

# Pacific Hake, *Merluccius productus*, Autecology: A Timely Review

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## Introduction

The Pacific hake (*Merluccius productus* Ayres 1855, also known as Pacific whiting), a gadoid species inhabiting waters off the west coast of North America (Fig. 1), is the most abundant groundfish in the California Current Large Marine Ecosystem (CCLME) (Sherman, 1991). The biomass of the coastal stock (fish age 3 and older which are susceptible to exploitation) was most recently estimated at 2.5 million metric tons (t) (Helser and Martell,

2007) (Fig. 2, top) and has supported average commercial landings of about 0.2 million t between 1966 and 2005 (Helser et al., 2006). The Pacific hake fishery currently has an annual landed value of about \$22 million in the U.S. and about \$14 million in Canada (values in U.S. dollars).<sup>1,2</sup> The commercial catch is mostly processed into surimi, headed and gutted products (Sylvia, 1995), and fillets (Helser et al., 2006), but it has also been used experimentally in such food products such as fish sauce (Lopetcharat and Park, 2002) and even hot dogs (Park et al., 1978).

Ecologically, Pacific hake play a dominant and key trophic role in the CCLME both as predator on euphausiids such as *Euphausia pacifica* and *Thysanoessa spinifera*, shrimp such as *Pandalus jordani*, and smaller finfishes such as the Pacific herring, *Clupea harengus pallasii*, and as prey for other

Pacific hake, larger finfishes such as lingcod, *Ophiodon elongatus*, large invertebrates such as Humboldt squid, *Dosidicus gigas*, seabirds such as the sooty shearwater, *Puffinus griseus*, and marine mammals such as the California sea lion, *Zalophus californianus californianus* (Livingston and Bailey, 1985; Buckley and Livingston, 1997; Baraff and Loughlin, 2000; Field et al., 2007).

Population reconstructions based on analysis of fish scales preserved in sediment cores show that the Pacific hake has been an abundant species in the CCLME for thousands of years (Soutar and Isaacs, 1969; Tunncliffe et al., 2001), but it has been studied and monitored intensively only since the 1960's (Alverson and Larkins, 1969), when a directed fishery began to develop. The long-term potential yield of Pacific hake depends upon its response to climate change and its role as both predator and prey (Methot and Dorn, 1995) in the CCLME.

Previous reviews (Best, 1963; Alverson and Larkins, 1969; Bailey et al., 1982; Stauffer, 1985; Methot and Dorn, 1995) described the incremental increase in the state of knowledge of

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<sup>1</sup>NMFS. 2004. Annual commercial landing statistics. Online at [http://www.st.nmfs.gov/st1/commercial/landings/annual\\_landings.html](http://www.st.nmfs.gov/st1/commercial/landings/annual_landings.html).

<sup>2</sup>Fisheries and Oceans Canada. 2004. Commercial catch statistics. Online at [http://www.pac.dfo-mpo.gc.ca/pages/data\\_e.htm](http://www.pac.dfo-mpo.gc.ca/pages/data_e.htm)

**ABSTRACT**—Pacific hake, *Merluccius productus*, the most abundant groundfish in the California Current Large Marine Ecosystem (CCLME), is a species of both commercial significance, supporting a large international fishery, and ecological importance, connecting other species as both predator and prey. Coastal Pacific hake migrations are characterized by movements between northern summer feeding areas and southern winter spawning areas, with variations in annual abundance, distribution, and the extent of these movements associated with varying climate-ocean con-

ditions. In general, warm (cool) years with enhanced (reduced) stratification and poleward (equatorward) transport are often related to good (poor) recruitment, increased (decreased) northward distribution, and reduced (enhanced) growth. However, the classic periodic pattern of annual migration and distribution may no longer be fully representative. Based on recent advances in the understanding of climate-ocean variability off the U.S. west coast, we hypothesize that the annual movements of Pacific hake are more responsive to climate-ocean variability than previously

thought, and further, that changes observed in Pacific hake distributions may reflect long-term changes in climate-ocean conditions in the CCLME. Therefore, an updated model of these relations is key to effective monitoring and management of this stock, as well as to devising scenarios of future change in the CCLME as a result of climate variations. The current state of knowledge of the relationship between the Pacific hake and its environment is reviewed, highlighting emerging ideas compared to those of the past, and priorities for future research are suggested.

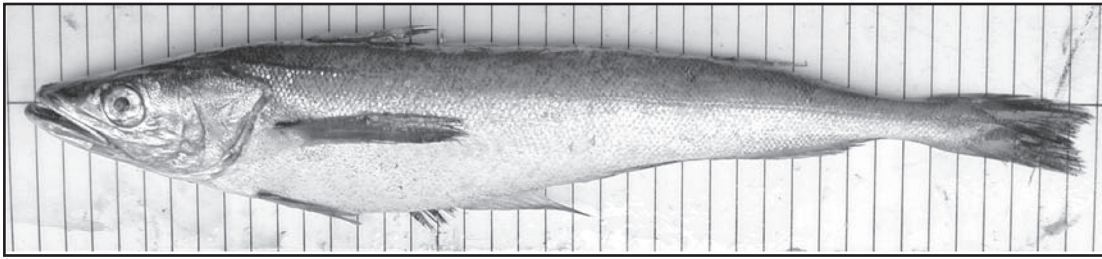


Figure 1.—Photo of an adult Pacific hake, *Merluccius productus*, which generally range from 35–75 cm in length. Photo by Dan Kamikawa, NMFS, Northwest Fisheries Science Center, Newport, Ore.

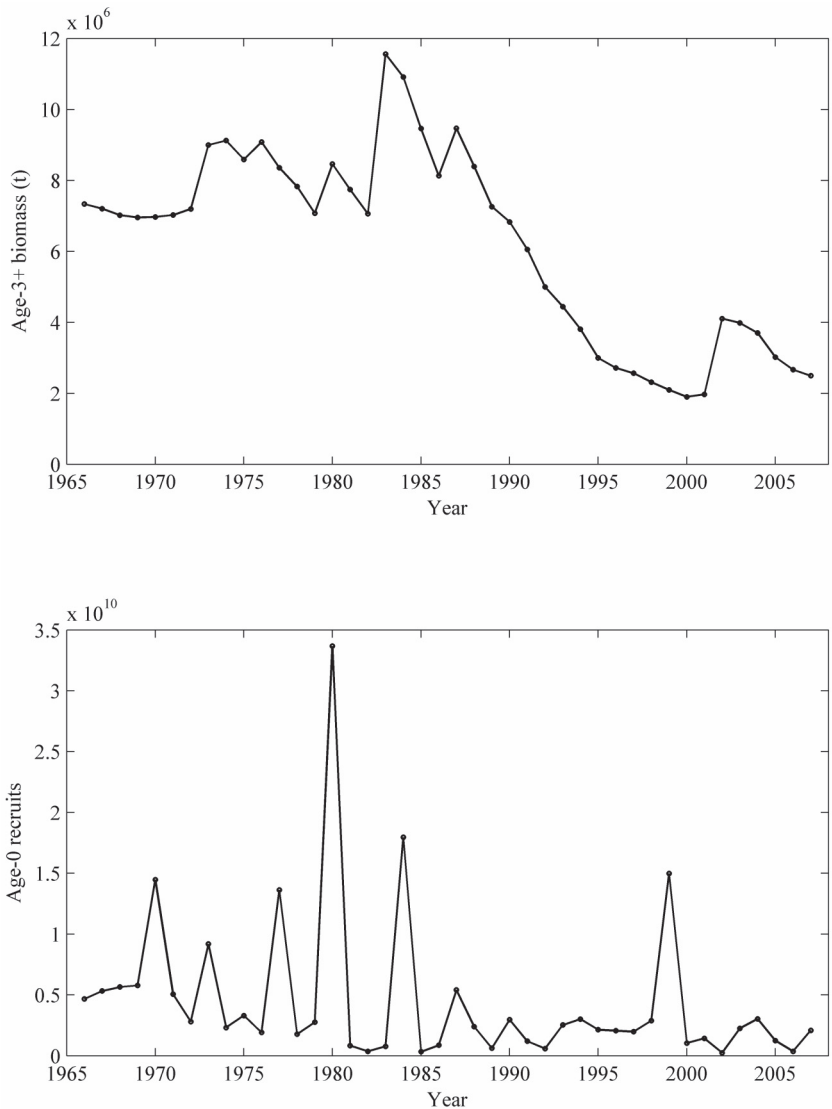


Figure 2.—Model estimated age 3+ biomass trajectory (in metric tons, top) and recruitment time series (in number of age-0 recruits, or the number of hake that survive their first year of life, bottom). From the most recent Pacific hake stock assessment (Helser and Martell, 2007).

Pacific hake at key times in the expansion of the commercial fishery and contributed to the fishery's rapid development since the 1960's. In the 28 year history (1977–2005) of the acoustics-trawl survey used to monitor the coastal hake stock, the ability to observe the fish has improved through advances in equipment and techniques, and our collective scientific understanding of the large influence of climate-ocean variability on marine species within the CCLME has increased. Since changes in climate-ocean conditions affecting the Pacific hake are likely to continue, there is a particular need to understand and devise scenarios of anticipated responses by such ecologically and economically important species. Neither the distribution nor the availability of the stock to resource monitoring surveys is known *a priori* and this uncertainty poses an obvious sampling issue for fisheries management in light of expected trends in oceanic and atmospheric warming (e.g. see Field et al., 2006a) in the foreseeable future. In this paper we review the main aspects of Pacific hake autecology, with an emphasis on the adult life stage, in order to identify key environmental relationships and associated biological mechanisms. Understanding physical processes in the CCLME is crucial to understanding the abundance and distribution of Pacific hake and to inferring how these fish are important indicators of the dynamics of the CCLME. We also highlight recent work on this topic and suggest the main directions for needed future research.

## Pacific Hake Autecology Overview

### Zoogeography, CCLME Dynamics, and Habitat

Pacific hake are widely distributed along the Pacific west coast of North America from Baja California to southeast Alaska (Alverson and Larkins, 1969; Dark et al., 1980; Bailey et al., 1982; Saunders and McFarlane, 1997; Wilson et al., 2000; Fig. 3). Three biologically and genetically distinct stocks are now recognized: a predominant coastal stock that migrates annually between southern California (lat. 25°N) and Queen Charlotte Sound (lat. 55°N), and two more restricted populations within Puget Sound and the Strait of Georgia (Iwamoto et al., 2004). Previously, a fourth “dwarf” Pacific hake stock had been recognized in the south off Baja California, but these fish are now considered a separate species (Vrooman and Paloma, 1976; Ermakov, 1982; Mathews, 1985; Grant and Leslie, 2001; Iwamoto et al., 2004). This review focuses on the migratory coastal stock of Pacific hake, which is a major biological component of the CCLME.

Well offshore of the western North American continental shelf break, a broad equatorward flow known as the California Current exists year round. However, along the shelf and slope off Washington, Oregon, and California, predominately northerly wind stress between April and September (summer) drives coastal upwelling and meandering equatorward surface flow, while southerly, downwelling-favorable winds and poleward flow prevail during the remaining (winter) months (Hickey, 1979; Huyer, 1983; Hickey, 1989a; Thomson et al., 1989; Strub and James, 2000; Fig. 4, top). Some poleward flow does occur close to shore during the summer, particularly west of Vancouver Island, B.C., where equatorward surface flow is mostly restricted to the outer shelf and slope (Thomson et al., 1989). In addition, jets, eddies, and filaments are common, especially in late summer and fall (Thomson et al., 1989; Huyer et al., 1998; Barth et al., 2000; Strub and

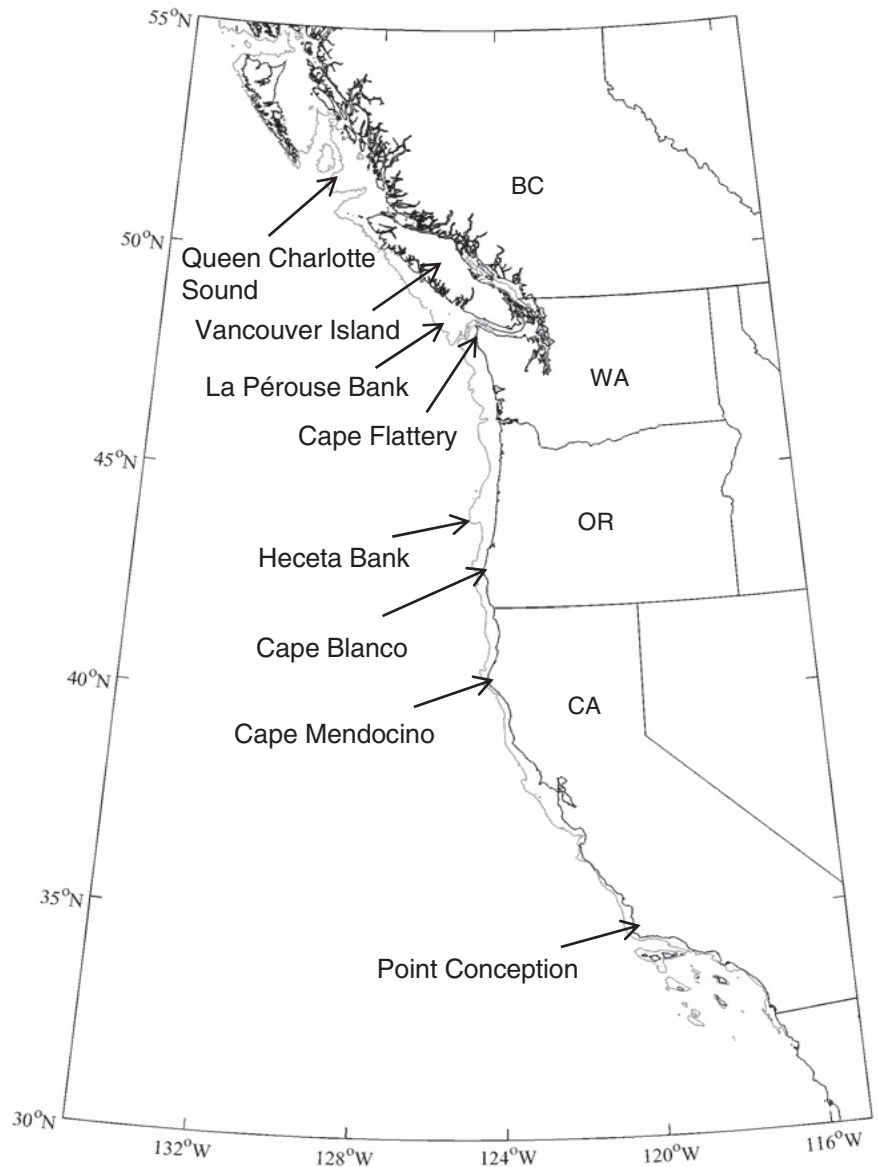


Figure 3.—Pacific coast waters inhabited by Pacific hake, showing physiographic and topographic features mentioned in the text. The 200 m depth contour (in gray) defines the continental shelf break.

