Do upwelling filaments result in predictable biological distributions in coastal upwelling ecosystems?

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ABSTRACT

We used satellite sea surface temperature (SST) images and in situ zooplankton data collected in four summers of field sampling in the northern California Current to address the question: Can the physical variables that indicate advective mesoscale circulation features (e.g. upwelling filaments) be used to infer biological distributions? Transects were selected from research cruises conducted when upwelling filaments were present in our study region and compared to transects occupied when filaments were not present. The hydrography and distribution of several indicator species of copepods were examined along each transect. SST in filaments ranged from 1.5 °C to 3.0 °C lower than the surrounding ocean water. Distributions of coastal and oceanic taxa reflected the SST patterns. Coastal taxa occurred offshore in higher abundances in cold upwelling filaments than in the surrounding warm ocean water. In contrast, species with oceanic and sub-tropical affinities were most abundant where warm surface water was present. Biomass and species abundances varied substantially among cruises and locations and so could not be quantitatively predicted by SST patterns. However, upwelling filaments consistently expanded the across-shelf region in which high zooplankton biomass occurred, 'spreading' the biomass from the continental shelf into offshore regions of the upwelling system. We conclude with a discussion of the sampling strategies necessary to capture ecosystem variability caused by these dynamic circulation features.

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1. Introduction

Zooplankton play a critical role in marine ecosystems as the link between primary and upper trophic level production, so advancing the methods by which we study controls on their distribution and abundance would further our understanding of ecosystem processes. Currently, the rate at which scientists are able to gather the species information necessary for such studies is hindered by the time commitment required for taxonomic identification. On the other hand, the relatively fast rate at which we can acquire physical measurements, such as those from satellite imagery, in situ floats, and moorings, allows us to observe the physical environment in near-real time over large spatial scales. Developing the ability to infer biological patterns from physical fields, and determining when such inferences are feasible, could therefore progress our understanding of ecosystem variability more quickly than by relying on relatively sparse biological data alone.

In the ocean, biological patterns of biomass and abundance often are the consequence of underlying physical processes, but can be overlaid with patterns generated by biological processes such as migrations, predation, and growth. In areas where bottom-up control dominates (e.g. upwelling ecosystems, extreme environments), there is temptation to infer biological patterns from observed physical patterns, but the multiple mechanisms that control biological patterns make it difficult to predict them from one or a few measures of correlative physical variables.

Upwelling filaments are seasonally important components of the circulation in all of the eastern boundary upwelling regions (Lutjeharms et al., 1991; Escribano and Hidalgo, 2000; Strub and James, 2000; Marchesiello et al., 2003; Barton and Aristegui, 2004; Waite et al., 2007). In the California Current, several strong upwelling filaments may concurrently develop along the coast during summer. These filaments are typically long (>100 km), narrow (<50 km), deep (>300 m) features with high zonal velocities exceeding 50 cm s^{-1} (Kosro and Huyer, 1986; Ramp et al., 1991). Their westward (offshore) transport of ~0.5–3.5 × 10^6 m^3 s^{-1} leads to large offshore net volume transport over their several-week lifetimes (Kosro and Huyer, 1986; Barth and Brink, 1987; Ramp et al., 1991; Barth et al., 2005). Several studies of individual filaments have demonstrated their contribution to offshore carbon flux (Marin et al., 2003; Morales et al., 2007; Keister et al., 2008), their potential for shaping species distributions by transporting coastal taxa from the nearshore upwelling area to the deep sea (e.g. Haury,

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1984; Mackas et al., 1991; Rodríguez et al., 1999), and their importance to upper trophic level organisms (Tynan et al., 2005). Studies of upwelling filaments have typically focused on single, strong circulation features which had clearly defined effects on biological distributions. However, the structure and intensity of upwelling filaments vary spatially and temporally (Keister and Strub, 2008), as do patterns in biological fields, so the effect of the circulation on biological distributions is also likely to vary.

In this study, we add to ongoing investigations of how mesoscale physical variability impacts biological patterns in coastal upwelling ecosystems by examining the relationship between the physical patterns and zooplankton distributions caused by upwelling filaments of varying structure in the northern California Current (NCC). We use examples of the physical and biological patterns from four summers of sampling in the NCC. Most cruises were part of monitoring programs in which regular sampling locations were occupied without regard to the conditions at the time of the cruise. During one cruise, we conducted adaptive sampling in which we targeted offshore expressions of mesoscale circulation features using satellite SST images to determine sampling locations. Here we use selected transects from these cruises and satellite SST images to investigate the degree to which zooplankton distributions are predictable from a characterization of the physical environment.

2. Predicted patterns

To explore the predictability of the physical-biological relationships, we first formed hypotheses of the zooplankton distributions we expected to find in relation to the observed physical fields. We hypothesized, based on our accumulated understanding of nearshore circulation in the NCC, that upwelling filaments identified in satellite SST images are advective features in which cold, nearshore water is transported off the continental shelf. We anticipated that shipboard sampling transects that crossed upwelling filaments would show zooplankton species distributions that reflected the hydrography. Specifically, we expected elevated biomass and elevated abundances of coastal taxa in the nearshore upwelling region and where cold filaments occurred offshore. We expected lower biomass and lower abundances of coastal taxa where warmer water occurred offshore. The opposite patterns in abundance of warm-water, oceanic taxa were predicted.

In contrast to patterns along transects which crossed upwelling filaments, we predicted that zooplankton distributions would show simple onshelf–offshelf gradients in abundance along transects where minimal offshore mesoscale structure was present. In those cases, we expected that elevated abundances of coastal taxa would be restricted to the nearshore upwelling region.

3. Methods

3.1. Physical-biological patterns

To investigate the relationship between upwelling filaments and zooplankton distributions, and the degree to which we could predict such relationships, we took the following four steps: (1) we used satellite SST images to select sampling transects which crossed cold upwelling filaments off of the continental shelf, (2) along those transects, we identified specific sampling locations where we hypothesized (based on satellite SST patterns) that coastal, cold-water taxa would occur offshore in relatively high abundance compared to surrounding warm-water locations, (3) we selected transects across which no upwelling filaments were visible in satellite SST images to contrast with transects along which such patterns in SST did occur and (4) along each selected

transect, we examined the *in situ* hydrography from CTD profiles and distributions of 'indicator species' (described below) from net tows to assess whether the predicted relationships occurred.

