SEASONAL OCCURRENCES OF HUMBOLDT SQUID (*DOSIDICUS GIGAS*) IN THE NORTHERN CALIFORNIA CURRENT SYSTEM

MARISA N. C. LITZ AND A. JASON PHILLIPS
Cooperative Institute for Marine Resources Studies
Oregon State University
2030 Marine Science Drive
Newport, OR 97365
Tel. 541-867-0148
Fax: 541-867-0389
Email: litzm@onid.orst.edu

RICHARD D. BRODEUR AND ROBERT L. EMMETT
Estuarine and Ocean Ecology Program
NOAA Fisheries Northwest Fisheries Science Center
Newport Research Station
2032 SE OSU Drive
Newport, OR 97365

ABSTRACT

Recent visits by Humboldt squid (*Dosidicus gigas*) to the northern California Current system (CCS) were suggested to be related to larger climatic events such as El Niño, global warming, and expansion and shoaling of the oxygen minimum zone. Due to their plasticity in foraging behavior, coupled with an increased availability of prey resources, these excursions may also represent opportunistic foraging explorations. Fisheries-independent surveys initiated by the Northwest Fisheries Science Center in 1998 first encountered Humboldt squid in coastal waters off central Oregon and Washington in 2004. Squid ranging from 36–79 cm mantle length were caught during the following six years of sampling (2004–2009), with individuals generally increasing in abundance shoreward in late summer. The highest observed densities were in 2009 and measured 1,671 squid $(10^6\ m^3)^{-1}$. Physical features associated with increased squid catch included station depth, subsurface water temperature, ocean salinity, ocean density, and dissolved oxygen. In addition, the arrival of Humboldt squid onto the shelf in late summer was coincident with declines of juvenile (10–30 cm total length) Pacific hake (*Merluccius productus*), in contrast to the typical increases of hake recorded in late summer during recent years. Our results suggest that predator-prey interactions and ocean conditions in the CCS epipelagic zone lead to seasonal expansions, yet unsuccessful colonization attempts, by Humboldt squid populations. Identifying the economic and ecological impacts of this newly arrived predator should be a top research priority.

INTRODUCTION

Humboldt squid (also known as jumbo flying squid *Dosidicus gigas*) have recently visited the northern California Current system (CCS) and have been documented as far north as southeast Alaska (Pearcy 2002; Cosgrove 2005; Brodeur et al. 2006; Rodhouse et al 2006; Wing 2006; Field et al. 2007; 2008; Rodhouse 2008). They are voracious predators that can grow to 2 m and 50 kg within a year (Zeidberg and Robison 2007), and Markaida et al. (2004) found that Humboldt squid in the Gulf of California have one of the highest absolute growth rates of any squid species. In recent years off the U.S. West Coast, Humboldt squid appear to overlap in time and space with commercially important species such as Pacific hake (*Merluccius productus*), Pacific sardine (*Sardinops sagax*), and rockfish (*Sebastes* spp.), and are of major interest because of their potential ecosystem impacts (Field et al. 2007; Holmes et al. 2008).

Humboldt squid invaded waters off southern and central California in large numbers during the mid-1930s (Clark and Phillips 1936) then were virtually or totally absent until a short period in the mid-1970s, then virtually absent again until the 1990s (Field et al. 2007). Off Oregon, they were not observed until the 1997 El Niño, when Humboldt squid and other warm water species were documented over the continental shelf and slope from June through November in sea surface temperatures ranging from 13.4 to 14.3°C (Pearcy 2002). Between 2002 and 2009, Humboldt squid undertook seasonal foraging visits to the northern CCS, with many reports of summertime beach strandings/landings by commercial, scientific, and recreational fisheries off Oregon, Washington, and British Columbia (Cosgrove 2005; Brodeur et al. 2006; Trudel et al. 2006). However, little is known about the seasonal and interannual variability in the large-scale distribution of Humboldt squid in the northern CCS.

Several environmental and ecological factors have been implicated as potential drivers of the appearance of Humboldt squid in temperate waters of the northern CCS, including warming ocean temperatures, shoaling, or expansion of the oxygen minimum zone (OMZ), and overfishing of subtropical predators in the Eastern Tropical Pacific (Pearcy 2002; Gilly et al. 2006; Field et al. 2007; Zeidberg and Robison 2007; Rodhouse 2008). We hypothesize that an abundance of potential prey in the CCS, namely juvenile (10–30 cm total length [TL]) Pacific hake, Pacific sardine, northern anchovy (*Engraulis mordax*), rockfish, and myctophids, may be an equally important explanation for episodic appearances of Humboldt squid in the northern CCS. However, the biological and environmental mechanisms driving seasonal Humboldt squid visits remain poorly understood.

Here we analyze fishery and oceanographic information collected by NOAA Fisheries Northwest Fisheries Science Center (NWFSC) during recent surveys off Oregon and Washington (2004–2009) to examine the seasonal and interannual patterns in the occurrence of Humboldt squid. Records from these surveys represent a limited, though valuable comprehensive seasonal and annual time series of Humboldt squid catches in the Pacific Northwest to date. The objectives of this study were to explore recent catch data and find some connectivity between physical oceanographic conditions and the observed sporadic spatial and temporal occurrence of Humboldt squid in the northern California Current to provide important baseline monitoring information which will serve the research community when designing new studies. We hypothesize that changes in physical oceanographic conditions play an important role in determining ecological habitat for Humboldt squid, but also that the interactive processes of biology, prey availability, and fisheries could play a role.

METHODS

The NWFSC surveyed spring-fall marine resources off Oregon and Washington (2004–2009) by fishing at night in two separate studies: the Stock Assessment Improvement Program, or SAIP study, initiated in 2004 (see Phillips et al. 2009), and the Predator study, initiated in 1998 (see Emmett et al. 2006). Both studies fished a Nordic 264-rope trawl behind a chartered fishing vessel, but the SAIP study fished the headrope at midwater (30 m), while the Predator study fished the headrope at the surface. The SAIP study regularly sampled four transects monthly during May–September (and in November 2004 and October 2005), with stations ranging from 5–100 nautical miles (nm) offshore. A total of 412 nighttime midwater trawls were conducted between Hecata Head, OR (44˚00N) and Willapa Bay, WA (46˚40N; table 1a.). The Predator study sampled 535 nighttime trawls along two transects (5–30 nm from shore) off the mouth of the Columbia River, OR (46˚10N) and Willapa Bay, WA (46˚40N) biweekly from April–August in 2004–2009 (table 1b). While SAIP study stations spanned the shelf break and slope (station depths ranged from 55 to 3,150 m), Predator study stations were located primarily on the shelf (depths ranged from 28 to 293 m).

