Available online at www.sciencedirect.com
ScienceDirect
Deep-Sea Research II 53 (2006) 3078–3098
DEEP-SEA RESEARCH PART II
www.elsevier.com/locate/dsr2

Cross-shelf distribution of copepods and the role of event-scale winds in a northern California upwelling zone

Katherine M. Papastephanou[a], Stephen M. Bollens[a,b,*], Anne M. Slaughter[a]

[a]*Department of Biology and the Romberg Tiburon Center for Environmental Studies, San Francisco State University, 1600 Holloway Ave., San Francisco, CA 94132, USA*

[b]*School of Biological Sciences, Washington State University Vancouver, 14204 NE Salmon Creek Avenue, Vancouver, WA 98686, USA*

Accepted 9 July 2006

Abstract

Cross-shelf distribution and abundance of copepod nauplii and copepodids were measured during three summer upwelling seasons (2000–2002) in a coastal upwelling zone off northern California. These 3 years varied considerably in the intensity of winds, abundance of chlorophyll, and water temperature. The cruises in 2000 were characterized by relaxation conditions, with generally high levels of chlorophyll and high water temperature. The cruises in 2001 and 2002 were dominated by strong and persistent upwelling events, leading to lower chlorophyll and water temperatures. The copepod assemblage was dominated by *Oithona* spp., *Acartia* spp. and *Pseudocalanus* spp., with *Metridia pacifica* (*lucens*), *Microsetella rosea*, *Oncaea* spp. and *Tortanus discaudatus* also common during all 3 years. The cross-shelf distribution of copepods was generally shifted offshore during upwelling and onshore during relaxation events, although some variability between species occurred. Abundance of all life stages generally exhibited a negative correlation with cross-shelf transport averaged over at least 1–4 days and lagged by 0–3 days, indicating lower abundances during and immediately after active upwelling. However, copepod nauplii seemed to respond positively to wind events lasting 1–5 days followed by a period of relaxation lasting 6 or 7 days. These rapid rates of change in abundance are probably too great to be due to in situ growth and reproduction alone; physical processes must also play a role. These results suggest a highly dynamic relationship between copepods and upwelling events off northern California, with species-specific responses to upwelling to be expected.

Keywords: Copepods; Nauplii; Cross-shelf transport; *Oithona* spp.; *Microsetella rosea*; *Oncaea* spp.

1. Introduction

The continental shelf off central and northern California is characterized by a strong eastern boundary current (the California Current) and seasonal winds. In the spring and summer, the area is dominated by equatorward winds that result in coastal upwelling and offshore movement of surface waters via Ekman transport, bringing colder and

*Corresponding author. School of Biological Sciences, Washington State University Vancouver, 14204 NE Salmon Creek Avenue, Vancouver, WA, 98686, USA. Tel.: +1 360 546 9116; fax: +1 360 546 9064.

E-mail address: bollens@vancouver.wsu.edu (S.M. Bollens).

0967-0645/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.dsr2.2006.07.014

nutrient-rich waters into the system. Periodic reversals of these winds can lead to downwelling conditions. The interplay of currents, reversing winds, offshore and onshore Ekman transport and varying coastline geometry creates complex patterns of water movement and ephemeral physical conditions, which in turn affect the organisms in the system.

The California Current system exhibits the high productivity at lower trophic levels that is typical of upwelling systems; it is rich in phytoplankton and zooplankton, especially during the active upwelling season. Copepods are an abundant component of the system biota and it is generally accepted that the events set in motion by coastal upwelling (addition of nutrients, increase in phytoplankton) result in increased copepod abundance. Planktonic organisms in the system are subject to alongshore and cross-shelf advection and their populations might be expected to move across the shelf according to the onshore–offshore water movement associated with coastal upwelling.

Numerous studies have examined the cross-shelf distribution of copepods during general upwelling conditions (Peterson et al., 1979; Verheye and Hutchings, 1988; Escribano and Hidalgo, 2000; Keister and Peterson, 2003; Morgan et al., 2003; Lamb and Peterson, 2005) with varying results. Some reported that upwelling had no effect on cross-shelf copepod distribution (Bernal and McGowan, 1981; Cross and Small, 1967). Others have investigated the behavioral mechanisms copepods might employ in order to avoid being advected beyond the shelf and out of the rich system, such as diel vertical migration (Smith et al., 1981a; Wroblewski, 1982; Batchelder et al., 2002), ontogenetic vertical migration (Verheye et al., 1992; Slagstad and Tande, 1996; Peterson, 1998) or both (Verheye et al., 1991; Verheye and Field, 1992). However, these studies focused on the overall pattern of offshore movement of surface water associated with upwelling. Models have shown that constant upwelling winds cannot explain the high productivity of upwelling systems or correlate to shelf retention of plankton (Wroblewski, 1980; Botsford et al., 2003). However, not much is known about the cross-shelf distributions of copepods as affected by water movement induced by much shorter-scale (several days) wind events. Such events may significantly influence copepod population distributions and abundances over the shelf. Smith et al. (1981b), for example, demonstrated that patterns of zooplankton composition and biomass can be significantly affected by cross-shelf advection fluctuations on a smaller (i.e. daily) time scale, and Dorman et al. (2005) recently examined this phenomenon in relation to euphausiids.

Additionally, it may be important to examine the role of not only those wind events that induce upwelling, but also relaxation from upwelling and even those wind events that lead to downwelling. For instance, despite high nutrients in the upwelling zone off northwest Africa, Jones and Halpern (1981) found that primary productivity remained low during upwelling winds until wind strength decreased. Similarly, Smith et al. (1986) reported that numbers of zooplankton taxa and individuals actually decreased as upwelling intensity increased, and found that copepod nauplii abundance increased during active downwelling. Peterson et al. (1988) found that several copepod taxa off the coast of Chile were low in abundance during active upwelling and higher during relaxation. Similar issues have been addressed with respect to meroplankton off the coast of northern California by Wing et al. (1995).

In the California Current system, periods of strong, equatorward alongshore winds that result in active upwelling are interspersed with winds of variable direction, strength and duration, leading to relaxation or downwelling. The interaction of upwelling favorable events and relaxation or downwelling conditions on very short time scales (i.e. event scales defined by individual wind "events") may have profound impacts on the biota in the upwelling zone. Our objective was to understand the relationship between event-scale winds and the distribution and numerical response of copepod populations. To achieve this, we recorded hourly wind data and repeatedly collected copepods from a cross-shelf transect during three upwelling seasons. By considering specific wind events in conjunction with the cross-shelf distribution and abundance of various life stages of several taxonomic groups of copepods, we examined not only the movement of copepod populations across the shelf, but also their relationship and numerical response to individual upwelling and relaxation events.

2. Materials and methods

Wind and sea-surface temperature data were obtained from the National Data Buoy Center (NDBC). Chlorophyll, copepod nauplii and

copepodid samples were collected from set locations along cross-shelf transects off Bodega Bay, CA, during three cruises in the spring/summer season of 2000, 2001 and 2002 on the R.V. *Point Sur* (Fig. 1). Not all sample types were collected at the same time or at all stations due to weather constraints and/or limited equipment availability time (Table 1).

2.1. Hydrographic data collection

Hourly values of sea-surface temperature, wind speed, and wind direction were downloaded from the NDBC website for station 46013 (Bodega Bay station at 38°13′37″N, 123°19′48″W) for spring 2000–2002. Wind direction was rotated 35° according to the orientation of the central California coastline, and adjusted wind direction data were used to calculate alongshore and cross-shelf components of wind speed data. Expected hourly cross-shelf Ekman transport values based on the alongshore wind vector and Coriolis were calculated according to Bakun (1973) and a 15-h moving average was applied. Additional temperature data were also collected from CTD casts using a Seabird 911 Plus CTD.

2.2. Chlorophyll data collection

Chlorophyll data were kindly provided by R. Dugdale and F. Wilkerson and methods are briefly outlined here (Wilkerson et al., 2006). Water samples of 280 or 50 ml (during blooms) were collected from a depth of 5 m in a 10-L Niskin bottle mounted on a Seabird 911 Plus CTD rosette apparatus. These samples were filtered onto 47-mm, 0.7-μm pore size Whatman GF/F filters, which were then stored at 4 °C until extraction and analysis in the lab (usually less than 2 weeks). Chlorophyll retained on the filters was extracted at room temperature in 90% acetone in the dark for 24 h and read before and after acidification with three drops 10% HCl on a Turner 10 fluorometer according to Strickland and Parsons (1972).

2.3. Zooplankton collection

Microzooplankton samples were collected from 10-L Niskin bottles mounted on the Seabird 911 CTD. Samples were collected from 5, 15 and 25 m water depths, filtered separately or together (if equal in volume) over 30-μm mesh and preserved in a borate-buffered 5–10% formalin-seawater solution. Mesozooplankton samples were collected using a 1.0 m (2000) or 0.5 m (2001 and 2002) diameter ring net with a 73-μm mesh. The ring net was hauled vertically from a depth of 200 m or from 5 m above the seafloor, whichever was shallower, to the surface at a rate of 10 m min^{-1}. Exact depth range of sampling was determined using a Vemco Minilog-TDR depth

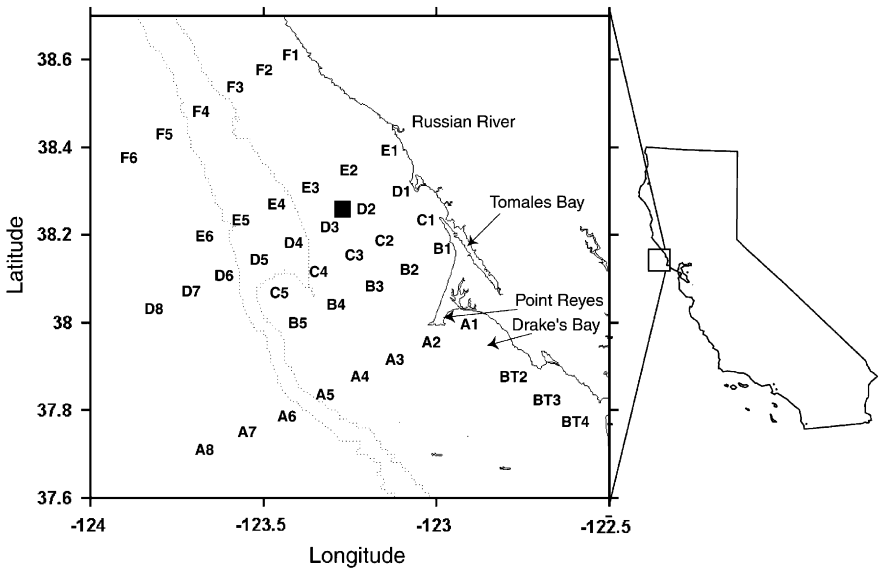

Fig. 1. Location of CoOP/WEST sampling stations and NDBC Station 46013 (■) in the study area off central California. 200 and 1000-m isobaths are represented by dotted lines (···).

