Humpback whale diets respond to variance in ocean climate and ecosystem conditions in the California Current

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Abstract

Large, migratory predators are often cited as sentinel species for ecosystem processes and climate-related changes, but their utility as indicators is dependent upon an understanding of their response to environmental variability. Documentation of the links between climate variability, ecosystem change and predator dynamics is absent for most top predators. Identifying species that may be useful indicators and elucidating these mechanistic links provides insight into current ecological dynamics and may inform predictions of future ecosystem responses to climatic change. We examine humpback whale response to environmental variability through stable isotope analysis of diet over a dynamic 20-year period (1993–2012) in the California Current System (CCS). Humpback whale diets captured two major shifts in oceanographic and ecological conditions in the CCS. Isotopic signatures reflect a diet dominated by krill during periods characterized by positive phases of the North Pacific Gyre Oscillation (NPGO), cool sea surface temperature (SST), strong upwelling and high krill biomass. In contrast, humpback whale diets are dominated by schooling fish when the NPGO is negative, SST is warmer, seasonal upwelling is delayed and anchovy and sardine populations display increased biomass and range expansion. These findings demonstrate that humpback whales trophically respond to ecosystem shifts, and as a result, their foraging behavior is a synoptic indicator of oceanographic and ecological conditions across the CCS. Multi-decadal examination of these sentinel species thus provides insight into biological consequences of interannual climate fluctuations, fundamental to advancing ecosystem predictions related to global climate change.

Keywords: cetacean foraging, climate change, ecosystem shifts, euphausiids, forage fish, North Pacific Gyre Oscillation, Pacific Decadal Oscillation, upwelling

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Introduction

The forecasting of future ecosystem states is dependent upon an understanding of the causal mechanisms that underlie natural and anthropogenically-mediated variability. While acquiring mechanistic understanding of ecological change is complex, top predators in the marine environment have often been suggested as indicators of ecosystem status and change (Hilty & Merenlender, 2000; Abraham & Sydeman, 2006; Becker *et al.*, 2007). However, due to the intricate physical and biological responses involved, a detailed understanding of the links between climate variability, ecosystem change and predator dynamics is absent for most top predators (Santora *et al.*, 2014). Identifying species that may be useful indicators and elucidating the mechanis-

tic links that exist between physical processes and the species' ecological response provides insight into current ecological and trophic dynamics, and may inform predictions of future responses in the face of climatic change.

Humpback whales (*Megaptera novaeangliae*) are a promising indicator species. They are distributed throughout the world's oceans and are the most extensively-studied of all large cetaceans (Fleming & Jackson, 2011). In most ocean basins, humpback whales migrate thousands of miles each season from low-latitude winter breeding areas to high-latitude feeding areas inhabited in the summer months (Baker *et al.*, 1986). They are capital breeders, fasting during migration and breeding while depending on blubber energy stores developed during the feeding season. To build the high energy reserves needed for migration and breeding activities, humpback whales require high-density prey patches (Hazen *et al.*, 2009). Humpback whales are believed to

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be largely opportunistic foragers and have been documented to feed on krill and small schooling fish (e.g. sardine, anchovy, sand lance and herring) (Baker *et al.*, 1985; Geraci *et al.*, 1989; Clapham *et al.*, 1997). Their prey consumption likely depends on the availability of different prey species and, given the high metabolic costs associated with rorqual feeding behavior (Goldbogen *et al.*, 2008), may be defined by certain prey density thresholds, below which feeding is not energetically beneficial. Therefore humpback whale prey composition is likely an indicator of dominant prey types in the ecosystem and underlying environmental drivers.

Historical evidence of temporal variability in diet composition in humpback whales exists from whaling data. Stomach contents of humpback whales killed at Moss Landing and Trinidad whaling stations in California varied with year and latitude (Clapham *et al.*, 1997). While sardines were common in the stomachs of whales killed in the 1920s, the stomach contents of whales killed between 1959 and 1962 were largely composed of anchovy (Rice, 1963, 1977). This switch coincides with the drastic decline in abundance of Pacific sardine stocks off California in the 1950s and the subsequent increase in abundance of anchovy stocks (Chavez *et al.*, 2003). Additionally, the main prey base of humpback whales in the Gulf of Maine was observed to shift from sand lance to capelin as the two prey species fluctuated in abundance during the mid-1960s to mid-1970s (Payne *et al.*, 1986). Humpback whale diet has also been observed to vary geographically. Historical records show that euphausiids were more commonly found in the stomachs of humpback whales caught from the Trinidad whaling station in northern California than in those caught from Moss Landing in central California (Clapham *et al.*, 1997). This high degree of foraging flexibility may be a significant contributor to this species' resilience as humpback whales have displayed some of the highest rates of population growth seen in any large whale over the last few decades (Barlow & Clapham, 1997; Zerbini *et al.*, 2010). However, little is yet known about the ecological factors that control the availability of humpback prey items and/or the frequency of changes in prey consumption.