At each station, the trawl was towed astern of the fishing vessel for 15–30 minutes at a vessel speed averaging 3.1 kts. The deployed trawl had a mouth opening of 12 m deep by 28 m wide (336 m^2) based on previous determinations using a third-wire Simrad FS3300 backwards-looking net sounder (Emmett et al. 2004). For midwater trawls, a knotless, 6.1 m long, 3-mm mesh liner was sewn into the cod end; for surface trawls, the liner was 8-mm mesh. During both studies, all individuals caught were identified to the lowest taxon level possible and enumerated. We measured 30 randomly selected individuals of each species for length. In the event of a very large catch, we counted and weighed a subsample of each species and used the measured weight of the remaining catch to estimate the total number of individuals caught. In addition, we collected environmental information, including temperature, salinity, and water density from the surface down to 100 m (or within 5 m from the bottom at stations <100 m depth) prior to each trawl by deploying a Sea-Bird SBE SEALOGGER 25 (SAIP study) or SBE 19 SEACAT (Predator study) CTD profiler. Beginning in September 2008, the SBE 25 SEALOGGER CTD was outfitted with a dissolved oxygen (DO) sensor to measure in situ concentrations (ml L^{-1}). All CTD sensors were calibrated annually prior to the start of each cruise season.

Because of a disproportionate amount of zero catches, the relationship between environmental factors and Humboldt squid caught in our trawls was examined by a two-step or conditional modeling approach, using exploratory Generalized Additive Models (GAMs) with the mgcv-package (Wood 2006) available for R (v2.10.1) software (The R Foundation for Statistical Computing, http://www.r-project.org). GAMs were chosen for habitat analysis because the relationship between Humboldt squid and environmental variables was expected to be of a complex form, not easily fitted by standard linear or nonlinear models. GAM fitting techniques have been employed to understand and predict variations in cephalopod abundance in many systems (Bellido et al. 2001; Denis et al. 2002; Tian et al. 2009).

Both binomial and conditional Poisson GAMs were fitted to filtered data sets gathered on Humboldt squid during the SAIP Study (2004-2009). Humboldt squid presence/absence was first modeled against environmental data using (1) a binomial family fit with a logit-link function, using only stations that were repeatedly sampled over the six years where Humboldt squid were captured (n = 315 hauls). Next, Humboldt squid abundance (count), was modeled using (2) a Poisson distri-

TABLE 1
Abbreviations, descriptions, and sources of the large-scale environmental variables used in the Generalized Additive Models (GAMs).

Abbreviation	Description and source
MEI	Multivariate El Niño-Southern Oscillation Index. From the NOAA Earth System Research Laboratory Web site: http://www.cdc.noaa.gov/ENSO/enso.mei_index.html.
PDO	Pacific Decadal Oscillation Index. From the University of Washington (Nathan Mantua administrator) Web site: http://jisao.washington.edu/pdo/.
UI	Upwelling Index for 45˚N, 125˚W. From the NOAA Southwest Fisheries Science Center Environmental Research Division live access server Web site: http://www.pfeg.noaa.gov/products/las.html.

TABLE 2
Research cruise dates for two NOAA Fisheries Northwest Fisheries Science Center studies occurring from 2004–2009: (a) the Stock Assessment Improvement Program (SAIP) study; and (b) the Predator study. Information presented for each cruise includes survey year, dates, latitude range (°N), distance range of stations offshore (in nautical miles), total number of transects, total trawls completed (and trawls containing Humboldt squid, *Dosidicus gigas* in parentheses), total number of *D. gigas* caught, and the associated dorsal mantle length range (ML in cm).

a. Stock Assessment Improvement Program (SAIP) study nighttime cruises 2004–2009

Year	Survey Dates	Start-end latitude	Distance range offshore	Number of transects	Total number of trawls (trawls containing *D. gigas*)	Total number of *D. gigas*	Length range
2004	6/30–7/01	44°40	5–85	1	5^{D}	–	–
2004	8/04–8/08	44°00–44°40	5–75	2	13	–	–
2004*	8/31–9/04	44°00–44°40	5–75	2	15 (4)	15	47–66
2004*	11/05–11/11	44°00–46°40	9–65	4	20 (8)	32	50–67
2005	6/07–6/11	44°00–46°40	10–45	4	15	–	–
2005*	7/11–7/14	44°00–46°40	10–40	3	11 (1)	1	52
2005	8/15–8/19	44°00–46°40	10–55	4	20	–	–
2005	9/19–9/23	44°40–46°40	10–55	3	14	–	–
2005*	10/19–10/24	44°00–46°40	9–65	4	21 (1)	1	62
2006	5/15–5/16	46°40	10–40	1	4	–	–
2006	6/15–6/17	46°10–46°40	10–40	2	7	–	–
2006*	8/07–8/11	44°00–46°40	10–55	4	18 (1)	70	46–63
2006*	9/24–8/28	44°00–46°40	10–55	4	20 (8)	33	51–68
2007	5/17–5/21	44°00–46°40	10–55	4	16	–	–
2007	6/16–6/20	44°00–46°40	10–55	4	16	–	–
2007	7/18–7/20	44°00–44°40	11–55	2	8	–	–
2007*	8/15–8/19	44°00–46°40	11–55	4	18 (5)	32	48–68
2007*	9/11–9/15	44°00–46°10	10–55	3	15 (3)	7	56–68
2008	5/18–5/21	44°00–46°10	20–55	3	12	–	–
2008	6/16–6/20	44°00–46°10	20–100	3	13	–	–
2008	7/15–7/19	44°00–46°40	20–55	4	15	–	–
2008	8/11–8/15	44°00–46°40	10–55	4	19	–	–
2008*	9/22–9/24	44°00–44°40	11–55	2	10 (1)	17	50–68
2009	5/16–5/20	44°00–46°40	11–55	4	17	–	–
2009	6/14–6/18	44°00–46°40	20–55	4	16	–	–
2009*	7/16–7/20	44°00–46°40	20–55	4	16 (1)	9	49–61
2009*	8/18–8/22	44°00–46°40	10–55	4	18 (6)	37	51–68
2009*	9/14–9/18	44°00–46°40	10–55	4	20 (9)	27	52–67

*Cruises with *D. gigas*

^{D}Two of these trawls occurred during the daytime

bution family with over-dispersed residual errors and a log link (Ciannelli et al. 2008; 2010), using only stations with positive squid catches (n = 48 hauls). GAMs took the general form:

1) SAIP *Dosidicus gigas* Presence/Absence ~ s (“Environmental Variable”)
2) SAIP *Dosidicus gigas* Count ~ Offset(ln(Volume Filtered)) + s(“Environmental Variable”)

The use of an offset term is necessary in Poisson-distributed models, which only accept integers as input variables (in our case squid catch). For these GAMs, the offset term was needed to standardize Humboldt squid catch by the volume filtered by the fishing net (in m^3). Humboldt squid captured in tows from the SAIP study were selected as response variables because Humboldt squid did not occur frequently enough in Predator study tows (n = 12) to allow a formal analysis. Environmental variables (covariates) considered included station depth, surface (5 m) and subsurface (20 m) temperature, salinity, density, and DO (September 2008 and May–September 2009 only). These two depth strata were chosen because they corresponded best with the mixed layer depth and maximum depth of the thermocline. Stratification in the water column was approximated by taking the difference between the surface and subsurface water properties (i.e., 5 m–20 m temperature, salinity, density, and DO). Biological covariates consisted of the five dominant potential prey densities (Field et al. 2007) including northern anchovy, juvenile Pacific hake, Pacific herring (*Clupea pallasi*), Pacific sardine, whitebait smelt (*Allosmerus elongatus*), and euphausiids (Euphausiidae). We also evaluated Humboldt squid in relation to three large scale environmental variables (MEI, UI, and PDO; table 1). Models were penalized for increased curvature or increased nodes and were evaluated based on minimizing Un-Biased Risk Estimator (UBRE) for the binomial model or Generalized Cross Validation (GCV) scores for the Poisson model (Wood 2006).

