

Population biology of euphausiids off northern California and effects of short time-scale wind events on *Euphausia pacifica*

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ABSTRACT: Variability in upwelling conditions has been shown to change the physical and biological characteristics of the water over the California shelf, including the population biology of the dominant euphausiid *Euphausia pacifica*. However, on a short time-scale (ca. weekly), far less is known, especially for larger planktonic animals like euphausiids. We examined *E. pacifica* abundance, size structure, oocyte composition, and euphausiid egg abundance in an upwelling region off northern California in June 2000, May and June 2001 and January 2002. Euphausiid egg abundance increased on a short time-scale during and after periods of relaxation and larval *E. pacifica* abundance decreased significantly during upwelling in June 2000 and January 2002, presumably due to interaction with offshore surface currents. Diel vertical migration out of the advective surface layer during the day by adults and juveniles may enhance shelf retention of euphausiids during upwelling events. Seasonally, a reduction in reproductive effort of *E. pacifica* (no. of oocytes female⁻¹) was observed during January 2002. Interannually, *E. pacifica* abundance was significantly higher during June 2000, a year of less intense upwelling, than in May and June 2001, a year of more intense upwelling. Thus, upwelling-favorable winds following periods of relaxation can lead to rapid increases in euphausiid egg abundance, but larval abundance, and perhaps juvenile and adult abundance as well, are likely to be negatively impacted locally by strong upwelling off Northern California.

KEY WORDS: Zooplankton · Euphausiid · Upwelling · Wind · Short time-scale · *Euphausia pacifica*

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INTRODUCTION

Coastal upwelling regions are some of the most productive areas in the world's oceans. The strength of upwelling can be highly variable, with local wind-forcing enhancing or diminishing upwelling depending on the magnitude and direction of the wind. The timing and duration of upwelling and relaxation events can also have significant effects on the physical and biological properties of the coastal ocean, including on a short time-scale. This short time-scale is variable, as it is dependent upon wind shifts from upwelling-favorable to relaxation (or downwelling)-favorable conditions. In our region of study, these wind events can range from a few days to a few weeks.

On the Northern California continental shelf, cross-shelf currents are coupled to atmospheric wind-forcing and move surface waters offshore during upwelling events (Steger et al. 2000). During relaxation events, studies on meroplankton settlement (Send et al. 1987, Wing et al. 1998) have described a shift to northerly and onshore flow of water, indicating a rapid response in currents to changes in wind patterns. Sea surface temperature (SST) also has been correlated to wind events, beginning to decrease approximately 1 d after the onset of upwelling-favorable winds (Winant et al. 1987, Largier et al. 1993, Wing et al. 1995b). Phytoplankton responds rapidly to wind events, increasing biomass and productivity as nutrients are input into the system by upwelling events (Barber & Smith 1981).

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Microzooplankton also respond to increases in phytoplankton via increased grazing (Boyd et al. 1980, Boyd & Smith 1983, Peterson et al. 1988) and increased biomass (Peterson et al. 1988). Thus, a significant amount of work has shown that off Northern California, water properties and small planktonic organisms respond to changes in short time-scale winds. However, little work has been done on the responses of larger planktonic organisms, such as euphausiids, to such events.

Euphausiids are a significant component of the zooplankton community in many upwelling regions and occupy an important place in marine food webs. They are omnivorous feeders (Ohman 1984, Barange et al. 1991, Gibbons et al. 1991, Suh et al. 1991, Båmstedt & Karlson 1998, Dilling et al. 1998, Gurney et al. 2001, Hernandez-Leon et al. 2001) and are consumed by many predators including seabirds (Ainley et al. 1996), pelagic fishes (Genin et al. 1988, Reilly et al. 1992, Tanasichuk 1999) and marine mammals (Fiedler et al. 1998). Euphausiids of the California Current have been the subject of many studies (Brinton 1960, 1962, Brinton & Wyllie 1976, Youngbluth 1976, Mullin & Conversi 1988, Simard & Mackas 1989), with some focusing only on the most dominant species of the Northern California region, *Euphausia pacifica* (Smiles & Pearcy 1971, Brinton 1976). Much of the work has focused on large temporal scales, examining seasonal and interannual differences in community structure and population biology, but not investigating short time-scale changes. Most of the previous studies have also taken place on a large spatial scale, extending well into oceanic waters, with less focus on the continental shelf region. The responses of euphausiids to short time-scale changes in their physical and biological environment in coastal upwelling regions have remained largely unstudied.

Summer wind patterns over the continental shelf of Northern California are driven by 2 relatively stationary pressure systems and are characterized by events of strong equatorward, alongshore winds (creating upwelling events), which can persist for extended periods of time (weeks). These winds are intensified in this particular region by the marine boundary layer and coastal mountain ranges (Halliwell & Allen 1987, Dorman & Winant 1995), creating one of the most consistently windy places on the west coast of North America during the summer. Winds of weaker magnitude,

more variable direction, and shorter duration (creating relaxation events) intersperse periods of strong equatorward, alongshore winds. In contrast, winter winds are governed by passage of intense cyclones and anticyclones and tend to fluctuate more than summertime wind conditions (Halliwell & Allen 1987). This decreases the opportunity for extended upwelling and promotes more stable or downwelling-favorable conditions.

