Foraging ecology during nesting influences body size in a pursuit-diving seabird

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ABSTRACT: Causes and consequences of differences in seabird foraging strategies between breeding colonies are not well understood. We tested whether body size of a pursuit-diving seabird, the thick-billed murre *Uria lomvia*, differs between breeding colonies and, if so, how size differences can be understood in the context of differences in foraging behavior, habitat use, and breeding performance. We measured adult murres over 3 seasons (2008 to 2010) at 2 of the Pribilof Islands, St. Paul and St. George, located on the continental shelf of the Bering Sea at different distances from the shelf break. Body mass and size were positively associated with deep diving and negatively associated with long flights, suggesting morphology influences foraging and commuting efficiency. Murres from St. Paul (farther from the shelf break) were larger than those from St. George (nearer the shelf break), foraged exclusively in the middle shelf domain, made deep dives during daylight, and fed on larger benthic prey. In contrast, smaller murres from St. George commuted greater distances to beyond the shelf break, made shallow dives at night, and fed on smaller, high-energy, schooling, vertical-migrating prey. Both foraging strategies resulted in similar chick-feeding rates and fledging success. The largest and the smallest murres experienced less stress during breeding compared to intermediate-sized murres, suggesting divergent selection for body size between islands. Nesting murres, as central-place foragers, may experience strong selection pressure on body size and other adaptive traits that reflect differences between breeding colonies in foraging ecology and the acquisition of resources for reproduction.

KEY WORDS: Body size · Foraging · Diving · Marine habitats · Stress levels · Bering Sea · Murres · Seabirds

INTRODUCTION

Foraging behavior is a critical factor affecting an animal's fitness because it directly affects survival and reproductive success. In marine environments, foraging by predators is generally 3-dimensional and food webs vary among marine habitats, such as neritic continental shelves vs. oceanic basins (Schabetsberger et al. 2000, Sims et al. 2005, Benoit-Bird et al. 2011). The timing and direction of vertically migrat-

ing prey varies with bathymetry (descent vs. ascent; Schabetsberger et al. 2000, Sims et al. 2005), which can affect prey availability to predators that forage at night or during twilight (Regular et al. 2010, Dias et al. 2012). Energy gain may also differ according to foraging habitat; in the Bering Sea, for example, krill are more abundant near the surface at night, and have higher energy content in the oceanic basin compared to the neritic shelf (Whitman 2010, Benoit-Bird et al. 2011, S. Heppell unpubl. data). Thus, the local environment exerts a strong influence on central-place foragers such as breeding seabirds (Paredes et al. 2012, Harding et al. 2013) because they are constrained by the need to provision offspring at the nest (Orians & Pearson 1979). In theory, individuals should exhibit foraging strategies that maximize their fitness, which is often translated into maximizing energy acquisition by simultaneously optimizing energy intake and expenditure rates (MacArthur & Pianka 1966).

Body size can affect the feeding efficiency of animals in different environments (Mittelbach 1981) and consequently influence survival and/or reproduction (Lynch 1977). In diving seabirds, optimal body size is predicated on foraging depth (Mori 2002). A large body size is associated with increased dive endurance, as oxygen storage capacity increases and specific metabolic rate decreases with increasing body size. Thus, larger animals can engage in deeper and longer dives (Halsey et al. 2006). Larger diving seabirds also swim faster (Watanabe et al. 2011) and feed on larger prey (Zavalaga et al. 2007). Large body mass is, however, disadvantageous for flapping flight because the power requirement for flight increases with size more rapidly than does available power (Pennycuick 2008). Cormorants (*Phalacrocorax* spp.) returning to their nests with heavy food loads for their chicks have higher wing loading and work harder than those flying out from the colony to forage (Wilson et al. 2006). Smaller brown boobies *Sula leucogaster* can fly longer distances, regardless of sex, highlighting the importance of body size (Lewis et al. 2005). Trade-offs between foraging range and diving capability are apparent in sexually dimorphic shags (*Phalacrocorax* spp.), where individual, gender, and colony differences in body size are associated with water depth of neighboring foraging habitats (Cook et al. 2013, Ratcliffe et al. 2013). In seabirds that lack or display only slight sexual dimorphism in body size, such as thick-billed murres *Uria lomvia*, the effects of body size on the foraging behavior of individuals are not predicted. However, among-colony differences in morphology (Gaston et al. 1984, Harding et al. 2013) and gender differences in foraging behavior at some colonies (Paredes et al. 2008) suggest otherwise.

Fitness costs associated with individual foraging strategies are difficult to measure in long-lived seabirds. Adult physiological stress, reflected in circulating levels of the hormone corticosterone (CORT), is a good indicator of foraging effort in seabirds (Harding et al. 2007) because CORT levels increase in breeding adults when food availability decreases near the colony (Kitaysky et al. 2010). The overproduction of CORT prolongs the mobilization of stored energy resources and renders the animal susceptible to fatigue and disease (Buchanan 2000). There is now abundant evidence that exposure of animals to high levels of CORT over an extended period can reduce immune functionality (Saino et al. 2003), cognitive abilities of individuals (Kitaysky et al. 2003), and survival (Romero & Wikelski 2001, Brown et al. 2005, Kitaysky et al. 2007, Goutte et al. 2010). Hence, individuals that manage to maintain low stress levels during reproduction, for example by maximizing energy acquisition through efficient foraging, would likely have higher fitness. Those that prioritize provisioning offspring by diverting resources from self-maintenance may have lower chances of survival when food supplies are reduced (Satterthwaite et al. 2010, 2012). Thus, changes in CORT levels may be a useful tool for inferring fitness-associated effects of variation in body size.

We examined how prey resource use influences foraging strategies, breeding performance, and body size of a pursuit-diving seabird, the thick-billed murre *Uria lomvia* (hereafter referred to as 'murre'), which is capable of flight, but at a very high energetic cost (Elliott et al. 2013). To test this, we used a 3 yr data set on GPS foraging locations and diving behavior of chick-rearing murres on 2 of the Pribilof Islands, St. Paul and St. George, which differ in oceanographic settings. Although both islands are situated on the continental shelf (<100 m depth), St. Paul is 3 times farther from the deep oceanic basin of the Bering Sea (>200 m depth) compared to St. George. Thus, we predicted different foraging strategies and diets of murres breeding on the 2 islands (Renner et al. 2012, Harding et al. 2013), and that these differences might be reflected in inter-colony differences in murre body size (Harding et al. 2013, Orben et al. 2015). In addition to colony effects, we investigated the effects of gender and individual foraging behavior (e.g. trip distance and diving) on body size, and used changes in stress levels to infer potential individual fitness costs. To make links to the

local environment, we used diving activity as a proxy for temporal and vertical prey availability among bathymetric habitats. Finally, we assessed inter-colony and inter-annual differences in breeding performance (chick-feeding rates, fledging success, and average prey size) and adult nutritional stress. Availability of key forage fish for murres is expected to be lower on the southeastern Bering Sea continental shelf during cold years, due to changes in ocean temperatures associated with sea-ice extent (Hollowed et al. 2012, Stabeno et al. 2012). Given that our study period encompassed 3 cold years, we expected to observe lower resilience to food shortages in murres from St. Paul, located farther from oceanic waters, compared to those from St. George (Byrd et al. 2008, Paredes et al. 2012).

MATERIALS AND METHODS

Field data collection

We studied thick-billed murres breeding at St. Paul Island (57° 7′ N, 170° 17′ W) and St. George Island (56° 36′ N, 169° 33′ W) in the Pribilof Islands, between June and September in 2008, 2009, and 2010. Both St. Paul and St. George are located in the middle domain of the continental shelf (50 to 100 m depth) of the southeastern Bering Sea, about 70 km from each other. St. Paul, however, is farther from the outer shelf domain (~30 km; 100 to 200 m depth) and the shelf slope domain (~90 km; >200 m depth). The breeding population of murres is in decline at St. Paul, estimated to be about 15 000 birds, and is relatively stable at St. George, estimated to be about 1.5 million birds (Byrd et al. 2008). Murres show slight sexual dimorphism at some colonies, with males being somewhat larger in most dimensions except wing length (Gaston & Hipfner 2000). Incubation lasts ~36 d in murres and both parents provision a single chick at the nest site for 15 to 25 d, after which the male is the sole caregiver at sea for a subsequent 3 to 4 wk.

We captured adult murres rearing 5- to 15-day-old chicks using a telescoping noose pole. At initial capture, each bird was weighed (±1 g) and a time–depth recorder (TDR, Lotek LAT1500 or 2500) and/or a GPS (TechnoSmart GiPSy-2) was attached following procedures described by Harding et al. (2013) (Table 1). Handling took ca. 10 to 15 min. Birds were recaptured after 42 ± 3.6 h and 54 ± 5.2 h at St. Paul and St. George, respectively. On recapture, instruments were removed, birds were reweighed, and wing

chord, tarsus, gape, and culmen length were measured. TDRs recorded depth every 1 to 3 s, with an absolute pressure accuracy of ±1% of full scale. GPS loggers were set to record locations at intervals of 1 to 60 s, with longer intervals more often used at St. George to ensure tracking during complete foraging trips to the Bering Sea slope.

