Lower foraging efficiency in immatures drives spatial segregation with breeding adults in a long-lived pelagic seabird

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Competition and, ultimately, adaptive specialization are the major ecological forces behind spatial segregation in foraging distributions, and are commonly driven by size-related differences in competitiveness between individuals of different sex, age or social status. However, such segregation can also be observed in long-lived monomorphic species, often between immature and breeding individuals. In many of these species, individuals often forage in patchy and potentially unpredictable environments in which resources can be spread over large scales and be difficult to find, and efficient foraging may require advanced cognitive skills (for example in navigation and memory). Particularly in species with deferred breeding, experience rather than size may be an important driver of segregation and may lead to differences in competitiveness between young and old, but whether there is a relationship between age, foraging efficiency and spatial segregation has never been properly investigated. Here we tested this hypothesis by simultaneously tracking individuals at different life stages in a long-lived seabird, the Manx shearwater, *Puffinus puffinus*, during a period of central-place foraging around the colony, to investigate spatial segregation, and by measuring foraging efficiency by combining an ethoinformatics approach and mass gain. We found substantial spatial segregation between immature and breeding adults. Compared with adults, immatures gained less mass per unit of time spent foraging and foraged in less productive waters, suggesting lower foraging efficiency, probably because of inexperience.
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Spatial segregation in foraging distributions driven by competition, which can eventually lead to adaptive specialization, is observed in a wide range of animal taxa, and often arises from size-related differences in competitiveness between individuals of different sex, age or social status (e.g. Durant, Kelly, & Caro, 2004; Gosler, 1987; Harcourt, Stewart, & Fossey, 1976; Webb, Marzluff, & Hepinstall-Cymerman, 2012). Long-lived animals with advanced cognitive capacities (vertebrates) may be able to exploit patchy, expansive and potentially unpredictable environments using individual memory and experience. This could provide a different mechanism driving spatial segregation, even in monomorphic species, if older, more experienced individuals competitively displace younger cohorts through enhanced foraging efficiency. Higher adult foraging efficiency could result from two (not mutually exclusive) mechanisms: first, adults could have superior hunting skills, resulting in a higher food gain per unit of time spent foraging in areas of similar productivity; second, adults may exploit areas of higher productivity. Either hypothesis would lead to age-related differences in space use correlated with differences in foraging efficiency. Spatial segregation between immature (nonbreeding) and breeding adults during all or part of the year occurs in many species (e.g. primates: Harcourt et al., 1976; other mammals: Cheney & Seyfarth, 1983; Durant et al., 2004; Jarman, 1974; birds: Webb et al., 2012; insects: Robertson & Cushing, 2011). Immatures have been found to disperse more and cover larger ranges than breeders, although in some species they have been reported to undertake smaller-scale movements than adults (Field, Bradshaw, Burton, Sumner, & Hindell, 2005). Understanding such differences is of paramount importance when considering the

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demography of a species or its conservation needs. It has been suggested that spatial segregation between immature and adult individuals may be due to differences in foraging experience (Lack, 1954), and lower foraging efficiency has been documented in some species (Daunt, Afanasyev, Adam, Croxall, & Wanless, 2007; Lefebvre, 1995; Le Vaillant et al., 2012; Maclean, 1986). The relationship between efficiency and spatial segregation, however, has never been properly tested. Here we investigated this relationship in a long-lived pelagic seabird, the Manx shearwater, *Puffinus puffinus*. Pelagic seabirds, like many other marine animals, are long-lived, with a prolonged immature period. They forage in an open and patchy environment which can be unpredictable, depending on the type of marine habitat used and the spatial and temporal scales of their foraging trips (Weimerskirch, 2007). This may not only give them more opportunities to segregate, but also make learning and experience particularly important in the development of the skills necessary to forage effectively, for example to navigate to distant areas in a featureless environment, to identify and memorize productive areas and often ephemeral prey distributions. This makes them particularly useful model organisms to study stage-related spatial segregation and changes in foraging skills over time; however, few studies have attempted to do so, mainly because of the logistical challenges involved with tracking nonbreeding individuals. Very little is known about the behaviour and distributions of immature pelagic seabirds (Lewison et al., 2012; Shillinger et al., 2012). Studies in penguins, albatrosses and a few large procellariiforms have found that immature seabirds may be more flexible in their destinations and cover a larger range during nonbreeding (usually long-distance) movements in the winter (Clarke, Kerry, Fowler, Lawless, & Eberhard, 2003; Kooyman, Kooyman, Horning, & Kooyman, 1996; Kooyman & Ponganis, 2007; Pelletier, Chiaradia, Kato, & Ropert-Coudert, 2014; Péron & Grémillet, 2013; Sherley et al., 2013; Thiebot, Delord, Marteau, & Weimerskirch, 2014; Trebilco, Gales, Baker, Terauds, & Sumner, 2008). However, few have investigated their foraging movements during the breeding season when both adults and immatures act as central-place foragers (Péron & Grémillet, 2013; Riotte-Lambert & Weimerskirch, 2013; Votier, Grecian, Patrick, & Newton, 2011). During this period, stage-related spatial segregation is likely to arise: parental duties force adults to return to the colony regularly because of changes in the cost–benefit trade-offs of different foraging locations. While immatures are not constrained to a colony, they tend to visit their natal colony (or others), generally during a restricted part of the breeding season, to prospect for future nest sites and mates (Dittmann & Becker, 2003; Harris, 1966; Major & Jones, 2011; Perrins, Harris, & Britton, 1973). Immature Scopoli's shearwaters, *Calonectris diomedea*, showed some spatial segregation from breeding adults, but the sample size and resolution of the data were too low to make any strong conclusion (Péron & Grémillet, 2013). Votier et al. (2011) showed that immature gannets, *Morus bassanus*, went further on longer foraging trips and visited other colonies on the way, unlike immature wandering albatrosses, *Diomedea exulans*, which engaged in shorter trips (in duration and distance; Riotte-Lambert & Weimerskirch, 2013). However, although both studies suggested that these differences could be a consequence of differences in foraging abilities, they did not test this hypothesis, which was our aim here.

Immature Manx shearwaters start to return to the colony in large numbers in their third year, and for 2–3 years spend over a month each summer regularly visiting the colony (Perrins et al., 1973). This makes them an ideal species to make simultaneous comparisons of the central-place foraging behaviour of immature

and breeding adults. In this study we investigated the relationship between efficiency and spatial segregation in Manx shearwaters by simultaneously tracking immature and breeding individuals with a mix of archival and remote-download GPS loggers. These allowed us to investigate potential spatial segregation while inferring individual foraging efficiency by combining an ethoinformatics analysis of the high-resolution GPS logs, to identify different behaviours at sea and estimate foraging effort, and at-colony measurements of foraging success (daily mass gain). We also examined proxies of marine productivity for the areas in which birds foraged to determine whether any segregation was related to potential differences in habitat quality.

METHODS

Ethical Note

All work adheres to the ASAB/ABS Guidelines for the Use of Animals in Research, and was conducted after ethical approval by the British Trust for Ornithology Unconventional Methods Technical Panel (permit C/5311), Natural Resources Wales, Skomer Island Advisory Committee and the University of Oxford's Local Ethical Review Process. To minimize disturbance, handling was kept to a minimum (<10 min for each deployment/retrieval). Similar techniques and loggers have been deployed on adult Manx shearwaters in this colony since 2007 and no significant effect was recorded (Dean et al., 2012; Freeman et al., 2013). When possible, lighter devices were deployed on immatures: on average the devices represented an extra 0.4% (ca. 1.4 g) of the immatures' body mass compared with adults, less than the 5 g accuracy of our weight measurements and equivalent to or less than loads shown to have no significant short-term effect in closely related species (Igual et al., 2004; Passos, Navarro, Giudici, & Gonzales-Solis, 2010). Therefore we are confident that our results are not biased by a greater impact on immatures. It was not possible to monitor the survival of immature birds as they do not return to a specific nest, but all adults had a breeding success similar to or higher than the rest of the colony after the experiment (Perrins et al. 2013–2014).