The purpose of this study was to examine the effects of short time-scale changes in wind patterns on euphausiids over the continental shelf of Northern California. In particular, we examined how winds affect euphausiid community composition and reproductive effort, as well as abundance, size structure and ovary composition, of the dominant euphausiid *Euphausia pacifica*. Seasonal and interannual changes were also examined and compared to findings from previous studies.

MATERIALS AND METHODS

Wind and SST data were collected from National Data Buoy Center (NDBC) stations, and chlorophyll *a* and zooplankton data were collected on the RV 'Point Sur' from a survey grid off Northern California (Fig. 1).

Physical data. Hourly values of wind speed, wind direction and SST were obtained from NDBC Stn 46013 (38° 13' 37" N, 123° 19' 48" W) during 2000 and

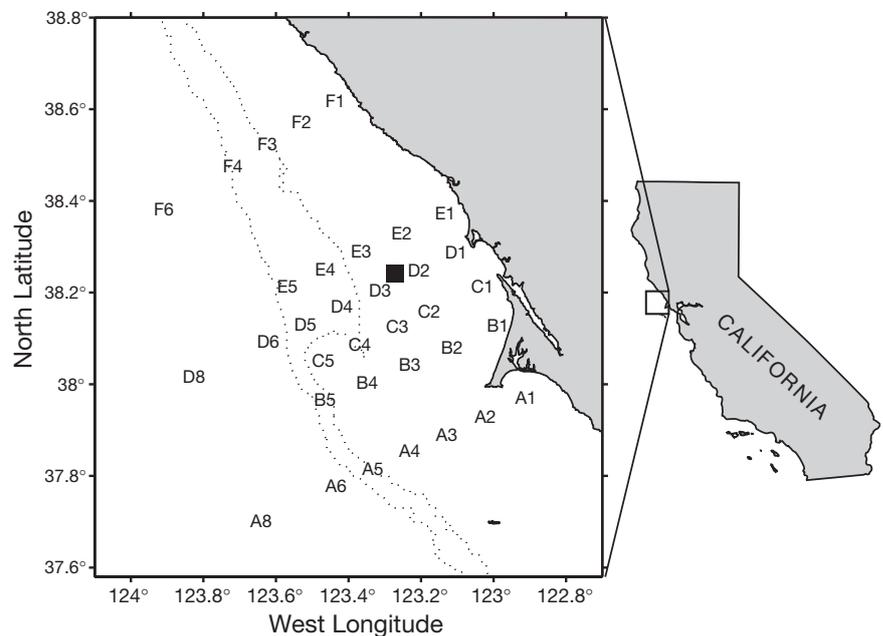


Fig. 1. Euphausiid sampling stations and NDBC Stn 46013 (■) within the study area off northern California; 200 and 1000 m isobaths represented by dotted lines

2001. Because NDBC Stn 46013 did not report data during January 2002, wind and SST data were collected from NDBC Stn 46026 (37° 45' 32" N, 122° 50' 00" W), located approximately 75 km to the southeast. Wind direction was rotated 40° into alignment with the coastline, and the wind speed and direction were broken up into alongshore and cross-shelf components. As wind data from January 2002 came from a location outside the study area, correlation analyses were run to determine the relationship between data from NDBC Stn 46026 and NDBC Stn 46013. Alongshore winds from these 2 stations were positively correlated during January 1999 ($r = 0.873$, $df = 455$, $p < 0.001$), January 2000 ($r = 0.904$, $df = 702$, $p < 0.001$), and January 2001 ($r = 0.891$, $df = 732$, $p < 0.001$) with an average regression slope of 0.7679 in the alongshore direction and 0.876 in the cross-shelf direction. While the stations showed similar trends during the 3 January months examined, wind speeds were slightly muted at NDBC Stn 46026. This variability in wind patterns between stations should be considered in examining the results. Temperature data were also collected from CTD casts using a Seabird 911 Plus CTD.

Biological data. Chlorophyll *a* water samples were collected in a 10 l Niskin bottle from a depth of 5 m at each station along our cruise track. Chlorophyll *a* concentration was measured via fluorometry for the entire population retained on a GF/F filter (nominal pore size 0.7 μm) using a protocol by Venrick & Hayward (1984), adapted from Holm-Hansen et al. (1965).

