

# SPATIAL AND TEMPORAL TRENDS IN POPULATION SIZE OF COMMON MURRES *URIA AALGE* NESTING IN COASTAL OREGON, 1988–2014

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## ABSTRACT

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Common Murres *Uria aalge* are upper trophic-level consumers and useful indicators of the impacts of anomalous climatic events and other perturbations, such as marine heatwaves, long-term change in ocean ecosystems, and changes in predator populations. We used an existing archive of aerial photographs of murre colonies along the coast of Oregon to expand available data on the number of murres nesting in that portion of the California Current ecosystem during 1988–2014. We completed counts of all murre colonies in Oregon *ca.* every 10 years, developed a stratified random sample of colonies representative of total counts, and completed sample counts *ca.* every three years. We documented a nearly 25% decline in the number of nesting murres in Oregon, with *ca.* 97,000 fewer counted in 2014 compared with 1988. Murre numbers declined by 74% (*ca.* –157,000 murres) along the northern coast of Oregon, increased by 105% (*ca.* +60,000 murres) along the central coast, and were nearly stable along the southern coast. The centroid of the Oregon breeding population shifted 84.4 km to the south during the study period. Most Oregon breeding colonies experienced growth rates that exceeded the maximum intrinsic growth rate and/or new breeding activity, indicating that philopatry was not strong and large numbers of murres immigrated or recruited from other colonies. Frequent shifts in colony sizes strongly implied substantial movement of murres among colonies throughout the study period, including those colonies on the southern coast where total numbers were stable. Predation and disturbance by Bald Eagles *Haliaeetus leucocephalus* are known drivers of higher murre mortality rates and lower reproductive success at colonies on the northern and central coasts. The recovering eagle population along the Oregon coast is likely the main factor causing high movement rates of murres among breeding sites, through the “ecology of fear.”

**Key words:** population trend, breeding distribution, Oregon, *Uria aalge*, Common Murre, breeding dispersal, eagle predation

## INTRODUCTION

Trends in the abundance of seabirds synthesize ecological impacts from long-term change in the marine environment (Parsons et al., 2008; Piatt et al., 2007). Seabird monitoring can be relatively simple and cost-effective, particularly for species that nest conspicuously and colonially. But long-term population trends are more informative as indicators and valuable for the management of ecosystems, because seabirds are long-lived, slow to mature, and produce few young—i.e., they exhibit a *k*-selected life history strategy (Hughes et al., 2017; Piatt et al., 2007). The Common Murre *Uria aalge* is one such species with potential as an indicator of decadal-scale changes in nearshore ocean conditions throughout its breeding range. Common Murres (hereinafter referred to as *murres*) are the most abundant seabird nesting in the state of Oregon and, as upper-trophic-level consumers, have an important influence on marine ecosystems of coastal Oregon (Carter et al., 2001; Naughton et al., 2007; Wiens & Scott, 1975).

As with most seabird species (Dias et al., 2019), murre abundance in Oregon is affected by multiple factors, many of them anthropogenic, including human disturbance, oil spills, fisheries bycatch, changes in prey abundance, climate change, and predation (Carter et al., 2001; Gladics et al., 2015; Hamel et al., 2009; Horton, 2014;

Piatt et al., 2020). The impacts of direct human disturbances, such as recreational kayakers and low-flying aircraft, on murres and other seabirds nesting in Oregon have been documented but not quantified (Carter et al., 2001; Stephensen et al., 2012). Impacts of oil spills on murres nesting in Oregon have been documented as recently as the *New Carissa* oil spill in 1999, estimated to have killed < 200 murres (Ford et al., 2001). Major impacts have been observed from other spills, however, such as the *Nestucca* spill in 1988 and the *Tenyo Maru* spill in 1991, which together killed 34,000–50,000 murres in neighboring Washington state; some portion of the murres killed nested in Oregon (Carter et al., 2001). Gillnetting is a potentially significant source of mortality but not in Oregon waters, where gillnetting is prohibited (Carter et al., 2001). Murres that nest in Oregon are susceptible to bycatch mortality during the non-breeding period in Washington and British Columbia, where gillnetting is legal (Hamel et al., 2009). Available data on other gear types indicate a low rate of fisheries bycatch for murres in Oregon (Jannot et al., 2021).

In recent decades, there have been significant changes in the physical and biotic oceanography of the northern California Current ecosystem, such as strong El Niño/La Niña events, anomalous upwelling events, development of anoxic zones, and marine heatwaves (Auth et al., 2018; Chan et al., 2008; Weber et

al., 2021). Murre populations are influenced by ocean conditions that impact the abundance of their primary prey, which are small schooling fish (Ainley et al., 2021; Erikstad et al., 2013; Renner et al., 2024; Strong & Duarte, 2023). At the Yaquina Head murre colony, on the central Oregon coast, sea surface temperatures, timing of spring transition from downwelling to upwelling, and the Pacific Decadal and North Pacific Gyre Oscillation indices were correlated with changes in the diet of murre chicks. In general, warmer sea surface temperatures have been associated with elevated levels of clupeids in the diet (e.g., Pacific herring *Clupea pallasii*, Pacific sardine *Sardinops sagax*) and lower murre reproductive success. When sea surface temperatures were cooler, the diet was dominated by Pacific sand lance *Ammodytes personatus*, northern anchovy *Engraulis mordax*, and flatfish (pleuronectiforms), and murre reproductive success was higher (Gladics et al., 2014, 2015). Of particular concern is the reduction in survival of murres during the recent marine heatwave of 2014–2016. This heatwave resulted in a major die-off of an estimated four million murres (50%) from the population in the Gulf of Alaska and the Bering Sea during 2015 and 2016 (Renner et al., 2024). Data are not available to assess the impact of this heatwave specifically on the abundance of nesting murres in Oregon, although data from beached bird surveys suggest that a large number of murres died across the California Current ecosystem (60,000–200,000 murres; Piatt et al., 2020). Anthropogenic climate change is predicted to increase the severity and frequency of these anomalous events, and as temperatures rise, the overall productivity of ocean systems will likely decrease (Ainsworth et al., 2011; Bryndum-Buchholz et al., 2019; Frölicher et al., 2018).

Predation pressure on nesting murres by Bald Eagles *Haliaeetus leucocephalus* (hereinafter referred to as *eagles*) and the associated disturbance to murre breeding colonies has been identified as a primary driver of change in the abundance of murres in coastal Oregon (Horton, 2014). The first known record of eagles affecting breeding colonies of murres in coastal Oregon was during the mid-1990s, when the population of eagles nesting along the coast was recovering from an earlier dramatic decline caused by the pesticide DDT (Buehler, 2022; Carter et al., 2001; Horton, 2014). Nesting eagles, while listed under the US Endangered Species Act, increased by an average of 7.3%/year in Oregon from 1978 to 2007 (Isaacs & Anthony, 2011). The statewide population was predicted to continue to increase by as much as 300% after monitoring ceased in 2007, prior to reaching carrying capacity.

Eagles prey on adult murres as well as murre eggs and chicks. Eagles cause nesting murres to flush (i.e., evacuate) from their breeding colonies, allowing secondary predators such as gulls (*Larus* spp.) and corvids (Northern Ravens *Corvus corax* and American Crows *C. brachyrhynchos*) to depredate eggs and chicks (Carter et al., 2001; Horton, 2014). Horton (2014) found that the reproductive success of murres was negatively correlated with the rate at which the Yaquina Head colony on the central Oregon Coast was disturbed by eagles—Yaquina Head being the only nesting site for murres in Oregon in which a multiyear time series (2007–2013) is available. Interestingly, the percentage of the colony that flushed when eagles were present was the best predictor of reproductive loss, highlighting the importance of the “ecology of fear” (Brown et al., 1999; Laundré et al., 2010) on murre reproductive success. Eagles were associated with reduced murre colony attendance, complete murre breeding failure, and delayed nesting phenology at Oregon murre colonies, particularly colonies along the northern and central

portions of the Oregon coast, where eagles were most prevalent (Horton, 2014). Similar impacts to seabird colonies caused by Bald Eagles and other sea eagles in the genus *Haliaeetus* have been noted elsewhere (Anker-Nilssen et al., 2023; Hipfner et al., 2012; Parrish, 1995; Parrish et al., 2001), including the redistribution of breeding murres among colonies within a metapopulation (Hipfner et al., 2012).

