

MARINE ECOSYSTEMS

Temporal variation in pelagic food chain length in response to environmental change

Rocio I. Ruiz-Cooley,^{1,2*} Tim Gerrodette,² Paul C. Fiedler,² Susan J. Chivers,² Kerri Danil,² Lisa T. Ballance^{2,3}

Climate variability alters nitrogen cycling, primary productivity, and dissolved oxygen concentration in marine ecosystems. We examined the role of this variability (as measured by six variables) on food chain length (FCL) in the California Current (CC) by reconstructing a time series of amino acid-specific $\delta^{15}\text{N}$ values derived from common dolphins, an apex pelagic predator, and using two FCL proxies. Strong declines in FCL were observed after the 1997–1999 El Niño Southern Oscillation (ENSO) event. Bayesian models revealed longer FCLs under intermediate conditions for surface temperature, chlorophyll concentration, multivariate ENSO index, and total plankton volume but not for hypoxic depth and nitrate concentration. Our results challenge the prevalent paradigm that suggested long-term stability in the food web structure in the CC and, instead, reveal that pelagic food webs respond strongly to disturbances associated with ENSO events, local oceanography, and ongoing changes in climate.

INTRODUCTION

Our oceans are changing at a rapid pace, altering the population dynamics of species with important ecological consequences over entire ecosystems. Over the past century, changes in the physical and chemical environment of marine ecosystems have altered biochemical cycles and primary production (1–3) and influenced the phenology and distribution of many species (4). Productivity, a primary factor influencing species diversity and food web stability (5), has declined in some ocean basins (6), with impacts on component species. In the Bering Sea, for example, marine mammal and bird populations have decreased in abundance in association with decreased carrying capacity related to climate change (7). El Niño Southern Oscillation (ENSO) events, a dominant physical mode of interannual climate variability with global effects, are projected to become more frequent and intense than in the previous decades (8, 9). Within the past 50 years, two extreme El Niño events (the warm phase of the ENSO) occurred only 14 years apart (1982–1983 and 1997–1998); they markedly reduced the abundance, survival, and fitness of many species and drove significant changes in community composition (10). Although the impacts of environmental variation on specific marine taxa have been studied for some time, less is known about its impacts on pelagic food web dynamics because of a lack of available methods for measuring food web length through time.

Food webs can interconnect a widely diverse group of species and promote ecosystem stability (11). However, biodiversity loss due to anthropogenic perturbations [for example, invasive species, removal of top predators, and climate change (12–14)] has already caused major changes in the marine food web structure (15). Food webs are delineated by the transfer of energy from primary producers to top predators through all trophic pathways among species within a community (16). Stable isotope analysis traces elemental flow throughout food webs, providing a metric for quantifying realized food chain length (FCL, defined by the energy web or trophic connections in the web) (17, 18). This approach has also been used in biogeochemistry to understand spatial and temporal variations of nitrogen compounds (3) and

in ecology to investigate feeding habits of species and trophic relationships (19). In the oceans, $\delta^{15}\text{N}$ from nitrate, primary producers, and particulate organic material vary in space and time (20), and animals integrate this baseline isotope variation through the diet, providing a record of both the biogeochemical environment and dietary preferences (17, 21). Hence, an animal's bulk tissue $\delta^{15}\text{N}$ values do not separate the effects of diet and primary producers. As such, obtaining suitable values near the base of the food web is essential for proper interpretation of data, to determine animal trophic positions and reconstruct food webs, but is quite difficult, especially for time series analysis.

The use of amino acid compound-specific isotope analysis (amino acid CSIA) has clarified some uncertainties from the bulk isotope record. It has been used for examining pathways of nitrogen transfer throughout food webs and for distinguishing the effects of baseline elemental sources and trophic position of consumers (22). Amino acid CSIA is becoming a key approach to identifying the habitat use and geographic origins of migratory species (23). At temporal scales, analysis of $\delta^{15}\text{N}$ amino acid in Hawaiian deep-sea corals time series samples identified a sharp decrease in baseline values that was linked to increasing nitrogen fixation in response to recent ocean warming (24). In the offshore California Current (CC), amino acid CSIA from sperm whales (*Physeter macrocephalus*), a top predator of the mesopelagic ocean, revealed ongoing changes in nitrogen biochemical cycling: $\delta^{15}\text{N}$ source amino acids have declined since 1993, whereas trophic amino acids did not exhibit a long-term trend (25). These studies illustrate the importance of animals as natural biological samplers of their habitat and the use of amino acid CSIA from tissues of resident predators to unravel changes in the animals' diet from habitat baseline values.

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has monitored the Southern California Bight (SCB; Fig. 1) for 65 years and is among the most studied marine regions in the world. There is a good understanding of the role of climate variability and its impacts on primary production and populations of many lower trophic level taxa, including zooplankton and fish. However, there is limited understanding of its effects on high trophic level species or entire food webs. Because apex predators integrate the biogeochemical characteristics of their habitat through diet, we used the short-beaked common dolphin (*Delphinus delphis*) as an ecosystem indicator. This odontocete species is an abundant generalist pelagic apex predator (trophic position, ~ 4.2) (26), feeds from the sea surface

¹Moss Landing Marine Laboratories, San Jose State University, Moss Landing, CA 95039, USA. ²Southwest Fisheries Science Center, National Oceanic and Atmospheric Administration Fisheries Service, La Jolla, CA 92037, USA. ³Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92037, USA.

*Corresponding author: Email: iruizcooley@mlml.calstate.edu

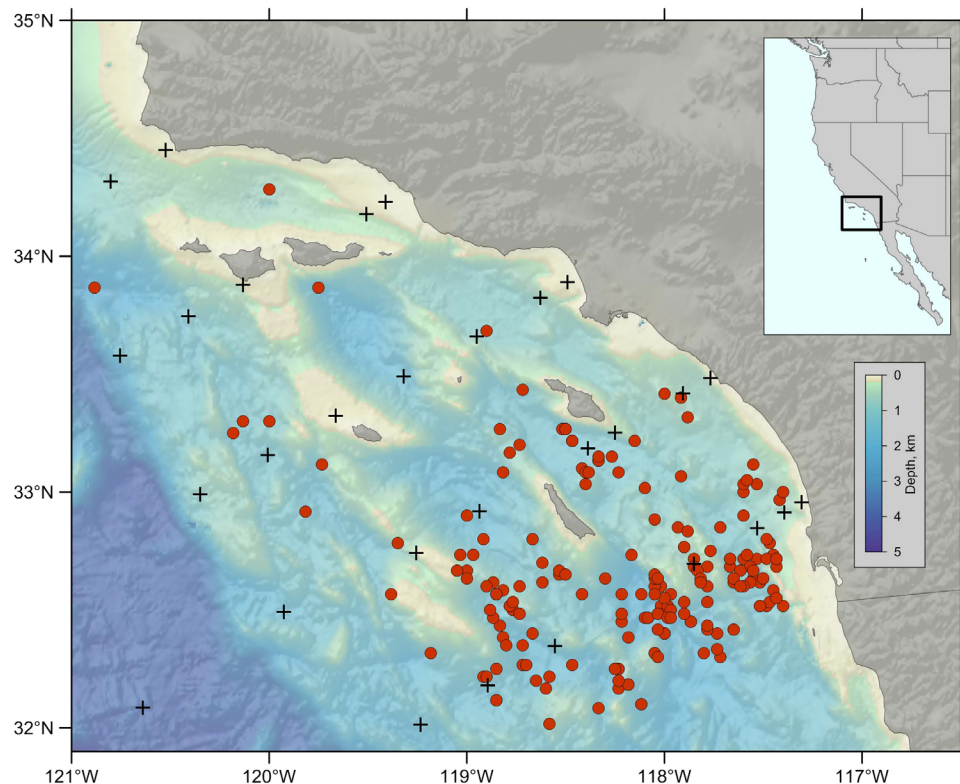


Fig. 1. The SCB with dolphin sampling locations and oceanographic stations. Sampling sites of *D. delphis* ($n = 204$) from 1990 to 2008 are indicated with red circles (○). The CalCOFI stations used to obtain in situ oceanographic data from the SCB are indicated with black crosses (+).

