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Environmental drivers and reproductive consequences of variation in the diet of a marine predator

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ABSTRACT

Ocean conditions can greatly impact lower trophic level prey assemblages in marine ecosystems, with effects of ocean state propagating to higher trophic levels. In many regions throughout their range, common murre (*Uria aalge*) exhibit narrow dietary breadth in feeding chicks and therefore are vulnerable to recruitment failures of dominant prey species during the breeding season. Contrastingly, common murres nesting in the northern California Current off Oregon, exhibit high species diversity and variability in dominant prey consumed. We studied the diets of common murres over 10 years between 1998 and 2011, a period in which the northern California Current experienced dramatic interannual variability in ocean conditions. Likewise, murre diets off Oregon varied considerably. Interannual variation in murre chick diets was influenced by environmental drivers occurring before and during the breeding season, and at both basin and local scales. While clupeids (likely Pacific herring, *Clupea pallasii*) were an important diet component throughout the study period, in some years murre diets were dominated by Pacific sand lance (*Ammodytes hexapterus*) and in other years by osmerids (likely whitebait smelt, *Allosmerus elongatus* and surf smelt, *Hypomesus pretiosus*). Years in which the Pacific Decadal Oscillation and local sea surface temperatures were higher during summer also showed elevated levels of clupeids in murre diets, while years with higher North Pacific Gyre Oscillation index values and greater local winter ichthyoplankton biomass had fewer clupeids and more sand lance or smelts. Years with higher values of the Northern Oscillation Index during summer and an earlier spring transition showed higher proportion of smelts in the diets. Nesting phenology and reproductive success were negatively correlated with gradients in sand lance and clupeids, respectively, reflecting demographic consequences of environmental variability mediated through bottom-up food web dynamics.

1. Introduction

1.1. Background

Predator–prey relationships are the most fundamental species interaction within an ecosystem (Vandermeer, 1972). Observations of marine predator diets increase our understanding of the mechanistic interactions between changes in ocean conditions and subsequent effects on predator populations and ecosystem dynamics. During the past two decades, the California Current System (CCS) has experienced increased variability in ocean conditions (Sydeman et al., 2013), including apparent but arrested regime shifts, delayed upwelling, and anomalous near-shore hypoxia (Barth et al., 2007; Bograd et al., 2009; Di Lorenzo et al., 2008). Changes in ocean conditions have also corresponded with changes in primary productivity, prey assemblages, prey availability and food-web dynamics in the CCS on multiple temporal scales (Ainley and Boekelheide, 1990; Ainley et al., 1993; Auth et al., 2011; Bograd et al., 2009; Brodeur et al., 2008; Lenarz et al., 1995; Ruzicka et al., 2012; Vanegas et al., 2008). Predators can buffer variations in resource availability by prey switching and/or changing foraging location to meet their metabolic needs and many marine predators are generalists at the population level with high interannual variability in diet or foraging location (Ainley et al., 2014). Much progress has been made on understanding the effects of ocean conditions on the diets and demographics of middle and upper trophic level taxa in the central California Current (cCCS) (Black et al., 2011; Sydeman et al., 2009, 2013; Wells et al., 2008). However, less is known about middle and upper trophic-level diets and demographic responses in the northern California Current (nCCS) (Eigner, 2009; Schrimpf et al., 2012).

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Seabirds are well suited for studies examining the causes and consequences of diet variability because they are numerous and conspicuous in the CCS and their breeding habits allow for observation of both diets and demographic parameters simultaneously (Ainley and Boekelheide, 1990).

1.2. Focal species

The common murre (*Uria aalge*), a pursuit diving seabird with a circumpolar boreal range, responds to basin and local scale climate variability at the population level (Irons et al., 2008; Parrish and Zador, 2003). Population level responses to changes in oceanographic conditions are mediated through prey availability, consequent diet, and ultimately reproductive success at the colony scale (Ainley and Boekelheide, 1990; Ainley et al., 1995b; Cairns, 1987). Common murres are generalist predators known to forage in coastal shelf and shelf break marine habitats on micro-nekton such as euphausiids and forage fish (Ainley et al., 1996; Oedekoven et al., 2001). They are largely found in waters overlying the continental shelf, with a maximum foraging range of approximately 60 km from the breeding colony and 150 m maximum depth (Ainley et al., 1996, 2002; Hatch et al., 2000; Hedd et al., 2009). Throughout much of their subpolar range, common murres often depend on a single or few species of mid-water schooling fishes to provision chicks, and can be vulnerable to breeding failures if key fish stocks are unavailable during the chick rearing period (Ainley and Boekelheide, 1990; Davoren and Montevecchi, 2003a,b; Gaston and Jones, 1998).

