



Modeled distribution and abundance of a pelagic seabird reveal trends in relation to fisheries

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ABSTRACT: The northern fulmar *Fulmarus glacialis* is one of the most visible and widespread seabirds in the eastern Bering Sea and Aleutian Islands. However, relatively little is known about its abundance, trends, or the factors that shape its distribution. We used a long-term pelagic dataset to model changes in fulmar at-sea distribution and abundance since the mid-1970s. We used an ensemble model, based on a weighted average of generalized additive model (GAM), multivariate adaptive regression splines (MARS), and random forest models to estimate the pelagic distribution and density of fulmars in the waters of the Aleutian Archipelago and Bering Sea. The most important predictor variables were colony effect, sea surface temperature, distribution of fisheries, location, and primary productivity. We calculated a time series from the ratio of observed to predicted values and found that fulmar at-sea abundance declined from the 1970s to the 2000s at a rate of 0.83 % (\pm 0.39 % SE) per annum. Interpolating fulmar densities on a spatial grid through time, we found that the center of fulmar distribution in the Bering Sea has shifted north, coinciding with a northward shift in fish catches and a warming ocean. Our study shows that fisheries are an important, but not the only factor, shaping fulmar distribution and abundance trends in the eastern Bering Sea and Aleutian Islands.

KEY WORDS: Aleutian Islands · Bering Sea · Distribution shifts · Fisheries · *Fulmarus glacialis* · Habitat modeling · Population trend

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INTRODUCTION

The northern fulmar *Fulmarus glacialis* is one of the most abundant and widespread seabirds of the Bering Sea and Aleutian Islands. Organisms that are easy to sample (such as seabirds) can serve as indicators of changes in the ecosystem on which they depend, responding with changes in abundance (Cury et al. 2011) and/or changes in distribution (e.g. Fisher 1952). Over the last 40 yr, the Bering Sea ecosystem has undergone considerable change (Coyle et al. 2011, Hunt et al. 2011). The management of fisheries

there has also changed, with both a reduction in the bycatch of seabirds and a reduction in the amount of fish waste discharged by fishing vessels (NMFS 2004). Here, we use a habitat model to ask what factors shape fulmar distribution in the Bering Sea and Aleutian Islands, and how the pelagic distribution and abundance of fulmars there may have changed since the mid-1970s. In particular, we relate changes in the distribution and abundance of fulmars to changes in fisheries practices in the eastern Bering Sea.

Beyond the Bering Sea, the northern fulmar is also found in the North Pacific and North Atlantic Oce-

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ans. Since the 1700s, the North Atlantic fulmar population has expanded dramatically in size and distribution. Two major sources of variation in the pelagic habitats occupied by fulmars are climate variability (which affects the marine food webs on which fulmars depend), and commercial fishing (which may have positive impacts via the provision of food, and negative impacts via mortality of birds caught in fishing gear). Both northern and southern *Fulmarus glacialis* fulmars have been shown to be sensitive to climate variation (Thompson & Ollason 2001, Jenouvrier et al. 2003), and it has been hypothesized that the North Atlantic fulmar population increase was a result of the abundance of supplementary food from fishing and whaling operations (Fisher 1952, Burg et al. 2003). There are no comparable historical data from the North Pacific Ocean, and even the present-day North Pacific fulmar population size is poorly known.

Our study focused on fulmars in the eastern Bering Sea and Aleutian Islands regions. Fulmar foraging trips during chick rearing are usually within 500 km of the colony (Weimerskirch et al. 2001), and breeding fulmars from the Bering Sea and Aleutian Islands spend most of their time within the Bering Sea region, with a few venturing farther south into the North Pacific and into Russian coastal waters during winter (Hatch et al. 2010). We therefore assumed that once colony location was accounted for, the pelagic distribution of fulmars in the Bering Sea and Aleutian Islands would provide an indication of the availability of their preferred prey, and changes in fulmar distribution and abundance over time would reveal changes in the Bering Sea/Aleutian Islands' ecosystem on which they depend.

Bering Sea and climate change

The Bering Sea is subject to climate variability over a wide variety of temporal scales (Stabeno et al. 2001) and is expected to be an area of rapid change as human-induced climate warming progresses (IPCC 2007). For example, over the past 35 yr, there have been major changes in the amount of seasonal sea ice present in the Bering Sea and the timing of its retreat in spring (Stabeno & Overland 2001, Overland & Stabeno 2004). In the northern Bering Sea, there is evidence that spring sea ice retreat has already advanced significantly, and that this change is impacting the amount and fate of primary production there (Grebmeier et al. 2006). Similarly, over the southeastern Bering Sea shelf, the timing of sea ice retreat has

been shown to affect the timing and fate of the spring bloom and its ability to support pelagic and benthic fish and shellfish resources (Hunt et al. 2002b, 2008, 2011, Orensanz et al. 2005, Mueter & Litzow 2008). Resulting changes in the distribution, abundance or availability of prey have been shown to affect the distribution, abundance, productivity, and survival of seabirds (e.g. Anderson & Piatt 1999, Baduini et al. 2001, Hunt et al. 2002a, 2008, Jahncke et al. 2005b, 2008, Byrd et al. 2008, Benowitz-Fredericks et al. 2008).

Food from fisheries

Like many other seabird species, fulmars are attracted to fishing vessels because they provide an abundant source of food (Garthe & Scherp 2003, Furness et al. 2007). Fisheries discharges offer an alternative food source to the natural diet and, as such, have the potential to open up previously unsuitable habitat, increase reproductive performance, and reduce the likelihood of starvation (Tasker et al. 2000, Montevecchi 2002). Although direct observations have suggested that fishing vessels have only a local (<10 km) effect on the distribution of fulmars at sea (Skov & Durinck 2001), satellite tracking has revealed large-scale alterations in the foraging behavior of shearwaters in the Mediterranean Sea when fishing vessels were operational (Bartumeus et al. 2010).

The extent to which fulmars in the Pacific feed on fishery discharge, however, is unclear. The natural diet of fulmars in areas with little or no fisheries consists largely of zooplankton (Phillips et al. 1999, Jahncke et al. 2005a), although live fish are also taken and may be an important part of the diet (Cherel et al. 2001). In the North Atlantic, in spite of the presence of large fisheries, fulmars have been shown to respond to climate change (Thompson & Ollason 2001), and the actual importance of fishery discharges, even in an area as heavily fished as the North Sea, has been called into question (Camphuysen & Garthe 1997, Phillips et al. 1999).

Over the past 4 decades there have been major changes in the management of Bering Sea and Aleutian Islands fisheries. Legislative efforts have since 1977 focused on reducing the bycatch of non-target fish species and increasing the proportional use of each fish caught, resulting in a reduction of discharges. Since 1975, water quality regulations of the US Environmental Protection Agency (40CFR408) have mandated that, with a few exceptions, all on-shore and at-sea processing facilities within the ex-

clusive economic zone (EEZ) must macerate all discharges (discards and offal) into pieces no greater than ½ inch in diameter. At least in some cases, maceration may increase food availability to seabirds (Furness et al. 2007). Because changes in fisheries practices in the Bering Sea coincided closely with changes in the Bering Sea climate, identification of their respective contributions to changes in fulmar populations is a challenge.

Fulmars killed as bycatch

Accidental bycatch of seabirds in trawl and long-line fisheries is a major global conservation concern (Melvin & Parrish 2001). Procellariiformes are especially vulnerable, with most albatross species now being classified as threatened, endangered, or critically endangered (BirdLife International 2008). Fulmars are the most common seabird species taken in Alaskan groundfish fisheries, with an average of 6500 birds killed annually between 1993 and 2004 (NMFS 2006). While this number is fairly small compared to the total Alaskan population of fulmars (estimated from colony counts to be around 1.5 million birds; Hatch 1993, Hatch & Nettleship 1998), fulmars commonly venture into international and Russian waters, especially in winter (Hatch et al. 2010). Estimating the size of the bycatch is especially difficult in those regions (Lewison & Crowder 2003), though recent information suggests that the bycatch of seabirds in the Russian Far East off the Kamchatka Peninsula is similar in magnitude to their bycatch mortality in Alaskan waters (Artyukhin et al. 2006, Anderson et al. 2011). Even small decreases in adult survival rates can lead to long-term declines in long-lived species (Weimerskirch & Jouventin 1987, Croxall et al. 1990, Tuck et al. 2001). Thus, with the general uncertainties about the total population size, the lack of fulmar population trend data, and a lack of comprehensive information on fishery bycatch Pacific-wide, concerns regarding at least localized effects on Alaska fulmar populations have been raised (see Hatch et al. 2010).