James, 2000; Fig. 4, top). During the winter months, the poleward Davidson Current dominates flow over the shelf and slope north of Point Conception. A subsurface poleward flow known as the California Undercurrent exists on the shelf and upper slope year-round (reviewed by Hickey, 1989b; Huyer et al., 1989; Thomson et al., 1989; Pierce et al., 2000; Fig. 4, bottom). The Undercur-

rent is nearly contiguous from lat. 33° to 51°N, with a relatively narrow core (10–20 km) at depths of 200–300 m where mean sustained velocities of 10 to 20 cm s<sup>-1</sup> have been recorded (Pierce et al., 2000).

Summer upwelling brings cool, dense, and nutrient-rich surface waters to the surface along the coast (Huyer, 1983; Hickey, 1989a), and the combi-

nation of Ekman transport, persistent, strong winds, and flow-topography interactions can draw this water many

kilometers from shore (Huyer, 1983; Barth et al., 2005). Off California, the upwelling is relatively steady

during the summer, but off Oregon and Washington it is usually episodic, with upwelling events lasting from days to weeks followed by periods of relaxation (Huyer et al., 1979; Huyer, 1983; Barth et al., 2000). In contrast, upwelled water rarely reaches the ocean surface off the west coast of Vancouver Island, because of the stabilizing effect of the large volumes of freshwater discharged from coastal rivers, but the upwelling is sufficient to bring nutrient rich waters into contact with the turbulent mixed surface layer (Thomson et al., 1989). These upwelling circulation and current patterns increase the CCLME's biological productivity (Mann and Lazier, 1996; Batchelder et al., 2002) and are the likely bases for the development of favorable feeding areas for Pacific hake during the summer months.

The fall transition from summer to winter conditions usually occurs in October, when storm events bring a reversal from prevailing northerly winds to southerly, downwelling-favorable winds and the appearance of the Davidson Current (Huyer et al., 1979; Thomson et al., 1989). The spring transition from winter to summer conditions occurs over a period of several days, as the return of northerly winds brings upwelling favorable oceanographic conditions and equatorward flow.

Long-term observations of wind, sea-level, and temperature observations indicate that the spring transition takes place earliest off northern California and propagates northward to British

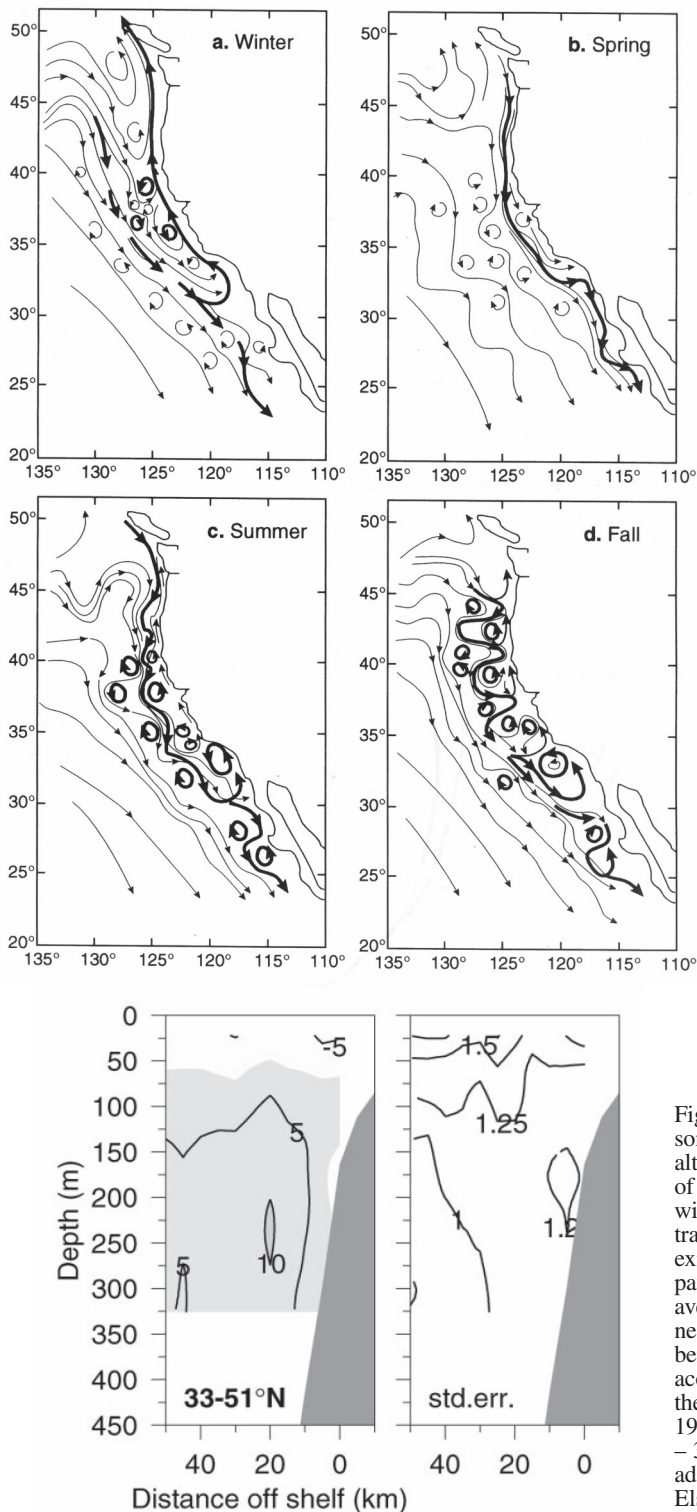


Figure 4.—Circulation in the CCLME. Conceptual drawing of seasonal evolution (top) based on the literature and analysis of satellite altimetry data, reprinted from Strub and James (2000), courtesy of Elsevier. Note prevailing poleward flow on shelf and slope in winter (a), and prevailing equatorward flow between spring and fall transition (b–d.) Seaward of the shelf and slope, equatorward flow exists all year. Meanders and eddies are superimposed upon broad patterns, particularly during summer and fall. At bottom, coastwide average velocity section showing equatorward flow (negative) near the surface and the poleward (positive) undercurrent beneath during summer 1995. This velocity section is based on acoustic Doppler current profiler (ADCP) data collected during the 1995 acoustics-trawl survey for Pacific hake (7 July–28 Aug. 1995). The depth range for this average section is from 22 m to 125–325 m, depending on bottom depth. See Pierce et al. (2000) for additional details. Reprinted from Pierce et al. (2000), courtesy of Elsevier, which gives additional details.

Table 1.—Life history intervals and defining morphological features in the ontogeny of teleost fish (adapted from Balon, 1975).

Interval	Start	End	Characteristics
Embryo	Fertilization	Absorption of the yolk-sac after hatching; exogenous feeding begins	Endogenous nutrition
Larva	Exogenous feeding begins	Formation or ossification of axial skeleton and fins fully differentiated; definitive organs developed	Exogenous nutrition, some embryonic organs
Juvenile	Axial skeleton ossified, fins fully differentiated, temporary organs replaced with definitive organs	First maturation of gametes	Rapid allometric growth
Adult	First maturation of gametes	Last maturation of gametes	Sexual maturity, spawning behavior
Senescent	Last maturation of gametes	Death	Arrested growth, gametes inferior or not produced

Columbia in about one week's time, usually between early February and late April (Thomson et al., 1989). However, the development of strong upwelling conditions is not always coincident with the spring transition, because their appearance is dependent on the strength and persistence of upwelling favorable winds over the continental slope. For example, in 2005 the spring transition off Vancouver Island occurred in late April, but persistent upwelling did not develop until late July<sup>3</sup> after the development of strong upwelling favorable wind stress in the northern California Current (Pierce et al., 2006; Fleischer et al.<sup>4</sup>).

Despite the aforementioned seasonal variability of the marine environment in the CCLME, climate forcing at interdecadal (e.g. regime shifts) and interannual time scales (e.g. El Niño/La Niña events) has also been identified (McFarlane et al., 2000; Benson and Trites, 2002; King, 2005). At present, regime shifts are only detectable retrospectively on the basis of coincidental changes in the distribution, survival, and abundance of many marine plankton and fish species (King, 2005). These changes are relatively abrupt, widespread, and may persist for decades, with effects cascading through all trophic levels in marine ecosystems.

Historical records provide evidence of regime shifts affecting the North Pacific in 1925, 1947, 1977, 1989, and most recently, 1998 (King, 2005). Ocean conditions in the CCLME after the 1998 regime shift can be summarized as a return to cooler, less stratified, and more biologically productive conditions with enhanced southward flow of water and organisms (King, 2005). Within these regimes, ocean conditions are affected by El Niño events, which generally result in a warming of coastal waters over the continental shelf and stronger poleward flow in the CCLME, and La Niña events, which couple cooling of surface temperatures with reduced poleward flow. In both cases, the impact of these events is measured relative to the existing ocean regime; hence no two El Niño or La Niña events will produce identical biological responses to organisms such as Pacific hake.

A warming trend during the late 20th century has been detected in all global oceans and accounts for a 1°C increase in average annual water temperature in the CCLME over the past 50 years (Palacios et al., 2004; Di Lorenzo et al., 2005). Based on abundances of tropical/subtropical (warmwater) and temperate/subpolar (coldwater) species of planktonic foraminifera shell casings in sediment cores from the Santa Barbara Basin, Field et al. (2006a) demonstrated that this recent warming trend is atypical of environmental variability in the CCLME during the preceding millennium and concluded that it represents a signal associated with anthropogenic warming, likely related to increases in atmospheric greenhouse gas concentrations since the late 1880's. This warming is likely to have widespread consequences for

the CCLME, including the spawning, recruitment, abundance, and distribution of the coastal Pacific hake stock.

In the following sections, we follow the general terminology conventions for fish life history intervals recommended by Balon (1975) (Table 1). For Pacific hake, the embryonic period lasts approximately 5–9 days after fertilization, but some exogenous feeding may occur before the yolk is fully absorbed; hake are 2.5–3.0 mm in length at this time (Bailey et al., 1982). The subsequent larval period lasts until about 20 days after fertilization, when the juvenile period begins with the onset of rapid growth (Bailey et al., 1982). Time until entry into the adult period is variable. At fork lengths of 37–40 cm and an age of 3, 50% of a Pacific hake cohort in the coastal stock is reproductively mature (Best, 1963; Methot and Dorn, 1995; Helser et al., 2006). It is uncertain when senescence might occur for Pacific hake, but it is known that they can live for more than 20 years (e.g. Fleischer et al., 2005), though hake older than about 15 years are very scarce (Methot and Dorn, 1995). The natural mortality rate for Pacific hake has been estimated at 0.20–0.30 year<sup>-1</sup> (Dorn, 1996; Helser et al., 2006).

### Embryos, Larvae, and Juveniles

Pacific hake eggs are spawned from January through March at depths of 100–500 m; the fertilized embryos and larvae remain beneath the mixed layer (Bailey, 1982). Classically, spawning was thought to occur in dense aggregations several hundred km offshore of southern and Baja California (Alverson and Larkins, 1969). However, indirect evidence of successful spawning north of this region has occasionally been

<sup>3</sup>Thomson, R. 2005. Fisheries and Oceans Canada, Institute for Ocean Sciences, 9860 West Saanich Road, P.O. Box 6000, Sidney, BC, V8L 4B2, Canada. Personal commun.

<sup>4</sup>Fleischer, G. W., K. D. Cooke, P. H. Ressler, R. E. Thomas, S. K. de Blois, and L. C. Hufnagle. The 2005 integrated acoustic and trawl survey of Pacific hake, *Merluccius productus*, in U.S. and Canadian waters off the Pacific coast. U.S. Dep. Commer., NOAA Tech. Memo. Manuscript in prep.

reported over the years (Bailey, 1980; Percy and Schoener, 1987; Hollowed, 1992; Dorn, 1996; Saunders and McFarlane, 1997; Benson et al., 2002). Spawning aggregations have seldom been observed directly (Alverson and Larkins, 1969; Nelson and Larkins, 1970; Bailey et al., 1982; Stauffer,

1985; Saunders and McFarlane, 1997; Saunders et al.<sup>5</sup>). Most of what is known about Pacific hake spawning has been inferred from collections of embryos and larvae during standard California Cooperative Oceanic Fisheries Investigations (CALCOFI) ichthyoplankton surveys (Bailey, 1981; Hollowed, 1992;

Horne and Smith, 1997; Mullin et al., 2000).<sup>6</sup> The gear used in the CALCOFI surveys (typically ring or bongo nets with 0.505–0.550mm mesh; Hollowed, 1992) may be inefficient for this species (Hollowed and Bailey, 1989). Other problems with these surveys include a reduction in spatial coverage over the years and difficulty in adequately sampling the apparently patchy and variable distribution of embryos and larvae both within and between years (Hollowed, 1992).

