The relationship between Pacific hake (*Merluccius productus*) distribution and poleward subsurface flow in the California Current System

Vera N. Agostini, Robert C. Francis, Anne B. Hollowed, Stephen D. Pierce, Chris Wilson, and Albert N. Hendrix

Abstract: In a search for ocean conditions potentially affecting the extent of Pacific hake (*Merluccius productus*) feeding migrations, we analyzed data collected in 1995 and 1998 by the National Marine Fisheries Service on abundance and distribution of hake (by echo integration), intensity and distribution of alongshore flow (from acoustic Doppler current profiler), and temperature (conductivity–temperature–depth profiles). Our results show that Pacific hake are associated with subsurface poleward flow and not a specific temperature range. Temporal and spatial patterns characterize both hake distribution and undercurrent characteristics during the two years of this study. We suggest that poleward flow in this area defines adult hake habitat, with flow properties aiding or impeding the poleward migration of the population. We conclude that although physical processes may not directly affect fish production, they may be the link between large-scale ocean–atmosphere variability and pelagic fish distribution.

Résumé : Dans notre recherche des conditions qui affectent potentiellement l'amplitude des migrations alimentaires du merlu du Pacifique (*Merluccius productus*), nous avons analysé des données récoltées en 1995 et 1998 par le National Marine Fisheries Service sur l'abondance et la répartition des merlus (par écho-intégration), l'intensité et la répartition de l'écoulement le long de la côte (à l'aide d'un enregistreur acoustique Doppler des profils de courant) et de la température (profils de conductivité–température–profondeur). Nos résultats montrent que le merlu du Pacifique est associé à l'écoulement vers le pôle qui se produit sous la surface, mais non à une gamme spécifique de températures. Durant les deux années de notre étude, tant la répartition des merlus que les caractéristiques des courants sous la surface suivent des patrons temporels et spatiaux. Nous pensons que l'écoulement vers le pôle dans cette région détermine l'habitat des merlus et que les caractéristiques de l'écoulement facilitent ou entravent la migration de la population vers le pôle. Nous concluons que, bien que les processus physiques peuvent ne pas affecter directement la production des poissons, ils peuvent servir de lien entre la variabilité à grande échelle de l'océan–atmosphère et la répartition des poissons pélagiques.

[Traduit par la Rédaction]

Introduction

The California Current (CC) ecosystem is one of the major eastern boundary current systems of the world, extending from Baja California to the northern tip of Vancouver Island (Fig. 1). The CC originates where the West Wind Drift divides, resulting from a divergence in wind patterns, into two branches near the coast of North America: a northern branch, the Alaska Current, and a southern branch, the CC (Ware and McFarlane 1989) (Fig. 1). The equatorward-flowing surface CC and the poleward-flowing subsurface California Undercurrent (CU) dominate large-scale circulation in this region

(Fig. 1). The CU flows poleward from Baja California to Vancouver Island throughout most of the year; it is a relatively narrow current (ca. 10–40 km) and strongest at depths of 100–300 m (Neshyba et al. 1989).

Ocean circulation in this area varies on seasonal, interannual, and interdecadal bases. Two dominant atmospheric pressure regimes drive most of the seasonal, as well as the interdecadal, variability: the Aleutian low pressure system (ALP) during winter and the North Pacific high pressure system during summer (Emery and Hamilton 1985; Mantua et al. 1997). Winds associated with these regimes drive the large-scale surface flow, as well as the local coastal surface

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Fig. 1. Schematic representation of general circulation along the west coast of North America. Box indicates area of study.

Fig. 2. Schematic representations of Pacific hake (*Merluccius productus*) migrations.
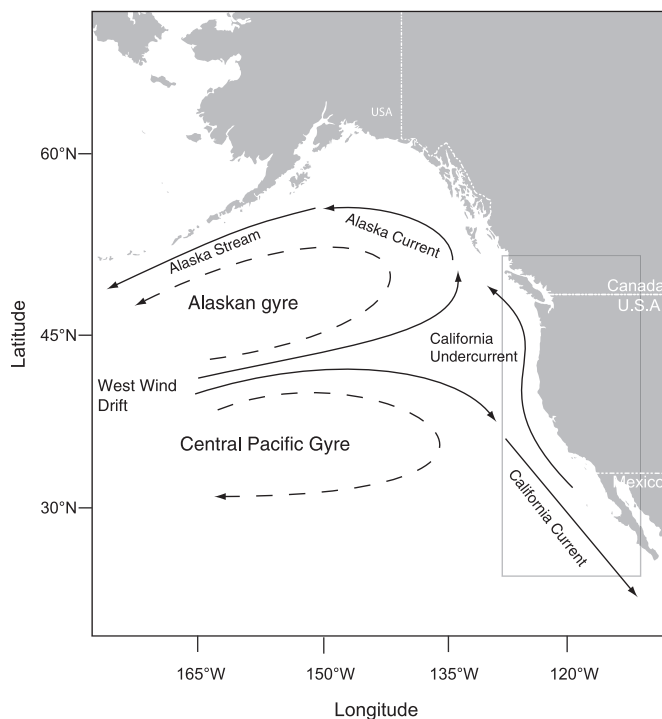
currents and onshore and offshore Ekman transport (Tabata 1975; Hickey 1979). Superimposed on this is the equatorially generated El Niño Southern Oscillation (ENSO), which leads to changes on an interannual scale. All of the above sources of variability affect a suite of local ocean conditions (Chelton 1981; Lynn and Simpson 1987; Strub et al. 1990). For example, El Niño can cause warming of the upper waters off the California coast, a depression of the nearshore thermocline, weakening of the CC, weakening in upwelling intensity, and an intensification of poleward flow (Chelton and Davis 1982; Hollowed 1992; Hickey 1998).

Variability in ocean conditions impacts production of a number of CC species (Francis and Hare 1994; Hare and Mantua 2000; Hollowed et al. 2001). There are four dominant coastal pelagic species in this system: northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), Pacific hake (*Merluccius productus*), and chub mackerel (*Scomber japonicus*). All of the adults of these species, with the exception of anchovy, conduct extensive migrations poleward in the summer to feed off the Pacific Northwest coast and equatorward in the winter to spawn off southern California (Benson et al. 2002). The northern limit of their feeding migrations appears to be related to oceanic seasons and to the northern boundary of the CC system (Ware and McFarlane 1989), the location of which varies according to climate conditions. Pacific hake (also referred to as Pacific whiting) account for 61% of the pelagic biomass in this system (Ware and McFarlane 1995) and belong mostly to the offshore population (Saunders and McFarlane 1997). There are also distinct populations of Pacific hake in the Strait of Georgia (McFarlane and Beamish 1985), Puget Sound (Pedersen 1985), and inlets of the west coast of Vancouver Island (Beamish and McFarlane 1985). The offshore population is
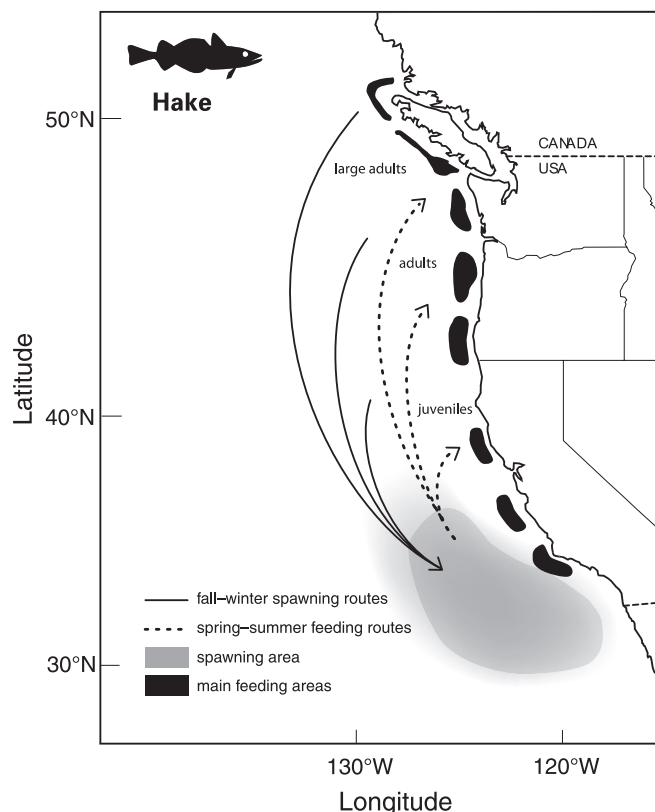
of greatest importance, as it contributes a large biomass for fisheries in both Canadian and United States (US) waters (Francis et al. 1989; Smith et al. 1990). A good deal of controversy and interest revolves around this fishery, as the largest and most valuable fish migrate further north (Beamish and McFarlane 1985) and dramatic variability in year-class strength (Bailey and Francis 1985) affects the interannual distribution of biomass and therefore yield of hake between Canada and the US (Swartzman et al. 1987).

