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Puffins Reveal Contrasting Relationships between Forage Fish and Ocean Climate in the North Pacific

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Running title: Puffins as samplers of Alaskan forage fish

ABSTRACT

Long-term studies of predator food habits (i.e., “predator-based sampling”) are useful for identifying patterns of spatial and temporal variability of forage nekton in marine ecosystems. We investigated temporal changes in forage fish availability and relationships to ocean climate by analyzing diet composition of three puffin species (horned puffin *Fratercula corniculata*, tufted puffin *F. cirrhata*, and rhinoceros auklet *Cerorhinca monocerata*) from five sites in the North Pacific from 1978-2012. Dominant forage species included squids and hexagrammids in the western Aleutians, gadids and Pacific sand lance (*Ammodytes personatus*) in the eastern Aleutians and western Gulf of Alaska (GoA), and sand lance and capelin (*Mallotus villosus*) in the northern and eastern GoA. Interannual fluctuations in forage availability dominated variability in the western Aleutians, whereas lower-frequency shifts in forage fish availability dominated elsewhere. We produced regional multivariate indicators of sand lance, capelin, and age-0 gadid availability by combining data across species and sites using Principal Components Analysis, and related these indices to environmental factors including sea level pressure, winds, and sea surface temperature. There was coherence in the availability of sand lance and capelin across the study area. Sand lance availability increased linearly with environmental conditions leading to warmer ocean temperatures, whereas capelin availability increased in a non-linear manner when environmental changes led to lower ocean temperatures. Long-term studies of puffin diet composition appear to be a promising tool for understanding the availability of these difficult-to-survey forage nekton in remote regions of the North Pacific.

KEY WORDS

puffins, capelin, gadids, sand lance, environmental conditions, sea level pressure, sea surface temperature, multivariate indicators, Principal Components Analysis

INTRODUCTION

Forage nekton include fishes, zooplankton, and squids that may be characterized by their central role in predator-prey relationships (Smith *et al*., 2011; Pikitch *et al*., 2014). Generally speaking, these small fish and squid, and medium-to-large zooplankton, are of exceptional trophic value owing to their abundance, tendency to form dense aggregations, and nutritional value. Many of these species are also high in essential lipids and proteins and thus play a disproportionate role in energy transfer from phytoplankton to consumers (Anthony *et al*., 2000), including species of economic and conservation concern (Cury *et al*., 2011; Hunsicker *et al*., 2011) and those targeted by fisheries (Smith *et al*., 2011;

Pikitch *et al*., 2014). In some areas, there is direct competition between human fisheries and top marine predators for food. For all of these reasons, documenting the dynamics of forage nekton communities over space and time is critical for assessing the 'health' and status of marine ecosystems (Cury *et al*., 2000; Aydin *et al*., 2007; Smith *et al*., 2011; Kaplan *et al*., 2013).

A comprehensive system for monitoring and evaluating change in forage nekton in marine ecosystems is vital, yet many of these prey communities remain poorly understood. In the Alaskan North Pacific, forage nekton distribution and abundance is known from studies that employ traditional small-scale sampling methods (e.g., mid-water trawls or beach seines; Anderson and Piatt, 1999; Robards *et al*., 2002; Abookire and Piatt, 2005), and, more recently, large-scale hydroacoustic-trawl surveys (e.g., Hollowed *et al*., 2012; Parker-Stetter *et al*., 2013; Ressler *et al*., 2012). However, with the exception of Anderson and Piatt (1999) and surveys conducted as part of the Bering Arctic Subarctic Integrated Survey (BASIS, http://www.afsc.noaa.gov/ABL/EMA/EMA_BASIS.php), none of these surveys were designed to target forage nekton over long time periods. Therefore, our understanding of temporal variation in forage nekton dynamics at regional to ecosystem scales in Alaska has been mostly inferred from incidental catch in large-scale fisheries surveys (Zador and Gaichas, 2010). Seabirds, however, are conspicuous, highly mobile samplers of the forage nekton community and for decades have been suggested to be reliable indicators of marine food supplies (Cairns, 1987; Piatt *et al*., 2007a,b). Data on seabird food habits may complement traditional fisheries-independent sampling and provide quantitative information on forage nekton availability (distribution, abundance, and spatial organization) (e.g., Hatch and Sanger, 1992; Davoren and Montevecchi, 2003; Mills *et al*., 2007; Sinclair *et al*., 2008; Thayer *et al*., 2008; Renner *et al*., 2012a; Hatch, 2013). Seabird diet composition may also be used to infer forage nekton relationships with habitat features and environmental conditions.

In Alaska, species of the families Ammodytidae (Pacific sand lance), Myctophidae (lanternfish), Osmeridae (capelin), Clupeidae (herring), Gadidae (pollock and cods), Hexagrammidae (age-0 greenlings), Scorpaenidae (rockfish), and Salmonidae (salmon), as well as Euphausiacea (krill), and Teuthidae (squids) are consumed by marine mammals and seabirds (Pauly *et al*., 1998; Sinclair *et al*., 2008; Renner *et al*., 2012a). Puffins (family Alcidae) forage heavily on small schooling fish throughout the spring and summer (including age-0 greenlings, rockfish, and salmon, and age-0 and age-1 pollock and cod), and thus are at least qualitative samplers of forage nekton availability during this critical period of productivity each year. Owing to their conspicuousness, the diet composition of puffins is easier to study than the food habits of fish or marine mammals. In this study, we integrate data on diet composition of puffin offspring at different colonies from multiple long-term studies with environmental indices derived from oceanographic data sets, and infer temporal variability in forage nekton availability over time and relative to ocean climate. Despite progressive fisheries management in Alaska that restricts targeted commercial fisheries on most species of forage nekton, knowledge of forage availability remains fragmentary. This study will help inform mandated ecosystem-based approaches to fisheries and wildlife management in Alaska in an environment strongly influenced by coupled climate-ecosystem variability (Francis and Hare, 1994; Pikitch *et al*., 2004).

METHODS

Data preparation

In Alaska, studies of puffin food habits have been conducted over large spatial and temporal scales. From the mid-1970s to the present, ~40 islands from Southeast Alaska, across the Gulf of Alaska (GoA), and throughout the Aleutian Islands have been regularly sampled as part of the Alaska Maritime National Wildlife Refuge seabird monitoring program as well as other directed studies by the U.S. Geological Survey Alaska Science Center. The sampling methodology is detailed by Hatch and Sanger (1992). In summary, puffins return from foraging with whole prey items carried in their bills, but are blocked from delivering to chicks by temporary placement of screens at their burrow entrance, leading the adult to drop prey on the screen. Prey items are collected, measured and identified in the field or later in the laboratory. For this study, we collated the dietary information for three species: horned (hereafter HOPU; *Fratercula corniculata*) and tufted puffins (TUPU; *F. cirrhata*), and rhinoceros auklet (RHAU; *Cerorhinca monocerata*). The data come from samples collected from 1978 through 2012. Each "bill load" delivered by adults may contain single or multiple prey items, and is considered a unique sample. The data we used were counts of identified prey species by sample. We summarized these data by sample because individual prey items within bill load are not independent from one another (Thayer *et al*., 2008, 2014). Over the entire time period, ~20,000 bill loads were obtained, consisting of ~100,000 individual prey items belonging to 122 species or higher taxonomic groupings (e.g., families such as Gadidae). For our analyses, we summarized a subset of these data from five sites (two of which consist of multiple islands) with > 9 years of data (Tables 1 and 2). We dropped sites which lacked at least ten samples within a given year. This resulting subset consisted of 13,804 bill loads (56% of the samples were from TUPU, 31% came from RHAU, and 13% were from HOPU) comprising 78,077 single prey items belonging to 64 species/taxonomic groups.

To investigate temporal variability in the forage fish availability, we simplified the dietary data into seven prey species and nine prey "groups" (Table 1). Prey analyzed as species were capelin (*Mallotus villosus*), lingcod (*Ophiodon elongatus*), Pacific herring (*Clupea pallasii*), Pacific sand lance (PSL; *Ammodytes personatus*), Pacific sandfish (*Trichodon trichodon*), prowfish (*Zaprora silenus*), and sablefish (*Anoplopoma fimbria*). We created a group for flatfish; this group was mainly arrowtooth flounder (*Atheresthes stomias*) and prey identified to family or order (Pleuronectiformes and Pleuronectidae), but also contained a few flathead sole (*Hippoglossoides elassodon*), Pacific halibut (*Hippoglossus stenolepis*), and Greenland turbot (*Reinhardtius hippoglossoides*) (Table 1). The gadid group was primarily composed of walleye pollock (*Gadus chalcogrammus*), but also included Pacific cod (*G. macrocephalus*), saffron cod (*Eleginus gracilis*), and Pacific tomcod (*Microgadus proximus*). Hexagrammids were mostly greenling (*Hexagrammos* spp.) and also included Atka mackerel (*Pleurogrammus monopterygius*). Mesopelagic fishes were primarily identified to the Family Myctophidae. Rockfish contained *Sebastes* spp. or prey identified as Family Scorpaenidae. Salmon included all prey identified within the genus *Oncorhynchus* or Family Salmonidae. Sculpins included several species within the families Cottidae, Hemitripteridae, and Psychrolutidae. The octopus group mostly included prey identified as Order Octopoda. Finally, most squid were identified as Family Gonatidae or Superorder Decabrachia.

In this analysis, we focused on percent by number as mass data were unavailable for many of the diet samples. We emphasized primary species in the forage nekton community by excluding rare and unidentified fishes, as well as non-cephalopod invertebrates (including all crustaceans). These exclusions accounted for ~6% of the total number of individual prey items identified and enumerated. Moreover, by excluding small prey species (e.g., euphausiids, which were numerically abundant) we lessened any biases associated with using percent by number instead of percent by mass or volume. We chose focal sites based on the availability of long time series data sets (Table 2). Assuming that birds foraging from some locations had overlapping foraging ranges and would be sampling the same local forage community, we created two island "complexes" (i.e., sites within 50 km of each other were pooled). In total, five sampling sites (islands or island complexes) were considered: Buldir Island in the western Aleutians, the Aiktak Complex in the eastern Aleutians, the Semidi Complex in the western GoA, Middleton Island in the central GoA, and St. Lazaria Island in the eastern GoA (Table 2, Fig. 1). At Buldir, Middleton, and Semidi Complex, more than one puffin species was studied: TUPU and HOPU were sampled at Buldir, TUPU and RHAU at Middleton, and all three puffin species at the

Semidi Complex. Only TUPU were studied at the Aiktak Complex and only RHAU were studied at St. Lazaria Island. For analyses, we evaluated percent composition by calculating the percent by number of each prey taxon per sample and then took the mean per year for each puffin-site.