Objectives

In this study, we sought not only to detect and describe changes in the pelagic distribution and abundance of fulmars, but also to examine whether we could relate any changes detected to either the effects of climate or the effects of changing commer-

cial fishing practices. We reasoned that if fulmars are primarily dependent on 'natural' prey such as zooplankton, changes in climate known to impact lower trophic levels should also affect these seabirds ('climate hypothesis'). Under the climate hypothesis, we would predict that fulmar distribution should show a fit with environmental variables related to trophic production. Likewise, if climate structures fulmar population dynamics, we would predict that fulmar populations should fluctuate with decadal-scale climate indices such as the Aleutian Low Pressure Index or North Pacific Gyre Oscillation (Di Lorenzo et al. 2008). By contrast, if fulmars depend to a large degree on fishery discharges, they should respond to variations in the distribution and quantity of catches of the Bering Sea fishing fleets ('fisheries hypothesis'). Under the fisheries hypothesis, we would expect the distribution of fishing activities to be a good predictor of fulmar distribution. We would also expect fulmar populations to respond to changes in fishery regulations, especially those affecting discards and bycatch.

MATERIALS AND METHODS

Study area and time periods covered

We bounded the study area by the Bering Strait in the north, the 200 nautical mile zone of the EEZ in the west and south, and the 159° W meridian in the east; this area comprises about 2.33 million km² (Fig. 1) and closely corresponds to the National Marine Fisheries Service reporting areas for the Bering Sea and Aleutian Islands (NMFS 2006). We chose this area because it has been well surveyed for pelagic seabirds and covers most of the fulmar breeding distribution in the North Pacific Ocean. We excluded the Russian part of the Bering Sea because we found no comparable data on fishery activities, and there was relatively light seabird survey coverage there. Our study area contains most of the fulmar colonies in the North Pacific, including the globally largest colony of the species (Fig. 1).

We further restricted our dataset by date from 1 May to 7 September, coinciding with the fulmar pre-breeding and breeding seasons, and thereby avoiding migrants and sea ice (arrival at colonies is between March in the south and May in the north; Hatch & Nettleship 1998) and the influx of fledglings (earliest reported fledging date from Alaska is 8 September; Hatch & Nettleship 1998). Survey coverage was also most comprehensive during these months.

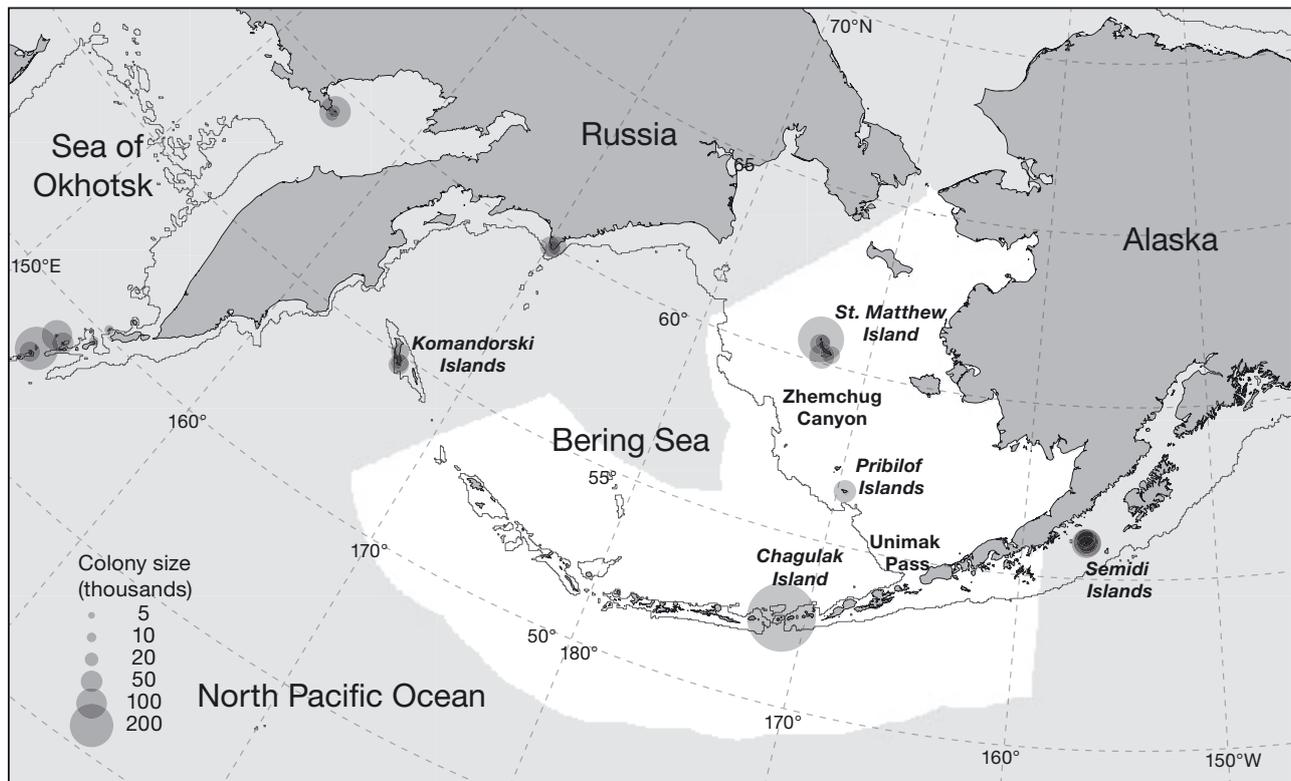


Fig. 1. *Fulmarus glacialis*. Study area: the Bering Sea and Aleutian parts of the Alaskan Exclusive Economic Zone (white). Also shown are the 400 m isobath (marking the edge of the continental shelf) and the colonies of northern fulmar

The northern half of the study area may be affected by seaice until early June, but few pelagic seabird surveys were conducted during May and June in the northern Bering Sea. The incorporation of monthly sea surface temperature into our distribution model should also address the issue of sea ice (see 'Modeling at-sea distribution and abundance').

Data sources, survey methods and correction factors

We combined pelagic seabird data from 5 principal data sources: (1) The North Pacific Pelagic Seabird Database (NPPSD; Drew & Piatt 2005), (2) pelagic seabird surveys conducted by G.L.H. and co-workers on process studies from the 1980s to the 2000s, (3) surveys around major seabird colonies of the Alaska Maritime National Wildlife Refuge (Byrd et al. 1997, Renner et al. 2008), (4) North Pacific Research Board (NPRB)-funded ships of opportunity project (Sydeman et al. 2010), and (5) the current pelagic seabird project run by K.J.K. on ships of opportunity, also with support from NPRB. All of these data sources have undergone QA/QC procedures for archiving in

the NPPSD. For the analysis here, we excluded aerial surveys and surveys without a defined transect width contained within the NPPSD. For additional information on the datasets and data collection methods used in the NPPSD, see publications employing NPPSD data e.g. Springer et al. 1999, Piatt & Springer 2003, Hunt et al. 2005, Piatt et al. 2006, Renner et al. 2008, Drew et al. 2010.

Pelagic seabird surveys prior to 1984 were recorded by hand on paper forms in pre-defined time bins, usually of 10 min duration. In later years (but still using the same basic methods of data collection), data were entered directly into a computer continuously with a time-stamp and GPS positions for each observation of a seabird. These records did not have a pre-imposed bin length. We divided computer-entered data into 3 km bins, equivalent to 10 min on a vessel traveling at 9 to 10 knots. At least since the late 1990s, geographic position fixes have been obtained exclusively from GPS, replacing positioning using Loran-C. Position errors of Loran-C are assumed to be less than 500 m and GPS fixes are accurate to less than 100 m.

All surveys used standard strip transect methods, usually with a strip width of 300 m, and counted all

birds on the water or feeding (Tasker et al. 1984). Two different methods for counting flying birds were used. Most surveys in the 1970s and 1980s counted all flying birds observed within the transect strip. Beginning in the 1980s, many surveys used the snapshot method (Tasker et al. 1984), which was adopted by most investigators by the 2000s. The ‘snapshot’ is a method designed to eliminate the bias introduced by birds flying fast compared to the usually slow-moving survey vessel. Flying birds are counted at a set instant in time in a survey box (typically 300 × 300 m) and again when the vessel has passed over this virtual box. Consequently, the snapshot method does not count every flying bird seen (as in ‘all flying birds’), but provides an estimate of the density of flying birds at sea that is not biased by the relative motion of the bird with respect to the ship, as is the case when all flying birds are counted (see Tasker et al. 1984).