As they grow, juvenile Pacific hake evidently move inshore from offshore areas where they were spawned to develop on the continental shelf and slope (Bailey, 1981; Grover et al., 2002). Juveniles have been collected in midwater trawl surveys by the California Department of Fish and Game (CDFG) (Bailey, 1981), in juvenile rockfish surveys conducted by the NMFS Southwest Fisheries Science Center (SWFSC) (Grover et al., 2002), and more recently in a joint survey initiative targeting Pacific hake and rockfish (*Sebastes* spp.) young-of-the-year juveniles conducted cooperatively by the NMFS Northwest Fisheries Science Center (NWFS) and the Pacific Whiting Conservation Cooperative (PWCC) (referred to herein as the NWFS-PWCC pre-recruit survey) (Phillips et al., 2007). Despite acknowledged difficulties (Hollowed, 1992) with surveys of embryos, larvae, and juveniles (Fig. 5), these data are still viewed as potentially useful indices of the strength of recruitment in Pacific hake stock assessments (Helser et al., 2006), as described further below.

Episodic strong year classes, varying as much as over two orders of magnitude (Bailey and Francis, 1985; Methot and Dorn, 1995), characterize the coastal

<sup>5</sup>Saunders, M. W., K. Cooke, M. Wyeth, G. A. McFarlane, and V. Wespestad. An echo-integration-trawl survey of pelagic fishes off the west coasts of Canada and the United States from January 10–February 6, 2001. Unpubl. rep. contact Ken Cooke, Fisheries and Oceans, Canada, Pacific Biological Station, Nanaimo, BC, V9T 6N7, Canada.

<sup>6</sup>NMFS, Southwest Fisheries Science Center. Pacific Hake Larvae Abundance and Spawning Center. Contact Richard Charter, SWFSC, 8604 La Jolla Shores Drive, La Jolla, CA 92037-1508. Online at <http://test.parsus.com/NOAA/Hake/>.

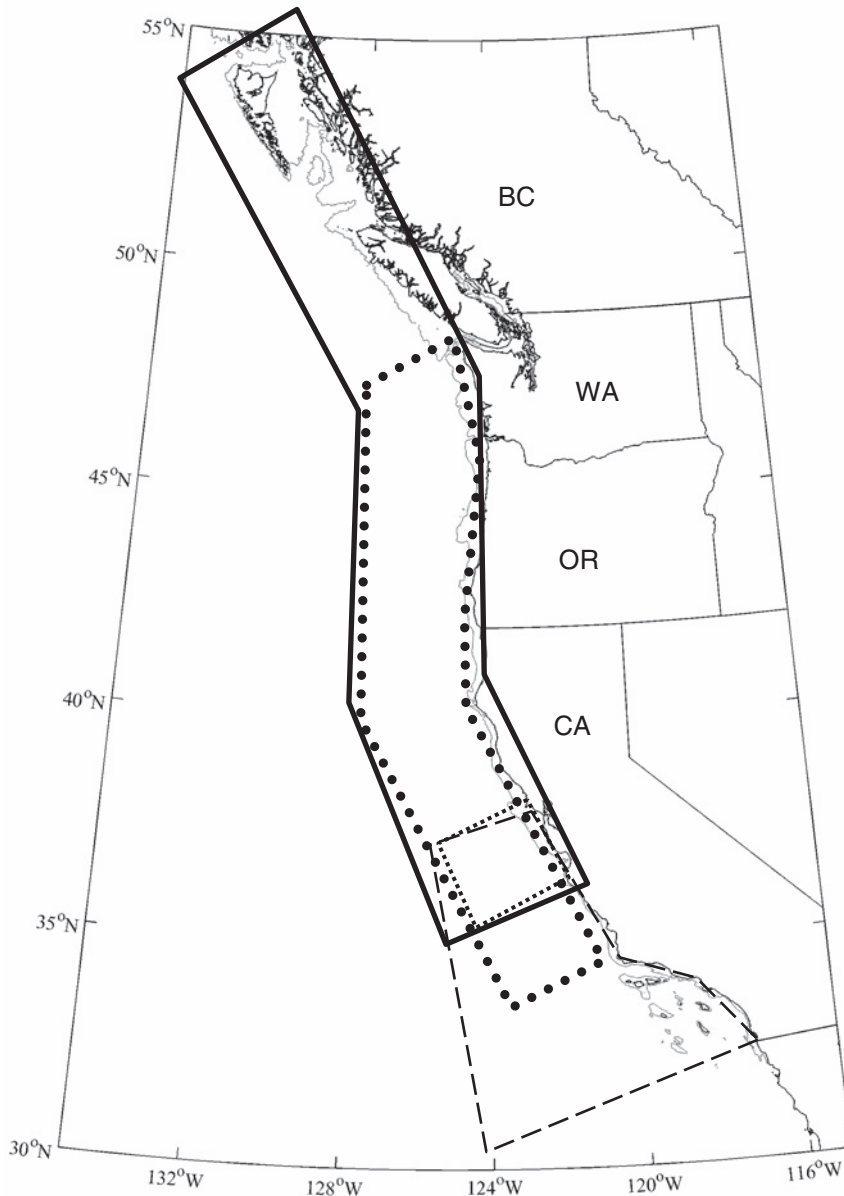


Figure 5.— Current spatial coverage of major monitoring surveys for Pacific hake: acoustics-trawl survey for adults (solid), NWFS-PWCC survey of prerecruits (dot), SWFSC of prerecruits (short dash), and CALCOFI larval surveys (long dash). The area covered by the surveys has changed over the years. The 200 m depth contour (in gray) defines the continental shelf break.

stock of Pacific hake (Fig. 2, bottom). These periodic strong recruitment events promote non-monotonic changes in stock abundance and subsequent harvest levels—typically resulting in periods of increases in both for several years followed by decline until the next strong recruitment event occurs.

Pacific hake recruitment fluctuates largely independent of spawning stock size, so a reliable stock-recruitment relationship, the fundamental relationship typically used to formulate harvest recommendations, has been difficult to establish (Bailey and Francis, 1985; Helser et al., 2006). Varying levels of mortality during the pre-recruit period is a common explanation for this observation in other species, and considerable research has provided evidence that the survival of larval Pacific hake is strongly influenced by the environmental conditions (such as upwelling, advection, and water temperature) experienced during the first few months after spawning (Bailey, 1981; Bailey and Francis, 1985; Bailey et al., 1986; Hollowed, 1992; Agostini, 2005). Cold ocean years often produce weaker year classes, while warm ocean years often produce strong, albeit more variable, year classes. Cold ocean years along the west coast are characterized not only by low water temperature and slower development rates for hake embryos and larvae, but also by stronger upwelling, equatorward transport, and offshore advection (the opposite conditions prevail in warm years). The mechanism for depressed Pacific hake recruitment in cooler years is not clear: it may be advection of embryos and larvae to unfavorable habitat, or the presence of different zooplankton prey and/or predator species brought in by advection during cooler years (Bailey, 1981; Hollowed, 1992; Agostini, 2005).

Although the biological mechanisms affecting recruitment in Pacific hake are not completely understood, most of the available evidence is consistent with the notion that the number of fish that survive to join older age classes and the fishery is strongly influenced by mortality during the first year of life. For example, Bailey et al. (1986) showed

that incidental catches of young-of-the-year (age 0) Pacific hake in CDFG pelagic fish surveys could be useful in forecasting the expected strength of year classes as they become vulnerable to fishing. Although juvenile catches may provide a useful index of year-class strength, Bailey and Francis (1985) and Hollowed (1992) argued that the strength of a year class may already be determined by the time the members of that class reach the juvenile stage, and that predatory and competitive forces at the juvenile stage are probably less important to recruitment than success at the larval stage.

Hollowed and Bailey (1989) contended that, as with Pacific hake larvae, high abundances of juvenile Pacific hake characterize strong year classes, and low juvenile abundances characterize weak year classes. Most of the interannual variability in recruitment was explained by density independent environmental factors. Hollowed and Bailey examined sea level, sea surface temperature, the depth of the 14°C isotherm, upwelling intensity, and temperature at 100 m from measurement stations and model data along the southern California coast and found that recruitment was higher when the 14°C isotherm was depressed and surface temperatures were higher than 15°C, both conditions that would characterize warm years with weak upwelling. Weak upwelling in January or February followed by strong upwelling in March led to stronger year classes. They proposed that Pacific hake larvae reach favorable habitat near the coast by the end of January during years with low upwelling and weak offshore transport. Subsequently, when upwelling increases later in the year, these larvae are protected from offshore transport and are able to take advantage of the upwelling-driven biological production that results. This conceptual model, which was a modification of the model originally presented by Bailey and Francis (1985) using a longer time series, was better able to explain variability in Pacific hake recruitment. Of course, there have been exceptions: 1999, an anomalously cool year in the CCLME (Schwing and Moore, 2000), produced

one of the strongest year classes since the late 1980's (Fleischer et al., 2005; Helser et al., 2006).

Hollowed et al. (2001) reviewed and analyzed patterns in northeast Pacific fish stock and climate index time series. Apropos of the present review, these authors found that Pacific hake (as well as other important gadoids in the Gulf of Alaska, walleye pollock, *Theragra chalcogramma*, and Pacific cod, *Gadus macrocephalus*) appeared to respond more strongly to interannual variability than to decadal climate variability, and they had a statistically higher proportion of strong year classes in unusually warm years than in other years. This result is not inconsistent with previous studies. They defined warm years not on the basis of low latitude El Niño phenomena, but on so-called “Niño North” conditions indicated by warm surface temperature anomalies in coastal waters north of the tropics. Niño North conditions did not always correspond to El Niño events. The frequency of favorable ocean conditions for recruitment has major implications for the size and variability of this stock, as years of strong recruitment store sufficient biomass to ensure survival during periods of unfavorable conditions (Hollowed et al., 2001).

## Adults

The distribution of the migrating coastal stock varies from about lat. 25°N to lat. 55°N, as the animals move north in summer and south in winter. Juvenile Pacific hake begin this annual feeding migration as they grow, and the northern extent of their migration increases with age, which is most likely related to fish length and swimming capability (Smith et al., 1990). Adults (i.e. fish age 3 and older, susceptible to exploitation) migrate from southern spawning areas to feed off Oregon, Washington, and British Columbia (approximately lat. 35°N to lat. 55°N) from April–May through September–October (Alverson and Larkins, 1969; Bailey et al., 1982; Francis, 1983; Stauffer, 1985; Dorn, 1995). Dorn (1997) applied geostatistical techniques to summer Pacific hake survey data for 1992 and 1995, estimat-

ing that the characteristic spatial scale of variability of these aggregations was between 20 and 30 km. Their cross-shelf distribution extends from the inner shelf out to waters more than 2,000 m deep, perhaps 40 km or more beyond the shelf break (Dorn, 1995).

#### *North–South Distribution*

Age structure, size distribution, and environmental conditions are all important factors determining the spatial distribution and annual coastwide migration of the Pacific hake stock and the availability of the fish to both monitoring surveys and commercial fishing operations. Usually the oldest, largest fish travel the greatest distances north into Canadian waters (Stauffer, 1985; Dorn, 1992) because they can apparently sustain higher swimming speeds (Ware, 1978; Francis, 1983). These fish also tend to be female in greater proportion, in part because females are on average larger than males (Dark, 1975; Beamish and McFarlane, 1985; Dorn, 1992). In addition, during warm years Pacific hake generally migrate further northward than in cool years (Dorn, 1995; Saunders and McFarlane, 1997; Wilson et al., 2000). Several key studies examining the interplay between these factors are discussed below.

Smith et al. (1990) studied the relationship between growth, fishing, oceanographic conditions, and length-at-age of Pacific hake found off Vancouver Island between 1976 and 1989. The Pacific hake samples they used in their analysis came from research and commercial trawl catches, and oceanographic data included time series of sea level height and sea surface temperature and salinity from Amphitrite Point (lat. 48°55'N, long. 125°32'W) and Tofino (lat. 49°09'N, long. 125°52.5'W). Growth and size-selective fishing pressure had the largest effect on mean length-at-age in their model, but they showed that oceanographic conditions also appeared to have a weak but significant influence. During warm years (higher sea level height, warmer surface temperatures, lower salinity, stronger poleward flow) Pacific hake were smaller on average than during cool years

(lower sea level height, cooler surface temperature, higher salinity, stronger equatorward flow). They attributed this difference to the effect of prevailing current patterns on Pacific hake migration under these different conditions. For instance, warm years were characterized by stronger poleward (or at least weaker than normal equatorward) flow, allowing smaller Pacific hake to migrate further northward into Canadian waters. By contrast, cooler years with stronger equatorward flow would allow only the larger, stronger Pacific hake to migrate further north.

Ware and McFarlane (1995) showed that warmer years (determined from sea surface temperatures measured at Amphitrite Point) were characterized by an increase in Pacific hake biomass in Canadian waters near La Pérouse Bank, an area just north of the Canada–U.S. border. Their analysis also showed an overlap in space and time between Pacific hake and euphausiid distributions around La Pérouse Bank, and they concluded that in warmer years Pacific hake deplete local euphausiid prey resources more quickly and move northward earlier than in cooler years, thus increasing predation pressure upon Pacific herring, *Clupea harengus pallasii*, stocks. Robinson and Ware (1999) used the simple regression between temperature and Pacific hake biomass that Ware and McFarlane developed to help parameterize a one-dimensional trophic model of the pelagic ecosystem in the La Pérouse Bank region, in which inter-annual variability in predator-prey relationships between Pacific hake, herring, and euphausiids were important.