Horton (2014) documented an increasing number of active eagle nests along the Oregon coast from 1978 to 2007, with the density of eagle nests being highest along the northern coast, intermediate along the central coast, and lowest along the southern coast. Census counts of breeding murres in Oregon (i.e., complete counts at all nesting colonies) during 1988 and 2006 indicated a decrease along the northern coast, an increase along the central coast, and no trend along the southern coast of Oregon during this 18-year period. The association between changes in regional density of eagle nests and occupancy of murre nesting colonies suggested that murres dispersed from northern Oregon nesting colonies to colonies further south in response to eagle disturbance. During this same period (1988–2006), the number of murres counted at a small subsample of colonies in Oregon was increasing, suggesting that the subsample was not representative of the total breeding population of murres in Oregon. Consequently, Horton was unable to reliably determine the trend in the total Oregon breeding population during 1988–2006. But Horton provided conclusive evidence that breeding murres moved among colony sites by documenting the number of new colonies that formed in the northern and central regions in 2006. No further studies of the temporal or spatial extent of movement by murres among colonies in Oregon have been conducted.

The objectives of our study were, for the period 1988–2014, to (1) determine the total breeding population size of Common Murres in each of three regions of the Oregon coast (northern, central, southern); (2) determine the trend in murre breeding population size for the entire coast of Oregon and within each region of the Oregon coast; and (3) evaluate and compare trends in murre breeding population size at the colony, colony complex, and regional scales as indicators of potential inter-colony movement rates by breeding adult murres.

## METHODS

### Breeding Population Size

The United States Fish and Wildlife Service (USFWS) conducted annual aerial photographic surveys from helicopters of all colonies of surface-nesting seabirds, including murres, along the coastline of Oregon from 46°N (Tillamook Head) to the southern boundary of the state (42°N; 444-km straight line distance) from 1988 to 2014 (Table 1, Fig. 1). A portion of the Oregon coastline, from 46.0°N to 46.25°N (about 28-km straight line distance), was omitted from surveys, because it did not include suitable habitat for murre colonies (i.e., rocky cliffs or islands). Survey data were collected annually for all known historical murre colony sites, and additional effort was made to search suitable habitat and identify newly established murre breeding colonies. Surveys were conducted over two to four days in early to mid-June (03–16 June), coincident with late incubation/early hatching of murres, during daylight hours with no precipitation and winds < 25 knots. During each survey, two passengers took overview and

detailed photographs of the entire colony area from a helicopter at 260–330 m above ground level. Photographs were taken at an oblique angle, using 35-mm film cameras with 100- to 400-mm and 24- to 105-mm lenses through 2008. Digital cameras were used after 2008.

We selected the highest quality photographs for each colony in a particular year. High-quality photographs were ones where murre were distinguishable from each other and the background (and where murre were not blocked by other murre or topographical features) and that could be stitched to other photographs. In 2008 and earlier, we projected 35-mm slides onto a wall lined with paper or whiteboard, marked each murre located on the nesting colony or in the water in the immediate vicinity of the colony with a pen or marker, and enumerated the marks. After 2008, we created mosaics of digital images using Adobe Photoshop or Microsoft Image Composite Editor and imported them to ArcGIS software. We added a point manually for each murre and tallied the points automatically. All counts included the entire colony area. To preserve and archive historical surveys stored on degrading film, approximately 63,000 35-mm slides generated through 2008 were scanned to high-resolution 2,400 dpi digital format (TIFF). We completed counts of colonies from these photographs using the software method described above.

Due to the time-consuming nature of counting colonies, it was not possible to complete counts of all murre at all breeding colonies (total census counts) in all years during the study period. We censused murre breeding colonies in 1994 and 2014 so that, with previously completed census counts, a statewide census was available for 1988, 1994, 2006, and 2014, or roughly at 10-year intervals. We also counted a representative sample of murre colonies nine times at roughly three-year intervals, in 1988, 1994, 1997, 2000, 2003, 2006, 2009, 2012, and 2014.

To select a representative sample of colonies to count at three-year intervals, we initially compiled a list of all colonies that were active during any of the four years when a total census count was conducted ( $n = 101$  colonies). Six additional murre colony locations were not active during any of the four census years and therefore were not included on the list. These excluded colonies had a limited

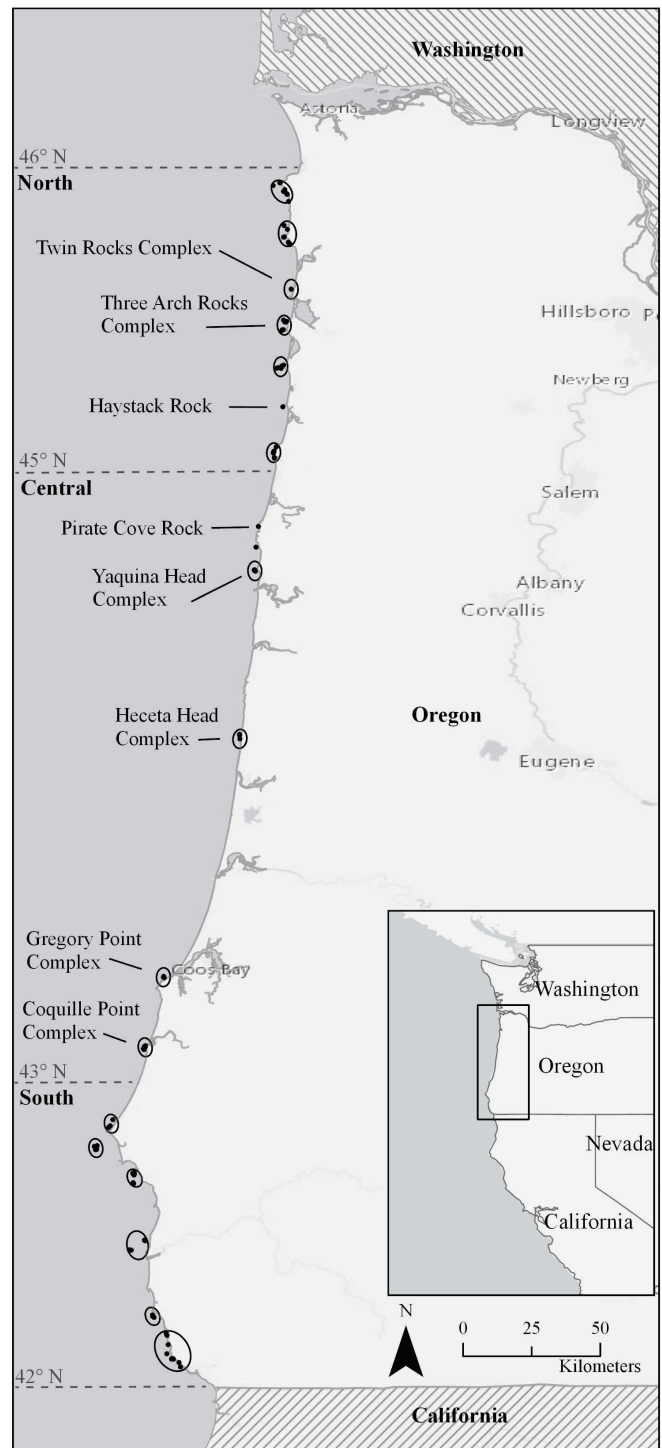
history of the presence of nesting murre during other years, either prior to the study period or a maximum of three years during the study period (range = 3–158 murre per excluded colony). Because

**TABLE 1**  
**Active Common Murre *Uria aalge* breeding colonies**  
**in the state of Oregon, categorized by geographic region**  
**and size class<sup>a</sup> during 1988, 1994, 2006, and 2014<sup>b</sup>**

| Region   | Number of colonies     |                           | Total | Latitudinal boundaries |
|----------|------------------------|---------------------------|-------|------------------------|
|          | Small<br>( $< 3,000$ ) | Large<br>( $\geq 3,000$ ) |       |                        |
| Northern | 29                     | 17                        | 46    | 46°N–45°N              |
| Central  | 13                     | 11                        | 24    | 45°N–43°N              |
| Southern | 17                     | 14                        | 31    | 43°N–42°N              |
| Total    | 59                     | 42                        | 101   | 46°N–42°N              |

<sup>a</sup> The maximum count of murre at each colony during the four census years was used to classify colonies as either small ( $< 3,000$  murre) or large ( $\geq 3,000$  murre).