Because many zooplankton taxa in our study area are either highly patchy or always in low abundance, we selected seven indicator species on which to focus our analysis and discussion. These taxa were all species of copepods that we expected, based on prior studies (Keister and Peterson, 2003; Morgan et al., 2003; Keister et al., 2008), to have the most predictable relationship to temperature in our study area. All tend to be in moderate to high abundance during the summer and have exhibited affinities to either warm, oceanic water or cold, upwelled water in the NCC. We focused on copepods, both because they comprise the dominant taxa in our study area (typically >80% by number), and because they are weak swimmers, so are strongly influenced by advection. We expect that other small zooplankton (e.g. euphausiid larvae, meroplankton) are subject to similar advective processes, but that larger taxa (e.g. adult euphausiids, chaetognaths, amphipods) may exhibit larger vertical migrations that de-couple their horizontal movements from the circulation considered here. Warm-water taxa include the copepods *Ctenocalanus vanus*, *Paracalanus parvus*, *Calanus pacificus*, and *Clausocalanus* spp. These taxa are found throughout the study area in winter, but are only found in warm, oceanic water during summer. Cold-water taxa include the copepods *Calanus marshallae*, *Acartia longiremis*, and *Pseudocalanus mimus*. These taxa are boreal, neritic taxa that are indicative of summer upwelling off Oregon and are absent in winter.

3.2. SST data

SST data from the Advanced Very High Resolution Radiometer (AVHRR) were captured with 1 km resolution and processed by Ocean Imaging of Solana Beach, CA (www.oceani.com) for the US Global Ocean Ecosystems Observations (GLOBEC) program. All are single-pass images which were either the images used to determine sampling locations during adaptive sampling (in August 2002) or were the clearest images available within 24 h of sampling, retrieved after sampling had occurred. The images used to guide sampling were attained 3–4 days prior to sampling (Table 1). For the transect occupied on 1 August 2002, SST patterns were very similar to those used to guide sampling, so the original image is shown. However, SST patterns had altered dramatically by the time sampling occurred along a southern transect on 6 August 2002, so an SST image from that sampling date is shown. Along each cross-shelf transect, the location of the strongest SST gradient was used to determine the position of the coastal upwelling front.

3.3. In situ sampling

In situ hydrographic and zooplankton data come from six cruises conducted as part of three different research programs during the summer upwelling season off Oregon and northern California. Cruises in July 1994 and June 1996 were conducted as anchovy and sardine egg and larval surveys. July 1999 and 2002 cruises were part of the US GLOBEC Long-Term Observations Program (LTOP). The August 2002 cruise was part of the GLOBEC Mesoscale Processes Studies.

Zooplankton sampling protocols differed among cruises. In 1994 and 1996, vertical net tows were conducted using the CALCOFI (California Cooperative Oceanic Fisheries Investigations) protocol (Smith et al., 1985). Tows were made from 5 m off the bottom, or from a maximum of 70 m, to the surface with a 150-μm mesh, 25-cm diameter CalVET net. In the other years, zooplankton were collected with a 202-μm mesh, 50-cm diameter ring net towed vertically from a maximum of 100 m to the surface. Therefore, abundances in 1994 and 1996 may be inflated compared

Table 1
Sampling and filament characteristics. All times are local (PDT). Maximum SST gradient is calculated as the maximum gradient in SST from inside to outside each filament. Total filament lifetime was estimated from SST images, from formation to breakdown.

Sampling start time	Time to complete (h)	SST image date/time	Filament present?	Max. SST gradient (°C/km)	Total filament lifetime	Lifetime before sampling
4 August 2002 06:00	14	1 August 2002 17:00	Yes	0.49	4 weeks	4 weeks
5 July 1999 14:00	12	5 July 1999 07:00	Yes	0.51	⩾5 weeks	2 weeks
25 July 1994 06:00	21	25 July 1994 17:00	Yes	0.30	1 week/2.5 weeks[a]	<4 days/1.5 weeks[a]
5 August 2002 23:00	23	6 August 2002 14:00	No	–	–	–
15 June 1996 08:00	15	14 June 1996 14:00	No	–	–	–
12 July 2002 05:00	23	12 July 2002 03:00	No	–	–	–

[a] Lifetime estimates are for both the northern extension and main body of the filament sampled in 1994 (see Fig. 1c).

to later years, so are not directly comparable. For all collections, a flowmeter was used to monitor the volume of water filtered. Samples were preserved in a 5% buffered formalin/seawater solution.

In the laboratory, zooplankton samples were diluted to 5–10 times the settled volume and subsampled with a 1.1-ml Stempel pipette. Two to four subsamples were counted. Zooplankton were identified to species and developmental stage. The abundance of each species (number of individuals m^{-3}) was calculated as total number of copepodite and adults (i.e. eggs and nauplii are excluded). Copepods from the genus *Clausocalanus* were identified to species in all but the 1994 and 1996 samples. All of the species of *Clausocalanus* that occur off the Oregon coast have warm-water affinities and tend to show similar distributions in relation to hydrographic variables (Peterson and Keister, 2002; Keister and Peterson, 2003). Therefore, we combined the *Clausocalanus* species for all analyses, though such grouping could result in smearing of signals if distributions varied among species.

Biomass values were calculated from stage-specific values found in the literature (e.g. Chisholm and Roff, 1990; Webber and Roff, 1995). None of the copepod species we focus on in this study (described below) are known to perform diel migration below the depth of our net casts in our area, even those that can be strong migrators (e.g. the copepods *Calanus* spp.), so day/night differences were not considered. Other studies in our area have shown little influence of diel migration on upper-100-m biomass or abundances (Peterson, 1972; Shaw and Robinson, 1998; Peterson and Keister, 2002). To assess the strength of patterns in this study, we will discuss 'strong' patterns, or 'significant differences,' as those across which biomass or abundance differed among stations by a factor of ⩾5 (confidence intervals of 2/3 of the mean), based on typical variances in zooplankton abundances observed in our research and from studies of zooplankton sampling methods by Wiebe and Holland (1968) and Wiebe (1971).

At each location where zooplankton were collected, we also performed a CTD cast for temperature, density, and salinity profiles. Profiles of all the variables are published in Keister (2008). Here, we show density profiles to a maximum depth of the zooplankton nets to show the relationship between the satellite SST images and *in situ* hydrography. Data were Kriged for presentation using Surfer 8.03 software (Golden Software Inc., 2002) and spherical semivariogram models. Profile data are from a minimum depth of 1 m, so do not capture the dynamics in the surface centimeters seen in satellite SST images.

4. Results

4.1. Hydrography

Sea surface temperature images showed variable circulation patterns with the complexity varying among years (Fig. 1). Strong upwelling filaments were present on 1 August 2002 and 5 July 1999 (Fig. 1a and b, respectively). A filament with a weaker SST

expression was present on 25 July 1994 (Fig. 1c). In contrast, no filaments occurred along transects sampled on 6 August 2002, 14 June 1996, or 12 July 2002 (Fig. 1d–f, respectively).