TABLE 2 (cont'd.)

Research cruise dates for two NOAA Fisheries Northwest Fisheries Science Center studies occurring from 2004–2009: (a) the Stock Assessment Improvement Program (SAIP) study; and (b) the Predator study. Information presented for each cruise includes survey year, dates, latitude range (°N), distance range of stations offshore (in nautical miles), total number of transects, total trawls completed (and trawls containing Humboldt squid, *Dosidicus gigas* in parentheses), total number of *D. gigas* caught, and the associated dorsal mantle length range (ML in cm).

b. Predator study nighttime cruises 2004–2009

Year	Survey Dates	Start-end latitude	Distance range offshore	Number of transects	Total number of trawls (trawls containing *D. gigas*)	Total number of *D. gigas*	Length range
2004	4/28–4/30	46°10–46°40	4–25	2	11	–	–
2004	5/08–5/10	46°10–46°40	4–30	2	12	–	–
2004	5/18–5/20	46°10–46°40	4–30	2	11	–	–
2004	5/29–5/31	46°10–46°40	4–30	2	12	–	–
2004	6/13–6/15	46°10–46°40	4–30	2	12	–	–
2004	6/13–6/25	46°10–46°40	4–30	2	12	–	–
2004	7/06–7/08	46°10–46°40	4–30	2	12	–	–
2004	7/17–7/19	46°10–46°40	4–30	2	12	–	–
2004	8/10–8/12	46°10–46°40	4–30	2	12	–	–
2005	4/19–4/21	46°10–46°40	4–30	2	12	–	–
2005	5/02–5/04	46°10–46°40	4–30	2	12	–	–
2005	5/12–5/14	46°10–46°40	4–30	2	12	–	–
2005	5/24–5/26	46°10–46°40	4–30	2	12	–	–
2005	6/04–6/06	46°10–46°40	4–30	2	12	–	–
2005	6/13–6/15	46°10–46°40	4–30	2	12	–	–
2005	6/26–6/28	46°10–46°40	4–30	2	12	–	–
2005	7/06–7/08	46°10–46°40	4–30	2	12	–	–
2005	7/30–8/01	46°10–46°40	4–25	2	11	–	–
2005	8/11–8/13	46°10–46°40	4–30	2	12	–	–
2006	5/11–5/13	46°10–46°40	4–30	2	12	–	–
2006	5/25–5/27	46°10–46°40	4–30	2	12	–	–
2006	6/01–6/03	46°10–46°40	4–30	2	12	–	–
2006	6/12–6/14	46°10–46°40	4–30	2	12	–	–
2006	7/05–7/07	46°10–46°40	4–30	2	12	–	–
2006	7/17–7/19	46°10–46°40	4–25	2	11	–	–
2006	8/15–8/17	46°10–46°40	4–30	2	12	–	–
2006*	8/28–8/30	46°10–46°40	4–30	2	12 (1)	2	59–63
2007	5/07–5/09	46°10–46°40	5–30	2	10	–	–
2007	5/22–5/24	46°10–46°40	5–25	2	10	–	–
2007	6/04–6/06	46°10–46°40	5–25	2	10	–	–
2007	6/21–6/23	46°10–46°40	5–25	2	9	–	–
2007	7/08–7/09	46°40	5–23	1	5	–	–
2007	7/23–7/25	46°10–46°40	5–25	2	10	–	–
2007	8/05–8/07	46°10–46°40	4–25	2	9	–	–
2007	8/21–8/23	46°10–46°40	4–25	2	10	–	–
2008	5/24–5/26	46°10–46°40	5–25	2	10	–	–
2008	6/12–6/14	46°10–46°40	5–25	2	9	–	–
2008	6/21–6/23	46°10–46°40	5–25	2	9	–	–
2008	7/01–7/03	46°10–46°40	5–25	2	10	–	–
2008	7/21–7/23	46°10–46°40	5–25	2	9	–	–
2008	8/05–8/07	46°10–46°40	4–30	2	12	–	–
2009	5/09–5/11	46°10–46°40	4–25	2	11	–	–
2009	5/23–5/25	46°10–46°40	5–25	2	10	–	–
2009	6/06–6/08	46°10–46°40	5–25	2	10	–	–
2009	6/20–6/22	46°10–46°40	5–25	2	9	–	–
2009*	7/07–7/09	46°10–46°40	5–25	2	9 (1)	5	51–56
2009	7/23–7/25	46°10–46°40	4–25	2	11	–	–
2009*	8/08–8/10	46°10–46°40	5–30	2	11 (1)	25	48–66
2009	8/23–8/25	46°10–46°40	4–30	2	12 (9)	2299	36–79

* Cruises with *D. gigas*

RESULTS

We caught Humboldt squid in 48 of 412 trawls and during every year of the SAIP study, representing a Frequency of Occurrence (FO) of 12% (table 2a). Dorsal mantle lengths (ML) for SAIP squid ranged from 46–68 cm over all years (table 2a). Length frequency histograms for SAIP study Humboldt squid catches by month and year is given in Figure 1. Comparisons of the SAIP squid lengths within each year by month found that squid significantly (t-tests, all $p < 0.05$) increased in size from

