REPRODUCTIVE INDICES OF COMMON MURRES *URIA AALGE* AND MARBLED MURRELETS *BRACHYRAMPHUS MARMORATUS* INDICATE MURRELETS ARE MORE RESILIENT DURING POOR YEARS

CRAIG S. STRONG[1] & ADAM DUARTE[2]

[1]*Crescent Coastal Research, 260 Hazeltime Road, Crescent City, California 95531, USA (strongcraig1@gmail.com)*
[2]*USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington 98512, USA (adam.duarte@usda.gov)*

Received 07 September 2022, accepted 10 April 2003

ABSTRACT

STRONG, C.S. & DUARTE, A. 2023. Reproductive indices of Common Murres *Uria aalge* and Marbled Murrelets *Brachyramphus marmoratus* indicate murrelets are more resilient during poor years. *Marine Ornithology* 51: 187–194.

Fledgling encounter rates at sea were used as measures of annual reproductive performance for Common Murres *Uria aalge* and Marbled Murrelets *Brachyramphus marmoratus* over 29 years in two marine biogeographic regions off the coast of Oregon, USA, north and south of Cape Blanco. In both bioregions, the adult murre population was much larger and the encounter rate of murre fledglings was much higher than for murrelets overall, but the apparent decline in productivity during El Niño events and years of poor foraging was significantly greater in murres than in murrelets. We conclude that murrelets are better at coping with variations in food availability as a function of ocean conditions. Different foraging strategies and body sizes may explain the differential success rates during years of low prey availability.

Key words: Common Murre, *Uria aalge*, Marbled Murrelet, *Brachyramphus marmoratus,* ENSO, California Current, seabird productivity, marine climate

INTRODUCTION

Seabird productivity is demonstrably affected by large-scale oceanographic events such as El Niño Southern Oscillation (ENSO; see Hodder & Graybill 1985, Schmidt *et al.* 2014) and, more recently, marine heat waves (Piatt *et al.* 2020). Such variation in ocean climate can lead to local and regional depressions in prey resources that, in turn, decrease seabird productivity (Becker & Beissinger 2003, Schneider 2018). With climate change, extreme weather events are becoming more common on the west coast of the continental USA, with likely large-scale effects on many seabird populations.

Common Murres *Uria aalge* (hereafter, murres) are abundant throughout the California Current System and were once considered to be a bastion of stability in their reproductive success. Indeed, reproductive success varied only slightly in the 1970s and 1980s, around 0.7 chicks per nest per year (standard deviation = 0.097, n = 12 study locations; Manuwal & Carter 2001). This, among other factors, has allowed murre populations to increase (Meade *et al.* 2013) and to recover from catastrophic or chronic impacts in localized regions, such as oil spills, fishery depletion, and bycatch (Carter *et al.* 2001, Warzybok *et al.* 2018). For the past 30+ years, murres breeding at colonies ranging from the state of Washington to central Oregon have faced increasing predation and disturbance from Bald Eagles *Haliaeetus leucocephalus* (hereafter, eagles; Parrish *et al.* 2001, Horton *et al.* 2014). Eagle numbers (and thus predation on and disturbance to murres) have expanded progressively south through Oregon since 1995, and multiple murre colonies have disappeared entirely (Naughton *et al.* 2007). Eagles eat relatively few adult murres; however, other factors such as adult murre displacement and secondary predation of murre chicks and eggs by gulls and crows, reproductive failure, and emigration due to chronic eagle disturbance are thought to be the most likely reasons for colony abandonment (Horton *et al.* 2014). Although more recent estimates are unavailable, an estimated 856 000 nesting murres were present on the Oregon coast around the turn of the century (Naughton *et al.* 2007). Presently, the highest abundances occur in southern Oregon, where numerous sea stacks and islands provide nesting habitat and where eagle predation has yet to have a documented impact.

Like murres, Marbled Murrelets *Brachyramphus marmoratus* (hereafter, murrelets) were once a very successful and abundant alcid on the west coast. The murrelet's downfall has been linked to industrial logging of the old-growth forest (1850–1980) that the species requires for nesting habitat (Marshall 1988, Nelson 1997). In this century, more forest habitat has been lost due to wildfires (Raphael *et al.* 2016, Betts *et al.* 2020). Predation on eggs and nestlings in the forest by corvids also remains a primary factor affecting the species (Nelson 1997). As such, the murrelet is currently listed as Threatened under the US Endangered Species Act, and as Threatened or Endangered in the states of Washington, Oregon, and California (McIver *et al.* 2021). There are 21 700 murrelets nesting along the west coast of the USA, including ~10 300 murrelets on the Oregon coast (Felis *et al.* 2020, McIver *et al.* 2021). In Oregon, murrelets now occur at peak abundance in the near-shore waters of central Oregon, adjacent to the largest stands of high-quality nesting habitat in the Siuslaw National Forest (Raphael *et al.* 2015, McIver *et al.* 2021).