4.1.1. Filaments present

On 1 August 2002, satellite SST showed a cold, cyclonically-rotating filament centered at 42.8°N 125.6°W that appears from the SST image to be rooted in the upwelling region just north of Cape Blanco, OR (Fig. 1a). The filament had been present in SST images for 4 weeks before our cruise, but developed into an eddy, separated from the upwelling region, and disappeared from satellite images a few days after the cruise. Our sampling transect crossed over the core of the cold filament. The SST patterns were strong: SST dropped 2.6 °C within the feature compared to SST on its shoreward side, with a maximum gradient of 0.49 °C km^{-1} (Table 1). *In situ* density (Fig. 2a) reflected the circulation pattern inferred from SSTs. Isopycnals domed upward at the stations between 125.4°W and 125.8°W that were identified as being in the cold filament (circled stations in Fig. 1a). Nearshore, uplifted isopycnals which are characteristic of strong coastal upwelling occurred.

In July 1999, satellite SST showed a cold upwelling filament extending seaward south of Cape Blanco (Fig. 1b). The filament had been present in SST images for 2 weeks prior to sampling and persisted for >3 weeks after. A transect at 41.9°N crossed from the cold nearshore area, over a region of slightly warmer (~14 °C) surface water, then across a strong SST gradient into the cold (12.2 °C) offshore filament. Hydrographic profiles (Fig. 2b) showed up-tilted isopycnals, both over the shelf indicating coastal upwelling, and offshore where the cold filament was apparent in the SST image.

In July 1994, SST was high throughout the region (Fig. 1c). An upwelling filament extended offshore of Cape Blanco, but the low range of SSTs across the filament indicated that it may not have been as strong as features sampled in other years. The main body of the filament had been present in SST images for ~1.5 weeks prior to sampling, but the northern branch of the filament that we sampled had been present for <4 days. Along our transect, SST was ~1.6 °C lower at the coolest point of the filament than in the warmer water toward shore; the maximum SST gradient was weaker than that of other filaments (Table 1). We identified the 5th and (secondarily) 4th stations from the seaward edge as 'in filament' locations (circled in Fig. 1c), although those stations fell on either side of the location where the coldest SST occurred. The *in situ* density structure shows upwardly domed isopycnals across the narrow tip of the upwelling filament (Fig. 2c). The density structure of the filament was stronger than implied by SSTs, which may have been influenced by surface solar heating.

4.1.2. Filaments absent

Along the three transects sampled when no upwelling filaments were present, SST images show broad areas of coastal upwelling
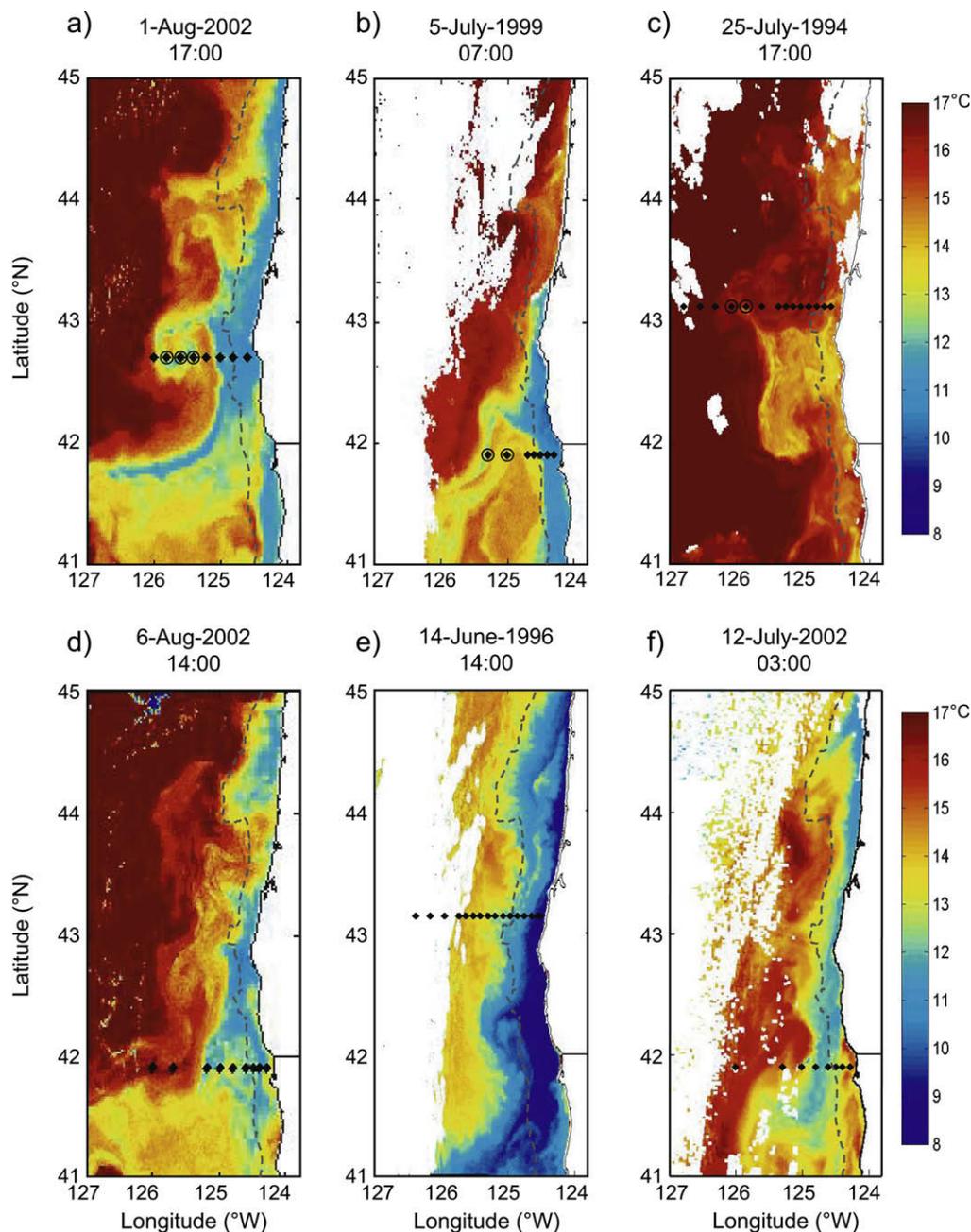
Fig. 1. Sea surface temperature maps from satellite AVHRR data. Locations of zooplankton net tows are marked and those occurring at cold, offshore locations in filaments are circled. Cloud masks are applied except in (d). Images are labeled by the local date and time of the satellite pass. CB = Cape Blanco, OR. The 180-m shelf break is shown as dashed lines.

nearshore, and warm oceanic water offshore (Fig. 1d–f). On 6 August, 2002, the *in situ* hydrography along 41.9°W (Fig. 2d) showed steeply sloped isopycnals which separated a broad area of high density water shoreward of 125.2°W from lower density water offshore. An upward doming of isopycnals occurred at the seaward edge of the upwelling region where a remnant of the southern filament seen in the 1 August image (Fig. 1a) may have lingered, now compressed against the upwelling region.

