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# Scientific observation program around Kerguelen Island, a ship-of-opportunity for bird and mammal data collection

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#### Abstract

Fishing activities targeting Patagonian toothfish (*Dissostichus eleginoides*) are conducted year round on the edge of the Kerguelen plateau. Since the early 2000s, scientific observers on board have been asked to collect data on both seabird and marine mammal abundances using standard protocols. Data collection is constrained in space (fishing activities occur only between 500 and 2 000 m depth) and time (effort declines in winter when quotas are caught and in February due to fishery closure) but represents the most important dataset of observations at sea in this area. Sixteen taxa of marine mammals and 37 taxa of birds were observed during the 2001–2017 period. This study provides the first insights on the spatio–temporal patterns of occurrence of some of these species. It also highlights the potential for data to be collected by fishing vessels targeting Patagonian toothfish used as ships of opportunity to investigate trends and distribution of seabirds and marine mammals in remote and difficult-to-access areas of the Southern Ocean.

# Programme d'observation scientifique autour des îles Kerguelen : plateforme d'opportunité pour la collecte de données sur les oiseaux et les mammifères

#### Résumé

Une activité de pêche ciblant la légine australe (*Dissostichus eleginoides*) est conduite toute l'année sur le bord du plateau de Kerguelen. Des observateurs scientifiques sont embarqués depuis le début des années 2000 et collectent des données d'abondance sur les oiseaux marins et les mammifères selon des protocoles standardisés. La collecte des données est contrainte dans l'espace (les activités de pêche occupent la frange de 500 à 2 000 mètres de fond) et dans le temps (l'effort diminue en hiver quand les quotas sont pris et en février quand la pêche est fermée) mais représente le jeu de données d'observations en mer le plus important pour cette zone. Seize taxons de mammifères marins et 37 taxons d'oiseaux marins ont été observés pendant la période 2001–2017. Cette étude fournit un premier aperçu des variations spatio-temporelles des occurrences pour certaines espèces. Elle souligne aussi le potentiel des données collectées à partir des navires de pêche ciblant la légine australe utilisés comme plateformes opportunistes pour étudier les tendances et les distributions d'oiseaux et mammifères marins dans des lieux reculés et difficiles d'accès de l'océan Austral.

Keywords: seabirds, marine mammals, Kerguelen, French EEZ, Southern Ocean, distribution.

KERGUELEN PLATEA

### Introduction

Observations at-sea, namely vessel-based data collection, have been for a long period of time the only way of getting data on the distribution of seabirds and marine mammals (Stahl, 1982, 1987; Péron et al., 2010). Vessel-based observations formed the basis of our knowledge on species distribution, more information was then added thanks to biologging (Péron et al., 2010; De Broyer et al., 2014; Delord et al., 2013) but remains limited by a minimum size for birds to be equipped and the access to the colonies.

A commercial longline fishery targeting Patagonian toothfish (Dissostichus eleginoides) has operated within the French exclusive economic zone (EEZ) of Kerguelen (south Indian Ocean) since the late 1990s. Seven fishing vessels operate year round, except around February when the fishery is closed in order to avoid seabird incidental by-catch (the starting date of the closure has changed slightly over time which explains why there are some data for this month). The fishing season starts on 1 September, thus activity declines in July and August toward the end of the season when quotas have been caught. Fishing effort is spatially distributed quite evenly between seasons. An average of three to four demersal longlines is deployed per day between 500 and 2 200 m depth. Fishing is prohibited in water <500 m deep to protect juvenile fish, which constrains observations to the edge of the plateau. Fishing effort is around 20 million hooks and 900 fishing days per year. For management purposes, fishery observers employed by the Terres Australes et Antarctiques Françaises (TAAF) administration observe all fishing operations. A scientific observation program is run by the Museum National d'Histoire Naturelle (MNHN). Amongst their numerous tasks (Gasco, 2011), since the early 2000s, observers have been asked to assess bird and marine mammal abundances. Many species are attracted by fishing activities, they are able to actively search, follow and interact with the boat (Barbraud et al., 2008, 2009; Collet et al., 2017; Tixier et al., 2010, 2014) facilitating observations. Other species are not attracted, thus are only observed opportunistically. This paper summarises the long-term observation data collected from fishing vessels used as ships of opportunity.