The marine habitats used by murres and murrelets overlap, with peak abundance for both species occurring in the very near-shore waters (< 1.5 km from shore, Strong 2009). Murrelets rarely occur beyond 4 km from the coast (Ralph & Miller 1995), in contrast to murres, which occur more broadly over the continental shelf (Lierness *et al.* 2021). Both species are primarily piscivorous during the nesting season when energetic demands are at their greatest (Matthews 1983, Burkett 1995, Nelson 1997), but they also prey on pelagic and near-shore invertebrates (Ainley *et al.* 1996, Becker & Beissinger 2003).

Nesting success can be directly quantified for murres at colonies, where individual pairs can be tracked throughout the season (e.g., Boekelheide *et al.* 1990, Burke & Montevecchi 2008). No such opportunity exists for murrelets because of their dispersed nesting high in mature trees across forested landscapes. However, decreased nesting propensity has been documented under lower-quality marine foraging conditions (Lorenz & Raphael 2018, Betts *et al*. 2020).

Recently fledged hatch-year (HY) birds of both species can be observed at sea and are distinguishable from adults by plumage. The abundance of HY birds on the water provides a useful and standardized indicator of relative productivity (Kuletz & Piatt 1999, Strong 2019). While the ratio of HY to adult birds has been used as a measure of productivity for murrelets (McShane *et al.* 2004), we instead used the encounter rate of HY birds at sea as an index of productivity. This avoids the assumption of equal distribution by age class.

We were interested in evaluating the existence of differences in relative productivity of murres and murrelets in response to variable ocean conditions along the Oregon coast. To accomplish this, we used the encounter rate of HY murres and murrelets during at-sea transect surveys over 29 years. Years were assessed as having poor prey availability based on ENSO, the marine heat wave of 2015–2017, and regional depressions in prey availability. We hypothesized that murrelet productivity would be less impacted by poor ocean conditions than murre productivity due to the murrelet's lower energetic needs (their average weight is just over one-fifth that of murres, Sibley 2003) and likely differences in foraging strategy.

METHODS

Study area

Our sampling area was the near-shore marine habitat of the Oregon coast (Fig. 1). This includes all of Conservation Zone 3 and the

Fig. 1. The coast of Oregon is indicated by the thick black vertical line on the inset map of the North America, and it is expanded to show higher-quality Marbled Murrelet *Brachyramphus marmoratus* nesting habitat (shaded areas) and the division between US Marbled Murrelet Recovery Plan Conservation Zones 3 and 4, relative to Cape Blanco. Figure adapted from Lorenz *et al.* (2021). Inset map: https://commons.wikimedia.org/wiki/File:Saint_Kitts_and_Nevis_in_North_America_(-mini_map_-rivers).svg.

Oregon portion of Conservation Zone 4, as designated in the Marbled Murrelet Recovery Plan (USFWS 1997). Differences in survey coverage of Zones 3 and 4 include less transect coverage in Zone 4, particularly prior to 2009, and alternating years of coverage between the Zones since 2014 (see Table 1). Also, the outer limit of sampling was set at 5 km in Zone 3 and at 3 km in Zone 4 (see Bentivoglio *et al.* (2002) for an explanation of the difference in sampled areas). The boundary between the Zones is at the mouth of Coos Bay, which closely approximates the bioregional division north and south of Cape Blanco, 60 km to the south (Fig. 1). In addition to being the westernmost point in the continental US, Cape Blanco divides a moderate upwelling regime along the largely straight and sandy beaches to the north from strong upwelling centers south of Cape Blanco (Bjorkstedt *et al.* 2017). The shoreline of Zone 4 in southern Oregon is also far more heterogenous, with frequent offshore reefs and sea stacks, sheltered coves, and a more variable bathymetry.

Data collection

This work was conducted as part of the Northwest Forest Plan Effectiveness Monitoring Program for the Marbled Murrelet (McIver *et al.* 2021). The goal of the program is to assess the abundance and trends of murrelets at sea. While murrelets are

TABLE 1
Summary of survey effort and fledgling (HY) detections for Common Murres *Uria aalge* and Marbled Murrelets *Brachyramphus marmoratus* by year and year quality in two regions on the coast of Oregon, USA