In June 1996 (Fig. 2e), widely spaced up-tilted isopycnals near the coast indicated the broad region of coastal upwelling visible in SSTs. A lens of low density water caused by the Columbia River plume (Huyer et al., 2005; Keister, 2008) was present in the surface layer between 125.2 and 126.2°W, causing domed isopycnals near surface, but not at depth.

In July 2002 (Fig. 2f), progressively deepening isopycnals seaward of the shelf break indicated a simple coastal-to-oceanic pattern, uninterrupted by advective circulation features. As in the SST images, no hydrographic structures characteristic of upwelling filaments were apparent offshore along the transect.

4.2. Copepod biomass patterns

Copepod biomass distributions showed the expected patterns in relation to SST and the hydrography, but to varying degrees among transects (Fig. 3). In general, biomass was highest inshore of the coastal upwelling fronts (indicated by dashed lines in Fig. 3) and at offshore stations that fell within the bounds of upwelling filaments (shaded regions in Fig. 3a–c). Patterns were complex where
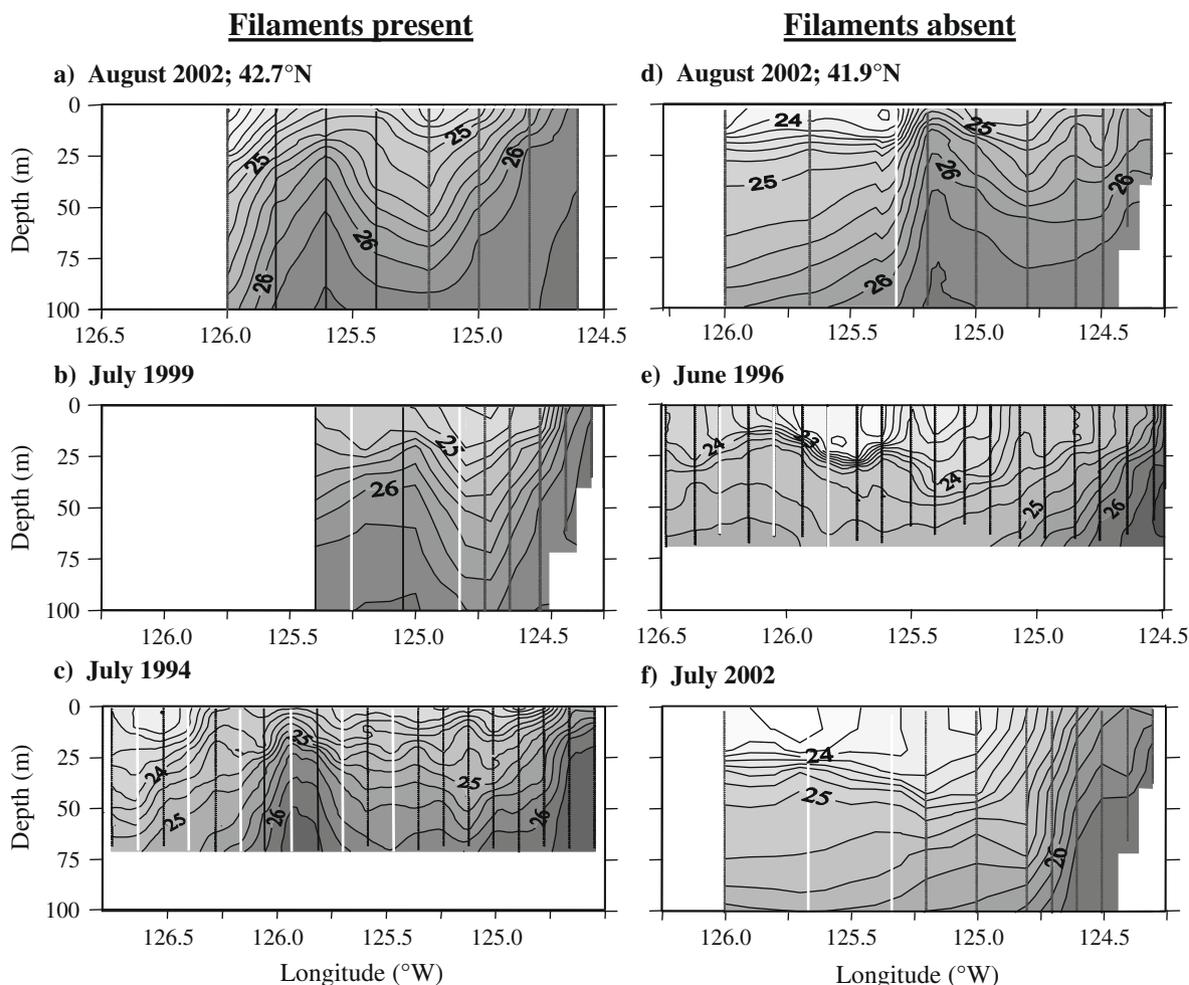
Fig. 2. Density along each transect from CTD casts, shown to the maximum depth of the zooplankton sampling. Stations occupied are indicated by vertical lines; white lines denote CTD stations where zooplankton were not also sampled; bold black vertical lines show locations of zooplankton stations that were within filaments (circled stations in Fig. 1a–c).

filaments were present. Along those transects, biomass at offshore locations was nearly as high as, or higher than, that found over the continental shelf. In sharp contrast, where filaments were absent (Fig. 3d–f), significantly higher biomass was found in the upwelling region than offshore. Simple high coastal, to low oceanic, biomass patterns were observed along all three transects.

Patterns along 42.7°N in August 2002 particularly strongly reflected the satellite SST and *in situ* hydrographic patterns (Fig. 1a, 2a, 3a). Total biomass was high in the upwelling area over the shelf (124.6–124.8°W), lower in the warmer, less dense water off the shelf (125.0–125.2°W), then significantly elevated in the cold, offshore filament (125.4–125.8°W). At the most offshore location (126.0°W), biomass was significantly lower than at the adjacent location within the filament. Patterns were also strong in July 1999 (Fig. 3b). Total copepod biomass was highest over the shelf and nearly as high at the two offshore stations within the filament. However, no station was significantly different than others.

The relationship between SST and biomass was not as clear in July 1994 (Fig. 3c). Biomass was slightly elevated at one station within the filament compared to stations in the warmer water towards shore, but biomass was also high at stations seaward of the filament. The expected pattern of high coastal biomass, lower off-shelf biomass, then high biomass again in the offshore filament, was ambiguously present. Copepod biomass was more uniformly spread over the transect in July 1994 compared to the other transects.

