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Density-dependent foraging and colony growth under varying environmental conditions in a pelagic seabird

Rachel D. Davies[1*], Sarah Wanless[2], Sue Lewis[3], Keith C. Hamer[1]

[1]School of Biology, University of Leeds, LS2 9JT, UK.

[2] Centre for Ecology & Hydrology, Bush Estate, Penicuik EH26 0QB, UK

[3]Institute of Evolutionary Biology, University of Edinburgh, EH9 3JT, UK

*Correspondence: bgy5rdd@leeds.ac.uk

ABSTRACT

Intra-specific competition for food resources affects both foraging behaviour and population growth rates in many species, highlighting a need to understand better how changing environmental conditions affect individuals in populations of different sizes. Using chick-rearing northern gannets as a model, we examined the influence of colony size on per capita population growth rates over two time-periods (1994-2000 and 2000-2009) and on foraging trip durations in each of two years (2000 and 2009) at 10 colonies in two separate regions of the UK and Ireland (the North Sea and the Celtic/Irish Sea). The slope of the relationship between population size and foraging trip duration in 2009 was less than one quarter of that in 2000, suggesting a much weaker influence of population size in 2009, presumably due to less intense intra-specific competition for prey resources at sea. There was also regional variation, with colonies in the Celtic/Irish Sea growing substantially slower for their size over the period between 2000 and 2009 than did colonies bordering the North Sea, whilst observed trip durations in 2009 were on average 13% shorter than predicted from population size at colonies bordering the North Sea but 32% longer than predicted at colonies in the Celtic and Irish Seas. These data suggest less favourable conditions for gannets in the latter region in recent years, and that annual variation in trip durations will be particularly marked at large colonies, making them especially vulnerable to adverse effects of low prey availability at sea.

Key-words:

Competition; Climate change; Northern gannets; *Morus bassanus*; North Sea; Populations

INTRODUCTION

There is growing concern over impacts of climate change on animal populations (Pearce-Higgins et al. 2010, Rolland et al. 2010, Davey et al. 2011). Recent studies have highlighted that in many cases, climate-related changes are also affected by population density (Rotella et al. 2009, Votier et al. 2009, Smallegange et al. 2011), but the mechanisms underlying such density-dependence are often unclear (Ahola et al. 2009, Laws & Belovsky 2010, Linares et al. 2010). In marine environments, the pace and direction of changes in climate over the past five decades have shown marked geographical variation (Burrows et al. 2011) but net warming has had a net negative impact on primary production (Behrenfeld et al. 2006, Boyce et al. 2010). There is also growing evidence that such decreases in production have been propagated to other trophic levels (Beaugrand et al. 2002, Behrenfeld et al. 2006), extending in some cases to higher marine predators such as seabirds (Wanless et al. 2007, Dorresteijn et al. 2012, Satterthwaite et al. 2012). Intense fishing pressure can also have cascading effects on marine food webs (Baum & Worm 2009) and the greatest threat to fish stocks is likely to be the combined effects of climate change and overfishing (Brander 2007). Recent studies have suggested that these combined effects can also have important consequences for seabird breeding success, survival and population stability (Frederiksen et al. 2004, Ainley & Blight 2009).

Many seabird species breed in dense colonies, making them potentially powerful models to examine density-dependent responses to changes in prey availability (Kitaysky et al. 2000, Ashbrook et al. 2010). In particular, foraging trip durations of many species are longer under poorer conditions (Hamer et al. 1993, Lewis et al. 2006, Riou et al. 2011) and also increase as a function of colony size, providing strong evidence of intra-specific competition for prey resources at sea (Lewis et al. 2001, Forero et al. 2002, Ainley et al. 2003). Changes in foraging conditions may thus be expected to have greater impacts on trip durations in larger populations (Hamer et al. 2006), but there are few data to test this prediction.