Offshore hake are believed to spawn between January and March each year at depths of 100–200 m (Fig. 2) off the coast of southern California or northern Mexico (Bailey et al. 1982; Bailey and Francis 1985). Offshore hake begin their seasonal northward feeding migration inshore (depths < 100 m) during late spring – early summer; in late fall, they move offshore and then return south to spawn (Bailey et al. 1982) (Fig. 2). Females have been reported to leave the spawning grounds and begin their migration north earlier than males (Saunders and McFarlane 1997). In summer, feeding hake are concentrated in large midwater aggregations centered on the shelf break from central Oregon to northern Vancouver Island (Saunders and McFarlane 1997). Their diet relies primarily on euphausiid in spring and summer and increases in piscivory with size (Bailey et al. 1982; Buckley and Livingston 1997). Cannibalism has been observed on the hake feeding grounds, with older larger hake eating smaller younger hake (Dorn 1995; Buckley and Livingston 1997).

The abundance of hake in Canadian waters has been related to temperature (Dorn 1995; Ware and McFarlane 1995;

Fig. 3. Acoustic backscatter signal representative of hake (*Merluccius productus*) abundance during (*a*) 1998 (warm year) and (*b*) 2001 (cold year). Data are from the National Marine Fisheries Service, Alaska Fisheries Science Center (NMFS–AFSC), Seattle, Washington.
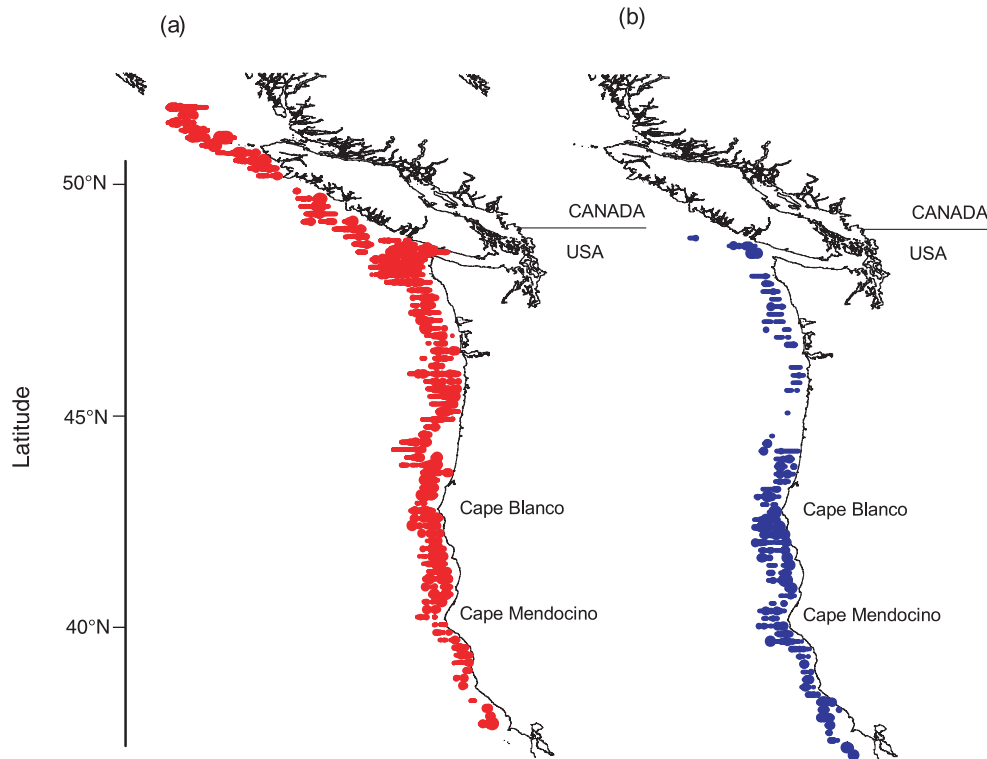
Benson et al. 2002). Hake have been located further north during warm years (Fig. 3) (Dorn 1991, 1995; Wilson and Guttormsen 1998); however, evidence for a relationship between hake distribution and temperature has been weak (Benson et al. 2002). A few authors have suggested that hake distribution may be related instead to poleward flow, with stronger flow aiding the migration of hake and weaker flow impeding it (Smith et al. 1990; Dorn 1995; Benson et al. 2002).

In this study, we use acoustic data to examine the distribution of hake in the CC system in relation to poleward flow and temperature. We test the hypothesis that hake distribution is related to poleward flow. We argue that although physical processes may not directly affect hake production, they may be the link between large-scale ocean–atmosphere variability and hake distribution along the west coast.

Materials and methods

Study area

In 1977, the National Marine Fishery Services (NMFS) began collecting data describing hake abundance and distribution along the west coast of North America; in 1992, the Canadian Department of Fisheries and Oceans (DFO) began collaboration with NMFS in this collection. Echo-integration summer acoustic trawl surveys have been conducted on a triennial basis along the continental shelf from California to the northern limit of hake aggregations in British Columbia (Fig. 3). Recently, survey efforts have extended into Alaskan waters. Details of the triennial surveys are available in Wilson and Guttormsen (1997) and Wilson et al. (2000). Surveys generally occurred from July to September off the west coast

of North America. Data were collected along parallel transects, uniformly spaced 18 km apart and 52 km long on average. Transects generally ran midshelf to midslope between the 50 m and 1500 m isobaths. To capture conditions from different climate regimes, survey data were analyzed from 1995 (a neutral year) and 1998 (an El Niño year).
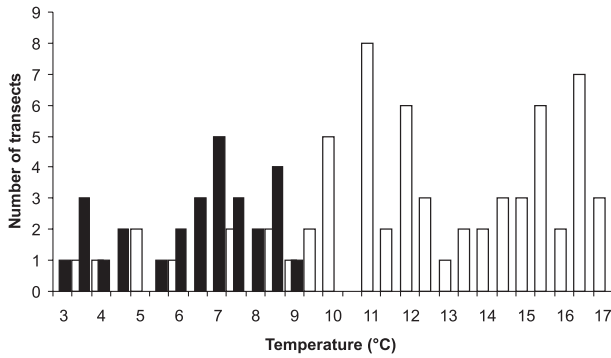
Biological data

Abundance and distribution of adult hake were derived from acoustic data collected using a quantitative echo-sounding system with split-beam transducers (38 kHz and 120 kHz; Simrad EK500; Simrad, Lynnwood, WA 98036, USA) mounted on the bottom of the vessel centerboard, 9 m below the surface. Data collected with the 38 kHz transducer were used in this study. Echo-integration data were sampled with a vertical resolution of about 9 m and a horizontal resolution of 1–2 m. Standard target strength–length relationships were used to convert acoustic backscatter into fish density. The target strength relationship used was TS = 20log$L$ – 68, where L represents fish length measured in centimetres. For detailed methods on data processing, see Wilson and Guttormsen (1997) and Wilson et al. (2000).

