

INTERACTIONS BETWEEN JUMBO SQUID (*DOSIDICUS GIGAS*) AND PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*) IN THE NORTHERN CALIFORNIA CURRENT IN 2007

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ABSTRACT

During a joint Canada-U.S. Pacific hake (*Merluccius productus*) acoustic-trawl survey in 2007, 82 jumbo squid (*Dosidicus gigas*) were captured at depths exceeding 300 m offshore of the continental shelf along Vancouver Island and the Queen Charlotte Islands. Because the acoustic signs associated with these captures were unusual, we compared 38 kHz echograms collected during trawls in which both hake and jumbo squid were caught with those from nearby trawls in which only hake or squid were caught. Hake appeared to be more widely dispersed or less densely aggregated when jumbo squid were captured concurrently. We hypothesize that squid predation causes an avoidance response in hake, thereby altering normal aggregation behavior. Although our evidence of jumbo squid predation on Pacific hake is limited to seven echogram comparisons, this new predator-prey interaction may lead to cascading trophic impacts in the northern California Current. On a practical level, our findings also suggest that the acoustic survey methods, which use a combination of visual echogram interpretation and trawling to verify target identification, will require adjustment. If hake are dispersed over larger coastal areas or do not aggregate as recognizable targets when jumbo squid are present, then additional ship time and other resources may be required for future acoustic-trawl surveys.

INTRODUCTION

Jumbo squid (*Dosidicus gigas*) were first sighted in northern California Current waters off Oregon in 1997 (Percy 2002) and in waters off Washington and British Columbia in 2004 (Cosgrove 2005; Trudel et al. 2006). Between 2002 and 2006, jumbo squid underwent a rapid range expansion from eastern tropical Pacific waters into the southern California Current (Field et al. 2007) that coincided with climate-related increases in regional sea surface temperature and declines in large predatory fish that prey on squid (e.g., Field et al. 2007; Zeidberg and Robison 2007). Local declines in Pacific hake (*Merluccius productus*) abundance in Monterey Bay between 1998 and 2005 (Zeidberg and Robison 2007) and Chilean hake (*M. gayi*) abundance off central Chile between 2000

and 2007 (Arancibia and Neira¹) may be related to increased jumbo squid predation as a result of range expansion (e.g., Field et al. 2007) or to shifts in hake distribution driven by climate-related changes in sea surface temperature (e.g., Smith et al. 1990).

Pacific hake is the most abundant groundfish in the California Current system and is an important commercial species in both Canada and the United States (Ressler et al. 2007). The coastal or offshore Pacific hake stock (referred to as hake hereafter) is the largest and most important of three stocks along the west coast of North America. This stock disperses from winter spawning grounds off southern California to northern feeding areas off the coasts of northern California, Oregon, Washington, and British Columbia during the summer months (June through August) where it forms dense midwater aggregations at depths of 150–300 m along the continental shelf break during daylight hours (Dorn 1995; Mackas et al. 1997).

Echo-integration trawl surveys (acoustic surveys) to assess the distribution and abundance of hake have been conducted since 1977 jointly by the United States National Marine Fisheries Service with Canada's Department of Fisheries and Oceans since 1992, under the auspices of the International Hake Treaty which recognizes that this stock is a transboundary resource. These surveys are conducted between June and September and target aggregations of adult hake (age 3 and older) along the continental shelf and upper slope from central California (36°N) to Dixon Entrance, British Columbia (54.7°N), or southeast Alaska, if necessary (fig. 1). Survey timing coincides with the completion of the annual northward migration and the full availability of hake to the survey (Nelson and Dark 1985). Acoustic backscatter data at 38 kHz attributed to hake are converted into estimates of biomass and abundance and verified using data from midwater and bottom trawls that confirm species composition and provide measurements of length,

¹Arancibia, H., and S. Neira. 2007. An overview of the present state of common hake (*Merluccius gayi*) stock with a forecast of its biomass including jumbo squid (*Dosidicus gigas*) prey-predator relationship in central Chile (33°S–39°S). Paper S-7 presented at California Cooperative Oceanic Fisheries Investigations Annual Science Conference 2007, Hubbs-SeaWorld Research Institute, San Diego, California, November 26–28, 2007.

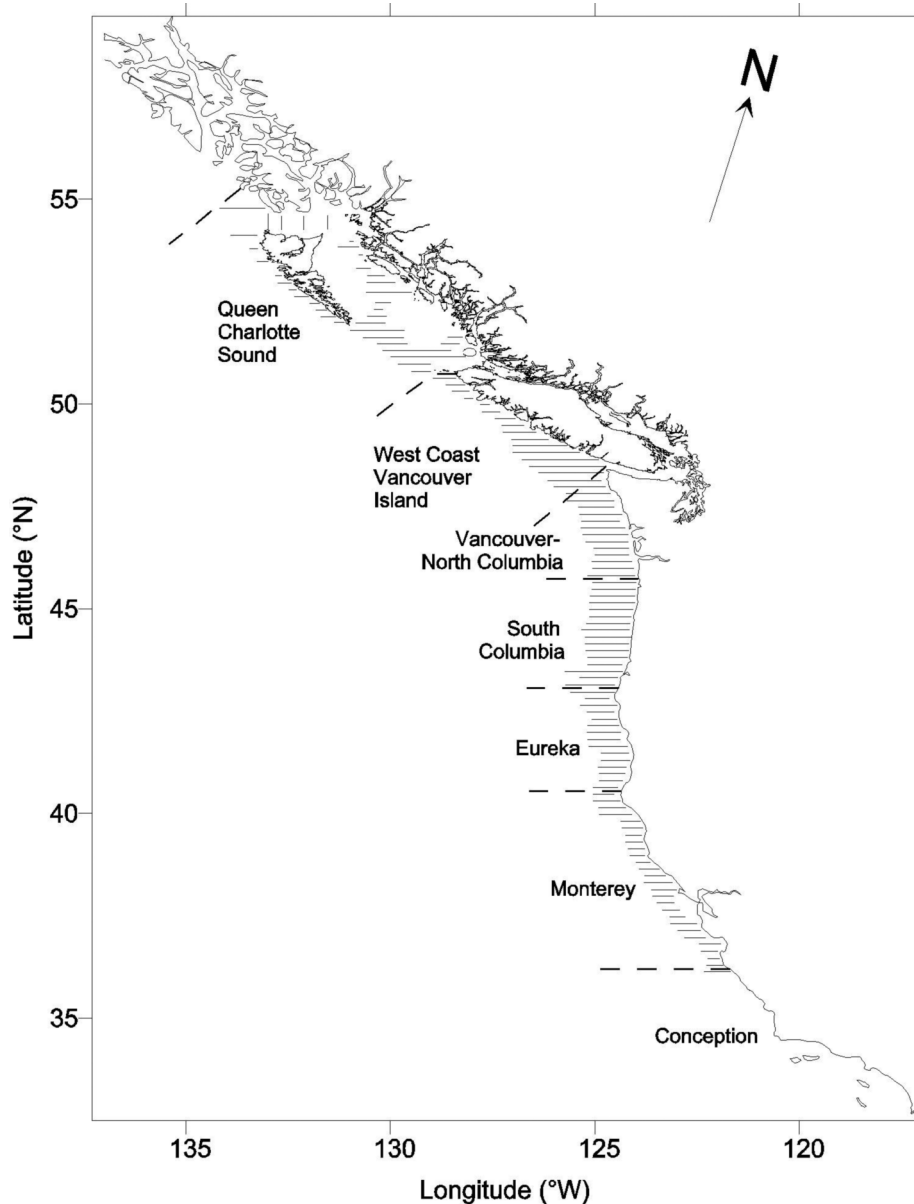


Figure 1. Generalized Pacific hake (*Merluccius productus*) acoustic survey transect pattern along the west coast of North America. Latitudinal location of transects in each survey may vary from those shown since placement is measured in 10 nmi intervals from a randomly chosen starting latitude south of Monterey, California. Statistical areas are from the International North Pacific Fishery Commission, with modifications in Canadian waters, and are used to group hake backscatter data for analysis.

weight, sex, and age. The acoustic surveys were conducted triennially between 1977 and 2001 and biennially from 2001 to 2007. The protocols and methodology used in these surveys are consistent with the best practices used worldwide (MacLennan and Simmonds 1992) and are fully described by Guttormsen et al. (2003) and Fleischer et al. (2005).