The bias in surveys not employing the snapshot method (or equivalent corrections) depends on the bird’s flying speed (which differs for each species), wind velocity, and wind direction in relation to that of the survey vessel (Spear et al. 1992). To meld datasets collected using these different survey methods, we divided the number of flying birds in a sample by a correction factor λ_m when the snapshot method was not used. Lacking empirical data for northern fulmar flight speeds, we used the value $\lambda_m = 2.3$ reported by van Franeker (1994) for the southern fulmar, an allopatric sibling-species of similar size and flying habits. To ensure that our analysis results were not driven by this correction factor, we also ran the same analyses with the minimal theoretically possible value of $\lambda_m = 1$ and with $\lambda_m = 5.0$, the highest value reported by van Franeker (1994). The $\lambda_m = 5.0$ was found for black-browed albatross *Thalassarche melanophrys*, a larger and considerably faster-flying species than the northern fulmars (especially in the conditions of the Southern Ocean). Since the correction factor increases with flying speed (Spear et al. 1997b), we are confident that the true correction factor is covered within these limits.

Densities and resulting at-sea population estimates reported here can be affected by other factors as well, including sea conditions, weather (rain, fog), observer skill, ship attraction, etc. (van der Meer & Camphuisen 1996). However, given a large sample size, reasonable population estimates, and therefore estimates of population trends, can be obtained from at-sea data (Spear et al. 1995, van der Meer & Leopold 1995, Clarke et al. 2003). We have no reason to suspect that the biases introduced by these factors have been sub-

ject to long-term change and therefore would not affect trend estimates of fulmar densities. Nonetheless, we recognize that our analysis suffers from several uncorrected biases. Reported estimates of at-sea densities should be viewed with this in mind.

Modeling at-sea distribution and abundance

Survey coverage was heterogeneous, but large sample sizes were obtained in every year (Table 1). While some areas were sampled extensively and in most years, other areas were surveyed only once, if at all. Since survey effort was occasionally focused in a subset of the study area, any observed spatial pattern could be based on differences in spatial coverage,

Table 1. *Fulmarus glacialis*. Sample sizes (number of 10 min or 3 km bins), total area surveyed and number of bins in which northern fulmars were detected for each year of the study

Year	n	Area (km ²)	N (fulmar > 0)
1975	1085	1646	606
1976	1300	1675	651
1977	1174	1396	921
1978	1919	1983	1399
1979	850	835	510
1980	1012	978	508
1981	2286	2122	1715
1982	2328	2528	1623
1983	1571	1467	1186
1984	882	1165	487
1985	972	919	651
1986	841	722	507
1987	863	757	717
1988	806	712	731
1989	1003	803	763
1990	317	288	225
1991	629	566	282
1992	1557	1352	1131
1993	1521	1333	1261
1994	1269	1084	342
1995	1039	934	754
1996	199	172	112
1997	2483	1664	1449
1998	2455	1983	1357
1999	2884	2384	1497
2000	123	162	118
2001	604	461	497
2002	1669	1270	763
2003	747	556	418
2004	2081	1469	1342
2005	898	758	602
2006	6608	4895	2825
2007	11598	8216	4632
2008	11808	6175	7025
2009	13746	7395	7948

unless differences in spatial coverage were accounted for by modeling. The heterogeneity of survey coverage also meant that not all portions of the study area received survey coverage in proportion to their areas in each time period. To compare observations in a particular year to an expected mean, we employed a spatial model of expected densities to compensate for the uneven survey coverage in space and time.

A schematic overview of our modeling approach is given in Fig. 2. To build a predictive model of the fulmar distribution in the Bering Sea and Aleutian Archipelago, we gathered a suite of raw and derived environmental and anthropogenic variables (Table 2, Fig. 3). All spatial data were projected into an Albers Equal Area projection with standard parameters for Alaska. We chose variables which we considered likely to be related to fulmar distribution at sea, and which were readily available. We assumed that most of these variables are not of direct importance to fulmars, but rather influence the distribution or near-surface availability of potential prey. For example, steep underwater slopes can upwell prey to the surface (Ladd et al. 2005), but only if the slopes are not too deep (Jahncke et al. 2005a). We used the slope of the log of bathymetry because by doing so, we emphasized the importance of slope in shallow over slope in deep water.

Distance from the colony (Colony effect) could be thought of as the default distribution for seabird densities at sea during the breeding season (Ashmole & Ashmole 1967). If the ocean environment was uniform without aggregations of prey, we would expect terrestrial, social, and random factors to determine the location and size of colonies. Due to geometric spreading (Kinder et al. 1983, Decker & Hunt 1996), we would expect that at-sea density of fulmars (F) at any given point (p) will be related to the distance from the colony. Combining n colonies, we postulate that this effect would be additive over all colonies, leading to the expected at-sea density of fulmars at any given point to be proportional to the size (s) of the colony i and the inverse of the point's distance (d) from the colony i :

$$F_p \propto \sum_{i=1}^{i=n} \frac{s_i}{d_{p,i}} \quad (1)$$

Assuming that a pelagic species such as a fulmar would be reluctant to fly over land other than to reach its nest, we did not use the Euclidean distance but rather the shortest distance over water. As a starting point, we used the point on shore closest to any given colony (Fig. 1). We included the contribution of all North Pacific fulmar colonies, even those outside the study area.

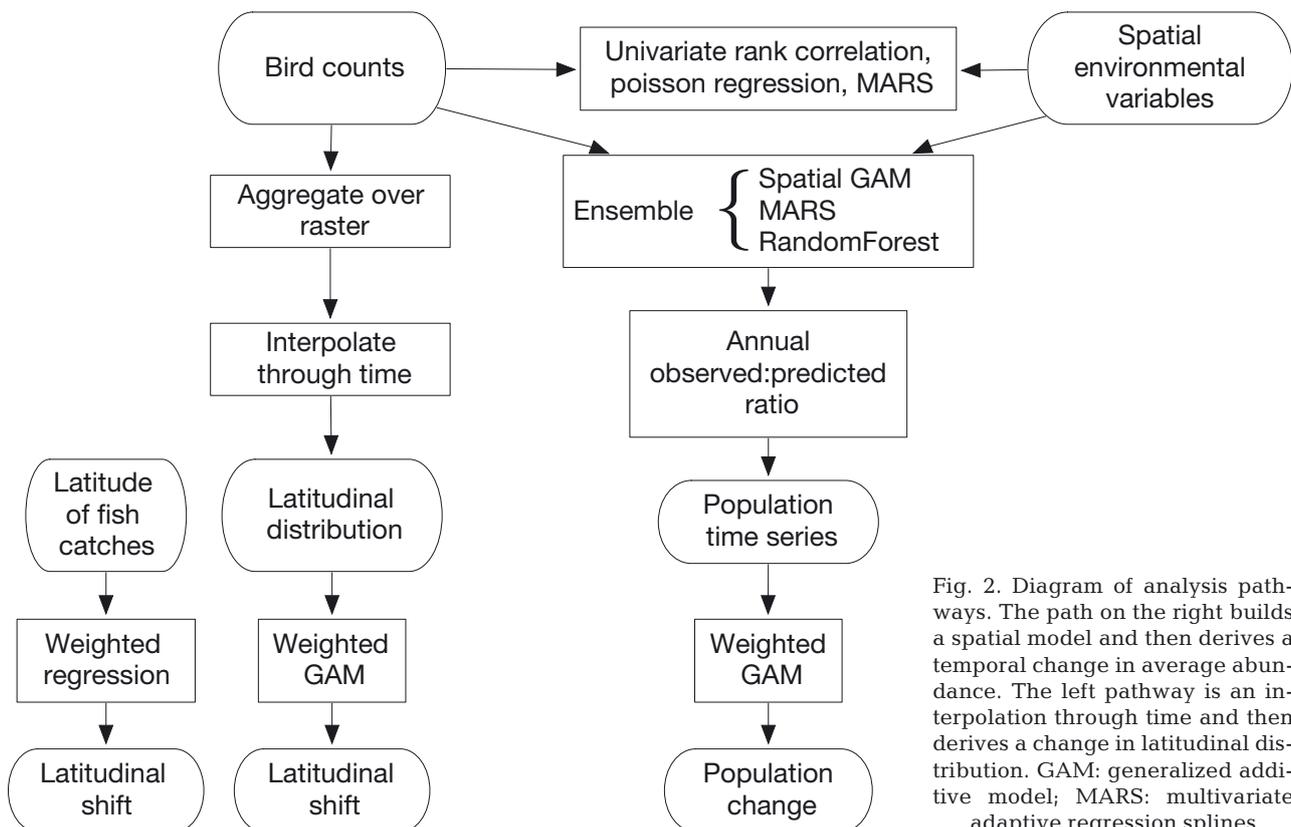


Fig. 2. Diagram of analysis pathways. The path on the right builds a spatial model and then derives a temporal change in average abundance. The left pathway is an interpolation through time and then derives a change in latitudinal distribution. GAM: generalized additive model; MARS: multivariate adaptive regression splines