4.3. Copepod species distributions

The cold-water copepod *C. marshallae* and its warm-water congener *C. pacificus* showed contrasting patterns of abundance along the transects (Fig. 4). *C. marshallae* showed strong patterns in relation to the hydrography—where filaments were present (Fig. 4a–c), abundances were significantly higher at one or more stations within the filament than at surrounding locations. When filaments were absent (Fig. 4d–f), abundances were much higher nearshore within the upwelling region than in the warm, oceanic water offshore. In contrast, *C. pacificus* tended to be most abundant in warm, offshore regions, and where warm surface water occurred between filaments and the coastal upwelling zone. However, overall, *C. pacificus* patterns were not as clear. Moderate numbers were unexpectedly found in the filaments in July 1999 and July 1994, and in the nearshore upwelling zone in June 1996.

Both of the cold-water copepods *P. mimus* and *A. longiremis* (Fig. 5) showed strong patterns in relation to the hydrography. In August 2002 (Fig. 5a) and July 1999 (Fig. 5b), both were significantly more abundant at one or more stations within filaments than at warmer shoreward and seaward locations. Again, the trend holds for July 1994, but is not as strong (Fig. 5c). The general onshore-to-offshore patterns were close to those predicted, but the specific locations of elevated offshore abundances were not—high abundances at 126.3°W and low abundances at 125.8°W contrasted with our initial expectations. Where filaments

Filaments present   Filaments absent
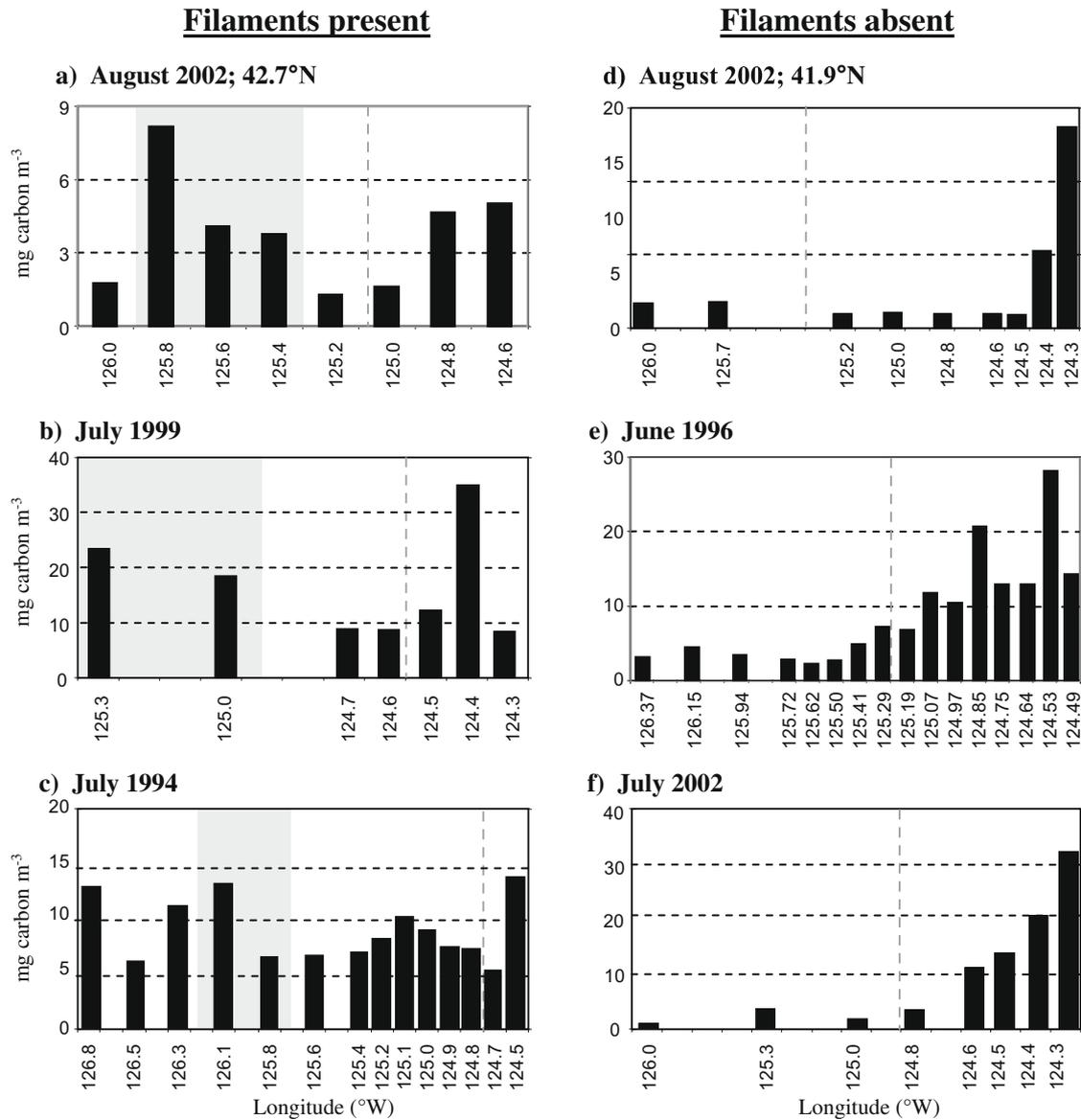
Fig. 3. Total copepod biomass along cross-shelf transects. Gray highlighting when filaments were present (panels a, b, c) indicate stations within the cold filaments, which are circled in the corresponding panels in Fig. 1. Vertical dashed lines show the location of the upwelling front. All stations sampled for zooplankton are labeled with their longitude.

were absent (Fig. 5d–f), patterns of both species were as predicted, with high numbers found only nearshore, and low numbers offshore.

When strong filaments were present in August 2002 and July 1999, the warm-water taxa *Clausocalanus* spp., *P. parvus*, and *C. vanus* were found in much lower abundances at the stations in the filaments than in the warmer water between the filaments and the coast (Fig. 6a and b). Abundances were especially high in the warm ocean water at the most offshore station in August 2002 (Fig. 6a). In July 1994, warm-water taxa tended to be less abundant in the cold filament and in the upwelling region than in warmer water (Fig. 6c), but *P. parvus* was abundant at the station at 126.1°W within the filament.

When filaments were absent (Fig. 6d–f), distributions of warm-water taxa were more variable. Along 41.9°N in August 2002 abundances were significantly higher at the offshore stations than in the upwelling region (Fig. 6d). Abundances in June 1996 and July 2002 were generally lower nearshore than offshore, but the distribution of *C. vanus* showed the opposite pattern in July 2002. In June 1996,

abundances of the warm-water species were highest near the edge of the upwelling area (Fig. 6e); warm-water taxa were abundant and fairly evenly distributed across the transect seaward of the upwelling region.