Bongo net zooplankton surveys (Table 1) were completed using 0.6 m diameter paired bongos fitted with 335 and 500 μm mesh nets to sample macrozooplankton such as euphausiids and larval fishes. Ring net surveys (Table 1) were completed using a 1.0 m diameter

ring fitted with a 73 μm mesh net in June 2000 and a 0.5 m diameter ring fitted with a 73 μm mesh net at all other sampling times to sample smaller zooplankton including early developmental stages of euphausiids. The bongo nets and ring net were towed from a depth of 200 m to the surface or from 5 m off the bottom, whichever was less. Bongo nets were towed obliquely at a ship speed of 2 knots and hauled back at 10 m min^{-1} . The ring net was hauled vertically at a rate of 10 m min^{-1} . Some studies have shown that towed net systems can underestimate adult euphausiid abundance (Pillar 1984, Hovekamp 1989, Sameoto et al. 1993). This possible underestimate, not quantified in this study, should not confound our results or interpretation, as we used the same bongo net system throughout our entire study. All nets were fitted with General Oceanics® flowmeters to determine the amount of water filtered by the net. Samples were preserved in a buffered 10% formalin–seawater solution for later analysis.

In the laboratory, subsamples of the preserved bongo samples were taken (if the total number of euphausiids was greater than approximately 400) using a 1 l Folsom splitter (target number of euphausiids in the subsample was 200). From the subsample, all euphausiids over 3 mm were identified, measured and sexed as male, female, or juvenile. Euphausiid species identification and sex determination was based on Brinton et al. (2000). A subsample of each preserved ring net sample was taken using a Stemple pipette and the euphausiid eggs were enumerated.

During June 2000 and May and June 2001, 1 station over the shelf and 1 station off the shelf from 4 of the 5 bongo net sampling periods (Table 1) were selected to examine female *Euphausia pacifica* ovary composition. During January 2002, 3 stations off the shelf were selected to examine ovary composition, being the only

stations where adult females were abundant. Adult females were selected from the entire sample, as enough adult females were not available from the subsamples used for community composition, abundance, and mean size analysis. For each of these stations, 10 adult females of a common size (19 to 23 mm; mean \pm SE = 21.8 \pm 0.13) were examined for external sexual characteristics, and each individual was weighed. The ovary was dissected out, weighed, and the oocytes of the ovary were sorted by maturity and enumerated. Oocyte maturity categories have not previously been reported for

Table 1. Zooplankton sampling: net used, dates sampled, and location (see Fig. 1)

Cruise dates	Net type	Survey dates	Stations sampled
June 1–30, 2000	Bongo (60 cm)	Jun 2–4	A1, 2, 4, 6, 8; D1–4, 6, 8 F1, 4, 6
	Ring (1.0 m)	Jun 4–5	B1–5; C1–5; D1–5 E1–5
	Bongo (60 cm)	Jun 17–19	A1, 2, 4, 6, 8 D1, 2, 4, 6, 8 F1, 2, 4, 6
	Ring (1.0 m)	Jun 24–25	C1–5; D1–5; E1–5
May 17–June 15, 2001	Bongo (60 cm)	May 19–21	A8; D1–4, 6, 8 F1, 2, 4, 6
	Ring (0.5 m)	May 23	D1–5
	Ring (0.5 m)	May 24	D1–4
	Ring (0.5 m)	May 27	D1–6
	Ring (0.5 m)	May 30	D1–6
	Bongo (60 cm)	Jun 3–7	A1, 2; D2, 3; F1, 2, 4, 6
	Bongo (60 cm)	Jun 11–13	A1–6, 8; D1–3, 8 F1, 2
January 8–24, 2002	Bongo (60 cm)	Jan 9–11	A1–4, 6, 8; D1–4, 6, 8 F1–4, 6
	Bongo (60 cm)	Jan 21–22	A1, 2, 4, 6; D1–4, 6

E. pacifica, and were therefore adapted from oocyte maturation work on the Antarctic species *E. superba* (Cuzin-Roudy & Amsler 1991).

Statistical analyses. Differences in euphausiid community composition (measured as species percentage of the euphausiid community), euphausiid egg abundance, *Euphausia pacifica* abundance, mean size and ovarian oocyte composition on short time, seasonal, and interannual scales were examined with Mann-Whitney *U*-tests. This test was selected instead of a Student's *t*-test as data normality could not be confidently determined due to small sample sizes. Where sample sizes were large (e.g. *E. pacifica* mean size), visual inspection of the data indicated non-normality. As exactly the same stations were not sampled during each survey, only those stations that were sampled in consecutive surveys were used in short time-scale analyses. Statistical analyses were run with SPSS 10.0®.

RESULTS

Wind, hydrographic and chlorophyll *a* data

Predominant winds tend to blow in an alongshore direction off Northern California (Halliwell & Allen 1987, Dorman & Winant 1995) and are closely coupled with cross-shelf transport of water (Steger et al. 2000). We observed cross-shelf winds to be much weaker in magnitude than alongshore winds (Fig. 2). Thus, in the following 'Results' and 'Discussion' sections, we refer only to the alongshore component of the wind, although the cross-shelf winds are shown in Fig. 2. Wind speed is presented with negative alongshore values representing northwesterly (equatorward) winds. This area experiences large variability in wind strength on many different time-scales, from hours to days to weeks, as seen in our June 2000, May and June 2001 and January 2002 data sets (Fig. 2). In the interest of clarity, the relative terms 'weak' and 'strong' events are used throughout to identify differing upwelling states, on a weekly time-scale, despite variability within any one event itself.