Table 2. Data sources and abbreviations for seascape variables used to model northern fulmar *Fulmarus glacialis* distribution. Since our dataset goes back to 1975, we used long-term averages (climatologies) for variables which change through time (i.e. SST and pprod). SST was the only variable for which we took the month of sampling into account

Variable name	Abbreviation	Explanation	Resolution (km)	Source
Bathymetry	bathy	Ocean depth interpolated from actual sounding and satellite-derived gravity data on a 30' grid	<0.9	GEBCO ^a
Slope of bathymetry	bathySl	First spatial derivative of bathymetry	5	
Slope of log-bathymetry	logBaSl	As bathymetry slope but derived from the log of bathymetry	5	
Bathymetric features	baFeat	Plains, ridges, channels, peaks and pits in the log of bathymetry	5	Wood (1996)
Distance to land	dLand	Distance to the nearest land	5	gshhs shoreline ^b
Colony effect	colony	Expected distribution assuming even dispersal from colonies (see Eq. 1)	5	Beringian Seabird Colony Catalog ^c
Sea surface temperature	SST	1985–2001 monthly average, derived from AVHRR satellite	4	NOAA ^d
Primary productivity	pprod	Averaged May to September, 2002–2009, derived from MODIS and Sea-WIFS ocean color and temperature	5	OSU ^e
Fish catch	fishCatch	Haul size of all fisheries combined	10	NOAA ^f

^awww.bodc.ac.uk//data/online_delivery/gebco/
^bwww.soest.hawaii.edu/wessel/gshhg/
^c<http://alaska.fws.gov/mbssp/mbm/northpacificseabirds/colonies/default.htm>
^dhttp://data.nodc.noaa.gov/pathfinder/Version5.0_Climatologies/1985_2001/Monthly/Combined/
^ewww.science.oregonstate.edu/ocean.productivity/
^fwww.afsc.noaa.gov/fma/spatial_data.htm

To identify Bathymetric features quantitatively, we made use of an algorithm developed for landscape analysis (Wood 1996) to characterize the shape of the log-bathymetry for each grid cell. After choosing an appropriate tolerance, a ridge, for example, was defined as a point that lies on a local convexity that is orthogonal to a line with no convexity/concavity (Wood 1996, GRASS Development Team 2009). Bathymetric feature was the only categorical variable in the set; the categories being pits, peaks, planes, ridges, saddles, and channels. We used log-bathymetry in the calculation of Bathymetry to, again, to emphasize shallow water features over those in deep water.

For Sea Surface temperature, we used monthly means (climatologies) across all years to build the models, and the mean across all months included in the dataset to make the predictions for the time series. Missing pixels near the shorelines of perpetually fog-shrouded islands and along the 180th meridian were interpolated from the adjacent pixels using a spline smoother.

Information on Fish catch was made available by the NMFS Alaska Fisheries Science Center observer program (AFSC Observer Program) at a coarse spatial resolution to protect confidentiality (Table 2). We aggregated the catches of all species of fin-

fish from all available years over a 10 km × 10 km vector-grid.

We used long-term means (climatologies) for the dynamic variables Sea surface Temperature, Primary productivity, Fish catch, and colony size (Colony effect) for 2 reasons: (1) Concurrent data was data not available for many years, especially for the 1970s and 1980s. (2) Our main objective was to use this model to look for temporal patterns in the observed:predicted ratios. Adding predictive variables that vary in time would improve the ability to estimate the functional response of fulmar density. However, the ability to detect trends in these ratios would be compromised, as some of that variability would already be explained by the long-term variability of the predictive variable. We were aware of the considerable interannual variation in some of these variables. However, our study area spanned such a large geographic space that we expected interannual variation to be small compared to spatial variation. While the model did not contain an annual component, the observed:predicted ratios of the dependent variable (Fulmar density) could still be analyzed on an annual basis. Because colony attendance varies considerably over the breeding season (Hatch 1989), we added the Day-of-year as a variable to the model.

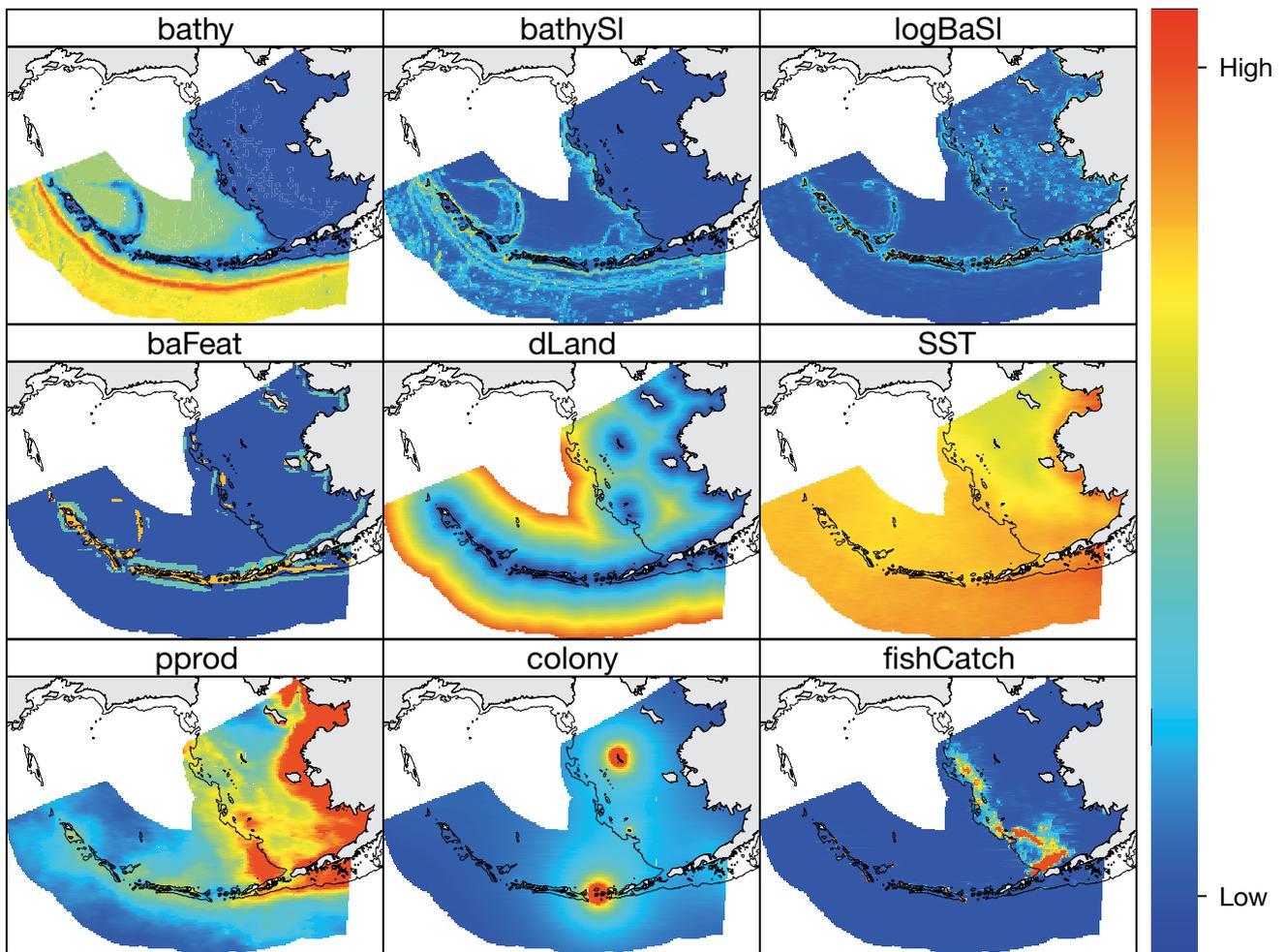


Fig. 3. Physical layers and fisheries catches used to predict northern fulmar *Fulmarus glacialis* densities. To show the spatial patterns better, we capped the upper 10th percentile of primary productivity, and the upper 1% of log bathymetry slope, colony effect, total fish catch, and longline catch (only for this figure, not the analysis). 'Bathymetric features' is the only nominal variable. Also shown is the 400 m isobath marking the continental slope. See Table 2 for abbreviations, variable explanations and sources

Abundance model

To model the counts of fulmars per transect, we used an ensemble approach—using the mean of 3 predictive models weighted by the inverse root mean squared error from 10-fold cross-validation: generalized additive model (GAM; Wood 2000, Clarke et al. 2003, Wood 2011), multivariate adaptive regression splines (MARS; Friedman 1991, Austin 2007, Hastie et al. 2009), and random forest (Cutler et al. 2007). Ensemble approaches are often superior to a single model (e.g. Burnham & Anderson 2002, Araújo & New 2007, Oppel et al. 2012).