In perhaps the most careful and complete study to date of environmental influences on Pacific hake annual migration, Dorn (1995) examined the relationship between monthly mean water temperatures along the west coast and the proportion of a given age class migrating into Canadian waters between 1977 and 1992. As earlier authors had proposed, Dorn (1995) also suggested that intensified northward currents and changes in prey distribution during warm years and El Niño events were likely mechanisms for increased north-

ward movement of the stock. Further, he showed that subsurface temperature anomalies were more closely correlated to Pacific hake migration than surface temperatures, and that temperatures in the “south” (lat. 30°N to lat. 42°N), where the Pacific hake begin their northward migration, were more important than the temperatures in the “north” (lat. 42°N to lat. 54°N), the feeding grounds. The southern temperature anomaly at 100 m during March–April explained the majority of inter-annual variation in the summertime abundance of Pacific hake in Canadian waters, and Dorn used this correlation to hindcast abundance for years between triennial surveys. The age structure of this stock was also important in his analysis, perhaps independent of environmental factors: older fish migrated further north than younger fish, the difference in mean distance migrated decreased between older age classes, and older age groups had a wider north–south distribution than younger age groups. Thus a change in age structure of the population, due to factors such as fishing pressure or patterns in recruitment, could alter the north–south distribution of the stock independent of, or in addition to, changes in climate-ocean conditions in the CCLME.

Although the empirical relationships reported by Dorn (1995) and Ware and McFarlane (1995) correctly capture the impact of temperature on the north–south distribution of Pacific hake, they do not conclusively establish the mechanisms by which water temperature influences Pacific hake population dynamics. Two possible mechanisms—current advection and active swimming in response to environmental cues—are thought to directly affect the summer distribution of adult Pacific hake (Smith et al., 1990; Dorn, 1995). The distribution that results from these mechanisms is affected by prevailing ocean conditions in the CCLME. The northward feeding migration begins during the winter, when poleward transport dominates. These conditions favor the northward movement of Pacific hake, and, all other factors being equal, larger and faster swimming fish will travel further north



in a given period of time. The onset of equatorward transport in surface waters and upwelling conditions after the spring transition could retard the northward movement of Pacific hake for the following reasons: they must swim against strong southward currents, they may be avoiding the coldest temperatures associated with upwelling of waters from below the thermocline, or they may find favorable feeding areas further south because the upwelling has supported high food productivity.

The beginning of the spring transition and the lag between this transition and the development of persistent upwelling are important influences on the distribution and abundance of Pacific hake in northern waters during the summer. Benson et al. (2002) reported an inverse relationship between acoustic survey estimates of Pacific hake biomass in Canadian waters from 1977 through 1998 and average upwelling anomaly over the preceding April, May, and June at 33°N, with the upwelling anomaly variable accounting for 77% of the variance in the Canadian biomass estimates. They contended that euphausiid prey availability driven by changes in ocean conditions, as well as the effect of prevailing currents on northward movement, were responsible. Emmett et al. (2006) linked the earlier appearance and increased abundance of Pacific hake off the Columbia River near the Oregon–Washington border to warm years with a late spring transition.

The evidence supporting the role of ocean conditions in the timing of the southward migration in fall is less compelling because there are fewer observations of these movements. In their review, Bailey et al. (1982) reported that Soviet fishery researchers had proposed a link between the winter appearance of the Davidson Current and the beginning of the southward migration. Thomson et al. (1989) noted that Pacific hake typically disappear from the La Pérouse area around the time of the fall transition and linked this disappearance to marked declines in production resulting from changes in oceanographic conditions associated with the fall transition. Based on observations of latitudinal

clines in the biological characteristics of spawning aggregations sampled in 1991, Saunders and McFarlane (1997) suggested that the southward migration of Pacific hake might be affected by mechanisms analogous to those influencing the northern displacement.

Pockets of resident Pacific hake, whose biomass is small relative to the migratory stock, have been reported in several inlets along the west coast of Vancouver Island (Beamish and McFarlane, 1985; Ware and McFarlane, 1995). Few data and little information are available because these small resident stocks inhabit areas not subject to established or even synoptic stock assessment surveys. These Pacific hake, though considered part of the coastal (not the Strait of Georgia) stock, are in this region year round and inhabit the large sounds during the summer. Pacific hake sampled in Barkley Sound in January 1983 were juvenile fish age 1 and 2 with fork lengths of 10–15 cm and 20–30 cm, respectively (Beamish and McFarlane, 1985). Small juvenile Pacific hake (< 30 cm) usually do not migrate north into Canadian waters during the summer, much less during the winter (Stauffer, 1985; Dorn, 1992), supporting the conclusion that the fish in Barkley Sound are part of a resident local spawning stock (Beamish and McFarlane, 1985). Possibly, these populations evolved because some individuals of the migratory stock did not migrate south to spawn because of warm ocean conditions and a delay in the fall transition.

McFarlane et al. (2000) and Benson et al. (2002) in fact contended that, since the mid 1990's, increasing numbers of Pacific hake from the coastal stock have remained off the west coast of Vancouver Island year-round and have successfully spawned, due to recent climate changes. Direct evidence of spawning individuals and spawning success in these areas are lacking at present, but more recent winter observations of adult Pacific hake as far north as Nootka Sound, Vancouver Island, by Saunders et al.<sup>5</sup> are also consistent with this view (Fig. 6). Though most of the reproductively mature fish Saunders et al. observed were located off southern

California, they also detected smaller numbers of both reproductively mature and immature Pacific hake throughout the surveyed area off the U.S. and Canadian west coasts.

There have been similar observations of adult Pacific hake present year-round in southeast Alaska.<sup>7</sup> In 1999, substantial numbers of these fish appeared in a year-round time series of Steller sea lion (*Eumetopias jubatus*) scat in the Frederick Sound area, near the Brothers Islands (~ lat. 57°17'N, long. 133°50'W). Between the inception of the time series in 1993 and 1999, only incidental and sporadic instances of Pacific hake had previously been observed. Midwater trawling conducted as part of ongoing studies of sea lion foraging documented midwater schools of adult Pacific hake in Frederick Sound, year-round during 2001–2004. These Pacific hake appeared to have remained well north of their traditional habitat after moving there following a strong El Niño event in 1997–98, though the northward movement of hake may have begun after a putative regime shift to warmer conditions in 1989 (Benson et al., 2002; footnote 7).

Changes in adult Pacific hake migration and distribution may in turn affect where and how well the embryos, larvae, and juveniles of succeeding year classes grow and survive. Bailey (1980) described a northward shift of Pacific hake spawning location between the mid 1960's and 1979, which he linked primarily to fishing pressure on older, larger individuals. Horne and Smith (1997) argued that the spawning locations of Pacific hake shifted north in warmer years and had moved 444 km toward the north between 1951 and 1984, based on modeling using CALCOFI collections of larval hake. They used temperatures >10°C at 100 m depth off Point Conception to define “warm years,” noting an anecdotal example of an instance where surface

<sup>7</sup>Sigler, M. 2006. NMFS Auke Bay Laboratory, 11305 Glacier Hwy, Juneau, AK 99801, and D. Tollit, Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, Vancouver, BC V6T 1Z4. Personal commun. and manuscript in prep.

temperature was cool, but temperature at 100 m was one of the warmest on record at that location. While both age structure and ocean conditions are dominant factors in determining the location of Pacific hake spawning in

a particular year, we suggest that the Horne and Smith study also fits more recent implications of a continued climate-mediated northward shift in the spawning location (Hollowed, 1992; Saunders and McFarlane, 1997;

McFarlane et al., 2000; Benson et al., 2002). These observations are at odds with the classical model of the annual Pacific hake life cycle as usually articulated (e.g. Alverson and Larkins, 1969; Bailey et al., 1982).

#### *Cross-shelf Distribution*

Pacific hake form dense daytime aggregations in regions of steeply sloping bathymetry along the shelf-break and near the edges of mid-shelf banks and basins, sometimes extending well offshore (Bailey et al., 1982; Dorn, 1995; Ware and McFarlane, 1995; Mackas et al., 1997; Swartzman, 2001). Pacific hake are found primarily between 50 and 500 m below the surface during the day, most commonly in aggregations between 150 and 250 m.

Pacific hake inhabit a three-dimensional environment where their response to temperature gradients may be an important mechanism driving their depth distribution since, unlike euphausiids, Pacific hake are sufficiently strong swimmers to overcome physical mechanisms related to flow-field structures. Swartzman (1997) found that the horizontal spatial pattern of Pacific hake along acoustics-trawl survey transects perpendicular to shore was related to temperature at the depth of the fish school, bottom depth, and latitude south of Cape Flattery in 1992. The depth of Pacific hake aggregations increased moving north from lat. 42° to lat. 46°N and moving out along the continental shelf to the shelf-break. This pattern probably reflects the latitudinal clines associated with the northern migration and ontogenetic effects on depth preferences: smaller, younger juvenile fish do not migrate as far north as older Pacific hake (Hollowed, 1992; Dorn, 1995; Ware and McFarlane, 1995; Horne and Smith, 1997), and juvenile Pacific hake exhibit a preference for shallower shelf locations than mature fish, which are generally most abundant near the shelf-break (Methot and Dorn, 1995; Saunders and McFarlane, 1997).

Swartzman's (1997) analysis did not explicitly account for age and size structure of the stock, however. Both the biomass of Pacific hake in aggregations

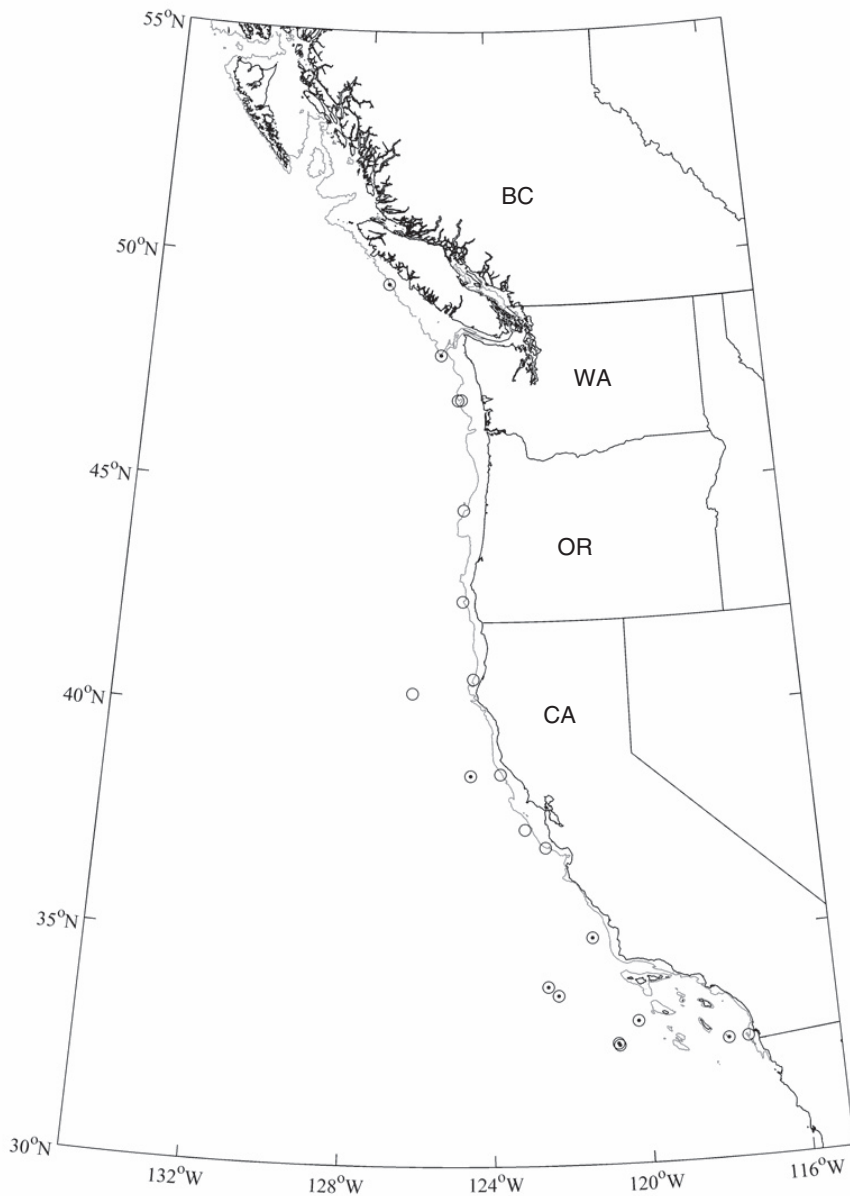


Figure 6.— Circles indicate the locations of 20 midwater trawls that captured Pacific hake during a winter survey off the west coasts of Canada and the United States, 10 Jan. – 6 Feb. 2001. These trawls were not used to estimate hake abundance; they were conducted to verify acoustically detected aggregations of Pacific hake. Dots indicate those trawls that captured reproductively mature Pacific hake whose maturity stage indicated they were either in preparation for spawning or had recently spawned. The 200 m depth contour (in gray) defines the continental shelf break. Data from Saunders et al. text footnote 5.

and the number of smaller clusters forming an aggregation were significantly affected by water temperature, bottom depth, and the depth below the surface. Clusters were larger and had more biomass in the north than in the south, and maximum biomass was observed in aggregations occupying temperatures around 7°C, although Pacific hake also occupied waters with temperatures ranging from 5° to 9°C. Swartzman noted that temperature and depth were closely correlated, making it hard to separate their effects.