	Zone 3, Central & northern Oregon					Zone 4, Southern Oregon				
	Survey effort		HY detections		Year quality	Survey effort		HY detections		Year quality
Year	km	Days	Murre	Murrelet		km	Days	Murre	Murrelet	
1992	361.1	7	0	14	Good	180.8	2	19	15	Good
1993	712.2	13	8	22	Poor	128.2	2	0	3	Poor
1994	0	0	No data		Good	0	0	No data		Good
1995	474.9	7	288	11	Good	80	1	104	2	Good
1996	498.5	9	7	5	Poor	319.2	6	95	7	Good
1997	699.2	10	100	24	Good	98	3	34	8	Good
1998	626.8	9	97	17	Poor	25	1	0	3	Poor
1999	532.8	7	563	28	Good	108	2	166	1	Good
2000	553.1	10	792	8	Good	131.2	4	210	7	Good
2001	551.7	9	1 078	13	Good	90.4	4	206	3	Good
2002	731.9	13	774	21	Good	52	1	51	2	Good
2003	643.9	14	184	4	Good	78.5	3	78	12	Good
2004	509.2	10	911	6	Good	67.3	3	110	0	Good
2005	323.1	6	27	0	Poor	70.6	1	6	0	Poor
2006	589.4	9	40	3	Good	112.3	3	40	13	Good
2007	549.2	9	136	0	Good	27.2	1	30	0	Good
2008	678.1	13	545	30	Good	96.3	3	366	6	Good
2009	383.8	8	705	11	Good	219.8	6	179	16	Good
2010	550.9	8	98	4	Poor	160.4	6	25	4	Poor
2011	624.9	9	158	8	Good	130	3	4	0	Good
2012	595.1	9	320	9	Good	77.2	2	58	4	Good
2013	729.8	8	615	58	Good	156.9	5	343	5	Good
2014	485.9	8	175	13	Good		0	No data		Good
2015		0	No data		?	208.3	5	116	8	Good
2016	565.5	10	21	3	Poor		0	No data		Poor
2017		0	No data		Poor	228.4	5	2	5	Poor
2018	463.8	8	234	11	Good		0	No data		Good
2019		0	No data		?	184.9	4	2	4	Poor
2020	680.4	12	365	14	Good		0	No data		Good
Total	14 115.2	235	8 518	337		3 030.9	76	2 244	128	

the focus of the research, data on all seabirds observed in the present study were collected using the same protocol consistently throughout the 29-year study period (Strong 2003, 2019).

Transects were conducted using a 21-foot vessel and a three-person crew consisting of an observer for each side of the boat and a vessel driver. While the vessel traveled at a speed of 10 knots (18 km/h) or less, each observer continuously scanned a 90° arc between the bow and the beam on their respective side, using binoculars only to confirm species identification or to observe plumage or behavior of murrelets. Search effort was directed primarily towards the bow quarters in order not to miss birds on the line (a critical assumption of line-transect sampling) and within 100 m of the vessel. All murrelet detections were recorded with information on group size, estimated perpendicular distance from the transect line (line-transect method), behavior, and age (HY vs. adult). All murre detections on the water and within 50 m of the boat (i.e., within a 100-m wide strip) were recorded, along with group size and age (also HY vs. adult). Surveys were conducted only in good weather conditions (Beaufort wind scale < 3). Data were recorded on hand-held micro audio recorders and later transcribed to electronic data forms.

Our protocol was consistent for the entire period (1992–2020), but the sampling design (i.e., where we planned transects in the near-shore area) changed in 2000 when the Northwest Forest Plan design was implemented. Prior to 2000, we ran transects parallel to the coast at 300–900 m from shore; to sample further offshore, we also conducted a set of parallel transects that were 4 km long at 500 m intervals, starting at randomly selected locations out to 3 km from shore (Strong 2003). The sampling design for the current monitoring program is described in detail by Raphael *et al.* (2007). In short, sampling was conducted within Conservation Zones. Within each zone, the coast was divided into 20-km long Primary Sampling Units (PSU). A transect was conducted through each PSU following a randomized transect route that was 350–5000 m offshore in Zone 3 and 400–3000 m offshore in Zone 4. Both designs sought to distribute survey effort geographically and temporally within the Conservation Zones.

California Current System productivity was categorized dichotomously as ‘good or average’ years and ‘poor’ years. Poor years were based on large-scale ENSO characteristics that affected both Zones in the study region. Regionally poor years, which affected productivity in only one of the Zones, were based on a combination of warm sea surface temperatures, low upwelling, adult die-offs, and colony abandonment. Details of how year quality was evaluated are in Appendix 1 (available online).

Statistical analysis

July data were chosen because both species have fledged young at sea by July, and because this is the month when most sampling effort occurred. Because there are differences in detectability of murre and murrelet HY birds at sea, as well as the different count methods used between species (line transect vs. strip survey), we analyzed the two species separately. For each species, we examined the relationship between juvenile count and day in July, zone, year quality, and the interaction between zone and year quality. We included an offset to account for variable effort (i.e., km traveled) among the different surveys, which means our response variable should be interpreted in terms of density. We also included random effects that varied by year to account for any potential temporal autocorrelation in the count data. The random effects were assumed to be normally distributed with a mean of 0 and an estimated variance. To improve convergence, day in July was standardized to have a mean of 0 and a standard deviation of 1 prior to model fitting. Although we originally fit Poisson generalized linear mixed-effect models (GLMMs) to these data, initial model checks found the observed variances were much greater than the modeled variances for both species—i.e., the data were over-dispersed (murrelet dispersion ratio: 2.58, $\chi^2 = 769.16$, $P < 0.001$; murre dispersion ratio: 47.54, $\chi^2 = 14500.33$, $P < 0.001$). Thus, we opted to fit negative binomial GLMMs. Notably, these models estimate the mean and variance of the distribution separately and are often flexible enough to efficiently handle over-dispersion in count data. All models were fitted using the “glmmTMB” package (Brooks *et al.* 2017) in program R (R Core Team 2019). We evaluated the fit of the negative binomial GLMMs by using each model to perform 10000 simulations with the “DHARMa” package (Hartig 2018). Using the output from these simulations, we visually examined quantile–quantile (Q–Q) plots of simulated scaled residuals versus expected residuals as well as plots that compared the simulated scaled residuals against the predicted value. Both diagnostics indicated good fit when the murrelet analysis incorporated a quadratic parameterization for the variance according to