Table 1
Summary of stations sampled for copepod nauplii and copepodids; n = number of samples

Cruise dates	Nauplii (niskin bottles)			Copepodids (ring net)		
	Samples dates (times)	Stations	n	Sample dates (times)	Stations	n
1–30 June 2000	3 June (03:05–08:00)	D1–D4	4	4 June (11:40–17:35)	D1–D5	5
	7 June (13:35)	D2	1	12 June (09:05–11:50)	D1–D3	3
	9 June (14:32–19:33)	D1–D3	3	24 June (05:58–22:23)	D1–D5	5
	11 June (08:33–21:21)	D1–D5	5	28–29 June (20:13–02:18)	D1–D5	5
	12 June (04:13–08:38)	D1–D5	5	Total		18
	13 June (09:05–11:10)	D2, D3	2			
	18–19 June (21:45–04:00)	D1, D2, D4	3			
	20 June (10:25, 23:19)	D2, D2	2			
	24 June (05:55–22:22)	D1–D5	5			
	26 June (10:25, 23:52)	D1, D1	2			
	28–29 June (19:52–02:16)	D1, D3–D5	4			
Total			36			
17 May–15 June 2001	19 May (18:50–23:40)	D1–D4	4	23 May (04:40–09:54)	D1–D5	5
	23 May (06:05–10:29)	D2–D5	4	24 May (07:49–14:45)	D1–D4	4
	24 May (08:19–12:20)	D2–D4	3	27 May (09:58–16:50)	D1–D5	5
	27 May (09:38–15:28)	D2–D5	4	30 May (12:04–18:18)	D1–D5	5
	28 May (09:48)	D2	1	5 June (12:25–20:03)	D1, D3, D4	3
	30 May (11:51–18:10)	D1–D5	5	6 June (01:00)	D5	1
	4 June (23:20)	D2	1	Total		23
	5–6 June (04:15–00:31)	D2, D3, D1–D5	7			
	8 June (01:14, 14:20)	D2, D2	2			
	10 June (00:53)	D1	1			
	13 June (09:12–14:09)	D1–D3	3			
	14 June (08:51)	D4	1			
Total			36			
30 May–28 June 2002	31 May–1 June (22:08–02:50)	D1–D3	3	3 June (05:05, 06:51)	D1, D2	2
	3 June (04:34–13:34)	D1–D5	5	16 June (04:12–12:37)	D2–D5	4
	4 June (08:38)	D1	1	18 June (14:46, 13:06)	D4, D5	2
	5 June (00:50, 10:02)	D1, D1	2	24–25 June (23:35–07:52)	D1–D5	5
	6 June (08:31)	D1	1			
	7 June (08:32)	D1	1			
	8 June (09:08)	D1	1			
	9 June (08:59–11:59)	D1–D3	3			
	16 June (03:45–14:38)	D1–D5	5			
	19 June (05:50, 07:39)	D3–D5	3			
	19 June (05:50, 07:39)	D1, D2	2			
	20 June (08:13)	D1	1			
	21 June (07:17, 13:40)	D1, D2	2			
	22 June (01:17)	D2	1			
	24–25 June (23:09–07:49)	D1, D2, D4, D5	4			
Total			35	Total		13

recorder in 2001 and 2002. The net was fitted with a General Oceanics flowmeter to determine the volume of water filtered. Mesozooplankton samples were preserved in a borate-buffered 7–10% formalin-seawater solution.

Samples from the D-line, or central line of the sampling area, were chosen for analysis because this transect was most frequently sampled. Additionally, moorings collecting physical data were located along this transect. Those stations with bottom depth less than 150 m (D1 and D2) are referred to as nearshore, and those stations with bottom depths greater than 150 m (D3, D4 and D5) are considered offshore.

2.4. Zooplankton enumeration and identification

In the laboratory, microzooplankton samples were analyzed for copepod nauplii by enumeration and identification of individuals under a Leica MZ6 stereomicroscope at 25.6–40 × total magnification. Nauplii were identified to genus when possible, or categorized according to size, developmental stage and general taxonomic group using Gibbons and Ogilvie (1933), Johnson (1934), Ogilvie (1953), Hirakawa (1974), Gibson and Grice (1978), Malt (1982) and Trujillo-Ortiz (1986). Calanoid nauplii that we were unable to identify to genus level were grouped according to size; individuals with body length measuring less than 150 μm during stages NI–III or less than 200 μm during stages NIII–VI were counted as "unidentified small calanoid" and larger individuals were counted as "unidentified large calanoid". Each of these groupings likely contained several taxa. Dense samples (containing >500 nauplii per sample) were split to 50% using a 1 L Folsom splitter to achieve ~200–300 individuals for enumeration and identification. Raw counts were divided by the volume of water filtered (and divided by Folsom split percentage, if applicable) to determine nauplii m^{-3}.

Mesozooplankton samples were analyzed for copepodids by enumeration and identification of individuals under a Leica MZ6 stereomicroscope at 16–40 × total magnification. A subsample of each sample (typically 0.02–0.1%) was taken with a 10-ml Stempel pipette to obtain 200–400 individuals for enumeration and identification to lowest possible taxon using Olson (1949), Dawson and Knatz (1980), Gardner and Szabo (1982) and Frost (1989). To achieve similar taxonomic groupings for direct comparison with nauplii data (e.g., plotting and statistical analyses), we combined all identified species of *Acartia* (*Acartia longiremis*, *Acartia tonsa* and *Acartia danae*) and *Oithona* (*Oithona similis*, *Oithona spinirostris*). *Acartia longiremis* and *Acartia tonsa* were more common than *Acartia danae*. In terms of *Oithona* spp., *Oithona similis* was the predominant species present, with *Oithona spinirostris* occurring rarely and in much lower abundances. Both *Pseudocalanus newmani* and *Pseudocalanus mimus* have been found in MOCNESS samples from the CoOP/WEST study, but as we were unable to distinguish the two species in our samples all individuals from the genus were grouped together as *Pseudocalanus* spp. Similarly, we were unable to distinguish between *Calanus marshallae* and *Calanus pacificus* and therefore grouped all individuals found into *Calanus* spp. We did not identify to species individuals in the grouping *Oncaea* spp. Those individuals from taxa not listed above, as well as some unidentified early copepodids, were grouped as "other". Raw counts were divided by the volume of water filtered during the net tow and subsample fraction to calculate individuals m^{-3}.

2.5. Correlation analysis

Hourly estimated Ekman offshore transport values (based on wind speed and direction) were averaged over 1–10 days starting 0 (no lag) and 19 days before each copepod sample was collected. We used this data to create a matrix of 200 Ekman transport values to compare to each copepod abundance estimate. Absolute abundance (individuals m^{-3}) of copepodids, nauplii, and total copepods were correlated with corresponding Ekman transport values using Matlab 5.3.

3. Results

3.1. Wind, upwelling, temperature and chlorophyll data

Wind conditions, upwelling indices, sea-surface temperature and station D2 chlorophyll concentrations varied inter-annually (Table 2). Each of the three spring/summer periods is described below.

May–June 2000 was characterized by prolonged periods (>4 days) of relaxation from upwelling winds, with episodes of low Ekman transport occurring in early June (around Year Day 155), preceded by a strong upwelling event, and again in mid and late June (YD 170, 180), each preceded by a moderate upwelling event (Fig. 2A). Sea-surface temperatures varied between 8.6 and 13.1 °C, with a mean of 10.6 °C. The value of 5m chlorophyll *a* at station D2 during the sampling period varied between 0.77 and 21.9 μg L^{-1}, with a mean of 10.3 μg L^{-1}. The mean upwelling index was 122 m^{-3} s^{-1} per 100 m coastline.

In contrast, May–June 2001 was characterized by stronger and more persistent upwelling winds, with much shorter periods of relaxation (<2 days). The mean hourly upwelling index was 201 m^{-3} s^{-1} per 100 m in 2001, compared with 122 m^{-3} s^{-1} per 100 m in 2000 (Fig. 2B and A). Sea-surface temperatures varied between 8.6 and 11.9 °C, with a mean of

Table 2
Summary of physical data collected at station D2 during CoOP-WEST sampling: SST and UI means for 1 May –30 June; chlorophyll means from cruise periods; SE = standard error

Sampling period	Sea surface temperature (°C) mean (SE)	Upwelling index ($m^3 s^{-1}$ per 100 m coastline) mean (SE)	5 m chlorophyll *a* ($\mu g L^{-1}$) mean (SE)
1 May–30 June 2000	10.6 (0.0)	122 (4.0)	10.3 (1.7)
	$n = 1413$	$n = 1413$	$n = 28$
1 May–30 June 2001	9.6 (0.0)	201 (4.4)	4.6 (1.1)
	$n = 1453$	$n = 1454$	$n = 19$
1 May–30 June 2002	9.3 (0.0)	228 (2.6)	3.0 (1.0)
	$n = 1460$	$n = 1460$	$n = 13$

9.6 °C. Chlorophyll *a* (5 m water depth) at station D2 during the sampling period was much lower than in 2000, varying between 0.2 and 7.2 $\mu g L^{-1}$ with a mean value of 4.6 $\mu g L^{-1}$.

May–June 2002 was characterized by three prolonged periods (>10 days) of strong upwelling and a few moderate episodes (2–3 days) of relaxation. In this and other respects, upwelling conditions during spring/summer 2002 were fairly similar to those in spring/summer 2001. Mean hourly upwelling index values was 228 $m^{-3} s^{-1}$ per 100 m (Fig. 2C). Sea-surface temperatures varied between 7.7 and 12.0 °C, with a mean of 9.3 °C. Five meter chlorophyll *a* at station D2 during the sampling period varied between 0.4 and 12.2 $\mu g L^{-1}$, with a mean of 3.0 $\mu g L^{-1}$.

3.2. Cross-shelf copepod distributions

The continental shelf copepod community was dominated by about seven taxa, with other groups represented in smaller numbers (Table 3). In order of decreasing abundance, copepod nauplii were primarily comprised of *Oithona* spp., *Acartia* spp., unidentified large calanoids, unidentified small calanoids, *Microsetella rosea*, *Oncaea* spp., and *Tortanus discaudatus* (Fig. 3). Similarly, copepodids were primarily comprised of *Oithona* spp. (e.g., *O. similis*, *O. spinirostris*), *Acartia* spp. (e.g., *A. longiremis*, *A. tonsa*, *A. danae*), *Pseudocalanus* spp., *Metridia pacifica* (*lucens*), *Microsetella rosea*, *Oncaea* spp. and *Tortanus discaudatus* (Fig. 4). Other species occasionally found in low abundance included *Corycaeus* spp., *Calanus* spp. (e.g., *C. marshallae*, *C. pacificus*), and *Eucalanus* spp. *Oithona* spp. were found at every station on every sample date. *Acartia* spp. and *Tortanus discaudatus* (a primarily estuarine species) were usually limited to the nearshore stations (D1 and D2). However, *Oithona* spp., *Acartia* spp., *Pseudocalanus* spp., *Metridia pacifica* (*lucens*), *Microsetella rosea*, *Oncaea* spp. and *Tortanus discaudatus* were all found at least once at each of the five stations over the course of this study. Copepod nauplii were generally much more abundant than copepodids, with maximum mean total abundances of nauplii approximately double those of copepodids (although the limited number of copepodid samples may affect the absolute values and interpretation of these data).

Considering the station-specific abundances in May–June 2000, copepod nauplii were more abundant at inshore stations (D1 and D2) than stations further offshore (Fig. 3A). *Oithona* spp. were dominant at the offshore stations (D3–D5), making up 57–72% of the total copepod nauplii present, and were also abundant at D1 and D2, but made up a smaller percentage of the assemblage (17.9% and 30.3%, respectively). *Acartia* spp. comprised 22.8% of the assemblage at D1, but was much less abundant (<2% of the assemblage) at all the other stations. Unidentified large and small calanoid copepod nauplii were present at all stations, but were a proportionally larger constituent of the nearshore copepod nauplii assemblage (unidentified large calanoids = 30.3% at D1, unidentified small calanoids = 43.2% at D2). *Tortanus discaudatus* was found only at D1 and D2 and made up a very small proportion of the assemblage (0.5% and 0.1%, respectively). *Microsetella rosea* also was found in small numbers, but increased steadily across the shelf, from 0.1% of the assemblage at D1 to 1.1% at D5, while *Oncaea* spp. varied from 0.1% to 0.9% of the assemblage with no apparent cross-shelf pattern.