Study Site and Model Species

The study was carried out on Skomer Island, Wales (51°44′N, 5°19′W), probably the largest Manx shearwater colony in the world (ca. 300 000 breeding pairs; Perrins et al., 2012), in June–July 2013 and 2014. Manx shearwaters are ca. 400 g, colonial, burrow-nesting, monomorphic seabirds which mainly breed on the Northeast Atlantic coast. The peak of attendance of immatures at the colony is between mid-June and mid-July (Harris, 1966; Perrins et al., 1973), which coincides with the end of the incubation period and the start of the chick-rearing period. Although hundreds of thousands of immatures visit the colony every year, their at-sea movements and behaviour during this period are currently unknown.

Deployment of Devices

Since immatures appear similar to adults they were identified first by their behaviour on the surface, for example prolonged amounts of time on the surface, long periods of immobility, prospecting movements, no strong directional movement towards a particular burrow, quick exploration of many burrows (Brooke, 1990), and then, after being caught by hand, by the

absence of a brood patch. Breeding adults in study burrows were monitored regularly, via an access hatch, from the start of the breeding season. We selected 50 immature birds (20 in 2013, 30 in 2014), 14 adults at the end of their incubation shift (four in 2013, 10 in 2014) and 13 chick-rearing adults (2013) for simultaneous device deployment (as breeding was later in 2014 all adults were still incubating during the peak of immature attendance at the colony, while in 2013 many nests had already hatched at the peak attendance and so we were able to track incubating and chick-rearing adults simultaneously). All birds were weighed and ringed with a metal ring from the British Trust for Ornithology. IgotU GT-120 (Mobile Action Technology Inc., Taiwan; both years) and remote-download Mataki trackers (Mataki.org; 2013), stripped of external casing and waterproofed in heatshrink tubing, were configured to record positions every 15 min (IgotU) or 60 min (Mataki). The latter were also configured to emit a radiosignal and look for a download base station every 30 min. These devices, made visible with retroreflective tape for retrieval, were attached to birds' backs using thin strips of marine tape (Tesa 4651 with water-soluble adhesive, see Guilford, Meade, Freeman, Biro, & Evans, 2008 for details of the methods), and designed to fall off within 2–3 weeks if the bird was not recaptured. Including waterproofing and tape, they weighed <19 g (IgotU) or <17 g (Mataki), which is under 5% of the average total individual body mass. A mix of Mataki and archival GPS loggers were deployed on immatures, while all adults carried an archival logger. Handling time was kept to a minimum (ca. 10 min) and birds were released in the colony after deployment.

Retrieval of Devices

In the 3 weeks following deployment, three observers were posted each night in the capture area, using low-intensity red light and night-vision scopes to observe the colony and look for immature study birds. In 2013, two remote-download base stations were also installed, each able to detect a radiosignal from any devices within ca. 200 m. Birds seen with a device were caught by the closest observer. In total, 20 immatures were recaptured, their device retrieved and data successfully downloaded. At least two more birds were seen but evaded recapture. For adults, burrows were inspected at regular intervals every night and birds returning had their device removed after 7 or more days or deployment, were weighed then replaced in the burrow. In the case of chick-rearing adults, they were first left for 30 min in the burrow to feed their chick. All 27 adults returned but six had lost their GPS, so in total we retrieved 21 trackers and successfully downloaded data from 19.

After device removal all birds were weighed using a spring balance (± 5 g). For chick-rearing adults the return mass was estimated as the mass of the adult after feeding its chick plus the overnight mass gain of the chick ($\times 0.5$ when both parents visited the nest that night).

Data Processing and Analysis

Only at-sea data (>5 km from the colony) were considered (apart from at-colony behaviour analyses), and interpolated to 1 min positions using piecewise cubic Hermite polynomials in MatLab (version R2013a, The MathWorks, Natick, MA, U.S.A.), as in Tremblay et al. (2006). Ground speed was calculated and a 90 km/h threshold applied to remove erroneous positions (Guilford et al.,

2008). Average flight speed was calculated on data >7 km/h (threshold obtained from our bimodal distribution of speed). Individual foraging trips were identified (range one to five trips per individual).

Statistics

We used linear mixed models (LMMs) to test the effect of breeding stage on foraging trip length, daily distance covered, maximum distance from the colony and average flight speed, and generalized linear mixed models (GLMMs) to test for differences in minimum and maximum latitudes (gamma distribution) and trip duration (Poisson distribution), with individual and year as random factors included in all models. In addition, using the bimodal distribution of trip length to choose a threshold of 3 days, we identified short and long trips and tested them separately, using the same models, to test whether the differences observed could be accounted for entirely by trip length alone. Because all incubating trips are >3 days, and to avoid potential issues with statistical power, breeding stages were not separated in this part of the analysis. *P* values were obtained by comparing our models to null models (with the random effects but without the fixed effect of interest) with a chi-square test.

Density kernels representing the core foraging distributions were calculated using a cell size of 2 km, with an optimal bandwidth of 86 km estimated by a least-squares cross-validation (sparr package, R; Geospatial Modelling Environment, Spatial Ecology Ltd, www.spatialecology.com/gme). Distribution overlaps were estimated with the adehabitat package in R, and significance levels were assessed using bootstrapping (i.e. each trip was randomly allocated to the adult or immature group, a new overlap was computed and compared to the observed value; this was repeated 1000 times for each of the 25, 50 and 95% kernels).

Distinctly different activities at sea, such as active foraging, resting or sustained flight, are reflected in distinguishable distributions of variables derived from the precision GPS tracks, such as speed and turning angle. These states can be statistically determined using Gaussian mixture models (GMMs). GMMS are hierarchical models which, given variables (here speed and turning angle) and a number of states, identify the most likely parameters (means and (co)variances and weights) of these states; the models then assign each data point with a probability of having been generated by each state and these can then be classified to their most probable state (see Bishop, 2006 for more details on the methods and Guilford et al., 2009; Freeman et al., 2010 for examples of use to classify animal behavioural states). We used Akaike's information criterion (AIC) to select the optimal number of states, three, which is consistent with other mixture models run on similar data sets for the same species (Dean et al., 2012; Freeman et al., 2013). Differences in the proportion of each behaviour between breeding stages were tested with LMMs. Differences in daily patterns of the three states between stages were tested with Kolmogorov–Smirnov tests. We tested the effect of mass on trip duration and potential differences in daily mass gain between stages with LMMs.

Sea surface temperature (SST, °C) and chlorophyll a concentrations (mg/m^3) were extracted from the NASA OceanColor websites (http://dx.doi.org/10.5067/Terra/MODIS_OC.2014.0 and http://dx.doi.org/10.5067/Aqua/MODIS_OC.2014.0) using data from the MODIS Terra and Aqua satellites, with a spatial resolution of 4 km and a temporal resolution of 8 days. Net primary productivity (NPP,

Table 1
Details of the mixed models comparing trip metrics between adults and immatures