Adult diets were sampled using the water off-loading (lavage) method (Renner et al. 2012), repeated twice to ensure empty stomachs (Neves et al. 2006). Both tagged and untagged birds were lavaged, and tagged birds were sampled only at recapture.

Adult time-budget watches (3 to 6 observation periods) were conducted during early, mid, and late chick rearing for determination of chick-feeding frequencies (meals h^{-1}), trip duration, and nest attendance (bird-min h^{-1}; Harding et al. 2007, 2013). At each colony in each year, marked birds were observed in a plot containing 7 to 15 breeding pairs from sunrise to sunset (15 to 16 h), and for 6 h on the following day after sunrise to record return times following overnight trips. In 2008 and 2009, observations of both tagged (n = 36) and control birds (n = 124) were recorded to test logger effects on activity budgets.

Chick diets were determined both during adult time-budget watches (see above) and dedicated chick-feeding watches during block periods (3 to 15 h) using a zoom spotting scope (×20 to 60) or binoculars (10 × 42). Murres deliver single prey items to their chicks, which are held lengthwise in the adult's bill, allowing prey identification and estimation of relative prey size. Prey were identified to the lowest possible taxonomic level (usually species), and visually assigned to a relative size less than, equal to, or longer than the gape length of the parent.

Fledging success (average number of chicks fledged/nest where a chick was hatched) was determined at each colony by the Alaska Maritime

Table 1. Summary of data loggers deployed in thick-billed murres at the Pribilof Islands during 2008, 2009, and 2010

| Year | Tags recovered/deployed | | | | Tags |
	TDR	GPS	GPS & TDR	Total	with data
St. Paul Island					
2008	12/13	0/0	2/5	14/18	13
2009	0/0	19/26	0/2	19/28	15
2010	0/0	3/3	32/40	35/43	28
St. George Island					
2008	18/21	4/5	3/6	25/32	24
2009	0/0	0/2	15/26	15/28	14
2010	0/0	0/0	29/41	29/41	28

National Wildlife Refuge long-term monitoring program (Renner et al. 2014). The same plots (n = 8 to 12), each containing 20 to 30 murre nest sites, were followed annually. Plots were checked every 3 to 6 d, and chicks were considered to have fledged if they disappeared from the nest site more than 15 d after hatching (Byrd et al. 2008).

We measured circulating levels of baseline CORT in adults to estimate level of nutritional stress as a proxy for adult survival probability (Satterthwaite et al. 2012). Birds were sampled according to a standardized technique, with a blood sample (<500 μl) collected within 3 min of capture (Benowitz-Fredericks et al. 2008). All blood samples were centrifuged, and plasma and red cells were frozen separately for later analysis of CORT in plasma (Kitaysky et al. 2010) and DNA sex determination of red cells (Griffiths et al. 1998) at the University of Alaska Fairbanks. Tagged birds were sampled both prior to tag deployment and at recapture for tag removal (St. Paul: n = 54; St. George: n = 45) to investigate changes in CORT levels in relation to body size (see below).

Data and statistical analysis

GPS locations from 122 trips were filtered and interpolated using MATLAB (MathWorks). Of these, 12% were considered incomplete for calculating trip distance (Table 1). Trips were classified by time of day (daytime vs. overnight, after Harding et al. 2013) and bathymetric habitat (middle shelf, outer shelf, or shelf slope). Overnight trips typically included daylight foraging, as trips were initiated as early as 18:00 h and ended after sunrise. Maximum trip distance (straight line distance between the nest site and the most distant trip location) was calculated and bathymetric habitat was determined using this location. As multiple trips were recorded from the same individuals, trip distance was analyzed using linear mixed models (LMMs) with colony, sex, and time of day as fixed effects. Year was excluded as a factor from our spatial analysis because sample sizes for year–colony combinations were too small to capture annual spatial variation (Soanes et al. 2013).

Dive data were first processed independently from tracking data using a zero-offset correction algorithm (IKNOS-DIVE, IKNOS toolbox; Y. Tremblay unpubl. data). A dive was deemed to have occurred when maximum depth was ≥2 m. We used maximum dive depth, dive duration, bottom time (time between the first and last inflection points at >80% of the maxi-

mum depth), ascent/descent rates (vertical speed), and dive efficiency (bottom time ÷ [dive duration + post-dive interval]) for between-colony comparisons of foraging on the middle shelf. Diving efficiency indicates the proportion of time a diver spends foraging relative to the duration of the complete dive cycle (Ydenberg & Clark 1989). Assuming the duration of a dive reflects a bird's foraging efficiency, we interpret diving efficiency as a proxy of feeding time. We excluded dives with post-dive intervals of longer than 60 s (29%; n = 4504) to avoid including time spent between diving bouts (Tremblay et al. 2003). From 101 birds, we recorded a total of 32 488 dives (n_{2008} = 16 597; n_{2009} = 4703; n_{2010} = 14 224), with a maximum recorded depth of 133 m. Dives were classified by daylight periods as diurnal (day hours), nocturnal (night hours) and crepuscular (twilight hours) following Harding et al. (2013), and frequencies were calculated by colony and sex. To account for possible differences in dive depth due to double tagging (GPS tag and TDR tag), we compared dive depths of birds with a single tag to those with 2 tags. We pooled diurnal dive data from both colonies (St. Paul: n = 39; St. George: n = 33) and years (2008 and 2010) to have a sufficient sample size. Using a LMM with tag number as a fixed effect and individual as a random effect, we found that dive depth did not differ with number of tags (GPS and TDR = 39.2 ± 2.4 m, n = 46; TDR only = 44.3 ± 3.2 m, n = 26; $F_{1,82.621}$ = 1.583, p = 0.212). Similar results were found for dive duration (p > 0.05). Therefore, data were combined for analysis of diving behavior; however, yearly comparisons were restricted to between 2008 and 2010 due to lack of dive data from St. Paul in 2009 (Table 1).

Dives were matched to linearly interpolated locations based on 40 trips from 34 individuals and assigned to the corresponding bathymetric habitat in ArcGIS 10.1. Distributions of frequency of dive locations and mean depth of all birds were plotted hourly to examine the effects of daylight among bathymetric habitats. Frequencies of dives in each bathymetric habitat, grouped by daylight periods, were compared using binomial generalized linear models with individual as a repeated measure. For each trip, we analyzed the number of dives and mean dive depth using LMMs, with colony and time of day as fixed effects. To avoid the confounding effect of the physical depth of each bathymetric region, we only used dives in the middle shelf domain in the LMMs of diving parameters, with colony and sex as fixed effects.

Body size was calculated using a principal component analysis on wing, tarsus, and culmen length measurements of all birds. Body mass was not in-

cluded in the analysis to account for possible differences in body condition. All variables were positively correlated with each other (all Pearson's product-moment correlations: p < 0.001). The first principal component (PC1) explained 50% of the variance, and all the variables loaded high (culmen: 0.5653; wing: 0.6219; tarsus: 0.5419). Therefore, PC1 scores were used as an index of body size, which we then tested with a general linear model (GLM) to determine the effect of colony and sex. PC1 scores were used to test the effect of individual body size on maximum distance (long trips ≥ median 27.2 km), and physiological changes in CORT levels (see below). Body mass was also tested in relation to mean dive depth and duration, and bottom of dives for each individual controlled by bathymetric habitat (middle shelf) using Pearson's product-moment correlations.

Adult diets were calculated as the percentage of occurrence of the total number of prey species found in stomach contents (Renner et al. 2012).

We obtained daytime and overnight trip duration, chick-feeding frequencies, and prey type and size from 55 and 69 breeding pairs at St. Paul and St. George, respectively. Chick diets were calculated based on the total prey identified at some taxonomic level (~49%; n = 1135). We reported frequencies of the main prey delivered by adults, considered to be those with >3% of occurrence. Prey size was analyzed between colonies, sexes, and years using chi-squared tests. The duration of daytime and overnight trips and chick-feeding frequencies were analyzed using LMMs, with colony and year as fixed effects and nest as a random effect.

Fledging success was analyzed using a binomial generalized linear model, with plot as a repeated measure, and colony and year as fixed effects.

CORT values were log-transformed before analysis. Values at first capture were tested using LMMs, with colony and year as fixed effects and individual as a random effect. CORT values of untagged birds rearing chicks (St. Paul: n = 180; St. George: n = 192) were used to test logger effects (see Supplement 1 at www.int-res.com/articles/suppl/m533p261_supp.pdf). Additional CORT samples from birds tagged with Centre for Environment, Fisheries and Aquaculture Science (CEFAS) TDRs (St. Paul: n = 44; St. George: n = 57) were used to test body size effect on the change in hormone concentrations between tag deployment and retrieval (ΔCORT). We found no differences among type of tagged birds ($F_{3,151}$ = 0.579, p = 0.196) or between colonies ($F_{1,151}$ = 0.0227, p = 0.880). ΔCORT was measured as the proportional change in CORT values before/after deployments,

and standardized by dividing by the initial CORT value. Positive ΔCORT values indicate increases in physiological stress and negative ones indicate decreases. ΔCORT was predicted using generalized least squares (GLS) and linear mixed effects models with heterogeneity controlled for sex and colony. Predictor variables included sex, colony, body size, and a quadratic term for body size (size^2). Model selection was conducted using the corrected Akaike's information criterion (AIC$_c$). For the full family of models and AIC$_c$ output, see Supplement 2.