In a dynamic ecosystem such as the California Current, a multidecadal investigation of humpback whale diet from 1993–2012 encapsulates a myriad of oceanographic conditions, providing insight into biological responses to variable physical environments. By examining humpback whale diet and changes in prey dynamics, as well as oceanographic and climatic indicators, a more integrative understanding of ecosystem response to climate variability may be gained. The objective of this study was to assess diet, as measured by stable isotopes, in a single feeding population of humpback whales (Calambokidis *et al.*, 1996) over decadal timescales, in conjunction with data on prey abundances and ocean climate indices to (1) determine whether humpback whales switch prey types over time, (2) illuminate the potential oceanographic and ecological causes of temporal changes in humpback whale diet and (3) explore the utility of humpback whales as indicators of ocean climate.

Materials and methods

Isotope studies

Stable isotope analysis is a powerful tool for trophic investigations, especially for species where stomach content data are unavailable (Kurle & Worthy, 2001; Newsome *et al.*, 2007; Kurle *et al.*, 2011). Diet composition, trophic level and geographic location of feeding can be inferred from isotopic signatures in the tissues of the predator, which reflect the isotopic ratios of its prey (Born *et al.*, 2003; Witteveen *et al.*, 2009a,b). Carbon isotope ratios (^{13}C/^{12}C) are indicative of the carbon source for primary production and can be used to infer geographic location (Farquhar *et al.*, 1989). Nitrogen isotope ratios (^{15}N/^{14}N) reflect trophic level as metabolic processes preferentially excrete ^{14}N, making higher trophic levels more enriched with ^{15}N (Post, 2002).

Humpback whale skin samples used for isotope analysis were collected from individual whales in the California Current ecosystem between 34° and 42°N latitude and 119° and 125°W longitude from 1993–2012 (Fig. S1). Sampling occurred from April to November when humpback whales are known to use this region for foraging. Samples were collected during NOAA Southwest Fisheries Science Center marine mammal survey cruises, and by Cascadia Research Collective and Moss Landing Marine Lab from small boats. All biopsy samples were acquired using a modified rifle or crossbow fitted with a hollow-tipped dart and included skin and a thin layer of blubber. Biopsy samples were frozen at −80°C or stored in ethanol (100%) or DMSO upon collection.

A total of 295 skin samples were analyzed for carbon and nitrogen stable isotope ratios in this study. Year-to-year variations in sample size reflect differences in field sampling effort. As the focus of this study is on inter-annual timescales, years with sample sizes of less than five were left out of most analyses as they may have been insufficient to be representative of an annual signal. Approximately 10 mg wet weight mass of skin from each biopsy sample was sliced into small pieces and dried for 24 h in a VirTis benchtop lyophilizer. Lipids were extracted using petroleum ether in a Dionex Accelerated Solvent Extractor and proteins were retained for analysis. Approximately 0.4–1.0 mg of each sample was sealed in tin capsules. Samples were then analyzed for δ^{15}N or δ^{13}C at the University of Florida, Gainesville Stable Isotope Geochemistry Lab using mass spectrometry (Carlo Erba NA 1500 CNS Elemental Analyzer and ConFlo II interface coupled with a Finnigan-MAT 252 isotope ratio mass spectrometer). Reference materials were Vienna Pee Dee Belemnite and atmospheric nitrogen gas for carbon and nitrogen stable isotope analyses,

respectively. USGS40 L-glutamic acid was used as an internal laboratory standard and was run at regular intervals during the analysis to calibrate the system. Stable isotope ratios were then reported as per mil using delta notation, computed as $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$ where X is ^{15}N or ^{13}C and R is the corresponding ratio of ^{15}N/^{14}N or ^{13}C/^{12}C. The precision of these repeat standard measurements was 0.1‰ for δ^{15}N and 0.05‰ for δ^{13}C.

Oceanographic and ecological covariates

The following environmental and prey variables were explored: sea surface temperature (SST), upwelling index, Pacific Decadal Oscillation (PDO) index, North Pacific Gyre Oscillation (NPGO) index, sea surface height (SSH) anomaly [as a proxy for El Nino Southern Oscillation (ENSO) index] and abundance anomalies of sardine, anchovy and krill. For each oceanographic variable, an annual anomaly was calculated to examine the interannual variability while minimizing the potential compounding effect of seasonal variability.

Physical oceanographic indices and prey time series were obtained from the following sources. Monthly SSH anomaly data from the California Current Ecosystem Long-Term Ecological Research program were used as a proxy for El Niño Southern Oscillation as it has been found to reflect both locally and remotely forced upwelling in the CCS (Bograd & Lynn, 2001). SSH data were obtained from http://oceaninformatics.ucsd.edu/datazoo/data/ccelter/datasets?action=view&id=153. The monthly mean values for the PDO were obtained from http://research.jisao.washington.edu/pdo/. The monthly mean values for the NPGO were obtained from http://www.o3d.org/npgo/. Average daily SST data were acquired from NOAA's National Data Buoy Center, buoy # 46026 located on the shelf, at 53 m water depth, 18 nautical miles west of San Francisco. Daily cumulative upwelling index values were obtained from the Pacific Fisheries Environmental Laboratory http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html. For this analysis, the upwelling data collected from 36°N 122°W were used. Both the SST and upwelling index data buoy locations were chosen because of their proximity to the majority of humpback whale sampling locations. The whale sampling locations are not uniformly geographically distributed and largely reflect preferred humpback whale habitat in the CCS. It should be noted that the scale of the SST and upwelling covariates is therefore regional while the ENSO, PDO and NPGO metrics represent basin-wide processes.