Physical data

Distribution and intensity of alongshore (north–south (N–S)) flow were derived from an RD instrument, a 153.6 kHz narrow-band, hull-mounted shipboard acoustic Doppler current profiler (ADCP). A vertical bin width of 8 m, a pulse length of 8 m, and an ensemble averaging time of 2.5 min were used. The depth range of good data (good pings > 30%) was typically 22–362 m. The ADCP was slaved to the Simrad EK500 to avoid interference. Presurvey tests con-

Fig. 4. Frequency distribution of temperature values in hake waters at survey stations during 1995 (solid bars) and 1998 (open bars).

Fig. 5. Frequency distribution of alongshore flow values (m·s^{-1}) in hake waters at survey transects during 1995 (solid bars) and 1998 (open bars). Positive values indicate poleward flow; negative values indicate equatorward flow.

firmed no interference between the two instruments when the ADCP was in water-pulse mode. When the ADCP bottom-track feature was enabled, however, an artificial signal was detected on the EK500. For this reason, bottom tracking was never enabled during the survey. GPS P-code navigation was used for position and gyrocompass was used for heading to determine absolute velocities. Tidal currents remain in the processed ADCP velocities. These are expected to be small (<0.05 m·s^{-1}) offshore of the shelfbreak (Erofeeva et al. 2003). For detailed ADCP processing methods, see Pierce et al. (2000).

Temperature information was derived from conductivity–temperature–depth (CTD) casts (1995, n = 200; 1998, n = 179) made at two or three locations where large aggregations of hake were observed, along every second or third transect, from the surface down to water depths of about 500 m.

Analysis

To describe the relationship between temperature, hake, and alongshore flow distribution the following values were computed for J transects (j = 1, 2, 3, ..., J), I_j stations in transect j (i = 1, 2, 3, ..., I_j), and $K_{i,j}$ depths at station i_j ($k_{i,j}$ = 1, 2, 3, ..., $K_{i,j}$).

Depth (in metres) of center of mass of poleward flow at station i and transect j (as in Pierce et al. 2000), hereafter referred to as core current, was determined by
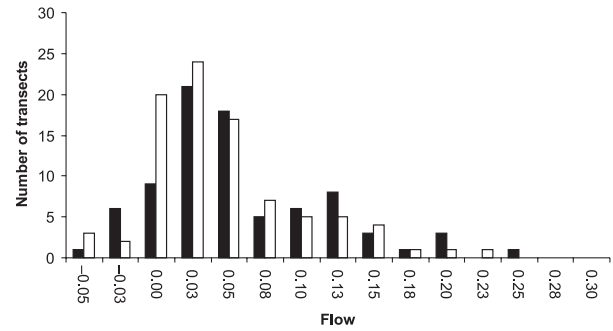
$$(1) \quad Z_{c_{i,j}} = \frac{\sum_{k=1}^{k_{i,j}} v_{i,j,k}\, z_{i,j,k}}{\sum_{k=1}^{k_{i,j}} v_{i,j,k}}$$

where $v_{i,j,k}$ represents raw poleward velocity at station i, transect j, and depth k; and $z_{i,j,k}$ is the depth of current measurement at station i, transect j, and depth k.

Weighted mean depth (in metres) of hake at each station i and transect j is determined as follows:

$$(2) \quad Z_{f_{i,j}} = \frac{\sum_{k=1}^{k_{i,j}} f_{i,j,k}\, z_{i,j,k}}{\sum_{k=1}^{k_{i,j}} f_{i,j,k}}$$

where $f_{i,j,k}$ is the number of fish at station i, transect j, and depth k; and $z_{i,j,k}$ is the depth of fish measurement at station i, transect j, and depth k.

The fish index at each station i and transect j is calculated by

$$(3) \quad FI_{i,j} = \frac{\sum_{k=1}^{k_{i,j}} f_{i,j,k}}{f_{max}}$$

where $f_{i,j,k}$ is as defined for eq. 1, and f_{max} is the maximum number of fish over the entire survey range.

Weighted alongshore flow velocity (cm·s^{-1}) at each station i and transect j (referred to hereafter as flow velocity of hake waters) is determined as follows:

$$(4) \quad v_{f_{i,j}} = \frac{\sum_{k=1}^{k_{i,j}} f_{i,j,k}\, v_{i,j,k}}{\sum_{k=1}^{k_{i,j}} f_{i,j,k}}$$

where $f_{i,j,k}$ is as defined earlier, and $v_{i,j,k}$ is the raw N–S flow velocity for bins where number of fish > 0 at station i, transect j, and depth k.

Mean alongshore flow velocity (cm·s^{-1}) at each station i and transect j is calculated by

$$(5) \quad v_{c_{i,j}} = \frac{\sum_{k=1}^{k_{i,j}} v_{i,j,k}}{n}$$

where $v_{i,j,k}$ is the raw N–S velocity at station i, transect j, and depth k, and n is the number of depth bins.

Weighted temperature (°C) at station i and transect j (referred to hereafter as temperature of hake waters) is determined as follows:

$$(6) \quad T_{f_{i,j}} = \frac{\sum_{k=1}^{k_{i,j}} T_{i,j,k}\, f_{i,j,k}}{\sum f_{i,j,k}}$$

