

Evidence for a Regime Shift After the 1997–1998 El Niño, Based on 1995, 1998, and 2001 Acoustic Surveys in the Pacific Eastern Boundary Current

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ABSTRACT: Increasing physical oceanographic evidence suggests that a regime shift, which featured increased equatorward surface winds and upwelling in the Eastern Pacific Boundary Current region, occurred following the 1997–1998 El Niño. We expect the signal of this change in biota to be stronger in euphausiids than in pelagic fishes such as Pacific hake (*Merluccius productus*) because lower trophic levels are more responsive to changes in upwelling and primary production. We used acoustic backscatter data from acoustic surveys in summer 1995, 1998, and 2001 to explore whether significant changes in abundance and distribution of euphausiids and fishes have occurred between 1995 and 2001. Graphical and statistical results show that the density of fish schools and euphausiid patches increased significantly south of Cape Blanco between 1995 and both 1998 and 2001. North of Cape Blanco there was no consistent change in euphausiid abundance, although both fish and euphausiid distributions in 2001 appear to be significantly higher nearshore than in the other years. Pelagic fish abundance distributions appeared more closely linked to El Niño than to regime shifts, with abundance shifted much farther north in 1998, an El Niño year, than in the other years, while 1995 and 2001 fish abundance distributions are similar to each other. The regime shift appears so far to have had a stronger effect on euphausiids than on pelagic fishes. The change in euphausiid abundance and distribution between the survey years was linked, through a conceptual model, to the relative strength of the poleward flowing California undercurrent and equatorward flowing California current and to the distribution and abundance of hake.

Introduction

The decade-scale behavior of the Eastern Pacific Boundary Current system (EPBC; California, Washington, Oregon, and British Columbia) appears to be dominated by regime shifts. Regimes are defined as multi-year periods of relatively stable conditions in physical data series (Beamish et al. 2000). Shifts between regimes are characterized by abrupt changes in species abundance, community composition, and trophic organization that occur concurrently with changes in large-scale climate systems. While these regime shifts have likely been taking place for centuries, only recently have such patterns been recognized (Francis and Hare 1994). The long-term response of biota in the north Pacific to decade-scale regime shifts has been well documented (reviewed in Benson and Trites 2002). The effects of regime shifts on biota are strong, long lasting, uncontrollable, and possibly predictable (Chavez et al. 2003). They represent a tapestry on which anthropogenic effects

in the nearshore ocean ecosystem play out, and strongly influence the effects of fisheries and other human activity in the ocean. These effects must be considered in any description of the coastal ecosystem and in all attempts at management, from setting fishing quotas to operating marine aquaculture systems, to hatchery-based fish population enhancement.

The emerging long-term climate picture suggests that regime shifts in the northeastern Pacific Ocean are linked to a strengthening or weakening of the Aleutian low frontal system, which appears to strengthen for long periods of time (e.g., decades) and be weak for similar time periods (Polovina et al. 1995). Prior to a major regime shift that occurred around 1976, atmospheric conditions exhibited a pattern of a strong North Pacific High. This was associated with vigorous anticyclonic winds resulting in strong upwelling favorable (equatorward) winds along most of the North American west coast (Parrish et al. 2000). After 1976, there was a weakening of the north Pacific High and strengthening of the Aleutian low. The typical large-scale wind anomaly in the Northeast

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Pacific was cyclonic (Parrish et al. 2000) and wind pattern anomalies were less favorable to upwelling in the EPBC. A second regime shift may have occurred around 1989 (Benson and Trites 2002).

The physical manifestation of regimes and their shifts in the northeastern Pacific Ocean has been encoded in a set of indexes that includes the Pacific Decadal Oscillation (PDO), which is the first empirical orthogonal component of North Pacific sea surface temperature (Mantua et al. 1997), the Aleutian Low Pressure index (ALPI; Beamish and Bouillon 1993), and the North Pacific Index (Trenberth and Hurrell 1995). Regime shifts often, but not always, show a consistent change in these indexes (Benson and Trites 2002). Although the PDO did not change around 1989, the ALPI and other large-scale indexes, such as the Pacific Circulation Index and the Pacific Inter-decade Oscillation Index, were much more positive between 1977–1989 than between 1990–1997 (Hare and Mantua 2000). The uniformly low recruitment of salmon stocks in the nearshore EPBC, while Alaskan stocks produced record runs (Beamish 1993; Francis and Hare 1994) during the 1990s suggests a different pattern for biota before and after 1989. Following the strong El Niño in 1997–1998 the north Pacific climate shifted during spring 1998 toward strong La Niña conditions, with a strengthening of the North Pacific High and concomitant increased coastal upwelling and lower coastal sea surface temperatures (Schwing et al. 1999). These conditions have persisted to the present and there is increasing evidence that this is a regime shift, rather than the result of an extended period of La Niña-like conditions (Parrish et al. 2000).

Regime shifts may be a chronic feature of the EPBC, because sediment cores show shifts in dominance between sardine and anchovy stocks over very long time scales (e.g., centuries; Baumgartner et al. 1992). Such annotated regime shift changes suggest that improving our understanding of how regime shifts of various kinds are likely to effect ecosystem dynamics can help put such long term management strategies as stock rebuilding, setting bycatch and target quotas, and assessing ecosystem health on a stronger scientific footing.