to a maximum depth of 280 m (27), and preys on a wide range of small-bodied epipelagic and mesopelagic taxa, mainly myctophids and other fish and squids from the deep scattering layer (27). This species is resident in the CC ecosystem (28) and thus should be a valuable ecosystem integrator and indicator. We quantified bulk and individual amino acid $\delta^{15}\text{N}$ values from skin tissue samples of *D. delphis* from 1991 to 2008 (Fig. 1) to examine interannual variability in FCL [the mean path length from the base of the food web or food web compartment to an apex predator (18, 29)]. Two proxies of FCL were calculated to examine temporal variability: (i) the isotopic difference ($\Delta^{15}\text{N}_{\text{Glu-Phe}}$) between the canonical trophic amino acid [glutamic acid (Glu)] and source amino acid [phenylalanine (Phe)] and (ii) the difference between the average trophic and source amino acids ($\Delta^{15}\text{N}_{\text{Tro-Src}}$). Our data set encompasses one major ENSO event in 1997–1998 and several weaker El Niños and La Niñas. This is the first study to present interannual variability in bulk and amino acid stable isotope ratios and to examine the effect of oceanographic variation over ecosystem nitrogen biochemistry, dolphin feeding status, and FCL.

RESULTS

Bulk nitrogen stable isotope values ($\delta^{15}\text{N}$) showed no evidence of a temporal trend from 1990 to 2008 ($n = 204$, $r^2 = 0.17$; Fig. 2). In contrast, our results reveal high interannual variability in $\delta^{15}\text{N}$ values for all amino acid isotope records (Glu, Phe, and average trophic and source amino acids) but with no evidence of linear temporal trends ($r^2 < 0.1$, $P > 0.2$; residuals are consistent with random error) (Fig. 2). Similarly, our two proxies of FCL, $\Delta^{15}\text{N}_{\text{Glu-Phe}}$ and $\Delta^{15}\text{N}_{\text{Tro-Src}}$, exhibited high variability over time with no linear trend (Fig. 3). These two proxies

displayed relatively similar patterns of variation with different amplitudes (Fig. 3). $\Delta^{15}\text{N}_{\text{Glu-Phe}}$ exhibited more variation because it is based on single amino acids at the trophic and source levels. $\Delta^{15}\text{N}_{\text{Tro-Src}}$ used data from all amino acids, but isotopic fractionation varied among amino acids (30), resulting in a wider isotopic variability within each group. Two strong declines ($\geq 10\%$) were observed for both FCL proxies coincident with the 1997–1998 El Niño event and from 2004 to 2006 coincident with the shoaling of the hypoxic depth (Figs. 3 and 4). Our hierarchical Bayesian models revealed that FCL varied in response to all environmental variables (Fig. 5 and table S1), with stronger patterns but wider Bayesian credibility intervals for $\text{FCL}_{\text{Glu-Phe}}$ than $\text{FCL}_{\text{Tro-Src}}$. Bayesian models revealed relatively similar patterns of variation for both $\text{FCL}_{\text{Glu-Phe}}$ and $\text{FCL}_{\text{Tro-Src}}$ in relation to surface temperature ($^{\circ}\text{C}$), chlorophyll (mean chlorophyll concentration in the euphotic zone; mg/m^3), multivariate ENSO index (MEI), and zooplankton (total plankton volume; $\text{cm}^3/1000 \text{ m}^3$). Longer FCLs were observed under intermediate conditions. In contrast, $\text{FCL}_{\text{Tro-Src}}$ was relatively flat for hypoxic depth (m) and nitrate (mean nitrate concentration in the euphotic zone; mM/kg), whereas $\text{FCL}_{\text{Glu-Phe}}$ exhibited a distinct pattern in relation to these two environmental variables. $\text{FCL}_{\text{Glu-Phe}}$ was shorter at negative values of hypoxic depth and increased with positive values. In contrast, we observed that $\text{FCL}_{\text{Glu-Phe}}$ was shorter at the highest nitrate and increased with lower nitrate concentrations (Fig. 5).

DISCUSSION

The lack of temporal trends in bulk nitrogen stable isotope values of common dolphins (Fig. 2) agrees with the lack of temporal trends that

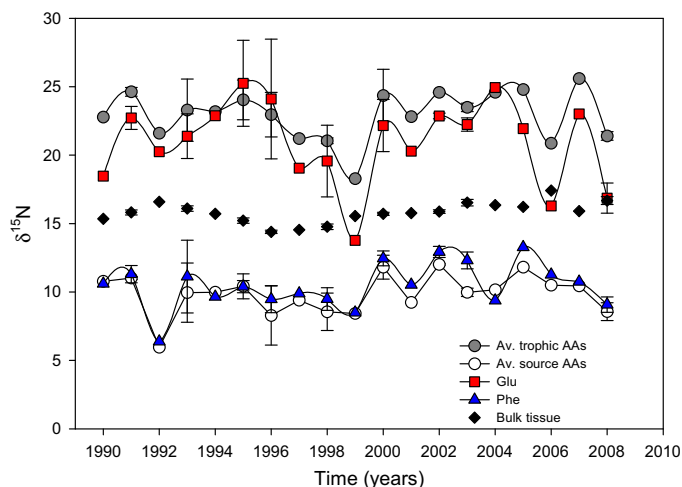


Fig. 2. Time series of nitrogen-stable isotope records. Interannual variation (mean ± 1 SE) in $\delta^{15}\text{N}$ (‰) of *D. delphis* skin tissue for bulk tissue ($n = 204$) and individual amino acids ($n = 28$): bulk tissue, Glu, Phe, average trophic amino acids (Av. trophic AAs), and average source amino acids (Av. source AAs) in the SCB.