Prey abundance anomaly data were gathered during Central California coast annual spring (May–June) rockfish midwater trawl surveys operated by the Fisheries Ecology Division of the Southwest Fisheries Science Center from 1993 to present. Approximately 100 midwater trawls are conducted annually with a geographic focus on the area from south of Monterey Bay to north of Point Reyes, CA. Data used in this study are the standardized annual anomalies from the log of mean catch rates. While numerous species are collected, analysis here focused on krill (predominantly *Euphausia pacifica* and *Thysanoessa spinifera*), anchovy (*Engraulis mordax*) and sardine (*Sardinops sagax*) because they are known humpback whale prey species in this area (Clapham *et al.*, 1997). Additionally, published δ^{15}N and δ^{13}C signatures of these prey species were reviewed to identify average values for the species as well as potential temporal and geographic variability that may occur.

Analytical methods

Isotope data were tested for normality using Lilliefor's adaptation of Kolmogorov–Smirnov test for large data sets, and for homogeneity of variance using Levene's Test. All statistical tests were performed in R (R package version 3.2.2, The R Foundation for Statistical Computing, Vienna, Austria), and results were interpreted with a significance level of $\alpha = 0.05$.

Prior to examining temporal variability in humpback whale isotope signatures, geographic structure within the CCS population was explored to ensure that geographic differences did not confound temporal patterns. The effect of latitude and longitude on both δ^{15}N and δ^{13}C was first tested using analysis of variance (ANOVA).

Interannual variation in humpback whale isotopic signatures was tested using ANOVA and Tukey's *post-hoc* test. Apparent temporal variation was further explored by comparing centroid location and dispersion metrics of three distinct time periods in bivariate isotopic space (Turner *et al.*, 2010). Additionally, isotopic niche was compared across the time series using Bayesian standard ellipse areas (Jackson *et al.*, 2011).

Since humpback whale diets are likely to respond nonlinearly to changes in habitat, generalized additive models (GAMs) were used to relate the value of isotope signatures to ecological and oceanographic covariates (Forney, 2000; Redfern *et al.*, 2006). GAMs are nonparametric models that can accommodate many different types of relationships between the examined variables and are therefore particularly effective at modeling complex ecological relationships (Hastie & Tibshirani, 1990). Prior to running the models, correlation among covariates was examined. Sardine and anchovy abundances were strongly correlated ($r^2 = 0.71$, $P \leq 0.05$) throughout the study period. Due to this correlation and the focus of our study question on potential prey switching between isotopically distinct diets dominated by fish or krill, we first ran two sets of GAMs to determine whether sardine or anchovy demonstrated greater explanatory power. Subsequent models were run with anchovy only, as the two species followed similar patterns of abundance throughout the study period. Both 1-year and 2-year lags between humpback whale isotope ratios and environmental variables were also explored to account for potential temporal lags between oceanographic conditions and prey availability. A stepwise forward–backward modeling approach was used in the *mgcv* package within R. Effective degrees of freedom for smoothing splines were determined by cross-validation within *mgcv*. Models were compared using Akaike's information criterion (AIC), with the final candidate models having the lowest AIC values.

Results

The data for both δ^{13}C and δ^{15}N did not deviate significantly from a normal distribution (δ^{15}N: $D = 0.0468$,

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$P = 0.1184$; $\delta^{13}C$: $D = 0.0285$, $P = 0.811$). Results from a subset of individuals of known sex (from the same years) confirmed that sexes did not significantly vary with respect to either $\delta^{15}N$ ($t_{34} = -0.93$, $P = 0.36$) or $\delta^{13}C$ ($t_{34} = -0.30$, $P = 0.76$). Sex was therefore not considered in subsequent analyses.

Interannual and geographic variability within the CCS humpback whale population

There was no indication of significant geographic variability in $\delta^{15}N$ and $\delta^{13}C$ within the CCS population with regard to latitude (ANOVA: $\delta^{15}N$ $F_{1,289} = 0.443$, $P = 0.506$; $\delta^{13}C$: $F_{1,288} = 0.789$, $P = 0.375$) or longitude

(ANOVA: $\delta^{15}N$ $F_{1,289} = 0.492$, $P = 0.484$; $\delta^{13}C$: $F_{1,288} = 0.426$, $P = 0.514$). Additionally, latitude and longitude were not included terms in any of the best GAM models for either $\delta^{15}N$ or $\delta^{13}C$.

