Global Change Biology

Global Change Biology (2014), doi: 10.1111/gcb.12502

Combined climate- and prey-mediated range expansion of Humboldt squid (*Dosidicus gigas*), a large marine predator in the California Current System

JULIA S. STEWART[1,2], ELLIOTT L. HAZEN[3,4], STEVEN J. BOGRAD[3], JARRETT E. K. BYRNES[5], DAVID G. FOLEY[3,4†], WILLIAM F. GILLY[1], BRUCE H. ROBISON[6] and JOHN C. FIELD[7]

[1]*National Center for Ecological Analysis and Synthesis, University of California at Santa Barbara, 735 State Street Suite 300, Santa Barbara, CA 93101, USA,* [2]*Hopkins Marine Station of Stanford University, 120 Oceanview Blvd, Pacific Grove, CA 93950, USA,* [3]*Environmental Research Division, NMFS Southwest Fisheries Science Center, NOAA, 1352 Lighthouse Avenue, Pacific Grove, CA 93950, USA,* [4]*Cooperative Institute for Marine Ecosystems and Climate, University of California, 1156 High Street, Santa Cruz, CA 95064, USA,* [5]*Department of Biology, University of Massachusetts Boston, 100 Morrissey Blvd, Boston, MA 02125, USA,* [6]*Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA,* [7]*Fisheries Ecology Division, NMFS Southwest Fisheries Science Center, NOAA, 110 Shaffer Road, Santa Cruz, CA 95060, USA*

Abstract

Climate-driven range shifts are ongoing in pelagic marine environments, and ecosystems must respond to combined effects of altered species distributions and environmental drivers. Hypoxic oxygen minimum zones (OMZs) in midwater environments are shoaling globally; this can affect distributions of species both geographically and vertically along with predator–prey dynamics. Humboldt (jumbo) squid (*Dosidicus gigas*) are highly migratory predators adapted to hypoxic conditions that may be deleterious to their competitors and predators. Consequently, OMZ shoaling may preferentially facilitate foraging opportunities for Humboldt squid. With two separate modeling approaches using unique, long-term data based on *in situ* observations of predator, prey, and environmental variables, our analyses suggest that Humboldt squid are indirectly affected by OMZ shoaling through effects on a primary food source, myctophid fishes. Our results suggest that this indirect linkage between hypoxia and foraging is an important driver of the ongoing range expansion of Humboldt squid in the northeastern Pacific Ocean.

Keywords: deep scattering layer, hypoxia, jumbo squid, oxygen minimum zones, pelagic

Received 30 September 2013 and accepted 8 November 2013

Introduction

Climate-driven range shifts due to rising temperatures have been increasingly documented in pelagic marine ecosystems (e.g., Perry *et al.*, 2005; Burrows *et al.*, 2011; Pinsky *et al.*, 2013); however, other oceanographic properties such as dissolved oxygen may also act as important drivers of range shifts and expansions (Gilly *et al.*, 2013). Dissolved oxygen in the water column affects the vertical (e.g., Seibel, 2011; Bianchi *et al.*, 2013) and geographical (Helly & Levin, 2004) distributions of many marine species due to their oxygen requirements at the depths they inhabit. Dissolved oxygen in the upper ocean decreases with depth, and the rate and extent of this decrease varies greatly with location. In certain areas of high surface productivity, particularly the temperate Humboldt (also called Peru) and California Current Systems (CCS) in the eastern Pacific Ocean, dissolved oxygen in midwater environments (100–1200 m) falls to extremely low values ($<20\ \mu\text{mol kg}^{-1}$ or ca. $0.5\ \text{ml l}^{-1}$), and such a midwater feature is called an oxygen minimum zone (OMZ) (Helly & Levin, 2004). During the last 50 years, OMZs have been shoaling, expanding horizontally, and intensifying in all areas where they occur (Stramma *et al.*, 2008), largely in response to warming surface waters and increased stratification, which inhibits transfer of atmospheric oxygen to depth (Keeling *et al.*, 2010).

In the southern CCS, a decrease in midwater oxygen concentration over the last 30 years (Bograd *et al.*, 2008) has been associated with a concomitant reduction in abundance of mesopelagic fish larvae (Koslow *et al.*, 2011). Koslow *et al.* hypothesized that OMZ shoaling may displace some members of the mesopelagic community vertically to shallower depths where increased daytime illumination heightens their susceptibility to visual predators. Such an effect would become more

---

Correspondence: Present address: J. S. Stewart, National Center for Ecological Synthesis and Analysis, University of California, 735 State Street, Santa Barbara, CA 93101, USA, tel. (805) 882 9218, fax (805) 892 2510, e-mail: jstewart@nceas.ucsb.edu

†Deceased.

prominent moving northward as shoaling progressed over time, because the upper boundary of the OMZ is deeper with increasing latitude (see fig. 2 of Helly & Levin, 2004). Redistribution of pelagic predators to follow these environmental changes could thus underlie a northward range expansion with complex ecosystem-wide effects.

Shoaling of the OMZ throughout the CCS has been suggested to be a contributing factor to the range expansion by Humboldt or jumbo squid (*Dosidicus gigas*) in this region in the past 15 years (Stewart *et al.*, 2013). Humboldt squid have been intermittently documented in California in the twentieth century (Croker, 1937; Mearns, 1988; Field *et al.*, 2007), but their presence has never been observed for such an extended time in California. They have also never been observed as far north – they have been frequently encountered in British Columbia (Cosgrove, 2005; Braid *et al.*, 2011), where stranded squid have been documented as prey of terrestrial predators (Barnes, 2009), and in 2005 they were observed in southwestern Alaska (Wing, 2006). Since their arrival in Monterey Bay, California in 1997, Humboldt squid have been routinely observed in surveys by remotely operated vehicles (ROVs) in most years since 2002 (Zeidberg & Robison, 2007; Stewart, 2012). As highly migratory predators (Stewart *et al.*, 2012), Humboldt squid prey on a large number of ecologically and economically important coastal species throughout the northern CCS, including Pacific hake (*Merluccius productus*) and market squid (*Doryteuthis* [formerly *Loligo*] *opalescens*), but their primary prey is mesopelagic micronekton, primarily myctophid fishes (Field *et al.*, 2007, 2013).

Like many myctophids and much of the hypoxia-tolerant mesopelagic community, Humboldt squid tend to spend daytime at midwater depths, where they can form part of the acoustic deep scattering layer (DSL) (Rosas-Luis *et al.*, 2011) and undertake a diel vertical migration to near-surface depths at night (Gilly *et al.*, 2006). Daytime depths for Humboldt squid are typically quite hypoxic, and occupancy of the OMZ for many hours (Stewart *et al.*, 2013) is possible through a suite of adaptations that includes reduced rapid jetting (Gilly *et al.*, 2012), metabolic suppression (Gilly *et al.*, 2006; Rosa & Seibel, 2010), and enhanced oxygen-binding by hemocyanin (Seibel, 2011).

Recent studies have found that Humboldt squid spend most time at oxygen concentrations somewhat higher than those in the OMZ proper. This hypoxic zone lies just above the OMZ, spanning the depth range where dissolved oxygen concentration is 20–60 μmol kg^{-1}, and has been called the oxygen limited zone (OLZ) (Stewart *et al.*, 2013). Often, DSL communities also occupy the OLZ during daytime (Koslow *et al.*, 2011). Constant access to prey within the DSL, along with the ability to withstand hypoxia, has led to the hypothesis that the Humboldt squid range expansion is facilitated by increased foraging opportunities as OMZs shoal and push the OLZ upwards, thereby compressing it (and the overlying epipelagic zone) vertically (Gilly *et al.*, 2013; Stewart *et al.*, 2013). Epipelagic predators such as billfish and mako sharks have habitat boundaries that are typically defined by both temperature and oxygen limits, and consequently their habitats are also impacted by vertical compression (e.g., Vetter *et al.*, 2008; Prince *et al.*, 2010; Stramma *et al.*, 2012).