$$V = \mu + \mu^2/\phi$$

and when the murre analysis incorporated a linear parameterization for the variance according to

$$V = \mu(1 + \phi)$$

RESULTS

Examination of the number of HY birds/km in July of each year for the two species show murres to generally have a much higher and much more variable encounter rate than murrelets (Fig. 2). Simple correlations of the HY encounter rate between the two species over the years was not significant in Zone 3 ($r = 0.1341$, $P = 0.275$) or Zone 4 ($r = -0.0543$, $P > 0.5$). Correlation within species between the two Zones was significant for murres ($r = 0.562$, $P = 0.003$) but not for murrelets ($r = -0.007$, $P > 0.5$).

For HY murrelets, we found that density significantly increased through July, and that Zone 4 had significantly higher densities than Zone 3 (Table 2). Although years considered to be of poor ocean condition had lower murrelet detection rates, the effect of year quality only approached significance (P$p = 0.073$; Table 2). Also, the effect of year quality on HY encounter rate did not vary by zone.

For HY murres, we also found that density significantly increased with day in July, and that Zone 4 had significantly higher densities than Zone 3. During years of poor ocean condition, HY density was significantly lower and the effect of year quality did not vary by zone. Notably, although both species had a negative relationship with poor ocean condition, the coefficient estimate for murres was more than two times the coefficient estimate for murrelets (Table 2).

DISCUSSION

We evaluated how apparent productivity varied across two geographic regions in response to variable ocean conditions for both murres and murrelets using 29 years of at-sea survey data. Overall,

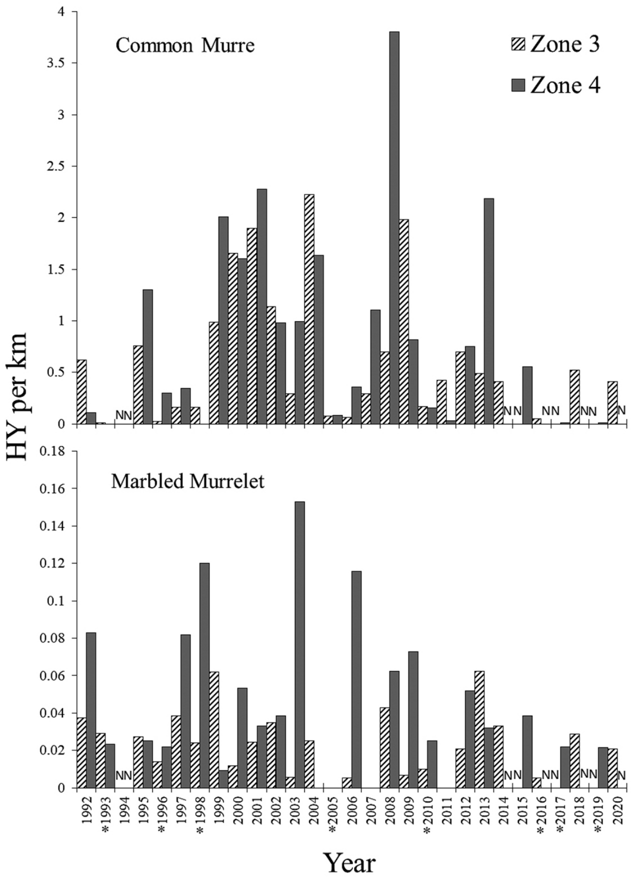

Fig. 2. Encounter rate of hatch-year (HY) Common Murres *Uria aalge* and Marbled Murrelets *Brachyramphus marmoratus* per survey km in US Marbled Murrelet Recovery Plan Conservation Zones 3 and 4 on the coast of Oregon, USA. N indicates years of no data and asterisks (*) on the x-axis are poor-quality years. Note the different scales on the y-axes.

in years of poor ocean condition for both regions off the Oregon coast, our results indicate that murrelets had a small reduction in HY densities compared to murres. It remains unclear whether the difference was due to the higher nutritional requirements of the larger-bodied murre or to different foraging strategies.

