Spatial ecology of closely-related taxa: the case of the little shearwater complex in the North Atlantic Ocean

Journal:	*Zoological Journal of the Linnean Society*
Manuscript ID	ZOJ-01-2020-3972.R1
Manuscript Type:	Original Article
Keywords:	North Atlantic < Geography, bird < Taxa, cryptic species < Taxonomy, feeding behaviour < Behaviour, feeding habits < Behaviour

Abstract:	Seabirds inhabiting vast water masses provide numerous intriguing examples where opposing phenomena such as natal and breeding philopatry vs vagility have dug cryptic taxonomic boundaries among closely-related taxa. The taxonomy of little shearwaters of the North Atlantic Ocean (Little–Audubon's shearwater complex, Puffinus assimilis-lherminieri) still remains unclear, and complementary information on non-breeding distributions and at-sea behaviour becomes essential to unravel divergent local adaptations to specific habitats. Using miniaturized light-level geolocators from seven study areas within the North Atlantic, we evaluated the spatial and habitat segregation, estimated the timing of their key life-cycle events, and described the at-sea behaviour of three taxa of these little shearwaters year-round to distinguish ecological patterns and specializations that could ultimately unravel potential lineage divergences. We also assessed morphometric data from birds that were breeding at each study area to further discuss potential adaptations to specific habitats. Our results showed that while birds from different taxa segregated in space and habitats, they share ecological plasticity, similar annual phenology and diel foraging behaviour. These ecological inconsistencies while defining the evolutionary stressors faced by these taxa do not suggest the existence of three Evolutionary Significant Units. However, they certainly confirm the fairly recent evolutionarily divergence among the three little shearwaters of the North Atlantic.

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Running title: Spatial ecology of little shearwaters

ABSTRACT

Seabirds inhabiting vast water masses provide numerous intriguing examples where opposing phenomena such as natal and breeding philopatry *vs* vagility have dug cryptic taxonomic boundaries among closely-related taxa. The taxonomy of little shearwaters of the North Atlantic Ocean (Little–Audubon's shearwater complex, *Puffinus assimilis-lherminieri*) still remains unclear, and complementary information on non-breeding distributions and at-sea behaviour becomes essential to unravel divergent local adaptations to specific habitats. Using miniaturized light-level geolocators from seven study areas within the North Atlantic, we evaluated the spatial and habitat segregation, estimated the timing of their key life-cycle events, and described the at-sea behaviour of three taxa of these little shearwaters year-round to distinguish ecological patterns and specializations that could ultimately unravel potential lineage divergences. We also assessed morphometric data from birds that were breeding at each study area to further discuss potential adaptations to specific habitats. Our results showed that while birds from different taxa segregated in space and habitats, they share ecological plasticity, similar annual phenology and diel foraging behaviour. These ecological inconsistencies while defining the evolutionary stressors faced by these taxa do not suggest the existence of three Evolutionary Significant Units. However, they certainly confirm the fairly recent evolutionarily divergence among the three little shearwaters of the North Atlantic.

KEYWORDS Activity patterns, at-sea distribution, Audubon's shearwater, Barolo shearwater, Boyd's shearwater, ecological segregation, evolutionary significant units, *Puffinus baroli*, *Puffinus boydi*, *Puffinus lherminieri*, speciation process.

INTRODUCTION

The identification of demographically isolated units is an important process within conservation biology for defining the conservation status of a given species and for developing and implementing conservation efforts (Palsbøll, Bérubé, & Allendorf, 2006). Management units (MU), which focus on the current population structure, are often defined for solving short-term management issues, while evolutionary significant units (ESU), more related to historical population structure, are defined for long-term conservation actions (Moritz, 1994). Often MUs or ESUs are delineated by assessing dispersal rates and using genetic structure and direct measures of gene flow within and among populations (Moritz, 1994; Schwartz, Luikart, & Waples, 2007). Outcomes of such population analyses solely based on genetic markers, however, often result in taxonomic boundaries that are unclear or not explicit (Gaines *et al.*, 2005; Keeney & Heist, 2006). In contrast, using multiple traits to assess population structure of closely related species can elucidate the mechanisms underlying observed genetic structuring of populations and therefore provide insight to ecological divergence (Friesen, Burg, & McCoy, 2007a). For example, in addition to colouration and biometrics, the annual phenology, spatio-temporal distribution, and behaviour of closely related taxa can each be used to better understand divergence among populations. A multi-faceted approach to the assessment of population structure can enhance the credibility of the identified MU/ESU and therefore better inform the evolutionary, ecological, and conservation implications of the underlying population structure (Crandall *et al.*, 2000; De Queiroz, 2007; Wiens, 2007; Tobias *et al.*, 2010).

Seabirds provide numerous examples where taxonomic boundaries between cryptic and closely-related taxa have been difficult to determine (e.g., Austin *et al.*, 2019). Isolation processes mediated through space and time (allopatry and allochrony, respectively) are important contributors to divergence between populations of many seabird taxa and likely contribute to speciation (Winker, 2010). For instance, high degrees of natal and breeding philopatry likely contribute to genetic differentiation among seabird populations (Friesen *et al.*, 2007a; Rayner *et* *al.*, 2011; Wiley *et al.*, 2012). In addition, habitat specialization and adaptations to specific oceanographic conditions may also promote ecological differentiation among breeding sites of the same species that are spatially-separated, often resulting in geographic differences in plumage, morphology, or vocalizations that may subsequently contribute to speciation, or conversely lead to assumed speciation when none may exist (Dearborn *et al.*, 2003; Burg & Croxall, 2004). Moreover, the presence of geographically-discrete wintering grounds in migratory species has often been considered as a good predictor of population genetic structuring (Friesen, 2015). In contrast, the great capacity for long-distance flight of most seabirds (i.e., vagility) and the absence of obvious physical barriers at sea pose opportunities for large-scale dispersal of individuals and hence a genetic mixture of widespread breeding populations. Taken together, these opposing phenomena (i.e., natal and breeding philopatry vs. vagility) result in the *seabird paradox* (Milot, Weimerskirch, & Bernatchez, 2008; Wiley *et al.*, 2012) which subsequently raises relevant questions related to the evolutionary divergence of closely-related yet vagile taxa. By assessing spatial and behavioural data of pelagic seabirds at sea, however, we can provide not only ecological insights (e.g., defining the vagility of taxa) but can also enhance our ability to assess the genetic structure, taxonomic delimitation and conservation status of seabird populations of a given species (Bickford *et al.*, 2007; Lascelles *et al.*, 2012). For instance, habitat use predicted with Species Distribution Models (SDM) may allow us to infer past distributions of given taxa (e.g., Svenning *et al.*, 2011), and spatial comparisons with their current at-sea distributions could unravel and be good proxies of immigration rates and hybridisation events between seabird colonies.

Many species within the Procellaridae have been and continue being the subject of genetic assessment in large part due to these species exhibiting both an isolation of breeding sites and high natal philopatry (Heidrich, Amengual, & Wink, 1998; Austin, Bretagnolle, & Pasquet, 2004; Wood *et al.*, 2017). For example, the taxonomy of little shearwaters (Little–Audubon's shearwater complex, *Puffinus assimilis–lherminieri*) has been revised several times over the last

100 years (Murphy, 1927; Heidrich *et al.*, 1998; Austin *et al.*, 2004; Olson, 2010), but it currently remains unsettled due to inconsistencies among studies (e.g., www.birdlife.org/globally-threatened-bird-forums/). Genetic evidence on most small *Puffinus* shearwaters (Austin *et al.*, 2004) suggests more genetic similarities among those taxa inhabiting the North Atlantic Ocean (*lherminieri-baroli-boydi*) compared to other species complexes from other ocean basins (e.g., the Australasian-Southern Ocean clade [*assimilis-tunneyi-kermadecensis-haurakiensis-elegans*] or the Indo-Pacific clade [*nicolae-colstoni-polynesiae-dichrous-bailloni-atrodorsalis-persicus-temptator*]). As currently classified, the most poorly supported taxonomic divisions occur among the taxa included in the North Atlantic clade. Two principal lineages or groups of species have been classically defined in the North Atlantic Ocean: the Audubon's shearwater (*P. lherminieri*, hereafter as PLHE) which breeds in the Caribbean and is characterized by pinkish-coloured feet, and the little shearwater (*P. assimilis*) which breeds in Macaronesia and is characterized by bluish feet and a smaller body (Murphy, 1927). Morphological and further genetic evidence suggested that little shearwaters from Macaronesia may actually include two differentiated lineages (Austin *et al.*, 2004; Brooke, 2004; Ramirez *et al.*, 2010): the Barolo shearwater (*P. assimilis baroli, P. lherminieri baroli* or *P. baroli*, hereafter PBAR) inhabiting Azores, Madeira, Salvages, and Canary Islands, and the Boyd's shearwater (*P. a. boydi, P. l. boydi* or *P. boydi*, PBOY) inhabiting several islands of the Cape Verde archipelago. There is evidence, however, that PBOY may be more closely related to PLHE in the Caribbean than to the more proximate breeding PBAR, and should instead be assigned to the taxon *P. lherminieri boydi* (Heidrich *et al.*, 1998). In fact, fossil evidence based on bone measurements suggests that PBOY inhabited Bermuda approximately 400,000 years BCE and therefore may have overlapped with the northern extent of current PLHE breeding habitat (Olson, 2010). Thus, given such phylogenetic and taxonomic uncertainties, the assessment of complementary information on non-breeding distribution, phenology, and at-sea behaviour can enhance our understanding of phenotypic plasticity and possible divergence within-among such closely-related taxa.