Here we test the hypothesis that mesopelagic prey abundance and distribution influences the species-wide response of Humboldt squid to OMZ shoaling, using a highly comprehensive and long-term predator–prey dataset. This unique dataset of Humboldt squid observations *in situ* and at-depth environmental data were acquired during ROV dives executed from 1997 to 2011 by The Monterey Bay Aquarium Research Institute (MBARI) in Monterey Bay. Using generalized additive models (GAMs), we identify biotic and abiotic variables affecting relative abundance of Humboldt squid in the Monterey Bay region and then use structural equation models (SEMs) to test the strength of the direct and indirect effects of these interactions. Our work identifies a key set of environmental and biological variables that appear to influence Humboldt squid abundance in the central CCS, which is a highly productive region rich with biodiversity and high economic value (Block *et al.*, 2011; Trebilco *et al.*, 2011). Results suggest that Humboldt squid in the CCS are most directly influenced by myctophid fishes, which in turn are affected by the depth of the upper boundary of the OMZ. This indirect link between OMZ depth and Humboldt squid provides an example of how a changing midwater environment can provide a pathway for range expansion of a major predator, through alterations of its forage resource (e.g., Tylianakis *et al.*, 2008; Sorte *et al.*, 2010).

Material and Methods

Data

Relative squid abundance. MBARI has been monitoring the midwater environment in the greater Monterey Bay region using ROVs since 1989 (Robison, 2004), and their unique dataset documents the first occurrences of Humboldt squid in 1997 (Zeidberg & Robison, 2007).

During each ROV dive, a conductivity–temperature–depth profiler equipped with an oxygen sensor (CTD-O) samples at 15 s intervals, creating a continuous time-series of environmental variables at depth as the ROV operates. Individual dives adhering to the constraints detailed below were identified, and *in situ* environmental data were accessed through

MBARI's internal database by S. Haddock. Observations of Humboldt squid and prey species adhering to the same constraints were accessed through MBARI's Video Annotation and Reference System (www.mbari.org/vars), processed to create a sightings per unit effort (SPUE) metric for each organism on each dive and synchronized with the CTD-O data of environmental variables at the time of each encounter.

Remotely operated vehicle dives included in this study adhered to six constraints. Dives must have: (i) occurred in the greater Monterey Bay area (35.5 °N–37.5 °N and 124 °W to the coastline; Fig. 1b); (ii) occurred during 1997–2011; (iii) had midwater ecology missions to ensure that conditions were appropriate and relatively consistent for viewing and documenting pelagic nekton (dive missions concerned with maintenance, benthic features or extremely small midwater fauna that were constrained by a video focal-range unsuitable for spotting large organisms were excluded); (iv) occurred during daytime (ca. 96% of all midwater dives); (v) had complete CTD-O time-series; and (vi) reached maximum depths within the OMZ where oxygen concentration was $\geq$0.5 ml l^{-1}, typically at ca. 500 m.

Sightings per unit effort (in units of squid per hour) for Humboldt squid was created by summing individual sightings that occurred during the ROV's descent between 250 and 940 m and dividing by hours of ROV effort within those depths. The depth constraint was added because ROV effort by depth was not uniform across dives and, when present, Humboldt squid were not observed continuously throughout the ROV's course (90% of all squid were observed between 250 and 940 m, and 80% of all observations occurred during the descent of the ROV; see Stewart, 2012). Standardizing the search effort and limiting data acquisition to the depth range where Humboldt squid are typically encountered provided a more consistent assessment of SPUE. Including effort expended where encounters with a particular species are not expected (or are extraordinarily rare) can mask important trends in the data (Maunder & Punt, 2004), and therefore this additional restriction was included to make effort as constant as possible through time (see Stewart, 2012; fig. 4–7). MBARI video lab technicians and JSS counted Humboldt squid from video footage collected with the ROV, using best judgment to avoid repeatedly counting the same individuals, and all analyses were completed under the assumption of independent sightings. ROV dives were conducted nearly every month, but to further reduce variability in effort (which ranged from 1 to 17 dives per month, Fig. 2a), we performed all analyses with combined bimonthly data.

Sightings per unit effort was also calculated for each of three key prey groups commonly encountered by the ROV on which Humboldt squid feed (Field *et al.*, 2007, 2013) for every eligible ROV dive during the study period. Prey SPUEs were created based on daytime depth distributions (90% level) for each group: Pacific hake (178–665 m), California market squid (49–406 m), and myctophids (248–703 m).

During the study period, several CTD instruments were used on the ROVs: a Falmouth MicroCTD (www.falmouth.

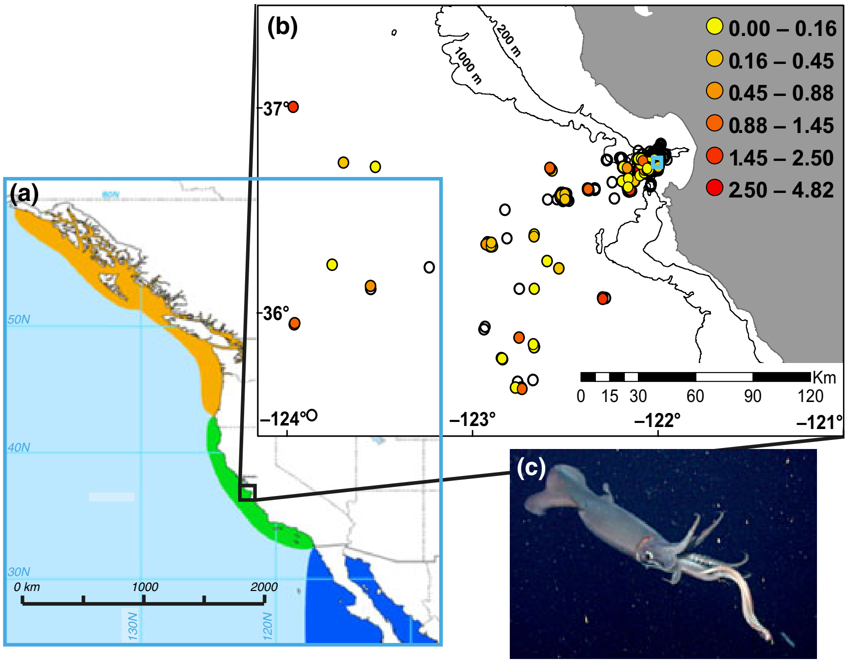

Fig. 1 (a) Map of Humboldt squid range expansion in the northeastern Pacific Ocean. Humboldt squid likely came to the Gulf of California and Mexico in the 1970s (blue: Gilly, 2005), were first observed in California and southern Oregon in 1997/1998 (green: Pearcy, 2002; Zeidberg & Robison, 2007) and further north in 2004–2005 (orange: e.g., Brodeur *et al.*, 2006; Wing, 2006). Black square shows the study area of Monterey Bay. (b) Black circles show mean locations of MBARI remotely operated vehicles (ROV) dives (n = 598), and colored shading indicates relative Humboldt squid SPUE on dives where they were encountered (n = 175). Blue box indicates the Midwater 1 study location. (c) A Humboldt squid hunting (still photo from ROV footage).

