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NOTES

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Defining areas of intensive foraging activity for a top marine predator, the Antarctic fur seal: Compromises between effort and accuracy

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Protected areas (i.e., reserves and parks) have become an important management tool in conservation of species and communities. One of the main initiatives for conservation of marine ecosystems is the implementation of Marine Protected Areas (MPA, Hooker & Gerber 2004) but they are often insufficient for an efficient protection of marine mammals (Hoyt, 2009). Effective conservation requires identification of Areas of Ecological Significance (AES) which correspond to areas that are critical to fulfill an animal's need to survive and reproduce (Hindell et al., 2011). For marine predators such as birds and pinnipeds these needs are considered mainly to correspond to foraging and corridor grounds (Hooker & Gerber, 2004; Hyrenbach, Forney, & Dayton, 2000). However, it is essential to understand the relationships between predators' behaviors, their habitat, and the resource consumed to identify their foraging grounds or Areas of Intensive Foraging Activity (AIFA) efficiently. For such predators, the identification of their AIFA thus represents the first step in determining their AES to act towards their effective conservation.

Over the past two decades, the development of powerful miniaturized biologgers has allowed the acquisition of important information on the behavior of wide-ranging marine predators at sea. Traditionally limited to horizontal tracks (i.e., localization devices such as Argos, Global Positioning System [GPS], or Global Location Sensor [GLS]) or diving parameters (i.e., depth data recording devices such as time-depth recorders [TDR]), a range of new sensors (i.e., Hall sensors, accelerometers, magnetometers, etc.) now provides much finer insights into the life of these animals. Biologgers, including such new sensors, make it possible to reconstruct 3-dimensional underwater paths of diving animals or to identify and quantify prey capture attempts. This has been done, for example, on king penguins, *Aptenodytes patagonicus* (Charrassin et al., 2001), Weddell seals, *Leptonychotes weddellii* (Plötz, Bornemann, Knust, Schröder, & Bester, 2001), Steller sea lions, *Eumetopias jubatus* (Viviant, Trites, Rosen, Monestiez, & Guinet, 2010), Antarctic fur seals (AFS), *Arctocephalus gazella* (Jeanniard-du-Dot, Trites, Arnould, & Guinet, 2017b; Viviant, Monestiez, & Guinet, 2014) and Southern elephant seals, *Mirounga leonina* (Vacquié-Garcia et al., 2012). These expensive loggers can record data at more than 20 Hz over weeks or months but are time-consuming, labor- and computing-intensive to analyze. Therefore, compromises need to be made between the cost of loggers (i.e., sample size), resolution of information collected (i.e., large vs. fine scale), and analytical constraints (i.e., qualitative vs. quantitative information; and rapid vs. time-consuming analyses) when it comes to conservation. A question thus arises as to whether such fine-scale data would provide a benefit to determining AIFA for conservation perspective, or whether information collected with more traditional data-loggers (i.e., GPS, TDR) would be sufficient to determine AIFA.

Antarctic fur seals are a ubiquitous top marine predator around the Subantarctic region that can provide large or fine-scale information on habitat use (Arthur et al., 2017; Bonadonna, Lea, Dehorter, & Guinet, 2001; Robinson, Goldsworthy, Van Den Hoff, & Hindell, 2002; Staniland, Reid, & Boyd, 2004). During the breeding season, females become central place foragers to nurse their pup for four months, alternating between foraging trips at sea (2–15 days) and nursing bouts on land to suckle their pup (Boyd, 1996; Forcada & Staniland, 2009; Guinet, Dubroca, Lea, & Goldsworthy, 2001). They are thus spatially and temporally tied to foraging areas close to breeding grounds that are of great importance for individuals and populations at this specific time of the year. These areas need to be identified in order to build efficient management tools such as MPAs.

Therefore, the objectives of this study were to (1) assess differences in spatial structures of AIFA based on three quantitative ecological indices as proxies of foraging activity extracted from loggers with increasing resolution, cost and complexity of analyses for breeding female AFS on the Kerguelen Islands, and (2) determine which resolution represents the best compromise between analysis effort and spatial accuracy to infer foraging areas in the context of sound and effective conservation of this top predator.

