Abundance and community composition of micronekton across a front off Southern California

ANA LIGIA LARA-LOPEZ*, PETER DAVISON AND JULIAN ANTHONY KOSLOW

SCRIPPS INSTITUTION OF OCEANOGRAPHY, UNIVERSITY OF CALIFORNIA SAN DIEGO, 9500 GILMAN DR., CA 92093-0218, USA

*CORRESPONDING AUTHOR: analigia@yahoo.com

Concurrent net and acoustic data were collected across a front off Southern California to assess its influence on the abundance, biomass and community composition of the micronekton. Higher abundance and biomass of vertically migratory mesopelagic fish (VMF) and euphausiids were found on the cooler mesotrophic (north) side of the front, whereas larval fish abundance was higher on the warmer oligotrophic (south) side. The biomass and community composition of non-VMF did not differ between the two sides of the front. The north was dominated by the euphausiid *Euphausia pacifica* and the myctophid *Diaphus theta*, whereas the south was dominated by *E. gibboides*, *E. recurva* and a combination of VMF species with warm water affinities. The larval fish assemblage in the north was dominated by the nearshore species *Engraulis mordax* and *Citharichthys* spp., whereas mesopelagic fish larvae dominated the south. Acoustic data revealed differences in the distribution of fish, euphausiids and the deep-scattering layer across the front. In particular, epipelagic fish were aggregated directly at the frontal interface in the area of enhanced plankton concentrations and may have contributed to higher plankton mortality and turnover rates at the front. In addition to being an area of high biological abundance, the front may be acting as a distributional boundary for several migratory species, as well as a locus of enhanced prey forage and the activity of epipelagic species.

KEYWORDS: micronekton; A-Front; fish; krill; mesopelagic; California Current

INTRODUCTION

Mesoscale variability of physical processes in the marine environment influences the distribution and community structure of pelagic organisms, as well as the temporal and spatial patterns of biological production and food web development (Haury, 1984; Garcon *et al.*, 2001; Lima *et al.*, 2002; Bost *et al.*, 2009; Eden *et al.*, 2009). Fronts are features where two water masses meet, forming strong horizontal gradients in water properties (Franks, 1992; Belkin *et al.*, 2009). They can be persistent or short-lived and are often associated with biological aggregations. Local primary production may be enhanced, and fronts may serve as spawning, nursery and feeding grounds for a variety of organisms at all trophic levels (Haury, 1984; Falkowski *et al.*, 1991; McGillicuddy *et al.*, 1998; Landry *et al.*, 2008; Belkin *et al.*, 2009). Often, changes in community composition and abundance of micronekton across fronts are abrupt and affect not only the surface waters but can also have an effect deeper in the water column through the export of organic matter (Backus *et al.*, 1969; Allison and Wishner, 1986; Angel, 1989; Baussant *et al.*, 1993; Pakhomov *et al.*, 1994). Persistent frontal regions have
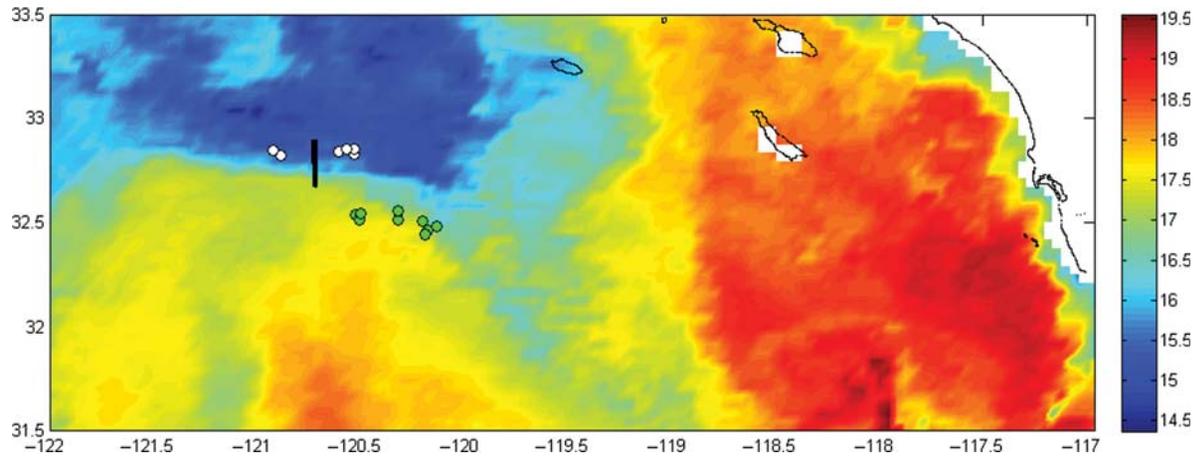
Fig. 1. Satellite image of sea surface temperatures showing the acoustic underway sampling at the A-Front (black line) and locations where the concurrent net and acoustic sampling took place in the water masses adjacent to the front (white and green circles).

also been shown to act as biogeographic boundaries, exhibiting substantial differences in community composition between adjacent water masses (Allison and Wishner, 1986; Anderson and Gardner, 1986; Angel, 1989; Sabates and Maso, 1990; Pakhomov *et al.*, 1994; Lima *et al.*, 2002; Belkin and Cornillon, 2007).

The central and southern regions of the California Current System are divided into two principal biogeographic provinces, based on topography, circulation patterns and floral and faunal distributions: the Oregonian and Californian Provinces (McGowan, 1971; Horn and Allen, 1978; Hickey, 1998; Horn *et al.*, 2006). The boundary between these provinces has variously been ascribed to Point Conception and to the region south from Los Angeles to San Diego at ~32–33°N (McGowan, 1971; Briggs, 1974; Newman, 1976; Horn and Allen, 1978; Doyle, 1985; Dawson, 2001; Dawson *et al.*, 2006; Horn *et al.*, 2006). The interaction between topography and remotely forced currents in the Southern California Bight south of Point Conception make the circulation complex, such that mesoscale features like fronts and eddies are common (Hickey, 1998; Hickey *et al.*, 2003; Caldeira *et al.*, 2005; Dong *et al.*, 2009). In this area, at ~32°N, there is often a frontal feature that extends east to west known as the Ensenada Front, where cold, chlorophyll-rich waters disappear abruptly (Pelaez and McGowan, 1986; Thomas and Strub, 1990; Haury *et al.*, 1993; Chereskin and Niiler, 1994). This frontal region has been noted to serve as a boundary for zooplankton and larval fish and marks the southern boundary of the biomass peak developed from the coastal upwelling off northern and central California (Thomas and Strub, 1990; Haury *et al.*, 1993; Moser and Smith, 1993; Chereskin and Niiler, 1994). In this study, we examine the potential role of a front with sharp

temperature and chlorophyll gradients (the "A-Front") that occurred in the vicinity of the Ensenada Front, as a distributional boundary for micronekton and a site of heightened ecological activity. This front extended in the east–west direction with warmer, less productive waters south of the front and cooler, more productive waters to the north (Landry, Ohman *et al.*, 2012). Current direction was also east to west with eastward flows higher in the front relative to the regions immediately to the south and north (Li *et al.*, 2012).

METHOD

Data collection

This study was undertaken as part of the California Current Ecosystem–Long-Term Ecological Research (CCE-LTER) Process Cruise (P0810), carried out during October 2008. The study site was located between 32–33°N and 120–121°W, ~230 km offshore (Fig. 1). The A-Front was identified using a combination of satellite imagery, a Moving Vessel Profiler (Ohman *et al.*, 2012) and an Advanced Laser Fluorescence System (Chekalyuk *et al.*, 2012). Process studies were carried out as Lagrangian-based experiments following satellite-tracked drifters in the water masses that interact at the A-Front. These studies included primary production experiments, carbon export and dissolve iron concentration estimates among others (Stukel, 2011; Ohman *et al.*, 2012). See Landry, Ohman *et al.* (Landry, Ohman *et al.*, 2012) for a full description of the study region and sampling design. During these process studies, concurrent multifrequency acoustic measurements and net sampling were carried out from 20 to 24

October 2008 in the cool productive waters (north) and from 26 to 27 October 2008 in the warm oligotrophic waters (south) to compare the micronekton community composition and ecological conditions in the water masses adjacent to the front. Net sampling in these water masses took place $\sim 25-50$ km away from the frontal feature itself (Fig. 1).

There were also four daytime crossings of the A-Front on October 24, during which acoustic data were recorded. However, the first two crossings were carried out at 20 km h^{-1}, too fast for good-quality acoustic data to be obtained, and vertical migration was underway during the fourth crossing. We therefore present data from the third crossing, which was carried out at 10 km h^{-1} in a north-to-south direction. Nevertheless, the distribution of backscattering was qualitatively similar during all crossings. Concurrent net sampling was not possible during this transect due to time constraints. Acoustic data were collected with a pole-mounted split-beam scientific echosounder (SIMRAD EK-60) equipped with four frequencies (38, 70, 120 and 200 kHz). The system was calibrated using the standard sphere method (Foote et al., 1987), and it was mounted on the port aft side of the vessel 3.4 m below the surface. Data were collected to a depth of 750 m with a ping rate of 0.5 ping s^{-1} and pulse length of 0.512 ms. Beam angles for the 70, 120 and 200 kHz transducers were 6°, and 12° for the 38 kHz. Acoustic data corresponding to trawls were processed and cleaned using Echoview® at a resolution of 1 ping and 1-m depth increments to the maximum depth of the trawl.

A total of seven shallow and eight deep oblique tows were taken during the Lagrangian-based experiments within the water masses adjacent to the A-Front with a Matsuda-Oozeki-Hu trawl (MOHT) with 5-m^2 mouth opening and 1.7-mm mesh Nitex netting (Oozeki et al., 2004). The towing speed was 1.25–1.5 m s^{-1}. Six of the eight deep tows were conducted in daylight, with all tows sampling to a mean depth of 774 m. Five of the seven shallow tows were conducted at night, with all tows sampling to a mean depth of 199 m. Total water volume filtered during each tow (m^3) was estimated using a TSK flowmeter attached to the frame at the mouth of the net. Trawl depth was recorded with a Wildlife Computers Mk9 archival tag. Samples were fixed on board in 5% buffered formalin–seawater solution, with fish sorted and preserved separately. Ashore, fish were identified to species, weighed, measured to the nearest millimeter and classified according to Davison (Davison, 2011) into three different groups: (a) vertically migratory fish (VMF), (b) non-VMF (NVMF), and (c) larvae. Category (a) comprised fish that remain at

mesopelagic depths during the day and migrate to the surface at night. It includes species for which only a portion of the population migrates vertically on a given night. Category (b) comprised species that do not migrate to the surface on a diel cycle. Zooplankton samples were subsampled with a Folsom splitter or a Stempel pipette, sorted to taxonomic groups and enumerated, with only euphausiids identified to species. Lengths and widths of 30 organisms from each taxonomic group of zooplankton were measured with an ocular micrometer under a dissecting microscope. Total abundance of organisms (ind. m^{-2}) was obtained by dividing the number of individuals by the volume filtered and multiplying by the maximum sampling depth.

