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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 murre nesting in the northern California Current off Oregon, exhibit high species diversity and variability in dominant prey consumed. We studied the diets of common murre 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.

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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

ENSO in the tropical Pacific based on six types of physical observations (Wolter, 1987; Wolter and Timlin, 1993). We obtained MEI values from the Earth Systems Research Laboratory – Physical Sciences Division (NOAA ESRL, <http://www.esrl.noaa.gov/psd/enso/mei/>). The NOI is the anomaly of sea level pressure difference between the North Pacific High and Darwin, Australia, and serves as measure of the strength of atmospheric circulation between the tropics and the North Pacific (Schwing et al., 2002). Positive NOI values correspond to increased winds, higher than average coastal upwelling and La Niña; the opposite conditions occur during periods with negative NOI (Schwing et al., 2002). We obtained values of the NOI from the Pacific Fisheries Environmental Laboratory (PFEL, <http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/>). The North Pacific Gyre Oscillation is the second dominant mode of sea surface height variability in the northeast Pacific and describes variability in wind-driven upwelling and horizontal advection on a regional and a basin scale (Di Lorenzo et al., 2008). Positive values of the NPGO have been correlated with higher salinity, nutrient, and chlorophyll-*a* values in the CCS (Di Lorenzo et al., 2009).

2.1.5. Local physical indices

Local and regional scale physical variables thought to effect forage fish availability to murre included monthly average SST for the spring (Jan–Apr) and summer (May–Sept), the date of the spring transition, seasonally averaged monthly upwelling, and seasonally averaged monthly local wind stress. Temperature is a very important factor in determining habitat suitability in marine environments, and can also serve as a proxy for many other physical processes in the coastal ocean, including upwelling and water stratification (Mann and Lazier, 2006). We obtained monthly average SST for the central Oregon coast from the National Oceanic and Atmospheric Administration National Buoy Data Center, Stonewall Banks Station 46050 (44°38'20" N 124°32'2" W) (http://www.ndbc.noaa.gov/station_page.php?station=46050). Where data were missing, we estimated missing values by conducting a linear regression of known data with in situ temperature measurements taken at station NH 15 (44°39'6" N, 124°24'42" W, $R^2 = 0.779$, $y = 0.847x + 1.956$). The date of the spring transition, which has been linked to ocean productivity and zooplankton and ichthyoplankton community composition in the CCS (Logerwell et al., 2003), is based on the date when the integrated cumulative upwelling reaches its minimum value (Bograd et al., 2009). This metric was obtained from the NOAA Northwest Fisheries Science Center Ocean Ecosystem Indicators website (<http://www.nwfsc.noaa.gov/research/divisions/fed/oeip/a-ecinhome.cfm>). We included two indices of upwelling because many aspects of biological productivity off the Oregon coast are strongly influenced by the strength and intensity of seasonal upwelling. Monthly upwelling index values for 45° N 125° W were obtained from the Pacific Fisheries Environmental Laboratory (PFEL, <http://www.pfeg.noaa.gov/>). The PFEL derives upwelling indices from 6-hourly gridded sea level pressure fields. We also included an index of upwelling based on local observations of winds developed by Pierce and Barth (2014, <http://damp.coas.oregonstate.edu/windstress/index.html>). The monthly values for along-shore wind stress (N/m²) at Newport, Oregon (Pierce and Barth, unpublished data) are derived from wind observations from the National Buoy Data Center (http://www.ndbc.noaa.gov/station_page.php?station=nwp03) following the methods described by Large and Pond (1981).

2.1.6. Local biological indices

Local biological indices available for the 1998–2002 and 2007–2011 periods included the northern copepod index (NCI), the copepod community index (CCI), the winter ichthyoplankton biomass index (WIB), and winter ichthyoplankton community index (WIC). The zooplankton community was sampled along the Newport Hydrographic line at station NH 5 (44°39'6" N, 124°10'36" W, 8 km from the Yaquina Head colony) following the methods described in Peterson and Keister (2003) and has been used to develop several indices based on species composition and biomass. The northern copepod index (NCI) is an index of the

biomass anomaly of cold water associated copepod species, including *Pseudocalanus mimus*, *Acartia longiremis*, and *Calanus marshallae* (Peterson and Keister, 2003; Peterson et al., 2012). The copepod community index (CCI) is composed of the principle axis of a nonmetric multidimensional scaling (nMDS) ordination of the copepod species community following the methods in Keister et al. (2011). Changes in these indices represent important changes in the quality of prey for forage fishes, with implications for fish survival and therefore availability to murre during chick rearing. We considered potential relationships between copepod indices collected both before (Jan–Apr) and during (May–Sept) the murre breeding season (monthly values were averaged across these periods to derive a single value). Ichthyoplankton are sampled also along the Newport Hydrographic Line (44°39'6" N, Brodeur et al., 2008) at stations 9–46 km from the murre colony. The samples collected from 1 January to 31 March are used to develop two ichthyoplankton indices (Daly et al., 2013). The winter ichthyoplankton biomass (WIB) index is the combined biomass (mg C 1000 m⁻³) of five taxa commonly found in juvenile coho and Chinook salmon diets (Cottidae, Osmeridae, *Sebastes* spp., *Ammodytes hexapterus*, *Engraulis mordax*) that also occur in diets of common murre (Daly et al., 2009, 2013). The winter ichthyoplankton community (WIC) index is the x-axis scores of an nMDS ordination of biomass values for all species in the ichthyoplankton community (Daly et al., 2013). Ichthyoplankton indices were available only for time periods preceding the murre breeding season (Jan–Mar).