Both $\delta^{15}N$ and $\delta^{13}C$ annual mean values varied to a comparable degree (approximately 2–3 ppm) across the study period and with a similar periodicity (Fig. S2). There appear to be two major shifts in isotope signatures (Fig. 1). Humpback whale signatures were less enriched during the early part of the study period until 2003 when there was a shift in both ratios to more positive values until 2006. This was followed by a subsequent return to more depleted values from 2010 to 2012, similar to levels observed in 1993–2002 (Fig. 1).
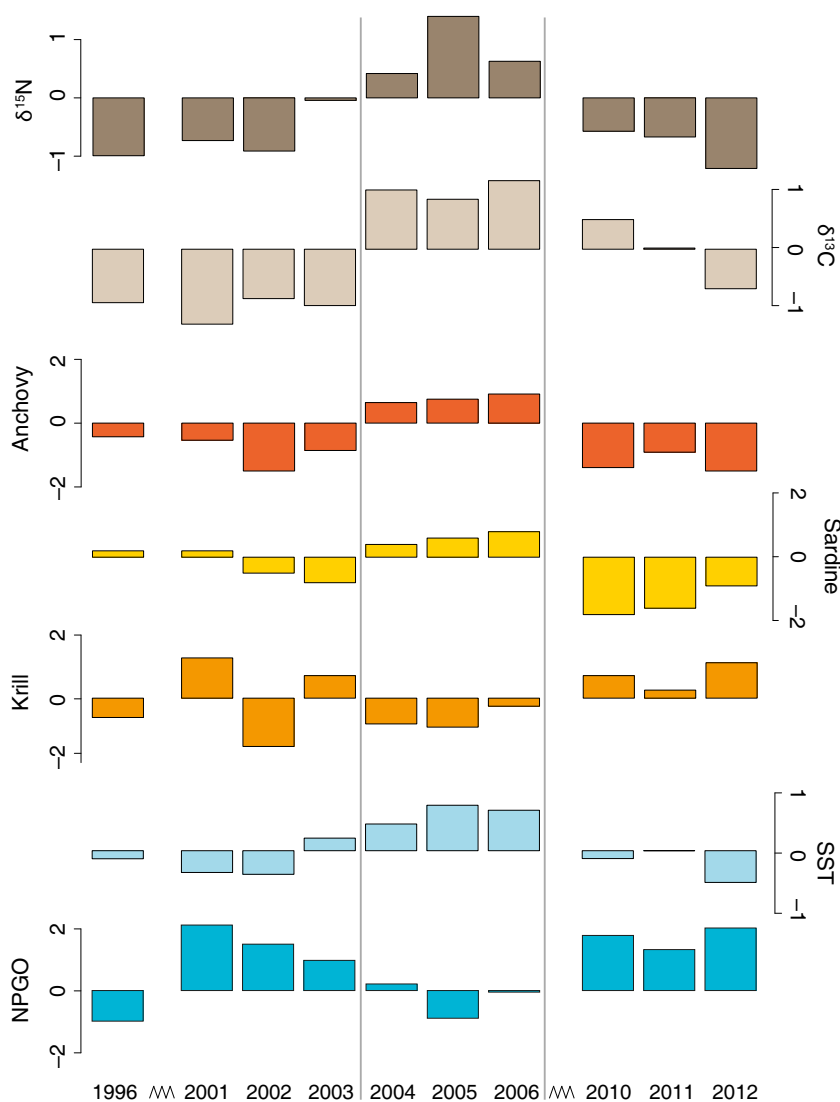

Fig. 1 Humpback whale $\delta^{15}N$ and $\delta^{13}C$ ratios, prey abundances and selected oceanographic indices represented in standard deviation units. The timing of the two hypothesized prey shifts is indicated by the vertical gray lines. Years with humpback whale sample sizes <5 are not shown.

The isotopic niche metric of Bayesian ellipse area indicates overlap between the early and late parts of the study period but no overlap with the middle years (Fig. S3). Though there is niche overlap between the early and late periods of the time series, it should be noted that all three periods occupy significantly different locations in isotopic space. Dispersion metrics of mean distance to centroid and nearest neighbor were similar across the three time periods, indicating that niche breadth was relatively consistent at these scales (Table S1). However, examination across individual years shows that variance was not homogenous, indicating differences in diet breadth between years (δ^{15}N: $F_{1, 15} = 3.7164, 5.695e{-}06$; δ^{13}C: $F_{1, 15} = 2.4415, 0.002303$).

Ecosystem Shifts

Our study period is characterized by high degrees of oceanographic variability, with regard to both large-scale oceanographic forcing as well as localized upwelling events. Both PDO and ENSO indices have been fluctuating at intervals of approximately 2–4 years for the last decade. The NPGO also switched between positive and negative phases three times between 1993 and 2012 (PaCOOS, 2013). In response to these oceanographic and climatic conditions, abundance of potential humpback whale prey species varied throughout the study period (PaCOOS, 2013). Anchovy and sardine abundances showed similar patterns of abundance to each other, with positive abundance anomalies from 2004 through 2006 (Fig. 1). Krill displayed an opposite pattern of abundance to the two fish species, with negative anomalies from 2004 to 2006 (Fig. 1). Though both 1-year and 2-year lags between humpback whale

isotope ratios and environmental variables were explored, neither significantly improved correlations, thus they were not considered further.

The best GAM, as assessed by AIC values, for humpback whale δ^{15}N included SST and krill abundance (Fig. 2). Models including anchovy and the upwelling index also performed well (within four AIC points). The relationship between δ^{15}N and SST was positive and generally linear, indicating that warmer years resulted in humpback whales feeding at higher trophic levels (Fig. 2a). The relationship between krill and δ^{15}N is slightly more complex. The GAM function resulting from the model with SST and krill is nonlinear and would suggest that both low and high densities of krill result in enriched δ^{15}N (Fig. 2b). However, comparison of our best model (krill and SST) with a single variable SST model shows that the AIC values are within five points of one another. SST and krill abundance are moderately though not significantly correlated ($r^2 = 0.1238$, $P = 0.07$) which may also drive some of the positive slope in the relationship between krill and δ^{15}N at high krill densities. Modeling δ^{15}N as a GAM function of the single variable krill indicated that, as expected, humpback whale δ^{15}N decreased with krill abundance (Fig. S4).