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Fig. 6. Distribution of alongshore flow (in color) and hake (*Merluccius productus*) aggregations (in black contours representing numbers of fish $\geq 16 \times 10^{-3}$ m^3) for (*a*) a transect located at 41°N sampled in 1995; (*b*) a transect located at 50°N sampled in 1995; (*c*) a transect located at 38°N sampled in 1998; and (*d*) a transect located at 51°N sampled in 1998. The bottom contour is also shown (solid area). Flow velocities greater than 0 indicate poleward flow; flow velocities less than 0 indicate equatorward flow.
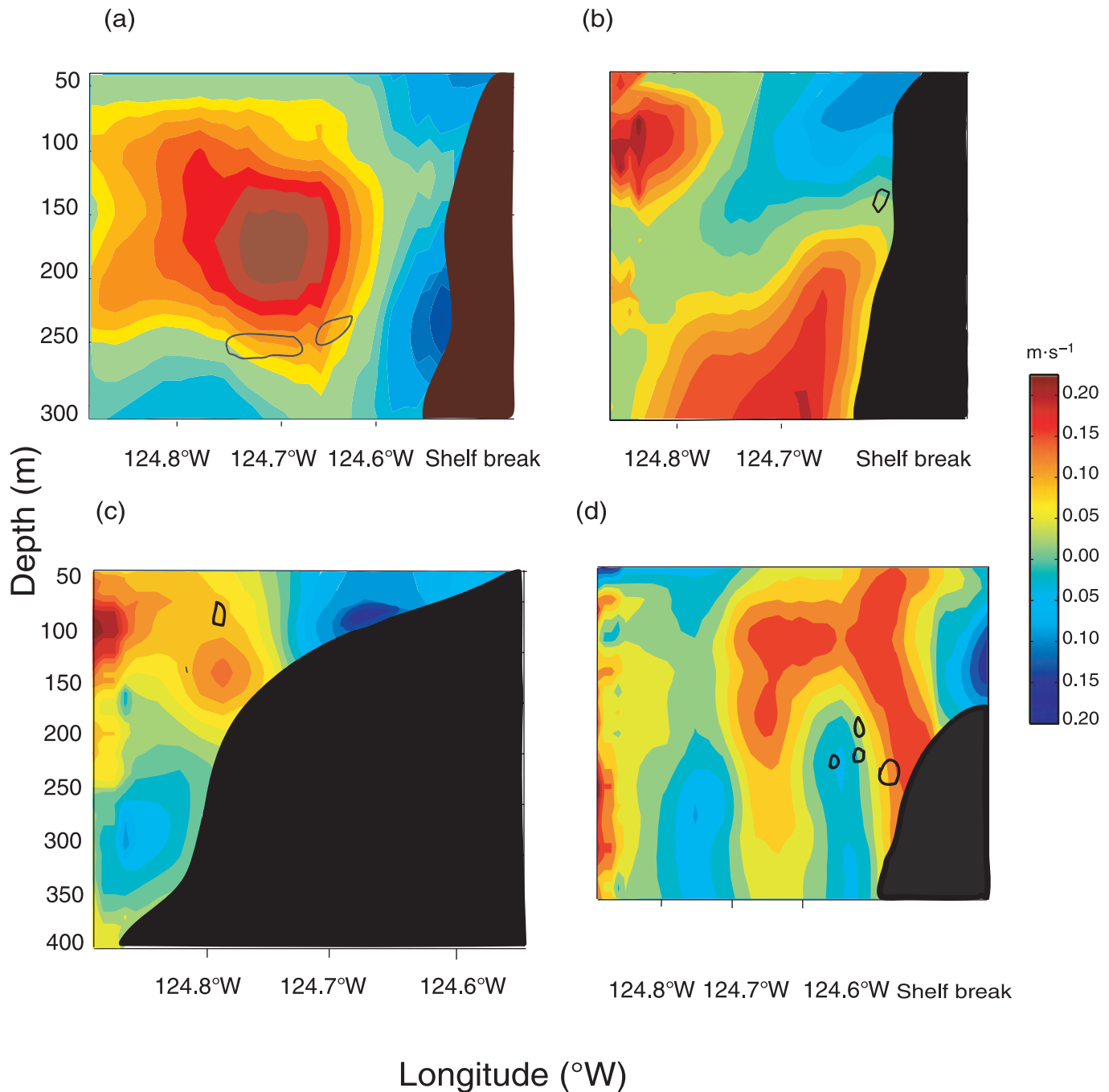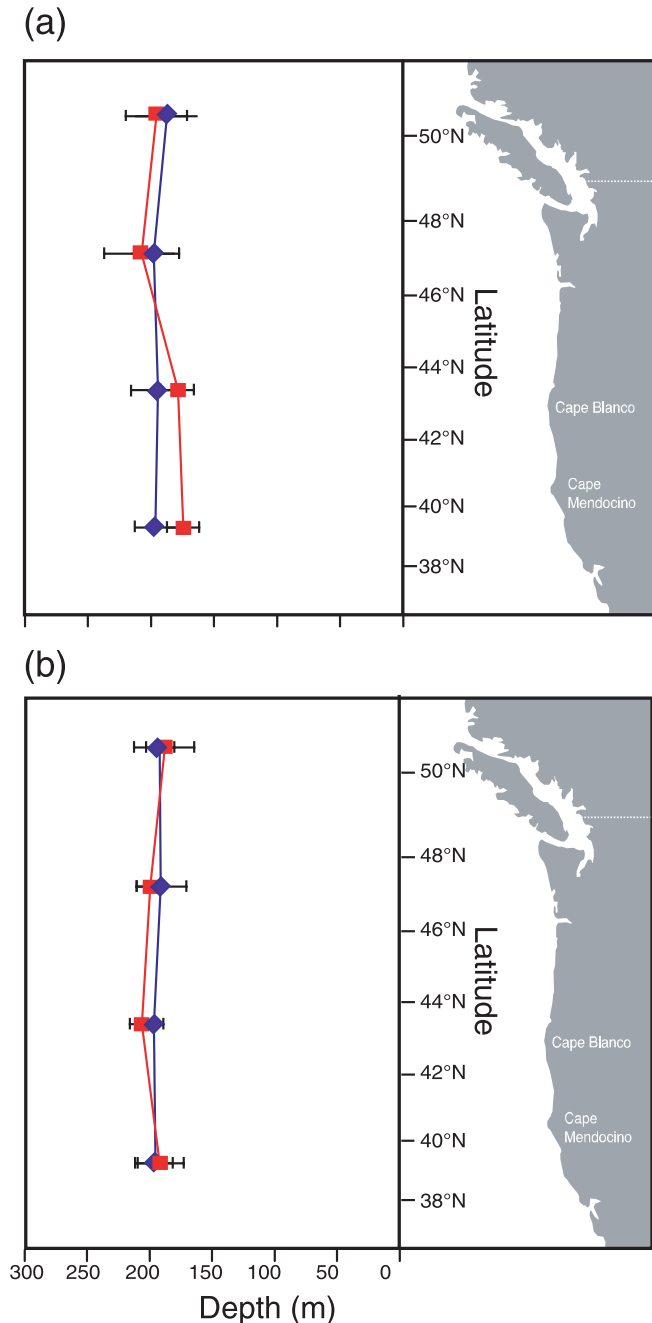

where $T_{i,j,k}$ is the temperature at station i, transect j, and depth k for bins where number of fish > 0, and $f_{i,j,k}$ is as defined earlier.