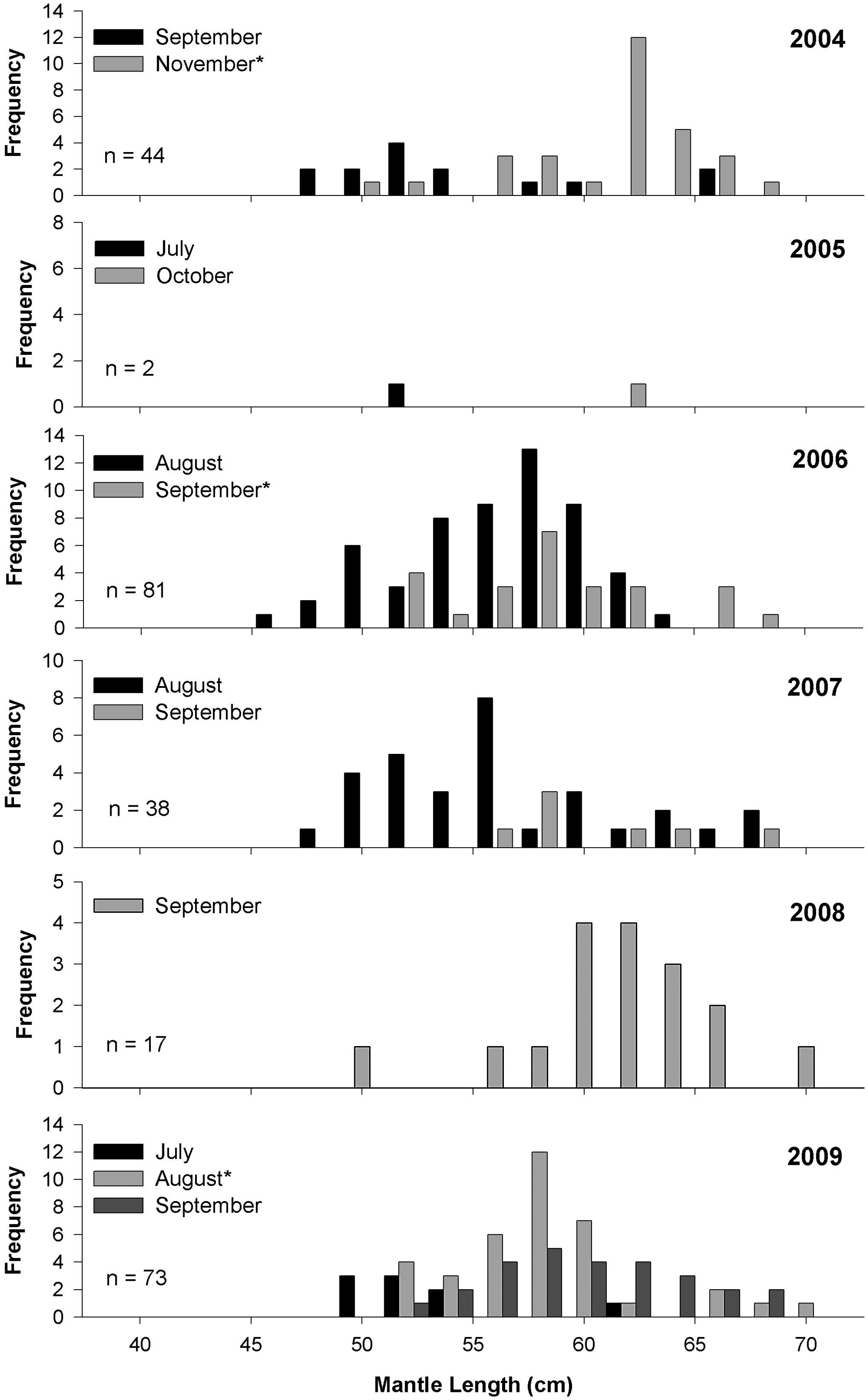

Figure 1. Length frequency histogram for dorsal mantle length (ML [cm]) measurements of Humboldt squid (*Dosidicus gigas*) caught in monthly Stock Assessment Improvement Program (SAIP) study nighttime midwater trawls shown in Figures 2 and 3 (n = 255). Only months with positive catches of *D. gigas* are presented. Months followed by a "*" represent months where lengths were significantly larger than measurements in a previous cruise. There were too few length measurements in 2005 and 2007 for statistical comparison.

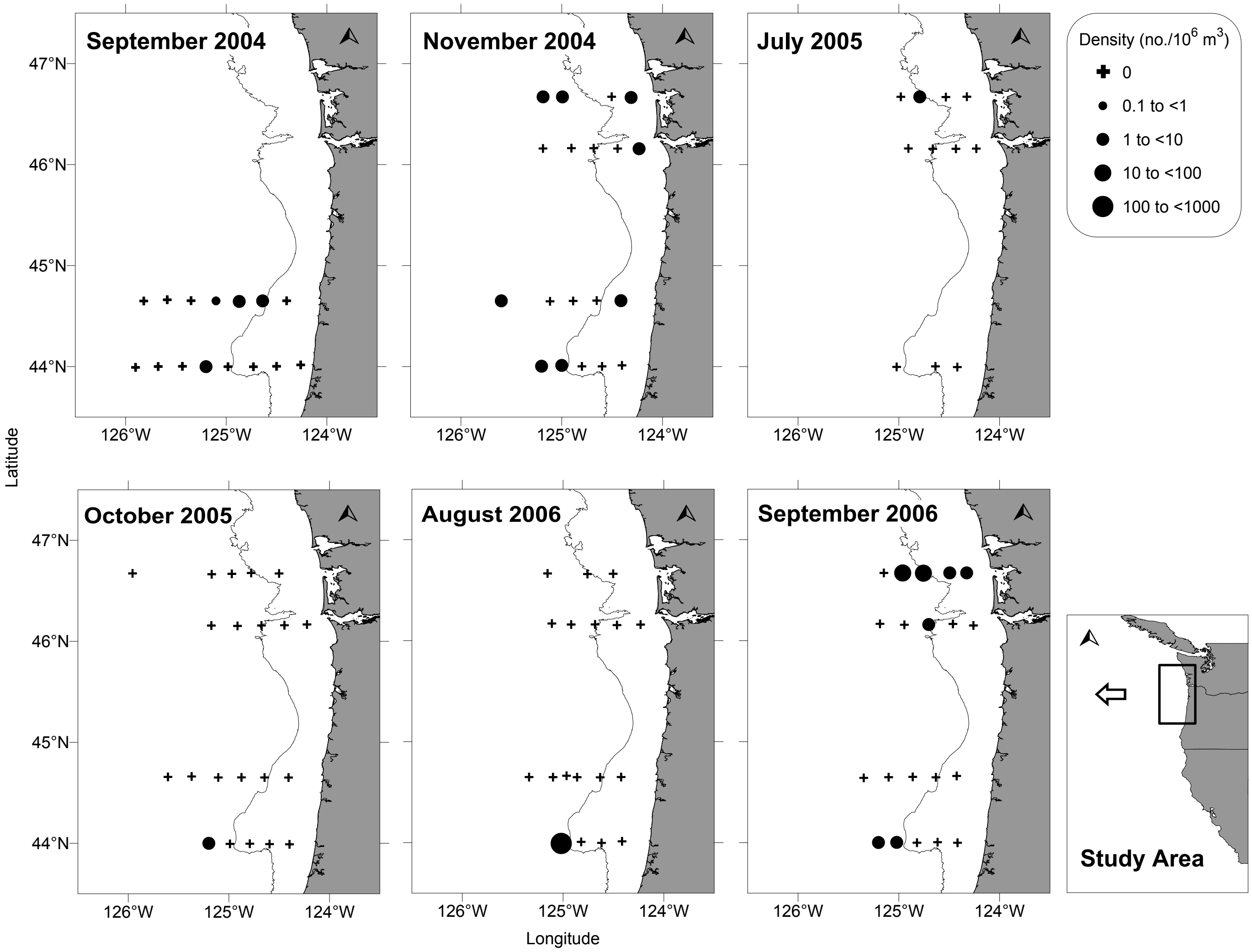

Figure 2. Maps showing the distribution and density (number [10^6 m^3]$^{-1}$) of Humboldt squid (*Dosidicus gigas*) captured during monthly spring-fall nighttime Stock Assessment Improvement Program (SAIP) study midwater trawls between 2004 and 2006. Each map shows the shelf break isobath (200 m) and trawls with zero squid catch are represented by a "+". Despite similar sampling grids, no Humboldt squid were captured in cruises during the following months: June–August 2004, June, August–September 2005, or May–June 2006 (not shown).