In 2001, mean copepod nauplii abundances were somewhat lower than in 2000 and did not exhibit the general cross-shelf gradient seen in 2000 (Fig. 3B). Compared to 2000, *Oithona* spp. made

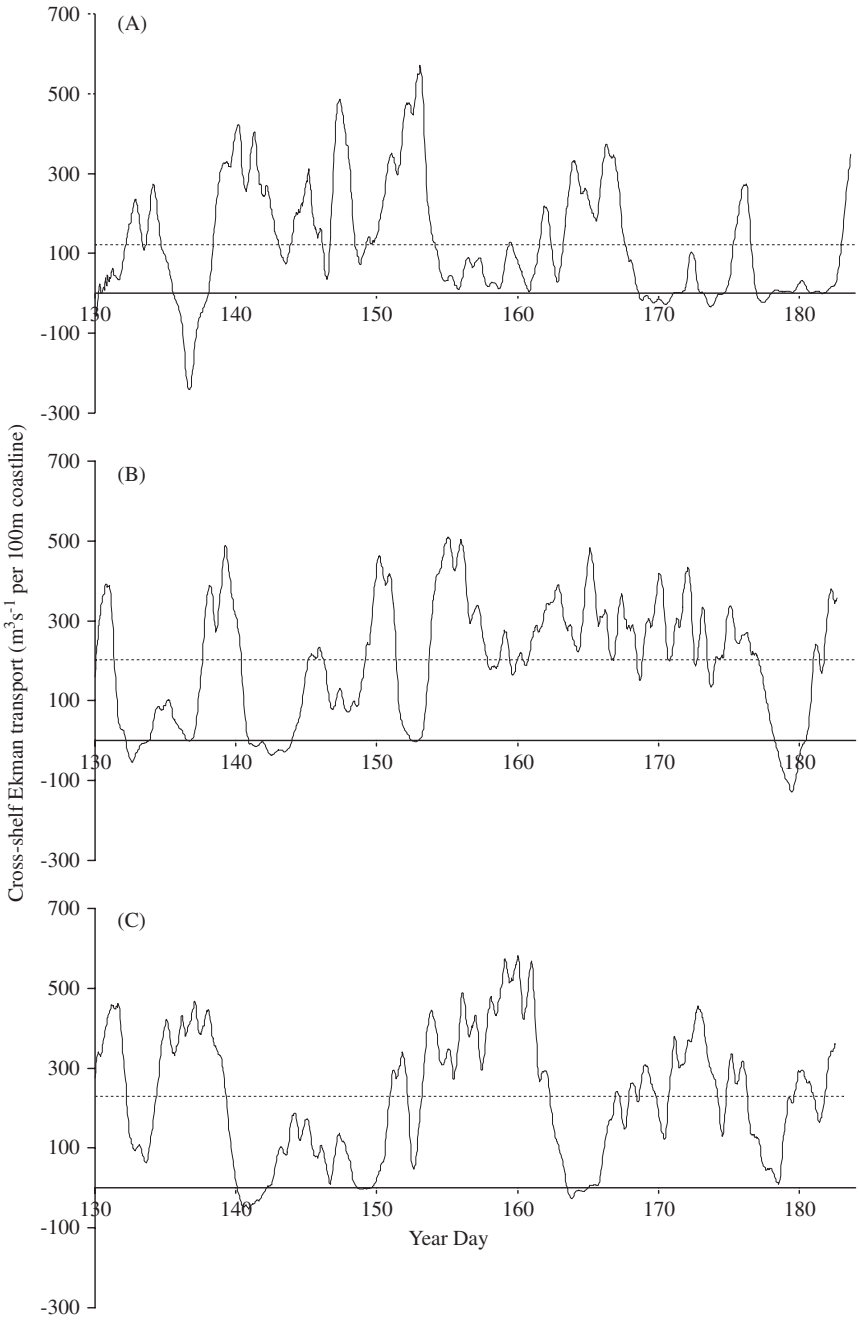

Fig. 2. Ekman upwelling index (15-h moving average calculated from alongshore vector of winds measured at NDBC buoy 46013 according to Bakun (1973)) during May–June of 2000 (A), 2001 (B), and 2002 (C). May–June average upwelling index represented by dashed line (----).

up a smaller percentage of the assemblage in 2001, ranging from 6.0% at D1 to 54.0% at D5. *Acartia* spp. were most abundant at D1, making up 42.4% of the assemblage. Unidentified large and small calanoids were common across the shelf and represented about 20–35% of the assemblage. *Tortanus discaudatus* was present across the shelf and was particularly abundant at D1 (4.8%). *Microsetella rosea* varied from 0.2% to 1.1%, with no discernable cross-shelf pattern apparent. The portion of the assemblage comprised by *Oncaea* spp. in 2001 was somewhat higher than in 2000,

Table 3
Mean copepodid abundance (individuals m^{-3}) and standard error (SE) from ring net D-line surveys

Taxon	Spring 2000		Spring 2001		Spring 2002	
	Mean	SE	Mean	SE	Mean	SE
Acartia longiremis	4	4	1344	928	31	24
Acartia spp.	3	3	3724	3392	358	358
Acartia tonsa	1957	1162	168	125	351	337
Aetidius armatus	1	1	2	2	1	1
Calanus spp.	50	18	11	5	6	2
Candacia bipinnata	0	0	0	0	1	1
Clausocalanus spp.	21	12	1	1	1	1
Corycaeus spp.	2	2	0	0	1	1
Ctenocalanus spp.	4	2	3	2	2	1
Epilabidocera spp.	2	2	0	0	4	4
Euaetideous spp.	0	0	1	0	0	0
Eucalanus californicus	2	1	2	1	22	10
Eucalanus hylinas	0	0	<1	<1	<1	<1
Euchaeta elongata	1	1	1	1	3	2
Euchirella curticauda	1	0	1	1	0	0
Euterpina acutifrons	0	0	0	0	71	71
Gaetanus spp.	0	0	0	0	<1	<1
Limnoithona spp.	2	2	0	0	0	0
Lubbockia spp.	1	1	30	29	0	0
Lucicutia spp.	0	0	1	1	5	3
Metridia pacifica (*lucens*)	131	44	106	27	181	42
Microsetella rosea	286	53	455	156	1087	529
Oithona similis	1515	159	903	112	766	118
Oncea spp.	195	34	258	43	753	286
Paracalanus spp.	4	4	1	1	0	0
Pseudocalanus spp.	2069	533	2165	508	622	294
Tortanus discaudatus	45	29	77	50	51	45
Unidentified copepodids	1934	1031	1450	684	74	28
Unidentified CI-CV *Ctenocalanus* + *Paracalanus* + *Clausocalanus* spp.	37	31	7	3	4	2

ranging from 1.4% at D1 to 0.4% at D5 (compared to 0.1–0.9% in 2000).

Mean copepod nauplii abundance in 2002 was generally lower than in 2000 and 2001, and showed no significant cross-shelf gradient (Fig. 3C). One consistent pattern observed during all three sampling periods was the cross-shelf gradient of *Oithona* spp., which, in 2002, increased from 11.5% at D1 to 49.3% at D5. *Acartia* spp. comprised 28.1% of the assemblage at D1, 7.9% to 10.1% from D2 to D4, and 7.5% at D5. Unidentified large calanoids made up between 9.4% (D4) and 36.2% (D1) of the assemblage, while small calanoids ranged between 9.4% (D1) and 40.0% (D3). *Tortanus discaudatus* ranged from 4.3% at D1 to 0.1% at D5. *Microsetella rosea* increased steadily from 0.6% of the assemblage at D1 to 1.7% at D5, while *Oncaea* spp. comprised more than 6.2% of the assemblage at D1, D4 and D5.

Copepodid abundance during May–June 2000 exhibited a striking decline with distance from shore (Fig. 4A). *Oithona* spp. were present at relatively similar abundances at all stations across the shelf, but its relative proportion to the entire assemblage varied from 7.2% at D1 to 51.2% at D5. *Acartia* spp. were only found near shore, making up 35.5% of the assemblage at D1 and 17.6% at D2. *Tortanus discaudatus*, similarly found only at nearshore stations, comprised 0.6% and 0.9% at D1 and D2, respectively. *Pseudocalanus* spp. were most abundant closer to shore, accounting for 47.7% of total copepodids at D2. *Metridia pacifica* (*lucens*), *Microsetella rosea* and *Oncaea* spp. all exhibited fairly similar abundances across the shelf, but

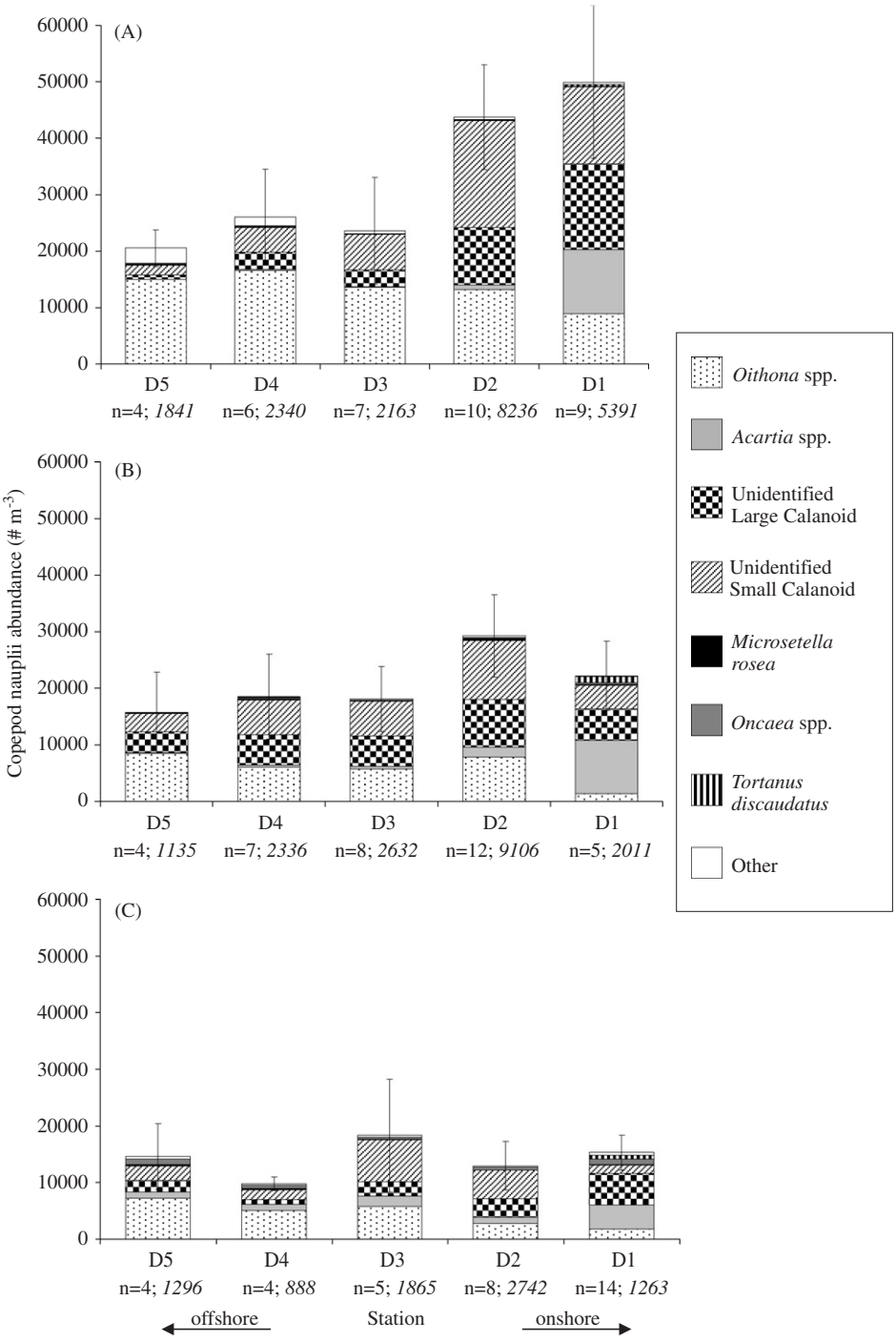

Fig. 3. Mean (±SE) cross-shelf abundance and distribution of copepod nauplii along the D-line, averaged over all sampling dates in June 2000 (A), May–June 2001 (B), and May–June 2002 (C). n = number of samples analyzed from a station and individuals counted (italics), e.g., $n = 4$ (samples); 1841 (individuals).

represented greater proportions of the copepod assemblage with increasing distance from shore. *Metridia pacifica (lucens)* increased from1.1% to 5.0%, *Microstella rosea* from 2.0% to 9.8%, and *Oncaea* spp. from 1.1% to 12.6% (D1–D5). Other species (“Other”) made up a considerable portion of