The best GAM for humpback whale δ^{13}C included anchovy, upwelling and PDO (Fig. 3). The same model with the addition of NPGO also performed well as did a model with just upwelling and anchovy. δ^{13}C values increased with the abundance of anchovy in the ecosystem, indicating a dominance of prey fish in humpback whale diets congruent with an availability of such prey in the ecosystem (Fig. 3a). δ^{13}C declined as upwelling increased, and NPGO entered positive phases, reflect-
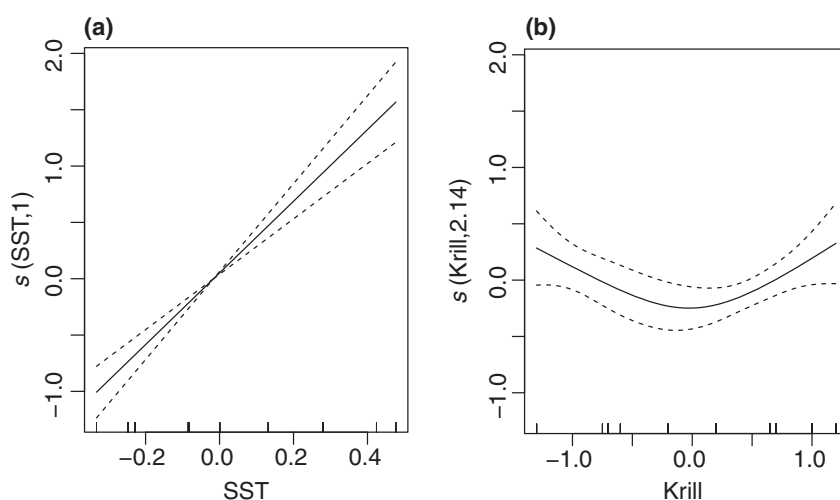

Fig. 2 Generalized additive model functions of humpback whale δ^{15}N in relation to (a) sea surface temperature and (b) krill abundance anomalies. Dashed lines are two standard error bars.

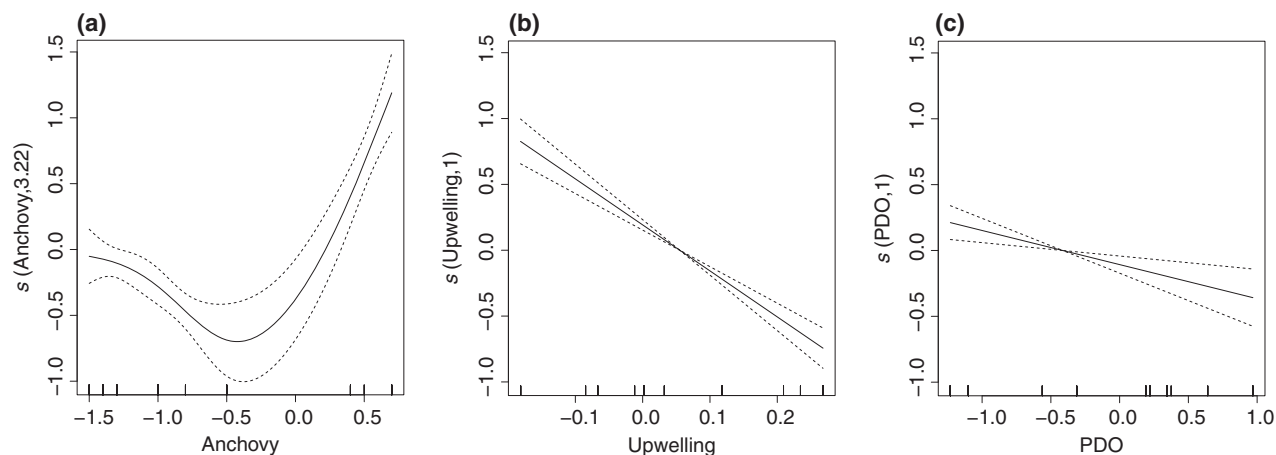**Fig. 3** Generalized additive model functions of humpback whale δ^{13}C in relation to (a) anchovy abundance, (b) upwelling, and (c) PDO anomalies. Dashed lines are two standard error bars. PDO, Pacific Decadal Oscillation.

ing humpback whale diets dominated by krill rather than fish under these oceanographic conditions (Fig. 3b). The relationship between PDO and δ^{13}C is slightly negative (Fig. 3c). However, further examination of this relationship in the two-variable models including PDO reveal that this relationship is more sinusoidal with moderate PDO values corresponding to elevated δ^{13}C while more extreme positive and negative values of PDO are concomitant with depleted δ^{13}C signatures.