We addressed the possible effects of instrumentation on birds' behavior in 3 ways: (1) frequencies of nest abandonment of tagged birds between colonies and years; (2) nest attendance, chick-feeding frequency, and trip duration between control and tagged birds in 2008 and 2009; and (3) CORT levels of tagged birds at recapture and control birds in 2010 (Supplement 1).

Statistical analysis was carried out using PASW Statistics 18 and R (R Development Core Team 2011). Residuals of the linear models (GLM and LMMs) met the assumptions for homogeneity and normality. Data for trip distance were log transformed before ANCOVA analysis in relation to body size. All LMMs were estimated with restricted maximum likelihood and used individual, nest, or plot as a random effect and variance component structure (scaled identity) unless otherwise noted. Bonferroni adjustments of p-values for multiple comparisons were carried out for all tests. For the GLS model of ΔCORT we used the default covariance structure, which assumes uncorrelated errors, as our variables displayed no autocorrelation (all variance inflation factors < 2). Count data or frequencies were compared between groups using binomial generalized linear models with individual as a repeated measure for larger samples (i.e. dives, fledging success) and chi-squared test for smaller samples (i.e. prey size). Means are expressed as ±SE unless otherwise noted. All comparisons are 2-tailed, and differences were considered significant when p < 0.05.

RESULTS

Foraging behavior, body size, and body mass

Murres from St. Paul were significantly larger than those from St. George ($F_{1,196}$ = 37.32, p < 0.0001) irrespective of sex ($F_{1,196}$ = 0.403, p = 0.527). Within colonies, males were larger than females ($F_{1,196}$ = 15.048, p < 0.0001; Fig. 1).
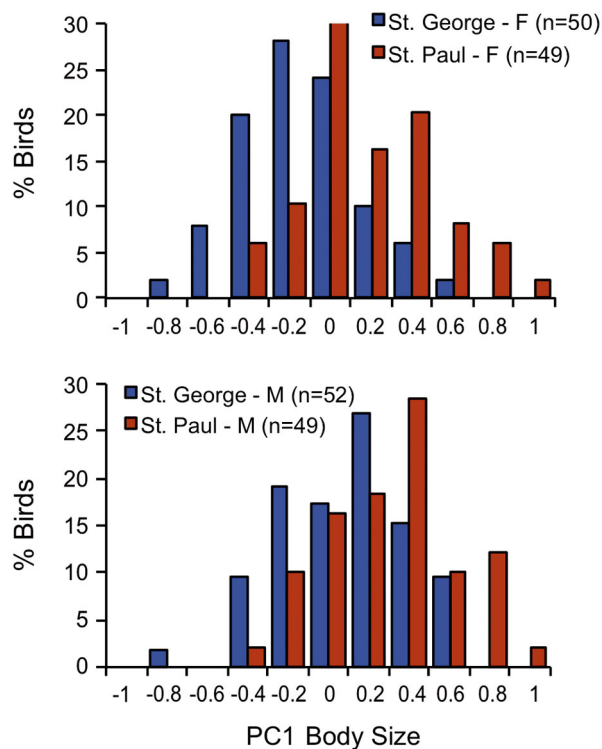
Fig. 1. Colony and sex differences in body size of thick-billed murres at the Pribilof Islands. Frequencies of PC1 scores (wing, tarsus, culmen) of body size are shown for St. George and St. Paul. Top panel: females (F); bottom panel: males (M)

Body size was highly correlated with body mass (Pearson's product-moment correlation: $r^2 = 0.663$, $p < 0.0001$; Fig. 2A). Body size was also highly correlated with the maximum distance of long foraging trips (greater than the median distance = 27.4 km) by individual murres (Pearson's $r^2 = -0.672$, n = 31, $p < 0.0001$). This latter relationship remained significant only for St. George murres when individuals from the 2 islands were analyzed separately (Fig. 2B).

The top ranked models of ΔCORT included the quadratic term for body size (see Supplement 2 at www.int-res.com/articles/suppl/m533p261_supp.pdf). Both relatively large and relatively small murres were able to maintain or reduce their physiological stress levels during chick rearing. Murres with large positive values for ΔCORT, and therefore with rapidly increasing stress, were those of intermediate size (both islands; Fig. 2C), which include larger murres from St. George and smaller murres from St. Paul.

Body mass of individual murres was significantly correlated to the duration of bottom time from dive profiles (r = 0.368, p = 0.007; Fig. 2D) over the middle shelf domain. Body mass was also positively cor-

related with mean dive depth and duration but was significant only for murres nesting on St. Paul (Fig. 2E,F).

Foraging behavior and habitat use

There were between-colony and day–night differences in foraging habitat use by thick-billed murres across years (Fig. 3; see also Supplement 3). All daytime trips (n = 50) and 70% of overnight trips (n = 57) occurred over the middle shelf domain. St. Paul murres (n = 57) foraged exclusively on the middle shelf. Murres from St. George foraged over the middle shelf (57%, n = 40 trips), but also made overnight foraging trips to the outer shelf (5%) and shelf slope (38%). Trip distance was affected by both colony and time of day. Murres from St. Paul traveled farther during daytime ($F_{1,32.976} = 9.654$, p = 0.004), while murres from St. George traveled farther during overnight trips. Overnight trips by St. George murres were mostly to the shelf slope ($F_{1,50.817} = 16.678$, p < 0.0001; Figs. 3 & 4A).

Over the middle shelf, murres from St. Paul dove deeper than those from St. George ($F_{1,33.652} = 9.389$, p = 0.004), regardless of time of day ($F_{1,33.652} = 0.614$, p = 0.439; Fig. 4B). Overnight trips were 5 to 6 times longer than daytime trips (see 'Adult diet and chick provisioning'). There were significantly more dives during overnight trips (76 to 84% greater) than during daytime trips ($F_{1,36} = 33.296$, p < 0.0001), but the number of dives per trip did not differ between colonies ($F_{1,36} = 2.457$, p = 0.126; 95% CI for St. Paul = 43.7 to 94.5 dives; 95% CI for St. George = 67.0 to 140.0 dives; Fig. 4C). There were no gender differences in foraging trip distance ($F_{1,53.824} = 0.060$, p = 0.808; 95% CI for males = 18.6 to 33.3 km; 95% CI for females = 15.7 to 33.4 km) irrespective of colony ($F_{1,53.824} = 0.004$, p = 0.948).