The documented changes in higher trophic levels in the EPBC that occur following regime shifts suggest that such changes also must be strong in the lower trophic levels that support them. Difficulties in detecting a regime shift in biota of a marine ecosystem, even when all environmental indicators suggest such a change has occurred, arise from the complexity of species interactions, the longevity of some of the fish species and their variable recruitment success (Myers and Pepin 1994), as well as the lack of long-term data sets for non-

commercially targeted species. We would expect that lower trophic levels respond more rapidly to regime shift than higher trophic levels (Hunt et al. 2002), which depend on the lower levels for successful growth and recruitment. With this in mind we have examined the abundance and spatial distribution of large zooplankton and fishes (patches and pelagic fishes from three acoustic surveys. The surveys transected the EPBC during the summers of 1995, 1998, and 2001 from mid-California to at least the Canadian border from nearshore to well beyond the shelf break and sampled at 10 nautical mile intervals. Image processing methods were used on the 38 and 120 kHz acoustic backscatter data to extract locations of large patches of euphausiids and schools of pelagic fishes (Swartzman 2001). Because Pacific hake (*Merluccius productus*) was dominant below the thermocline during the daytime (80–90% of biomass in trawls; Wilson and Guttormsen 1997) and almost all transects were conducted during the daytime (Wilson and Guttormsen 1997), we assumed that all the acoustically determined fish schools below the thermocline were hake. The euphausiids *Euphausia pacifica* and *Thysanoessa spinifera*, dominated the large zooplankton (McKelvey 2001), and regions where backscatter at 120 kHz was larger than that at 38 kHz were found to comprise almost 100% of zooplankton taken in Methot tows along the survey tracks (McKelvey 2001).

We examine whether the proposed regime shift in 1997–1998 (Hare and Mantua 2000) is detectable from the abundance and distribution of euphausiid patches and hake schools, and, if so, to determine when this change occurred (i.e., between 1995 and 1998 or between 1998 and 2001).

Methods

Data from summer acoustic surveys in 1995, 1998, and 2001 on the R/V *Miller Freeman* were provided by the National Marine Fisheries Service (NMFS), Alaska Fisheries Science Center Marine Acoustics group (Wilson and Guttormsen 1997, 1998; Guttormsen 2001). These included acoustic backscatter data collected at 38 and 120 kHz using a SIMRAD EK-500 echosounder system center board-mounted at 9-m depth, onshore-offshore and alongshore current estimates collected using a 150 kHz Acoustic Doppler Current Profiler (ADCP), conductivity-temperature-depth sensor and expendable bathythermograph data collected during the cruise, fishing data collected using an Aleutian Wing Trawl (midwater) and an otter trawl (bottom), and zooplankton data collected using a Methot net sampler.

The distributions of both fish schools and zooplankton patches along the survey transects were

mapped using thresholds and morphological filtering applied to the 38 kHz echograms (for the fish) and to both the 38 and 120 kHz echograms (for the zooplankton; Swartzman et al. 1999a; Swartzman 2001). The methods were applied to echograms collected for 5-nautical mile bins, each having 1000×500 (horizontal \times vertical) pixels covering the same swath of ocean below the survey ship with pixel resolution of about 9 m horizontal and between 0.2 and 2.0 m vertical (depending on bottom depth). Fish schools were identified by first applying a backscatter threshold to the 38 kHz echograms between -40 and -54 dB (i.e., everything within this backscatter range was set to 1 and outside was set to 0; Swartzman 2001). A morphological filter with a 3×2 pixel (horizontal \times vertical) binary structuring element (Haralick and Shapiro 1992) was then used to identify contiguous groups of pixels satisfying the threshold constraints, while eliminating isolated pixels smaller than the structuring element (i.e., small schools or image noise). Others have found the actual filtering operations, a morphological opening followed by a closing, effective for fish school identification (Reid and Simmonds 1993; Barange 1994). The resulting binary image was multiplied by the original image and a connected component algorithm (Haralick and Shapiro 1992) was used to convert each fish school (i.e., a contiguous group of pixels having nonbackground-level backscatter after applying the algorithm) to a row of a table where each column is an attribute of the school. Attributes include location (fish school center latitude, longitude, and depth), size (fish school area, width, and height), shape (fractal dimension, eccentricity, sinuousness, 8 boundary points defining a bounding polygon for the school), intensity (mean, maximum, and minimum backscatter, backscatter variance), and environment (bottom depth). As mentioned earlier, based on the dominance of trawl catches below the thermocline by Pacific hake (Wilson and Guttormsen 1998) we assume that the fish schools in this zone were entirely hake.

The algorithm for zooplankton (euphausiid) patch identification used a threshold between -62 and -54 dB. All pixels outside this threshold range for the 120 kHz echogram were set to the background backscatter level (-100 dB) in both the 120 and 38 kHz echograms. These thresholds were determined using a geometric bent cylinder model for backscatter from euphausiids within the 15–25 mm size range (Stanton et al. 1993) and expected density ranges based on Methot trawl densities (Swartzman 2001). An image was then constructed of the difference between the two threshold images (120–38 kHz image) and a $+5$ dB threshold

was applied to the resultant image. All pixels having backscatter at 120 kHz at least 5 dB greater than that at 38 kHz was set to the 1 and the rest of the pixels to 0. A binary morphological opening and closing using a 3×3 structuring element was applied next (Swartzman 2001). As with the fish school identification, the morphological filter identifies contiguous groups of pixels satisfying the threshold conditions but eliminates isolated groups of pixels (or individual pixels) smaller than the structuring element. Finally, the resulting binary image was multiplied by the 120 kHz echogram and, similar to the fish school identification, a connected component algorithm was used to label the patches and calculate patch attributes (Swartzman et al. 1999b; Swartzman 2001).

The euphausiid patch algorithm uses the observation (based on in situ measurements and geometric models) that backscatter from most adult euphausiid species (15–25 mm in length) at 120 kHz is significantly higher than backscatter at 38 kHz (Stanton et al. 1993; Mitson et al. 1996). In the present case, this technique identified patches of zooplankton independent of fish schools (Swartzman et al. 1999a; Swartzman 2001). Comparison of zooplankton net samples from the 1995 survey with acoustic backscatter at the two frequencies (McKelvey 2001) corroborated that the net samples were composed of almost 100% euphausiids when backscatter at 120 kHz was higher than that at 38 kHz. We assume that the zooplankton patches were composed entirely of euphausiids. The high resolution of backscatter images (i.e., 9.0 m horizontal resolution and 0.2–2.0 m vertical resolution) made it possible to clearly identify patch and school boundaries.

