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

Thesis · December 2018

Stephanie Schneider
H. T. Harvey & Associates

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

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Stephanie R. Schneider

December 2018

The Designated Thesis Committee Approves the Thesis Titled

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

by

Stephanie R. Schneider

APPROVED FOR THE DEPARTMENT OF MARINE SCIENCE

SAN JOSÉ STATE UNIVERSITY

December 2018

Birgitte I. McDonald, Ph.D.	Moss Landing Marine Laboratories
Thomas P. Connolly, Ph.D.	Moss Landing Marine Laboratories
Daniel C. Barton, Ph.D.	Department of Wildlife, Humboldt State University

ABSTRACT

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

by Stephanie R. Schneider

Common Murre (*Uria aalge*) are the most abundant avian apex predator nesting in the California Current System (CCS) and nesting is the most energetically demanding phase of their lifecycle. The preyscape within flight distance of their nesting colony determines whether murres produce young, how hard they must work to do so, and what prey types are available to them. This study characterized the reproductive performance, foraging effort, and prey composition of murres nesting at a previously unstudied and large nesting colony in the CCS, Castle Rock National Wildlife Refuge, over an 11-year period (2007 - 2017) intended to capture a representative range of prey conditions. Timing of upwelling, coincident with seasonal increase in prey, accounted for 70% of the variability in nest initiation by murres. Reproductive success averaged 61% and, even in the most successful years, murres approached their behavioral limit to increase foraging effort and obtain adequate prey; crossing this threshold resulted in chicks being left unattended and widespread nest failure in 3 study years (2007, 2016, and 2017). Smelt and rockfish dominated the diet in good years and anchovy dominated in bad years. Prey available to murres nesting at this large colony closely matched the amount of prey required for them to produce young and, based on current conditions, even small shifts causing demand to exceed availability could result in large-scale reproductive failure of murres as well as other seabirds nesting here.

ACKNOWLEDGMENTS

I am indebted to the efforts of the individuals that initiated the seabird research at Castle Rock National Wildlife Refuge, especially Dr. Richard T. Golightly (Professor Emeritus, Humboldt State University) and Eric T. Nelson (Refuge Manager, Humboldt Bay National Wildlife Refuge). This research program was first conceptualized in 2000 but was not actualized until 2006, and Rick and Eric were integral to the inception and continuation of this research. This research extended much longer that originally planned, and this longevity is a testament to the unwavering commitment and dedication of the core individuals to overcome persistent logistical and financial challenges.

I am thankful to all the individuals that have assisted with this research over the years. Although this list is not exhaustive, additional collaborators were essential to the success of this research. Konrad Schaad (SeeMore Wildlife Systems) helped develop and install the camera system and provided unlimited technical support even after SeeMore Wildlife went out of business. Pia Gabriel (Humboldt State University) oversaw many administrative aspects of the project and regularly assisted with installation and removal of gear on the island, often without pay and once on Thanksgiving. Gerry McChesney (Manager of Farallon Islands National Wildlife Refuge and Common Murre Restoration Project) was integral to the early development of this project and willingly offered his expert advice, boat driving abilities, and outdated electronic equipment. Lisa Eigner, Mike Cunha, and Katie Rian (prior M.S. students on this project) mentored me as I assumed responsibility for the scientific and electronic aspects. Ken Griggs, Kurt Roblek, and Steve Lewis (Humboldt Bay National Wildlife Refuge) each uniquely contributed to

the needs of this research and all braved the zodiac ride to the island, often highlighted by bloody knuckles and a renewed respect for the ocean. The U.S. Coast Guard Sector Humboldt Bay assisted with transportation to the island when boat-based transport was not possible. The efforts of Terry Hofstra, Candace Tinkler and John Christopher (Redwood National and State Parks) facilitated video transmission from the island to the mainland and provided creative solutions for public outreach. Lynn Roberts (U.S. Fish & Wildlife Service) always expressed great interest in the project and had a skill for finding funding opportunities when they were needed most. Last, but not least, are the field technicians that assisted with data collection over the years (Aguilar S, Bishop C, Cole M, Donnell A, Epperson J, Foster L, Lindsey J, Lockerby C, Trost A, Tucci L, Zarnes C).

I extend my greatest gratitude to my advisor, Dr. Gitte McDonald, for taking me on as her first graduate student and having confidence that I would succeed. Her mentoring helped me to improve both as a scientist and as an individual. For the duration of my time at Moss Landing Marine Laboratory she treated me like a colleague as we worked together in various capacities— learning the marine birds of Monterey Bay, serving as a graduate assistant for physiology and advanced statistics (twice!), providing mutual editorial assistance, and co-mentoring a cool REU student. Thank you!

My other committee members both provided advice and instruction that was integral to improving the theoretical and quantitative aspects of this thesis, it was an honor to receive their constructive suggestions and guidance throughout the process. Dan, a special thanks for your eagerness to speak your mind. Tom, thanks for being the first person to give me the skills and inspiration to program in Python and beyond!

TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

Apex predators, organisms that forage at the top of the food web, play a crucial role in maintaining the balance of food webs by keeping prey populations in check (Heithaus et al. 2008; Terborgh and Estes 2010). To survive and reproduce, however, they require an abundance of energy in the form of prey. Because there is inefficiency in the transfer of energy from one trophic level to the next, only highly productive and/or large ecosystems contain adequate prey to sustain predator populations (Lindeman 1942; Block et al. 2011; Scales et al. 2014; Young et al. 2015). In the ocean, the most productive areas are eastern boundary currents (GLOBEC 1992), such as the California Current System (CCS), which are characterized by wind-driven upwelling of nutrient-rich water (Hickey 1998). These productive regions attract marine predators throughout their annual cycle (Block et al. 2011). Although these upwelling zones are productive, the variability in the strength and timing of seasonal winds cause order-of-magnitude differences in their primary productivity (McGowan et al. 1998; Chavez and Messié 2009). This variability permeates through the food web, resulting in dramatic fluctuations of the abundance and composition of prey (Croll et al. 2005; Frederiksen et al. 2006). Marine predators must be able to cope with this variable preyscape. Understanding the mechanisms by which predators cope with this variability, and the limits of their ability to compensate, provides insight into their resiliency to withstand a changing marine system (Piatt et al. 2007; Frederiksen and Haug 2015; Young et al. 2015; Keogan et al. 2018).

Seabirds are unique marine predators whose nesting phenology, reproductive success, foraging effort and diet depends on, and rapidly reflects, the abundance and composition of prey in the marine environment (Montevecchi 1993; Diamond and Devlin 2003; Frederiksen et al. 2007; Piatt et al. 2007; Einoder 2009). The breeding season is the most energetically demanding part of the seabird lifecycle (Schreiber and Burger 2001; Watanuki et al. 2009), and sufficient prey is critical to a successful outcome (Scott et al. 2006; Cury et al. 2011). One mechanism by which many birds ensure that energy will be available to meet demands is to time nesting to coincide with the peak availability of prey (Shultz et al. 2009; Votier et al. 2009; Watanuki et al. 2009; Thackeray et al. 2010; Gilg et al. 2012); in the CCS, this occurs following the onset of upwelling in spring. Once nesting initiates, seabirds must remain within flight distance of their breeding colony to incubate eggs and feed chicks such that areas accessible for foraging are drastically reduced relative to non-breeding periods due to this shift to central-place foraging (Orians and Pearson 1979). For the duration of nesting, seabirds are entirely reliant on the prey available within flight distance of their breeding colonies to meet the needs of themselves and their young (Birt et al. 1987). To maintain adequate provisioning despite localized variability in the preyscape during this time, seabirds must modify their foraging effort and prey choice to compensate (Lewis et al. 2001; Burke and Montevecchi 2009; Pichegru et al. 2010), minimizing effort when prey are readily available and maximizing effort when prey become difficult to acquire. Thus, the prey community within flight distance of breeding colonies determines when seabirds should initiate nesting, if seabirds can meet the energetic needs of their young, how hard they must work to do so, and what prey types they can find.

The most abundant seabird nesting in the CCS is the Common Murre (*Uria aalge*; hereafter murre), a piscivorous pursuit diver. Changes in the population size of murres are slow to reflect sub-lethal reductions in marine productivity since they can survive for decades without reproducing (Diamond and Devlin 2003; Ainley and Hyrenbach 2010). In contrast, murre reproductive performance, foraging effort, and diet reflect variability in the local prey community in the span of days and weeks (Ainley et al. 1996; Diamond and Devlin 2003; Schrimpf et al. 2012; Gladics et al. 2014). Murres typically fledge young even in years when prey are relatively scarce (Boekelheide et al. 1990). They compensate for reductions in prey by increasing their foraging effort (Burger and Piatt 1990; Harding et al. 2007); when prey are abundant, chick-rearing murres spend up to 40% of their day together at the colony but, as prey become scarce, time spent at the colony is traded for time searching for prey so that chicks are adequately fed. Although rare, during periods of extreme prey scarcity, murres have been observed to leave chicks unattended at the colony while both members of a chick-rearing pair search for prey (Ainley et al. 2002; Ashbrook et al. 2008; Eigner 2009).

Common murre are easily observed at the colony, are diurnally active, and deliver whole prey to their chick. Therefore, colony-based surveys are an effective method to quantify their reproductive performance, time-allocation, and the composition of prey fed to chicks. These metrics are essential to identify the mechanisms that underly changes in abundance, gain insights into seabird population health, and facilitate development of a baseline characterization of the seabird prey community from which to detect future change (Diamond and Devlin 2003; Einoder 2009; Gaston et al. 2009). Colony-based studies of murres can also provide insights into whether behavioral flexibility exists, both among and within individuals, and determine the consequence for reproductive success (Bolnick et al. 2003; Grémillet and Charmantier 2010).

The most comprehensive colony-based studies of murres nesting in the CCS are from the Farallon Islands (1971-2018), a major seabird colony in central California (Boekelheide et al. 1990). It is often assumed that observations from the Farallon Islands are generalizable to a broader oceanographic region, inclusive of Castle Rock in northern California, due to oceanographic similarities (GLOBEC 1992; Batchhelder et al. 2002; Tynan et al. 2005; Roth et al. 2008; Bjorkstedt et al. 2012). However, there is mounting evidence that marine productivity is not homogenous across this region of the CCS (Barth et al. 2005; Huyer et al. 2005; Reese and Brodeur 2006; Bograd et al. 2009). Castle Rock provided nesting habitat for more than 10% of murres nesting in the CCS at the time of the last state-wide seabird count in California (Carter et al. 1992) and has continued to increase at an average rate of 5% annually since then (Barton et al. 2017). Despite its importance to murres nesting in the CCS, Castle Rock has received little attention beyond intermittent aerial censuses to estimate the number of nesting adults beyond this current project (Jaques 2007; USFWS 2009). Furthermore, long-term seabird studies within a 300 km radius of Castle Rock have not previously occurred, with the nearest long-term studies at the Farallon Islands to the south and Yaquina Head to the north. If differences exist across the CCS, long-term measures of reproductive performance and foraging effort in this region will provide information needed to assess population-level dynamics and the resiliency of murres to withstand environmental change across the CCS (Satterthwaite et al. 2012; Oro 2014; Frederiksen and Haug 2015).