During the breeding season of 2012 (from January to March), eighteen healthy-looking lactating females AFS were randomly selected at the colony of Pointe Suzanne on the southeast of the Kerguelen Islands (49°07′S, 70°45′E) in the Southern Ocean. Females were captured with a hoop net and then carried to a close restraint board where they were anesthetized with isoflurane gas. All females were each equipped with a GPS logger (MK10 Fastloc, Wildlife Computers, Redmond, WA; 105 L × 56 W × 30 H, 213 g), a Daily Diary tag (DD, TDR 10 F 238, Wildlife Computers; 105 L × 56 W × 30 H, 213 g) on their back, and a tri-axial accelerometer (GCDC-X6 or X8, Gulf Coast Data Concepts, Waveland, MS; 54 L × 32 W × 16 H, 34 g) on their head. Loggers were attached using a 5-min epoxy glue. MK10 loggers were set to record GPS locations every 5 min, the DD recorded depth (±0.5 m) every second and acceleration in 3-dimensions at 16 Hz, and the GCDC-X6 or X8 recorded head tri-axial acceleration also at 16 Hz. After recovery from the procedures, animals were released into the colony. Recapture and device removal were undertaken after a single foraging trip. GPS data were originally published by Jeanniard-du-Dot et al. (2017b) while DD and accelerometer data were originally published by Jeanniard-du-Dot et al. (2017a).

Time series of diving behaviors were reconstructed using a custom-made program developed within R 2.6.1. Drifts in the pressure sensors were corrected prior to analysis using a zero-offset correction. Dives were defined as periods underwater below 3 m and longer than 4 s. Given known records for maximum dive depth of 300 m and duration of 300 s (Lea, Hindell, Guinet, & Goldsworthy, 2002) readings above these values were considered erroneous and discarded (<0.1% of the total dive number). Dive durations and maximum dive depths were derived for each selected dive. Distances traveled at the surface of the ocean (horizontal distances) were calculated by measuring the linear distance between two successive GPS locations taking into account the curvature of the Earth using the Haversine formula (Sinnott, 1984). GPS locations have a high spatial (<100 m) and temporal resolution (one location every 5 min), so GPS tracks did not require filtering (Tremblay et al., 2006). Time of day (nighttime vs. daylight) was categorized for each data point using solar angles at GPS positions and time recorded by the MK10. Nighttime was defined as periods when solar angles were <6° (thus including dawn and dusk) and daylight when solar angles were >6°.

To assess prey capture attempts (PrCA), the data and methodology developed by Jeanniard-du-Dot et al. (2017b) were used. Only acceleration signals recorded while the animals were below a depth of 3 m were kept for analyses.

To spatialize each foraging index, the area around the Kerguelen Islands was split into 0.2° × 0.2° grid cells (~15.7 km × 22.3 km) GPS locations along individual tracks were linearly interpolated every second between two GPS points and then combined to the 1 Hz dive data to define precise dive locations. Foraging activity was then spatially estimated within these cells by (1) deriving the time spent per unit area (TSPA) from location data only as TSPA assumes that residence times increase in profitable patches (Cezilly & Benhamou, 1996; Fauchald & Tveraa, 2003; Kareiva & Odell, 1987); (2) extracting time spent diving per unit area (TSDA) in each cell from location and depth data (dive time is assumed to reflect feeding behaviors, as fur seals are thought to rest and travel at the surface of the ocean during the day, and to only dive to significant depths for foraging at night; Boyd, 1996; Staniland et al., 2004); and (3) spatially georeferencing PrCA derived from acceleration data with corresponding GPS locations within the grid (PrCA are an index of feeding events; Viviant et al., 2010; Volpov et al., 2015). TSPA over the whole trip duration were compare to the TSPA at night.

A Fuzzy Kappa approach was used to compare the index maps produced. A fuzzy-based map comparison consists of a cell-by-cell comparison, which takes into account the neighboring cells to assess levels of similarities between maps (Hagen, 2003; Visser & De Nijs, 2006). As these maps were numerical, they were categorized by dividing the maximum TSPA, TSDA, or PrCA values by the chosen number of categories n = 10. Values were then assigned to a category between 1 and n if they were included in an interval of values between $i * (n - 1)$ and $i * n$. This methodology allows taking into account levels of similarities between categories (Hagen, 2003). When defining categories to compare usage maps, uncertainty and vagueness (or fuzziness in this context) may exist. For this reason the fuzziness of categories was represented by expressing degrees of similarity between two categories (Hagen, 2003). Similarities between two categories were set with a number between 0 (distinct) and 1 (identical) according to their degree of similarity, for example, a category 10 (represented in dark-red cells) is more similar to a category 7 (orange cells), than to a category 3 (light-green cells, Table S1) (Hagen, 2003). For all map comparisons an exponential decay function with a halving distance of two cells and the same categorical similarity matrix (Table S1) were used. Two indices were then calculated to assess the level of similarity between two maps, the average similarity index and the Fuzzy Kappa index. The average similarity index ranges from 0 (total disagreement) to 1 (fully identical) (Hagen, 2003). The Fuzzy Kappa index (Landis & Koch, 1977) ranges from 0 to 1 with values between 0 and 0.40 representing poor to fair similarity, 0.41 and 0.60 moderate similarity, 0.61 and 0.80 substantial similarity, and 0.81 and 1.00 almost perfect match. Fuzzy Kappa analyses were performed on categorized maps within the Map Comparison Kit 3 software (version 3.2.3., Hagen 2003).

