

Non-stationary seabird responses reveal shifting ENSO dynamics in the northeast Pacific

Annie E. Schmidt^{1,2,*}, Louis W. Botsford¹, John M. Eadie¹, Russell W. Bradley², Emanuele Di Lorenzo³, Jaime Jahncke²

¹Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, One Shields Ave., Davis, California 95616, USA

²Point Blue Conservation Science, 3820 Cypress Dr. #11, Petaluma, California 94954, USA

³School of Earth and Atmospheric Sciences, Georgia Institute of Technology, 311 Ferst Drive, Atlanta, Georgia 30332-0340, USA

ABSTRACT: The impacts of the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) on the ecology of the northeast Pacific are well known. However, recently there has been a shift in the dominance of El Niño events from the eastern Pacific (canonical) El Niño, to the central Pacific (Modoki) El Niño, concurrent with a strengthening of the North Pacific Gyre Oscillation (NPGO). Our examination of ocean conditions and seabird reproductive success in central California shows that the way these physical factors affect the pelagic food web is also changing. Reproduction of Cassin's auklet *Ptycoramphus aleuticus* and Brandt's cormorant *Phalacrocorax penicillatus*, species that forage at different trophic levels, responded primarily to ENSO variability from the 1970s to the 1990s. By 1995, however, NPGO had become the dominant variable determining Cassin's auklet reproductive success. Eventually, NPGO also became correlated with Brandt's cormorant success but in the opposite direction to Cassin's auklet. Thus, during the mid-1990s, the correlation between the reproduction of these 2 species weakened and eventually became inversely correlated. This shift from coherent reproduction, presumably bottom-up driven, to an inverse relationship between the 2 species suggests that the structure of the local marine food web changed as the equatorial forcing changed. This non-stationary response of seabirds to physical forcing is cause for concern since predictions of future ecosystem productivity and effects of climate change rely on the assumption that a species' response to environmental conditions is consistent over time.

KEY WORDS: Non-stationary · Seabird · California Current · Climate change · Reproductive success · Ocean conditions · Sliding correlation

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INTRODUCTION

In the California Current, annual productivity of the food web is stimulated by the seasonal, wind-driven upwelling of nutrients (Mann & Lazier 2006). The timing and strength of coastal upwelling is highly variable and low upwelling, warm water periods such as during an El Niño, can dramatically reduce productivity throughout the California Current (King

et al. 2011). Upwelling and productivity in this region may also be significantly influenced by large-scale phenomena such as the Pacific Decadal Oscillation (PDO, McGowan et al. 1998, Mantua & Hare 2002) and the North Pacific Gyre Oscillation (NPGO, Di Lorenzo et al. 2008, 2009). The PDO describes the dominant mode of spatial variability in sea surface temperature (SST) in the North Pacific (poleward of 20°N). Its temporal signature is an El Niño-like pat-

tern that varies on a decadal rather than annual scale and has been shown to be important in biological productivity (Mantua et al. 1997). In contrast, the NPGO index is defined as the second dominant mode of spatial variability in sea surface height in the northeast Pacific. It is associated with decadal scale variations in the circulation of the North Pacific Gyre (Di Lorenzo et al. 2008).

Fluctuations in the PDO and NPGO have been linked to major regime shifts in both physical oceanographic conditions (Di Lorenzo et al. 2008, Yeh et al. 2011) and biological communities (Mantua et al. 1997, Hare & Mantua 2000, Peterson & Schwing 2003, Cloern et al. 2010). Regime shifts in the PDO are driven by changes in the intensity of the Aleutian Low, and positive phases are associated with decreased productivity in the California Current (Mantua et al. 1997). A major regime shift in the PDO occurred in the winter of 1976–1977 with a well-documented response observed at many trophic levels in the marine community (McGowan et al. 1998, Hare & Mantua 2000). Another apparent shift occurred in the winter of 1988–1989, but the observed responses were somewhat less clear (Hare & Mantua 2000). Meanwhile, the NPGO has emerged as an influential factor determining more recent patterns in SST variability. One recent analysis suggested the ocean regime shift detected in 1988 and 1989 was, in fact, primarily driven by changes in the NPGO (Yeh et al. 2011). Additionally, variability in the NPGO has increased in recent decades (Di Lorenzo et al. 2008, Sydeman et al. 2013). This shift in the amount of variance explained by the NPGO tracks the shift in El Niño Southern Oscillation (ENSO) type from the canonical eastern Pacific El Niño to the central Pacific or Modoki El Niño (Di Lorenzo et al. 2010), which some studies suggest will become more frequent as a response to climate change (Yeh et al. 2009).

