

## DIRECT AND INDIRECT EFFECTS: INTERACTIONS BETWEEN BALD EAGLES AND COMMON MURRES

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**Abstract.** We have studied the changing demography of a colonial seabird, the Common Murre, *Uria aalge*, at a single site on the Washington coast. Whereas informal estimates suggest a steep population increase at Tatoosh Island from ~1975 to 1990, more rigorous censuses from 1991–1999 indicate that the population has subsequently declined at a rate of ~3% per year. The primary factor causing this decline appears to be increasing numbers of Bald Eagles, *Haliaeetus leucocephalus*, visiting the site, where eagles inflict both direct mortality due to eagle predation on adult murre and indirect mortality due to eagle facilitation of gull and crow predation on murre eggs. To explore the contribution of eagles to the observed population decline, we used age-specific vital rates drawn from the literature to develop a wide range of plausible models of murre demography. We found that the match between the projected and observed murre numbers is generally much improved by the inclusion of eagle effects. Our study highlights three general challenges to conservation and management practitioners. First, the difficulty of multispecies management may be exacerbated by successful restoration of high-trophic-level consumers, such as eagles, which may generate subsequent declines in their prey species. Second, indirect effects are usually subtle and often difficult to observe but, as in this case, may contribute substantially to the decline of focal species. Finally, when viewed in the context of the balance between local production and mortality, population trends are difficult to interpret without an explicit understanding of immigration/emigration rates and patterns.

**Key words:** Bald Eagle; Common Murre; *Haliaeetus leucocephalus*; indirect effects; multispecies; predation; reproductive success; survivorship; Tatoosh Island, Washington (USA); *Uria aalge*.

### INTRODUCTION

Conservation attention has focused primarily on individual species with declining populations, and only secondarily on the broader ecological consequences of changing population size. However, no species lives in isolation; each is imbedded in a matrix of interactions, and it is these interactions that often determine a species' survival. As the number of threatened species continues to grow, ecological communities will increasingly include multiple species of conservation concern—a problem that underscores the need to consider the broader community and ecosystem-level consequences of management actions that have historically targeted only single species.

One popular approach to multispecies conservation is the use of umbrella species, species such as large carnivorous animals whose requirements might encompass those of many additional species (Noss et al. 1996). However, recovery of upper-trophic-level species can potentially lead to declines in other (prey) species of concern. For example, recovery of Peregrine Falcons, *Falco peregrinus*, was associated with declines in local populations of Cassin's and Rhinoceros Auklets (*Ptychoramphus aleutica* and *Cerorhinca mon-*

*ocerata*; Paine et al. 1990). With Peregrines, the effects result from clear direct impacts of predators on prey. However, field observation and controlled manipulations are increasingly identifying that the consequences of both direct interactions and the associated indirect effects must be considered if population changes in multispecies assemblages are to be properly interpreted.

Indirect effects in particular have been relatively unexplored. Such effects occur “when the impact of one species on another requires the presence of a third species” (Wootton 1994a) and operate through two general, nonexclusive mechanisms (Wootton 1994b). First, interaction chains involve linked pairs of direct interactions, for instance those producing trophic cascades (Paine 1980, Carpenter and Kitchell 1993). Second, in interaction modifications, one species changes the intensity of relationship between two or more other species (e.g., Crowder and Cooper 1982). Ecologists remain uncertain about how to identify and quantify the role that indirect effects exercise in community dynamics and organization (Paine 1980, Wootton 1994a) although both theoretical and field studies indicate that indirect effects account for approximately half the total interaction in ecosystems (Schoener 1993, Menge 1995). Studies like those of Slagsvold (1980), Paine et al. (1990), Spencer et al. (1991), and Marquis and Whe-

lan (1994), all involving birds as major participants, suggest that indirect effects are important determinants of interaction outcomes. Finally, in contrast to direct effects, indirect effects can be much more difficult to predict a priori—a fact that makes indirect effects especially problematic for multispecies management decisions.

Our paper quantifies the natural history of an experimentally intractable interaction whose consequences stem mainly from indirect effects. We quantified the relative importance of direct and indirect effects in the relationship between a federally protected apex predator, the Bald Eagle, *Haliaeetus leucocephalus*, and one of its many prey species, the Common Murre, *Uria aalge*, a species of concern in the state of Washington. We present 9 yr of observational data on murre demography and the varying interactions between eagles and murres at one of the largest and most speciose seabird colonies in Washington State: Tatoosh Island. In addition, we employ simple demographic models to tease out the relative importance of direct versus indirect influences under a variety of population scenarios. Our intent is to highlight the management dilemma associated with successful restoration of a high trophic level consumer, and add to the meager but growing understanding of the major role indirect effects play in influencing vertebrate population dynamics and natural resource management.

## METHODS

### Study site

Tatoosh Island (48°24' N, 124°44' W), ~0.6 km off the northwest tip of the Olympic Peninsula of Washington State, is a complex of flat-topped rocky islets (land area ~6 ha). Tatoosh has a lengthy history of human occupation, beginning in antiquity with the Makah Tribe. Europeans began managing a lighthouse there in 1854, and the island remained permanently inhabited until 1976, at which time the U.S. Coast Guard station was automated and all personnel and their pets removed. We believe the human factor in the dynamics reported below to be minimal. The island has no resident small mammals; river otters, *Lutra canadensis*, are observed on ~10% of our trips.

Tatoosh is inhabited by 10 species of breeding seabirds (Paine et al. 1990). Most conspicuous among these, in both abundance and diurnal habits, are the murres and Glaucous-winged Gulls, *Larus glaucescens*. Two predatory species, Bald Eagles and Peregrine Falcons, visit throughout the year and represent known mortality sources for the island's seabirds although neither predator breeds on the island (Paine et al. 1990). Other hawks and owls are either migratory transients or occasional visitors from the adjacent mainland and are of no known ecological consequence. Although no threat to adult seabirds, gulls and Northwestern Crows, *Corvus caurinus*, can be major consumers of eggs, es-

pecially those of murres and cormorants (*Phalacrocorax* spp.). Both species gain access to murre eggs primarily when eagles flush murres from their nesting sites. In the absence of eagles, this indirectly facilitated mortality appears to be uncommon.

### Estimating murre presence on Tatoosh

From 1991–1999, 11 index plots on the island were regularly censused for murres throughout the murre nesting season. These data were used to produce counting correction factors as a function of time of day and of season, as well as of interobserver variation. Total island attendance (defined as the number of birds present on the colony during the count) was recorded at least once during each nesting season (after eggs had been laid but before chicks began to fledge). Smaller subcolonies (<300 birds) were counted directly, whereas attendance in larger subcolonies was estimated by counting a subplot accounting for ~25% of the total area. In this paper, total island attendance is a sum of these counts and/or estimates, corrected for differences in timing of observations and differences among observers. To obtain total breeding population, we multiplied attendance by 1.6 to account for foraging birds (after Takekawa et al. 1990).