Statistical analyses

We used PRIMER v6 (PRIMER-E Ltd., 2006) to contrast puffin diet composition among sites, species, and years. We used Analysis of Similarity (ANOSIM), followed by similarity percentages (SIMPER), to compare diet composition between puffin species within sites. ANOSIM tests the null hypothesis that no assemblage differences exist between groups of samples (Clarke and Gorley, 2006). SIMPER provides interpretation of differences among groups when they have been found (Clarke and Gorley, 2006). We conducted this analysis to determine if we could combine data between species, or if each dietary time series would have to be considered independently. In all cases, puffin species showed significant dissimilarities in diet composition (Table S1), so we could not combine them for temporal analyses. Second, we compared diet similarities between sites, stratified by species. These comparisons were restricted to compatible time series: TUPU at Middleton vs. the Aiktak Complex, RHAU at Semidi Complex vs. Middleton, RHAU at Middleton vs. St. Lazaria, and RHAU at the Semidi Complex vs. St. Lazaria. As was the case between species, we found significant dissimilarities in the forage fish taken between sites, with the exception of RHAU at the Semidi Complex and Middleton (Table S2), and therefore also stratified our temporal analyses by site. Third, to examine changes in diet composition over time, we calculated the percentage by number by sample by year and tested for the significance of variation among year (as well as “year periods”, see Supplementary Material) using ANOSIM/SIMPER. We tested for among-year differences to investigate interannual variability in diet composition (see Results).

Temporal variation of forage nekton species was investigated by exploring the use of each prey species across time using Principal Components Analysis (PCA) (Jolliffe, 2002; Mills *et al.,* 2007). To conduct PCA, we collated all annual data for sand lance, gadids, and capelin, which were the dominant forage fish used across most sites and are thought to be “preferred prey” in most locations (Decker *et al*., 1995; Renner *et al.*, 2012a). Squids and hexagrammids would also have been appropriate targets for multivariate indicators, but were only dominant prey in the western Aleutians (see Results). PCA requires that data sets have no missing values. For sites with one year of missing data, we averaged the two years of data before and after the missing point, assuming a monotonic change in the consumption of a particular forage fish species. In a few instances only one year before or after was available for estimating the missing data point, so we repeated the adjacent value for the missing year. For sand lance and gadids, a total of nine annual values for each species were estimated using this procedure (each representing 9.4% of the total data matrix for these species). For capelin, six annual values were estimated (7.5% of the matrix). The assumption of monotonic change appears reasonable for sand lance and capelin, but may be less appropriate for age-0 gadids where production and recruitment are more irregular (Mueter *et al*., 2011; Hollowed *et al*., 2012). The resulting data matrices for forage fish PCA included five puffin-sites for sand lance and gadids (n = 95 site-years, 1994-2012), and four puffin-sites for capelin (n = 80 site-years, 1993-2012). We retained the resulting first and second principal components for analysis against environmental conditions.

To investigate environmental correlations, we conducted analyses on sea surface temperature (SST), sea level pressure (SLP), and winds, variables known to affect marine productivity (Hunt *et al*., 2002; Hunt and Stabeno, 2005). Monthly environmental data were collated for the three local oceanographic variables in 4° longitude x 3° latitude boxes overlaid on each of the five sites where puffin food habits were studied (Fig. 1). SST and SLP data were obtained from Hadley Met Office reconstructions (Rayner *et al*., 2003; www.metoffice.gov.uk; July 2014), and wind speed data were obtained from iCOADS (Woodruff *et al*., 2011; www.icoads.noaa.gov; July 2014). Wind speed was represented by zonal (u) and meridional (v) wind components. We integrated the local-scale environmental data (u and v winds, SLP, and SST) across sites using PCA, and used the first and second principal components for further analysis. We used multiple regression and Spearman rank correlation to test for relationships between the seabird-based forage fish indices (sand lance and capelin) and annually-averaged environmental principal components (PCs) in the same year. We used annually-averaged data due to autocorrelation in these variables, particularly those associated with ocean temperature (Mendelssohn and Schwing, 2002); essentially, the annual values reflect seasonal values.

RESULTS

Puffin diet composition by site, species, and year

Puffin diet composition at the westernmost site, Buldir, was dominated by squids and hexagrammids, with lesser amounts of gadids and sand lance (Fig. 2). Sand lance and gadids were the prevalent prey at the Semidi and Aiktak complexes in the western and central GoA (Fig. 2). Sand lance, capelin, and herring were dominant at the eastern GoA sites of Middleton and St. Lazaria (Figs. 2 and 3). When stratified by species and site, diet composition varied significantly by year (Table 3). For HOPU and TUPU at the Semidi Complex, sand lance was dominant in all years (Fig. 2). For TUPU at the Aiktak Complex, gadids were commonly observed, primarily in the early 1990s and after 2008, but sand lance dominated in the late 1990s and early 2000s (Fig. 2). At Middleton, sand lance was the predominant TUPU diet item from the mid-1990s to mid-2000s, but decreased afterwards when herring, and to a lesser degree, capelin were taken with greater frequency. For RHAU at the Semidi Complex, sand lance dominated the diet in all years (Fig. 3). At Middleton, sand lance was the predominant RHAU diet item until the late 2000s, when capelin became more important (Fig. 3). At St. Lazaria, from the late 1990s through the mid-2000s, and again beginning in 2011, sand lance and capelin were present in nearly equal proportions. In remaining years when sand lance use was low, herring and hexagrammids were taken in greater amounts (Fig. 3).

Multivariate indicators of forage fish availability

$PC1_{\text{Pacific sand lance}}$ (hereafter $PC1_{PSL}$) explained 51% of the variation in sand lance use among puffin species and sites, with another 23% explained by $PC2_{PSL}$ (Table 4a). Coherence across species and sites was evident. $PC1_{PSL}$ was strongly associated (loadings >|0.2|) with TUPU at Buldir, Middleton, and Aiktak Complex and RHAU at Middleton; RHAU at St. Lazaria loaded strongly on $PC2_{PSL}$ and showed a slightly different pattern of temporal variability (Table 4a). We interpret $PC1_{PSL}$ as reflecting low-frequency variability in sand lance availability (Fig. 4a). Values were high from the late 1990s through mid-2000s, but lower prior to 1997 and from 2006-2012 (Fig. 4a). We interpret $PC2_{PSL}$ as reflecting interannual variation in sand lance availability near St. Lazaria in Southeast Alaska (Table 4a).

$PC1_{\text{capelin}}$ explained 44% of the variation in capelin availability among puffin species and sites, while $PC2_{\text{capelin}}$ explained 30% of the variation (Table 4b). All puffins and sites were strongly associated (loadings >|0.2|) with both $PC1_{\text{capelin}}$ and $PC2_{\text{capelin}}$, although $PC2_{\text{capelin}}$ loaded negatively for RHAU and TUPU at Middleton and positively for RHAU at St. Lazaria and TUPU at Aiktak Complex (Table 4b). Similar to sand lance, we interpret $PC1_{\text{capelin}}$ as reflecting low-frequency variability in capelin availability (Fig. 4b), but in this case values were low from the early 1990s through mid-2000s and increased after 2006. We interpret $PC2_{\text{capelin}}$ as predominantly reflecting interannual variation at St. Lazaria (Table 4b).

$PC1_{\text{gadids}}$ explained 49% of the variation in gadid abundance trends among puffin species and sites, while $PC2_{\text{gadids}}$ explained 21% (Table 4c). All puffin-sites with the exception of TUPU at Buldir were strongly associated with $PC1_{gadids}$. TUPU at Buldir was the only time series to show peak gadid availability in 2006 and thus loaded strongly onto $PC2_{gadids}$ (Table 4c, Fig. 4c). We interpret $PC1_{gadids}$ as reflecting interannual variability in gadid availability for most puffin-sites and $PC2_{gadids}$ as reflecting variability at Buldir (Table 4c, Fig. 4c).

Forage fish availability and environmental conditions

We developed indicators of temporal environmental variability by combining information on SLP, SST, and winds using PCA (Fig. 5). $PC1_{environment}$ reflected SST variability at the Aiktak Complex and GoA study sites (Semidi Complex and Middleton). We interpret $PC2_{environment}$ as an indicator of atmospheric (SLP) and wind variability across sites, but loadings on $PC2_{environment}$ were not particularly strong and our interpretation is limited. $PC1_{environment}$ was positively correlated with $PC1_{PSL}$ (Table 5, Fig. 6a). By itself, $PC2_{environment}$ did not correlate to $PC1_{PSL}$, but a negative relationship was evident in the multiple regression (Table 5, Fig. 6b), which appears to be mostly related to the negative effect of meridional winds at Middleton (Table S3). The multiple regression examining the relationship of environmental conditions and $PC1_{PSL}$ explained 61% of the variance in this variable (Table 5). In contrast, $PC1_{environment}$ was *negatively* correlated with $PC1_{capelin}$ (Table 5, Fig. 6c). This relationship appears to be weakly non-linear (Fig. 6c), but the quadratic regression term with $PC1_{environment}$ was not significant ($P>0.05$). $PC2_{environment}$ was not correlated with $PC1_{capelin}$ (Table 5, Fig. 6d). Additional site-specific correlations between $PC1_{PSL}$ and $PC1_{capelin}$ and SST, SLP, and wind indices are provided (Table S3).