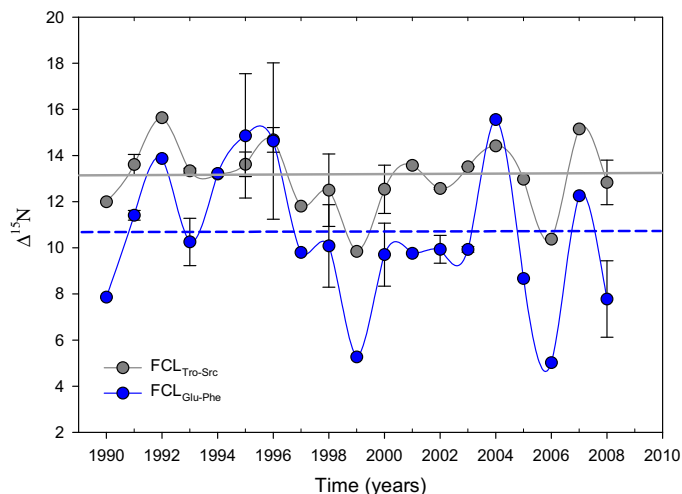


Fig. 3. Interannual variation (mean ± 1 SE) in $\delta^{15}\text{N}$ (‰) FCL proxies: $\Delta^{15}\text{N}_{\text{Glu-Phe}}$ and $\Delta^{15}\text{N}_{\text{Tro-Src}}$. Solid lines connect annual mean values. Horizontal lines represent the mean values for each FCL proxy as follows: $\Delta^{15}\text{N}_{\text{Glu-Phe}}$ (dashed blue line) and $\Delta^{15}\text{N}_{\text{Tro-Src}}$ (solid gray line).

has been observed in zooplankton $\delta^{15}\text{N}_{\text{bulk}}$ values from 1950 to 2002, which was interpreted as evidence for long-term stability and ecosystem resilience in nitrogen cycling and food web structure off southern California (31, 32). In contrast to the bulk $\delta^{15}\text{N}$ record, we observed a high interannual variability in $\delta^{15}\text{N}$ values for Glu, Phe, and average trophic and source amino acids (Fig. 2). Low values of Glu and trophic amino acids occurred during the major ENSO event of 1997–1998 and again in 2006. This large variability in trophic amino acid has not been detected before in any ecosystem. Previous studies using amino acid-specific isotope ratios observed continuously decreasing $\delta^{15}\text{N}$ values for source amino acids and not for trophic amino acids, indicating declining primary producer values, in the western North Atlantic (33), the subtropical North Pacific (24), and the offshore CC (25), possibly driven by recent changes in elemental cycling associated with climate change. In California, Phe $\delta^{15}\text{N}$ values from three zooplankton species were higher in the 1997–1998 El Niño

than the 1999 La Niña, indicating differing nitrogen assimilation rates by primary producers (34). We found relatively similar Phe patterns with *D. delphis* (Fig. 2), confirming that this predator captures variability associated with low trophic level consumers at the base of the SCB food web. Our two FCL proxies exhibited strong declines after the 1997–1998 El Niño event and after 2004, coincident with the shoaling of the hypoxic depth (Figs. 3 and 4). These results are not consistent with the long-term stability in the food web structure in the SCB proposed by previous studies (31, 32). Instead, the observed high temporal variability in FCL ($\Delta^{15}\text{N}_{\text{Glu-Phe}}$ and $\Delta^{15}\text{N}_{\text{Tro-Src}}$) suggested that pelagic communities, and therefore the food web structure, may exhibit major changes in response to environmental variability.

Marine food webs tend to be generally structured according to body size because prey are generally smaller than their predators (35) and the predator-prey mass ratio is relatively constant across marine ecosystems (36). Because *D. delphis* preys on a wide range of smaller-sized epipelagic and mesopelagic taxa, mainly fish and squids from the deep scattering layer, but limited by dolphin beak size and shape (37), we suggest that three main factors could contribute to variation in FCL isotope proxies in *D. delphis*: (i) shifts in diet between optimal and suboptimal preys because they are likely associated with changes in protein quantity, quality, trophic position, and links; (ii) significant changes in community assemblages of the deep scattering layer by the addition or removal of important trophic components and links in the food web; and (iii) strong shifts in nitrogen cycling that affect the abundance, distribution, and species composition of phytoplankton and planktivorous consumers. Knowing which oceanographic variables drive major changes in epipelagic and mesopelagic communities is the key to understanding variability in FCL in the SCB. Studies of mesopelagic fish recognized that SST and midwater oxygen concentrations strongly influence fish assemblages and diversity in the SCB (38, 39). Furthermore, SCB pelagic communities are highly influenced by the California Undercurrent, which brings warm waters from the south to nearshore pelagic communities, and by cold waters advected south by the CC that primarily influence offshore communities (39, 40). Because community stability and trophic structure are highly related (41), fluctuations in the strength and properties of these two currents would have a major impact on the stability of the pelagic community composition and organization of species into different trophic levels.

FCL_{Glu-Phe} was shorter at negative hypoxic depth values and increased with positive values (Fig. 5). Negative hypoxic depth anomalies mean that the hypoxic depth has shoaled (38, 42) and likely compressed the vertical habitat for species intolerant of low oxygen concentrations (42–44). Temporarily, this could benefit *D. delphis* and other predators because many prey items would be closer to the surface. For prey populations, mortality rates due to predation would increase for prey closer to the surface and also for nonmobile prey species intolerant of low oxygen concentration. Higher mortality rates may lead to reduction or even extirpation of some local prey populations, and this may explain the observed low FCL during negative hypoxic depth values within our period of study. Global change models have predicted that dissolved oxygen concentrations will decline by approximately 20 to 40% in mesopelagic ecosystems over the coming century (45). If the rate of decline in dissolved oxygen concentration continues and is as high as predicted, it would be difficult for other species to occupy empty niches, and therefore, a shorter FCL would be expected as a result of local extinctions with low replacement.

An asymmetrical unimodal relationship and a linear decline were observed for the FCL proxies in association with surface temperature