To quantify the observed rate of population decline, we fit a simple exponential model to the observed time series of attendance estimates. Although the observed fluctuations in murre numbers probably result from a combination of observation error and environmental variation (or process error), assuming only observation error generally provides a reasonably robust fit (Polachek et al. 1993). We therefore assumed that the random component in the observed attendance estimates was due to observation error:

$$N_{\text{obs},t+1} = (\lambda N_{\text{pred},t}) \exp[Z_t \sigma - (\sigma^2/2)]$$

where  $N_{\text{obs},t}$  is the observed population size at time  $t$ ;  $N_{\text{pred},t}$  is the predicted population size at time  $t$ ;  $\lambda$ , the key unknown parameter to be estimated from the data, is the annual rate of population growth;  $Z_t$  is a normally distributed random variable with mean of zero and standard deviation of 1; and  $\sigma$  is the standard deviation of the observation error (Hilborn and Mangel 1997). We searched over values of  $\lambda$ ,  $N_0$  (initial population size), and  $\sigma$  to produce a likelihood profile for  $\lambda$ . The maximum likelihood estimate of  $\lambda$  is the value that minimizes the negative log-likelihood (NLL):

$$\begin{aligned} \text{NLL}(N_{\text{obs},t} | \lambda, N_0, \sigma) \\ = \sum_{t=1}^8 -\frac{1}{2} \ln \left( \frac{1}{2\pi\sigma^2} \right) + \frac{\{\ln(N_{\text{obs},t}) - \ln(N_{\text{pred},t})\}^2}{2\sigma^2}. \end{aligned}$$

In addition, we fit one-dimensional confidence limits for  $\lambda$ , allowing the other parameters to vary so as to minimize NLLs. The upper and lower 95% confidence limits for  $\lambda$  are the values that cause the NLL to exceed the minimum NLL + 1.92 (Hilborn and Mangel 1997).

### *Estimating eagle pressure*

Three independent data collection efforts have assessed eagle presence in the coastal area surrounding Tatoosh: a habitat scale measure of successful nest sites, a site-specific measure of eagle numbers, and a site-specific measure of eagle activity. In 1971, the Washington Department of Fish and Wildlife initiated fixed-wing airplane surveys for eagle territories on the Olympic Peninsula. From 1980–1985, data were collected in April and June, and from 1986–1999, the June survey was conducted by helicopter. In 1989, the number of surveys was doubled (i.e., increased from two per year to four per year) in response to the *Nestucca* oil spill (A. MacMillan, *personal comment*). We use the number of eyries producing young (active eyries) within a 25 km radius of Tatoosh as our habitat scale measure.

Second, our site-specific measure of eagle numbers is the mean number of eagles per trip sighted during the months when murres and eagles overlap in the region each year. Although murres do not colonize the island until June, eagles and murres are both present in the general vicinity of the island from March to mid-July. RTP first visited Tatoosh in 1968, and since 1972 has spent 20–78 d/yr there, usually in 3–5-d trips over all seasons. During the late spring to early fall, approximately two trips per month were made to the island. Records of eagle sightings have been kept since 1979. Eagle numbers were conservatively estimated as the maximum number of adults and/or immatures observed simultaneously during each trip. Trip data were averaged within each year (sample size, e.g., trips, ranged from four to nine).

Finally, our measure of site-specific activity is hourly eagle flight activity, defined as the mean number of eagles flying past a promontory (Burning Barrel Point, BBPT) affording a simultaneous view of several murre subcolonies (>60% of the island's total population), the mainland, and the main eagle roosting areas on Tatoosh. Observations were made in 0.5-h blocks, evenly spaced over each trip (2–10 d), starting at 0500 and ending at 2200 (~620 h in total, 1991–1999). Because eagle flight activity is not uniform across the day, data were standardized such that all clock hours contributed evenly to a combined annual mean. Eagle flights/h provide a record of eagle activity as witnessed by the murres, regardless of the number of individual eagles in the area.

Because both eagle abundance and activity are important factors determining prey response, all three measures (1991 through 1999) were combined in a single principal component score (PC1) reflecting eagle pressure on the Tatoosh murre colony. Because curve fitting is simplified when all values are positive, graphs display  $(PC1 + 1)$ .

### *Effects of eagles on murres*

Eagles were potentially present ~17.5 h/d (0500–2130) and had the opportunity to take adult murres from

the colony over a 50 d period from 1 June (approximate date murres settle on the island) through 20 July (approximate date eagles depart). In most years, eagles were witnessed taking adult murres during the course of observations at BBPT. Because only a fraction (range 10–15%) of the total daylight hours over any one season were spent in observation at this location, total mortality of adult murres due to eagle predation was estimated by standardizing the observed kills by percent time observed. In years when no kills were observed (1991 and 1993), we used two potential estimates of the kill rate: a low end estimate of zero and a high end estimate just below the lowest observed number of kills in any year (one in 1992). The high-end values were standardized by hours observed in 1991 and 1993, respectively. To relate estimated annual kill rate to an effect on the murres, standardized kill rates are expressed as a percentage of the breeding population in a given year.

Murres respond to eagle presence with a series of escalating group behaviors culminating in temporary evacuation of the nesting area. Frequent evacuation leads to depressed reproductive success via loss of eggs to gulls and crows (Parrish 1995). Although murres occasionally evacuate in response to disturbances other than eagles, these events are relatively rare (Parrish 1995). We used evacuations as a measure of prey response to predator activity. In this case, flyby rate rather than the integrated measure of eagle pressure (i.e., PC1 score) was used because eagles flying over the murre nesting area are the proximate predator signal to which murres respond (regardless of how many eagles are in the area). Total number of witnessed evacuations was standardized to account for differences in observation time among years. Data are from 1992–1999.

Habitat-specific annual reproductive success was measured for murre pairs nesting in seven monitored subcolonies: four crevices and three cliff-top nesting areas (~50% of the breeding population). Because reproductive success differed between these two habitat types, annual island-wide reproductive success was calculated by multiplying habitat-specific success by the percentage of the total island population occupying each habitat. For logistic regression using reproductive success as the dependent variable, a subset of 50 monitored nests (where the percentage in each habitat type was chosen according to its representation across the entire colony) was randomly chosen from among all monitored nests within a year. This number was chosen to both maximize and equilibrate sample size among years.

### *Effects of climate on murres*

Because changes in ocean conditions, most notably primary production associated with upwelling, can affect the murres' food supply and thus reproductive success, we examined the effects of four indices of climate variability on murre reproductive success, using data

TABLE 1. Form of the Leslie matrix used to project murre population change.

$$\mathbf{M} = \begin{bmatrix}
 0 & 0 & 0 & r_4 b_4 m_4 / 2 & r_5 b_5 m_5 / 2 & r_6 b_6 m_6 / 2 & r_7 b_7 m_7 / 2 & r_8 b_8 m_8 / 2 & r_{9+} b_{9+} m_{9+} / 2 \\
 p_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & p_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & p_3 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & p_4 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & p_5 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & p_6 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & p_7 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_8 & p_{9+}
 \end{bmatrix}$$

from 1992 (first year of reproductive success data) through 1999. We manufactured annual indices based on monthly anomalies in four climatic measures: (1) the Pacific Decadal Oscillation (PDO), an index of extratropical sea surface temperature (SST) widely used to track annual and interdecadal climate variability in the North Pacific (Mantua et al. 1997; threshold set at 1.0); (2) the West Coast Sea Surface Temperature, an integrated measure of coastal SST (Climate Prediction Center;<sup>4</sup> threshold set at 1.0); (3) the extratropical Northern Oscillation Index (NOIx), an index of sea level pressure difference between the North Pacific High and Darwin, Australia (Schwing et al. 2001; threshold set at -2.0); and (4) a more local measure, the monthly sea surface temperature anomalies within a two degree square centered on 125° W, 49° N as assessed by the National Oceanic and Atmospheric Administration (NOAA) ship of opportunity program COADS (Climate Data Center;<sup>5</sup> threshold set at 1.0). For each climatic measure we recorded the number of months in which the reported anomaly exceeded a threshold value in a direction likely to reduce murre production. Years ran from September through August (e.g., the 1992 signal encompassed September 1991 through August 1992), to reflect the breeding cycle of the murre. These indices were used as predictor variables in a logistic regression of murre reproductive success.