Data analyses

A variety of sound-scattering models were applied to estimate frequency-dependent target strengths (TSs) of the fish and invertebrates collected (Table I). For each organism type, acoustic backscattering cross-sections (σ_{bs}) were determined, based on the geometric shape, size, orientation and material properties of the organisms, and the acoustic frequency. Organisms were subsequently classified according to the shape of their TS-frequency spectra into three acoustic groups: (i) with gas inclusion, (ii) large without gas inclusion and (iii) small without gas inclusion. The group classification corresponds to the size of the organism relative to the wavelength (λ) of sound. Group 1 organisms scatter in the geometric region ($ka > 1$), group 2 scatter in the region between Rayleigh and geometric characteristics ($ka = 1$ indicates the transition between regions) and group 3 scatter in only the Rayleigh region ($ka < 1$). The wave number is represented by k and relates to λ by $k = 2\pi/\lambda$, and a is the equivalent spherical radius of the organism. Abundance of organisms was estimated from multifrequency backscatter (s_v) and the mean TS of the frequency spectra from each acoustic group using non-negative least-squares inversion (Holliday, 1977; Greenlaw, 1979). The loss of the high-frequency data (120 and 200 kHz) due to sound absorption makes this method unsuitable for estimating abundances below ~ 150 m of depth. A combination of relative frequency response, $r(f) = s_v(f)/s_{v38}$, and the difference in mean volume backscatter (ΔMVBS) between frequencies (Madureira et al., 1993; Miyashita et al., 1997; Kang et al., 2002; Korneliussen and Ona, 2002) was used to estimate the acoustic abundance of NVMF at depths below 200 m using Echoview®. Because only two frequencies (38 and 70 kHz) can be used to estimate abundance at depths below 200 m, it is difficult to discriminate organisms with an air inclusion from those

Table I: Scattering models, material properties and orientation used to estimate acoustic backscattering cross-sections for invertebrates and fish based on MOHT catches

Taxa	Model	g	h	Tilt angle	Tilt angle (SD)	Reference
Euphausiids	Bent cylinder (DWBA)	1.037[a]	1.011[a]	1.9[b]	42.3[b]	Mikami *et al.* (2000)[a] and De Robertis *et al.* (2003)[b]
Copepods	Prolate spheroid (DWBA)	1.00	1.012	0	30	Matsukura *et al.* (2009)
Pteropods (limacina)	Spherical elastic shell	1.732	1.732	—	—	Lawson *et al.* (2004)
Decapods (<25 mm)	Bent cylinder (DWBA)	1.043[a]	1.064[a]	20[b]	20[b]	Chu *et al.* (2000)[a] and Chu *et al.* (1993)[b]
Decapods (≥25 mm)	Bent cylinder (DWBA)	1.041[a]	1.078[a]	20[b]	20[b]	Chu and Wiebe (2005)[a] and Chu *et al.* (1993)[b]
Siphonophore (pneumatophore)	Gas sphere	0.0012	0.22	—	—	Warren *et al.* (2001)
Amphipods	Bent cylinder (DWBA)	1.058	1.058	0	30	Lawson *et al.* (2004)
Chaetognath	Bent cylinder (DWBA)	1.014[a]	1.03[b]	0	30	Smith *et al.* (2010)[a] and Lawson *et al.* (2004)[b]
Ostracods	Bent cylinder (DWBA)	1.03	1.03	0	30	Lawson *et al.* (2004)
Polychaete	Bent cylinder (DWBA)	1.03	1.03	0	30	Lawson *et al.* (2004)
Salp	Bent cylinder (DWBA)	1.002	1.001	0	30	Wiebe *et al.* (2009)
Zoea	Bent cylinder (DWBA)	1.058	1.058	0	30	Lawson *et al.* (2004)
Fish body	Fluid-filled cylinder	[a]	1.020[b]	0	0	Davison, (2011)[a] and Yasuma *et al.* (2006)[b]
Fish swimbladder	Gas sphere	—	—	—	—	

Invertebrate models for fluid-like organisms are as per Stanton *et al.* (Stanton *et al.*, 1998), Stanton and Chu (Stanton and Chu, 2000) and Anderson (Anderson, 1950). A hybrid model was used for the pneumatophore of physonect siphonophores following Lavery *et al.* (Lavery *et al.*, 2007). Fish bodies were modeled as a fluid-filled cylinder per Stanton (Stanton, 1988). The fish with swimbladder was modeled as a gas sphere per Anderson (Anderson, 1950) and Medwin and Clay (Medwin and Clay, 1997) with the assumptions that gas volume was 80% of that required for neutral buoyancy and that the gas was at the temperature and pressure of the seawater at 50 m of depth. Material property values used for invertebrates were based on literature values with references included in the table. Corresponding references are indicated by the alphabet "a". *g*, density contrast between surrounding water and the organism; *h*, sound-speed contrast between surrounding water and the organism; SD, standard deviation; DWBA, distorted-wave born approximation.

without. Both methods were therefore used for comparison. Values of ΔMVBS of <5 dB between 70 and 38 kHz and an $s_{v70}/s_{v38} < 1$ were deemed to be organisms with an air inclusion. Similarly, a combination of $r(f)$ and ΔMVBS was used to estimate the acoustic abundance of fish and euphausiids during the underway transect measurements across the A-Front. Because only acoustic data were collected during these transects, the identity of the epipelagic schooling fish observed within the front itself (where the isopycnals shoaled and the hydrographic gradients were largest) could not be identified. Abundance estimates during the underway acoustic sampling are therefore expressed as relative acoustic backscatter (NASC, $m^2 \, nmi^{-2}$).

Acoustic data collected concurrently with night-time tows in the water masses adjacent to the front were used to estimate the abundance of VMF and NVMF species. Larval fish abundances could not be estimated acoustically since they could not be distinguished from other fish or invertebrates with the frequency range in our study. Euphausiids were identified using ΔMVBS, and their abundance was estimated by dividing the resulting s_v by their mean σ_{bs}.

Net abundances (ind. m^{-2}) and biomass (g WW m^{-2}) for larval fish, VMF and NVMF were estimated for all tows except those conducted during daytime in the upper 200 m, when avoidance led to extremely low catches. Euphausiid biomass (g WW m^{-2}) was estimated using the following relationship for length (L) versus carbon content (C): $\log C$ (μg) $= -0.473 + 3.174 \log L$ (Lavaniegos and Ohman, 2007), with C subsequently converted into wet weight (WW) as $\log WW$ (g) $= -1.537 + 0.852 \log C$ (mg) (Wiebe, 1988).

One-way ANOVAs (SPSS®) were used to compare abundances and wet weight biomass (WW) in the two sampling areas north and south of the front. Data that did not pass parametric test assumptions (Levene statistics) were log-transformed before analysis. Cluster analyses were performed to assess differences in community composition on the two sides of the front using PRIMER® statistical software. The analyses were based on the Bray–Curtis similarity matrix among tows based on euphausiid, VMF, NVMF and larval fish abundances (ind. m^{-2}). A SIMPER (similarity percentages) routine was applied to determine which species contributed most to the dissimilarities between clusters.

RESULTS

Overall, the number of species of euphausiids, fish and particularly larval fish was higher in the water mass south of the front (Tables II and III). However, the

Table II: Families and species of fish caught with nets in the water masses north and south of the front in Southern California during October 2008, their respective abundance (ind. m^{-2}), biomass (g WW m^{-2}) size range and life history

	Abundance				Biomass				Size range		
	North		South		North		South				
	Adult	Larvae	Adult	Larvae	Adult	Larvae	Adult	Larvae	North (mm)	South (mm)	Life history
Alepocephalidae											
Alepocephalus tenebrosus	0.02 ± 0.02	<0.01 ± < 0.01	0.01 ± 0.01		0.01 ± 0.02	<0.01 ± < 0.01	<0.01 ± < 0.01		18–50	36–37	M,B
Anoplogastridae											
Anoplogaster cornuta	0.01 ± 0.01				0.17 ± 0.29				98		B
Bathylagidae											
Bathylagoides wesethi[a]	0.08 ± 0.06	0.01 ± 0.02	0.15 ± 0.13	0.07 ± 0.08	0.03 ± 0.02	<0.01 ± < 0.01	0.05 ± 0.04	<0.01 ± < 0.01	19–65	18–72	M
Leuroglossus stilbius[a]	0.04 ± 0.03		0.01 ± 0.02		0.01 ± < 0.01		<0.01 ± < 0.01		25–34	24–28	M
Lipolagus ochotensis[a]	0.01 ± 0.01		<0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.02		<0.01 ± 0.01	<0.01 ± < 0.01	52	22–57	M
Blenniidae											
Hypsoblennius jenkinsi[b]		<0.01 ± 0.01				<0.01 ± < 0.01					D
Chiasmodontidae											
Chiasmodon niger			<0.01 ± 0.01				0.04 ± 0.09			103	B
Engraulidae											
Engraulis mordax[b]		0.05 ± 0.07				<0.01 ± < 0.01					E
Gobiidae											
Rhinogobiops nicholsi[b]		<0.01 ± 0.01		<0.01 ± < 0.01		<0.01 ± < 0.01		<0.01 ± < 0.01			D
Gonostomatidae											
Cyclothone acclinidens	1.91 ± 0.39		2.41 ± 1.94		0.53 ± 0.02		0.69 ± 0.59		17–55	16–56	M,B
Cyclothone atraria	0.04 ± 0.05		0.01 ± 0.02		0.01 ± 0.01		<0.01 ± 0.01		28–45	35–45	M,B
Cyclothone pallida	0.03 ± 0.03				0.02 ± 0.04				45–60		M,B
Cyclothone pseudopallida	0.05 ± 0.04		0.06 ± 0.03		0.01 ± 0.01		0.01 ± < 0.01		27–43	25–43	M,B
Cyclothone signata	3.43 ± 0.37		3.59 ± 0.54	0.01 ± 0.02	0.17 ± 0.12		0.12 ± 0.12	<0.01 ± < 0.01	15–36	14–34	M,B
Cyclothone sp.	0.05 ± 0.05		1.03 ± 1.29		0.02 ± 0.03		0.2 ± 0.26		23–51	12–55	M,B
Melamphaidae											
Melamphaes lugubris	0.04 ± 0.05		<0.01 ± 0.01	0.01 ± 0.01	0.04 ± 0.07		<0.01 ± 0.01	<0.01 ± < 0.01	22–48	32	M
Melamphaes parvus	0.01 ± 0.02		0.02 ± 0.02		<0.01 ± 0.01		0.04 ± 0.06		29	17–60	M
Poromitra crassiceps	0.03 ± 0.04		0.04 ± 0.03		0.01 ± 0.01		0.01 ± 0.01		18–29	19–38	M
Scopelogadus mizolepis	0.08 ± 0.02		0.08 ± 0.01	<0.01 ± 0.01	0.22 ± 0.2		0.13 ± 0.12	<0.01 ± < 0.01	38–80	10–83	M
Microstomatidae											
Microstoma microstoma	0.01 ± 0.02		<0.01 ± < 0.01		<0.01 ± < 0.01				16	35	B
Myctophidae											
Ceratoscopelus townsendi[a]			0.04 ± 0.04				0.05 ± 0.05			25–53	M
Diaphus theta[a]	0.87 ± 0.81		0.16 ± 0.11	0.07 ± 0.08	0.18 ± 0.14		0.03 ± 0.04	<0.01 ± < 0.01	13–55	12–60	M
Diogenichthys atlanticus[a]	<0.01 ± 0.01		0.02 ± 0.02	0.02 ± 0.03	<0.01 ± < 0.01		<0.01 ± < 0.01	<0.01 ± < 0.01	15	18–26	M
Diogenichthys laternatus[a]			<0.01 ± < 0.01				<0.01 ± < 0.01			19	M
Loweina rara[b]				<0.01 ± < 0.01				<0.01 ± < 0.01			M
Nannobrachium hawaiiensis			<0.01 ± 0.01				<0.01 ± 0.01			46–56	M

Species											
Nannobrachium regale	0.01 ± 0.02		<0.01 ± 0.01		0.02 ± 0.03		0.01 ± 0.02		59	57	M
Nannobrachium ritteri[a]	0.33 ± 0.21		0.15 ± 0.09	0.01 ± 0.01	0.57 ± 0.36		0.3 ± 0.24	<0.01 ± 0.01	22–92	17–98	M
Notolychnus valdiviae[a]	<0.01 ± 0.01		<0.01 ± 0.01		<0.01 ± <0.01		<0.01 ± <0.01		22	15–21	M
Notoscopelus resplendens[a]			<0.01 ± <0.01	<0.01 ± <0.01			<0.01 ± 0.01	<0.01 ± <0.01		54	M
Parvilux ingens	0.02 ± 0.01		0.03 ± 0.05		0.08 ± 0.08		0.22 ± 0.34		37–85	18–153	M
Protomyctophum crockery	0.07 ± 0.05	0.04 ± 0.04	0.1 ± 0.04	0.12 ± 0.12	<0.01 ± <0.01	<0.01 ± <0.01	0.01 ± 0.01	<0.01 ± <0.01	15–28	11–36	M
Stenobrachius leucopsarus[a]	0.24 ± 0.13		0.18 ± 0.11	<0.01 ± 0.01	0.08 ± 0.04		0.03 ± 0.03	<0.01 ± 0.01	20–71	21–72	M
Symbolophorus californiensis[a]	0.01 ± 0.01	0.01 ± 0.01	0.04 ± 0.04	0.03 ± 0.02	<0.01 ± <0.01	<0.01 ± <0.01	0.03 ± 0.02	<0.01 ± <0.01	24–37	25–53	M
Tarletonbeania crenularis[a]	0.03 ± 0.02	0.01 ± 0.01	<0.01 ± 0.01	<0.01 ± 0.01	<0.01 ± <0.01	<0.01 ± <0.01	<0.01 ± <0.01	<0.01 ± <0.01	20–29	23	M
Triphoturus mexicanus[a]	0.49 ± 0.32	0.02 ± 0.02	0.39 ± 0.27	0.03 ± 0.03	0.33 ± 0.31	<0.01 ± <0.01	0.22 ± 0.21	<0.01 ± <0.01	15–68	14–69	M
Nemichthyidae											
Avocettina infans			<0.01 ± 0.01				0.05 ± 0.11			562	M
Nemichthys scolopaceus	<0.01 ± 0.01				0.01 ± 0.03				599		M
Notosudidae											
Scopelosaurus harryi			<0.01 ± 0.01				<0.01 ± <0.01			41–49	M
Ophidiidae											
Chilara taylori	<0.01 ± 0.01		<0.01 ± <0.01		<0.01 ± <0.01		<0.01 ± <0.01		62	49	D
Opisthoproctidae											
Macropinna microstoma	0.01 ± 0.02			<0.01 ± 0.01	0.01 ± 0.01			<0.01 ± <0.01	26		B
Paralepididae											
Lestidiops ringens[b]		<0.01 ± 0.01		0.01 ± 0.01		<0.01 ± <0.01		<0.01 ± <0.01			M
Paralichthyidae											
Citharichthys sordidus[b]		0.03 ± 0.06		<0.01 ± 0.01		<0.01 ± <0.01		<0.01 ± <0.01			D
Citharichthys stigmaeus[b]		0.12 ± 0.11		<0.01 ± 0.01		<0.01 ± <0.01		<0.01 ± <0.01			D
Phosichthyidae											
Ichthyococcus irregularis	0.01 ± 0.01				<0.01 ± <0.01				18–22		M
Vinciguerria lucetia[a]	0.01 ± 0.01		0.08 ± 0.05	0.09 ± 0.06	<0.01 ± <0.01		<0.01 ± <0.01	<0.01 ± <0.01	20–23	14–26	M
Platytroctidae											
Holtbyrnia latifrons	0.03 ± 0.04	<0.01 ± 0.01	0.08 ± 0.03		<0.01 ± <0.01	<0.01 ± <0.01	0.01 ± 0.01		15–23	13–40	MB
Mirorictus taningi	0.01 ± 0.01				0.06 ± 0.11				95		D
Sagamichthys abei	0.02 ± 0.02		0.02 ± 0.02		0.16 ± 0.27		<0.01 ± <0.01		16–24	13–28	MB
Pleuronectidae											
Microstomus pacificus[b]				<0.01 ± 0.01				<0.01 ± <0.01			D
Scopelarchidae											
Benthalbella dentata[b]		0.01 ± 0.01		<0.01 ± 0.01		<0.01 ± <0.01		<0.01 ± <0.01			M
Rosenblattichthys volucris[b]				<0.01 ± 0.01				<0.01 ± <0.01			M
Scopelarchus analis[b]				0.03 ± 0.03				<0.01 ± <0.01			M
Sebastidae											
Sebastes sp.[b]		0.01 ± 0.01				<0.01 ± <0.01					D
Sebastolobus altivelis			<0.01 ± 0.01				<0.01 ± <0.01			18	D
Sternoptychidae											
Argyropelecus affinis	0.13 ± 0.14		0.08 ± 0.03		0.15 ± 0.22		0.15 ± 0.12		10–62	13–71	M