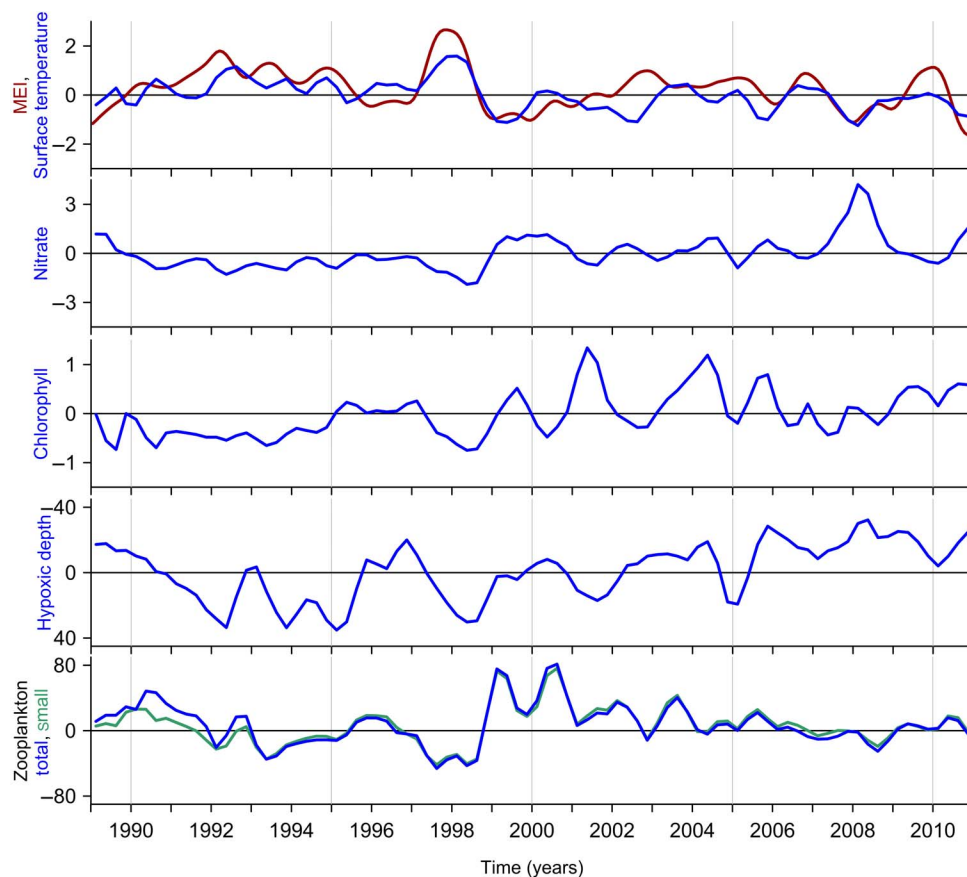


Fig. 4. Time series of environmental variables. The MEI (www.cdc.noaa.gov/people/klaus.wolter/MEI/mei.html) and five in situ oceanographic data anomalies (www.calcofi.org/data): surface temperature (°C), nitrate (mean nitrate concentration in the euphotic zone; mM/kg), chlorophyll (mean chlorophyll concentration in the euphotic zone; mg/m³), hypoxic depth (m; axis reversed), and zooplankton (total and small plankton volume; cm³/1000 m³). Series are LOWESS (locally weighted scatterplot smoothing) smoothed with a 1-year window (13 months for MEI, five quarters for the in situ CalCOFI variables).

and nitrate, respectively (Fig. 5). Shorter FCL was observed at the highest nitrate and coldest surface temperatures, whereas the longest FCL occurred at the lowest nitrate concentrations but intermediate surface temperature for FCL_{Glu-Phe} (Fig. 5). These results may be associated with differences in phytoplankton size and species composition. Longer food webs are common in oceanic oligotrophic waters because phytoplankton size is small and protozoans play an important role as intermediary links between phytoplankton and zooplankton (46). On the other hand, shorter food webs occur in cold coastal upwelling areas because of the dominance of large diatoms that are a direct food source for zooplankton and fish (46). Shorter food webs may occur in waters of the SCB where cold surface temperature and high-nutrient conditions, advected from upwelling centers to the north, favor diatoms. The size structure of plankton assemblages has been associated with the rate of wind-forced upwelling in the CC; therefore, climate change effects on upwelling are expected to affect community structure (47). Furthermore, availability of optimal prey species for *D. delphis* may be higher under cold productive environmental conditions leading to higher dietary specialization and stronger trophic interactions. In contrast, diversification in primary producers, zooplankton, and perhaps mid trophic level consumers—lengthening food webs at low trophic levels—possibly occurs during warm periods with weak upwelling.

The SCB was influenced by two El Niños (1991–1992 and 1997–1998) and two La Niñas (1998–2001 and 2007–2008) during the pe-

riod of study (Fig. 4). The first sharp continuous declines in FCLs ($\Delta^{15}\text{N}_{\text{Tro-Src}}$ and $\Delta^{15}\text{N}_{\text{Glu-Phe}}$) occurred from 1996 to 1999, with a moderate recovery from 1999 to 2000, coincident with a strong La Niña event (Fig. 3). The 1997–1998 El Niño, which dissipated in mid-1998 by the quick development of La Niña in the tropics and strong coastal upwelling and high primary production in the CC, was one of the strongest of the 20th century (48, 49). Our results indicate a short FCL during both El Niño (positive MEI values) and La Niña (negative MEI values) and a longer FCL under intermediate MEI conditions (Fig. 5). According to the ecological disturbance hypothesis for terrestrial and aquatic systems, the food web length and complexity of trophic interactions should decline during events of extreme and/or frequent disturbances due to the removal of species not resistant to perturbation (50). Hence, the effect of ENSO events, and transitions between these events, can pose significant stress to entire communities (51). During the 1997–1998 El Niño, for instance, the California coastal waters were highly influenced by the enhancement of the poleward countercurrent/undercurrent that transported warmer and more saline waters than normal and deepened the thermocline (51). These environmental changes had severe effects on coastal populations at all trophic levels: Primary production and macrozooplankton biomass were reduced significantly; the distribution range of some mesopelagic species, such as the jumbo squid (*Dosidicus gigas*), increased, whereas the abundance of some fish and seabird populations decreased; and,