2.2. Comparison of murre diets at Yaquina Head to other sites in the CCS

We drew on published studies of murre diets at Tatoosh Island, located on the inner shelf of the nCCS, and Southeast Farallon Island, on the outer shelf of the cCCS, to better understand how murre diets observed at Yaquina Head fit within the range of murre diets in the CCS as a whole (Mills et al., 2007; Schrimpf et al., 2012). We only included years in which diet data were collected concurrently at all three sites (1998–2002). Observers' ability to identify prey varied across sites, so prey types were combined into eight general taxonomic categories for analysis. Prey items that could not be identified to the family level or lower were excluded from statistical analysis.

2.3. Analysis

2.3.1. Data screening and transformation

Prey were combined into 12, ecologically relevant taxonomic categories. Prey species or groups that comprised ≤1% of overall diet for that year or were not identified using the photographic sampling method were omitted from the analysis, as recommended by McCune and Grace (2002). Prey categories retained for analyses summed to ≥95% of the diet by count. We summed the counts of prey by prey category during each sampling year and then divided this value by the total for that year to obtain the annual proportion of the diet contributed by each prey species. There were no outliers (>2 SD cutoff) in the dataset, and thus all years were retained in the analysis.

2.3.2. Statistical analysis

All multivariate statistical analyses were conducted using PC-ORD v. 6.0 (McCune and Mefford, 2011) and R v. 2.14.1 (www.r-project.org). A nonparametric, multi-response permutation procedure (MRPP) was used to test the null hypothesis of no significant difference between the samples collected using traditional trained observer techniques and those collected using digital photographs (Mielke and Berry, 2001). We used Sørensen's (Bray–Curtis) distance to compare the similarity of years within these two a priori groups to the similarity of diets within years across groups. MRPP analysis returns a chance-corrected within group agreement (A-value) which ranges from –1 to 1. An A-value of zero signifies that the similarity of sample units within groups is equal to that which would be expected by chance and, therefore, there is no

difference between groups. An A-value of 1 results if all sample units within a group are identical to one another and, therefore, there are strong differences between groups. In ecological studies, it is common to have A-values of <0.1 that are significant and values of 0.3 or greater are considered high (McCune and Grace, 2002).

We employed a multivariate ordination technique, nonmetric multidimensional scaling (Kruskal, 1964), to reduce the dimensionality of the prey composition data and allow for a visual representation of prey community structure across study years. We selected nMDS among ordination techniques because it is considered to be the most robust ordination approach for ecological data with non-linear relationships (McCune and Grace, 2002). We evaluated the dimensionality of ordinations using a scree plot, which describes the improvement of fit (decrease in stress) as dimensions are added to the ordination (McCune and Mefford, 2011). In a scree plot, the final stress, a measure of the goodness of fit, of the NMS ordination of the real data is examined against the final stress of an NMS ordination of randomized data in relation to the number of dimensions included in the ordination. The instability, the standard deviation of stress over the preceding 10 iterations of the NMS run, was evaluated using the final instability of the two dimensional solutions against the 10^{-4} value recommended by (McCune and Grace, 2002). Sørensen's distance was used in all cases, with a random starting configuration and 50 runs using real data and up to 200 iterations per run. We evaluated the usefulness of the ordination in describing patterns in the original data by examining the stress, and conducting post-hoc regressions of the distances between sample units in the ordination against distances between sample units in the original diet data. The post-hoc regression of distances between sample units in the ordination versus the original diet dataset provided a measure of variance (i.e. an R^2 value) in the original diet data explained by the ordination.

We conducted an examination of correlations between ordination axes and individual dietary components (Table 1), a number of environmental variables (Table 2) and two demographic parameters. Environmental variables with large correlation coefficients ($R^2 \geq 0.4$) were considered biologically meaningful results. We did not conduct statistical tests for significance of these correlations because ordination scores do not meet the assumption of independence (McCune and Grace, 2002). We overlaid the correlations of these variables graphically with the ordination. The length of the line is proportional to the strength of the correlation, while the angle indicates with which axes the variable is correlated. For example, a variable correlated with axis 1 but not axis 2 will be parallel to axis 1 and orthogonal with axis 2.

To ascertain relationships in murre diets across sites in the CCS, we used agglomerative hierarchical clustering analysis. We used Sørensen's distance and Flexible β as a linking method. Groups were examined using a cut-off level that was biologically meaningful, but retained at a level where 60% of the information remained. The percent information remaining is a function of the amount of information lost at each step

Table 1
Correlations of prey species with NMS axes 1 & 2.