Continued

	Abundance				Biomass				Size range		
	North		South		North		South		North (mm)	South (mm)	Life history
	Adult	Larvae	Adult	Larvae	Adult	Larvae	Adult	Larvae			
Argyropelecus hemigymnus	0.06 ± 0.06		0.23 ± 0.06		<0.01 ± < 0.01		0.02 ± 0.01		9–14	9–29	M
Argyropelecus lychnus	0.01 ± 0.01		<0.01 ± 0.01		<0.01 ± < 0.01		0.01 ± 0.02		14–24	36	M
Argyropelecus sladeni	0.21 ± 0.08		0.05 ± 0.05		0.06 ± 0.05		0.03 ± 0.03		9–39	9–45	M
Danaphos oculatus	0.05 ± 0.04	<0.01 ± 0.01	0.13 ± 0.11	0.01 ± 0.03	<0.01 ± < 0.01	<0.01 ± < 0.01	0.02 ± 0.02	<0.01 ± < 0.01	18–27	19–41	M
Sternoptyx diaphana			0.01 ± 0.01				<0.01 ± < 0.01			12–20	MB
Sternoptyx obscura			0.02 ± 0.02				0.01 ± < 0.01			12–27	MB
Sternoptyx pseudobscura			<0.01 ± 0.01				<0.01 ± 0.01			23	MB
Stomiidae											
Aristostomias scintillans	0.01 ± 0.01		<0.01 ± 0.01		0.02 ± 0.04		<0.01 ± 0.01		77	47	M
Bathophilus flemingi	0 ± 0.01				0.02 ± 0.03				89		M
Borostomias panamensis			<0.01 ± 0.01				0.25 ± 0.55			213	B
Chauliodus macouni	0.02 ± 0.02	0.03 ± 0.02	0.01 ± 0.01	0.02 ± 0.02	<0.01 ± < 0.01	<0.01 ± < 0.01	<0.01 ± < 0.01	<0.01 ± < 0.01	38–43	36–37	M
Idiacanthus antrostomus	0.13 ± 0.06		0.03 ± 0.03	0.18 ± 0.07	0.09 ± 0.02		0.12 ± 0.28	<0.01 ± < 0.01	61–332	52–422	M
Tactostoma macropus	0.02 ± 0.03		0.01 ± 0.01		0.45 ± 0.78		<0.01 ± < 0.01		58–301	62–67	M
Photonectes margarita			<0.01 ± < 0.01				0.03 ± 0.06			134	M
Stomias atriventer	0.04 ± 0.02	<0.01 ± 0.01	0.01 ± 0.01		0.16 ± 0.2	<0.01 ± < 0.01	0.04 ± 0.09		33–184	33–165	M
Tetragonuridae											
Tetragonurus cuvieri[b]		<0.01 ± < 0.01	0.01 ± 0.01	<0.01 ± 0.01				<0.01 ± < 0.01			
Total	32.97	2.15	52.22	6.65	15.90	0.08	19.44	0.18			

M, mesopelagic; B, bathypelagic; D, demersal; E, epipelagic.
[a]VMF.
[b]Larvae only.

Table III: Species of euphausiids caught with nets in the water masses north and south of the front in Southern California during October 2008, their respective abundance (ind. m^{-2}) and biomass (g WW m^{-2})

	Abundance		Biomass	
	North	South	North	South
Bentheuphausia amblyops	0.37 ± 0.58	0.11 ± 0.22	<0.01 ± 0.01	0 ± 0.01
Euphausia gibboides		14.62 ± 7.84		0.27 ± 0.15
Euphausia mutica		0.67 ± 1.02		0.01 ± 0.03
Euphausia pacifica	357.69 ± 423.23	7.7 ± 6.86	4.71 ± 4.91	0.17 ± 0.14
Euphausia recurva	0.65 ± 1.59	3.31 ± 2.38	0.02 ± 0.04	0.08 ± 0.05
Nematoscelis difficilis	28.99 ± 25.17	9.56 ± 9.85	0.61 ± 0.47	0.17 ± 0.18
Nematoscelis tenella		0.06 ± 0.19		<0.01 ± 0.01
Stylocheiron longicorne		0.3 ± 0.54		0.01 ± 0.02
Stylocheiron maximum		0.68 ± 0.97		0.02 ± 0.03
Thysanoessa gregaria	0.44 ± 0.55		0.01 ± 0.02	
Thysanoessa spinifera	0.16 ± 0.4		<0.01 ± 0.01	
Unidentified	13.98 ± 27.84	3.37 ± 1.89	0.05 ± 0.09	0.08 ± 0.04

Table IV: Results of one-way ANOVAs comparing estimated abundance and biomass of euphausiids, larval fish, VMF and NVMF and three mesopelagic species between the north and south water masses using acoustics and net data collected concurrently during the process experiments

	Abundance				Biomass			
	F-value	*P*-value	Mean north	Mean south	F-value	*P*-value	Mean north	Mean south
Net								
Euphausiids	6.11	*	1.69	0.13	9.45	**	2.96	0.34
Larval fish	7.08	*	0.35	0.78	3.12	NS	0.02	0.03
VMF	10.70	**	2.51	1.40	9.46	*	1.46	0.82
NVMF	5.27	NS	6.57	8.08	0.17	NS	2.73	2.49
Acoustic								
Euphausiids	35.58	***	601.93	22.94	9.45	**	26.25	1.00
VMF	41.18	***	16.68	2.19	52.13	**	11.22	1.73
NVMF	2.99	NS	2.50	1.58	2.99	NS	0.90	0.57
N. ritteri	12.16	**	0.39	0.16				
S. leucopsarus	3.63	NS	0.29	0.2				
T. mexicanus	1.16	NS	0.23	0.24				
B wesethi	1.71	NS	0.1	0.17				
S. californiensis	3.95	NS	0.01	0.05				
V. lucetia	10.81	**	0.01	0.09				

NS, not significant.
*$P < 0.05$.
**$P < 0.01$.

abundance and biomass of most groups were higher in the water mass north of the front. For most groups, there were substantial differences in species composition between water masses.

Euphausiids

Euphausiid abundance and biomass estimates from MOHT samples were an order of magnitude higher in the northern water mass (1.7 ± 2.3 ind. m^{-2}, 3.0 ± 2.9 g WW m^{-2}) than the south (0.1 ± 0.1 ind. m^{-2}, 0.3 ± 0.2 g WW m^{-2}). These differences were significant at $P < 0.05$. Likewise, acoustic estimates of abundance and biomass were significantly higher in the

north of the front (602 ± 307 ind. m^{-2}, 26.3 ± 13.4 g WW m^{-2}) than the south (22.9 ± 23.7 ind. m^{-2}, 1 ± 1 g WW m^{-2}) (Table IV, Fig. 2). However, acoustic estimates of euphausiid abundance were 2 orders of magnitude higher than MOHT-based estimates, and biomass estimates based on acoustics were an order of magnitude higher. Classification based on euphausiid species composition clearly separated the assemblages from the two water masses, with less than 50% similarity between them (Fig. 3a). *Euphausia pacifica* was the dominant species in the northern water mass, accounting for ~88% of the catch. *Nematoscelis difficilis* and *E. gibboides* dominated the southern assemblage, accounting for ~56% of the catch (Fig. 3b). In addition,
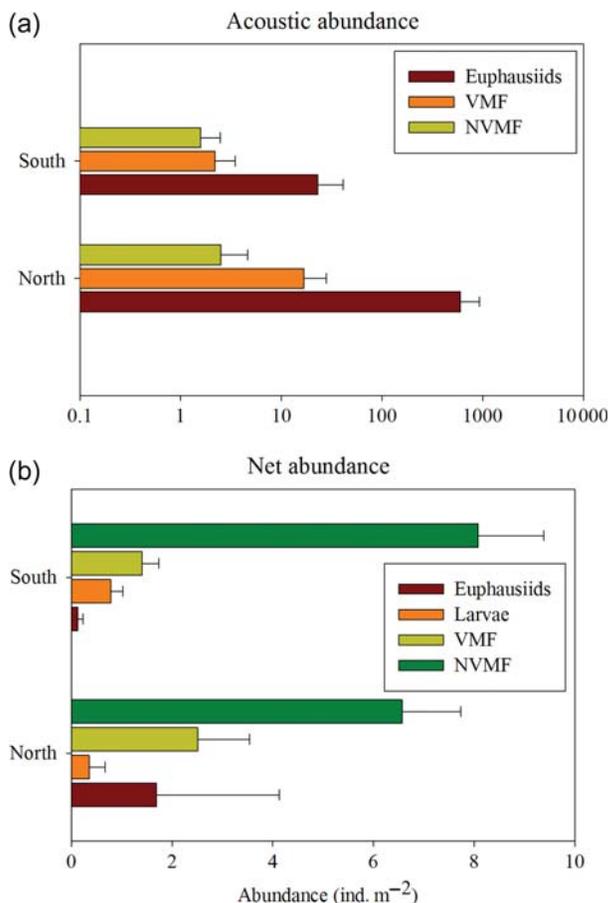
Fig. 2. (**a**) Acoustic and (**b**) net estimates of abundance of euphausiids, VMF, NVMF and larval fish. Acoustic abundance in log-scale.

there was a significant difference (ANOVA, $P < 0.05$) in the size distribution of euphausiids with larger organisms in the northern samples, mean length 12.6 ± 2.7 mm, compared with 11.3 ± 3.1 mm in the south.

Vertically migratory fish

The abundance and the biomass of VMF estimated from the MOHT samples were also significantly higher in the northern water mass (2.5 ± 0.8 ind. m^{-2}, 1.4 ± 0.2 g WW m^{-2}) than the south (1.4 ± 0.4 ind. m^{-2}, 0.8 ± 0.4 g WW m^{-2}) (Table IV, Fig. 2). This pattern was also observed in the acoustic data, although the magnitude of the difference was greater, with both abundance and biomass ~ 10 times higher to the north (16.7 ± 4.6 ind. m^{-2}, 11.2 ± 4.3 g WW m^{-2}) than to the south ($2.2 \pm S0.8$ ind. m^{-2}, 1.7 ± 0.4 g WW m^{-2}). There was again an order of magnitude difference between acoustic and net estimates of abundance and biomass. A clear separation in the community

composition between both water masses was evident with less than 60% similarity between them. *Diaphus theta* dominated the assemblage in the north, where it comprised $\sim 43\%$ of the fish sampled, compared with $\sim 13\%$ to the south. However, *Stenobrachius leucopsarus*, *Triphoturus mexicanus* and *Nannobrachium ritteri* contributed similar to the fish abundance in the two water masses with ~ 12, 27 and 13%, respectively. Despite this similarity in percent contributions, their abundances were higher in the northern water mass, although the difference was only significant for *N. ritteri* (Table IV). The percentage contributions to the assemblage of *Bathylagoides wesethi*, *Symbolophorus californiensis* and *Vinciguerria lucetia* were ≥ 3 times higher to the south (Fig. 4a and b), but only *V. lucetia* was significantly more abundant in those samples. *Ceratoscopelus townsendi* was absent in the water mass north of the front yet contributed 3% to the assemblage in the water mass south of the front. Several less abundant species exhibited marked differences in abundance between water masses adjacent to the front: *Diogenichthys laternatus* was absent in the north, *D. atlanticus* was 10 times more abundant in the south and *Tarletonbeania crenularis* was 10-fold more abundant in the north. Trends in biomass reflected those in abundance, with $\sim 70\%$ similarity between the two water masses (Fig. 5a and b).