Within the British Isles, northern gannets *Morus bassanus* (hereafter gannets) breed at colonies differing in size from tens to tens of thousands of pairs (Wanless et al. 2005). They are generalist predators, able to exploit a wide variety of species and sizes of prey, including lipid-rich fish such as mackerel (*Scomber scomber*) and sandeels (mainly *Ammodytes marinus*) in addition to discards from fishing vessels (Hamer et al. 2000, Lewis et al. 2003). Most British colonies are increasing in size, with smaller colonies having higher per capita growth rates (Wanless et al. 2005). In addition, direct observations of nest attendance have revealed a positive relationship between colony size and the mean foraging trip durations of breeding birds, both among colonies of different sizes in the same year and, from the limited longitudinal data available, within individual colonies as they grow (Lewis et al. 2001). However, trip durations and foraging ranges at one of the largest gannet colonies in the UK were found to be much longer in years when sandeel stocks around the colony were low (Hamer et al. 2007a), suggesting that impacts of changes in prey availability may outweigh those of changes in population size. Yet it is not known whether birds at colonies of different sizes were similarly affected. Lewis et al. (2006) found that chronically poor conditions resulted in greater foraging effort by Cape gannets *Morus capensis* even at small colonies, highlighting a need to understand better how changing environmental conditions affect birds in populations of varying size.

Here we resampled the same colonies as those studied in 2000 by Lewis et al. (2001), after a further nine years of population growth. Lewis et al. (2001) found no evidence of any spatial variation in the effects of population size, but since then, several studies have identified strong regional structure in breeding productivity and population trends of seabirds within Britain and Ireland (Frederiksen et al. 2007, Cook et al. 2011). In particular, for gannets, the Celtic and Irish Sea region was considered ecologically distinct from the North Sea region, including Fair Isle and Shetland, on the basis of consistent variation in abundance at breeding colonies (Fig 3 in Cook et al. 2011). In the North Sea region, several species of seabird have experienced declining breeding success since the mid 1980s (Burthe et al. 2012), but breeding productivity in 2009 was higher than it had been for a number of years including 2000, possibly due to increased availability of sandeels in 2009 (JNCC 2011). Stocks of mackerel in the southern, western and northern North Sea were also 30% higher in 2009 than in 2000 (4.0×10^3 tonnes and 3.1×10^3 tonnes, respectively; data from ICES 2010). Hence we predicted less intense competition, i.e. a smaller influence of population size on foraging trip durations, at North Sea colonies in 2009 compared to 2000.

In contrast to the North Sea, there was little evidence for any increases in prey availability or quality within the Celtic or Irish Seas in 2009 and some evidence of recent declines in prey biomass in this region (JNCC 2011, Riou et al. 2011). As a result of this difference between the two regions in 2009, we predicted less difference between years in the relationship between population size and trip duration at colonies in the Celtic and Irish Seas than in the North Sea, resulting in significant interactions between the effects of population size, year and region on trip duration. We also examined the per capita growth rates of our study colonies over the periods 1994-2000 and 2000-2009. We assessed whether the relationship between population size and growth rate was similar in each time-period or whether it was affected by changing environmental conditions, resulting in significant two-way or three-way interactions between the effects of population size, time-period and region on per capita growth rate.

METHODS

Fieldwork took place from June to August 2000 and 2009 at nine gannet colonies around the coast of Britain and Ireland. A tenth colony (Lambay, established in 2007) was also sampled in 2009 (Fig 1). Counts of Apparently Occupied Sites (AOS), made from aerial photographs combined with visits to colonies, both with a maximum sampling error of around 5-10% (Wanless et al. 2005), were obtained from the literature (Murray & Wanless 1997, Wanless et al. 2005, Murray 2011), together with more recent unpublished data for some colonies (see acknowledgements). Five of the nine colonies sampled in 2000 were counted that year. Population sizes for the other four colonies (two counted in 1999, one in 1998 and one in 1995) were adjusted using colony-specific per capita growth rates recorded between 1994 and 2004 (Murray & Wanless 1997, Lewis et al. 2001, Wanless et al. 2005) to estimate the additional increase in population size since the most recent count (in practice these increments were < 3% of population size). Six of the 10 colonies sampled in 2009 were counted that year. The other four were last counted in 2004 (n=2) or 2008 (n=2) and population sizes for these colonies in 2009 were estimated by assuming that per capita growth rates recorded between 1994 and 2004 or 2008 were maintained until 2009. The remaining colony (Ailsa Craig) decreased slightly in size between 1994 and 2004 (Wanless et al. 2005) but has shown no further decreases since then (B. Zonfrillo pers comm.) and so we assumed the same size in 2009 as in 2004.