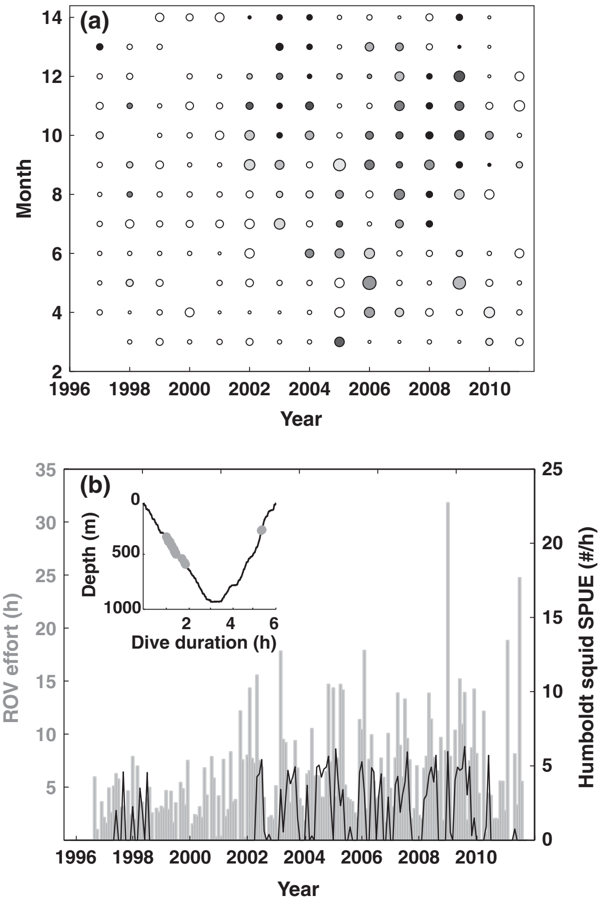

Fig. 2 Monthly remotely operated vehicles (ROV) effort and Humboldt squid observations. (a) ROV dives each year, from March (month 3) to the following February (month 14) to best represent the timing of squid abundance in the CCS (Field *et al.*, 2013). Circle size represents the number of ROV dives each month (min = 1 dive, max = 17 dives); months with no midwater ROV dives have no circle. Shading illustrates Humboldt squid frequency of occurrence (unshaded = 0%, black = 100%). Dives occurred nearly every month of each year, and Humboldt squid were most often encountered in the fall through winter months. (b) Summed monthly ROV search effort (h) and Humboldt squid sightings per unit effort (SPUE, squid per hour) from 1997 to 2011. Inset in (b) illustrates a typical ROV midwater dive occurring to ca. 950 m depth over 6 h, with gray dots indicating independent Humboldt squid sightings. Data for (a) and (b) are presented for illustrative purposes for all dives adhering to the first five constraints (n = 775; see Methods); the sixth constraint (n = 598; reaching a maximum depth within the oxygen minimum zones OMZ) was also applied for all modeling analyses.

com) with Seabird Electronics SBE13 or SBE43 oxygen sensor (www.seabird.com), and Seabird Electronics SBE19Plus with SBE43 and Aanderaa Optode 3830 oxygen sensors (www.aadi.no). Data were managed and SPUEs were calculated using MATLAB 7.8 (2010b, MathWorks, Natick, MA, USA).

Environmental variables. Twenty-four variables that could potentially influence Humboldt squid SPUE were included in the modeling analyses (see Table S1). The variables were based on our understanding of the presence of Humboldt squid in the CCS (Stewart, 2012; Field *et al.*, 2013), their habitat encountered during daily vertical migrations (ranging from ca. 500 m during the daytime to <25 m at night) (Stewart *et al.*, 2013), and interactions with key prey (Field *et al.*, 2007, 2013). Most variables (e.g., depth and strength of thermocline or oxycline) were calculated from data collected by the ROVs by first fitting a smoothing spline and calculating standard deviation in temperature and oxygen profiles over a 15 m moving window. Thermocline depth was determined by the depth at which the maximum change in temperature occurred, and thermocline strength was determined by the value at the depth of maximum change. Analogous parameters were defined for oxygen concentration. In addition, four broad-scale variables [Bakun Upwelling Index, Northern Oscillation Index, Pacific Decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO)] were modeled as well.

With these, we used GAMs and model selection techniques to identify a subset of variables that had significant interactions with Humboldt squid SPUE, thereby reducing the total number of variables considerably. Those found to be significant were used in SEMs to test the direct and indirect relationships among the identified variables.

Modeling

Generalized additive modeling. To identify important interactions between Humboldt squid, habitat characteristics and prey, we used GAM. GAM is a form of linear regression that uses local smoothing splines to fit predictor variables to their response in an additive framework (Wood, 2006), in this case, Humboldt squid SPUE. Exploratory data analysis indicated a high degree of overdispersion (high variability) in the data, so we explored link functions and ultimately used a quasi-Poisson distribution with log link. Prey observations with the ROV (myctophids, market squid, and hake) were adjusted for non-normality with the transformation $\log(x + 0.1)$. In the GAM fitting process, we used an iterative technique whereby we started with an initial, full model with all variables and selectively removed and readded individual terms based on the lowest Akaike Information Criterion (Burnham & Anderson, 2002) and highest r^2 values to decide upon a parsimonious model. GAMs were run using the *mcgv* package (Wood, 2006) in R 2.15.2 (CRAN 2012).

Structural equation modeling. To further understand the direct and indirect effects of different physical and biological variables on squid, we used SEM. Briefly, SEM is a statistical approach to parameterize and test causal models describing the hypothesized relationships between multiple variables, to solve a set of equations implied by a path diagram (Hox & Bechger, 1998; Grace & Bollen, 2005). As we used maximum likelihood based SEM with covariance matrices (Grace & Bollen, 2005), all relationships are assumed to be linear and additive (in contrast to the assumptions of the GAM). We specified a model that included candidate variables identified from the most parsimonious GAM approach that were consistent with our previous knowledge of the system, with a few additional oceanographic-scale indicators because we were interested to see if these larger-scale indicators had effects that were not captured in the GAM approach. The SEM provides a more powerful means of identifying the degree to which the relationships among variables are hierarchically dependent.

Using SEM, we were able to corroborate GAM results by independently testing for variables affecting Humboldt squid SPUE and further examine the identified correlative relationships by testing hypotheses of direct and indirect relationships. We ultimately tested 23 hypothetical links between variables, working within the constraints of the data. For example, although upwelling intensity decreases with distance from shore (Huyer, 1983) and may be a contributing variable to Humboldt squid distribution, this link was not included since Bakun upwelling indices are calculated at a fixed point from shore.

Structural equation models were fit using the *lavaan* package (Rosseel, 2011) in R 2.15.2 (CRAN 2012) by bootstrapping (1000 draws). As our data were highly zero inflated (see below), we ran the SEM with only positive dives (dives where Humboldt squid were observed). Prey data were transformed as described above.

Historic hypoxia in CCS

Finally, historic CTD-O casts were acquired from the World Ocean Database 2009 (www.nodc.noaa.gov/OC5/WOD09/pr_wod09.html) and analyzed using Ocean Dataview (http://odv.awi.de/). Dissolved oxygen data from the Monterey Bay region from 1950 to 1980 were selected and exported. Data were primarily available from two comprehensive sampling periods: 1950–1959 and 1970–1979. Average depths for the upper boundaries of the OMZ (0.5 ml l^{-1}) and OLZ (1.5 ml l^{-1}) were determined by interpolation using MATLAB (2010b, Mathworks). These historic depths were compared with present-day values calculated from ROV CTD-O casts occurring in the area of the Monterey Bay Midwater 1 station (blue box in Fig. 1b).

Results

Data

From 1997 to 2011, MBARI conducted 589 dives adhering to the study criteria, resulting in 808.8 h of search effort in Humboldt squid habitat. Dives occurred nearly every month during the study period (Fig. 2a), and we assume the probability of detecting an individual squid if one was present was equal for all dives throughout the study period. Humboldt squid were encountered on 175 of these dives near the Midwater 1 transect location, where most effort was expended (Fig. 1b). After an initial pulse of Humboldt squid sightings in this region associated with the 1997/1998 El Niño (Fig. 2b), Humboldt squid were not seen until 2002, and were then encountered in every year through 2010. However, Humboldt squid sightings ceased after 2010 (except a single encounter in 2011), perhaps in conjunction with a strong La Niña event (Bjorkstedt *et al*., 2011) following an El Niño Modoki in 2009–2010 that also affected distribution of Humboldt squid in the Gulf of California (Hoving *et al*., 2013).

Median annual daytime depths for Humboldt squid and their prey were calculated and are displayed in Fig. 3 along with mean depths of the OLZ and the OMZ. During the daytime, Humboldt squid were closely associated with the upper boundary of the OMZ at ca. 500 m (Fig. 3a), whereas myctophids and Pacific hake aggregated within the OLZ at ca. 400 and 350 m, rarely being observed within the OMZ (Figs 3b, c). California market squid were encountered mostly above the OLZ (Fig. 3d). Historically, the upper boundary of the OMZ in Monterey Bay was much deeper than that during the study period: 640 m in 1950–1959 and 590 m in 1970–1979 vs. ca. 500 m at present (Fig. 3, Table 1). During this period, the upper boundary of the OLZ has changed very little, thus resulting in compression of the OLZ but not of the overlying epipelagic zone.