Larval fish

In contrast to euphausiids and VMF, larval fish were significantly more abundant in net tows from the southern water mass (0.8 ± 0.3 ind. m^{-2}) than the north (0.4 ± 0.3 ind. m^{-2}), with no significant difference in biomass (Table IV, Fig. 2). There was less than 30% similarity in community composition of larval fish between water masses north and south of the front. Oceanic mesopelagic species dominated the larval fish community in the southern water mass, whereas the north was dominated by nearshore species, such as the sand dabs, *Citharichthys stigmaeus* and *C. sordidus*, and anchovy, *Engraulis mordax*, which together accounted for $\sim 58\%$ of the larval fish in those samples. Larvae from mesopelagic species such as *Idiacanthus antrostomus*, *V. lucetia* and *D. theta* were absent in the northern water mass, but accounted for 49% of the larval fish in the southern samples. Larvae of *E. mordax* were absent to the south but accounted for 13% of the larval fish from northern samples (Fig. 6a and b).

Non-vertically migratory fish

NVMF species showed no significant difference in abundance or biomass between the two water masses
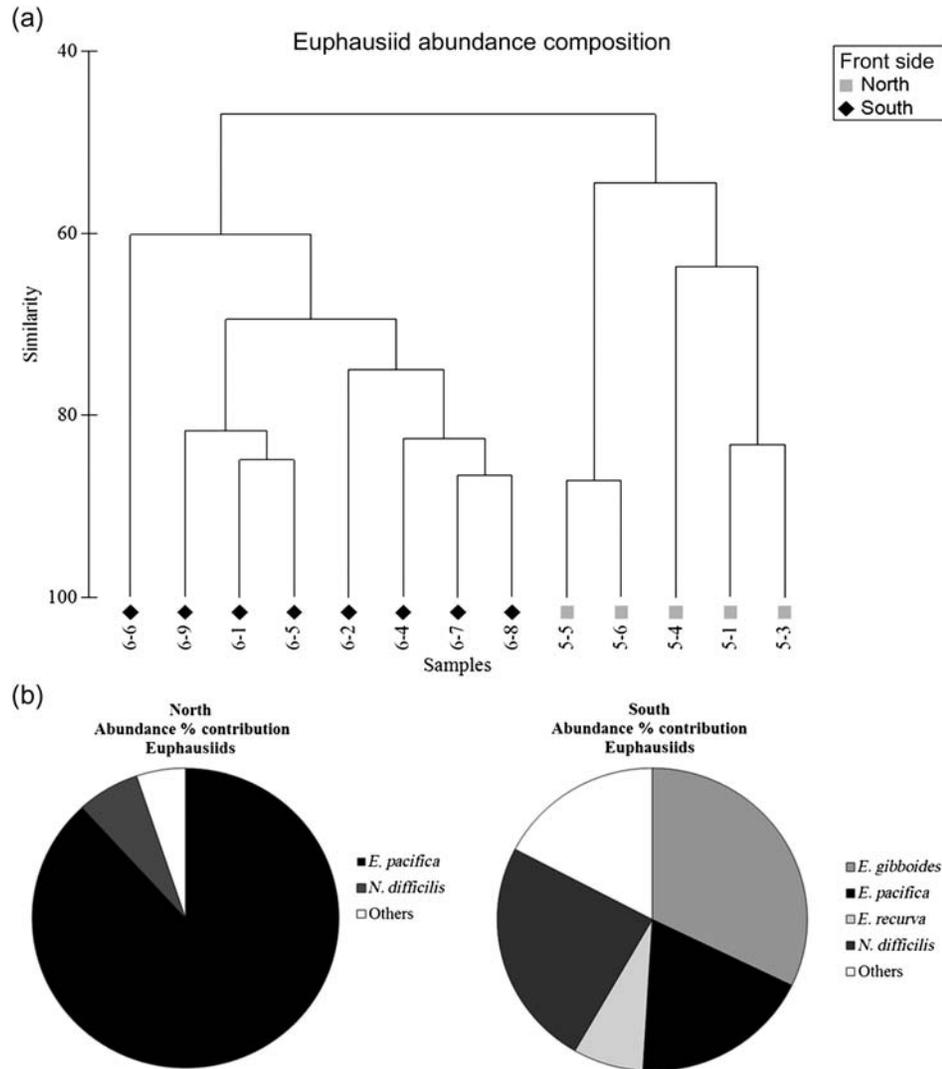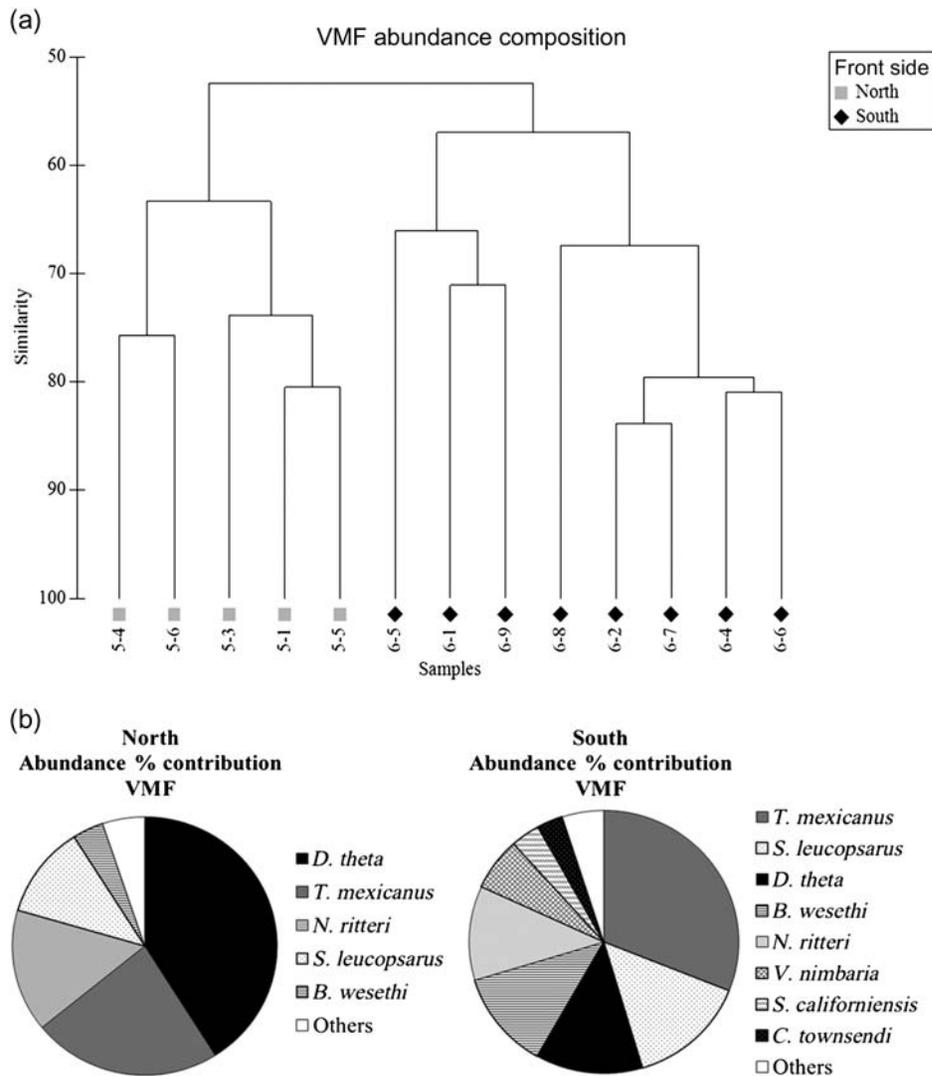
Fig. 3. (**a**) Cluster analyses of euphausiid abundance composition and (**b**) abundance % contribution of euphausiid species in the north and south water masses.

(Table IV, Fig. 2). Similarly, their community composition did not separate clearly the two water masses across the front (Figs 7a and 8a). Two species of *Cyclothone*, *C. signata* and *C. acclinidens*, together accounted for over 80% of NVMF abundance in both water masses. Biomass was more evenly distributed among species with *C. acclinidens*, *Parvilux ingens*, *Scopelogadus mizolepis*, *C. signata*, *Argyropelecus affinis* and *I. antrostomus* accounting for ~50% of the biomass in the north and 70% in the south (Figs 7b and 8b).

Distributions at the A-front

A high-density patch of acoustically identified euphausiids ($127 \, m^2 \, nmi^{-2}$) was found at the northern interface of the A-Front during the daytime transects, with almost none at the southern interface ($0.96 \, m^2 \, nmi^{-2}$) (Fig. 9a). Three features were apparent for fish in relation to the A-Front in these four transects. First, a conspicuous, dense aggregation was present in the surface waters at the front itself, with a more dispersed distribution away from it (Fig. 9b). On the other hand, fish from the deep-scattering layer (DSL) did not concentrate at the front, but were distributed in a layer across it. However, there was a discontinuity in the vertical structure of the DSL at the front, which appeared more compact and deeper (~350 m) in the southern interface, rising to ~200 m at the front and appearing more dispersed at the northern interface (Fig. 9b). Third, a secondary, deeper (400–500 m)
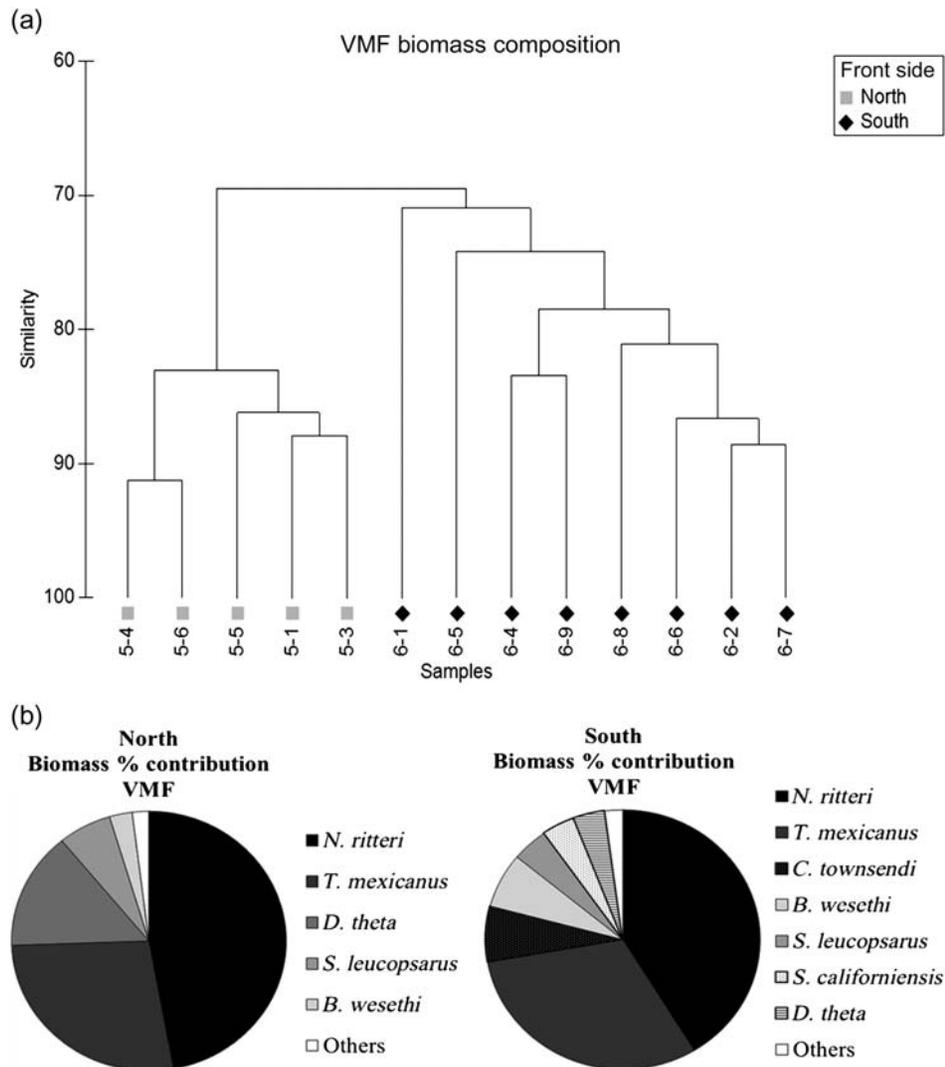
Fig. 4. (**a**) Cluster analyses of VMF abundance composition and (**b**) abundance % contribution of VMF species in the north and south water masses.

sublayer within the DSL was observed to extend north of the front.