#### Material and methods

Scientific observers received training courses provided by the MNHN on species identification and counting methods, including the provision of identification materials (Gasco et al., 2015) and a self-training tool to help memorise bird names (Gasco and Martin, 2016). At the end of their first trip, when possible, their identification performance was tested during their debriefing by using a picture slide show and asking them to identify the different species of birds.

Line hauling occurred mainly during the day at low speed (2.5 knots), allowing birds and mammals attending the vessel to be observed easily; observers were asked to:

- (i) count and identify all visible birds to genus or species, in a 360° arc around the vessel, in day light, once per day at the end of the afternoon, only during hauling of the line. Those observations last 10 minutes and are conducted from outside by walking around the upper deck of the vessel
- (ii) collect data on presence of seals, killer whale
   (Orcinus orca) and sperm whale (Physeter macrocephalus) during hauling of each set, if light and weather conditions allowed
- (iii) collect observations opportunistically on other cetacean species
- (iv) photograph cetaceans (Gasco et al., 2013, 2016).

Data were stored at the museum in the 'Pecheker' data base (Martin and Pruvost, 2007). Protocols are considered to have been stable and robust since 2001 for birds and 2003 for marine mammals.

Photographs of cetaceans were used to complete the main dataset (when identification could not be made at sea) and to confirm identification of less common species. The results of the bird identification tests, when available, were used to assess observers' skills for each species, if an observer failed to identify at least 75% of the representation for a species, then data for this species were excluded, overall 22.7% of the data collected were excluded through this method to increase data quality. One observation for birds corresponds to the number of individuals counted around the vessel on a daily basis, one observation for marine mammals corresponds to the number of individuals detected around the ship during the hauling of one line. Marine mammal and bird observations were pooled on a  $0.2^{\circ}$  spatial grid basis and were weighted by the number of observations made in each cell, only cells with a minimum of 20 observations were taken into account for mammals and a minimum of five for birds.

Some species are difficult to tell apart at sea and were grouped together:

- (i) *Diomedea epomophora / sanfordi* correspond to *D. epomophora* and *D. sanfordi*
- (ii) Thalassarche cauta sensu lato correspond to T. cauta cauta and T. cauta steadi
- (iii) *Pachyptila* spp. correspond to unidentified species of prions
- (iv) *Arctocephalus* spp. correspond mostly to *A. gazella* but some might have been *A. tropicalis*
- (v) *Eudyptes* spp. correspond to *E. chrysolophus* and *E. chrysocome filholi*
- (vi) Sterna spp. correspond to unidentified terns.

Some species can be told apart only at short distance and were grouped when observed at longer distance:

- (i) *Macronectes* spp. correspond to *M. halli* and *M. giganteus*
- (ii) unidentified storm petrels correspond to *Fregetta tropica* and *Oceanites oceanicus*
- (iii) *Phoebetria* sp. correspond to *P. palpebrata* and *P. fusca*.

Lastly, the rare species were included only if pictures were available to confirm identification.

# Results

Since 2003, 33 571 observations were conducted for marine mammals. Observers counted 98 357 individuals of 16 taxa (Table 1). Four taxa, fur seals (*Arctocephalus* spp.), long-finned pilot whales (*Globicephala melas*), hourglass dolphins (*Lagenorhynchus cruciger*) and sperm whales made up 98.4% of mammals observed.

From 2003 to 2016 observers counted 7 214 256 birds of 37 taxa (Table 2).