Herein, I characterize murre reproductive performance, foraging effort, and prey composition of Common Murres nesting at Castle Rock National Wildlife Refuge using an 11-year time series (2007 - 2017) with the intention of capturing a representative range of prey conditions. Measures of reproductive performance included the phenology of nest initiation and the success of those nests. Since reproduction is often timed to match peak availability of prey, the timing of nest initiation by murres at Castle Rock was predicted to vary as a function of the seasonal onset of upwelling. Since murres are known to nest successfully across a wide spectrum of marine conditions, murres nesting at Castle Rock were predicted to be consistently successful except in years when prey accessible from the colony were too scarce for individuals to maintain adequate provisioning. During the chick-rearing period, murres must capture adequate prey each day to keep themselves and their chick alive and, therefore, fluctuations in the ease of finding prey should be reflected by a suite of metrics that relate to foraging effort. For years in which prey were difficult to acquire, I predicted that chick-rearing pairs would minimize time spent together at the colony (co-attendance), leave chicks alone at the colony to maximize time searching for prey, increase the duration of foraging trips, experience lower success of chick-provisioning trips, and feed chicks fewer times per day relative to years when prey were easy to acquire. Finally, prey fed to chicks were identified to assess the composition and stability of the prey community over the study period. Although prior knowledge about murre diet in this area of the CCS is limited, recent studies indicate that the physical environment of the CCS may exhibit greater latitudinal heterogeneity than previously thought and, as such, the prey community near Castle may be distinct from other well-studied regions of the CCS.

METHODS

Study Area

Castle Rock is a 6.82-hectare island (Del Norte County Assessor’s Office 1954, 1967) located in the CCS approximately 0.8 km offshore from Crescent City, CA (Figure 1; 41^{o} 43´37´´N, 124^{o}15´00´´W). Castle Rock provides nesting habitat to all 11 seabird species that nest in this region of the CCS (Carter et al. 1992; Jaques 2007) and, based on the 1989 statewide seabird census, supports a significant percentage of seabirds nesting in California (Carter et al. 1992). To minimize disturbance to seabirds while they nest at Castle Rock, a video-based monitoring system (SeeMore Wildlife Systems Inc., Homer, Alaska) with two visible-light video cameras capable of real-time panoramic scanning (360^{o}), tilting (120^{o}), zooming, and auto-focusing were installed on the island in 2006 near the top of a rocky slope on the north side of the island (Cunha et al. 2008). Except for being a localized site with good visibility, the location of the camera system was randomly selected and does not contain unique habitat features that would enhance or diminish reproductive efforts of seabirds. As such, it is assumed that observations of seabirds within the vicinity of the monitoring system provide a representative sample of the entire colony. All video of the island, including surveys, were recorded at high resolution (29 frames per second at a resolution of 720x480 pixels) and hard drives were archived at Humboldt State University. All research at Castle Rock associated with this video-based monitoring system has been approved by Humboldt State University’s IACUC (Protocol #’s: 05/06.W.70.A, 08/09.W.54.A, 11/12.W.88-E, 15/16.W.01-E) and recognized by San Jose State University’s IACUC (Protocol #: AAA-10).

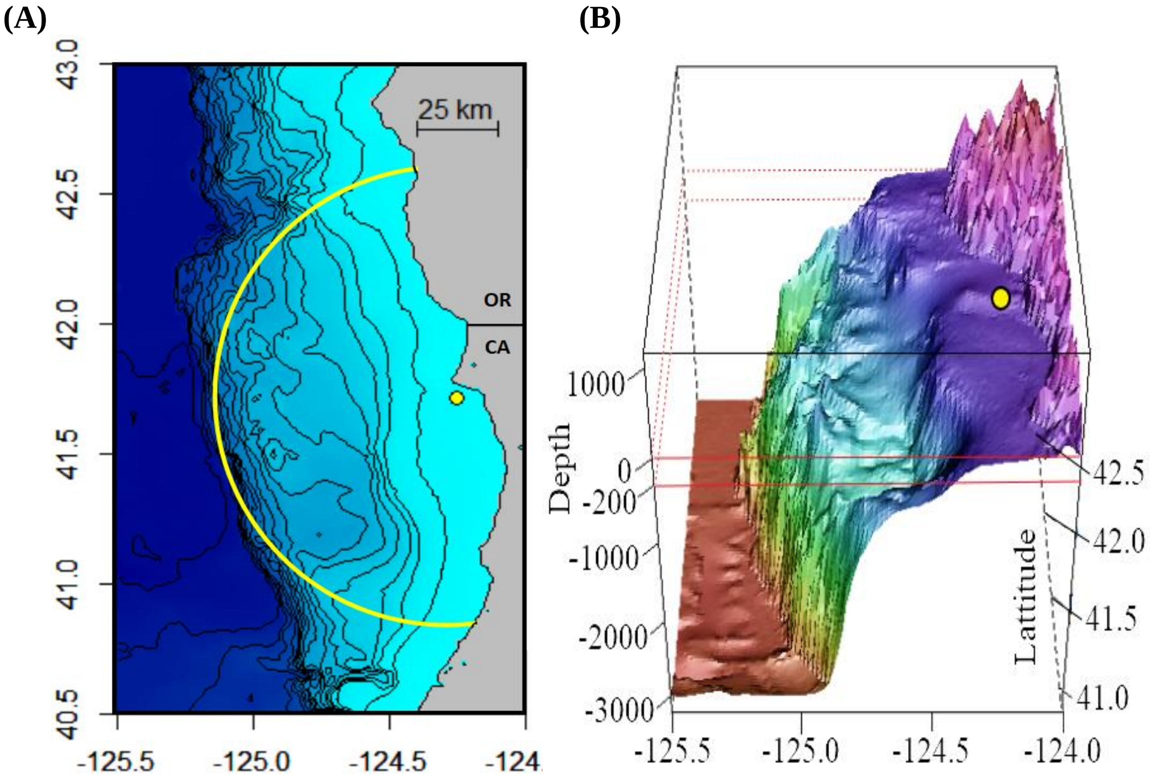


Figure 1. (A) Location of Castle Rock National Wildlife Refuge (yellow dot) with maximum foraging range (100 km; Ainley et al. 2002; Piatt, Harding, M.T. Shultz, et al. 2007) for Common Murres nesting at this colony (yellow line) and (B) bathymetric profile of the 100 km foraging range with the maximum diving range of murres (0 - 200 m; Piatt and Nettleship 1985; Hedd et al. 2009; Regular et al. 2011) bounded by the red lines.

Colony-based Surveys

Surveys were conducted to assess: the timing of nesting and reproductive success (nest surveys), murre foraging effort and chick provisioning rates (time-allocation surveys), and prey community composition (diet surveys) during each breeding season between 2007 and 2017. To ensure validity of interannual and cross-colony comparisons, all surveys followed specific protocols that approximated methods used at other breeding colonies in the CCS (Boekelheide et al. 1990; Suryan et al. 2014; Fuller et al. 2015).

Nest Surveys

Nest surveys were used to quantify the timing of nest initiation, the overall success of nests, and identify causes of failure. Nests included in these surveys were near the monitoring system because it was necessary to make detailed observations of breeding pairs, eggs, and chicks. In 2007 and 2008, all nests (~60) within a 25 m^2 area were observed and, in 2009, this area was doubled to include more nests (~120). To ensure accurate identification of each nest, still-images of the survey area were generated, and each site was labeled with a unique number. These surveys required a remote observer to move the cameras to view each nest and determine if an egg or chick was present. Observations began prior to nest initiation and continued every other day until all nesting attempts were completed.

Murres lay a single egg on bare ground, and nesting is initiated with the laying of this egg. The overall success of nests is defined as the number of nests initiated that successfully fledged young. There are two components that contribute to overall nesting success: hatching success, a measure of the proportion of eggs laid that hatched, and fledging success, proportion of chicks (based on hatched eggs) that successfully fledged. Distinction between these two periods is important because of differences in energy demands and sources of mortality. Chicks were considered fledged if they were documented alive at the colony for a minimum of 15 days and were not known to perish afterwards. This 15-day period was based on the duration of chick-rearing reported from various murre colonies in the CCS and elsewhere (Boekelheide et al. 1990) and has been commonly used in the CCS to quantify murre nest success (Eigner 2009; Fuller et al. 2015).

Time-allocation Surveys

Time-allocation surveys were used to make inferences about the ease of finding prey using a suite of metrics known to be related to foraging effort, specifically the duration chick-rearing pairs spend together at the colony, the duration chicks are left alone at the colony, the duration and success of foraging trips, and chick provisioning rates. Time-allocation surveys required an observer to position the camera to record 12 - 24 chick-rearing pairs simultaneously. Once positioned, the camera remained stationary for an entire day (from dawn until dusk). This method resulted in all focal sites being clustered in the same area of the colony; it is unlikely that this biased observations because these parameters are influenced by prey availability rather than site quality (Harding et al. 2007; Smout et al. 2013). Time-allocation surveys began when 66% of the chicks hatched and continued until all chicks at focal sites left the colony as determined by nest surveys (approximately 3 - 4 weeks). Each year, time-allocation surveys occurred six to eight days apart since they required a full day in which no other surveys occurred.

Video recordings of each time-allocation survey were subsequently reviewed to quantify daily time-allocation and provisioning rates for each site using methods described by Parker (2005) and Eigner (2009). Data for time-allocation surveys were collected from the video recordings, rather than in real-time, because recordings could be paused and re-watched to ensure that all arrivals, departures, and chick-provisioning events at each nest-site were observed. During video review, the exact time of all arrivals, departures, and chick-provisioning events at each nest-site was noted. A visual scan of each chick-rearing pair occurred every 15 minutes to confirm that arrivals and departures were not missed. If an arrival or departure was missed, the observer re-reviewed the previous 15 minutes of video to determine the exact time of the relevant change. When an individual briefly left its site (e.g., to kleptoparasitize a neighboring murre) but remained at the island, this event was not classified as a departure event. Additionally, when chicks were left unattended at the colony, an individual from a neighboring site would sometimes brood the unattended chick; although the chick was under the supervision of an adult, for purposes of quantifying the time-allocation of chick-rearing pairs, these chicks were still classified as unattended until one of their parents returned.

Diet Surveys

Diet surveys were used to assess variability in the composition of prey brought to the colony by murres during chick-rearing. Diet surveys focused on all murres within ~100 m of the camera system to ensure that enough detail for prey identification was recorded. Diet surveys required an observer to actively scan through the colony and locate adult murres possessing prey. Once located, the observer re-focused the camera onto the prey to maximize recording of morphological characteristic needed for identification. Surveys began when 10% of eggs had hatched and continued until 90% of the chicks had fledged, as determined by nest surveys.

In 2007 through 2009, the schedule of surveys followed a specific protocol developed by the Common Murre Restoration Project in central California (Eigner 2009; Fuller et al. 2015). This called for two types of surveys: entire-day surveys (06:00 - 20:00 PDT) that occurred three times during the chick-rearing period at weekly intervals, and two-hour surveys that occurred daily (except one day per week when time-allocation surveys occurred). Daylight hours were broken into seven 2-hour intervals (beginning at 06:00 and ending at 20:00) and were surveyed on a rotating schedule such that each interval was sampled approximately every seven days. In 2010, this protocol was modified to maximize the total number of prey identified and, since prey deliveries were most frequent between 06:00 and 08:00 (Golightly and Schneider 2016), diet surveys in 2010 through 2016 occurred six days per week during this time interval. Each prey observed during diet surveys were recorded and archived as individual video files to ease identification.

Video of each prey delivery was subsequently reviewed and identified to the most specific level possible using characters such as fin placement, distance between fins, tail shape and body shape based on descriptions provided by guides specific to fishes and murre prey items of the Pacific Coast (Eschmeyer and Herald 1983; Papish 1996; Eigner 2009; Orben 2009; Golightly and Schneider 2016). Video facilitated accurate identification of prey as they could be viewed from various angles, video could be reviewed frame by frame, and experts could be consulted to confirm ID of each prey type. During the identification process, coordinates (x,y) indicating the position of each prey were noted (these coordinates are exact and built into the monitoring system). If more than one prey was observed at the same location during a survey, these prey were directly compared to guarantee that each prey observation was unique.