DISCUSSION

Several studies have examined the influence of meso-scale features, such as fronts, on mid-trophic levels. In some cases, these frontal features coincided with major biogeographic boundaries (Backus *et al.*, 1969; Angel, 1989; Baussant *et al.*, 1993; Bertrand *et al.*, 1999; Sassa *et al.*, 2002). Similarly, this study showed strong differences in community composition and abundance of mesopelagic fish and euphausiids between the water masses on either side of the A-Front.

Previous studies in this region have reported differences in primary productivity and the abundances of larval fish and zooplankton across a front known as the Ensenada Front, which is located at ∼32°N where the flow of the California Current turns shoreward, separating warm oligotrophic from cool, more productive waters (Haury *et al.*, 1993; Moser and Smith, 1993; Venrick, 2000). It is a semi-persistent feature that has been detected most of the year with a considerable loss of pigment to the south but small temperature gradients (Pelaez and McGowan, 1986; Haury *et al.*, 1993). The location, orientation and temperature and productivity characteristics of the waters across the A-Front bear some resemblance to the Ensenada Front. However, previous studies of the Ensenada Front did not observe

Fig. 5. (a) Cluster analyses of VMF biomass composition and (b) biomass % contribution of VMF species in the north and south water masses.

an accumulation of biomass at the front itself, despite finding higher biomass north of the front and differences in species distributions (Haury *et al.*, 1993; Moser and Smith, 1993; Venrick, 2000), so we have not given the A-Front the same designation.

Differences in community composition and abundance in the adjacent water masses

Euphausiids

Euphausia pacifica is the dominant euphausiid in the North Pacific, particularly in the Subarctic Gyres and Transition Zone, i.e. the area where Subarctic water meets Subtropical water, extending to the California Current region in the eastern Pacific (Brinton, 1962; Mauchline and Fisher, 1969; Shaw *et al.*, 2010). Its

range extends from the Bering Sea to 30 or 25°N off the California coast and 36°N off the Japan coast (Brinton, 1962; Hong, 1969). *Euphausia pacifica* has cold water affinities, and its distribution in the California Current is linked to upwelled or Subarctic water (Brinton, 1962; Iguchi and Ikeda, 1995). On the other hand, *E. gibboides* and *E. recurva* have an affinity for warmer waters, whereas *N. difficilis* is intermediate (Brinton, 1962; Brinton and Townsend, 2003). The distribution of *E. pacifica*, *E. gibboides* and *E. recurva* across the A-Front reflected their temperature preferences, with the abundance of *E. pacifica* decreasing dramatically south of the front, where *E. recurva* abundance increased. *Euphausia gibboides* was present only south of the front. *Nematoscelis difficilis*, on the other hand, did not exhibit a clear difference across the front: its percentage
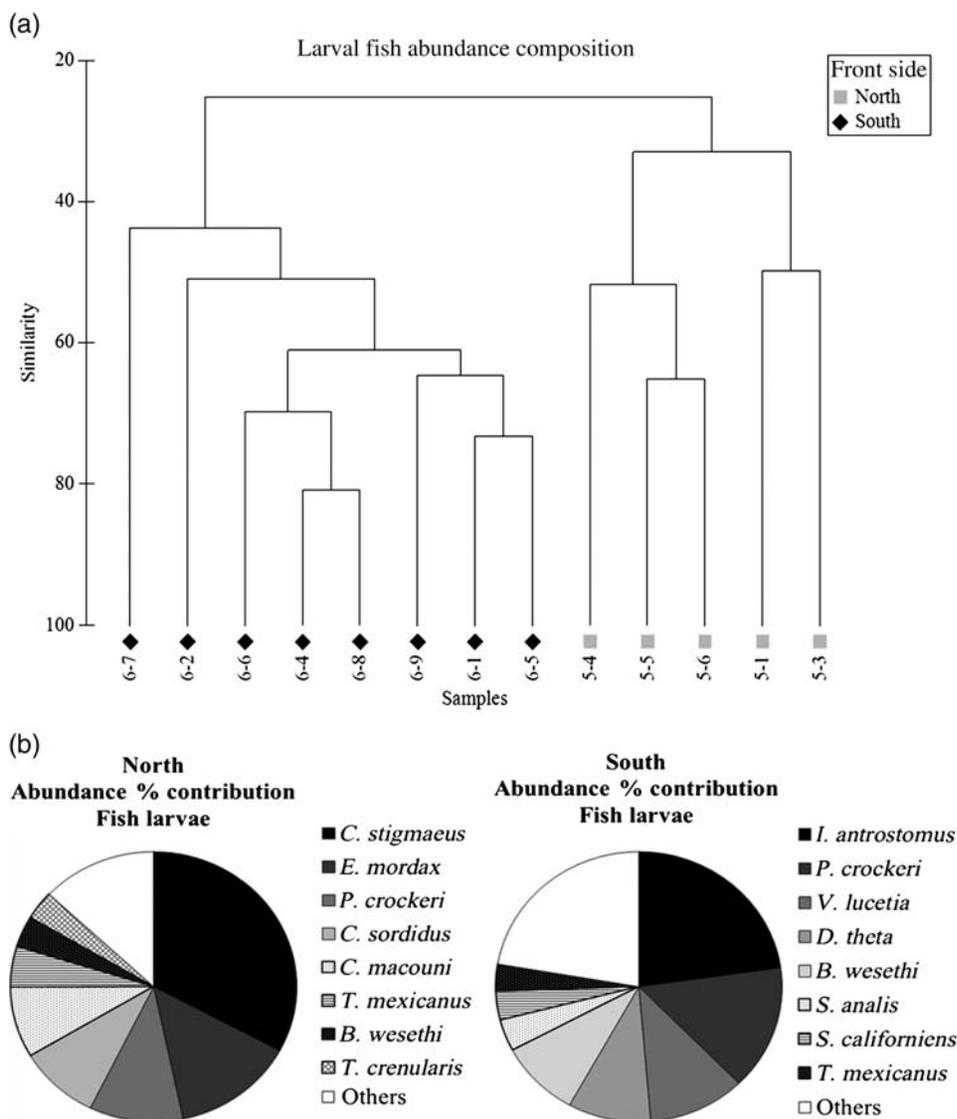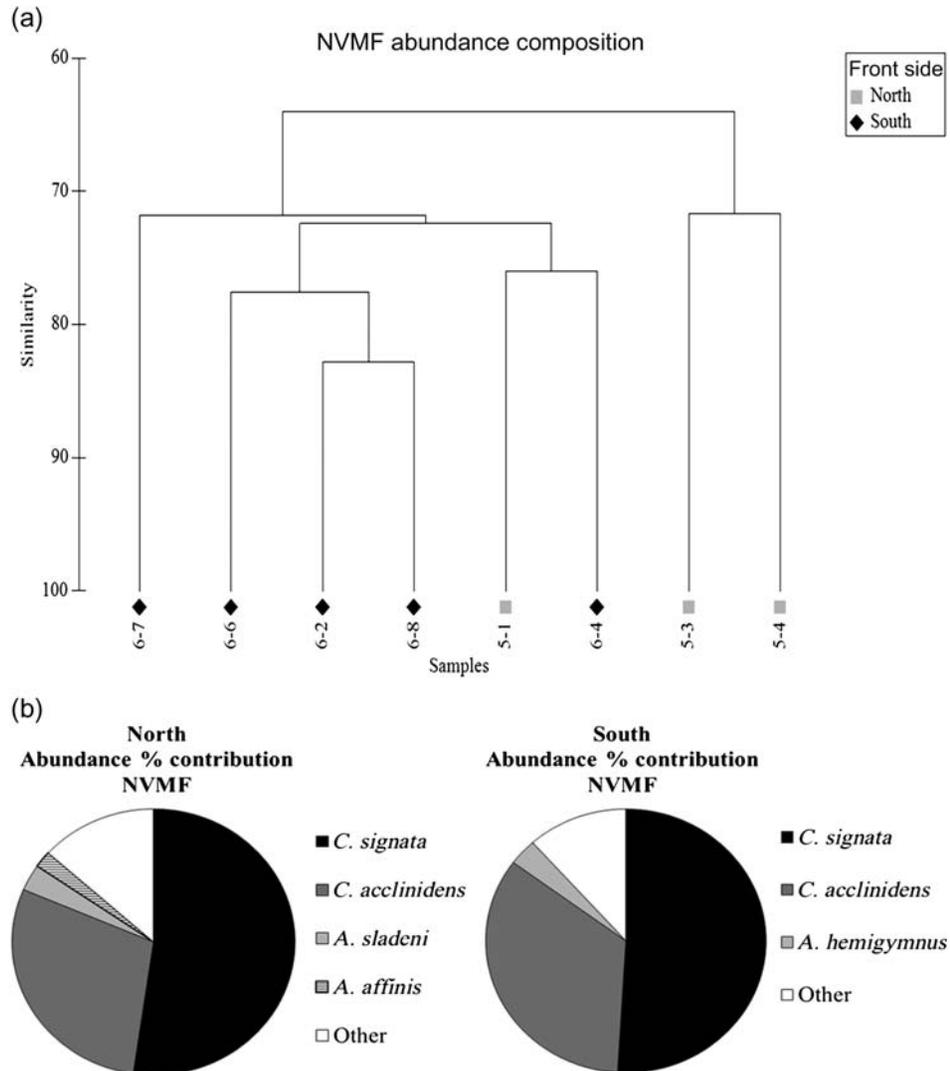
Fig. 6. (**a**) Cluster analyses of larval fish abundance composition and (**b**) abundance % contribution of larval fish species in the north and south water masses.

contribution to the community was greater south of the front, but its abundance was higher north of it. This species is widespread in the California Current and is second in abundance after *E. pacifica* in the Transition Zone (Brinton, 1962; Brinton and Townsend, 2003).

Fish
Cluster analyses indicated that most of the differences in the abundance of fish across the front were due to the VMF species, *D. theta*, *C. townsendi*, *B. wesethi* and *V. lucetia*: cold water species such as *D. theta* were more abundant to the north and those with warm water affinities, *V. lucetia*, *B. wesethi* and *C. townsendi*, were more abundant or limited to the south (Gjosaeter and

Kawaguchi, 1980; Loeb *et al.*, 1983; Moser and Smith, 1993). This pattern, which we observed for the adults and juveniles of these species, was similar to that reported across the Ensenada front for their larval stages, with a decrease in larval *D. theta* abundance and an increase in larval *V. lucetia*, *C. townsendi* and *B. wesethi* south of the Ensenada Front (Moser and Smith, 1993). Similarly, the distribution of the adults of less abundant VMF species, *T. crenularis*, *S. californiensis*, *D. atlanticus* and *D. laternatus*, followed trends consistent with the distributions described previously for the larvae off Central and Southern California (Loeb *et al.*, 1983; Moser and Smith, 1993), with *T. crenularis* less abundant and the latter three species more abundant in the south. The
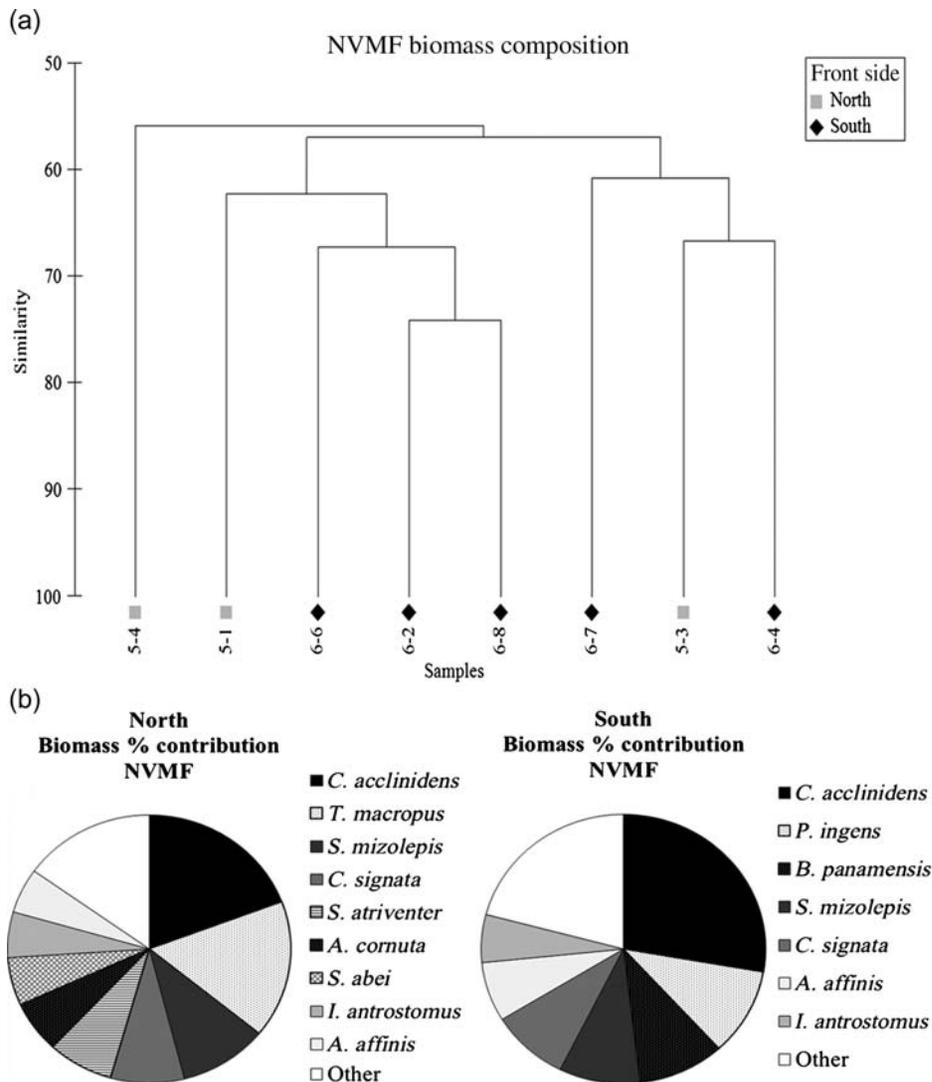
Fig. 7. (**a**) Cluster analyses of NVMF abundance composition and (**b**) abundance % contribution of NVMF species in the north and south water masses.

differences in north–south distributions for most of these fish species suggest that the A-Front may be acting as an important distributional boundary, separating significantly different pelagic habitats.