Understanding how populations respond to environmental variability is critical for managing marine ecosystems and predicting the ecological consequences of climate change. Typically, researchers investigate the relationship between the environment and an ecological response by fitting a statistical model. If a relationship is found, it is assumed to be statistically stationary such that the relationship will hold into the future (e.g. Jenouvrier et al. 2009). However, the relationships themselves may change over time and become non-stationary (Kirby & Beaugrand 2009, Hidalgo et al. 2012). For example, a sliding correlation in Kirby & Beaugrand (2009) revealed that the positive relationship between cod

Gadus morhua L. and SST shifted in the 1970s to a negative relationship, coinciding with an increase in the 10 yr mean SST. The shifting importance and dynamics of El Niño, PDO, and NPGO in the North Pacific prompts the question: Are marine food webs and upper trophic level predators responding to these physical phenomena in the same manner as in the past?

Here, we use over 40 yr of data collected on seabirds breeding on the Farallon Islands in central California to investigate whether changing ocean conditions are evoking new responses in the pelagic food web. Data on seabird ecology, particularly annual reproductive success, reflects conditions in the broader marine ecosystem. For example, seabird reproductive success has been shown to respond rapidly to interannual changes in the availability of forage fish abundance (Aebischer et al. 1990, Thayer et al. 2008). We use data on 2 seabird species, Brandt's cormorant *Phalacrocorax penicillatus* and Cassin's auklet *Ptycoramphus aleuticus*, that have recently exhibited unusual, opposing trends in productivity. Brandt's cormorant and Cassin's auklet forage at different trophic levels—Cassin's auklet forage primarily on euphausiid krill during the breeding season (Abraham & Sydeman 2004, 2006) while Brandt's cormorant forage on a variety of small fish, including juvenile rockfish *Sebastes* spp. and northern anchovy *Engraulis mordax* (Ainley et al. 1981). Because primary productivity in the California Current is largely driven by seasonal upwelling of nutrients, we expect annual productivity to be positively correlated across trophic levels through bottom-up forcing (Aebischer et al. 1990, Ware & Thomson 2005). Thus, the opposing trends in productivity between these 2 seabird species are unusual and somewhat paradoxical. The long-term study on the Farallon Islands affords a unique opportunity to define the relationships between seabird reproductive success and the environment for sympatric species feeding at different trophic levels in a comparative way.

We show that the correlations between seabird reproductive success and ocean conditions have changed markedly over time, especially for Cassin's auklet, leading to the recent divergence in reproductive success of the 2 species. The relationships between seabird reproductive success and El Niño and NPGO in particular stand out as being particularly dynamic. This non-stationarity illustrates that fundamental shifts in relationships once thought to be stable are already complicating our ability to predict the consequences of future change.

METHODS

Study site and species

Point Blue Conservation Science has studied Cassin's auklet and Brandt's cormorant populations on Southeast Farallon Island (SFI), part of the Farallon National Wildlife Refuge (37° 42' N, 123° 00' W), since 1971 (Ainley & Boekelheide 1990). Cassin's auklets are small (~170 g) seabirds that lay a single egg per attempt in rock crevices or burrows excavated in soil. Brandt's cormorants build nests on the surface and typically lay 2 to 4 eggs (Ainley & Boekelheide 1990). Cassin's auklet nesting success was measured by following breeding attempts in artificial nest boxes placed around the island. Nesting attempts of Brandt's cormorant were studied from a blind overlooking a colony of up to 900 pairs (for full details on data collection methods see Ainley & Boekelheide 1990). Annual reproductive success for both species was defined as the mean number of chicks fledged per breeding attempt.

Oceanographic conditions

We computed correlations between reproductive success of each species and several measures of ocean conditions. To develop a complete understanding of how the seabird reproductive success related to ocean conditions at several spatial and temporal scales, we included 3 local scale variables, SST, sea level height (SLH) and Bakun's Upwelling Index (UI), in addition to basin-scale variables relating to the ENSO, PDO and NPGO (Fig. 1). Generally, stronger upwelling leads to lower sea level at the coast and lower SST (Mann & Lazier 2006). During El Niño events, upwelling is reduced and SLH and SST both increase so these can also be considered as local measures of ENSO or ENSO-like conditions. Daily SST was measured at SFI (see Abraham & Sydeman 2004 for full details), and we used monthly averages of SLH data from at the University of Hawaii station maintained at the mouth of the San Francisco Bay, CA, USA.