September to November 2004, August to September 2006, July to August 2009, but not from August to September 2007 or 2009. Visual inspection of Humboldt squid densities and distributions for cruises with positive catches indicated that most squid were found off the shelf before August, but moved onto the shelf in later months (figs. 2 and 3).

Minimum DO concentration (ml L^{-1}) typically was observed near the bottom of each CTD cast, as expected, and at times reached levels considered hypoxic for some organisms (<1.40 ml L^{-1}). We plotted minimum DO values integrated over our entire sampling grid for cruises after 2008 in Figure 3, with Humboldt squid densities and distributions overlaid over the DO values. The highest densities of Humboldt squid occurred in August 2009 and were in hypoxic nearshore waters off the Columbia River (fig. 3).

Catches of Humboldt squid from surface trawls conducted by the Predator study in 2004–2009 were much rarer than the SAIP study. The FO for Predator study trawls was only 2% (12 of 535 trawls; table 2b). Furthermore, 11 of the 12 positive squid trawls during the Predator study were in 2009, with the only other positive trawl in July 2006. However, in August 2009, 43% of all Predator study trawls contained Humboldt squid, including one 30 minute surface trawl 20 nm off the mouth of the Columbia River at a station depth of 135 m, which contained 1,872 individuals (density of 1,671 squid [10^6 m^3]$^{-1}$) and estimated biomass of ~25 metric tons [mt]). These individuals showed tremendous size variation, ranging from 36 to 79 cm ML (table 2b) and their density far exceeded densities (25 squid [10^6 m^3]$^{-1}$) measured within their native range of the Gulf of California during March and April 2007 and November

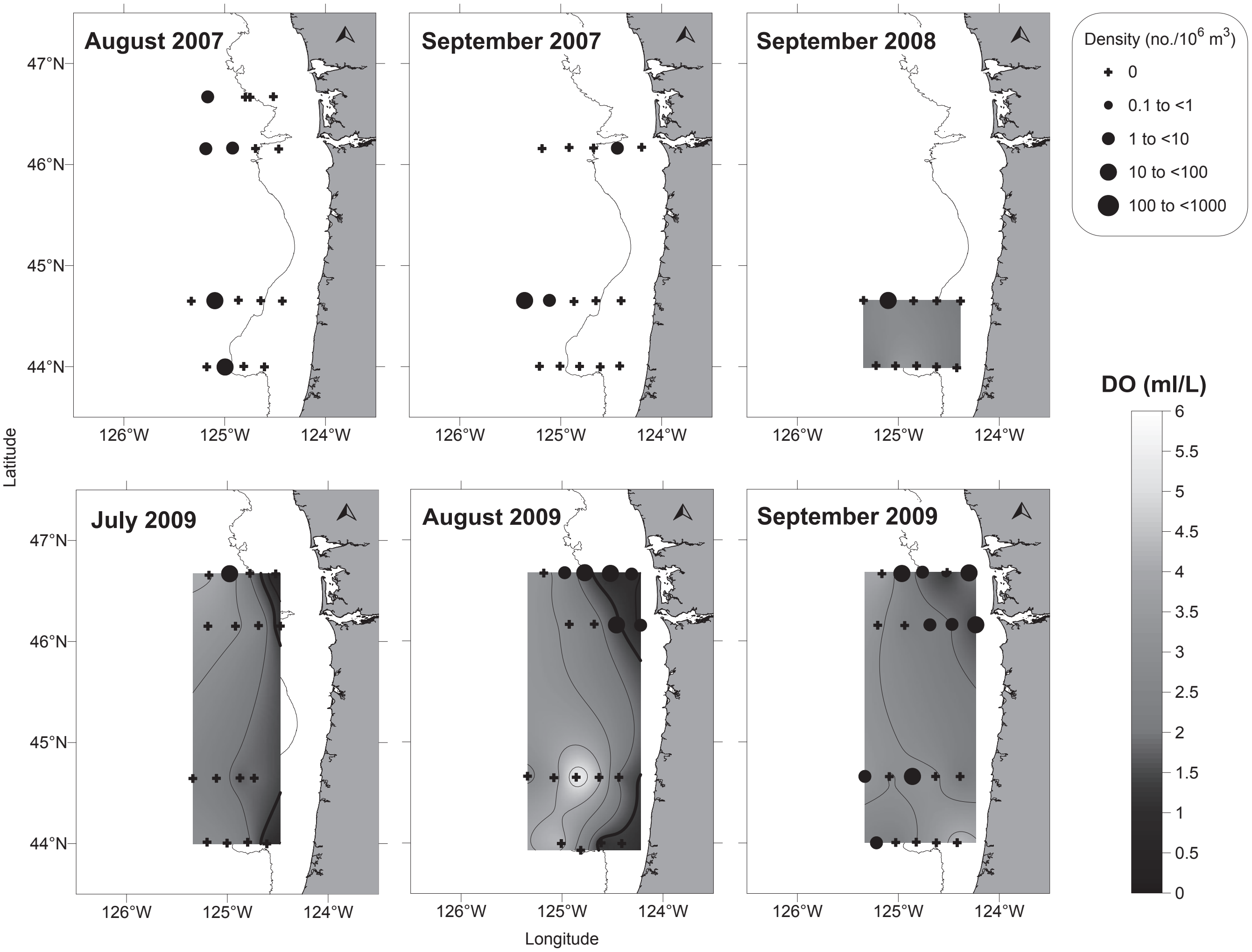

Figure 3. Maps showing the distribution and density (number $[10^6\ m^3]^{-1}$) of Humboldt squid (*Dosidicus gigas*) captured during monthly spring-fall nighttime Stock Assessment Improvement Program (SAIP) study midwater trawls between 2007 and 2009. Each map shows the shelf break isobath (200 m) and trawls with zero squid catch are represented by a "+". Despite similar sampling grids, no Humboldt squid were captured in cruises during the following months: May–July 2007, May–August 2008, May–June 2006, or May–June 2009 (not shown). Beginning in 2008, we measured dissolved oxygen (DO) concentration (ml L^{-1}) from the surface to 100 m depth (or within 5 m of the bottom in stations where the depth <100 m) prior to each trawl. The last four panels show minimum DO values measured over the water column. Note the aggregation of Humboldt squid in the area of hypoxic DO conditions (>1.4 ml L^{-1}; dark black contour) during August 2009 on the shelf of the two northernmost transects (Willapa Bay and Columbia River).

2008 (Matteson and Benoit-Bird 2009). At the time of capture, large numbers of squid were observed at the surface near the vessel along with schools of adult Pacific sardine breaking the surface (personal observation).