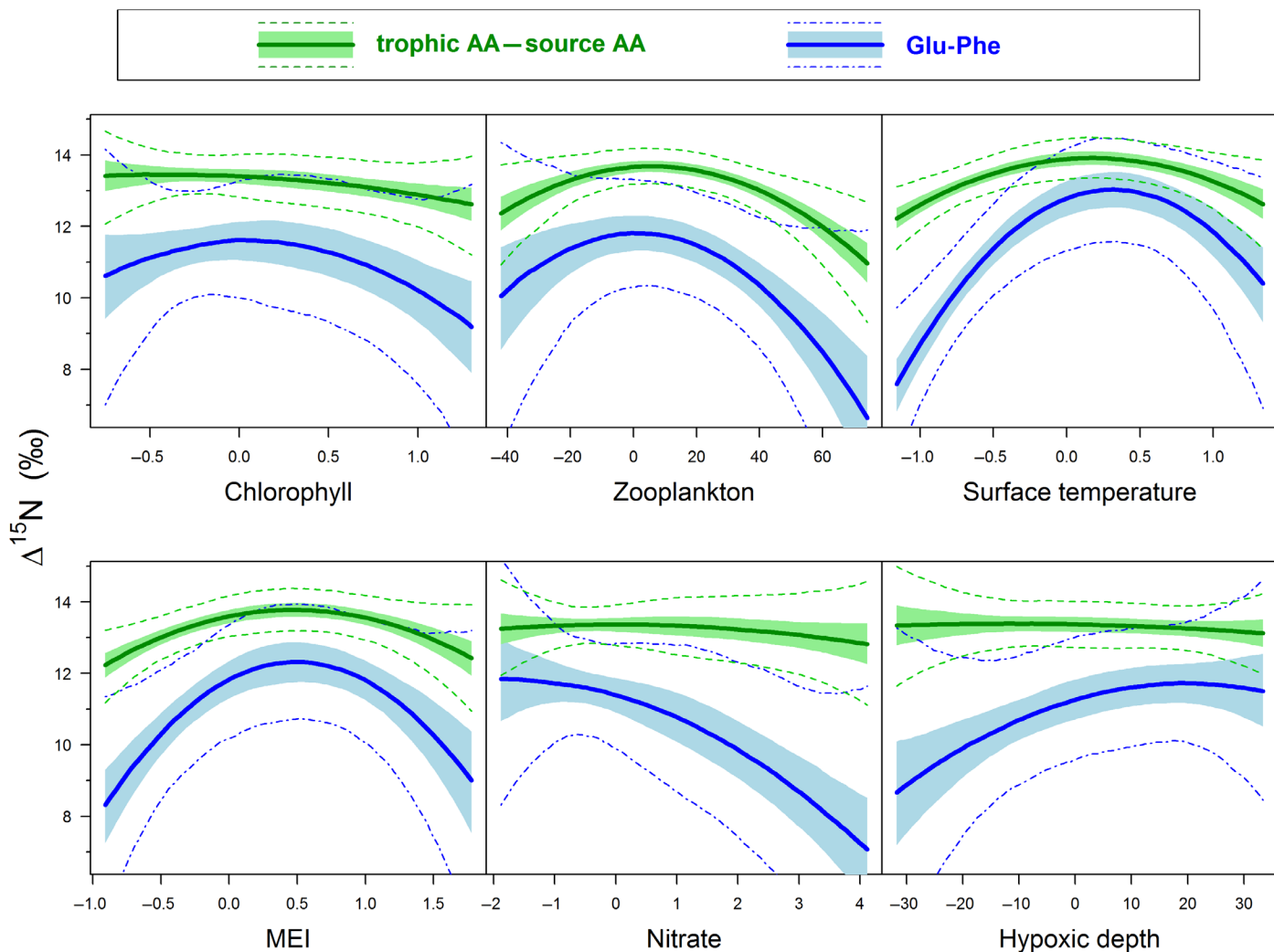


Fig. 5. FCL, measured as trophic amino acids–source amino acids ($\Delta^{15}\text{N}_{\text{Tro-Src}}$) or Glu-Phe ($\Delta^{15}\text{N}_{\text{Glu-Phe}}$), as a function of six oceanographic variables. The solid lines are the medians of the posteriors from the hierarchical Bayesian model. The shaded areas include the central 50%, and the broken lines include the central 95% of the posterior density.

overall, the feeding and reproductive success for many species were affected (48, 51–54). These changes in life history traits and population dynamics likely reduced and/or removed populations of many species, including important components of the food web (51, 52, 54), possibly favoring a shorter FCL.

Short FCL was also associated with La Niña (Fig. 5). The additive effect of a combination of factors may explain this pattern: (i) Abrupt changes from El Niño to La Niña conditions likely disrupted trophic links by removing species intolerant to sharp changes between warm and cold conditions; (ii) dominance of large diatoms in cold, nutrient-rich upwelling areas can promote a shorter FCL (46); and (iii) mesopelagic ichthyoplankton diversity was reduced during La Niña conditions due to greater offshore transport in the SCB (39). The loss of some trophic links during El Niño years could have been compensated by the appearance and increase in abundance of rare species, such as the jumbo squid, *D. gigas*, and others, because El Niño conditions typically bring warmer water species to southern Californian waters (55). This may explain why FCL is slightly higher during El Niño compared with La Niña (Fig. 5).

Our indicator of primary production, chlorophyll, was associated with lower $\delta^{15}\text{N}$ values at the lowest and highest levels (Fig. 5), but

patterns were weak. Overall, primary production is the central constraint of diversity (56), yet the importance of primary productivity in explaining variability in FCL has been debated for decades (18). Energetic efficiency predictions suggest that FCL should increase with an increasing amount of energy or limiting resources available to consumers (57). However, our results disagree with this prediction; we found a longer FCL at moderate levels of primary production and not at the highest levels. Some studies have concluded that systems with high resource availability and frequent disturbances can facilitate increased abundance in species that truncate FCL due to their limited vulnerability to predation (58). As previously noted, primary production, species richness, and assemblages of pelagic communities in the SCB strongly fluctuate in association with ENSO and the interplay between the California Undercurrent and the CC (39, 40). For instance, the 1998 La Niña had the highest values of primary production, but fish species evenness was low, while fish species richness was higher during the 1997–1998 El Niño because of the presence of rare species transported by the California Undercurrent (39).

Primary production is positively correlated with zooplankton volumes (fig. S3). Total plankton volume represents plankton without any sampled nekton (adult and juvenile fish, squid, octopi, and adult pelagic crabs), whereas small plankton volume excludes large plankton (>5 ml),

such as jellyfish and tunicates. We estimated a longer FCL (indicated by both isotope proxies) at average levels of zooplankton, and a shorter FCL at both extremes (Fig. 5). In the SCB, the biomass and species composition of zooplankton overall, particularly pelagic tunicates, were highly variable from 1951 to 1999, coincident with a decline in zooplankton biomass and ocean warming; the opposite pattern occurred after 1999 (59), coincident with higher primary production and colder temperatures (Fig. 4). Our time series indicated that total and small zooplankton are nearly equal between 1990 and 2008, except from 1990 to 1993 (Fig. 4), when tunicates and jellyfish were proportionately more abundant. Considering the observed trends, we propose two different mechanisms at extreme levels of primary production and zooplankton to explain variation in FCL. When primary production and zooplankton are high, densities of higher trophic level predators could be high as well, and higher consumption rates by these predators could ultimately suppress the abundance of prey species or extirpate some prey populations, resulting in a shorter FCL. In contrast, when primary production and zooplankton are low, densities of optimal prey and many other species are likely low, which may increase trophic omnivory and reduce FCL (60). Furthermore, high population size of fast-growing species, such as jellyfish and tunicates, can effectively truncate trophic interactions and FCL because these organisms can reach large biomass at low food concentrations, but many jellyfish and tunicate species avoid predation because of their low nutrient value (59, 61).

Decades of research indicate that habitat stability, resource availability, community organization, and ecosystem size [through species diversity and habitat heterogeneity (60)] are highly related and play a key role in determining FCL (18). In pelagic marine ecosystems, only a few studies have been able to quantify FCL through time and investigate the effect of environmental variability on FCL. Our study shows that *D. delphis* can serve as an important ecosystem indicator for tracking variability in baseline values, trophic status, and FCL using stable isotope analysis of individual amino acids. This study analyzes the first time series of amino acid isotope values from a top predator of the SCB to provide insights into changes in FCL; the results provide strong evidence that pelagic food webs rapidly change in response to environmental conditions. Specifically, the observed temporal variability in $\Delta^{15}\text{N}_{\text{Tro-Src}}$ and $\Delta^{15}\text{N}_{\text{Glu-Phe}}$ and a hierarchical model revealed how food web length markedly shifted in response to interannual variation in local oceanography and basin-scale processes, such as ENSO. We suggest potential mechanisms for explaining some of the patterns in FCL proxies in relation to environmental factors influencing the time series from 1990 to 2008 and for the value of *D. delphis* as an ecosystem indicator for epipelagic and mesopelagic food webs in the SCB. SCB pelagic FCL seems to recover from episodic environmental stresses, such as the 1997–1999 ENSO event. However, it is unknown what FCL $\delta^{15}\text{N}$ values would indicate a state of equilibrium for the SCB in the absence of environmental and anthropogenic perturbations. Looking into the future, trends of declining dissolved oxygen concentrations and stronger ENSO events are more evident in recent years, and global change models predict that these trends will continue to intensify. This is a major concern because rapid continuous changes in elemental cycling, reduction in dissolved oxygen concentrations, primary production, and fish densities would have a profound effect on the fitness and survival of many animal populations, including important fisheries resources and endangered species, and on species diversity in general. Integrating the approach presented in this study for future monitoring efforts will help to understand variability in FCL in response to climate change.