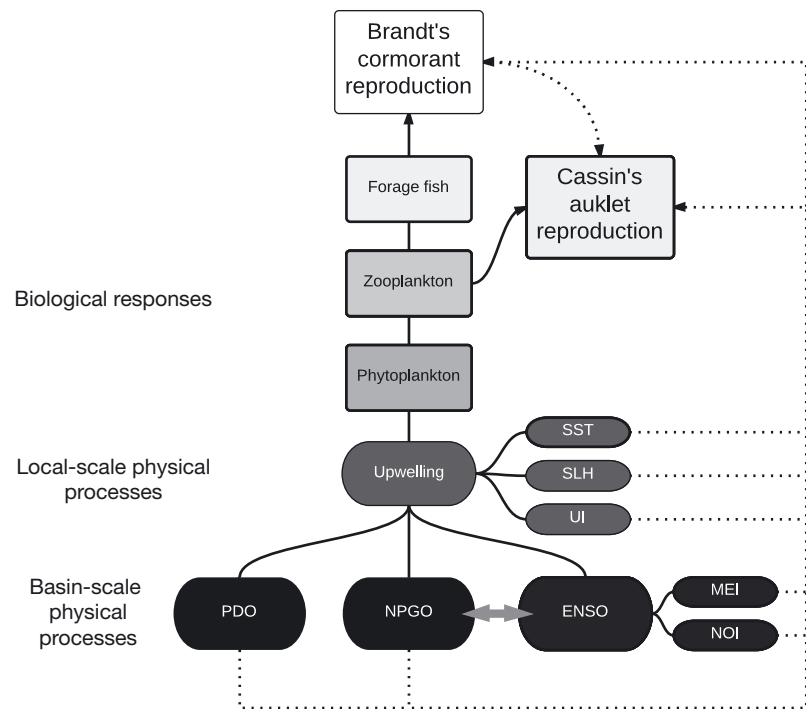


Fig. 1. Dominant relationships between various environmental variables and food web responses. Basin-scale variables describing conditions in the North Pacific, the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) influence the strength of local upwelling. Basin-scale indices, the Multivariate ENSO Index (MEI) and the Northern Oscillation Index (NOI), describe the strength of the ENSO. Double-headed grey arrow represents the atmospheric teleconnection between NPGO and ENSO (see 'Discussion'). Upwelling is measured indirectly through local measures of sea surface temperature (SST), sea level height (SLH), and Bakun's Upwelling Index (UI). Solid lines represent relationships that were not directly examined; dotted lines represent the indirect relationships that were the primary focus of the analysis

We used the Northern Oscillation Index (NOI) and the Multivariate ENSO Index (MEI) to characterize broad-scale El Niño conditions. The NOI and MEI fluctuate on an annual scale and indicate variation in ENSO as it is expressed in the North Pacific and at the equator, respectively. Positive values of the NOI indicate La Niña, and negative values indicate El Niño conditions at high latitudes (Schwing et al. 2002). In contrast, positive values of MEI are associated with El Niño, and negative values of the MEI are associated with La Niña (Wolter & Timlin 1998).

All oceanographic data were accessed from public sources online (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m499p249_supp.pdf for full details on data sources). For each index, we used the months from the October prior to the breeding season through June of the breeding season. This encompasses the pre-breeding conditioning period

as well as egg laying and incubation in most years (Ainley & Boekelheide 1990). Since the majority of nest failures occur during the incubation phase for both species (Ainley & Boekelheide 1990), we considered these months to be the most important in determining final reproductive success. Instead of averaging ocean conditions over an entire season (e.g. breeding and/or non-breeding season), we examined variability on a finer temporal scale by calculating bi-monthly averages for each variable from October to June (e.g. mean Oct–Nov SST, mean Nov–Oct SST etc.).

Statistical analysis

To establish when the reproductive success of the 2 species began to diverge, we calculated the Pearson correlation coefficient between the annual reproductive success of Brandt's cormorant and the annual reproductive success of Cassin's auklet using a sliding correlation with windows of 5 to 20 yr. The varying window length allowed us to compare temporal resolution with statistical significance: shorter correlation periods allow greater resolution for detecting the time of a shift in correlation but are less often significant.