Discussion

While top predators are often cited as indicator species for ecosystem processes and conditions, their utility as indicators is dependent upon an understanding of their response to environmental variability. Top-predator responses are likely cumulative integrations of links between predator foraging behavior, mid-trophic level prey dynamics and oceanographic conditions (Hilty & Merenlender, 2000; Abraham & Sydeman, 2004; Sydeman et al., 2013). The dynamic oceanographic conditions that occurred during our study period resulted in temporal variability in humpback whale isotope ratios and provided insight into multi-trophic level responses to interannual variability in ocean climate patterns. Our study period captured two major shifts in isotopic ratios of California humpback whales (Fig. 1). These shifts appear to be a result of a switch in humpback whale dominant prey type from krill to fish and back. These prey switches reflect availability of prey in the system and changing oceanographic conditions (Fig. 1). Support for this hypothesis includes carbon and nitrogen isotope ratios of humpback whales, time series of prey abundances and time series of oceanographic con-

ditions. By integrating all of these lines of evidence over the course of the 20-year study period, a more thorough understanding of the relationships between climate, prey and predators is gained (Fig. 4).

Throughout several years at the start of the time series, SST was cool, southward transport in the CCS was strong, and both NPGO and upwelling were positive (Goericke et al., 2004; PaCOOS, 2011). These climatic and oceanographic conditions had impacts on the biology of the CCS that propagated up the food chain. NPGO has been correlated with the strength and timing of upwelling favorable winds, with NPGO+ years characterized by earlier spring transitions that result in longer and more vigorous upwelling seasons (Di Lorenzo et al., 2008, 2009; Chenillat et al., 2012). This increased upwelling led to elevated levels of nutrients and more abundant zooplankton populations. Krill occurred in greater densities and consequently represented the dominant species in humpback whale diets, driving humpback whale δ^{15}N and δ^{13}C to be more depleted (PaCOOS, 2011). Though the values reported for krill abundance in 2002 would suggest low krill availability to humpback whales, the prey data used here may not fully capture the abundance or density of krill in all years in the CCS. Other data available for the region, such as record-high reproduction of the krill-dependent planktivorous Cassin's auklets (*Ptychoramphus aleuticus*), indicate that krill was abundant in the CCS, but the timing or geographic coverage of the SWFSC surveys may have been mismatched with the peak in krill abundance in the ecosystem (Abraham & Sydeman, 2004; Sydeman et al., 2013). Spatially, krill are typically found adjacent to upwelling centers, where prey and nutrients are readily available, yet transport is slightly weaker allowing for better krill
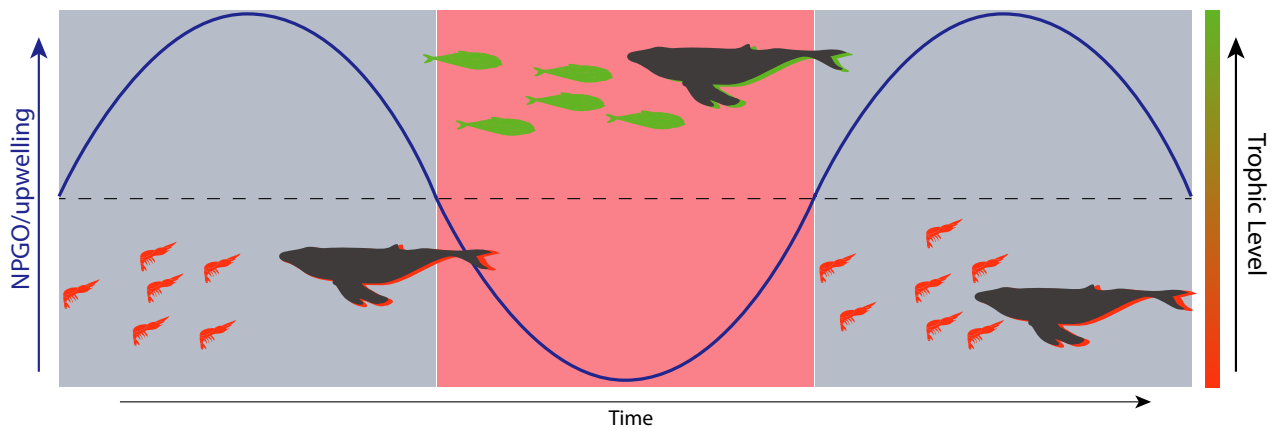
Fig. 4 Conceptual diagram displaying the proposed relationship between oceanographic forcing, prey abundance and humpback whale foraging. A positive phase of the North Pacific Gyre Oscillation (NPGO) (blue line) is correlated with increased upwelling and more abundant krill populations resulting in lower trophic level humpback whale diets (color bar on right side of diagram and position of whale). As the NPGO switches to a negative phase, upwelling is reduced, and krill populations decline while sardine and anchovy populations increase driving the diet of humpback whales to be at a higher trophic level.

retention (Santora *et al.*, 2011a,b). Known krill hotspots coincide geographically with documented whale foraging hotspots (Croll *et al.*, 1998; Fiedler *et al.*, 1998).