Transect coverage for the three summers of acoustic survey data (1995, 1998, and 2001) followed an almost identical track in each year, so we were able to compare the surveys transect by transect. Because the spatial area covered by the surveys was so large, the survey area was divided into 4 regions whose boundaries were selected to account for different ocean environments north and south of major capes as well as the Columbia River plume (Hickey 1979). The region south of Cape Mendocino was denoted South, while the regions between Capes Blanco and Mendocino and between Cape Blanco and the Columbia River were termed Blanco South and Blanco North, respectively, and the region north of the Columbia River was called North. The cross-shelf transects were divided into offshore, shelf-break, and nearshore or shelf domains. The 200-m isobath was used as the boundary between shelf (nearshore) and shelf-break domains and the 800-m isobath as the

boundary between shelf-break and offshore domains.

The 3 survey years were compared using boxplots, which show the distribution of fish and euphausiid acoustic abundance between years for each region and domain. The acoustic biomass density for fish and euphausiids (biomass per transect km) was modeled using generalized additive models (GAM; Hastie and Tibshirani 1990) as a function of the survey year, survey region, survey domain, and their interactions. GAM is a nonparametric regression method that models the mean of the dependent variable (in this case hake or euphausiid acoustic biomass) as the sum of a number of unspecified functions or smooths of the covariates and their interactions. The underlying distribution may be any distribution from the exponential family (which includes the Poisson, Normal, Binomial, and Gamma distributions). In this case a normal distribution was assumed. GAM finds the covariates that are most associated with changes in the mean biomass by recursively fitting spline smooth functions of a single covariate at a time (with the others held constant). The recursion continues until the deviance (a measure of variance similar to standard deviation) converges. The sampling units in these tests are transects, which are treated as replicates within each region. The GAM models the fish or euphausiid acoustic biomass km^{-1} for each transect as a function of the domain, region, and year covariates. GAM offers the advantage over linear regression in that it does not specify a functional relationship between the dependent variable and covariates and can identify unspecified nonlinear relationships.

Paired-difference *t*-tests for the density of hake school and euphausiid patch biomass (biomass per transect km) were used to test for differences between years in pairs in each region and domain. The paired-difference *t*-tests were run to test the null hypothesis of no difference in abundance of euphausiid patches and fish schools. We chose this latter approach to get the most powerful discrimination between years. Because we lacked replicates for transects within a year, we were unable to test for a transect effect using GAM. The significance of most interaction effects in the GAM (see results section) suggested that separate analysis of transects within regions was appropriate. Although it may seem unlikely that the transect-effect within a region is significant, because the same transects were followed in each year, the paired-difference test allows us to eliminate variability within a region that may be due to a transect effect. Biomass is used synonymously with acoustic biomass in each patch or school, an index proportional to true biomass but not calibrated. The same index applies

equally to all three surveys and the numbers are equivalent. Biomass density (biomass km^{-1}) refers to the total acoustic biomass of fish or euphausiids contained in schools and patches divided by the length of the transect segment in each domain.

Results

Boxplot comparisons of the fish school and euphausiid patch density between the three survey years are given in Figs. 1 and 2. The boxplots show the median (filled square), inter-quartile range (lines), and mean (unfilled squares) for all transects and each year in each region and domain.

For all three years the shelf break generally had the highest abundance for both hake schools and euphausiid patches (Figs. 1 and 2). This is supported by GAM results, which indicated significant year, region, and domain effects for both fish and euphausiids (Fig. 3, $p < 0.001$). The GAM also gave significant two and three-way interactions for all covariates ($p < 0.05$) except the domain-region interaction for euphausiids. The overall euphausiid abundance was lower in 1995 than in 1998 or 2001 (Fig. 3), and the regions around Cape Blanco (Blanco North and Blanco South) had, on average, higher euphausiid density than the North and South regions (Fig. 3).

Besides the overlap of high densities of fish and euphausiids along the shelf break in all three study years there was also a persistent deep layer of euphausiids extending offshore from the shelf break during the daytime (Swartzman 2001). Both features are apparent from a perusal of transect plots for the entire survey (shown in Swartzman [2001]; they are the red polygons in the offshore domain in the two sets of transects shown in Fig. 4).

Interpretation of the main-effect patterns suggested by the GAM analysis is limited due to the significance of higher order interactions. Interaction effects (e.g., differences between years varying with region) were clarified by results of the paired difference tests (results denoted by capital letters A, B, C, and AB in Figs. 1 and 2). These tests indicate that the euphausiid abundance south of Cape Blanco was higher in 2001 and 1998 than in 1995 (Fig. 2, $p < 0.05$). Temporal changes in euphausiid abundance were not evident north of Cape Blanco (Fig. 2), although there appeared to be significant shift of euphausiids toward the shelf area in 2001, compared with 1995 and 1998 (Fig. 2). Hake abundance was higher south of Cape Blanco in 1995 and 2001, while north of Cape Blanco it was highest in 1998 (Fig. 1).

Averages of core poleward undercurrent volume ($\text{m}^3 \text{s}^{-1}$) and surface equatorward current volume of the California Current Ecosystem, computed from ADCP data (Pierce and Kosro unpublished