To aid in spatial analysis, values were averaged over each transect, as well as over four latitudinal blocks (32.5°N–37.5°N, 37.5°N–42.5°N, 42.5°N–47.5°N, 47.5°N–52.5°N). The latitudinal blocks were chosen to coincide with important topographic features, such as capes and promontories, known to influence the oceanography of the region (Hickey

1979). Differences between 1995 and 1998 mean average temperature, flow, and distance of fish from shelf were tested using two-sample *t* tests. Also, to effectively isolate waters where subsurface poleward flow usually occurs, the values above were computed in two ways: (*i*) including measurements from all depths bins, and (*ii*) including only measurements from 120–330 m depth bins (hereafter referred to as subsurface). Any values at depths shallower than 120 m probably do not represent CU flow (Pierce et al. 2000). Also,

Fig. 7. Depth of (*a*) fish and (*b*) core current averaged over four latitudinal blocks (32.5°N–37.5°N, 37.5°N–42.5°N, 42.5°N–47.5°N, 47.5°N–52.5°N). Values for 1995, ♦; values for 1998, ■.
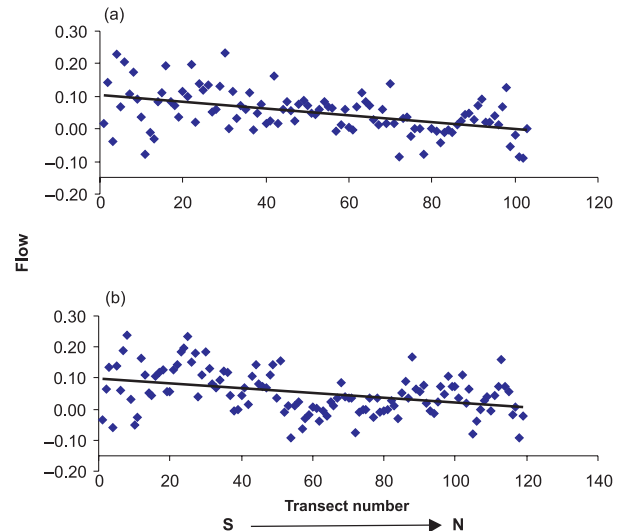

(a)

(b)

Fig. 8. Average speed of subsurface alongshore flow (m·s^{-1}; negative values indicate equatorward flow; positive values indicate poleward flow) at each transect. Values are averaged over the 120 m to 330 m depth bins. (*a*) 1998, (*b*) 1995.


hake were usually not detected at depths shallower than 120 m. Alongshore flow (N–S) will be referred to as "flow" throughout this paper.

Results

To explore the relationship between hake distribution and temperature, we computed average temperature ($\overline{T}$) of hake waters for each CTD station. A frequency histogram of these values reveals that hake occur in waters of a wide range of temperatures (from a minimum of 3.5 °C to a maximum of 17.5 °C) (Fig. 4). As expected, temperatures of hake waters were significantly higher during 1998, an El Niño year ($\overline{T}$ = 12.2 °C, s^2 = 12.1), compared with during 1995, a neutral year ($\overline{T}$ = 5.3 °C, s^2 = 7.0) (p << 0.01, df = 81, t test for difference between means).

In contrast, average subsurface flow speed in hake waters (Fig. 5) indicates that fish were in waters with a much narrower range of values (between –0.05 and 0.25 m·s^{-1}, where negative values indicate equatorward flow and positive values indicate poleward flow) compared with the temperature values reported above, with most of the flow between 0.025 and 0.075 m·s^{-1}, speeds reported to be typical of the poleward-flowing undercurrent (Pierce et al. 2000). Average subsurface flow speed of hake waters was higher during 1995 ($\overline{x}$ = 0.05 m·s^{-1}, s^2 = 0.004) compared with during 1998 ($\overline{x}$ = 0.03 m·s^{-1}, s^2 = 0.003) (p = 0.04, df = 160, t test for difference between means). Similar results were found when considering flow at all depths.

Sections of flow overlaid with hake distribution and abundance data were plotted for each transect, revealing a picture of a ubiquitous core of poleward flow at depth, with its strength and location varying both inshore and offshore and at depth for the two years sampled. Complex flow patterns were evident in each section. The view of geostrophic flow in any one section is confused by the presence of barotropic tidal currents, baroclinic tidal currents, and inertial oscillations (Pierce et al. 2000). For sections where fish were present, concentrations were almost always observed on the edge of the core poleward flow (Figs. 6a–6d). Depth of fish and core current averaged over latitudinal blocks were similar (Fig. 7) during both 1995 and 1998, with average depths ranging mostly between 170 and 220 m. Depth of core current values are consistent with results from Pierce et al. (2000), as well as with historical estimates of undercurrent depth (Neshyba et al. 1989).

The alongshore subsurface layer flow speeds show significant scatter during both years (Fig. 8), probably because of

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Fig. 9. Observed acoustic Doppler current profiler velocity vectors (depth averaged 120–330 m) from a subsection of the National Marine Fisheries Service – Department of Fisheries and Oceans survey for (*a*) 1995 and (*b*) 1998. Black lines parallel to the coast represent the 50 m, 100 m, and 200 m isobaths.
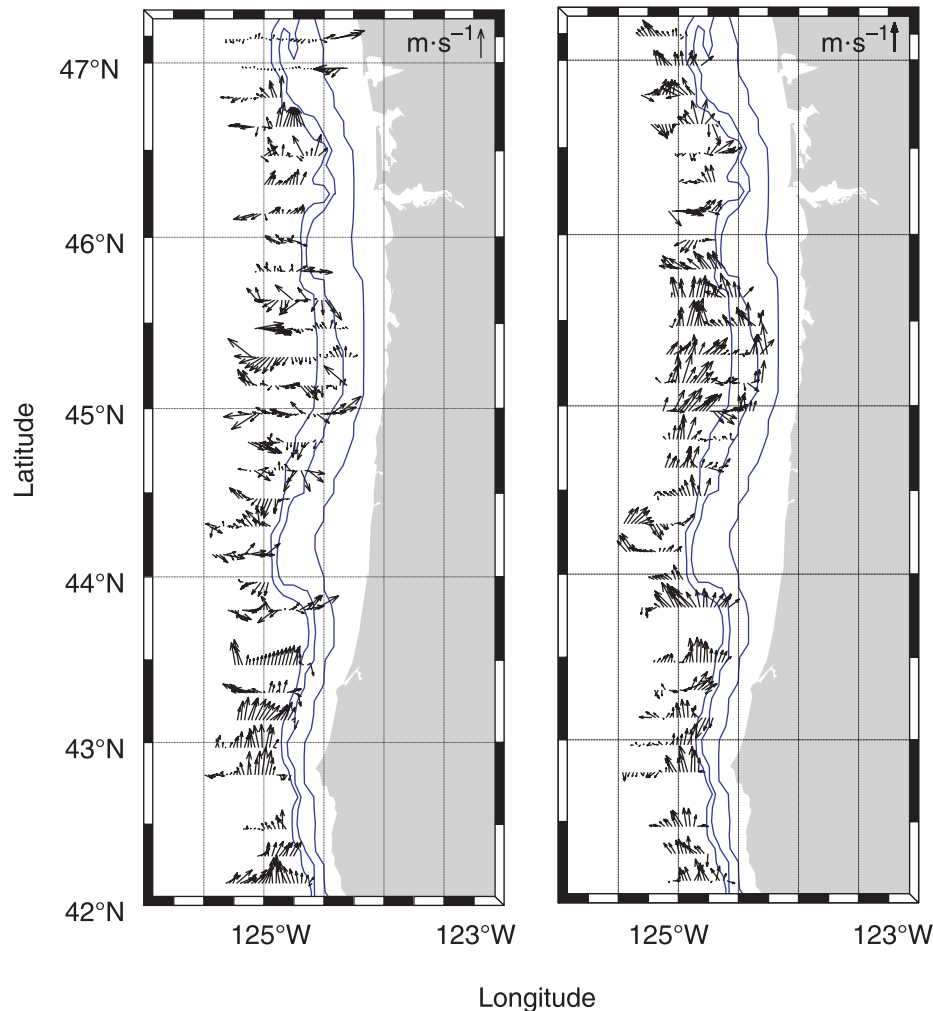
the presence of unresolved tidal, inertial, and other phenomena. A statistically significant large-scale trend with latitude is evident in both plots by classical least squares fit as in Pierce et al. (2000). The core velocities decrease poleward. Current vectors for the subsurface layer (120–330 m) clearly show poleward flow during both years, but the presence of other oceanic phenomena is also obvious (Fig. 9). Fish index (FI) values computed for each transect indicate that the distribution of hake is variable along the coast, but there is a northward shift of the population in 1998 (Fig. 10); large amounts of hake were found north of 50°N (FI between 0.4 and 1) during 1998 in comparison with small (FI < 0.1) to no amounts of hake found in this area during 1995.