<sup>b</sup> The four years included are the years when a total census count of murre on breeding colonies was conducted.



**Fig. 1.** Map showing all Common Murre *Uria aalge* breeding colonies along the Oregon coast during 1988–2014. Breeding colonies ( $n = 101$ ) are represented by black dots. Colony complexes ( $n = 16$ ) are represented by open ellipses and include all colonies within 5 km of each other. The coastline was separated into three geographic regions, each with a similar number of large colonies that were  $\geq 3,000$  individuals. Geographic regions (northern, central, and southern) are bounded by latitudinal lines.

new murre colonies became active or were discovered during the study period, the number of colonies increased each census year. As a result, there were colonies active in later years for which photographs were not available in earlier years. We assumed that colonies without photographs were not active during those years. Photographs were available for 80%, 82%, 95%, and 100% of the 101 colonies on the list for the 1988, 1994, 2006, and 2014 census counts, respectively.

We stratified the sample of colonies for counting at three-year intervals by colony size and geographic location, based loosely on an approach described by Bridgeland et al. (2018). We classified colonies by the maximum number of murre counted during a total census year as small (< 3,000 murre) or large ( $\geq$  3,000 murre). We divided the Oregon coastline into three geographic regions (northern, central, and southern), each with roughly the same number of large colonies and with specific boundaries determined by degree of latitude (Table 1, Fig. 1). Regional boundaries differed from those used by Horton (2014). We subsampled the colonies randomly to include nine large and six small colonies from each region (15 colonies per region, 45 colonies total). These same 45 colonies were counted during each year when a subsample of colonies was counted. We used colony designations listed in the Oregon Seabird Colony Catalog (Naughton et al., 2007; i.e., individual rocks, islands, or short stretches of coastline).

Many murre colonies along the coast of Oregon are located in clusters in close proximity to each other. These clusters have been referred to as “colony complexes” (Carter et al., 2001; Naughton et al., 2007), within which nearby colonies are more likely to interact (e.g., murre from an expanding colony form a new colony on an adjacent rock; Carter et al., 2001). We defined colony complexes as all colonies within 5 km of each other. Using this criterion, only three individual colonies of the 101 murre colonies along the Oregon coast were not part of a colony complex. The murre colony complexes used in the present study differed somewhat from those listed in the Oregon Seabird Colony Catalog (Naughton et al., 2007) because we consistently applied the criterion (within 5 km of each other) to identify colony clusters.

### Population Centroid

To describe the overall shift in distribution of nesting murre along the Oregon Coast during the study period, we calculated the geographic centroid of the breeding population of murre (mean colony location weighted by colony size) for each census year. We calculated the centroid based on latitude but excluded longitude given the small longitudinal variation among colonies. Latitude of breeding colonies was obtained from Naughton et al. (2007).

### Indicators of Inter-Colony Movements

We used the formula  $(N_{\text{end}}/N_{\text{start}})^{1/\text{years}}$  to calculate average annual population growth rates between consecutive census counts for each murre colony. We also calculated population growth rates for each colony complex, consisting of two or more colonies in close proximity to each other, so that short-distance movements (< 5 km) among adjacent murre colonies would not be included in growth rate calculations. We assumed the maximum intrinsic growth rate ( $R_{\text{max}}$ ) for Common Murre was 5.5% (Cox et al., 2024) and that annual growth rates in colony size that exceeded 5.5% indicated immigration of murre to a colony or colony complex.

### Statistical Analysis

We assessed trends in statewide and regional population size using the sum of murre counted at the subsample of colonies during 1988–2014. We used quasi-Poisson models to accommodate overdispersion and back-transformed estimates of the percentage change in population size each year. We tested for autocorrelation in standardized counts and standardized residuals for both statewide and regional trend models. For the model of statewide counts, there was autocorrelation of standardized residuals at a two-sample lag in the autocorrelation function plot and correlation test (Box-Ljung test;  $p = .03$ ) that was eliminated with the addition of a single AR(2) term to the regression model. Small sample size prevented us from adding further parameters to address remaining cyclicity of residuals of the model. We found significant autocorrelation of standardized counts at a three-sample lag in the autocorrelation function plot and correlation test (Box-Ljung test;  $p < .001$ ) for the regional trend model. We did not include an autoregressive term in the model, because there was no evidence to suggest a relationship to regional counts (three-sample lag;  $p = .89$ ). Small sample size prevented inclusion of additional parameters in the model. We present descriptive statistics only for census data and data calculated using census data (i.e., growth rates and population centroid) due to small sample size ( $n = 4$ ). All analyses were performed with the R statistical packages “psych,” “MASS,” “dplyr,” and “AICcmodavg” (R Core Team 2024).

### RESULTS

Of the 101 active murre breeding colonies in Oregon during 1988–2014 (Table 1, Fig. 1), most were located within the Oregon Coast National Wildlife Refuge Complex, including Oregon Islands National Wildlife Refuge, Cape Meares National Wildlife Refuge, and Three Arch Rocks National Wildlife Refuge. Two colonies were located on state-owned land at Cape Lookout State Park and Heceta Head Lighthouse State Scenic Viewpoint. Murre nested on both mainland cliffs and rocky islands up to 6.5 km from shore. Nearly half (45.5%) of the 101 murre colonies were located along the northern coast of Oregon, 23.8% along the central coast, and 30.7% along the southern coast.

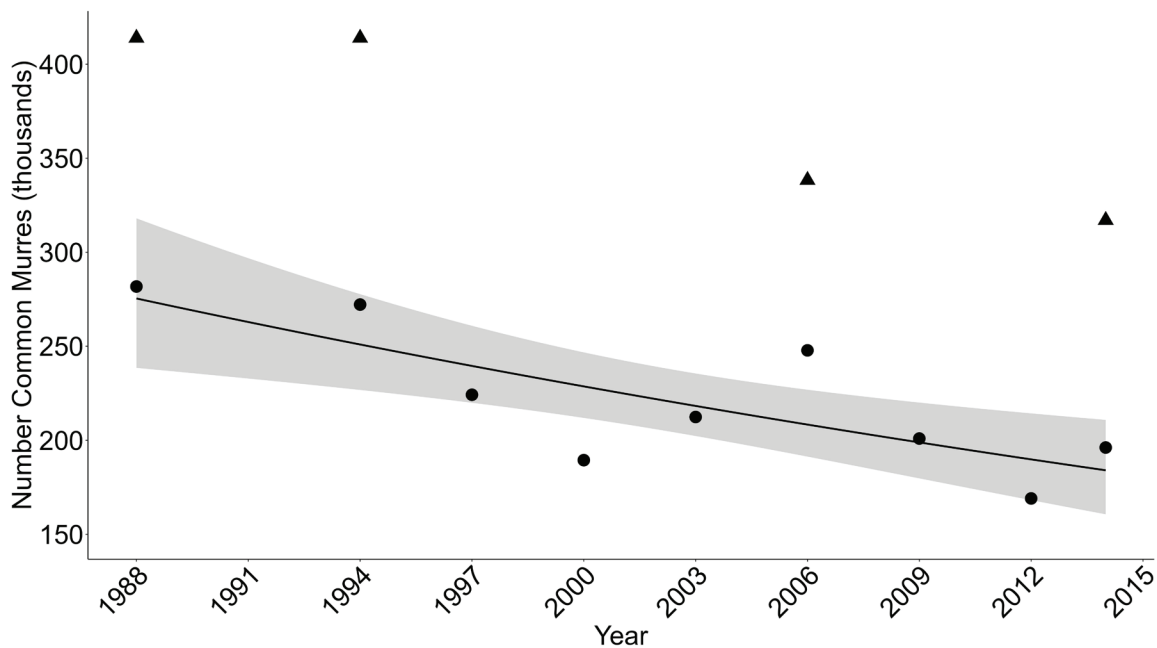
The census count of murre at all colonies in Oregon in 2014 (317,050 murre) was 23.4% lower than the initial census count in 1988 (413,918 murre; Table 2, Fig. 2). The total number of murre in the 45 subsampled breeding colonies declined by 2.25%/year during the same period (95% confidence interval [CI] =  $-1.18\%$  to  $-3.32\%$ ;  $p = .02$ ). The centroid of the censused population shifted southward by 87.5 km ( $0.7869^\circ$  latitude) between 1988 and 2014 (Fig. 3). The mean centroid latitude for all colonies was  $44.0441^\circ\text{N}$  during 1988–2006 and  $43.4600^\circ\text{N}$  during 2009–2014.