To determine foraging trip durations, around 20 chick-rearing pairs at each colony (2000, 18-24 pairs; 2009, 19-30 pairs) were observed during daylight hours (sunrise to sunset) for an average of 41 hours each (2000, 16-60hrs; 2009, 16-64hrs). Following Hamer et al. (1993) and Lewis et al. (2001), the arrival and departure times of foraging adults were recorded to the nearest minute and used to calculate a daily changeover rate at each colony (number of changeovers observed divided by the nest-days of observation). The mean trip duration at each colony was then calculated by dividing the time available per day for undertaking foraging trips (24 hours minus the mean time adults spent together at the nest) by the estimated changeover rate. To account for possible changes in trip durations as chicks grew, chicks were aged using a combination of observed hatch dates and plumage characteristics (Nelson 2002). The median age of all chicks observed was 7 weeks in 2000 and 5 weeks 2009.

All statistical analyses were carried out using R version 2.12.1 (R-Development-Core-Team 2010). We used a linear mixed effects model (LME) (Pinheiro & Bates 2000) using the package 'nlme' to examine whether the relationship between natural log (Log_e) population size (log-transformed to normalize the data and because population growth is a multiplicative rather than additive effect) and per capita growth rate differed over the periods 1994-2000 and 2000-2009. This model included region (North Sea or Celtic/Irish Sea, as defined by Cook et al. 2011) as a fixed effect and colony identity as a random effect to account for repeated measures (see Fig 1 for locations of colonies; the model had the form: per capita growth rate ~ initial $\log_e$ colony size + (initial $\log_e$ colony size * time period) + (initial $\log_e$ colony size * time period * region) + random =(~1| colony), with a Gaussian error distribution). We then used an additional LME to examine how the relationship between square root colony size and foraging trip duration differed between years. This model also included two potential confounding effects (median chick age and total number of nest-hours of observation at each colony) and had the form: trip duration (hours) = square-root colony size + (square-root colony size * year) + (square-root colony size * region) + chick age + nest-hours + random =(1| colony), with a Gaussian error distribution. Colony size was square-root transformed for this second analysis, following Lewis et al. (2001), because the area covered by birds at sea increases with the square of the mean foraging radius. To check the robustness of our analyses, we compared each full model with the minimum adequate model (Crawley 2007) following serial deletion of non-significant terms (Mundry & Nunn 2009). To check that our analysis was not affected by errors in estimating population sizes, we also re-ran each model using extreme population sizes, assuming no further growth of any colonies since the most recent counts. This had no qualitative effect on our results in either case, and so we are confident that any errors in estimating population sizes did not affect our conclusions.

In contrast to foraging trip durations, mean travel speeds at sea show remarkable consistency between different colonies and years (Grémillet et al. 2006, Hamer et al. 2007, Votier et al. 2010). Hence, in addition to trip durations, we also estimated foraging ranges each year, using telemetry data to calibrate foraging range against trip duration, following Hamer et al. (2001).

RESULTS

Population sizes and per capita growth rates

Study colonies differed in size from 188 AOS (Ireland's Eye) to 45,569 AOS (Bass Rock) in 2000 and from 158 AOS (Lambay) to 52,292 AOS (Bass Rock) in 2009. With the exception of Ailsa Craig (see Methods), all colonies increased in size between 2000 and 2009 (Fig 1). Per capita population growth rates between 1994 and 2000 and between 2000 and 2009 were significantly negatively related to population size in 1994 and 2000, respectively (LME; $F_{1,7} = 27.3$, $P = 0.001$) with no difference in this relationship over the two time-periods (two-way interaction; $F_{1,7} = 1.0$, $P > 0.05$; 1994-2000: $b = -1.953$, 2000-2009: $b = -3.675$; Fig 2). However, colonies in the Celtic/Irish Sea region (I, G and A) grew substantially and significantly more slowly for their size over the period between 2000 and 2009 than did colonies bordering the North Sea (three-way interaction; $F_{2,6} = 9.2$, $P < 0.05$; Fig 2).

Foraging trip durations

There was a significant positive relationship between current population size (square root transformed AOS) and mean trip duration (TD) during chick rearing in both 2000 and 2009 (LME; $F_{1,5} = 28.97$, $P = 0.01$) but with a much steeper slope, indicating a much stronger influence of population size, in 2000 (TD (hours) = [0.069*Sqrt colony size(AOS)] + 6.39) than in 2009 (TD (hours) = [0.011*Sqrt colony size(AOS)] + 8.08); two-way interaction between square-root colony size and year; $F_{1,5} = 8.73$, $P < 0.05$; Fig 3). Population size also explained much more of the variation in trip duration among colonies in 2000 ($R^2 = 0.76$) than in 2009 ($R^2 = 0.43$). Despite the increases in population sizes over the study period, birds at all but the two smallest colonies studied in 2000 (Ireland's Eye and Troup Head) made shorter trips in 2009 than in 2000 (Fig 3), suggesting that in most cases, changes in environmental conditions had a stronger effect on trip durations than did the increases in colony size.