Winds were strong northwesterly (alongshore) during May and June of 2000 and 2001, and were weaker and more variable during January 2002. Our sampling during June of 2000 was preceded by a strong wind event (7 d mean = -11.3 m s^{-1}). Wind speed decreased throughout the sampling period, averaging -5.3 m s^{-1} during the first 2 wk and -2.6 m s^{-1} during the last 2 wk (Fig. 2A). The entire sampling period was characterized by weaker than average winds (sample period mean = -4.19 m s^{-1}) compared to monthly averaged winds from 1981 to 1999 (June mean = -6.73 m s^{-1})

(data not shown). Upwelling, as measured by the Bakun upwelling index (Bakun 1973), prior to sampling (January to May 2000) was below average in 4 of the 5 months.

Sampling during May and June 2001 was preceded by a fairly weak wind event (7 d mean = -3.3 m s^{-1}). Wind speed increased over the course of the cruise from an average of -6.2 m s^{-1} during the first 2 wk to -11.4 m s^{-1} during the final 2 wk (Fig. 2B). Winds were, on average, stronger (sample period mean = -8.81 m s^{-1}) than monthly averaged winds from 1981 to 1999 (May and June mean = -6.77 m s^{-1}) (data not shown) and relaxation events were less pronounced in magnitude and duration than in June 2000 (Fig. 2A,B). Upwelling prior to sampling (January to May 2001) was above average in 4 of the 5 months.

Winds in January 2002 exhibited a more significant cross-shelf component than in the summers of 2000 and 2001 but, like summertime winds, exhibited significant variability in the alongshore direction. The 7 d averaged wind speed changed from $+2.9 \text{ m s}^{-1}$ before the first sampling period to -5.5 m s^{-1} before the second sampling (Fig. 2C).

SSTs were positively correlated to northwesterly wind strength during 2000 and 2001 ($r = 0.705$, $df = 57$, $p < 0.001$). During the relatively low-wind year of 2000, daily averaged SST ranged from 9°C at the beginning of our sampling to 13°C at the end of sampling, following 2 wk of low wind (Fig. 3A). In 2001, daily averaged SST was less variable and generally cooler, ranging from 9 to 10.5°C (Fig. 3B). Daily averages of SST in January 2002 showed little variability, ranging from 10.5 to 12°C , decreasing slightly as northwesterly winds increased toward the end of our sampling period (Fig. 3C). Spatially, SST was more variable in the cross-shelf direction during June 2000, with higher temperatures offshore and colder water over the continental shelf (Fig. 4A). During May and June 2001 and January 2002, however, little cross-shelf variability in SST was evident (Fig. 4C,E).

Chlorophyll *a* concentrations at Stn D2 (Fig. 1) were highly variable, ranging from 33 to $<1 \mu\text{g l}^{-1}$ during June 2000 and from 15 to $<1 \mu\text{g l}^{-1}$ during May and June 2001 (Fig. 3A,B). Both peaks in chlorophyll *a* occurred after periods of intense winds were followed by a few days of relaxed winds. Chlorophyll *a* concentrations during January 2002 showed little variability and were quite low, ranging from 2 to $<1 \mu\text{g l}^{-1}$ (Fig. 3C). Spatially, the highest concentrations of chlorophyll *a* were evident over the continental shelf and to the south of the study area during May and June 2000 and 2001 (Fig. 4B,D). There was little variability in the cross-shelf or along-shelf direction during January 2002 (Fig. 4F).

Euphausiid community composition

The euphausiid community was primarily comprised of *Euphausia pacifica* and *Thysanoessa spinifera*. *E. pacifica* was the most dominant euphausiid, comprising 77.3% of the community in offshore and mid-shelf

waters, but only 10.9% of the community in water <50 m deep. *T. spinifera* was dominant over the inner shelf in water <50 m deep, comprising 88.8% of the community (Fig. 5A–D), but comprising only 17.0% of the community in water >50 m deep. These cross-shelf differences in species percentages between stations in