Prey categories	R^2 (sign of correlation)			
	NMS 1		NMS 2	
Pacific sand lance (<i>Ammodytes hexapterus</i>)	0.875	(+)	0.190	(-)
Herring, sardine, shad (Clupeidae)	0.004	(+)	0.908	(+)
Sculpins (Cottidae)	0.134	(-)	0.272	(-)
Northern anchovy (<i>Engraulis mordax</i>)	0.339	(-)	0.074	(+)
Hake and cods (Gadiformes)	<0.001	(-)	0.002	(+)
Lingcod and greenlings (Hexagrammidae)	0.044	(-)	0.141	(-)
Squids (Cephalopoda)	0.008	(+)	0.085	(+)
Smelts (Osmeridae)	0.737	(-)	0.167	(-)
Flatfishes (Pleuronectiformes)	0.144	(-)	0.011	(+)
Salmon (<i>Oncorhynchus</i> spp.)	0.135	(-)	0.010	(-)
Rockfishes (<i>Sebastes</i> spp.)	0.001	(+)	0.365	(-)

The strength (R^2) of the correlation and the direction (+ or -) are shown and all correlations with an $R^2 > 0.4$ are highlighted in bold.

Table 2
Correlations of environmental variables with NMS axes 1 & 2.

	Environmental index	Months	R^2 (sign of correlation)			
			NMS 1		NMS 2	
Basin	PDO	Oct–Apr	0.016	(-)	0.190	(+)
	PDO	Oct–Dec	0.001	(-)	0.338	(+)
	PDO	Jan–Apr	0.035	(-)	0.086	(+)
	PDO	May–Aug	0.110	(-)	0.500	(+)
	MEI	Oct–Apr	0.032	(-)	0.278	(+)
	MEI	Oct–Dec	0.031	(-)	0.322	(+)
	MEI	Jan–Apr	0.031	(-)	0.243	(+)
	MEI	May–Aug	0.120	(+)	0.199	(+)
	NOI	Oct–Apr	0.102	(+)	0.046	(-)
	NOI	Oct–Dec	0.133	(+)	0.214	(-)
	NOI	Jan–Apr	0.073	(+)	0.004	(-)
	NOI	May–Aug	0.404	(-)	0.010	(-)
	NPGO	Oct–Apr	0.010	(-)	0.452	(-)
	NPGO	Oct–Dec	< 0.001	(+)	0.656	(-)
	NPGO	Jan–Apr	0.011	(+)	0.597	(-)
Local	NPGO	May–Aug	0.001	(+)	0.543	(-)
	SST	Oct–Apr	0.011	(-)	0.238	(+)
	SST	Oct–Dec	0.002	(+)	0.331	(+)
	SST	Jan–Apr	0.046	(-)	0.160	(+)
	SST	May–Aug	0.033	(-)	0.677	(+)
	Spring transition	Julian date	0.635	(-)	0.000	(+)
	Upwelling index	Oct–Apr	0.089	(+)	<0.001	(+)
	Upwelling index	Oct–Dec	0.132	(+)	<0.001	(-)
	Upwelling index	Jan–Apr	0.049	(+)	<0.001	(+)
	Upwelling index	May–Sept	0.023	(+)	<0.001	(+)
	Local wind stress	Oct–Apr	0.001	(-)	0.001	(+)
	Local wind stress	Oct–Dec	0.034	(-)	<0.001	(-)
	Local wind stress	Jan–Apr	0.006	(+)	0.002	(+)
	Local wind stress	May–Aug	0.013	(+)	0.057	(-)
	Biological	CCI	Jan–Apr	0.068	(-)	0.081
CCI		May–Aug	0.054	(-)	0.238	(+)
NCI		Jan–Apr	0.011	(+)	0.027	(-)
NCI		May–Aug	0.021	(-)	0.314	(-)
WIC		Jan–Mar	<0.001	(-)	0.109	(+)
WIB		Jan–Mar	0.004	(+)	0.863	(-)

The strength (R^2) of the correlation and the direction (+ or -) are displayed below, with all correlations with an $R^2 > 0.4$ are highlighted in bold.

of hierarchical cluster analysis. We also conducted an MRPP analysis to determine if the groups that we established were significantly different from one another.

3. Results

3.1. Murre demographics

Common murre median hatch date occurred between 13 June and 8 July (164–189 days since January 1st) and reproductive success varied from a low of 20% in 1998 to a high of 90% in 2002. Phenology was relatively stable during the early study period (1998–2002, median hatch date = 166, min = 164, max = 172) but was significantly later during the later study period (2007–2011, median hatch date = 178, min = 175, max = 189) (Welch's two sample t-test, $df = 5.587$, $p = 0.007$). There were no relationships between phenology and fecundity.