We investigated how relationships between seabird reproductive success and the environment changed by calculating Pearson correlation coefficient between the reproductive success of each species and the bi-monthly averages for each oceanographic variable for a 10 yr sliding window. We chose the 10 yr window as a good representation of the trade-off between resolution and significance. The sliding correlation approach is well suited to detecting temporal change in a relationship. However, because of the large number of correlation coefficients calculated, the probability identifying at least one spurious relationship as significant is very high. With this in mind, the p-value of any single correlation in isolation must be considered with caution. Nevertheless, we would not expect to see strong temporal coherence in the pattern of correlations by chance alone. Therefore, correlations where $p < 0.05$ for multiple months within a year, or for multiple correlation periods across years, can be considered largely robust to Type I error. We did not employ wavelet coherence analysis because, rather than identifying temporal changes, wavelet coherence calculates the cross-correlation between 2 time series in terms of frequency content. It is limited in timescale and would smooth the temporal changes

we were particularly interested in identifying (Torrence & Compo 1998). For comparison to the shorter-term correlations, we also calculated the total correlation (across all years) between each bi-monthly average of oceanographic variables and the reproductive success of each species. We tested all time series for autocorrelation and applied a correction to the degrees of freedom where appropriate. If autocorrelation is present in only one of the time series used in a correlation, then no correction to the degrees of freedom is necessary (Botsford & Paulsen 2000). Where autocorrelation was present in both time series under consideration, we adjusted the degrees of freedom used to calculate p-values according to this equation:

$$\frac{1}{\text{EDF}} = \frac{1}{N} + \frac{2}{N} \sum_{j=1}^D \frac{N-j}{N} \rho_{xx}^{(j)} \rho_{yy}^{(j)} \quad (1)$$

from Botsford & Paulsen (2000), where EDF is the effective degrees of freedom, N = length of series, $\rho_{xx}^{(j)}$ is the autocorrelation of series x at lag j , and $\rho_{yy}^{(j)}$ is the autocorrelation of series y at lag j . For the sliding correlations, we estimated autocorrelation for 10 yr windows so we limited D (max lag) ≤ 5 to allow sufficient data to estimate a correlation. If the 2 time series are autocorrelated in opposite directions (i.e. one positively and one negatively autocorrelated), this equation will sometimes result in $\text{EDF} > N$, so we also limited EDF to not exceed $N - 2$. This method is more appropriate than a regression with an autoregressive moving average (ARMA) error structure because with ARMA models, one loses sight of how the different time scales (or frequencies) of variability affect results by effectively reducing the number of degrees of freedom (Pyper & Peterman 1998). All analyses were conducted using the statistical computing program R (version 2.13.2, R Development Core Team 2011).

There was no significant autocorrelation in the Brandt's cormorant reproductive success time series (Fig. S1A in the Supplement), so we did not adjust the degrees of freedom when calculating the significance of the correlation coefficients (Botsford & Paulsen 2000). The Cassin's auklet reproductive success series was significantly autocorrelated at lags of 1, 4, and 5 yr (Fig. S1B). Overall, the oceanographic series exhibited very little autocorrelation (Fig. S2 in the supplement). Autocorrelation was significant only in PDO and NPGO, so the degrees of freedom for correlations calculated between Cassin's auklet reproductive success and PDO and NPGO were adjusted accordingly.

RESULTS

Reproductive success of Brandt's cormorant and Cassin's auklet covaried for the majority of the time series (Fig. 2B). At longer window lengths (20 yr window), the correlation was positive and significant ($r = 0.5\text{--}0.7$, $p = 0.0006\text{--}0.02$) from 1973 through 2004. However, correlations calculated for lengths of 5 to 14 yr all indicated that a change occurred in the mid-1990s. At that point, the correlation between the reproductive success of Brandt's cormorant and Cassin's auklet began to decrease and switched to a negative correlation beginning in 1999 (in the 5 yr window). After 1999, Brandt's cormorant and Cassin's auklet reproductive success became increasingly negatively correlated, significantly so for the last 10 yr (2003–2012) of the study ($r = -0.73$, $p = 0.017$). This recent inverse correlation between these 2 species is unique and unprecedented in the time series.