A plot of alongshore subsurface flow in hake waters averaged over each transect (Fig. 11) also clearly portrays mostly poleward flow during both years of this study, although variable equatorward flow characterizes some regions (e.g., 44°N–46°N in 1995 and 48°N–50°N in 1998). During 1995, northward flow was measured at 81% of the transects and southward flow at 19% of the transects; during 1998, northerly flow was measured at 85% of the transects and southerly flow at 15%. Interesting latitudinal patterns can also be

observed. A transition point in undercurrent strength just north of Cape Blanco is evident (Fig. 11). Pierce et al. (2000) also found a similar transition point in their analysis of the undercurrent. Our analysis indicates that both 1995 and 1998 flow speed north of Cape Blanco diminishes, with subsurface flow velocity being more southward in 1995 than in 1998 (Fig. 11). The distance from the shelf of maximum alongshore subsurface flow is more variable in 1995 than in 1998 and gets closer to the shelf north of 45°N with areas of on-shelf flow (Fig. 12). Maximum alongshore subsurface flow in the southern portion of the survey area (south of 44°N) is significantly closer to the shelf in 1998 ($\bar{X} = 15$, $s^2 = 146$) than in 1995 ($\bar{X} = 19$, $s^2 = 77$, $p < 0.05$) but gets farther away and never migrates onto the shelf north of 44°N in 1998 ($\bar{X} = 28$, $s^2 = 428$) compared with in 1995 ($\bar{X} = 11$, $s^2 = 511$, $p \ll 0.05$). Distances of maximum fish densities follow this pattern, with maximum fish densities south of 44°N observed slightly (although not significantly) closer to the shelf break in 1998 ($\bar{X} = 10$, $s^2 = 108$) compared with 1995 ($\bar{X} = 12$, $s^2 = 113$). Overall maximum fish distances from the shelf break in 1998 are highly variable and increase northward along the coast.

Fig. 10. Fish index (number of fish per transect/maximum number of fish over survey area) by survey transect in (*a*) 1995 and (*b*) 1998.
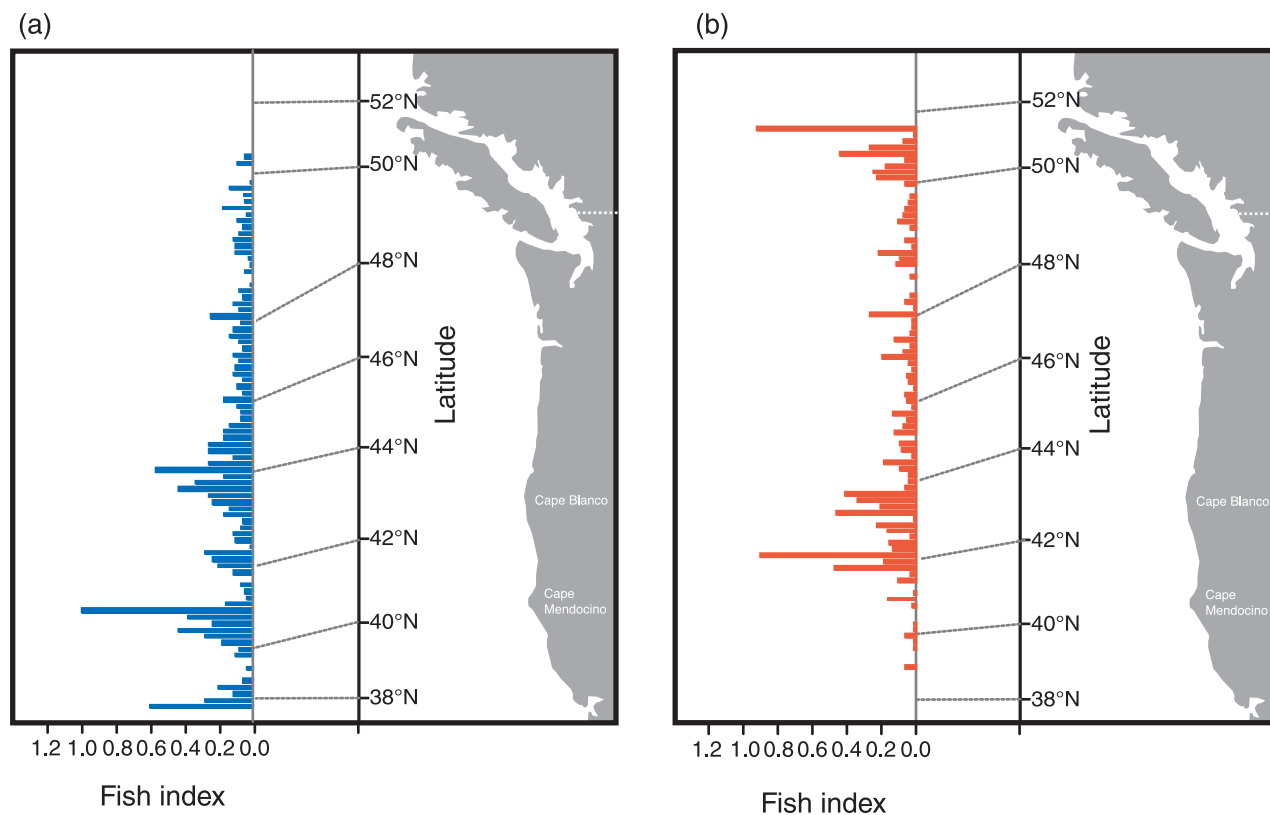