Nine taxa accounted for 99.4% of the bird observations: wandering albatross (*Diomedea exulans*), grey-headed albatross (*Thalassarche chrysostoma*), black-browed albatross (*Thalassarche melanophris*), Cape petrel (*Daption capense*), giant petrels (*Macronectes* spp.), storm petrels (Oceanitidae), white-chinned petrel (*Procellaria aequinoctialis*) and grey petrel (*Procellaria cinerea*). Some species were very rarely observed, for example southern bottlenose whale (*Hyperoodon planifrons*), Buller's albatross (*Thalassarche bulleri*), spectacled petrel (*Procellaria conspicillata*) and snow petrel (*Pagodroma nivea*).

### Mammals

Main species of marine mammals developed in this document are illustrated in Figure 1.

Fur seals were most abundant off the eastern and southern sides of the island and also in a small spot in the north between 46.5–47.5°S and 70–70.5°E (Figure 2a). Numbers per observation declined over the study period (Figure 2b). Fur seals were most abundant from June to November (Figure 2c).

Long-finned pilot whales were mostly observed along the western edge of the plateau (Figure 3a). The number of individuals per observation were higher in 2010 and 2011 and have been low since 2012 (Figure 3b).

Hourglass dolphins were observed in different locations in the north and the east of the plateau with no clear trend (Figure 4a). Observations increased gradually to reach a maximum in 2009 and then decreased rapidly to remain at low levels until 2017 (Figure 4b). This species is observed more frequently during the first half of the year (Figure 4c).

Killer whales were mostly observed on the western part of the plateau's edge (Figure 5a). No trend was observed between years; there were no observations in some years (Figure 5b). Observations per month show no clear trend (Figure 5c).

| Order, sub-order, family | Taxa                                     | Total  |
|--------------------------|------------------------------------------|--------|
| Cetacea                  |                                          |        |
| Mysticeti                |                                          |        |
| Balaenidae               |                                          |        |
|                          | Eubalaena australis                      | 3      |
| Balaenopteridae          |                                          |        |
|                          | Balaenoptera bonaerensis                 | 30     |
|                          | Balaenoptera musculus                    | 4      |
|                          | Balaenoptera physalus                    | 8      |
|                          | Megaptera novaeangliae                   | 17     |
|                          | unidentified baleen whales               | 72     |
| Odontoceti               |                                          |        |
| Physeteridae             |                                          |        |
|                          | Physeter macrocephalus                   | 35 031 |
| Ziphiidae                |                                          |        |
|                          | Hyperoodon planifrons                    | 6      |
| Delphinidae              |                                          |        |
|                          | Cephalorhynchus commersonii kerguelensis | 197    |
|                          | Globicephala melas                       | 11 599 |
|                          | Lagenorhynchus cruciger                  | 1 813  |
|                          | Lissodelphis peronii                     | 825    |
|                          | Orcinus orca                             | 328    |
| Carnivora                |                                          |        |
| Caniformia               |                                          |        |
| Phocidae                 |                                          |        |
|                          | Hydrurga leptonyx                        | 18     |
|                          | Mirounga leonina                         | 6      |
| Otariidae                |                                          |        |
|                          | Arctocephalus spp.                       | 46 368 |