Model results

Generalized additive modeling. Generalized additive modeling results identified seven variables that significantly influenced Humboldt squid SPUE, including four environmental variables (OMZ depth, upwelling, NOI, and thermocline strength), one spatial variable (distance offshore from the shelf), and two prey variables (myctophids and hake) (Table 2; Fig. 4). The reduced, final model explained 46.7% of the variance in squid sightings (adjusted r^2), with 63.2% deviance explained (a measure of the goodness of fit). Year and month were important components to account for unexplained variance in the model, as many environmental parameters vary seasonally or annually.

Relationships between Humboldt squid SPUE and these variables had a variety of non-linear forms (Figs 4a–g), but Humboldt squid SPUE generally increased with SPUE for myctophids (Fig. 4a) and Pacific hake (Fig. 4c), supporting the hypothesis that abundance of these prey species is related to Humboldt squid abundance (Figs 4a, c). California market squid were not found to have a significant relationship to Humboldt squid SPUE (results not shown). Although most ROV effort was concentrated near shore (Fig. 1), Humboldt squid SPUE increased monotonically with distance from the shelf (Fig. 4b).

Environmental factors appeared to have complex relationships to Humboldt squid SPUE. SPUE was higher at low values of the NOI (Fig. 4d), which

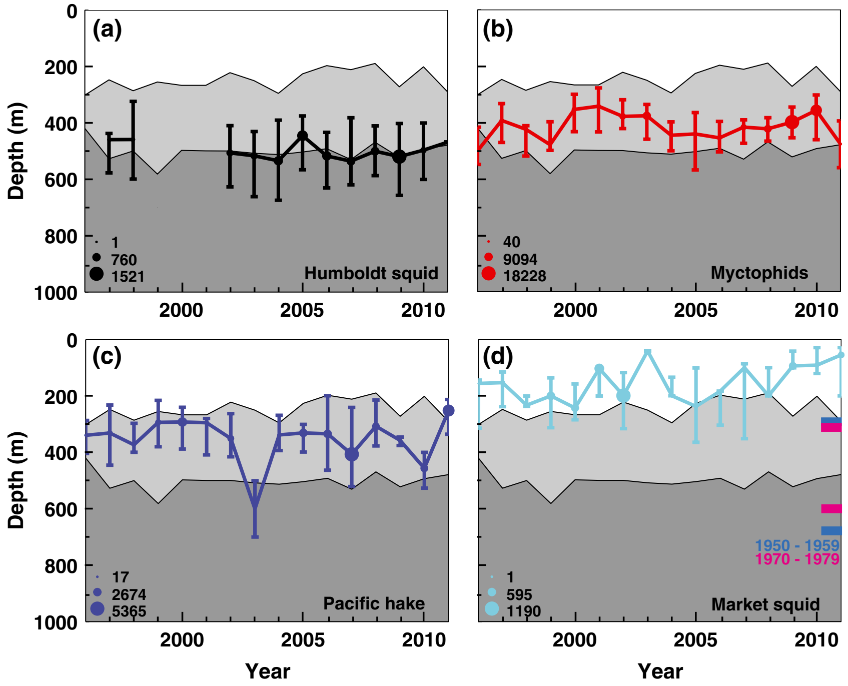

Fig. 3 Annual depth distributions and abundance of (a) Humboldt squid, (b) myctophid fishes, (c) Pacific hake, and (d) market squid in relation to hypoxia. Light gray illustrates the mean depth-range of the oxygen limited zone (OLZ; between 0.5 and 1.5 ml l^{-1} dissolved oxygen concentration); darker gray indicates the mean depth range of the oxygen minimum zone (OMZ, <0.5 ml l^{-1} dissolved oxygen). Circles show relative encounter rates for each species, with actual values indicated. In (d), historic oxygen data from the World Ocean Atlas was used to calculate OLZ and OMZ values for the same area for the indicated time periods (see Table 2).

Table 1 Comparison of historic average depths of the OMZ and OLZ (1950–1959 and 1970–1979; World Ocean Database 2009) and average depths from the current study (1997–2011)

	OMZ			OLZ		
	1950–1959	1970–1979	1997–2011	1950–1959	1970–1979	1997–2011
n	211	67	589	254	177	706
Mean depth	637.76	586.60	500.50	301.56	310.45	262.60
SD	98.44	72.93	42.20	57.88	45.15	66.4

OMZ, oxygen minimum zone; OLZ, oxygen limited zone.
All depths are in meters.

suggests a positive relationship with El Niño conditions. El Niño is generally associated with reduced upwelling and low productivity in the northern CCS, and a negative correlation with upwelling is evident in Fig. 4f. OMZ depth was also a significant contributor to the model fit, with squid SPUE decreasing monotonically with OMZ depth (Fig. 4g), but this relationship was weak. A similar pattern was evident for thermocline strength (Fig. 4e). Contribution from all other variables was also modest. In particular, the upper boundary of the OLZ was not significant, nor were any other variables calculated to describe conditions related to the oxycline (see Table S1).

Structural equation modeling. Broadly, our SEM results show that two variables have significant direct effects on Humboldt squid SPUE: myctophid SPUE and distance from the shelf (Fig. 5). Bollen–Stine bootstrapped r^2 tests show that the structure of our model was consistent with the data ($n = 175$, $P = 0.057$, and Table S2; SEM P-values of >0.05 demonstrate that the model results lack significant differences between the actual data and the ideal data the model would expect). The effects of OMZ depth and other physical factors on Humboldt squid SPUE were all accounted for by their effects on myctophid SPUE. Myctophids themselves were directly influenced by OMZ depth, with fewer

Table 2 Generalized additive model (GAM) results for Humboldt squid sightings per unit effort (SPUE) in relation to environmental and prey predictor variables

	Estimated df	*F* statistic	*P*-value	Change in deviance (%)	r^2
Myctophid SPUE	2.263	31.259	4.44E–29	14.20	0.304
Dist from shelf	1.006	16.527	5.89E–16	7.00	0.399
Hake SPUE	2.596	10.945	1.52E–10	6.26	0.406
NOI	3.997	7.354	6.73E–06	3.10	0.416
Thermocline strength	3.565	4.541	4.86E–04	1.14	0.441
Upwelling	2.459	3.652	5.56E–04	1.96	0.447
OMZ depth	0.907	2.568	6.02E–04	1.17	0.461
Total				63.20	0.467

GAM output parameters from the most parsimonious model are shown, illustrating estimated degrees of freedom per term (estimated df), *F*-statistic, *P*-value, and change in deviance when the term is removed from the model, and r^2 value with the term removed. The percentages show a percentage of the total (63.2 for deviance and 0.467 for r^2).