There are no experimental observations in the literature to establish preferred temperature ranges for Pacific hake. In the field, acoustic surveys of Pacific hake collect temperature measurements during midwater trawls and conduct a limited number of conductivity-temperature-depth (CTD) profiles. Although the midwater trawls are conducted to verify acoustic observations and are not random samples or of standard duration, they do indicate the temperatures at the depths and locations where hake were observed and captured. In the 2003 and 2005 acoustics-trawl surveys, the distribution of temperatures from trawls in which more than 50 hake were caught ranged from 5° to 11°C, averaging 6.98°C (SD 0.89) (Fig. 7, top; Fleischer et al., 2005). This is similar to the findings of Swartzman (1997) and those of prior acoustics-trawl surveys (Wilson and Guttormsen, 1997; Wilson et al., 2000; Guttormsen et al.<sup>8</sup>). However, in 2003 and 2005 these water temperatures were not significantly different from those hauls in which less than 50 hake (an incidental catch size) were captured (two-sample T-test,  $t=0.90$ ,  $df=159$ ,  $p=0.37$ ), and in fact these temperatures were typical of much of the water column that was sampled (Fig. 7, middle and bottom). Temperatures from hauls in which less than 50 hake were caught averaged 6.82°C (SD 1.13), and the average median profile temperature from CTD profiles was 7.56°C (SD 1.12).

Pacific hake are obviously able to live within a range of temperatures, as their distribution during anomalous years shows. For example, Agostini (2005)

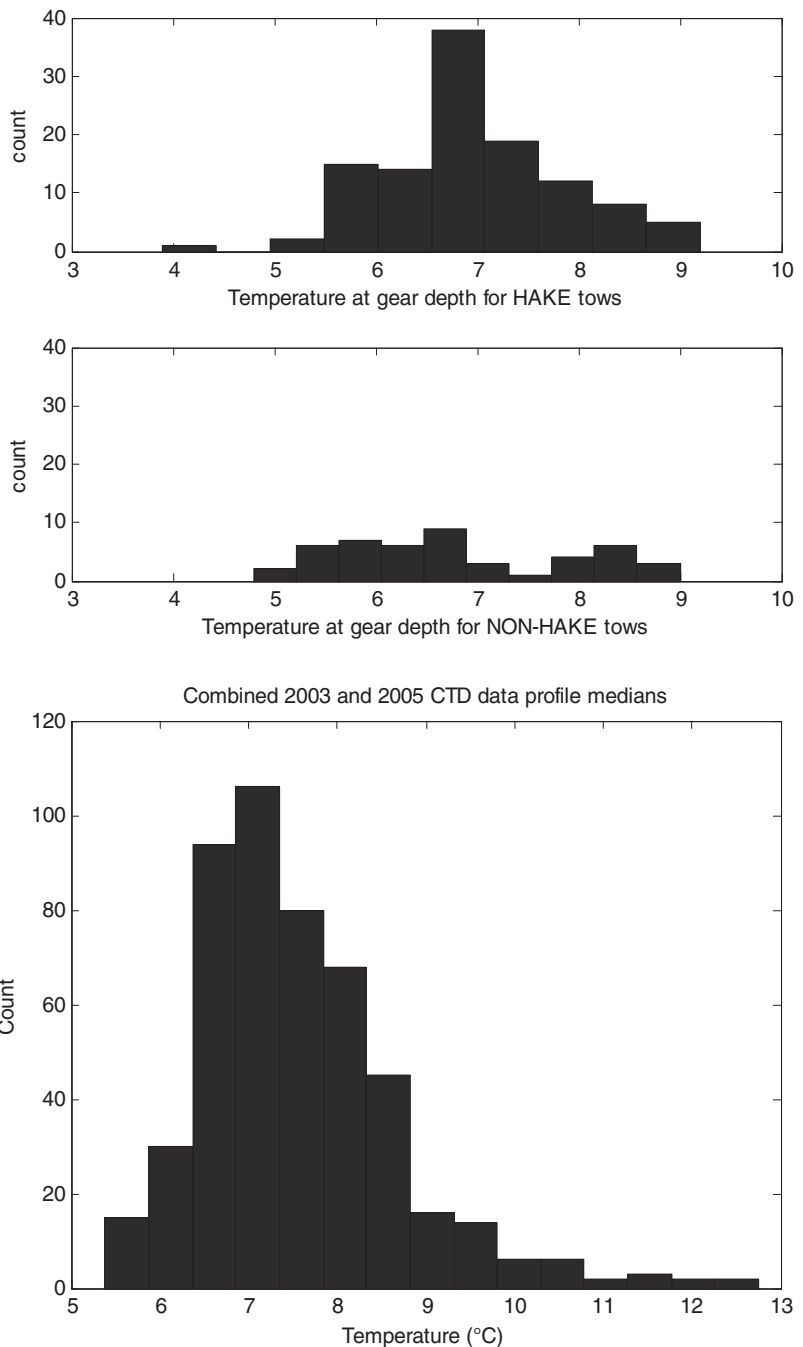


Figure 7.—Top, temperatures from sensors located on the headrope of midwater and bottom trawls that captured more than 50 Pacific hake during the 2003 and 2005 acoustics-trawl surveys of Pacific hake. Middle, temperatures from sensors located on the headrope of midwater and bottom trawls from the same surveys that captured less than 50 Pacific hake. Bottom, median temperatures from CTD profiles from the same surveys.

<sup>8</sup>Guttormsen, M. A., C. D. Wilson, K. Cooke, M. W. Saunders, D. R. McKelvey, and R. Kieser. 2003. Echo integration-trawl survey of Pacific hake, *Merluccius productus*, off the Pacific coast

of the United States and Canada during June–August 2001. AFSC Processed Report 2003-12, Alaska Fisheries Science Center, NMFS, NOAA, US Department of Commerce, Seattle, WA, 81 p.

and Agostini et al. (2006) used hake survey biomass, CTD data from summer 1998 (when ocean conditions were very warm on the west coast at the end of an El Niño event) to show that hake were observed in much warmer waters on average (mean 12.2°C, SD 3.5) than in 1995 (mean 5.3°C, SD 2.6). Note that average temperatures from midwater trawls reflect the narrow depth range of a targeted hake aggregation, while Agostini (2005) and Agostini et al. (2006) related hake found throughout the water column to averages of temperatures from nearby CTD profiles.

We infer that there are other important determinants of the vertical distribution of Pacific hake, since temperature and depth are correlated with other factors, including currents and prey availability. Pacific hake are often found in close spatial proximity to aggregations of euphausiids (Mackas et al., 1997; Swartzman, 1997; Swartzman, 2001; Swartzman and Hickey, 2003), an important Pacific hake prey during the summer (Livingston, 1983; Livingston and Bailey, 1985; Tanasichuk et al., 1991; Ware and McFarlane, 1995; Buckley and Livingston, 1997). The relationship between euphausiids and Pacific hake may be strongest for smaller fish, since Pacific hake become increasingly piscivorous with age (Livingston, 1983; Livingston and Bailey, 1985; Tanasichuk et al., 1991). The mechanisms driving the spatial aggregation patterns of euphausiids and Pacific hake need not be the same for each of these organisms to produce the observed similarities in distribution patterns of each species. The available evidence supports the hypothesis that two mechanisms directly affect the cross-shelf distribution of Pacific hake on their feeding grounds during the summer and may be responsible for the strong overlap and spatial proximity of euphausiids and Pacific hake (Mackas et al., 1997; Swartzman, 2001): oceanographic conditions, including flow-field dynamics and predator-prey dynamics.

Bailey et al. (1982) noted that Pacific hake make a progressive movement from onshore to offshore from early to late in the summer feeding season; he speculated that this movement was

related to the seasonal dynamics of the California Undercurrent. However, Tanasichuk et al. (1991) and Tanasichuk (1999, 2002) contended that predator-prey dynamics have a dominant role when Pacific hake first arrive at feeding areas on the shelf off Vancouver Island, resulting in an inshore distribution early in the summer because the higher temperatures of these shallower waters support higher productivity.

Mackas et al. (1997) held that the decline in euphausiid abundance off the west coast of Vancouver Island later in late summer, and the development of upwelling-driven high productivity offshore, led to a shift in Pacific hake distribution towards the shelf-break, where flow-field dynamics became more important influences on Pacific hake distribution. In that study, late summer distributions of Pacific hake on La Pérouse Bank occurred in a band 5–10 km wide at the shelf-break coinciding with upwelling and subsequent doming of density surfaces. Based on vertical and horizontal offsets between the distributions of Pacific hake and euphausiids, Mackas et al. (1997) concluded that both Pacific hake and euphausiids were independently orienting to environmental gradients produced by turbulence associated with vertical and horizontal current shears at the shelf-break.

In a study of much broader spatial scope, Swartzman (2001) found that the spatial proximity of euphausiids and Pacific hake was dominated by overlap at or near the shelf-break based on acoustic data from the 1995 and 1998 Pacific hake acoustics-trawl surveys; Swartzman and Hickey (2003) report similar results in an analysis of data from 1995, 1998, and 2001. High abundance Pacific hake schools were often close to high abundance euphausiid patches when these aggregations were close to the shelf-break, but this pattern of overlap was far less obvious along portions of transects further offshore. Swartzman (2001) suggests a simple causal sequence in which euphausiids sense and orient to oceanographic factors (bottom depth, temperature, flow) and Pacific hake sense and orient to euphausiids to explain the aggregation patterns that he

observed. Several recent studies have linked the distribution of euphausiid aggregations off the west coast to the California Undercurrent (Swartzman et al., 2005) and mesoscale physical processes in the CCLME (Ressler et al., 2005; Pierce et al.<sup>9</sup>).

#### *Diel and Seasonal Migrations*

In addition to their seasonal, coast-wide migration, adult Pacific hake also migrate on shorter time scales during most of the year. They form well-defined pelagic schools during the day, mostly between depths of 50 and 500 m, disperse and undertake a diel vertical migration toward the surface at dusk, and then migrate back to mid-water depths during the daytime, except during spawning, when they neither feed nor migrate vertically (Best, 1963; Alverson and Larkins, 1969; Nelson and Larkins, 1970; Bailey et al., 1982; Stauffer, 1985). The vertical migration is usually thought to facilitate predation upon fish and zooplankton in the water column (Alton and Nelson, 1970), but few careful and complete studies of diel Pacific hake feeding behavior have been done.

Livingston (1983) showed that stomach fullness was irregular in samples collected over a 24 hour period, but was highest at around 1800 h, well before dusk in mid summer. Tanasichuk et al. (1991) contended that Pacific hake in his study fed periodically during the daytime throughout the feeding season. The Livingston (1983) and Tanasichuk et al. (1991) studies suggest significant feeding bouts during daytime, after midnight, and in the early morning, in contrast to previous reports of primarily nighttime feeding (Alton and Nelson, 1970; Rexstad and Pikitch, 1986). However, these conclusions of preferential nighttime feeding by Pacific hake were inferred from daytime stomach fullness data and Pacific hake diel behavior, while Livingston (1983) and Tanasichuk et al. (1991) collected Pacific hake stom-

<sup>9</sup>Pierce, S. D., J. A. Barth, W. T. Peterson, and T. J. Cowles. Bioacoustical analysis of zooplankton distributions during mesoscale surveys in the Northern California Current System. Deep-Sea Res. I. Manuscript in prep.

achs during both night and day in their studies. Still, Krutzikowsky and Emmett (2005) recently compared daytime and nighttime catches of pelagic surface trawls, in which Pacific hake appeared only at night, and reported that stomach contents of those fish suggested active nighttime feeding. It may be that feeding by Pacific hake occurs during both night and day, depending on prey availability (Emmett et al., 2006), and that Pacific hake migrate vertically both to seek prey and also to avoid other visual predators in surface waters during the daytime.

This sort of tradeoff between risk and reward for vertical migration is well discussed for both zooplankton and fish in the literature (Angel, 1985; Neilson and Perry, 1990; De Robertis, 2002). Vertical migration could also have bioenergetic advantages for Pacific hake if the growth efficiency of the animal is greater at lower temperatures in deeper water (e.g. 7° to 8°C for Pacific hake), but feeding rates and feeding efficiency are greater at higher temperatures near the surface. In this scenario, it would be advantageous for hake to feed at the higher temperatures for a short time and digest, assimilate, and grow at the lower temperatures. As with other marine fishes, diel migration may be a facultative behavior (Neilson and Perry, 1990) for Pacific hake, influenced by several important factors (prey, light, avoidance of predation, metabolism) and sensitive to local environmental conditions.

#### Prey and Predation

Larvae and smaller juvenile hake feed on copepod eggs, copepods, and juvenile euphausiids (Sumida and Moser, 1980; Grover et al., 2002; Cass-Calay, 2003). The diet of large juveniles and adults is composed largely of euphausiids, fish, and pandalid shrimp, with evidence of adult cannibalism on juveniles (Alton and Nelson, 1970; Bailey et al., 1982; Livingston, 1983; Livingston and Bailey, 1985; Rexstad and Pikitch, 1986; Brodeur et al., 1987; Tanasichuk et al., 1991; Buckley and Livingston, 1997; Buckley et al., 1999; Tanasichuk, 1999; Romaine et al., 2002; Tanasichuk, 2002). The amount of cannibalism of adults upon juveniles (intra-cohort can-

nibalism is not common) is probably related to the amount of spatial overlap between juvenile and adult fish, which could vary annually as the distribution of the hake stock changes (Buckley and Livingston, 1997). The daily ration for juvenile and adult Pacific hake has been estimated variously between 0.4 and 3.5% of body weight per day in the literature (Francis, 1983; Livingston, 1983; Rexstad and Pikitch, 1986; Tanasichuk et al., 1991).

Pacific hake is probably the most important consumer of zooplankton and forage fish in the CCLME (Field, 2004). Larger zooplankton and fish become more important dietary components as Pacific hake grow larger, implying a strong interaction between size and the prey that the Pacific hake are able to capture, but the availability of suitable prey in the environment and the spatial and temporal overlap between the predator and these prey are probably equally important (Livingston and Bailey, 1985). Larger fish most likely have more flexibility in prey size and type. Pacific hake appear to be opportunistic feeders (Best, 1963), particularly upon schooling or aggregating prey (Livingston and Bailey, 1985), and anecdotal evidence suggests they can be voracious predators on whatever becomes available (e.g. Hobson and Howard, 1989).