There were distinct differences between colonies in diving activity with respect to time of day (χ^2 (1) = 21.209, p < 0.0001, n = 4598 dives; Fig. 4D). The odds ratio for nocturnal diving was 6.23 times higher for individual murres from St. George than St. Paul. Of all dives recorded at St. Paul (n = 10344 dives) and St. George (n = 20477 dives), 70 vs. 42% and 4 vs. 33% occurred during the day and night, respectively. The incidence of crepuscular diving was similar between the 2 colonies (25 to 26%). Male murres from St. Paul dove more often during the day (82%, n = 3594) compared to their female counterparts (59%, n = 5059); otherwise, there were no gender differences in the incidence of diving. In general, diurnal dives made
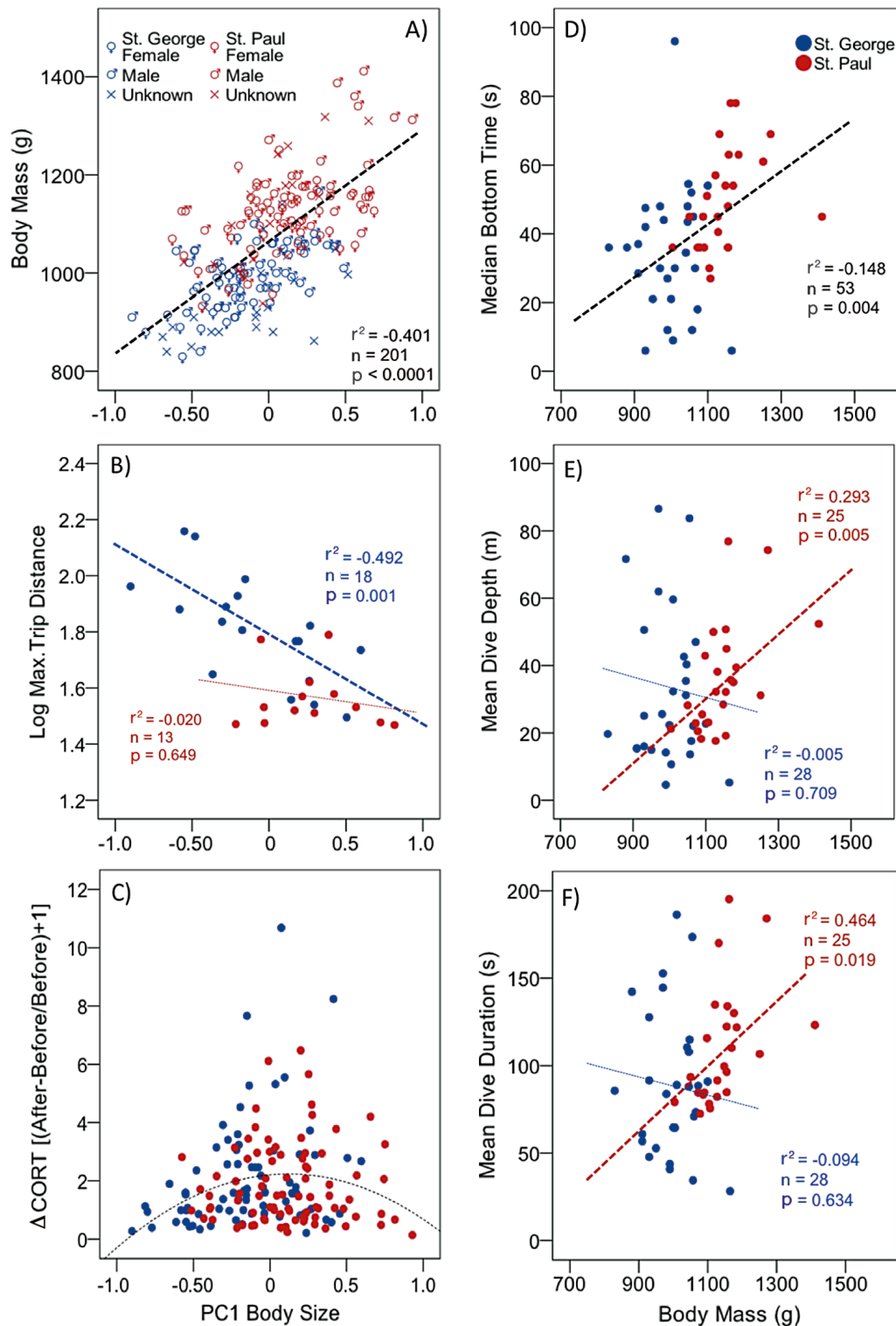
Fig. 2. Relationships between body size, body mass, foraging behavior, and stress levels in thick-billed murres breeding at St. Paul and St. George islands. PC1 body size scores were obtained from wing, tarsus, and culmen measurements. Body size in relation to (A) body mass including gender; (B) maximum trip distance (long trips ≥ median, 27.4 km); and (C) ΔCORT levels (n = 161 birds). Body mass in relation to (D) median bottom time; (E) mean dive depth; and (F) mean dive duration of individual dives. Fitted lines and correlation results are matched by colony color: St. Paul (red); St. George (blue); or both (black) if pooled data from both colonies were correlated
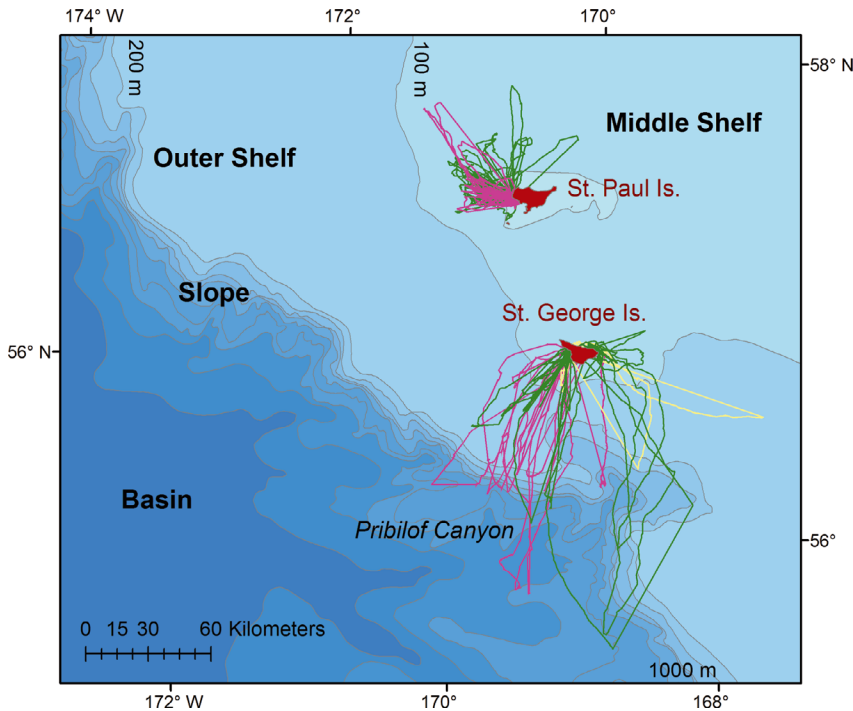
Fig. 3. GPS tracking of thick-billed murres breeding at the Pribilof Islands (St. Paul and St. George) on the southeastern Bering Sea shelf. Color tracks refer to years: 2008 (light yellow); 2009 (pink); and 2010 (green). Number of birds: 0, 18, 28 for St. Paul; 4, 12, 11 for St. George in 2008, 2009, and 2010, respectively

Here, murres dove more often during the day (χ^2 (2) = 21.209, p < 0.0001, odds ratio$_{middle\ shelf}$ = 5.7, n = 6795 dives) than the other 2 deeper regions, where diving was more likely to occur at night (χ^2 (2) = 62.56, p < 0.0001, odds ratio$_{outer\ shelf\ \&\ slope}$ = 4.6). No differences among habitats were found for murres diving at the crepuscular period (χ^2 (2) = 1.691, p = 0.429). On average, dive depth differed among habitat types ($F_{1,9,352.4}$ = 56.353, p < 0.0001); murres dove deeper over the middle shelf domain compared to the outer shelf and shelf slope domains, and they also dove deeper over the outer shelf domain than over the shelf slope domain (post hoc tests: all p < 0.0001).

Over the middle shelf, the depth and duration of dives by murres differed between both colony and sex. Males from St. Paul dove deeper and longer than those from St. George (depth: $F_{1,17.58}$ = 10.537, p = 0.005; duration: $F_{1,17.551}$ = 13.674, p = 0.002), but there were no differences in dive depth or duration between colonies for females (depth: $F_{1,21.63}$ = 0.624, p = 0.438; duration: $F_{1,20.738}$ = 0.118, p = 0.735; 95% CI for St. Paul = 82.2 to 114.0 min; 95% CI for St. George = 68.8 to 117.6 min; Table 2). Bottom time ($F_{1,38.851}$ = 17.814, p < 0.0001), ascent rate ($F_{1,39.225}$ = 11.198, p = 0.002), descent rate ($F_{1,39.108}$ = 7.893, p = 0.008), and diving efficiency ($F_{1,34.76}$ = 8.516, p = 0.006) were all greater for St. Paul murres than for St. George, regardless of sex (Table 2).

by murres were deeper (40.4 ± 0.3 m) than crepuscular (17.2 ± 0.2 m) or nocturnal dives (8.1 ± 0.2 m).

Among foraging habitats, murre diving activity (Fig. 5A,C,E) and mean dive depth (Fig. 5B,D,F) varied across the 24 h period, with a relatively low incidence of diving activity between 01:00 h and 04:00 h (Alaska Daylight Time) over the middle shelf (Fig. 5A).
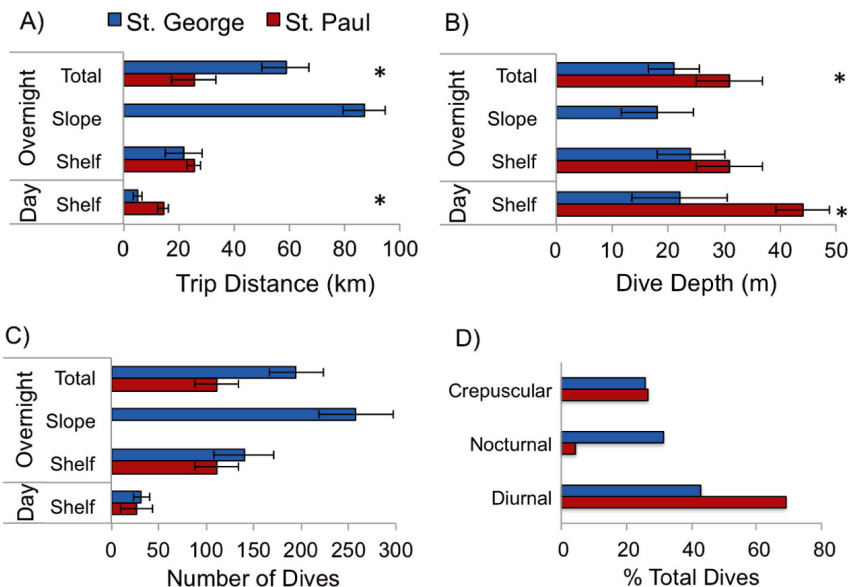