Relationships between reproductive success and most physical oceanographic conditions were highly variable and non-stationary (Fig. 3). Beginning in the mid-1970s, reproductive success for both species was negatively correlated with the ENSO variable, MEI (Fig. 3B,E). After the 1980–1989 window, the correlation between Cassin's auklet reproductive success and MEI variables weakened and remained weak for the remainder of the study period (Fig. 3E). In contrast, Brandt's cormorant reproductive success re-

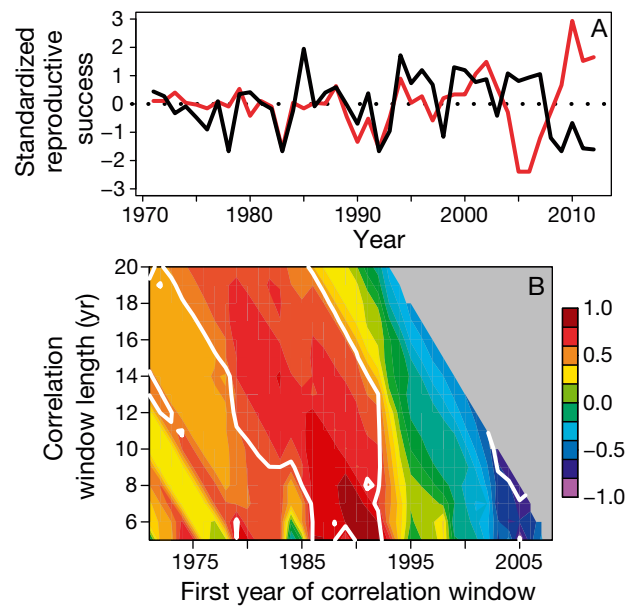


Fig. 2. (A) Long-term reproductive success time series for Brandt's cormorant and Cassin's auklet. Each series is centered and divided by its SD. Reproductive success is measured as the mean number of chicks fledged per breeding pair. Brandt's cormorant is shown in black; Cassin's auklet shown in red. (B) Sliding correlation between Cassin's auklet reproductive success and Brandt's cormorant reproductive success over sliding window lengths of 5 to 20 yr. Year on the x-axis represents the first year of the correlation window. Correlation coefficient is plotted in color; white line represents the $p = 0.05$ contour (i.e. within the contour $p < 0.05$)