Statistical Analyses

All analyses were done in R (R Development Core Team 2017). If data did not meet the assumptions of parametric tests described below (e.g., normality and homoscedacity), bootstrapping techniques were used to assess statistical significance and, if necessary, homogenous subsets were identified using a Sequential Bonferroni Correction. Unless otherwise noted, all results are reported as $\bar{x} \pm SE$.

Nest Phenology

Nests for which egg lay dates were accurate to ± 3 days were used to determine if the average date of nest initiation varied across the 11-year period. Replacement clutches, sometimes initiated following failure of a first clutch, were not used in this analysis. Interannual variability was assessed using an analysis of variance (ANOVA) and, if necessary, homogenous subsets were identified using Tukey's HSD (Tukey 1949).

It is widely recognized that the "spring transition" to upwelling favorable conditions has physical and ecological significance and various approaches for tracking this phenomenon have been proposed including those based strictly on physical attributes associated with upwelling (Logerwell et al. 2003; Barth et al. 2007; Holt and Mantua 2009) as well as those that also account for biological attributes indicative of this transition (Peterson et al. 2011). Because of the various methods available, I determined the date of spring transition using two different methods: (1) a cumulative approach widely used by physical oceanographers to determine the date of spring transition (Bograd et al. 2009) based on the logic that this phenomena has cumulative effects on the ecosystem and (2) a running mean approach that used a 7-day centered running mean to highlight underlying trends occurring at a scale matching the lag in time between the onset of upwelling and development of phytoplankton blooms (4-8 days; Hutchings et al. 2009; Thompson et al. 2012; Kämpf and Chapman 2016). These blooms form the base of the food web and are essential for energy transfer to higher trophic levels.

Both the cumulative and running mean approach rely on the same wind-derived coastal upwelling index (UI), an estimate of the amount of water being upwelled or downwelled (m^3 s^{-1}) for a 100 m segment of coastline (Bakun 1973; NOAA 2018), to identify the date of spring transition. Because the timing of this transition varied latitudinally (Bograd et al. 2009), only UI data from the latitude nearest Castle Rock (42^{o}N, 125 ^{o}W) was used. The cumulative approach of determining the date of spring transition required that the daily mean UI be integrated beginning on January 1st through the end of the year. The date of spring transition was identified as the date when this cumulative upwelling index (CUI) reached its minimum value, representing the point at which upwelling became net positive each year. Because the UI was derived from localized wind patterns, there was substantial day-to-day variability that masked lower frequency transitions from downwelling dominated to upwelling dominated. The running mean approach required that the UI be averaged using a 7-day running mean and then each day be classified as exhibiting moderate to strong downwelling (UI < -10), transitional (-10 < UI < 10), or moderate to strong upwelling (UI > 10). The date of spring transition was identified as the date in which moderate to strong upwelling occurred for at least 10 days and was not interrupted by a transition to moderate to strong downwelling for a sustained period (> 7 days). The logic behind these cut-off dates was that 10 days of moderate to strong upwelling should be sufficient to allow the transfer of energy from a phytoplankton bloom to primary and secondary consumers (Hutchings et al. 2009; Thompson et al. 2012; Kämpf and Chapman 2016) and that this transfer of energy to higher trophic levels would only be halted if the nutrient supply to phytoplankton was interrupted for longer than one week; in the absence of nutrients, phytoplankton abundance can decline as fast as it increased (Cloern 1996; Saito et al. 2006).

Once the date of spring transition was identified using both the cumulative and average approached summarized above, this relationship between this date and the nest initiation by murres was assessed using a linear regression. For this analysis, the date of first nest was used rather than the average initiation date because the date of first nest was known to ± 1 day and was, therefore, more accurate.

Reproductive Success

The sampling protocol for nest surveys ensured that most nests were detected in less than 48 hours from their initiation and, once detected, were observed every other day for the duration of the nesting attempt. As such, it was not necessary to adjust estimates of success to account for nests that may have failed prior to detection or nests that were not able to be checked at regular intervals. Thus, the probability of successful nesting, hatching, and fledging for each year was estimated by fitting generalized linear models (GLM) to binomial survival data (0 = failure, 1 = success) using a logit link function (Aebischer 1999; Johnson 2007; Post van der Burg et al. 2010). The Log Odds estimate of success from these GLMs was back transformed to probability of success and homogenous subsets were identified using Tukey’s HSD. These estimates excluded replacement nests which, for Common Murres, are uncommon and typically fail (Manuwal et al. 2000; Golightly and Schneider 2016). For nests that failed, the stage and cause of failure was quantified to identify drivers of nest failure.

Foraging Effort

Annual variation in foraging effort and success, in terms of providing food to chicks, was assessed using a suite of behaviors. Specific parameters of interest were the proportion of daylight hours when both members of chick-rearing pairs were present at the colony; the proportion of daylight hours when chicks were left alone at the colony; the duration of each trip to sea; the percent of trips to sea that individuals successfully procured prey for their chick; and the frequency of chick provisioning. ANOVAs were used to test for interannual variability and homogenous subsets were identified using Tukey’s HSD. To determine if the frequency of chick provisioning was related to the probability of chick mortality, each chick-rearing pair was categorized as successful or unsuccessful in fledging a chick (based on nest survey data) and a logistic regression was used.

Prey Composition

To quantify the compositional dissimilarity of the prey community across years, a non-metric multidimensional scaling based on a Bray-Curtis dissimilarity matrix was used (Bray and Curtis 1957; Beals 1984). Each day with at least 10 identified prey were included. Unidentified prey were excluded from this analysis because the ability to identify prey was limited only by the duration of observation and resulting zoom level achieved by the camera system rather than the actual identity of the prey and unidentified prey should not have bearing on prey composition in this study. Species-specific counts were standardized by the total prey identified per day because the total number of prey observed was a sampling artifact rather than reflective of actual differences in the prey community (Clarke and Warwick 2001). Additionally, relative abundance was not transformed and the contribution of rarer species was not amplified (Clarke and Warwick 2001). A stress plot was used to validate that the ordination was successful in preserving the original dissimilarities of the multidimensional data. A Similarity Percentage (SIMPER) analysis was then used to determine which prey types drive annual variation diet (Clarke 1993). To identify homogenous subsets, a Permutational Multivariate Analysis of Variance (PERMANOVA) with 10,000 iterations was used (Anderson and Walsh 2013).

RESULTS

The 11-year time series of Common Murre reproductive performance, foraging effort, and prey composition was successfully compiled from nest, time-allocation, and diet surveys at Castle Rock. However, in 2012 the video monitoring system failed early in the nesting season so only the earliest egg lay dates were recorded and only the date of the first egg observation could be determined in 2012.

Reproductive Performance

The timing and outcomes of 856 nests (86 ± 8 pairs per year) were determined between 2007 and 2017. The timing of nest initiation was different between years (ANOVA: $F_{9,846} = 190.5$, $p < 0.001$), with average egg lay date having a 25-day range over the 11 years (Figure 2); the earliest nest initiation occurred on 27-April in 2008 and latest nest initiation occurred on 22-May in 2010 and 2017 (Figure 2). Although the average date of nest initiation in 2012 could not be quantified due to premature failure of the camera system, the first egg was not observed until 15-May which was two days later than the first egg in 2017 and thirteen days later than the first egg in 2010; this indicated that the average date of nest initiation would have been later in 2012 relative to all other years. Nest initiation was earlier in years when the seasonal onset of upwelling happened early and was later in years when the transition was relatively late based on dates determined by both the cumulative approach (Figure 3A; Linear regression: $y = 0.190x + 110.0$, $R^2 = 0.571$, $F_{1,9} = 12.0$, $p = 0.007$) and the average approach (Figure 3B; Linear regression: $y = 0.204x + 108.5$, $R^2 = 0.704$, $F_{1,9} = 17.3$, $p = 0.001$).

Except for 2016 and 2017, nests initiated by murres at Castle Rock were relatively successful and interannual variability in success was minimal (Figure 4). For all years combined, nest success averaged 60.4% (95% CI: 57.1 - 63.3%), hatching success averaged 73.6% (95% CI: 70.6 - 76.5%), and fledging success averaged 82.2% (95% CI: 79.1 - 85.1%). Fledging success tended to be equal to or greater than hatching success except in 2016 and 2017 when chick mortality was 73.3% and 99.9%, respectively (Figure 4). Across all years, 226 nests failed at the egg stage and the primary causes of failure were abandonment (24%), failure to hatch despite incubation (19%), and disappearance of the egg (57%). An additional 113 nests failed at the chick stage, with 1 instance of starvation directly observed (0.8%), chicks observed dead at their nest (30%), and disappearance of the chick (69%). Based on all formal surveys and incidental observations of the colony, predation of eggs was never witnessed but there have been a limited number of instances in which chicks were observed being predated by Western Gulls (*Larus occidentalis*).

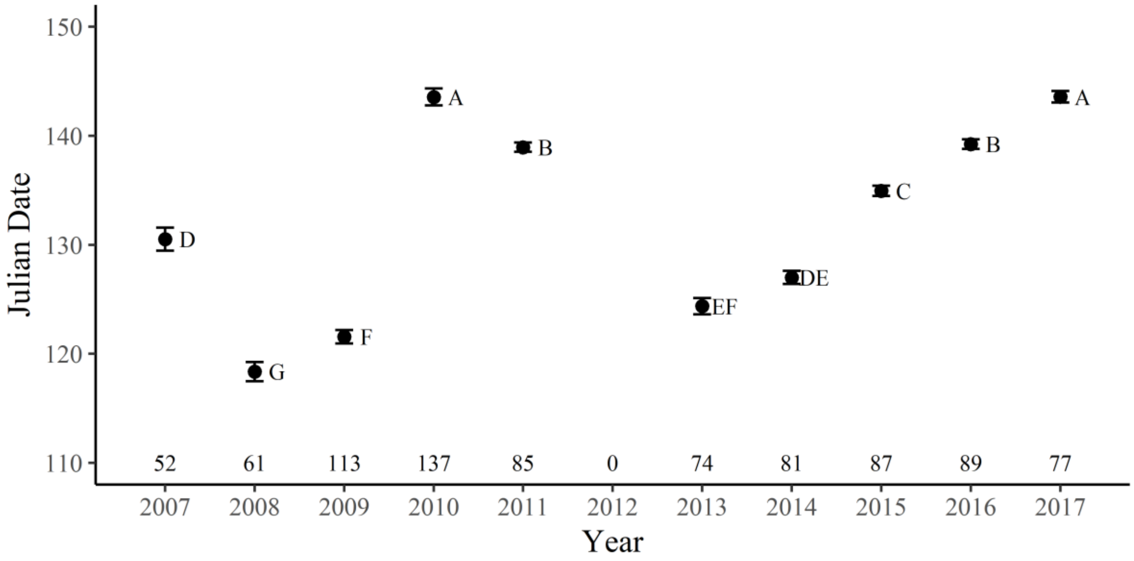


Figure 2. The timing of nest initiation by Common Murre at Castle Rock from 2007 to 2017. These calculations only included first clutches (no replacement nests) and the date of initiation was accurate to ± 3 days. Circular markers indicate the mean and error bars represent the standard error. Letters adjacent to each marker indicate homogenous subsets and sample sizes are indicated above each year.