Fig. 4. Foraging and diving behavior of GPS-tracked thick-billed murres at St. Paul and St. George islands in 2009 and 2010. Means ± SE of parameters are shown according to daytime and overnight trips and bathymetric habitat type (shelf: 100 to 200 m depth; slope: >200 m depth). Dive data for trips available in 2010 only. (A) maximum trip distance (St. George: n = 38 trips; St. Paul: n = 105; *daytime: p = 0.006; overnight: p < 0.0001). (B) Mean dive depth per trip (St. George: n = 20 trips; St. Paul: n = 21; *daytime and overnight: p = 0.013). (C) Number of dives per trip (St. George: n = 20 trips; St. Paul: n = 21 trips). (D) Frequency of dives according to daylight periods based in sunrise/sunset hours
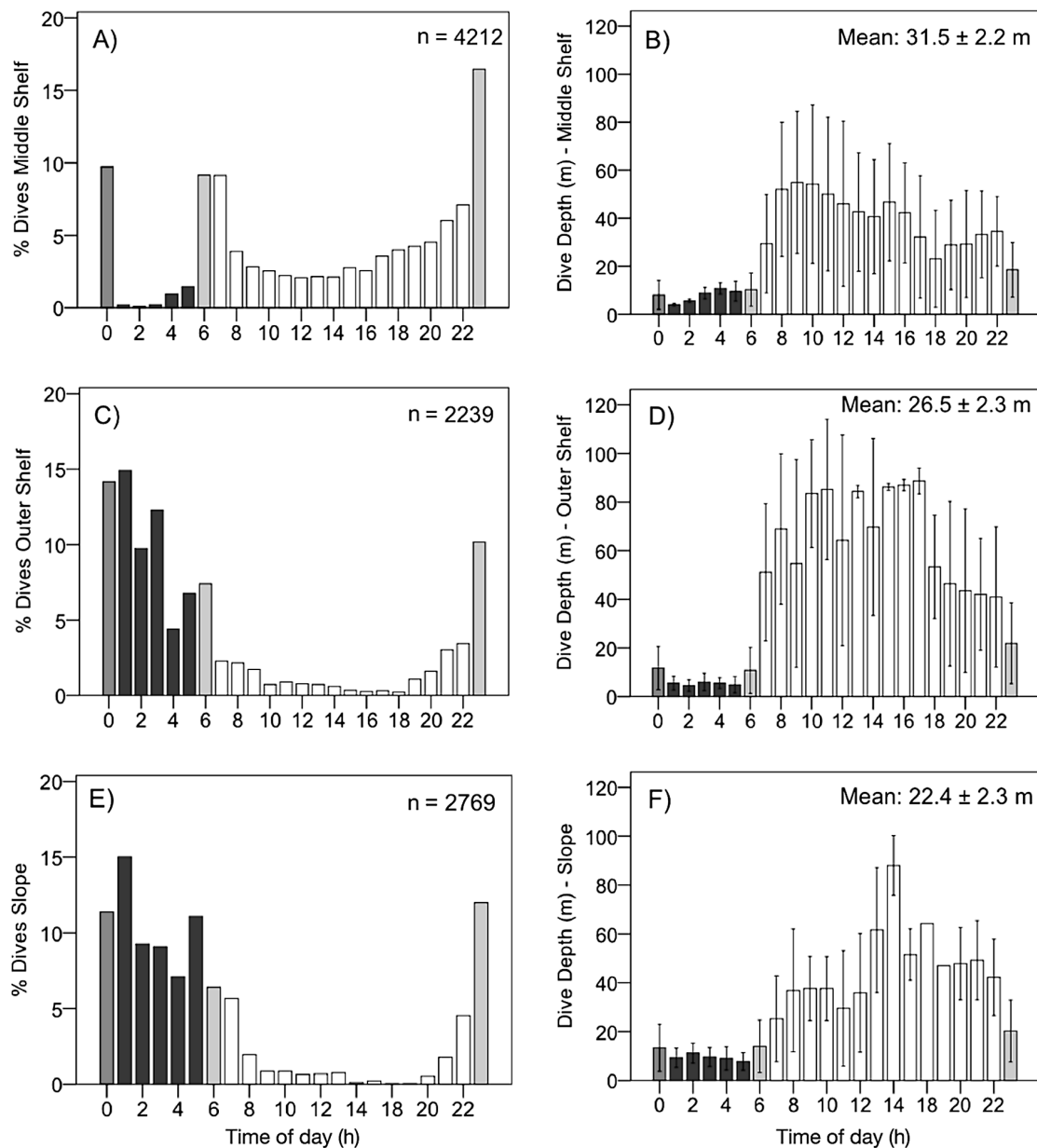
Fig. 5. Hourly distributions of diving activity and depth (means ± SE) of thick-billed murres according to bathymetric habitat type in 2010. (A,B) Middle shelf (<100 m depth); (C,D) outer shelf (100 to 200 m depth); and (D,E) shelf slope (>200 m depth). Color bars indicate daylight periods: nocturnal (black); crepuscular (light and dark grey); and diurnal (white)

Adult diet and chick provisioning

Adult murres from St. Paul fed on a variety of fish species, such as eelpouts (*Lycodes* spp.), pricklebacks (Stichaeidae), Pacific sandlance *Ammodytes hexapterus*, and gadids (Gadidae), whereas murres from St. George fed primarily on squid (63 to 77%, n = 107; Fig. 6). Foraging trips during the day that ended with the delivery of a chick meal to the nest were longer for St. Paul murres (165 ± 13.9 min) than for St. George

murres (123 ± 11.9 min; $F_{1,105.3}$ = 5.763, p = 0.018), regardless of year ($F_{2,203.48}$ = 2.664, p = 0.072). No differences in trip duration between colonies were found for overnight trips (p > 0.05; 95% CI for St. Paul = 787.5 to 894.7 min; 95% CI for St. George = 799.0 to 927.0 min). Murres from both colonies made longer overnight trips in 2008 than in 2009 (post hoc tests: p = 0.044).

Chick diets resembled prey captured in the middle shelf because they were obtained mostly during day-

Table 2. Between-island differences in diving behavior of thick-billed murres at the Pribilof Islands, controlled by bathymetry on the Bering Sea middle shelf (<100 m depth). Mean ± SE

	n	Maximum depth (m)[a]	Dive duration (s)[a]	Bottom time (s)[b]	Descent rate (m s^{-1})[b]	Ascent rate (m s^{-1})[b]	Dive efficiency[b]
St. Paul Island							
Female	15	28.3 ± 3.9	98.0 ± 7.8	47.9 ± 3.5	0.88 ± 0.03	0.97 ± 0.05	0.40 ± 0.02
Male	10	45.5 ± 4.8	127.5 ± 9.7	53.8 ± 4.4	0.94 ± 0.04	1.1 ± 0.07	0.36 ± 0.03
St. George Island							
Female	9	34.5 ± 6.0	93.2 ± 12.1	32.3 ± 5.6	0.83 ± 0.05	0.83 ± 0.08	0.35 ± 0.03
Male	10	23.0 ± 4.8	74.8 ± 9.7	30.7 ± 4.5	0.76 ± 0.04	0.77 ± 0.06	0.32 ± 0.03

[a]Significant differences between islands, males only, p < 0.005
[b]Significant differences between islands, regardless of sex, p < 0.008

time trips. Both male and female murres from St. Paul delivered predominately benthic fish (81%, n = 278 total items) to their chicks, while murres from St. George delivered both squid (55%) and benthic fish (38%, n = 260; Fig. 6). In 2008, murres delivered fewer squid (25 vs. 44 to 75 items) at St. George and fewer gadids (2 vs. 12 to 16 items) at St. Paul than in 2009 or 2010, suggesting lower availability of the main prey species at each colony and overall reduced breeding performance (see below).

Breeding performance

Chick-feeding rates did not differ between colonies ($F_{1,231}$ = 0.744, p = 0.389; St. Paul 95% CI = 0.07 to 0.14 feeds h^{-1}; St. George 95% CI = 0.09 to 0.15 feeds h^{-1}), but did differ between years ($F_{1,231}$ = 14.016, p < 0.0001; Fig. 7A). Murres fed chicks less often in 2008 and 2010 compared to 2009 (post hoc Tukey tests: p < 0.0001). Similarly, fledging success did not differ

between colonies ($F_{1,1144}$ = 2.824, p = 0.093; St. Paul 95% CI = 0.79 to 0.87 fledglings per nest where a chick hatched; St. George 95% CI = 0.74 to 0.83 fledglings per nest), but did differ between years ($F_{2,1144}$ = 10.724, p < 0.0001; Fig. 7B). Murres had lower fledging success in 2008 compared to 2009 or 2010 (post hoc tests: p < 0.006), and there was no difference in fledging success between 2009 and 2010 (p = 0.309). In 2008, the average prey size delivered to murre chicks was smaller at both St. Paul and St. George; St. Paul murres delivered more medium-sized fish relative to large fish (χ^2_2 = 53.77, p < 0.0001) and St. George murres delivered more small fish relative to medium and large fish (χ^2_2 = 22.76, p < 0.0001; Fig. 7C). Murres from St. Paul delivered large prey more frequently than those from St. George in both 2009 (χ^2_2 = 40.37, p < 0.0001) and 2010 (χ^2_2 = 19.84, p < 0.0001). There were no gender differences in the proportions of different size classes of prey delivered to nests (St. Paul: χ^2_2 = 1.08, p = 0.58; St. George: χ^2_2 = 0.485, p = 0.78).
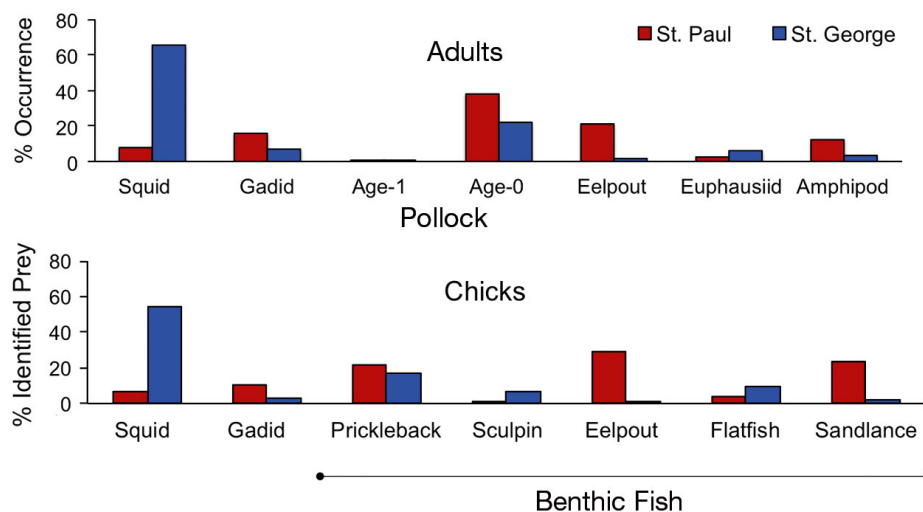