However, in our study, the larvae of *D. theta* were found only in the water mass south of the front, in contrast to the findings of Moser and Smith (Moser and Smith, 1993). This segregation of *D. theta*'s developmental stages across a frontal system has also been reported in the Western North Pacific where a demographic shift between adults and juveniles of *D. theta* was observed across the Oyashio Front (Sassa *et al.*, 2002). The difference in the distribution of *D. theta* larvae compared with the adults and juveniles in the water masses adjacent to the A-Front could be related to differences

in the size spectrum of food particles across the front (Li *et al.*, 2012; Ohman *et al.*, 2012; Taylor *et al.*, 2012). Thus, the high abundance of juveniles and adults of *D. theta* was coincident with high abundances of relatively large potential prey, *E. pacifica* and copepods to the north, whereas the larval stage coincided with smaller phytoplankton and zooplankton particles to the south (Hopkins *et al.*, 1996; Gartner *et al.*, 1997; Moku *et al.*, 2000; Brodeur and Yamamura, 2005; Suntsov and Brodeur, 2008).

No significant difference in distribution was found across the front for *S. leucopsarus*. Although we categorized this species as a vertical migrator, it has been observed to have substantial nocturnal peaks in abundance at depth as well as in near-surface waters,

Fig. 8. (**a**) Cluster analyses of NVMF biomass composition and (**b**) biomass % contribution of NVMF species in the north and south water masses.

indicating that only part of the population vertically migrates (Pearcy et al., 1977). Its distribution across the front, in fact, seems to more closely resemble that of the non-migratory fish.

The larval assemblage north of the A-Front represented species associated with the shelf region such as *E. mordax*, *C. stigmaeus* and *C. sordidus*, all with more northerly distributions and cold water affinities. Moser and Smith (Moser and Smith, 1993) also found these species in the more productive waters north of the Ensenada Front. Although all these species are coastal, their larvae are pelagic and can be transported offshore in the Southern California circulation (Moser and Smith, 1993). It is also likely that anchovies were spawning within the frontal region (see below).

Cyclothone signata and *C. acclinidens* were the most abundant NVMF species. These species dominate mesopelagic and bathypelagic non-migratory fish assemblages in the California Current, with *C. signata* occurring predominantly at 250–500 m and *C. acclinidens* at 500–900 m (Dewitt, 1972; Bailey and Robison, 1986; Miya and Nemoto, 1991). Although Moser and Smith (Moser and Smith, 1993) reported that the larvae of *Cyclothone* were predominantly in the warm waters south of the Ensenada front, we found that the abundance of the adults did not appear to be influenced by the A-Front. However, *Cyclothone* larvae live in near-surface waters (Miya and Nemoto, 1991), where the influence of frontal features is stronger. In contrast, the center of distribution for adult *Cyclothone* is 400 m or deeper
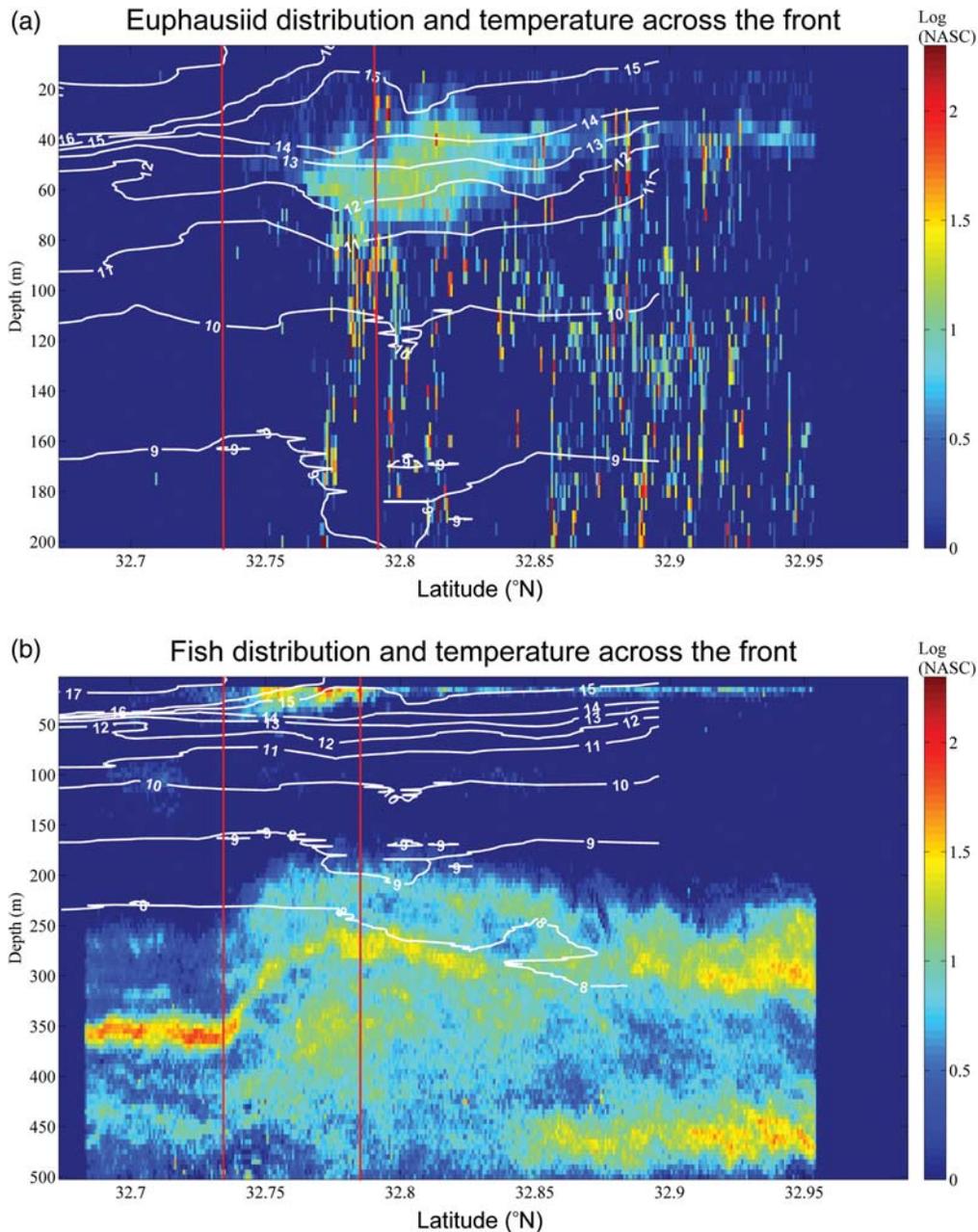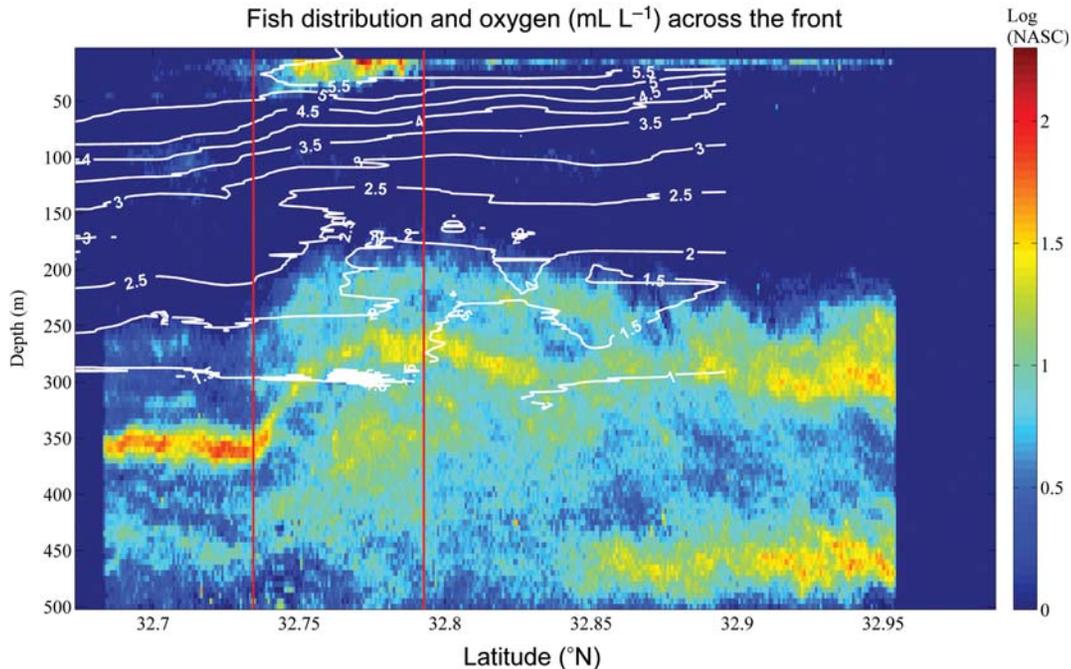
Fig. 9. Underway N-S acoustic sampling of the A-Front showing the abundance distribution of (**a**) euphausiids and (**b**) fish measured by the acoustics during the third crossing of the A-Front conducted at daytime at a speed of 10 km h^{-1}. Seawater temperature contour is overlaid to show the frontal boundary, indicated between the red lines.

(Willis and Pearcy, 1982), below the depth directly influenced by the frontal circulation. These species of *Cyclothone* are found throughout the southern California Current region (Moser, 1996). We note that Backus *et al.* (Backus *et al.*, 1969), examining the distribution of meso- and bathypelagic fish across a front in the Sargasso Sea, similarly found a significant difference in species assemblages across the front, but only among the vertical migrators.

The A-front

In regions of abrupt horizontal change separating water masses with very different physical properties, it is expected that biological communities will also differ significantly (Lutjeharms *et al.*, 1985; Ainley and DeMaster, 1990; Pakhomov *et al.*, 1994; Belkin *et al.*, 2009; Bost *et al.*, 2009). In the present study, the biological changes across the front were most evident from the acoustical data, which showed dense

Fig. 10. Underway N-S acoustic sampling of the A-Front showing the abundance distribution of fish measured by the acoustics during the third crossing of the A-Front conducted at daytime at a speed of 10 km h^{-1}. Oxygen concentration contour is overlaid and the frontal boundary is indicated between the red lines.

aggregations of fish and krill at the precise location of the front in the upper 100 m. Because the acoustic data were collected during daylight, the aggregated fish at the front were probably anchovies: anchovy larvae (*E. mordax*) hatch 3–4 days after spawning (Zweifel and Lasker, 1976) and were among the more abundant fish larvae north of the front, even though our cruise was outside the winter–spring peak period of anchovy spawning. Also, conditions at the front constituted prime anchovy habitat, with its high values of Chl *a* near the surface (Taylor *et al.*, 2012), preponderance of larger particles such as zooplankton and large diatoms, and high geostrophic flow (Bakun and Broad, 2003; Rykaczewski and Checkley, 2008; Weber and McClatchie, 2010; Li *et al.*, 2012). The concentrations of epipelagic fish at the front suggest that plankton mortality and removal processes may be higher at the front, consistent with the indications of elevated plankton productivity there: elevated phytoplankton photosynthetic efficiency (Wang *et al.*, 2012), bacterial secondary production (Samo *et al.*, 2012) and the ratio of copepod nauplii to adults (Ohman *et al.*, 2012).