The earliest confirmed incidental catches of jumbo squid in the acoustic survey time-series (1977–2007) occurred in 2003 (Fleischer et al. 2005), although a specimen, lost before the Royal British Columbia Museum

could confirm identification, was caught during the 1998 survey (K. Cooke, Fisheries and Oceans Canada, pers. comm.). Several authors have suggested that the recent range expansion of jumbo squid in the eastern Pacific Ocean may result in increased predation on hake (e.g., Field et al. 2007; Zeidberg and Robison 2007) and this predation combined with high fishing mortality will mean that hake are unlikely to be effective competitors with jumbo squid (Rodhouse 2008). In this paper, we document jumbo squid catches during hake acoustic surveys conducted between 2001 and 2007. We focus on

2007 sightings because unusual acoustic signs recorded during this survey led us to hypothesize that interactions between jumbo squid and hake were affecting normal hake aggregation behavior.

METHODS

Our data sets consist of trawl catch data and acoustic backscatter data per unit area ($s_A - m^2/nmi^2$) collected during acoustic surveys of hake in 2001, 2003, 2005, and 2007. The trawl data set consists of numbers and total weights (kg) of all recognizable species as well as length, sex, maturity, and condition data for hake. Raw acoustic data from Simrad 38 kHz and 120 kHz split-beam transducers in the 2001 and 2003 surveys and Simrad 18, 38, 120, and 200 kHz split-beam transducers in the 2005 and 2007 surveys were logged, but the 38 kHz acoustic signals are the primary data source for quantitative hake acoustic backscatter (s_A) measurements. Data from other frequencies were used qualitatively as aids in determining hake water column distributions.

Acoustic data were collected with Simrad EK500 (2001, 2003) or EK60 (2005, 2007) scientific echosounding systems. The transducers were located on a hydraulic ram that was extended 1.2 m below the keel to 5.2 m below the surface (CCGS *W.E. Ricker*) or on a centerboard that held the transducers 9 m below the surface (NOAA RV *Miller Freeman*). Acoustic sample rates were automatically determined based on sound propagation and internal processing constraints, but ping intervals typically ranged from 0.5 s in shallow waters to 2.5 s at water column depths >1000 m. The acoustic systems were calibrated in the field before, sometimes during, and after the survey by suspending copper spheres with known backscattering cross-sections below the transducers and measuring the acoustic returns using standard procedures described by Foote et al. (1987) and

MacLennan and Simmonds (1992). Split-beam target strength and echo-integration data were collected to calculate echosounder gain parameters and beam patterns during calibration.

Acoustic data (s_A) were collected along east-west oriented transects spaced at 18.5 km (10 nautical miles) intervals from a randomly chosen starting latitude south of Monterey, California (fig. 1). The inshore and offshore ends of each line were established when hake were no longer detectable acoustically or, in the absence of hake, from 50 m depth inshore to 1500 m depth offshore. Both the southern and northern limits of the survey grid were initially based on historical knowledge of hake distribution patterns and environmental conditions prior to a survey. Near real-time satellite data on coastal ocean conditions and commercial fishing reports were reviewed at sea to ensure that survey coverage encompassed the full expanse of the hake distribution at the time of each survey. Acoustic data were collected at vessel speeds of 9–12 knots (4.6–6.1 m/s) and only during the day when hake were acoustically detectable and aggregations recognizable on the echogram. Shortly after sunset and throughout the night, hake disperse in the water column, mixing with other species and reforming in discrete layers around sunrise (Guttormsen et al. 2003; Fleischer et al. 2005).

Midwater and bottom trawls were used to obtain representative catches of species composition and size distributions of organisms detected acoustically. Trawls were conducted based on the occurrence and pattern of backscattering layers observed at the time of each survey rather than using a sampling design with predetermined locations and effort. Distinct layers of intense backscatter consistent with high densities of hake were the highest priority for trawl sampling, but other types of backscattering features, both in terms of marginal areas

TABLE 1
Summary of integrated acoustic and trawl surveys conducted jointly by Canada and the United States since 2001.

	2001 ^a	2003	2005	2007
Vessel	<i>Miller Freeman; W.E. Ricker</i>	<i>W.E. Ricker</i>	<i>Miller Freeman</i>	<i>Miller Freeman</i>
Survey dates	15 June–29 July, 6–18 August	29 June–01 September	20 June–19 August	19 June–21 August
Start–end latitudes (°N)	36.2–50.2; 50.2–54.8	36.1–51.4	35.7–54.8	35.8–54.8
Acoustic frequencies (kHz)	38, 120	38, 120	18, 38, 120, 200	18, 38, 120, 200
Vessel speed (m/s)	6.0; 4.6	4.6–5.1	5.6–6.1	5.6–6.1
Number of transect lines	81; 49	115	106	133
Total survey distance (km)	4,870; 640	6,756	21,246	21,201
Trawl Gear ^b (Number of trawls)	AWT (72), PNE (14), PRT (41)	PRT (88), PYT (18)	AWT (61), PNE (2)	AWT (82), PNE (10)
Biomass estimate (x 10 ⁶ t)	0.74	1.84	1.26	0.88
% biomass—Canada	10	20.3	40.4	25.3
% biomass—United States	90	79.7	59.6	74.7
Reference	Guttormsen et al. (2003)	Fleischer et al. (2005)	Fleischer et al. unpubl. ms ^c	

^aOrder of column values is RV *Miller Freeman* followed by CCGS *W.E. Ricker*; both ships used the same acoustic frequencies.

^bAWT—Aleutian wing midwater trawl with a codend of 3.2 cm; PNE—polyethylene Nor’eastern bottom trawl with a 3.2 cm codend mesh liner; PRT—Polish rope midwater trawl with 1 cm codend mesh; PYT—Poly-Yankee 36 bottom trawl with 2.5 cm codend liner.

^cFleischer, G. W., K. D. Cooke, P. H. Ressler, R. E. Thomas, S. K. de Blois, and L. C. Hufnagle. In prep. The 2005 integrated acoustic and trawl survey of Pacific hake, *Merluccius productus*, in U.S. and Canadian waters off the Pacific coast. U.S. Dept. Comm., NOAA Tech. Memo.

TABLE 2
 Aquatic species accounting for $\geq 90\%$ of biomass in pelagic and bottom trawls during hake
 echo-integration trawl surveys, 2001–2007. Figures are proportion of total catch weight in each survey.
 Data taken from Guttormsen et al. (2003), Fleischer et al. (2005), and Fleischer et al.^a

Species	2001		2003		2005		2007	
	Pelagic	Bottom	Pelagic	Bottom	Pelagic	Bottom	Pelagic	Bottom
Pacific hake	66.9	60.1	78.6	72.7	86.9	56.1	91.4	
Pacific herring	10.6		3.4					
walleye pollock	8.8			1.6				
spiny dogfish	3.9	0.9	6.7		1.0	37.8	1.2	
canary rockfish							1.8	
splitnose rockfish		15.1		3.3	3.3			
yellowtail rockfish	6.1		1.0		2.7		2.9	
widow rockfish					1.7			
yellowmouth rockfish			4.0		1.1			
Pacific ocean perch		10.8	1.2	2.4	1.1			
chillipepper rockfish			1.6	2.1				
silvergray rockfish				2.5				
sharpchin rockfish		2.7						
redstripe rockfish		1.2						
stripetail rockfish				1.7				
Pacific sanddab		1.8						
arrowtooth flounder				1.9				
rex sole				1.1				
Dover sole		1.2		1.7				
jumbo squid	0	0	0.4	0	<0.1	0	1.0	

^aFleischer, G. W., K. D. Cooke, P. H. Ressler, R. E. Thomas, S. K. de Blois, and L. C. Hufnagle. In prep. The 2005 integrated acoustic and trawl survey of Pacific hake, *Merluccius productus*, in U.S. and Canadian waters off the Pacific coast. U.S. Dept. Comm., NOAA Tech. Memo.

of low fish density and putative aggregations of species other than hake, were also sampled (Fleischer et al. 2005). Because the trawls targeted hake for verification of acoustic sign and because tow effort and locations were not standardized between surveys, neither relative nor absolute abundances of incidental species can be inferred from the trawl data.