	All trips pooled				Short trips (≤3 days)				Long trips (>3 days)			
	Mean±SE	Parameter estimates	Statistic	P	Mean±SE	Parameter estimates	Statistic	P	Mean±SE	Parameter estimates	Statistic	P
Trip duration (days) GLMM (Poisson distribution)	Inc=9.3±1.2 CR=4.9±0.7 Imm=3.7±0.6	Imm:Inc: 0.9±0.1 Imm:CR: 0.3±0.2 Inc:CR: 0.5±0.3	Z=3.17 Z=1.55 Z=1.86	**0.002** 0.121 0.012	A=1.1±0.1 I=1.6±0.2	N/A	N/A	N/A	A=8.3±0.5 I=6.5±0.9	N/A	N/A	N/A
Distance/day (km) LMM	Inc=209±28 CR=221±14 Imm=179±8	Imm:Inc: 28.8±25.6 Imm:CR: 49.1±18 Inc:CR: 20.3±28.6	t=1.12 t=2.72 t=0.71	0.499 **0.028** 0.659	A=275.6±18.4 I=193.2±11.8	-1.51±0.11	ΔlogLik=4.52 ΔAIC=-7.04 χ^2_1=9.04	**0.003**	A=188.9±10.9 I=160.4±10.4	-1.26±0.10	ΔlogLik=1.88 ΔAIC=-1.75 χ^2_1=3.75	0.052
Max distance from colony (km) LMM	Inc=248±53 CR=201±37 Imm=135±14	Imm:Inc: 1.8±1.5 Imm:CR: 6.7±1.3 Inc:CR: 0.5±0.3	t=2.49 t=2.30 t=1.02	**0.035** **0.035** 0.312	A=99.5±6.0 I=92.5±8.7	-1.03±1.06	ΔlogLik=0 ΔAIC=1.99 χ^2_1=0.01	0.919	A=309.6±44.4 I=194.0±22.7	1.5 E-3±0.8 E-3	ΔlogLik=2.84 ΔAIC=-4.63 χ^2_1=6.36	**0.012**
Mean flight speed (km/h) LMM	Inc=20.3±1.4 CR=23.0±0.7 Imm=18.2±0.6	Imm:Inc: 2.4±1.3 Imm:CR: 1.5±1.2 Inc:CR: -4.9±1.9	t=1.16 t=5.25 t=-2.65	0.230 **<0.001** 0.230	A=25.2±1.16 I=17.9±0.9	-11.1±1.8	ΔlogLik=7.97 ΔAIC=-13.93 χ^2_1=15.94	**<0.001**	A=21.0±0.6 I=18.5±0.8	-2.41±1.0	ΔlogLik=2.78 ΔAIC=-3.56 χ^2_1=5.55	**0.018**
Max latitude (°) GLMM (γ - distribution)	Inc=54.4±1.6 CR=52.9±0.3 Imm=51.9±0.1	Imm:Inc: -7.8±2.7 E-4 Imm:CR: -3.8±2.2 E-4 Inc:CR: 0.9±1.8 E-4	t=-2.92 t=-1.75 t=-0.47	**0.004** 0.080 0.341	A=52.3±0.1 I=51.8±0.04	1.7 E-4±0.4 E-4	t=-4.3	**<0.001**	A=53.7±0.5 I=52.2±0.1	4.7 E-4±2.3 E-4	t=1.97	**0.049**
Min latitude (°) GLMM (γ - distribution)	Inc=51.5±0.1 CR=51.4±0.1 Imm=51.1±0.09	Imm:Inc: -1.7±1.0 E-4 Imm:CR: -2.4±1.1 E-4 Inc:CR: -0.7±1.4 E-4	t=-1.63 t=-2.21 t=-0.54	0.104 **0.027** 0.589	A=51.5±0.1 I=51.1±0.09	1.9 E-4±1.1 E-4	t=1.74	0.081	A=51.4±0.1 I=51.0±0.2	1.8 E-4±1.1 E-4	t=1.65	0.098

Imm = immatures, Inc = incubating adults, CR = chick-rearing adults. For each test we indicate the mean ± SE of the dependent variable, the type of model, the test statistics, the parameter estimates and the P value. Significant values are in bold.

mg/m^2/day) data (8 km resolution), estimated from chlorophyll, light and photosynthetic efficiency values using the vertically generalized production model algorithm, were obtained from the Ocean Productivity website (www.science.oregonstate.edu/ocean.productivity). Each location in our tracking data set was assigned an SST, chlorophyll a and NPP value, and after log transformation of NPP and chlorophyll a concentration, LMMs were used to test for differences between groups, with individual and year included as random effects.

RESULTS

Differences in Foraging Trips

We compared 29 trips from six incubating and 13 chick-rearing adults and 36 trips from 20 immatures. The foraging trips of immatures were significantly shorter than those of incubating adults but not of chick-rearing adults (Table 1, Fig. 1a). Immatures also covered less distance than chick-rearing adults each day (Table 1, Fig. 1b), and stayed closer to the colony than all adults, even after we removed one extraordinarily long incubating adult trip to the Atlantic (Table 1, Fig. 1c). Chick-rearing adults' mean flight speeds were also significantly higher than immatures' (Table 1, Fig. 1d).

To investigate these differences further and test whether they could be accounted for entirely by trip length (which varied substantially between immatures: range 1–15 days), we analysed short and long trips separately. The distribution of trip durations was bimodal, which allowed us to identify a threshold of 3 days to classify trips as long (>3 days, $N_{immature}$ = 15, N_{adult} = 19) or short (≤3 days, $N_{immature}$ = 21, N_{adult} = 10). Adults covered more distance each day but the difference was only significant on short trips (Table 1). They still travelled further from the colony but only on long trips, even without the long adult trip to the Atlantic (Table 1). Adults' mean flight speed remained higher than immatures' on both short and long trips (Table 1).

Spatial Segregation

We found significant differences between the destinations of adult and immature birds. On average, adults went to significantly higher latitudes than immatures (GLMM (gamma): N = 65, parameter estimate 5.4 E-4 ± 2.6 E-4, t = 107.4, P = 0.029; Fig. 1e), while immatures went significantly further south (GLMM (gamma): N = 65, parameter estimate 2.0 E-4 ± 0.8 E-4, t = 200.1, P = 0.013; Fig. 1f). This held when we looked at short and long trips separately (Table 1). There were differences between the occupancy contours of adults and immatures, at the 95%, 50% and 25% density levels. The overlap of the core distributions of adults and immatures, which was below 20% at the 50% occupancy level and below 5% at the 25% occupancy level, was significantly lower than expected by chance at the 25% and 50% level (25%: 4% overlap, P = 0.020; 50%: 19% overlap, P = 0.045; 95%: 83%, P = 0.377; P values obtained from bootstrapping with 1000 iterations; Fig. 2). These differences were not due to different trip durations between groups, as the overlap between adults and immatures remained small when we looked at short and long trips separately (Fig. 2c). Overlap of core distributions occurred near the colony, near the southern Irish coast and in the middle of the Celtic Sea. The most striking segregation was in the Irish Sea, which was visited by a single immature but over 50% of adults. This was not due to the Irish Sea trips taking too long for immatures: all adult trips in the Irish Sea lasted 6–12 days and only one of seven immature trips in this range of duration was to the Irish Sea (versus 10 of 18 for adults). Rather than the Irish Sea, the south Celtic Sea and around the Cornish peninsula were used disproportionally by immatures; over 40% ventured south of the Bristol
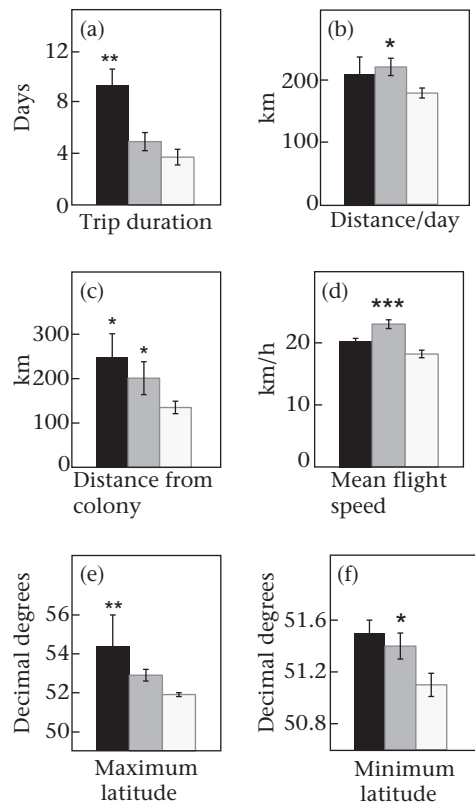
Figure 1. Trip characteristics of immatures (white), incubating (black) and chick-rearing (grey) adults: (a) trip duration, (b) distance covered per day, (c) maximum distance from the colony, (d) mean flight speed, (e) maximum latitude and (f) minimum latitude (mean ± ± SE). Asterisks represent significant differences between adults and immatures: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. For significance levels between incubating and chick-rearing adults see Table 1.