Generalized cross-validation allows selection of the smoothing parameters in a GAM to be tuned as if checking it against an independent dataset, thereby

avoiding overfitting. MARS is a non-parametric extension of generalized linear models, automatically allowing for non-linearities and interactions between variables. The implementation used here ('earth') allows for hinges, joining 2 straight lines, rather than smooth splines. Variables and hinges are selected through a step-wise process.

Random forest is an ensemble method in itself, combining the ideas of 'bagging' and random selection of features. From a bootstrap sample, a large number of regression trees are fitted (here 500) using randomly chosen variables on each node. Trees are fully grown (rather than pruned), and the results of all trees are averaged for the final prediction. While providing highly accurate predictions, random forest models tend to be difficult to interpret. Used here for

the predictive regression of abundance, random forest has been shown to be a superior method for presence/absence and diversity distribution models (Marmion et al. 2009, Knudby et al. 2010), but has seen only limited use in abundance models so far.

All variables listed in Table 2 were allowed to enter the respective models. In the case of the GAM, we allowed Bathymetry, Sea surface temperature, and Day-of-year (Day) to be smooth functions. The GAM model was specified as:

$$\log\left(N_s + \frac{N_f}{\lambda_m}\right) = \beta_1 s_{1j} \text{Day} + \beta_2 s_2 \text{bathy} + \beta_3 \text{bathyS1} + \beta_5 \text{dLand} + \beta_6 \log(\text{colony}) + \beta_7 \text{pprod} + \beta_8 \text{fishCatch} + \beta_{9s3} \text{SST} + \beta_{10} \text{baFeat}_{\text{planar}} + \beta_{11} \text{baFeat}_{\text{slope}} + \beta_{12} \text{baFeat}_{\text{ridge}} + \beta_{14} \text{baFeat}_{\text{channel}} + \beta_{14} \text{baFeat}_{\text{mount}} + \beta_{16s4x} + \beta_{17s6y} + \beta_{18s6x} : y + \log(\text{Area}) + \epsilon \quad (2)$$

where N_s is the number of swimming, and N_f the number of flying fulmars counted during a transect segment. The flux correction factor λ_m was used to allow comparison between the 2 methods (m) used for flying birds; $\lambda_m = 1$ when the snap-shot method was used. Applying the correction factor λ_m to the area offset instead of the count numbers was not possible because swimming and flying birds are counted simultaneously, but the correction only needs to be applied to the flying birds. β_{1-18} are the individual parameters fitted by the model, and s_{1-6} are smooth spline functions. The degree of smoothing was determined through generalized cross-validation (Wood 2000), and variables were selected through shrinkage.

We considered 2 error distributions: the negative binomial and the quasi-Poisson, both of which allow for overdispersion. Ver Hoef & Boveng (2007) showed that the quasi-Poisson distribution gave greater weight to large aggregations and was therefore more appropriate when a high proportion of the total population was found in a few large aggregations. In our sample, we found that over 50% of all birds were in flocks larger than 60 birds, while the mean flock size was only 14 birds. We therefore built our models using the quasi-Poisson distribution. We used a log-link function and $\log(\text{bin-area})$ as an offset. The offset allowed us to model discrete counts per bin, while taking different bin sizes into account, thereby effectively modeling density rather than counts. The MARS and random forest models were set up equivalently, but without the terms for geographic location.

To estimate variable importance, we made predictions for each variable over its observed range, while

holding the remaining variables constant at their respective means. We computed the standard deviation of the predicted counts and scaled them relative to the variable with the greatest variance.

Time series

To test whether fulmar abundance in the Bering Sea has responded to observed changes in climate and changes in fishing practices, we derived a time series of the fulmar at-sea abundance (NOFU). Using the ensemble model, we predicted counts over a 10 km grid of the entire study area. For each grid cell we used the mean of the continuous, and the mode of categorical variables. Day-of-year was set to 30 July, which usually falls in the incubation period for northern colonies and around hatch time for southern colonies. We chose this date because colony attendance during these phases is comparatively constant (Hatch 1989).

From the sum, P , of this predicted at-sea abundance, we derived annual abundance estimates by applying the mean ratio of fitted F to observed values O to P for every year a from Year 1 to Year N_a :

$$\text{NOFU}_a = P \frac{\sum_{i=1}^{i=N_a} \frac{F_{i,a}}{O_{i,a}} \sum O}{N_a \sum F} \quad (3)$$

We fitted a GAM to the annual estimates, to allow for variations in the population trajectory over this rather long period of time. We set the smoothing parameter through generalized cross-validation. We calculated 95% confidence intervals for the annual population estimates by bootstrapping the ratio $\frac{F_i}{O_i}$ using 999 replicates. The caveat to these confidence intervals is that not only the number of 3 km or 10 min bins, but also the spatial coverage varies between years. While there was good coverage in the early and the late parts of the study period, for some years only a few localized surveys are available. The confidence limits are a valid estimate of the uncertainty within the sampled area, but can only be indicative for the entire study area when sampling is geographically limited. To address this uncertainty for individual years (which is also a function of the varying sample size over years), we weighted the GAM by the inverse of the range of the confidence interval. For comparison, we applied these steps not only to the ensemble model, but to the MARS, GAM, and random forest habitat models as well.

Change in latitudinal distribution

To test for shifts in the latitudinal distribution of fulmars while accounting for the heterogeneity of the dataset, we averaged densities over a 10 km × 10 km grid, assuming that data within any one grid-cell were comparable through time (Fig. 2). Missing data, i.e. grid cells that were not surveyed in any 1 yr, were interpolated through time (but not space). Missing values in the earliest and latest years were replaced with the closest neighbor in time. The now complete matrix could be analyzed for changes in latitude (center of gravity) by using mean density per grid cell as weights in a regression of latitude (of grid cell) over time. We used a cross-validated GAM for fulmars and for comparison a weighted linear regression for the shorter time series of fish catches.

Software tools

We used R (R Development Core Team 2011) for almost all calculations. GRASS GIS (Neteler & Mitasova 2008) in conjunction with the R packages 'sp' and 'spgrass6' were used for all GIS operations. Models were fit using R with the packages 'lme4' (GLMM), 'mgcv' (GAM), 'earth' (MARS), and 'randomForest' (Liaw & Wiener 2002).

RESULTS

Distribution

We found fulmars throughout most of our study area. A plot of the observed densities, averaged over the entire time period, revealed high concentrations along the outer continental shelf and along the Aleutian Archipelago (Fig. 4). Two off-shore hotspots stand out: one to the south-west of Saint Matthew Island and one between the Pribilof Islands and Unimak Pass (see Fig. 1 for locations). Areas where fulmars were found at zero or near-zero densities included the shallow waters of the inner domain of the Bering Sea, and areas far off-shore over the deep waters of the Bering Sea Basin and the North Pacific.

Model selection and variable importance

Fulmar density showed the strongest relationship with Bathymetric features based on a Poisson regression and a univariate MARS model (Table 3). Fulmar densities were higher over underwater ridges than over other features like flats or channels. Spearman rank correlations with fulmar density were strongest with Colony effect, Bathymetry and Fish Catch, but could not be calculated for Bathymetric Features. Slope of bathymetry and Sea surface temperature had similarly high values of ρ , whereas ρ values of the slope of Log-bathymetry, Primary productivity and Distance to land were close to zero. The best univariate MARS models after Colony effect were based on Bathymetric features (ridges), Fish catch, and Bathymetry. Primary productivity and Distance to land ranked low in all of the univariate model sets.