For the SAIP study, GAMs (table 3, fig. 4) provided best-fit models and significant ($p < 0.05$) environmental variables for Humboldt squid catch data. For the binomial GAMs, salinity ranked best as an explanatory variable for Humboldt squid presence/absence (table 3, fig. 4a). For the Poisson distribution GAMs, station depth and subsurface water temperature, salinity and density at 20 m were all significantly ($p < 0.05$) associated with Humboldt squid and ranked best (lowest GCV scores without being overfit) among all models (table 3), with larger squid catches associated with a station depth of approximately 1000 m, and water at 20 m measuring 11–13°C, 32.4–32.8 psu, and 24.5–25.0 kg m^{-3}, respectively (fig. 4b). No large-scale environmental variables were reliably associated with Humboldt squid catches because of model over-fitting (fig. 4). GAMs run with a limited data set in which measurements of DO were included yielded insignificant results. Additionally, no biotic factors (prey fish) were significant variables explaining Humboldt squid catch in SAIP study tows, partially because there were too few prey measurements to allow a formal analysis.

Despite higher Humboldt squid FO in SAIP study cruises compared to Predator study cruises from 2004–2009, we observed the highest overall squid densities during Predator study cruises in 2009 (eight cruises alto-

TABLE 3
Output for Humboldt squid (*Dosidicus gigas*) two-part conditional Generalized Additive Models (GAMs), showing the association between Humboldt squid catch and environmental covariates from the Stock Assessment Improvement Program (SAIP) study. The left side (1) shows the results of GAMs from 315 tows (2004–2009) using a binomial family fit with a logit-link function on Humboldt squid presence-absence data. Individual covariates were individually explored and can be ranked by Un-Biased Risk Estimator (UBRE) score (smallest to largest). The associated p-values, fit, adjusted R-squared values, and percent deviance explained are also given. The right side (2) shows results from over-dispersed Poisson GAMs using only the 48 positive tows for squid catch fit with catch data and the log of the volume filtered. Environmental covariates for these GAMs are ranked by Generalized Cross Validation (GCV) score; associated p-values, fit, adjusted R-squared values, and percent deviance explained are also presented. The best models based on lowest UBRE/GCV scores are shown in bold. Covariates examined, but excluded from the analyses because of insufficient data or over fitting include: the large-scale environmental variables: MEI, PDO and UI; dissolved oxygen concentration, the difference between 5 and 20 m temperature, and the associated prey densities of northern anchovy (*Engraulis mordax*), juvenile (10–30 cm total length) Pacific hake (*Merluccius productus*), Pacific herring (*Clupea pallasi*), Pacific sardine (*Sardinops sagax*), whitebait smelt (*Allosmerus elongatus*), and euphausiids (Euphausiidae) from each tow.

	1. Binomial GAMs (n = 315 hauls)					2. Over-dispersed Poisson GAMs (n = 48 hauls)				
Variable	UBRE	p-value	Fit	Adjusted R-sq	Deviance Explained (%)	GCV	p-value	Fit	Adjusted R-sq	Deviance Explained (%)
Salinity 20 m	**–0.169**	*	+	**0.035**	**5.0**	**12.483**	**	+/–	**–0.348**	**39.1**
Density 20 m	–0.123	n.s.	n.s.	0.005	1.3	**12.573**	**	+/–	**–0.265**	**49.7**
Station Depth	–0.134	n.s.	n.s.	–0.003	0.1	**14.228**	***	+/–	**–0.778**	**30.7**
Salinity 5 m	**–0.163**	**	+	**0.026**	**3.5**	14.823	*	overfit	–0.853	41.8
Temperature 20 m	–0.147	n.s.	overfit	0.036	4.9	**15.566**	*	+/–	**–0.939**	**22.1**
Density 5 m	–0.126	n.s.	n.s.	0.004	1.7	16.097	*	overfit	–0.445	41.8
Salinity Difference	–0.143	n.s.	n.s.	0.005	1.1	16.171	n.s.	n.s.	–1.110	19.3
Density Difference	–0.139	n.s.	n.s.	0.023	4.3	17.608	n.s.	n.s.	–1.460	17.7
Temperature 5 m	–0.167	n.s.	overfit	0.043	6.7	18.650	n.s.	n.s.	–3.170	0.6

Significance codes: 'n.s.' $p > 0.05$ '*' $p < 0.05$ '**' $p < 0.01$ '***' $p < 0.001$

gether). We compared the time-series of squid density, sea surface temperature (SST at 3 m), and potential prey density (juvenile hake) observations from each Predator study cruise in 2009 (fig. 5). The PDO Index was in phase with SST measured at the effective sampling depth of our surface trawls (3 m; fig. 5a), and was more representative of in situ ocean conditions measured during the eight Predator study cruises of 2009 than either the MEI or UI (not shown). A clear pattern emerged between increasing SST (and PDO Index) and increasing juvenile hake density through August. However, when we began catching Humboldt squid at high densities in August 2009, juvenile hake density fell to zero (fig. 5).

DISCUSSION

Changes in ocean conditions probably contributed to northward seasonal expansions of Humboldt squid to waters off Oregon and Washington from 2004–2009. The NWFSC first captured Humboldt squid in 2004, while surveying marine resources using midwater trawls offshore of Hecata Head, OR as part of the SAIP study (fig. 2). In 2006, we recorded the first incidence of Humboldt squid in surface trawls during the Predator study (table 2b). The summer of 2006 was particularly noteworthy due to a severe expanse of hypoxic water ranging across the shelf in nearshore waters from Cape Perpetua, OR (44˚17) north to La Push, WA (47˚54) (Chan et al. 2008). Seasonal hypoxia has been observed in nearshore waters off Oregon and Washington in all years beginning in 2002, although the most severe event occurred in the summer of 2006 (Chan et al. 2008). The repeated hypoxic events off Oregon and Washington are considered by some to be a symptom of climate change (Grantham et al. 2004; Levin et al. 2009). Humboldt squid are extremely tolerant of low DO (Gilly et al. 2006), and on this basis we hypothesize that the low DO in shelf waters off Oregon and Washington may be suitable habitat for these aggressive predators.

During August and September 2006, we retained a subsample of Humboldt squid from the SAIP study and Field et al. (2007) conducted a dietary analysis on these specimens (n = 24; mean ML = 54 cm in August and 58 cm in September). Although net feeding may have biased results (Field et al. 2007), primary prey items in decreasing order of abundance included juvenile Pacific hake, northern lampfish (*Stenobrachius leucopsarus*), blue lanternfish (*Tarletonbeania crenularis*), Pacific sardine, euphausiids, and shortbelly rockfish (*Sebastes jordani*). Other prey items included crustaceans, pteropods, cephalopods, other unidentified coastal pelagics, mesopelagics, and flatfish. While not necessarily representative for their whole distribution range, these findings are consistent with other diet studies that found Humboldt squid prey on sardine (Ehrhardt et al. 1983; Markaida and Sosa-Nishizaki