For both species, we found that HY densities were higher in Zone 4 and that densities increased with increasing day in July. Day in July was expected to be significantly positive, as more HY fledge to sea through the month for both species. Higher HY densities in Zone 4 could be expected among murres, since eagle depredation or disturbance are not presently known to affect HY production in the Oregon portion of Zone 4. However, one might expect the opposite pattern for murrelets, whose peak densities occur in central Oregon. There is some evidence that HY murrelets relocate soon after arriving at sea (Kuletz & Piatt 1999, Strong 2013), a pattern that may help explain why we found HY murrelets densities to be higher in Zone 4. Murrelet HY movements could also explain the lack of correlation between the two species. The very low murrelet HY encounter rates we described in both Zones are consistent with those found in virtually all other research on the species south of Canada (Beissinger 1995, Nelson 1997, McShane *et al.* 2004, Peery *et al.* 2006, Peery *et al.* 2007, Lorenz & Raphael 2018). Because murrelet populations are not declining as would be predicted from using either these low encounter rates or adult:HY ratios at sea (Beissinger 1995, McShane *et al.* 2004), we suspect that HY murrelets at sea are disproportionately undetected due to avoidance of survey vessels. While it is not possible to quantify that which is not seen, one behavioral characteristic of recently fledged HY murrelets at sea is rapid evasive diving (Strong 1998). Despite this unknown, the consistency of survey methods and vessel size throughout the study period allow our comparisons of relative productivity measures to be valid.

Amidst the extensive research on murres, specialization in foraging locations and prey species have been demonstrated even within the same colony (Pratte *et al.* 2017, Gulka & Davoren 2019). Prey switching is also well documented when the primary prey species is in short supply (Ainley *et al.* 1995). Murre parents also compensate in poor years by expending more energy to bring higher quantities of smaller, less energetic prey to their chick (Schrimpf *et al.*

TABLE 2
Results of the negative binomial generalized linear mixed-effect models of at-sea counts for Common Murres *Uria aalge* and Marbled Murrelets *Brachyramphus marmoratus*

	Intercept	Day in July	Zone 4	Poor years	Zone × year	Random effect	Over-dispersion
Marbled Murrelet							
Mean	–3.751	0.442	0.658	–0.456	–0.096	0.010	0.824
Standard error	0.119	0.086	0.229	0.254	0.464		
Z	–31.431	5.128	2.878	–1.794	–0.207		
P	< 0.001	< 0.001	0.004	0.073	0.836		
Common Murre							
Mean	–0.770	0.486	0.822	–0.928	–0.748	0.288	71.2
Standard error	0.160	0.064	0.158	0.311	0.499		
Z	–4.820	7.582	5.194	–2.990	–1.499		
P	< 0.001	< 0.001	< 0.001	0.003	0.134		

2012). Such flexibility has been considered a buffer in maintaining adequate chick provisioning (Harding *et al.* 2007, Schrimpf *et al.* 2012). At some point, however, prey resources can be so limited for a species that breeding-age adults either do not attempt breeding or fail to find enough prey for chick development, and reproductive success falls (Ronconi & Burger 2008, Schneider 2018). Murre father-chick pairs may travel beyond the surveyed waters during poor years in search of prey, which is an alternative explanation for our results. Moving offshore beyond the surveyed waters is possible, but it is unlikely to reduce competition or to increase prey encounters in bad years since we compared only those exceptionally poor years where seabird productivity was demonstrably limited. Though ocean conditions (a proxy for prey availability) do affect murrelet nesting propensity (Betts *et al.* 2020), our results indicate that murres are more affected and that this is occurring at a similar rate in the two regions, with and without the presence of eagle predation on murres. Of note is that, while eagle impacts on murres are undocumented in southern Oregon, disturbance effects have been noted in northern California (D. Barton pers. comm.). Murres have shown some acclimation to eagle predation in Washington, and numbers there have rebounded somewhat (Thomas & Lyons 2017).

While we have confidence in the support of our hypothesis based on this analysis, we have no information on the mechanism by which murrelets fare better in severely limiting years. The much smaller body size of murrelets is a consideration simply because less energy is required for their maintenance, and in seasons of low prey availability, murrelets may still have reserves to provide for chicks, whereas adult murres may only be able to maintain themselves. But there is more to the story than body size. A speculative hypothesis is that murres may be more reliant on schooling prey and murrelets are better able to catch individual prey. In poor years, forage fish schools are reduced or absent, but individual prey fish may still be found, which could result in the pattern uncovered in this study. This is also consistent with colonially nesting seabirds relying on one another to locate large prey patches (Ward & Zahavi 1973, Weimerskirch *et al.* 2010). Murrelets have little or no opportunity to employ the 'information center' potential that densely colonial species can use, but they apparently have some other foraging abilities that are unavailable to murres. An analysis of fine-scale distribution of murre and murrelet foraging groupings at sea may shed some light on this concept. Information on forage fish abundance, variation, and distribution in the study area remains sorely lacking.

ACKNOWLEDGEMENTS

It was Kim Nelson who pointed out the need and opportunity for this work in 1991. The Oregon Department of Fish and Wildlife supported this research through the 1990s, thanks to the efforts of Robin Brown and Martin Nugent (retired). The US Fish and Wildlife Service supported surveys since 2000 as an element of Northwest Forest Plan. We thank Naomi Bentivoglio, Patrick Jodice, Mark Huff, Gary Falxa, Deanna Lynch, and Bill McIver for their roles in coordinating this work, and the at-sea working group for maintaining the high standards of our data collection. This work was possible only with the dedicated effort of a great many capable field biologists who took part in the research over the years. This manuscript benefitted greatly by thoughtful reviews from Scott Pearson and David Ainley. The use of trade or firm names in this publication is for reader information and does not imply endorsement by the US Government of any product or service.