Fig. 6. Diets of thick-billed murres (adults and chicks) at St. Paul and St. George islands during 2008 to 2010. Proportion of main prey species all years combined. Chick diets resemble prey obtained in the middle shelf. Flatfish (Pleuronectidae) were offered by the parents but often not swallowed by the chicks
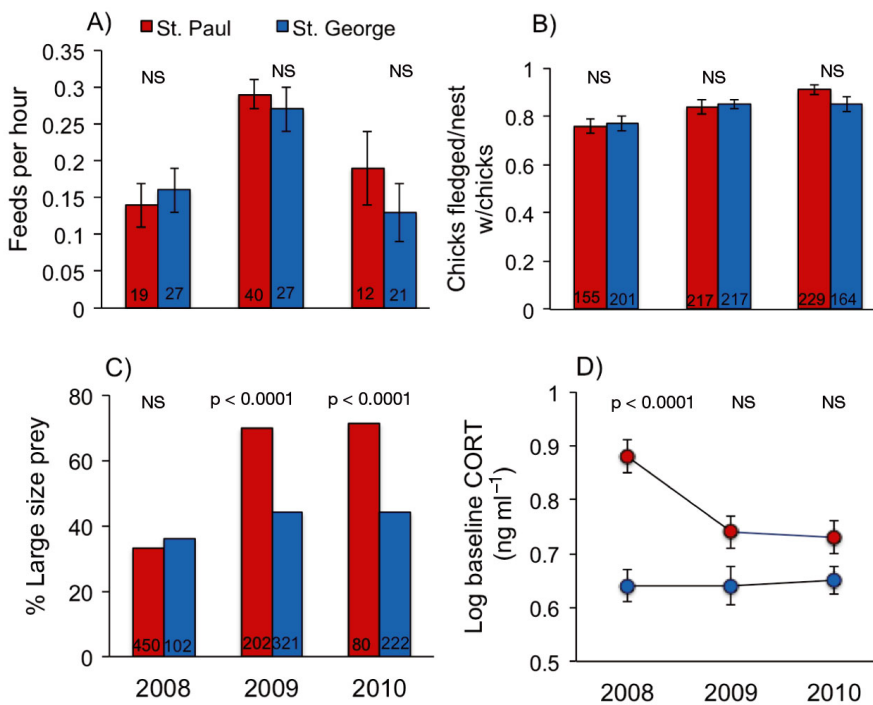
Fig. 7. Breeding performance and prey size of untagged thick-billed murres at St. Paul and St. George islands during 2008 to 2010. (A) Chick-feeding frequency; (B) fledging success (number of chicks fledged per nest with chicks); (C) proportion of large prey delivered to chicks; and (D) adult nutritional stress (St. Paul: 2008 = 59, 2009 = 89, 2010 = 92 individuals; St. George: 2008 = 89, 2009 = 90, 2010 = 97 individuals). Values in bars represent sample sizes of nests (A,B) or prey items (C). Means ± SE. NS = not statistically significant

DISCUSSION

At 2 geographically close breeding colonies of thick-billed murres where body size was divergent, we found evidence that supported the influence of body size on foraging strategies and physiological stress levels. Larger murres from St. Paul dove more efficiently during daylight hours in neritic waters, while smaller birds from St. George performed extensive overnight foraging trips in oceanic habitats. Larger birds at St. Paul or smaller ones at St. George incurred less stress than intermediate-sized birds in the study region. Of the 2 murre colonies, the St. Paul colony was more affected by relatively poor foraging conditions on the middle shelf during the study period, which was apparent in poor adult condition, rather than lower fledging rates of offspring.

Foraging patterns with respect to habitat and time of day

The temporal patterns in the diving behavior of murres, specifically deep diurnal dives, intermediate crepuscular dives, and shallow nocturnal dives (Elliott et al. 2008, Paredes et al. 2008, Harding et al. 2013), were similar in the 3 habitat domains used in this study. Nonetheless, the various hourly activity levels, ranging from no diving to repeated diving at night, likely reflects the different behavior of vertically migrating prey species in the different Bering Sea domains (Arkhipkin et al. 1998, Swartzman et al. 1999, Benoit-Bird et al. 2011). For instance, the nocturnal gap in diving by murres in the middle shelf domain coincides with the nocturnal cessation in feeding by juvenile pollock, the main forage fish species (Brodeur et al. 2000), and a decrease in concentrations of the amphipod *Themisto libellula* near the surface (Fortier et al. 2001). Conversely, the intense shallow diving (<10 m) by murres in the outer shelf and slope domains coincides with the higher nocturnal concentration of euphausiids and squid compared to the middle shelf domain (Sinclair & Stabeno 2002, Benoit-Bird et al. 2011). Whether there is an inverse vertical migration of zooplankton (descend instead of ascend at night) in the Bering Sea middle shelf domain compared to deeper regions

There were no inter-annual differences in CORT levels of murres from St. George (p > 0.05); for murres from St. Paul, CORT levels in 2008 were different from 2009 and 2010 (post hoc Tukey tests, 2008 to 2009: p = 0.022; 2008 to 2010: p = 0.015; Fig. 7D). A significant colony × year interaction in murre CORT levels ($F_{2, 433}$ = 10.264, p = 0.0404) indicated that murres from St. Paul had significantly higher CORT levels than those from St. George in 2008 (post hoc test: p < 0.0001), but not in 2009 (p = 0.144) or 2010 (p = 0.363).

Effect of instrumentation

There was no apparent effect of double-tagging on trip duration compared to control birds, or dive depth compared to TDR birds. Nevertheless, double-instrumented birds had lower nest attendance, chick-feeding rates (1 of 2 yr) and higher stress levels than non-or single-tagged birds (see Supplement 1). Thus, double-tagged birds appeared to work harder to raise chicks, although foraging patterns were apparently less affected.

beyond the shelf break, as has been found in other studies (e.g. Sims et al. 2005), is unknown.

Given that murres from St. Paul foraged entirely in the middle shelf domain, and previous studies of St. Paul murre diets (Sinclair et al. 2008, Renner et al. 2012) suggest that crustaceans were not readily available at night, the predominantly diurnal and benthic foraging strategy observed is not surprising. The longer daytime foraging trips by St. Paul murres (Kitaysky et al. 2000) may serve to restore adult reserves, while St. George murres appear to achieve this goal by foraging in more distant oceanic habitats at night. The more nocturnal foraging strategy of murres from St. George, however, may reflect relatively poor foraging conditions in the middle shelf domain during the present study. In years when the availability of juvenile pollock is higher in the middle shelf domain, diving by St. George murres is less nocturnal and averages deeper (Takahashi et al. 2008), suggesting increased usage of nearby shelves during the daytime foraging.

Overall, differences in foraging strategies and dive depths by murres from St. George and St. Paul were apparently influenced by the proximity of foraging habitats and the temporal availability of prey in those habitats, as has been found in other seabirds (Cook et al. 2013, Ratcliffe et al. 2013).

Foraging strategies, gender, and body size

Murres of the average body size at each colony, larger at St. Paul and smaller at St. George, foraged more efficiently than intermediate-sized ones, as suggested by lower stress levels. For St. George murres, body size was negatively correlated with the maximum distance of individual foraging trips. Given that, within a species, flight costs increase with body size in birds (Schmidt-Wellenburg et al. 2007), smaller body size would reduce flight costs to more distant foraging habitats. For murres from St. George, this means easier access to predictable and energetically cost-effective foraging opportunities in the shelf slope domain. For murres from St. Paul, however, the commute to the slope domain was 3 times farther than for St. George murres, mitigating any energetic profitability. Instead, larger body size for St. Paul murres may confer a greater flexibility for foraging on a variety of prey at greater depths in the middle shelf domain due to enhanced oxygen storage and foraging speed (Halsey et al. 2006, Watanabe et al. 2011). This was particularly true for female murres from St. Paul, whose diving efficiency, and

potentially foraging efficiency, were greater than for females from St. George. Arguably, the parameter 'diving efficiency' could possibly underestimate successful feeding during V-shaped dives because they lack the bottom time ('feeding time') that characterizes U-shaped dives (Machovsky Capuska et al. 2011). Assuming murres capture squid, sandlance, and gadids during V-shaped dives (Elliott et al. 2008), we do not anticipate differences in diving efficiency between the colonies based on diet frequencies. For murres from either island, bottom time of individual dives increased with body mass, which significantly correlated with body size. Dive depth and duration, however, increased with body mass only in individuals from the St. Paul colony, which included larger murres. However, the relationship between maximum foraging trip distance and body size was only significant for individuals from the St. George colony, which included smaller murres. These results suggest that either relatively large or relatively small body size was associated with 2 distinctly different foraging modes in this seabird species.