Euphausiids nearly always appear as a very important component of Pacific hake diet, but some studies, reviewed by Bailey et al. (1982) and Livingston (1983) have demonstrated seasonal patterns in the mix of prey types utilized throughout the CCLME. Observed dietary shifts have been from primarily euphausiid prey to increased consumption of Pacific herring in late summer off Vancouver Island (Tanasichuk et al., 1991; Ware and McFarlane, 1995), and from mostly fish prey to euphausiids in the summertime off Oregon and Washington (Brodeur et al., 1987).

Interrannual variation in Pacific hake diet has also been reported, including changes in the proportion of euphausiids and fish eaten and the species present (Livingston, 1983; Brodeur et al., 1987; Buckley and Livingston, 1997). Tanasichuk (2002) reported that Pacific hake

daily ration varied significantly among years during 1985–98 in August off Vancouver Island, but the proportion of the daily ration composed of euphausiids (mostly *Thysanoessa spinifera* >17 mm in length) averaged 89% even as euphausiid prey became less abundant. Nelson (2004) reported that consumption of euphausiids by Pacific hake was reduced during the 1997–98 El Niño, supplanted in the diet by Pacific herring in the larger, more piscivorous fish (> 50 cm in length); he attributed this change to an interannual shift in the availability of euphausiids and Pacific herring. Smaller Pacific hake that were not able to consume herring suffered a reduction in diet quality and perhaps growth. Similarly, some authors reported that Pacific hake growth was depressed during the 1983–84 El Niño (Hollowed and Francis, 1987; Francis et al.<sup>10</sup>), perhaps due to reduced euphausiid abundance (Miller et al., 1985; Rexstad and Pikitch, 1986). Pacific hake appear to respond to changes in climate-ocean conditions and prey fields, but moving from descriptive observations to predictive relationships between Pacific hake, the variability in prey species (such as euphausiids and herring) abundance, and oceanographic conditions at different scales has been difficult (Hayward, 2000; Mackas et al., 2001; Benson et al., 2002; Tanasichuk, 2002; Field et al., 2006b).

In addition to being a significant predatory force in the CCLME, Pacific hake are also important prey for other species. During early ontogeny, Pacific hake embryos and larvae are preyed upon by copepods, amphipods, and gelatinous zooplankton (Bailey and Yen, 1983; Livingston and Bailey, 1985). Pacific hake juveniles and adults are also prey for other nekton, including dogfish, *Squalus acanthias*; sablefish, *Anoplopoma fimbria*; lingcod, *Ophiodon elongates*; arrowtooth flounder, *Atheresthes stomias*; rockfishes, *Sebastes*

<sup>10</sup>Francis, R. C., G. A. McFarlane, A. B. Hollowed, G. L. Swartzman, and W. M. Getz. 1984. Status and management of the Pacific hake (*Merluccius productus*) resource and fishery off the west coast of the United States and Canada. Northwest and Alaska Fisheries Center Processed Report NWAFC-84-18, 73 p.

spp.; tunas, *Thunnus* spp. (Fiscus, 1979; Livingston and Bailey, 1985); as well as apex predators such as marine mammals (reviewed by Fiscus, 1979; Ainley et al., 1982; and Baraff and Loughlin, 2000) and seabirds (Livingston and Bailey, 1985; Field, 2004). The predation of Humboldt squid (*Dosidicus gigas*) upon adult Pacific hake has recently received attention (Zeidberg and Robison, 2007; Field et al., 2007) as these squid have become more common in the northern CCLME. Thus, Pacific hake form an important link between upper and lower trophic levels.

Pacific hake is the most abundant groundfish off the North American west coast, south of Alaska (Methot and Dorn, 1995), and its biomass—the largest of any single groundfish species in the CCLME—supports a substantial fishery and exerts a wide influence as both predator and prey (Field, 2004). Changes in the migration and distribution of Pacific hake could alter its predatory impact upon populations ranging from ocean shrimp, *Pandalus jordani* (Hannah, 1995), and euphausiids to forage fishes, juvenile salmon, *Oncorhynchus* spp. (Emmett, 2006), and younger age classes of Pacific hake (Buckley and Livingston, 1997), as well as alter its availability as prey to marine mammals (Ainley et al., 1982) and seabirds (Livingston and Bailey, 1985). Francis (2003) proclaimed Pacific hake the “poster child of the California Current”, emphasizing that this fish “[serves] as a massive stabilizing bridge between the northern and southern parts of the California Current ecosystem” and is distributed “in response to physical and biological cues which vary greatly from year to year.” The distribution, abundance, and behavior of coastal Pacific hake is sensitive to climate-ocean conditions, making it a useful biological indicator of changes in the CCLME (Benson et al., 2002).

### **Fishery, Management, and Monitoring**

#### **A Brief History of the Fishery**

Methot and Dorn (1995) and Sylvia (1995) reviewed the history of the

fishery and market for Pacific hake. During the 1960’s, the fishery for Pacific hake in the United States initially developed as a tiny domestic fishery, with annual landings of only hundreds to a few thousand tons. Beginning in 1966, the fishery was dominated by a much larger, mostly foreign effort, with annual landings averaging 137,000 t. The foreign fishery was in turn eclipsed by a joint-venture fishery in the early 1980’s. An exclusively domestic fishery was eventually established in 1991, with offshore factory and catcher vessels, vessels delivering to shoreside processing plants, and tribal fisheries splitting the U.S. allocation. The development of the Pacific hake fishery in Canadian waters was largely similar (Beamish and McFarlane, 1985; Helser et al., 2006), becoming a mostly domestic, shoreside fishery by 2001 and now allocated using individual vessel quotas.

The early stages of the fishery produced mainly fillets, headed and gutted products, and fish meal, mostly for foreign markets. Initially, there was very little market in either the United States or Canada for the catch, due to problems with rapid softening of the flesh related to the presence of the parasites in the genus *Kudoa* (Kabata and Whitaker, 1981, 1985, 1986). By the early 1990’s, quality problems were overcome by rapid cooling techniques and enzyme inhibitors, and the development of processed Pacific hake products, such as surimi, has made the fishery more profitable (Methot and Dorn, 1995).

Like other fisheries on the west coast, the Pacific hake fishery is monitored by observers. Currently, observers are mainly concerned with monitoring total catch and accounting for bycatch of other fish stocks (which constitutes a small fraction of the total Pacific hake catch, but can be relatively significant for very depleted stocks). They also collect biological samples for stock assessment-related scientific work. Deployment of U.S. fishery observers to monitor the catch on foreign vessels in the Pacific hake fishery began in 1977, more than two decades before most other U.S. west coast fisheries carried observers. Domestic factory and catcher

vessels in the Pacific hake fishery voluntarily began carrying observers in 1991, in what was essentially an outgrowth of the observing conducted on many of these same vessels in the Alaska wall-eye pollock, *Theragra chalcogramma*, fishery. Vessels delivering Pacific hake to shoreside plants at first operated under experimental fishing permits and did not carry observers, but complete observer coverage in the U.S. Pacific hake fishery is now mandatory, with human observers monitoring offshore factory and catcher vessels, and cameras and port samplers monitoring the catch of vessels delivering to shoreside plants (Tuttle<sup>11</sup>). In Canada, fishery observers were first deployed on foreign vessels targeting Pacific hake in 1987. Since 1996, on-board observers have monitored and sampled the catch of all domestic groundfish vessels, and all landed catch from trawlers is subject to dockside monitoring (McFarlane, 2001).

### **Management Strategy and Challenges**

Pacific hake are caught commercially by mostly midwater trawling during April–November in offshore waters along the coasts of northern California, Oregon, Washington, and British Columbia (Helser et al., 2006). A quota is set annually, and fish are harvested by both Canadian and U.S. fishing fleets. In past years, landings have exceeded the international coast-wide total allowable catch (by an average of 14% between 1991 and 1999) due to disagreements on the allocation between Canadian and U.S. fisheries, but since 2000 the coast-wide catch has been maintained within the quota (Helser et al., 2006).

In November 2003, Canada and the United States signed a new binational treaty for the joint management of Pacific hake to establish a process under which the total allowable catch (TAC) is decided and the fishery is managed. Under the new agreement, 26.12% of the TAC will be allocated to Canada and 73.88% will be allocated to the United

<sup>11</sup>Tuttle, V. 2007. NMFS, Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112. Personal commun.

States. The terms of the treaty have not yet been fully implemented by either nation, but the most recent stock assessments and management activities have conformed to the spirit therein (Helsler et al., 2006).

Utilization of the TAC is limited not only by the status of the Pacific hake stock, but also the bycatch of other species in the Pacific hake fishery. While this bycatch represents a relatively small fraction of the annual landings in the Pacific hake fishery, it is large enough to exceed limits on other severely depressed West Coast groundfish stocks, including several species of rockfish (*Sebastes* spp.) (Helsler et al., 2006; He et al.<sup>12</sup>).

As noted, the Pacific hake stock is characterized by low recruitment punctuated by very strong year classes, so the fishery must be managed to maintain the stock until the next large year class appears. The best indicator of potential recruitment remains the monitoring of larvae and juvenile abundance, as discussed earlier. Helsler and Martell (2007) describe the most recent stock assessment, including history of the time series, sources of data, and model development (see also Fig. 2). Primary data inputs to the assessment model include catch and age data from the fishery, recruitment indices from larval and juvenile surveys and the biennial (formerly triennial) joint U.S.–Canada acoustics-trawl survey of adult Pacific hake. The latter survey is the only fishery-independent measure now used to assess the adult stock.

### **The Acoustics-Trawl Survey: Monitoring the Recruited Pacific Hake Stock**

Fishery-independent acoustic surveys to assess the distribution and abundance of the coastal stock of Pacific hake have been conducted since 1977 by NMFS, and jointly with Fisheries and Oceans Canada since 1995, based on the recog-

nition that this stock is a transboundary resource (Fleischer et al., 2005). The current survey design is based upon knowledge of the biology of the fish and the historical distribution of the stock, past survey coverage, statistical considerations, and logistical constraints. It assumes that the surveyed area encompasses the entire summer range of the recruited stock, and that most or all of the stock is available to the survey techniques at the time of the survey.

Broadly speaking, the survey measures volume backscattering strength ( $S_v$ ) at 38 kHz along east–west oriented transects spaced at 18.5 km (10 n.mi.) intervals along the U.S. and Canadian west coasts (Fig. 5). Backscatter attributed to Pacific hake is integrated into units of backscatter per unit area ( $s_A$ ) and then converted into an estimate of Pacific hake biomass and numbers using information from concurrent midwater and bottom trawling (Fleischer et al., 2005). These data are incorporated into the Pacific hake stock assessment model (Helsler et al., 2006). Basic oceanographic information is also collected during the survey, including regular CTD profiles.

The survey takes place in the summer months (between June and September), when adult Pacific hake are found at the northern extent of their annual coastal migration along the continental shelf and slope (Alverson and Larkins, 1969; Bailey et al., 1982). Typically, the survey stretches from near Monterey, Calif. (lat. 36°30'N), to Queen Charlotte Sound, B.C. (lat. 54°30'N), extends from about 50 m of water nearshore to water depths of 1,500 m or more, and requires about 65–75 days to complete, including coverage of both U.S. and Canadian waters. The survey was a triennial effort until 2003, when a biennial schedule was implemented to increase the frequency of the stock status information required for management.

The design of Pacific hake monitoring surveys since the mid 1970's reflects the state of knowledge of adult Pacific hake distribution during the summer feeding season, since the survey is intended to capture the entire population. The survey design was changed in the early 1990's

(Dorn et al., 1994; Dorn, 1996; Wilson and Guttormsen, 1997) to increase the offshore extent (to 1,500 m water depth) and northward extent (as far as south-east Alaska, lat. 58°N) of the survey, to account for significant portions of the population in those areas during some years (Saunders and McFarlane, 1997; Fleischer et al.<sup>13</sup>).

It is unclear whether these changes were necessary solely because of changes in Pacific hake distributional patterns since the survey was first designed (Dark et al., 1980; Nelson and Dark, 1985), or because in later years fractions of the population that had always been “missed” by the old sampling design and gear were detected. The entire Pacific hake stock assessment time series was retrospectively adjusted using “expansion factors” for these changes in sampling design (Dorn et al., 1994; Dorn, 1996; Wilson and Guttormsen, 1997).

Major areas of uncertainty in this survey are pointed out in recent stock assessments (e.g. Helsler et al., 2006) and Stock Assessment Review (STAR) Panel<sup>14</sup> reports. Topics identified as major contributors to the uncertainty in survey-based biomass estimates and requiring additional research include (among others) the relationship between acoustic target strength and length for Pacific hake, a key parameter for acoustics-based biomass estimates (Traynor, 1996; Fleischer et al., 2005; Henderson, 2005); improved information on life history parameters, including growth rates and maturity; and the effect of climate-ocean conditions on movement patterns (expansion/contraction) of the stock and their effect on survey selectivity and the availability of the stock to the survey technique (the catchability of the survey, or  $q$ ) during different survey years.

<sup>13</sup>Fleischer, G. W., P. H. Ressler, R. E. Thomas, S. K. de Blois, and L. H. Hufnagle. 2005. NWFSC regional protocols for the joint Canadian and U.S. Pacific hake acoustic survey. NMFS, Northwest Fisheries Science Center (NWFSC), Fishery Resource Analysis and Monitoring Division Acoustics Team.

<sup>14</sup>STAR panel. 2006. Report of the joint Canadian and U.S. Pacific hake/whiting Stock Assessment Review Panel. 6–9 Feb., 2005, Seattle, WA. Online at <http://www.pcouncil.org/groundfish/gfstocks.html>.

<sup>12</sup>He, X., S. V. Ralston, A. D. Maccall, D. E. Pearson, and E. J. Dick. 2003. Status of the widow rockfish resource in 2003. Draft submitted to the June 2003 council meeting. Online at <http://www.pcouncil.org/groundfish/gfsafe0803/gfsafe0803.html>.