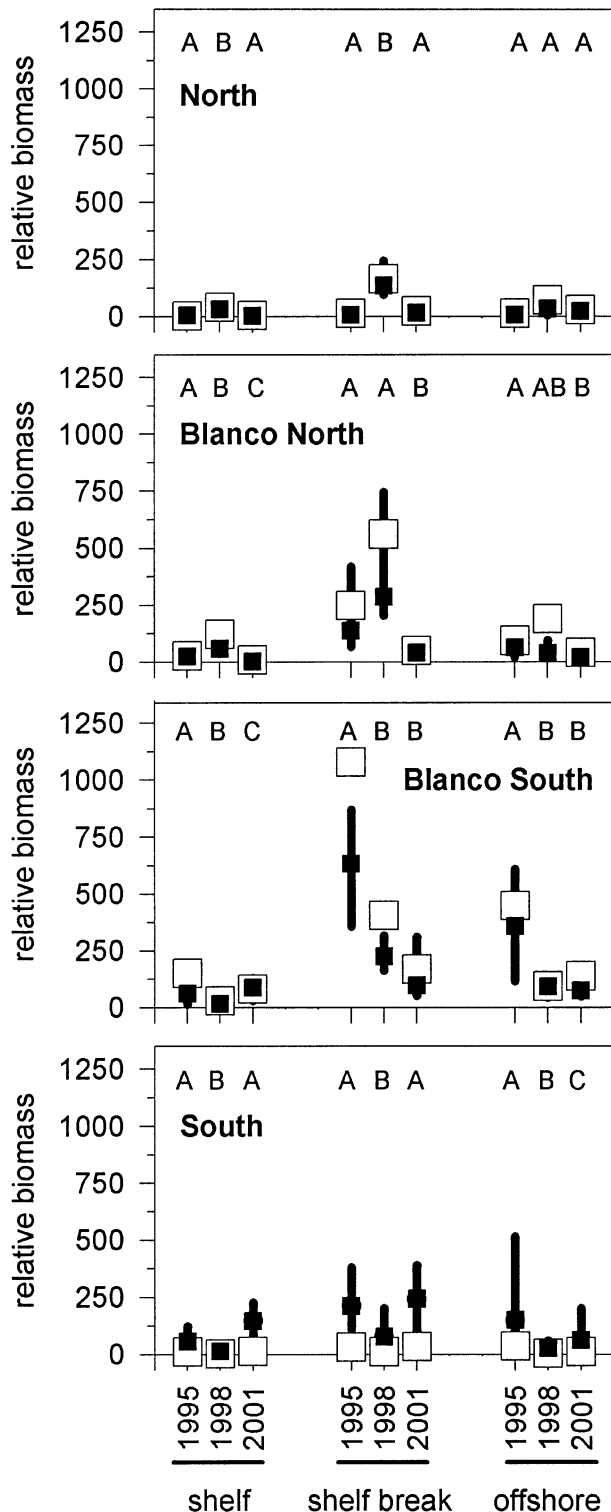


Fig. 1. Boxplots comparing the acoustic biomass density (biomass km^{-1}) between years for Pacific hake schools in the nearshore (shelf), shelf-break, and offshore domains for the regions north of the Columbia River (North), north of Cape Blanco to the Columbia River (Blanco North), south of Cape Blanco to Cape Mendocino (Blanco South), and south of Cape Men-

docino (South). Filled squares indicate medians, with 50% quartiles shown as vertical lines. Unfilled squares indicate means. The letters A, B, C, and AB are used to show the results of paired-difference tests, based on significant differences at $p < 0.075$. Years that are statistically different from each other are labeled with different letters. AB is used to denote a year that is not significantly different from either other year when the other years are significantly different from each other.

Discussion

The observed euphausiid distribution pattern in the three study years appears to be linked to diel migration of the euphausiids, to differences in current and wind patterns between the three survey years, and to differences in the distribution of the major summer euphausiid predator, Pacific hake (Wilson and Guttormsen 1998). The shelf-break domain had generally the highest abundance of hake and euphausiids in all years. Euphausiid abundance was elevated south of Cape Blanco in 1998 and 2001 compared with 1995. Euphausiid abundance was relatively higher on the shelf north of Cape Blanco in 2001 than it is in other years. Hake abundance was highest south of Cape Blanco in 1995 and 2001 and north of Cape Blanco in 1998.

The regions north and south of Cape Blanco have significant oceanographic differences that may influence the distribution of euphausiids. Wind forcing in summer and coastal upwelling are generally weaker north of Cape Blanco than they are to the south (Hickey 1979, 1998; Hickey and Banas 2003). The coastline north of Cape Blanco is relatively straight and upwelled water and organisms tend to be confined to the shelf (Hickey 1998; Hickey and Banas 2003; Fig. 4). South of Cape Blanco the coastline is irregular, and wind-generated coastal jets tend to separate from the shelf at the promontories to form meandering jets that can extend hundreds of kilometers away from the coast (Fig. 4; Strub et al. 1991). The jets provide a mechanism for carrying cold, salty, chlorophyll-rich, recently upwelled water away from the coast. Meandering jets can sometimes be traced continuously from Cape Blanco, where they separate from the shelf, to southern California (Strub et al. 1991). The area south of Cape Blanco often has primary production extending much farther offshore than the area north of Cape Blanco. The pattern of shelf-bound upwelling north of Cape Blanco and jets and eddies south of Cape Blanco is expected to be enhanced after the 1997–1998 regime shift

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docino (South). Filled squares indicate medians, with 50% quartiles shown as vertical lines. Unfilled squares indicate means. The letters A, B, C, and AB are used to show the results of paired-difference tests, based on significant differences at $p < 0.075$. Years that are statistically different from each other are labeled with different letters. AB is used to denote a year that is not significantly different from either other year when the other years are significantly different from each other.