In the past two decades, ecologists have benefitted from vast improvements in our ability to collect animal movement data on diverse taxa through animal-borne technology, such as Global Location Sensors (GLS, also referred as geolocators). Tracking multiple individuals from different colonies using increasingly-smaller geolocators has provided new insights into year-round spatial ecology, annual phenology, foraging activity, and subsequently ecological divergence of several closely-related taxa (Pollet *et al.*, 2014; Orben *et al.*, 2015; Ramos *et al.*, 2016; Paiva *et al.*, 2018; Austin *et al.*, 2019). In this study, using miniaturized geolocators from seven breeding colonies of little shearwaters in the North Atlantic, we (1) define accurate phenological schedules, (2) identify foraging areas used during breeding and non-breeding periods, (3) assess spatio-temporal distributions, (4) characterize marine habitat, and (5) describe at-sea activity patterns throughout their annual cycle, to ultimately improve understanding of the evolutionary processes acting on these taxa. One of the main goals of this study was to test whether spatial segregation/overlap among individuals of different colonies is related to the geographic distance between those breeding sites, expecting that segregation year round will be higher between colonies of different taxa. In addition, if birds segregate clearly in space and habitat, we expect to model and better predict spatial distributions of populations within the same taxon than those distributions of other taxa, and this should be maximized during the non-breeding season when birds are not constrained by breeding duties. Similarly, we expect populations segregating in space to differ accordingly in their phenology and/or in their activity budgets, due to facing and exploiting different environments. By all these means, and in combination with morphological data, we finally provide evidence on how ecological and behavioural processes can be central to understanding patterns of evolutionary differentiation amongst closely-related populations, particularly in wide-ranging marine vertebrates, such as the little shearwaters of the North Atlantic.

METHODS

Studied species and sampling design

Little shearwaters are long-lived, colonial breeders that nest in rock crevices or burrows on remote islands (Vanderwerf *et al.*, 2015; Precheur *et al.*, 2016). Three differentiated taxa breed in the North Atlantic Ocean (Table 1): PLHE breeds throughout the Caribbean (including a few islands off the coast of Brazil; Bradley & Norton, 2009), PBAR breeds throughout the northern Macaronesian archipelagos (Azores, Madeira, Salvages, and Canary Is.), and PBOY breeds throughout the archipelago of Cape Verde. Breeding periods are long (ca. 6 months), and begin during the northern winter (from early December to late May) with peak laying occurring late January (references in Table 1). Wing moult (i.e., remige feather moult) begins in May-June at the end of the breeding period, and finishes in August-September at the end of the non-breeding period (Monteiro *et al.*, 1999). These small, black and white shearwaters are pursuit-diving seabirds with specific adaptations for underwater swimming, including flattened tarsi and humeri, short wings, and high wing-loading (Warham, 1990; Burger, 2001). They dive mainly in the upper 15 m of the water column, primarily feeding on small juvenile squid, fish and crustaceans (Neves *et al.*, 2012; Ramos *et al.*, 2015), all of which perform diel vertical migrations (DVM) up to the epipelagic zone while following zooplankton diel movements (Davoren *et al.*, 2010). Most populations are small and of high conservation concern regionally (Table 1); however, the International Union for Conservation of Nature (IUCN) lists the entire little shearwater complex of the North Atlantic (*P. lherminieri-baroli-boydi*) as a Least Concern species (www.iucnredlist.org/).

The present study was conducted at seven breeding colonies of the species spread throughout the Caribbean and Macaronesian regions (Fig. 1, and see Table 1 for population numbers). Sampling was conducted at different periods during an eight-year span: Bahamas in 2008, Martinique in 2012-2014, Azores in 2007, Madeira in 2011-2013, Salvages in 2008-2012, Raso in 2007-2008, and Cima in 2009-2013.

Morphometric data

Differences in morphological traits among taxa can be used to delineate provisional taxonomic boundaries among lineages, and these can subsequently be complemented with genetic, behavioural and ecological descriptors (Gómez-Díaz, González-Solís, & Peinado, 2009). Here, we collected standard morphometric measurements while deploying geolocators at each breeding site, including some colonies where no recoveries were achieved (e.g., Trinidad Tobago and Canary Islands; Table 2). We compared morphometrics among colonies using those measurements sampled in most colonies: culmen, tarsus (measured with callipers, to the nearest 0.01mm), and wing length (measured with wing ruler, to the nearest 0.5mm) as well as body mass (measured with spring balances, to the nearest 5g; Fig. S1 in Appendix S2). We also used tarsus and wing length measurements to build a similarity matrix based on the Euclidean distance for all pairwise comparisons among eight breeding colonies to construct an unrooted tree of similarities (Fig. S2 in Appendix S2) using the neighbour-joining clustering analysis implemented in the R package *ape* (Paradis, 2017).

Tracking data: representativeness and spatio-temporal analysis

At each colony, various models of geolocators were attached to bands on the legs of PLHE (n = 69 tags), PBAR (n = 64) and PBOY (n = 100) breeding adults, while incubating an egg or rearing a chick (see Table S1 in Appendix S2). We recaptured the birds and recovered the tags approximately one year after deployment (see Table S1 in Appendix S2 for specific numbers of deployments and recoveries at each colony). Before deployment and after recovery, every tag was calibrated to estimate sun elevation angles (ranging from −6.4 to −2.9). We applied an overall light threshold value of 20 and specific estimates of sun elevation angles to process light levels provided by the tags, and converted these to 2 locations per day, with an average accuracy of ~200 km (or ~ 2°; Phillips *et al.*, 2004).

When delineating areas used by a given population, an analysis of representativeness is strongly recommended when sample sizes are small or when high variability in distribution occurs within and between individuals (Delord *et al.*, 2014). In such cases, a small number of tracked individuals may not be representative of the space use of the entire population (Lascelles *et al.*, 2016). Therefore, we conducted a representativeness analysis that allowed us to assess how robust our datasets were. Specific data gathering, filtering procedures and representativeness analysis on spatial data are described in Appendix S1.

Kernel density Utilization Distributions (UD) were estimated using Dynamic Brownian Bridge Movement Models (DBBMM; Kranstauber *et al.*, 2012). The method, highly recommended in migratory studies at large spatial scales (Horne *et al.*, 2007; Palm *et al.*, 2015), allows calculating the probability of an animal use in between locations by accounting for: distance and elapsed time between successive locations, location error, variable animal's mobility (i.e., Brownian motion variance) as well as temporal autocorrelation in location data (Kranstauber *et al.*, 2012). Using the R package *move* (Kranstauber *et al.*, 2012), we calculated cumulative probability contours for specific UDs: 5% UDs to estimate the centroids of the non-breeding ranges for each sampled colony/taxon, 50% UDs to estimate core areas of the habitat used by sampled colonies/taxa within a given period (Lascelles *et al.*, 2016), and 95% UDs to measure potential overlap among individuals and taxa.

From complete year-round tracks, we estimated five phenological and spatial parameters: (1) departure date from breeding site, (2) arrival date at breeding site, (3) duration of the non-breeding period (in days), (4) area exploited throughout the non-breeding period (as indicated by the 50% UDs; in 10^6 km^2), and (5) non-breeding range (orthometric distance between the breeding colony and the centroid of the 5% non-breeding UDs; in km). Timing of departure and arrival of individual birds at the different breeding areas were determined visually while plotting raw positions. These dates allowed us to define breeding and non-breeding periods of each colony (Fig. 2). We used the 'kerneloverlap' function in the *adehabitatHR* R package (Calenge *et al.*, 2006) to calculate the spatial overlap among individuals as the average of all individual-paired 95%

UDs overlaps from birds tagged at the same colony during the same year, separately for the breeding and non-breeding periods (Table S4 in Appendix S2). Therefore, spatial data for each taxon were combined across years for subsequent analyses (Fig. 3). We evaluated the effect of taxon on these non-breeding parameters by fitting a set of candidate Linear Mixed Models (LMM), with sampled colony (nested within taxon) and year as random effects (Table 3). Model selection was based on the Akaike Information Criterion corrected for small sample size (AICc; Burnham & Anderson, 1998). LMM selection procedures are fully described in Appendix S1.

For the analysis of spatial distribution, we first estimated the importance of specific areas across the North Atlantic Ocean for little shearwaters, at the species complex level (Fig. 1). To do so, we enumerated the number of positions of each taxon that were located within each 200 x 200 km cell. These positions' counts were then weighed by considering the total numbers of positions in each taxon/dataset (*i.e.*, the sampling effort per colony site), and multiplied by the size of the population of origin (estimated as 2*number of breeding pairs; Table 1). By these means, we obtained an estimate of the intensity of use of areas by adult little shearwaters across the species complex distribution (Fig. 1).

To evaluate the spatio-temporal overlap among the considered colonies of little shearwaters, we estimated the use of specific areas across the North Atlantic Ocean by mapping the occurrence of different taxa within every 200×200 km cell, separately during four annual periods (*i.e.*, January–March, April–June, July–September, October–December; Figs 3 & 4). We also calculated the spatial overlap between the areas used during each of these four periods (95% UDs; Table S4 in Appendix S2) between the three taxa using the 'kerneloverlap' function of the *adehabitatHR* package. To test the significance of overlaps, we first generated a null expectation by creating kernels from colony-paired data that had been randomly assigned using the same sample sizes as the original colonies and subsequently calculated the overlap. By randomizing this procedure 1,000 times, we determined whether observed spatial overlap was greater than expected by chance, and generated a *P*-value for each overlap (as the proportion of randomized overlaps that were smaller than the observed overlap; Breed *et al.*, 2006).