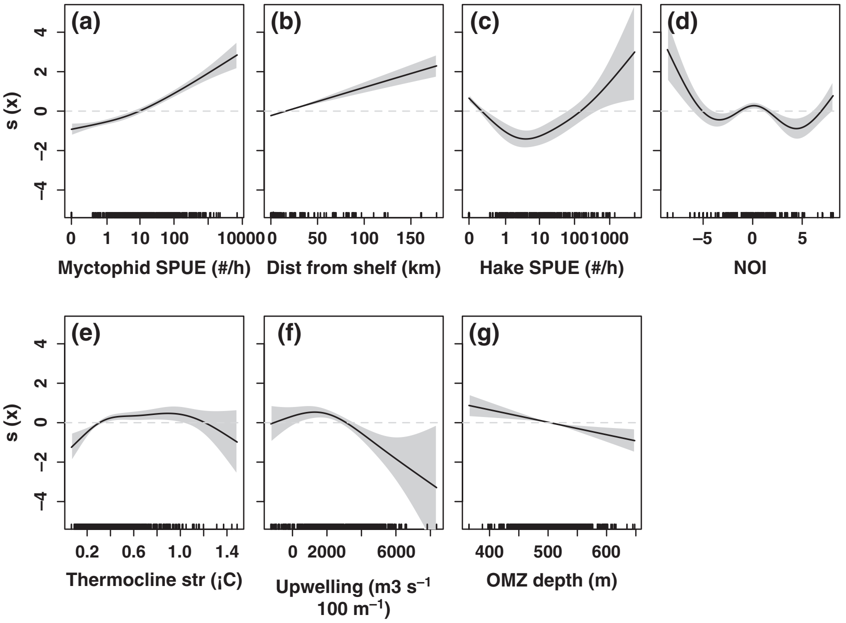

Fig. 4 Generalized additive model (GAM) plots for variables with significant relationships with Humboldt squid sightings per unit effort (SPUE). Covariates (e.g., predictor variables, *x*-axis) are plotted against the spline of the covariate (*y*-axis), and show the relationship between the covariate and response variable (=Humboldt squid SPUE), with all other covariates held constant. *Y*-axis therefore represent how the response variable changes relative to its own mean following changes in the covariate. Plots are presented in order of strength of the relationships between predictor variables and response variable: (a) myctophid SPUE is the strongest; (b) distance to the 200 m isobath; (c) Pacific hake SPUE; (d) Northern Oscillation Index, (NOI); (e) thermocline strength; (f) 30-day cumulative upwelling window; and (g) oxygen minimum zones (OMZ) depth. Each panel demonstrates the relationship between that individual variable and Humboldt squid SPUE, given the effects of all other significant variables. Vertical axes display the splined effects of the predictor variables, with error shaded.

fish sighted as OMZ depth decreased. Distance from the shelf break directly influenced many variables, with a positive relationship to thermocline strength and Humboldt squid SPUE, and a negative relationship to OMZ depth and Pacific hake SPUE.

Hypoxic OMZ depth was directly affected by large-scale ocean processes, including NPGO and PDO, which reflect low-frequency, basin-scale climate variability. NOI could also indirectly affect the OMZ depth by affecting upwelling and thermocline strength, although this relationship was weak. In general, the results of SEM modeling strongly suggest that the abundance of Humboldt squid is directly coupled to the availability of myctophid prey and only

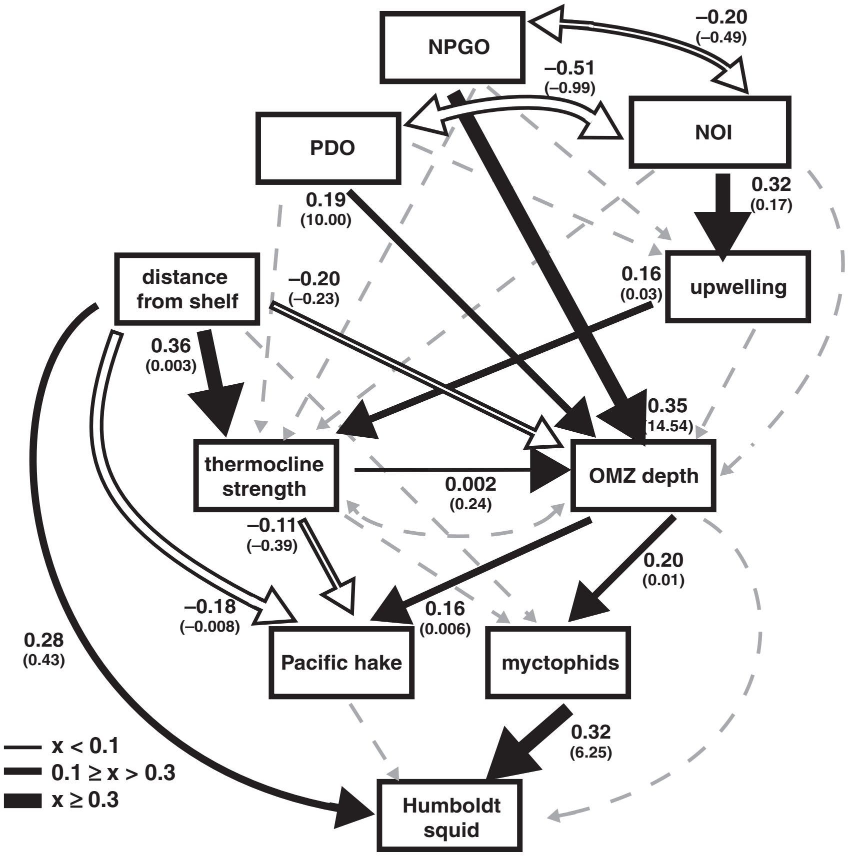

Fig. 5 Finalized path diagram of relationships tested using structural equation modeling (SEM). Lines between variables indicate relationships tested in the final model; significant relationships are black and non-significant are gray and dashed. Significant relationships are presented with line thickness representing the standardized coefficients (=slopes; bold values), and unstandardized coefficients (values in parentheses), with black showing positive coefficients and outlined showing negative coefficients. Standardizing the coefficients is based on the standard deviations of the variables, which makes the coefficients comparable and that the standard deviation of one variable is interpretably equivalent to that of another (Grace & Bollen, 2005). The overall model had a Bollen–Stine bootstrapped *P*-value of 0.057 (df = 18; see Table S2). For further details, see Table S1.

indirectly to environmental factors through prey abundance.

Discussion

In this study, we test the hypothesis that the Humboldt squid range expansion is influenced by the shoaling of the OMZ (Stewart *et al.*, 2013), which could also cause the daytime community of mesopelagic micronekton to alter its vertical distribution (Koslow *et al.*, 2011). By using two different modeling approaches, we were able to support these ideas and identify likely pathways, suggesting that an expanding OMZ influences Humboldt squid abundance in the greater Monterey Bay area indirectly, through its effect on prey species (myctophid fishes).

Our work used a unique, long-term fisheries-independent dataset of *in situ* observations of animals observed nearly monthly, and also focused on dissolved oxygen at midwater depths, a parameter related to vertical distribution of squid in the study area (Stewart *et al.*, 2013). Dissolved oxygen is becoming increasingly important in studies of climate-change effects on the behavior and distribution of top predators (Stramma *et al.*, 2012), but studies of mechanisms mediating these responses remain extremely rare. Oceanic OMZ shoaling is thought to be primarily driven by a warming climate (Keeling *et al.*, 2010), and this factor will undoubtedly be important in the predicted northward shift of many top pelagic predators in the eastern Pacific (Hazen *et al.*, 2012).

Significant effects on Humboldt squid SPUE

Results from both GAMs and SEMs identified myctophid fishes as having the strongest effect on the relative abundance of Humboldt squid in the region of Monterey Bay (Figs 4 and 5). Small mesopelagic fishes, primarily myctophids of several genera and the photoicthyid *Vinciguerria lucetia*, have been identified the major prey of Humboldt squid throughout its range, including the CCS (Nigmatullin *et al*., 2001; Markaida & Sosa-Nishizaki, 2003; Field *et al*., 2007, 2013; Markaida *et al*., 2008; Rosas-Luis *et al*., 2011). Correlations between changes in the populations sizes of *Dosidicus* and *Vinciguerria* have previously been noted in the Peru Current System (Argüelles *et al*., 2008; Rosas-Luis *et al*., 2011), but our approach is the first to quantitatively evaluate the effects of apparent prey abundance (in this case all myctophids) on squid abundance within the context of other physical and biological variables. This approach revealed that myctophid SPUE was the strongest effect and strongest direct effector in the GAM and SEM, respectively.

Humboldt squid were found mostly at the boundary of the OMZ and OLZ (Fig. 2a), which is consistent with observations of vertical movement of individuals using archival satellite tags deployed in the same geographic area and distance from the shelf (Stewart, 2012). Myctophids were primarily found somewhat shallower than this depth, in the middle of the OLZ (Fig. 2b), and the strongest variable influencing myctophid SPUE was OMZ depth (Fig. 5) [separate GAM models run with myctophid SPUE as the dependent variable suggest the same, although the models explain only a small portion of the variance in myctophid SPUE (results not shown)]. Why myctophid SPUE should be driven by OMZ depth is not clear, but it may reflect heightened ROV-sampling of myctophids as they become concentrated in a compressed OLZ.