REFERENCES

AINLEY, D.G., SPEAR, L.B., ALLEN, S.G. & RIBIC, C.A. 1996. Temporal and spatial patterns in the diet of the Common Murre in California waters. *The Condor* 98: 691–705.

AINLEY, D.G., SYDEMAN, W.J., & NORTON, J. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. *Marine Ecology Progress Series* 118: 69–79.

BECKER, B.H. & BEISSINGER, S.R. 2003. Scale-dependent habitat selection by a nearshore seabird, the Marbled Murrelet, in a highly dynamic upwelling system. *Marine Ecology Progress Series* 256: 243–255.

BEISSINGER, S.R. 1995. Population trends of the Marbled Murrelet projected from demographic analyses. In: RALPH, C.J., HUNT, G.L., JR., RAPHAEL, M.G. & PIATT, J.F. (Eds.). *Ecology and Conservation of the Marbled Murrelet.* General Technical Report PSW-GTR-152. Albany, USA: US Forest Service, Pacific Southwest Research Station.

BENTIVOGLIO, N., BALDWIN, J., JODICE, P.G.R. ET AL. 2002. *Northwest Forest Plan Marbled Murrelet Effectiveness Monitoring: 2000 Annual Report.* Portland, USA: US Fish & Wildlife Service.

BETTS, M.G., NORTHRUP, J.M., BAILEY-GUERRERO, J.A. ET AL. 2020 Squeezed by a habitat split: Warm ocean conditions and old-forest loss interact to reduce long-term occupancy of a threatened seabird. *Conservation Letters* 13: e12745. doi:10.1111/conl.12745

BJORKSTEDT, E.P., GARCÍA-REYES, M. LOSEKOOT, M., SYDEMAN, W., LARGIER, J. & TISSOT, B. 2017. *Oceanographic context for baseline characterization and future evaluation of MPAs along California's North Coast.* Technical report to California Sea Grant for Projects. R/MPA-31A, R/MPA-31B, and R/MPA-31C. Arcata, USA: California Polytechnical University, Humboldt.

BOEKELHEIDE, R.J., AINLEY, D.G, MORRELL, S.H., HUBER, H.R. & LEWIS, T.J. 1990. Common Murre. In: AINLEY, D.G. & BOEKELHEIDE, R.J. (Eds.). *Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community.* Stanford, USA: Stanford University Press.

BROOKS, M.E., KRISTENSEN, K. & VAN BENTHEM, K.J. ET AL. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9: 378–400.

BURKE, C.M. & MONTEVECCHI, W.A. 2008. Fish and chicks: Forage fish and chick success in co-existing auks. *Waterbirds* 31: 372–384.

BURKETT, E.E. 1995. Marbled Murrelet food habits and prey ecology. In: RALPH, C.J., HUNT, G.L., JR., RAPHAEL, M.G. & PIATT, J.F. (Eds.). *Ecology and Conservation of the Marbled Murrelet.* General Technical Report PSW-GTR-152. Albany, USA: US Forest Service, Pacific Southwest Research Station.

CARTER, H.R., WILSON, U.W., LOWE, R.W. ET AL. 2001. Population trends of the Common Murre (*Uria aalge californica*). In: MANUWAL, D.A., CARTER, H.R. ZIMMERMAN, T.S. & ORTHMEYER, D.L. (Eds.). *Biology and Conservation of the Common Murre in California, Oregon, Washington, and British Columbia. Volume 1: Natural History and Population Trends.* Information and Technology Report USGS/BRD/ITR-2000-0012. Washington, USA: US Geological Survey, Biological Resources Division.

FELIS, J.J., KELSEY, E.C., ADAMS, J., HORTON, C. & WHITE, L. 2020. *Abundance and productivity of Marbled Murrelets (*Brachyramphus marmoratus*) off central California during the 2019 breeding season.* Data Series 1123. Santa Cruz, USA: US Geological Survey. doi:10.3133/ds1123

GULKA, J. & DAVOREN. G.K. 2019. High individual flexibility in the foraging behavior of a marine predator, the Common Murre. *Marine Biology* 166: 83. doi:10.1007/s00227-019-3530-4

HARDING, A.M.A., PIATT, J. F., SCHMUTZ, J.A. ET AL. 2007. Prey density and the behavioral flexibility of a marine predator, the Common Murre (*Uria aalge*). *Ecology* 88: 2024–2033. doi:10.1890/06-1695.1

HARTIG, F. 2018. *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models.* R package version 0.2.0. Regensburg, Germany: University of Regensburg. [Accessed at https://CRAN.R-project.org/package=DHARMa on 06 February 2021.]