From 1988 to 2014, the number of murre counted at colonies along the northern coast of Oregon declined by 73.6% ( $-156,569$  murre), while the number of murre counted at colonies along the central coast increased by 104.5% ( $+60,264$  murre; Table 2, Fig. 4). The number of murre counted at colonies along the southern coast declined by only 0.4% ( $-563$  murre), indicating a nearly stable breeding population. The number of murre counted at the 15 subsampled colonies along the northern coast declined by 6.55%/year during 1988–2014 (95% CI =  $-4.68\%$  to  $-8.42\%$  per year;  $p < .001$ ). The number counted at the 15 subsampled colonies along the central coast increased by 3.35%/year (95% CI =  $1.18\%$

**TABLE 2**  
The number of Common Murres *Uria aalge* counted at breeding colonies within each of three regions along the coast of Oregon during 1988–2014<sup>a</sup>

| Year | Total census |         |          |         | Subsample |         |          |         |
|------|--------------|---------|----------|---------|-----------|---------|----------|---------|
|      | Northern     | Central | Southern | Total   | Northern  | Central | Southern | Total   |
| 1988 | 212,676      | 57,659  | 143,583  | 413,918 | 135,614   | 37,256  | 108,912  | 281,782 |
| 1994 | 172,003      | 66,112  | 175,818  | 413,933 | 102,795   | 40,103  | 129,277  | 272,175 |
| 1997 | –            | –       | –        | –       | 107,014   | 31,396  | 85,808   | 224,218 |
| 2000 | –            | –       | –        | –       | 60,797    | 49,452  | 79,188   | 189,437 |
| 2003 | –            | –       | –        | –       | 66,079    | 58,213  | 88,095   | 212,387 |
| 2006 | 107,814      | 107,880 | 122,656  | 338,350 | 77,055    | 76,767  | 94,003   | 247,825 |
| 2009 | –            | –       | –        | –       | 16,819    | 80,383  | 103,728  | 200,930 |
| 2012 | –            | –       | –        | –       | 10,395    | 67,225  | 91,457   | 169,077 |
| 2014 | 56,107       | 117,923 | 143,020  | 317,050 | 29,765    | 73,835  | 92,547   | 196,147 |

<sup>a</sup> Census counts (i.e., counts of every colony) were completed in each of four years during the study period (1988, 1994, 2006, and 2014). A subsample of colonies was counted in each of the nine years listed between 1988 and 2014.



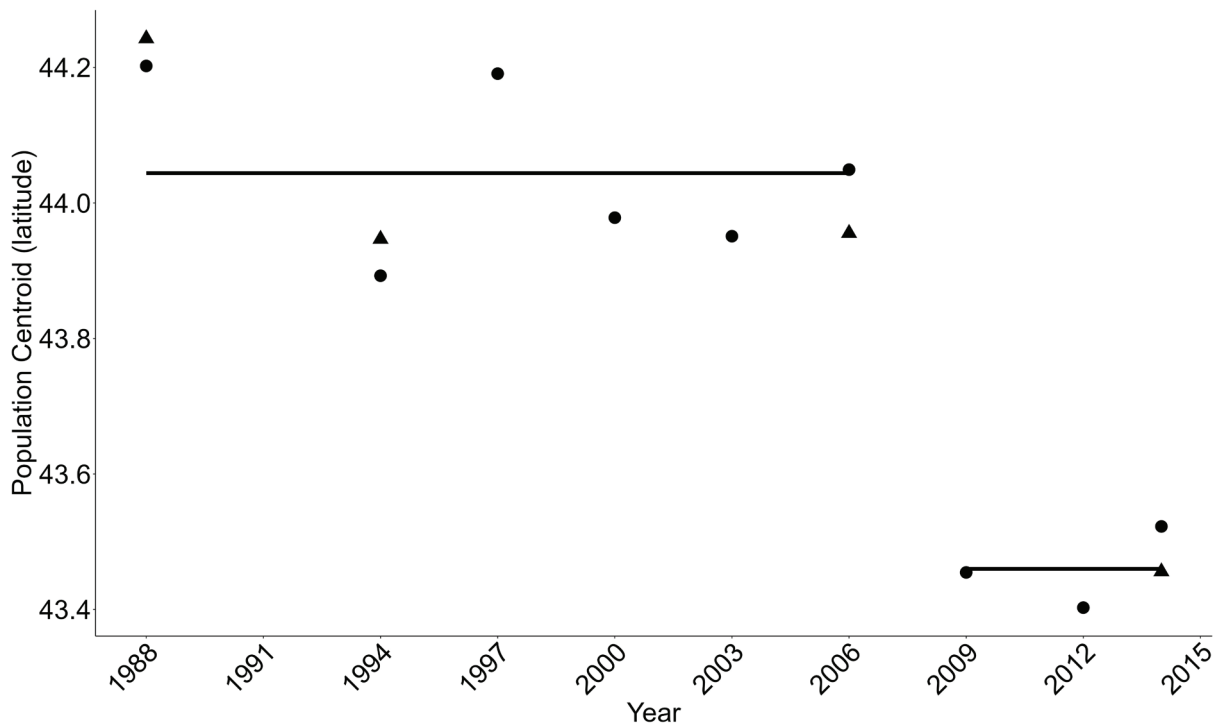
**Fig. 2.** The total number of Common Murres *Uria aalge* counted at all active breeding colonies in Oregon during four census years (filled triangles), and the number of murres counted at 45 subsampled colonies along the Oregon coast (filled circles) during 1988–2014. The line represents a fitted linear trend, and the shaded area represents the 95% confidence interval of the trend line. A trend line and 95% confidence interval were not calculated for the statewide census counts due to small sample size ( $n = 4$ ).

to 5.85% per year;  $p = .008$ ). There was no significant trend in numbers of murres nesting at the 15 subsampled colonies along the southern coast ( $p = .40$ ) during the study period.

The number of active murre breeding colonies along the Oregon Coast varied among the four years when a total census count was conducted, with 60%–71% of the 101 total colony locations active during a given census (Table 3). Trends in the number of active colonies mirrored trends in the number of murres counted, with a decrease in the number of active colonies along the northern coast, an increase along the central coast, and stable numbers along the

southern coast. Fourteen of the 45 colonies within our subsample first became active after the study began in 1988. Of these 14 incipient colonies, three were located along the northern coast and were small ( $< 3,000$  murres). Six small and five large colonies ( $\geq 3,000$  murres) became established along the central coast during the study period.