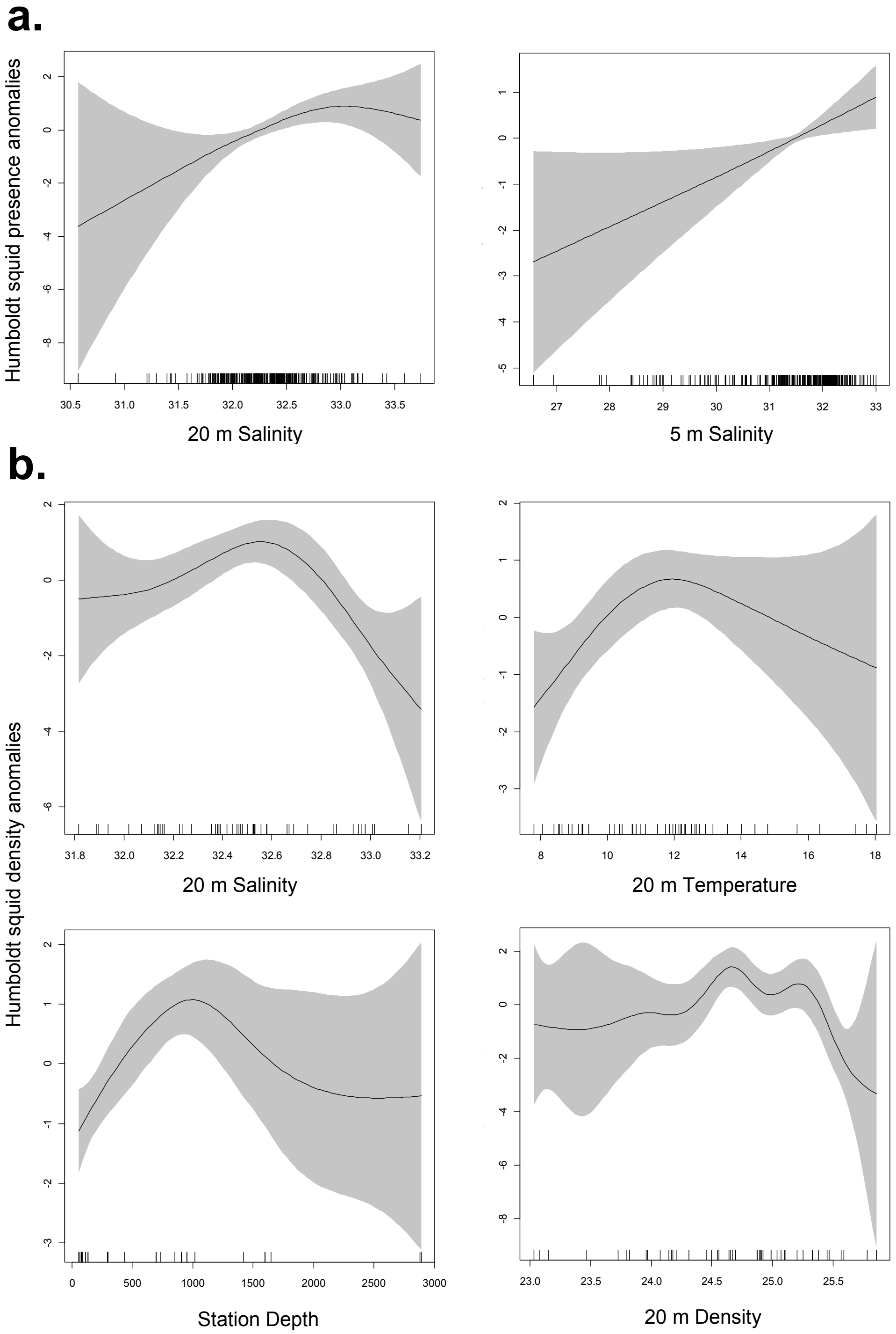

Figure 4. Significant outputs for the environmental variables used to fit the (a) binomial distribution, and (b) over-dispersed Poisson distribution Generalized Additive Models (GAMs) shown in Table 1. Variation in covariate main effects are shown along the x-axes, whereas the y-axes represent spline smoother functions for Humboldt squid (*Dosidicus gigas*). The grey area represents 95% confidence intervals surrounding the covariate main effect.

2003), hake (Markaida and Sosa-Nishizaki 2003), mackerel (Sato 1976; Ehrhardt et al. 1983), and anchovies (Sato 1976; Markaida et al. 2008), all of which are major fisheries in the CCS that could be impacted by range expansion of this predator. Furthermore, recent evidence of predatory attacks on juvenile and adult Pacific salmon (*Oncorhynchus* spp.; L. Weitkamp, NWFSC Newport and J. Field, SWFSC Santa Cruz, personal communication) suggests that salmonids may be impacted by Humboldt squid predators as well. There is clearly a need to develop alternative Humboldt squid diet sampling strategies to better understand their prey field for future work.