On the west coast of North America, common murre diets can vary annually. Studies in the cCCS have shown prey switching in response to variable oceanographic conditions and changes in prey availability (Ainley and Boekelheide, 1990; Ainley et al., 1993; Miller and Sydeman, 2004; Mills et al., 2007). In nCCS, interannual variability and between-site differences have been documented as well (Eigner, 2009). At Tatoosh Island, in the nCCS, Parrish and Zador (2003) and Schrimpf et al. (2012) observed prey switching among a handful of dominant prey species as a mechanism to buffer environmental variability, whereas further north at Triangle Island in the transition zone between the California Current and the Alaska Current, Hipfner and Greenwood (2008) observed little variability in murre diets, despite highly variable oceanographic conditions. Less is known about murre diets off Oregon, near the latitudinal midpoint of murre research sites in the CCS, despite the fact that murre numbers in this region dwarf those to the north and south (Manuwal et al., 2001; Naughton et al., 2007).

1.3. Objectives and hypotheses

In this study, we used a multivariate ordination approach to assess the effects of basin and local scale environmental variability and variation in the zooplankton and ichthyoplankton community on the diets of common murres (correlations with $R^2 \geq 0.4$) at a breeding colony in the nCCS. We also determined how diets at this site relate to common murre diets elsewhere in the CCS. We hypothesized that environmental factors both before and during the breeding season would affect prey availability and thus murre diets, as has been noted in the cCCS. We were also interested in how changes in diets might correlate with murre nesting phenology and fecundity.

2. Material and methods

2.1. Data collection

2.1.1. Study site

We collected all diet and demographic data at Yaquina Head, Newport, Oregon (44°40′30″ N, 124°04′35″ W). Approximately 70,000 common murres nest at this colony, along with seven other species of seabirds (Naughton et al., 2007). All observations of murres were made at two large sub-colonies, Colony Rock and Flat Top Rock, containing approximately 50,000 and 17,000 breeding murres respectively. Our observation points at the base and gallery deck of the Yaquina Head lighthouse were approximately 100–150 m from nesting murres.

2.1.2. Demographic data collection

We monitored the reproductive success of 12–25 breeding pairs in each of 6–12 plots on the two subcolonies throughout the breeding season (April–August). Within these plots, we closely observed breeding birds, recorded when eggs were laid and then followed the success of each breeding pair through egg incubation and chick rearing at approximately 1- to 3-day intervals. We used the median hatch date to measure breeding phenology. Reproductive success was calculated as the percentage of eggs laid which produced chicks that fledged. Actual observations of fledging events were rare and, therefore, we used the age of murre chicks to determine if a chick fledged or rather disappeared because of likely mortality. Murre chicks may begin leaving the colony when 15 days old (Ainley et al., 2002) and therefore, chicks that remained on the colony ≥15 days were considered successfully reared to fledging age. We attempted to reduce the influence of top-down effects of murre predators at this colony by excluding plots in which all pairs failed from our calculation of overall reproductive success, which occurred in 2 of the 10 years (Suryan et al., 2006).

2.1.3. Diet data collection

Common murres, if tending a chick, return from foraging trips with a single prey item, generally carried with the tail of the prey item extending past the tip of the murre's bill. The visible portions of the prey item can be used to identify prey type to the family, genus, or species level. Murre prey items were identified using trained observers and digital photographs. Observations were concentrated in the morning (0600–1100 h) during chick rearing (May–August) throughout the study period (1998–2011). During 1998–2002, trained observers worked in pairs for 30–60 min daily to identify murre prey items between 3 May and 19 July, 1998–2002. No data were collected from 2003 to 2006. During 2007–2011, common murre prey were identified using digital photographs (Larson and Craig, 2006) between the hours of 0630–1800, 2–5 days per week, 22 June–9 August, 2007–2011. We used a Canon EOS T2i digital SLR camera with a 50 mm lens attached to a Swarovski 20–60 × 80 mm STM spotting scope. Trained observers and photographers were 95–105 m from the birds holding fish. Photographs were examined in the lab, allowing for both a closer examination of the prey, more time to make an identification decision, and the ability to consult fish identification experts. Prey were identified to the lowest taxonomic level possible. Several prey species identified by trained observers were difficult to distinguish in photographic samples and thus were combined into more general taxonomic groups to allow analysis of the entire time series. Prey items that could not be identified to the family level or lower were excluded from statistical analysis.

2.1.4. Basin scale physical indices

We used monthly values of basin scale environmental variables that correlate with biological variability in the North Pacific, including the Pacific Decadal Oscillation (PDO), Multivariate El Niño/Southern Oscillation Index (MEI), Northern Oscillation Index (NOI) and the North Pacific Gyre Oscillation (NPGO). The PDO is the leading principal component of North Pacific monthly sea surface temperature (SST) variability poleward of 20° N since 1900 (Mantua et al., 1997) and can be strongly correlated with changes in fish populations (Alheit and Bakun, 2010; Mantua et al., 1997). We obtained values for the PDO from the Joint Institute for Study of the Atmosphere and Ocean, University of Washington (http://jisao.washington.edu/pdo/). Periodic fluctuations in SST in the Pacific, termed El Niño Southern Oscillation (ENSO) with El Niño during warm anomalies and La Niña during cool anomalies, are well known to cause widespread atmospheric, oceanographic and biological changes throughout the north Pacific. The MEI is a multivariate, standardized measure of the strength of