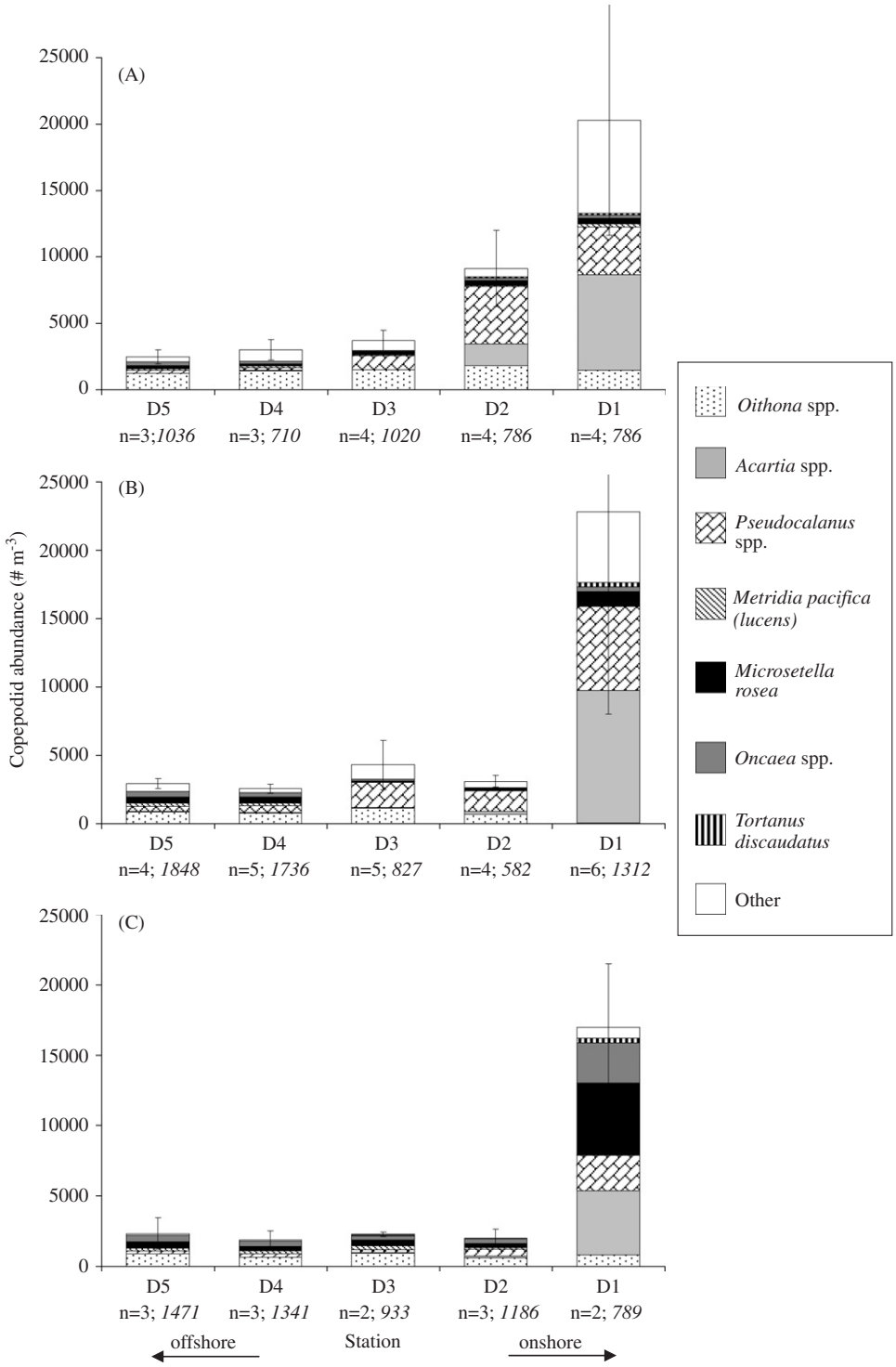

Fig. 4. Mean (±SE) cross-shelf abundance and distribution of copepodids along the D-line, averaged over all sampling dates in June 2000 (A), May–June 2001 (B), and May–June 2002 (C). n = number of samples analyzed from a station and individuals counted (italics), e.g., $n = 3$ (samples); 1036 (individuals).

the assemblage (34.7%) at D1 and decreased with distance from shore.

Copepodid abundances in 2001 showed many patterns similar to 2000, although with slightly lower abundances (Fig. 4B). Mean copepodid abundances were much higher (ca. 7 fold) at D1 than at any other station on the D line. As in 2000, *Acartia* spp. made up a large portion of the assemblage at D1 (42.8%), *Pseudocalanus* spp. were highly abundant nearshore (48.0% at D2), and *Metridia pacifica* (*lucens*), *Microsetella rosea*, and *Oncaea* spp. abundances all increased with increasing distance from shore (D1–D5). *Metridia pacifica* (*lucens*) and *Oncaea* spp. were present at proportions similar to 2000, but the proportion of *Microsetella rosea* in 2001 was higher than 2000 (4.6% at D1, 15.7% at D5). *Tortanus discaudatus* was only present at D1 (1.6%). A marked difference between 2000 and 2001 is the near-absence of *Oithona* spp. at D1 (only 0.1%).

In 2002, copepodids again showed highest abundance at D1 and much lower abundances at all other D stations (Fig. 4C). *Acartia* spp. was again dominant at D1 (26.9%). *Pseudocalanus* spp. were again most abundant closer to shore, making up 23.9% of the assemblage at D2. *Oithona* spp. increased from 4.7% at D1 to 37.8% at D5. *Microsetella rosea* varied from 14.5% to 19.8% between D2 and D5, with a maximum of 29.9% at D1. *Tortanus discaudatus*, found only at D1 and D2 during previous years, was found further from shore (at D3) in 2002. Both *Oncaea* spp. and *Microsetella rosea* made up larger portions of the assemblages at all stations in 2002 than in 2000 and 2001; *Oncaea* spp. ranged between 13.2% and 18.4% with no discernable cross-shelf pattern.

3.3. Copepod abundance in relation to temporal patterns of winds

Copepod nauplii and copepodid abundances were generally lower during active upwelling and higher during periods of relaxation (Fig. 5). We ran correlations of copepod nauplii and copepodid abundances with Ekman transport values integrated over various time periods (1–10 days) and lagged by different time periods (0–19 days). No apparent patterns were evident when we grouped nearshore and midshelf station (D1–D3) data and compared them to grouped data from outer shelf and offshore stations (D4 and D5). We also examined total nauplii abundances between stations and years and found them to be highly variable.

Total nauplii abundance (all taxa combined) was consistently negatively correlated with Ekman transport (i.e. low abundances corresponded to high upwelling index values). Specifically, nauplii abundance at D2 was negatively correlated ($p<0.05$) with Ekman transport averaged over 1–8 days and lagged by 0–2 days, depending on the year (Table 4). In 2000 only, naupliar abundance was positively correlated with transport when transport was averaged over 1–5 days and lagged by 6 or 7 days. In 2001 only, additional negative correlations were found with transport averaged over 1–5 days and lagged 9–11 days. Otherwise, patterns of total nauplii between stations and years were highly variable.

Considering individual taxa separately yielded additional patterns (results not shown). For instance, significant negative correlations between *Oithona* spp. naupliar abundance at D2 and transport were apparent when transport was averaged over 1–8 days and lagged by 0–1 days (all years). Several significant correlations were found between *Microsetella rosea* nauplii and transport, although no consistent patterns emerged. Interestingly, *Microsetella rosea* nauplii abundance was generally positively correlated with transport when lagged by 0–10 days at D3 and D5 in 2001, whereas the previous taxa tended to be negatively correlated with transport when the lag time was short. *Oncaea* spp. nauplii similarly exhibited a positive correlation to transport when lag periods were short; this correlation was found at stations D1–D3 for all 3 years. Correlations between abundance of early (NI–III) unidentified calanoid nauplii and transport were highly variable, but were generally negative at stations D2–D5 when transport was lagged by less than 13 days and positive when transport was lagged by more than 13 days. Late stage (NIV–VI) unidentified calanoid nauplii showed a consistent negative correlation pattern only in 2000, when transport was averaged over 5–10 days and lagged by 5–16 days.

Total copepodids (all taxa combined) also yielded variable correlations between abundance at D2 and Ekman transport, although correlations were consistently negative (Table 5). In 2000, significant negative correlations occurred when transport was averaged over 1–2 days and lagged for 2–3 days, and again when averaged over 5–10 days and lagged 10–12 days. Correlation patterns in 2001 were similar to those in 2000: negative significant correlations were apparent when averaged over

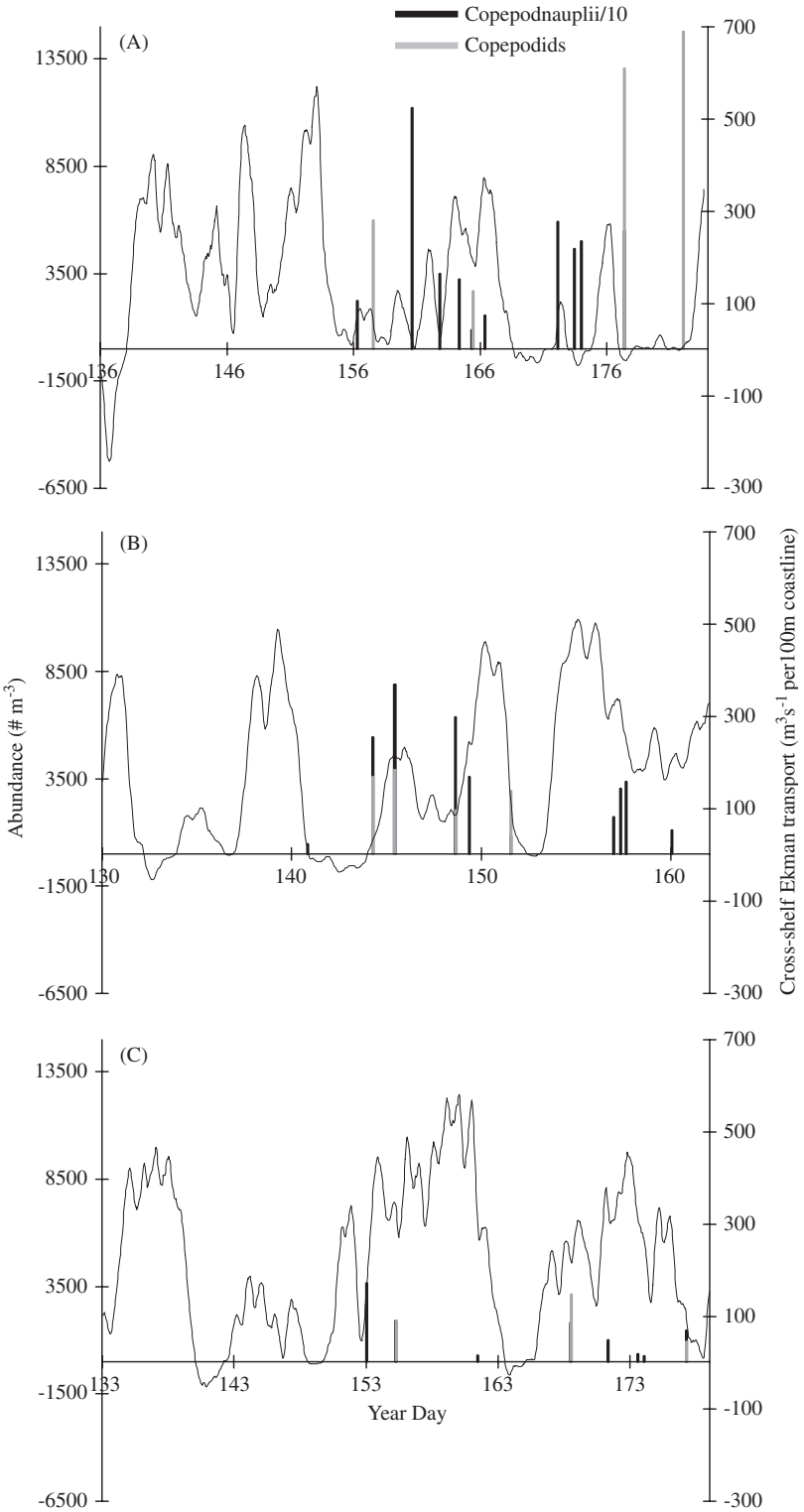

Fig. 5. Ekman upwelling index (15-h moving average) and time series of abundances of copepod nauplii (divided by 10) and copepodids at station D2 in 2000 (A), 2001 (B), and 2002 (C).