HODDER, J. & GRAYBILL, M.R. 1985. Reproduction and survival of seabirds in Oregon during the 1982–1983 El Niño. *The Condor* 87: 535–541.

HORTON, C.A., SURYAN, R.M., DUGGER, K.M. ET AL. 2014. Return of a native predator: Colonial seabird response to an expanding Bald Eagle population. In: HORTON, C.A. *Top-Down Influences of Bald Eagles on Common Murre Populations in Oregon*. MSc thesis. Corvallis, USA: Oregon State University.

LIERNESS, J., ADAMS, J., BALLANCE, L.T. ET AL. 2021. *Modeling At-Sea Density of Marine Birds to Support Renewable Energy Planning on the Pacific Outer Continental Shelf of the Contiguous United States*. OCS Study, BOEM 2021-014. Camarillo, USA: US Department of the Interior, Bureau of Ocean Energy Management.

LORENZ, T.J. & RAPHAEL, M.G. 2018. Declining Marbled Murrelet density, but not productivity, in the San Juan Islands, Washington, USA. *The Condor* 120: 201–222. doi:10.1650/CONDOR-17-122.1

LORENZ, T.J., RAPHAEL, M.G., YOUNG, R.D., LYNCH, D., NELSON, S.K. & MCIVER, W.R. 2021. *Status and trend of nesting habitat for the Marbled Murrelet under the Northwest Forest Plan, 1993 to 2017.* General Technical Report PNW-GTR-998. Portland, USA: US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

KULETZ, J.K. & PIATT, J.F. 1999. Juvenile Marbled Murrelet nurseries and the productivity index. *The Wilson Bulletin* 111: 257–261.

MANUWAL, D.A. & CARTER, H.R. 2001. Natural history of the Common Murre. In: MANUWAL, D.A., CARTER, H.R., ZIMMERMAN, T.S. & ORTHMEYER, D.L. (Eds.). *Biology and Conservation of the Common Murre in California, Oregon, Washington, and British Columbia. Vol. 1: Natural History and Population Trends.* Information and Technology Report USGS/BRD/ITR-2000-0012 Washington, USA: US Geological Survey, Biological Resources Division.

MARSHALL, D.B. 1988. *Status of the Marbled Murrelet in North America: With Special Emphasis on Populations in California, Oregon, and Washington.* Biological Report 88, US Fish & Wildlife Service. Portland, USA: Audubon Society of Portland.

MATTHEWS, D.R. 1983. *Feeding ecology of the Common Murre,* Uria aalge*, off the Oregon Coast.* MSc thesis. Corvallis, USA: Oregon State University.

MCIVER, W.R., PEARSON, S.F., STRONG, C.S. ET AL. 2021. *Status and Trend of Marbled Murrelet Populations in the Northwest Forest Plan Area, 2000 to 2018.* General Technical Report PNW-GTR-996. Portland, USA: US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

MCSHANE, C., HAMER, T., CARTER, H. ET AL. 2004. *Evaluation Report for the 5-Year Status Review of the Marbled Murrelet in Washington, Oregon and California.* Unpublished report. Seattle, USA: EDAW, Inc.

MEADE, J., HATCHWELL, B.J., BLANCHARD, J.L. & BIRKHEAD, T.R. 2013. The population increase of Common Guillemots *Uria aalge* on Skomer Island is explained by intrinsic demographic properties. *Journal of Avian Biology* 44: 55–61.

NAUGHTON, M.B., PITKIN, D.S., LOWE, R.W., SO, K.J. & STRONG, C.S. 2007. *Catalog of Oregon Seabird Colonies.* Biological Technical Publication BTP-R1009-2007. Washington, USA: US Fish and Wildlife Service.

NELSON, S.K. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). In: POOLE, A.F. & GILL, F.B. (Eds.) *The Birds of North America, No. 276*. Philadelphia, USA: The Academy of Natural Sciences; Washington, USA: The American Ornithologists' Union.

PARRISH, J.K., MARVIER, M. & PAINE, R.T. 2001. Direct and indirect effects: Interactions between Bald Eagles and Common Murres. *Ecological Applications* 11: 1858–1869.

PEERY, M.Z., BECKER, B.H. & BEISSINGER, S.R. 2006. Combining demographic and count-based approaches to identify source–sink dynamics of a threatened seabird. *Ecological Applications* 16: 1516–1528.

PEERY, M.Z., BECKER, B.H. & BEISSINGER, S.R. 2007. Age ratios as estimators of productivity: Testing assumptions on a threatened seabird, the Marbled Murrelet. *The Auk* 124: 224–240.

PIATT, J.F., PARRISH J.K., RENNER H.M. ET AL. 2020. Extreme mortality and reproductive failure of Common Murres resulting from the northeast Pacific marine heatwave of 2014–2016. *PLoS One* 15: e0226087. doi:10.1371/journal.pone.0226087

PRATTE, I., ROBERTSON, G.J. & MALLORY, M.L. 2017. Four sympatrically nesting auks show clear resource segregation in their foraging environments. *Marine Ecology Progress Series* 572: 243–254. doi:10.3354/meps12144

R CORE TEAM. 2019. *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

RALPH, C.J. & MILLER, S.L. 1995. Offshore population estimates of Marbled Murrelets in California. In: RALPH, C.J., HUNT, G.L., JR. RAPHAEL, M.G. & PIATT, J.F. (Eds.). *Ecology and Conservation of the Marbled Murrelet*. General Technical Report PSW-GTR-152. Albany, USA: Pacific Southwest Research Station, Forest Service.