Research vessels and trawl gear used for surveying hake varied with survey year, although the majority of effort and catches were with midwater trawls (tab. 1). Either a Polish rope trawl (PRT) with 20 m vertical opening and 1 cm codend mesh (CCGS *W. E. Ricker*) or an Aleutian wing trawl (AWT) fitted with a 3.2 cm or 1.2 cm codend mesh liner (NOAA RV *Miller Freeman*) were used for midwater and near-bottom sampling. Bottom trawls were made using a Poly-Yankee 36 research trawl (PYR) with a 4–5 m vertical opening, roller gear on the footrope, and a 2.5 cm codend mesh liner (CCGS *W. E. Ricker*) or with a polyethylene Nor'eastern (PNE) high opening bottom trawl (NOAA RV *Miller Freeman*) fitted with roller gear and a 3.2 cm codend mesh liner (Guttormsen et al. 2003). We compiled data on jumbo squid catches and locations from all surveys, beginning with the 2001 survey. Echograms were catalogued (S. de Blois, U.S. National Marine Fisheries Service, Seattle, Washington, unpubl. data) to illustrate characteristic backscatter patterns for targets verified with trawl catches during the 2005 and 2007 surveys. Using the results from the 2007 survey, we visually compared

and contrasted 38 kHz echograms at locations with catches of both hake and jumbo squid and echograms at nearby locations in which trawl catches were dominated by hake alone.

RESULTS

Pacific hake were the dominant species by weight in both pelagic and bottom trawl catches (tab. 2), consistent with the targeted approach to trawling for acoustic sign verification during the acoustic surveys. Spiny dogfish (*Squalus acanthias*) and a variety of rockfish species (*Sebastes* spp.) were the most common incidental species in these catches. Incidental catches of rockfish are not unusual since trawling is often conducted in areas where hake and rockfish are known to mix (e.g., northwest tip of Vancouver Island) in order to assign proportions to the mixed acoustic signal for species-specific biomass estimates. The first verified catches of jumbo squid in the acoustic survey time-series (1977–2007) occurred in two trawls near San Francisco in 2003 at depths of 317 and 434 m (tab. 2; fig. 2). The number of squid caught in hake trawls increased from 67 (66 in a single tow) in 2003 to 82 from seven tows in 2007. Total trawl effort (the number of trawls regardless of the length of the tow) was 106, 63, and 92 in the 2003, 2005, and 2007 surveys, respectively (fig. 3). The low catch of only three jumbo squid in three tows in 2005 does not necessarily reflect squid dynamics since operational constraints reduced overall trawling effort during this survey. The aver-

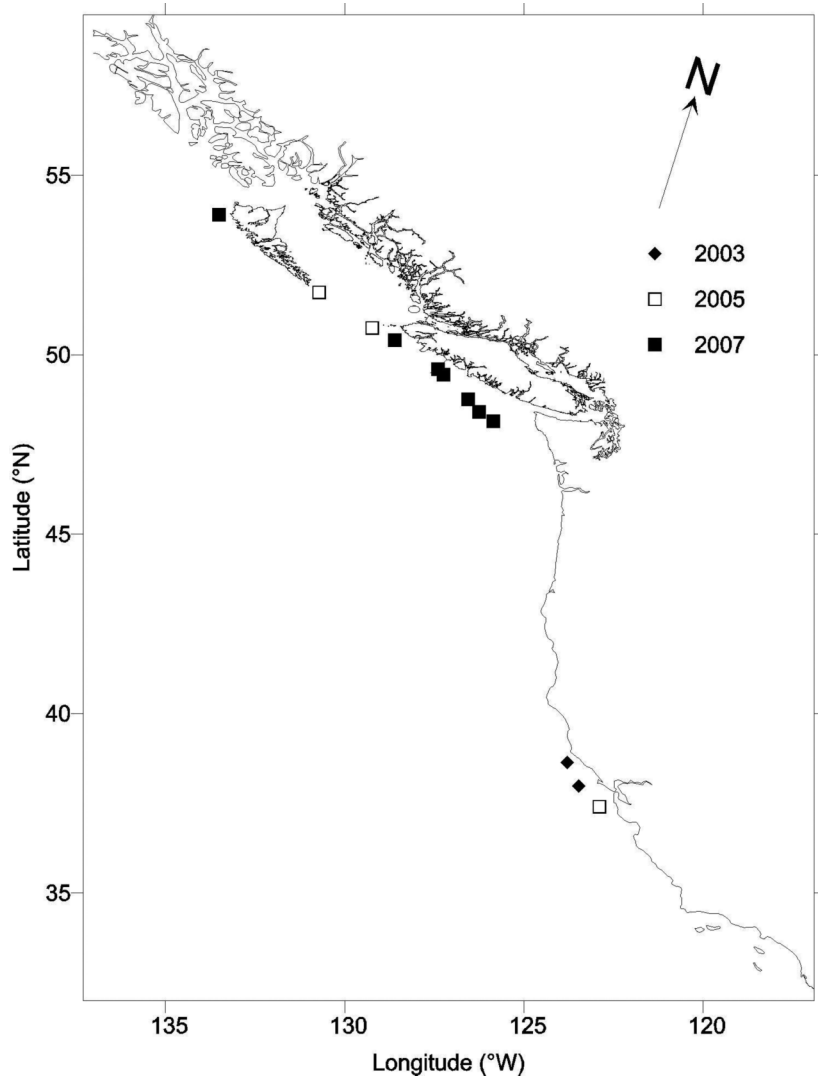


Figure 2. Jumbo squid (*Dosidicus gigas*) catch locations during 2003, 2005, and 2007 hake (*Merluccius productus*) acoustic surveys of the Pacific coast of North America.

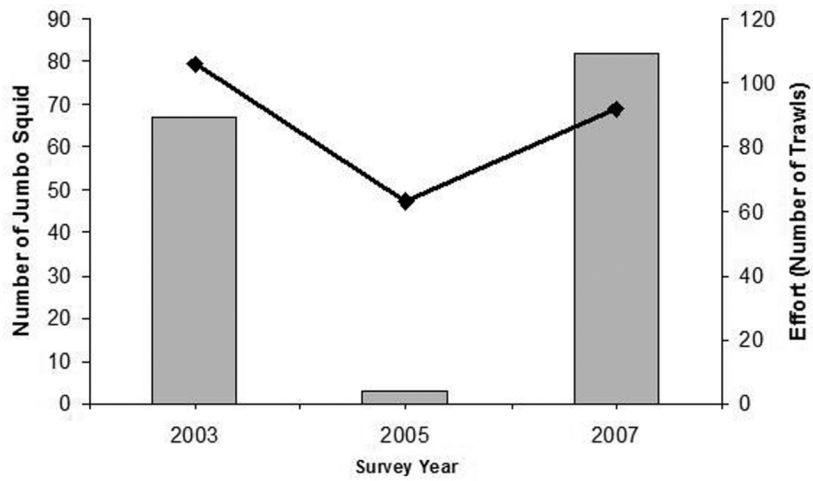


Figure 3. Total jumbo squid (*Dosidicus gigas*) catches (bars, left axis) and trawl effort (line, right axis) during 2003, 2005, and 2007 hake (*Merluccius productus*) acoustic surveys of the Pacific coast of North America.

age size of captured squid was similar in all years (5.4 kg in 2003, 5.0 kg in 2005, 5.7 kg in 2007). Jumbo squid were captured with hake in seven pelagic trawls north of 48°N in 2007 (fig. 2) and west of the shelf break at an average depth of 366 m (ranging from 330–400 m). One midwater tow in 2007 (Transect 75, the most southern 2007 location shown in fig. 2) captured jumbo squid at a depth of 400 m but no hake. The majority of recent jumbo squid catches (84 of 85 in 2005 and 2007 combined) were north of 48°N (fig. 2) at depths ranging from 172 to 405 m, at or west of the continental shelf break (defined as the 200 m isobath).