Fig. 11. Subsurface alongshore flow speed (m·s^{-1}) in hake waters for (*a*) 1995 and (*b*) 1998. Positive values indicate poleward flow; negative values indicate equatorward flow.
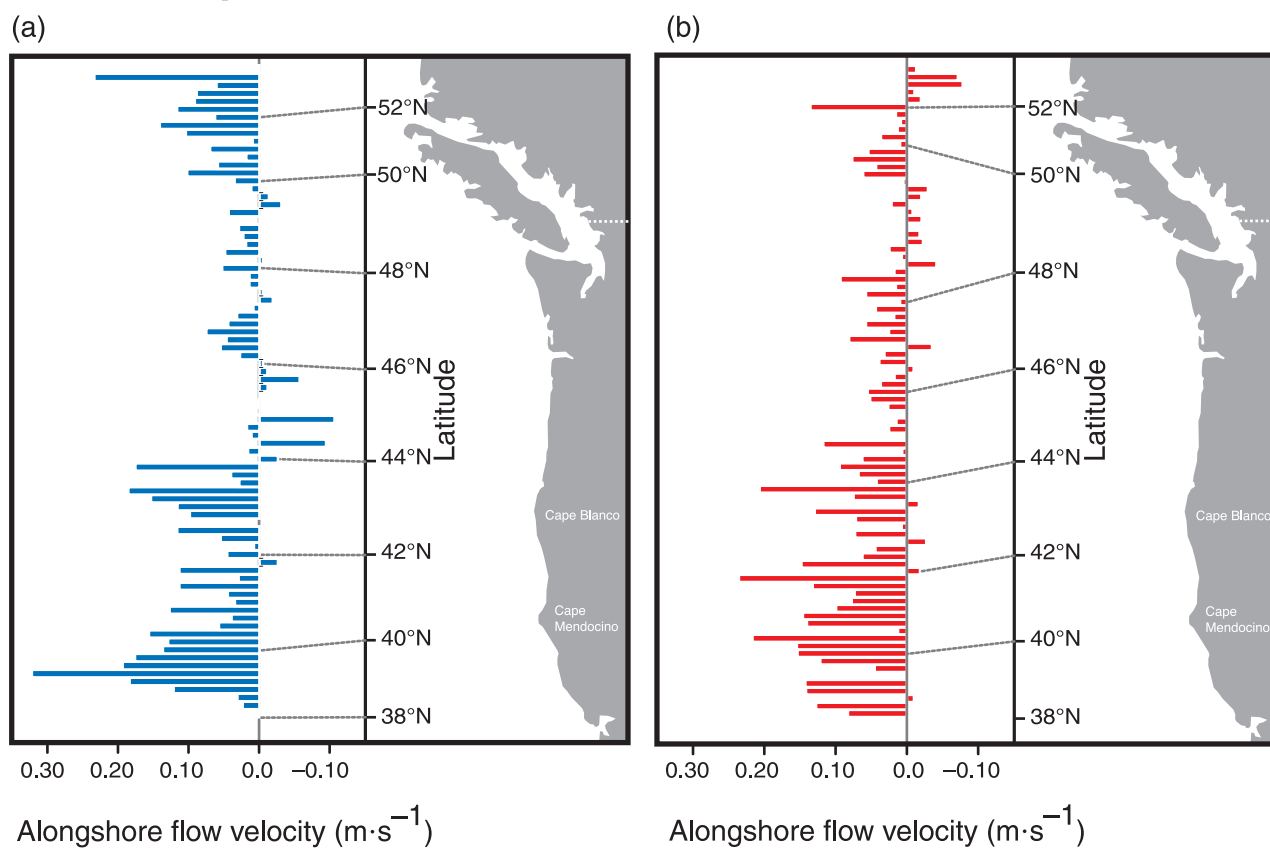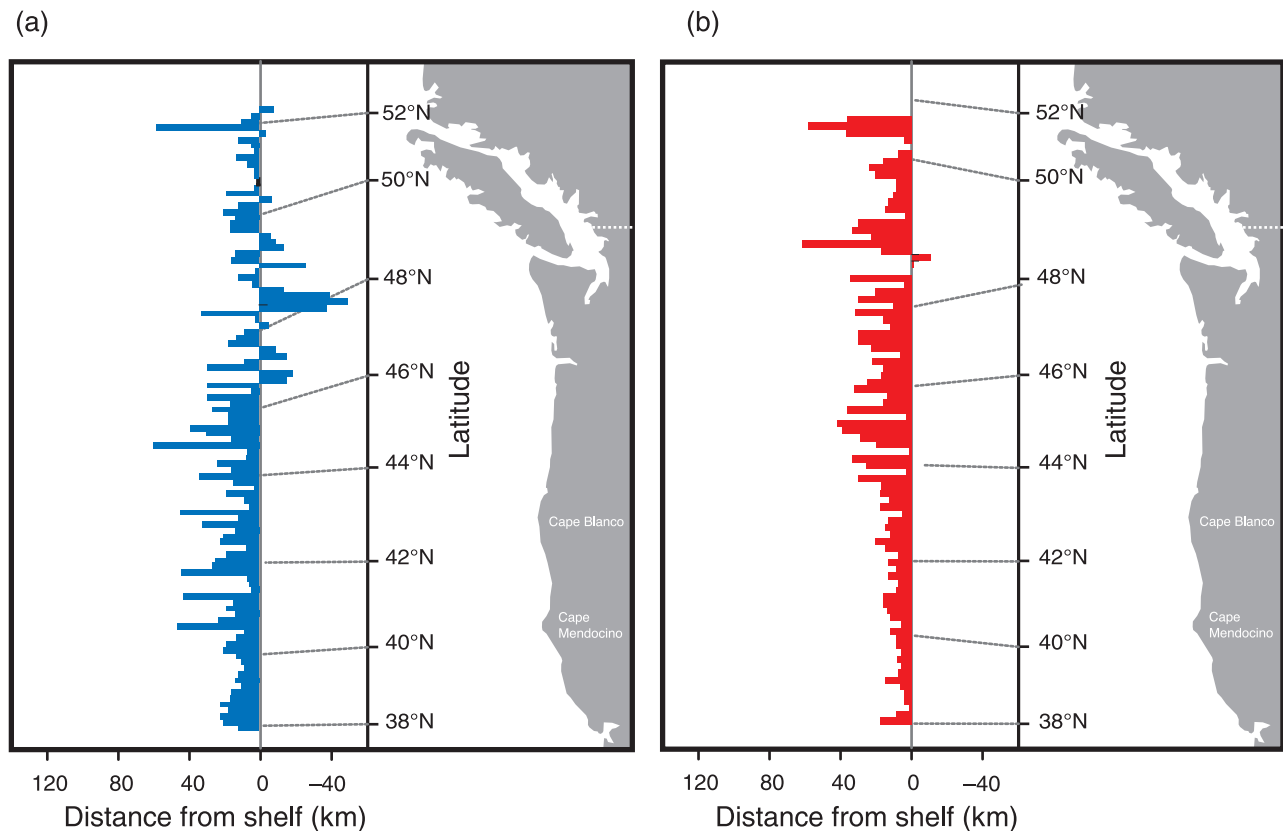
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Fig. 12. Distance from shelf (bottom depth = 150 m) of maximum subsurface alongshore flow (m·s⁻¹) in (*a*) 1995 and (*b*) 1998. Negative values indicated on-shelf location; positive values indicate off-shelf location.

Discussion

The results of our analysis suggest that Pacific hake habitat is associated with subsurface poleward flow and not a specific temperature range. Temperature has been one of the most widespread indices used to relate environmental conditions to abundance and distribution of fish populations. Temperature is known to influence the physiology of some species (Durant et al. 2003) and can be useful as an index of oceanic conditions impacting fish abundance and (or) distribution. However, if a specific process associated with the index has not been identified, the relationship is not likely to hold during different climate regimes and will therefore not be useful to researchers and managers. For example, Benson et al. (2002) looked at how sea surface temperature (SST) and upwelling relate to the presence of hake in Canadian waters. The relationship with SST only existed until a shift to a new climate regime occurred. Upwelling was found to be a better predictor of hake abundance in Canadian waters. The authors note that this type of index includes transport and winds more explicitly and may thus be a better predictor. The influence of transport processes on poleward hake migration was also observed by Smith et al. (1990), who looked at the relationship between a number of oceanographic parameters and the observed length-at-age pattern for Pacific hake sampled off Vancouver Island. Sea-level height, commonly used as an index of transport, had the strongest relationship to interannual variability in hake mean lengths-at-age in Canadian waters. The authors find that years of stronger than normal surface poleward flow (or weaker than

normal equatorward flow) result in more, smaller hake arriving off southern Vancouver Island. This suggests that northward migration of hake is assisted in years of strong poleward flow. Dorn's (1995) analysis also suggests that poleward flow influences northward migration of hake.