To predict the spatial distribution of fulmar abundances, we built an ensemble model, based on GAM, MARS, and random forest models, using all predictor variables simultaneously. Model weights for the GAM, MARS and random forest models were practically equal at 0.332, 0.335 and 0.333, respectively. To visualize the structure of the ensemble model, we plotted the effect of each variable in the model, holding all other vari-

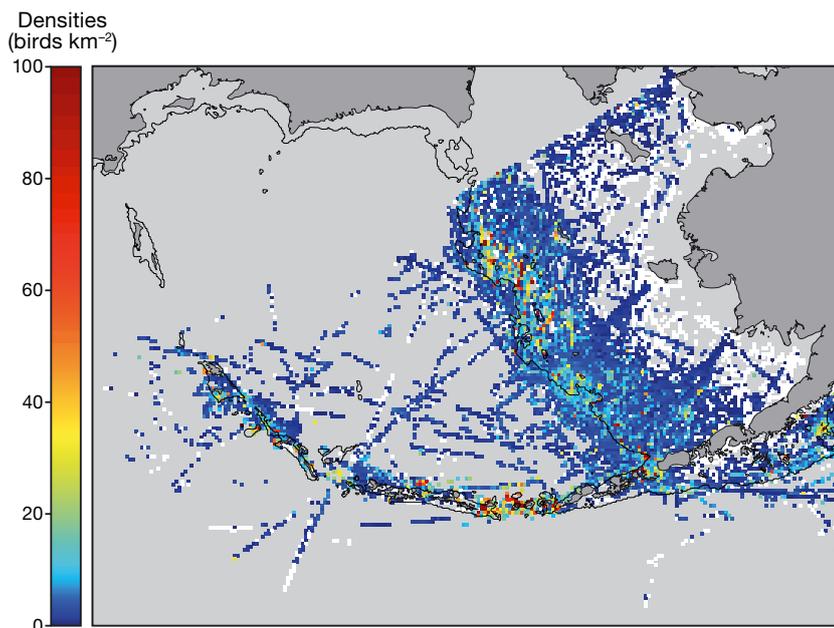


Fig. 4. *Fulmarus glacialis*. Observed average densities (birds km⁻²) of northern fulmars between May and early September in the Bering Sea between 1975 and 2009 within a 10 km × 10 km grid. Gray pixels were not surveyed; white pixels were surveyed but no birds were found. Densities above 100 birds km⁻² were truncated

Table 3. *Fulmarus glacialis*. Univariate models explaining northern fulmar distribution, contrasting natural factors and fisheries. We show Spearman's ρ from rank correlation with fulmar density, the difference in deviance of a Poisson regression on fulmar counts (with a survey-area offset) and the best Poisson model (low values indicating a better fitting model), and the r^2 of the respective multivariate adaptive regression splines (MARS) model. Note that here only the MARS model allows for a non-monotonous relationship. The table is sorted by the mean rank \bar{k} of the 3 measures

Variable	ρ	Δ deviance	MARS r^2	\bar{k}
Bathymetric features		0	0.002	1.5
Colony effect	0.24	10383	0.00889	1.7
Bathymetry	0.27	43109	0.00126	3
Fish catch	0.23	46977	0.00144	4
Sea surface temperature	0.17	46606	0	5.5
Primary productivity	-0.04	42873	0	5.5
Distance to land	0.01	59536	0.00118	6.7
Slope of bathymetry	0.07	67860	0	7.2
Slope of log-bathymetry	0.02	64049	0	7.5

ables constant (Fig. 5). Colony effect was the single most important predictor. Other important predictors included Sea surface temperature, Fish catch and Geographic location (x and y). The effect of Fish catch showed a threshold above which additional fishing activity would lead to only minor increases in fulmar densities. The function of Day-of-year on fulmar densities was somewhat bell-shaped, peaking in early July.

The predicted at-sea distribution showed high concentrations of fulmars on the Bering Sea continental shelf close to the shelf break, and in the Aleutian Archipelago (Fig. 6). Localized hotspots were found around the largest colony on Chagulak Island and in adjacent passes, in the 'elbow' north of Unimak Pass, and at an off-shore area on the shelf adjacent to Zhemchug Canyon. Low densities were predicted for shallow coastal waters and deep off-shore waters. The predicted hotspots were also found in the aggregated observed data in the form of spatially smaller but denser aggregations (Fig. 4). The different models agreed on the hotspot around Chagulak, but differed in the predicted extent and size of some of the other areas of high density. We based the following time series analysis on the predictive ensemble model.

Time series

Using the annual deviations from the locally-predicted at-sea densities, we derived a time series of fulmar at-sea abundance. A GAM of the time

series showed a decline from an average at-sea density of 6.75 ± 0.53 birds km^{-2} in 1975 to 5.10 ± 0.40 birds km^{-2} by 2009 at a constant rate of $-0.83 \pm 0.39\%$ (SE) per year (Fig. 7). This translates to a total decline of 24.7% over the time period from 1975 to 2009. Note that all models showed a decline, but estimates of at-sea abundance as well as shape of the trend varied considerably among model results. Generalized cross-validation supported several nodes in the abundance trends of all models other than the ensemble model—the trend of which was reduced to a straight line. These patterns were similar when using the extreme values (1 or 5) for the correction factor of flying birds λ . Using these extreme

values of λ , the estimated annual rates of decline for the ensemble model were $1.4 \pm 0.39\%$ for $\lambda = 1$, and $0.35 \pm 0.45\%$ for $\lambda = 5$, respectively.

Given that the temporal GAM from the spatial ensemble model failed to reveal changes in the slope of the abundance trend over the years, we refrained from a formal analysis relating this trend to climate or biological variables. While any time series with a strong directional trend will show a high correlation with the trend in fulmar abundance, the inherent autocorrelation precludes a convincing quantitative argument for causal relationships.

Changes in distribution

Using a temporal GAM of latitude, weighted by interpolated densities within $10 \text{ km} \times 10 \text{ km}$ grid cells, we looked for changes in distribution over time. We found a northward shift in the center-of-gravity of fulmar distribution in the Bering Sea (excluding the Aleutian Archipelago). A similar, but 3 times faster shift northward was found in the distribution of fishery catches (Fig. 8). While fulmar densities have seen increases in the north, the distributional shift in fishery catch was largely due to reduced catches in the southern Bering Sea, rather than a range-expansion at the northern edge (Fig. 8b). Although the temporal GAM allowed for a flexible model, the level of smoothing chosen by generalized cross-validation resulted in a straight line.

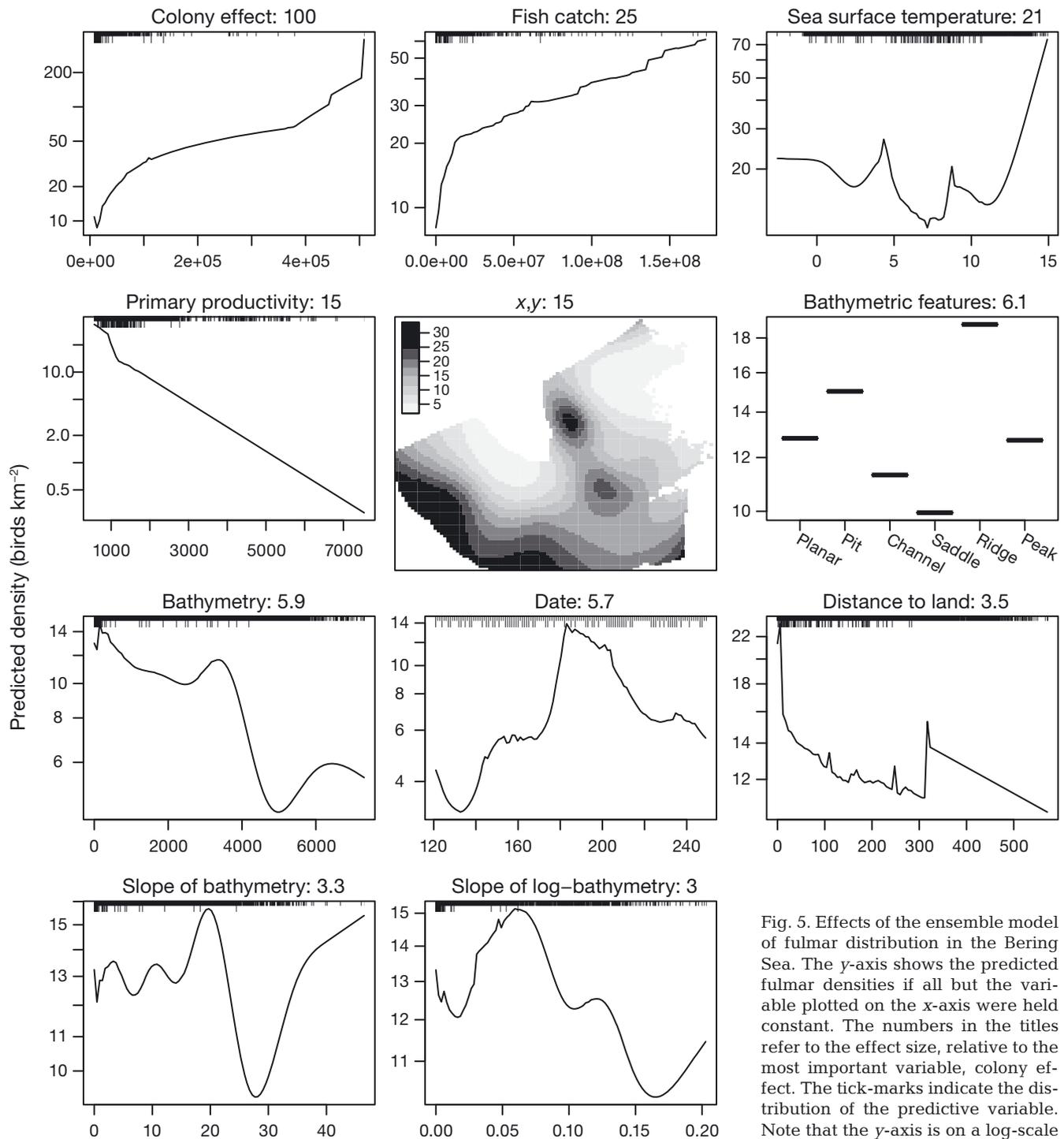


Fig. 5. Effects of the ensemble model of fulmar distribution in the Bering Sea. The y-axis shows the predicted fulmar densities if all but the variable plotted on the x-axis were held constant. The numbers in the titles refer to the effect size, relative to the most important variable, colony effect. The tick-marks indicate the distribution of the predictive variable. Note that the y-axis is on a log-scale