Since our analysis in this paper relies on echogram interpretation, we provide a brief description of echograms and their contents. An echogram displays the location of backscatter (targets) in the water column with respect to depth below the transducer vertically, and distance travelled by a survey vessel horizontally. A depth grid at 50 m intervals and a distance grid at 0.5 nmi intervals are overlaid on the echogram to facilitate orientation and interpretation. The choice of vertical and horizontal intervals is arbitrary and can be changed to suit different users. The spacing of the distance grid (vertical lines in the echograms that follow) is constant when vessel speed is constant, but will change when the vessel slows (wider) or increases (narrower) speed. The strongest echoes are returned by the bottom, which typically appears as a heavy dark trace overlaid with a lighter bottom tracking line produced by the echosounder (and referred to as the sounder-detected bottom). When water depth is shallow (<200 m) and the bottom is composed of hard substrates, second and third bottom echoes will appear below the first or true bottom echo (see figs. 4A, 5B, 6B for examples of multiple bottom echoes). Echoes above the bottom trace represent targets (plankton, fish) in the water column. Fish and plankton are identified by the visual pattern of these echoes, their location in the water column relative to bottom features, and the intensity and density of echoes at different frequencies (higher frequencies detect smaller organisms such as plankton, lower frequencies are better at detecting larger organisms, such as fish) combined with trawl sampling to verify user interpretations. Echograms display echo intensity on a logarithmic scale (dB) using a color scheme derived by Simrad (1993) for the EK500 echosounder, which represents low echo intensity with “cold” colors (green, blue, grey) and high echo intensity with “warm” colors (yellow, orange, red). We produced the echograms in this paper as grey-scale images (figs. 4–6), but the original color images are available from the authors by request. In the echograms that follow, echo intensity is displayed on a grey scale, with light to moderately-dark greys corresponding to low s_A in the water column (low fish density) and dark grey to black corresponding to

high s_A in the water column (high fish density). Areas with no echo returns, or where acoustic signal intensity falls below a minimum threshold of –69 dB, are white. The threshold is used to remove acoustic noise and echoes from organisms too small to be hake. The bottom appears as a broad grey zone outlined with a lighter grey trace line that follows the bathymetry and represents the sounder-detected bottom.

Hake show two distinctive visual patterns on the 38 kHz echogram at normal vessel survey speeds during the day in the vicinity of the shelf break based on signal intensity, morphological criteria, and relative density in the water column. A low-density pattern consists of a diffuse speckled band of small grey groups or layers of fish spread over a broad depth range as on Transect 55 in 2007 (grey regions outlined by polygons in fig. 4A). This low-density scatter often includes other small meso-pelagic fishes such as Myctophidae (lanternfishes) and plankton (light grey targets underlying the polygons in fig. 4A). Conversely, high densities of hake produce distinct clusters (schools) or a W-shaped band of darker grey tones and black that may continue relatively unbroken for distances up to several kilometers (dark grey patterns in polygon in fig. 4B). The high-density patterns generally span a narrower depth stratum than the low-density pattern and these aggregations are usually composed entirely of hake.

The low- and high-density backscatter patterns also differ with respect to their location in the water column relative to bottom features. For example, the low-density pattern in Figure 4A (in the polygons) is not associated with specific bottom features since it usually occurs 200 m or more below the surface and offshore of the shelf edge, but was observed at depths exceeding 500 m in 2007. Low-density hake aggregations remain discernable within the meso-pelagic acoustic sign attributable primarily to Myctophidae (below the polygons in fig. 4A) in the absence of jumbo squid. In contrast, the high-density pattern is typically observed at or near the shelf break and usually maintains itself within the 200–300 m depth range (fig. 4B). The offshore extent of the high-density hake scattering layer is thought to be associated with high productivity zones linked to ocean upwelling conditions (Mackas et al. 1997; Ressler et al. 2007).

Other species commonly observed during the acoustic survey are also recognizable using signal intensity, morphology, and location criteria. For example, lanternfishes (Myctophidae) largely comprise an indistinct layer of varying intensity, at water depths below 300 m (moderate to dark grey targets in the water below 300 m in fig. 5A). Pacific herring (*Clupea pallasii*) and sardine (*Sardinops sagax*) form dense schools near the surface (<50 m) and produce a characteristic intense (black) “double echo” signal, consisting of an echo in the water column (rec-

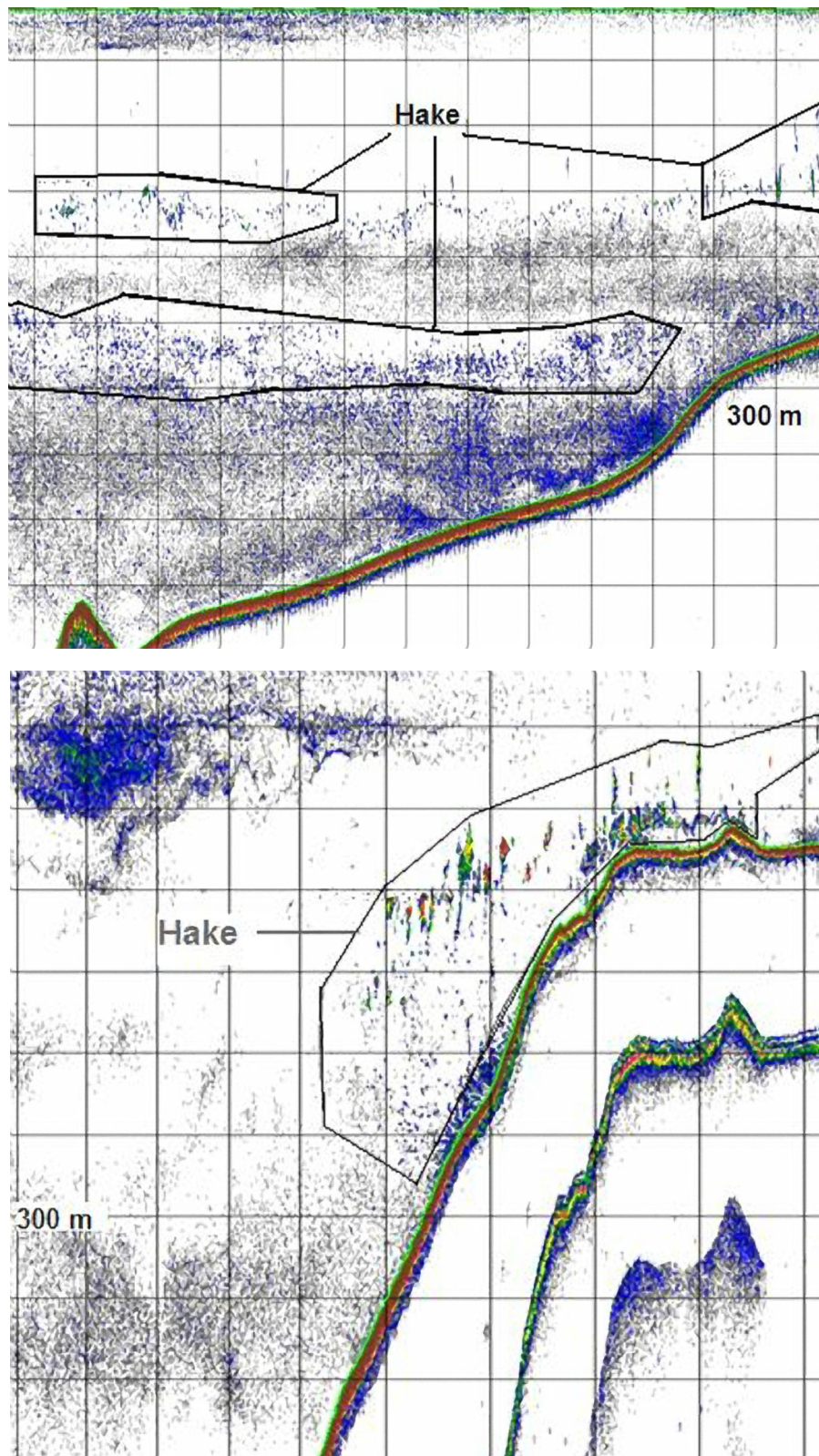


Figure 4. Grey scale examples of low- (A) and high- (B) density hake (*Merluccius productus*) backscatter patterns in 38 kHz echograms observed during the 2007 hake survey. The low-density pattern (in the polygons) was observed on Transect 55 (44.8°N) off Newport, Oregon, at a depth of 260 m on 10 July 2007 at 08:00. The high-density pattern was observed on Transect 29 (40.55°N) off Cape Mendocino, California, at a depth of 120 m on 29 June 2007 at 17:30. Horizontal lines are 50 m depth intervals (300 m is marked) and vertical lines are spaced at 0.5 nmi intervals.