Channel and even south of the U.K. into the English Channel, while only 10% of the adults went to such low latitudes (and none to the English Channel). Both groups foraged in the Celtic Sea, but more adults favoured the Irish south coast while more immatures foraged along the coast of north Wales.

At-sea Behaviour

The optimum number of behavioural states identified with our Gaussian mixture model was three (Appendix Fig. A1). The three states are taken to identify approximately foraging (low speed, high turning angle), sustained flight (high speed, low turning angle) and resting (low speed, low turning angle; Table 2, Fig. 3).

Birds spent most of their time 'resting' on the water, with 'foraging' the second and 'sustained flight' the least common behavioural class at sea. All adults and immatures spent similar proportions of time flying (LMM: immatures versus incubating adults: parameter estimate 0.03 ± 0.03, $t = 0.92$, $P = 0.60$; immatures versus chick-rearing adults: parameter estimate 0.04 ± 0.02, $t = 2.4$, $P = 0.51$; incubating versus chick-rearing adults: parameter estimate -0.02 ± 0.03, $t = -0.63$, $P = 0.70$). However, immatures spent less time foraging and more time resting than incubating adults (LMMs: foraging: immatures versus incubating adults: parameter estimate 0.03 ± 0.01, $t = 2.34$, $P = 0.023$; immatures versus chick-rearing adults: parameter estimate -0.005 ± 0.01, $t = -0.06$, $P = 0.33$; incubating versus chick-rearing adults: parameter estimate -0.03 ± 0.02, $t = -2.33$, $P = 0.07$; resting: immatures versus incubating adults: parameter estimate -0.06 ± 0.02, $t = -2.24$, $P = 0.044$; immatures versus

chick-rearing adults: parameter estimate -0.05 ± 0.02, $t = -2.56$, $P = 0.134$; incubating versus chick-rearing adults: parameter estimate 0.006 ± 0.03, $t = 0.23$, $P = 0.65$).

Despite adults and immatures travelling to largely separate locations, the patterns of daily activity were similar between stages (Kolmogorov–Smirnov tests: $N_{immature} = 16$, $N_{incubating\ adult} = 6$, $N_{chick-rearing\ adult} = 13$: foraging: immatures versus incubating adults: $D = 0.17$, $P = 0.89$; immatures versus chick-rearing adults: $D = 0.20$, $P = 0.67$; incubating versus chick-rearing adults: $D = 0.25$, $P = 0.44$; flying: immatures versus incubating adults: $D = 0.25$, $P = 0.44$; immatures versus chick-rearing adults: $D = 0.33$, $P = 0.14$; incubating versus chick-rearing adults: $D = 0.25$, $P = 0.44$; resting: immatures versus incubating adults: $D = 0.25$, $P = 0.44$; immatures versus chick-rearing adults: $D = 0.13$, $P = 0.99$; incubating versus chick-rearing adults: $D = 0.21$, $P = 0.67$; Fig. 4), and were also similar to timings previously found in this species (Dean et al., 2012). Foraging occurred across the daylight hours with a slight increase towards the end of the afternoon. Resting occurred mostly at night, but also occupied a significant part of the day, especially the middle. Flying occurred predominantly by day, with distinct peaks around sunrise and before sunset, when birds left or arrived near the colony.

Daily Mass Gain

Immature birds were significantly lighter than adults prior to tracking (364 ± 5 g versus 405 ± 5 g; $N_{immature} = 20$, $N_{adult} = 19$; t test: $t_{36.9} = 5.59$, $P < 0.001$). Lighter immatures tended to go on shorter foraging trips (LMM: $N = 20$, parameter estimate 0.01 ± 4.1 E-3, $Z = 3.17$, $P = 0.002$), but this was not the case in adults, even when we controlled for breeding stage (LMM: $N = 19$, parameter estimate 0.002 ± 0.004, $Z = -0.56$, $P = 0.58$). In addition, immatures gained significantly less mass per day (-0.59 ± 0.7 g/day on average) than incubating birds (5.6 ± 1.8 g/day on average; LMM: parameter estimate 6.22 ± 1.69, $t = 3.7$, $P < 0.001$) and chick-rearing birds (2.0 ± 0.9 g/day on average; LMM: parameter estimate 2.59 ± 1.29, $t = 2.0$, $P = 0.05$), while adults also differed significantly between stages (LMM: parameter estimate 3.63 ± 1.79, $t = 2.0$, $P = 0.05$). The difference between adults and immatures held when we looked at daily mass gain per unit of time spent foraging: while there was no significant difference between chick-rearing and incubating birds (LMM: parameter estimate 0.02 ± 0.64, $t = 0.47$, $P = 0.161$), immatures gained significantly less mass per unit of time spent foraging than either incubating or chick-rearing adults (LMMs: incubating: parameter estimate -1.25 ± 0.36, $t = -3.47$, $P = 0.001$; chick-rearing: parameter estimate -0.62 ± 0.26, $t = -2.37$, $P = 0.026$). To check whether the differences in efficiency were simply an effect of body condition, we tested whether bird mass had an effect on efficiency (mass gain per unit of time spent foraging) in adults and immatures: we did not find any significant differences in adults but there was a nearly significant trend in immatures (LMMs: immatures: $N = 20$, parameter estimate -0.01 ± 0.005, $\chi^2_1 = 3.76$, $P = 0.053$; adults: $N = 19$, parameter estimate -0.11 ± 0.8, $\chi^2_1 = 2.21$, $P = 0.137$). The trend was negative, i.e. heavier immatures tended to be less efficient than lighter immatures.

Marine Productivity

Immatures foraged in areas of significantly lower estimated net primary productivity than adults (1873 ± 8 versus 2349 ± 10 mg/m^2/day; LMM: $N_{immature} = 20$ (9844 locations), $N_{adult} = 19$ (15912 locations), parameter estimate -0.21 ± 0.08, $\chi^2_1 = 6.61$, $P = 0.010$). When looking at breeding stages separately, we found that the difference was significant between immatures and chick-rearing
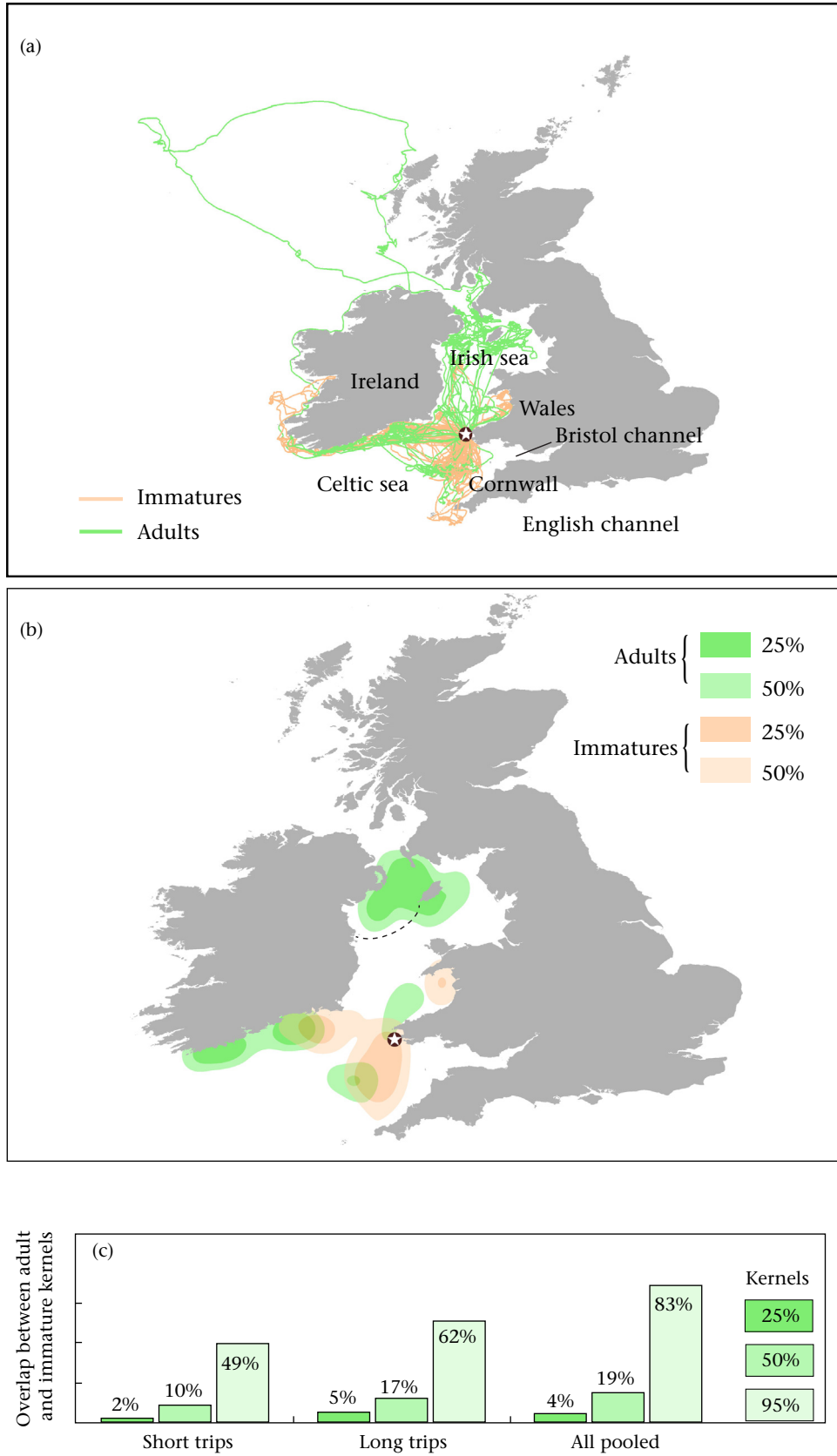
Figure 2. (a) Raw tracks from the 20 immature (orange) and 19 adult (green) shearwaters in 2013 and 2014. (b) 50% and 25% occupancy kernels of immatures and adults calculated on the whole data set. The colony is indicated with a star, and the approximate position of the Irish Sea front with a dashed line. (c) Overlap between 25%, 50% and 95% occupancy kernels of adults and immatures, with all trips pooled (*N* = 65) or separated by trip duration (short: *N* = 31; long: *N* = 34).