There was also a significant effect of region in the model ($F_{1,8} = 7.36$, $P < 0.05$), with observed trip durations in 2009 on average 32% longer than predicted from colony size (i.e. above the fitted regression line for 2009) at colonies in the Celtic and Irish Seas, but 13% shorter than predicted (i.e. below the regression line) at colonies bordering the North Sea (Fig 3). This difference between regions was confirmed by running separate linear models for each year; there was a significant two-way interaction between square-root colony size and region in 2009 ($F_{2,7} = 7.56$, $P < 0.05$) but not in 2000 ($F_{2,6} = 2.82$, $P = 0.1$). There was a small but significant additional effect of chick age (F = 13.83, P = 0.03) but no effect of the number of nest-hours of observation (ns).

To assess further the difference between years and regions in the influence of colony size, we used the relationship between colony size and trip durations found in 2000 to predict trip durations from colony sizes in 2009. Observed trip durations in 2009 were shorter than predicted at all six colonies bordering the North Sea but longer than predicted at three of the four study colonies in the Celtic and Irish Sea, the exception being the colony on Ailsa Craig (Fig 4).

DISCUSSION

The slope of the relationship between population size and foraging trip duration in 2009 was less than one quarter of that in 2000 (Fig 3), suggesting a much weaker influence of population size in 2009, presumably due to less intense intra-specific competition for prey resources at sea. Gannets compete mainly through passive interference due to prey disturbance rather than by depleting prey (Lewis et al. 2001, Camphuysen 2011), but lower prey abundance can nonetheless lead to greater competition through fewer, smaller and/or shorter-lasting occurrences of prey close to the surface within the vertical foraging ranges of birds (Lewis et al. 2002). Gannets may also compete directly for discards from fishing vessels, which comprise about 15% of the diet at colonies in the UK (Hamer et al. 2007; Votier et al. 2010). Changes in prey availability can result in birds altering their activity at sea (e.g. the proportion of time spent resting on the water; Monaghan et al. 1994, Litzow & Piatt 2003) without any effect on trip durations (Lescroël & Bost 2005, Garthe et al. 2011), but large reductions in prey availability are likely to exceed this buffering capacity, resulting in longer trips, especially at large colonies where birds have less flexibility in their time/activity budgets owing to their greater foraging effort (Lewis et al. 2004, Hamer et al. 2007a).

Trips at most colonies were shorter in 2009 than in 2000, despite all but one of these colonies increasing in size since 2000. Hence the impact of changes in prey availability between years exceeded that of changes in colony sizes in most cases. However, trips at the two smallest colonies studied in 2000 (Troup Head and Ireland's Eye) were longer in 2009, because annual variation in density-dependence had little effect on trip durations at these small colonies (Fig 3). Hence the main influence on trip duration in these two cases was from colony growth. This has important implications for the use of trip durations to monitor marine environments (Furness & Camphuysen 1997, Hamer et al. 2006), because even large changes in prey availability will have relatively little effect on trip durations at small colonies.

A recent analysis of seabird monitoring data for the UK identified two separate ecologically coherent regions for gannets, corresponding with the North Sea and the Celtic/Irish Sea, within which trends in abundance varied in a consistent fashion (Cook et al. 2011). In support of this distinction, we found that colonies in the Celtic/Irish Sea region grew significantly more slowly for their size over the period between 2000 and 2009 than did colonies bordering the North Sea. We also found that observed trip durations in 2009 were shorter than predicted at colonies bordering the North Sea, but longer than predicted at colonies in the Celtic and Irish Seas. These data suggest less favourable environmental conditions in the latter region over recent years, similar to the impacts of low food availability on trip durations and population trajectories of Cape gannets *Morus capensis* in southern Africa (Lewis et al. 2006). This suggestion is also supported by recent data showing longer trips than expected from population size at a gannet colony in Brittany (Grémillet et al. 2006), long foraging trips and poor chick growth of Manx shearwaters *Puffinus puffinus* since 2007 at a colony in SW

Wales (Riou et al. 2011) and decreases in overwinter survival of adult guillemots *Uria aalge* and razorbills *Alca torda* breeding in Wales (Votier et al. 2005).