Changes in DSL depth and distribution across fronts have been previously reported to be apparently influenced by environmental factors (Conte *et al.*, 1986; Baussant *et al.*, 1993). The DSL in our study varied in depth, thickness and number of layers across the A-Front. This appears consistent with differences in the distributions of light and oxygen with depth across the front. Light plays an important role in the vertical structure of the DSL, since organisms have been observed to follow particular isolumes (Kampa, 1971; Clarke, 1973; Smith and Laver, 1981; Drazen *et al.*, 2011). Higher phytoplankton concentrations in the northern water mass led to an increase in light attenuation there relative to the oligotrophic water column in the south (Li *et al.*, 2012), which could explain the shallower distribution of the DSL at the northern interface of the front. However, dissolved oxygen isopleths also shoaled north of the front following a similar distribution pattern as that of the DSL, with the upper edge of the DSL coinciding with the 2 mL L^{-1} isopleth (Fig. 10). A close relationship between the depth of the DSL and oxygen levels in the CalCOFI region in Southern California has been reported previously (Koslow *et al.*, 2011). Unfortunately, oxygen data were collected only down to 300 m in our study and no irradiance data were collected at the front itself, so we cannot more definitively determine the factors that influenced the depth distribution of the DSL across the A-Front. Nevertheless, it is clear that there is a relationship between environmental factors and biological distributions across the A-Front.

The abundance of euphausiids, estimated acoustically from our north–south underway transect, was higher over the front and to the north of it, decreasing significantly to the south. This is consistent with the results of

zooplankton vertical hauls, taken in the upper 100 m with bongo nets, at nine stations immediately following the acoustical survey (i.e. the same night of 24–25 October 2008), which also showed higher euphausiid abundance at the front and north of it (Ohman *et al.*, 2012). It is apparent that euphausiid abundance here was associated with the cooler, more saline water mass with higher primary productivity north of the front (Landry, Ohman *et al.*, 2012). However, the acoustic distribution of euphausiids did not precisely overlap with the area of highest phytoplankton concentration located at the front itself (Taylor *et al.*, 2012). This could be either an artifact of the acoustics or due to predation by the epipelagic fish located immediately over the front. The high concentration of epipelagic fish with air-filled swimbladders located immediately over the front could have masked organisms in the area with reduced acoustic reflectivity, such as euphausiids. Alternatively, predation by the anchovies or other epipelagic fish concentrated at the front could have left a gap in the euphausiid distribution (Genin *et al.*, 1994).

In summary, there have been few studies on the influence of fronts in the distribution of the mesopelagic micronekton globally (Backus *et al.*, 1969; Angel, 1989; Baussant *et al.*, 1993; Koubbi, 1993; Beamish *et al.*, 1999), and none in the southern California Current. There have been particularly few that have combined the use of acoustics and trawl sampling, which enables improved estimates of abundance and biomass, compensating for the substantial biases resulting from net avoidance and escapement. Acoustics also provides high-resolution data on horizontal and vertical distributions. This enabled us to observe particularly high concentrations of fish directly at the front and sharp discontinuities in fish and euphausiid distributions there. Notably, only the vertically migratory or near surface fish appeared to be strongly influenced by the frontal boundary, consistent with previous observations across a front in the Sargasso Sea (Backus *et al.*, 1969). However, although NVMF species did not show differences in species composition across the front, changes in the DSL indicate that the A-Front influenced deep-water distributions. Quantitative study of the influence of fronts on deep-water trophodynamics and biogeochemistry remains an important area for future investigation.

ACKNOWLEDGEMENTS

FUNDING

REFERENCES

Ainley, D. G. and DeMaster, P. D. (1990) The upper trophic levels in polar marine ecosystems. In Smith, J. W. (ed.), *Polar Oceanography, Part B, Chemistry, Biology and Geology.* Academic Press, San Diego, pp. 599–630.

Allison, S. K. and Wishner, K. F. (1986) Spatial and temporal patterns of zooplankton biomass across the Gulf-Stream. *Mar. Ecol. Prog. Ser.*, **31**, 233–244.

Anderson, J. T. and Gardner, G. A. (1986) Plankton communities and physical oceanography observed on the southeast shoal region, Grand Bank of Newfoundland. *J. Plankton Res.*, **8**, 1111–1135.

Anderson, V. C. (1950) Sound scattering from a fluid sphere. *J. Acoust. Soc. Am.*, **22**, 426–431.

Angel, M. V. (1989) Vertical profiles of pelagic communities in the vicinity of the Azores Front and their implications to deep ocean ecology. *Prog. Oceanogr.*, **22**, 1–46.

Backus, R. H., Craddock, J. E., Haedrich, R. L. *et al.* (1969) Mesopelagic fishes and thermal fronts in Western Sargasso Sea. *Mar. Biol.*, **3**, 87–106.

Bailey, T. G. and Robison, B. H. (1986) Food availability as a selective factor on the chemical compositions of midwater fishes in the eastern North Pacific. *Mar. Biol.*, **91**, 131–141.

Bakun, A. and Broad, K. (2003) Environmental 'loopholes' and fish population dynamics: comparative pattern recognition with focus on El Nino effects in the Pacific. *Fish. Oceanogr.*, **12**, 458–473.

Baussant, T., Gasser, B., Gorsky, G. *et al.* (1993) Mesopelagic micronekton and macrozooplankton observed by echosounding, multiple-net sampling and video profiling across the Almeria-Oran Front (W Mediterranean Sea). *Ann. Inst. Oceanogr.*, **69**, 87–93.

Beamish, R. J., Leask, K. D., Ivanov, O. A. *et al.* (1999) The ecology, distribution, and abundance of midwater fishes of the Subarctic Pacific gyres. *Prog. Oceanogr.*, **43**, 399–442.

Belkin, I. M. and Cornillon, P. C. (2007) Fronts in the world ocean's large marine ecosystems. ICES Document CM 2007/D: 21. 33 pp.

Belkin, I. M., Cornillon, P. C. and Sherman, K. (2009) Fronts in large marine ecosystems. *Prog. Oceanogr.*, **81**, 223–236.

Bertrand, A., Le Borgne, R. and Josse, E. (1999) Acoustic characterisation of micronekton distribution in French Polynesia. *Mar. Ecol. Prog. Ser.*, **191**, 127–140.

Bost, C. A., Cotte, C., Bailleul, F. *et al.* (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J. Mar. Syst.*, **78**, 363–376.

Briggs, J. C. (1974) *Marine Zoogeography.* McGraw-Hill, New York.

Brinton, E. (1962) The distribution of Pacific euphausiids. *Bull. Scripps Inst. Oceanogr.*, **8**, 51–269.

Brinton, E. and Townsend, A. (2003) Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. *Deep-Sea Res. Part II*, **50**, 2449–2472.

Brodeur, R. and Yamamura, O. (2005) *Micronekton of the North Pacific.* PICES Institute of Ocean Sciences, Report No. 30, Sydney, BC, Canada.

Caldeira, R. M. A., Marchesiello, P., Nezlin, N. P. *et al.* (2005) Island wakes in the Southern California Bight. *J. Geoph. Res. Ocean*, **110**, 26.

Chekalyuk, A. M., Landry, M. R., Goericke, R. *et al.* (2012) Laser fluorescence analysis of phytoplankton across a frontal zone in the California Current ecosystem. *J. Plankton Res.*, **34**, 761–777.

Chereskin, T. K. and Niiler, P. P. (1994) Circulation in the Ensenada Front—September 1988. *Deep-Sea Res. Part I*, **41**, 1251–1287.

Chu, D., Foote, K. G. and Stanton, T. K. (1993) Further analysis of target strength measurements of Antarctic krill at 38 and 120 kHz: comparison with deformed cylinder model and inference of orientation distribution. *J. Acoust. Soc. Am.*, **93**, 2985–2988.

Chu, D. and Wiebe, P. H. (2005) Measurements of sound-speed and density contrasts of zooplankton in Antarctic waters. *ICES J. Mar. Sci.*, **62**, 818–831.

Chu,, D., Wiebe, P. H. and Stanton, T. K. *et al.* (2000) Measurements of the material properties of live marine organisms and their influence on acoustic scattering. *Proceedings of the OCEANS 2000 MTS/IEEE International Symposium*, 11–14 September 2000. Providence, RI. Vol. 3, pp. 1963–1967.

Clarke, T. A. (1973) Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. *Fish. Bull.*, **71**, 401–434.

Conte, M. H., Bishop, J. K. B. and Backus, R. H. (1986) Nonmigratory, 12-kHz, deep scattering layers of Sargasso Sea origin in warm-core rings. *Deep-Sea Res.*, **33**, 1869–1884.

Davison, P. (2011) The buoyancy of mesopelagic fishes from the northeast Pacific Ocean and its implications for acoustic backscatter. *ICES J. Mar. Sci.*, **68**, 2064–2074.

Dawson, M. N. (2001) Phylogeography in coastal marine animals: a solution for California? *J. Biogeogr.*, **28**, 723–736.

Dawson, M. N., Waples, R. S. and Bernardi, G. (2006) Phylogeography. In Allen, L. G., Pondella, D. J. II and Horn, M. H. (eds), *The Ecology of Marine Fishes*. University of California Press, Berkeley, pp. 26–54.

De Robertis, A., Schell, C. and Jaffe, J. S. (2003) Acoustic observations of the swimming behavior of the euphausiid *Euphausia pacifica* Hansen. *ICES J. Mar. Sci.*, **60**, 885–898.

Dewitt, F. A. (1972) Bathymetric distribution of 2 common deep-sea fishes, *Cyclothone acclinidens* and *Cyclothone signata*, off Southern California. *Copeia*, **88**, 88–96.

Dong, C. M., Idica, E. Y. and McWilliams, J. C. (2009) Circulation and multiple-scale variability in the Southern California Bight. *Prog Oceanogr.*, **82**, 168–190.

Doyle, R. F. (1985) Biogeographical Studies of Rocky Shores Near Point Conception, California. Thesis, University of California.

Drazen, J. C., De Forest, L. G. and Domokos, R. (2011) Micronekton abundance and biomass in Hawaiian waters as influenced by seamounts, eddies, and the moon. *Deep-Sea Res. Part I Oceanogr. Res. Pap.*, **58**, 557–566.

Eden, B. R., Steinberg, D. K., Goldthwait, S. A. *et al.* (2009) Zooplankton community structure in a cyclonic and mode-water eddy in the Sargasso Sea. *Deep-Sea Res. Part I*, **56**, 1757–1776.

Falkowski, P. G., Ziemann, D., Kolber, Z. *et al.* (1991) Role of eddy pumping in enhancing primary production in the ocean. *Nature*, **352**, 55–58.

Foote, K. G., Knudsen, H. P., Vestnes, G. *et al.* (1987) Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Cooperative Research Report, No. 144, 70 pp.

Franks, P. J. S. (1992) Phytoplankton blooms at fronts—patterns, scales, and physical forcing mechanisms. *Rev. Aquat. Sci.*, **6**, 121–137.

Garcon, V. A., Oschlies, S., Doney, D. *et al.* (2001) The role of mesoscale variability on plankton dynamics in the North Atlantic. *Deep-Sea Res. Part II*, **48**, 2199–2226.

Gartner, J. V., Crabtree, R. E. and Sulak, K. J. (1997) Feeding at depth. In Randall, D. J. and Farrell, A. P. (eds), *Deep-Sea Fishes*. Academic Press, London.

Genin, A., Greene, C. H., Haury, L. R. *et al.* (1994) Zooplankton patch dynamics: daily gap formation over abrupt topography. *Deep-Sea Res. Part I*, **41**, 941–951.

Gjosaeter, J. and Kawaguchi, K. (1980) A review of the world resources of mesopelagic fish. Food and Agriculture Organization of the United Nations, Report No. 193. FAO, Rome.

Greenlaw, C. F. (1979) Acoustical estimation of zooplankton populations. *Limnol. Oceanogr.*, **24**, 226–242.

Haury, L. R. (1984) An offshore eddy in the California Current System. 4: plankton distributions. *Prog. Oceanogr.*, **13**, 95–111.

Haury, L. R., Venrick, E. L., Fey, C. L. *et al.* (1993) The Ensenada Front: July 1985. *CalCOFI Reports*, 34 San Diego.

Hickey, B. M. (1998) Coastal oceanography of Western North America from the tip of Baja California to Vancouver Island. In: Robinson, A. R. and Brink, K. H. (eds), *The Sea*. J Wiley and Sons Inc., New York, pp. 345–393.

Hickey, B. M., Dobbins, E. L. and Allen, S. E. (2003) Local and remote forcing of currents and temperature in the central Southern California Bight. *J. Geoph. Res. Ocean*, **108**, 26.

Holliday, D. V. (1977) Extracting bio-physical information from acoustic signatures of marine organisms. In Andersen, N. R. and Zahuranec, B. J. (eds), *Oceanic Sound Scattering Prediction*. Plenum Press, New York, pp. 619–624.