3.2. Murre diet community structure

We did not detect any difference in prey composition (MRPP, $A = -0.006$, $p = 0.55$) between years in which sampling was conducted using trained observers (1998–2002) and years when we used digital photographs (2007–2011). We collected an average of 585 (range: 36–1510) identifiable bill loads, including >12 prey species. Relative proportions varied annually, with smelts (Osmeridae), Pacific sand lance (*A. hexapterus*), and clupeids, likely Pacific herring (*Clupea pallasii*) contributing 65% to 95% of the diet, across all sampling years (Fig. 1).

Our evaluation of the usefulness of the two dimensional nMDS ordination using a post-hoc regression of distances between samples (years) in the ordination of murre chick diets with distances between samples in the original data showed that the ordination explained 93.0% of the variance in the diets, with an acceptably low final stress of 4.94 and low final instability. The ordination axes were orthogonal and captured similar amounts of the variance in the original diet matrix (Axis 1: $R^2 = 0.515$; Axis 2: $R^2 = 0.415$). The nMDS ordination of diets did not reveal any distinct clustering of years by diet type; rather sampling years were distributed relatively evenly across the ordination space (Fig. 2). We found that three prey types had strong correlations ($R^2 \geq 0.4$) with ordination axes (Table 1). Axis 1 was positively correlated ($R^2 = 0.765$) with Pacific sand lance, and negatively correlated ($R^2 = 0.737$) with the abundance of smelts. Axis 2 was positively correlated ($R^2 = 0.908$) with clupeids.

Prey categories comprising smaller proportions of murre diets showed weaker relationships with ordination axes. Northern anchovy, sculpins, and flatfishes were negatively related with axis 1 ($R^2 = 0.339, 0.134, 0.144$, respectively). Sculpins (Cottidae) were positively correlated with axis 2 ($R^2 = 0.272$). Rockfishes (*Sebastes* spp.), smelts, and hexagrammids were negatively correlated with axis 2 ($R^2 = 0.365, 0.176, 0.141$, respectively).

3.3. Environmental variables and murre diets

3.3.1. Basin-scale indices

Three of the four basin-scale environmental indices (summer NOI, summer PDO, and NPGO) were strongly correlated with murre diets (Fig. 2, Table 2). The May–September values of the NOI were negatively

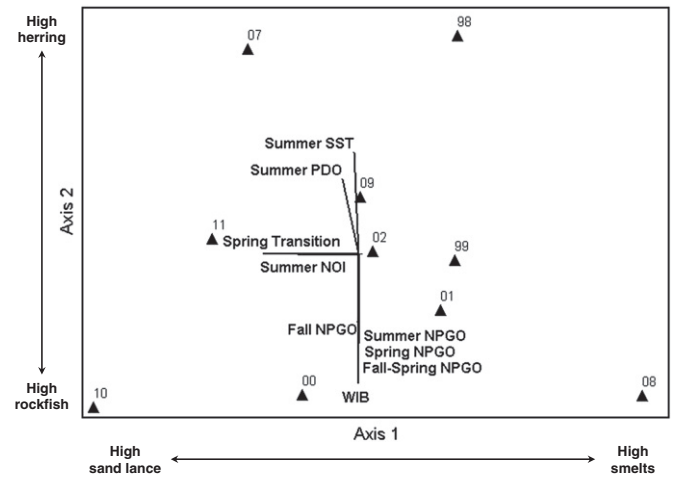


Fig. 2. Correlation of environmental variables with nonmetric multidimensional scaling axes 1 & 2 explaining variation in murre diet at Yaquina Head, Oregon. Triangles represent sampling years. Environmental variables with correlations larger than $R^2 \geq 0.4$ are shown, including sea surface temperature (SST), Pacific Decadal Oscillation (PDO), Northern Oscillation Index (NOI), North Pacific Gyre Oscillation (NPGO), spring transition and Winter Ichthyoplankton Biomass index (WIB).

correlated with axis 1 ($R^2 = 0.404$), thus high NOI values corresponded to years in which the murre diets were dominated by smelts and were lower when dominated by sand lance. The May–September values of the PDO were positively correlated with axis 2 ($R^2 = 0.500$), indicating that years with positive PDO values had higher abundances of clupeids,