At Ailsa Craig, in the northern Irish Sea, population size decreased slightly between 1995 and 2000 (Wanless et al. 2005) but mean trip duration in relation to population size was lower in 2009 than at more southerly colonies (Fig 4). We have no data on diets of birds or prey biomasses in this region but this difference suggests more favourable environmental conditions within the northern Irish Sea in more recent years. This corresponds with both a suspected northerly shift in the foraging areas of Manx shearwaters from the south of the region (Guilford et al. 2008) and large increases in populations of guillemots and razorbills at nearby Rathlin Island, following steep declines between 1999 and 2007 (Allen et al. 2011).

In contrast to gannets, which have maintained consistently high breeding success over this period (Hamer et al. 2007a, JNCC 2011), several species of seabird at colonies in the North Sea have experienced declining breeding success since the mid 1980s (Burthe et al. 2012) and greatly reduced adult survival since the mid-2000s (Lahoz-Monfort et al. 2011). This difference partly reflects the greater flexibility of gannets in terms of diet and foraging ranges (Hamer et al. 2007a, Hamer et al. 2009) and may also be linked to recent increases in North Sea stocks of mackerel (ICES 2010), which are too large to be taken by most other seabirds in the region and may compete with them for prey species such as sandeels (Furness 2002, Frederiksen et al. 2007, Langoy et al. 2012), but have been the main component in the diet of gannets at the large colony on Bass Rock in recent years (> 80% by frequency; R.D. Davies et al. unpubl.data).

The consistency between different colonies and years in the mean travel speeds of gannets at sea (Grémillet et al. 2006, Hamer et al. 2007a, Votier et al. 2010b) can be used in conjunction with the relationship between colony size and trip duration to project foraging ranges and hence at-sea distributions for additional colonies (Grecian et al. 2012; Fig 3). However, the results of this study highlight the importance of accounting for temporal variation in the latter relationship to avoid mismatches between observed and predicted foraging ranges.

The observed difference between years in the effect of population size on gannet foraging behaviour means that annual variation in trip durations will be particularly marked at large colonies, making them especially vulnerable to adverse effects of low prey availability. Long foraging trips result in chicks receiving less food per unit time, assuming food loads are no larger after long trips (Lewis et al. 2006), and also increase the likelihood of adults leaving chicks unattended and at risk of being washed from the nest during poor weather, exposed to cold temperatures or attacked by conspecifics (Nelson 2002, Lewis et al. 2004). There is no evidence to date of a relationship between colony size and breeding success in gannets (Lewis et al. 2001), but such a relationship has been observed in some other species (Hunt et al. 1986, Kitaysky et al. 2000) and evidence from one large gannet colony suggests that in years of poor food availability, adults have very little leeway to increase foraging effort any further without likely adverse effects on chick survival (Hamer et al. 2007a).

Finally, there is evidence that gannets from large colonies recruit into smaller colonies (Moss et al. 2002, Votier et al. 2011), so it is possible that trip durations and provisioning rates play a role in influencing where birds choose to breed for the first time (Lewis et al. 2001). Our data indicate that the difference in trip durations between large and small colonies is most marked during adverse foraging conditions, and so differences in recruitment rate may have contributed towards both the observed negative density-dependent growth of populations and the lower per capita growth rates since 2000 at colonies in the Celtic and Irish Sea (Fig 2).

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FIGURES

Figure 1. Locations and sizes of the ten gannet colonies studied in 2000 and 2009 (A, Ailsa Craig; BR, Bass Rock; B, Bempton Cliffs; F, Fair Isle; G, Great Saltee; H, Hermaness; I,

Ireland's Eye; L, Lambay; N, Noss; T, Troup Head). Colony sizes (number of apparently occupied sites, square-root transformed) are shown for 2000 (grey bars) and 2009 (black bars). The area of each circle is proportional to colony size in 2009. Scales on the y axes differ among colonies.

Figure 2. The relationship between $\log_e$ population size (AOS) and percentage per capita population growth rate from 1994 to 2000 (A) and from 2000 to 2009 (B). North Sea colonies: filled circles, Celtic/Irish Sea colonies: open circles. In 2000-2009, there was a significant difference between colonies in the North Sea (solid regression line) and the Celtic/Irish Sea (dashed regression line).