Most female fur seals headed southeast of the colony (n = 12), while six females traveled east to northeast of the colony. They traveled 437 ± 274 km (158–1,054 km) at a maximum distance of 175 ± 121 km from the colony (48–430 km). Overall animals spent 23.2% ± 14.4% of their time diving during which they made a total of 2,737 ± 1,927 prey capture attempts, with a total of 2,697 ± 1,884 capture attempts occurring at nighttime.

Female fur seals spent most of their time east and northeast of the islands on the Kerguelen Plateau at the edge of the 500 m isobaths or along the shelf break at the 1,000 m isobaths (TSPA, Figure 1a). Their TSDA was mainly localized along the 500 m isobaths just east of the Kerguelen Islands (Figure 1c). Most of the feeding attempts occurred at the 500 m isobath close to the colony, but interestingly, other areas, such as those on 1,000 m isobath southeast of the Plateau, where seals spent time diving did not lead to as many PrCA (Figure 1d). Fuzzy cell-by-cell comparisons between the different categorized maps showed that TSPA, TSDA, and number of PrCA were overall highly similar (Figure 2, Table 1). Areas where AFS spent most of their time and dived the most showed the strongest similarities (average similarity = 0.96 and Fuzzy Kappa = 0.61).

Furthermore, areas where AFS spent the most of their time at night and where they foraged the most (PrCA) were also highly similar (Table 1). Finally, areas where AFS foraged and dived the most had the weakest similarity. Overall AES derived from full GPS location tracks (including daytime and nighttime) or partial tracks (nighttime) were highly similar (average similarity = 0.97 and Fuzzy Kappa = 0.65). Interestingly, TSPA over the whole trip duration did not differ from the TSPA at night only (similarity = 0.96, Fuzzy Kappa = 0.64, Table 1). Likewise, areas where AFS