*Modeling murre demography: the importance of direct and indirect effects of eagles*

Finally, we explored the contribution of direct and indirect effects of eagles to the observed decline of murre on Tatoosh. Specifically, we evaluated the empirical support for four sets of density-independent and deterministic age-specific matrix models of murre demography. The first set of models (baseline matrices) describes the population growth of murre in the absence of eagles. The three remaining sets are modifications of the baseline models that incorporate direct effects, indirect effects, or both direct and indirect effects of eagles.

<sup>4</sup> URL: <www.cpc.ncep.noaa.gov>

<sup>5</sup> URL: <www.cdc.noaa.gov>

Because detailed demographic data were not available for the Common Murre colony on Tatoosh, four sets of age-specific vital rates were estimated using published data on banded Common and Thick-billed Murres: probability of survival from age  $x - 1$  to  $x$  ( $p_x$ ), proportion of survivors of age  $x$  returning to the breeding colony ( $r_x$ ), proportion of on-colony birds of age  $x$  attempting to breed ( $b_x$ ), and reproductive success of age  $x$  breeders, ( $m_x$ ). Although Common Murres can live >30 yr, our model included only nine age classes, with all murre aged 9 yr and older lumped into a single age class (Table 1). Values for reproductive success of age  $x$  breeders ( $m_x$ ) are divided by two because the matrices are based on demography of females.

An extensive literature search for vital rate data published on Common and Thick-billed Murres revealed that no single murre colony had been assessed for all age-specific data needed to parameterize our models. However, in some cases, more than one data source was available for a given parameter. Therefore, we selected values according to the following operational rules in order of priority: (1) use parameters from a same-species colony within the Pacific region and during a coincident time period; (2) use parameters from a distant (e.g., Atlantic) same-species colony within a coincident time period; (3) use parameters from a sister-species colony within a coincident time period; (4) use parameters from a same-species colony in the Atlantic but from earlier decades (Table 2).

Using the vital rate values described in Table 2, we constructed 24 different baseline matrices, corresponding to all possible combinations of parameter sets (three sets of  $p_1$ - $p_5$  values, two sets of  $p_6$  and  $p_7$  values, two sets of  $p_8$  and  $p_{9+}$  values, two sets of  $r_3$ - $r_6$  values). For each baseline model, we constructed an initial (1991) population vector (assuming the population was at stable age distribution) and projected the population forward eight years in a density-independent manner:

$$\mathbf{N}_{x,t+1} = \mathbf{M}\mathbf{N}_{x,t}$$

where  $\mathbf{N}_{x,t}$  is a column vector of age-specific murre abundance at time  $t$  and  $\mathbf{M}$  is a  $9 \times 9$  Leslie matrix of the form shown in Table 1. For each year of the projection, we recorded the following:

TABLE 2. Estimation of parameter values used to construct 24 unique matrices describing murre population growth in the absence of eagles.

| Parameters                                 | Methods   |
|--|---|
| a) Details of parameter estimation methods |   |
| $p_1-p_5$                                  | Birkhead and Hudson (1977), Hudson (1985), and Hatchwell and Birkhead (1991) report Atlantic Common Murre survival to 5 yr. Gaston et al. (1994) report survival to 3 and to 5 yr for Thick-Billed Murres, based on band returns corrected for emigration. We constructed three sets of age-specific survival rates which encompass all reported values assessed at 3 and 5 yr.   |
| $p_6-p_7$                                  | We found no data on survival at age 6 or 7 yr. We used the medium $p_5$ value as a low estimate and the low $p_8$ value as a high estimate.   |
| $p_8-p_{9+}$                               | Adult survival has been reported by Sydeman (1993) for Common Murres in the California Current System, as well as more generally for Atlantic Common Murres which are "experienced breeders" by Birkhead and Hudson (1977), Hudson (1985), Harris (1991), and Hatchwell and Birkhead (1991). We used Sydeman's (1993) predator-free adult survival estimate as a high estimate and mean across all Atlantic values as a low estimate.   |
| $r_1-r_{9+}$                               | We constructed two sets of age-specific return rates $r_2-r_{7+}$ using data reported for Atlantic Common Murres by Swann and Ramsay (1983; reports ages 3 to 7 yr) and Hudson (1985; reports ages 2 to 6 yr). We assumed age-1 birds do not return to the colony. We corrected values reported in the literature by dividing each $r_x$ value by $l_x$ , the probability of surviving from age 0 to $x$ based on mean $p_x$ values.  |
| $b_1-b_{9+}$                               | The proportion of the returning population that attempts to breed has been reported by Harris et al. (1994) for Atlantic Common Murres and by Gaston et al. (1994) and DeForest and Gaston (1996) for Thick-Billed Murres. We assumed birds <4 yr old do not attempt to breed. For $b_4-b_8$ we used values reported in Harris et al. (1994). For age 9+ birds, we used the complement of the proportion of experienced breeders present but not breeding as reported by Harris and Wanless (1995) for Atlantic Common Murres.  |
| $m_x$                                      | We considered colony-wide reproductive success of Common Murres in the California Current System in the late 1980s-early 1990s ( $m_x = 0.805$ fledglings per pair) reported by Sydeman and Eddy (1995) as most indicative of what baseline (i.e., eagle-free) conditions might have been on Tatoosh. This value is slightly conservative, as a mean of all nonoverlapping Atlantic Common Murre colony values (excluding values attributed to food shortages or low nesting density) mean reproductive success was 0.813 (SD = 0.105, $N = 6$ ; Birkhead 1977, Birkhead and Hudson 1977, Hedgren 1980, Hudson 1985, Harris 1991, Hatchwell and Birkhead 1991, Harris and Wanless 1995, Regehr and Rodway 1999). Colony-wide Common Murre reproductive success values from the Gulf of Alaska and Bering Sea are consistently less than values from other areas, a result attributed to food availability and weather constraints (Hatch and Hatch 1990, Murphy and Schauer 1994). Although Hedgren (1980) reports $m_x$ values for Atlantic Common Murres with known years of experience (first-time, 1 yr, and 2+ yr), these values could not be easily translated into age-specific values. We used the only age-specific reproductive success values, which were for Thick-Billed Murres in the Atlantic ( $m_{3-5} = 0.20$ , $m_{6-8} = 0.41$ , $m_{9+} = 0.83$ ; Gaston et al. 1994, DeForest and Gaston 1996), but applied a uniform correction factor 0.03 to bring the colony-wide mean reproductive success up to ~0.8 fledglings per pair. |

b) Parameter values

| Age (x) | $p_x$ |      |       | $r_x$  |       | $b_x$ | $m_x$ |
|---------|-------|------|-------|--------|-------|-------|-------|
|         | Low   | Med  | High  | Low    | High  |       |       |
| 1       | 0.62  | 0.70 | 0.76  | 0†     |       | 0     | 0     |
| 2       | 0.70  | 0.78 | 0.82  | 0.056† |       | 0     | 0     |
| 3       | 0.72  | 0.80 | 0.85  | 0.254  | 0.188 | 0     | 0     |
| 4       | 0.74  | 0.82 | 0.87  | 0.460  | 0.595 | 0.01  | 0.23  |
| 5       | 0.76  | 0.84 | 0.89  | 0.373  | 0.764 | 0.17  | 0.23  |
| 6       | 0.84  |      | 0.921 | 0.577  | 0.602 | 0.53  | 0.46  |
| 7       | 0.84  |      | 0.921 | 0.886† |       | 0.54  | 0.46  |
| 8       | 0.921 |      | 0.939 | 0.950† |       | 0.68  | 0.46  |
| 9+      | 0.921 |      | 0.939 | 0.950† |       | 0.922 | 0.86  |

† See explanation in part (a) of table.

$$NI_t = \mathbf{N}_{x,t} \mathbf{r}_x$$

where  $NI_t$  is the number of age  $x$  murres present on-island at time  $t$  and  $\mathbf{r}_x$  is a row vector of age-specific probabilities of returning to Tatoosh Island.