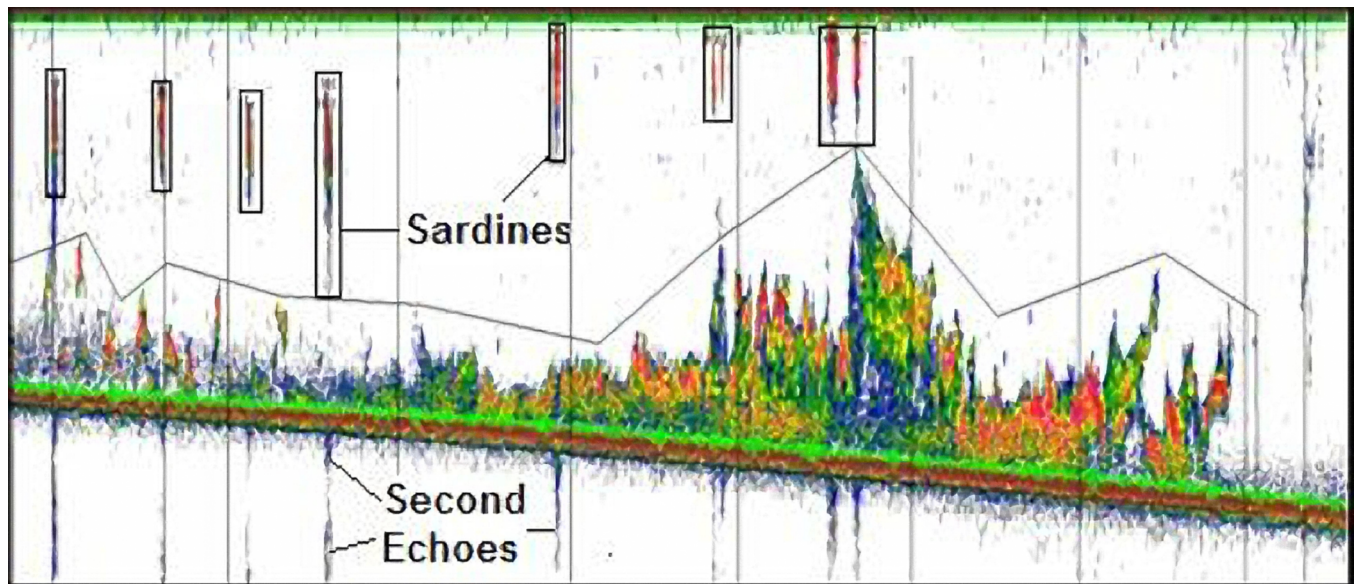
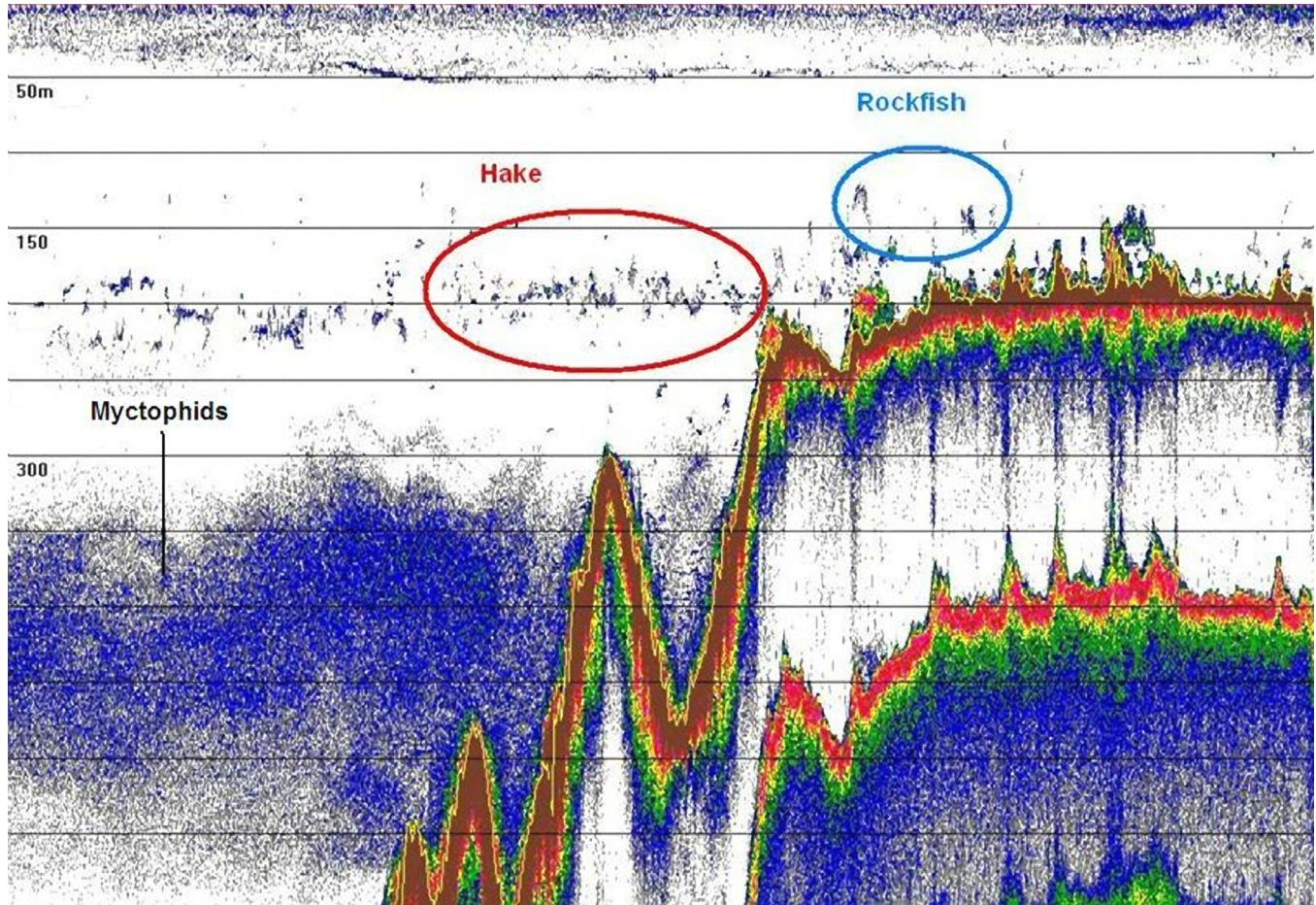


Figure 5. (A) Backscatter patterns near the continental shelf break in 38 kHz echograms from plankton at the surface to 50 m depth, rockfish chimney stacks, hake (*Merluccius productus*), and myctophids below 300 m. The bottom contour trace begins at 600 m depth and rises to 200 m. (B) Double echo returns from dense aggregations of sardine (*Sardinops sagax*) (within polygons) in shallow water over the continental shelf. A second echo aligned in the vertical plane to high-density fish schools can be seen below the bottom contour trace. Vertical lines represent 0.5 nmi intervals along the transect line.