DISCUSSION

Alaskan puffins consume a wide diversity of forage nekton. In this study, we documented 64 species/species-groups of forage fishes, squids, and octopus captured by puffins for chick provisioning. We can describe this high diet diversity due to the long-term nature of this study, with sampling over 35 years (1978-2012 and continuing). It has been reported that TUPU take a wider variety of prey than do HOPU and RHAU (Piatt and Kitaysky, 2002a,b; Hedd *et al.*, 2006). We corroborate this result in our study with the utilization of a much larger comparative database. Considering only nektonic prey identified to species, TUPU took 41 prey species, whereas HOPU and RHAU consumed 24 and 21 species, respectively. This suggests that TUPU are a more generalist predator. A more detailed analysis of diet composition between seabird species focused on prey species, rather than families or some of the coarse taxonomic groupings used here, would help identify factors affecting diet diversity in these puffins.

While puffin diet was diverse in general, a few species tended to dominate across time and space. Considering the five sites investigated here, we showed that the diets of puffins at Buldir, our western-most site, were dominated by squids and hexagrammids, whereas in the eastern Aleutians and western GoA, puffins consumed gadids and sand lance, and in the central and eastern GoA, they consumed sand lance, capelin, and herring. The split between the more oceanic western Aleutian site (Buldir) and the eastern Aleutians and GoA is in accordance with changes in the physical and biological environments to the east and west of Samalga Pass (Hunt and Stabeno, 2005; Ladd *et al*., 2005 a,b). To the east, biological communities are comprised mostly of shelf-based species (in this case gadids, sand lance, and capelin) whereas to the west, a community of open-ocean species resides (e.g., squids). Details of this geographic variability across the Aleutian chain are being addressed elsewhere (Piatt *et al*. submitted).

Multivariate synthesis, modes of temporal variability, and relationships to ocean climate

The main goal and advantage in combining data sets across species and sites is in establishing patterns of change and coherence at large (regional) scales amid the noise typical of most biological time series (Sydeman *et al*., 2001; Frederiksen *et al*., 2007; Zador *et al*., 2013). For the most common prey species of puffins—sand lance, capelin, and gadids—we used the observed spatial and species-specific variability to derive multivariate forage nekton indicators (Table 4). We did not attempt to develop multivariate indicators for squid and hexamgrammids because so few were identified to species, and those groups were largely found only at the western site (Buldir), making a synthesis by PCA unnecessary (i.e., PCA results would simply reflect availability at Buldir).

Our PCA-derived indicators revealed temporal and spatial coherence in the availability of sand lance and capelin. The dominant pattern in sand lance ($PC1_{PSL}$) reflected variability from the western Aleutians to the central GoA, whereas $PC2_{PSL}$ reflected trends in the eastern GoA (as well as an inverse trend at Buldir). It appeared that changes at St. Lazaria preceded changes at the other sites, but our time series is inadequate to consider this a robust pattern. The dominant sand lance temporal pattern shows higher abundance from 1997 through 2004, then low sand lance availability from 2005 through 2011. The temporal trend differed at St. Lazaria, with $PC2_{PSL}$ revealing consistently moderate availability from 1994 through 2004, followed by decline from 2005 through 2009. Sand lance were not taken by puffins much anywhere after 2007-2008, which may correspond to a large-scale ecosystem shift at that time (Hatch, 2013) or slightly earlier (Peterson and Schwing, 2003; Litzow and Mueter, 2014).

The dominant capelin pattern was strongest in the western and central GoA and less so in the eastern GoA. Buldir was not included in the capelin PCA because no capelin were observed in diet samples there. Our analyses show a major stepwise (apparent threshold) increase in capelin availability starting in 2007 (Fig. 4c); capelin were not consistently prevalent in the puffin diets at Middleton until that year (Hatch, 2013). The positive loadings of the Aiktak Complex and St. Lazaria and negative loadings of Middleton on $PC2_{capelin}$ suggest that this is an indicator of variability in the availability of capelin between coastal (Aiktak Complex and St. Lazaria) and offshore (Middleton) habitats. For most of the time series, the use of capelin in these habitats was largely out of phase, thus $PC2_{capelin}$ may be an indicator of capelin presence/absence in offshore habitats. This may also help to explain why the abundance trends from the small-mesh survey, which has been restricted to coastal areas in recent years, do not match the changes evident in the prey captured by puffins (Orsmeth, 2012). Apparent non-linear (threshold-like) shifts in capelin abundance have been described by others in Alaska. Anderson and Piatt (1999) showed that capelin in the small-mesh survey in the western GoA peaked in the late 1970s, declined to lower levels in the early to mid-1980s, then largely disappeared from trawl catches after 1985. In the central GoA, Hatch (2013) documented a stepwise increase in capelin in the diets of kittiwakes starting in 2008. Our PCA on capelin availability confirms that this species is characterized by non-linear changes with respect to our multivariate index of environmental conditions, which reflects a combination of atmospheric and oceanographic variables. Other multivariate indicators of temporal variation in forage fish in marine ecosystems are rare. In the central-northern California Current, dietary data from three species of seabirds and Chinook salmon were combined using PCA to develop indices for pelagic schooling juvenile rockfish (*Sebastes* spp.), an important forage fish in the region (Mills *et al*., 2007). Other than that, no other study focused on using seabirds as indicators of forage fish availability has combined data from multiple top predators, though Hatch and Sanger (1992) combined data across sites in the eastern Aleutians to characterize age-0 pollock abundance, and Thayer *et al*. (2008) examined forage nekton in RHAU diet at multiple sites from Japan to California.

Given the temporal coherence in the availability of sand lance by puffins across Alaska, our results suggest that patterns of change are likely related to large-scale climatic factors. Indeed, we found that sand lance presence in the puffin diet was linearly and positively related to ocean temperature (and negatively related to sea level pressure), while capelin abundance in the diet was negatively related to temperature. These relationships may reflect the biogeography of these species, since capelin is a boreal species (Rose, 2005), whereas sand lance is a more temperate species. Sand lance growth has been positively related to temperature in Cook Inlet, Alaska (Robards *et al.*, 2002), and abundance has been positively related to temperature in the North Sea and Japan Sea (van der Kooij *et al.*, 2008; Murase *et al.*, 2009). However, Arnott and Ruxton (2002) and Hedd *et al.* (2006) reported that sand lance recruitment declines under warmer conditions in the North Sea and southeastern Gulf of Alaska, respectively. Doyle *et al.* (2009) also showed a negative relationship between larval sand lance abundance and temperature, represented by the Pacific Decadal Oscillation, in the western GoA. Notably, we found regional differences in the response of sand lance to environmental/temperature change (Table S3). Sand lance (abundance and recruitment) may actually respond to temperature variation in a "dome-shaped" manner, positively in a lower temperature range and negatively in a high temperature range, as suggested by others for the southeastern GoA (Bertram *et al.*, 2001; Hedd *et al.*, 2006). If this is the case, it is noteworthy that for the time period analyzed, with the possible exception of St. Lazaria Island in SE Alaska, the environmental conditions leading to potential negative relationships between sand lance and temperature were not experienced. Dome-shaped relationships with temperature have also been established for other fish, including pollock in the Bering Sea (Coyle *et al.*, 2011).

Capelin biophysical relationships are clearer (Decker *et al.*, 1995). In Alaska, Arimitsu *et al.* (2008) and Renner *et al.* (2012b) showed that within relatively warm regions or time periods in the GoA, capelin were spatially associated with colder, glacially-modified waters found in fjords and large embayments. In the Northwest Atlantic, Buren *et al.* (2014) showed capelin recruitment to be enhanced when ice retreat is delayed, leading to colder temperatures in the region. Further evidence of capelin association with colder water comes from the Bering Sea where Yang *et al.* (2005) demonstrated greater groundfish depredation on capelin north of the ice edge compared to south of it, which may reflect differences in habitat preferences, or differential predation rates in waters of varying temperature. Therefore, despite some variability in sand lance biophysical relationships, it seems likely that of the two species, sand lance prefers warmer conditions more than capelin do, and the relationships we derived between $\mathrm{PC1}_{\mathrm{PSL}}$, $\mathrm{PC1}_{\mathrm{capelin}}$, and $\mathrm{PC1}_{\mathrm{environment}}$ are in accordance with findings from previous studies on these species. The contrasting relationships are interesting, and may be related to life history and habitat requirements of these species (Winemiller, 2005). Sand lance require nearshore shelf habitats and sand for spawning and burrowing. These habitats are shallow, generally warmer, and may be more productive than deeper water habitats. Capelin also spawn on sandy beaches or nearshore benthic habitats, but are often found offshore and in deeper waters where juveniles go to feed and grow, and adults gather briefly before spawning. Sand lance are unusual in that they spawn in late fall, and larvae emerge during winter when prey are scarce but less variable (Robards *et al*., 1999). Capelin typically spawn in late spring (April-June), and larvae emerge into a productive but more variable environment (Arimitsu *et al*., 2008).

Availability or abundance?

The lack of detailed information on forage nekton distribution and abundance across Alaska was a primary motivation for this study. A key question thus remains: do puffin diets reflect forage fish abundance in the environment, or do the patterns in diet composition just reflect variation in prey selection and shifts in prey preferences? Few studies have actually demonstrated that seabird diets track prey (forage fish) population abundance (e.g., Mills *et al*., 2007). In order to address this question, one needs concurrent long-term data on forage nekton availability within the foraging ambit of the birds under study, as well as knowledge of the spatial distribution of the prey species (G.L. Hunt, Jr., pers. comm.). In particular, if the foraging ambits of the birds are within the central portion of the prey distribution, there may be huge changes in the periphery of the prey distribution that will not be detected. Likewise, if the birds are sampling the periphery of prey distribution, large swings in diet composition may occur with relatively minor changes in overall forage nekton abundance (Hunt, 1991). Nonetheless, several lines of evidence suggest that Alaskan puffin diet composition aligns with forage fish abundance in the environment as inferred from both fisheries and fisheries-independent surveys. First, Anderson and Piatt (1999) described changes in forage nekton based on fisheries-independent small-mesh surveys in the western GoA from 1953 through 1997 and found shifts in forage abundance in association with the 1977 regime shift to warmer conditions (Mantua *et al*., 1997; Litzow, 2006). Similarly, although at a slightly different time period, our study showed that capelin declined rapidly in the GoA during the early 1980s and remained scarce through the 1990s. Second, Doyle and Mier (2012) summarized relative abundance of gadids, capelin, and sand lance from multi-decadal ichthyoplankton surveys in the western GoA, including bongo net (333-µm mesh) sampling from 1981 to the present. While a full analysis is beyond the scope of this study, preliminary correlation analyses indicate coherence between the ichthyoplankton data set and our puffin-based indices of abundance: rank correlation was strong for gadids ($PC1_{gadids}$: $\rho = 0.525$, $p = 0.025$, $n = 18$; $PC2_{gadids}$: $\rho = 0.123$, $p =$

0.627, n = 18), but weak for sand lance ($PC1_{PSL}$: $\rho = -0.090$, p = 0.723, n = 18; $PC2_{PSL}$: $\rho = -0.084$, p = 0.742, n = 18). The weak relationship with sand lance is expected as the puffins take both age-0 and age-1 fish, and this may mask any relationships with larval abundance in the environment. We were unable to make these comparisons with age-0 capelin, the size taken by puffins, because they are adept at avoiding plankton nets (M. Doyle, University of Washington, USA, pers. comm.).