Figure 3. The relationship between mean foraging trip duration (hours) and population size (square-root transformed to be proportional to the number of birds at sea) in 2000 (triangles) and 2009 (circles). Open symbols, Irish/Celtic Sea colonies; Filled symbols, North Sea colonies (A, Ailsa Craig; BR, Bass Rock; B, Bempton Cliffs; F, Fair Isle; G, Great Saltee; H, Hermaness; I, Ireland's Eye; L, Lambay; N, Noss; T, Troup Head).

Figure 4. Observed (O) and predicted (P) trip durations (hours), with associated standard errors, at different colonies in 2009. Predictions were based on population sizes in 2009, using the relationship between square-root population size and trip duration that was observed in 2000 (A, Ailsa Craig; BR, Bass Rock; B, Bempton Cliffs; F, Fair Isle; G, Great Saltee; H, Hermaness; I, Ireland's Eye; L, Lambay; N, Noss; T, Troup Head).

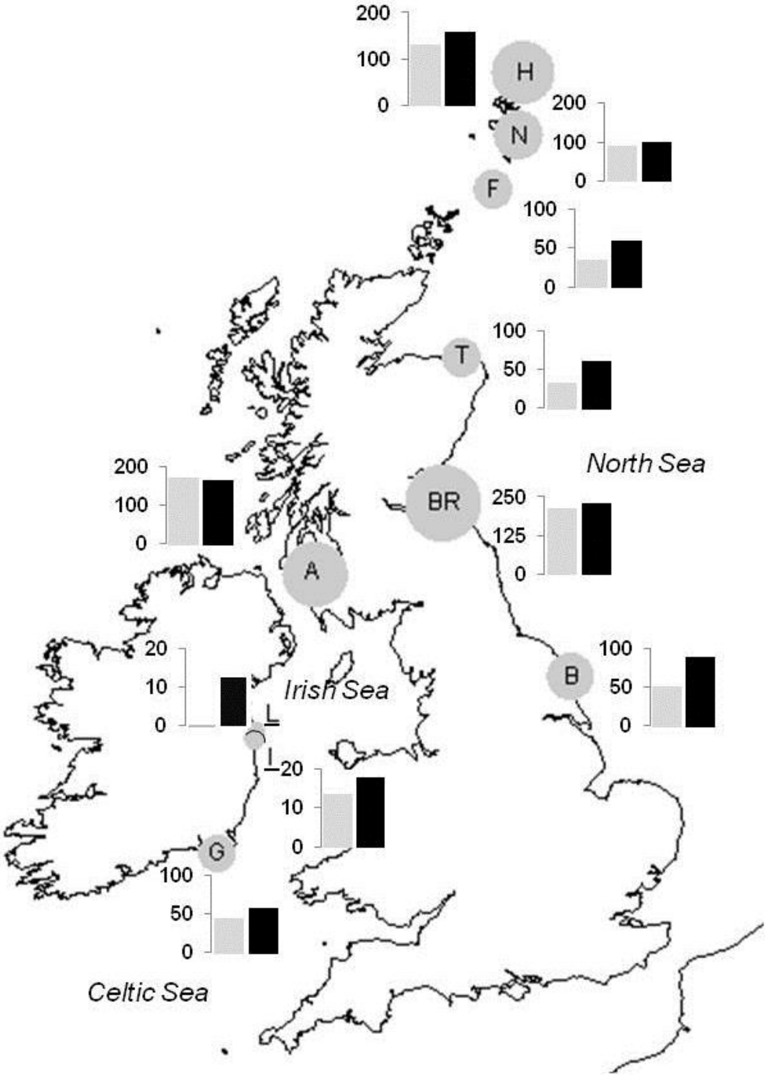

200
100
0
H
N
200
100
0
F
100
50
0
T
100
50
0
North Sea
200
100
0
BR
250
125
0
A
20
10
0
Irish Sea
L
I
20
10
0
B
100
50
0
G
100
50
0
Celtic Sea

Figure 1.