We calculated the NLL for each baseline matrix as

$$NLL(N_{obs,t} | \mathbf{M}, NI_0, \sigma) = \sum_{t=1}^8 -\frac{1}{2} \ln \left( \frac{1}{2\pi\sigma^2} \right) + \frac{\{\ln(NI_{obs,t}) - \ln(NI_{pred,t})\}^2}{2\sigma^2}$$

assuming that the differences between the observed and

predicted estimates of the on-island population were due to observation error and allowing the initial number of on-island murres,  $NI_0$ , and the standard deviation of the observation error,  $\sigma$ , to converge to their most likely values given the constrained value of  $\mathbf{M}$ .

Next we altered each of the 24 matrices to add: (1) only direct effects of eagles, (2) only indirect effects of eagles, and (3) both direct and indirect eagle effects. Direct effects of eagle predation were incorporated into the baseline demographic model as a reduction in the survival probabilities of murres present on Tatoosh. We

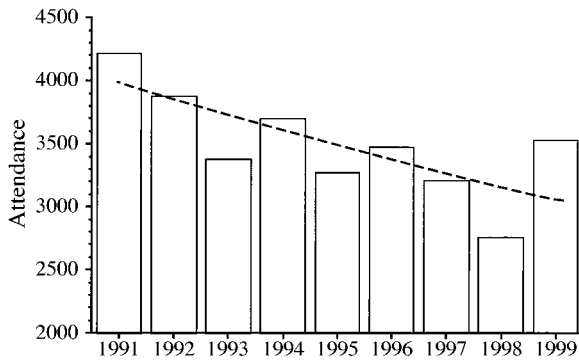


FIG. 1. Annual attendance estimate (bars) for Common Murres nesting on Tatoosh Island. The dashed line represents a fitted exponential decline, with a population growth rate of  $\lambda = 0.969$ .

used the asymptote of the observed relationship between the kill rate and eagle pressure on Tatoosh to estimate the mean maximum strength of this direct effect (See *Results*; Fig. 4;  $\mu = 0.022$ ). Because only the portion of the adult population that returns to the breeding colony is subjected to eagle predation, the transition probability for adults of age  $x$  becomes:  $(1 - r_x)p_x + r_x p_x(1 - \mu)$ . We found the stable age distribution for each of these modified matrices, projected the population forward 8 yr, and calculated the NLL as described above.

Indirect effects result because adult murres evacuate the nesting area when eagles fly over, leaving their eggs susceptible to gull and crow predation (Parrish 1995). Thus, to incorporate indirect effects of eagles into our models, we rescaled the baseline  $m_x$  values by the ratio of murre reproductive success in the presence of eagles (see *Results*; Table 3) to murre reproductive success in the absence of eagles (calculated from baseline matrices,  $\sim 0.80$ ; Sydeman and Eddy 1995). We again projected the populations and calculated the NLL for each of the 24 modified matrices. A final set of models incorporated both direct and indirect eagle effects. To compare the relative support for each of the four models, we asked which model had the lowest mean NLL for each of the 24 baseline matrices.

## RESULTS

### *Trends in murre attendance and eagle presence*

Murre attendance on Tatoosh Island has been in decline since annual censuses were initiated in 1991. Maximum likelihood fit of an exponential model of population growth indicates that observed attendance has dropped at a rate of  $\sim 3\%$  per year for a cumulative decline of 22.4% over the 1991–1999 period (maximum likelihood estimate of  $\lambda = 0.9688$ ,  $N_0 = 3930$ ,  $\sigma = 0.08$ ; Fig. 1). The 95% confidence interval for  $\lambda$  was 0.947–0.991.

In contrast, the abundance of Bald Eagles has been steadily increasing over recent decades. First, the num-

ber of eaglet-producing eyries within a 25 km radius of Tatoosh Island has increased dramatically since the early 1980s (Fig. 2A). Since survey effort doubled in 1989, the habitat has accommodated an additional nesting pair almost every year (least squares linear regression: eyries =  $a + b \times \text{year}$ ;  $b = 0.827$ ,  $R^2 = 0.64$ ,  $F_{1,9} = 18.452$ ,  $P = 0.002$ ). The mean number of eagles sighted on Tatoosh from March through July has also risen significantly over recent years (Fig. 2B: least squares linear regression, eagles =  $a + b \times \text{year}$ ;  $b = 0.234$ ,  $R^2 = 0.73$ ,  $F_{1,17} = 48.742$ ,  $P < 0.0001$ ). However, eagle activity (number of eagle flyovers) did not mirror the steady increase in eagle abundance (Fig. 2C: least squares linear regression, activity =  $a + b \times \text{year}$ ;  $b = 0.313$ ,  $F_{1,8} = 4.678$ ,  $P = 0.067$ ), and instead fluctuated from year to year with a sudden increase in 1998 and 1999 (mean of 6.26 eagles per hour).

These three measures of eagle abundance and activity (1991 through 1999) were combined in a single first principal component score (“eagle pressure,” hereafter), explaining 75% of the total variance in these three measures (Table 4). This index of eagle pressure tends to increase over time (Fig. 3: least squares linear regression: eagle pressure =  $a + b \times \text{year}$ ;  $b = 0.272$ ,  $R^2 = 0.491$ ,  $F_{1,7} = 8.725$ ,  $P = 0.021$ ), and is significantly related to the decrease in murre attendance through 1998 (least squares linear regression: attendance =  $a + b \times \text{eagle pressure}$ ;  $b = -646.7$ ,  $R^2 = 0.473$ ,  $F_{1,6} = 7.281$ ,  $P = 0.036$ ). However, the relationship between murre attendance and eagle pressure is substantially weakened with the inclusion of the 1999 attendance data ( $F_{1,7} = 0.818$ ,  $P = 0.396$ ).

### *Effects of eagles on murres*

To address the relationship between eagle pressure and murre population response, we used two variants of the percent of the murre population killed by eagles. Our low-end estimate incorporates zeros (i.e., no kills) for the years 1991 and 1993 when no kills were wit-

TABLE 3. Annual reproductive success of Common Murres nesting in crevices (four monitored subcolonies) and on cliff-tops (three monitored subcolonies) on Tatoosh Island, Washington.

| Year             | Crevice   | Cliff-top  | % Crevice | Island-wide |
|------------------|-----------|------------|-----------|-------------|
| 1992             | 0.79 (43) | 0.37 (100) | 0.22      | 0.46        |
| 1993             | 0.43 (28) | 0.19 (100) | 0.19      | 0.24        |
| 1994             | 0.79 (57) | 0.23 (100) | 0.25      | 0.37        |
| 1995             | 0.87 (60) | 0.34 (100) | 0.41      | 0.56        |
| 1996             | 0.03 (71) | 0.49 (104) | 0.47      | 0.27        |
| 1997             | 0.85 (75) | 0.59 (150) | 0.45      | 0.71        |
| 1998             | 0.07 (63) | 0.16 (140) | 0.53      | 0.11        |
| 1999             | 0.00 (97) | 0.20 (200) | 0.55      | 0.09        |
| Mean (1992–1999) |           |            |           | 0.3511      |

*Notes:* Numbers in parentheses are total pairs monitored. Percentage of the attending population nesting in each habitat type is used to weight reproductive success and determine a single annual island-wide value.