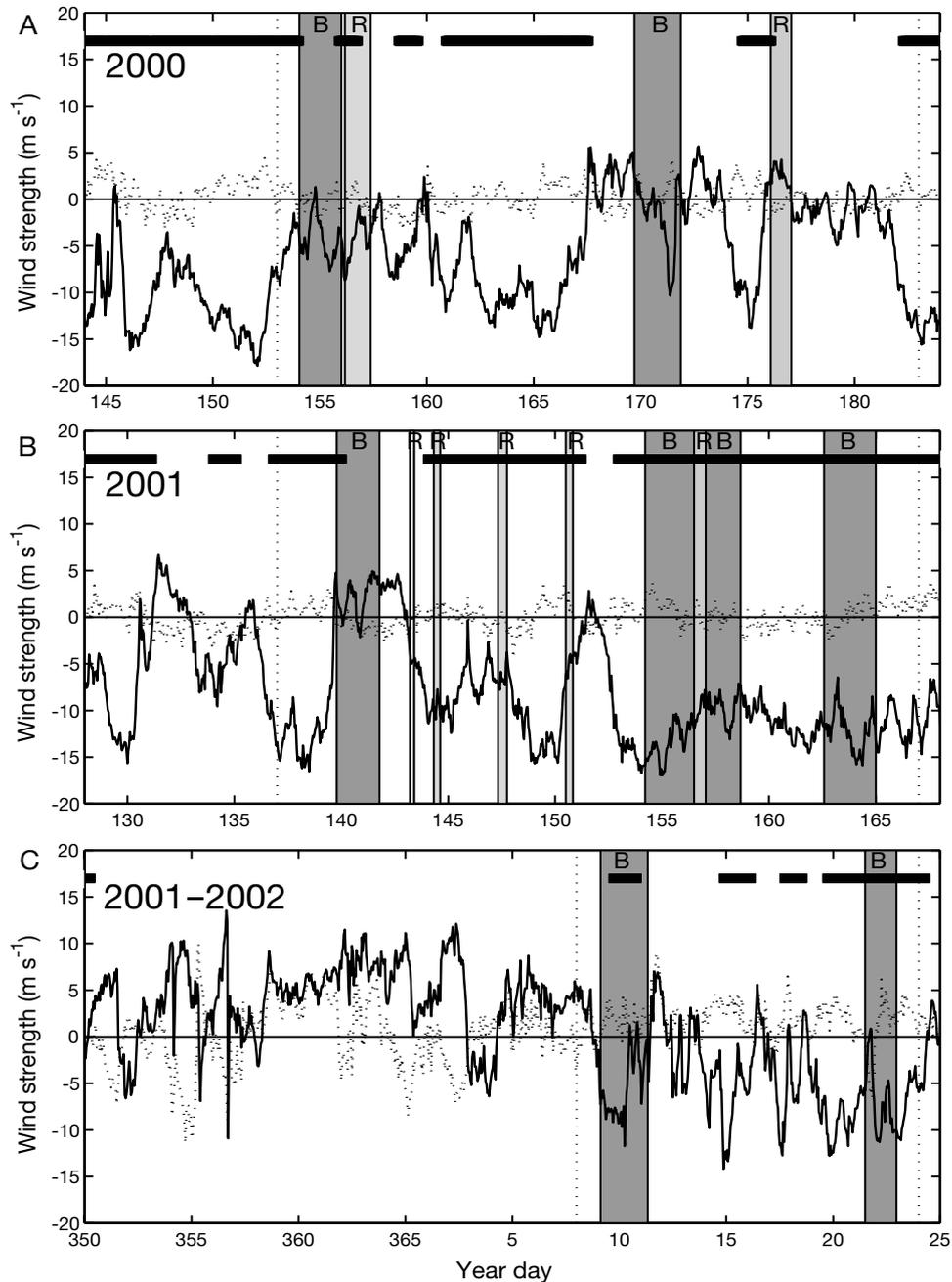


Fig. 2. Alongshore (continuous curves) and cross-shelf (dotted curves) wind speed for NDBC Stn 46013 for (A) May 23 to July 1, 2000 and (B) May 7 to June 16, 2001, and for NDBC Stn 46026 for (C) December 15, 2001 to January 25, 2002. Negative/positive values of wind speed represent NW/SE wind directions; dotted vertical lines show cruise start and end dates; shaded B and R areas show times of bongo net and ring net surveys, respectively; horizontal black bars represent periods of upwelling when 6 h running average of alongshore, northwesterly wind speed was $>5 \text{ m s}^{-1}$

<50 m of water and those in >50 m of water were highly significant for both *E. pacifica* ($U = 451$, no. of observations in Sample 1 [n_1] = 10, no. of observations in Sample 2 [n_2] = 47, $p < 0.001$) and *T. spinifera* ($U = 453$, $n_1 = 10$, $n_2 = 47$, $p < 0.001$).