MATERIALS AND METHODS

A total of 204 skin samples were obtained from dolphins incidentally killed in drift and small-mesh gillnet fisheries operating in the SCB from 1991 to 2008 (Fig. 1). We used $\delta^{15}\text{N}$ values of amino acids that track the base of the food web [source amino acids: Phe (phenylalanine), Met (methionine), Lys (lysine), and Tyr (tyrosine)] and animal trophic status [trophic amino acids: Asp (aspartic acid), Ile (isoleucine), Ala (alanine), Glu (glutamic acid), Leu (leucine), Pro (proline), and Val (valine)] (fig. S1) (30, 62). Furthermore, we calculated the isotopic difference between Glu and Phe ($\Delta^{15}\text{N}_{\text{Glu-Phe}}$) and between the average trophic and source amino acids ($\Delta^{15}\text{N}_{\text{Tro-Src}}$) to examine the variability in FCL of SCB *D. delphis*. Using both isotope measurements to track FCL is a conservative approach to detecting patterns because any source and trophic amino acid reflect variability at the base of the food web and animal trophic status, respectively. Glu and Phe are considered the canonical trophic and source amino acids, respectively, because Glu is abundant in animal tissues, central for nitrogen cycling, and undergoes substantial isotopic fractionation with trophic step, whereas Phe is the most stable source amino acid with the lowest trophic enrichment value among taxa from all trophic levels (30).

We used hierarchical Bayesian models to understand patterns of temporal variation in FCL in relation to changes in the environment. We used the MEI as a climatic index for ENSO (www.cdc.noaa.gov/people/klaus.wolter/MEI/mei.html) and five oceanographic variables collected in situ from the CalCOFI program from 1990 to 2008. CalCOFI has regularly conducted surveys to study physical, chemical, and biological oceanography since 1951 (<http://calcofi.org>). FCL, either as $\text{FCL}_{\text{Glu-Phe}}$ or $\text{FCL}_{\text{Tro-Src}}$ was estimated and modeled as a function of the MEI and regional quarterly anomalies of five environmental variables: surface temperature ($^{\circ}\text{C}$), nitrate ($\mu\text{M/liter}$), chlorophyll (mg/m^3), zooplankton ($\text{cm}^3/1000 \text{ m}^3$), and hypoxic depth (m) (Fig. 4). Surface temperature is a basic physiologic parameter for many organisms, but anomalies also reflect changes in mixing and advection of surface waters. Nitrate represents nutrient availability in the euphotic zone and is an important determinant of primary productivity in these nutrient-limited waters. Chlorophyll is a measure of phytoplankton biomass or primary production in the euphotic zone, the near-surface waters where photosynthesis exceeds respiration. Zooplankton volume is an approximate index of biomass at intermediate levels of the food web (59). Hypoxic depth is a measure of the vertical extent of the regional oxygen minimum zone, which affects the distribution and composition of mesopelagic communities (38). FCL was modeled as a quadratic function of each environmental variable 6 months before the time of dolphin tissue sample collection because there is a lag (unknown) for top predators to integrate changes in both baseline isotope values and community composition across the food web. The quarterly oceanographic series or monthly MEI series values were spline-interpolated to daily values, and then, for each dolphin skin sample, daily values were averaged for the 70 days preceding the day 6 months before the sample date. The 70-day average accounts for an additional 35 days lead time, based on the half-time of skin migration cells from the basal lamina to the outermost surface on delphinids (35 days) (63) and the half-life turnover rate for $\delta^{15}\text{N}$ values in skin tissues from captive dolphins (64).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/3/10/e1701140/DC1>

fig. S1. Biplot for the principal component analysis of short-beaked common dolphin (*D. delphis*) $\delta^{15}\text{N}$ values.

fig. S2. The $\delta^{15}\text{N}$ values of individual amino acids in skin samples of *D. delphis*: trophic amino acids are those amino acids strongly enriched in ^{15}N (blue), and source amino acids refer to those amino acids with low isotopic fractionation (green).

fig. S3. Correlation matrix among oceanographic variables.

table S1. Summary of WAIC (widely applicable information criterion) scores for food web length at a 6-month lag using hierarchical Bayesian models.

table S2. Mean $\delta^{15}\text{N}$ values of bulk skin tissue samples and individual amino acids (for abbreviations, see description in amino acid stable isotope analysis) from *D. delphis* collected in the SCB.

References (65–76)