Third, and perhaps most significantly, it is well known that pollock stocks are characterized by occasional strong recruitment events that can lead to dominant year classes in the population (Bailey, 2000; Mueter *et al*., 2011). Indeed, back-calculating from fisheries statistics, the 2006 year class for Aleutian pollock and the 1994 year class for GoA pollock have been identified as strong year classes (Barbeaux *et al*., 2013; Dorn *et al*., 2013), and these strong year classes were observed as the age-0 cohort in the puffin diets. For example, with the exception of gadids taken by puffins at the Aiktak Complex (mostly walleye pollock; Table 1), gadids were largely uncommon outside of short-term 'pulses' of abundance at other sites. At Buldir, gadids comprised over 50% of the TUPU prey in 1992 and 2006 and were either absent or <20% of the prey in all other years. Furthermore, our PCA demonstrated that while low-frequency, multi-year change was the dominant mode of variability for sand lance and capelin (see below), interannual variability was the dominant mode of variability for gadids (Table 4, Fig. 4c). This may reflect serial correlation in recruitment of sand lance and capelin in response to varying climatic conditions, a feature that differentiates them from gadids, which do not show any evidence of serial correlation in the puffin diets. Alternatively, the apparent serial correlation in the take of sand lance and capelin may be related to the predators' ability to take multiple age classes of these prey, as they do not grow to a size puffins cannot consume (in contrast to gadids; G.L. Hunt, Jr., pers. comm.). $PC1_{gadid}$ is interpreted to reflect change in gadid use in the GoA, whereas $PC2_{gadid}$ reflects trends in the western Aleutians. Thus, the high abundance of gadids in the puffin chick diets in the GoA in 1994-1995 and in the western Aleutians in 2006 appears to correspond with the strong recruitment events for this species throughout its range in Alaska. We plan to correlate the puffin data with recruitment indices from stock assessments in a future study, but we conclude here that both the basic observations and multivariate syntheses of the dietary data suggest that puffins are tracking the availability of forage nekton in the environment.

Implications for ecosystem management

Assessing the status of remote marine ecosystems requires ecological indicators of mid trophic level forage nekton availability. Globally, one of the challenges is to design and test indicators that have clear relationships to ecosystem "productivity", especially with regard to the conservation and management of upper trophic level species (fish, birds, and mammals). Indicators of the distribution and abundance (hence availability) of forage nekton populations that support predator-prey relationships should enable more sustainable use of marine resources (Hunsicker *et al*., 2011). The focal forage fishes in this study, capelin, sand lance, and age-0 gadids, as well as age-0 hexagrammids and squids, provide the 'preyscape' for piscivorous fishes important to commercial fisheries in Alaska, seabirds, and marine mammals. Poor foraging conditions, meaning few forage fish, can have negative impacts on commercially-targeted species. For example, periodic occurrences of "mushy halibut syndrome", in which the flesh of Pacific halibut is abnormally opaque and flaccid, and hence of inferior quality for human consumption, is thought to be related to nutritional deficiencies (http://www.iphc.int/research/biology/mushy-halibut.html). Thus, understanding the determinants of the abundance and availability of these forage fish may have broad application, beyond population predictions, to informing management of fisheries and wildlife species. In addition, links between abundances of age-0 gadids in puffin prey and strong pollock year classes may serve as early indications of recruitment strength. Given the importance of capelin and sand lance to the ecosystem, the North Pacific Fisheries Management Council has a long-standing policy prohibiting fisheries targeting these species (Witherell *et al*., 2000). This progressive policy is based primarily on assumed relationships between forage nekton and fish, seabird, and marine mammal productivity. Given the nature of this policy, more information about sand lance and capelin, as well as other key forage fish, can help to ensure that ongoing management supports key ecosystem functions in the region.

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The data analyzed in this paper are contained in a composite database ("puffin_diet_ALASKA_NPRB1213", version date February 2014) and reflect a compilation of ongoing studies on Alaskan seabird food habits (e.g., prey species, length and mass) by the Alaska Maritime National Wildlife Refuge (AMNWR, Homer, AK), the U.S. Geological Survey Alaska Science Center (USGS, Anchorage, AK), and Institute for Seabird Research and Conservation (ISRC, Anchorage, AK). Data from these original sources were harmonized and merged by the Farallon Institute, with the resulting derived database presenting standardized information on puffin diet composition and prey metrics. As studies of puffin food habits are continuing as part of ongoing AMNWR, USGS, and ISRC research, we note that newer data are available than what are contained in the database used in this paper (contact the primary data holders listed above). Support for analysis of these data was provided by the North Pacific Research Board under project 1213. To the multitude of people who sampled puffin food habits in the region over the years we offer sincere gratitude. In addition to authors S.A.H. and M.A., puffin diet samples were processed (identified and measured in the field or lab) by Kathy Turco, Rick Hibpshman, and Sarah Schoen. We also thank Kerim Aydin, Shannon Fitzgerald, Andy Whitehouse, George Hunt, and anonymous reviewers for reviewing earlier versions of this manuscript, and Julie A. Thayer and Franz Mueter for discussions regarding analysis of diet composition data. The scientific results and conclusions, as well as any views of opinions expressed herein, are those of the authors and do not necessarily reflect those of the USFWS, NOAA, USGS, or any other governmental agency. Any mention of trade names is for descriptive purposes only and does not constitute endorsement by the federal government.

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Table 1. Species contained within the 16 prey groups observed at the sites in this study. The percentage of each species in each group (of fish identified to the species level) is shown in parentheses.

Prey Group	**Prey Species**	**Prey Common Name**
Capelin	*Mallotus villosus*	Capelin
Flatfish	*Atheresthes stomias (71%)*	Arrowtooth flounder
	Pleuronectiformes	Flatfish
	Pleuronectidae	Right-eyed flatfish
	Hippoglossoides elassodon (18%)	Flathead sole
	Reinhardtius hippoglossoides (6%)	Greenland turbot
	Hippoglossus stenolepis (5%)	Pacific halibut
	Lepidopsetta spp.	Rock sole
	Glyptocephalus zachirus (<1%)	Rex sole
	Limanda spp.	Limanda spp.
Gadid	*Gadus chalcogrammus (90%)*	Walleye pollock
	Gadidae	Gadid
	Gadus macrocephalus (9%)	Pacific cod
	Microgadus proximus (<1%)	Pacific tomcod
	Eleginus gracilis (<1%)	Saffron cod
Hexagrammid	Hexagrammidae	Greenling
	Hexagrammos decagrammus (82%)	Kelp greenling
	Pleurogrammus monopterygius (17%)	Atka mackerel
	Hexagrammos lagocephalus (<1%)	Rock greenling
	Hexagrammos octogrammus (<1%)	Masked greenling
	Hexagrammos stelleri (<1%)	White-spotted greenling
Lingcod	*Ophiodon elongatus*	Lingcod
Mesopelagic	Myctophidae	Lanternfish
	Stenobrachius leucopsarus (86%)	Northern lampfish
	Stenobrachius nannochir (14%)	Garnet lampfish
Octopus	Octopoda	Octopus
	Octopodidae	Octopus
Pacific herring	*Clupea pallasii*	Pacific herring
Pacific sand lance	*Ammodytes personatus*	Pacific sand lance
Pacific sandfish	*Trichodon trichodon*	Pacific sandfish
Prowfish	*Zaprora silenus*	Prowfish
Rockfish	Scorpaenidae	Rockfish
	Sebastes spp.	Sebastes rockfish

	Sebastes aleutianus (42%)	Rougheye rockfish
	Sebastes melanops (47%)	Black rockfish
	Sebastes jordani (11%)	Shortbelly rockfish
Sablefish	*Anoplopoma fimbria*	Sablefish
Salmon	*Oncorhynchus spp.*	Salmon
	Oncorhynchus gorbuscha (72%)	Pink salmon
	Salmonidae	Salmonid
	Oncorhynchus nerka (7%)	Sockeye salmon
	Oncorhynchus tshawytscha (5%)	Chinook salmon
	Oncorhynchus keta (16%)	Chum salmon
	Oncorhynchus kisutch (<1%)	Coho salmon
Sculpin	Cottidae	Sculpin
	Phallocottus obtusus (60%)	Spineless sculpin
	Hemilepidotus jordani (19%)	Yellow Irish lord
	Hemilepidotus hemilepidotus (17%)	Red Irish lord
	Hemilepidotus spp.	Irish lord
	Icelus spiniger (<1%)	Thorny sculpin
	Triglops forficatus (<1%)	Scissortail sculpin
	Triglops pingelii (2%)	Ribbed sculpin
	Triglops spp.	Triglops sp.
	Psychrolutes paradoxus (1%)	Tadpole sculpin
	Blepsias bilobus (<1%)	Crested sculpin
	Blepsias cirrhosus (<1%)	Silver-spotted sculpin
	Hemitripterus bolini (<1%)	Bigmouth sculpin
	Nautichthys oculofasciatus (<1%)	Sailfin sculpin
Squid	Decabrachia	Squid
	Gonatidae	Squid
	Cephalopoda:Gonatidae	Squid
	Gonatus kamtschaticus (96%)	Squid
	Berryteuthis magister (2%)	Squid
	Gonatopsis makko (2%)	Squid

Table 2. Characteristics of the time series used in this study. Puffins: tufted puffin (TUPU), horned puffin (HOPU), and rhinoceros auklet (RHAU).