DISCUSSION

Modeling of at-sea data revealed high densities of fulmars along the edge of the continental shelf, around the major colony of Chagulak Island, and near Zhemchug Canyon. Our model indicates that fulmars have declined by 0.83% per annum, or about

24% from 1975 to 2009. Additionally, the center of gravity of fulmar at-sea distribution has shifted northward, coinciding with a northward shift in the distribution of fish catches.

While a large proportion of the literature is concerned with modeling distribution of occurrence from presence/absence or presence-only data, com-

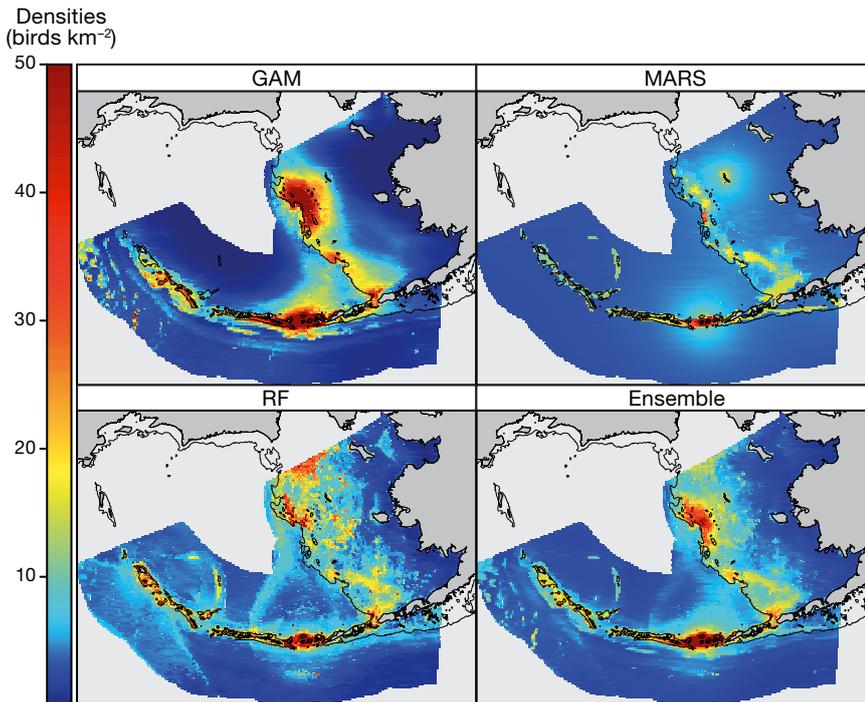


Fig. 6. *Fulmarus glacialis*. Distribution of northern fulmar at-sea densities in the Bering Sea and Aleutian Archipelago as predicted by 3 different predictive models and an ensemble of those 3 for 30 July, based on data from the breeding season (May–early September) and the years 1975–2009. Color scale is capped at a density of 50 birds km^{-2} . Note the general agreement in large-scale patterns, but differences in size and location of high-density areas on the Bering Sea shelf, the north of which is only sparsely surveyed (Fig. 5). GAM: generalized additive model; MARS: multivariate adaptive regression splines; RF: random forest model

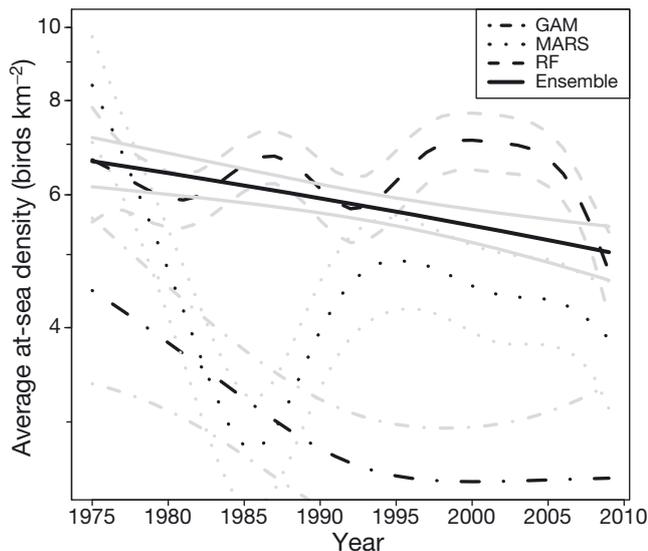


Fig. 7. *Fulmarus glacialis*. Estimated trends of northern fulmar densities in the Bering Sea as indicated by at-sea surveys, based on ratios of observations to predictions of one of 4 different spatial models, including an ensemble model. Annual estimates were smoothed using cross-validated temporal GAMs, weighted by the inverse range of the confidence intervals of the annual estimates. Shown are the temporal GAMs with their standard errors in gray. Note that the y-axis is scaled logarithmically

paratively little attention has been paid to modeling the spatial distribution of abundance. Ensemble models have performed well in a previous study (Oppel et al. 2012), but more research in this field is clearly needed. It may appear peculiar that the ensemble model (an average of the 3 other distribution models) resulted in a lower population estimate than the GAM, MARS or random forest models (Fig. 7). We interpret this as a result of slight differences in the predicted location of hotspots, especially on the Bering Sea shelf. Our results show that model selection can affect the results and their interpretation considerably (see Figs. 6 & 7).

Colony effect was the most important variable predicting fulmar distribution and abundance during the breeding season. Colony location is a prominent feature in almost any telemetry study, but is rarely used in vessel-based at-sea studies (but see Kinder et al. 1983, Decker & Hunt 1996, Huettmann & Diamond 2001, McSorley et al. 2006). For large-

scale studies and species with overlapping foraging areas between adjacent colonies, a multi-colony approach, as shown here, is necessary. Many of the extant fulmar colonies in the Bering Sea are long-established, driven by factors predating the advent of modern fisheries in the region. Those hotspots of fulmar densities that overlap with commercial fishing activities are in near-shelf-edge areas that appear to be suitable fulmar habitat elsewhere in the North Pacific. What makes these zones particularly attractive is the combination of natural and anthropogenic food.

Both the univariate exploration, as well as the ensemble model, indicated that Fish catch was an important variable for explaining the distribution of fulmars. We suggest that the explanatory importance of Fish catch reflects the importance of fishing activity as the underlying reason for the northward shift in the pelagic distribution of fulmars in the Bering Sea. We are unaware of any data suggesting a northward shift in the location of fulmar colonies, or of the numbers of individuals attending extant fulmar colonies, although if the northward shift of the foraging range is long-lasting, we would expect a gradual northward shift of the breeding population.