Table 2
Metrics of the three classes of behaviour as identified by a Gaussian mixture model

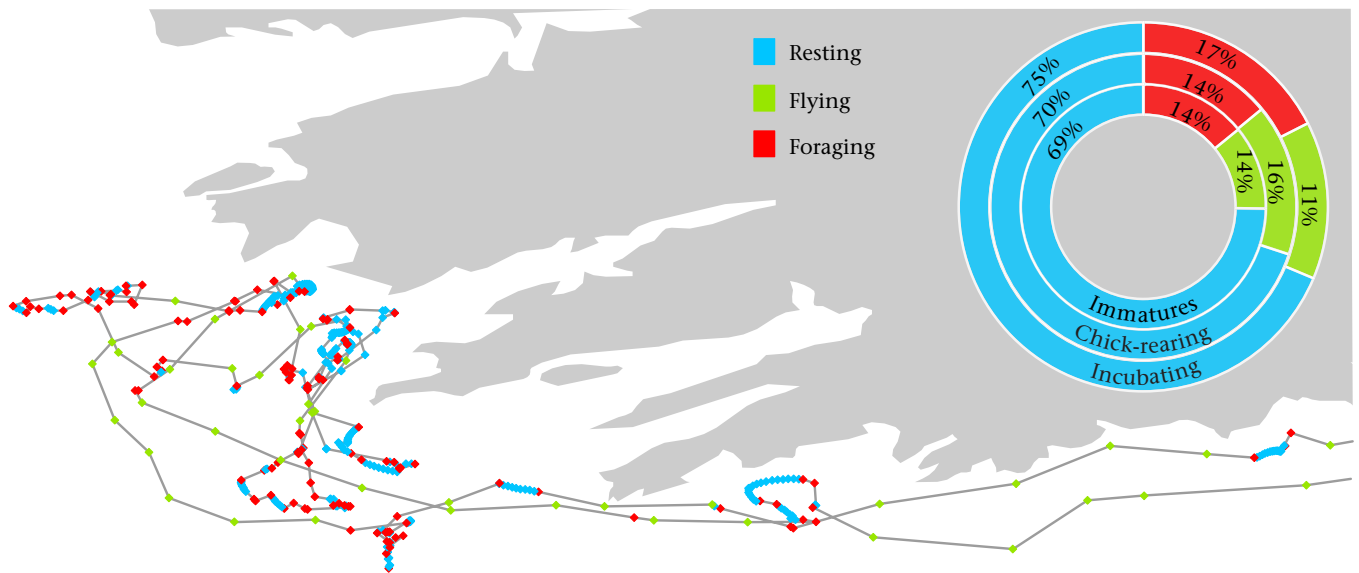|	Ground speed (km/h)	Turning angle (°)	% Time in incubating adults	% Time in chick-rearing adults	% Time in immatures
Class 1: 'foraging'	5.85±0.10	129.56±0.52	17.5±0.1	14.0±0.8	14.1±0.5
Class 2: 'sustained flight'	34.19±0.20	19.32±0.47	13.8±3.1	16.0±1.6	11.1±1.0
Class 3: 'resting'	4.01±0.04	21.35±0.21	68.6±3.2	69.9±1.4	74.7±1.0

Figure 3. Example of behavioural classification of part of a foraging trip, and percentage of time spent foraging (red), flying (green) and resting (blue) for immatures, incubating and chick-rearing adults across the whole data set.

birds (1873 ± 8 versus 2453 ± 12 mg/m^2/day; LMM: $N_{\text{chick-rearing adults}} = 13$ (10950 locations), parameter estimate -0.30 ± 0.08, $\chi^2_1 = 10.03$, $P = 0.002$), but not incubating birds (LMM: $N_{\text{incubating adults}} = 6$ (4962 locations), parameter estimate -0.11 ± 0.11, $\chi^2_1 = 1.11$, $P = 0.291$). There was no difference between incubating and chick-rearing adults (parameter estimate -0.19 ± 0.14, $\chi^2_1 = 1.99$, $P = 0.159$). We obtained similar results by looking at the foraging, flying and sitting states separately, although the effect was less obvious for flying (Table 3). Differences in chlorophyll a levels were the same as those obtained with net primary productivity, with immatures generally exploiting areas of lower chlorophyll a concentrations; the only difference from net primary productivity being a lack of difference in flying locations between any stages. Although adults seemed to occupy areas of slightly lower SSTs, there were no significant differences with immatures (Table 3).

DISCUSSION

By comparing simultaneously precision-tracked foraging trips of different life stages we were able to investigate the foraging distributions of immatures and breeding adults under identical environmental circumstances. At the same time, we used an ethoinformatics analysis, and a proxy for foraging success (mass gain), to estimate individual foraging efficiencies. We found that immatures were substantially spatially segregated from adults in their foraging destinations, and that this was not an effect of constraints on trip duration or flight distance: on average, immatures foraged closer to the colony than adults and their trips

were of similar duration to the trips of chick-rearing adults (but shorter than incubating trips). In addition, they covered similar distances per day, and at similar flight speed, to incubating birds (but shorter distances and at lower flight speed than chick-rearing adults). Although there were small differences in measured speeds and trip durations between immatures and chick-rearing (although not incubating) adults, which may indicate that immatures are less efficient in sustained flight, these differences are not sufficient to deny immatures access to the core areas exploited by adults in our study. Critically, we found that immatures gained less mass per unit of time spent engaged in foraging-related behaviour, suggesting that they are less efficient at foraging than adults. There are several potential causes of this effect. One possibility is that immatures are inferior competitors because they are lighter than adults (ca. 10% lighter in our data set), and are competitively excluded from the best foraging areas. However, we found no evidence that heavier birds were better at foraging: there was no effect of mass on foraging efficiency in adults, and only a nearly significant, but negative, trend in immatures, indicating that heavier immatures do not forage more effectively. Furthermore, we found that while lighter immatures did go on shorter trips, this was not the case in adults, whether they were incubating an egg or rearing a chick. Thus, the differences we observed between adults and immatures cannot be readily explained by differences in body condition alone.