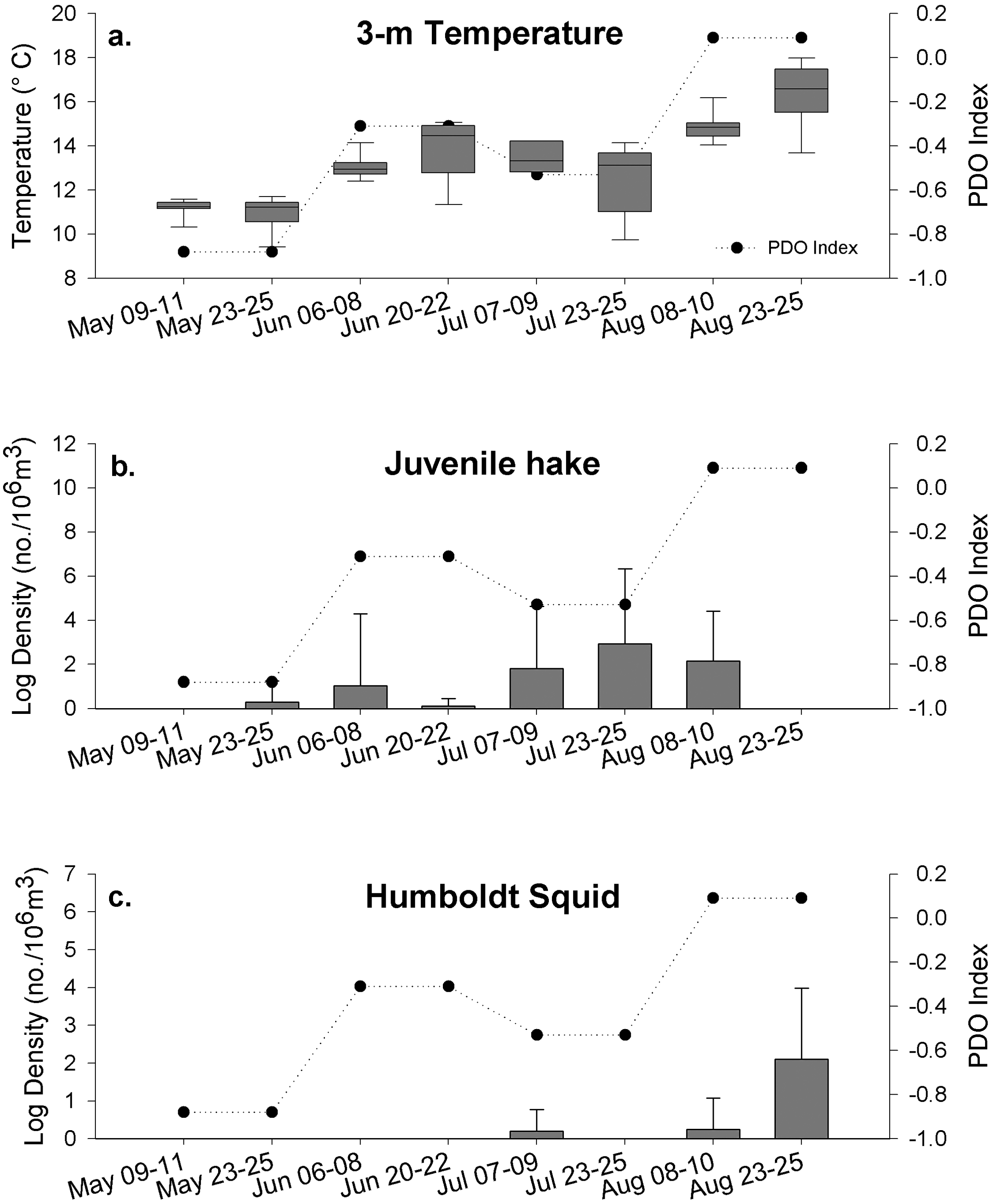

Figure 5. Plots showing (a) surface (3 m) temperature; (b) density (number [10^6 m^3]$^{-1}$) of juvenile (10–30 cm total length) Pacific hake (*Merluccius productus*); and (c) density (number [10^6 m^3]$^{-1}$) of Humboldt squid (*Dosidicus gigas*) recorded during the eight NOAA Fisheries Northwest Fisheries Science Center Predator study cruises conducted biweekly between May and August 2009 (dates on x-axis). Overlaid behind each plot is the monthly value of the Pacific Decadal Oscillation (PDO) Index during each sampling period. Note the absence of juvenile Pacific hake during the last cruise (August 23–25, 2009), coincident with high densities of Humboldt squid.

Humboldt squid have been shown to exhibit tremendous variability in their growth rates and age at maturity (Keyl et al. 2008). In both the SAIP and Predator studies, squid captured earlier in the sampling season (July–August) tended to be smaller than squid captured in later cruises (September–November), which we hypothesize is related to growth (fig. 1). However, as an aggressive and fast-growing predator, capable of migrating up to 30 km day^{-1} and making diel vertical migrations upwards of 1,000 m (Gilly et al. 2006), the physiological and energetic demands of growing so large so quickly, coupled with a semelparous reproductive strategy, make growth patterns in individuals encountered during our study difficult to estimate.

Humboldt squid are opportunistic predators, yet Pacific hake ranging from 2–42 cm TL represented the most numerically important prey item from northern CCS samples in diet studies to date (Field et al. 2007). Prior to the 1997 El Niño, juvenile Pacific hake were rarely documented in the northern CCS. Recent surveys have revealed northward expansion of hake spawning and juvenile recruitment habitat (Phillips et al. 2007; Ressler et al. 2007), which overlaps with the observed range expansion of Humboldt squid from 2004–2009. We found that juvenile hake densities were reduced coincident with Humboldt squid presence in the northern CCS in 2009 (fig. 5), which was unexpected given that juvenile hake density within our study area in recent years increased in late summer (Emmett et al. 2006; Phillips et al. 2007). However, the degree to which this was significant is unknown. Total commercial U.S. landings of Pacific hake decreased from 248 thousand mt in 2008 to 122 thousand mt in 2009, a reduction of 51% (Stewart et al. 2011), and similarly low total U.S. commercial hake landings were reported in 2010 (161 thousand mt). Holmes et al. (2008) suggested that squid predation as well as secondary effects on schooling behavior and distribution of Pacific hake was important to this fishery, but the primary reason for the decline in total U.S. hake catches in 2009 and 2010 was the decline in coastwide allowable catches (optimal yield), based on stock assessment results (Stewart et al. 2011).

While it is unlikely that the current data sources will be able to detect squid-related changes in population dynamics, our results indicate that the top-down effects of predation exerted on Pacific hake by Humboldt squid could have a negative effect on recruitment of this important species. Currently, Pacific hake represent the largest fishery along the U.S West Coast. There is evidence from the Chilean hake fishery that squid may have a large and adverse impact on abundance due to direct predation of individuals of all sizes (Alarcón-Muñoz et al. 2008). Ongoing research at the NWFSC includes developing an index of hake recruitment in the northern California Current, quantifying the bioenergetic effects of the Humboldt squid on prey resources in this region (e.g., Field et al. 2007), and modeling the potential ecosystem impacts of Humboldt squid on extant fish populations.

Our GAM analyses confirmed that Humboldt squid was most likely to occur in warmer (12–14°C) water temperatures in water at approximately 1000 m depth. Subsurface salinity was also a significant covariant with Humboldt squid density, revealing the importance of understanding the physical and biological dynamics of the epipelagic region as an area of opportunistic predation. Follow-up work should include more detailed and broader scale distribution information and include data from daytime trawling and/or acoustics. Unfortunately, there were too few DO measurements to provide meaningful results in our GAMs, although we still consider DO a reasonable explanatory abiotic variable for future consideration, particularly given the observed association between squid and DO in August 2009 (fig. 3). Our GAM findings are consistent with observations from recent tagging (Gilly et al. 2006) and diet (Field et al. 2007; Markaida et al. 2008) studies implicating that the dynamics of the upper boundary of the OMZ is important to Humboldt squid foraging ecology. We conclude that the physical properties (including the OMZ) and source water (from basin-wide phenomenon such as El Niño) of the epipelagic region determines community structure within the northern CCS, and is critical in determining seasonal Humboldt squid foraging visits.

The fact that no biotic factors (prey fish density) ranked as significant covariates with Humboldt squid in SAIP tows in any of our GAMs was related to differences in catchability of the prey sampled at 30 m in SAIP study midwater tows, patchy distribution both temporally and spatially for the prey field and Humboldt squid, and perhaps predator avoidance (table 3, fig. 4). The reliance on midwater trawl caught data from night efforts is too limiting to draw strong conclusions owing to the highly variable catchability of the different species, variability of diurnal behavior among the different prey species and the highly variable day-night depth distributions among all species. Many prey fish in the northern CCS are at the surface at night (Emmett et al. 2004; 2006), and therefore sampling the density and distribution of prey fishes is best accomplished by fishing at the surface at night. The effect of surface-caught prey (from Predator study catches) on Humboldt squid density is not represented in the biotic variables presented in our GAM analysis, and should be addressed in future studies.

Despite similar sampling efforts by the NWFSC in 2010, no Humboldt squid were caught off Oregon and Washington from May–September (Litz unpublished data). Based on these results, we conclude that ocean conditions were not favorable in 2010 to support a northerly shift of Humboldt squid and/or that available prey resources were not as abundant in 2010 as in other years. In addition, the lack of any known occurrences of larval or juvenile specimens in the northern CCS implies there was no Humboldt squid spawning or recruitment off Oregon and Washington during 2008–2009, and that the seasonal visits of Humboldt squid to the northern CCS during the period from 2004 to 2009 were opportunistic and probably related to feeding and not reproduction. However, ongoing research efforts in waters off Oregon and Washington will continue to monitor future Humboldt squid foraging visits, habitat associations, and predator-prey relationships within the northern California Current.

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