Table 4
Correlation coefficients (R) for copepod nauplii abundance at D2 and upwelling index

No. of days over which upwelling values were averaged	Lag (days) between upwelling value and sampling date													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
2000														
1	*−0.506*	*−0.410*	*−0.561*	*−0.348*	*−0.305*	*−0.095*	0.240	**0.769**	0.519	0.409	0.172	*−0.289*	*−0.146*	*−0.183*
2	*−0.525*	*−0.607*	*−0.489*	*−0.346*	*−0.221*	0.067	0.625	**0.696**	0.552	0.342	*−0.083*	*−0.258*	*−0.182*	*−0.443*
3	*−0.614*	*−0.589*	*−0.441*	*−0.296*	*−0.095*	0.484	0.623	**0.693**	0.532	0.125	*−0.135*	*−0.268*	*−0.377*	*−0.369*
4	***−0.647***	*−0.536*	*−0.397*	*−0.215*	0.321	0.518	**0.639**	**0.711**	0.354	0.051	*−0.190*	*−0.429*	*−0.347*	*−0.396*
5	*−0.611*	*−0.499*	*−0.332*	0.124	0.397	0.566	**0.676**	0.614	0.289	*−0.036*	*−0.364*	*−0.397*	*−0.373*	*−0.458*
6	*−0.592*	*−0.449*	*−0.022*	0.238	0.468	0.606	0.613	0.588	0.192	*−0.235*	*−0.333*	*−0.404*	*−0.421*	*−0.400*
7	*−0.567*	*−0.131*	0.123	0.317	0.513	0.555	0.624	0.530	*−0.044*	*−0.219*	*−0.351*	*−0.440*	*−0.373*	*−0.260*
8	*−0.282*	*−0.052*	0.211	0.357	0.456	0.575	0.608	0.298	*−0.066*	*−0.253*	*−0.394*	*−0.405*	*−0.253*	*−0.133*
9	*−0.065*	*−0.155*	0.252	0.295	0.468	0.590	0.382	0.207	*−0.117*	*−0.312*	*−0.366*	*−0.300*	*−0.147*	*−0.055*
10	*−0.050*	*−0.303*	0.186	0.281	0.454	0.359	0.274	0.118	*−0.195*	*−0.290*	*−0.267*	*−0.207*	*−0.084*	*−0.144*
2001	0	1	2	3	4	5	6	7	8	9	10	11	12	13
1	*−0.585*	***−0.703***	*−0.524*	*−0.389*	*−0.240*	*−0.132*	0.046	0.254	0.274	*−0.112*	*−0.204*	*−0.528*	*−0.576*	*−0.184*
2	***−0.676***	***−0.636***	*−0.538*	*−0.357*	*−0.188*	*−0.057*	0.163	0.327	0.037	*−0.159*	*−0.474*	***−0.644***	*−0.418*	0.007
3	***−0.643***	***−0.656***	*−0.595*	*−0.299*	*−0.149*	0.072	0.232	0.231	*−0.063*	*−0.340*	***−0.726***	*−0.598*	*−0.268*	0.049
4	***−0.666***	***−0.764***	*−0.528*	*−0.245*	*−0.039*	0.140	0.206	0.074	*−0.231*	*−0.565*	***−0.745***	*−0.515*	*−0.194*	0.032
5	***−0.778***	***−0.745***	*−0.433*	*−0.137*	0.019	0.104	0.094	*−0.110*	*−0.438*	***−0.625***	***−0.612***	*−0.426*	*−0.185*	0.087
6	***−0.779***	***−0.624***	*−0.301*	*−0.083*	*−0.021*	0.017	*−0.083*	*−0.329*	*−0.521*	*−0.510*	*−0.515*	*−0.404*	*−0.117*	0.192
7	***−0.662***	*−0.479*	*−0.243*	*−0.115*	*−0.081*	*−0.143*	*−0.289*	*−0.511*	*−0.435*	*−0.450*	*−0.527*	*−0.336*	0.002	0.130
8	*−0.523*	*−0.425*	*−0.269*	*−0.157*	*−0.211*	*−0.338*	*−0.498*	*−0.438*	*−0.389*	*−0.488*	*−0.499*	*−0.188*	*−0.036*	*−0.024*
9	*−0.476*	*−0.455*	*−0.297*	*−0.265*	*−0.367*	*−0.483*	*−0.441*	*−0.379*	*−0.440*	*−0.502*	*−0.314*	*−0.198*	*−0.190*	0.098
10	*−0.511*	*−0.475*	*−0.387*	*−0.392*	*−0.437*	*−0.366*	*−0.352*	*−0.496*	*−0.441*	*−0.356*	*−0.302*	*−0.369*	*−0.068*	0.244
2002	0	1	2	3	4	5	6	7	8	9	10	11	12	13
1	*−0.728*	*−0.419*	***−0.812***	*−0.547*	*−0.686*	*−0.483*	*−0.477*	*−0.040*	0.364	*−0.096*	*−0.118*	*−0.313*	*−0.472*	*−0.403*
2	*−0.625*	*−0.703*	***−0.758***	*−0.647*	*−0.629*	*−0.505*	*−0.242*	0.181	0.236	*−0.009*	*−0.238*	*−0.408*	*−0.454*	*−0.267*
3	***−0.744***	*−0.699*	***−0.748***	*−0.648*	*−0.636*	*−0.352*	*−0.011*	0.156	0.126	*−0.138*	*−0.354*	*−0.430*	*−0.353*	*−0.209*
4	***−0.742***	***−0.717***	***−0.724***	*−0.674*	*−0.519*	*−0.150*	0.024	0.091	−0.006	*−0.274*	*−0.402*	*−0.364*	*−0.304*	*−0.129*
5	***−0.758***	*−0.701*	***−0.735***	*−0.589*	*−0.345*	*−0.089*	*−0.011*	*−0.015*	*−0.153*	*−0.344*	*−0.357*	*−0.327*	*−0.243*	*−0.099*
6	***−0.744***	***−0.715***	*−0.672*	*−0.451*	*−0.258*	*−0.109*	*−0.098*	*−0.151*	*−0.239*	*−0.319*	*−0.330*	*−0.278*	*−0.215*	*−0.067*
7	***−0.752***	*−0.663*	*−0.575*	*−0.362*	*−0.263*	*−0.187*	*−0.218*	*−0.237*	*−0.233*	*−0.302*	*−0.284*	*−0.254*	*−0.187*	*−0.119*
8	***−0.707***	*−0.587*	*−0.493*	*−0.358*	*−0.334*	*−0.300*	*−0.294*	*−0.236*	*−0.226*	*−0.261*	*−0.264*	*−0.234*	*−0.217*	*−0.081*
9	*−0.651*	*−0.519*	*−0.486*	*−0.428*	*−0.434*	*−0.369*	*−0.287*	*−0.232*	*−0.186*	*−0.246*	*−0.249*	*−0.257*	*−0.178*	0.009
10	*−0.593*	*−0.519*	*−0.549*	*−0.526*	*−0.495*	*−0.355*	*−0.284*	*−0.194*	*−0.194*	*−0.237*	*−0.272*	*−0.221*	*−0.092*	0.020

Rows indicate number of days over which upwelling values were averaged; columns correspond to duration (number of days) of lag. Negative values are in *italics*; **bold** numbers have p values <0.05; **underlined** numbers have p values <0.01.

1–2 days and lagged 2–3 days, generally positive when averaged over 1–6 days and lagged by 2–6 days, and negative again when averaged over 5–8 days and lagged by 7–8 days. In 2002, total copepodid abundance was negatively correlated to transport when transport was averaged over 1–8 days and lagged 0–2 days, but generally positive when lagged by 5–12 days.

As with copepod nauplii data, correlation patterns became clearer when copepodid taxa were considered individually (results not shown). Correlations between *Oithona* spp. copepodids and transport were most significant in 2002: negative when transport was lagged 0–4 days, positive when lagged by 5–12 days, and negative when lagged by more than 13 days. Results from *Acartia* spp. copepodids were more mixed, with significantly negative correlations to transport averaged over 5–9 days and lagged by 9 days in 2000, and positive correlations with transport lagged by 0–4 days in 2001.

Pseudocalanus spp. copepodid abundance was consistently negatively correlated with Ekman transport when lagged by 2–5 days and positively correlated when lagged by 6–10 or more days during 2000 and 2001. This pattern, interestingly, was

Table 5
Correlation coefficients (R) for copepodid abundance at D2 and upwelling index