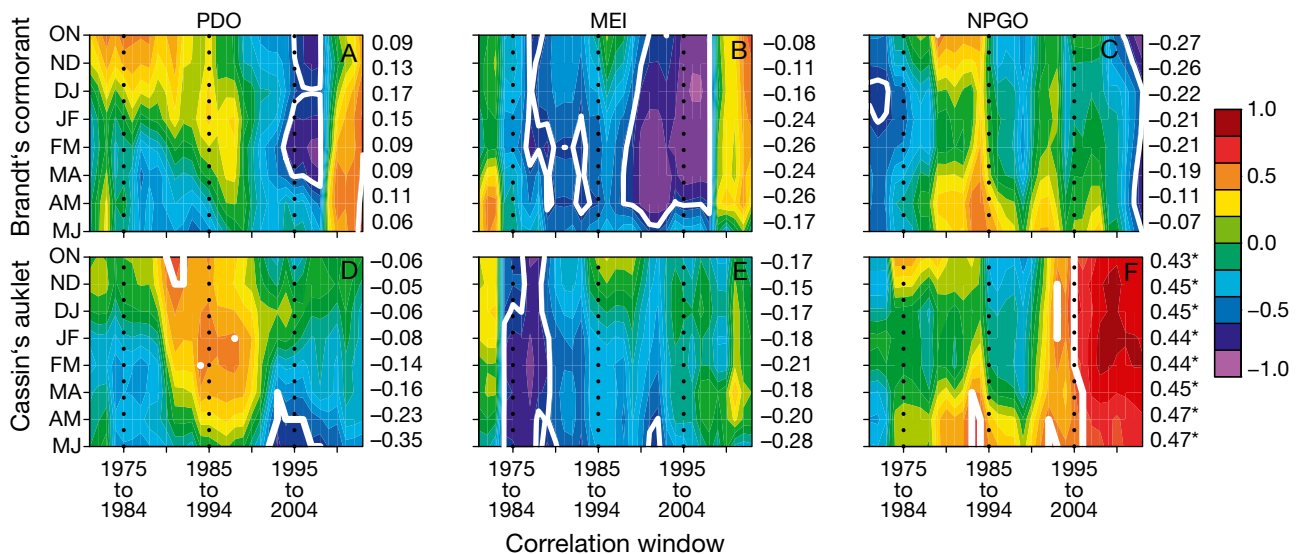


Fig. 3. The 10 yr sliding correlation between seabird reproductive success and the Pacific Decadal Oscillation (PDO), the Multivariate ENSO Index (MEI), and the North Pacific Gyre Oscillation (NPGO). Each panel shows the results from correlating the bi-monthly averages of one oceanographic variable to seabird reproductive success. (A–C) Results from Brandt's cormorant; (D–F) results from Cassin's auklet. Months are shown on the y-axis (ON = mean Oct–Nov, ND = mean Nov–Dec, etc.); x-axis is the 10 yr correlation window. Correlation coefficients are plotted in color; white line represents the $p = 0.05$ contour (i.e. within the contour $p < 0.05$). Total correlation (including all years) for each 2 mo period shown to the right of each panel. Total correlation values where $p < 0.05$ are represented with an asterisk

mained negatively correlated with MEI through the 1998–2007 period. Beginning with the 1999–2008 period, the correlation between MEI and Brandt's cormorant reproductive success also disappeared, a second indication of non-stationarity. In fact, the relationships between many of the oceanographic variables and Brandt's cormorant reproductive success weaken as soon as 2008 enters the correlation window, suggesting that the dramatic decrease in reproductive success that began in 2008 was not related to ENSO or related variables such as SLH and SST (Figs. 2A, 3, & S3 in the Supplement).

Meanwhile, for Cassin's auklet, the NPGO replaced ENSO as the dominant environmental process associated with reproductive success. Beginning in the mid-1990s, Cassin's auklet reproductive success was consistently correlated only with NPGO (Fig. 3F). This positive correlation was very strong and persisted through the end of the study period across all months examined (periods beginning 1996 through 2003, $r = 0.6–0.9$, $p = 0.0004–0.05$). The timing of this emerging relationship between Cassin's auklet and NPGO is striking given that it arose at the same time that Cassin's auklet reproductive success began to diverge from Brandt's cormorant (Figs. 2B & 3F). In comparison, Brandt's cormorant reproductive success was correlated with winter NPGO values early on but did not appear to be robust (the correlation is only visible over a 3 mo period, Dec–Feb and only persists for 2 correlation periods, Fig. 3C). After the 1973–1982 period, the correlation with NPGO virtually disappeared. It was only in the most recent 10 yr (2003–2012) that the correlation reappeared and became consistently strong and significant across all months ($r = -0.62–0.89$, $p = 0.0006–0.05$, Fig. 3). Since the relationship between NPGO and Brandt's cormorant reproductive success has only recently re-emerged, and only been present for one correlation window, it is not yet clear how important or robust it will be.

Interestingly, PDO did not seem to be an important variable directly; it showed little correlation with the reproductive success of either species, with the exception of a brief period beginning in the 1990s (Fig. 3A,D). For both species, the UI, SST, SLH and the NOI showed correlation patterns that were similar to MEI, with SLH and NOI being the most similar. The area of significant correlation for UI and SST was smaller, indicating the over-

all connection to these 2 indices was weaker (Fig. S3 in the Supplement).

Most oceanographic variables were not significantly related to seabird reproductive success when the correlation was calculated using the complete time series. The major exception was NPGO, which was positively correlated with Cassin's auklet reproductive success over all months even when including all years (Fig. 3F). The correlations between Cassin's auklet reproductive success and Apr–May (AM) and May–Jun (MJ) SLH and NOI were also marginally significant ($p \approx 0.05$) when including all years (Table S3 in the Supplement). The only variable that was significantly correlated to Brandt's cormorant reproductive success when all years were included was the ENSO variable NOI during Feb–Mar (Table S2).

DISCUSSION

El Niño events are known to influence annual productivity in the California Current (Botsford & Lawrence 2002, Chavez et al. 2002) and the response of seabird reproductive success early in the study confirmed this relationship. However, the correlation between ENSO and Cassin's auklet reproductive success weakened after 1988 (Fig. 3). Although ENSO continued to influence Brandt's cormorant reproductive success for almost 20 additional years, this relationship also subsequently disappeared (Fig. 4). The reproductive success of both species is now correlated only with NPGO, although this relationship emerged much earlier for Cassin's auklet