The average annual population growth rate exceeded  $R_{\max}$  at 35 colonies (35%) between consecutive censuses at least once during the study period: 11 of 46 colonies (24%) along the northern coast, 11 of 24 colonies (46%) along the central coast,

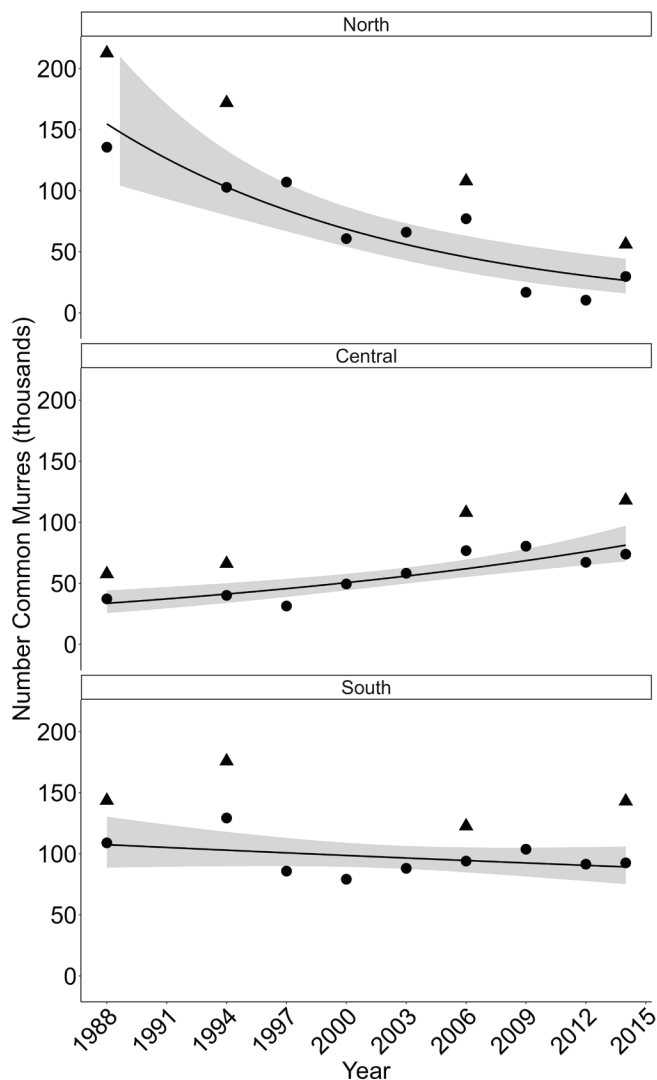


**Fig. 3.** The centroid of Common Murres *Uria aalge* counted at all breeding colonies along the Oregon coast during four census years (filled triangles) and of murres counted at 45 subsampled colonies (filled circles) between 1988 and 2014. Lines represent the average population centroid during 1988–2006 and during 2009–2014.

and 13 of 31 colonies (42%) along the southern coast (Table 4). The greatest average population growth rate for a colony during the study period was 64%/year between the 1994 and 2006 total censuses at the Heceta Head South colony at Heceta Head along the central coast, which resulted from an increase of 1,112 murres. The largest change in number of murres between census counts at a single colony also occurred along the central coast between 1994 and 2006, an increase of 27,696 murres at the Colony Rock colony at Yaquina Head, with an average growth rate of 10%/year. Murres nested at 42 different colonies during the 1994, 2006, and/or 2014 census counts that were inactive during the previous census count, indicating the formation of a new colony or recolonization (hereinafter referred to as new colony formation): 20 new colonies (43% of all northern coast colonies) formed along the northern coast, 19 new colonies (79%) formed along the central coast, and three new colonies (10%) formed along the southern coast (Table 4). The largest count of murres at a colony that was inactive during a previous census count was at the Table Rock colony at Coquille Point along the central coast, where 5,392 murres were counted in 2014. Over the course of the study, 67 of all 101 murre colonies in Oregon (66%) experienced either a growth rate that exceeded  $R_{\max}$  or the formation of a new breeding colony that was not present during the previous census count, or both. The number of colonies with high growth rates and/or new colony formation shifted from primarily the northern and central coastlines of the state in 1994 to mostly the central and southern coastlines of the state by 2014.

Ninety-eight of the 101 active murre colonies in Oregon during 1988–2014 were located within 5 km of other active murre colonies and, therefore, were part of a colony complex (Table 5, Fig. 1), whereas just three murre colonies were more isolated and not part

of a colony complex. Out of a total of 16 murre colony complexes in Oregon during the study period, five complexes included two to four murre colonies each, seven included five to seven murre colonies each, and four included nine to 12 murre colonies each. Three of the 16 colony complexes first became active after the study began: one along the northern coast (Twin Rocks colony complex) and two along the central coast (Heceta Head and Gregory Point colony complexes). The first record of murres breeding at two of the three isolated colonies occurred during the study period: one along the northern coast (Haystack Rock) and one along the central coast (Pirate Cove Rock). Six of the 19 colony complexes and isolated colonies (32%) experienced average annual population growth rates that exceeded  $R_{\max}$  (+5.5% per annum; Cox et al., 2024) during at least one time period between total censuses: two along the northern coast, three along the central coast, and one along the southern coast of Oregon (Table 6). The greatest average annual population growth rate at a colony complex or isolated colony was 63% at the Heceta Head colony complex along the central coast, which increased by 2,374 individuals between 1994 and 2006. The largest change in number of murres at a colony complex or isolated colony was +40,419 at the Yaquina Head colony complex between 1994 and 2006 (average annual growth rate = 12%). Colony complexes and isolated colonies were not all consistently active throughout the study period. During the 1994, 2006, and 2014 census counts, nesting murres were counted at five colony complexes or isolated colonies (26%) where no murre nesting activity had occurred during the previous census survey, providing more support for high movement rates among colony complexes by breeding adults. Counts of murres at these new colony complexes and isolated colonies were relatively small, with a maximum of 1,548 murres counted at the Pirate Cove Rock colony on the central



**Fig. 4.** Trends in the numbers of Common Murres *Uria aalge* counted at Oregon breeding colonies during 1988–2014. Count data for all colonies in each of four census years (filled triangles), as well as 15 subsampled colonies per region in nine years (filled circles), are presented for the northern (top panel), central (center panel), and southern (bottom panel) regions of the Oregon coast. Lines represent fitted curvilinear trends, and shaded areas represent 95% confidence intervals of those trends. A trend line and 95% confidence intervals were not calculated for total census counts due to small sample size ( $n = 4$ ).

Oregon coast in 2014, the first record of nesting at this location. The colony complexes and isolated colonies with population growth rates exceeding  $R_{\max}$  or where new colony complexes formed were primarily located along the northern coast in 1994 but shifted largely to the southern coast by 2014.

The Three Arch Rocks/Cape Meares colony complex was the largest in Oregon during the study period; it included three large colonies within Three Arch Rocks National Wildlife Refuge and another two large colonies plus two small colonies in Cape Meares National Wildlife Refuge. We counted 132,066 murres at this colony complex in 1988 and 42,602 murres in 2014, a decrease of 89,464 murres (Fig. 5, Table 5). This represents 92.4% of the overall

decline in numbers of murres breeding in Oregon between 1988 and 2014. In contrast, the Yaquina Head colony complex, about 90 km further south, nearly quadrupled in size during 1988–2006, to a maximum of 55,519 murres (the second-largest colony complex in Oregon in 2006), but decreased by 43% by 2014. The number of murres counted at the Coquille Point colony complex, about 260 km to the south of the Three Arch Rocks/Cape Meares colony complex, increased by about 250% during the study period to a maximum of 74,080 murres, making it the largest colony complex along the Oregon coast by 2014 (Fig. 5, Table 5).