REFERENCES AND NOTES

- P. M. Vitousek, H. A. Mooney, J. Lubchenco, J. M. Melillo, Human domination of Earth's ecosystems. *Science* **277**, 494–499 (1997).
- P. G. Falkowski, T. Fenchel, E. F. Delong, The microbial engines that drive Earth's biogeochemical cycles. *Science* **320**, 1034–1039 (2008).
- N. Gruber, J. N. Galloway, An Earth-system perspective of the global nitrogen cycle. *Nature* **451**, 293–296 (2008).
- G.-R. Walther, E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, F. Bairlein, Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002).
- L. Oksanen, S. D. Fretwell, J. Arruda, P. Niemela, Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* **118**, 240–261 (1981).
- D. M. Karl, R. R. Bidigare, R. M. Letelier, Long-term changes in plankton community structure and productivity in the North Pacific Subtropical Gyre: The domain shift hypothesis. *Deep Sea Res. Part II* **48**, 1449–1470 (2001).
- D. M. Schell, Declining carrying capacity in the Bering Sea: Isotopic evidence from whale baleen. *Limnol. Oceanogr.* **45**, 459–462 (2000).
- A. Timmermann, J. Oberhuber, A. Bacher, M. Esch, M. Latif, E. Roeckner, Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* **398**, 694–697 (1999).
- W. Cai, S. Borlace, M. Lengaigne, P. van Rensch, M. Collins, G. Vecchi, A. Timmermann, A. Santoso, M. J. McPhaden, L. Wu, M. H. England, G. Wang, E. Guilyardi, F.-F. Jin, Increasing frequency of extreme El Niño events due to greenhouse warming. *Nat. Clim. Change* **4**, 111–116 (2014).
- P. C. Fiedler, Environmental change in the eastern tropical Pacific Ocean: Review of ENSO and decadal variability. *Mar. Ecol. Prog. Ser.* **244**, 265–283 (2002).
- E. P. Odum, G. W. Barrett, *Fundamentals of Ecology* (JSTOR, 1971), vol. 3.
- J. E. Byrnes, P. L. Reynolds, J. J. Stachowicz, Invasions and extinctions reshape coastal marine food webs. *PLOS ONE* **2**, e295 (2007).
- D. Pauly, V. Christensen, J. Dalsgaard, R. Froese, F. Torres Jr., Fishing down marine food webs. *Science* **279**, 860–863 (1998).
- J. B. Jackson, M. X. Kirby, W. H. Berger, K. A. Bjørndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlanson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, R. R. Warner, Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–637 (2001).
- J. E. Duffy, Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.* **6**, 680–687 (2003).
- R. T. Paine, Road maps of interactions or grist for theoretical development? *Ecology* **69**, 1648–1654 (1988).
- D. M. Post, Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* **83**, 703–718 (2002).
- D. M. Post, The long and short of food-chain length. *Trends Ecol. Evol.* **17**, 269–277 (2002).
- N. J. P. Owens, Natural variations in ^{15}N in the marine environment. *Adv. Mar. Biol.* **24**, 389–451 (1988).
- C. J. Somes, A. Schmittner, E. D. Galbraith, M. F. Lehmann, M. A. Altabet, J. P. Montoya, R. M. Letelier, A. C. Mix, A. Bourbonnais, M. Eby, Simulating the global distribution of nitrogen isotopes in the ocean. *Global Biogeochem. Cycles* **24**, GB4019 (2010).
- R. I. Ruiz-Cooley, T. Gerrodette, Tracking large-scale latitudinal patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ along the E Pacific using epi-mesopelagic squid as indicators. *Ecosphere* **3**, 1–17 (2012).
- J. W. McClelland, J. P. Montoya, Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. *Ecology* **83**, 2173–2180 (2002).
- R. I. Ruiz-Cooley, L. T. Ballance, M. D. McCarthy, Range expansion of the jumbo squid in the NE Pacific: $\delta^{15}\text{N}$ decrypts multiple origins, migration and habitat use. *PLOS ONE* **8**, e59651 (2013).
- O. A. Sherwood, T. P. Guilderson, F. C. Batista, J. T. Schiff, M. D. McCarthy, Increasing subtropical North Pacific Ocean nitrogen fixation since the Little Ice Age. *Nature* **505**, 78–81 (2014).
- R. I. Ruiz-Cooley, P. L. Koch, P. C. Fiedler, M. D. McCarthy, Carbon and nitrogen isotopes from top predator amino acids reveal rapidly shifting ocean biochemistry in the outer California Current. *PLOS ONE* **9**, e110355 (2014).
- D. Pauly, A. W. Trites, E. Capuli, V. Christensen, Diet composition and trophic levels of marine mammals. *ICES J. Mar. Sci.* **55**, 467–481 (1998).
- W. E. Evans, PhD. Dissertation, University of California at Los Angeles, Los Angeles (1975).
- K. A. Forney, Preliminary estimates of cetacean abundance along the US west coast and within four National Marine Sanctuaries during 2005, (NOAA Technical Memorandum NOAA-NMFS-SWFSC-TM-406, 2007).
- P. Yodzis, Energy flow and the vertical structure of real ecosystems. *Oecologia* **65**, 86–88 (1984).
- K. W. McMahon, M. D. McCarthy, Embracing variability in amino acid $\delta^{15}\text{N}$ fractionation: Mechanisms, implications, and applications for trophic ecology. *Ecosphere* **7**, e01511 (2016).
- G. H. Rau, M. D. Ohman, A. Pierrot-Bults, Linking nitrogen dynamics to climate variability off central California: A 51 year record based on $^{15}\text{N}/^{14}\text{N}$ in CalCOFI zooplankton. *Deep Sea Res. Part II* **50**, 2431–2447 (2003).
- M. D. Ohman, G. H. Rau, P. M. Hull, Multi-decadal variations in stable N isotopes of California Current zooplankton. *Deep Sea Res. Part I* **60**, 46–55 (2012).
- O. A. Sherwood, M. F. Lehmann, C. J. Schubert, D. B. Scott, M. D. McCarthy, Nutrient regime shift in the western North Atlantic indicated by compound-specific $\delta^{15}\text{N}$ of deep-sea gorgonian corals. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 1011–1015 (2011).
- M. Décima, M. R. Landry, B. N. Popp, Environmental perturbation effects on baseline $\delta^{15}\text{N}$ values and zooplankton trophic flexibility in the southern California Current Ecosystem. *Limnol. Oceanogr.* **58**, 624–634 (2013).
- R. W. Sheldon, A. Prakash, W. H. Sutcliffe Jr., The size distribution of particles in the ocean. *Limnol. Oceanogr.* **17**, 327–340 (1972).
- C. Barnes, D. Maxwell, D. C. Reuman, S. Jennings, Global patterns in predator-prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology* **91**, 222–232 (2010).
- L. Osnes-Erie, “Food habits of common dolphin (*Delphinus delphis* and *D. capensis*) and off California,” thesis, San Jose State University (1999).
- J. A. Koslow, R. Goericke, W. Watson, Fish assemblages in the southern California Current: Relationships with climate, 1951–2008. *Fish. Oceanogr.* **22**, 207–219 (2013).
- S. McClatchie, A. R. Thompson, S. R. Alin, S. Siedlecki, W. Watson, S. J. Bograd, The influence of Pacific Equatorial Water on fish diversity in the southern California Current System. *J. Geophys. Res. Oceans* **121**, 6121–6136 (2016).
- D. M. Checkley Jr., J. A. Barth, Patterns and processes in the California Current System. *Prog. Oceanogr.* **83**, 49–64 (2009).
- R. MacArthur, Fluctuations of animal populations and a measure of community stability. *Ecology* **36**, 533–536 (1955).
- J. A. Koslow, R. Goericke, A. Lara-Lopez, W. Watson, Impact of declining intermediate-water oxygen on deepwater fishes in the California Current. *Mar. Ecol. Prog. Ser.* **436**, 207–218 (2011).
- S. J. Bograd, C. G. Castro, E. Di Lorenzo, D. M. Palacios, H. Bailey, W. Gilly, F. P. Chavez, Oxygen declines and the shoaling of the hypoxic boundary in the California Current. *Geophys. Res. Lett.* **35**, L12607 (2008).
- S. McClatchie, R. Goericke, R. Cosgrove, G. Auad, R. Vetter, Oxygen in the Southern California Bight: Multidecadal trends and implications for demersal fisheries. *Geophys. Res. Lett.* **37**, L19602 (2010).
- G. Shaffer, S. M. Olsen, J. O. P. Pedersen, Long-term ocean oxygen depletion in response to carbon dioxide emissions from fossil fuels. *Nat. Geosci.* **2**, 105–109 (2009).
- M. P. Seki, J. J. Polovina, Ocean gyre ecosystems. *The Encyclopedia of Ocean Sciences* **4**, 1959–1964 (2001).
- R. R. Rykaczewski, D. M. Checkley, Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 1965–1970 (2008).
- S. J. Bograd, R. J. Lynn, Long-term variability in the southern California Current System. *Deep Sea Res. Part II* **50**, 2355–2370 (2003).
- F. B. Schwing, C. S. Moore, S. Ralston, K. M. Sakuma, Record coastal upwelling in the California Current in 1999. *Cal. Coop. Ocean. Fish. Invest. Rep.* **41**, 148–160 (2000).
- B. A. Menge, J. P. Sutherland, Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* **130**, 730–757 (1987).
- R. J. Lynn, C. A. Collins, A. W. Mantyla, F. B. Schwing, T. Baumgartner, T. L. Hayward, T. Murphree, K. M. Sakuma, J. Garcia, K. D. Hyrenbach, A. Shankle, M. J. Tegner, The state of the California Current, 1997–1998: Transition to El Niño conditions. *Cal. Coop. Ocean. Fish. Invest. Rep.* **39**, 25–49 (1998).
- T. L. Hayward, El Niño 1997–98 in the coastal waters of southern California: A timeline of events. *Cal. Coop. Ocean. Fish. Invest. Rep.* **41**, 98–116 (2000).
- S. J. Bograd, R. J. Lynn, Physical-biological coupling in the California Current during the 1997–99 El Niño-La Niña cycle. *Geophys. Res. Lett.* **28**, 275–278 (2001).
- F. C. Chavez, J. T. Pennington, C. G. Castro, J. P. Ryan, R. P. Michisaki, B. Schlining, P. Walz, K. R. Buck, A. McFadyen, C. A. Collins, Biological and chemical consequences of the 1997–1998 El Niño in central California waters. *Prog. Oceanogr.* **54**, 205–232 (2002).
- H. Song, A. J. Miller, S. McClatchie, E. D. Weber, K. M. Nieto, D. M. Checkley Jr., Application of a data-assimilation model to variability of Pacific sardine spawning and survivor habitats with ENSO in the California Current System. *J. Geophys. Res.* **117**, C03009 (2012).