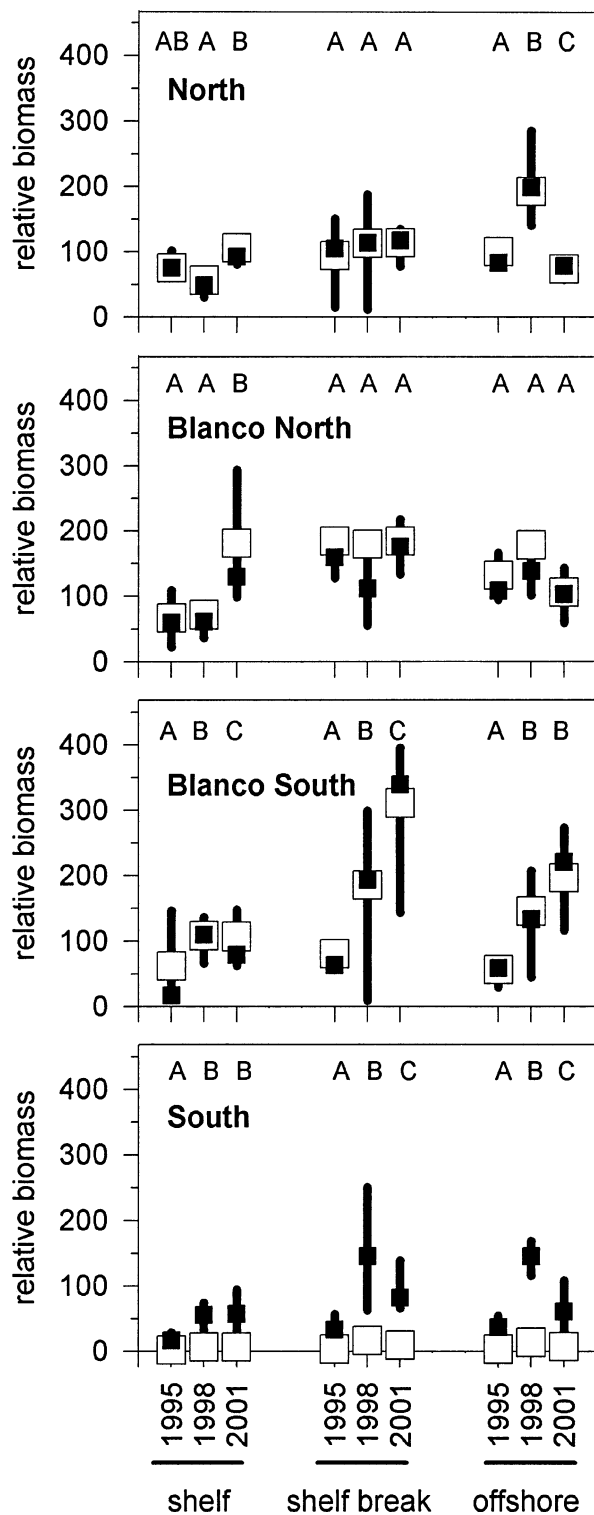


Fig. 2. Boxplots comparing the acoustic biomass density (biomass km^{-3}) between years for euphausiid patches in the nearshore (shelf), shelf-break, and offshore domains for the regions north of the Columbia River (North), north of Cape Blanco to the Columbia River (Blanco North), south of Cape Blanco to Cape Mendocino (Blanco South), and south of Cape Men-

(i.e., more consistent upwelling conditions off the coast during summer, Thomas and Strub 2001).

Euphausiids in the deep layer migrate on a diel cycle, probably as a predator avoidance mechanism, moving up in the water column to feed at dusk (Peterson personal communication based on observations over several years throughout the year on the Newport line, extending 50 km off Newport, Oregon; DeRobertis et al. 2000). Vertically migrating adult euphausiids, with a maximum sustainable swim speed of $6\text{--}8\text{ cm s}^{-1}$ (Kils 1993), cannot maintain position swimming against the undercurrent due to its high speed (average speed of $10\text{--}20\text{ cm s}^{-1}$; Pierce et al. 1999). Because of diel migration euphausiids move between a deeper, poleward flowing undercurrent during the daytime to a surface, generally equatorward flowing, current during the night. The relative volume of the poleward flowing California undercurrent and equatorward flowing surface currents may influence the amount of transport north incurred by vertically migrating euphausiids.

In our conceptual model of euphausiid abundance and distribution between the three years, strong wind driven upwelling generally resulted in higher euphausiid abundance in all domains south of Cape Blanco, as occurred in 1998 and 2001 (Fig. 1), while north of Cape Blanco, because production tended to be confined to the shelf region, strong upwelling resulted in higher euphausiid abundance mostly in the shelf and shelf-break regions. There were two other influential factors—relative hake abundance, which influenced predation pressure on euphausiids, and the strength of the undercurrent, which we hypothesize influenced the relative north-south distribution of euphausiids by affecting their transport.

The summer of 1995, during the pre-regime shift period, would be expected to be a period of weaker surface currents and reduced upwelling and primary production (Chavez et al. 2003; Table 1). Analysis of ADCP data on the 1995 summer survey demonstrated the existence of a consistent, high velocity undercurrent as far north as 44°N (Pierce et al. 1999) and lower volume surface currents, especially south of Cape Blanco (Table 1). We suggest that the strong undercurrent and rel-

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docino (South). Filled squares indicate medians, with 50% quartiles shown as vertical lines. Unfilled squares indicate means. The letters A, B, C, and AB are used to show the results of paired-difference tests, based on significant differences at $p < 0.075$. Years that are statistically different from each other are labeled with different letters. AB is used to denote a year that is not significantly different from either other year when the other years are significantly different from each other.

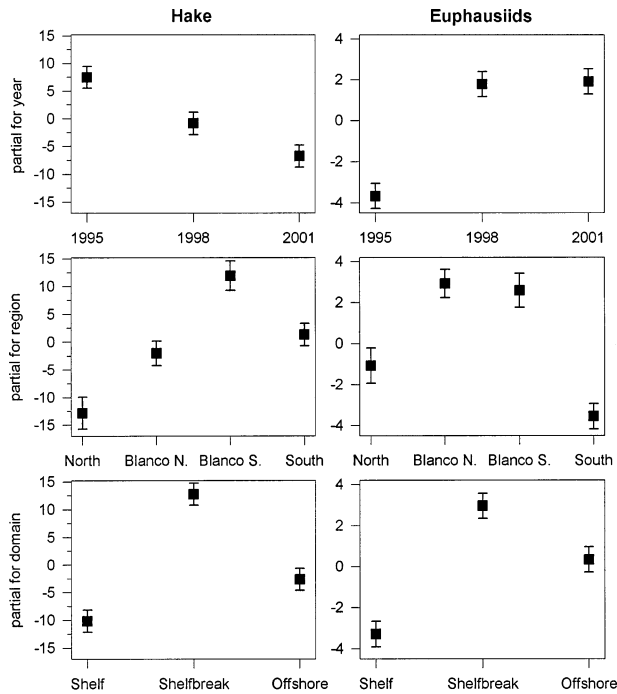


Fig. 3. Results of GAM analysis for fish (left panels) and euphausiid (right panels) acoustic abundance as a function of year, region, and domain. One standard error bars surround the average effect of each covariate.

atively weak surface current south of Cape Blanco in summer (Table 1) and the very high abundance of hake in that region resulted in low euphausiid abundance due to euphausiid transport further north and euphausiid removal through predation. North of Cape Blanco in 1995, we hypothesize that the low hake abundance and the net transport of euphausiids from further south resulted in high euphausiid abundance.