## DISCUSSION

We confirmed that changes in the size and distribution of murre breeding colonies in the three regions of the Oregon coast first described by Horton (2014) were indicative of population trends, and that those trends continued after 2006, the end of her study period. We found new and compelling evidence that there were substantial movements of breeding murres among colonies, among colony complexes, and between regions along the Oregon coast during 1988–2014. Population growth rates and new breeding activity at the colony and colony-complex levels indicate that movement rates of murres among colonies within colony complexes were greater than movement rates between colony complexes. This difference was expected given the greater distances between colony complexes compared with distances between colonies within a colony complex. Two-thirds of all colony sites and one-third of all colony complexes had average annual colony growth rates exceeding the maximum intrinsic rate of increase ( $R_{\max}$ ). These high colony growth rates—and a relatively high rate of new breeding colony formation—indicate that movement rates of breeding murres among colonies and colony complexes were extremely high for a seabird species that is generally considered philopatric (Ainley et al., 2021). In the absence of mark-recapture data, however, we cannot estimate murre movement rates between colonies in a complex, between colony complexes within the same region, between colony complexes in adjacent regions of the Oregon coast, or between Oregon and other states. Because the breeding population of murres was nearly stable along the southern coast of Oregon during 1988–2014, we were surprised to detect colonies and colony complexes with average annual growth rates greater than  $R_{\max}$  in this region and that the overall number of colonies and colony complexes with high growth rates was similar to the northern and central regions. Large changes in the numbers of murres counted at the three largest colony complexes in Oregon illustrate the southward shift in population centroid in Oregon between 1988–2006 and 2014 (Fig. 5). The patterns of population change among these three colony complexes are consistent with Horton's (2014) hypothesis that large numbers of murres dispersed from colonies along the northern coast to colonies further south through time.

Maximum intrinsic population growth rate in a closed system ( $R_{\max}$ ) for Common Murres under ideal conditions is estimated to be 5.5%/year (90% CI: 3.8%–6.9%) assuming 44% survival to breeding age, 97% annual adult survival, and productivity of 0.69 chicks/breeding pair (Cox et al., 2024). These survival and productivity values are comparable to maximum estimates reported for populations in the California Current ecosystem (Lee et al., 2008; Porquez et al., 2021; Sarzo et al., 2019). Much lower survival and productivity have been reported for murres in the California Current ecosystem when conditions were not favorable. For example, Parrish et al. (2001) observed eagles depredating up to 2% of adult murres nesting on

**TABLE 3**  
**The number of active Common Murre *Uria aalge* breeding colonies along the Oregon Coast during 1988–2014<sup>a</sup>**

| Year | Total census |         |          |       | Subsample |         |          |       |
|------|--------------|---------|----------|-------|-----------|---------|----------|-------|
|      | Northern     | Central | Southern | Total | Northern  | Central | Southern | Total |
| 1988 | 28           | 5       | 28       | 61    | 12        | 4       | 15       | 31    |
| 1994 | 30           | 12      | 28       | 70    | 12        | 9       | 15       | 36    |
| 1997 | –            | –       | –        | –     | 12        | 9       | 14       | 35    |
| 2000 | –            | –       | –        | –     | 13        | 9       | 15       | 37    |
| 2003 | –            | –       | –        | –     | 11        | 8       | 15       | 34    |
| 2006 | 28           | 17      | 27       | 72    | 11        | 11      | 15       | 37    |
| 2009 | –            | –       | –        | –     | 8         | 11      | 15       | 34    |
| 2012 | –            | –       | –        | –     | 10        | 12      | 15       | 37    |
| 2014 | 23           | 18      | 28       | 69    | 8         | 11      | 14       | 33    |

<sup>a</sup> All breeding colonies were censused in 1988, 1994, 2006, and 2014. A subsample of colonies was counted in each of the nine years listed between 1988 and 2014.

Tatoosh Island in Washington during a breeding season. In Oregon, mean nesting success at Yaquina Head declined from 0.69 chicks/pair during 2007–2010 to 0.23 chicks/pair during 2011–2014, apparently due to increasing eagle disturbance and predation. In four of the following seven years, there was an unprecedented near

or complete nesting failure apparently due, at least in part, to eagle disturbance (Porquez et al., 2021).

The observed change in the distribution of the murre breeding population in Oregon during the study period was likely the

**TABLE 4**  
**The numbers and proportions of Common Murre *Uria aalge* breeding colonies in Oregon with high average annual population growth rates or detection of new colony formation during 1988–2014<sup>a</sup>**

| Period <sup>b</sup>    | Region <sup>c</sup> | High growth rate |         | New colony formation |         | Total <sup>d</sup> |         |
|------------------------|---------------------|------------------|---------|----------------------|---------|--------------------|---------|
|                        |                     | Number           | Percent | Number               | Percent | Number             | Percent |
| 1988–1994              | Northern            | 5                | 11%     | 4                    | 9%      | 9                  | 20%     |
|                        | Central             | 1                | 4%      | 7                    | 29%     | 8                  | 33%     |
|                        | Southern            | 4                | 13%     | 1                    | 3%      | 5                  | 16%     |
|                        | Total               | 10               | 10%     | 12                   | 12%     | 22                 | 22%     |
| 1994–2006              | Northern            | 8                | 17%     | 9                    | 20%     | 17                 | 37%     |
|                        | Central             | 7                | 29%     | 7                    | 29%     | 14                 | 58%     |
|                        | Southern            | 2                | 6%      | 0                    | 0%      | 2                  | 6%      |
|                        | Total               | 17               | 17%     | 16                   | 16%     | 33                 | 33%     |
| 2006–2014              | Northern            | 0                | 0%      | 8                    | 17%     | 8                  | 17%     |
|                        | Central             | 4                | 17%     | 6                    | 25%     | 10                 | 42%     |
|                        | Southern            | 10               | 32%     | 2                    | 6%      | 12                 | 39%     |
|                        | Total               | 14               | 14%     | 16                   | 16%     | 30                 | 30%     |
| Overall<br>(1988–2014) | Northern            | 11               | 24%     | 20                   | 43%     | 30                 | 65%     |
|                        | Central             | 11               | 46%     | 19                   | 79%     | 21                 | 88%     |
|                        | Southern            | 13               | 42%     | 3                    | 10%     | 16                 | 52%     |
|                        | Total               | 35               | 35%     | 42                   | 42%     | 67                 | 66%     |

<sup>a</sup> Colonies where average annual population growth rates exceeded  $R_{\max}$  (+5.5%) are included under “high growth rate”; colonies where a newly formed colony or recolonization was detected are included under “new colony formation.”

<sup>b</sup> The 27-year study period was separated into three shorter periods bounded by the years of the statewide census counts of all murre colonies.

<sup>c</sup> Murre colonies were separated into three regions of the Oregon coast: northern, central, and southern.

<sup>d</sup> “Total” includes breeding colonies with “high growth rate,” “new colony formation,” or both.