Temporal and spatial patterns characterize both hake distribution and undercurrent characteristics during the two years of this study. The distribution of Pacific hake shifted north in 1998, with higher densities of fish observed north of 50°N. This shift north can not be explained by a higher number of older fish in the population, because the estimated population's age distribution in 1995 and 1998 are similar, as shown by Helser and Dorn (2001). Instead, favorable flow characteristics could have facilitated the migration of hake north in 1998. The flow was more ubiquitous and coherent in 1998 than in 1995. The literature suggests stronger undercurrent during warm years (Bograd et al. 2001; Lynn and Bograd 2002; Bograd and Lynn 2003). S.D. Pierce and P.M. Kosro (unpublished data cited in Swartzman and Hickey (2003)) report higher average undercurrent volume transport (m³·s⁻¹) in 1998 than in both 1995 and 2001. Swartzman et al. (2005) also report on higher undercurrent volume transport (m³·s⁻¹) in specific areas of the CC system.

Flow geometry, such as distance from the shelf and area covered, also differs between the two years of this study. In 1998, subsurface poleward flow was significantly closer to the shelf in the southern part of the survey area (south of 44°N). Swartzman et al. (2005) also found poleward transport to be closer to the shelf in 1998 than in 1995. Along specific sections of the coastline (e.g., from 44.5°N to 46°N

and from 48°N to 50°N), alongshore flow was mostly poleward in 1998 and mostly equatorward in 1995. Flow geometry, as well as flow velocity, are likely to affect hake distribution. There is evidence of a higher concentration of prey at shelf-edge environments (Mackas et al. 1980, 1997; Simard and Mackas 1989). Being at the edge of a current closer to the shelf break (as was the case in 1998 in the southern portion of the survey) probably gives hake better access to prey usually found in higher concentrations along the shelf. This is particularly important for younger, thus smaller, hake typically found in the southern portion of the survey area. Thus, the proximity to the shelf break of the flow in the southern area of the survey during 1998 could have facilitated access that year to richer feeding grounds for the smaller, younger fish in the population.

Based on the results of this analysis, we hypothesize that one of the ways that climate influences the population dynamics of hake is by affecting the physical structure of adult hake habitat, expanding and contracting the amount available. We suggest that subsurface poleward flow in this area defines adult hake habitat, with flow properties aiding or impeding the poleward migration of the population. This may be especially true for the southern half of the hake distribution where smaller fish are closer to shore in the juvenile nursery grounds and thus flow closer to the coast is probably easier for them to detect. Favorable current characteristics during warm years (e.g., coherent ubiquitous flow along the coast located close to the shelf break) may facilitate the hake feeding migration north to richer feeding grounds and access to prey along the way. These conditions may also facilitate migration of smaller younger fish that would otherwise have a hard time covering long distances. For example, Smith et al. (1990), as well as Benson et al. (2002), found evidence of a greater number of smaller hake present in Canadian waters during 1998. Wilson and Guttormsen (1997, 1998) found 95% of hake caught off the coast of Washington in 1995 to be above 42 cm in fork length, whereas only 50% in 1998 were in this size category. The presence of smaller younger hake further north could also lead to an increased spatial overlap of age classes and potentially a higher rate of cannibalism during warm years. Field (2004) reports on differences in the amount of hake present in hake diets during warm and cold years, with up to 70% of hake prey being smaller hake during warmer years compared with less than 1% during cooler years.

Our hypothesis that poleward flow defines the amount and location of adult hake habitat might lead the reader to believe that we do not consider food availability to be important. This is not the case. Pacific hake migrations are first and foremost motivated by a search for food and are therefore primarily governed by factors related to food availability. The physical structure of the water column is one of these factors, as it probably influences the distribution of hake prey (i.e., euphausiids) that for the most part are not as able to retain position in the water column in regions of strong flow (Swartzman and Hickey 2003; Ressler, et al. 2005; Swartzman et al. 2005). Swartzman (2001) and Swartzman and Hickey (2003) investigated the relationship between the distribution of euphausiids and hake along the west coast of North America. They found a consistent overlap of large plankton patches and fish shoals near the shelf break, although the degree of clustering between years differed depending on latitude. However, Mackas et al. (1997) pointed out that despite the apparent relationship between euphausiids, hake, and bathymetry evident at a coarser scale (tens of kilometres), this relationship did not hold at a finer scale. Their analysis highlighted the importance of cues provided by flow fields. They did not find an overlap in space between plankton and hake at a finer scale; hake patches were located either above or below euphausiid patches and both organisms seemed to be associated with specific bathymetric contours. Sensory spheres of both zooplankton and fish are quite small (Mackas et al. 1997). Mackas et al. (1997) suggested that hake are cued by their immediate surrounding flow field, rather than by the surrounding bathymetry or prey density (both at ranges ≥10 m).

We also note that hake spawning ground are not fixed but rather variable in location (Sakuma and Ralston 1997; Horne and Smith 1997). It is conceivable that adults could migrate further north in some years when the spawning migration does not extend as far south as other years. However, the degree of variation observed for spawning ground location in consecutive years (Horne and Smith 1997) is too small to justify the observed degree of variation in adult hake distribution. The most appreciable latitudinal changes in spawning grounds location are observed when integrating data over long periods (Horne and Smith 1997). Thus, although spawning ground location may affect the distribution of adult hake, we don't believe it to be potentially a dominant factor in this study.

We propose that Pacific hake gain evolutionary benefits by positioning themselves relative to poleward flow. One advantage is that being at the edge of this current puts them in or close to a location where the food supply is likely to be high (the shelf break). Another advantage is that they expend less energy during their northward migration. What determines competitive advantage of a certain life history strategy over another is ultimately related to energy gain and expenditure. Food allows individuals to gain that energy, but migrating long distances contributes to expending it. Close examination of hake life history traits reveals that hake time their migration in relation to the seasonality of the current. Females, for example, leave the spawning grounds earlier, beginning their migration when the poleward current intensity peaks (Saunders and McFarlane 1997). This suggests that Pacific hake have evolved to take advantage of poleward flow during their feeding migrations. Hake are active swimmers and do not need the current to migrate north. Poleward flow simply allows them to complete their migrations expending less energy and to gain access to new energy by accessing richer northern feeding grounds. There is evidence of poleward flow facilitating hake migration in other areas of the world (Sanchez and Gil 2000). The fact that distant populations are affected by similar environmental processes leads us to believe that an association with poleward flow must provide competitive advantages to this species.

The factors influencing hake year-class strength are multiple and complex; hence, a linear relationship between subsurface poleward flow and the hake production time series will likely not be found. For example, conditions on the larval and juvenile nursery grounds are of primary importance, as is the impact that the fishery has on the population. Here we have

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formulated hypotheses to explain the variability in hake migration and adult hake habitat that are a part of this puzzle. All of these factors come together to produce the observed production variability. Similar changes in migration patterns have been observed for other CC pelagic species, e.g., sardine and mackerel (Beamish et al. 2000). One thing seems clear: pelagic fish are good indicators of shifts in ocean conditions as their life histories are so tightly related to atmosphere and ocean conditions. This leads us to believe that in the future, pelagic fish distribution might be used as an indicator of climate change. We will, however, only be able to do so if we understand the processes that link climate and pelagic fish production and distribution. This study is a step in that direction.

Acknowledgments

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