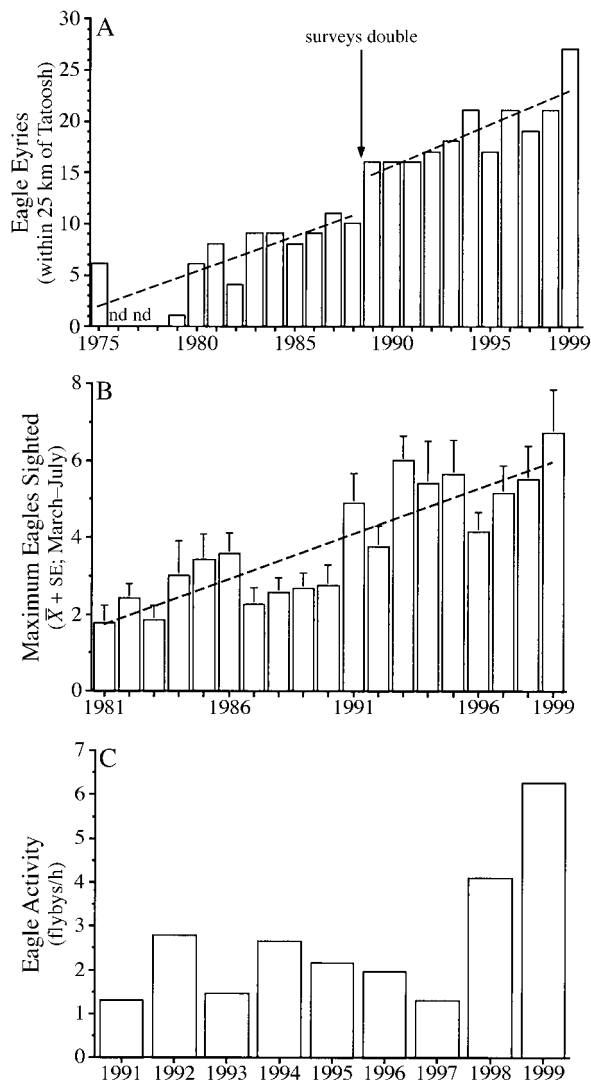


FIG. 2. (A) The number of reproductively active Bald Eagle eyries within 25 km of Tatoosh Island. Note that data before and after 1989 are treated separately; nd = no data. The dashed line is from least-squares linear regression. (B) The annual mean of the maximum number of Bald Eagles sighted simultaneously per research trip to Tatoosh Island. Dashed line is as in (A). (C) An annual estimate of the number of times any eagle flew by our observation promontory on Tatoosh Island, standardized to flybys/h.

nished. Our high-end estimate incorporates the kill rate from the next lowest year, adjusted for hours of observation in 1991 and 1993. In both cases a logistic curve provided a better fit than a linear regression, suggesting the proportion of the murre breeding population killed by eagles is a positive but saturating function of eagle pressure, maximized at just over 2% (Fig. 4; logistic curve fit, high end dataset, kills =  $a(1 - \exp[-b(\text{eagle pressure} + 1)])$ , asymptote ( $\mu$ ) and 95% confidence interval =  $2.22\% \pm 0.97\%$ ,  $R^2 = 0.763$ ; low end dataset,  $a = 2.41\% \pm 1.80\%$ ,  $R^2 = 0.704$ ). This pattern makes sense in light of the behavioral

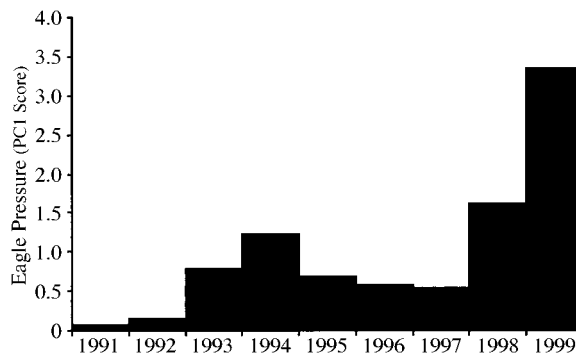


FIG. 3. An annual index of eagle pressure on Tatoosh Island: the first principal component score of active eagle eyries, mean maximum eagles seen, and eagle flybys/h (see Fig. 2).

response of attending murres to visiting eagles: murres respond to eagle overflights, assessed as eagle activity, by temporarily evacuating their ledges for the relative safety of the water (Fig. 5; logistic curve fit: evacuations =  $a(1 - \exp(-b \times \text{overflights}))$ , asymptote and 95% confidence limits =  $1.678 \pm 1.135$ ,  $R^2 = 0.714$ ). The same analysis with eagle pressure provided a poorer fit ( $R^2 = 0.602$ ), as did linear regressions (overflights,  $R^2 = 0.541$ ; eagle pressure,  $R^2 = 0.502$ ). However, because adult murres are not susceptible to eagle predation once they reach the water, there is some point beyond which further increases in eagle pressure would not necessarily translate into additional mortality of adult murres.

Although adult murres are safe once they reach water, their evacuation during eagle overflights renders their eggs extremely vulnerable to other sources of mortality. In particular, there is increased predation of murre eggs by gulls and crows during and after murre evacuation. In fact, murres in monitored nesting areas that were most strongly affected by eagle disturbance displayed the highest evacuation rates and suffered complete reproductive failure (Parrish 1995).

To determine the degree to which eagle pressure, as opposed to climate variability, was forcing reproductive success, we first conducted an exploratory analysis to determine which single climate index was most highly correlated with reproductive success. Seabird reproductive success, more than colony attendance, is

TABLE 4. Component loadings and variance explained by a principle component analysis of three measures of eagle abundance and activity (see text for details).

| Component loadings           | PC 1<br>(eagle<br>pressure) | PC 2   | PC 3   |
|------------------------------|-----------------------------|--------|--------|
| Active eyries                | 0.927                       | 0.238  | -0.292 |
| Eagle sightings              | 0.753                       | -0.658 | 0.022  |
| Eagle flybys                 | 0.912                       | 0.302  | 0.278  |
| Variance explained           | 2.257                       | 0.580  | 0.163  |
| Total variance explained (%) | 75.3                        | 19.3   | 5.4    |

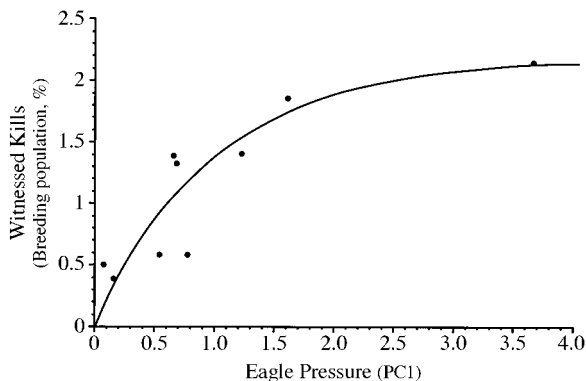


FIG. 4. The number of Common Murre kills by Bald Eagles we witnessed annually, standardized to accommodate differences in annual hours of observation, and expressed as a percentage of the annual breeding population on Tatoosh Island, as a function of eagle pressure index. Data points from 1991 and 1993 are high-end values. The line is a logistic curve with an asymptote of 2.22.