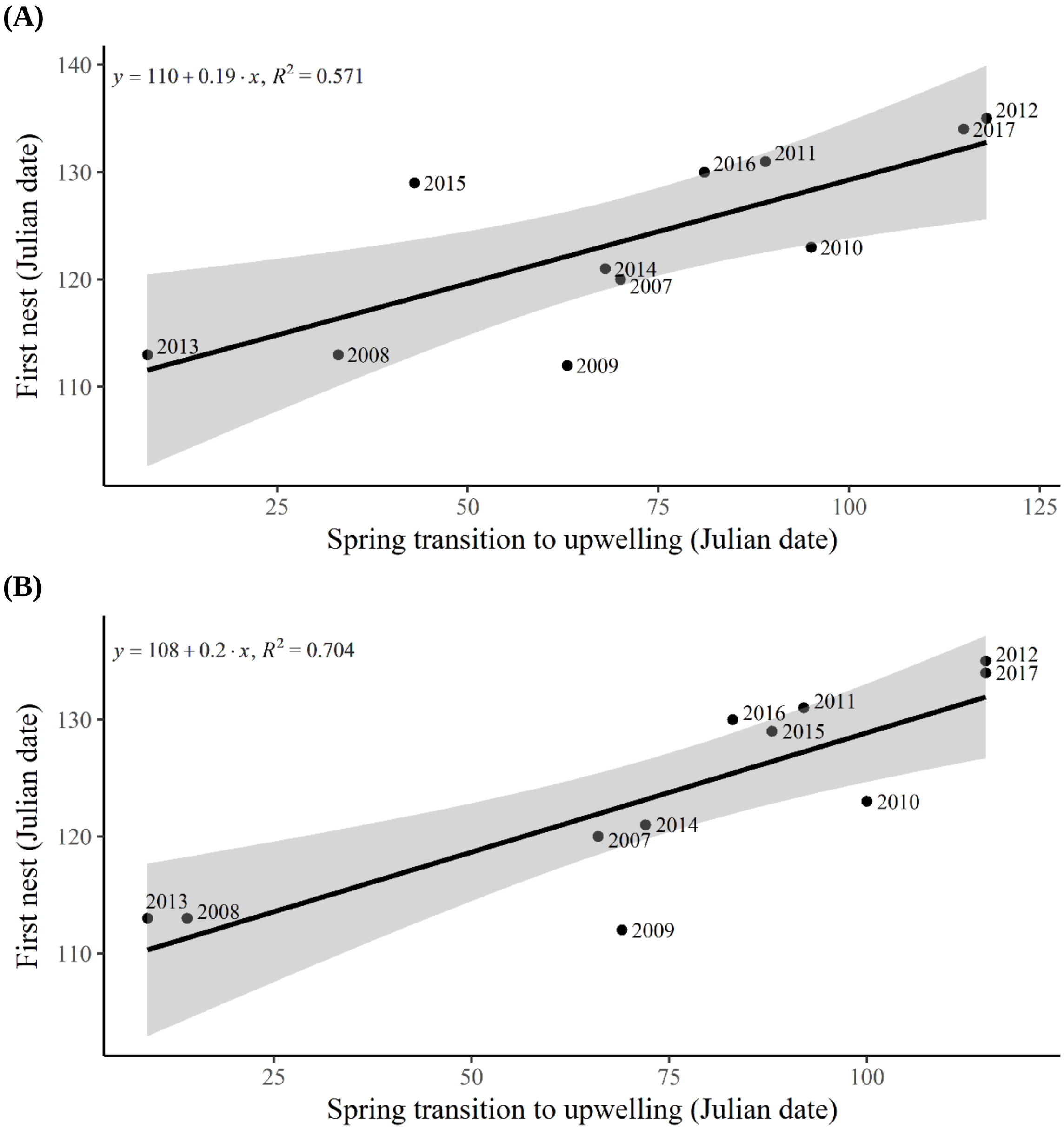
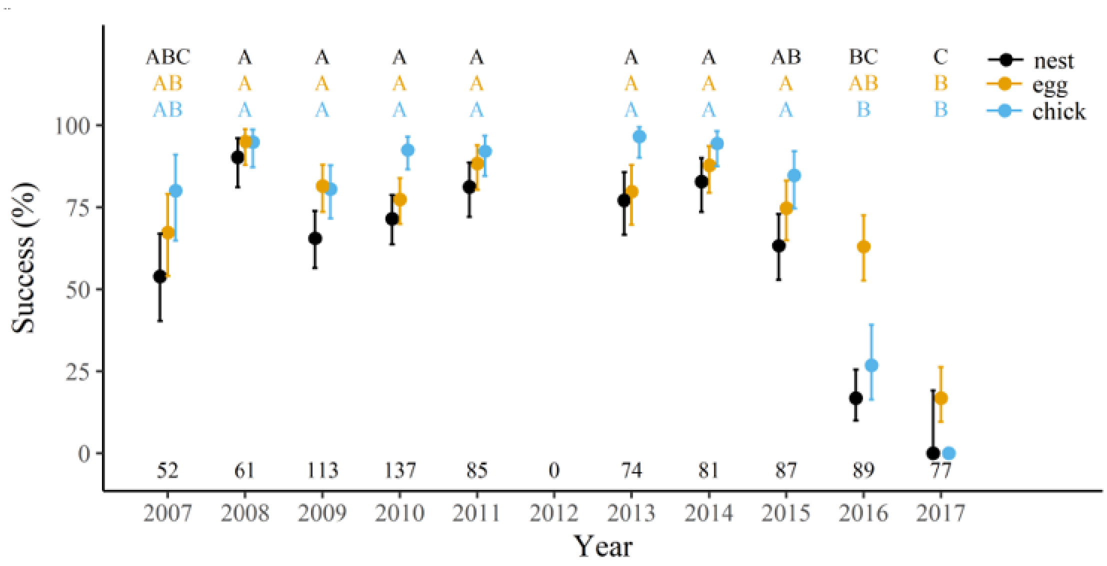


Figure 3. Relationship between the date of first egg observation at Castle Rock and the seasonal onset of upwelling based on (A) the cumulative approach for determining the date of spring transition and (B) the average approach for determining the date of spring transition. These calculations only included first clutches (no replacement nests) and the date of first egg observation was accurate to ± 1 day. Solid lines represent the linear relationship described by the equations at the top of each figure and shaded areas represent the 95% confidence limit for each line.



¶

Figure 4. Reproductive success of Common Murre nesting at Castle Rock from 2007 to 2017 as estimated by fitting a generalized linear model to binomial survival data. The proportion of nests that were successful (nest) are depicted for each year. Circular markers indicate the mean and error bars represent the 95% confidence intervals. Estimates of hatching (egg) and fledging (chick) success, the two components of nest success, are also depicted. Letters indicating homogenous subsets as determined by Tukey’s HSD were indicated above the data and color coded for clarity. Replacement nests were not included in these calculations.

Foraging Effort

To quantify behaviors indicative of foraging effort by murres, 159 chick-rearing pairs were observed between 2007 and 2017. Over this 11-year period, 476 hours of video from 24 observation days were reviewed for these purposes. In 2016, only the earliest of the time-allocation surveys occurred as many chicks died within days of hatching and chick-rearing pairs were not dense enough for time-allocation surveys. In 2017, all chicks died within a few days of hatching (oldest chick was 8 days) and there were no chick-rearing pairs available for time-allocation surveys.

All behaviors associated with forging effort varied as a function of year. The percent of daylight hours that chick-rearing pairs spent co-attending their chick at the colony was lowest in 2007, 2008, and 2016, averaging 1.3%, and was greatest in 2014 at 5.6% (Figure 5; Bootstrapping: trials = 10000, $F_{8,150} = 17.8$, $p < 0.001$). The percent of daylight hours that chicks were left unattended at the colony was greatest in 2007 at 24.9% and relatively minimal for all other years, ranging between 0.01 - 7.2% (Figure 5; Bootstrapping: trials = 10000, $F_{8,150} = 8.5$, $p < 0.001$). The average duration of at-sea trips ranged from 2.1 hours in 2013 to 6.7 hours in 2017 (Figure 6; Bootstrapping: trials = 10000, $F_{8,150} = 8.3$, $p = 0.004$). The percent of trips to sea that murres successfully returned with prey for chicks approached 100% in 2013 and remained at or above 90% in all years except 2007 and 2016, when trip success was 85% and 66%, respectively (Figure 7; Bootstrapping: trials = 10000, $F_{8,150} = 5.5$, $p = 0.026$).

The number of prey that chicks consumed in a day varied from year-to-year (ANOVA: $F_{8,150} = 10.48$, $p < 0.001$), ranging from 1.9 prey per day in 2016 to 6.4 prey per day in 2013 (Figure 8). As the number of prey fed to chicks decreased, there was a corresponding increase in probability of chick fatality presumably due to starvation (Figure 9; Logistic regression: z-stat = 3.95, df = 150, $p < 0.001$); based on this regression, chicks must be fed a minimum of 1.8 prey per day for survival probability to be 75%.

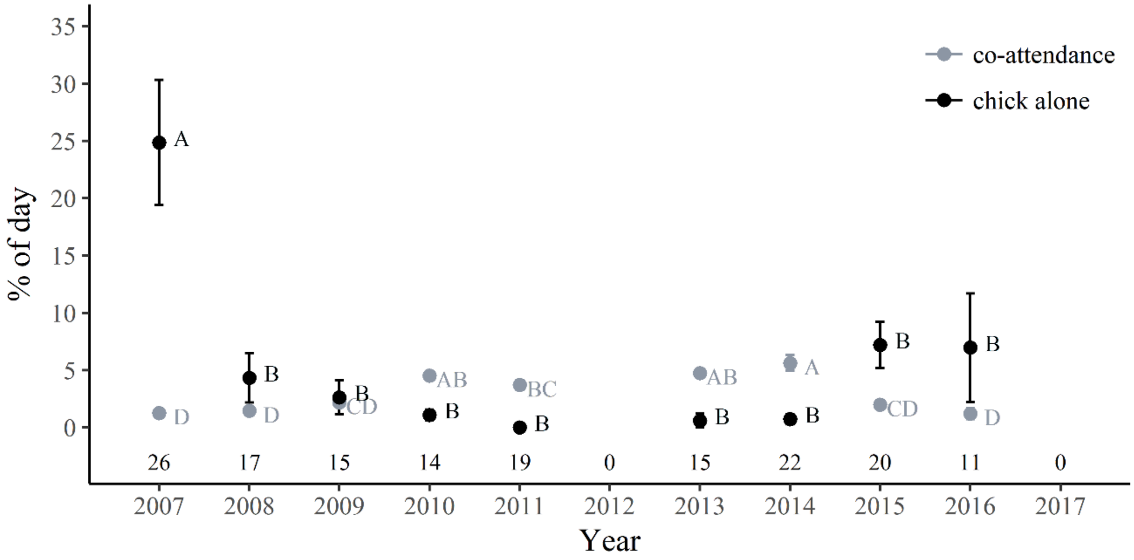


Figure 5. The amount of time that chick-rearing murres spent together with their chick (co-attendance) and the amount of time that chick-rearing murres left chicks unattended (chick alone) at Castle Rock from 2007 through 2017. Circular markers indicate the mean and error bars represent the standard error. Letters adjacent to each marker indicate homogenous subsets and sample sizes are indicated above each year.