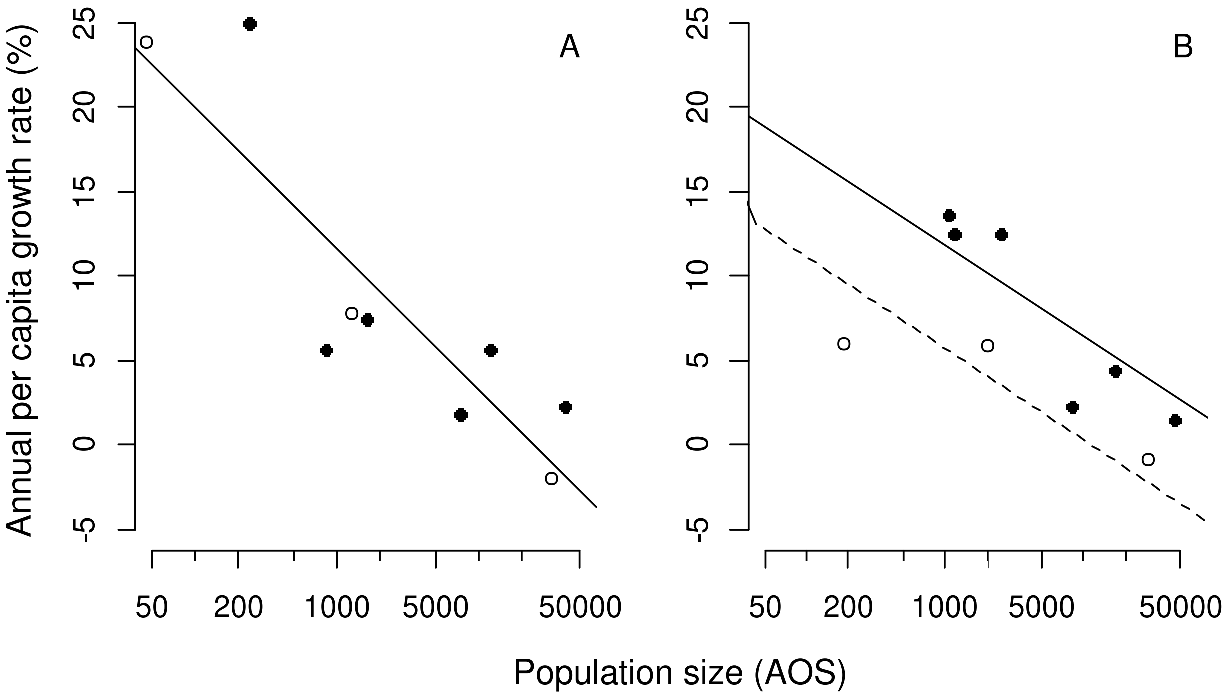

A
B
Annual per capita growth rate (%)
25
20
15
10
5
0
-5
50
200
1000
5000
50000
Population size (AOS)

Figure 2.