thought to be affected by regional to global climate change (Furness et al. 1993). Anomalies of two North Pacific indices (PDO, NOIx), one coastal regional index (WCSST), and one local index (COADS SST) were used. No climate variables were significant predictors of Tatoosh Island Common Murre reproductive performance; however, the local variable (COADS SST anomaly) provided the best fit (Table 5). A logistic regression including both eagle pressure and local climate pressure (i.e., COADS) substantiated this result. Whereas eagle pressure was a highly significant factor affecting murre reproductive success, climate was not (eagle pressure, Wald statistic = 10.941,  $P = 0.001$ ; climate, Wald statistic = 1.365,  $P = 0.243$ ;  $N = 400$ ). The relationship between eagle pressure and island-wide reproductive success appears to be exponential (reproductive success =  $a \times \exp(b \times \text{eagle pressure})$ ,

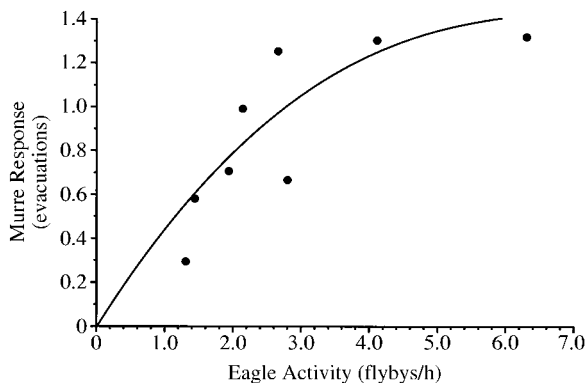


FIG. 5. Annual evacuations by Common Murres of their nesting areas (standardized to accommodate differences in annual hours of observation) as a function of eagle activity on Tatoosh Island, expressed as the annual mean number of eagles flying by our observation promontory (per hour). The line is a logistic curve with an asymptote of 1.68.

TABLE 5. Linear regressions of reproductive success against four indices of climate variability.

| Variable | Sample size   | F     | df  | P     |
|----------|---------------|-------|-----|-------|
| PDO      | 1992–1999 (8) | 0.163 | 1,6 | 0.700 |
| WCSST    | 1992–1999 (8) | 0.106 | 1,6 | 0.756 |
| NOIx     | 1992–1999 (8) | 0.154 | 1,6 | 0.708 |
| COADS    | 1992–1999 (8) | 4.373 | 1,6 | 0.105 |

$R^2 = 0.647$ , Fig. 6). A linear regression provided a nearly significant relationship, but a weaker fit ( $R^2 = 0.647$ ,  $P = 0.07$ ). Thus, as eagles drive murres to continuously evacuate, a small percentage of breeders remain successful. These parents either nest in locations not accessed by eagles in a given year (J. Parrish, *personal observation*), or nest in limited portions of nesting areas not accessible to eagles (e.g., underneath protective vegetation, Parrish and Paine 1996).

*Modeling murre demography: the importance of direct and indirect effects of eagles*

We used 24 different baseline demographic matrices to explore the relative contributions of direct effects (eagle predation on adult murres) and indirect effects (reductions in murre reproductive success during evacuations triggered by eagle overflights) to the recent decline in the Tatoosh murre colony. The likelihoods of the unaltered baseline models, describing the possible patterns of growth for a murre population in the absence of eagle predation, were compared to the likelihoods of the same matrices altered to include eagle effects.

For the vast majority of parameter combinations (22 out of 24 matrices), models that included some form of eagle effect provided the best fit to the observed decline in murre attendance (Table 6). Lambdas of best fit models ranged between 0.96 and 0.98. In the two cases where we assumed low survival at all stages, the baseline model (with no eagle effects) provided the best fit to the observed murre attendance values. In these two cases, adding eagle effects caused the predicted

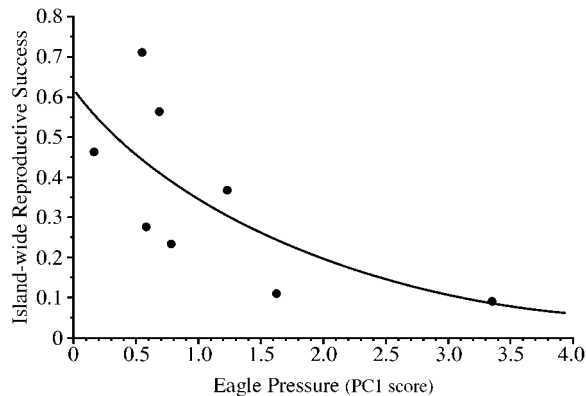


FIG. 6. Reproductive success (fledglings/pair) of Tatoosh Island Common Murres as a function of eagle pressure index.

TABLE 6. The "winning" population model (left column) that minimizes the NLL (right columns) for each of 24 combinations of input vital rates (survival, center columns; return, right column headings).

| Winning model (sample size)      | $p_1-p_3$ | $p_6-p_7$ | $p_8-p_{9+}$ | NLL           |                |
|----------------------------------|-----------|-----------|--------------|---------------|----------------|
|                                  |           |           |              | low $r_3-r_6$ | high $r_3-r_6$ |
| Baseline, no eagle effects (2)   | low       | low       | low          | -9.6497       | -9.6573        |
| Direct effects (6)               | low       | low       | high         | -9.8688       | -9.8810        |
|                                  | low       | high      | low          | -9.9518       | -9.9660        |
|                                  | low       | high      | high         | -9.4050       | -9.4115        |
| Indirect effects (2)             | med.      | low       | low          | -8.8990       | -8.8745        |
| Direct and indirect effects (14) | med.      | low       | high         | -8.9652       | -9.0732        |
|                                  | med.      | high      | low          | -8.7595       | -8.9270        |
|                                  | med.      | high      | high         | -8.7133       | -8.5480        |
|                                  | high      | low       | low          | -8.7124       | -8.7791        |
|                                  | high      | low       | high         | -8.3621       | -8.1034        |
|                                  | high      | high      | low          | -8.2630       | -8.0141        |
|                                  | high      | high      | high         | -7.2868       | -6.8722        |

Notes: See Table 2b for baseline parameter values. Except in cases where all survival values were low, models incorporating either direct effects, indirect effects, or both, were superior.

population to shrink too quickly compared to the observed population. However, because our observations clearly document both direct and indirect effects of eagles on Tatoosh murre, either the survival rates of murre on Tatoosh must be higher than indicated by our lowest assumption set or the Tatoosh population was being supplemented by immigration during the years of observation.

For all other combinations of input values, we found that models including direct and/or indirect mortality due to eagles were the most likely models. In particular, for 14 of the 24 parameter combinations, models including both direct and indirect effects predict population changes that are most consistent with the observed rate of decline.

In general, survival of the youngest murre most strongly affected exactly which form of eagle effects was most likely. Specifically, when survival of the youngest age classes was assumed to be low but in combination with high survival of older murre, the most likely models included direct effects of eagles (i.e., a reduction in adult survival). On the other hand, if survival of young age classes was assumed to be medium or high, the most likely models incorporated indirect effects (i.e., a reduction in reproductive success) or the combination of direct and indirect effects. In other words, as the survival of the youngest age classes increased across the parameter sets, the importance of indirect effects (mortality of chicks) also increased.