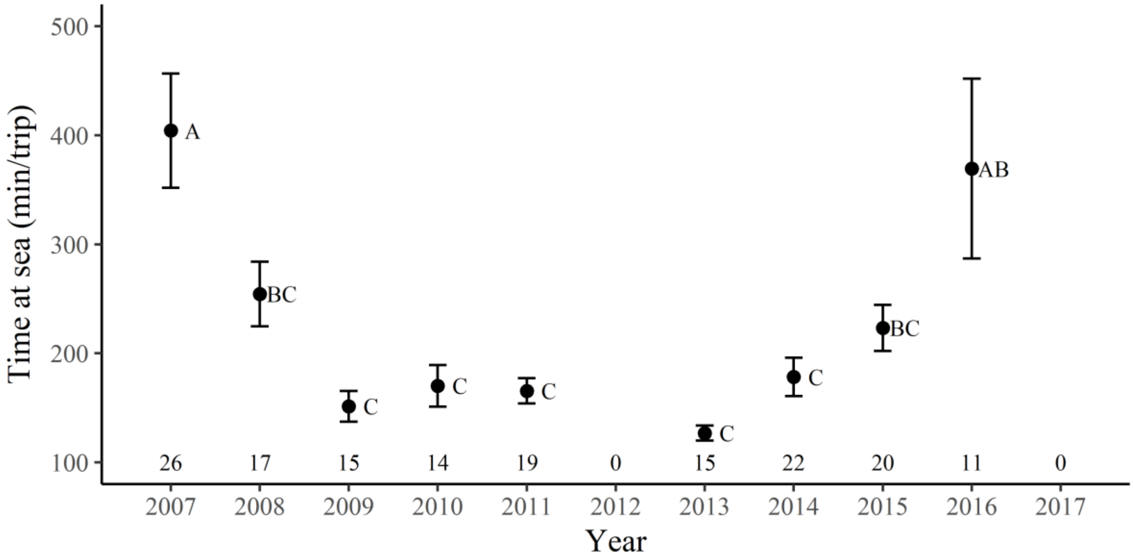


Figure 6. Duration of trips to sea made by chick-rearing murres at Castle Rock from 2007 through 2017. Circular markers indicate the mean and error bars represent the standard error. Letters adjacent to each marker indicate homogenous subsets and sample sizes are indicated above each year.

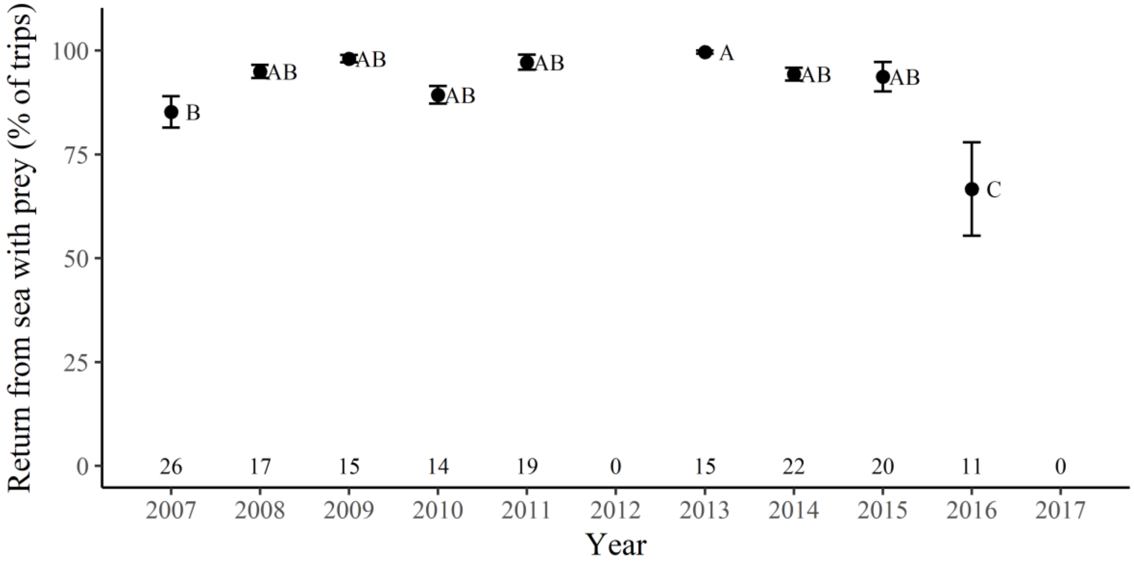


Figure 7. Percent of trips to sea that chick-rearing murres successfully returned from foraging trips with prey for their chick at Castle Rock from 2007 through 2017. Circular markers indicate the mean and error bars represent the standard error. Letters adjacent to each marker indicate homogenous subsets and sample sizes are indicated above each year.

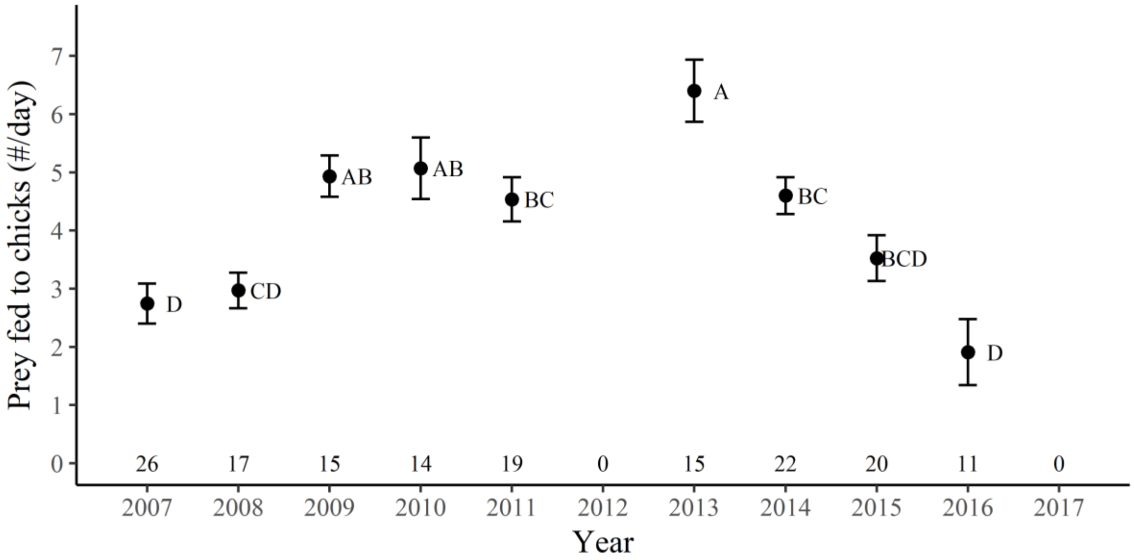


Figure 8. Frequency of chick provisioning at Castle Rock from 2007 through 2017. Circular markers indicate the mean and error bars represent the standard error. Letters adjacent to each marker indicate homogenous subsets and sample sizes are indicated above each year.

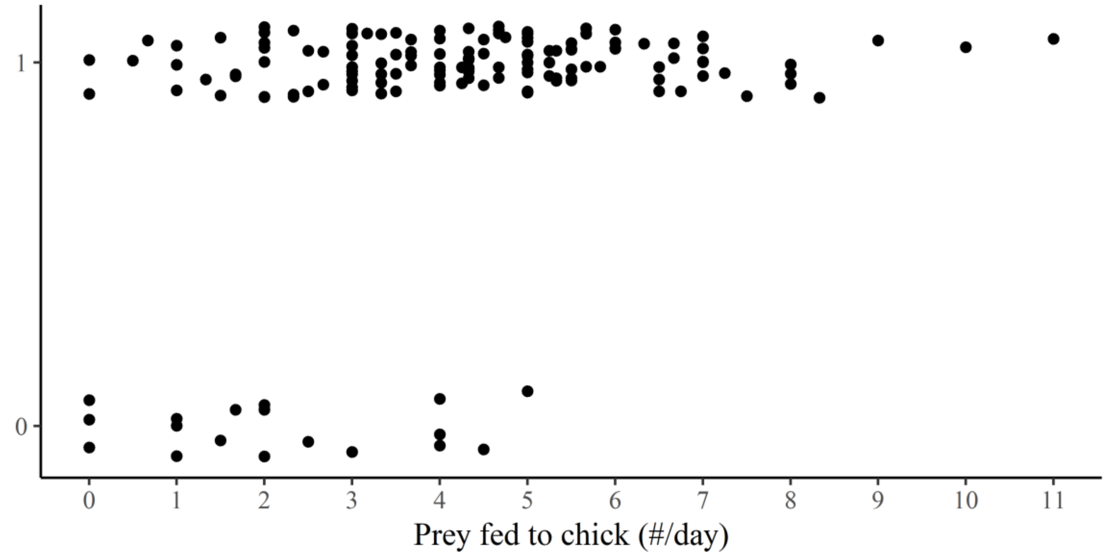


Figure 9. Occurrence of chick mortality (0 = died, 1 = survived) as a function of chick provisioning rate at Castle Rock. Points are offset from each other in respect to the y-axis to avoid over plotting.

Prey Composition

Between 2007 and 2017, 600 hours of diet surveys were conducted. During these surveys, 5166 prey deliveries were observed and 3964 of these were subsequently identified. In total, 96.8% of prey were classified at least to family, 31% were further classified to genus, and 7.8% were identified to species. In all, 20 distinct prey types were identified (range: 12 - 15 per year). Despite a diversity of prey, 87.2% of all prey identified were one of three prey types: smelt (Osmeridae), rockfish (*Sebastes sp.*), and salmon (Salmonidae; Figure 10). Until 2016, smelt (59.1% of prey) and rockfish (23.3% of prey) were the two most common prey types observed each year. However, in 2016 and presumably 2017 northern anchovy (*Engraulis mordax*) became more prevalent in the diet.

Prey composition varied across the 11-year study period (PERMANOVA: trials = 10000, $F_{8,134} = 5.07$, $p < 0.001$). The year with the most compositionally distinct prey was 2009, which was the only year that rockfish were regularly missing (54% of surveys reported 0 rockfish in 2009) while smelt dominated and could account for more than 90% of prey delivered on a given day (Figure 11). All other years were compositional variants of 2008 and there were three primary variants on the prey community observed in 2008: one that was very typically composed of smelt, rockfish, and salmon (2010); one that was composed of smelt and rockfish but lacked salmon and had a greater proportion of squid (2011, 2014); and one that was dominated by anchovy and lacked rockfish and salmon (2016; Figure 11). Intermediate years were 2007, 2013, 2015 (Figure 11).

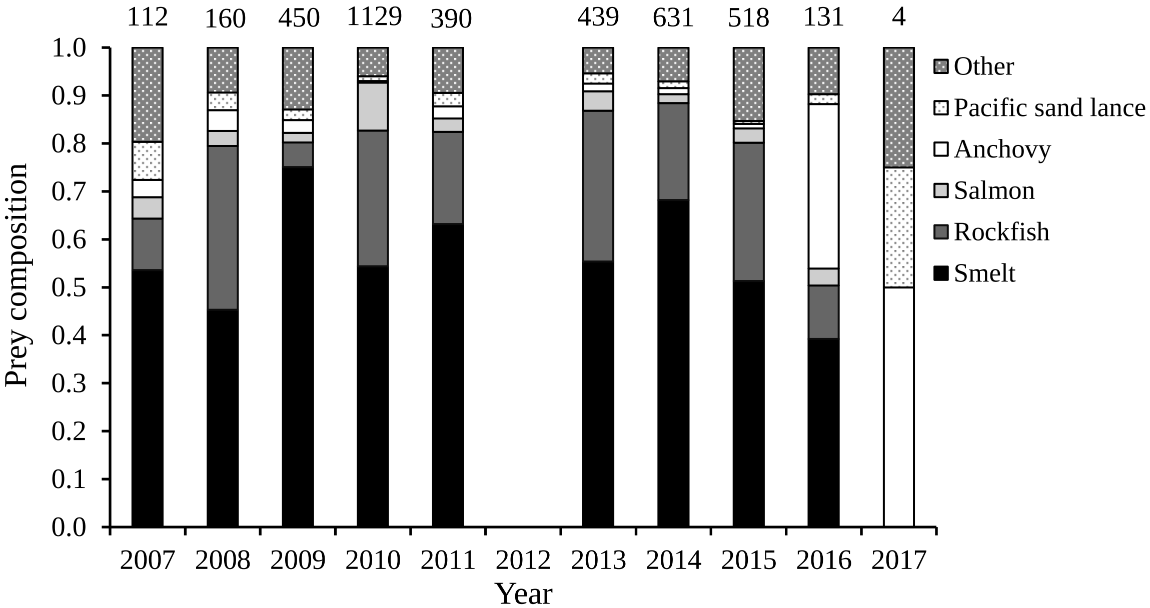


Figure 10. Composition of prey delivered to chicks at Castle Rock by Common Murre. Unidentified prey were excluded, the number of prey identified each year is indicated by the numbers above each bar.