Island	Complex	Puffin	Time Series	No. Years Data	Latitude	Longitude

Buldir		TUPU	1988-2012	22	52.36	175.92
		HOPU	1988-2012	21		
Aiktak	Aiktak	TUPU	1986-2012	24	54.19	-164.84
Kaligagan			2012	1	54.15	-164.91
Round			2012	1	54.20	-164.78
Baby			2012	1	53.99	-166.07
Tangagm			1986	1	54.00	-166.06
Puffin			1991-2012	5	54.15	-165.53
Chowiet	Semidi	RHAU	1979-2012	11	56.03	-156.70
Suklik		TUPU	1979-1995	9	56.05	-156.64
		HOPU	1979-1995	9		
Middleton		TUPU	1978-2012	23	59.44	-146.33
		RHAU	1978-2012	23		
St. Lazaria		RHAU	1994-2012	19	56.99	-135.70

Table 3. Interannual variability in diets of puffin species on each island using Analysis of Similarity. Low values of Global R indicate significant interannual variation in diet composition. Puffins: tufted puffin (TUPU), horned puffin (HOPU), and rhinoceros auklet (RHAU).

Site	Puffin	Global R	p-value
Buldir	TUPU	0.233	0.001
	HOPU	0.233	0.001
Aiktak Complex	TUPU	0.161	0.001
Semidi Complex	TUPU	0.127	0.001
	HOPU	0.130	0.001
	RHAU	0.059	0.003
Middleton	TUPU	0.292	0.001
	RHAU	0.121	0.001
St. Lazaria	RHAU	0.148	0.003

Table 4. Results of PCA on (a) Pacific sand lance, (b) capelin, and (c) gadids across species and sites. Gray shading indicates eigenvector loadings of >|0.2|. Puffins: tufted puffin (TUPU) and rhinoceros auklet (RHAU).

(a) Pacific sand lance

Component	Eigenvalue	Proportion	Cumulative
1	2.5337	0.5067	0.5067
2	1.1533	0.2307	0.7374

	Eigenvectors	
Variable	1	2
TUPU Buldir	0.3888	-0.4583
TUPU Aiktak Complex	0.4936	-0.0635
RHAU Middleton	0.5573	0.2290
TUPU Middleton	0.5384	0.0434
RHAU St. Lazaria	0.0685	0.8553

(b) Capelin

Component	Eigenvalue	Proportion	Cumulative
1	1.7612	0.4403	0.4403
2	1.1892	0.2973	0.7376

	Eigenvectors	
Variable	1	2
TUPU Aiktak Complex	0.4238	0.4766
RHAU Middleton	0.6297	-0.2267
TUPU Middleton	0.5859	-0.4501
RHAU St. Lazaria	0.2839	0.7203

(c) Gadids

Component	Eigenvalue	Proportion	Cumulative
1	2.4480	0.4896	0.4896
2	1.0306	0.2061	0.6957

	Eigenvectors	
Variable	1	2
TUPU Buldir	0.0033	0.9689
TUPU Aiktak Complex	0.4482	0.1870
RHAU Middleton	0.5476	-0.0248
TUPU Middleton	0.5531	-0.1571
RHAU St. Lazaria	0.4397	0.0306

Table 5. Results of multiple regression and Spearman rank correlation between environmental and fish indicators ($PC1_{PSL}$ and $PC1_{capelin}$).

Pacific Sand Lance			Regression				Spearman	
Environmental predictor	N	F	p-value	R^2	t	p>|t|	Rho	p-value
$PC1_{environment}$	19	12.41	0.001	0.608	4.03	0.001	0.586	0.008
$PC2_{environment}$					-2.93	0.010	-0.344	0.149

Capelin			Regression				Spearman	
Environmental predictor	N	F	p-value	R^2	t	p>|t|	Rho	p-value
$PC1_{environment}$	19	6.90	0.007	0.463	-3.59	0.002	-0.660	0.002
$PC2_{environment}$					0.96	0.350	0.154	0.528

Figure 1. Study area, study sites, and boxes (outlining areas for which data were averaged) used to develop environmental indices.

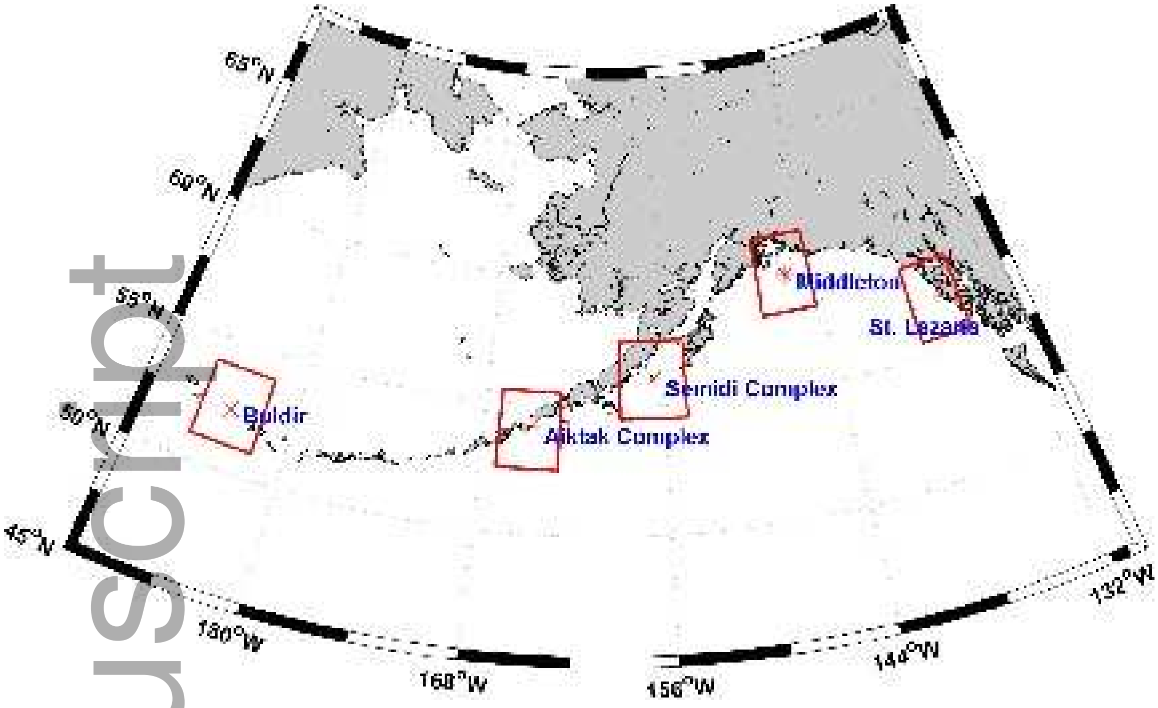
Figure 2. Horned puffin (HOPU) and tufted puffin (TUPU) diet composition by site, 1978-2012.

Figure 3. Diet composition of rhinoceros auklet (RHAU) by site, 1978-2012.

Figure 4. Results of PCA on forage fish (see Table 3 for eigenvector loadings). (a) $PC1_{PSL}$ and $PC2_{PSL}$, (b) $PC1_{capelin}$ and $PC2_{capelin}$, and (c) $PC1_{gadids}$ and $PC2_{gadids}$ through time.

Figure 5. Scores (bottom) of $PC1_{environment}$ and $PC2_{environment}$ through time, 1994-2012. Colors of loadings (top panels) correspond to zonal wind (u, blue), meridional wind (y, red), SLP (magenta) and SST (green), for the sites Buldir, Aiktak Complex, Semidi Complex, Middleton, and St. Lazaria. EV: explained variance.

Figure 6. Relationships between forage fish and environmental principal components. (a) $PC1_{environment}$ and $PC1_{PSL}$ with linear regression, (b) $PC2_{environment}$ and $PC1_{PSL}$ with linear regression, (c) $PC1_{environment}$ and $PC1_{capelin}$ with quadratic regression, and (d) $PC2_{environment}$ and $PC1_{capelin}$. PSL: Pacific sand lance.