Environmental data and habitat modelling

All remote sensing products were extracted from NOAA CoastWatch (coastwatch.pfeg.noaa.gov/). We considered bathymetry (BAT, m), surface chlorophyll *a* concentration (CHLa, mg m^{-3}), sea surface salinity (SAL, g of salt per kg of water), sea surface temperature (SST, °C), and wind speed (WIND, m s^{-1}). The static BAT variable and monthly composites of CHLa, SST, and WIND (dynamic variables downloaded for each year from 2007 to 2013) were rescaled to a common spatial resolution of 2°, which matches the average accuracy of geolocation data. Gradients for BAT, CHLa, and SST were also considered (BATG, CHLG, and SSTG, respectively). Within each year, monthly values of dynamic variables were averaged for the breeding and non-breeding periods, i.e., from December to April and from June to August, respectively (processing of the environmental data is detailed in Appendix S1). Habitat suitability models were developed through Ensemble Species Distribution Models (ESDM; Marmion *et al.*, 2009) using the function 'ensemble_modelling' from the package *SSDM* (Schmitt *et al.*, 2017). Diverse modelling algorithms (GAM, MARS, GBM, CTA, RF, MaxEnt, ANN, and SVM) were conducted with non-redundant variables (with pairwise correlations [r] < 0.6) for each colony, taxon and season (20 models in total; Table 4): BAT, BATG, CHLa, CHLG, SST, SSTG, and WIND. The participation of each algorithm to the final ensembled model was weighed by its Area Under the Curve (AUC, Fielding and Bell 1997) statistic (Table 4; details in Appendix S1). From ESDMs, we first evaluated consistency or plasticity in the habitat preferences throughout the annual cycle of each taxa. Second, we also projected potential breeding habitats of each taxon using non-breeding ESDMs of other taxa (i.e., fitting non-breeding ESDMs with those selected environmental variables but estimated for the breeding season; Table 5 & Fig. 5), with the ultimate goal of unravelling different marine habitat preferences among taxa. The approach of projecting breeding habitat with non-breeding models allude to the idea that birds during the non-breeding period behave with no environmental constraints imposed by breeding duties and their habitat preferences should clearly reflect those that the species is more adapted for.

Analysis of activity data

Geolocators record immersion in sea water every 3 seconds using 2 electrodes, and provide a value (0 to 200) corresponding to the sum of positive tests in each 10-minute period. These data can be transformed to the proportion of time the logger is immersed (*i.e.*, wet) indicating the bird is on the sea surface or diving. Time in 'wet' mode cannot distinguish between these two states (i.e., inactive on the water surface or actively foraging via pursuit diving; Brown, Bourne, & Wahl, 1978; Burger, 2001) although we expect that time spent diving to be much shorter than the resting time (Aguilar *et al.*, 2003; Dean *et al.*, 2013; Péron *et al.*, 2013; Shoji *et al.*, 2016). Combining light and immersion data, we defined time spent incubating as those darkness periods in the burrow occurring during daylight, and, we therefore excluded such incubation periods from this analysis. However, other relevant breeding activities (in terms of daily time) occurred at the colony during darkness periods (i.e., nest-defence, pairing and chick-rearing duties) and cannot be distinguished from that time of flying, and therefore, they precluded us from using the time in dry mode as a proxy of behaviour.

To evaluate potential seasonal differences in the daily activity budgets among taxa, we first modelled the dynamics of time spent on the water throughout the annual cycle in the seven sampled colonies using LMMs with Gaussian error structure and an identity-link function, and considering sampled colony (nested within taxon), year and individual (nested within colony) as random effects (Table S5 in Appendix S2). We evaluated the associations between taxon, annual season and daylight (i.e., day or night) factors with the time spent on water. For visualisation we also modelled activity budgets using Generalized Additive Mixed Models (GAMM; Fig. 6) to differentiate behavioural patterns throughout the year in relation to different breeding stages (breeding, migrating, wintering). Filtering methods for the activity data, and LMM and GAMM selection procedures are described in Appendix S1. Finally, time spent in contact with salt-water at night during the non-breeding season was modelled against moonlight levels (obtained from the 'moonAngle' function in the *oce* package of R (Kelley, 2018) as percentage of illuminated moon, i.e., from 0 during a new moon to 100% during a full moon) in a similar LMM framework (Table 4), and using locally-weighted non-parametric regressions at colony level (Fig. S5 in Appendix S2; Jacoby, 2000).

RESULTS

Morphometrics and size

Body size differed among little shearwaters from the eight colonies sampled (Table 2). Even though measurements were taken by different researchers within a given taxon, and a slight bias could be thus introduced, PLHE were consistently and significantly heavier and larger in their culmen, tarsus and wing lengths than PBAR and PBOY, and PBAR displayed the shortest wing length among the three taxa (Fig. S1 in Appendix S2). The eight colonies we sampled were subsequently grouped by taxon according to their body size (i.e., tarsus and wing lengths) in the similarity tree (Fig. S2 in Appendix S2).

Spatio-temporal distribution

The recovery rate of geolocators deployed was 62.3% (43/69) for PLHE, 51.6% (33/64) for PBAR and 53.0% (53/100) for PBOY (Table S1 in Appendix S2). We obtained 99 complete tracks from 76 individual shearwaters (PLHE n = 22, PBAR n = 32, PBOY n = 45; Table S3 in Appendix S2). After filtering, we obtained 48,097 positions, of which 52.5% and 47.5% were assigned to breeding and non-breeding periods, respectively. Representativeness analysis revealed that all datasets (grouped by colony and season) adequately represented the spatial variability of target colonies (Table S2 in Appendix S2). In addition, spatial overlaps among individuals of the same colony and year of sampling were relatively high, and, as expected, they were higher during the breeding than during the non-breeding period (Table S4 in Appendix S2). Overall, these results not only highlighted the representativeness of our datasets, but also the relatively small and consistent range of the foraging areas used for each colony. However, although the spatial distributions of these populations are representative and relevant, PLHE from Bahamans and PBAR from the Azores, in particular, should be treated with caution because their assessments were derived from only a few available tracks.

At the species complex level, adult little shearwaters occur widely across the North Atlantic Ocean, with an obvious gap along the Sargasso Sea, and with a higher concentration of shearwaters along the Gulf Stream in the western North Atlantic (Fig. 1). The concentration of birds along the Gulf Stream is likely due to that the Bahamas Archipelago supporting larger breeding populations compared to other regions and taxa in this study (Mackin, 2016).

There was substantial variation in timing of migration (Fig. 2) and in the spatial characteristics of non-breeding distributions among and within taxa (Fig. 3). Based on AICc values, the best-supported models explaining these differences always included taxon as a variable (Table 3). In addition, the random term for colony accounted for a relevant proportion of the total variance in most cases. In contrast, little to no variability was accounted for by the year effect. Timing of breeding and migration appeared to differ among the three taxa in a few weeks. PBOY initiated breeding earliest (Fig. 2), arriving at the colony in late August and departing in early May. Timing was consistent between the two colonies of PBOY we sampled (Table 3 & Table S3 in Appendix S2). PBAR showed more variable arrival dates at the colony depending on the sampled colony and ranging from early October to mid-December, while departure dates appeared to be similar among the three sampled colonies and occurred in mid-May. PLHE initiated breeding the latest among the species sampled, but dates varied from mid-September to mid-December among colonies. Departure dates occurred primarily in mid-June for PLHE. The duration of the breeding season was similar in PLHE and PBOY (242 ± 46 and 247 ± 16 days, respectively, as median ± SE), but much shorter for PBAR (194 ± 50 days on average). The distance between breeding colonies to the centroid of the core non-breeding area was greater in PLHE and PBOY compared to PBAR (Table 3). PBAR showed the shortest distance to the centroid of the non-breeding area, although it had the longest non-breeding period (Table 3).

At the population level, distributions of all sampled colonies were concentrated within 500 – 600 km of the colony during breeding seasons, although a few PBAR from Madeira and Azores also visited an area between the Azores and Iceland, around the Charlie-Gibbs Fracture Zone in the Mid-Atlantic Ridge (either early or late in the breeding season; Fig. 3d). Throughout the breeding season, there was a slight spatio-temporal overlap among colonies of PBAR and PBOY (0.2-13.8%; Fig. 3 & Table S4 in Appendix S2) within different oceanic areas in Macaronesian waters. Both sampled colonies of PBOY shared non-breeding habitat in a relatively restricted area in the mid-equatorial Atlantic Ocean, north of the Saint Peter and Saint Paul archipelago (0°55’ N, 29°20’ W; hereafter Saint Paul’s Rocks). Populations of PBAR also shared common non-breeding areas, although there was a slight tendency for segregation between birds from Salvages (mostly using the Canary Current) and those from Azores and Madeira (inhabiting Azorean and Iberian-Portuguese waters; Fig. 3). The two sampled colonies of PLHE segregated completely, not only during the non-breeding period but also throughout the year (Table S4 in Appendix S2). Interestingly, PLHE and PBOY overlapped slightly during the non-breeding season (July-September; 1.6-8.4%) along the Amazon reef located off the mouth of the Amazon River (Fig. 3). Finally, spatial overlaps between distribution estimates of all sampled colonies related exponentially to the geographic distance between such colonies year-round (Fig. 4).

Habitat modelling

The AUCs obtained from the ESDMs were generally large. The importance of each variable and its contribution to the models differed among taxa, colonies, and seasons (Table 4). The environmental determinants that most explained distributions of little shearwaters during the breeding season varied among the three taxa (Table 4). The overall breeding distribution of PLHE was most strongly related to BATG; of PBAR to SAL and SST; and of PBOY to BATG and SAL. In contrast, the non-breeding distributions of most colonies of little shearwaters were influenced by BATG and SST (Table 4). PBOY, as well as colonies of PBAR from the Azores and Madeira, used shallow areas, while PLHE and the colony of PBAR from the Salvages used steeper areas near the American and African continental shelves, respectively (Fig. S4a in Appendix S2). Similarly, each taxon inhabited a certain range of SST, PLHE using the warmest waters, PBAR using the coldest ones, and PBOY using mid-range temperatures of the sea (Fig. S4b in Appendix S2). Finally, suitable breeding habitats for each taxon, as derived from non-breeding ESDMs, did predict well neither breeding foraging areas of that taxon nor those of other taxa (Table 5 & Fig. 5). This result was particularly acute for PBOY and their respective sampled colonies. Only non-breeding ESDMs for PBAR and their respective sampled colonies seemed to predict reasonably well their breeding distributions as well as those of other taxa (Table 5).