Hypoxic OMZ depth itself was directly influenced by large-scale environmental forcing, including the NPGO and the PDO, but not by higher frequency environmental forcing, such as seasonal upwelling. Our coupled GAM and SEM results show that broad-scale forcing (PDO, NPGO, and NOI) does affect Humboldt squid SPUE through a shoaling OMZ (and PDO has been shown to affect midwater oxygen through movement of the thermocline, Deutsch *et al*., 2011), but this effect is indirect and is transmitted through a more direct effect of OMZ shoaling on myctophid density.

Model results differ between approaches with regard to Pacific hake: *M. productus* SPUE was found to be the third-most important effect by the GAM, but it was not a significant direct effect on Humboldt squid SPUE by the SEM. A negative relationship between Humboldt squid and hake abundance was previously noted (Zeidberg & Robison, 2007), and hake are known to be an important part of Humboldt squid diet in the CCS (Field *et al*., 2013) as well as in southern hemisphere (Ibáñez *et al*., 2008). Our model results are consistent with the idea that Humboldt squid is an opportunistic predator (Gilly & Markaida, 2007; Bazzino *et al*., 2010; Argüelles *et al*., 2012) that is more likely to be attracted to an area when hake are available in greater numbers (Fig. 4c), and a large squid population might significantly deplete the hake population in a given area though predation (Zeidberg & Robison, 2007).

Both GAM and SEM models also identified the distance offshore from the shelf as the second most-influential variable, identifying that Humboldt squid SPUE increases with increasing distance from shore. This relationship may simply reflect the oceanic nature of this species, but it could also be linked to upwelling, since coastal upwelling shows a negative relationship with squid SPUE (Fig. 4f). Although a significant contributor in both models, upwelling was not a strong or direct contributor to Humboldt squid SPUE (Figs 4f and 5). Humboldt squid are generally absent or in low abundance in the Monterey Bay area during peak upwelling (normally during early summer but variable year-to-year: Zeidberg & Robison, 2007; Stewart, 2012). Upwelling has been shown to have indirect effects on several marine predators by affecting primary productivity and forage resources, and this could potentially affect myctophid fishes when upwelling winds are relaxed and they may form denser communities nearshore. Prolonged periods with weak winds also lead to delayed onset of annual upwelling, which occurred most notably in 2005 (Schwing *et al*., 2006; Barth *et al*., 2007). While many species across multiple trophic levels were negatively affected by delayed upwelling in 2005, including Cassin's auklets (Sydeman *et al*., 2006; Bjorkstedt *et al*., 2011) and outmigrating Chinook salmon smolts (Lindley *et al*., 2009), Humboldt squid thrived during this year with some of the greatest numbers ever observed, and the greatest extent of their range expansion into southeast Alaska (Wing, 2006). Presumably this out-of-phase relationship between Humboldt squid and other predators in conjunction with the lack of upwelling confers some competitive advantage to the squid.

Humboldt squid and fisheries

Monterey Bay Aquarium Research Institute's unique long-term data not only serve as an indicator of relative abundance of both Humboldt squid and their prey but also provide high-resolution environmental sampling at depth on appropriate temporal and spatial scales to test the importance of environmental and biological drivers of abundance. SPUE can be considered a proxy to catch-per-unit effort, a metric used in fisheries science to assess relative abundance of fish populations in formal stock assessments. Although Humboldt squid is not currently targeted commercially in northern CCS, this highly migratory and opportunistic predator has demonstrated potential to affect important commercial fisheries (Field *et al.*, 2013). For example, Humboldt squid have caused complications for quantifying and therefore managing Pacific hake (Holmes *et al.*, 2008), the largest fishery (by volume) on the continental US west coast and Canada (Stewart *et al.*, 2011). As Humboldt squid are highly migratory (Stewart *et al.*, 2012) and are thought to make long-distance foraging migrations through California waters to and from the Pacific Northwest seasonally (Field *et al.*, 2013), SPUE as an indicator of relative abundance off central California could be a valuable management tool for these more northern regions.

From a Pacific basin-wide perspective, Humboldt squid represent an increasingly important target for commercial fisheries, and this species has been the world's largest commercial invertebrate fishery for most years since 2004 (Food & Agriculture Organization, 2011). The vast majority of these landings are derived from the Humboldt (Peru) Current System, and dramatic changes in abundance and life-history characteristics of Humboldt squid have occurred in this region during the period of our study (mid-1990s through 2011), with several environmental and trophic drives being considered (Argüelles *et al.*, 2008; Keyl *et al.*, 2011). The OMZ is unusually shallow in this highly productive region, and effects of periodic OMZ shoaling on the distribution and abundance of Peruvian anchoveta, the largest single-species fishery in the world, have been reported (Bertrand *et al.*, 2010, 2011). It is highly likely that both cyclic and monotonic changes in the depth of the OMZ in this region also have major impacts on abundance and distribution of Humboldt squid and their prey as well. Given the size and value of the squid fishery, this issue has significant economic importance.

Humboldt squid range expansion

Range expansion of Humboldt squid in the northern CCS, as well as in the southern hemisphere (Alarcón-Muñoz *et al.*, 2008), is an ongoing phenomenon, and a comprehensive understanding of the exact mechanisms is not yet possible. Nevertheless, this paper provides important insight concerning the effects of environmental and biological interactions on the abundance of these important predators. Long-term climate change in marine ecosystems involves both types of drivers in a complex set of interactions (Doney *et al.*, 2012) that may be teased apart to some extent by modeling approaches like that presented in this paper. Moreover, the long-term consequences of these changes may provide insight into substantive impacts throughout marine ecosystems, as cephalopod populations are highly sensitive to climate dynamics, and have a major influence on the trophic dynamics of the ecosystems they inhabit (Rodhouse & Nigmatullin, 1996; Coll *et al.*, 2013).

Any explanation of long-term range expansion of Humboldt squid in the CCS must accommodate the annual long-distance migrations that this species undertakes to its northern range limit from suitable spawning grounds outside of the northern CCS (Staaf *et al.*, 2011; Field *et al.*, 2013). Because the northern range limit is defined on a seasonal basis (late summer and early autumn), range expansion in this case is more accurately viewed as a migratory trajectory of increasing amplitude that is more variable than the migrations of sardines and Pacific hake to the rich waters off the Pacific Northwest (e.g., Ware & Thomson, 2005; Agostini *et al.*, 2006). As chronic OMZ shoaling continues, OLZ compression and deoxygenation of the euphotic zone will proceed northward and/or intensify throughout the current range of Humboldt squid. Our results suggest that this feature affects myctophids in a way that benefits Humboldt squid, possibly by concentrating them in a compressed OLZ where they are more vulnerable to visual predators (Koslow *et al.*, 2011). This concentrating effect may also underlie the apparent increase in myctophid abundance (based on SPUE), which in principle could mask the decrease due to heightened predation. While our results suggest that food (myctophid) availability is a stronger determinant of Humboldt squid abundance than are environmental drivers once the squid are in the CCS, the identities of annual environmental drivers that are most critical in controlling annual migrations remain unclear.

Humboldt squid have clearly demonstrated dramatic changes in geographical distribution, habitat preference, age at maturity, and life span in response to short-term environmental variability such as El Niño (Argüelles *et al.*, 2008, 2012 Keyl *et al.*, 2011; Hoving *et al.*, 2013). Our results suggest that large-scale environmental drivers occurring on a much longer temporal scale (e.g., OMZ shoaling and PDO) have indirect effects on the abundance of Humboldt squid in the northern CCS through changes in the abundance of prey (myctophid fishes), or rather the density of their prey, although this measure was beyond the scope of our study. As OMZs continue to shoal (Keeling *et al.*, 2010) along with temperature increases (Burrows *et al.*, 2011) and other heightened ecosystem impacts of climate change (Doney *et al.*, 2012), Humboldt squid will likely continue their range expansions and affect predator–prey dynamics in new ecosystems.