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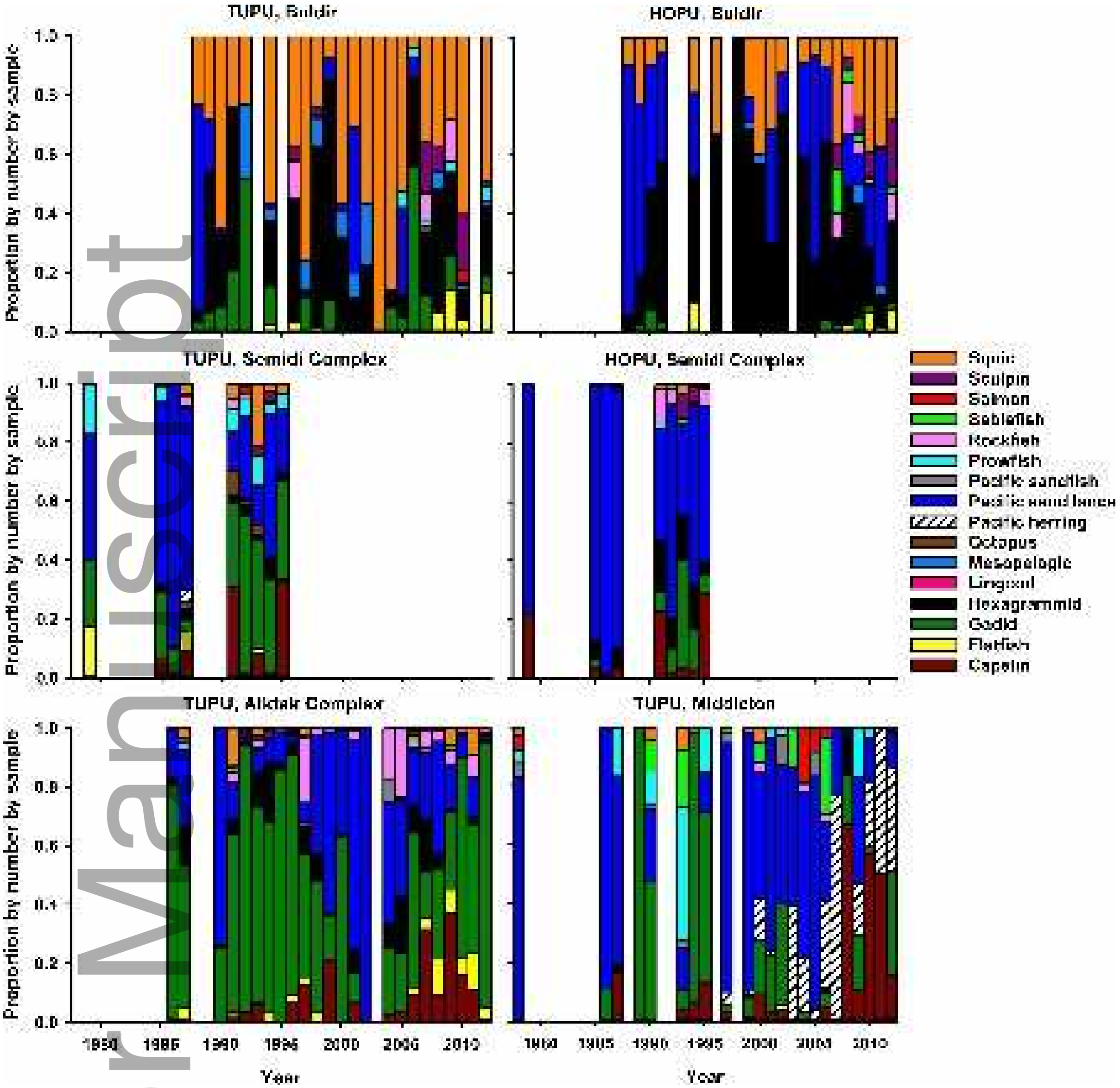

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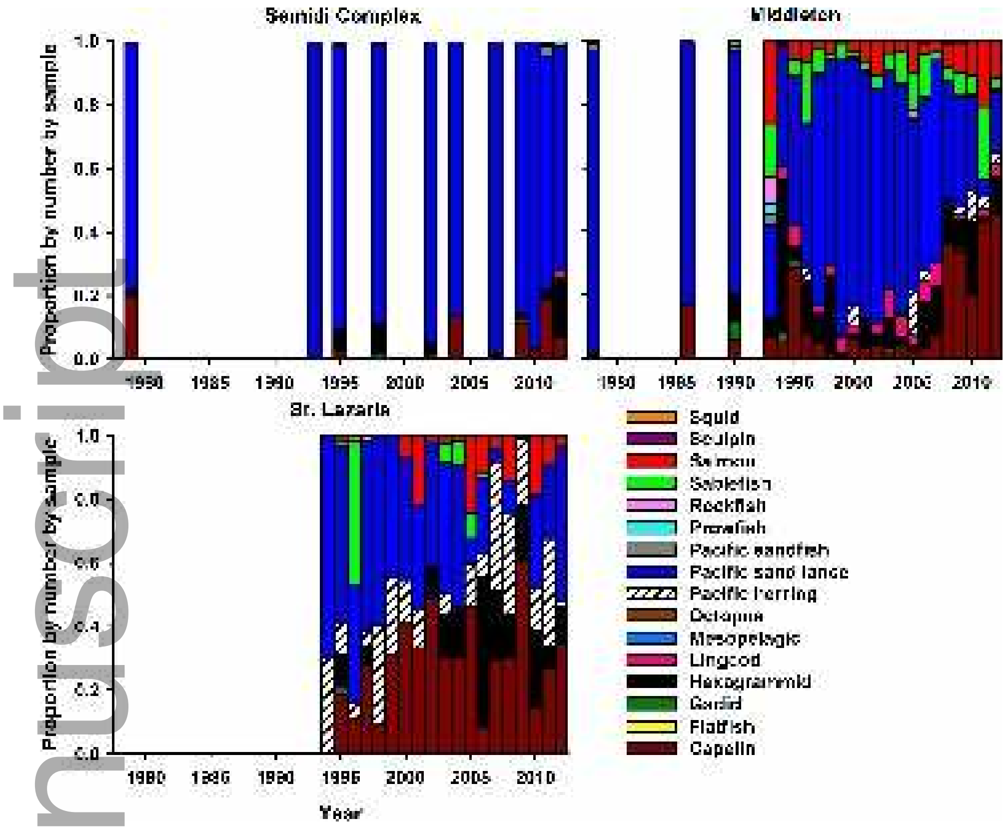

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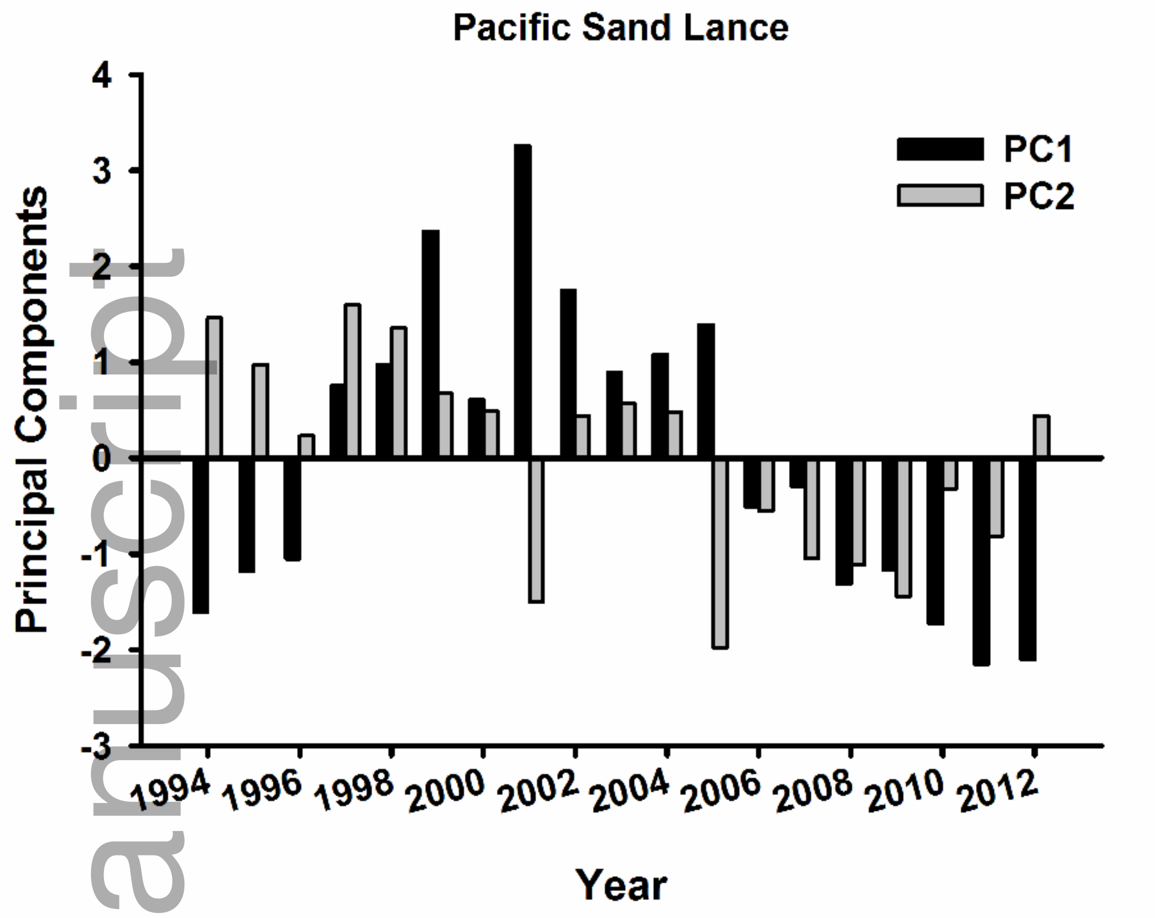

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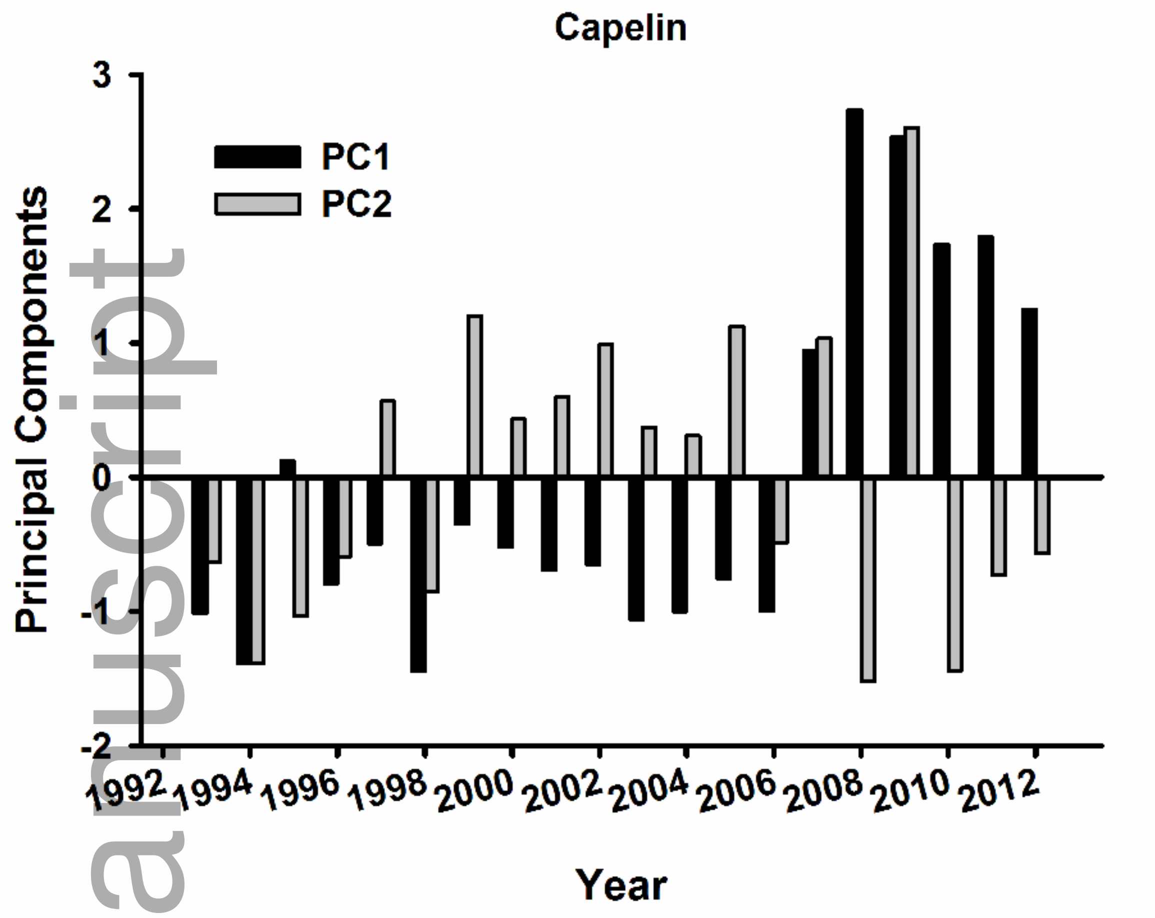