From 2004–2006, the NPGO was negative, SST was warmer in the summers and seasonal summer upwelling was delayed (Mackas *et al.*, 2006; Schwing *et al.*, 2006; Barth *et al.*, 2007; Dorman *et al.*, 2011). Anomalously strong poleward winter currents, associated with positive PDO conditions, advected krill further north in the winter. This, in combination with the delayed upwelling, resulted in krill being too far north early in the upwelling season and therefore missing their optimal foraging window during spring phytoplankton blooms (Dorman *et al.*, 2011). These events led to anomalously low population abundances of krill (Dorman *et al.*, 2011; PaCOOS, 2011). Simultaneously, these warmer more stable conditions allowed sardine and anchovy populations to increase and, especially for sardine, expand their range further north (Brodeur *et al.*, 2006; Zwolinski *et al.*, 2012). The range expansion and biomass increase likely resulted in sardine and anchovy being more available to humpback whales feeding in the central California Current and led to elevated $\delta^{15}N$ and $\delta^{13}C$ values in humpback whale diets. Other predators in the CCS displayed foraging behavior that supports this interpretation. Scat samples from California sea lions were anomalously dominated by anchovy, sardine and rockfish. Blue whales, which feed on euphausiids, were distributed more widely throughout the CCS and further north than previous years, possibly in response to poor euphausiid recruitment in nearshore feeding areas (Peterson *et al.*, 2006).

In 2010–2012, krill were again present in high densities while both sardine and anchovy were anomalously low in abundance through the CCS (Fig. 1). Concurrently, humpback whale diets displayed low $\delta^{15}N$ and $\delta^{13}C$. It is worth noting that 2010 has a unique combination of $\delta^{15}N$ and $\delta^{13}C$ signatures (Fig. 1). $\delta^{15}N$ signatures suggest a krill-dominated diet, yet $\delta^{13}C$ is more enriched than would be expected from such a diet. While a krill-dominated diet is consistent with prey availability and oceanographic indices that year, it is possible that krill may have had a slightly elevated $\delta^{13}C$ signature in 2010. Three possible scenarios may have led to an elevated $\delta^{13}C$ signature. The CCS was characterized in 2010 by a transition in early spring from a brief El Niño period to La Niña, with increased seasonal upwelling resuming in June/July (Bjorkstedt *et al.*, 2011). Such conditions may have aggregated euphausiids closer to the shore, where food chains are enriched in $\delta^{13}C$ compared to pelagic habitats (Checkley & Barth, 2009; Bjorkstedt *et al.*, 2011). Secondly, the composition of euphausiid prey may have altered euphausiid isotopic signatures. The community composition of copepods in 2010 was anomalously subtropical, dominated by less lipid-rich species, which may have elevated the resulting $\delta^{13}C$ signatures seen in humpback whales in 2010 (McConnaughey & McRoy, 1979; PaCOOS, 2011). Finally, the euphausiid community may have been slightly altered by a very brief positive PDO that occurred in 2010. Positive phases of PDO are associated with enhanced northward transport which can result in an incursion of a more subtropical krill species, *Nyctiphanes simplex*, into the CCS (Di Lorenzo & Ohman, 2013). The enriched $\delta^{13}C$ signature of *N. simplex*, as compared to *E. pacifica*, would have resulted in an elevated $\delta^{13}C$ signature in

humpback whales if this species comprised a greater proportion of the euphausiid community in 2010.

Isotope ratios suggest that the variance observed in humpback whale diet, throughout our study period, is indicative of a full trophic level shift. $\delta^{15}N$ and $\delta^{13}C$ of humpback whale diet varied by ~2‰ between the early, middle and late years of the study period (Fig. S2). Published values for krill (*T. spinifera* and *E. pacifica*) $\delta^{15}N$ and $\delta^{13}C$ vary from values for anchovy and sardine also by approximately 2‰ (Sydeman *et al.*, 1997; Becker *et al.*, 2007; Brodeur *et al.*, 2008; Miller *et al.*, 2008, 2013). However, this prey switch hypothesis assumes that there exists little to no change in basal isotopic signatures in the food web throughout the study period. Given the importance of temporal variability highlighted by this study, it would be preferable to have prey samples from all years of our study. However, it is difficult to obtain samples with the geographic coverage that is comparable to the humpback population range over the 20-year timescale examined. A review of the literature provided isotope values for prey samples collected in 1993, 1994, 1996–2002, 2007 and 2009 in the CCS (Sydeman *et al.*, 1997; Becker *et al.*, 2007; Brodeur *et al.*, 2008; Miller *et al.*, 2008, 2013). All $\delta^{15}N$ and $\delta^{13}C$ values for krill were found to be comparable despite the different sampling years. This was also the case for sardine and anchovy, suggesting that basal signatures were relatively stable throughout the time period examined. Additionally, there was no overlap of carbon or nitrogen ratios between krill and these two forage fish species, allowing diets dominated by fish and krill to be isotopically discriminated. This suggests that a prey switch in humpback whale diet is the most parsimonious explanation for the observed humpback whale temporal isotope variability.

Previous research on the distribution and habitat use of cetaceans in the CCS complement our findings here. Habitat models of humpback distribution reveal that whales were concentrated in a smaller area during the foraging season in both 2001 and 2008, in the same regions where persistent krill hotspots have been identified (Santora *et al.*, 2011a; Becker *et al.*, 2012). In contrast, in 2005, humpback whales were found to be more widely spread throughout the CCS extending into the California Bight (Becker *et al.*, 2012). While an examination of geographic variability is beyond the scope of the present study, it can be hypothesized that the observed and predicted cetacean densities reported by Becker *et al.* (2012) were the result of changes in location by humpback whales in order to exploit the most dominant prey resource in those years.