**TABLE 5**  
**The number of Common Murres *Uria aalge* counted at all breeding colonies in Oregon in 1988, 1994, 2006, and 2014<sup>a</sup>**

| Region   | Colony complex                    | Average latitude<br>(°N) | Census year |        |        |        |
|----------|-----------------------------------|--------------------------|-------------|--------|--------|--------|
|          |                                   |                          | 1988        | 1994   | 2006   | 2014   |
| Northern | Tillamook Head to Haystack Rock   | 45.921810                | 35,164      | 33,363 | 27,259 | 4,337  |
|          | Castle Rock to Cape Falcon        | 45.761574                | 10,859      | 9,672  | 2,350  | 2,061  |
|          | Twin Rocks                        | 45.597246                | 0           | 4      | 150    | 128    |
|          | Three Arch Rocks and Cape Meares  | 45.479435                | 132,066     | 93,727 | 65,873 | 42,602 |
|          | Cape Lookout                      | 45.341945                | 9,801       | 8,744  | 7,450  | 5,200  |
|          | Haystack Rock <sup>b</sup>        | 45.211794                | 0           | 28     | 291    | 124    |
|          | Cascade Head                      | 45.061201                | 24,786      | 26,465 | 4,441  | 1,655  |
| Central  | Pirate Cove Rock <sup>b</sup>     | 44.819627                | 0           | 0      | 0      | 1,548  |
|          | Gull Rock <sup>b</sup>            | 44.751837                | 13,730      | 11,278 | 0      | 0      |
|          | Yaquina Head                      | 44.675829                | 14,134      | 15,100 | 55,519 | 31,132 |
|          | Heceta Head                       | 44.133979                | 0           | 7      | 2,381  | 3,555  |
|          | Gregory Point                     | 43.343060                | 0           | 0      | 1,438  | 7,608  |
|          | Coquille Point                    | 43.112719                | 29,795      | 39,727 | 48,542 | 74,080 |
| Southern | Cape Blanco North                 | 42.860899                | 25,068      | 25,810 | 21,915 | 19,866 |
|          | Orford Reef                       | 42.783537                | 22,702      | 24,076 | 25,983 | 31,589 |
|          | Redfish Rocks                     | 42.690020                | 28,227      | 38,288 | 22,653 | 30,629 |
|          | Hubbard Mound to Rogue River Reef | 42.464635                | 17,520      | 21,555 | 15,880 | 16,093 |
|          | Mack Reef                         | 42.231840                | 14,210      | 21,753 | 15,569 | 26,020 |
|          | Thomas Point to Goat Island       | 42.112720                | 35,856      | 44,336 | 20,656 | 18,823 |

<sup>a</sup> Colonies were grouped into 16 colony complexes (i.e., all colonies within 5 km of each other); three colonies were isolated and not part of a colony complex. The location of each complex is indicated by the average latitude of colonies within each colony complex.

<sup>b</sup> Isolated colony with no murre colony within 5 km.

result of the dramatic increase in numbers of Bald Eagles, especially along the northern coast (Isaacs & Anthony, 2011), as has been demonstrated elsewhere in the California Current ecosystem (Hipfner et al., 2012; Parrish et al., 2001). Murres move to new nesting locations in response to repeated, focused disturbance by eagles at a particular colony or colony complex (Parrish et al., 2001). Horton (2014) concluded that eagles were having a major impact on reproductive success of murres, as well as the number and size of murre colonies, along much of the Oregon coast. Disturbance of murre colonies by eagles and predation events by eagles and secondary predators such as gulls caused complete reproductive failure at the Pillar Rock colony in the Three Arch Rocks/Cape Meares colony complex along the northern coast of Oregon in 2012 (Horton, 2014). Consistent with this observation, we found anecdotal evidence that Bald Eagles were responsible for the major decline in numbers of murres breeding throughout the Three Arch Rocks/Cape Meares colony complex, historically the largest murre colony complex within the California Current ecosystem (Carter et al., 2001). We identified two to four eagles in aerial photographs of the two colonies that were counted within this complex in each of 2009, 2012, and 2014.

Eagles are recognized as the primary factor influencing reproductive success of murres at the Yaquina Head colony complex, the largest colony complex in the central coast region (Weber et al., 2021).

However, murre diet composition has also been monitored at this colony complex, and annual variation in murre diets has been shown to influence murre reproductive success (Gladics et al., 2015), suggesting that bottom-up forces also influence murre productivity at this location (Lyons, 2022; Weber et al., 2021). Evidence from Tatoosh Island in Washington suggests that both eagles and ocean conditions influence the distribution and size of murre colonies. Predation and disturbance of murres by eagles was the main driver of population dynamics at this location (Parrish et al., 2001). During anomalously warm years, however, ocean conditions, rather than eagle predation and disturbance, drove reproductive success and colony attendance of murres (Parrish et al., 2001). Environmental conditions also influenced colonization and persistence of new nesting areas within the Tatoosh Island colony complex (Zador et al., 2009). Our study ended in 2014, the same year that an unprecedented marine heatwave was first detected in the northeastern Pacific (Piatt et al., 2020). The influence of climate and ocean conditions on the breeding population of murres in Oregon will become more apparent when murre census data are available from the decade after the present study period.

The available data are too limited to determine the relative importance of eagle disturbance and ocean conditions as drivers of the decline in the Oregon breeding population of murres during 1988–2014. Emigration to colonies in northern California and, to a lesser extent,

TABLE 6

The numbers and proportions of Common Murre *Uria aalge* breeding colony complexes or isolated colonies<sup>a</sup> in Oregon with high average annual population growth rates or detection of new colony complexes during 1988–2014<sup>b</sup>

| Period <sup>c</sup>    | Region <sup>d</sup> | High growth rate |         | New colony complex formation |         | Total <sup>e</sup> |         |
|------------------------|---------------------|------------------|---------|------------------------------|---------|--------------------|---------|
|                        |                     | Number           | Percent | Number                       | Percent | Number             | Percent |
| 1988–1994              | Northern            | 0                | 0%      | 2                            | 29%     | 2                  | 29%     |
|                        | Central             | 0                | 0%      | 1                            | 17%     | 1                  | 17%     |
|                        | Southern            | 1                | 17%     | 0                            | 0%      | 1                  | 17%     |
|                        | Total               | 1                | 5%      | 3                            | 16%     | 4                  | 21%     |
| 1994–2006              | Northern            | 2                | 29%     | 0                            | 0%      | 2                  | 29%     |
|                        | Central             | 2                | 33%     | 1                            | 17%     | 3                  | 50%     |
|                        | Southern            | 0                | 0%      | 0                            | 0%      | 0                  | 0%      |
|                        | Total               | 4                | 21%     | 1                            | 5%      | 5                  | 26%     |
| 2006–2014              | Northern            | 0                | 0%      | 0                            | 0%      | 0                  | 0%      |
|                        | Central             | 1                | 17%     | 1                            | 17%     | 2                  | 33%     |
|                        | Southern            | 1                | 17%     | 0                            | 0%      | 1                  | 17%     |
|                        | Total               | 2                | 11%     | 1                            | 5%      | 3                  | 16%     |
| Overall<br>(1988–2014) | Northern            | 2                | 29%     | 2                            | 29%     | 2                  | 29%     |
|                        | Central             | 3                | 50%     | 3                            | 50%     | 4                  | 67%     |
|                        | Southern            | 1                | 17%     | 0                            | 0%      | 1                  | 17%     |
|                        | Total               | 6                | 32%     | 5                            | 26%     | 7                  | 37%     |

<sup>a</sup> Breeding colony complexes include colonies within 5 km of each other, while isolated colonies are those with no other murre colonies within 5 km.

<sup>b</sup> Colonies where average annual population growth rates exceeded  $R_{\max}$  (+5.5%) are included under “high growth rate”; colony complexes where a newly formed colony complex or recolonization was detected are included under “new colony complex formation.”

<sup>c</sup> The 27-year study period was separated into three shorter periods bounded by the years of the statewide census counts of all murre colonies in Oregon.