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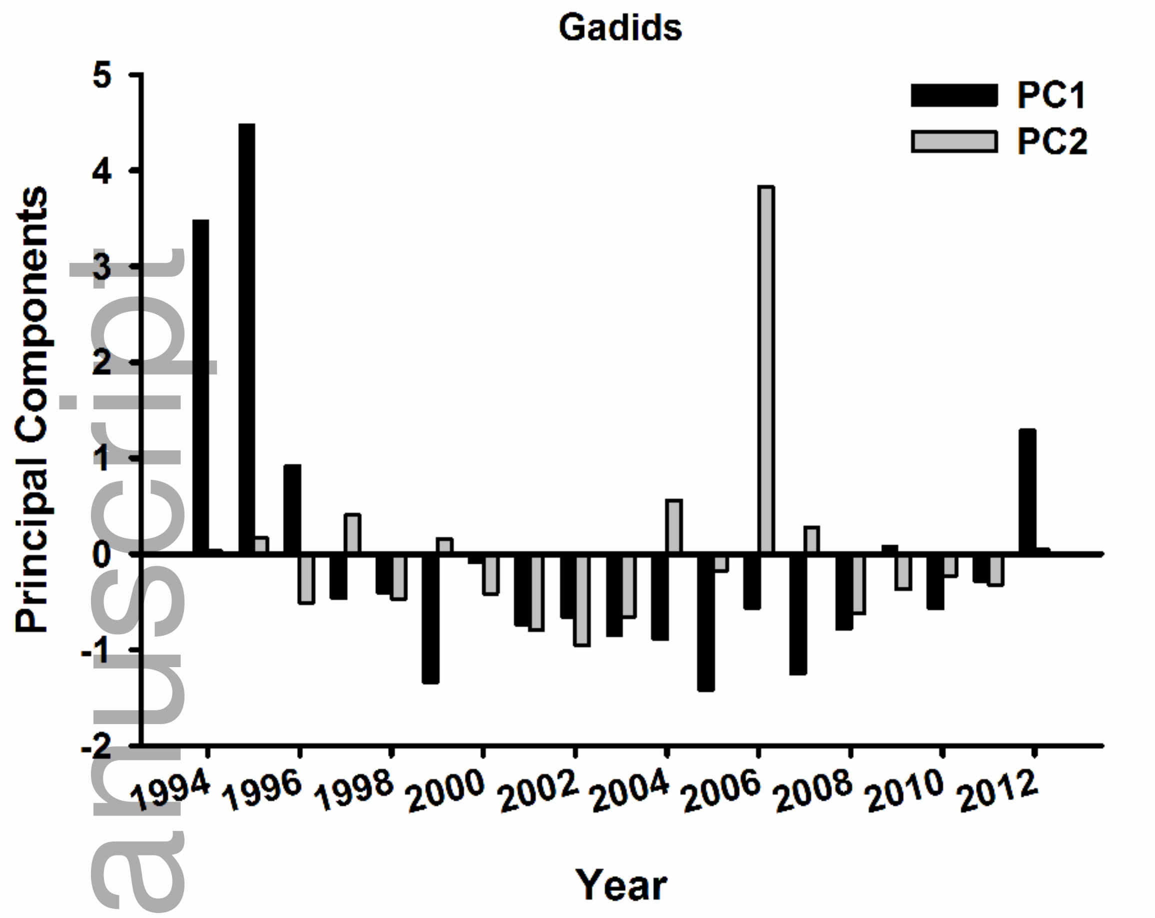

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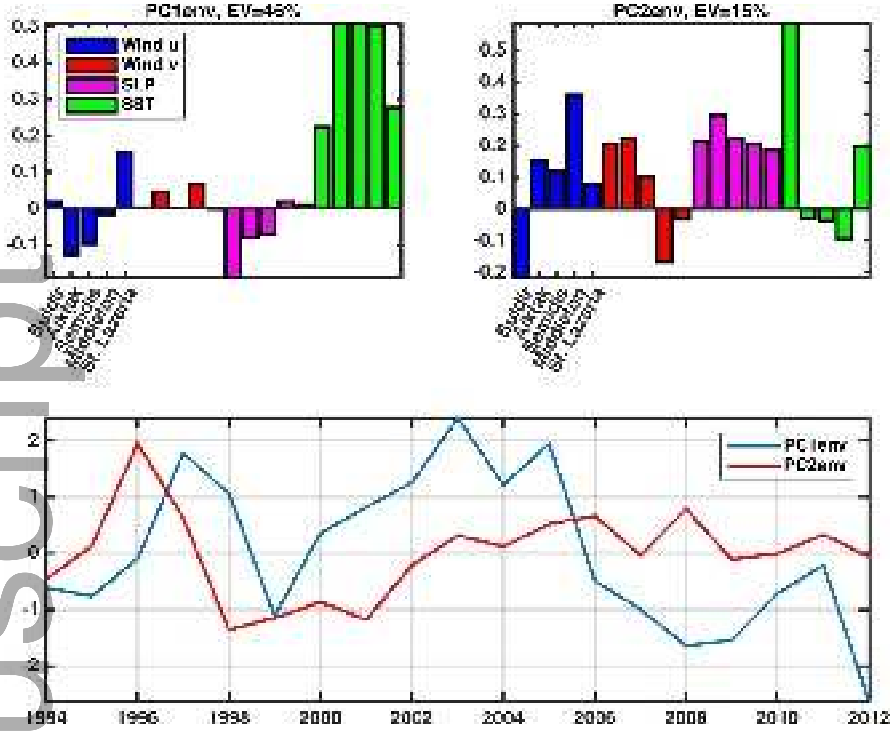

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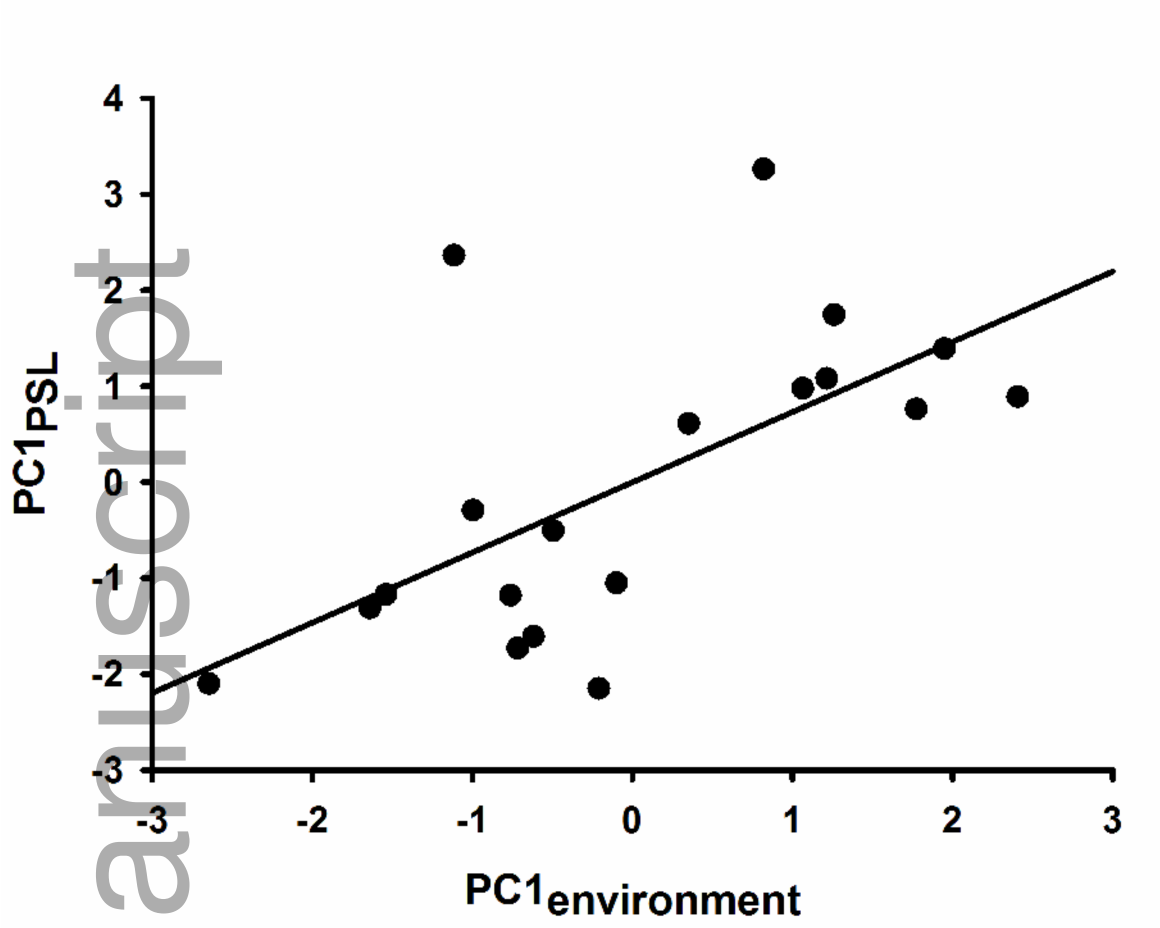