At-sea activity

Analysis of at-sea activity patterns revealed heterogeneity among taxa, seasons, and daylight and darkness periods, as well as a slight influence of moonlight on activity during the non-breeding season (Table S5 in Appendix S2). The proportion of time on water was highest in PBOY compared to the other taxa. All three taxa, however, spent more time on water during the non-breeding season (year-round activity in Fig. 6 and Table S5 in Appendix S2), and time on water decreased considerably around dawn and dusk year-round (circadian activity in Fig. 6). Nocturnal activity during the non-breeding season was influenced by moonlight in PLHE and PBOY (Table S5 in Appendix S2); birds tended to be slightly more active during moonlit nights, and flew less on nights close to the new moon (Fig. S5 in Appendix S2). In all cases, individual variability was higher than any other random effect we considered, and neither colony nor year of sampling contributed to this variability (Table S5 in Appendix S2).

DISCUSSION

Spatio-temporal segregation and colony distances among little shearwaters of the North Atlantic

All little shearwater populations performed short-distance migrations from their respective breeding sites to non-breeding areas, most of them within the North Atlantic Ocean. The three taxa distributed across the North Atlantic, with clear avoidance of the oligotrophic waters of the Sargasso Sea. Specific oceanographic features of this area could make it uninhabitable by these species; however, other seabird species such as White-tailed Tropicbirds (*Phaethon lepturus*; Mejías *et al.*, 2017) and Trindade petrels (*Pterodroma arminjoniana*; Ramos *et al.*, 2017) are known to exploit this vast area of the North Atlantic. In addition, assuming the meridional limit of the North Atlantic Ocean lies at 8ºN (e.g., Stramma & England, 1999), three of the tracked colonies used waters at South/Central Atlantic during the non-breeding season. Thus, contrary to what was assumed for the taxa (Sinclair, Brooke, & Randall, 1982; Austin *et al.*, 2004), the species complex (or the low-level clade composed by PLHE, PBAR and PBOY) is not strictly resident of the North Atlantic Ocean. Finally, we caution that our data from little shearwaters in the North Atlantic (i.e., Fig. 1) are based solely on adult birds, and that movements of birds in their early life stages, i.e., inexperienced juveniles and immatures, which can represent a relevant percentage of the entire population of long-lived species (e.g., Tuck *et al.*, 2015), are so far unknown.

The colonies of little shearwaters we studied segregated clearly in space during the non-breeding period, with specific foraging grounds for colonies of different taxa, but also for some colonies within the same taxon. The two surveyed colonies of PBOY shared common breeding and non-breeding areas around the colony and in the mid-Atlantic, respectively. In contrast, the breeding and non-breeding habitats were segregated, partially or completely, between colonies within PBAR and PLHE. Variability in non-breeding destinations was relatively low among individuals of the same colony, in most cases migrating to and exploiting a common single non-breeding area. As expected, the observed spatial segregation between colonies and taxa during the non-breeding period was explained by the relatively large distances among colony sites (Fig. 4) and generally modest movements between the non-breeding grounds and the breeding colony. This short-distance migratory behaviour of little shearwaters is consistent with their short wings and relatively high wing loading (Warham, 1990). This morphology allows little shearwaters to dive efficiently but limit their long-distance movements based on a flapping and heavy flight (Hedenström, 1993). Alternatively, their parapatric distribution, both during the breeding and non-breeding periods, may also be explained by the need to avoid heterospecific and conspecific competitors (Cairns, 1989; Wakefield *et al.*, 2013). Either direct or indirect competition for limited resources at sea may imply costs in terms of reduced foraging efficiency, which would promote segregation in habitat use by birds from different colonies in terms of time (Friesen *et al.*, 2007b), space (González-Solís, Croxall, & Afanasyev, 2008) or diet (Wilson, 2010). However, current population size estimates of most populations of little shearwaters of the North Atlantic are rather small (see Table 1) and, therefore, do not provide support for concluding competition underlies the current distribution of birds from sampled colonies during the non-breeding season. Nevertheless, this possibility should not be completely dismissed given that the current distribution of these birds may reflect historic competition when populations were larger and more broadly distributed. Finally, and to be conclusive on this hypothesis (i.e., intra-specific competition as a key feature when explaining the non-breeding distributions of different colonies), additional sampling should be considered; for example, tracking individuals from colonies of the Greater Antilles, the Canary Islands and other islands of Cabo Verde for PLHE, PBAR, and PBOY, respectively.

Overall, the segregation pattern we described for each taxon should be taken into account when discussing the genetic diversity of the taxa we studied, as we would expect genetic differentiation to be higher among colonies that clearly segregate in space than among colonies sharing non-breeding grounds, and therefore, sharing habitat preferences (Friesen, 2015).

Predicting spatio-temporal distributions of little shearwaters

The aforementioned spatial segregation between colonies and taxa could also result from habitat specialization. Differing body sizes among taxa suggested a certain degree of specialization and differential environmental preferences while foraging (Sausner *et al.*, 2016; Fischer *et al.*, 2018; Masello *et al.*, 2019). Habitat suitability models of the non-breeding season, when birds are not constrained by central-place foraging, suggested that the slope of the sea floor and the sea surface temperature (i.e., BATG and SST in Table 4) influenced the distribution of most shearwater populations. In general, specific ranges of these variables existed for each taxon during the non-breeding season. These habitat specializations, the absence of overlap between the main foraging grounds of the three taxa, and the fact that ESDMs of a certain taxon did not predict distributions of another taxa, could be the result of divergent ecological adaptations of each colony/taxon to specific prey adapted to differential oceanic features (Mindel *et al.*, 2016; Hidalgo *et al.*, 2017), a factor that could contribute to or ultimately result in speciation. However, the fact that non-breeding ESDMs of a certain taxon did not predict well the breeding distribution of such a taxon is incompatible with the hypothesis of existence of a robust ecological differentiation between the three little shearwaters from the North Atlantic. These results clearly suggested that birds, colonies and taxa face very different environments year round and they can adapt their plastic foraging behaviour to such differential circumstances. Overall, based on our environmental modelling approach, we can conclude that little shearwaters are able to forage in a vast array of marine habitats, presumably, independently of their taxonomic status.

Phenology and foraging behaviour of little shearwaters

We reported that little shearwaters of the North Atlantic breed during the Northern Hemisphere cool season, from September to May-June. Cold-season breeders in subtropical regions of the Atlantic are rather rare, particularly among marine vertebrates (Friesen *et al.*, 2007b; Ramos *et al.*, 2016). Breeding during the cold season may be an ancestral adaptation of the species to avoid other abundant competitors for food at sea or burrows at the colony site, as Bulwer's petrels (*Bulweria bulwerii*), Cory's shearwaters (*Calonectris borealis*), and Cape Verde shearwaters appear to do (*C. edwardsii*; Ramos *et al.*, 1997; Fagundes *et al.*, 2016; Paiva *et al.*, 2016). However, this hypothesis is unlikely to apply given that PLHE does not compete with any other seabird for burrows, but shows a similar phenology to PBAR and PBOY. We would predict the species would rapidly respond to this lack of competition by shifting their breeding period if the current phase was suboptimal. Independently of the origin and cause of such breeding schedule, we found rather similar phenological calendars among the three taxa, only displaced by approximately one month depending on the taxon.

Activity of little shearwaters at sea was also similar among colonies and the three taxa, although it varied throughout the annual cycle. As expected, little shearwaters spend longer periods on the water surface during the non-breeding phase, when they are relieved from their breeding duties and they only need to forage for self-provisioning. However, we found slight differences in the proportion of time spent on the water among colonies that might be explained by some differential environmental features at the specific foraging grounds of each colony. For instance, birds from colonies exploiting neritic waters (i.e., both colonies of PLHE and PBAR from Salvages) tended to spend more time flying compared to birds from colonies inhabiting oceanic areas (i.e., PBOY and PBAR from Azores and Madeira). This confirms the aforementioned behavioural plasticity among taxa (see the previous section) and even between colonies of the same taxon when facing different foraging habitats (Neves *et al.*, 2012; Paiva *et al.*, 2016).Similar circadian behaviour was also reported for each colony and taxon. Flight behaviour remained relatively low and constant throughout daytime and night-time for both seasons of any taxa. However, foraging activity clearly increased during crepuscular hours. These crepuscular behaviours of all little shearwaters suggest that the three taxa rely on such DVM prey, which are more accessible near the surface when light intensities are high enough to allow prey detection and (i.e., during both twilight periods; Regular *et al.*, 2010). In this regard, other seabirds such as Bulwer's petrels and other larger shearwaters (such as Cory's and Cape Verde shearwaters) might not be able to dive deep enough to capture such prey during twilight periods (Monteiro *et al.*, 1996; Mougin & Mougin, 2000). Thus, our data suggested that the three taxa shared prey preferences across their breeding range (mostly relying on DVM prey), although a certain degree of foraging specialization may still exist among the different exploited habitats (i.e., neritic vs. oceanic).

Overall, the similarity in breeding phenology, and both year-round and circadian foraging behaviours among taxa could suggest either similar environmental constrictions at each breeding site that could condition these schedules, or alternatively, a relatively recent evolutionary divergence among the taxa that still preserve an ancestral calendar. Although our study concluded that taxa segregate clearly in space and in marine habitat along the North Atlantic, the similar phenology and at-sea activity budgets throughout colonies and taxa should reflect a relatively recent evolutionary divergence among the three little shearwaters of the North Atlantic.