No. of days over which upwelling values were averaged	Lag (days) between upwelling value and sampling date													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
2000														
1	*−0.901*	*−0.390*	***−0.964***	***−0.967***	*−0.413*	*−0.296*	*−0.204*	*−0.564*	*−0.947*	*−0.200*	*−0.008*	*−0.244*	*−0.885*	*−0.638*
2	*−0.658*	*−0.512*	***−0.986***	*−0.646*	*−0.374*	*−0.354*	*−0.340*	*−0.771*	*−0.501*	*−0.096*	*−0.119*	*−0.714*	*−0.791*	*−0.756*
3	*−0.703*	*−0.837*	*−0.704*	*−0.535*	*−0.334*	*−0.321*	*−0.508*	*−0.524*	*−0.277*	*−0.167*	*−0.555*	*−0.692*	*−0.836*	*−0.744*
4	*−0.864*	*−0.877*	*−0.581*	*−0.463*	*−0.365*	*−0.428*	*−0.421*	*−0.348*	*−0.316*	*−0.546*	*−0.606*	*−0.763*	*−0.874*	*−0.823*
5	*−0.950*	*−0.759*	*−0.502*	*−0.476*	*−0.431*	*−0.385*	*−0.332*	*−0.383*	*−0.621*	*−0.621*	*−0.712*	*−0.798*	***−0.981***	*−0.787*
6	*−0.870*	*−0.657*	*−0.509*	*−0.527*	*−0.397*	*−0.331*	*−0.383*	*−0.650*	*−0.677*	*−0.736*	*−0.740*	*−0.938*	***−0.971***	*−0.754*
7	*−0.776*	*−0.654*	*−0.557*	*−0.484*	*−0.354*	*−0.380*	*−0.644*	*−0.709*	*−0.779*	*−0.754*	*−0.845*	***−0.992***	*−0.940*	*−0.745*
8	*−0.753*	*−0.682*	*−0.511*	*−0.437*	*−0.390*	*−0.611*	*−0.730*	*−0.806*	*−0.798*	*−0.805*	*−0.946*	***−0.991***	*−0.924*	*−0.688*
9	*−0.775*	*−0.618*	*−0.463*	*−0.472*	*−0.567*	*−0.714*	*−0.828*	*−0.818*	*−0.834*	*−0.891*	***−0.977***	***−0.978***	*−0.853*	*−0.666*
10	*−0.709*	*−0.551*	*−0.497*	*−0.628*	*−0.660*	*−0.806*	*−0.819*	*−0.831*	*−0.901*	*−0.921*	***−0.993***	*−0.896*	*−0.822*	*−0.659*
2001	0	1	2	3	4	5	6	7	8	9	10	11	12	13
1	*−0.108*	*−0.409*	*−0.935*	***−0.957***	0.368	**0.978**	**0.995**	0.676	*−0.765*	*−0.778*	*−0.736*	*−0.321*	*−0.176*	0.112
2	*−0.285*	*−0.651*	***−0.983***	*−0.071*	0.777	**0.997**	0.889	0.057	*−0.773*	*−0.771*	*−0.855*	*−0.246*	*−0.043*	0.898
3	*−0.490*	*−0.782*	*−0.579*	0.601	0.918	0.976	0.709	*−0.471*	*−0.772*	*−0.938*	*−0.647*	*−0.139*	0.383	**0.973**
4	*−0.622*	*−0.628*	0.231	0.858	**0.992**	0.929	0.092	−0.571	*−0.916*	*−0.946*	*−0.470*	0.141	0.612	0.933
5	*−0.533*	*−0.111*	0.748	**0.980**	**0.960**	0.635	*−0.238*	*−0.740*	***−0.993***	*−0.825*	−0.242	0.338	0.658	0.818
6	*−0.128*	0.434	**0.975**	0.924	0.745	0.221	*−0.437*	*−0.908*	*−0.939*	*−0.830*	0.030	0.431	0.682	0.785
7	0.300	0.773	0.911	0.598	0.408	0.119	*−0.709*	***−0.966***	***−0.980***	*−0.736*	0.217	0.472	0.921	0.744
8	0.566	0.767	0.340	0.198	0.460	*−0.024*	*−0.867*	*−0.892*	***−0.980***	*−0.514*	0.206	0.752	0.936	0.763
9	0.460	*−0.146*	*−0.153*	0.094	0.962	0.150	*−0.322*	*−0.761*	*−0.924*	*−0.721*	0.760	0.844	0.719	0.658
10	*−0.186*	*−0.767*	*−0.534*	*−0.410*	0.383	0.794	0.241	*−0.770*	*−0.877*	*−0.786*	0.940	0.545	0.646	0.767
2002	0	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0.193	*−0.541*	*−0.932*	*−0.912*	*−0.984*	*−0.646*	0.263	0.655	0.609	0.751	0.830	0.987	0.940	0.868
2	*−0.181*	*−0.933*	*−0.982*	*−0.995*	*−0.889*	*−0.260*	0.497	0.630	0.681	0.783	0.942	0.965	0.910	0.747
3	*−0.603*	*−0.921*	***−1.000***	*−0.984*	*−0.687*	0.121	0.546	0.674	0.719	0.879	0.941	0.941	0.827	0.544
4	*−0.787*	*−0.986*	*−0.979*	*−0.895*	*−0.353*	0.310	0.609	0.704	0.811	0.899	0.924	0.878	0.715	0.300
5	*−0.941*	***−0.998***	*−0.901*	*−0.677*	*−0.038*	0.438	0.648	0.784	0.846	0.893	0.872	0.806	0.582	*−0.154*
6	*−0.997*	*−0.955*	*−0.722*	*−0.331*	0.182	0.504	0.732	0.821	0.850	0.852	0.809	0.725	0.317	*−0.713*
7	*−0.988*	*−0.823*	*−0.419*	*−0.039*	0.290	0.616	0.777	0.828	0.819	0.799	0.743	0.574	*−0.223*	*−0.932*
8	*−0.891*	*−0.533*	*−0.138*	0.113	0.450	0.687	0.791	0.802	0.770	0.745	0.630	0.255	*−0.723*	*−0.974*
9	*−0.588*	*−0.226*	0.017	0.323	0.564	0.715	0.770	0.758	0.722	0.660	0.421	*−0.296*	*−0.892*	*−0.961*
10	*−0.231*	*−0.049*	0.233	0.481	0.615	0.703	0.726	0.714	0.650	0.529	0.062	*−0.716*	*−0.888*	*−0.954*

Rows indicate number of days over which upwelling values were averaged; columns correspond to duration (number of days) of lag. Negative values are in *italics*, **bold** numbers have p values <0.05; **underlined** numbers have p values <0.01.

reversed (positive–negative) at all stations in 2002. There was a significant positive correlation between *Microsetella rosea* and Ekman transport when transport was averaged over 1–4 days and lagged by about 5 days. This general pattern of positive correlations when transport was lagged only a short time (0–5 days) was consistent across all stations and years for *Microsetella rosea*. This pattern of positive correlations also occurred between abundance of *Oncaea* spp. and transport at all stations in 2000 and was apparent after a slightly longer lag (6–8 days) at the outer shelf stations in 2001 and 2002.

3.4. Copepod distribution and abundance: upwelling versus relaxation conditions

In an effort to directly compare the copepod response to upwelling vs. relaxation conditions, we chose data collected along a cross-shelf transect during a time span that included one active upwelling period and one relaxation period (May–-June 2000). This was the only cruise that provided samples where nauplii and copepodids were sampled at all cross-shelf stations (D1–D5) during both upwelling and relaxation conditions. During active upwelling, copepod nauplii abundances were

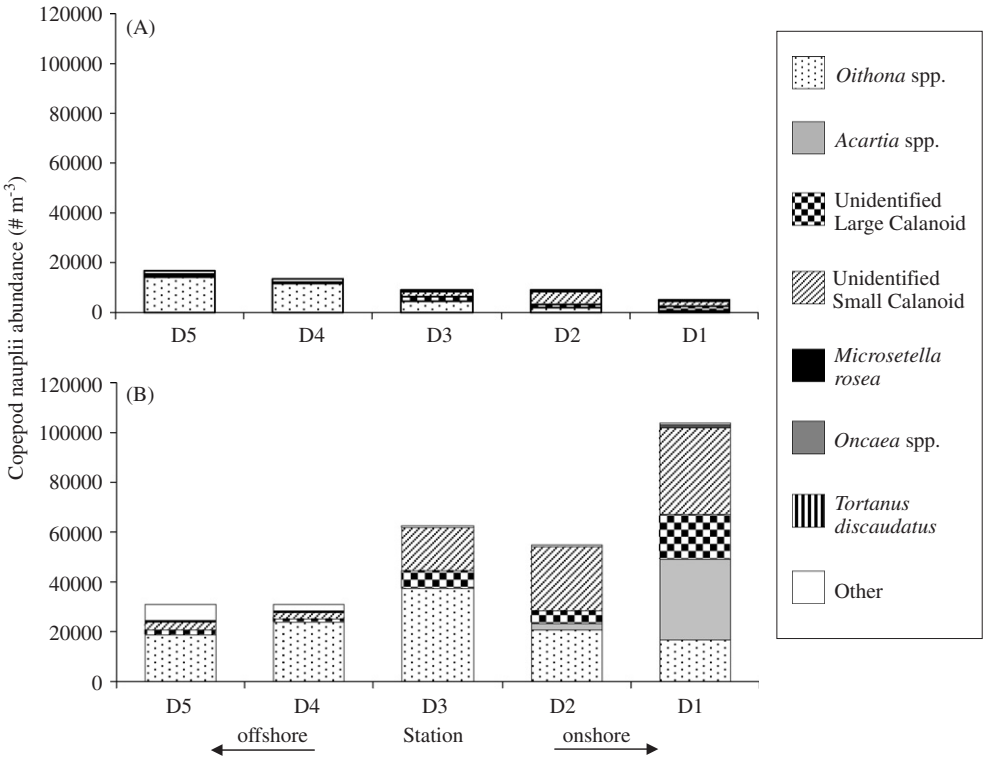

Fig. 6. Cross-shelf abundance and distribution of copepod nauplii along D-line during active upwelling on 12 June 2000 (A) and during relaxation from upwelling on 24 June 2000 (B).

low (less than 20,000 m^{-3}) at all stations and increased slightly with distance from shore (D1–D5) (Fig. 6A). During relaxation, nauplii abundances were generally much higher than during active upwelling, particularly inshore, with decreasing abundance with distance from shore (D1–D5) (Fig. 6B). During both conditions, *Oithona* spp. made up a larger portion of the assemblage at offshore stations than nearshore stations, but was relatively more abundant at nearshore stations during relaxation. *Acartia* spp. and unidentified calanoids were more abundant inshore during relaxation than upwelling.

Copepodid stages also exhibited different patterns of distribution and abundance during active upwelling and relaxation; they were generally more abundant during relaxation, especially at nearshore stations (Fig. 7A and B). They exhibited a different cross-shelf pattern than nauplii during upwelling. During relaxation, the cross-shelf gradient was more pronounced for copepodids than for nauplii. *Pseudocalanus* spp. represented a large portion of the assemblage inshore during both active upwelling and relaxation conditions, but was proportionately more abundant than other copepodid taxa at D3. *Oithona* spp. were more abundant at D2 during relaxation, as were *Acartia* spp. at D1. A cross-shelf gradient of decreasing copepodid abundance with increasing distance from shore (D1–D5) was apparent during both upwelling and relaxation, but the pattern was much more pronounced during relaxation. In addition, a larger proportion of "other" (identified and unidentified) taxa were present inshore during relaxation.

4. Discussion

Among the primary differences between the upwelling seasons of 2000, 2001 and 2002 were the durations of wind-driven upwelling and the intervening periods of relaxation, which resulted in differences in water temperature and chlorophyll *a*. Mean water temperatures and chlorophyll abundances were lower during periods dominated by active upwelling (2001 and 2002) compared to extended periods of relaxation from upwelling (2000).

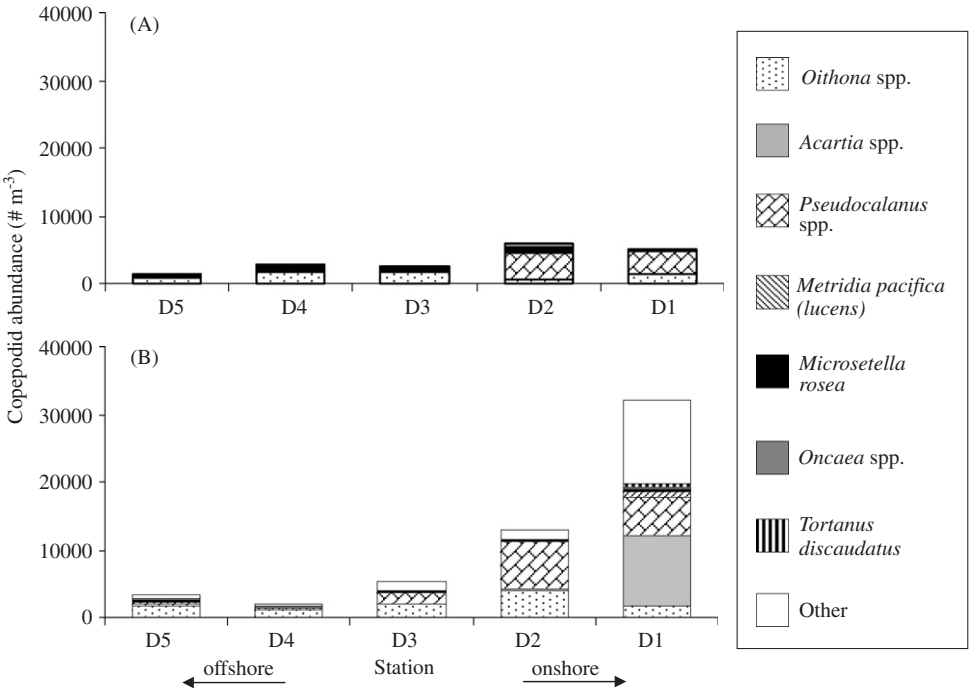

Fig. 7. Cross-shelf abundance and distribution of copepodids along D-line during active upwelling on 4 June 2000 (A) and during relaxation from upwelling on 24 June 2000 (B).