Alternatively (or in addition), immatures may be less effective foragers because they lack individually acquired experience which may enable adults to recall the locations of the best foraging areas under different conditions, recognize the signals indicative of prey
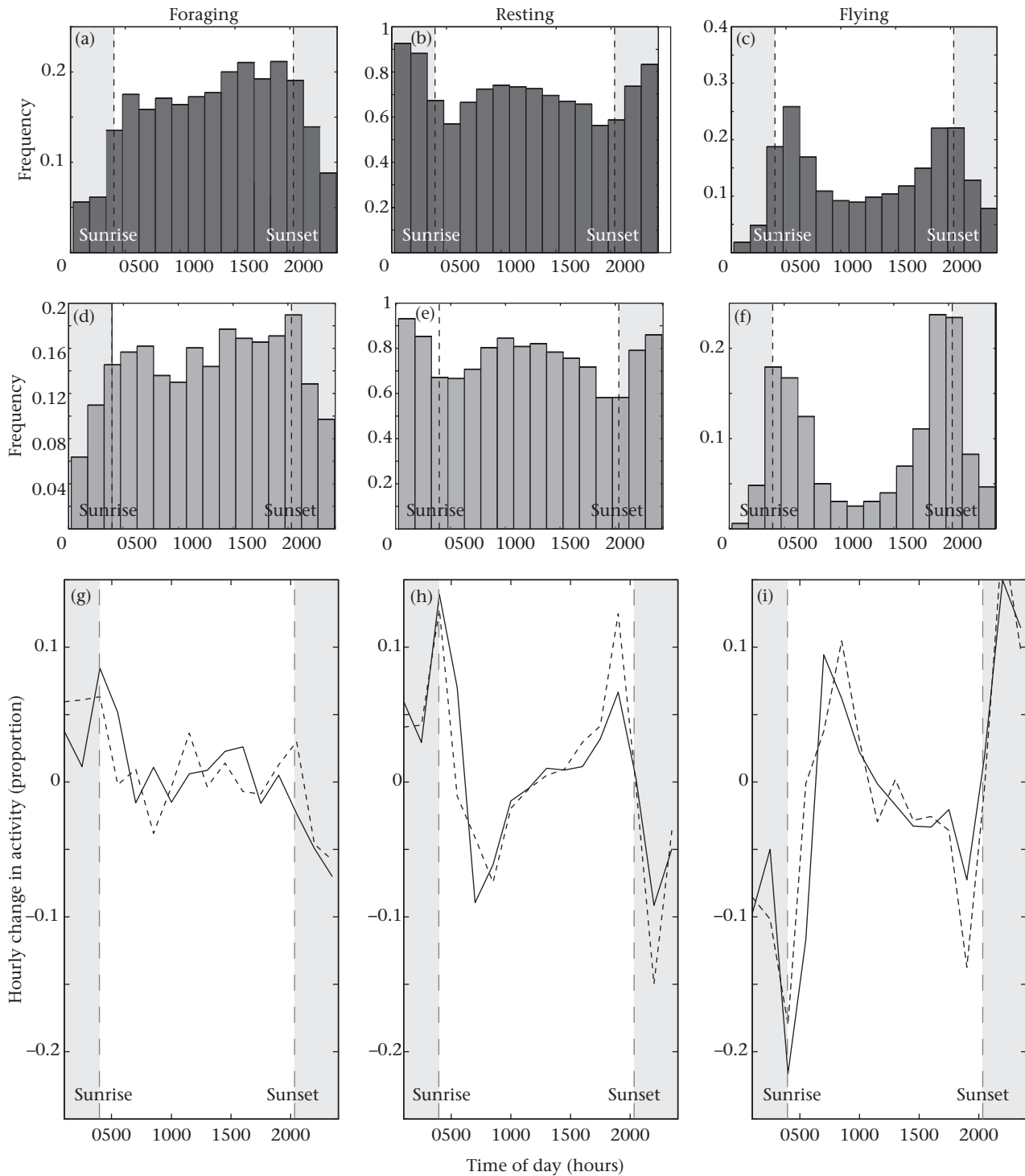
Figure 4. Stacked histograms of (a, d, g) foraging, (b, e, h) resting and (c, f, i) flying behaviours against time of day for (a, b, c) adults and (d, e, f) immatures, and (g, h, i) their hourly variation for adults (continuous lines) and immatures (dashed lines). The y-axis represents a change in proportion, e.g. if the percentage of adults flying is 10% between 1600 and 1700 hours and 25% between 1700 and 1800 hours, the value for 1700 hours will be 0.15. On all six graphs night-time is represented by a light grey background, and sunrise and sunset with grey dashed vertical lines.

presence or hunt prey more effectively (e.g. by diving at different depths; Le Vaillant et al., 2012), in an environment in which prey is patchy, often ephemeral and predictable only on a complex spatiotemporal scale. We found that immatures exploited areas that were significantly less productive than those used by chick-rearing adults, with lower primary productivity and chlorophyll a

levels. Incubating adults also visited areas of higher productivity than immatures (although less so than chick-rearing adults), but the differences were not significant, which could result from our small sample size of incubating adults. These results support the idea that the lower foraging efficiency of immatures is at least partly due to their exploitation of less productive areas; however,

Table 3
Differences in net primary productivity, chlorophyll a and sea-surface temperature between locations visited by immatures and adults for each behavioural state

	Foraging (N_{Imm}=1811, N_{Inc}=1048, N_{CR}=2052)	Sitting (N_{Imm}=7105, N_{Inc}=3172, N_{CR}=7547)	Flying (N_{Imm}=928, N_{Inc}=742, N_{CR}=1351)
Net primary productivity (mg/m²/day)	Imm: 1843±18 Inc: 2106±37 CR: 2526±28 Imm:Inc: χ^2_1=1.2, P=0.269 **Imm:CR: χ^2_1=18.7, P<0.001** Inc:CR: χ^2_1=2.2, P=0.139	Imm: 1866±10 Inc: 2142±21 CR: 2443±15 Imm:Inc: χ^2_1=1.4, P=0.238 **Imm:CR: χ^2_1=9.9, P=0.002** Inc:CR: χ^2_1=1.9, P=0.172	Imm: 1983±27 Inc: 2121± 39 CR: 2401±34 Imm:Inc: χ^2_1=0.2, P=0.682 **Imm:CR: χ^2_1=4.2, P=0.040** Inc:CR: χ^2_1=1.1, P=0.269
Chlorophyll a (mg/m³)	Imm: 1.08±0.02 Inc: 1.53±0.10 CR: 2.30±0.07 Imm:Inc: χ^2_1=3.3, P=0.068 **Imm:CR: χ^2_1=10.5, P=0.001** Inc:CR: χ^2_1=1.14, P=0.285	Imm: 1.13±0.02 Inc: 1.51±0.06 CR: 2.11±0.04 Imm:Inc: χ^2_1=2.8, P=0.094 **Imm:CR: χ^2_1=9.8, P=0.002** Inc:CR: χ^2_1=1.0, P=0.313	Imm: 1.23±0.04 Inc: 1.58±0.08 CR: 1.67±0.03 Imm:Inc: χ^2_1=1.0, P=0.318 Imm:CR: χ^2_1=2.7, P=0.097 Inc:CR: χ^2_1=13.7, P=0.711
SST (°C)	Imm: 17.2±0.03 Inc: 16.4±0.05 CR: 16.9±0.04 Imm:Inc: χ^2_1=1.5, P=0.228 Imm:CR: χ^2_1=0.1, P=0.718 Inc:CR: χ^2_1=0.4, P=0.515	Imm: 17.1±0.1 Inc: 16.4±0.03 CR: 16.9±0.02 Imm:Inc: χ^2_1=1.7, P=0.190 Imm:CR: χ^2_1=0.05, P=0.825 Inc:CR: χ^2_1=0.6, P=0.435	Imm: 16.7±0.04 Inc: 15.8±0.06 CR: 16.6±0.05 Imm:Inc: χ^2_1=2.5, P=0.111 Imm:CR: χ^2_1=0.03, P=0.873 Inc:CR: χ^2_1=0.7, P=0.473