Phylogeographic and conservation implications

Identifying cryptic and recently-divergent taxa can have important conservation implications (Bickford *et al.*, 2007). Three intrinsic factors that are non-exclusive are often considered to contribute to population differentiation in seabirds (Friesen *et al.*, 2007a; Friesen, 2015): high philopatry, spatio-temporal segregation of foraging areas used year-round, and breeding asynchrony. Little shearwaters display strong natal philopatry and breeding-site fidelity (Precheur *et al.*, 2016). Our results showed that the three taxa performed short-distance migrations and essentially segregated completely in foraging areas during breeding as well as in non-breeding areas (displaying a parapatric distribution during breeding and non-breeding periods). However, our results also showed that the three taxa share similar phenologies, similar foraging habits (both daily and annually), and that specific populations of different taxa displayed similar ecological and behavioural specializations to different marine habitats. Moreover, based on our environmental modelling we concluded that individuals and colonies of little shearwaters are able to behave plastically year-round and adapt to very different marine habitats, diminishing importance of habitat specialization to that potential ecological differentiation/speciation. Thus, while some of these factors may restrict gene flow among populations of little shearwaters (i.e., high philopatry, and spatio-temporal segregation) and suggest the existence of three distinct ESUs, others alternatively indicate population homogenization (i.e., breeding synchrony, similar phenology, ecological plasticity as well as similar at-sea behaviour). The inconsistencies in the ecological evidence we provided here are in line with previous genetic results suggesting a recent evolutionary divergence of the three taxa (Austin *et al.*, 2004). Such inconsistencies claim for more genome-wide comparative data on the studied populations that would benefit and solve the present question about the taxonomic status of these shearwaters. The Little-Audubon's shearwater complex is currently classified as Least Concern by the IUCN, but if genetic analyses supported three distinct ESUs, then smaller effective population sizes would be likely for each taxon and subsequently a re-evaluation of the current conservation status of these taxa would be warranted.

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Table 1. Little shearwaters from the North Atlantic Ocean (*Puffinus lherminieri-baroli-boydi* complex). Geographical characteristics of sampled populations, minimum estimated breeding pairs, conservation status (assessed regionally, according IUCN Red List of Threatened Species, version 3.1) and approximate breeding period of their main populations. The seven-sampled populations included in the study are depicted in bold.

Taxon	Breeding population	Sampled colony	Longitude (°)	Latitude (°)	Estimated population (in pairs)	Population status	Breeding period	Reference
Audubon's shearwater	Bermuda Archipelago				Extirpated	Extinct	?	Mackin, 2016
Puffinus lherminieri **(PLHE)**	**Bahamas Archipelago**	Exumas, Cay Sal Bank	-76.69	24.42	12,350	Least Concern	Mar-Jul	Mackin, 2016
	Greater Antilles (Cuba, Puerto Rico)				790	?	Mar-Jul	Rodríguez et al., 2008
	Lesser Antilles (Virgin Islands to Panama Coast)	Hardy Islet (Martinique)	-61.83	14.42	175	?	Jan-Jun	Lowrie et al., 2013
	islands off the coast of Brazil				10–15	Critically Endangered	Jun-Oct	Mestre et al., 2009 / Lopes et al., 2014
Barolo shearwater	**Azores Archipelago**	Vila Islet (Santa Maria)	-25.17	36.94	840–1,530		Oct-May	Monteiro et al., 1999
Puffinus baroli **(PBAR)**	**Madeira Archipelago**	Cima Islet (Porto Santo)	-16.32	33.08	150–300		Dec-May	Paiva et al., 2016
	Salvages Archipelago	Selvagem Grande	-15.87	30.14	1,383–3,689		Dec-May	Fagundes, unpublished data
	Canary Archipelago				400			Rodríguez & Rodríguez, 2009
Boyd's shearwater	**Cape Verde Archipelago**	Raso Island	-24.60	16.61	5,000	Endangered	Jan-Jun	Brooke, 2004
Puffinus boydi **(PBOY)**		Cima Islet (Brava)	-24.64	14.97				

Table 2. Seven morphometric characteristics and mass (mean ± SD) of little shearwaters sampled at nine breeding locations throughout the breeding distribution of the involved taxa. Notice that two sampled colonies do not include geolocation data (Tobago and Canary Islands).

Taxon	Sampled colony	n	Culmen (mm)	Maximum bill depth (mm)	Bill depth at nostril (mm)	Bill-head (mm)	Tarsus (mm)	Wing length (mm)	Wing span (mm)	Mass (g)
Audubon's shearwater (PLHE)										
	Bahamas	745	29.7 ± 1.3	NA	NA	NA	41.7 ± 2.4	205.1 ± 4.9	NA	215.3 ± 21.5
	Martinique	52	28.5 ± 1.2	6.9 ± 0.5	NA	NA	41.2 ± 1.2	207.2 ± 4.8	NA	209.9 ± 15.2
	Tobago	32	29.8 ± 1.4	NA	NA	NA	NA	203.7 ± 4.4	NA	223.6 ± 17.0
Barolo shearwater (PBAR)										
	Azores	48	25.4 ± 0.9	8.1 ± 1.2	5.8 ± 0.6	65.0 ± 1.5	37.6 ± 0.9	181.1 ± 3.6	605.8 ± 11.7	170.7 ± 15.5
	Madeira	67	NA	NA	NA	NA	37.3 ± 0.9	182.6 ± 3.8	NA	169.3 ± 17.1
	Salvages	74	NA	NA	NA	NA	36.7 ± 0.9	181.1 ± 3.9	NA	162.3 ± 14.8
	Canary	15	25.4 ± 0.9	8.5 ± 0.4	5.8 ± 0.4	65.1 ± 1.6	37.1 ± 0.7	182.6 ± 2.8	613.8 ± 4.6	182.1 ± 13.0
Boyd's shearwater (PBOY)										
	Raso	142	25.3 ± 1.0	8.8 ± 0.6	6.1 ± 0.5	63.6 ± 1.6	37.4 ± 1.1	187.9 ± 4.1	627.7 ± 11.4	163.5 ± 17.5
	Cima	91	25.1 ± 1.1	8.8 ± 0.5	5.8 ± 0.4	62.9 ± 1.7	37.1 ± 1.0	186.1 ± 3.7	622.0 ± 11.1	151.3 ± 14.9

Table 3. Linear Mixed Models (LMM) testing for taxon effect on five migration characteristics of little shearwater from seven North Atlantic colonies. (a) Results of Akaike's Information Criterion (AIC) analysis for the two competing models: with and without taxon factor. Values refer to AIC adjusted for small sample sizes (AICc). The best-supported model (in bold) included in all the five cases taxon as a fixed effect. (b) Parameter estimates (± Standard Error, SE, or Standard Deviance, SD) from the best-supported taxon-dependent LMMs. All evaluated models included sampled colony (nested within taxon) and year of sampling as random effects.

a)	Colony departure date	Colony arrival date	Duration of the non-breeding period (days)	Area of the non-breeding period (10^6 km^2)	Non-breeding range (distance from colony; in km)
AICc					
Taxon	**865.5**	**1010.1**	**996.6**	**912.5**	**1477.8**
Constant	918.9	1076.8	1041.5	946.6	1530.5
b)					
Fixed effects (estimate ± SE)					
PLHE	15 Jun ± 5.7	02 Nov ± 18.8	136.6 ± 16.1	33.5 ± 8.8	1326.5 ± 247.4
PBAR	15 May ± 4.9	30 Oct ± 15.1	168.8 ± 12.9	58.1 ± 7.0	798.4 ± 200.0
PBOY	04 May ± 4.6	28 Aug ± 17.1	117.4 ± 14.5	37.1 ± 7.5	1433.1 ± 230.3
Random effect (variance ± SD)					
Sampled colony (within taxon)	96.5 ± 9.8	492.1 ± 22.2	348.9 ± 18.7	78.5 ± 8.9	86073 ± 293
Year	0.0 ± 0.0	36.3 ± 6.0	0.0 ± 0.0	16.9 ± 4.1	27298 ± 165
Residual	315.9 ± 17.8	1436.6 ± 37.9	1275.7 ± 35.7	536.0 ± 23.2	168981 ± 411

Table 4. Estimates of model fit and relative importance (contribution percentage) of the environmental variables to the probability of occurrence of each colony and taxon (values over 15.0% in bold). Separate models were built for each breeding (from December to April; DJFMA) and non-breeding (June to August; JJA) periods. AUC: area under the receiver operating characteristic curve; BAT: bathymetry; BATG: gradient of BAT; CHLa: chlorophyll *a* concentration; SAL: salinity; SST: sea surface temperature; WIND: wind speed.

Locality/Taxon	period	AUC	BAT	BATG	CHLa	SAL	SST	WIND
Bahamas	DJFMA	0.752	8.7	**31.2**	3.8	**32.4**	10.8	13.1
Martinique	DJFMA	0.721	10.4	11.3	8.0	**41.2**	10.5	**18.7**
Azores	DJFMA	0.753	**26.6**	**33.6**	9.9	8.0	12.7	9.1
Madeira	DJFMA	0.712	12.3	11.7	8.9	10.6	**36.5**	**20.0**
Salvages	DJFMA	0.719	12.1	**38.9**	6.4	11.2	8.5	**22.8**
Cima	DJFMA	0.806	6.0	**15.9**	**21.0**	11.3	**20.9**	**24.9**
Raso	DJFMA	0.775	14.0	14.9	**20.8**	11.5	**26.9**	12.0
PLHE	DJFMA	0.827	6.4	**41.7**	4.0	**19.7**	14.8	13.3
PBAR	DJFMA	0.911	4.0	11.2	8.7	**22.9**	**47.4**	5.8
PBOY	DJFMA	0.934	13.3	**29.0**	12.1	**21.6**	7.0	**17.0**
Bahamas	JJA	0.801	9.1	**25.7**	4.8	8.5	**37.7**	14.1
Martinique	JJA	0.785	8.5	**16.9**	8.2	**17.3**	**30.1**	**19.0**
Azores	JJA	0.770	12.1	**35.6**	5.0	12.7	**25.4**	9.2
Madeira	JJA	0.769	**24.5**	12.8	8.7	9.4	**36.6**	7.9
Salvages	JJA	0.740	**18.4**	**27.1**	4.7	**17.2**	**27.9**	4.8
Cima	JJA	0.773	9.5	6.1	9.8	**19.2**	**39.6**	**15.7**
Raso	JJA	0.780	14.1	**15.9**	10.7	**33.9**	**15.3**	10.1
PLHE	JJA	0.891	7.7	**50.4**	7.1	14.2	3.9	**16.7**
PBAR	JJA	0.816	**16.0**	**15.8**	8.4	9.8	**29.6**	**20.5**
PBOY	JJA	0.968	**15.5**	**16.5**	10.9	10.2	**26.1**	**20.8**

Table 5. Evaluation of non-breeding habitat suitability models (10 models computed for JJA and detailed in Table 4) projected to the breeding period (DJFMA) of all seven sampled colonies, including projections at taxa level (i.e., PLHE, PBAR, and PBOY). Average values of presence probability (p as mean ± SD) estimated from breeding-projected non-breeding habitat suitability models for the geographic locations recorded during the breeding period range from 0 (null habitat use estimation) to 1 (excellent habitat use estimation).