## DISCUSSION

### *Predation as a driving force*

It appears that the murre population was steadily increasing on Tatoosh Island prior to 1990 (Paine et al. 1990). At present, however, the Common Murre populations are in decline on Tatoosh (Fig. 1), as well as in Washington State generally (Wilson 1991). Mean-

while, eagles are increasing numerically (Fig. 2), appear to have become with time and experience more effective murre predators (Fig. 3), and have exerted chronic and increasingly serious indirect effects (Table 3, Fig. 6). In light of our data, we anticipate eagle effects to continue to increase and to become an increasingly important factor in murre population decline on Tatoosh. Although regional extinction is unlikely, and global extinction due to this cause exceedingly improbable (worldwide, Common Murre populations are robust, with numbers estimated to be in the millions), the current trends do not favor murre on a local scale.

Depressed reproductive success as an indirect function of eagle presence is not limited to Tatoosh (e.g., Douglas and Reimchen 1988, Norman et al. 1989). Verbeek (1982) detailed a similar situation on Mandarte Island (British Columbia) involving Bald Eagle facilitation of Double-crested Cormorant (*P. auritus*) egg predation by Northwestern Crows. In our system, the indirect effects derive from a behaviorally mediated interaction modification: increasing eagle visitation to the island promotes nest site evacuation by murre (Fig. 3), strongly facilitating egg predation by gulls and crows regardless of the actual number of individual eagles present. Although indirect eagle effects have strengthened over the decade, on a year to year basis the pattern is much more noisy (e.g., 1996 vs. 1997) as eagles turn their attentions from one nesting area to the next and breeding murre abandon sites and colonize others (J. Parrish, unpublished data).

Our findings suggest that the importance of direct and indirect interactions can depend substantially on the functional form of the relationships among the various species. In this case, the direct effects between eagles and murre are limited because murre that have retreated to rafts on the water are relatively safe from eagle predation. In contrast, indirect effects only be-

come limiting as reproductive success approaches zero. Our models suggest that the relative importance of direct vs. indirect effects may change as a function of age-specific survival; a parameter which may be influenced by other factors, such as climate variability. Some reviews (e.g., Schoener 1993) have suggested that indirect effects should generally be weaker than direct effects; however, both theoretical (Yodzis 1988) and field studies (Paine et al. 1990, Wootton 1994b, Menge 1995) indicate that at least half the change in ecosystems can be attributed to indirect effects. Our study implicates indirect effects as a major force currently driving murre population dynamics, probably accounting for a substantial portion of the observed decline in murre numbers.

*Are other factors driving murre population dynamics?*

Wilson (1991) argued that murre population decline along the coast of Washington was precipitated by El Niño and other anomalous warm water events. In our study, regional sea surface temperature anomaly could not explain patterns in murre reproductive success. Thus, while it is well known that seabird population dynamics can be driven by changes in the physical structuring of food availability stemming from changes in climatic conditions (Ainley et al. 1995), this does not seem to be an overarching factor affecting the Tatoosh murre population except perhaps in the most dire of years (e.g., 1993, 1998).

Two other factors potentially reducing murre abundance are the frequency and intensity of oil spills, and fisheries by-catch. The most recent oil spill was the sinking of the *Tenyo Maru*, a Japanese fishing vessel, within 35 km of Tatoosh in July 1991. Although 3157 murre carcasses were recovered from this spill, there is scant evidence that even very large spills continue to affect either survival or reproductive success eight years beyond the spill date (Piatt and Anderson 1996). More likely, this spill's effects were most pronounced on reproductive success in 1991 (excluded from our data) and on attendance in 1992 (although attendance was not exceptionally low in 1992; Fig. 1).

Gillnet fisheries, principally for sockeye salmon, *Oncorhynchus nerka*, exist in the eastern Strait of Juan de Fuca, Puget Sound, and the Strait of Georgia. Seabirds, primarily murre, are caught in these nets (Melvin et al. 1999). However, effort in this fishery has declined drastically over the last decade. During the 1990s, nontreaty sockeye landings have decreased 85%, a mean loss of 42 000 salmon each year (1990–1999; linear regression, landings =  $a + b \times \text{year}$ ;  $b = -42.68$ ,  $F_{1,8} = 8.386$ ,  $P = 0.020$ ). In 1999, there were no openings for the commercial nontribal gillnet fishery. Since 1997, nontreaty fishermen have been required to fish with modified nets that significantly decrease seabird by-catch. Moreover, this fishery occurs in August and September, when Tatoosh breeders are still on the col-

ony, some 140 km away. Thus, although by-catch in these fisheries undoubtedly accounts for some of the mortality experienced by the Tatoosh murre population, the effect would have been most massive in the 1980s and early 1990s when the fishery was at its peak and the Tatoosh murre population was increasing. Moreover, by-catch can not account for the depressed reproductive success observed on Tatoosh.

Although a panoply of anthropogenic factors affect survival of the Tatoosh Island Common Murres, it is clear that the major factor affecting this population is eagles, and that substantial impacts of this predator can result from indirect effects. These data provide a quantitative example of the strength of indirect effects in structuring a seabird population, and highlight the annual variability of this interaction as predator and prey continue to adapt behaviorally to the presence and activity of each other. Both our data and our model results strongly support the contention that indirect effects are ecologically significant and therefore imply that management and conservation strategies must be set in a broader, multispecies context. The fact that both species are of conservation concern, murre locally and eagles nationally, only serves to complicate the situation. Traditional single-species management, for example managing murre but not eagles or gulls, would be fruitless.

*Spatial dynamics: murre populations are not closed*

Insular populations generally, and colonially nesting seabirds especially, are spatially structured populations, characterized by distinct breeding aggregations and locale-specific reproductive and mortality rates, linked by dispersal to form metapopulations (Buckley and Downer 1992). Our models treated the Tatoosh population as closed and stable, two assumptions which are probably invalid. In fact, immigration in the 1980s was likely responsible for the exceptionally rapid rise in murre numbers. We used an estimate of murre abundance in 1979 from Paine et al. (1990; Fig. 4), to estimate the rate of murre population growth between 1979 and 1991 (our first attendance data point). Because annual attendance estimates were not available, the annual population growth rate for this period was calculated as  $(N_{1991}/N_{1979})^{1/12} = 1.289$ . It is exceedingly unlikely that a closed population of murre could increase by 29% per year. For example, the growth rate predicted by our rosierest baseline model (assuming highest survival and return rates plus no eagle effects) is only ~4% per year. Immigration probably continues to contribute to murre attendance on Tatoosh, as is possibly indicated by the jump in attendance following years of especially intense climatic disruption (e.g., 1992 to 1993, 1998 to 1999; Fig. 1).

Without knowing the rates of emigration to other murre colonies, it is impossible to determine whether Tatoosh was a demographic source, although it is obviously now a sink (sensu Pulliam 1988). Furthermore,

the actual imbalance between local reproductive output and mortality may be underestimated if immigration has continued; one of Pulliam's (1988) points was that numerical trends could be misleading. Seabirds, because of their social behavior and colonial nesting proclivities, could be prime candidates for this demographic pattern. In this interpretation, Tatoosh will continue to be a demographic "trap," attracting immigrants who may be consumed by eagles and whose eggs are likely to be destroyed by gulls and crows. As neighboring colonies decline to near zero (Wilson 1991), Tatoosh becomes an ever more isolated stepping stone between the expanding colonies along the Oregon coast and those in the Gulf of Alaska.

If retention of biodiversity at both local and regional scales is a goal of natural resource management, biologically intricate relationships such as we have described must be disentangled quantitatively. The issue becomes more complicated when major component species are of conservation concern. Whether multi-species management is possible, and what the goals and implementation strategies should be, are challenges left for the future.