4.1. Copepod community composition, abundance, and cross-shelf distribution

The copepod community composition was consistent over our 3-year course of sampling (all major taxa were found at least once at every station during all three sampling periods). Copepod assemblages were dominated by *Oithona* spp. and *Acartia* spp., and included a substantial proportion of *Pseudocalanus* spp. and *Metridia pacifica* (*lucens*). Unidentified calanoids made up the largest percentage of the nauplii assemblage, with *Microsetella rosea*, *Oncaea* spp. and *Tortanus discaudatus* also present. These results are consistent with Peterson and Keister (2002), who found all of these taxa except *Tortanus discaudatus* in at least 20% of their samples collected near the California-Oregon border. The consistently high abundance of *Oithona* spp. in our samples was not surprising; Bigelow (1926) described *Oithona similis* as the most abundant and ubiquitous copepod in the world. In addition, Gallienne and Robins (2001) suggested that *Oithona* spp. have been historically undersampled by large mesh sizes and underrepresented in the literature. Our mesh sizes of 30 μm (nauplii) and 73 μm (copepodids) were small enough to retain *Oithona* spp.

Copepodid abundances were much lower than nauplii abundances, as expected. We found generally higher copepodid abundances inshore, especially *Pseudocalanus* spp. and *Acartia* spp., with *Oncaea* spp. and *Microsetella rosea* representing the highest proportions of the offshore assemblages. These findings are consistent with Morgan et al. (2003), who reported an on-shelf copepod biomass 2.8 times greater than off-shelf biomass (based on a shelf break at 180 m) and identified *Calanus marshallae*, *Pseudocalanus mimus*, and *Acartia longiremis* as indicators of continental shelf waters in Oregon.

4.2. Effects of upwelling

Our correlation analysis attempted to relate abundance of copepods to calculated Ekman cross-shelf transport. As such, we examined only one of many factors potentially affecting copepod abundance and distribution within this dynamic system; these calculations did not include information about other physical factors (advection of copepods out of the system, offshore wind-stress curl, coastal topography, alongshore transport) or biological processes (birth, development and growth

rates, vertical migration). We can, however, compare patterns of changes in abundance to general patterns of upwelling.

We found a positive correlation between total copepod nauplii abundance and cross-shelf transport averaged over 1–5 days and lagged by 6–7 days in 2000, a year characterized by prolonged periods of relaxation and higher chlorophyll. In the simplest model of the biological response to upwelling, upwelled water brings nutrients into surface waters, where they become available to phytoplankton, resulting in an increase in chlorophyll, and zooplankton (e.g., copepods) respond in turn to this abundant food source by reproducing. In reality, however, it appears that the biological components of the system require not only the introduction of nutrients into the system during coastal upwelling, but also an opportunity to use those nutrients before they are advected out of the system. The generally negative correlations in 2001 and 2002, years dominated by active upwelling, imply that the copepods simply were not able to utilize the nutrients and phytoplankton before they were quickly advected off the shelf or sank out of the system.

One of the most striking taxon-specific patterns we observed was a general negative correlation between *Oithona* spp. nauplii abundance and Ekman transport; *Oithona* spp. were a significant component of the assemblage at every station, but were found in lowest numbers during and just after high values of Ekman transport. This may be due to advection out of the system, as we suspect, or alternatively, from either mortality or vertical migration out of surface waters to avoid increased turbulence (Incze et al., 2001) (both of which were beyond our means of measuring).

On the other hand, we found a consistently positive correlation between Ekman transport and abundance of all stages of both *Microsetella rosea* and *Oncaea* spp. These taxa made up larger percentages of the assemblage at the offshore stations, but exhibited this positive numerical response to upwelling at all stations. The lag time for this positive response was brief (0–6 days), so the high abundance of these taxa could not have been the result of a reproductive response to the particular upwelling event to which their abundance was being correlated. Also, this positive correlation was seen concurrently in both naupliar and copepodid stages, implying the existence of a standing population prior to any given upwelling event. Keister and Peterson (2003) identified *Microsetella* spp. and *Oncaea* spp. as indicators of El Niño conditions in the upwelling zone off Oregon, implying origins to the south (e.g., off California) for these populations. Additionally, Morgan et al. (2003) identified both of these taxa as indicators of off-shelf copepod populations. It is possible that these two taxa are adapted to offshore conditions, such as lower food (chlorophyll) availability, and thus seem to dominate the system when other, nearshore taxa move out of the system during active upwelling. The vertical distribution of these two genera, about which very little is known, might be another possible explanation for the different numerical response of these taxa to upwelling compared to that of other copepods in our study.

Previous research on the effects of upwelling on copepods has yielded mixed results: Smith et al. (1986) found the fewest taxa and lowest abundance of copepods during the strongest upwelling off Pt. Conception, CA. Similarly, Peterson et al. (1988) reported that off Chile, *Acartia tonsa*, *Calanoides patagoniensis*, and *Paracalanus parvus* were found in low abundance during active upwelling and high abundance during relaxation, but *Oithona* spp., *Oncaea* spp., *Centropages brachiatus*, and *Calanus chilensis* exhibited no consistent relationship with upwelling. Our correlations indicate there are some regular patterns of change in copepod abundance in response to wind events off northern California, although species-specific responses are to be expected.

With respect to possible distributional changes, Pillar (1986) reported that persistent mild upwelling off the southern and southwest coasts of Africa resulted in displacement of copepod populations such that peaks in abundance were found offshore. Blackburn (1979) reported similar findings in the upwelling zone off northwest Africa. We did not see this pattern in copepodids, but copepod nauplii, on the other hand, were indeed less abundant nearshore during years with persistent upwelling (2001 and 2002). Copepod nauplii abundance was higher at inshore stations during periods of relaxed winds (2000) and less abundant during strong persistent upwelling-favorable winds (2001 and 2002). Their more uniform cross-shelf distribution in 2001 and 2002 is most easily explained by cross-shelf advection of naupliar stages during upwelling. The increased presence of *Acartia* spp., usually a coastal taxon, at offshore stations in 2002 also might be explained, at least in part, by cross-shelf advection.

In our one direct comparison of an individual upwelling event followed by an individual relaxation event (Fig. 7), we observed abundances of offshore copepodids and nearshore nauplii that were lower during active upwelling and higher during relaxation. This general decrease in zooplankton abundance during active upwelling is consistent with Dorman et al. (2005), who found lower abundances of *Euphausia pacifica* during active upwelling in this same system. Similarly, Smith et al. (1986) reported a decrease in copepod abundance during upwelling, but noted that the percentage of the assemblage comprised by *C. pacificus*, *P. parvus* and *Oithona* spp. increased as upwelling strength increased. Our data support this finding for *Oithona* spp. and *Pseudocalanus* spp. copepodids, which made up a larger percentage of the nearshore assemblage during upwelling than during periods of relaxation. Smith et al. (1986) also found that peaks of nauplii did not occur near the coast, but always coincided with areas of elevated chlorophyll *a*, and were most abundant and farthest from the coast during upwelling. We also found higher abundances of nauplii at offshore stations during upwelling, perhaps due to cross-shelf advection.

Why would different copepod taxa have such dissimilar responses to upwelling? Different behaviors may have evolved as a way to avoid competition for space and resources. For instance, Williams and Conway (1980) reported differing vertical migration behavior patterns which minimized competition between species (*Calanus finmarchicus* and *Calanus helgolandicus*) with sympatric distributions. These different behaviors and distributional patterns lead to different feeding regimes and strategies, and may simplify resource partitioning for taxa co-occurring in an upwelling zone. Such differential vertical distributions may in turn have different implications for each taxon's transport and/or retention on the shelf, and thus their relationship to wind events.

The general increase in abundance of both copepod nauplii and copepodids between upwelling and relaxation events in June 2000 (Figs. 6 and 7) may be due to several factors, as their numbers are affected by both physical factors (advection) and biological factors (reproduction, predation, etc.). While it is not possible with our data to determine the effect of each of these factors, we can examine their relative importance. For instance, copepod nauplii abundance at station D1 increased dramatically over this 12-day period, from $4890\,m^{-3}$ during upwelling to $103{,}826\,m^{-3}$ during relaxation (>21-fold increase) (Fig. 6). Based on exponential population growth, an increase of this magnitude would require a growth rate of $0.254\,d^{-1}$. However, adjusted to the mean temperature of 10 °C measured during our sampling, maximum intrinsic rates of increase for dominant taxa are generally much less than this: approximately $0.12\,d^{-1}$ for *Oithona* spp. (Sabatini and Kiørboe, 1994; Huntley and Lopez, 1992), $0.14\,d^{-1}$ for *Acartia* spp. (Wroblewski, 1980; Huntley and Lopez, 1992), and $0.15\,d^{-1}$ for *Pseudocalanus* spp. (Huntley and Lopez, 1992). Estimates of maximum intrinsic rates of increase usually assume a stable age distribution; even higher rates are theoretically possible in a situation where a population is dominated by adults that reproduce and yields an age distribution that is skewed towards young stages (Bollens, 1988). With respect to copepodids, abundance increased at D1 between upwelling and relaxation events 20 days apart from 5114 to $32{,}000\,m^{-3}$, a 6-fold increase (Fig. 7). This increase would require a growth rate of at least $0.092\,d^{-1}$, which is possible based on maximum growth rates in the literature, but unlikely since such estimates assume no predation or other mortality. Therefore, it is unlikely that our observed changes in abundance were solely due to biological processes; advective processes must have had an impact.

In addition to cross-shelf flow, equatorward alongshore water movement occurs during upwelling-favorable wind events in northern California; this also affects plankton distribution. Huyer (1983) described a southward coastal jet off the coast of Oregon with maximum displacement occurring 15–20 km offshore. Bernal and McGowan (1981) reported that changes in zooplankton biomass during upwelling were uncorrelated with upwelling and were better predicted by transport from the north. Wing et al. (1995) found abundance of meroplankton off northern California to be positively affected by reversal of alongshore currents (i.e. from southerly to northerly) associated with relaxation of upwelling conditions. Thus, the distribution and abundance patterns of copepods we observed are probably associated with alongshore flow patterns in addition to cross-shelf advection.

General offshore movement of upwelled water at the surface is not the only physical oceanographic factor affecting cross-shelf distribution to consider;

an undercurrent of reverse direction also may occur (Huyer, 1983). During active upwelling, copepods may vertically migrate into this layer to be transported back towards shore and avoid being swept out of the upwelling system; this may explain the pronounced pattern of high inshore copepodid abundance seen in 2002. Peterson (1998) presented a model of ontogenetic migration of *Calanus marshallae* in an upwelling zone in which copepod egg-laying occurred near shore, development occurred as individuals were advected offshore, and sinking of stage CV into the deep onshore current resulted in transport back inshore for egg-laying. This model predicted a broad distribution of life stages across the shelf, yet we consistently found all copepodid taxa except *Oithona* spp. to be more abundant close to the shore; perhaps our sampling to a maximum of 200 m was not deep enough to capture all individuals employing diel vertical migration in deeper water.

In addition to alongshore currents and deep countercurrents, other large-scale circulation patterns may affect copepod distribution in this region, such as jets, eddies and flow patterns affected by coastal topography. Huntley et al. (2000) reported distinctly different zooplankton populations in a jet from the California Current and a cyclonic eddy that resulted from it. Lamb and Peterson (2005) suggested that a recirculating gyre off the coast of Oregon may be responsible for nearshore retention of plankton during active upwelling. In and around our (WEST) study site off northern California, Kuebel Cervantes and Allen (2006) modeled recirculation of water displaced offshore by Pt. Reyes and back onshore to the south. Similarly, Vander Woude et al. (2006) used satellite observations to describe two retentive embayments, one north of Pt Reyes and one south of Pt. Reyes (Drakes Bay). The degree to which these recirculation features affect zooplankton populations, however, is currently unknown.

In interpreting our results, it is also necessary to consider possible confounding factors. In a system as dynamic as the northern California coastal upwelling zone, periods of upwelling and relaxation vary in duration and can alternate rapidly. Therefore when calculating our correlations, we cannot always isolate the long-term effects of an individual upwelling event. Correlations occurring at longer lag times (e.g., the significant negative correlation between *Oithona* spp. copepodid abundance and transport lagged over more than 13 days in 2002) may include the effects of several individual wind events.