# Table 1:Number of individuals of marine mammals sighted per species from 2003<br/>to 2017.

| Order         | Family     | Taxa                          | Total         |
|---------------|------------|-------------------------------|---------------|
| Charadrii     | formes     |                               |               |
|               | Stercorar  | iidae                         |               |
|               |            | Catharacta lönnbergi          | 230           |
|               |            | Catharacta maccormicki        | 28            |
|               | Laridae    | ~                             | • • •         |
| <b>D</b> 11 1 |            | Sterna spp.                   | 260           |
| Procellari    | itormes    | 1                             |               |
|               | Diomeder   |                               | 4 410         |
|               |            | Diomedea epomophora/sanfordi  | 4 412         |
|               |            | Diomedea exulans              | 515 200       |
|               |            | Phoebetria fusca              | 176           |
|               |            | Phoebetria palpebrata         | 1 999         |
|               |            | <i>Phoebetria</i> sp.         | 275           |
|               |            | Thalassarche bulleri          | 500           |
|               |            | Thalassarche cauta sensu lato | 505           |
|               |            | Thalassarche chlororhynchos   | 395           |
|               |            | Thalassarche chrysostoma      | 89 049        |
|               |            | Thalassarche melanophris      | 1 031 067     |
|               | o :::      | Thalassarche salvini          | 30            |
|               | Oceanitid  | ae                            | (7.4)         |
|               |            | Fregetta tropica              | 67 616        |
|               |            | Oceanites oceanicus           | 251 351       |
|               | D 11 '     | Unidentified storm petrels    | 136 111       |
|               | Procellari | idae                          | 1 0 0 0 ( 4 0 |
|               |            | Daption capense               | 1 238 643     |
|               |            | Fulmarus glacialoides         | 1 902         |
|               |            | Halobaena caerulea            | 4 160         |
|               |            | Aphrodroma brevirostris       | 2             |
|               |            | Macronectes giganteus         | 11 447        |
|               |            | Macronectes halli             | 399 651       |
|               |            | Macronectes spp.              | 2 423 763     |
|               |            | Pachyptila spp.               | 26419         |
|               |            | Pagodroma nivea               | 004.54        |
|               |            | Procellaria aequinoctialis    | 934 761       |
|               |            | Procellaria cinerea           | 73 828        |
|               |            | Procellaria conspicillata     | 2.77          |
|               |            | Pterodroma macroptera         | 373           |
|               |            | Pterodroma mollis             | 7             |
|               |            | Puffinus gravis               | 2             |
| a 1 · ·       | C          | Thalassoica antarctica        | 167           |
| Sphenisci     | tomes      | 1                             |               |
|               | Sphenisci  | dae                           |               |
|               |            | <i>Eudyptes</i> spp.          | 102           |
|               |            | Aptenodytes patagonicus       | 35            |
|               |            | Pygoscelis papua              | 237           |
|               |            | unidentified penguins         | 50            |

Table 2: Number of seabirds counted per species for the 2001–2016 period.



Figure 1: (a) fur seal (*Arctocephalus* spp.), (b) long-finned pilot whales (*Globicephala melas*), (c) hourglass dolphin (*Lagenorhynchus cruciger*), (d) killer whale (*Orcinus orca*), and (e) sperm whale (*Physeter macrocephalus*).



Figure 2: Abundance of fur seals (*Arctocephalus* spp.): (a) around the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per 0.2° size grid cell and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.



Figure 3: Distribution of long-finned pilot whales (*Globicephala melas*): (a) within the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per 0.2° size grid cell and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.



Figure 4: Distribution of hourglass dolphins (*Lagenorhynchus cruciger*): (a) around the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per 0.2° size grid cell and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.



Figure 5: Distribution of orcas (*Orcinus orca*): (a) around the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per  $0.2^{\circ}$  size grid cell and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.

Sperm whales were observed all around the plateau with higher densities in the northeast of the island, and lower densities in the south and southeast of the area (Figure 6a). Numbers have remained stable since 2003 (Figure 6b), and fewer were observed during mid-winter (Figure 6c).

#### Seabirds

Main species of seabirds developed in this document are illustrated in Figure 7.

Cape petrels were observed in larger numbers in the south of the plateau than in the north (Figure 8a), the average number of birds per observation varied between years with no clear trends (Figure 8b), this species was clearly observed in greater numbers from June to November (Figure 8c).

Wandering albatrosses were observed in greater numbers in the northwestern part of the area (Figure 9a). Average number of individuals increased from 2001 to 2007 to reach 40 individuals per observation and then decreased to around 20 and remained quite constant after that (Figure 9b). Number of individuals per observation were lower during winter months (Figure 9c).