Seasonally, *Euphausia pacifica* dominated the community composition in both summer (65.6%) and

winter (74.1%) (Fig. 5). The percentage of *Thysanoessa spinifera* was significantly lower in winter (6.8%), than in summer (29.6%) ($U = 894.5$, $n_1 = 23$, $n_2 = 57$, $p < 0.01$) (Fig. 5); 2 other species that were present only in trace amounts during May and June 2000 and 2001, but to a greater degree in January 2002, were *Nematoscelis difficilis* and *Stylocheiron*

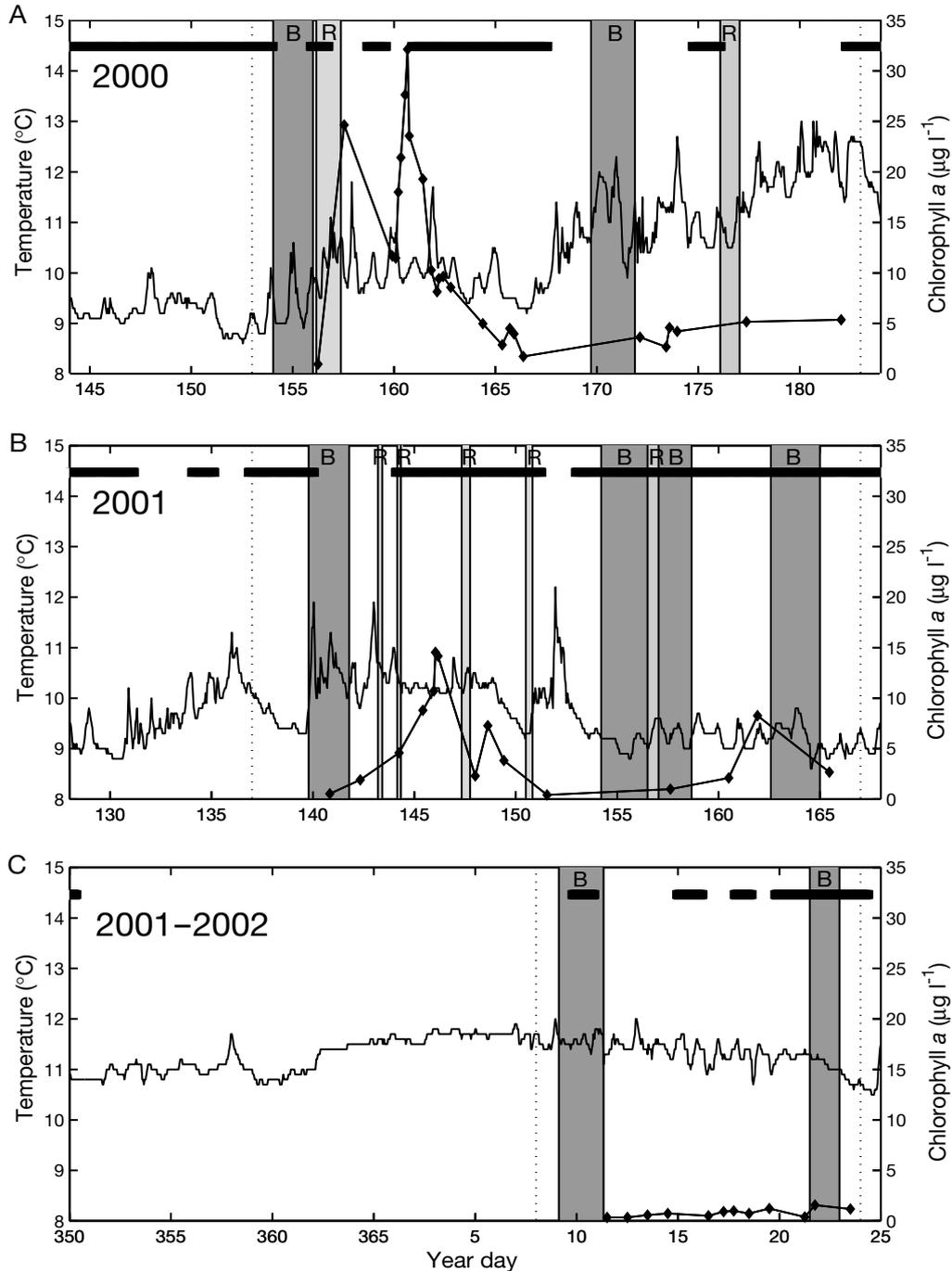


Fig. 3. Sea surface temperature for NDBC Stn 46013 (—) and chlorophyll *a* for Stn D2 (—◆—) for (A) May 23 to July 1, 2000 and (B) May 7 to June 16, 2001; and (C) sea surface temperature for NDBC Stn 46026 (—) and chlorophyll *a* for Stn D2 (—◆—) for December 15, 2001 to January 25, 2002. Further details as in Fig. 2

longicorne. *N. difficilis* comprised 6.4% of the community during summer and 17.5% during winter ($U = 1076$, $n_1 = 23$, $n_2 = 57$, $p < 0.01$), while *S. longicorne* comprised 3.7% of the community during summer and 10.8% during the winter (Fig. 5E,F) ($U = 903$, $n_1 = 23$, $n_2 = 57$, $p < 0.01$). There was

little interannual change in the community composition between June 2000 and May and June 2001 (Fig. 5A–D). As *E. pacifica* was the dominant euphausiid during both winter and summer, and only more limited data are available on other species, we focus primarily on *E. pacifica*.