In accordance with colony-associated foraging, very small murres from St. George and very large murres from St. Paul maintained or reduced their level of physiological stress during the chick-rearing period. In contrast, medium-sized murres were more likely to suffer an increase in stress level, which could negatively affect reproductive success (Schultner et al. 2013) and survival (Kitaysky et al. 2007, Goutte et al. 2010). Thus, both smaller murres nesting on St. George and larger murres nesting on St. Paul apparently experienced lower levels of stress, and were therefore better adapted to their respective foraging habitats. Within each colony, males averaged significantly larger than females, but gender differences in foraging behavior (e.g. time of day, dive depth) were more apparent on St. Paul, the colony with greater gender differences in body size. Given that gender differences in murre body size can differ between colonies (Paredes et al. 2008, Elliott et al. 2010), the nature of nearby foraging habitats could explain such differences, rather than sexual selection acting to refine gender-specific phenotypes.

Foraging strategies and breeding performance

Our results suggest that flexible foragers, such as thick-billed murres (Burger & Piatt 1990, Harding et al. 2007), allocate resources toward chick survival by increasing foraging effort during food shortages.

Despite distinctly different foraging strategies at the 2 islands, murres from both colonies had similar chick meal delivery rates and fledging success during the present 3 yr study, in agreement with trends over the last 35 yr (Renner et al. 2014). Nonetheless, murres from St. Paul, farther removed from the oceanic habitats than murres from St. George, were less able to cope with an apparent food shortage in the middle shelf domain, as indicated by higher stress levels in 2008. During that breeding season, murres from both colonies made longer trips overnight, delivered fewer and smaller prey to their chicks, and had lower fledging success than during 2009 and 2010, when the availability of juvenile pollock (Benoit-Bird et al. 2011) and amphipods *T. libellula* (Pinchuk et al. 2013) in the middle shelf domain was higher. Previous studies on stress levels (Benowitz-Fredericks et al. 2008) and field metabolic rates (Kitaysky et al. 2000) suggested that murres from St. Paul work harder to meet their energy requirements for reproduction. Adults from St. George fed more on oceanic prey with higher energy densities (e.g. squid and krill; Whitman 2010, S. Heppell unpubl. data), perhaps allowing the maintenance of energy reserves, as indicated by lower stress levels across years. Adult mortality mediated through elevated baseline CORT levels of murres in poor years could contribute to the declining breeding population of thick-billed murres at St. Paul, similar to that of black-legged kittiwakes *Rissa tridactyla* (Paredes et al. 2014).

Causes and consequences of body-size divergence between colonies

Differences in the body size of thick-billed murres between colonies may have arisen from size-dependent immigration/recruitment or from divergent selection. Murres exhibit a high degree of colony philopatry (Gaston 1984), which would suggest a role for divergent selection in the observed colony-specific differences in body size. Young murres, however, could recruit to non-natal colonies based on body size, thereby producing the observed body-size difference between colonies without the necessity of genetic structuring among colonies (Harris et al. 1996). Another possible scenario is that body size is an adaptive trait selected at each colony to maximize foraging efficiency in adjacent marine habitats. Breeding adults of the optimal body size at each colony might have greater chances of survival during food shortages, especially at the declining colony on

St. Paul. Although many factors could influence the microevolution of body size, it appears that the most prevalent mechanism is prey size and availability (Grant & Grant 2002, Boback & Montgomerie 2003). To our knowledge, there are no published studies of the genetic structure of thick-billed murres breeding on the Pribilof Islands; however, evidence from other studies on alcids indicates no genetic differentiation among colonies, despite significant differences in morphology among and within them (Gaston 1984, Moen 1991, Birt-Friesen et al. 1992, Ibarguchi et al. 2011). An additional consideration is the large inter-annual variability in ocean conditions near the Pribilof Islands (Stabeno et al. 2012), which could lead to dynamic size–performance relationships in a long-lived seabird.

This study is the first step toward understanding divergent body size between and within murre colonies. In the future, adding more colonies and the molecular investigation of micro-evolutionary processes would be essential to support the initial findings reported here.

In conclusion, the body size of thick-billed murres nesting on the Pribilof Islands appears to be associated with the differential use of foraging habitats and prey types at the 2 main breeding colonies. Larger murres nesting on St. Paul were better suited for exploiting larger benthic prey in nearby foraging habitats in the middle shelf domain. In contrast, smaller murres nesting on St. George were better suited for flying longer distances to forage on vertically migrating oceanic prey that were present near the surface at night. Although these differences were not reflected in inter-colony variations in fledging success, higher stress levels in murres nesting at the St. Paul colony farther from the shelf break suggest that parental effort incurred a fitness cost during years of low food availability. Our study provides the first evidence of divergent selection for body size in seabirds that rely on proficiency in both diving and flying during foraging. These results suggest that foraging habitats within commuting distance of breeding colonies are the ultimate factor selecting for body-size differences at the individual, gender, and colony levels.

LITERATURE CITED

Arkhipkin AI, Bizikov VA, Verkhunov VA (1998) Distribution and growth in juveniles of the squid *Berryteuthis magister* (Cephalopoda, Gonatidae) in the western Bering Sea. Sarsia 83:45–54

Benoit-Bird K, Kuletz K, Heppell S, Jones N, Hoover B (2011) Active acoustic examination of the diving behavior of murres foraging on patchy prey. Mar Ecol Prog Ser 443:217–235

Benowitz-Fredericks ZM, Shultz MT, Kitaysky AS (2008) Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. Deep-Sea Res II 55:1868–1876

Birt-Friesen V, Montevecchi W, Gaston AJ (1992) Genetic structure of thick-billed murre (*Uria lomvia*) populations examined using direct sequence analysis of amplified DNA. Evolution 46:267–272

Boback SM, Montgomerie WL (2003) Body size evolution in snakes: evidence from island populations. Copeia 2003: 81–94

Brodeur RD, Wilson MT, Ciannelli L (2000) Spatial and temporal variability in feeding and condition of age-0 walleye pollock (*Theragra chalcogramma*) in frontal regions of the Bering Sea. ICES J Mar Sci 57:256–264

Brown CR, Brown MB, Raouf SA, Smith LC, Wingfield JC (2005) Effects of endogenous steroid hormone levels on annual survival in cliff swallows. Ecology 86:1034–1046

Buchanan KL (2000) Stress and the evolution of condition-dependent signals. Trends Ecol Evol 15:157–160

Burger AE, Piatt JF (1990) Flexible time budgets in breeding common murres: buffers against variable prey abundance. Stud Avian Biol 14:71–83

Byrd GV, Schmutz JA, Renner HM (2008) Contrasting population trends of piscivorous seabirds in the Pribilof Islands: a 30-year perspective. Deep-Sea Res II 55:1846–1855

Cook TR, Lescroël A, Cherel Y, Kato A, Bost CA (2013) Can foraging ecology drive the evolution of body size in a diving endotherm? PLOS ONE 8:e56297

Dias MP, Granadeiro JP, Catry P (2012) Working the day or the night shift? Foraging schedules of Cory's shearwaters vary according to marine habitat. Mar Ecol Prog Ser 467: 245–252

Elliott KH, Davoren GK, Gaston AJ (2008) Time allocation by a deep-diving bird reflects prey type and energy gain. Anim Behav 75:1301–1310

Elliott KH, Gaston AJ, Crump D (2010) Sex-specific behaviour by a monomorphic seabird represents risk partitioning. Behav Ecol 21:1024–1032

Elliott KH, Ricklefs RE, Gaston AJ, Hatch SA and others (2013) High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. Proc Natl Acad Sci 110:9380–9384

Fortier M, Fortier L, Hattori H, Saito H, Legendre L (2001) Visual predators and the diel vertical migration of copepods under Arctic Sea ice during the midnight sun. J Plankton Res 23:1263–1278

Gaston AJ (1984) Phenotypic variation among thick-billed murres from colonies in Hudson Strait. Arctic 37:284–287

Gaston AJ, Hipfner JM (2000) Thick-billed murre (*Uria lomvia*). In: Poole A, Gill F (eds) The birds of North America, No. 497. The birds of North America Inc. Philadelphia, PA

Goutte A, Angelier F, Welcker J, Moe B and others (2010) Long-term survival effect of corticosterone manipulation in black-legged kittiwakes. Gen Com Endocrinol 167: 246–251

Grant PR, Grant BR (2002) Unpredictable evolution in a 30-year study of Darwin's finches. Science 296:707–711

Griffiths R, Double MC, Orr K, Dawson RJG (1998) A DNA test to sex most birds. Mol Ecol 7:1071–1075