Acknowledgements

We dedicate this manuscript to our colleague and coauthor Dave Foley, a generous and unparalleled colleague, mentor, and friend. We thank R. Sherlock and S. Haddock for accessing MBARI data from the internal VARS and Expedition Databases. We also thank MBARI's ROV pilots and ships' crew and the data and video teams, particularly S. Von Thun, B. Schlining, K. Schlining, and L. Kuntz. We thank P. Daniel and A. Booth for making the maps. A. Booth, D. Staaf, P. Daniel, L. Zeidberg, R. Thomas, I. Stewart, W. Sydeman, M. Hunsicker, and B. Wells provided helpful discussion and support. Y. Rosseel created the *lavaan* package and graciously provided guidance. S. Haddock provided invaluable instruction on data management and processing without which this project would not have been possible (Haddock & Dunn, 2011). Funding was provided by the David and Lucile Packard Foundation, the National Science Foundation, California Sea Grant, and the NOAA Fisheries and the Environment (FATE) program. Authors declare no conflict of interest.

References

Agostini V, Francis RC, Hollowed AB, Pierce SD, Wilson C, Hendrix AN (2006) The relationship between Pacific hake (*Merluccius productus*) distribution and poleward subsurface flow in the California Current System. *Canadian Journal of Fisheries Aquatic Science*, **63**, 2648–2659.

Alarcón-Muñoz R, Cubillos L, Gatica C (2008) Jumbo squid (*Dosidicus gigas*) biomass off central Chile effects on Chilean hake (*Merluccius gayi*). *CalCOFI Reports*, **49**, 157–166.

Argüelles J, Tafur R, Taipe A, Villegas P, Keyl F, Dominguez N, Salazar M (2008) Size increment of jumbo flying squid *Dosidicus gigas* mature females in Peruvian waters 1989–2004. *Progress in Oceanography*, **79**, 308–312.

Argüelles J, Lorrain A, Cherel Y *et al.* (2012) Tracking habitat and resource use for the jumbo squid *Dosidicus gigas*: a stable isotope analysis in the northern Humboldt Current System. *Marine Biology*, **159**, 2105–2116.

Barnes WC (2009) Available at: http://tofinophotography.wordpress.com/category/wildlife/humboldt-squid (accessed 01 October 2013).

Barth J, Menge B, Lubchenco J *et al.* (2007) Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California Current. *Proceedings of the National Academy of Sciences*, **104**, 3719–3724.

Bazzino G, Gilly WF, Markaida U, Salinas-Zavala CA, Ramos-Castillejos J (2010) Horizontal movements vertical-habitat utilization and diet of the jumbo squid (*Dosidicus gigas*) in the Pacific Ocean off Baja California Sur Mexico. *Progress in Oceanography*, **86**, 59–71.

Bertrand A, Ballon M, Chaigneau A (2010) Acoustic observation of living organisms reveals the upper limit of the oxygen minimum zone. *PLoS ONE*, **5**, e10330.

Bertrand A, Chaigneau A, Peraltilla S, Ledesma J, Graco M, Monetti F, Chavez FP (2011) Oxygen: a fundamental property regulating pelagic ecosystem structure in the coastal southeastern tropical Pacific. *PLoS ONE*, **6**, e29558.

Bianchi D, Galbraith ED, Carozza DA, Mislan KAS, Stock CA (2013) Intensification of open-ocean oxygen depletion by vertically migrating animals. *Nature Geoscience*, **6**, 545–548.

Bjorkstedt E, Goericke R, McClatchie S *et al.* (2011) State of the California Current 2010–2011: regionally variable responses to a strong (but fleeting?) La Niña. *CalCOFI Reports*, **52**, 36–68.

Block B, Jonsen I, Jorgensen S *et al.* (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature*, **475**, 86–90.

Bograd SJ, Castro C, Di Lorenzo E, Palacios D, Bailey H, Gilly WF, Chavez FP (2008) Oxygen declines and the shoaling of the hypoxic boundary in the California Current. *Geophysical Research Letters*, **35**, 1–6.

Braid HE, Deeds J, DeGrasse SL, Wilson JJ, Osborne J, Hanner RH (2011) Preying on commercial fisheries and accumulating paralytic shellfish toxins: a dietary analysis of invasive *Dosidicus gigas* (*Cephalopoda Ommastrephidae*) stranded in Pacific Canada. *Marine Biology*, **159**, 25–31.

Brodeur R, Ralston S, Emmett R, Trudel M, Auth T, Phillips A (2006) Anomalous pelagic nekton abundance distribution and apparent recruitment in the northern California Current in 2004 and 2005. *Geophysical Research Letters*, **33**, L22S08.

Burnham KP, Anderson DR (2002) *Model Selection and Multi-Modal Inference: A Practical Information-Theoretic Approach* (2nd edn). Springer, New York.

Burrows MT, Schoeman DS, Buckley LB *et al.* (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science*, **334**, 652–655.

Coll M, Navarro J, Olson RJ, Christensen V (2013) Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. *Deep-Sea Research II*, **95**, 21–36.

Cosgrove JA (2005) The first specimens of Humboldt squid in British Columbia. *PICES Press*, **13**, 30–31.

Croker RS (1937) Further notes on the jumbo squid *Dosidicus gigas*. *California Department of Fish Game Fish Bulletin*, **23**, 246–247.

Deutsch C, Brix H, Ito T, Frenzel H, Thompson L (2011) Climate-forced variability of ocean hypoxia. *Science*, **333**, 336–339.

Doney SC, Ruckelshaus M, Duffy JE (2012) Climate change impacts on marine ecosystems. *Annual Review in Marine Science*, **4**, 11–37.

Food and Agriculture Organization (2011) Capture production by principal species in 2011. Available at: ftp://ftp.fao.org/fi/stat/summary/a1e.pdf (accessed 20 November 2013).

Field JC, Baltz K, Phillips AJ, Walker WA (2007) Range expansion and trophic interactions of the jumbo squid *Dosidicus gigas* in the California Current. *CalCOFI Reports*, **48**, 1–16.

Field JC, Elliger C, Baltz K *et al.* (2013) Foraging ecology and movement patterns of jumbo squid (*Dosidicus gigas*) in the California Current System. *Deep-Sea Research Part II*, **95**, 37–51.

Gilly WF (2005) Spreading and stranding of Humboldt squid. Monterey Bay National Marine Sanctuary, 1–3.

Gilly WF, Markaida U (2007) Perspectives on *Dosidicus gigas* in a changing world. In: *The Role of Squid in Open Ocean Ecosystems* (edsOlson RJ, Young JW), 94p. Report of a GLOBEC-CLIOTOP/PFRP workshop 16-17 November 2006 Honolulu Hawaii USA. GLOBEC Report 24, vi. GLOBEC, Honolulu, USA.

Gilly WF, Markaida U, Baxter CH *et al.* (2006) Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Marine Ecology Progress Series*, **324**, 1–17.

Gilly WF, Zeidberg LD, Booth JAT, Stewart JS, Marshall G, Abernathy K, Bell LE (2012) Locomotion and behavior of Humboldt squid *Dosidicus gigas* in relation to natural hypoxia in the Gulf of California Mexico. *Journal of Experimental Biology*, **215**, 3175–3190.

Gilly WF, Beman JM, Litvin SY, Robison BH (2013) Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annual Review of Marine Science*, **5**, 393–420.

Grace JB, Bollen KA (2005) Interpreting the results from multiple regression and structural equation models. *Bulletin of the Ecological Society of America*, **86**, 283–295.

Haddock SH, Dunn C (2011) *Practical Computing for Biologists* (1st edn). Sinauer Associates, Sunderland, MA, USA.

Hazen EL, Jorgensen S, Rykaczewski RR *et al.* (2012) Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change*, **2**, 1–5.

Helly J, Levin L (2004) Global distribution of naturally occurring marine hypoxia on continental margins. *Deep-Sea Research Part I*, **51**, 1159–1168.