Recent research into climate-ocean patterns and processes in the CCLME and their relevance for Pacific hake recruitment, distribution, and abundance, all have direct bearing upon improved Pacific hake stock assessment.

### **Recent Observations of Climate-Ocean Influences on the Distribution of Pacific Hake**

The influence of climate-ocean conditions on the Pacific hake has been recognized during the major reviews of the state of knowledge of the stock over the past 20 years (Bailey et al., 1982; Stauffer, 1985; Methot and Dorn, 1995). As we have noted in this review, the survival of Pacific hake larvae and juveniles are linked to processes such as upwelling and advection, thereby affecting recruitment in different years and the strength of different year classes. It is also widely recognized that the annual coast-wide migrations of adult Pacific hake change in different climate ocean conditions, a phenomenon most dramatic during anomalous years.

But the mechanisms underlying these phenomena have not been fully elucidated, and perhaps as a consequence, these observations have been slow to change the conceptual model of Pacific hake autecology and have not been fully incorporated into the stock assessments that drive management decisions. Some early Pacific hake assessments used different recruitment curves during warm v. cold conditions (Swartzman et al., 1983; Hollowed and Francis, 1987; Francis et al.<sup>10</sup>), but the current stock assessment construct does not explicitly use environmental covariates (Helser et al., 2006), although its modeling of selectivity may implicitly incorporate the effect of ocean conditions on Pacific hake distribution (Agostini, 2005).

However, there is an increasing trend of environmental factors being explicitly handled in stock assessment models (Schirripa and Colbert, 2006). In the 10 years since the last major review of the status of knowledge of the Pacific hake stock (Methot and Dorn, 1995), there have been several recent advances in our understanding of climate-ocean influences upon Pacific hake. In large

part, the last 10 years have provided new data with which to evaluate some longstanding ideas about Pacific hake abundance and distribution.

### **Northward Shift in Spawning Location**

It is likely that coastal Pacific hake are spawning further north now than suggested by the classic model as articulated by Alverson and Larkins (1969), Bailey et al. (1982), and by most published papers on this species, one notable exception being the review of climate influences on North Pacific fish stocks by McFarlane et al. (2000). Unusual distributions of age-0 Pacific hake (Pearcy and Schoener et al., 1987; Dorn, 1996) imply that spawning events north of California can occur during warm ocean periods, and that the traditional model of hake annual migration, originally formulated in the late 1960's, should be revised to so that it can accommodate such observations (Fig. 8).

We further hypothesize that more northerly spawning events have continued through the 1990's and into the 21st century, and that these events reflect a general sensitivity of adult Pacific hake distribution not only to anomalously warm and cool years, but also to longer-term warming in climate-ocean conditions in the CCLME (McFarlane et al., 2000; Mendelssohn et al., 2003; Palacios et al., 2004; King, 2005; Field et al., 2006a).

Assuming that the distribution of young-of-the-year fish indicates the location of offshore adult spawner concentrations, more recent reports of young-of-the-year hake off Oregon, Washington (Phillips et al., 2007), and Vancouver Island (Cooke<sup>15</sup>) in mid summer (Brodeur et al., 2006) are consistent with this pattern. The design of the survey presently conducted by NMFS-PWCC (Phillips et al., 2007) includes parts of the northern California, Oregon, and Washington coasts not sampled by previous larval and juvenile surveys which focused on central and

southern California (Grover et al., 2002; Fig. 5). NMFS-PWCC results show a distinct northern shift in the distribution of young-of-the-year hake, with age-0 individuals detected as far north as 47°N since 2001. Given our knowledge of how embryos and larvae disperse from spawning areas, these observations are hard to reconcile with the past convention that depicts spawning aggregations only occurring in the deep waters off the Southern California Bight.

Future research should incorporate a new conceptual model of Pacific hake annual migration, in which 1) the average spawning location can shift northward from southern California, and 2) the location of spawning is variable with groups of Pacific hake spawning in different places, well north of where the classic model would suggest during some years (Fig. 8). Studies of the variability in hake recruitment that only consider processes within the classical southern spawning area (Mullin et al., 2000) are no longer adequate.

### **Pacific Hake Distribution and Growth in Relation to Climate-Ocean Processes**

As we have noted, studies investigating inter-annual variation in the distribution of Pacific hake in relation to ocean variability have reported a progressive increase in northern dispersal throughout the 1990's and into the 2000's. The increased northern displacement in the 1990's occurred during a period of warmer surface temperatures and reduced upwelling and stratification of coastal waters following the 1989 regime shift (King, 2005) and was related to warmer surface waters and stronger poleward flow in the spring (Ware and McFarlane, 1995; Swartzman and Hickey, 2003).

Benson et al. (2002) hypothesized that the 1989 regime shift also differentially affected the availability of euphausiids in the northern and southern regions of the CCLME, with feeding conditions in the north improved relative to those in the south, resulting in faster growth of juveniles in the northern regions during the 1990's. This progressive increase in northern distribution culminated with

<sup>15</sup>Cooke, K. 2006. Fisheries and Oceans, Canada, Pacific Biological Station, Nanaimo, BC V9T 6N7. Personal commun.



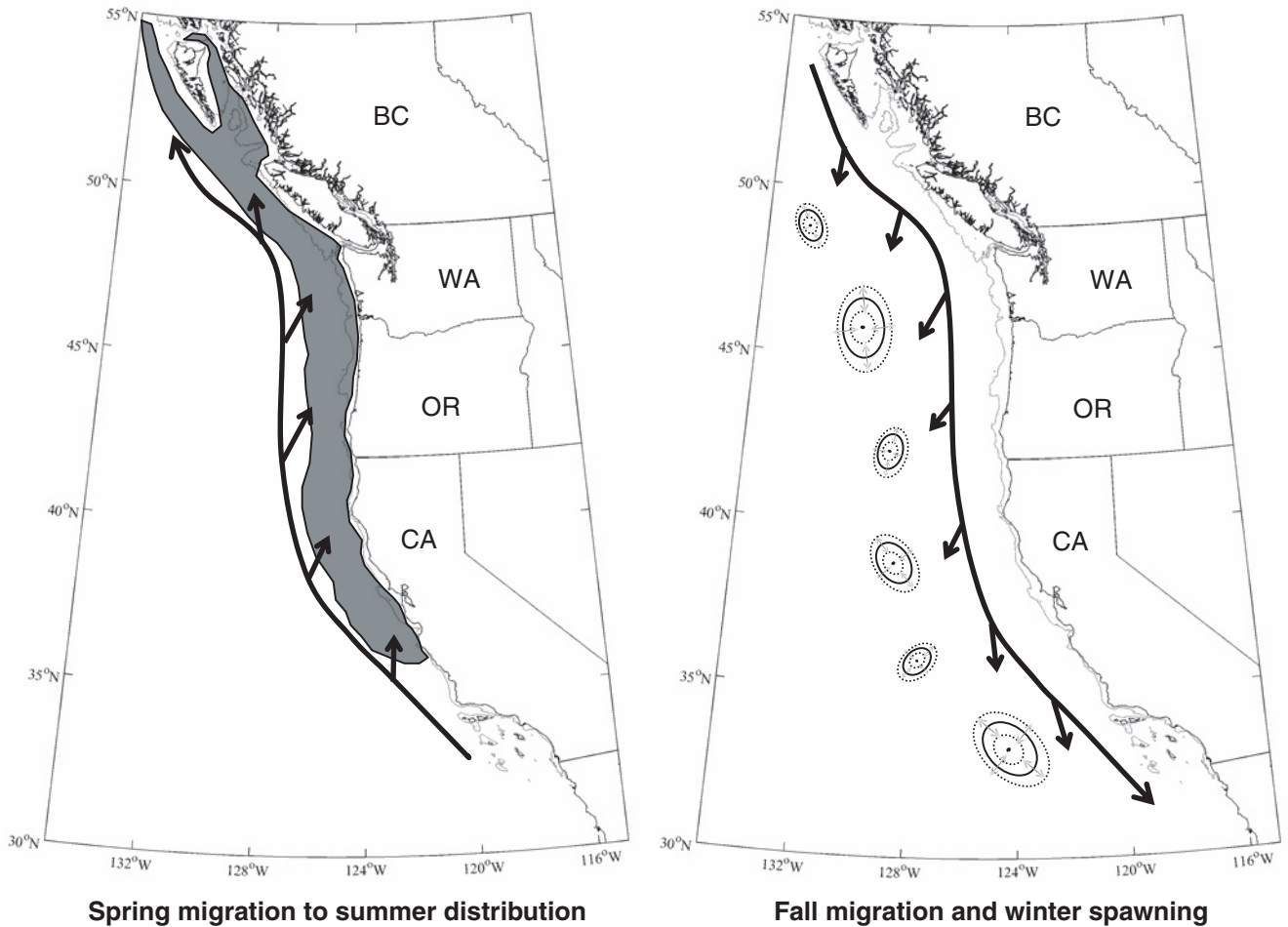


Figure 8.—Left, shaded area represents summer distribution of adults on shelf and slope in recent years. Right, ovals represent variable, patchy offshore spawning locations, inferred from recent collections of larvae and young juveniles and reports of a northward shift of spawning location in the literature. Arrows indicate the general direction of movement and migration in both panels. The 200 m isobath is shown in gray.

the cataloguing of measurable quantities of Pacific hake biomass as far north as southeast Alaska during the strong 1997–98 ENSO event (Wilson and Guttormsen, 1997; Wilson et al., 2000).

These changes in Pacific hake distribution represent a shift in the distribution of the entire stock rather than a range expansion or contraction (Benson et al., 2002), which is demonstrated by the fact that the proportion of the total Pacific hake biomass in Canadian waters increased while the proportion off southern California decreased during this period (Swartzman and Hickey, 2003), especially during the 1998 acous-

tic survey. The observed relationship between age, length, and northward migration distance that we have noted also implies that younger, smaller fish will increasingly appear in Canadian waters during warmer climate-ocean conditions.

Recent acoustic survey observations (Fig. 9) continue to show that the summer Pacific hake distribution includes areas north of Vancouver Island (ca. lat. 50°N) which were not considered typical Pacific hake habitat prior to the 1992 survey. Particularly dramatic are northward shifts in distribution in 1998 after a strong El Niño event, a

southward shift in 2001 (Wilson et al., 2000; Guttormsen et al.<sup>8</sup>) after a series of cool La Niña years (Schwing et al., 2002), and subsequent movement back northward in 2003 (Fleischer et al., 2005) and 2005 (Fleischer et al.<sup>4</sup>) during years characterized by warmer ocean conditions and delayed upwelling in the CCLME (Brodeur et al., 2006; Pierce et al., 2006). These patterns reinforce the presence of both a relationship between shifts in north–south distribution and inter-annual physical variability, and a pattern of increasing northward dispersal during a longer-term trend of rising ocean temperatures. Such observations

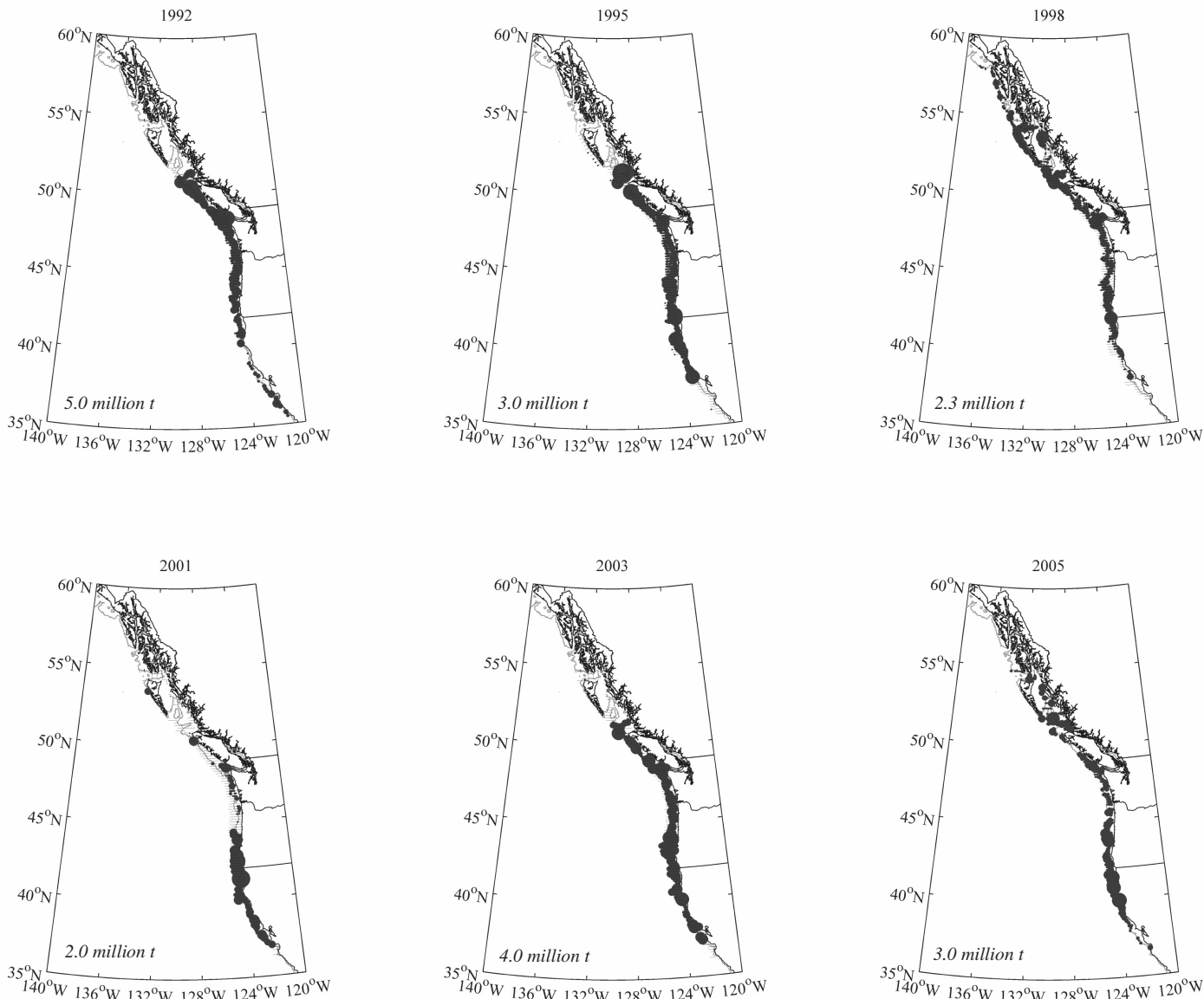


Figure 9.—The dark shaded area represents the coast-wide distribution of Pacific hake biomass during joint U.S.–Canadian acoustics-trawl surveys between 1992 and 2005. The total stock biomass from the corresponding year, estimated by the assessment model (Helser and Martell, 2007), is indicated in the lower left corner of each panel. Survey transects are indicated by solid east-west black lines, the coastline is shown in black, and the 200 m isobath is shown in gray. Between 1992 and 2001, U.S. and Canadian surveys were conducted semi-independently and their coverage overlapped in Canadian waters; for clarity, in these areas of overlap the data from Canadian surveys are not shown. Most transects have a north-south spacing of 10 n.mi., but note finer scale sampling off Vancouver Island in 1992, 1995, and 1998. For further information on these surveys, see Dorn et al. (1994), Wilson and Guttormsen (1997), Wilson et al. (2000), Fleischer et al. (2005), Fleischer et al., text footnote 4, and Guttormsen et al., text footnote 8.

not only hold promise for understanding and forecasting hake distribution, but they also imply that Pacific hake might be useful indicators of change within this ecosystem.