5. Discussion

In all cruises, patterns in zooplankton distributions were related to patterns in satellite SST, but the strength of the relationships varied greatly among cruises and taxa. The largest differences in zooplankton biomass and abundances associated with filaments occurred across filaments which had the largest gradients in SST. Weaker and less predictable biological patterns occurred where SST features were weaker. Patterns along all of the transects that crossed filaments contrasted with those along transects that did not cross filaments. When filaments were not present, coastal taxa were abundant only in the upwelling region over the shelf and were absent or in low numbers in oceanic water.

Filaments present   ## Filaments absent
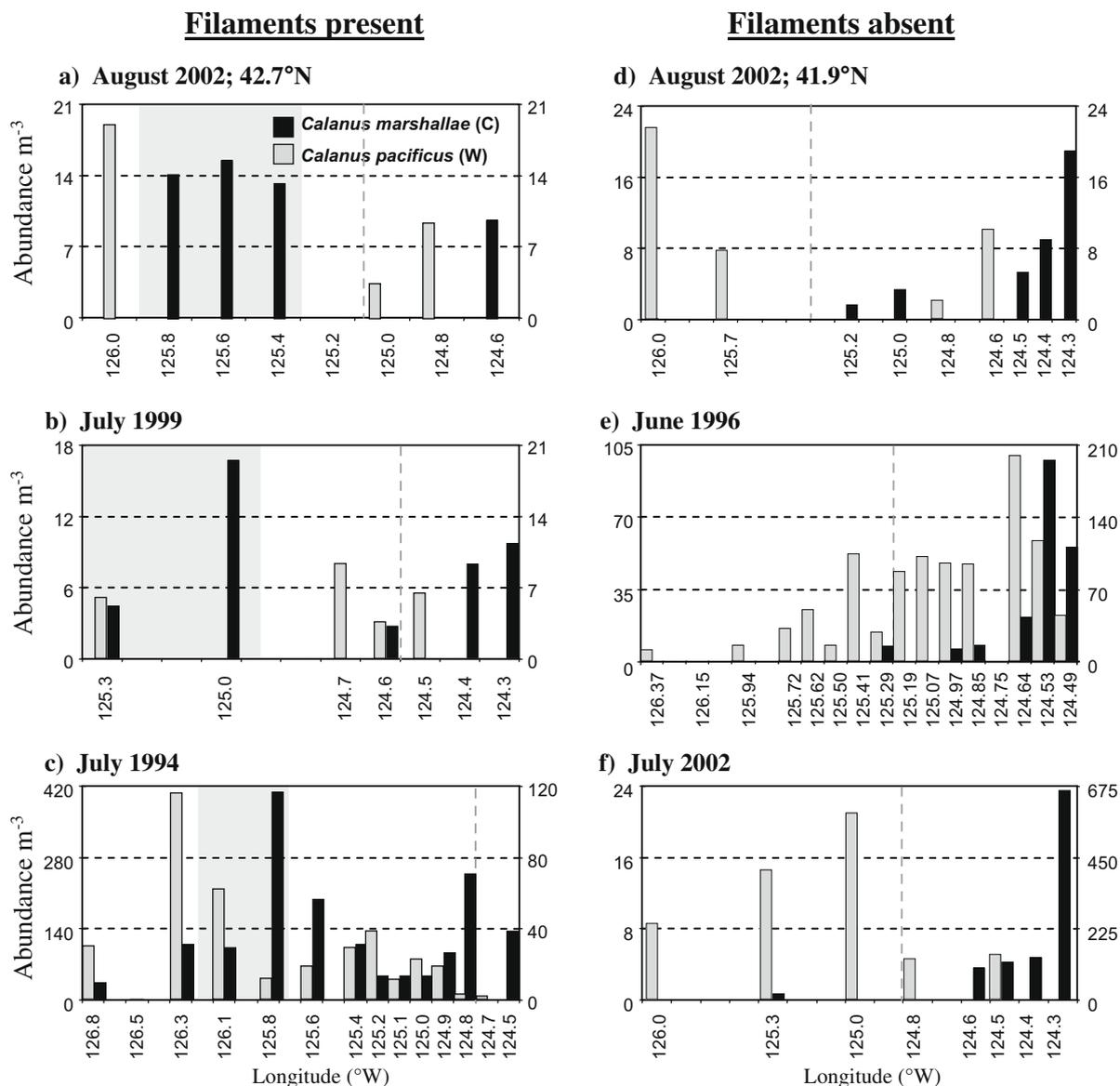
Fig. 4. Abundances of the cold-water (C) copepod *Calanus marshallae* and warm-water (W) copepod *Calanus pacificus* along cross-shelf transects. *C. marshallae* abundances are on the second (right) axis. All else as in Fig. 3.

5.1. Ecological impacts

Distinct patterns of elevated biomass and abundances of coastal, cold-water taxa within upwelling filaments demonstrate the ecological consequences of the circulation. These features act as a mechanism to transfer a portion of the high shelf production offshore to the deep California Current. Previous studies in the Northeast Pacific (Mackas and Yelland, 1999; Keister et al., 2008) have found that mesoscale circulation features result in seaward displacement of only a small portion of the coastal biomass. However, species patterns in several of the cruises here and in eddies off Vancouver Island (Mackas and Galbraith, 2002) indicate that at some times and locations, abundances can be as high or higher in offshore features than over the shelf.

The ecological impacts of individual upwelling filaments and eddies have been documented in several studies. These circulation features result in locally elevated plankton biomass and production, and may result in significant losses to some shelf populations (Mackas et al., 1991; Smith and Lane, 1991; Yebra et al., 2004; Keister et al., 2008). Upper trophic level organisms aggregate at the fronts created by the features (Tynan et al.,

2005), implying that their piscine prey are also more abundant there.

One important effect of the upwelling filaments sampled in this study is that they resulted in biomass that was spread more broadly between the coastal and ocean zone than when the circulation features were absent. Along transects without filaments, biomass was significantly (>10×) higher over the shelf than at offshore locations in all cruises (Fig. 3d–f). In contrast, biomass ranged only ~3–4× along transects that crossed filaments, and was never significantly higher over the shelf than in the filaments offshore (Fig. 3a–c). Because some populations which prey upon zooplankton mainly occur over the shelf whereas others mainly occur over the slope and offshore (e.g. fish larvae, Auth and Brodeur, 2006), the large temporal and spatial variability that occurs as a result of the circulation patterns is likely to have consequences for the success of different planktivorous populations.