Although 1997–1998 featured a strong El Niño with a strengthened California undercurrent, by summer 1998 conditions along the coast also had strong upwelling symptomatic of La Niña conditions (Schwing et al. 2002). By summer 1998 feeding conditions were favorable for euphausiids. Pacific hake was most abundant north of Cape Blanco in 1998 (Fig. 1). The strong northward migration of Pacific hake in 1998 is thought to be due to El Niño impacts that preceded the sampling period (Wilson and Guttormsen 1998). The Pacific hake migration in 1998 extended as far north as

the Queen Charlotte Islands (Wilson and Guttormsen 1998), and its distribution was similar in its northward shift to the hake summer distribution in 1992, another El Niño year (Swartzman 1997). South of Cape Blanco, we hypothesize that the low hake abundance in the South region in summer 1998 (Fig. 1) and high primary production allowed euphausiids to rebound rapidly from earlier El Niño conditions, resulting in high euphausiid abundance. Stronger jets and eddies south of Cape Blanco by summer 1998 (Schwing et al. 2002) may have extended the effective euphausiid feeding range further offshore resulting in high offshore euphausiid abundance.

North of Cape Blanco hake abundance was high, especially south of the Columbia River in the Blanco South region (Table 1). Despite strong upwelling and good euphausiid feeding conditions in this region during summer 1998 (Schwing et al. 2002; Table 1), predation pressure by hake must have been significant. We hypothesize that predation pressure by hake tended to shift euphausiid abundance offshore. Euphausiids offshore might have reduced susceptibility to predation, because they can migrate to a depth with low enough light conditions to provide some refuge from predation during the daytime (De Robertis et al. 2000), whereas euphausiids on the shelf are limited by the bottom depth from so doing. Euphausiid abundance north of Cape Blanco may have been increased during summer 1998 through transport of euphausiids from further south. The undercurrent during summer 1998 was stronger than in 1995 (Table 1).

In 2001, cooler regime conditions had been dominant for several years (Chavez et al. 2003). The more consistent equatorward winds created a stronger, more persistent equatorward current system. Furthermore, these conditions may have deepened the layer of equatorward flowing water and displaced the undercurrent further offshore (Barth personal communication). Because of the possible strengthening of the equatorward flowing surface current, the vertically migrating euphausiids might have had less net transport north than in years when the surface current was weaker (e.g., 1995). Jets and eddies south of Cape Blanco (e.g., Fig. 4) may have extended the range of high phytoplankton biomass further offshore in this region,

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Fig. 4. High resolution (1 km²) SeaWiFS image taken on July 1, 2001 between latitudes 40°N and 45°N showing phytoplankton chlorophyll *a* (mg km⁻²) density. The survey track of the 2001 survey is overlaid on the image in red. Transect comparisons at 41°N and 45°N for 1995, 1998, and 2001 show fish schools (blue polygons) and euphausiid patches (red polygons) along the transects from depth 15–400 m, with the bottom (when above 400 m) shown as a solid line. The hue of each polygon is proportional to the biomass in that school or patch. Color scales vary year-to-year, and maximum patch and school biomass are labeled at their centers.