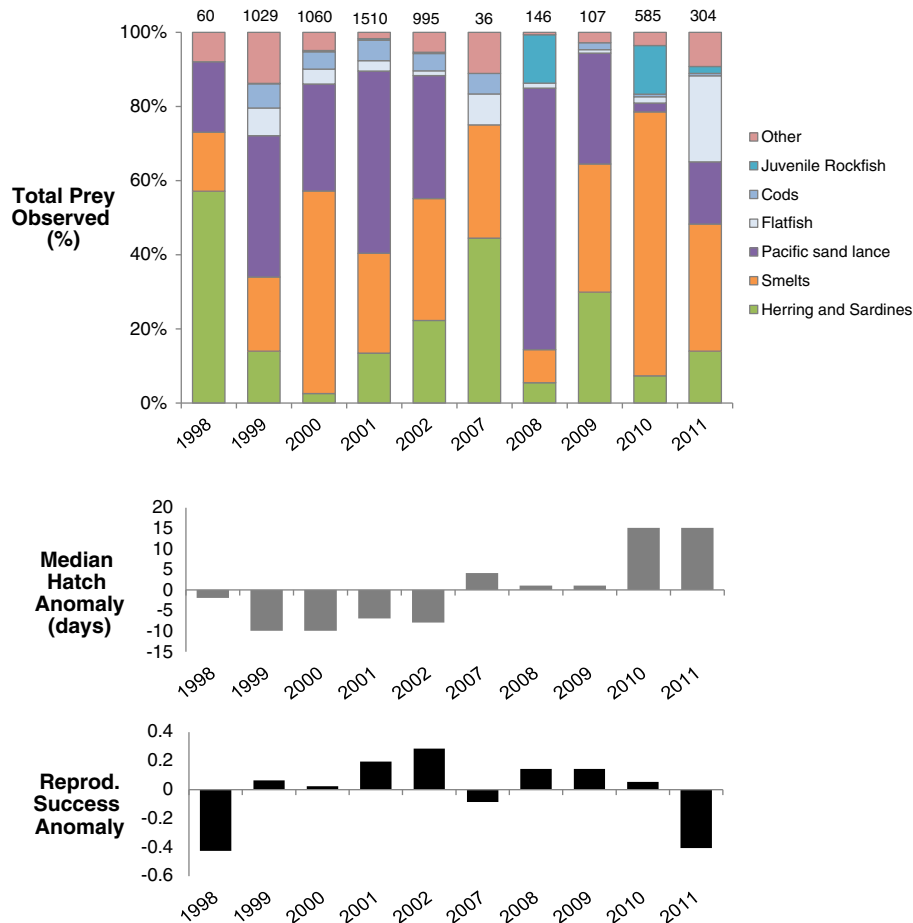


Fig. 1. Proportion of total number of prey observed in common murre diets, median hatch date anomaly, and reproductive success anomaly at Yaquina Head, Oregon. Numbers shown above each bar for diets are the total number of identifiable samples collected during that sampling year.

and lower smelt and sand lance values. The NPGO was negatively correlated with axis 2 for all time periods (Oct–Apr: $R^2 = 0.452$, Oct–Dec: $R^2 = 0.656$, Jan–Apr: $R^2 = 0.597$, May–Sept: $R^2 = 0.543$). We did not find any strong correlations between the MEI and murre diets. Aside from the NPGO, we did not detect any strong correlations with basin scale indices for time periods before the murre breeding season.

3.3.2. Local and biological indices

We found that the spring transition was negatively correlated with axis 1 (Fig. 2, Table 2). The local SST was positively correlated with axis 2 ($R^2 = 0.677$), showing a similar pattern as the PDO. Higher SST was associated with years in which the PDO was also higher and diets contained more clupeids. Both WIB and NCI were negatively correlated with axis 2 ($R^2 = 0.863$, $R^2 = 0.314$, respectively), thus in phase with NPGO and out of phase with PDO and SST in correlations with axis 2. Similar to basin scale indices, we did not find any correlations with physical variables occurring prior to the breeding season.

3.4. Demographic variables and murre diets

We observed correlations between both demographic variables and murre diets. Median hatch date was negatively correlated with axis 1 ($R^2 = 0.346$), and reproductive success was negatively correlated with axis 2 ($R^2 = 0.305$). Neither correlation, however, was strong (i.e. $R^2 \geq 0.4$). Hatch date and reproductive success correlations with orthogonal NMS axes reinforced that these demographic parameters were not correlated with one another (Fig. 3).

3.5. Murre diets at Yaquina Head and other sites in the CCS

The hierarchical clustering of diets across sites in the CCS revealed three distinct clusters, with sites on the inner shelf of the nCCS (Tatoosh, and Yaquina Head) comprising one group and the Southeast Farallon Island diets split into two groups (Fig. 4, MRPP A = 0.451, $p < 0.001$). The diets at Tatoosh and Yaquina Head were primarily composed of herring/sardines, smelts and Pacific sand lance, while juvenile rockfishes and anchovies contributed a very small portion. The diets at Southeast Farallon Island were clearly differentiated from the diets at the two sites in the nCCS, with the dominance of juvenile rockfishes and northern anchovy likely driving the difference that we observed. The Southeast Farallon Island diets were split into an earlier period that was dominated by anchovy/sardine ($\geq 40\%$, 1998–2000) and a

later period when juvenile rockfishes were a higher proportion of the diets ($\geq 50\%$, 2001–2002).

4. Discussion

4.1. Variation in murre diet community

We observed gradients among the three primary prey types under varying ocean conditions, suggesting that multiple environmental factors drive interannual changes in murre diets at Yaquina Head. Alongside the three dominant prey types, several smaller components of the diet followed similar patterns of variation. We observed that years higher in smelts also had elevated levels of northern anchovy and flatfishes, consistent with previous observations of associations between whitebait smelt, northern anchovy and Pacific sanddab (*Citharichthys sordidus*) in the nCCS (Brodeur et al., 2005). Sculpins (Cottidae) and squids (Cephalopoda) were also more abundant in murre diets in years with higher amounts of clupeids, while rockfishes were less abundant.