Imm = immatures, Inc = incubating adults, CR = chick-rearing adults. The numbers presented are means ± SE, and the statistics are from LMMs. Significant differences are in bold.

this does not rule out the possibility that they are also less skilled at hunting which could itself push them into less productive waters through competition with adults. In our data set, the clearest segregation occurred in the Irish Sea: over 50% of adults visited the Irish Sea front (a known seabird hotspot for several species including Manx shearwaters; Begg & Reid, 1997; Pollock, Reid, Webb, & Tasker, 1997), but no immature did, even though it was well within their range (in duration and distance). It seems unlikely that this absence can simply be explained by their inability to find this area, as large flocks of Manx shearwaters can be seen flying to and from it in the breeding season (Durazo, Harrison, & Hill, 1998). This suggests that immatures were competitively excluded from this area. The only immature going to the Irish Sea (which did not reach the front) was one of the heaviest (third of 20) and within the range of adult mass; furthermore, unlike the other immatures we tracked, it shared the same burrow each night with the same bird (with a small brood patch), and remained in a burrow for 24 h on two occasions during the tracking period. This suggests that this bird was most likely a prebreeder with a newly established burrow or a breeder that failed early enough in the season for its brood patch to disappear. There may be a threshold (triggered by mass, age or experience) above which it becomes worth facing intraspecific competition in the Irish Sea. This may also be the same threshold that triggers the start of breeding, as is also observed in albatrosses (Weimerskirch, 1992). Displacement of immatures from the Irish Sea is unlikely to occur by direct aggression from the adults, but is more likely to result from differential competitiveness: immatures visiting the Irish Sea could be outcompeted by adults and their superior foraging skills, and therefore the gain from foraging in areas less exploited by adults may outweigh the cost of the lower productivity of these areas.

Poorer foraging ability in immatures has often been invoked as the main reason for their higher mortality observed in many species (Ashmole, 1963; Lack, 1954). Immatures' improvement of foraging with experience has been suggested in several taxa (Lefebvre, 1995; Mazur & Seher, 2008) including seabirds (Daunt et al., 2007; Yoda, Kohno, & Naito, 2004), and may continue after reaching adulthood (Haug, Paiva, Werner, & Ramos, 2015). Furthermore, despite a lack of difference in bill and wing length

with age ruling out the physical inability to catch the same prey as adults, Manx shearwaters are known to increase in mass until at least age 6 years (Brooke, 1978). Tracking data of immature wandering albatrosses visiting their colony during the breeding season revealed that immatures, like our shearwaters, took shorter trips than breeding adults and covered shorter distances (Riotte-Lambert & Weimerskirch, 2013; Weimerskirch et al., 2013); these authors suggested that immatures may stay nearer the colony (where they are likely to experience higher competition for resources) to learn how to deal with the competition constraints of central-place foraging near the colony, which they will encounter once they start breeding. On the other hand, immature gannets, M. bassanus, covered longer distances and went on longer trips than chick-rearing adults between regular visits to the colony, interestingly also visiting other colonies during their trips (Votier et al., 2011). Here, the authors argued the longer trips of immature gannets were a way to avoid high intraspecific competition near the colony. The limitation of these studies is that the tracking of immatures and adults was not simultaneous but occurred in different years, and so the differences may be masked or increased by different environmental conditions. Although our results strongly indicate a lower foraging efficiency of immature shearwaters, they tended to go on shorter trips and to spend less time foraging than some adults, despite being lighter. They may be under less pressure than adults to exploit the most profitable areas because they do not need to build reserves for incubation shifts or to feed a chick. This would imply the existence of a cost or risk to travel to more productive areas, which breeders benefit from paying or taking. During the short period during which they visit the colony each year, immatures may also prioritize frequent colony visits to prospect for burrows and improve their social skills over foraging. Therefore, the spatial segregation we observed in our study may result not only from the inexperience of immatures at foraging, but also from their inexperience at adult life in general.

Conclusion

Our study reveals for the first time the simultaneous foraging movements of adult and immature seabirds during the breeding

season, hereby addressing the issue of between-year differences in environmental conditions potentially confounding the findings of previous studies. In addition, by measuring the foraging success of the birds, we estimated and compared foraging efficiency between immatures and breeders. Our findings highlight substantial spatial segregation between adults and immatures during central-place foraging around the colony, and lower foraging efficiency in immatures, which is not driven by differences in body condition and therefore is most likely to be the result of inexperience. This is driving the spatial segregation we observed in which the inferior competitors (immatures) were excluded from the significantly more productive foraging areas visited by adults. Our findings provide the strongest evidence to date that within-species spatial segregation in long-lived animals can be driven by differences in foraging experience, which may in turn lead to intraspecific competition.