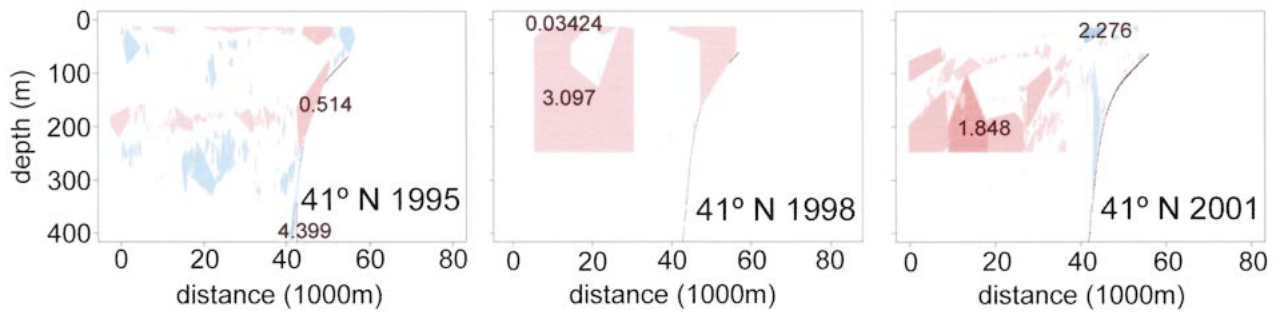
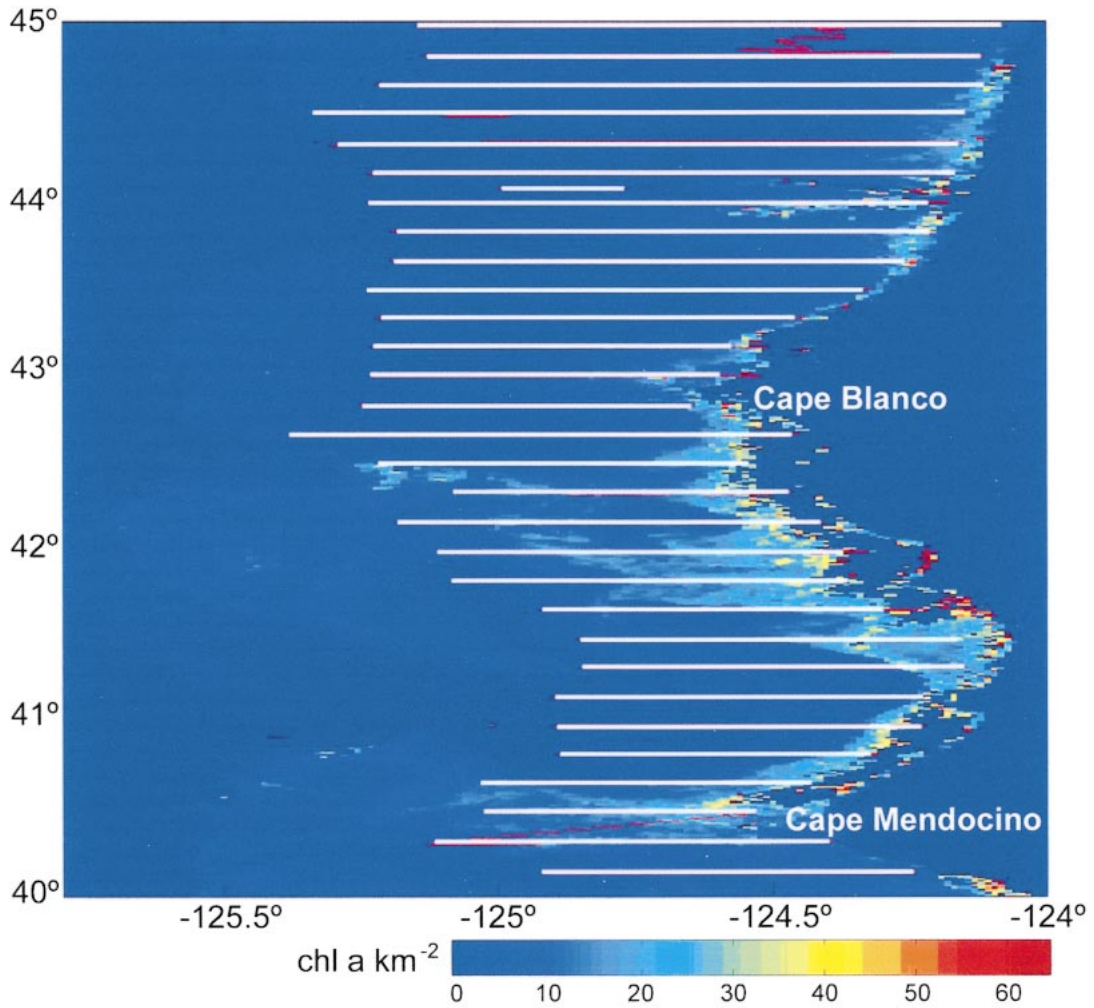
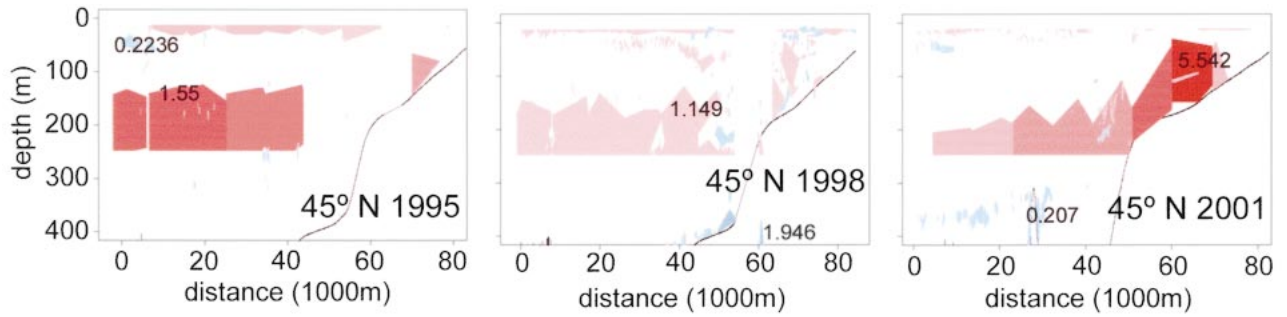


TABLE 1. Mean core undercurrent and surface current volumes ($\text{m}^3 \text{s}^{-1}$) per transect and an average upwelling index in the region south of Cape Blanco (South), between Capes Blanco and Mendocino (Blanco South), Cape Blanco to the Columbia River (Blanco North), and north of the Columbia River (North) for the summer 1995 and 1998 cruises. Standard errors of the mean for each region are given in parentheses. A minus sign means equatorward flowing current. The upwelling index is an average for June–August (Pacific Fisheries Environmental Laboratory upwelling index, <http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/PFELindices.html>).

Year/Region	South	Blanco South	Blanco North	North
1995 undercurrent	7,350 (1,022)	6,592 (997)	2,120 (725)	3,019 (428)
1998 undercurrent	9,318 (1,644)	15,208 (2,419)	11,101 (2,914)	4,246 (1,136)
1995 surface current	-491 (104)	-731 (292)	-645 (229)	-645 (295)
1998 surface current	-1,283 (378)	-836 (348)	-1,670 (502)	-499 (146)
1995 upwelling	155	85	42	19
1998 upwelling	263	209	83	42
2001 upwelling	298	237	64	32

providing better feeding conditions for euphausiids further offshore south of Cape Blanco than north of Cape Blanco. North of Cape Blanco, hake abundance in 2001 was extremely low, while it was high in all domains south of Cape Blanco (Fig. 1). South of Cape Blanco in summer 2001 we hypothesize the high euphausiid abundance observed, despite the relatively high hake abundance in the region, resulted from high primary production extending offshore due to jets and eddies and less net transport north than in other years. North of Cape Blanco we hypothesize that good feeding conditions for euphausiids and low hake predation pressure resulted in high levels of euphausiids despite less transport of euphausiids from further south. The very low hake abundance in this region reduced predation pressure on euphausiids, resulting in their elevated abundance along the shelf (Fig. 2).