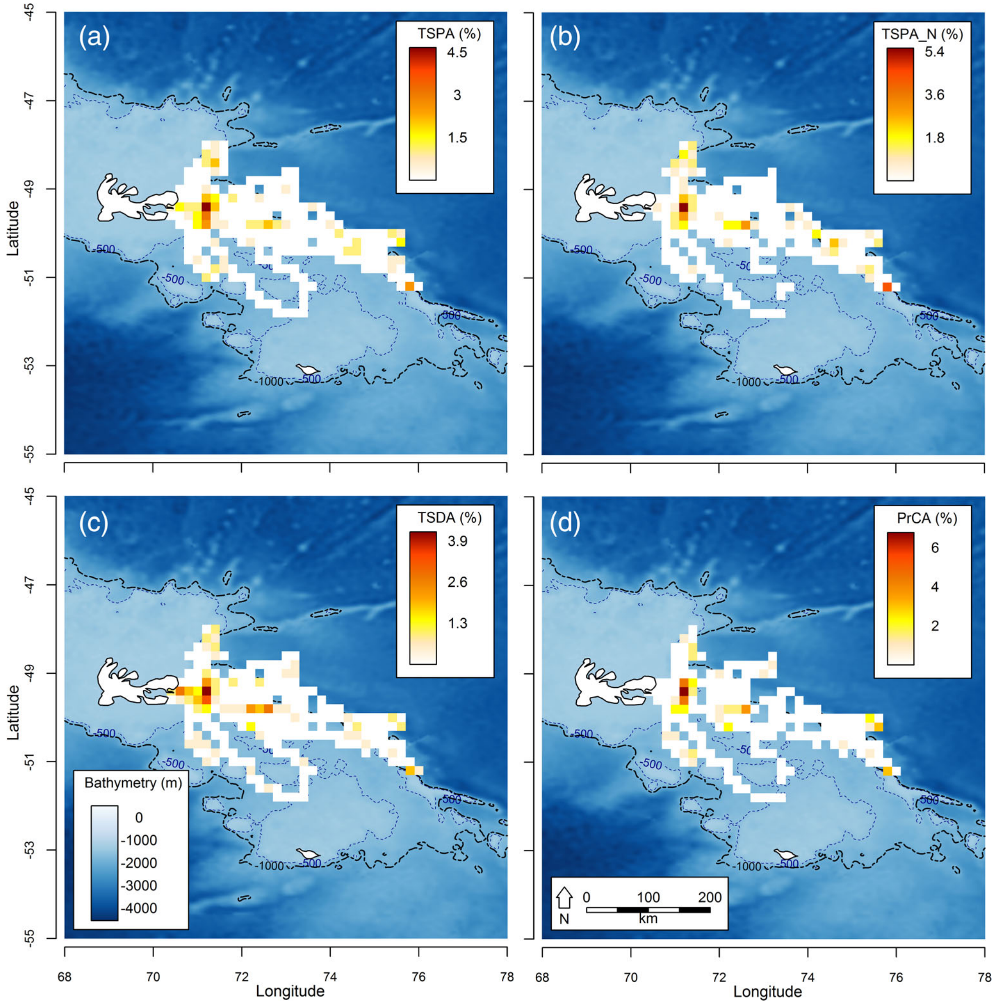

FIGURE 1 Spatial representations of (a) time spent per unit area (including daytime and nighttime), (b) Time spent per unit area at night (including dawn and dusk), (c) time spent diving per unit area, and (d) prey capture attempts per unit area. Values are represented in proportions of time per cell or prey capture attempts per cell from low (light colors) to high (bright colors). Blue dotted lines show the 500 m contours and black dashed lines show the 1,000 m contours.

dived and foraged the most over the whole trip duration did not differ from those where they dived and foraged the most at nighttime (Table 1). Fuzzy Kappa comparisons showed strong similarities between all maps tested (Figure 2).

Areas of intensive foraging activity for Antarctic fur seals breeding on the Kerguelen Islands were assessed based on three ecological indices as foraging proxies (time spent per area, time spent diving per area, and location of prey capture attempts) extracted from three types of data with different resolutions (~2 GPS locations/hr, dive data at 1 Hz, acceleration at 16 Hz). Fairly similar AIFA from these three different indices were shown. Consequently, finer-scale data, such as areas where the diving or the feeding attempts occurred, did not provide added value to determine AIFA accurately compared to the simpler TSPA from GPS locations. Tracking data are often the only source of information previously or currently collected on several wide-ranging marine species and our results showed that they provide sufficient information on habitat use to define important areas accurately within their habitat.