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#### LITERATURE CITED

- Ainley, D. G., W. J. Sydeman, and J. Norton. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. *Marine Ecology Progress Series* **118**:69-79.
- Birkhead, T. R. 1977. The effect of habitat and density on breeding success in the common guillemot (*Uria aalge*). *Journal of Animal Ecology* **46**:751-764.
- Birkhead, T. R., and P. J. Hudson. 1977. Population parameters for the Common Guillemot *Uria aalge*. *Ornis Scandinavica* **8**:145-154.
- Buckley, P. A., and R. Downer. 1992. Modelling metapopulation dynamics for single species of seabirds. Pages 563-585 in D. R. McCullough and R. H. Berrett, editors. *Wildlife 2001: populations*. Elsevier Applied Science, New York, New York, USA.
- Carpenter, S. R., and J. F. Kitchell. 1993. *The trophic cascade*. Cambridge University Press, Cambridge, UK.
- Crowder, L. G., and W. E. Cooper. 1982. Habitat structural complexity and the interactions between bluegills and their prey. *Ecology* **63**:1802-1813.
- DeForest, L. N., and A. J. Gaston. 1996. The effect of age on timing of breeding and reproductive success in the thick-billed murre. *Ecology* **77**:1501-1511.
- Douglas, S. D., and T. E. Reimchen. 1988. Reproductive phenology and early survivorship in red-throated loons, *Gavia stellata*. *Canadian Field Naturalist* **102**:701-704.
- Furness, R. W., J. J. D. Greenwood, and P. J. Jarvis. 1993. Can birds be used to monitor the environment? Pages 1-41 in R. W. Furness and J. J. D. Greenwood, editors. *Birds as monitors of environmental change*. Chapman and Hall, New York, New York, USA.
- Gaston, A. J., L. DeForest, G. Donaldson, and D. G. Noble. 1994. Population parameters of Thick-billed Murres at Coats Island, Northwest Territories, Canada. *Condor* **96**:935-948.
- Harris, M. P. 1991. Population changes in British Common Murres and Atlantic Puffins, 1969-88. Pages 52-61 in A. J. Gaston and R. D. Elliot, editors. *Studies of high-latitude seabirds. 2. Conservation biology of Thick-Billed Murres in the northwest Atlantic*. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Harris, M. P., D. J. Halley, and R. L. Swann. 1994. Age of first breeding in Common Murres. *Auk* **111**:207-209.
- Harris, M. P., and S. Wanless. 1995. Survival and non-breeding of adult Common Guillemots *Uria aalge*. *Ibis* **137**:192-197.
- Hatch, S., and M. A. Hatch. 1990. Components of breeding productivity in a marine bird community: key factors and concordance. *Canadian Journal of Zoology* **68**:1680-1690.
- Hatchwell, B. J., and T. R. Birkhead. 1991. Population dynamics of Common Guillemots *Uria aalge* on Skomer Island, Wales. *Ornis Scandinavica* **22**:55-59.
- Hedgren, S. 1980. Reproductive success of guillemots *Uria aalge* on the island of Stora Karlsö. *Ornis Fennica* **57**:49-57.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, New Jersey, USA.
- Hudson, P. J. 1985. Population parameters for the Atlantic Alcidae. Pages 233-261 in D. N. Nettleship and T. R. Birkhead, editors. *The Atlantic Alcidae: the evolution, distribution and biology of the Auks inhabiting the Atlantic Ocean and adjacent water areas*. Academic Press, New York, New York, USA.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* **78**:1069-1078.
- Marquis, R. J., and C. F. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* **75**:2007-2014.
- Melvin, E. F., J. K. Parrish, and L. L. Conquest. 1999. Novel tools to reduce seabird bycatch in coastal gillnet fisheries. *Conservation Biology* **13**:1386-1397.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* **65**:21-74.
- Murphy, E. C., and J. H. Schauer. 1994. Numbers, breeding chronology, and breeding success of Common Murres at Bluff, Alaska, in 1975-1991. *Canadian Journal of Zoology* **72**:2105-2118.
- Norman, D. N., A. M. Breault, and I. E. Moul. 1989. Bald eagle incursions and predation at great blue heron colonies. *Colonial Waterbirds* **12**:215-217.
- Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* **10**:949-963.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**:667-685.

- Paine, R. T., J. T. Wootton, and P. D. Boersma. 1990. Direct and indirect effects on peregrine falcon predation on seabird abundance. *Auk* **107**:1–9.
- Parrish, J. K. 1995. Influence of group size and habitat type on reproductive success on Common Murres (*Uria aalge*). *Auk* **112**:390–401.
- Parrish, J. K., and R. T. Paine. 1996. Ecological interactions and habitat modification in nesting Common Murres, *Uria aalge*. *Bird Conservation International* **6**:261–269.
- Piatt, J. F., and P. Anderson. 1996. Response of Common Murres to the *Exxon Valdez* oil spill and long-term changes in the Gulf of Alaska Marine Ecosystem. Pages 720–737 in S. D. Rice, R. B. Spies, D. A. Wolfe, and B. A. Wright, editors. Proceedings of the *Exxon Valdez* Oil Spill Symposium, American Fisheries Society Symposium **18**.
- Polacheck, T., R. Hilborn, and A. E. Punt. 1993. Fitting surplus production models: comparing methods and measuring uncertainty. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:2597–2607.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**:652–661.
- Regehr, H. M., and M. S. Rodway. 1999. Seabird breeding performance during two years of delayed capelin arrival in the northwest Atlantic: a multi-species comparison. *Waterbirds* **22**:60–67.
- Schoener, T. W. 1993. On the relative importance of direct versus indirect effects in ecological communities. Pages 365–415 in H. Kawanabe, J. E. Cohen, and J. K. Iwasaki, editors. *Mutualism and community organizations*. Oxford University Press, Oxford, UK.
- Schwing, F. B., T. Murphree, and P. Green. 2001. A climate index for the Northeast Pacific. *Progress in Oceanography*, *in press*.
- Slagsvold, T. 1980. Habitat selection in birds: on the presence of other bird species with special regard to *Turdus pilaris*. *Journal of Animal Ecology* **49**:523–526.
- Spencer, C. N., B. R. McClelland, and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and the eagle displacement. *BioScience* **41**:14–21.
- Swann, R. L., and A. D. K. Ramsay. 1983. Movements from and age of return to an expanding Scottish Guillemot colony. *Bird Study* **30**:207–214.
- Sydeman, W. J. 1993. Survivorship of Common Murres on Southeast Farallon Island, California. *Ornis Scandinavica* **24**:135–141.
- Sydeman, W. J., and J. O. Eddy. 1995. Repeatability in laying date and its relationship to individual quality for Common Murres. *Condor* **97**:1048–1052.
- Takekawa, J. E., H. R. Carter, and T. E. Harvey. 1990. Decline of the Common Murre in central California, 1980–1986. *Studies in Avian Biology* **14**:149–163.
- Verbeek, N. A. M. 1982. Egg predation by northwestern crows: its association with human and bald eagle activity. *Auk* **99**:347–352.
- Wilson, U. W. 1991. Responses of three seabird species to El Niño events and other warm episodes on the Washington coast, 1979–1990. *Condor* **93**:853–858.
- Wootton, J. T. 1994a. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* **25**:443–466.
- Wootton, J. T. 1994b. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* **75**:151–165.
- Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* **69**:508–515.