5.2. Deviations from expected patterns

Biological patterns tended to reflect SST patterns, particularly where SST gradients were large. However, absolute, or even rela-

## Filaments present   ## Filaments absent
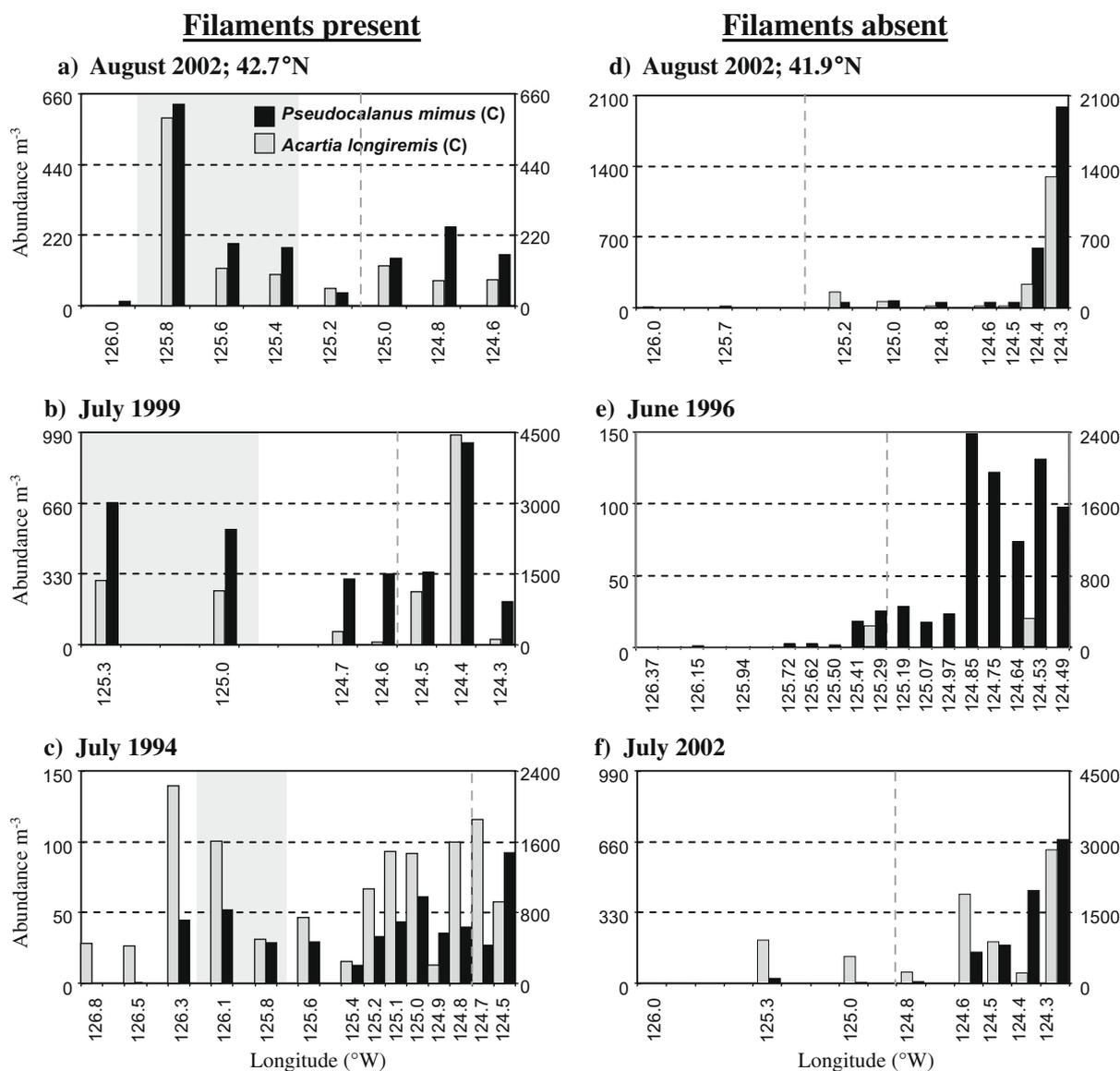
Fig. 5. Abundances of the cold-water (C) copepods *Pseudocalanus mimus* and *Acartia longiremis* along cross-shelf transects. *P. mimus* abundances are on the second (right) axis. All else as in Fig. 4.

tive, abundances of taxa at any particular station were not predictable. There are several possible reasons for the deviations from expected patterns. One of the largest potential factors is the temporal and spatial variability of abundances in the coastal source waters of circulation features. Temporally, biomass and abundances of individual taxa in our study area vary on intra-seasonal, seasonal, and interannual scales (Peterson and Miller, 1977; Keister and Peterson, 2003). The variability is such that taxa may be absent from locations where, at other times, they dominate. Spatial patchiness can be just as extreme and may result in higher or lower than 'expected' abundances in offshore circulation features. Distributions across the filament along 42.7°N in August 2002 (Figs. 4a, 5a) show this potential effect – abundances of coastal taxa were higher in the circulation feature than on the shelf. Because the timescales of advection within these features (on the order of 1–3 weeks transport from nearshore to offshore) were probably too short for growth to significantly influence the biomass or population structure, the elevated offshore abundances likely reflected higher abundances over the shelf in the source waters to the north compared to abundances on the shelf at the latitude sampled.

While an absence of species from locations where they were expected may have been due to temporal variability or patchiness in source waters, the occurrence of species where we did not predict them from SST patterns was most likely due to mixing or the vertical shear of water masses. Oceanic boundaries are biologically 'leaky' (Mackas and Coyle, 2005), and mixing of water masses in advective environments is high, resulting in mixed zooplankton communities. Shear of water types via surface layer Ekman transport or vertically-sheared circulation leads to stratified water columns containing multiple community types, across which vertical net tows integrate. In July 1994, the mix of cold and warm-water species we observed at stations in the filament (Figs. 4c, 5c, 6c) may have resulted from shearing and mixing along the boundaries of the feature, which was relatively narrow compared to others (Fig. 2).