Locality/Taxon for the **non-breeding** model projections	Locality/Taxon for the **breeding** positions	Average p
Bahamas	Bahamas	0.57 ± 0.16
	Martinique	0.29 ± 0.08
	Azores	0.48 ± 0.07
	Madeira	0.57 ± 0.10
	Salvages	0.64 ± 0.08
	Cima	0.44 ± 0.14
	Raso	0.53 ± 0.11
Martinique	Bahamas	0.12 ± 0.05
	Martinique	0.51 ± 0.19
	Azores	0.11 ± 0.05
	Madeira	0.08 ± 0.04
	Salvages	0.06 ± 0.04
	Cima	0.10 ± 0.06
	Raso	0.08 ± 0.05
Azores	Bahamas	0.11 ± 0.11
	Martinique	0.05 ± 0.04
	Azores	0.57 ± 0.13
	Madeira	0.47 ± 0.21
	Salvages	0.34 ± 0.21
	Cima	0.28 ± 0.15
	Raso	0.30 ± 0.17
Cima	Bahamas	0.25 ± 0.18
	Martinique	0.53 ± 0.12
	Azores	0.05 ± 0.03
	Madeira	0.06 ± 0.05
	Salvages	0.06 ± 0.05
	Cima	0.28 ± 0.21
	Raso	0.18 ± 0.15
Raso	Bahamas	0.24 ± 0.09
	Martinique	0.48 ± 0.11
	Azores	0.27 ± 0.05
	Madeira	0.20 ± 0.07
	Salvages	0.14 ± 0.08
	Cima	0.38 ± 0.14
	Raso	0.29 ± 0.12
PLHE	PLHE	0.24 ± 0.08
	PBAR	0.12 ± 0.05
	PBOY	0.10 ± 0.03
PBAR	PLHE	0.22 ± 0.13
	PBAR	0.55 ± 0.15
	PBOY	0.48 ± 0.20
PBOY	PLHE	0.01 ± 0.01

Madeira	Bahamas	0.66 ± 0.15
	Martinique	0.38 ± 0.09
	Azores	0.74 ± 0.10
	Madeira	0.81 ± 0.11
	Salvages	0.89 ± 0.07
	Cima	0.59 ± 0.23
	Raso	0.72 ± 0.19
Salvages	Bahamas	0.64 ± 0.11
	Martinique	0.45 ± 0.12
	Azores	0.56 ± 0.11
	Madeira	0.65 ± 0.11
	Salvages	0.74 ± 0.08
	Cima	0.50 ± 0.17
	Raso	0.60 ± 0.15

PBAR	0.14 ± 0.02
PBOY	0.03 ± 0.01

FIGURES

Figure 1. Distribution of seven colonies of little shearwaters that breed in the North Atlantic Ocean (*Puffinus assimilis–lherminieri* complex). Grid map shows the number of locations that fall in each 2×2° cell (units in birds/cell), corrected by the sampling effort on the population of origin (i.e., total number of positions from that colony site) and multiplied by the size of that population of origin (see Table 1). Additionally, specific kernel density distributions (50% UDs) are depicted in continuous lines for the breeding season and in dash-dotted lines for the non-breeding season for each of the sampled colonies (in purples for PLHE, in blues for PBAR, and in greens for PBOY). The number of tracks of each sampled colony is shown in brackets. Coloured circles show the location of the respective breeding colonies. Small dark grey points show locations of colonies not sampled in this study. Exclusive Economic Zones (EEZs) are also shown in light grey dashed lines. The bird silhouette represents a PBAR, courtesy of Martí Franch.

Figure 2. Annual phenologies of the seven breeding colonies of little shearwaters that breed in the North Atlantic Ocean (*Puffinus assimilis–lherminieri* complex) that we sampled. Breeding period is depicted in orange and non-breeding period in blue (as median values). Additionally, individual values are plotted over each bar.

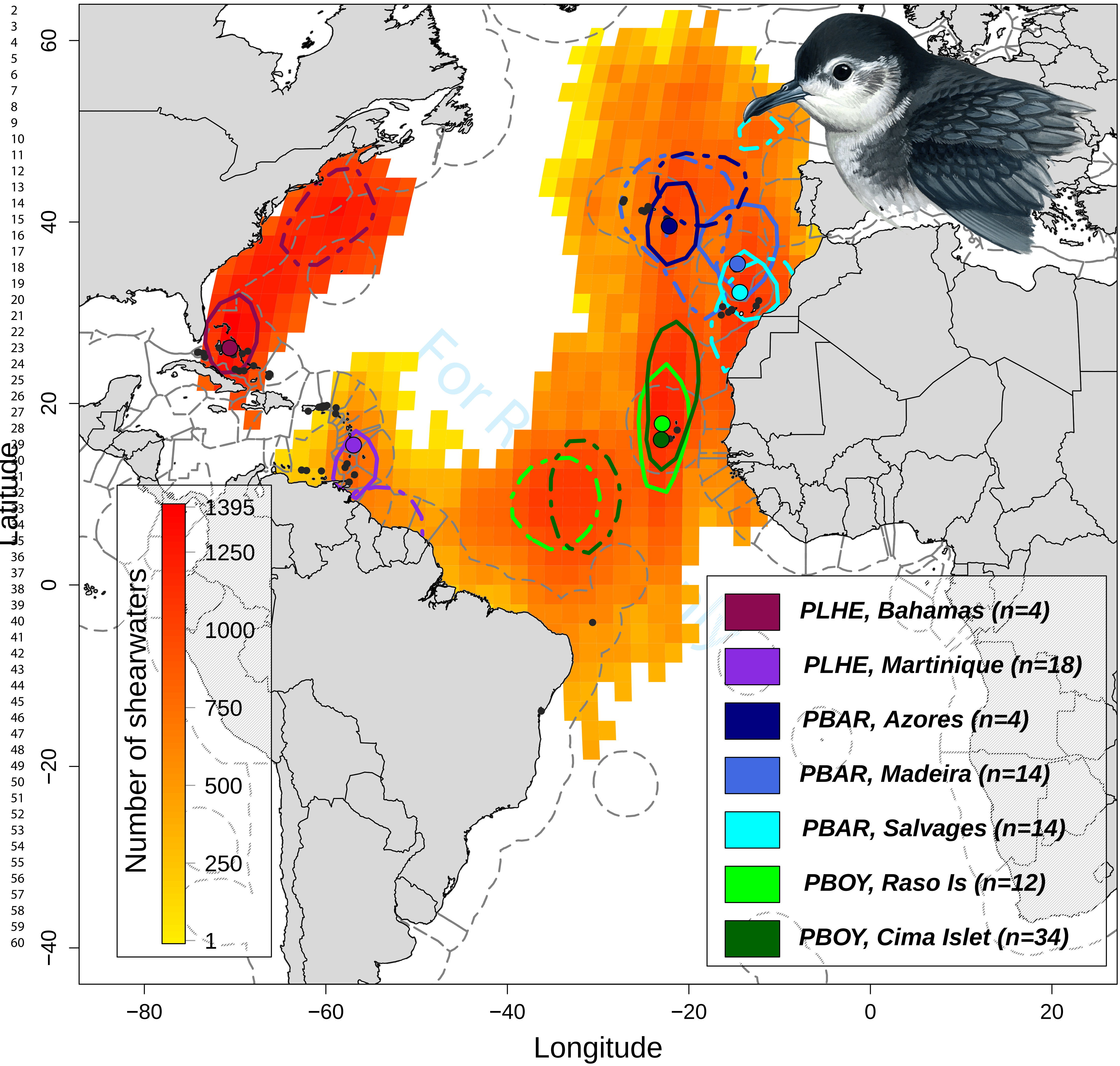
Figure 3. Spatio-temporal overlap among little shearwater that breed along the North Atlantic Ocean (in a, b, c and d, for January-March, April-June, July-September, and October-December periods, respectively). The number of taxa that overlap in every 2×2° cell is plotted as grid maps (light and dark orange for one and two taxa, respectively). Kernel density distributions (50% UDs) are also depicted on the respective grid map for each of the sampled colonies (in purples for PLHE, in blues for PBAR, and in greens for PBOY). Coloured circles show the location of the respective breeding colonies.