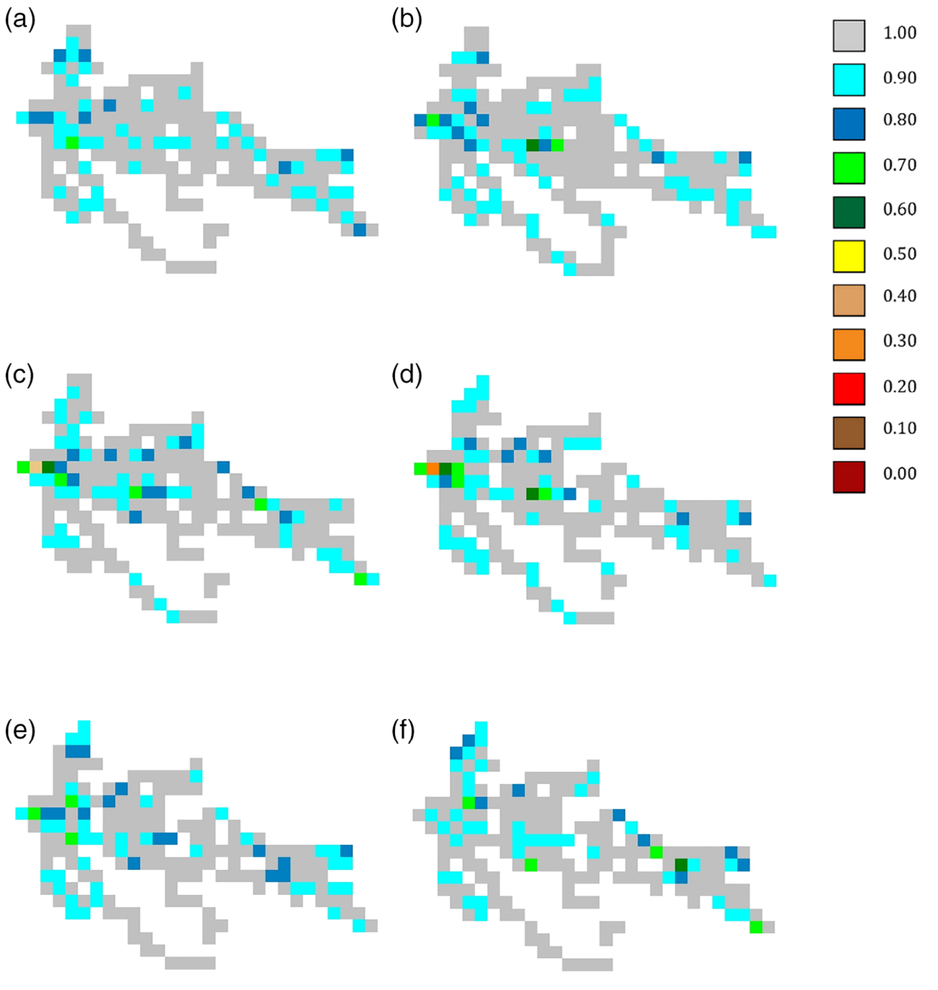

FIGURE 2 Fuzzy Kappa comparison maps of (a) time spent per unit area (TSPA, daylight + nighttime) with the Time spent per unit area at nighttime only (TSPA_N), (b) time spent diving per unit area (TSDA) with TSPA, (c) TSDA with TSPA_N, (d) prey capture attempts per unit area (PrCA) with TSDA, (e) PrCA with TSPA and (f) PrCA with TSPA_N. Darker color (red) indicate a weak similarity (0) between the same cell of the two maps, while green and blue colors indicate a strong similarity. Gray cells show identical cells (1).

TABLE 1 Average Similarity and Fuzzy Kappa coefficients for map comparisons between the three quantitative ecological indices, time spent diving per unit area (TSDA), number of prey capture attempts per unit area (PrCA), and time spent per unit area (over the whole trip duration [TSPA, including daytime and nighttime], and at nighttime only [TSPA at night]).

Test	Average Similarity	Fuzzy Kappa
PrCA vs. TSDA	0.95	0.53
PrCA vs. TSPA	0.95	0.54
PrCA vs. TSPA at night	0.96	0.54
TSDA vs. TSPA	0.96	0.61
TSDA vs. TSPA at night	0.95	0.53
TSPA vs. TSPA at night	0.96	0.64

It is difficult to assert that these results are applicable beyond this species and the spatio-temporal scale of the study, although this was already suggested (Louzao et al., 2011). Antarctic fur seals are pelagic nocturnal central place foragers with time-activity budgets and dive behaviors reflecting their foraging strategies. Given the very similar time-activity budgets and dive behaviors between pelagic divers, such as New Zealand sea lions, *Phocarctos hookeri* (Costa & Gales, 2000), northern fur seals, *Callorhinus ursinus* (Battaile, Sakamoto, Nordstrom, Rosen, & Trites, 2015) and Galápagos sea lions, *Zalophus wollebaeki* (Villegas-Amtmann, McDonald, Páez-Rosas, Aurioles-Gamboa, & Costa, 2017), as well as their prey capture attempt rates (Jeanniard-du-Dot, Trites, & Arnould, 2018; Jeanniard-du-Dot et al., 2017b; Viviant, Jeanniard-du-Dot, Monestiez, Authier, & Guinet, 2016) it would not be surprising that this method would be applicable to these other species as well. It is possible that a stronger uncoupling between PrCA and TSPA (inclusive of all foraging behaviors) or TSDA would occur in years of difficult environmental conditions when prey were less available, accessible, or predictable. This would occur, as animals would increase their search behavior and likely be less successful at capturing prey per dive. However, some of these AFS spent time diving in the middle and eastern part of the Kerguelen Plateau while not attempting to capture prey often. This indicated either a less successful foraging strategy/location, or animals feeding on fewer but larger prey. Yet this foraging strategy on the plateau was still accurately represented by the TSPA index compared to PrCA despite a slightly smaller similarity index in these areas (Table 1). AFS tend to increase their time at sea rather than their diving effort during years of difficult conditions (Trillmich, 1990), which suggests that TSPA would remain as accurate as TSDA in various environmental conditions, including less “predictable” ones. However, this requires testing before extrapolating to predators with foraging strategies that entail different time-activity budgets and dive patterns such as benthic divers that spend more time at sea diving throughout the day to prey on less patchily distributed prey. Testing on populations of top predators that include different foraging strategies, such as the California sea lions (*Zalophus californianus*), for example, (McHuron et al., 2016) would also be interesting.