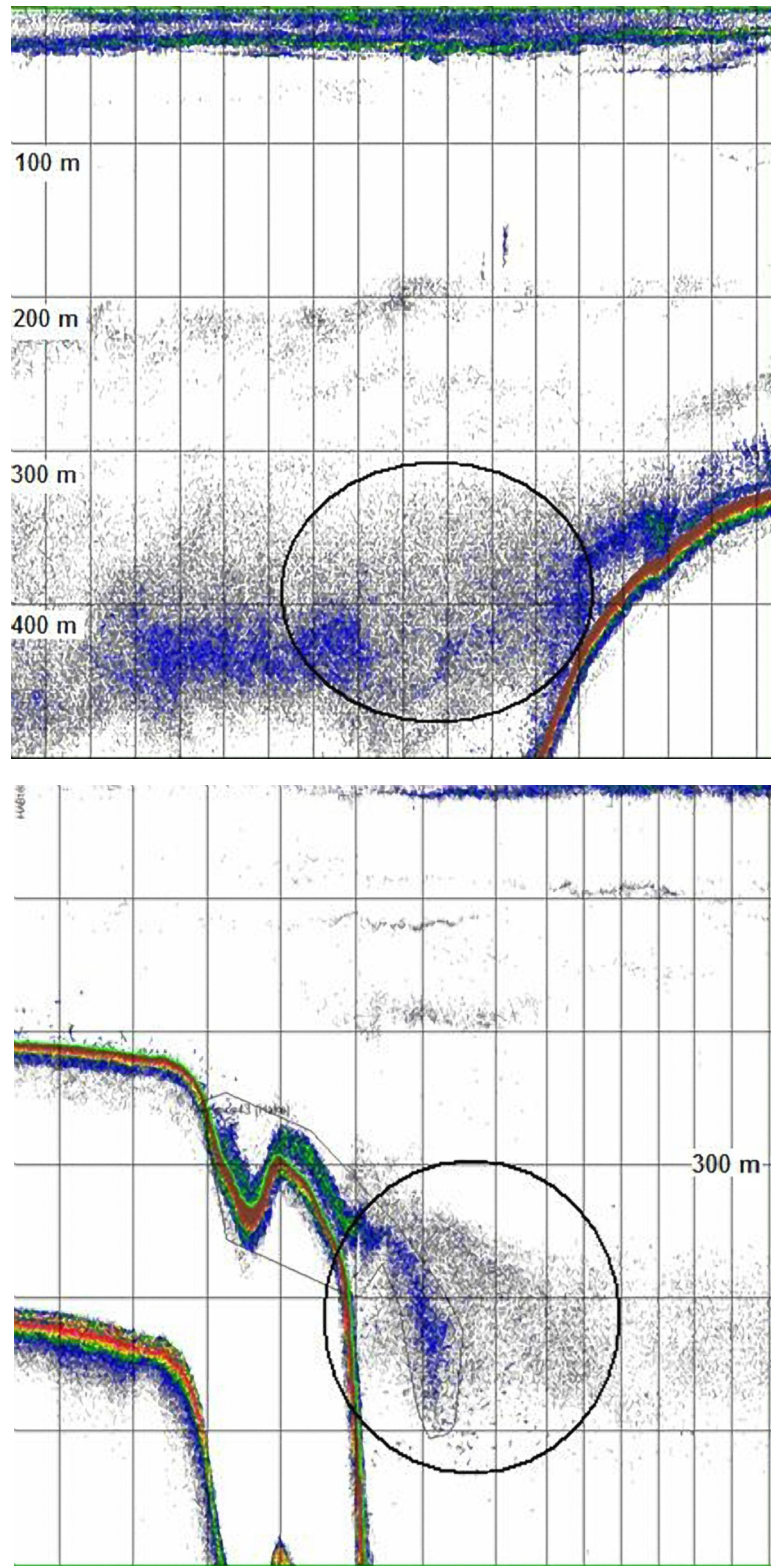


Figure 6. Two examples of mixed hake-jumbo squid backscatter patterns at 38 kHz (circled in A and B) which were considered atypical in 2007 because they resemble low-density layers usually characteristic of meso-pelagic Myctophidae, but contained hake (*Merluccius productus*). (A) Hake and jumbo squid (*Dosidicus gigas*) observed on transects 79 near La Pérouse Bank, British Columbia (48.8°N), at a depth of 350 m on 02 Aug 2007 at 20:25. Trawling on this sign resulted in a catch of 133.5 kg, consisting of 88% jumbo squid and 17% hake. (B) Hake-jumbo squid echogram observed on Transect 89 off northern Vancouver Island (50.5°N), at a depth of 330 m on 07 Aug 2007 at 07:26. A trawl catch of 553 kg consisted of 79% hake and 20% jumbo squid. Horizontal lines are 50 m depth intervals (300 m is marked) and vertical lines are spaced at 0.5 nmi intervals.

tangular polygons in the water column in fig. 5B) and a false echo below the bottom. The sardine aggregations in Figure 5B appear to be moving into or out of a larger aggregation near the bottom. Rockfish (*Sebastes* spp.) typically orient in vertical “chimney stack” formations in association with high-relief bottom types at the shelf edge or further inshore (fig. 5A).

Backscatter patterns at 38 kHz attributable to a mixture of hake and jumbo squid at the locations identified in Figure 3 differed from the hake backscatter patterns observed previously in 2007 and in earlier surveys. A wide diffuse band with few discernable groups and low signal intensity (grey) at depths >300 m was observed at 38 kHz (grey targets in the ellipses in figs. 6A and B). These morphological and signal-intensity features more often characterize myctophid layers (e.g., fig. 5A) rather than a low-density hake layer. In addition, the location of these layers, which were in close association with the shelf break below 300 m and near the bottom, was atypical of hake distribution patterns observed in other surveys. The pattern of hake distribution that we expected, based on experience in previous surveys, is one consisting of a uniform depth distribution across the shelf break, regardless of density. Hake may be near bottom inshore of the edge (fig. 4B) but usually maintain themselves within the zone of high productivity at depths of 200–300 m when seaward of the shelf break (fig. 4A). The unusual patterns observed in 2007 (figs. 6A and B) were only noted in Canadian waters north of 48°N. The normal pattern of hake distribution is related to coastal upwelling conditions, which were not unusual in 2007 relative to the long-term average (fig. 7A), and sea surface temperature, which was near-normal in 2007 (fig. 7B).

DISCUSSION

Jumbo squid is a large, short-lived, pelagic predator. Growth is rapid and allows squid to attain maximum sizes of 1.0–1.2 m dorsal mantle lengths and 30–50 kg during a life span of one to two years (Argüelles et al. 2001; Nigmatullin et al. 2001). Reproduction occurs year round, but peaks in spring and summer, and potential fecundity ranges between 0.3 and 13 million oocytes (Nigmatullin et al. 2001). Migrations for feeding in the summer and fall and spawning in the spring and summer are common (Nigmatullin et al. 2001) and may result in daily movements >30 km (Gilly et al. 2006). Jumbo squid are opportunistic predators of small pelagic and meso-pelagic fishes such as herring and sardines, other cephalopods, and pelagic crustaceans (e.g., Nigmatullin et al. 2001; Markaida and Sosa-Nishizaki 2003; Markaida 2006) and they undertake a diel vertical migration at dusk into near-surface waters to forage (Nigmatullin et al. 2001; Gilly et al. 2006). Tagging studies have demonstrated that squid in the Gulf of California occupy wa-

ters below 250 m during daylight hours and that they tolerate and forage in hypoxic conditions in the oxygen minimum layer at these depths because they are able to physiologically reduce oxygen consumption rates under hypoxic conditions (Gilly et al. 2001). Since the probability of catching squid in the upper-mixed layer of the water column during the day is low, future surveys targeting jumbo squid in the northern California Current should implement a sampling strategy that focuses on sampling between dusk and dawn. Short life span, high growth and reproductive rates, and aggressive predation coupled with physiological adaptations that permit tolerance of hypoxic conditions unfavorable to other species are ideal characteristics for invading species and confer competitive advantages to jumbo squid.

Jumbo squid inhabit tropical and subtropical eastern Pacific waters from Chile to the Gulf of California (Nigmatullin et al. 2001) and have spread into the waters off southern and central California (Field et al. 2007) and the Humboldt Current system off Peru (Yamashiro et al. 2007²). The earliest anecdotal reports of jumbo squid in eastern Pacific Ocean coastal waters north of central California are two 1997 reports of large numbers off Oregon (Percy 2002) and an unconfirmed sighting off Yakutat, Alaska (Cosgrove and Sendall 2004³), which were linked by these authors to the strong 1997–98 El Niño event. Cosgrove and Sendall (2004) also reported that jumbo squid were caught well offshore of Vancouver Island during research surveys along the Line P oceanographic line sometime between 1994 and 1998, although this has not been verified or documented by a taxonomic specialist. Following these initial observations, further sightings of jumbo squid were rare until the summer and fall of 2004 and 2005, when incidental catches were made by pelagic fisheries and research surveys off Washington and British Columbia and as far north as Sitka, Alaska (Cosgrove 2005; Trudel et al. 2006; Wing 2006). These jumbo squid occurrences were also considered transient summer range extensions as a result of warm climate-related ocean conditions, rather than El Niño events (Trudel et al. 2006; fig. 7B). The earliest verified catches of jumbo squid during hake acoustic surveys occurred in 2003 off central California. The next survey in 2005 recorded incidental catches in northern California Current waters, and in 2007 incidental catches

²Yamashiro, C., R. Castillo, N. Dominguez, C. Paulino, L. Vasquez, and L. Mariategui. 2007. Distribution and abundance of jumbo squid (*Dosidicus gigas*) off the Peruvian coast and their relationships to environmental conditions. Paper S-2 presented at California Cooperative Oceanic Fisheries Investigations Annual Science Conference 2007, Hubbs-SeaWorld Research Institute, San Diego, California, November 26–28, 2007.