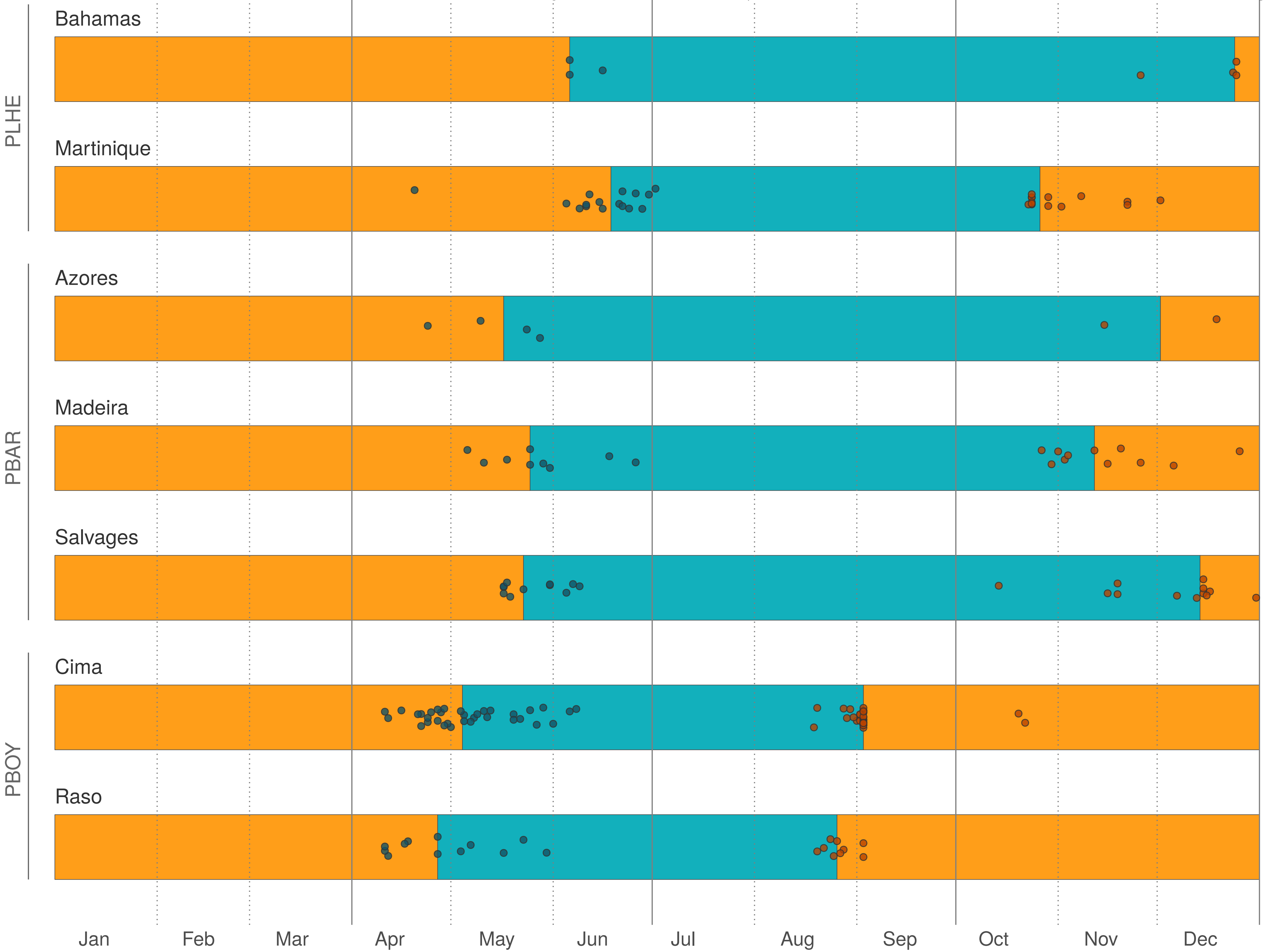
Figure 4. Estimated spatial overlap (in %) in the 95% kernel UDs of every pair of sampled colonies of little shearwater is shown for specific time periods against the distance between such pairs of colonies.

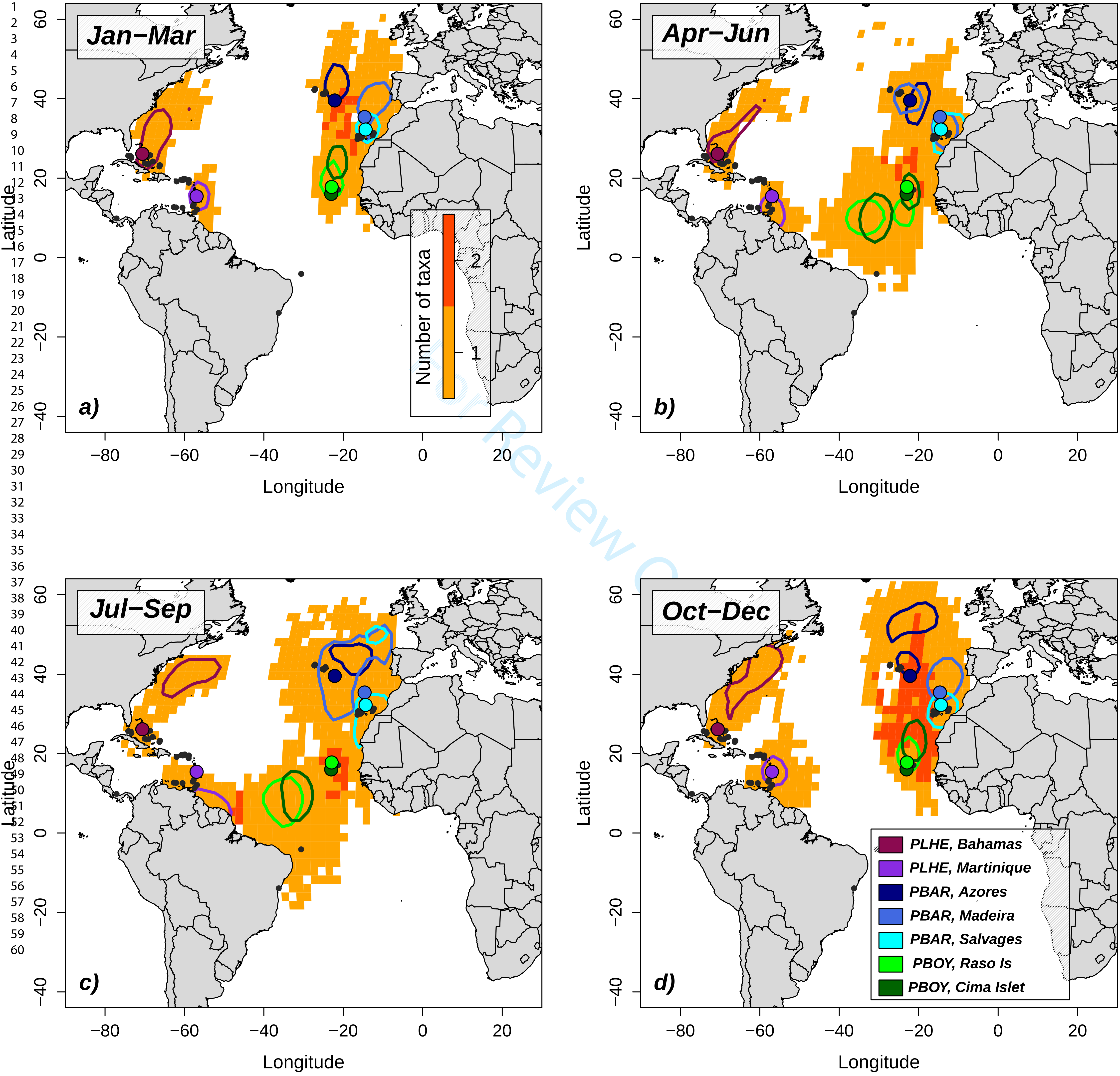
Exponential regressions for each period are displayed in coloured lines. Paired colonies belonging to the same taxon are displayed in thicker dots.

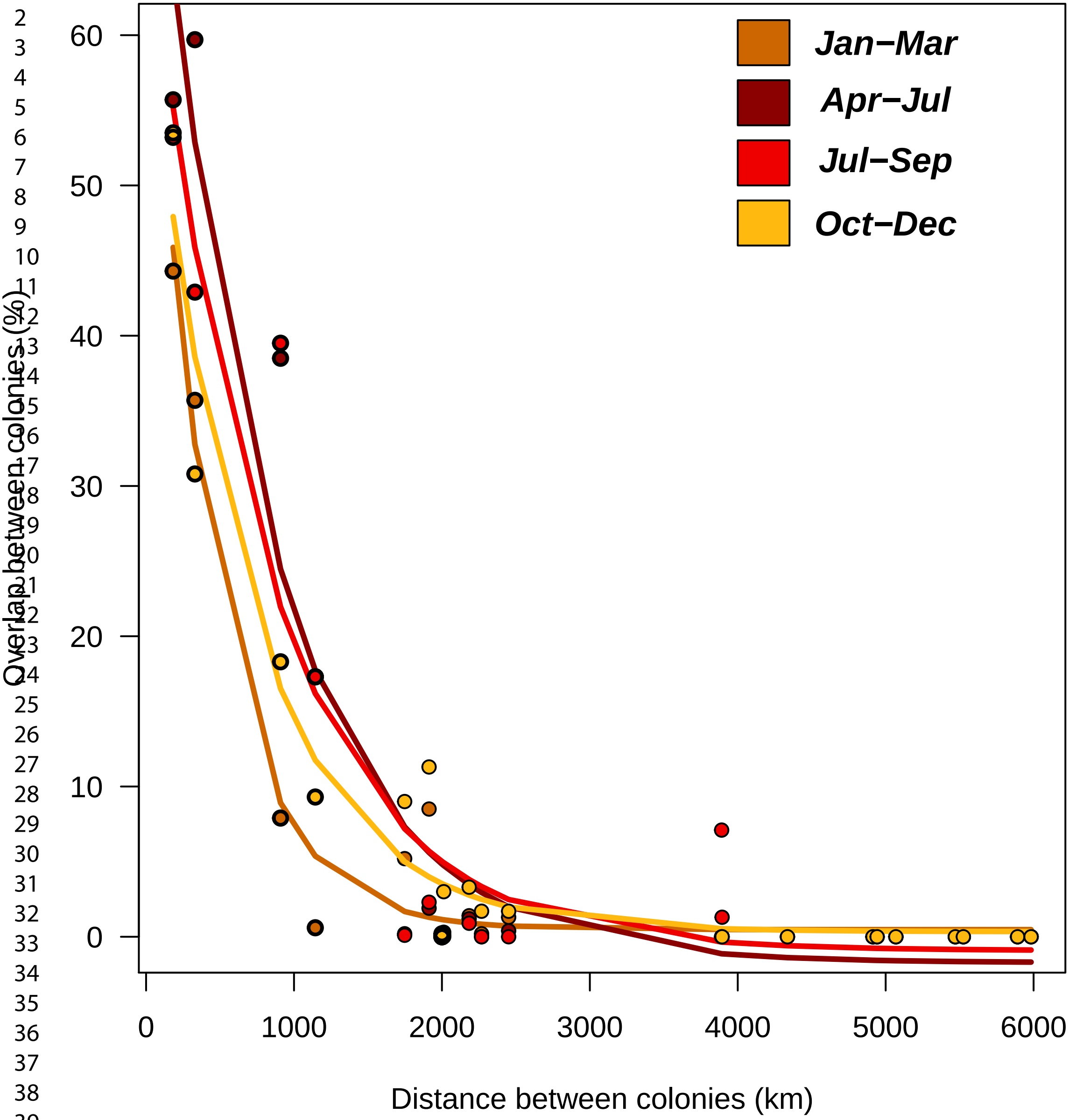
Figure 5. Spatial projection of the habitat suitability of PLHE (a), PBAR (b), and PBOY (c) for the breeding period. Initial habitat modelling was performed with the non-breeding positions of the individuals of each taxon and the environmental conditions of that non-breeding season. The three probability maps were built for the breeding season of each taxon using the respective and aforementioned non-breeding habitat models but fitted with the environmental conditions during the breeding season. Suitability values range from 0 (not suitable habitat) to 1 (most suitable habitat). 50%UD kernels of the breeding distribution of the taxa not included in each modelling were also depicted in continuous lines (in purples for PLHE, in blues for PBAR, and in greens for PBOY). Coloured circles show the location of those breeding colonies not included in the respective modelling.