The foraging locations of the studied seals was previously shown for Kerguelen colonies (Bonadonna et al., 2001; Guinet et al., 2001; Lea et al., 2008; Lea & Dubroca, 2003) and for colonies at the Macquarie Islands (Robinson et al., 2002) or South Georgia (Boyd, Staniland, & Martin, 2002; Staniland, Morton, Robinson, Malone, & Forcada, 2011; Staniland et al., 2004). At the Kerguelen Islands, ~25% of the Southern elephant seal population was also found generally diving around the 500 m contours on the eastern, northeastern, and southeastern parts of the Plateau (O'Toole, Hindell, Charrassin, & Guinet, 2014). In 2014, Delord et al. (2014) also identified key foraging areas of 10 species of birds that correspond to specific oceanographic features such as these breaks. In their recent study, Thiers, Delord, Bost, Guinet, and Weimerskirch (2017) used tracks from nine species of marine birds and pinnipeds breeding at the Kerguelen Islands to infer high-importance areas, or AES, for this top marine predator community. Overall, they showed that highest values of TSPA occurred near the colonies and to the eastern side of the Islands. The AIFA defined in this study for AFS are thus in agreement with these predictions for this community of top predators.

Antarctic fur seal colonies from Cap Noir and Pointe Suzanne likely use the same AIFA (Lea et al., 2008). However AIFA of a more remote colony breeding at Iles Nuageuses (located on the western side of the Kerguelen Islands and ~160 km distant from the two other colonies (Bonadonna et al., 2001; Lea et al., 2008) may differ. Similarly, AFS breeding on Heard Island occupy a different spatial area on the plateau than the ones from this study even if with similar oceanographic features (Hindell et al., 2011). Effective species-specific AIFA thus need to take into account the local needs of spatially segregated colonies including remote ones.

There is thus a trade-off possible between the cost of loggers and the sample size of individuals tagged within the whole range of their breeding distribution. Given that simpler GPS/TDR tags are less expensive and provide similar information to newer sensors in regards to defining foraging areas, the deployment of less expensive loggers (GPS) on more individuals from different colonies is recommended to obtain a better picture of AIFA at the species level rather than collecting finer-scale data (acceleration, etc.) on fewer animals. In comparison to summer studies, winter tracks of AFS from South Georgia, Prince Edward Islands, and South Shetland Islands (Arthur et al., 2017; Boyd et al., 2002; Staniland, Robinson, Silk, Warren, & Trathan, 2012) revealed that AFS mainly travel farther away from the colony and exploit highly productive waters associated with bathymetric features, shelves and breaks, and fronts (subantarctic and polar fronts). This suggests that even for understudied seasons, TSPA provides enough information to highlight feeding grounds, and that investing in finer-scale loggers would not be necessary. Finally, as environmental processes might shift in time (Lombard et al., 2007), identifying these AIFA over years would be necessary to ensure a dynamic identification of all foraging grounds for efficient management (Hindell et al., 2011).

To conclude, the use of GPS loggers was found to be the most cost- and effort-effective biologging technology to accurately collect relevant information to establish efficient AIFA of a wide-ranging marine predator. In our case, it would be judicious to researchers to focus on lower resolution data and alleviate the financial burden and labor effort attached to higher-resolution data in the context of delimiting MPAs. Efforts should rather be invested in increasing sample size throughout the spatial and temporal ranges of studied species. The AIFA identified in this study is vital to AFS and other species for foraging and by extension crucial to maintain healthy reproduction and survival rates.

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AUTHORS' CONTRIBUTIONS

Fabien Vivier, Tiphaine Jeanniard-du-Dot, and Christophe Guinet conceived the ideas and designed methodology; Tiphaine Jeanniard-du-Dot collected the data; Fabien Vivier and Tiphaine Jeanniard-du-Dot analyzed the data; Fabien Vivier, Tiphaine Jeanniard-du-Dot, and Christophe Guinet led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Daily diary and accelerometer data are deposited in the Dryad Digital Repository and are accessible at https://doi.org/10.5061/dryad.n8s3c.

GPS data are deposited on the Dryad Digital Repository and available at https://doi.org/10.5061/dryad.269qr.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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