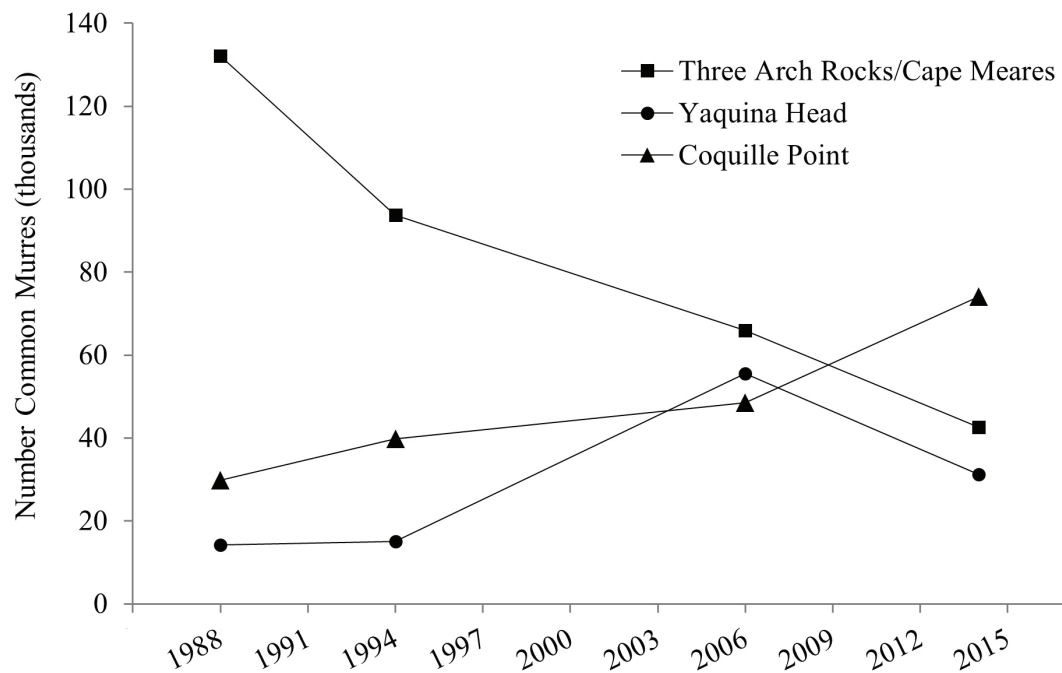
<sup>d</sup> Murre colony complexes were separated into three regions of the Oregon coast: northern, central, and southern.

<sup>e</sup> “Total” includes colony complexes with “high growth rate,” “new colony formation,” or both.

northern Washington is one plausible explanation for the decline in Oregon, given the high apparent movement rates among colonies and colony complexes in Oregon. The dramatic increases in size of murre breeding colonies along the northern and central coasts of California imply high rates of immigration that may reflect better foraging conditions for murre in that part of the California Current ecosystem. But declines in survival, productivity, and recruitment at murre breeding colonies in Oregon, especially northern Oregon, due to eagles are also a reasonable explanation. Murres are characterized by low productivity, low post-fledging survival, and delayed maturity (Ainley et al., 2021). Consequently, small decreases in adult survival rates and, to a lesser extent, juvenile survival rates can have an outsized impact on population trends (Lee et al., 2008; Meade et al., 2013; Sarzo et al., 2019). While there were no large-scale mortality events due to starvation or oil spills that could explain the decline in the murre breeding population along the northern coast of Oregon during the study period (Jones et al., 2024), the dramatic increase in the density of nesting eagles during 1988–2007 was noteworthy (Isaacs & Anthony, 2011).

At the start of our study period (1988–1989), there were more than 400,000 murres counted at all colonies along the coast of Oregon,

approximately two-thirds of the total breeding population of murres within the California Current ecosystem (Carter et al., 2001). By 2014, Oregon was no longer where most murres in the California Current population nested, because about 100,000 fewer murres were counted throughout Oregon compared with 1988/89. During this same period, murre colonies along the northern and central coasts of California grew by about 336,000 murres and 400,000 murres, respectively (Ainley et al., 2021; Barton et al., 2017; Capitolo et al., 2006). The estimated annual growth rates of some murre colonies in northern California were as high as 82%, indicating that many murres immigrated to these colonies (Barton et al., 2017). In Washington state, the breeding population of murres increased by about 15,000 individuals and shifted toward the northern coast of Washington from 1996 to 2015 (Ainley et al., 2021; Thomas & Lyons, 2017). The increases in numbers of breeding murres from the early 1990s to 2014–2015 in northern and central California and in northern Washington represent, at least partly, recovery from prior oil spills, fisheries bycatch, and El Niño events (Ainley et al., 2021; Carter et al., 2001; Thomas & Lyons, 2017). The only regional murre population declines in the California Current ecosystem during this period occurred along the southern Washington coast (Thomas & Lyons, 2017) and along the northern Oregon coast.



**Fig. 5.** The total number of Common Murres *Uria aalge* counted at the three largest colony complexes along the Oregon coast during 1988–2014. Colony complexes include all colonies within 5 km of each other. The Three Arch Rocks/Cape Meares colony complex is in the northern region, the Yaquina Head colony complex is in the central region, and the Coquille Point colony complex is near the southern boundary of the central region.

This study used a randomized subsample of breeding colonies stratified by colony size and geographic location based on Bridgeland et al. (2018). The colonies subsampled in previous studies were selected subjectively to be representative of the available nesting habitat, but the largest colonies were excluded from the subsample because it was too time consuming to count these colonies (Carter et al., 2001). This earlier approach failed to yield a representative sample of the total murre breeding population in Oregon over time (Horton, 2014). Our subsample of colonies adequately represented the statewide and regional trends of census counts of all colonies. The accuracy of the current study was likely improved by an increase in the proportion of the total population sampled. For example, the current study's subsample of murre colonies counted in 1988 includes 68% of the total number of murres censused in 1988, whereas the earlier study's sample included just 14% of the total number of murres counted in 1988 (Carter et al., 2001).

We did not use a correction factor to account for breeding individuals away from the colony at the time of the survey. Although a correction factor has been calculated for multiple colonies in California (Ainley et al., 2021; Warzybok et al., 2018), it is unlikely to be appropriate for all colonies in Oregon over the study period given the variable dynamics influencing colony attendance (Carter et al., 2001; Harris et al., 2015). Instead, we used direct counts of murres attending colonies to assess population trends. If we apply the California correction factor  $k = 1.67$  to the total census counts in Oregon for comparison (Ainley et al., 2021; Carter et al., 2001; Thomas & Lyons, 2017), we produce rough estimates of the total Oregon breeding population size of 691,243 murres in 1988, 691,268 in 1994, 565,048 in 2006, and 529,475 in 2014. Our estimate of the total number of breeding murres in Oregon in 1988 is approximately 3% lower than that reported by Carter et al. (2001), because we relied solely on aerial survey counts and did

not include boat-based counts. Our specific results are not directly comparable with the estimates provided by Ainley et al. (2021) due to differing methods; Ainley et al. (2021) estimated there were 628,708 murres nesting in Oregon in 2009.

An investigation into the metapopulation dynamics of murres throughout the California Current ecosystem is key to our ability to distinguish between population declines and dispersal/redistribution of the breeding population. We recommend that future census counts of all breeding colonies of murres along the coast of Oregon be synchronized with similar efforts in Washington and California, as they were in 1988/89 and in 2014/15. This is of particular importance given the potential for movement of murres among colonies across state boundaries within the California Current ecosystem. The high inter-colony and interregional movement rates of nesting murres found by this study demonstrate that periodic (i.e., every 10 years) statewide census counts of breeding murres at all colonies are critical to confirm population trends from counts of a subsample of colonies. Because this study only analyzed the available data on murre colony sizes through 2014, any potential impacts of the 2014–2016 marine heatwave in the northeastern Pacific on murre population trends in Oregon are unknown. Counts of Oregon murre colonies from aerial photographs taken after 2014 would reveal whether the heatwave caused a major die-off of murres nesting in Oregon, as it did for murres nesting in the northern Gulf of Alaska and the Bering Sea (Renner et al., 2024). Given the frequent movement of murres among colonies, protection of historical colony sites is advisable to allow murres to respond to variable conditions across years.

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## AUTHOR CONTRIBUTIONS

KSB: Conceptualization (equal), methodology (equal), investigation (lead), formal analysis, writing—original draft preparation, writing—review and editing (lead). JP: Conceptualization (equal), methodology (equal), investigation (support), writing—review and editing (support). RS: Funding acquisition (lead), conceptualization (equal), methodology (equal), writing—review and editing (support). SS: Funding acquisition (support), conceptualization (equal), writing—review and editing (support), methodology (equal). DEL: Conceptualization (equal), methodology (equal), investigation (support), writing—review and editing (support).

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