³Cosgrove, J. A., and K. A. Sendall. 2004. First records of *Dosidicus gigas*, the Humboldt squid, in the temperate north-eastern Pacific. Available at: http://www.royalbcmuseum.bc.ca/Content_Files/Files/Collections%20and%20Research/Natural%20History/Dosidicus_paper.pdf

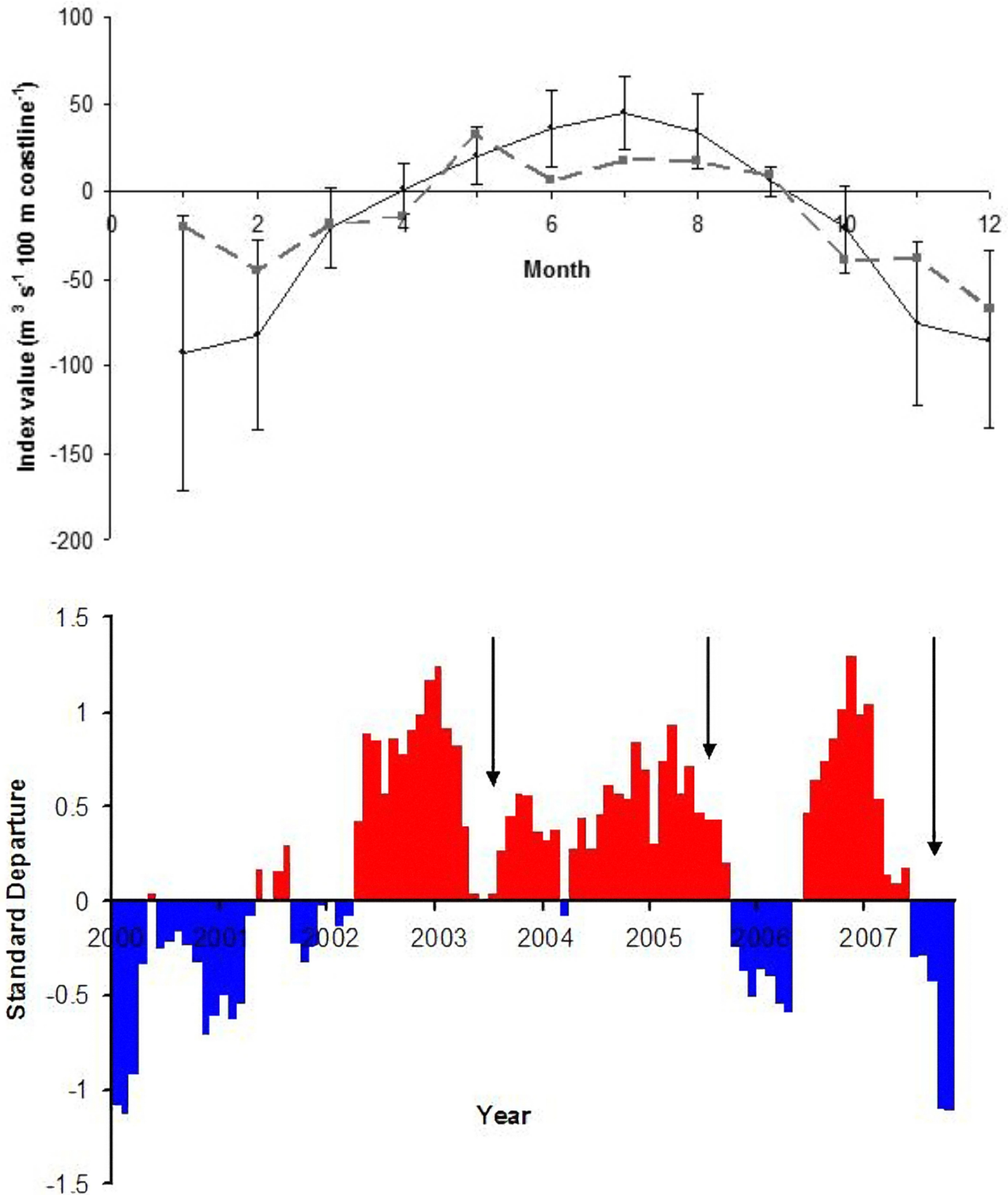


Figure 7. (A) Monthly average upwelling index values ± 1 standard deviation for the 1967–91 period at 48°N , 125°W (solid line) and monthly average upwelling values for 2007 (dashed line) at the same location. Positive values denote upwelling and negative values denote downwelling. Data retrieved from http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html. See http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/how_computed.html for index computation. (B) Multivariate El Niño-Southern Oscillation index time-series showing periods of warmer (above the x-axis) and cooler (below the x-axis) ocean conditions, 2000–2007. Arrows mark the approximate timing of hake acoustic surveys in 2003, 2005, and 2007. The MEI is the first unrotated principal component of six variables including sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky. See Wolter and Timlin (1998) for details. Numerical values of the MEI time-series are available at: <http://www.cdc.noaa.gov/people/klaus.wolter/MEI/table.htm>.

were made exclusively in these northern waters. The 2007 data do not appear to be a sampling artifact since the distribution of trawl locations and effort between San Francisco and Vancouver Island was not noticeably different from previous surveys.

At present, a self-sustaining population of jumbo squid is likely established off southern and central California as a result of the invasion that occurred in the 2002–06 period (Field et al. 2007; Zeidberg and Robison 2007; Rodhouse 2008). We hypothesize that multiple invasions have occurred in the northern temperate waters of the California Current since 1997 (and perhaps earlier) when climate-related ocean conditions were favorable (warm sea surface temperatures, enhance poleward transport of water), but these occupations did not appear to last very long and have not established a sustained population at present. The evidence supporting this hypothesis consists of anecdotal sightings and incidental catches of squid described above, which show a gap of several years between the earliest reports and more recent sightings. Similar evidence of multiple invasions in Monterey Bay is documented by Zeidberg and Robison (2007).

Our catches of jumbo squid during the 2007 hake survey were notable because the visual appearance of 38 kHz echograms associated with the mixed hake-jumbo squid trawls differed from hake-only trawl echograms. Regional hake distribution is related to sea surface temperature along with coastal upwelling and food production at the shelf break (e.g., Smith et al. 1990; Mackas et al. 1997; Benson et al. 2002), but coastal upwelling conditions in 2007 were not unusual relative to long-term averages (fig. 7A), and sea surface temperatures were near-normal (fig. 7B). Thus, the change in hake behavior is not a regional response to climate-related changes in ocean conditions but may be a response to more localized factors. We hypothesize that jumbo squid predation led to increased swimming activity and dispersal of hake, resulting in the diffuse, less dense aggregation pattern observed near the shelf break in some of the 2007 echograms. We recognize that the evidence supporting this hypothesis is limited to only a few instances in which our trawl catches verified a mixed hake-jumbo squid species composition in 2007 and that this evidence depends on the reliability of the echogram patterns that we described and our association between these patterns and catches. Our echogram interpretations are based on a time series of observations and verifications from trawling operations that provide biological samples of acoustic returns. These interpretations are subjective because judgment is involved, but this subjectivity is reduced through the use of a common group of interpreters for many surveys, the compilation of a catalogue of verified characteristic distribution patterns attributable to various species, including hake, and the

development of standardized protocols for scrutinizing and interpreting echograms. Historically, trawling effort at depths >300 m probably has not exceeded 10% in any survey since the low s_A at these depths translates to low hake biomass, which is not a sampling priority given limited vessel availability. However, we have sufficient experience sampling these deep indistinct layers to be confident that they consist primarily of small meso-pelagic species such as Myctophidae (see fig. 5A). Despite these caveats, the implications of this hake-jumbo squid interaction hypothesis for Pacific hake acoustic surveys are significant since the acoustic signs associated with mixed hake-squid catches likely would be attributed to small meso-pelagic fishes (e.g., myctophids or lanternfishes in fig. 5A) in the absence of evidence to the contrary. This interpretation would mean that hake in these mixtures will not contribute to overall biomass estimates. If our hypothesis is true and jumbo squid alter the aggregation pattern of hake, then additional ship time and trawling effort may be required in future surveys to identify and verify acoustic signs attributable to hake.