RAPHAEL, M.G., BALDWIN, J., FALXA, G.A. ET AL. 2007. *Regional Population Monitoring of the Marbled Murrelet: Field and Analytical Methods.* General Technical Report PNW-GTR-716. Portland, USA: US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

RAPHAEL, M.G., FALXA, G.A., LYNCH, D. ET AL. 2016. Status and trend of nesting habitat for the Marbled Murrelet under the Northwest Forest Plan. In: FALXA, G.A. & RAPHAEL, M.G. (Eds.). *Northwest Forest Plan—The First 20 Years (1994–2013): Status and Trend of Marbled Murrelet Populations and Nesting Habitat.* General Technical Report PNW-GTR-933. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

RAPHAEL, M.G., SHIRK, A.J., FALXA, G.A. & PEARSON S.F. 2015. Habitat associations of Marbled Murrelets during the nesting season in nearshore waters along the Washington to California coast. *Journal of Marine Systems* 146: 17–25. doi:10.1016/j.jmarsys.2014.06.010

RONCONI, R.A. & BURGER, A.E. 2008. Limited foraging flexibility: Increased foraging effort by a marine predator does not buffer against scarce prey. *Marine Ecology Progress Series* 366: 245–258.

SCHMIDT, A.E., BOTSFORD, L.W., EADIE, J.M. ET AL. 2014. Non-stationary seabird responses reveal shifting ENSO dynamics in the northeast Pacific. *Marine Ecology Progress Series* 499: 249–258. doi:10.3354/meps10629

SCHNEIDER, S.R. 2018. *Reproductive Performance, Foraging Effort, and Diet of an Apex Predator, the Common Murre, at One of the Largest Nesting Colonies in the California Current System*. MSc thesis. Moss Landing, USA: San Jose State University.

SCHRIMPF, M.B., PARRISH, J.K. & PEARSON, S.F. 2012. Trade-offs in prey quality and quantity revealed through behavioral compensation of breeding seabirds. *Marine Ecology Progress Series* 460: 247–259.

SIBLEY, D.A. 2003. *The Sibley Field Guide to Birds of Western North America.* New York, USA: Alfred A. Knopf, Inc.

STRONG, C.S. 1998. Techniques for Marbled Murrelet age determination in the field. *Pacific Seabirds* 25: 6–8.

STRONG, C.S. 2003. Decline of the Marbled Murrelet population on the central Oregon coast during the 1990s. *Northwestern Naturalist* 84: 31–37.

STRONG, C.S. 2009. *Seabird Abundance and Distribution during Summer off the Oregon and Southern Washington Coast.* National Fish and Wildlife Foundation Contract no. 2005-0127-006. Report prepared for the US Fish and Wildlife Service, Oregon State Fish and Wildlife Office. Crescent City, USA: Crescent Coastal Research.

STRONG, C.S. 2013. *Marine micro-habitat selection by fledgling and older Marbled Murrelets in Oregon and northern California coastal waters: Where are the kids?* Abstract presented to the Pacific Seabird Group at their 40th annual meeting, 20–24 February 2013. Portland, Oregon: Pacific Seabird Group.

STRONG, C.S. 2019. *Marbled Murrelet Population Monitoring at Sea during 2019: Results from Southern Oregon and Northern California.* US Fish & Wildlife Service cooperative agreements no. F16AC00554 and F18AC00326. Crescent City, USA: Crescent Coastal Research. Available upon request to strongcraig1@gmail.com

THOMAS, S.M. & LYONS, J.E. 2017. Population trends and distribution of Common Murre *Uria aalge* colonies in Washington, 1996–2015. *Marine Ornithology* 45: 95–102.

USFWS (US FISH & WILDLIFE SERVICE). 1997. *Recovery Plan for the Threatened Marbled Murrelet (*Brachyramphus marmoratus*) in Washington, Oregon, and California*. Portland, USA: USFWS.

WARD, P. & ZAHAVI, A. 1973. The importance of certain assemblages of birds as "information-centres" for food-finding. *Ibis* 115: 517–534.

WARZYBOK, P., SANTORA, J.A., AINLEY, D.G. ET AL. 2018. Prey switching and consumption by seabirds in the central California Current upwelling ecosystem: Implications for forage fish management. *Journal of Marine Systems* 185: 25–39.

WEIMERSKIRCH, H., BERTRAND, S., SILVA, J., MARQUES, J.C. & GOYA, E. 2010. Use of social information in seabirds: Compass rafts indicate the heading of food patches. *PLoS One* 5: e9928. doi:10.1371/journal.pone.0009928