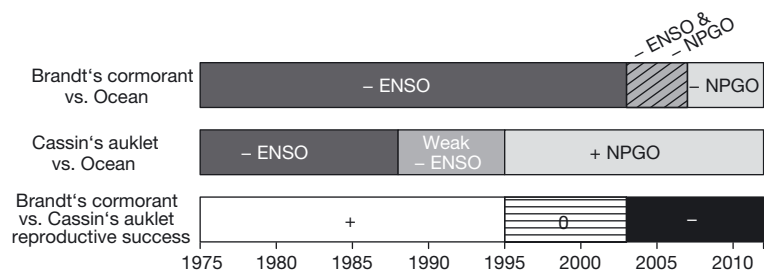


Fig. 4. Dominant relationships over the study period. Bottom bar shows that the relationship between the reproductive success of the 2 species, Brandt's cormorant and Cassin's auklet, was positive (white) from 1975–1995, not correlated (horizontal stripes) from 1995–2003, and negatively correlated (black) from 2003–2012. Middle and top bars show how the dominant relationships between each species' reproductive success and ocean conditions changed over the study period. A strong relationship with ENSO (timing illustrated using MEI but patterns similar for NOI and SLH) shown in dark grey, weak (not significant) relationship with ENSO in medium grey, strong relationships with both MEI and NPGO in light grey with diagonal stripes, and relationship with NPGO in light grey. Negative relationship indicated with '-' and positive with '+'. Year of change is along the horizontal axis. Abbreviations defined in Fig. 1

and is too recent for Brandt's cormorant to judge its true biological significance. Nonetheless, this is the first indication that the influence of ENSO on seabirds in central California may be waning while NPGO is becoming the dominant signal forcing seabird reproductive dynamics.

The stationarity of empirical relationships is rarely addressed when making predictions based on statistical models. The results presented here demonstrate that this fundamental assumption should be stated and evaluated. Had we continued to use the relationships defined early in the study to predict seabird responses to ocean conditions, we would have risked being critically misled since the relationships between ENSO and seabird reproductive success in the 1970s and 1980s did not predict the responses of either species in the last 10 yr of the study. On the other hand, it is worth noting that although the North Pacific has experienced several regime shifts associated with changes in the PDO and NPGO over the course of this study, the reproductive responses of the seabirds observed here were not due a regime shift in the typical sense. If the seabirds were simply responding to changing values of the PDO and NPGO, that response should have been apparent as a consistent correlation across all years. Yet, in most cases, individual oceanic variables were not correlated to reproductive success when all years were included. Instead, it was the correlation itself that changed over time. This implies that it is the response of seabirds, and consequently the response of the food web, that is changing over time, not just the value of the ocean indices.

Changes in both the nature of ENSO and the variability of the NPGO are almost certainly playing a role in shifting seabird responses. The amplitude of variability in NPGO has been increasing (Di Lorenzo et al. 2008, Sydeman et al. 2013), and there is some indication that NPGO values have become more positive overall in recent decades. In fact, the 10 yr mean (Oct–Jun) of NPGO switched from negative to highly positive during the same period that Cassin's auklet reproductive success began to track NPGO and diverged from Brandt's cormorant reproductive success (Fig. 5). The recent divergence in the reproductive success of the 2 species implies that significant changes have taken place in the structure of the marine food web. The response to physical ocean conditions of the species feeding at the higher trophic level (Brandt's cormorant) is now opposite rather than parallel to that of the species feeding at the lower trophic level (Cassin's auklet, Figs. 1 & 2). Since the reproductive success of seabirds is thought to be deter-

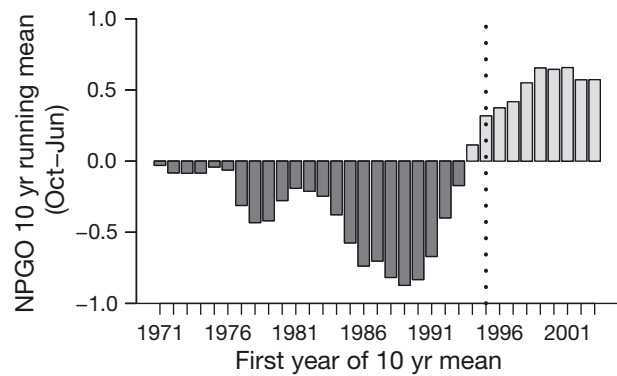


Fig. 5. The 10 yr running mean of Oct–Jun North Pacific Gyre Oscillation (NPGO). Positive anomalies plotted in light grey; negative anomalies plotted in dark grey. Dotted line marks the beginning of the positive (10 yr) correlation with Cassin's auklet reproductive success

mined primarily by prey availability (Piatt et al. 2007), the inverse responses of these 2 seabirds suggests that the response of zooplankton and forage fish to ocean conditions has become decoupled. The availability of these organisms no longer follows parallel trends and implies that strictly bottom-up processes may no longer dominate this particular food web. Our results indicate this change occurred sometime after the mid-1990s and represents a significant shift in energy flow and structure of the marine food web.

