, G., Costa, D., Goebel, M., and Robinson, P. 2011. Electronic tracking tag programming is critical to data collection for behavioral time-series analysis. *Ecosphere*, 2: 1–11.
- Brown, S., Bearhop, S., Harrod, C., and McDonald, R. 2012. A review of spatial and temporal variation in grey and common seal diet in the United Kingdom and Ireland. *Journal of Marine Biology Association, U.K.*, 92: 1711–1722.
- Chouinard, G., Swain, D., Hammill, M., and Poirier, G. 2005. Covariation between grey seal (*Halichoerus grypus*) abundance and natural mortality of cod (*Gadus morhua*) in the southern gulf of St Lawrence. *Canadian Journal of Fisheries and Aquatic Science*, 62: 1991–2000.
- Christensen, V., Guénette, S., Heymans, J., Walters, C., Watson, R., Zeller, D., and Pauly, D. 2003. Hundred-year decline of North Atlantic predatory fishes. *Fish and Fisheries*, 4: 1–24.
- Cronin, M. A., Zuur, A. F., Rogan, E., and McConnell, B. J. 2009. Using mobile phone telemetry to investigate the haul-out behavior of harbor seals *Phoca vitulina vitulina*. *Endangered Species Research*, 10: 255–267.
- Cronin, M. A., Gerritsen, H. D., and Reid, D. G. 2012. Evidence of low spatial overlap between grey seals and a specific whitefish fishery off the west coast of Ireland. *Biological Conservation*, 150: 136–142.
- Cunningham, L., Baxter, J., Boyd, I., Duck, C., Lonergan, M., Moss, S., and McConnell, B. 2009. Harbour seal movements and haul-out patterns: implications for monitoring and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 19: 398–407.
- Dujon, A., Lindstrom, R. T., and Hays, G. C. 2014. The accuracy of Fastloc-GPS locations and implications for animal tracking. *Methods in Ecology and Evolution*, 5: 1162–1169.
- Fedak, M., and Anderson, S. 1987. Estimating the energy requirements of seals from weight changes. *In: Marine Mammal Energetics*. Ed. by A. Huntley, D. Costa, G. Worthy, and M. Castellini. Allen Press, Lawrence, pp. 205–226.
- Fedak, M. A., Lovell, P., and Grant, S. M. 2001. Two approaches to compressing and interpreting time-depth information as collected by time-depth recorders and satellite-linked recorders. *Marine Mammal Science*, 17: 94–110.
- Gerondeau, M., Barbraud, C., Ridoux, V., and Vincent, C. 2007. Abundance estimate and seasonal patterns of grey seal (*Halichoerus grypus*) occurrence in Brittany, France, as assessed by photo-identification and capture-mark-recapture. *Journal of Marine Biological Association, UK*, 87: 365–372.
- Goldsworthy, S., Bulman C., He X., Larcome J. and Littan C. 2003. Trophic interactions between marine mammals and Australian fisheries: An ecosystem approach. *In: Marine Mammals - Fisheries, Tourism and Management Issues*. Ed. by N. Gales, M. Hindell, and R. Kirkwood. CSIRO Publishing, Collingwood, Victoria, Australia, pp. 62–69.
- Goulet, A. M., Hammill, M., and Barrette, C. 2001. Movements and diving of grey seal females (*Halichoerus grypus*) in the Gulf of St. Lawrence, Canada. *Polar Biology*, 24: 432–439.
- Hamilton, E. 1983. Seals and science vs seals and culls. *Marine Pollution Bulletin*, 14: 37–38.
- Hammond, P., McConnell, B., and Fedak, M. A. 1993. Grey seals off the east coast of Britain: distribution and movements at sea. *Symposium of the Zoological Society of London*, 66: 211–224.
- Hammond, P. S., Hall, A. J., and Prime, J. H. 1994. The diet of grey seals around Orkney and other island and mainland sites in north-eastern Scotland. *Journal of Applied Ecology*, 31: 340–350.
- Härkönen, T., Brasseur, S., Teilmann, J., Vincent, C., Dietz, R., Abt, K., and Reijnders, P. 2007. Status of grey seals along mainland Europe from the Southwestern Baltic to France. *NAMMCO Scientific Publications*, 6: 57–68.