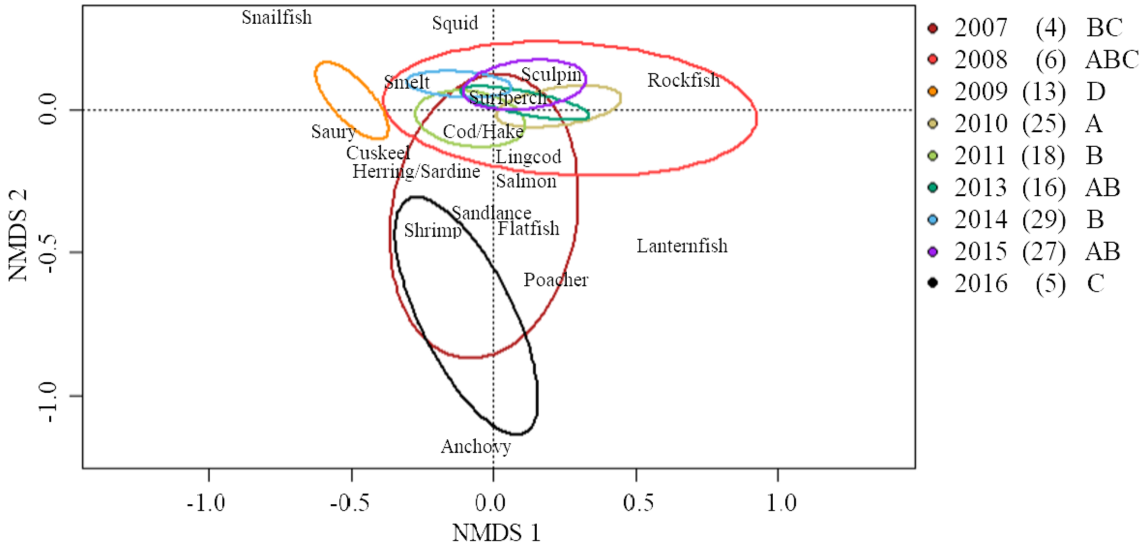


Figure 11. Nonmetric multidimensional scaling (NMDS) of the prey community accessible to Common Murres feeding chicks at Castle Rock from 2007 to 2016. Next to each year in parentheses is the number of surveys per year included in this analysis and letters that indicate homogenous subsets. Observations from 2017 were excluded due to limited observations of prey in that year.

DISCUSSION

Castle Rock is one of the largest murre colonies in the CCS and is distant from other colonies where similar studies have been undertaken. Thus, information gained from this study enhances our understanding of murre reproductive performance, time allocation, and chick diet in an area of the CCS where there is currently no baseline understanding of these parameters. The long-term nature of this dataset allowed for the observation of a representative range of prey conditions for murres nesting at Castle Rock. As predicted, the onset of upwelling was positively related to the date of nest initiation for both methods used to identify the seasonal transition to upwelling favorable conditions. Reproduction was relatively successful in all years except when prey were more difficult to obtain, as indicated by the suite of metrics that reflect foraging effort. Specifically, metrics indicative of foraging effort usually varied in a predictable way: in instances of increased foraging effort, the duration of co-attendance was minimized, the duration of chicks being left alone was increased, the duration of foraging trips was increased, the success of foraging trips decreased, and the provisioning rate of chicks decreased. This increased foraging effort coincided with years of low reproductive success. This study highlights the need of chicks to eat frequently and, if prey were not delivered at least 2 times per day, the reproductive success dropped below average. Furthermore, it seemed that prey availably, rather than prey composition, influenced the reproductive success of murres. This is confounded because years of poor reproduction overlapped with compositional shifts towards anchovy. However, anchovy is high in energy content and murres elsewhere have reproduce successfully even when anchovy was a predominant prey delivered to chicks (Ainley et al. 1990; Boekelheide et al. 1990).

The phenology of nesting by many seabirds, including murres, often matches seasonal increases in productivity of the local environment to ensure synchrony between the most energetically demanding phases of the seabird lifecycle and peak availability of their prey (Grémillet and Boulinier 2009; Reed et al. 2009; Watanuki et al. 2009). In the CCS, seasonal increases in productivity occur in late winter and early spring due to changes in prevailing wind patterns that cause deep, nutrient-rich water to reach the surface. The timing of nest initiation by murres at Castle Rock was positively related to, and followed, this seasonal increase of marine productivity. The delay between upwelling and nest initiation averaged 48.9 to 52.5 days based on the cumulative and average approach of identifying the date of spring transition, respectively. This delay likely results from a lag between environmental inputs needed for increased productivity and the transfer of this energy to higher trophic levels (Cushing 1978; Croll et al. 2005; Thompson et al. 2012). As the ocean continues to warm and alter the seasonal timing and strength of winds that drive upwelling in the CCS (Xiu et al. 2018), differential changes among trophic levels may result in desynchronization of seabird reproduction and the peak availability of their prey (Thackeray et al. 2010; Keogan et al. 2018).

Reproduction was typically successful at Castle Rock between 2007 and 2017, with prey abundance being the primary factor influencing success. Although the majority of murres successfully produced chicks in most years, murres nesting here maximized the time they spend searching for prey, even the best years. At Castle Rock, the amount of time chick-rearing pairs spent together at the colony never exceeded 5% and chicks were frequently left unattended as both parents searched for prey at-sea. This is in contrast to other well-studied colonies where chick-rearing murres typically spent at least 10% of the day together at the colony (Burger and Piatt 1990; Uttley et al. 1994; Zador and Piatt 1999; Davoren and Montevecchi 2003; Harding et al. 2007) and rarely left chicks unattended except in times of extreme prey scarcity (Ainley et al. 2002; Harding et al. 2007) often coincident with widespread starvation and chick mortality (Ashbrook et al. 2008).

Additional evidence that murres nesting at Castle Rock have currently approached their limit to behaviorally compensate for further reductions in prey is provided by observations from 2007, 2016, and 2017. In 2007, chick-rearing murres left chicks unattended for 25% of daylight hours and foraging trips were 3 times longer than the year with the shortest foraging trip. The majority (88%) of trips to sea ended with prey being delivered to chicks and chick-rearing pairs were able to maintain this level of effort for the duration of chick-rearing. In 2016, foraging duration was similar to 2007 with relatively long foraging trips (6.2 hours per trip); despite this similarity in duration, the success of trips was reduced in 2016 relative to 2017, with just 66% of trips to sea ending with prey delivery to chicks. In these conditions, only 25% of chick-rearing pairs were able to maintain this level of effort for the duration of chick-rearing. In 2017, many breeding pairs abandoned their nest before eggs hatched and chick-rearing adults were unable to find enough food to keep chicks alive for more than a few days; the oldest chick observed was 8 days and multiple chicks were observed dying at their nest presumably due to starvation.

Although prey availability in the waters surrounding Castle Rock was characterized by identifying prey returned to the colony by chick-rearing murres, this observation is relevant to other marine predators that live and reproduce in this area of the CCS. It is likely that there is great overlap in the prey base and foraging environment of murres and other seabirds, especially pursuit-diving piscivores such as other Alcids (guillemots, puffins, and some auklets) and cormorants. Sympatrically nesting seabirds experience similar foraging conditions because the distance they can travel from the colony to forage is limited by their need to incubate eggs and feed chicks (Orians and Pearson 1979; Elliott et al. 2009; Fauchald 2009). Although the maximum foraging range is species-specific, physical adaptations of diving seabirds such as Alcids and cormorants can have energetic trade-offs and limit their ability to fly long distances (Pennycuick 1987). Like murres, many piscivorious species nesting in the CCS opportunistically capture prey, which leads to dietary overlap as prey composition is determined by availability (Ainley et al. 1990; Forero et al. 2004; Gladics et al. 2014; Webb and Harvey 2014). Furthermore, prey tend to concentrate in specific areas where ocean productivity is greatest (Bost et al. 2009; Fauchald 2009; Bouchet et al. 2015). This aggregation of prey resources causes seabirds to forage in multi-species feeding flocks, further facilitating overlap of their prey base (Diamond 1983) despite some specialization (Ainley et al. 1990). Based on long-term observations at the Farallon Islands, the diets of piscivorious species can overlap extensively, especially in years when upwelling is strong and prey are abundant (Ainley et al. 1990; Ainley et al. 1996; Ainley et al. 2005). Because sympatrically nesting seabirds rely on the same prey community, observations of murres foraging effort and fledging success can provide insights into the overall ability of a colony to meet the energy needs of other nesting seabirds; in years when murres have difficulty obtaining adequate prey for chicks, it is likely that various other seabird species nesting at this location also struggle to feed their young.

This baseline characterization of murre behavior at Castle Rock indicates that the energy required to support nesting of an estimated 238,000 murres and thousands of other seabirds almost matches the energy available within flight distance of this breeding colony (corrected by the standard factor of 1.67 for murres to account for absent breeders; Carter et al. 2001; Thomas and Lyons 2017). Any event that shifts this balance could result in large-scale reproductive failure of seabirds nesting at Castle Rock similar to 2016 and 2017. A trend analysis of murres nesting at Castle Rock estimated their abundance increased at an average rate of 6.9% per year between 2007 and 2014 (Barton et al. 2017). If this growth trajectory has continued since 2014, this could partially explain the widespread failure observed in recent years. Because Castle Rock is one of the most populous seabird breeding colonies in the CCS and provides habitat for a major proportion of murres (and other seabirds) that nest in the CCS, consecutive years of failure at Castle Rock could potentially impact seabird abundance across the CCS.

In addition to improving understanding of population dynamics and potential conservation needs of seabird populations nesting in the CCS, studies at Castle Rock can improve knowledge of the mechanisms by which apex predators survive and reproduce even when prey become scarce (Bolnick et al. 2003). As indicated earlier, Castle Rock is distinct from other well-studied colonies in the CCS because, currently, food limitation and bottom-up processes drive the reproductive success of seabirds nesting there. Because prey available to murres nesting at Castle Rock is, in most years, just enough to support successful reproduction, studies investigating of the extremes of behavioral flexibility to compensate for scarce prey can occur at this location. Related to this, rarely reported behaviors including chicks left alone at the colony, conspecific attacks on chicks, and intraspecific kleptoparasitism can be better understood.