Storm petrels were mostly encountered in the northern part of the study area (Figure 10a). The number of individuals per observation was quite



Figure 6: Distribution of sperm whales (Physeter macrocephalus): (a) around the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per  $0.2^{\circ}$  size grid cell and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.



Figure 7: a) Cape petrel (*Daption capense*), (b) wandering albatross (*Diomedea exulans*), (c) storm petrels (Oceanitidae), (d) giant petrel (*Macronectes* spp.), (e) white-chinned petrels (*Procellaria aequinoctialis*), (f) grey petrel (*Procellaria cinerea*), (g) grey-headed albatross (*Thalassarche chrysostoma*), and (h) black-browed albatross (*Thalassarche melanophris*).



Figure 8: Distribution of Cape petrels (*Daption capense*): (a) around the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per 0.2° size grid cell and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.



Figure 9: Distribution of wandering albatrosses (*Diomedea exulans*): (a) around the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per 0.2° size grid cell and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.



Figure 10: Distribution of storm petrels (Oceanitidae): (a) around the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per 0.2° size grid cell and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.

constant between 2001 and 2006, then suddenly dropped in 2007 to nearly zero, then increased in 2009 and then decreased to less than 10 in 2016 (Figure 10b). Storm petrels were mainly present during summer (November to May) (Figure 10c).

Giant petrels were observed in large numbers evenly distributed in the observed area with a concentration in the northeast of the island (Figure 11a), numbers of individuals per observation were quite constant except in 2007 (Figure 11b), they were observed all year round with more observations during winter with a small peak in July (Figure 11c).

White-chinned petrels were observed quite evenly in the observed area except around Skiff Bank, west of the main plateau (Figure 12a; -49.5, 63). Number of individuals per observation decreased over the study period (Figure 12b). This species was observed only during the summer breeding season, with a peak in February (Figure 12c).

Grey petrels were observed throughout the study area (Figure 13a), mainly in winter (Figure 13c). The number of individuals per observation showed higher values between 2003 and 2006 and was low until 2017 (Figure 13b).

Grey-headed albatrosses were observed in higher numbers per observation in the northwestern part of the observed area (Figure 14a), number of individuals per observation decreased slightly over time (Figure 14b), this species was present in lower numbers during summer months (Figure 14c).



Figure 11: Distribution of northern and southern giant petrels (*Macronectes* spp.): (a) around the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per  $0.2^{\circ}$  size grid and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.



Figure 12: Distribution of white-chinned petrels (*Procellaria aequinoctialis*): (a) around the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per 0.2° size grid cell and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.



Figure 13: Distribution of grey petrel (*Procellaria cinerea*): (a) around the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per  $0.2^{\circ}$  size grid cell and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.



Figure 14: Distribution of grey-headed albatrosses (*Thalassarche chrysostoma*): (a) around the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per  $0.2^{\circ}$  size grid cell and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.



Figure 15: Distribution of black-browed albatrosses (*Thalassarche melanophris*): (a) around the northern part of the Kerguelen Plateau. Colour scale represents the average number of individuals per observation per  $0.2^{\circ}$  size grid cell and grey line represents the 500 m isobath; (b) trends in the average number counted per day per year; (c) seasonal trends in abundance at fishing vessels.

Black-browed albatross were observed throughout the study area (Figure 15a), number of individuals per observation reached about 30, except in 2006 and 2007 when it reached up to 100 individuals per observation (Figure 15b). This species was observed all year round but in lower numbers in winter (Figure 15c).