- Harvey, J., Côté, S., and Hammill, M. 2008. The ecology of 3-D space use in a sexually dimorphic mammal. *Ecography*, 31: 371–380.
- Harwood, J. and Greenwood J. 1985. Competition between British grey seals and fisheries. *In Marine Mammals and Fisheries*. Ed. by J. Beddington R. Beverton, and D. Lavigne. George Allen & Unwin, London, pp. 153–169.
- Haug, T., Hammill, M., and Olafsdottir, D. 2007. Grey seals in the North Atlantic and the Baltic. *Nammco Scientific Publications*, 6: 227.
- Hily, C. and Glemarec, M. 1999. Environnement naturel de l'Iroise – Bilan des connaissances et intérêt patrimonial. Rapport d'étude DIREN Bretagne/Université de Bretagne Occidentale, 83 PP. *In French*
- ICES. 2013. Report of the ICES Advisory Committee 2013. ICES Advice, 2013. Book 5. p. 416.
- ICES. 2014. Report of the Inter-Benchmark Protocol for Sea Bass in the Irish Sea, Celtic Sea, English Channel and Southern North Sea (IBP Bass), 1 January–30 April 2014, By correspondence. ICES CM 2014/ACOM:45. pp. 218.
- Jounela, P., Suuronen, P., Millar, R., and Koljonen, M. L. 2006. Interactions between grey seal (*Halichoerus grypus*), Atlantic salmon (*Salmo salar*), and harvest controls on the salmon fishery in the Gulf of Botnia. *ICES Journal of Marine Science*, 63: 936–945.
- Königson, S., Fjälling, A., Fjälling, A., and Lunneryd, S. 2007. Grey seal induced catch losses in the herring gillnet fisheries in the northern Baltic. *NAMMCO Scientific Publications*, 6: 203–213.
- Leeper, R., Lavigne, D., Corkeron, P., and Johnston, D. 2010. Towards a precautionary approach to managing Canada's commercial harp seal hunt. *ICES Journal of Marine Science*, 67: 316–320.
- Lesage, V., Hammill, M., and Kovacs, K. 1999. Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology*, 77: 74–87.
- Lowry, L., Laist, D., Gilmartin, W., and Antonelis, G. 2011. Recovery of the hawaiian monk seal (*Monachus schauinslandi*): a review of conservation efforts, 1972 to 2010, and thoughts for the future. *Aquatic Mammals*, 37: 397–419.
- Matthiopoulos, J., Smout, S., Winship, A. J., Thompson, D., Boyd, I. L., and Harwood, J. 2008. Getting beneath the surface of marine mammal – fisheries competition. *Mammal Review*, 38: 167–188.
- McConnell, B., Chambers, C., and Fedak, M. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the southern ocean. *Antarctic Science*, 4: 393–398.
- McConnell, B. J., Fedak, M. A., Lovell, P., and Hammond, P. S. 1999. Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology*, 36: 573–590.
- Muller, H., Blanck, B., Dumas, F., Lekien, F., and Mariette, V. 2009. Estimating the Lagrangian residual circulation in the Iroise Sea. *Journal of Marine Systems*, 78: 517–536.
- Myers, A., Lovell, P., and Hays, G. 2006. Tools for studying animal behaviour: validation of dive profiles relayed via the Argos satellite system. *Animal Behaviour*, 71: 989–993.
- NAMMCO 1996. Report of the scientific committee ad hoc working group on grey seals. NAMMCO. NAMMCO, Tromso, Norway, pp. 97–178.
- Oksanen, S., Ahola, M., Lehtonen, E., and Kunasranta, M. 2014. Using movement data of Baltic grey seals to examine foraging-site fidelity: implications for seal–fishery conflict mitigation. *Marine Ecological Progress Series*, 507: 297–308.
- Photopoulou, T., Fedak, M. A., Matthiopoulos, J., McConnell, B. J., and Lovell, P. 2015a. The generalized data management and collection protocol for Conductivity-Temperature-Depth Satellite Relay Data Loggers. *Animal Biotelemetry*, 3: 1–11.
- Photopoulou, T., Lovell, P., Fedak, M. A., Thomas, L., and Matthiopoulos, J. 2015b. Efficient abstracting of dive profiles

- using a broken-stick model. *Methods in Ecology and Evolution*, 6: 278–288.