The potential ecosystem impacts of jumbo squid are not known with certainty at present. Zeidberg and Robison (2007) correlated the jumbo squid expansion into Monterey Bay with interactive effects of declines in top predators and climate-related changes in ocean conditions, but did not explicate causal mechanisms leading to declining hake abundance. Field et al. (2007) found that jumbo squid in the California Current preyed heavily on groundfish in the 15–45 cm size range, including hake and several rockfish species (*Sebastes* spp.). These authors also found that larger hake and rockfish were more frequently consumed during winter months off of central California, which is consistent with the migratory pattern of Pacific hake. Jumbo squid caught in winter months tended to be larger (Field et al. 2007) than those caught at other times and were presumably better able to feed on adult fish. Jumbo squid stomachs were not sampled during hake surveys in 2003, 2005, or 2007, so direct evidence of predatory activity on hake is not available. However, the diel vertical foraging migration of jumbo squid at dusk (Gilly et al. 2006) coincides with a vertical migration by hake into near-surface waters after dusk (Ressler et al. 2007), resulting in substantial overlaps in time and space. Further, the ability of jumbo squid to tolerate hypoxic conditions may be advantageous in establishing a multi-generational sustained population in northern waters of the California Current. Whitney et al. (2007) have documented a 17%–30% decrease in oxygen (20–40 $\mu\text{mol}/\text{kg}$) in the depth range 125–300 m at Ocean Station Papa (OSP, 50°N, 145°W) coupled with a shoaling of the hypoxic boundary (defined as 60 $\mu\text{mol O}_2/\text{kg}$) from ~400 to 300 m between 1956 and 2006. These findings are noteworthy because

they imply that hypoxic waters are moving eastward across the Pacific Ocean in the Subarctic Gyre, because coastal upwelling from Oregon to British Columbia draws waters from depths ranging between 100 and >250 m, and because they result in the simple projection that shelf and slope ecosystems will lose oxygenated habitat (Whitney et al. 2007). Species such as jumbo squid that tolerate low oxygen may expand their ranges, but pelagic species such as hake will either shift their distribution or perish. Given the potential overlaps in time and space between hake and jumbo squid, the hypothesis that hake are unlikely to be effective competitors with jumbo squid (Rodhouse 2008), and the knowledge that hake is the most abundant groundfish in the California Current and a key trophic linkage in this system (Ressler et al. 2007), there is ample cause for concern about potential ecosystem impacts. Ecosystem impact modeling that targets trophic interactions associated with jumbo squid invasions is warranted.

We used a simple visual comparison approach to identify mixed hake-jumbo squid acoustic signs. If the presence of jumbo squid continues to increase and disrupt hake behavior, then the application of more sophisticated techniques to identify hake and jumbo squid acoustic signs may be justified. For example, Benoit-Bird et al. (2008) estimated that the average in situ target strength (a measure of acoustic reflectivity) of jumbo squid was about -27.5 dB at 38 kHz, which compares to average in situ values of -33.2 and -35.5 dB reported for hake by Henderson and Horne (2007). These kinds of data could be used as filters in an image analysis procedure designed to automate the isolation and classification of echograms.

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LITERATURE CITED

- Argüelles, J., P. G. Rodhouse, P. Villegas, and G. Castillo. 2001. Age, growth and population structure of the jumbo flying squid *Dosidicus gigas* in Peruvian waters. *Fish. Res.* 54:51–61.
- Benoit-Bird, K. J., W. F. Gilly, W. W. L. Au, and B. Mate. 2008. Controlled and *in situ* target strengths of the jumbo squid *Dosidicus gigas* and identification of potential acoustic scattering sources. *J. Acoust. Soc. Am.* 123:1318–1328.
- Benson, A. J., G. A. McFarlane, S. E. Allen, and J. F. Dower. 2002. Changes in Pacific hake (*Merluccius productus*) migration patterns and juvenile growth related to the 1989 regime shift. *Can. J. Fish. Aquat. Sci.* 59:1969–1979.
- Cosgrove, J. A. 2005. The first specimens of Humboldt squid in British Columbia. *PICES Press* 13(2):30–31.
- Dorn, M. W. 1995. The effects of age composition and oceanographic conditions on the annual migration of Pacific whiting, *Merluccius productus*. *Calif. Coop. Oceanic Fish. Invest. Rep.* 36:97–105.
- Field, J. C., K. Baltz, A. J. Phillips, and W. A. Walker. 2007. Range expansion and trophic interactions of the jumbo squid, *Dosidicus gigas*, in the California Current. *Calif. Coop. Oceanic Fish. Invest. Rep.* 48:131–145.
- Fleischer, G. W., K. D. Cooke, P. H. Ressler, R. E. Thomas, S. K. de Blois, L. C. Hufnagle, A. R. Kronlund, J. A. Holmes, and C. D. Wilson. 2005. The 2003 integrated acoustic and trawl survey of Pacific hake, *Merluccius productus*, in U.S. and Canadian waters off the Pacific coast. U.S. Dept. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-NWFSC-65, 45 pp.
- Foote, K. G., H. P. Knudsen, G. Vestnes, D. N. MacLennan, and E. J. Simmonds. 1987. Calibration of acoustic instruments for fish density estimation: A practical guide. *ICES Coop. Res. Rep.* 144 pp.
- Gilly, W. F., U. Markaida, C. H. Baxter, B. A. Block, A. Boustany, L. Zeidberg, K. Reisenbichler, B. Robison, G. Bazzino, and C. Salinas. 2006. Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Mar. Ecol. Prog. Ser.* 324:1–17.
- Guttormsen, M. A., C. D. Wilson, K. Cooke, M. W. Saunders, D. R. McKelvey, and R. Keiser. 2003. Echo-integration trawl survey of Pacific hake, *Merluccius productus*, off the Pacific coast of the United States and Canada during June–August 2001. U.S. Dept. Comm., NOAA, AFSC Processed Rep. 2003–12, 80 p.
- Henderson, M. J., and J. K. Horne. 2007. Comparison of *in situ*, *ex situ*, and backscatter model estimates of Pacific hake (*Merluccius productus*) target strength. *Can. J. Fish. Aquat. Sci.* 64:1718–1794.
- Mackas, D. L., R. Kieser, M. Saunders, D. R. Yelland, R. M. Brown, and D. F. Moore. 1997. Aggregation of euphausiids and Pacific hake (*Merluccius productus*) along the outer continental shelf off Vancouver Island. *Can. J. Fish. Aquat. Sci.* 54:2080–2096.
- MacLennan, D. N., and E. J. Simmonds. 1992. *Fisheries acoustics*. London, UK: Chapman and Hall. 325 pp.
- Markaida, U. 2006. Food and feeding of jumbo squid *Dosidicus gigas* in the Gulf of California and adjacent waters after the 1997–98 El Niño event. *Fish. Res.* 79: 16–27.
- Markaida, U., and O. Sosa-Nishizaki. 2003. Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *J. Mar. Bio. Assn. U.K.* 83:507–522.
- Nelson, M. O., and T. A. Dark. 1985. Results of the coastal Pacific hake, *Merluccius productus*, survey. *Mar. Fish. Rev.* 47:82–94.
- Nigmatullin, Ch. M., K. N. Nesis, and A. I. Arkhipkin. 2001. A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae). *Fish. Res.* 54:9–19.
- Pearcy, W. G. 2002. Marine nekton off Oregon and the 1997–98 El Niño. *Prog. Oceanogr.* 54:399–403.
- Ressler, P. H., J. A. Holmes, G. W. Fleischer, R. E. Thomas, and K. D. Cooke. 2007. Pacific hake (*Merluccius productus*) autecology: A timely review. *Mar. Fish. Rev.* 69: 1–24.
- Rodhouse, P. G. 2008. Large-scale range expansion and variability in ommastrephid squid populations: a short review. *Calif. Coop. Oceanic Fish. Invest. Rep.* 49.
- Smith, B. D., G. A. McFarlane, and M. W. Saunders. 1990. Variation in Pacific hake (*Merluccius productus*) summer length-at-age near southern Vancouver Island and its relationship to fishing and oceanography. *Can. J. Fish. Aquat. Sci.* 47:2195–2211.
- Simrad. 1993. Simrad EK500 scientific echo sounder reference manuals V4.01. Simrad Subsea A/S, Strandpromenaden 50, Box 111, N-3191 Horten, Norway.
- Trudel, M., G. Gillespie, J. Cosgrove, and B. Wing. 2006. Warm water species in British Columbia and Alaska. *In* State of the Pacific Ocean 2005. DFO Science Ocean Status Rep. 2006/001. pp 53–70. Available at: <http://www.pac.dfo-mpo.gc.ca/sci/psarc/OSRs/StateofOceans2005fml.pdf>
- Whitney, F. A., H. J. Freeland, and M. Robert. 2007. Persistently declining oxygen levels in the interior waters of the eastern subarctic Pacific. *Prog. Oceanogr.* 75:179–199.
- Wing, B. L. 2006. Unusual invertebrates and fish observed in the Gulf of Alaska, 2004–2005. *PICES Press* 14(2):26–28.
- Wolter, K., and M. S. Timlin. 1998. Measuring the strength of ENSO events—how does 1997/98 rank? *Weather* 53:315–324.
- Zeidberg, L. D., and B. H. Robison. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proc. Nat. Acad. Sci. U.S.A.* 104: 12948–12950.