The proposition that ocean conditions affect Pacific hake distribution is not a new idea. The last 10 years have led to a better understanding of the strong link of Pacific hake distribution to climate-related physical processes in the CCLME (McFarlane et al., 2000; King, 2005; Field et al., 2006a), as well as the luxury of a longer time series with which to evaluate the fluctuations of the Pacific hake stock under different environmental conditions. Temperature is easily measured and has predictive power (Dorn, 1995; Ware and McFarlane, 1995), but it may not be the key variable that affects the distribution of Pacific hake, as other authors have suspected (Benson et al., 2002).

We have already discussed covariation of Pacific hake distributions with flow regimes and prey distribution: the work of Mackas et al. (1997), Swartzman (2001), Swartzman and Hickey (2003), and Benson et al. (2002) argues strongly that these are key to understanding Pacific hake distribution. Agostini (2005) and Agostini et al. (2006) recently examined and modeled the distribution of adult Pacific hake with respect to the location and intensity of the poleward undercurrent during 1995 and 1998, providing further support for this sort of link. Agostini's major finding is that Pacific hake aggregated close to the poleward flow of the California Undercurrent, perhaps in response to cues in the flow field. She showed that there was a dome-shaped relationship between Pacific hake habitat favorability and current speed, in which Pacific hake are most often found in areas of poleward flow (Fig. 10). Agostini (2005) used this relation to model the southern part of Pacific hake habitat (ca. lat. 38°–43°N), and found that there was more favorable habitat (based on a model using flow and bottom depth as predictors and accounting for autocorrelation in the data set) in 1998 than 1995 (51% vs. 16%). The model used subsurface flow between 120 and 330 m and bottom depth as

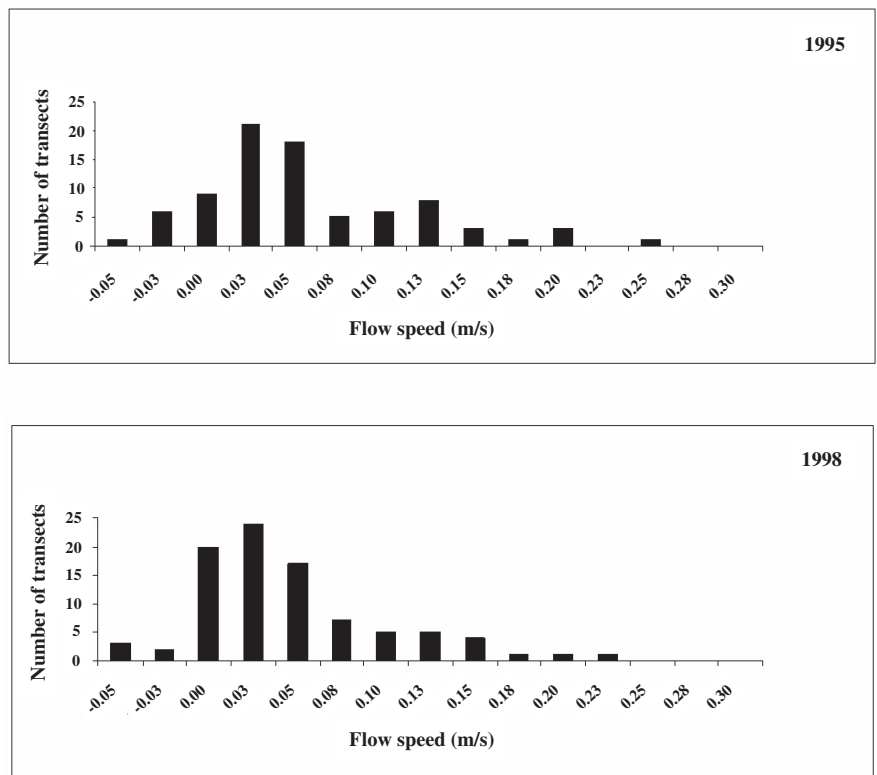


Figure 10.—Frequency distribution of alongshore flow, averaged over survey transects from depths where Pacific hake were present, based on acoustics-trawl survey data from 1995 and 1998. Positive flow speeds are poleward, characteristic of the California Undercurrent, while negative values indicate equatorward flow. Modified from Agostini (2005) with permission.

predictors, but it did not explicitly account for the possible influence of the age structure of the population.

As we have noted, climate-ocean conditions not only affect the behavior of the Pacific hake, in terms of movements and migration, but also their growth. A recent study by Colbert et al.<sup>16</sup> showed that oceanographic conditions could explain much of the variability in Pacific hake otolith growth increments formed between 1970 and 2002, reinforcing a link between the size of these increments and climate-ocean conditions (Dorn, 1992; MacLellan and Saunders, 1995). This link provides strong support

for a relationship between Pacific hake growth, adult distribution and migration, and climate-ocean processes.

### Pacific Hake Trophic Impact and Importance

As noted, Pacific hake have a wide ranging trophic impact and importance in the CCLME. This feature has been recognized previously, but only recently have improvements in our understanding of climate-ocean processes, associated biological impacts in the CCLME, and computational improvements made realistic ecosystem-wide model simulations possible. A northward distributional shift, for example, could alter the predatory impact of Pacific hake as well as influence its availability to top predators.

Field (2004) recently formulated a mass balance model of the CCLME,

<sup>16</sup>Colbert, J. J., M. J. Schirripa, and O. Rodriguez. Interannual changes in Pacific hake (*Merluccius productus*) growth in relation to oceanographic conditions. Contact J. Colbert, Oregon State University, 2032 S.E. Marine Science Dr., Newport, OR 97365. Manuscript in prep.

primarily to explore the idea of ecosystem-based fisheries management (Field et al., 2006b). The model includes physical forcing as well as biological data to simulate different climate-ocean conditions, and includes zooplankton, fish, and higher predators represented as single species or groups of species. Inclusion of climate indices significantly improved the fit of the model. Moreover, Pacific hake was identified by the model as a key species in the CCLME: changes in its relatively substantial abundance have wide-ranging effects, both upon forage fishes and upon the apex predators that feed on Pacific hake (Fig. 11; Agostini, 2005). As a better functional understanding of climate-ocean effects emerges, such models can be used to test hypothesis and forecast future scenarios, based on assumed future environmental conditions.

## Research Needs and Priorities

We suggest the following priorities for future Pacific hake monitoring and research efforts.

- 1) Analyze climate and Pacific hake acoustics-trawl survey data from 1992 to present to look for predictive relationships between Pacific hake distribution and recent climate and oceanographic data. The spatial distribution of the Pacific hake stock affects its availability to both monitoring surveys and the commercial fishery. The most careful model of ocean influences on northward migration by Pacific hake, formulated by Dorn (1995), was based only on data through 1992. Modeling of distribution must include both oceanographic

factors (such as temperature, time of spring transition, climate indices, and current patterns) and the age structure of the population. A predictive relationship will allow an evaluation of past survey data and improvements in the design and execution of future surveys. It will also allow better forecasts of Pacific hake distribution and ecosystem impact under different hypothetical climate-ocean scenarios.

- 2) Pursue improvements to the biennial acoustics-trawl survey, including possible adjustments to the current design based on improved understanding of relationships between ocean conditions and Pacific hake distribution, as well as better knowledge of a key acoustic parameter, target strength. Continue to conduct spatially expanded surveys of larval and juvenile stages as an index of recruitment. These research priorities closely coincide with many of the recommendations of the STAR panel convened to review the most recent stock assessment.<sup>14</sup>
- 3) Investigate mechanisms underlying observed correlations between physical oceanographic parameters and Pacific hake distribution. This will require regular collection of physical oceanographic data as well as sampling of the potential prey field which, if sufficient time and resources are allocated, could be accomplished in concert with the biennial acoustics-trawl survey. Smaller, dedicated studies of diel feeding behavior, prey consumption, and the available prey field that focus on the goal of establishing links between relevant physical variables and prey distribution are needed. These could also allow a better understanding of the mechanisms that drive Pacific hake abundance and distribution, improving monitoring and assessment of this species.
- 4) Develop the means for better information on Pacific hake during the non summer months (after they have left the northern feeding

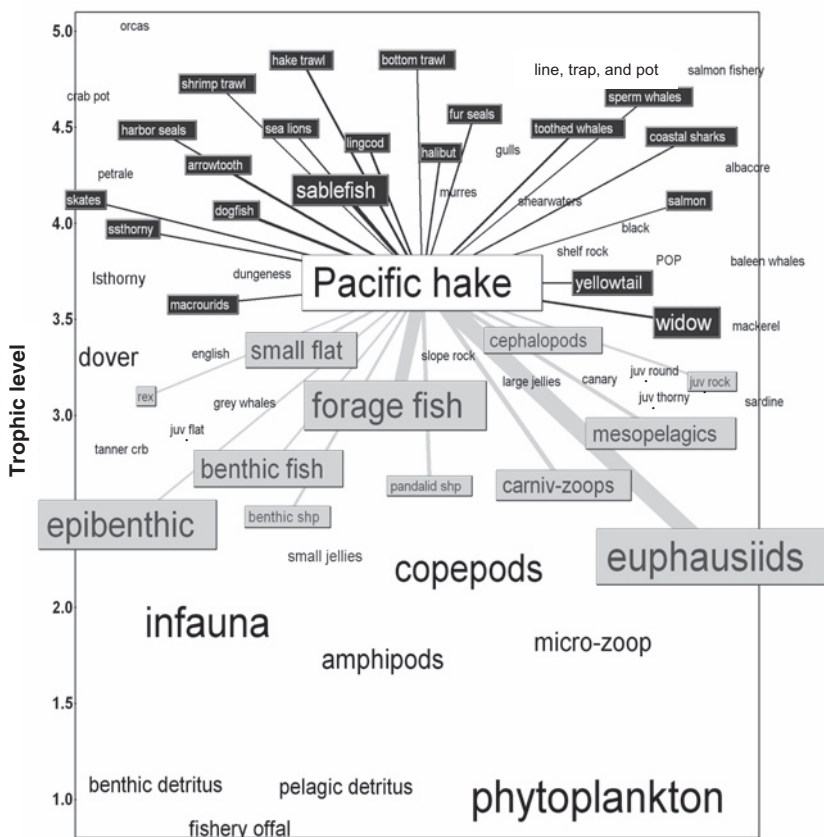


Figure 11.—The trophic position of the Pacific hake in a recent model of the CCLME. Predators on Pacific hake are shown in black boxes, prey in gray boxes, and ecosystem model components not directly connected to Pacific hake in plain text. Modified from Field (2004) with permission.

grounds) since relatively few data on Pacific hake have been collected during this time of the year. Bailey et al. (1982) noted that efforts to tag Pacific hake had proved unsuccessful, but recent advances in tagging technology may facilitate these kinds of studies. Other avenues include developing partnerships with the commercial fishing industry that could be used to gather this information using commercial vessels or by utilizing emerging broad-scale acoustic sampling technologies (Makris et al., 2006). Directly quantifying spawning location and biomass by surveying likely areas would yield important insights into distributional changes and recruitment patterns.

- 5) Explore possible scenarios of future Pacific hake abundance, distribution, and growth to predict possible impacts in the CCLME. This effort should employ a combination of stock assessment models and food web models in simulations of possible future climate-ocean conditions.
- 6) Investigate the use of Pacific hake as an indicator species to biological changes in the CCLME, particularly in the face of changing climate-ocean conditions (e.g. King, 2005; The Pacific Coast Ocean Observing System, <http://www.pacoos.org/>). Pacific hake may be an appropriate species for such monitoring, both because of the sensitivity of its distribution to changes in ocean conditions and its ecological and commercial importance in the CCLME.

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1; and various authors (as noted in the text) that shared their works-in-progress with us for the purpose of our review. J. J. Colbert, M. W. Dorn, and R. L. Emmett, and several anonymous reviewers provided useful comments on previous drafts of this manuscript. The source of coastline data used in figures was the National Geophysical Data Center Coastline Extractor at <http://rimmer.ngdc.noaa.gov/coast/>. C. Whitmire helped provide the 200 m bathymetry contours.

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