The inclusion of both large-scale forcing indices (NPGO and PDO) and local upwelling conditions (SST, CUI and SSH) in this study provides useful information for future research that aims to predict top-predator responses to ocean climate forcing. While numerous top-predator studies have explored relationships between large-scale indices and predator distributions, identifying climate-to-prey-to-predator correlations over multiple years is less common (Zacharias & Roff, 2001). Findings here suggest that both indices of large-scale climate variability as well as local oceanographic processes are central to understanding mechanisms underlying prey availability and top predator responses. Both NPGO and PDO were important in our models. Recent work has provided insight into the ecological consequences of the NPGO (Di Lorenzo *et al.*, 2008, 2009; Chenillat *et al.*, 2012). NPGO modulates the strength of winter nearshore winds, accelerating the transition to spring upwelling during NPGO+ years and increasing the overall length and magnitude of the upwelling season (Chenillat *et al.*, 2012). This increased coastal upwelling has been linked to elevated salinity, nutrients and chlorophyll which drive concomitant changes in phytoplankton and lead to elevated zooplankton populations (Di Lorenzo *et al.*, 2008, 2009). Such conditions are consistent with periods when humpback whale diets were dominated by zooplankton. While NPGO captures changes in coastal upwelling and resulting productivity, PDO is more strongly correlated with the strength of alongshore surface transport and variability in the dominance of cold-water or warm-water zooplankton species (Keister *et al.*, 2011; Di Lorenzo & Ohman, 2013; Di Lorenzo *et al.*, 2013). PDO is strongly correlated with SST in the CCS, and both SST and PDO have been correlated with variability in sardine and anchovy abundance (Checkley *et al.*, 2000; Zwolinski & Demer, 2012; Lindegren & Checkley, 2013; Lindegren *et al.*, 2013) . Consequently, both alongshore transport and coastal upwelling are likely impacting relative prey abundances and therefore important in the determination of humpback whale trophic behavior. Additionally, the geographic influence of these climatic indices is diverse as the link between NPGO and upwelling is strong for the central CCS, while upwelling variability is more tightly correlated with PDO in the northern CCS (Di Lorenzo *et al.*, 2008; Chenillat *et al.*, 2012). The inclusion of both PDO and NPGO in our models, as well as the upwelling index, is therefore consistent with the CCS-wide geographic scope of our study area.

Observational studies as well as global warming projection models find evidence for amplification of NPGO variance (and concurrent stabilization or reduction in PDO variance) that suggests NPGO may play an increasingly important role in Pacific ecosystem conditions (Di Lorenzo *et al.*, 2008; Sydeman *et al.*, 2013). Other studies predict increasing coastal upwelling

under future climate change scenarios but with uncertain consequences in light of expected phenological shifts in upwelling seasons, concurrent increasing temperatures and stratification, and changes in nutrient supply (Bakun, 1990; Durant *et al.*, 2007; Rykaczewski & Dunne, 2010; Black *et al.*, 2011; Sydeman *et al.*, 2014; Bakun *et al.*, 2015). Results here suggest that these projected changes in climate forcing and upwelling dynamics will affect the prey composition available to humpback whales. Though the specific diet alterations are uncertain, the foraging flexibility documented here might confer greater population resilience in the face of a changing ocean climate for humpback whales. However, more stenophagous cetaceans, such as blue whales, may be forced to adapt through other means, such as shifts in geographic range (Hazen *et al.*, 2012).

Ecosystem responses to global climate change are likely to be complex, regionally varied and poorly predicted by monitoring of primary production metrics alone (Kearney *et al.*, 2013; Chust *et al.*, 2014). The forecasting of future ecosystem states may be improved through the inclusion of multiple indicators of food-web dynamics, energy flow and physical–biological relationships (Friedland *et al.*, 2012; Fu *et al.*, 2012). Recent studies suggest that changes in environmental conditions and at lower trophic levels can be amplified at higher trophic levels due to nonlinear responses of biological communities and predatory interactions (Friedland *et al.*, 2012; Stock *et al.*, 2014). The present examination of higher trophic-level response to climate variability suggests that humpback whales are useful indicators of ecosystem dynamics in the CCS. Their foraging behavior is a synoptic result of dynamic physical and biological conditions in the CCS, reflecting changes across multiple trophic levels due to contemporary climate variability and ultimately informing potential responses across these trophic levels due to climate change. Though variations in oceanographic conditions are occurring across daily and monthly timescales, the present examination of annual and multi-year scales provides useful insight into the scales most relevant to top-predator foraging and population-level responses. Long-term data sets of predator and prey data are limited; however, future trophic ecology studies should emphasize interannual temporal coverage and continuity. Insights into biological responses to large-scale and regional physical forcing, such as those reported here, are fundamental to advancing ecosystem predictions related to global climate change.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Map of study area with humpback whale sample locations shown color-coded by year of collection.

Figure S2. δ^{15}N and δ^{13}C values measured in 295 skin samples from humpback whales collected in the California Current from 1993–2012.

Figure S3. δ^{15}N and δ^{13}C values measured in 295 skin samples from humpback whales collected in the California Current from 1993–2012.

Figure S4. Generalized additive model function of humpback whale δ^{15}N in relation to krill abundance anomalies only.

Table S1. Centroid locations and dispersion metrics for isotope samples collected during three different time periods of the study in the California Current Ecosystem.

Table S2. Summary of generalized additive models relating humpback whale δ^{15}N and δ^{13}C to prey abundance anomalies and oceanographic variables.