#### Discussion

The dataset collected by observers from this remote area provides a long time series of a large range of marine predators, some of which were very rarely observed in this area. The data represents the vast majority of observations at sea available in this part of the world (Péron et al., 2010; Ropert-Coudert et al., 2014) and has been used in recent studies (Fontaine et al. 2015, Labadie et al., 2018; Tixier et al., 2016)

First insight in the data shows great variation in space and time that could be related to prey distribution movement or availability, species breeding cycle, oceanographic differences or population changes (natural or linked to fishery mortality). For example, the number of fur seals observed from vessels is decreasing whereas the population of Antarctic fur seals (*Arctocephalus gazella*) on Kerguelen Island is increasing at 3 to 4% per year (CEBC-CNRS, unpublished data). The data showed some clear seasonal patterns in occurrence, for example, most species are more common during their breeding season (i.e. for white-chinned petrel, Barbraud et al., 2008; Delord et al., 2010), but Cape petrels or grey-headed albatrosses are more common in the winter (nonbreeding season), strongly suggesting that most of the birds around Kerguelen at this time are nonbreeding visitors from farther south (e.g. Clay et al., 2016; Delord et al., 2013, 2016).

Interestingly, some similarities across species in spatio-temporal patterns in the data were visible. For instance, an important change (an increase in black-browed albatross observations and a decrease in grey petrel and giant petrel observations) is observed around 2007. Other species showed similar spatial distribution patterns in the number of individuals per observation (sperm whales, wandering albatrosses and grey-headed albatrosses were observed in greater numbers in the north/northwest; pilot whales and killer whales in the west; fur seals and Cape petrels in the south). Whether these patterns correlate with the natural feeding ecology of these species should be further investigated.

The way long-term trends observed in the data concur with changes in the local or regional breeding populations varied with the spatio–temporal distribution of species. For seabirds for instance, trends did broadly concur even for long-distance migratory species as wandering albatross (Delord et al., 2008; CEBC-CNRS, unpublished data), grey petrel or white-chinned petrel (Barbraud et al., 2009). Nevertheless, long-term data on local breeding population trends remains deficient for part of the species (storm petrels sp., gadfly petrels *Pterodroma* sp. or giant petrels).

Data collected on birds and marine mammals from fishing vessels may therefore be valuable in investigating the temporal trends and the spatial distribution of a broad range of species. However, these data may involve some bias altering their interpretation and inference in regard to natural patterns of wild populations. The non-even distribution and the attractiveness of fishing vessels for many species of seabirds and some species of marine mammals is likely to be the most relevant bias to account for when using these data for ecological studies. Previous studies have examined the extent to which these species may modify their natural foraging behaviour to switch to interaction with fisheries, and the distance to vessels at which these behavioural changes occur (Collet et al., 2017). Fishing activity impacts the observed distribution by attracting some species of predators: Antarctic fur seal, killer whale and sperm whale depredate fish caught on the line (Roche et al., 2007; Tixier et al., 2010, 2014; Guinet et al., 2014; Janc et al., 2018), seabirds feed on offal and bait, sometimes resulting in incidental mortality of the birds (Delord et al., 2005, 2010; McInnes et al., 2017). Animals following the boat from one observation to the next is another potential bias that needs to be taken into account (Collet et al., 2017). How the numbers of scavenging animals attending fishing vessels respond to changes in population size is unknown, but it is unlikely to be a linear relationship. If there is some upper limit on how many individuals can profitably scavenge at vessels, the number of a species at vessels might remain constant even if its numbers are increasing or decreasing. Also, numbers at vessels might change if feeding conditions elsewhere change, without any change in population size. Finally, there might be interspecific interactions - if species 1 becomes more abundant and its numbers go up at vessels, they may displace species 2.

The data collected from fishing vessels are supportive of other, more accurate, measures of population size such as colony counts, at least for seabirds and seals, despite potential bias.

### Conclusions

This work follows the first synthesis of Robineau and Duhamel (2006) for cetaceans and is a first full insight into the marine mammal and seabird data collected by observers. It gives an overview of the potential of the dataset for species distribution models. The dataset is constrained by the geographical area fished by vessels, yet observers spend more than 900 days at sea each year and collect unique data on species. Data collected at sea can be complementary to land-based studies such as long-term breeding population censuses, demographic surveys or tracking studies (Weimerskirch et al., 2003; Barbraud et al., 2012; Delord et al., 2013).

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