The diets observed during this study contain many of the same prey species in adult murre (not feeding chicks) collected as stomach samples between 1979 and 1982 in waters off the central and southern Oregon Coast and in the Columbia River plume, but in very different proportions (Matthews, 1983; Varoujean and Matthews, 1983). Pacific herring was an important component of diets among murre collected near Newport in 1982, but smelts and sand lance each contributed $< 2\%$ of the diets (Matthews, 1983). Diets in murre collected over four years near Coos Bay showed a great deal of interannual variation (Matthews, 1983), which we observed in our study as well. Diets of murre collected in the Columbia River Plume were dominated ($> 75\%$) by northern anchovy and Pacific tomcod (*Microgadus proximus*) (Varoujean and Matthews, 1983), which were only minor dietary constituents in our observations at Yaquina Head. Matthews (1983) also found at least some evidence of geographic variation in diets, with murre collected within 2 km of the Yaquina Bay jetties containing greater amounts of coho salmon (*Oncorhynchus kisutch*) and larval crabs (*Cancer* spp.) and fewer market squid (*Doryteuthis (Loligo) opalescens*).

Murre diets at Yaquina Head were similar to murre diets in some other regions of the nCCS. Observations in the nCCS, at Tatoosh Island on the inner shelf of the Washington Coast, were similar to the diets that we observed at Yaquina Head (cf. Parrish and Zador, 2003). Pacific herring, smelts, and sand lance accounted for $> 80\%$ of the chick diet at Tatoosh Island (Parrish and Zador, 2003; Schrimpf et al., 2012). It appears that these three prey (herring, smelts and sand lance) compose the typical diets for murre off Oregon and Washington and that prey switching may be an important strategy for murre throughout the nCCS (Schrimpf et al., 2012). The similarity in murre diets off Oregon and Washington also appears consistent with what has been observed in northern California at Castle Rock, where murre consumed large amounts of smelts and some sand lance (Eigner, 2009). Further south in the cCCS, murre nesting at near-shore Devil's Slide Rock show some similarity to the diets of Yaquina Head murre with appreciable amounts of smelts and sand lance, though clupeids/anchovy were also an important component of the diets (Eigner, 2009). In contrast, murre diets at Southeast Farallon Island in the cCCS differ markedly from the majority of murre colonies in the northern California Current. Juvenile rockfishes are a dominant prey item for murre nesting near the shelf break at the Farallon Islands (Ainley et al., 1993; Miller and Sydeman, 2004), in contrast to $\leq 10\%$ for murre diets at Yaquina Head and other nCCS near-shore colonies. When data were collected concurrently at sites throughout the CCS (Fig. 4, 1998–2002 for Tatoosh, Yaquina Head and Southeast Farallon Island) the diets at the two northern, inshore colonies (Tatoosh Island and Yaquina Head) were relatively coherent, but in contrast with the rockfish and anchovy dominated diets of murre nesting at the more southern, shelf-break colony (Southeast Farallon Island). The inshore–offshore difference in diet is also apparent among murre collected at sea (Ainley et al., 1996). Yaquina

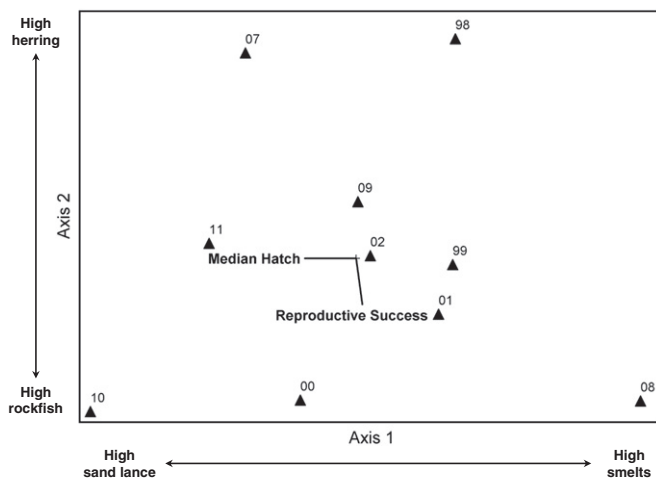


Fig. 3. Correlation of demographic variables with nonmetric multidimensional scaling axes 1 & 2 explaining variation in murre diet at Yaquina Head, Oregon. Triangles represent sampling years.