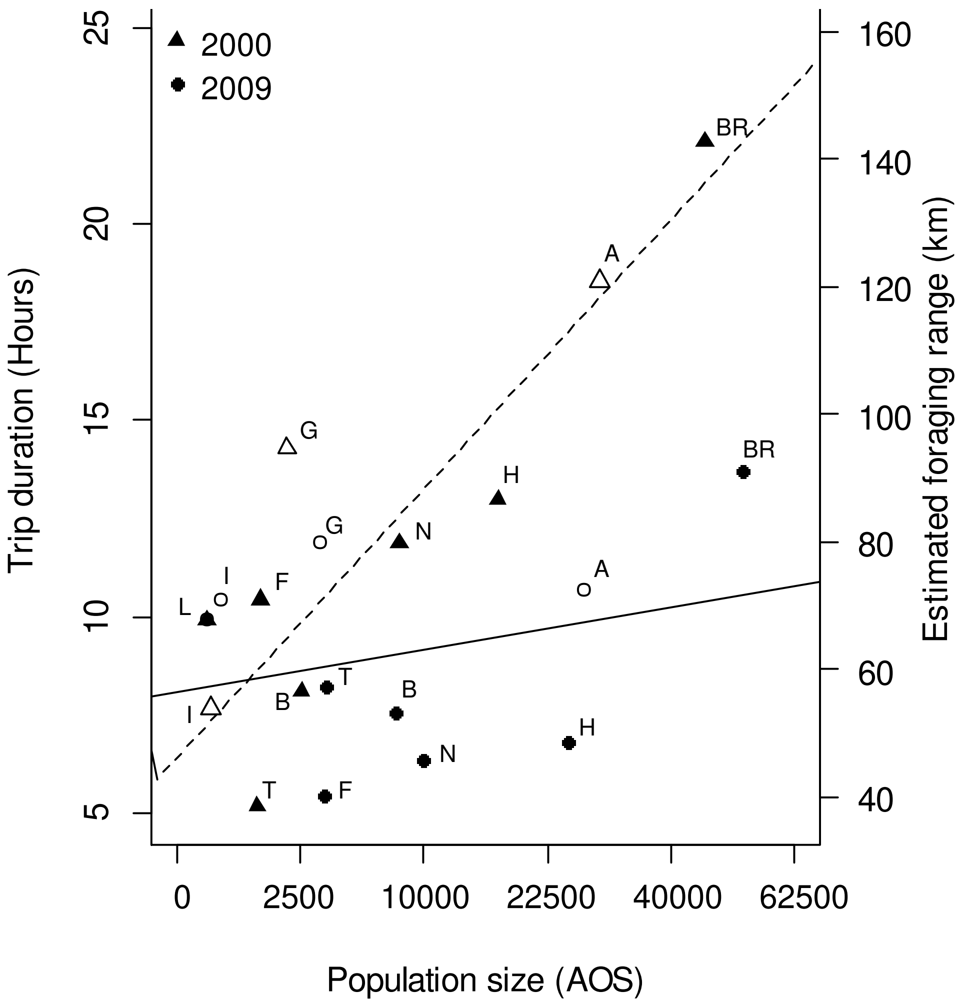
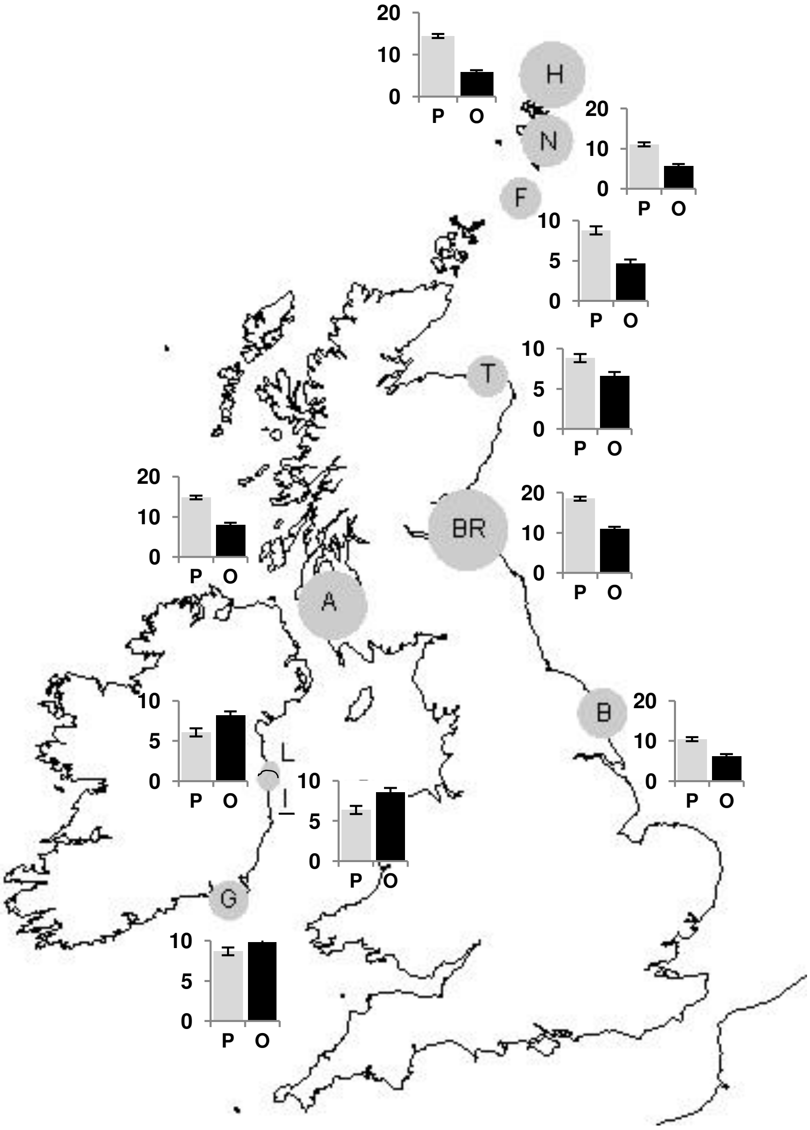

2000
2009
Trip duration (Hours)
Estimated foraging range (km)
Population size (AOS)
5
10
15
20
25
40
60
80
100
120
140
160
0
2500
10000
22500
40000
62500
BR
A
G
H
N
F
I
L
B
T
B
T
F
N
H
BR
A
G
I

Figure 3.



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551 Figure 4.