Other mechanisms that may affect the relationship between physical and biological patterns are predation, behavior, and vertical circulation. For example, vertical Ekman pumping may cause localized areas of cold surface water and increased biomass in the deep ocean (Brock and McClain, 1992), but not the presence
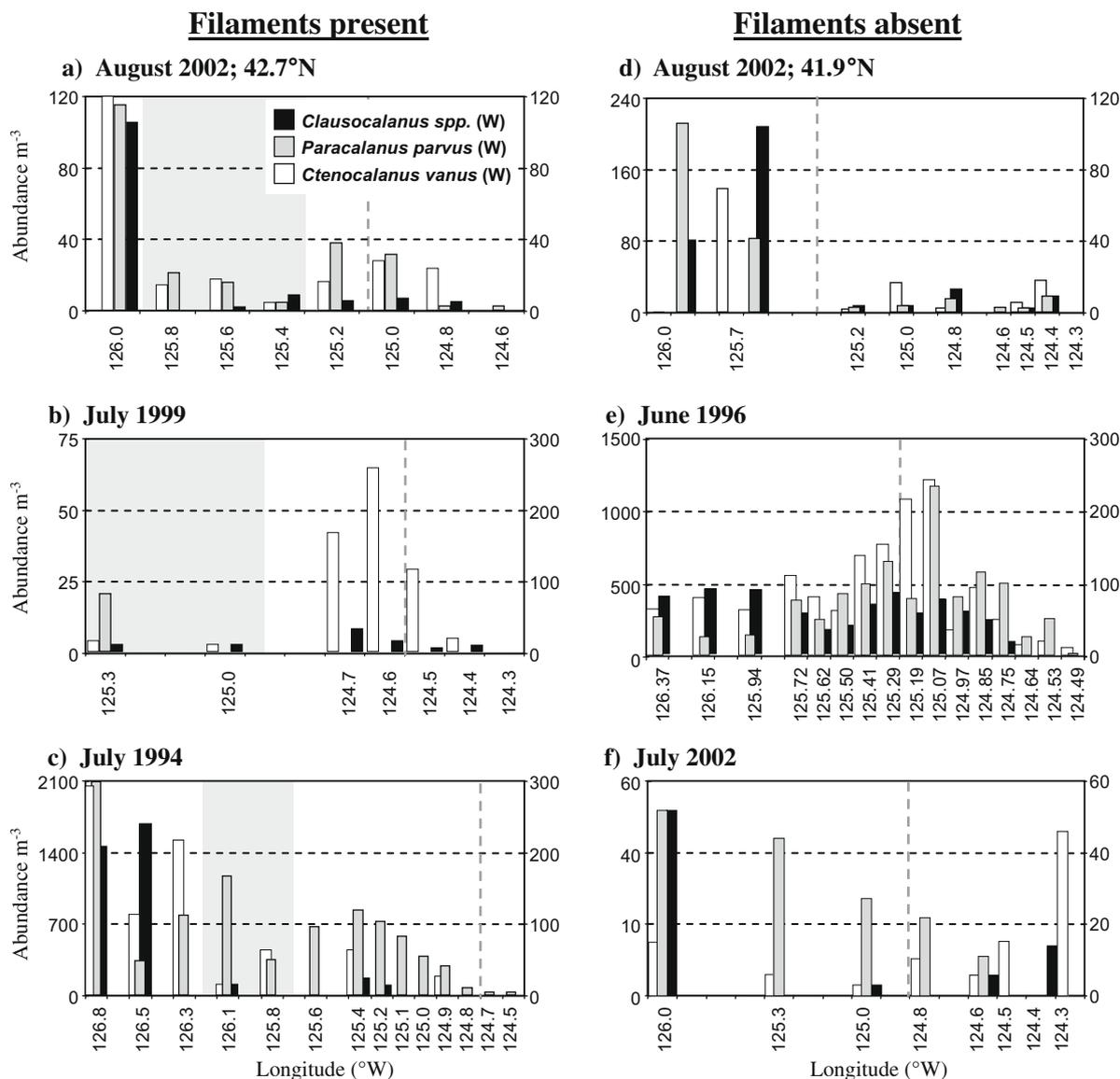
Fig. 6. Abundances of the warm-water (W) copepods *Clausocalanus* spp., *Paracalanus parvus,* and *Ctenocalanus vanus* along cross-shelf transects. *Clausocalanus* spp. and *C. vanus* abundances are on the second (right) axis. All else as in Fig. 4.

of coastal taxa. Alternatively, high mortality or behaviors (e.g. vertical migration) that lead to loss of taxa from circulation features could de-couple the physical and biological patterns.

5.3. Field sampling design

Our experience is that sampling strategies based on occupation of pre-determined, widely spaced sampling locations, such as those used in many monitoring programs, are not sufficient to capture the variability due to dynamic circulation features. Sampling must either occur with high enough spatial resolution to ensure sampling of features when/where they occur, or must incorporate adaptive sampling in which stations are chosen based on a recent view of the hydrography. In the California Current, some mesoscale circulation features can have spatial scales of >200 km, making them easy to sample with pre-planned transects, but the smaller mesoscale features we measured in this study have spatial scales of <50 km along one zonal or meridional axis. Such features require sampling every 15–20 km to resolve the spatial patterns.

Adaptive sampling is better suited to capturing dynamic features, but requires knowledge of the spatial pattern in hydrography at the time of sampling. Satellite SST images can be used to guide sampling in regions where circulation features result in visible surface temperature gradients (e.g. Fig. 1) but cannot always be obtained while at sea. An understanding of the dynamics and temporal scales of the local circulation is needed to make decisions based on 'old' images. This 'intuition-guided' sampling should be supported by shipboard under-way data for real-time assessment of the ship's position relative to observed hydrographic features, or by conducting an acoustic Doppler current profile (ADCP) section before selecting sampling stations to help sample as close to the center of features as possible.

6. Conclusions

In the California Current, as in other boundary current ecosystems, circulation is a dominant force structuring distributions of zooplankton, particularly during summer upwelling. In this study, we explored the degree to which we can use observed physical

patterns to infer biological patterns. We found that the strength of the relationship between the circulation patterns (here inferred from SST) and the zooplankton distributions largely depended upon the strength of the physical patterns. Using examples from research cruises conducted during four summers, we found that we can predict that elevated zooplankton biomass and abundances of coastal organisms will occur offshore when advective circulation features are present and will not occur offshore in the absence of such features. The predictive ability arose from our fundamental understanding of the mechanism behind the relationships—i.e. the dynamics of offshore advection of coastal water masses and the associated plankton in upwelling filaments. We were not able to predict the abundances of taxa at any location or the presence/absence of specific taxa at specific locations. The predictive ability ended with a generalization of 'relative abundance' patterns because patchy abundances, interannual variability in populations, biologically-driven processes, and mixing of water masses added uncertainty.

Adequate sampling of patterns in the environment such that the important ecosystem processes are captured is a continuous challenge in ecology, particularly in pelagic ecology where the environment itself is not just changing in time, but is also moving in space over fixed locations. The balance between temporal and spatial resolution prevents synoptic observations over large scales and makes designing sampling strategies to quantitatively assess patterns difficult. However, because dynamic circulation features can result in localized hot-spots of production and biomass and may substantially contribute to the overall production of systems in which they occur (Michaels, 2007), future studies must give careful thought to designing sampling strategies that capture these patterns on the mesoscale.

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