Studies at Castle Rock are also essential to understanding variability in the preyscape across the CCS. When compared with long-term studies of murre diet at other locations in the CCS, prey composition near Castle Rock was distinct. Smelt and rockfish dominated murre diet at Castle Rock. Murres in central California typically consume Northern Anchovy, other clupieds, and rockfish (Ainley et al. 1990; Roth et al. 2008; Eigner 2009). In fact, the prey community at Castle Rock was more like areas north of Point Blanco, based on reports from at Yaquina Head during the same period (Gladics et al. 2014; Suryan et al. 2014; Gladics et al. 2015). This was especially true in 2010, when smelt and rockfish accounted for about 80% of all prey observed at both Yaquina Head and Castle Rock. Despite similarities between the prey communities near Yaquina Head and Castle Rock, there were also noticeable differences; rockfish abundance was generally much lower at Yaquina Head and prey types uncommon at Castle Rock (including herring, sardine, flatfish, and Pacific sand lance) were prevalent in the diet of murres at Yaquina Head (Gladics et al. 2015). The observations of chick diet at Castle

Rock confirm that prey communities are not homogenous between northern and central regions of California and diet studies at Castle Rock enhance understanding of both spatial and temporal variability in prey composition across the CCS.

Conclusions

Ultimately, this study provided a robust understanding of a previously unstudied region of the CCS in terms of the ability of murres, and potentially other seabirds, to produce young, how hard they must work to do so, and what prey types are available to them. This information is essential to accurately assess the population health of murres nesting in the CCS and to better understand temporal and spatial heterogeneity in the preyscape of the CCS. As predicted, the timing of upwelling accounted for 70% of the variability in the nesting phenology of murres and provides evidence that murres are sensitive to and can alter the timing of nesting to match peak availability of prey. Despite timing nest initiation to coincide with greater abundance of prey, availability was barely sufficient to meet the needs of the colony and in all years of this study murres neared the limits of their ability to behaviorally compensate; crossing this threshold resulted in widespread nest abandonment and chick starvation. Because of this fine balance that currently exists between prey availability and the needs of seabirds nesting at Castle Rock, even small shifts that cause demands to exceed availability will likely result in large-scale reproductive failure of seabirds nesting at Castle Rock.

REFERENCES

Aebischer NJ. 1999. Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. Bird Study. 46:S22–S31.

Ainley DG, Hyrenbach KD. 2010. Top-down and bottom-up factors affecting seabird population trends in the California Current System (1985-2006). Prog Oceanogr. 84:242–254.

Ainley DG, Nettleship DN, Carter HR, Storey AE. 2002. Common Murre (Uria aalge), Ver. 2.0. In: Poole A, editor. The birds of North America online. Ithaca (NY): Cornell Lab of Ornithology. doi: 10.2172/bna.666.

Ainley DG, Spear LB, Allen SG, Ribic CA. 1996. Temporal and spatial patterns in the diet of the Common Murre in California waters. Condor. 98:691–705.

Ainley DG, Spear LB, Tynan CT, Barth JA, Pierce SD, Ford RG, Cowles TJ. 2005. Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. Deep Res Part II. 52:123–143.

Ainley DG, Strong CS, Penniman TM, Boekelheide RJ. 1990. Feeding ecology of Farallon seabirds. In: Ainley DG, Boekelheide RJ, editors. Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community. Stanford (CA): Stanford University Press. p. 51–127.

Anderson MJ, Walsh DCI. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecol Monogr. 83:557–574.

Ashbrook K, Wanless S, Harris MP, Hamer KC. 2008. Hitting the buffers: conspecific aggression undermines benefits of colonial breeding under adverse conditions. Biol Lett. 4:630–633.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-1971. Washington (DC): U.S. Department of Commerce. (NOAA Technical Report NMFS SSRF-671). 103 p.

Barth JA, Menge BA, Lubchenco J, Chan F, Bane JM, Kirincic AR, McManus MA, Nielsen KJ, Pierce SD, Washburn L. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California Current. PNAS. 104:3719–3724.

Barth JA, Pierce SD, Cowles TJ. 2005. Mesoscale structure and its seasonal evolution in the northern California Current System. Deep Res Part II. 52:5–28.

Barton DC, Capitolo PJ, McChesney GJ, Carter HR, Golightly RT, Tyler WB. 2017. Trends in seabird abundance. In: Golightly RT, Barton DC, Robinette DP, editors. Comprehensive seabird monitoring for the characterization and future evaluation of Marine Protected Areas in California’s North Coast Study Region. Arcata (CA):

Humboldt State University, Department of Wildlife. p. 17–48.

Batchhelder H, Barth JA, Kosro PM, Strub T, Brodeur RD, Peterson WT, Tynan CT, Ohman MD, Botsford L, Powell T, et al. 2002. The GLOBEC Northeast Pacific California Current System Program. Oceanography. 15:36–47.

Beals EW. 1984. Bray-curtis ordination: an effective strategy for analysis of multivariate ecological data. Adv Ecol Res. 14:1–55.

Birt VL, Birt TP, Goulet D, Cairns DK, Montevecchi WA. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Mar Ecol Prog Ser. 40:205–208.

Bjorkstedt EP, Goericke R, McClatchie S, Weber ED. 2012. State of the California Current 2011 – 2012 : ecosystems respond to local forcing as La Niña wavers and wanes. Calif Coop Ocean Fish Investig Rep. 53:41–76.

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed GA, Harrison AL, et al. 2011. Tracking apex marine predator movements in a dynamic ocean. Nature. 475:86–90.

Boekelheide RJ, Ainley DG, Morrell SH, Huber HR, Lewis TJ. 1990. Common Murre. In: Ainley DG, Boekelheide RJ, editors. Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community. Stanford (CA): Stanford University Press. p. 245–275.

Bograd SJ, Schroeder ID, Sarkar N, Qiu X, Sydeman WJ, Schwing FB. 2009. Phenology of coastal upwelling in the California Current. Geophys Res Lett. 36:1–5.

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003. The ecology of individuals: incidence and implications of individual specialization. Am Nat. 161:1–28.

Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H. 2009. The importance of oceanographic fronts to marine birds and mammals of the southern oceans. J Mar Syst. 78:363–376.

Bouchet PJ, Meeuwig JJ, Kent CPS, Letessier TB, Jenner CK. 2015. Topographic determinants of mobile vertebrate predator hotspots: current knowledge and future directions. Biol Rev. 90:699–728.

Bray JR, Curtis JT. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr. 27:325–349.

Burger AE, Piatt JF. 1990. Flexible time budgets in breeding Common Murres:Buffers against variable prey abundance. Stud Avian Biol. 14:71–83.

Burke CM, Montevecchi WA. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. J Zool. 278:354–361.

Carter HR, McChesney GJ, Jaques DL, Strong CS, Parker MW, Takekawa JE, Jory DL, Whitworth DL. 1992. Breeding populations of seabirds in California, 1989 – 1991. Vol. 1. Dixon (CA): U.S. Fish & Wildlife Service, Northern Prairie Wildlife Research Center. 471 p.

Carter HR, Wilson UW, Lowe RW, Rodway MS, Manuwal DA, Takekawa JE, Yee JL. 2001. Population trends of the Common Murre (Uria aalge californica). In: Manuwal DA, Carter HR, Zimmerman TS, Orthmeyer DL, editors. Biology and conservation of the Common Murre in California, Oregon, Washington, and British Columbia. Vol. 1. Washington (DC): U.S. Geological Survey, Information and Technology Report USGS/BRD/ITR– 2000-0012. p. 33–132.

Chavez FP, Messié M. 2009. A comparison of eastern boundary upwelling ecosystems. Prog Oceanogr. 83:80–96.

Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. Aust J Ecol. 18:117–143.

Clarke KR, Warwick RM. 2001. Change in marine communities: an approach to statistical analysis and intertpretation. 2nd ed. Plymouth (UK): PRIMER-E Ltd. 176 p.

Cloern JE. 1996. Phytoplankton bloom dynamics in coastal ecosystems: a review with some general lessons with sustained investigation of San Francisco Bay, California. Rev Geophys. 34:127–168.

Croll DA, Marinovic B, Benson SR, Chavez FP, Black N, Ternullo R, Tershy BR. 2005. From wind to whales: trophic links in a coastal upwelling system. Mar Ecol Prog Ser. 289:117–130.

Cunha MJ, Golightly RT, Nelson ET, McChesney GJ. 2008. Development of methods for monitoring seabirds on Castle Rock NWR. Arcata (CA): Humboldt State University, Department of Wildlife. 27 p.

Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T, Crawford RJM, Furness RW, Mills JA, Murphy EJ, Österblom H, Paleczny M, et al. 2011. Global seabird response to forage fish depletion: one-third for the birds. Science. 334:1703–1706.

Cushing DH. 1978. Upper trophic levels in upwelling areas. In: Boje R, Tomczak M, editors. Upwelling Ecosystems. New York (NY): Springer-Verlag. p. 101–110.

Davoren GK, Montevecchi WA. 2003. Consequences of foraging trip duration on provisioning behaviour and fledging condition of Common Murres Uria aalgae. J Avian Biol. 34:44–53.

Diamond AW. 1983. Feeding overlap in some tropical and temperate seabird communities. Stud Avian Biol. 8:24–46.

Diamond AW, Devlin CM. 2003. Seabirds as indicators of changes in marine ecosystems: ecological monitoring on Machias Seal Island. Environ Monit Assess.

88:153–175.

Eigner LE. 2009. Spatial and temporal variation in prey use of Common Murres at two disjunct colonies in the California Current System. [MS Thesis]. Arcata (CA): Humboldt State University, Department of Wildlife. 57 p.

Einoder LD. 2009. A review of the use of seabirds as indicators in fisheries and ecosystem management. Fish Res. 95:6–13.

Elliott KH, Woo KJ, Gaston AJ, Benvenuti S, Dall'Antonia L, Davoren GK. 2009. Central-place foraging in an arctic seabird provides evidence for Storer-Ashmole's halo. Auk. 126:613–625.

Eschmeyer WN, Herald ES. 1983. A field guide to Pacific coast fishes. Boston (MA): Houghton Mifflin. 336 p.

Fauchald P. 2009. Spatial interaction between seabirds and prey: review and synthesis. Mar Ecol Prog Ser. 391:139–151.

Forero MG, Bortolotti GR, Hobson KA, Donazar JA, Bertelloti M, Blanco G. 2004. High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. J Anim Ecol. 73:789–801.

Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J Anim Ecol. 75:1259–1268.

Frederiksen M, Haug T. 2015. Editorial: climate change and marine top predators. Front Ecol Evol. 3:136–138.

Frederiksen M, Mavor RA, Wanless S. 2007. Seabirds as environmental indicators: the advantages of combining data sets. Mar Ecol Prog Ser. 352:205–211.

Fuller AR, McChesney GJ, Anderson JC, Berger RW, Zimmerman JA, Potter RJ, White BC, Windsor JA, Golightly RT. 2015. Restoration and monitoring of Common Murre colonies in central California: annual report 2014. Arcata (CA): Humboldt State University, Department of Wildlife. 68 p.

Gaston AJ, Bertram DF, Boyne AW, Chardine JW, Davoren GK, Diamond AW, Hedd A, Montevecchi WA, Hipfner JM, Lemon MJF, et al. 2009. Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography and food webs. Environ Rev. 17:267–286.

Gilg O, Kovacs KM, Aars J, Fort J, Gauthier G, Grémillet D, Ims RA, Meltofte H, Moreau J, Post E, et al. 2012. Climate change and the ecology and evolution of Arctic vertebrates. Ann N Y Acad Sci. 1249:166–190.

Gladics AJ, Suryan RM, Brodeur RD, Segui LM, Filliger LZ. 2014. Constancy and change in marine predator diets across a shift in oceanographic conditions in the northern California Current. Mar Biol. 161:837–851.

Gladics AJ, Suryan RM, Parrish JK, Horton CA, Daly EA, Peterson WT. 2015. Environmental drivers and reproductive consequences of variation in the diet of a marine predator. J Mar Syst. 146:72–81.

GLOBEC. 1992. Global ocean ecosystems dynamics: report on climate change and the California Current ecosystem. Davis (CA): U. S. Global Change Research Program, Eastern Boundary Current Program. 85 p.