An aspect of euphausiid distribution that does not appear to fit the conceptual model is the relatively high abundance of euphausiids offshore during both 1995 and 1998 north of the Columbia River (North region) under very different hake abundance conditions (low in 1995 and high in 1998). It has been hypothesized that there is enhanced upwelling near submarine canyons north of the Columbia River even during lower wind-driven upwelling periods providing a possible stable food resource for euphausiids (Hickey 1998). This has been corroborated by analysis of the acoustic survey data for 1995 and 1998, which found higher euphausiid abundance on transects in the North region crossing submarine canyons than those that do not (Swartzman 2001).

A common feature in all three surveys was the consistent high abundance of both hake and euphausiids along the shelf break in all years and regions (Figs. 1–3). This may be a result of a compromise between predation risk and feeding conditions. Phytoplankton abundance was usually highest in the shelf region (Fig. 4) and predation

susceptibility for euphausiids also was highest there because of restricted depth range (De Robertis et al. 2000). The shelf-break domain may be deep enough to provide reduced susceptibility to daytime predation but close enough to the shelf to have higher phytoplankton availability. Moving up in the water column to feed at dusk places euphausiids at increased risk of predation, especially on clear moonlit nights (De Robertis et al. 2000). The presence of euphausiids in higher abundance in the shelf-break domain may attract hake to the area. It is difficult to separate the results of predation (i.e., removal of euphausiids through predation) from the behavioral response to predation (i.e., attraction to an area because it provides some refuge from predation).

An increasing body of evidence suggests that there have been significant changes in the California Current ecosystem since the 1997–1998 regime shift. There have been apparent shifts in the dominant species of copepods, from higher abundance of warm water species prior to 1998 to increased abundance of cold water species (Peterson unpublished data). This pattern has been observed off the Oregon and Washington (Peterson and Mackas 2001), British Columbia (Mackas et al. 2001; Peterson and Mackas 2001), and California (Ohmann unpublished data) coasts. High abundance of cold water copepod species reflects increased transport out of the subarctic Pacific and coastal Gulf of Alaska. This may also result in greater input of nutrients in the transported water and greater productivity in the northern California Current. Increased nutrient levels also would result from increased upwelling.

Enhanced primary and secondary production and increased abundance of cold water copepod species may enhance recruitment of euphausiids and planktivorous fishes (anchovies and smelts; Peterson unpublished data), and could help survival of smolt salmon, which feed largely on euphausiids and small pelagic fishes that feed on euphausiids

(Brodeur et al. 1992). Salmon appear to respond rapidly to the changed feeding environment resulting from regime shifts, because they have a critical smolt period on first entry into the ocean (Logerwell et al. in press).

While survival of juvenile coho smolts off Oregon was greater than 5% during the early 1970s it decreased to less than 2% in the 1980s and less than 1% in the 1990s (Logerwell et al. 2003). Juvenile coho survival has increased steadily since the 1999 brood year, from 2% in 1999 to 5% in 2001. Increased chinook salmon survival on the Columbia River is reflected in greatly increased runs, with the 2001 run above Bonneville Dam being among the highest ever recorded, with the proportion of survivals being comparable to pre-1976 values. Generally, increased upwelling and cooler surface water conditions favor coho and chinook ocean survival (Magnusson and Hilborn 2003). Additional evidence for an increase in planktivorous fishes after the 1997–1998 regime shift was the predominance during the nighttime in summer 2001 of large aggregations of small planktivorous pelagic fishes (anchovy, saury, myctophids, and capelin) feeding in dense aggregations of euphausiids near the surface (Swartzman unpublished data). Parrish and Zador (2003) found that the common murre (*Uria aalge*) colony attendance on Tatoosh Island, Washington, rebounded in 1999 after many low attendance years and has remained higher. Since common murre feed mainly on small pelagic fish (eulachon, herring, sandlance) this might reflect an increase in abundance of small pelagic fish since 1999.

Decade-scale changes in the ocean environment, reflected in indexes such as the PDO, have a strong effect on biota in the EPBC. We have shown that in two summer acoustic surveys, arguably after the 1997–1998 regime shift, the distribution of euphausiids was significantly different and their abundance significantly higher than in the single summer survey conducted before the regime shift. Comparison of the three surveys did not show any consistent pattern in the abundance and distribution of Pacific hake that can be related to the effects of the regime shift. Changes in euphausiid distribution and abundance may be linked to changes in primary production, in the relative strength of the equatorward flowing surface and poleward flowing undercurrent, and to the relative abundance of hake (predatory pelagic fish). While there were not a sufficient number of surveys before and after the regime shift to demonstrate that the differences observed here are characteristic of the two regimes, the results are consistent with a regime shift mediated change in the euphausiid abundance and distribution. The middle survey,

1998, was a swing year, the survey being taken on the cusp between a strong El Niño and a strong La Niña year, which reduces the value of that survey in providing evidence concerning the effects of regime shifts. The differences in distribution and abundance of euphausiids between the 1995 and 1998 surveys appear to be linked to the same upwelling, current-dominated migration and predation features that appear to affect the euphausiid abundance and distribution in the other survey years. Changes in euphausiid abundance and distribution may influence the abundance of many pelagic consumers such as salmon smolts, herring, and anchovy. The interaction of oceanographic, feeding, and predation dynamics appear to characterize the biotic results of regime shifts. Results from only three surveys present tantalizing evidence to this effect. The patterns would undoubtedly be more forthcoming if more frequent acoustic surveys were conducted.

These results were based on analysis of data collected as part of surveys conducted to assess the abundance of Pacific hake (Guttormsen 2001). We were able, through detailed analysis of the acoustic data, to extrapolate results to multiple trophic levels and address, albeit tentatively, issues concerning the interaction of currents, bathymetry, pelagic fish, and euphausiids. We believe that mesoscale, multi-year, and multi-trophic studies, such as this one, can help to explain long-term changes in nearshore marine environments, and serve as a powerful tool for aiding fisheries managers and marine policy makers in their recent expanded emphasis on ecosystem based fishery management (Ecosystem Based Fisheries Management 1999).

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