Hong, S. Y. (1969) The euphausiid crustaceans of Korean waters. In Marr, J. C. (ed.), *The Kuroshio (a Symposium on the Japan Current)*. East-West Center Press, University of Hawaii, Honolulu, pp. 291–300.

Hopkins, T. L., Sutton, T. T. and Lancraft, T. M. (1996) The trophic structure and predation impact of a low latitude midwater fish assemblage. *Prog Oceanogr.*, **38**, 205–239.

Horn, M. H. and Allen, L. G. (1978) A distributional analysis of California coastal marine fishes. *J. Biogeogr.*, **5**, 23–42.

Horn, M. H., Allen, L. G. and Lea, R. N. (2006) Biogeography. In Allen, L. G., Pondella, D. J. II and Horn, M. H. (eds). *The Ecology of*

Marine Fishes. Californian and Adjacent Waters. University of California Press, Berkeley.

Iguchi, N. and Ikeda, T. (1995) Growth, metabolism and growth efficiency of a euphausiid crustacean *Euphausia pacifica* in the Southern Japan Sea, as influenced by temperature. *J. Plankton Res.*, **17**, 1757–1769.

Kampa, E. M. (1971) Photoenvironment and sonic scattering. In Farquhar, G. (ed.), *Proceedings of an international symposium on biological sound scattering in the ocean*. Maury Center for Ocean Science, Washington, DC, pp. 51–59.

Kang, M., Furusawa, M. and Miyashita, K. (2002) Effective and accurate use of difference in mean volume backscattering strength to identify fish and plankton. *ICES J. Mar. Sci.*, **59**, 794–804.

Korneliussen, R. J. and Ona, E. (2002) An operational system for processing and visualizing multi-frequency acoustic data. *ICES J. Mar. Sci.*, **59**, 291–313.

Koslow, J. A., Goericke, R., Lara-Lopez, A. *et al.* (2011) Impact of declining intermediate-water oxygen on deepwater fishes in the California Current. *Mar. Ecol. Prog. Ser.*, **436**, 207–218.

Koubbi, P. (1993) Influence of the frontal zones on ichthyoplankton and mesopelagic fish assemblages in the Crozet Basin (Indian sector of the Southern Ocean). *Polar Biol.*, **13**, 557–564.

Landry, M. R., Decima, M., Simmons, M. P. *et al.* (2008) Mesozooplankton biomass and grazing responses to Cyclone Opal, a subtropical mesoscale eddy. *Deep-Sea Res. Part II*, **55**, 1378–1388.

Landry, M. R., Ohman, M. D. *et al.* (2012) Pelagic community responses to a deep-water front in the California Current Ecosystem: overview of the A-Front study. *J. Plankton Res.*, **34**, 739–748.

Lavaniegos, B. E. and Ohman, M. D. (2007) Coherence of long-term variations of zooplankton in two sectors of the California Current System. *Prog. Oceanogr.*, **75**, 42–69.

Lavery, A. C., Wiebe, P. H., Stanton, T. K. *et al.* (2007) Determining dominant scatterers of sound in mixed zooplankton populations. *J. Acoust. Soc. Am.*, **122**, 3304–3326.

Lawson, G. L., Wiebe, P. H., Ashjian, C. J. *et al.* (2004) Acoustically-inferred zooplankton distribution in relation to hydrography west of the Antarctic Peninsula. *Deep-Sea Res. Part II*, **51**, 2041–2072.

Lima, I. D., Olson, D. B. and Doney, S. C. (2002) Biological response to frontal dynamics and mesoscale variability in oligotrophic environments: biological production and community structure. *J. Geoph. Res. Ocean*, **107**, 1–20.

Li, Q. P., Franks, P. J. S., Ohman, M. D. *et al.* (2012) Enhanced nitrate fluxes and biological processes at a frontal zone in the southern California Current system. *J. Plankton Res.*, **34**, 790–801.

Loeb, V., Smith, P. E. and Moser, H. G. (1983) Recurrent groups of larval fish species in the California Current Area. *CalCOFI Reports*, 24, pp. 152–164.

Lutjeharms, J. R. E., Walters, N. M. and Allanson, B. R. (1985) Oceanic frontal systems and biological enhancement. In Siegfried, W. R., Condy, P. R. and Laws, R. M. (eds). *Antarctic Nutrient Cycles and Food Webs*. Springer-Verlag, Heidelberg, pp. 11–21.

Madureira, L. S. P., Everson, I. and Murphy, E. J. (1993) Interpretation of acoustic data at 2 frequencies to discriminate between Antarctic krill (*Euphausia superba* Dana) and other scatterers. *J. Plankton Res.*, **15**, 787–802.

Matsukura, R., Yasuma, H., Murase, H. *et al.* (2009) Measurements of density contrast and sound-speed contrast for target strength estimation of *Neocalanus* copepods (*Neocalanus cristatus* and *Neocalanus plumchrus*) in the North Pacific Ocean. *Fish. Sci.*, **75**, 1377–1387.

Mauchline, J. and Fisher, L. R. (1969) The biology of euphausiids. *Adv. Mar. Biol.*, **7**, 1–454.

McGillicuddy, D. J., Robinson, A. R., Siegel, D. A. *et al.* (1998) Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature*, **394**, 263–266.

McGowan, J. A. (1971) Oceanic biogeography of the Pacific. In Funnell, B. M. and Riedel, W. R. (eds), *The Micropaleontology of Oceans*. Cambridge University Press, Cambridge, UK.

Medwin, H. and Clay, C. S. (1997) *Fundamentals of Acoustic Oceanography*. Academic Press, Burlington.

Mikami, H., Mukai, T. and Iida, K. (2000) Measurements of density and sound speed contrasts for estimating krill target strength using theoretical scattering models. *Nippon Suisan Gakkaishi*, **66**, 682–689.

Miya, M. and Nemoto, T. (1991) Comparative life histories of the mesopelagic and bathypelagic fishes of the genus *Cyclothone* (Pisces: Gonostomatidae) in Sagami Bay, Central Japan. *Deep-Sea Res. Part A*, **38**, 67–89.

Miyashita, K., Aoki, I., Seno, K. *et al.* (1997) Acoustic identification of isada krill, *Euphausia pacifica* Hansen, off the Sanriku coast, northeastern Japan. *Fish. Oceanogr.*, **6**, 266–271.

Moku, M., Kawaguchi, K., Watanabe, H. *et al.* (2000) Feeding habits of three dominant myctophid fishes, *Diaphus theta*, *Stenobrachius leucopsarus* and S-nannochir, in the subarctic and transitional waters of the western North Pacific. *Mar. Ecol. Prog. Ser.*, **207**, 129–140.

Moser, H. G. (1996) The early stages of fishes in the California Current. *CalCOFI Atlas*, **33**, 1505 pp.

Moser, H. G. and Smith, P. E. (1993) Larval fish assemblages of the California Current region and their horizontal and vertical distributions across a front. *Bull. Mar. Sci.*, **53**, 645–691.

Newman, W. A. (1976) Californian transition zone: significance of short-range endemics. In Gray, J. and Boucot, A. J. (eds), *Historical Biogeography, Plate Tectonics and the Changing Environment*. Oregon State University Press, Oregon, pp. 399–416.

Ohman, M. D., Powell, J., Picheral, M. *et al.* (2012) Mesozooplankton and particulate matter responses to a deep-water frontal system in the southern California Current System. *J. Plankton Res.*, **34**, 815–827.

Oozeki, Y., Hu, F. X., Kubota, H. *et al.* (2004) Newly designed quantitative frame trawl for sampling larval and juvenile pelagic fish. *Fish. Sci.*, **70**, 223–232.

Pakhomov, E. A., Perissinotto, R. and McQuaid, C. D. (1994) Comparative structure of the macrozooplankton micronekton communities of the subtropical and Antarctic polar fronts. *Mar. Ecol. Prog. Ser.*, **111**, 155–169.

Pearcy, W. G., Krygier, E. E., Mesecar, R. *et al.* (1977) Vertical distribution and migration of oceanic micronekton off Oregon. *Deep-Sea Res.*, **24**, 223–245.

Pelaez, J. and McGowan, J. A. (1986) Phytoplankton pigment patterns in the California Current as determined by satellite. *Limnol. Oceanogr.*, **31**, 927–950.

Rykaczewski, R. R. and Checkley, D. M. (2008) Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proc. Natl Acad. Sci. USA*, **105**, 1965–1970.

Sabates, A. and Maso, M. (1990) Effect of a shelf slope front on the spatial distribution of the mesopelagic fish larvae in the Western Mediterranean. *Deep-Sea Res. Part A*, **37**, 1085–1098.

Samo, T. J., Pedler, B. E., Ball, I. G. *et al*. (2012) Microbial distribution and activity across a water mass frontal zone in the California Current Ecosystem. *J. Plankton Res.*, **34**, 802–814.

Sassa, C., Kawaguchi, K., Kinoshita, T. *et al*. (2002) Assemblages of vertical migratory mesopelagic fish in the transitional region of the western North Pacific. *Fish. Oceanogr.*, **11**, 193–204.

Shaw, C. T., Peterson, W. T. and Feinberg, L. R. (2010) Growth of *Euphausia pacifica* in the upwelling zone off the Oregon coast. *Deep-Sea Res. Part II*, **57**, 584–593.

Smith, J. N., Ressler, P. H. and Warren, J. D. (2010) Material properties of euphausiids and other zooplankton from the Bering Sea. *J. Acoust. Soc. Am.*, **128**, 2664–2680.

Smith, K. L. and Laver, M. B. (1981) Respiration of the bathypelagic fish *Cyclothone acclinidens*. *Mar. Biol.*, **61**, 261–266.

Stanton, T. K. (1988) Sound scattering by cylinders of finite length. I. Fluid cylinders. *J. Acoust. Soc. Am.*, **83**, 55–63.

Stanton, T. K. and Chu, D. Z. (2000) Review and recommendations for the modelling of acoustic scattering by fluid-like elongated zooplankton: euphausiids and copepods. *ICES J. Mar. Sci.*, **57**, 793–807.

Stanton, T. K., Chu, D. Z. and Wiebe, P. H. (1998) Sound scattering by several zooplankton groups. II. Scattering models. *J. Acoust. Soc. Am.*, **103**, 236–253.

Stukel, M. R. (2011) Trophic cycling and carbon export relationships in the California Current Ecosystem. *Limnol. Oceanogr.*, **56**, 1866–1878.

Suntsov, A. V. and Brodeur, R. D. (2008) Trophic ecology of three dominant myctophid species in the northern California Current region. *Mar. Ecol. Prog. Ser.*, **373**, 81–96.

Taylor, A. G., Goericke, R., Landry, M. R. *et al*. (2012) Sharp gradients in phytoplankton community structure across a frontal zone in the California Current Ecosystem. *J. Plankton Res.*, **34**, 778–789.

Thomas, A. C. and Strub, P. T. (1990) Seasonal and interannual variability of pigment concentration across a California Current frontal zone. *J. Geophys. Res.*, **95**, 13023–13042.

Venrick, E. L. (2000) Summer in the Ensenada Front: the distribution of phytoplankton species, July 1985 and September 1988. *J. Plankton Res.*, **22**, 813–841.

Wang, H., Schieber, B., Seegers, B. *et al*. (2012) Bio-optics and photophysiology across a strong frontal gradient in the California Current Ecosystem. *J. Plankton Res.*, in press.

Warren, J. D., Stanton, T. K., Benfield, M. C. *et al*. (2001) In situ measurements of acoustic target strengths of gas-bearing siphonophores. *ICES J. Mar. Sci.*, **58**, 740–749.

Weber, E. D. and McClatchie, S. (2010) Predictive models of northern anchovy *Engraulis mordax* and Pacific sardine *Sardinops sagax* spawning habitat in the California Current. *Mar. Ecol. Prog. Ser.*, **406**, 251–263.

Wiebe, P. H. (1988) Functional regression equations for zooplankton displacement volume, wet weight, dry weight and carbon: a correction. *Fish. Bull.*, **86**, 833–835.

Wiebe, P. H., Chu, D. Z., Kaartvedt, S. *et al*. (2009) The acoustic properties of *Salpa thompsoni*. *ICES J. Mar. Sci.*, **67**, 583–593.

Willis, J. M. and Pearcy, W. G. (1982) Vertical distribution and migration of fishes of the lower mesopelagic zone off Oregon. *Mar. Biol.*, **70**, 87–98.

Yasuma, H., Takao, Y., Sawada, K. *et al*. (2006) Target strength of the lanternfish, *Stenobrachius leucopsarus* (family Myctophidae), a fish without an airbladder, measured in the Bering Sea. *ICES J. Mar. Sci.*, **63**, 683–692.

Zweifel, J. R. and Lasker, R. (1976) Pre-hatch and posthatch growth of fishes—general model. *Fish. Bull.*, **74**, 609–621.