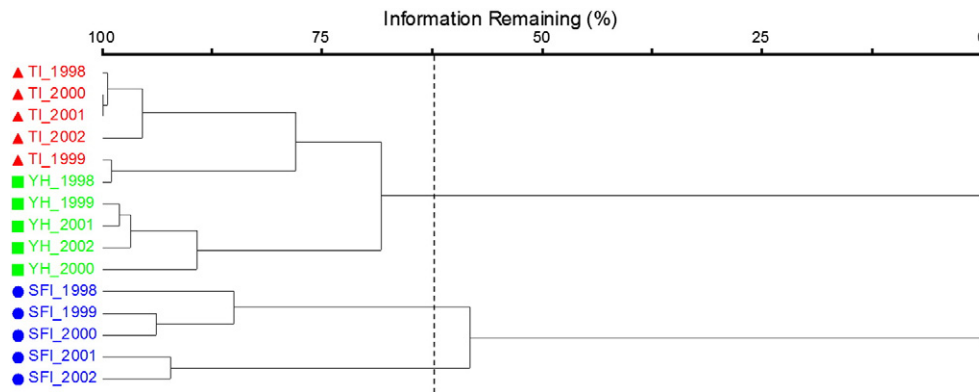


Fig. 4. Cluster dendrogram of murre diets from three sites in the CCS (1998–2002) as determined by agglomerative hierarchical cluster analysis. Dashed line marks the level (percent information remaining) at which groups were established in the dendrogram. The percent information remaining is a function of the amount of information lost at each step of hierarchical cluster analysis. Tatoosh Island diets (labeled TI, red triangle) adapted from Schrimpf et al. (2012, Supplemental materials), Yaquina Head diets (labeled YH, green square) are from this study, and the Southeast Farallon Island diets (labeled SFI, blue circle) adapted from Miller and Sydeman (2004).

Head murre, however, consistently relied more on Pacific sand lance than those nesting at all other colonies.

4.2. Environmental drivers of variable diets

We observed changes in murre diets associated with temperature related indices (PDO, SST), an atmospheric circulation related index (NOI), and indices related to productivity at lower trophic levels (WIB, NCI). We observed warm water periods, with clupeids in murre diets, associated with elevated PDO and local SST values. Sand lance, northern anchovy and flatfishes contributed more to the diet in years of cooler SST and greater NOI values during the summer. This pattern is consistent with alternations between “cool anchovy regimes” and “warm sardine regimes” throughout the Pacific (Chavez et al., 2003). The association among clupeids, cottids, and squid during warmer water conditions is not entirely consistent with previous observations of increased squid abundance with lower SST elsewhere in the CCS (Brodeur et al., 2005; Zeidberg, 2006). In contradiction with previous studies of local fish communities sampled at sites further offshore (e.g. Auth and Brodeur, 2006), higher consumption of rockfishes in murre diet at Yaquina Head was not associated with warm SST. As noted in the CCS, the intensity and frequency of upwelling and relaxation periods change the availability of prey over shelf waters, which in turn alters murre’s foraging area and thus diet (Ainley et al., 1991, 1993, 1996). This phenomenon is likely applicable to the nCCS as well.

Enhanced atmospheric teleconnections between the tropics and the North Pacific during the summer were associated with higher amounts of smelts and lower amounts of sand lance in murre diets. While the bio-physical mechanisms are unclear, it almost certainly is related to altered availability of these prey (see Ainley et al., 1995a).

Biomass values for ichthyoplankton during the winter preceding the murre breeding season and northern lipid rich copepod biomass anomaly during the summer were associated with murre diets that were lower in clupeids but higher in sand lance, smelts, and rockfishes. By extension, periods with lower SST and negative PDO values were years with high biomass values of zooplankton and ichthyoplankton (i.e. our WIB and NCI), which is consistent with previous findings (Peterson and Keister, 2003; Peterson et al., 2012). There are likely both direct and indirect trophic connections between the ichthyoplankton captured in the WIB and the mix of young-of-year and age 1 + fishes fed to murre chicks in the following summer. Some species of ichthyoplankton captured in the WIB can achieve sufficient growth to become available as prey for murre chicks just months later during the summer, in particular Pacific sand lance and Pacific herring, which we observed in murre diets at sizes that correspond to YOY fishes. Other components of the WIB more likely reflect good foraging conditions for both larval and age 1 + fishes,

which may help explain why elevated WIB also related to higher amounts of smelts in murre diets along with sand lance and rockfishes. The indices based on community composition (CCI, WIC) may represent changes in prey that are less important to the food web that supports murre.

Surprisingly, we did not observe any relationships between physical indices measured prior to the murre breeding season and murre diets. This contrasts with cCCS colonies, where timing of upwelling and other environmental variables preceding the breeding season influence both diets and reproductive success in murre and other seabirds (Ainley and Boekelheide, 1990; Ainley et al., 1993; Black et al., 2010). Obviously, temporal lags exist between the physical indices measured at the basin scale and corresponding physical and biological changes in the area immediately surrounding the murre colony. It may be that the more immediate atmospheric forcing components exert a larger influence on the murre foraging behavior and prey availability than components that require longer to take effect.