Halsey LG, Blackburn TM, Butler PJ (2006) A comparative analysis of the diving behaviour of birds and mammals. Funct Ecol 20:889–899

Harding AM, Piatt J, Schmutz J, Schultz M and others (2007) Prey density and the behavioral flexibility of a marine predator: the common murre (*Uria aalge*). Ecology 88: 2024–2033

Harding A, Paredes R, Suryan R, Roby D and others (2013) Does location really matter? An inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea. Deep-Sea Res II 94:178–191

Harris MP, Wanless S, Barton TR (1996) Site use and fidelity in the common guillemot *Uria aalge*. Ibis 138:399–404

Hollowed AB, Barbeaux SJ, Cokelet ED, Farley E and others (2012) Effects of climate variations on pelagic ocean habitats and their role in structuring forage fish distributions in the Bering Sea. Deep-Sea Res II 65–70:230–250

Ibarguchi G, Gaston AJ, Friesen VL (2011) Philopatry, morphological divergence, and kin groups: structuring in thick-billed murres *Uria lomvia* within a colony in Arctic Canada. J Avian Biol 42:134–150

Kitaysky AS, Hunt Jr. GL, Flint EN, Rubega MA, Decker MB (2000) Resource allocation in breeding seabirds: responses to fluctuations in their food supply. Mar Ecol Prog Ser 206:283–296

Kitaysky AS, Kitaiskaia EV, Piatt JF, Wingfield JC (2003) Benefits and costs of increased levels of corticosterone in seabird chicks. Horm Behav 43:140–149

Kitaysky AS, Piatt JF, Wingfield JC (2007) Stress hormones link food availability and population processes in seabirds. Mar Ecol Prog Ser 352:245–258

Kitaysky AS, Piatt JF, Hatch S, Kitaiskaia EV and others (2010) Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. Funct Ecol 24:625–637

Lewis S, Schreiber EA, Daunt F, Schenk GA and others (2005) Sex-specific foraging behaviour in tropical boobies: Does size matter? Ibis 147:408–414

Lynch M (1977) Fitness and optimal body size in zooplankton populations. Ecology 58:763–774

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609

Machovsky Capuska GE, Vaughn RL, Würsig B, Katzir G, Raubenheimer D (2011) Dive strategies and foraging effort in the Australasian gannet *Morus serrator* revealed by underwater videography. Mar Ecol Prog Ser 442: 255–261

Mittelbach GG (1981) Foraging efficiency and body size: a study of optimal diet and habitat use. Ecology 62: 1370–1386

Moen SM (1991) Morphologic and genetic variation among breeding colonies of the Atlantic puffin (*Fratercula arctica*). Auk 108:755–763

Mori Y (2002) Optimal diving behaviour for foraging in relation to body size. J Evol Biol 15:269–276

Neves VC, Bolton M, Monteiro LR (2006) Validation of the water offloading technique for diet assessment: an experimental study with Cory's shearwaters (*Calonectris diomedea*). J Ornithol 147:474–478

Orben RA, Paredes R, Irons DB, Roby DD, Shaffer SA (in press) Body size predicts individual winter foraging strategies of thick-billed murres in the Bering Sea. J Anim Ecol, doi: 10.1111/1365-2656.12410

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) Analysis of ecological systems. Ohio State University Press, Columbus, OH, p 154–177

Paredes R, Jones IL, Boness DJ, Tremblay Y, Renner M (2008) Sex-specific differences in diving behaviour of two sympatric Alcini species: thick-billed murres and razorbills. Can J Zool 86:610–622

Paredes R, Harding AMA, Irons DB, Roby DD and others (2012) Proximity to multiple foraging habitats enhances seabirds' resilience to local food shortages. Mar Ecol Prog Ser 471:253–269

Paredes R, Orben R, Suryan RM, Irons DB and others (2014) Foraging responses of black-legged kittiwakes to prolonged food-shortages around colonies on the Bering Sea shelf. PLOS ONE 9:e92520

Pennycuick CJ (2008) Modelling the flying bird. Academic Press, London

Pinchuk AI, Coyle KO, Farley EV, Renner HM (2013) Emergence of the Arctic *Themisto libellula* (Amphipoda: Hyperiidae) on the southeastern Bering Sea shelf as a result of the recent cooling, and its potential impact on the pelagic food web. ICES J Mar Sci 70:1244–1254

R Development Core Team (2011), R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org

Ratcliffe N, Takahashi A, O'Sullivan C, Adlard S and others (2013) The roles of sex, mass and individual specialisation in partitioning foraging-depth niches of a pursuit-diving predator. PLOS ONE 8:e79107

Regular PM, Davoren GK, Hedd, A, Montevecchi WA (2010) Crepuscular foraging by a pursuit-diving seabird: tactics of common murres in response to the diel vertical migration of capelin. Mar Ecol Prog Ser 415:295–304

Renner HM, Mueter F, Drummond B, Warzybok J, Sinclair EH (2012) Patterns of change in diets of two piscivorous seabird species during 35 years in the Pribilof Islands. Deep-Sea Res II 65–70:273–291

Renner H, Drummond B, Benson AM, Paredes R (2014) Reproductive success of kittiwakes and murres in sequential stages of the nesting period: relationships with diet and oceanography. Deep-Sea Res II 109: 251–265

Romero LM, Wikelski M (2001) Corticosterone levels predict survival probabilities of Galapagos marine aguanas during El Niño events. PNAS 98:7366–7370

Saino N, Suffritti C, Martinelli R, Rubolini D, Møller AP (2003) Immune response covaries with corticosterone plasma levels under experimentally stressful conditions in nestling barn swallows (*Hirundo rustica*). Behav Ecol 14:318–325

Satterthwaite W, Kitaysky AS, Hatch SA, Piatt JF, Mangel M (2010) Unifying quantitative life-history theory and field endocrinology to assess prudent parenthood in a long-lived seabird. Evol Ecol Res 12:779–792

Satterthwaite WH, Kitaysky AS, Mangel M (2012) Linking climate variability, productivity and stress to demography in a long-lived seabird. Mar Ecol Prog Ser 454: 221–235

Schabetsberger R, Brodeur RD, Ciannelli L, Napp JM, Swartzman GL (2000) Diel vertical migration and interaction of zooplankton and juvenile walleye pollock (*Theragra chalcogramma*) at a frontal region near the Pribilof Islands, Bering Sea. ICES J Mar Sci 57: 1283–1295

Schmidt-Wellenburg CA, Biebach H, Daan S, Visser GH (2007) Energy expenditure and wing beat frequency in relation to body mass in free flying barn swallows (*Hirundo rustica*). J Comp Physiol B 177:327–337

Schultner J, Kitaysky AS, Gabrielsen GW, Hatch SA, Bech C (2013) Differential reproductive responses to stress reveal the role of life-history strategies within a species. Proc R Soc B 280:20132090

Sims DW, Southall EJ, Tarling G, Metcalfe JD (2005) Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. J Anim Ecol 74: 755–761

Sinclair E, Stabeno P (2002) Mesopelagic nekton and associated physics of the southeastern Bering Sea. Deep-Sea Res II 49:6127–6145

Sinclair EH, Vlietstra LS, Johnson DS, Zeppelin TK and others (2008) Patterns in prey use among fur seals and seabirds in the Pribilof Islands. Deep-Sea Res Part II 55: 1897–1918

Soanes LM, Arnould JPY, Dodd SG, Sumner MD, Green JA (2013) How many seabirds do we need to track to define home-range area? J Appl Ecol 50:671–679

Stabeno PJ, Kachel NB, Moore SE, Napp JM and others (2012) Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep-Sea Res II 65–70:31–45

Swartzman G, Brodeur R, Napp J, Hunt G and others (1999) Spatial proximity of age-0 walleye pollock (*Theragra chalcogramma*) to zooplankton near the Pribilof Islands, Bering Sea, Alaska. ICES J Mar Sci 56:545–560

Takahashi A, Matsumoto K, Hunt GL, Shultz MT and others (2008) Thick-billed murres use different diving behaviors in mixed and stratified waters. Deep-Sea Res II 55: 1837–1845

Tremblay Y, Cherel Y, Oremus M, Tveraa T, Chastel O (2003) Unconventional ventral attachment of time-depth recorders as a new method for investigating time budget and diving behaviour of seabirds. J Exp Biol 206: 1929–1940

Watanabe YY, Takahashi A, Sato K, Viviant M, Bost CA (2011) Poor flight performance in deep-diving cormorants. J Exp Biol 214:412–421

Whitman L (2010) Variation in the energy density of forage fishes and invertebrates from the southeastern Bering Sea. MSc dissertation, Oregon State University, Corvallis, OR

Wilson RP, White CR, Quintana F, Halsey LG and others (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. J Anim Ecol 75:1081–1090

Ydenberg RC, Clark CW (1989) Aerobiosis and anaerobiosis during diving by western grebes: an optimal foraging approach. J Theor Biol 139:437–449

Zavalaga CB, Benvenuti S, Dall'Antonia L, Emslie SD (2007) Diving behavior of blue-footed boobies *Sula nebouxii* in northern Peru in relation to sex, body size and prey type. Mar Ecol Prog Ser 336:291–303