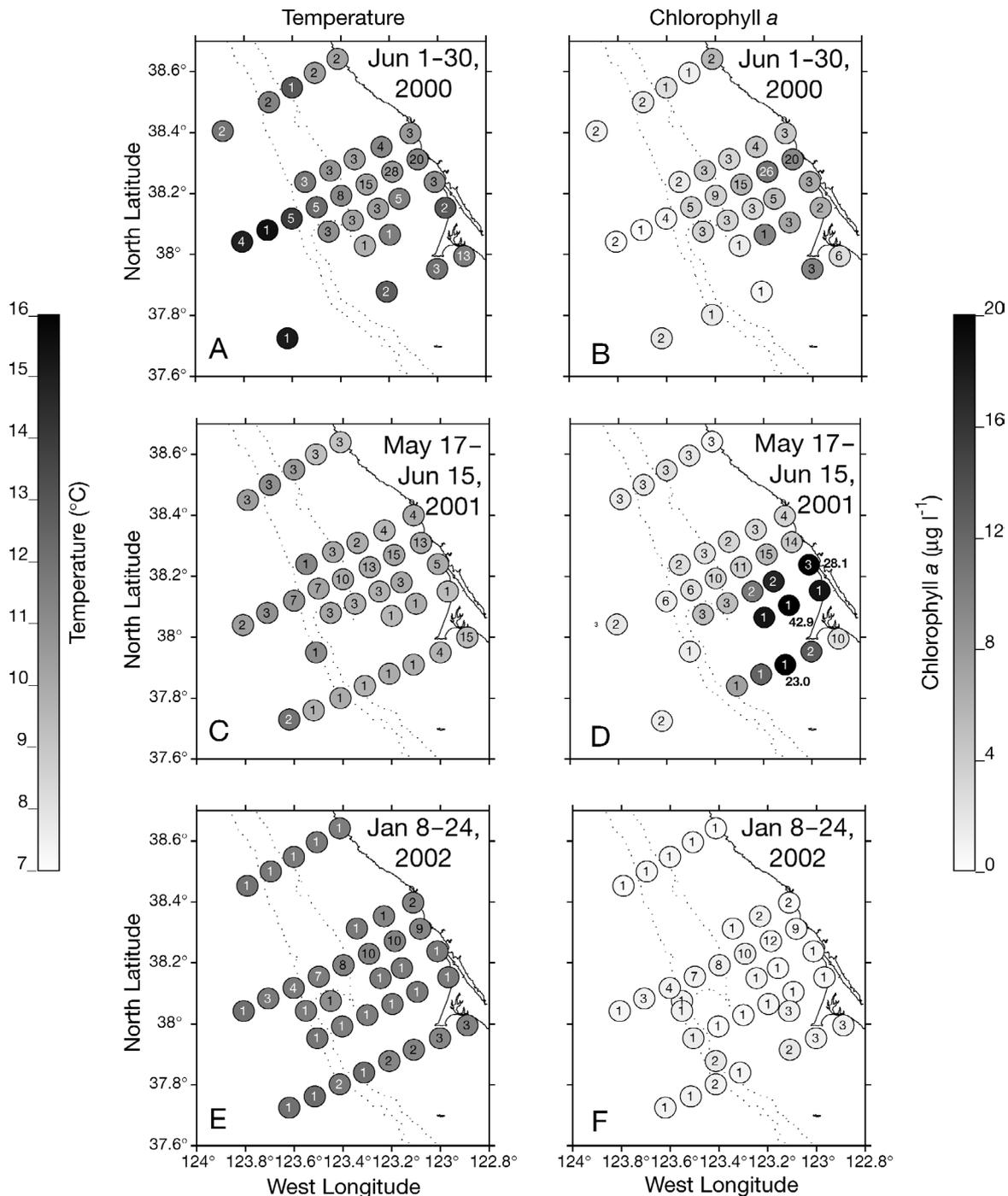


Fig. 4. Sea surface temperature and chlorophyll a for (A,B) June 1 to 30, 2000, (C,D) May 17 to June 15, 2001, and (E,F) January 8 to 24, 2002. Numbers in circles are no. of samples

***Euphausia pacifica* abundance**

Abundance of *Euphausia pacifica* did not change significantly on a short time-scale in response to different wind strengths over the course of either summer-time sampling period. Average abundance (ind. m⁻³ ± SE) changed from 8.3 ± 2.38 to 7.2 ± 2.45 from early to mid-June during 2000 (Fig. 6A,B) and from 2.3 ± 0.91 to 3.8 ± 1.30 over the course of sampling during 2001 (Fig. 6C,D). Abundance of the smallest size class of *E. pacifica* sampled in the bongo nets, 3 to 5 mm, was significantly lower during periods of upwelling in June

2000 ($U = 143, n_1 = 14, n_2 = 14, p < 0.05$), but not in May and June 2001. Abundance of total (mostly larval) *E. pacifica* decreased significantly ($U = 64, n_1 = 9, n_2 = 9, p < 0.05$) from 10.8 ± 6.79 ind. m⁻³ just after an extended relaxation event to 0.8 ± 0.43 ind. m⁻³ after an upwelling event in January 2002 (Fig. 6E,F).