56. G. E. Hutchinson, Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159 (1959).
57. D. Pauly, V. Christensen, Primary production required to sustain global fisheries. *Nature* **374**, 255–257 (1994).
58. M. A. Leibold, Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.* **134**, 922–949 (1989).
59. B. E. Lavaniegos, M. D. Ohman, Long-term changes in pelagic tunicates of the California Current. *Deep Sea Res. Part II* **50**, 2473–2498 (2003).
60. D. M. Post, M. L. Pace, N. G. Hairston Jr., Ecosystem size determines food-chain length in lakes. *Nature* **405**, 1047–1049 (2000).
61. J. L. Acuña, Pelagic tunicates: Why gelatinous? *Am. Nat.* **158**, 100–107 (2001).
62. Y. Chikaraishi, N. O. Ogawa, Y. Kashiyama, Y. Takano, H. Suga, A. Tomitani, H. Miyashita, H. Kitazato, N. Ohkouchi, Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnol. Oceanogr.* **7**, 740–750 (2009).
63. B. D. Hicks, D. J. St. Aubin, J. R. Geraci, W. R. Brown, Epidermal growth in the bottlenose dolphin, *Tursiops truncatus*. *J. Invest. Dermatol.* **85**, 60–63 (1985).
64. N. E. Browning, C. Dold, I.-F. Jack, G. A. Worthy, Isotope turnover rates and diet–tissue discrimination in skin of ex situ bottlenose dolphins (*Tursiops truncatus*). *J. Exp. Biol.* **217**, 214–221 (2014).
65. A. K. Styring, A. Kuhl, T. D. J. Knowles, R. A. Fraser, A. Bogaard, R. P. Evershed, Practical considerations in the determination of compound-specific amino acid $\delta^{15}\text{N}$ values in animal and plant tissues by gas chromatography-combustion-isotope ratio mass spectrometry, following derivatisation to their *N*-acetylisopropyl esters. *Rapid Commun. Mass Spectrom.* **26**, 2328–2334 (2012).
66. R. G. Walsh, S. He, C. T. Yarnes, Compound-specific $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of amino acids: A rapid, chloroformate-based method for ecological studies. *Rapid Commun. Mass Spectrom.* **28**, 96–108 (2014).
67. S. O. Hoskin, S. Gavet, E. Milne, G. E. Loble, Does glutamine act as a substrate for transamination reactions in the liver of fed and fasted sheep? *Br. J. Nutr.* **85**, 591–597 (2001).
68. M. L. Calleja, F. Batista, M. Peacock, R. Kudela, M. D. McCarthy, Changes in compound specific $\delta^{15}\text{N}$ amino acid signatures and D/L ratios in marine dissolved organic matter induced by heterotrophic bacterial reworking. *Mar. Chem.* **32–44** (2013).
69. D. J. Lunn, A. Thomas, N. Best, D. Spiegelhalter, WinBUGS—A Bayesian modelling framework: Concepts, structure, and extensibility. *Stat. Comput.* **10**, 325–337 (2000).
70. A. Thomas, B. O'Hara, U. Ligges, S. Sturtz, Making BUGS open. *R News* **6**, 12–17 (2006).
71. A. Gelman, Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Anal.* **1**, 515–534 (2006).
72. M. Plummer, N. Best, K. Cowles, K. Vines, CODA: Convergence diagnosis and output analysis for MCMC. *R News* **16**, 7–11 (2006).
73. S. Watanabe, Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *J. Mach. Learn. Res.* **11**, 3571–3594 (2010).
74. A. Gelman, J. Hwang, A. Vehtari, Understanding predictive information criteria for Bayesian models. *Stat. Comput.* **24**, 997–1016 (2014).
75. A. Vehtari, A. Gelman, J. Gabry, Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**, 1413–1432 (2017).
76. A. Gelman, I. Pardoe, Bayesian measures of explained variance and pooling in multilevel (hierarchical) models. *Technometrics* **48**, 241–251 (2006).

Acknowledgments: The CalCOFI data were provided by the Scripps Institution of Oceanography. We thank the National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service's West Coast Regional Office in Long Beach, CA for implementing the fisheries observer program, and the fisheries observers who collected the samples used in this study. All the samples used in this paper came from fisheries bycaught animals; Institutional Animal Care and Use Committee is not applicable. We thank S. McClatchie [Southwest Fisheries Science Center (SWFSC)–NOAA] and our anonymous reviewers for providing constructive criticism to this manuscript. **Funding:** The funding for this research was provided by the SWFSC, NOAA Fisheries, and the National Research Council, National Academies. **Author contributions:** Participated in the design and/or interpretation of the reported experiments or results: R.I.R.C., T.G., and P.C.F. Participated in the acquisition and analysis of data: R.I.R.C., T.G., P.C.F., S.C., and K.D. Primarily responsible for a particular, specialized role in the research: R.I.R.C., T.G., P.C.F., S.C., and K.D. Participated in drafting and/or revising the manuscript: R.I.R.C., T.G., P.C.F., and L.T.B. Provided administrative, technical, and supervisory support: L.T.B. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors. All samples and data are archived at the SWFSC. Mean $\delta^{15}\text{N}$ values of bulk skin tissue samples and individual amino acids are available in table S2.

Submitted 3 April 2017
 Accepted 20 September 2017
 Published 18 October 2017
 10.1126/sciadv.1701140

Citation: R. I. Ruiz-Coolley, T. Gerrodette, P. C. Fiedler, S. J. Chivers, K. Danil, L. T. Ballance, Temporal variation in pelagic food chain length in response to environmental change. *Sci. Adv.* **3**, e1701140 (2017).

Temporal variation in pelagic food chain length in response to environmental change

Rocio I. Ruiz-Coleley, Tim Gerrodette, Paul C. Fiedler, Susan J. Chivers, Kerri Danil and Lisa T. Ballance

Sci Adv **3** (10), e1701140.
DOI: 10.1126/sciadv.1701140

ARTICLE TOOLS

<http://advances.sciencemag.org/content/3/10/e1701140>

SUPPLEMENTARY MATERIALS

<http://advances.sciencemag.org/content/suppl/2017/10/16/3.10.e1701140.DC1>

REFERENCES

This article cites 71 articles, 7 of which you can access for free
<http://advances.sciencemag.org/content/3/10/e1701140#BIBL>

PERMISSIONS

<http://www.sciencemag.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of Service](#)

Science Advances (ISSN 2375-2548) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. The title *Science Advances* is a registered trademark of AAAS.

Copyright © 2017 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works. Distributed under a Creative Commons Attribution NonCommercial License 4.0 (CC BY-NC).