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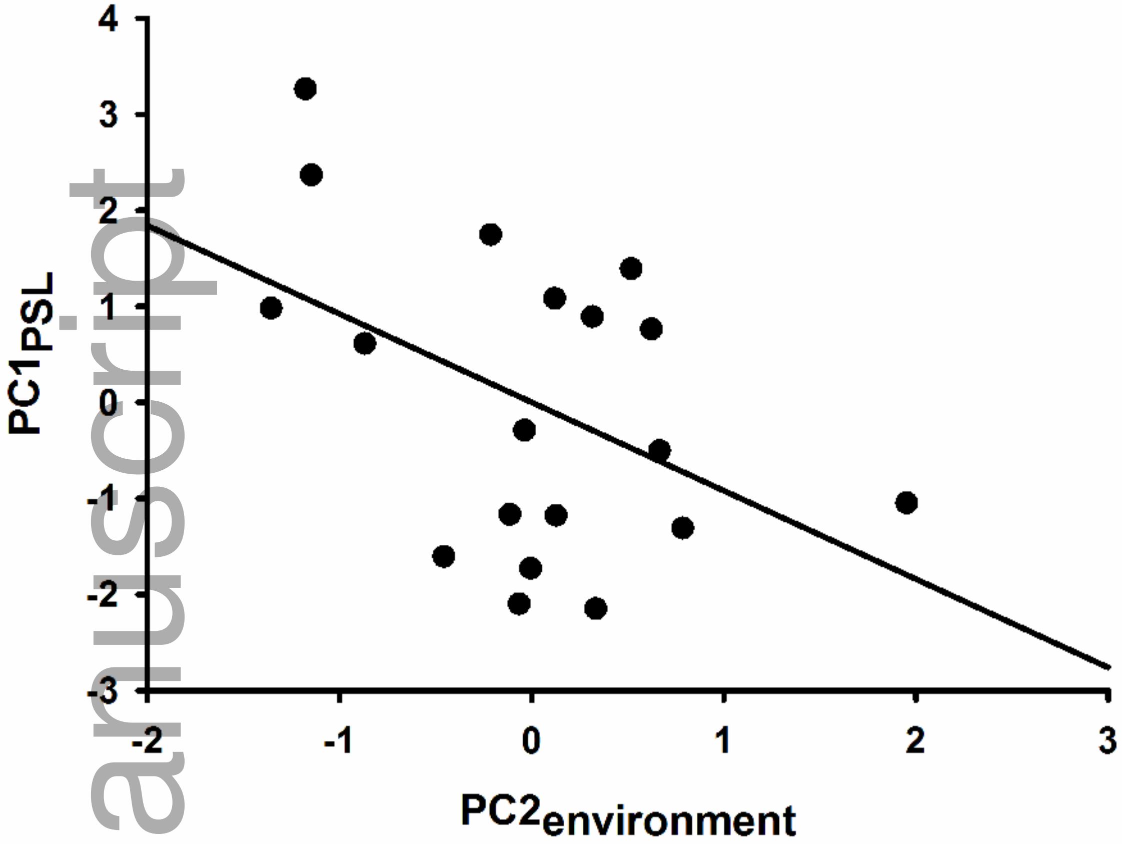

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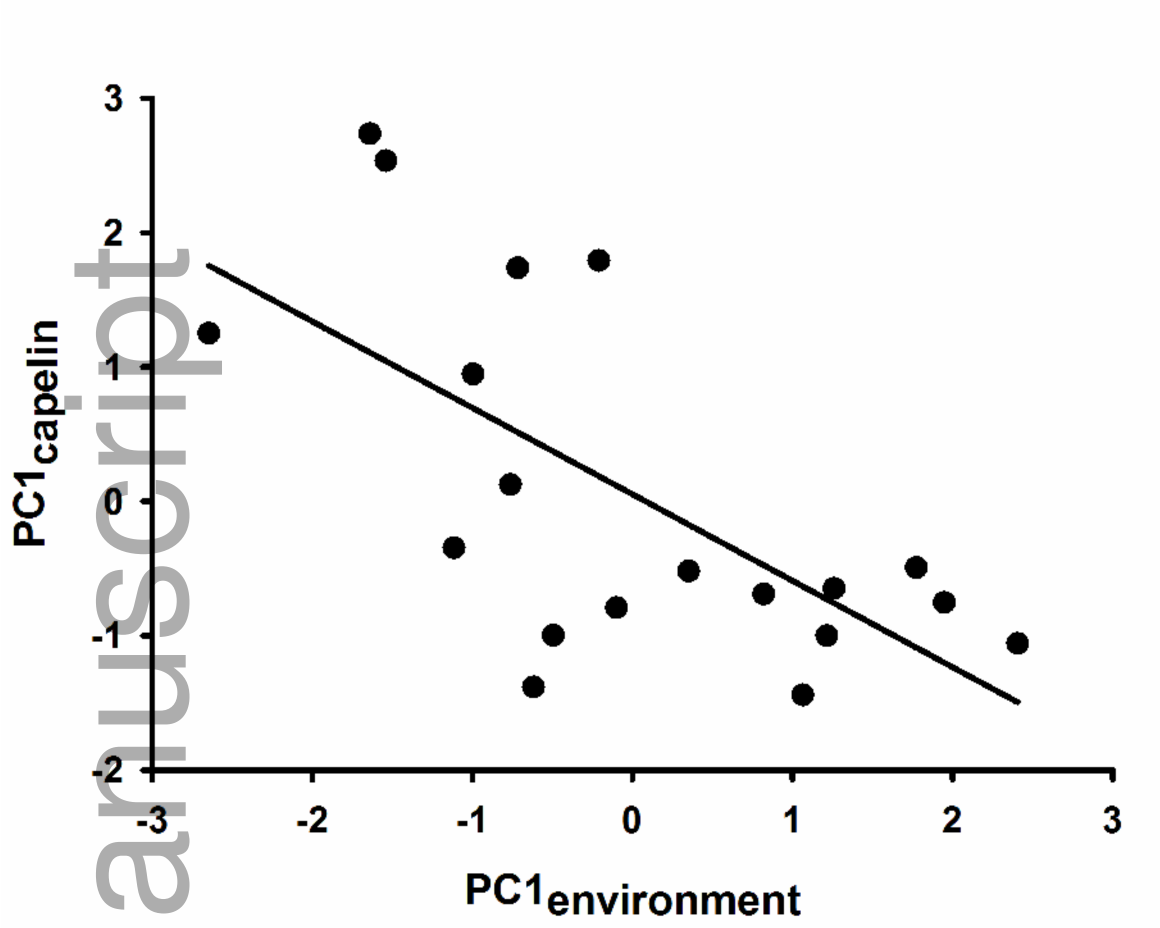

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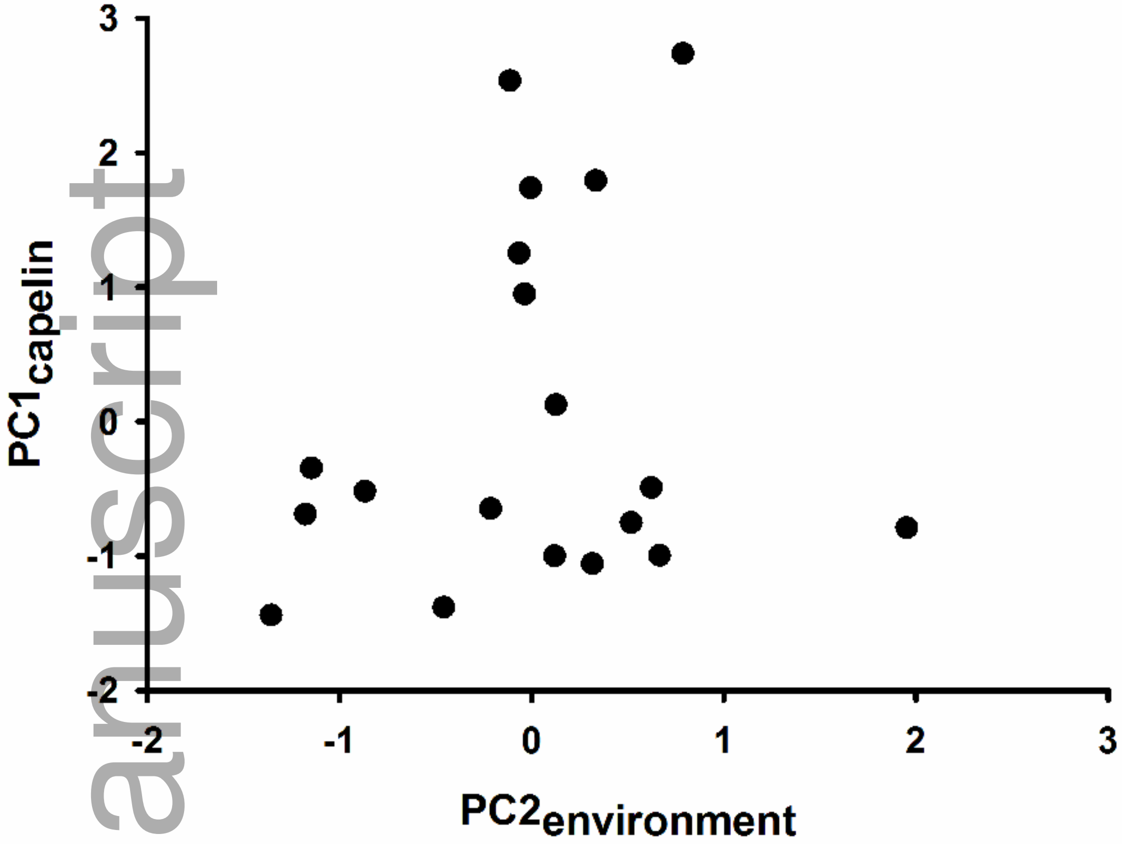

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