Golightly RT, Schneider SR. 2016. Seabird investigations at Castle Rock National Wildlife Refuge: 2006-2012 report. Arcata (CA): Humboldt State University, Depaerment of Wildlife. 62 p.

Grémillet D, Boulinier T. 2009. Spatial ecology and conservation of seabirds facing global climate change: a review. Mar Ecol Prog Ser. 391:121–137.

Grémillet D, Charmantier A. 2010. Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. Ecol Appl. 20:1498–1503.

Harding AMA, Piatt JF, Schmutz JA. 2007. Seabird behavior as an indicator of food supplies: sensitivity across the breeding season. Mar Ecol Prog Ser. 352:269–274.

Hedd A, Regular PM, Montevecchi WA, Buren AD, Burke CM, Fifield DA. 2009. Going deep: Common Murres dive into frigid water for aggregated, persistent and slow-moving capelin. Mar Biol. 156:741–751.

Heithaus MR, Frid A, Wirsing AJ, Worm B. 2008. Predicting ecological consequences of marine top predator declines. Trends Ecol Evol. 23:202–210.

Hickey BM. 1998. Coastal oceanography of western North America from the tip of Baja California to Vancouver Island. In: Brink KH, Robinson AR, editors. The sea. New York (NY): Wiley and Sons, Inc. p. 345–393.

Holt CA, Mantua N. 2009. Defining spring transition: Regional indices for the california current system. Mar Ecol Prog Ser. 393:285–299.

Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Verheye HMS, Bartholomae CH, van der Plas AK, Louw D, Kreiner A, Ostrowski M, et al. 2009. The Benguela Current: an ecosystem of four components. Prog Oceanogr. 83:15–32.

Huyer A, Fleischbein JH, Keister JE, Kosro PM, Perlin N, Smith RL, Wheeler PA. 2005. Two coastal upwelling domains in the northern California Current System. J Mar Resea. 63:901–929.

Jaques DL. 2007. Castle Rock National Wildlife Refuge information synthesis. Loleta (CA): U.S. Fish & Wildlife Service, Humboldt Bay National Wildlife Refuge Complex. 82 p.

Johnson DH. 2007. Methods of estimating nest success: an historical tour. Stud Avian

Biol. 34:1–12.

Kämpf J, Chapman P. 2016. Upwelling systems of the world. New York (NY): Springer International Publishing. 433 p.

Keogan K, Daunt F, Wanless S, Phillips RA, Walling CA, Agnew P, Ainley DG, Anker-Nilssen T, Ballard G, Barrett RT, et al. 2018. Global phenological insensitivity to shifting ocean temperatures among seabirds. Nat Clim Chang. 8:313–317.

Lewis S, Sherratt TN, Hamer KC, Wanless S. 2001. Evidence of intra-specific competition for food in a pelagic seabird. Nature. 412:816–819.

Lindeman RL. 1942. The trophic-dynamic aspect of ecology. Bull Math Biol. 23:399–417.

Logerwell EA, Mantua N, Lawson PW, Francis RC, Agostini VN. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (Oncorhynchus kisutch) marine survival. Fish Oceanogr. 12:554–568.

Manuwal DA, Carter HR, Zimmerman TS, Orthmeyer DL. 2000. Biology and Conservation of the Common Murre in California, Oregon, Washington, and British Columbia Volume 1: natural history and population trends. Washington (DC): U.S. Geological Survey, Biological Resources Division. (USGS/BRD/ITR- 2000-0012). 132 p.

McGowan JA, Cayan DR, Dorman LM. 1998. Climate-ocean variability and ecosystem response in the northeast Pacific. Science. 281:210–217.

Montevecchi WA. 1993. Birds as indicators of change in marine prey stocks. In: Furness RW, Greenwood JJD, editors. Birds as monitors of environmental change. London (UK): Chapman and Hall.

[NOAA] National Oceanic and Atmospheric Administration. 1967–2018. Daily upwelling indices database [internet]. Pacific Grove (CA): Pacific Fisheries Environmental Laboratory. https://www.pfeg.noaa.gov/products/PFELData/upwell/daily/p08dayac.all

Orben R. 2009. BSIERP Seabird Telemetry Flying Fish Guide. St. George Island (AK): Bering Sea Integrated Ecosystem Research Program.

Orians GH, Pearson NE. 1979. On the ecology of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR, editors. Analysis of ecological systems. Columbus (OH): Ohio State University Press. p. 155–177.

Oro D. 2014. Seabirds and climate: knowledge, pitfalls, and opportunities. Front Ecol Evol. 2:1–12.

Papish R. 1996. A field guide to murre bill loads. Anchorage (AK), Alaska Science Center, CISeaFFS Project.

Parker MW. 2005. Comparison of breeding performance, co-attendance and chick provisioning rates of breeding Common Murres (Uria aalge) as early indicators for ecological monitoring. [MS Thesis]. Arcata (CA): Humboldt State University, Department of Wildlife. 53 p.

Pennycuick CJ. 1987. Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: ornithodolite observations. J Exp Biol. 34:778.

Peterson WT, Morgan CA, Casillas E, Fisher JL, Ferguson JW. 2011. Ocean ecosystem indicators of salmon marine survival in the Northern California Current. Newport (OR): Northwest Fisheries Science Center National Marine Fisheries Service, Northwest Fisheries Science Center, Fish Ecology Division. 76 p.

Piatt JF, Nettleship DN. 1985. Diving depths of four alcids. Auk. 102:293–297.

Piatt JF, Sydeman WJ, Wiese F. 2007. Introduction: a modern role for seabirds as indicators. Mar Ecol Prog Ser. 352:199–204.

Pichegru L, Ryan PG, Crawford RJM, Van der Lingen CD, Grémillet D. 2010. Behavioural inertia places a top marine predator at risk from environmental change in the Benguela Upwelling System. Mar Biol. 157:537–544.

Post van der Burg M, Powell LA, Tyre AJ. 2010. Finding the smoothest path to success: model complexity and the consideration of nonlinear patterns in nest-survival data. Condor. 112:421–431.

R Development Core Team. 2017. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. http://www.R-project.org.

Reed TE, Warzybok P, Wilson AJ, Bradley RW, Wanless S, Sydeman WJ. 2009. Timing is everything: flexible phenology and shifting selection in a colonial seabird. J Anim Ecol. 78:376–387.

Reese DC, Brodeur RD. 2006. Identifying and characterizing biological hotspots in the northern California Current. Deep Res Part II. 53:291–314.

Regular PM, Hedd A, Montevecchi WA. 2011. Fishing in the dark: a pursuit-diving seabird modifies foraging behaviour in response to nocturnal light levels. PLoS One. 6:2007–2010.

Roth JE, Nur N, Warzybok P, Sydeman WJ. 2008. Annual prey consumption of a dominant seabird, the Common Murre, in the California Current System. ICES J Mar Sci. 65:1046–1056.

Saito H, Tsuda A, Nojiri Y, Nishioka J, Takeda S, Kiyosawa H, Kudo I, Noiri Y, Ono T, Taira Y, et al. 2006. Nutrient and phytoplankton dynamics during the stationary and declining phases of a phytoplankton bloom induced by iron-enrichment in the eastern subarctic Pacific. Deep Res Part II. 53:2168–2181.

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

Scales KL, Miller PI, Hawkes L, Ingram SN, Sims DW, Votier SC. 2014. On the front line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. J Appl Ecol. 51:1575–1583.

Schreiber EA, Burger J. 2001. Biology of marine birds. Boca Raton (FL): CRC Press. 722 p.

Schrimpf MB, Parrish JK, Pearson SF. 2012. Trade-offs in prey quality and quantity revealed through the behavioral compensation of breeding seabirds. Mar Ecol Prog Ser. 460:247–259.

Scott BE, Sharples J, Wanless S, Ross ON, Frederiksen M, Daunt F. 2006. The use of biologically meaningful oceanographic indices to separate the effects of climate and fisheries on seabird breeding success. In: Boyd IL, Wanless S, Camphuysen CJ, editors. Top predators in marine ecosystems: their role in monitoring and management. Cambridge (UK): Cambridge University Press. p. 46–62.

Shultz MT, Piatt JF, Harding AMA, Kettle AB, Van Pelt TI. 2009. Timing of breeding and reproductive performance in murres and kittiwakes reflect mismatched seasonal prey dynamics. Mar Ecol Prog Ser. 393:247–258.

Smout S, Rindorf A, Wanless S, Daunt F, Harris MP, Matthiopoulos J. 2013. Seabirds maintain offspring provisioning rate despite fluctuations in prey abundance: a multi-species functional response for guillemots in the North Sea. J Appl Ecol. 50:1071–1079.

Suryan RM, Throckmorton I, Gladics AJ, Porquez JM, Fernandez L. 2014. Yaquina Head seabird colony monitoring 2014 season summary. Newport (OR): Oregon State University, Hatfield Marine Science Center. 10 p.

Terborgh J, Estes JA, editors. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Washington (DC): Island Press. 452 p.

Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright PW, Carvalho L, et al. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Glob Chang Biol. 16:3304–3313.

Thomas SM, Lyons JE. 2017. Population trends and distribution of Common Murre Uria aalge colonies in Washington, 1996–2015. Mar Ornithol. 45:95–102.

Thompson SA, Sydeman WJ, Santora JA, Black BA, Suryan RM, Calambokidis J, Peterson WT, Bograd SJ. 2012. Linking predators to seasonality of upwelling: using food web indicators and path analysis to infer trophic connections. Prog Oceanogr.

101:106–120.

Tukey JW. 1949. Comparing individual means in the analysis of variance. Biometrics. 5:99–114.

Tynan CT, Ainley DG, Barth JA, Cowles TJ, Pierce SD, Spear LB. 2005. Cetacean distributions relative to ocean processes in the northern California Current System. Deep Res Part II. 52:145–167.

[USFWS] U.S. Fish & Wildlife Service. 2009. Humboldt Bay National Wildlife Refuge: Draft Comprehensive Conservation Plan and Environmental Assessment. Loleta (CA): U.S. Fish and Wildlife Service, Humboldt Bay National Wildlife Refuge Complex. 144 p.

Uttley JD, Walton P, Monaghan P, Austin G. 1994. The effects of food abundance on breeding performance and adult time budgets of guillemots Uria aalge. Ibis. 136:205–213.

Votier SC, Hatchwell BJ, Mears M, Birkhead TR. 2009. Changes in the timing of egg-laying of a colonialseabird in relation to population size and environmental conditions. Mar Ecol Prog Ser. 393:225–233.

Watanuki Y, Ito M, Deguchi T, Minobe S. 2009. Climate-forced seasonal mismatch between the hatching of Rhinoceros Auklets and the availability of anchovy. Mar Ecol Prog Ser. 393:259–271.

Webb LA, Harvey JT. 2014. Diet of a piscivorous seabird reveals spatiotemporal variation in abundance of forage fishes in the Monterey Bay region. J Mar Syst. 146:59–71.

Xiu P, Chai F, Curchitser EN, Castruccio FS. 2018. Future changes in coastal upwelling ecosystems with global warming: the case of the California Current System. Sci Rep. 8:1–9.

Young JW, Hunt BP V, Cook TR, Llopiz JK, Hazen EL, Pethybridge HR, Ceccarelli D, Lorrain A, Olson RJ, Allain V, et al. 2015. The trophodynamics of marine top predators: current knowledge, recent advances and challenges. Deep Res Part II. 113:170–187.

Zador SG, Piatt JF. 1999. Time-budgets of Common Murres at a declining and increasing colony in Alaska. Condor. 101:149–152.