Some environmental drivers effect murre diet composition in both the cCCS and nCCS, while others do not. Oscillations in the PDO have been tied to shifts in murre diets over longer temporal scales (Miller and Sydeman, 2004) and studies of another piscivorous seabird, the rhinoceros auklet (*Cerorhinca monocerata*), found negative correlations between local SST and the proportion of preferred prey in the diet (Thayer et al., 2008). Although our study examined a much shorter time period, PDO and SST were related to diet composition at Yaquina Head. There were several relationships that we expected to observe based on previous studies in the cCCS and studies in the nCCS on other marine predators that were not evident in our study. Seasonal upwelling is recognized as an important environmental driver of biological productivity in eastern boundary currents like the CCS (Mann and Lazier, 2006), and has been related to components of murre diets (Ainley et al., 1993), but did not show direct relationships with murre diets in our study. Likewise, MEI was not directly related to the diet community, though other studies have observed effects of El Niño on murre diets (Ainley and Boekelheide, 1990; Ainley et al., 1995a; Miller and Sydeman, 2004).

4.3. Reproductive consequences of variable diets

We found that when murre diets at Yaquina Head contained fewer clupeids, accompanied by negative PDO and SST anomalies, their reproductive success was higher. Similar relationships were found at the Tatoosh Island breeding site in the nCCS, where both PDO and local SST were negatively correlated with colony attendance and showed weak negative correlations with reproductive success (Parrish and Zador, 2003). Both reproductive success and diets could be responding independently to the same environmental drivers, but as has been observed in

other seabird colonies (Harding et al., 2007; Jodice et al., 2006; Suryan et al., 2000), it appears that prey abundance and proximity to the colony (availability) is critical to reproductive success for murrets at Yaquina Head.

It is unclear if changes in murre diet represent changes in prey availability or flexible foraging responses on the part of individual murrets. There is evidence for diet specialization at the individual level in the closely related thick-billed murre nesting in the Canadian high arctic (Elliott et al., 2009a; Woo et al., 2008), wherein individual murrets repeatedly seek the same prey type year after year but the colony exhibits interannual variation in diets, as different foraging strategies gain success. However, thick-billed murrets and common murrets nesting in the same area have been shown to have different diets and foraging strategies (Birkhead and Nettleship, 1987). The degree to which common murrets in the CCS exhibit individual diet specialization remains unknown. If murrets are responding with behavioral flexibility, the years when clupeids dominated the diet could have been when adult murrets had to travel further to obtain prey to provision chicks. Murrets are known to buffer reproductive success with flexible time budgets (Burger and Piatt, 1990) but longer foraging trip durations have also been related to reduced reproductive success during more extreme prey shortages (Zador and Piatt, 1999). At Yaquina Head, the gradient in murre diets ranging from smelts and sand lance low on axis 2 to clupeids higher on axis 2 may represent a shift in foraging location between years. Smelts and sand lance are known to have a more inshore distribution, while clupeids are more abundant further offshore (Brodeur et al., 2005; Emmett et al., 2006; Kaltenberg et al., 2010). During years with higher sea level pressure in the North Pacific and enhanced coastal upwelling, we would expect greater availability of forage fish overall (Brodeur et al., 2005) and potentially greater prey availability in the area immediately surrounding the colony. Increased prey availability might allow murrets, a central place forager, to forage closer to the colony on coastally distributed species such as smelts and sand lance with subsequent energetic ramifications on chick growth and reproductive success (Burke and Montevecchi, 2009; Elliott et al., 2009b). Unfortunately, we do not have a consistent measure of murre foraging duration across the entire time series, nor were we able to track individual foraging responses over time and thus cannot account for changes in parental provisioning efforts or individual foraging specialization.

Many factors can influence breeding phenology and reproductive success, including bottom-up factors such as prey availability as well as top-down factors like disturbance and predation risk. In the cases where the timing of prey availability triggers birds to adjust their nesting phenology, then we observe close relationships between phenology, diets and breeding success (Abraham and Sydeman, 2004). At Yaquina Head, the median hatch date observed in 2011 was more than two weeks later than the median hatch observed at the beginning of the time series, yet we found no difference between the diets observed during the earlier period and those observed during the later period of the time series. Concurrently, predation and disturbance at this colony have increased during the pre-laying and laying periods in recent years (Horton, 2014) and it is possible that murrets are delaying breeding in response to elevated disturbance and predation risk on colony prior to egg laying. Similar patterns were observed at Tatoosh off the northern Washington Coast, where disturbance by bald eagles (*Haliaeetus leucocephalus*) and peregrine falcons (*Falco peregrinus*) was likely the primary cause of breeding failures in recent years (Schrimpf et al., 2012). A continued shift in murre phenology might eventually result in a mismatch with the arrival of preferred prey within their foraging range of the breeding colony. Top-down effects at Yaquina Head likely precluded finding stronger relationships between environmental drivers, diets and demographics, as has been reported on murrets elsewhere in the CCS (Ainley and Boekelheide, 1990; Ainley et al., 1995a; Black et al., 2010; Parrish and Zador, 2003).

Prey consumption by murrets varies with both physical and biological conditions at basin and local scales, and we have identified the

environmental conditions most closely related with murre diet variation at Yaquina Head. Additional work is needed to better understand the spatio-temporal foraging dynamics that serve as the mechanistic link between environmental variation, murre foraging behavior, diets, and demographics.

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