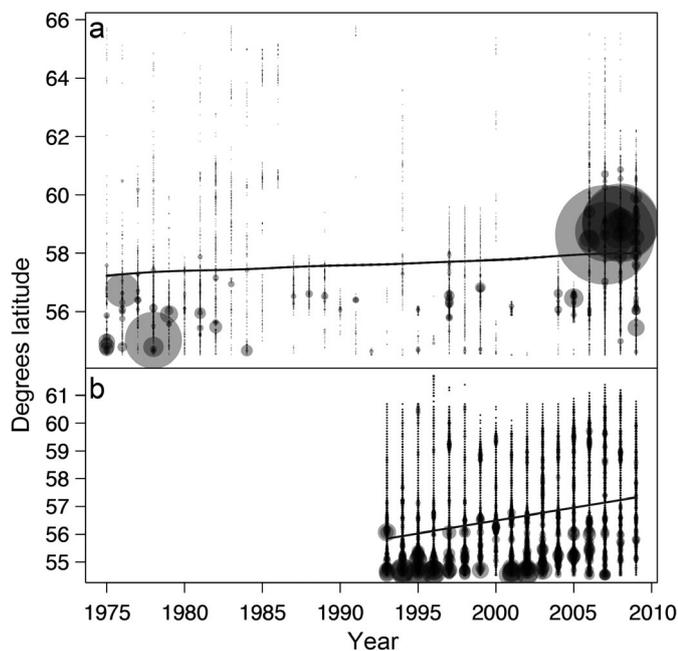


Fig. 8. Change in the latitudinal distribution of (a) northern fulmars and (b) fisheries catches in the Bering Sea (excluding Aleutian Islands). Both datasets were first aggregated over a 10 km × 10 km grid, so each data point represents one grid cell. Size of the circles is proportional to (a) the size of the average bird density (prior to interpolation) and (b) fish landings per grid cell. Regression slopes translate to a northwards shift in distribution at a rate of $2.43 \text{ km yr}^{-1} \pm 0.06 \text{ km yr}^{-1}$ in fulmars and $10.30 \text{ km yr}^{-1} \pm 0.06 \text{ km yr}^{-1}$ in fish catches. Note that the shift in the center of gravity of the fisheries is due to a reduction in fish catches in the south rather than an expansion at the northern extreme. Confidence intervals are too narrow to be clearly visible. A cross-validated weighted temporal GAM of the fulmar distribution did not differ from the straight line, suggesting that the straight line is the best predictor supported by the data

Bathymetric features, principally bathymetric ridges, ranked highly when taken by themselves, but their importance was much reduced in the ensemble model. Bathymetric ridges were particularly prominent along the continental shelf break, emphasizing the shelf-edge as an important habitat feature of fulmars. While much of the Bering Sea fishing activity also occurs near the shelf edge (Fig. 3), there are numerous exceptions where shelf-edge habitat is not fished or where large fisheries occur away from shelf edge habitat. We found only weak correlations between fulmar density and Sea surface temperature, and even weaker correlations with Primary productivity. Primary productivity was more important in the ensemble model. We have no ready explanation as to why the relationship between Primary productivity and Fulmar density is negative, however.

Using the ensemble model, we can produce an estimate of fulmar at-sea abundance independent of colony-based counts by multiplying the average predicted density (from Fig. 7 by the size of the study area (2.33 million km²). This would yield an at-sea population of 15.7 million in 1975 that declined to 11.9 million birds by 2009. This estimate does not include birds attending an egg or chick on land. The North Pacific seabird colony database covers the entire range of fulmars in the Pacific and lists a total of 2.2 million individual breeding fulmars (not pairs; Migratory Bird Management 2010). Considering only birds breeding within the study area would leave us with an estimated 984 000 breeding birds. Adjusting for 30% non-breeders (Hatch 1987), we get 3.1 million and 1.4 million for the North Pacific and the study area, respectively.

We suggest that this discrepancy between the at-sea-based estimate and the colony-based estimate of about an order of magnitude has 2 causes: (1) vessel attraction leads to an overestimation of actual fulmar at-sea densities. (2) The largest fulmar colonies host considerably more birds than the colony catalog suggests. Hyrenbach (2001) reported that ship-based surveys overestimate albatross densities off California by a factor of 4. While observers in our study were instructed not to count obviously ship-following birds, there is no known antidote against ship-attraction.

Additional at-sea surveys (especially close to the major colonies) would help to reduce the uncertainties of model predictions. There is a need for better estimates of the effects of vessel attraction and ship following on standard survey methods and how these vary across species and group sizes.

If detectability were a source of a major bias in this study, we would have expected an at-sea population estimate lower than the comparable estimate from terrestrial data. Because our ship-based population estimates were higher than those based on colony counts, it is reasonable to assume that detectability was at most a minor source of bias to the at-sea population estimate.

There is no established method for estimating the enormous numbers of fulmars breeding in the largest colonies. The slopes of Chagulak Island are near-vertical and usually covered in fog (Fig. 9). The counts of this colony were incomplete, at best, and given the clouds of fulmars circling this island, it is easy to imagine that the actual numbers are substantially larger than the estimate in the current version of the colony catalog.

It is likely that our finding of a decline in the number of fulmars at sea is correct. We have corrected for

the change in methods for the recording of flying birds, and biases such as ship attraction or detectability are unlikely to have changed over the course of the study period. Using a generation length of 18.8 yr (Jones et al. 2008), the decline extrapolated from our analysis for Pacific fulmars over 3 generations is $(1 - 0.0083)^{3 \times 18.8} \approx 1 - 0.38$. A 38% decline over 3 generations meets the IUCN criteria A2 for 'vulnerable' (IUCN 2001).

Fisheries can be both a source of mortality and a source of food for seabirds such as fulmars. Population declines of some seabird species, especially albatrosses, have been linked to high mortality rates of adult birds as bycatch, especially in longline fisheries (Tuck et al. 2001, Arnold et al. 2006, Delord et al. 2008). Fulmars are the most common seabird species accidentally killed in Alaskan fisheries (Dietrich & Fitzgerald 2010). Our estimate of the at-sea abundance of fulmars confirms that the total number of birds in the population dwarf the number of birds accidentally killed in fisheries, even during the height of fisheries bycatch of fulmars in the late 1990s, when over 16000 fulmars were killed in a single year (Melvin et al. 2004). Bycatch mitigation measures (Melvin & Parrish 2001, Melvin et al. 2001), which have been implemented since the late 1990s and are now mandatory, have been highly successful and have dramatically reduced the number of birds killed (Moore et al. 2009).

Conversely, fishing vessels bring otherwise inaccessible fish to the surface, which can be taken by fulmars when the catch is being hauled up or when

bycatch and offal are being discharged. While no fulmar population is known to rely exclusively on discards or offal, anthropogenic food plays an important role at least in some populations (Phillips et al. 1999). As expected under the hypothesis that discharge should have a positive effect on fulmar populations, a decline in the tonnage of fish caught (Bailey 2000) coincided with the decline of fulmars documented here.

Total fishery catch provides a consistent metric over the decades of food available to scavenging seabirds as long as fishing and especially fish processing methods do not change over time. However, over the 4 decades of this study, political and economic factors have influenced rates, types, and locations of discards and offal discharged into the Bering Sea. Examples include the reorganization of the fishery from largely international to domestic by the Magnuson-Stevenson Act, the rising value of fish as a commodity, and the adoption of ecosystem-based fisheries management.

Estimates by NMFS of fisheries discharge (discards and offal combined) for the largest Bering Sea fishery, the midwater-trawl pollock fishery, are available from 1996 to 2005, during which time discharge declined by about a quarter (A. E. Edwards unpubl. data). The midwater-trawl fishery is highly selective and has a much lower discard rate of entirely-unwanted fish (currently <1%) compared to the pelagic trawl or longline fisheries (>10%). However, the larger catches and considerable at-sea processing facilities of the midwater trawl fishery result in higher total discharge rates of macerated offal, which forms the majority of the fisheries-discharge made available to fulmars in the Bering Sea.

A series of changes to processing standards in the 1990s enabled retention of a greater proportion of each marketable fish, thereby reducing the offal discharge rate, and also increased the proportion of the total catch that was processed on shore. Consequently, the proportion of the catch made available to scavenging fulmars relative to the total fisheries catch of the Bering Sea declined during the late 1990s (A. E. Edwards unpubl. data). However, given that the temporal GAM of the ensemble model resulted in a straight line, we have no strong evidence linking



Fig. 9. Small section of the world's largest fulmar colony at Chagulak Island, Alaska. No quantitative census has ever been conducted on this island, nor has a method been proposed how this could be done. Photo: M. Renner

changes in fishing or processing standards with the change in fulmar populations.

A major climatic regime shift in the North Pacific in the late 1970s is believed to have triggered large-scale changes in the organization of the ecosystem in the Gulf of Alaska (Anderson & Piatt 1999). Considerable changes in the ecosystem of the Bering Sea have been observed on a similar time scale (Trites et al. 2007, Mueter & Litzow 2008). The drop in fish catches with an associated drop in discharge and supplementary food provides an immediate mechanism for changes in fulmar populations. However, we cannot distinguish between this and the possibility that fisheries and fulmars were merely affected by the same underlying changes in the ecosystem.

CONCLUSIONS

By comparing a model of a seabird species' at-sea abundance distribution to observed data, we developed a novel approach for population monitoring. Our analyses suggest that there has been a substantial decline in the numbers of fulmars present at sea in the eastern Bering Sea and Aleutian Islands since the 1970s. Not surprisingly, fisheries play an important, but not the most important, role in shaping the pelagic distribution and abundance of fulmars in the Bering Sea and Aleutian Archipelago. We found that a northward shift in the pelagic distribution of fulmars coincided with changes in the location of fisheries catches. However, we could not determine the relative importance of fisheries or climate-related changes in the food web as factors in the changes in the size of the fulmar population based on at-sea observations.

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