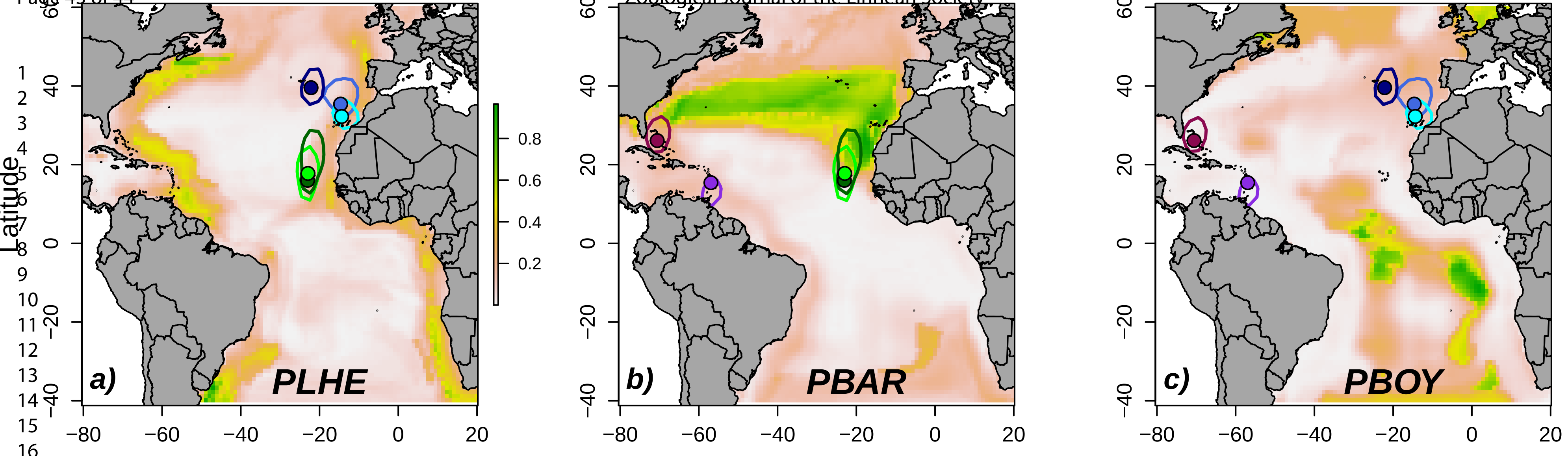
Figure 6. Daily activity budgets throughout the annual cycle (left-hand panels) for the PLHE (a) in purples, for PBAR (b) in blues, and for PBOY (c) in greens (different colour tones correspond to different sampled colonies). The solid lines correspond to the mean for each sampled colony estimated using Generalized Additive Mixed Models (GAMM), and the coloured regions around the means represent the associated 95% CI of the slopes. Raw data points are also plotted in the background. Coloured vertical lines correspond to mean dates of starting outward migrations (in dashed lines) and arriving at the breeding ground (in continuous lines) for each sampled colony. First dates in the burrow (estimated as the first day of every individual that the logger recorded 6 hours in continuous dry mode) are also shown as coloured ticks for every individual bird at the bottom of each subplot. Circadian activity (right-hand panels) is also modelled using GAMMs and shown as hourly time (in min) spent on the water, separately for breeding and non-breeding periods, for each sampled colony. Coloured vertical dashed lines correspond to mean of daily sunrise and sunset timings, for each sampled colony and period.

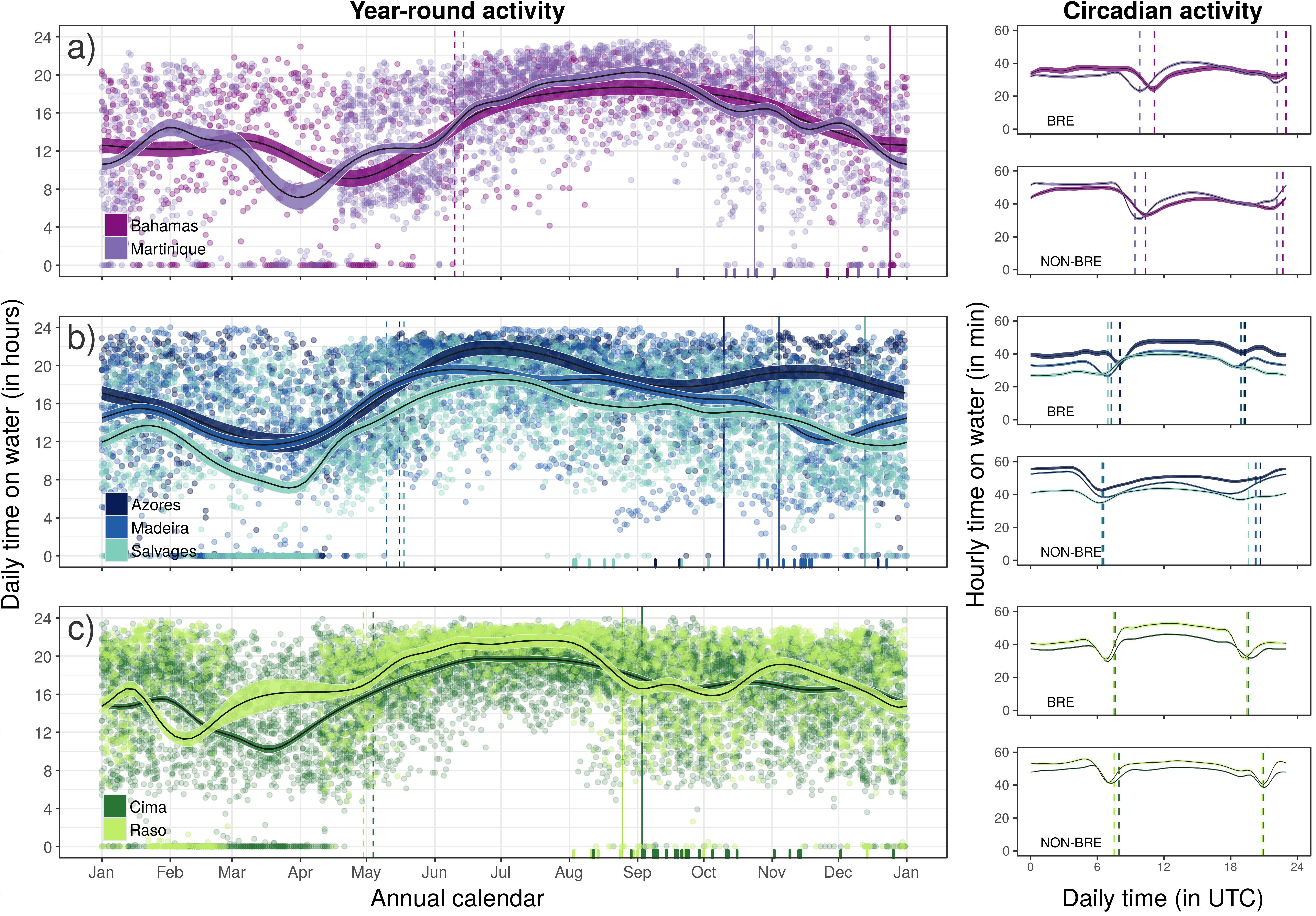

60
40
20
0
−20
−40
Latitude
−80
−60
−40
−20
0
20
Longitude
Number of shearwaters
1395
1250
1000
750
500
250
1
PLHE, Bahamas (n=4)
PLHE, Martinique (n=18)
PBAR, Azores (n=4)
PBAR, Madeira (n=14)
PBAR, Salvages (n=14)
PBOY, Raso Is (n=12)
PBOY, Cima Islet (n=34)


PLHE
Bahamas
Martinique
PBAR
Azores
Madeira
Salvages
PBOY
Cima
Raso
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec


Jan−Mar
Apr−Jun
Jul−Sep
Oct−Dec
a)
b)
c)
d)
Number of taxa
1
2
Latitude
Longitude
60
40
20
0
−20
−40
−80
−60
−40
−20
0
20
PLHE, Bahamas
PLHE, Martinique
PBAR, Azores
PBAR, Madeira
PBAR, Salvages
PBOY, Raso Is
PBOY, Cima Islet


Jan−Mar
Apr−Jul
Jul−Sep
Oct−Dec
Overlap between colonies (%)
60
50
40
30
20
10
0
0
1000
2000
3000
4000
5000
6000
Distance between colonies (km)


Latitude
60
40
20
0
−20
−40
−80
−60
−40
−20
0
20
0.8
0.6
0.4
0.2
a)
PLHE
b)
PBAR
c)
PBOY


Year-round activity
Circadian activity
a)
b)
c)
Bahamas
Martinique
Azores
Madeira
Salvages
Cima
Raso
BRE
NON-BRE
Daily time on water (in hours)
Hourly time on water (in min)
Annual calendar
Daily time (in UTC)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
0
4
8
12
16
20
24
0
20
40
60
0
6
12
18
24