Holmes J, Cooke K, Cronkite G (2008) Interactions between jumbo squid (*Dosidicus gigas*) and Pacific hake (*Merluccius productus*) in the northern California Current in 2007. *CalCOFI Reports*, **49**, 129–141.

Hoving H-J, Gilly WF, Markaida U *et al.* (2013) Extreme plasticity in life-history strategy allows a migratory predator (Jumbo Squid) to cope with a changing climate. *Global Change Biology*, **19**, 2089–2103.

Hox J, Bechger T (1998) An introduction to structural equation modelling. *Family Science Review*, **11**, 354–373.

Huyer A (1983) Coastal upwelling in the California Current System. *Progress in Oceanography*, **12**, 259–284.

Ibáñez CM, Arancibia H, Cubillos L (2008) Biases in determining the diet of jumbo squid *Dosidicus gigas* (D'Orbigny 1835) (*Cephalopoda Ommastrephidae*) off southern-central Chile (34S-40S). *Helgoland Marine Research*, **62**, 331–338.

Keeling RF, Körtzinger A, Gruber N (2010) Ocean deoxygenation in a warming world. *Annual Review of Marine Science*, **2**, 199–229.

Keyl F, Argüelles J, Tafur R (2011) Interannual variability in size structure age and growth of jumbo squid (*Dosidicus gigas*) assessed by modal progression analysis. *ICES Journal of Marine Science*, **68**, 507–518.

Koslow J, Goericke R, Lara-Lopez A, Watson W (2011) Impact of declining intermediate-water oxygen on deepwater fishes in the California Current. *Marine Ecology Progress Series*, **436**, 207–218.

Lindley ST, Grimes CB, Mohr MS *et al.* (2009) What caused the Sacramento River fall Chinook stock collapse? NOAA Tech Memo NMFS NOAA-TM-NMFS-SWFSC-447.

Markaida U, Sosa-Nishizaki O (2003) Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *Journal of the Marine Biological Association of the UK*, **83**, 507–522.

Markaida U, Gilly WF, Salinas-Zavala CA, Rosas-Luis R, Booth JAT (2008) Food and feeding of jumbo squid *Dosidicus gigas* in the central Gulf of California during 2005–2007. *CalCOFI Reports*, **49**, 90–103.

Maunder M, Punt A (2004) Standardizing catch and effort data: a review of recent approaches. *Fisheries Research*, **70**, 141–159.

Mearns AJ (1988) The "odd fish": unusual occurrences of marine life as indicators of changing ocean conditions. In: *Marine Organisms as Indicators D* (eds Soule F, Kleppel GS), pp. 137–176. Springer-Verlag, New York, NY.

Nigmatullin CM, Nesis KN, Arkhipkin AI (2001) A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: ommastrephidae). *Fisheries Research*, **54**, 9–19.

Pearcy W (2002) Marine nekton off Oregon and the 1997–98 El Nino. *Progress in Oceanography*, **54**, 399–403.

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science*, **308**, 1912–1915.

Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track local climate velocities. *Science*, **341**, 1239–1242.

Prince ED, Luo J, Goodyear CP *et al.* (2010) Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes. *Fisheries Oceanography*, **19**, 448–462.

Robison BH (2004) Deep pelagic biology. *Journal of Experimental Marine Biology and Ecology*, **300**, 253–272.

Rodhouse PG, Nigmatullin ChM (1996) Role as consumers. *Philosophical Transaction of the royal society of London*, **351**, 1003–1022.

Rosa R, Seibel BA (2010) Metabolic physiology of the Humboldt squid *Dosidicus gigas*: implications for vertical migration in a pronounced oxygen minimum zone. *Progress in Oceanography*, **86**, 72–80.

Rosas-Luis R, Tafur-Jimenez R, Alegre-Norza AR, Castillo-Valderrama PR, Cornejo-Urbina RM, Salinas-Zavala CA, Sanchez P (2011) Trophic relationships between the jumbo squid (*Dosidicus gigas*) and the lightfish (*Vinciguerria lucetia*) in the Humboldt Current System off Peru. *Scientia Marina*, **75**, 549–557.

Rosseel Y (2011) *Lavaan: An R Package for Structural Equation Modeling and more Version 0.5-9 (BETA)*. 1–33. Available at: R Project: http://cran.r-project.org/web/packages/lavaan/index.html (accessed 10 December 2012).

Schwing FB, Bond NA, Bograd SJ, Mitchell T, Alexander MA, Mantua N (2006) Delayed coastal upwelling along the US West Coast in 2005: a historical perspective. *Geophysical Research Letters*, **33**, L22S01.

Seibel BA (2011) Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *Journal of Experimental Biology*, **214**, 326–336.

Sorte CJB, Williams SL, Carlton JT (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography*, **19**, 303–316.

Staaf DJ, Zeidberg LD, Gilly WF (2011) Effects of temperature on embryonic development of the Humboldt squid *Dosidicus gigas*. *Marine Ecology Progress Series*, **441**, 165–175.

Stewart IJ, Forrest RE, Grandin C, Hamel OS, Hicks AC, Martell SJD, Taylor IG (2011) *Status of the Pacific hake (whiting) stock in US and Canadian waters in 2011*. Joint US and Canadian Hake Technical Working Group Report, 1–207.

Stewart JS (2012) Humboldt squid in the northern California Current System. PhD thesis, Stanford University Stanford California USA. 193. Available at: http://purl.stanford.edu/pb685tk3754 (accessed 31 May 2013).

Stewart JS, Hazen EL, Foley DG, Bograd SJ, Gilly WF (2012) Marine predator migration during range expansion: Humboldt squid *Dosidicus gigas* in the northern California Current System. *Marine Ecology Progress Series*, **471**, 135–150.

Stewart JS, Field JC, Markaida U, Gilly WF (2013) Behavioral ecology of jumbo squid (*Dosidicus gigas*) in relation to oxygen minimum zones. *Deep-Sea Research Part II*, **95**, 197–208.

Stramma L, Johnson GC, Sprintall J, Mohrholz V (2008) Expanding oxygen-minimum zones in the tropical oceans. *Science*, **320**, 655–658.

Stramma L, Prince E, Schmidtko S *et al.* (2012) Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nature Climate Change*, **2**, 33–37.

Sydeman W, Bradley R, Warzybok P *et al.* (2006) Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate 2005: unusual atmospheric blocking. *Geophysical Research Letters*, **33**, L22S09.

Trebilco R, Halpern BS, Flemming JM, Field C, Blanchard W, Worm B (2011) Mapping species richness and human impact drivers to inform global pelagic conservation prioritisation. *Biological Conservation*, **144**, 1758–1766.

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.

Vetter R, Kohin S, Preti A, McClatchie S, Dewar H (2008) Predatory interactions and niche overlap between mako shark *Isurus oxyrinchus* and jumbo squid *Dosidicus gigas* in the California Current. *CalCOFI Reports*, **49**, 142–156.

Ware DM, Thomson RE (2005) Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. *Science*, **308**, 1280–1284.

Wing BL (2006) Unusual invertebrates and fish observed in the Gulf of Alaska 2004–2005. *PICES Press*, **142**, 26–28.

Wood SN (2006) *Generalized Additive Models: An Introduction with R*. Vol. 66. Chapman & Hall. The R Project: http://cran.r-project.org/web/packages/mgcv/index.html (accessed 10 December 2012).

Zeidberg LD, Robison BH (2007) Invasive range expansion by the Humboldt squid *Dosidicus gigas* in the eastern north Pacific. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 12948–12950.

Supporting Information

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

Table S1. Twenty-four exploratory variables tested with the generalized additive model (GAM). Humboldt squid, Pacific hake, and myctophid SPUE, thermocline strength, OMZ depth, and distance from shelf are from data collected by MBARI. Upwelling, Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), and North Oscillation Index (NOI) were accessed from NOAA websites.
Table S2. Finalized structural equation model for Humboldt squid (Bollen–Stine bootstrap, $P = 0.057$; df = 18).