References

Ashmole, N. P. (1963). The regulation of numbers of tropical oceanic birds. *Ibis, 103b*(3), 458–473.
Begg, G. S., & Reid, J. B. (1997). Spatial variation in seabird density at a shallow sea tidal mixing front in the Irish Sea. *ICES Journal of Marine Science, 54*(4), 552–565.
Bishop, C. M. (2006). *Pattern recognition and machine learning.* New York, NY: Springer-Verlag.
Brooke, M. (1978). Weights and measurements of Manx shearwater, *Puffinus puffinus. Journal of Zoology, 186*, 359–374.
Brooke, M. (1990). *The Manx shearwater.* London, U.K.: Poyser.
Cheney, D. L., & Seyfarth, R. M. (1983). Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. *The American Naturalist, 122*(3), 392–412.
Clarke, J., Kerry, K., Fowler, C., Lawless, R., & Eberhard, S. (2003). Post-fledging and winter migration of Adelie penguins *Pygoscelis adeliae* in the Mawson region of East Antarctica. *Marine Ecology Progress Series, 248*, 267–278.
Daunt, F., Afanasyev, V., Adam, A., Croxall, J. P., & Wanless, S. (2007). From cradle to early grave: juvenile mortality in European shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. *Biology Letters, 3*(4), 371–374.
Dean, B., Freeman, R., Kirk, H., Leonard, K., Phillips, R. A., Perrins, C., et al. (2012). Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *Journal of The Royal Society Interface, 10*(78), 1–12.
Dittmann, T., & Becker, P. H. (2003). Sex, age, experience and condition as factors affecting arrival date in prospecting common terns, *Sterna hirundo. Animal Behaviour, 65*(5), 981–986.
Durant, S. M., Kelly, M., & Caro, T. M. (2004). Factors affecting life and death in Serengeti cheetahs: environment, age, and sociality. *Behavioral Ecology, 15*(1), 11–22.
Durazo, R., Harrison, N. M., & Hill, A. E. (1998). Seabird observations at a tidal mixing front in the Irish Sea. *Estuarine, Coastal and Shelf Science, 47*(2), 153–164.
Field, I. C., Bradshaw, C. J. A., Burton, H. R., Sumner, M. D., & Hindell, M. A. (2005). Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals (*Mirounga leonina*). *Oecologia, 142*(1), 127–135.
Freeman, R., Dean, B., Kirk, H., Leonard, K., Phillips, R. A., Perrins, C., et al. (2013). Predictive ethoinformatics reveals the complex migratory behaviour of a pelagic seabird, the Manx shearwater. *Journal of The Royal Society Interface, 10*(84), 1–8.
Freeman, R., Dennis, T., Landers, T., Thompson, D., Bell, E., Walker, M., et al. (2010). Black petrels (*Procellaria parkinsoni*) patrol the ocean shelf-break: GPS tracking of a vulnerable procellariiform seabird. *PLoS One, 5*(2).
Gosler, A. G. (1987). Pattern and process in the bill morphology of the great tit *Parus major. Ibis, 129*, 451–476.
Guilford, T., Meade, J., Freeman, R., Biro, D., & Evans, T. (2008). GPS tracking of the foraging movements of Manx Shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales. *Ibis, 150*(3), 462–473.
Guilford, T., Meade, J., Willis, J., Phillips, R. A., Boyle, D., Roberts, S., et al. (2009). Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proceedings of the Royal Society B: Biological Sciences, 276*(1660), 1215–1223.
Harcourt, A., Stewart, K., & Fossey, D. (1976). Male emigration and female transfer in wild mountain gorilla. *Nature, 263*(5574), 226–227.
Harris, M. P. (1966). Age of return to colony, age of breeding and adult survival of Manx shearwaters. *Bird Study, 13*(1), 84–95.
Haug, F. D., Paiva, V. H., Werner, A. C., & Ramos, J. A. (2015). Foraging by experienced and inexperienced Cory's shearwater along a 3-year period of ameliorating foraging conditions. *Marine Biology, 162*(3), 649–660.
Igual, J. M., Forero, M. G., Tavecchia, G., González-Solis, J., Martínez-Abraín, A., Hobson, K. A., et al. (2004). Short-term effects of data-loggers on Cory's shearwater (*Calonectris diomedea*). *Marine Biology, 146*(3), 619–624.
Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour, 48*(1), 215–267.
Kooyman, G. L., Kooyman, T. G., Horning, M., & Kooyman, C. A. (1996). Penguin dispersal after fledging. *Nature, 383*(6599), 397.
Kooyman, G. L., & Ponganis, P. J. (2007). The initial journey of juvenile emperor penguins. *Aquatic Conservation-Marine and Freshwater Ecosystems, 17*, S37–S43.
Lack, D. L. (1954). *The natural regulation of animal numbers.* Oxford, U.K.: Clarendon Press.
Le Vaillant, M., Wilson, R. P., Kato, A., Saraux, C., Hanuise, N., Prud'Homme, O., et al. (2012). King penguins adjust their diving behaviour with age. *Journal of Experimental Biology, 215*(21), 3685–3692.
Lefebvre, L. (1995). Culturally-transmitted feeding-behavior in primates—evidence for accelerating learning rates. *Primates, 36*(2), 227–239.
Lewison, R., Oro, D., Godley, B. J., Underhill, L., Bearhop, S., Wilson, R. P., et al. (2012). Research priorities for seabirds: improving conservation and management in the 21st century. *Endangered Species Research, 17*(2), 93–121.
Maclean, A. (1986). Age-specific foraging ability and the Evolution of deferred breeding in 3 species of Gulls. *Wilson Bulletin, 98*(2), 267–279.
Major, H. L., & Jones, I. L. (2011). An Experimental study of the use of social information by prospecting nocturnal burrow-nesting seabirds. *The Condor, 113*(3), 572–580.
Mazur, R., & Seher, V. (2008). Socially learned foraging behaviour in wild black bears, *Ursus americanus. Animal Behaviour, 75*, 1503–1508.
Passos, C., Navarro, J. L., Giudici, A., & Gonzales-Solis, J. (2010). Effects of extra mass on the pelagic behavior of a seabird. *The Auk, 127*(1), 100–107.
Pelletier, L., Chiaradia, A., Kato, A., & Ropert-Coudert, Y. (2014). Fine-scale spatial age segregation in the limited foraging area of an inshore seabird species, the little penguin. *Oecologia, 176*(2), 399–408.
Péron, C., & Grémillet, D. (2013). Tracking through life stages: adult, immature and juvenile Autumn migration in a long-lived seabird. *PLoS One, 8*(8), e72713.
Perrins, C., Boyle, D., Baer, J., Bueche, B., Cole, T., Kipling, R., et al. (2013–2014). Seabird monitoring on Skomer Island 2013–2014. *JNCC Reports, 294–295.*
Perrins, C. M., Harris, M. P., & Britton, C. K. (1973). Survival of Manx shearwaters *Puffinus puffinus. Ibis, 115*(4), 535–548.
Perrins, C., Wood, M., Garroway, C., Boyle, D., Oakes, N., Revera, R., et al. (2012). A whole-island census of the Manx shearwaters *Puffinus puffinus* breeding on Skomer Island in 2011. *Seabird, 25*, 1–13.
Pollock, C., Reid, J., Webb, A., & Tasker, M. (1997). The distribution of seabirds and cetaceans in the waters around Ireland. *JNCC Report, 267*, 1–167.
Riotte-Lambert, L., & Weimerskirch, H. (2013). Do naive juvenile seabirds forage differently from adults? *Proceedings of the Royal Society B: Biological Sciences, 280*(1768), 20131434.
Robertson, S. L., & Cushing, J. M. (2011). Spatial segregation in stage-structured populations with an application to tribolium. *Journal of Biological Dynamics, 5*(5), 398–409.
Sherley, R. B., Ludynia, K., Lamont, T., Roux, J.-P., Crawford, R. J. M., & Underhill, L. G. (2013). The initial journey of an endangered penguin: implications for seabird conservation. *Endangered Species Research, 21*(1), 89–95.
Shillinger, G., Bailey, H., Bograd, S., Hazen, E., Hamann, M., Gaspar, P., et al. (2012). Tagging through the stages: technical and ecological challenges in observing life histories through biologging. *Marine Ecology Progress Series, 457*, 165–170.

Thiebot, J.-B., Delord, K., Marteau, C., & Weimerskirch, H. (2014). Stage-dependent distribution of the critically endangered Amsterdam albatross in relation to economic exclusive zones. *Endangered Species Research, 23*(3), 263–276.

Trebilco, R., Gales, R., Baker, G. B., Terauds, A., & Sumner, M. D. (2008). At sea movement of Macquarie Island giant petrels: Relationships with marine protected areas and Regional Fisheries Management Organisations. *Biological Conservation, 141*(12), 2942–2958.

Tremblay, Y., Shaffer, S. A., Fowler, S. L., Kuhn, C. E., McDonald, B. I., Weise, M. J., et al. (2006). Interpolation of animal tracking data in a fluid environment. *Journal of Experimental Biology, 209*(1), 128–140.

Votier, S., Grecian, W. J., Patrick, S., & Newton, J. (2011). Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology, 158*(2), 355–362.

Webb, W. C., Marzluff, J. M., & Hepinstall-Cymerman, J. (2012). Differences in space use by common ravens in relation to sex, breeding status, and kinship. *The Condor, 114*(3), 584–594.

Weimerskirch, H. (1992). Reproductive effort in long-lived birds–age-specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos, 64*(3), 464–473.

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Research Part Ii-Topical Studies in Oceanography, 54*(3–4), 211–223.

Weimerskirch, H., Cherel, Y., Delord, K., Jaeger, A., Patrick, S. C., & Riotte-Lambert, L. (2013). Lifetime foraging patterns of the wandering albatross: life on the move! *Journal of Experimental Marine Biology and Ecology, 450*, 68–78.

Yoda, K., Kohno, H., & Naito, Y. (2004). Development of flight performance in the brown booby. *Proceedings of the Royal Society B: Biological Sciences, 271*, S240–S242.
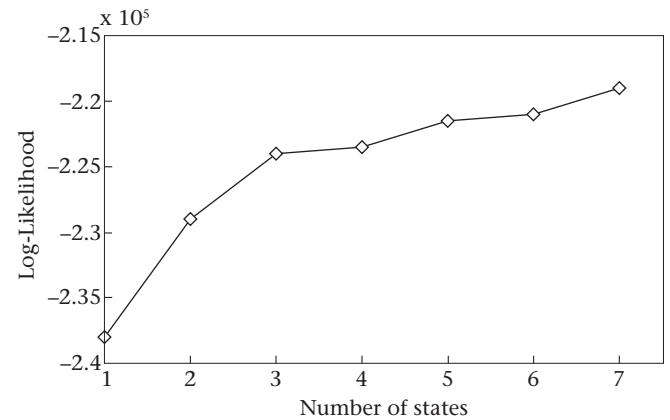
Appendix

Figure A1. Log-likelihood of Gaussian mixture models with different numbers of states, used to identify the optimum number of behavioural states (3).