- Pierce, G., and Boyle, P. 1991. A review of methods for diet analysis in piscivorous marine mammals. *Oceanographic Marine Biology Annual Review*, 29: 409–486.
- Ridou, V., Spitz, J., Vincent, C., and Waltion, M. J. 2007. Grey seal diet at the southern limit of its European distribution: combining dietary analyses and fatty acid profiles. *Journal of Marine Biological Association, UK*, 87: 255–264.
- Rocklin, D., Levrel, H., Drogou, M., Herfaut, J., and Veron, G. 2014. Combining Telephone Surveys and Fishing Catches Self-Report: The French Sea Bass Recreational Fishery Assessment. *PLoS One*, 9: e87271. doi:10.1371/journal.pone.0087271.
- Sjöberg, M., Fedak, M., and McConnell, B. J. 1995. Movements and diurnal behaviour patterns in a baltic grey seal (*Halichoerus grypus*). *Polar Biology*, 15: 593–595.
- Sjöberg, M., and Ball, J. 2000. Grey seal, *Halichoerus grypus*, habitat selection around haulout sites in the Baltic Sea: bathymetry or central-place foraging? *Canadian Journal of Zoology*, 78: 1661–1667.
- Smith, L., Link, J., Cadrin, S., and Palka, D. 2015. Consumption by marine mammals on the Northeast US continental shelf. *Ecological Applications*, 25: 373–389.
- Smout, S., Rindorf, A., Hammond, P., Harwood, J., and Matthiopoulos, J. 2014. Modelling prey consumption and switching by UK grey seals. *ICES Journal of Marine Science*, 71: 71–89.
- Sparling, C.E. 2003. Causes and consequences of variation in the energy expenditure in grey seals (*Halichoerus grypus*). PhD thesis, University of St Andrews, UK. p 257.
- Sparling, C.E., and Smout, S.C. 2003. Population energy budget for UK North Sea grey seals. SCOS Briefing paper 03/9. SCOS Advice 2003, SMRU. [http://soi.st-andrews.ac.uk/documents/SCOS\\_03\\_v7.pdf](http://soi.st-andrews.ac.uk/documents/SCOS_03_v7.pdf)
- Speakman, J. R. 2000. The cost of living: field metabolic rates of small mammals. *Advances in Ecological Research*, 30: 177–297.
- Spitz, J., Mouroucq, E., Schoen, V., and Ridoux, V. 2010. Proximate composition and energy content of forage species from the bay of Biscay: high- or low-quality food? *ICES Journal of Marine Science*, 67: 909–915.
- Summers, C. 1978. Trends in the size of British grey seal populations. *Journal of Applied Ecology*, 15: 395–400.
- Thompson, D., Hammond, P. S., Nicholas, K. S., and Fedak, M. A. 1991. Movements, diving and foraging behavior of grey seals. *Journal of Zoology, London*, 224: 223–232.
- Trzcinski, M., Mohn, R., and Bowen, W. 2006. Continued decline of an Atlantic cod population: how important is gray seal predation? *Ecological Applications*, 16: 2276–2292.
- Vincent, C., Meynier, L., and Ridoux, V. 2001. Photo-identification in grey seals: legibility and stability of natural markings. *Mammalia*, 65: 363–372.
- Vincent, C., McConnell, B. J., Ridoux, V., and Fedak, M. A. 2002. Assessment of Argos location accuracy from satellite tags deployed on captive grey seals. *Marine Mammal Science*, 18: 156–166.
- Vincent, C., Fedak, M. A., McConnell, B. J., Meynier, L., Saint-Jean, C., and Ridoux, V. 2005. Status and conservation of the grey seal, *Halichoerus grypus*, in France. *Biological Conservation*, 126: 62–73.
- Walpole, M., and Leader-Williams, N. 2002. Tourism and flagship species in conservation. *Biodiversity and Conservation*, 11: 543–547.
- Wilson, S. C., Mo, G., and Sipila, T. 2001. Legal protection for seals in small populations in European Community and Mediterranean coastal waters. *Mammalia*, 65: 335–348.
- Zacharias, M., and Roff, J. 2001. Use of focal species in marine conservation and management: a review and critique. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 11: 59–76.

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