In summary, we observed that the community composition of copepods in the upwelling region off northern California was quite stable during three consecutive upwelling seasons. Many of these taxa exhibited consistent numerical and/or distributional responses to upwelling transport, but others did not. The cross-shelf distribution of copepods was generally shifted offshore during upwelling and inshore during relaxation events. Copepod nauplii and copepodid abundances were generally much higher in this upwelling zone during relaxation than during active upwelling. Abundances of all life stages generally exhibited a negative correlation with cross-shelf transport averaged over at least 1–4 days and lagged by 0–3 days (with *Microsetella rosea* and *Oncaea* spp. being notable exceptions). Copepod nauplii, on the other hand, seemed to respond positively to wind events lasting 1–5 days followed by a period of relaxation lasting 6 or 7 days. Understanding the exact timescales for different copepod species to respond to individual wind events will require combining field data such as ours with coupled physical–biological models of upwelling ecosystems (e.g., Batchelder et al., 2002; Botsford et al., 2003; Botsford et al., 2006), as well as additional information on the life histories of these particular taxa.

Acknowledgements

We thank Sean Avent, Jeff Dorman, Tessa Johnson and the officers and crew of the R.V. *Point Sur* for assistance in the field. We would also like to thank the Frances Wilkerson and Dick Dugdale labs for providing chlorophyll data and members of Toby Garfield's lab for assistance in writing computer programs. Gratitude is extended to the other members of the CoOP/WEST group for their input and guidance. This project was funded by the National Science Foundation (NSF Grant # OCE-9908072 to S.M. Bollens).

References

Bakun, A., 1973. Coastal upwelling indices, west coast of North America, 1946–71. US Department of Commerce, NOAA Technical Reports NMFS SSRF-671.

Batchelder, H.P., Edwards, C.A., Powell, T.M., 2002. Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally

influenced diel vertical migration on demographic success and nearshore retention. Progress in Oceanography 53 (2–4), 307–333.

Bernal, P.A., McGowan, J.A., 1981. Advection and upwelling in the California Current. In: Richards, F.A. (Ed.), Coastal Upwelling. American Geophysical Union, Washington, DC, pp. 381–399.

Bigelow, J.M., 1926. Plankton of the offshore waters of the Gulf of Maine. Bulletin of the US Bureau of Fisheries 40, 1–507.

Blackburn, M., 1979. Zooplankton in an upwelling area off northwest Africa: composition, distribution and ecology. Deep-Sea Research 26 (1A), 41–56.

Bollens, S.M., 1988. A model of the predatory impact of larval marine fish on the population dynamics of their zooplankton prey. Journal of Plankton Research 10 (5), 887–906.

Botsford, L.W., Lawrence, C.A., Dever, E.P., Hastings, A., Largier, J., 2003. Wind strength and biological productivity in upwelling systems: an idealized study. Fisheries Oceanography 12 (4–5), 245–259.

Botsford, L.W., Lawrence, C.A., Dever, E.P., Hastings, A., Largier, J., 2006. Effects of variable winds on biological productivity on continental shelves in coastal upwelling systems. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2006.07.011].

Cross, F.A., Small, L.F., 1967. Copepod indicators of surface water movements off the Oregon coast. Limnology and Oceanography 12 (1), 60–72.

Dawson, J., Knatz, G., 1980. Illustrated key to the planktonic copepods of San Pedro Bay, California. Technical Reports of the Allan Hancock Foundation #2. Institute for Marine and Coastal Studies, University of Southern California, 106pp.

Dorman, J.G., Bollens, S.M., Slaughter, A.M., 2005. Population biology of euphausiids off northern California and effects of short time-scale wind events on *Euphausia pacifica*. Marine Ecology Progress Series 288, 183–198.

Escribano, R., Hidalgo, P., 2000. Spatial distribution of copepods in the north of the Humboldt Current region off Chile during coastal upwelling. Journal of the Marine Biological Association of the United Kingdom 80 (2), 283–290.

Frost, B., 1989. A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. Canadian Journal of Zoology 67, 525–551.

Gallienne, C.P., Robins, D.B., 2001. Is *Oithona* the most important copepod in the world's oceans? Journal of Plankton Research 23 (12), 1421–1432.

Gardner, G., Szabo, I., 1982. British Columbia pelagic marine copepoda: an identification manual and annotated bibliography. Canadian Special Publication of Fisheries and Aquatic Sciences (62), 536pp.

Gibbons, S.G., Ogilvie, H.S., 1933. The development stages of *Oithona helgolandica* and *Oithona spinirostris*, with a note of the occurrence of body spines in cyclopoid nauplii. Journal of the Marine Biological Association of the United Kingdom 18, 529–550.

Gibson, V.R., Grice, G.O., 1978. The developmental stages of a species of *Corycaeus* (Copepoda: Cyclopoida) from Saanich Island, British Columbia. Canadian Journal of Zoology 56, 66–74.

Hirakawa, K., 1974. Biology of a pelagic harpacticoid copepod, *Microstella norvegica* Boeck in Oshoro Bay, Hokkaido. I. life history. Bulletin of the Plankton Society of Japan 21 (1), 41–54.

Huntley, M.E., Lopez, M.D.G., 1992. Temperature-dependent production of marine copepods: a global synthesis. The American Naturalist 140 (2), 201–242.

Huntley, M.E., Gonzalez, A., Zhu, Y., Zhou, M., Irigoien, X., 2000. Zooplankton dynamics in a mesoscale eddy-jet system off California. Marine Ecology Progress Series 201, 165–178.

Huyer, A., 1983. Coastal upwelling in the California Current system. Progress in Oceanography 12, 259–284.

Incze, L.S., Hebert, D., Wolff, N., Oakey, N., Dye, D., 2001. Changes in copepod distributions associated with increased turbulence from wind stress. Marine Ecology Progress Series 231, 229–240.

Johnson, M.W., 1934. The life history of the copepod *Tortanus discaudatus* (Thompson and Scott). Biological Bulletin 67 (1), 182–200.

Jones, B.H., Halpern, D., 1981. Biological and physical aspects of a coastal upwelling event observed during March–April 1974 off northwest Africa. Deep-Sea Research 28 (1A), 71–81.

Keister, J.E., Peterson, W., 2003. Zonal and seasonal variations in zooplankton community structure off the central Oregon coast, 1998–2000. Progress in Oceanography 57 (3–4), 341–361.

Kuebel Cervantes, B.T., Allen, J.S., 2006. Numerical model simulations of continental shelf flows off northern California. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2006.07.004].

Lamb, J., Peterson, W., 2005. Ecological zonation of zooplankton in the COAST study region off central Oregon in June and August 2001 with consideration of retention mechanisms. Journal of Geophysical Research 110 (C10), C10S15.

Malt, S., 1982. Developmental stages of *Oncaea media* Giesbrecht, 1891 and *Oncaea subtilis* Giesbrecht, 1892. Bulletin of the British Museum of Natural History, Zoology 43 (3), 129–151.

Morgan, C.A., Peterson, W.T., Emmett, R.L., 2003. Onshore–offshore variations in copepod community structure off the Oregon coast during the summer upwelling season. Marine Ecology Progress Series 249, 223–236.

Ogilvie, H.S., 1953. Copepod nauplii. Journal du Conseil International pour l'exploration du Mer Zooplankton Sheet 50.

Olson, J.B., 1949. Pelagic cyclopoid copepods of the coastal waters of Oregon, California and Lower California. Ph.D. Thesis, University of California, Los Angeles.

Peterson, W., 1998. Life cycle strategies of copepods in coastal upwelling zones. Journal of Marine Systems 15 (1–4), 313–326.

Peterson, W.T., Keister, J.E., 2002. The effect of a large cape on distribution patterns of coastal and oceanic copepods off Oregon and northern California during the 1998–1999 El Niño-La Niña. Progress in Oceanography 53, 389–411.

Peterson, W.T., Miller, C.B., Hutchinson, A., 1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. Deep-Sea Research 26 (5A), 467–494.

Peterson, W.T., Arcos, D.F., McManus, G.B., Dam, H., Bellantoni, D., Johnson, T., Tiselius, P., 1988. The nearshore zone during coastal upwelling: daily variability and coupling between primary and secondary production off central Chile. Progress in Oceanography 20 (1), 1–40.

Pillar, S.C., 1986. Temporal and spatial variations in copepod and euphausiid biomass off the southern and south–western

coasts of South Africa in 1977/78. South African Journal of Marine Science 4, 219–229.

Sabatini, M., Kiørboe, T., 1994. Egg production, growth and development of the cyclopoid copepod *Oithona similis*. Journal of Plankton Research 16 (10), 1329–1351.

Slagstad, D., Tande, K.S., 1996. The importance of seasonal vertical migration in across shelf transport of *Calanus finmarchicus*. Ophelia 44 (1–3), 189–205.

Smith, S.L., Boyd, C.M., Lane, P.V.Z., 1981a. Short term variation in the vertical distribution of small copepods off the coast of northern Peru. In: Richards, F.A. (Ed.), Coastal Upwelling. American Geophysical Union, Washington, DC, pp. 417–426.

Smith, S.L., Brink, K.H., Santander, H., Cowles, T.J., Huyer, A., 1981b. The effect of advection on variations in zooplankton at a single location near Cabo Nazca, Peru. In: Richards, F.A. (Ed.), Coastal Upwelling. American Geophysical Union, Washington, DC, pp. 400–410.

Smith, S.L., Jones, B.H., Atkinson, L.P., Brink, K.H., 1986. Zooplankton in the upwelling fronts off Pt. Conception, California. In: Nihoul, J.C.J. (Ed.), Marine Interfaces Ecohydrodynamics (Elsevier Oceanography Series vol. 42). Elsevier, New York, pp. 195–214.

Strickland, J.D.H., Parsons, T.R., 1972. Spectrophotometric determination of chlorophylls and total carotenoids. In: Strickland, J., Parsons, T. (Eds.), A Practical Handbook of Seawater Analysis. Fisheries Research Board of Canada, Bulletin #167, Ottawa, pp. 185–196.

Trujillo-Ortiz, A., 1986. Life cycle of the marine calanoid copepod *Acartia californiensis* Trinast reared under laboratory conditions. California Cooperative Oceanic Fisheries Investigations Reports 27, 188–204.

Vander Woude, A.J., Largier, J.L., Kudela, R.M., 2006. Nearshore retention of upwelled waters north and south of Point Reyes (northern California) — patterns of surface temperature and chlorophyll observed in CoOP WEST. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2006.07.003].

Verheye, H.M., Field, J.G., 1992. Vertical distribution and diel vertical migration of *Calanoides carinatus* (Kroeyer, 1849) developmental stages in the southern Benguela upwelling region. Journal of Experimental Marine Biology and Ecology 158, 123–140.

Verheye, H.M., Hutchings, L., 1988. Horizontal and vertical distribution of zooplankton biomass in the southern Benguela, May 1983. South African Journal of Marine Science 6, 255–265.

Verheye, H.M., Hutchings, L., Peterson, W.T., 1991. Life history and population maintenance strategies of *Calanoides carinatus* (Copepoda: Calanoida) in the southern Benguela ecosystem. South African Journal of Marine Science 11, 179–191.

Verheye, H.M., Hutchings, L., Huggett, J.A., Painting, S.J., 1992. Mesozooplankton dynamics in the Benguela ecosystem, with emphasis on the herbivorous copepods. South African Journal of Marine Science 12, 561–584.

Wilkerson, F.P., Lassiter, A.M., Dugdale, R.C., Marchi, A., Hogue, V.E., 2006. The phytoplankton bloom response to wind events and upwelled nutrients during the CoOP-WEST study. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2006.07.007].

Williams, R., Conway, D.V.P., 1980. Vertical distributions of *Calanus finmarchicus* and *C. helgolandicus* (Crustacea: Copepoda). Marine Biology 60 (1), 57–61.

Wing, S.R., Botsford, L.W., Largier, J.L., Morgan, L.E., 1995. Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Marine Ecology Progress Series 128, 199–211.

Wroblewski, J.S., 1980. A simulation of the distribution of *Acartia clausi* during Oregon Upwelling, August 1973. Journal of Plankton Research 2 (1), 43–68.

Wroblewski, J.S., 1982. Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone—a simulation. Deep-Sea Research 29 (6A), 665–686.