While the mechanism behind this trophic disconnect remains unclear, the increasingly positive values of NPGO (Fig. 5) may be important since the positive phase is associated with earlier spring transitions to upwelling favorable conditions in the California Current (Chenillat et al. 2012). The shift in the timing of upwelling may affect trophic levels differently and lead to a mismatch in availability between secondary and upper level consumers (Edwards & Richardson 2004). For example, earlier spring transitions associated with positive NPGO values can result in colder than usual water temperature earlier in the year. Cold temperatures may reduce spawning of forage fish (Weber & McClatchie 2010) as well as lead to slower growth of fish larvae, leaving them susceptible to predation longer (Takasuka et al. 2007). Euphausiids, the primary prey of Cassin's auklet, are known to be predators of fish larvae, particularly northern anchovy, an important prey item for Brandt's cormorant (Theilacker et al. 1993). Thus, increasing euphausiid abundance earlier in the year may compound the negative impacts of slower growth by also increasing the number of predators that encounter fish larvae. In this way, increasing euphausiid abundance could actually be detrimental

to fish recruitment. This type of interaction, where the adult stage of a species exerts predation pressure on the larval stage of its predator, was also proposed by Agostini et al. (2007) to explain alternating abundance of zooplankton and Pacific sardine *Sardinops sagax* in southern California.

While there is no direct evidence that this specific mechanism is occurring, there is corroborating evidence indicating important changes in the structure of the food web from several other studies. For example, Ainley & Hyrenbach (2010) showed the number of humpback whales in central California increased dramatically after the mid-1990s. Humpbacks are potential competitors with both Cassin's auklet and Brandt's cormorant since they forage on small pelagic fish as well as krill. Additionally, long-term declines in rockfish *Sebastes* spp., which are important forage fish, have been documented (Field et al. 2010, Ralston et al. 2013), and changes in zooplankton species composition have occurred (Batten & Welch 2004). Although there is no immediately apparent explanation for how these changes might result in shifting the indirect relationships between oceanographic variables and seabird responses, they do paint a picture of a rapidly changing pelagic ecosystem.

Numerous studies have noted that the nature of ENSO events appears to be changing, perhaps as a result of climate change (Kao & Yu 2009, Yeh et al. 2009, McPhaden 2012). The occurrence of ENSO events in the last decade has increased in frequency to once every 2.8 yr, up from once every 4 yr in the previous 20 yr (McPhaden 2012). Furthermore, 3 of the last 4 ENSO events were of a newly identified central Pacific warming (modoki) type (McPhaden 2012). During this type of ENSO event, the center of the warm water anomaly occurs in the central Pacific rather than the eastern Pacific, as in a conventional ENSO (Ashok et al. 2007, Kao & Yu 2009). This is significant because SST anomalies associated with central Pacific warming of El Niño modoki force changes in atmospheric circulation that in turn drive the low-frequency variability of the NPGO (Di Lorenzo et al. 2010). Thus, the increasing frequency of El Niño modoki may be at least partly responsible for the observed increase in the variability of NPGO and the changing response of seabirds to the NPGO.

Understanding what leads to non-stationarity in the response of an organism to physical processes is clearly complex and probably dependent on the specific ecological interactions within a system. As a result of over 4 decades of continuous monitoring on the Farallon Islands, we were able to take the first

step of identifying when new relationships between seabird reproduction and ocean conditions began to emerge. The sliding correlation approach was particularly useful in this context because it allowed us to examine temporal changes both within and across years without choosing an arbitrary change point. To thoroughly understand the mechanisms of the observed non-stationarity, we now need to develop process-based models that take into account specific interactions and intermediate links between the physical forcing and a species response (e.g. Dorman et al. 2011). Significant data challenges have so far hampered development of such models for higher trophic organisms. Nonetheless, these models will be necessary to move us beyond the use of correlation analyses with large-scale climate indices that may be inadequate for tracking the physical forcing relevant to a species through time. Such models could increase the empirical basis for prediction by including known mechanisms and additional observable variables, providing a more robust approach towards estimating how species may respond to environmental change and reducing uncertainties in climate change predictions.

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