Seasonally, no significant difference in abundance of *Euphausia pacifica* was observed. However, abundance of *E. pacifica* was significantly higher in June 2000 (7.9 ± 1.63 ind. m⁻³), than in May and June 2001 (3.6 ± 1.03 ind. m⁻³) ($U = 595, n_1 = 28, n_2 = 32, p < 0.05$) (Fig. 6A–D).

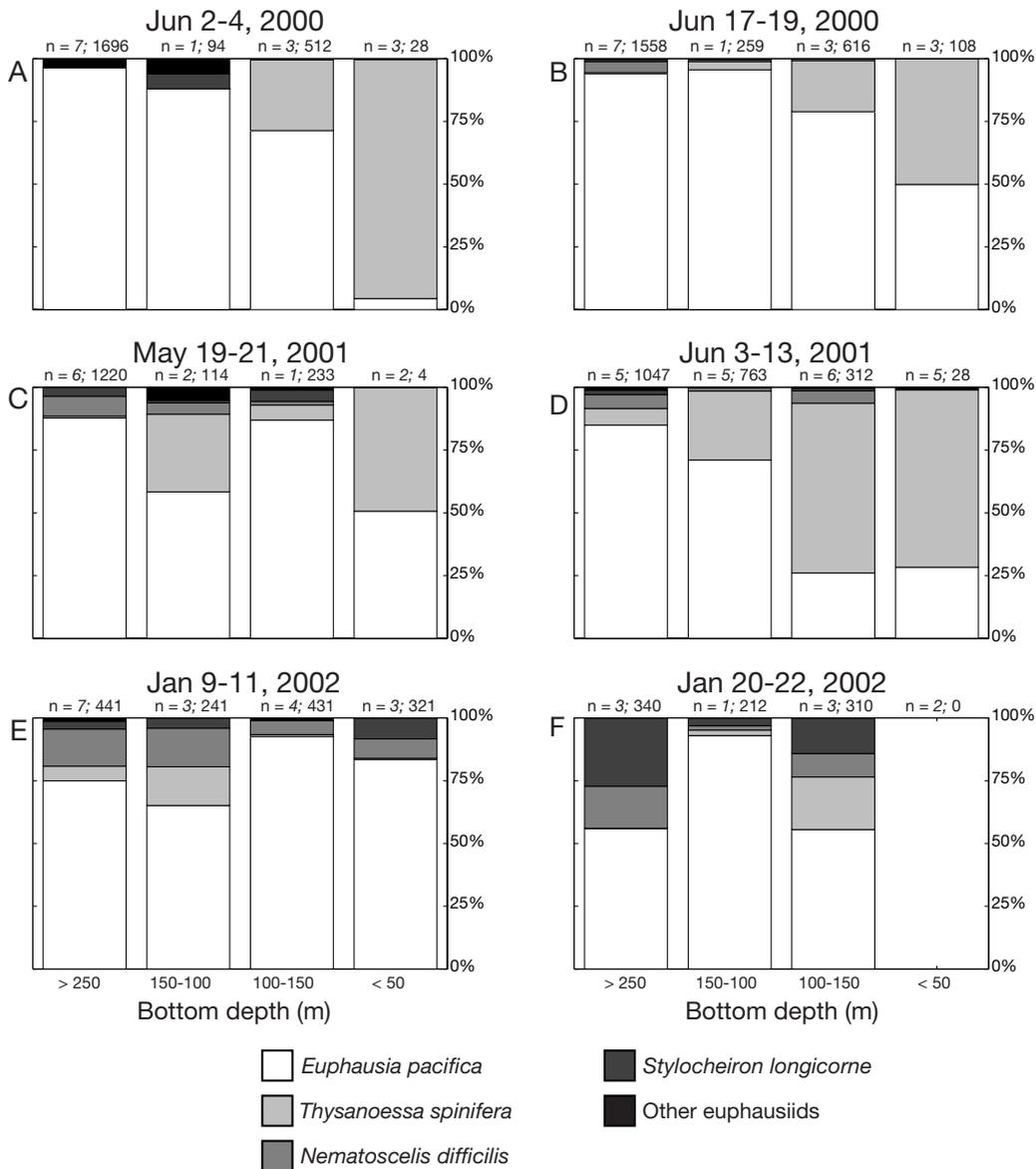


Fig. 5. Euphausiid community composition across continental shelf for (A) June 2 to 4, 2000, (B) June 17 to 19, 2000, (C) May 19 to 21, 2001, (D) June 3 to 13, 2001, (E) January 9 to 11, 2002, and (F) January 20 to 22, 2002. n: numbers of stations (italics), followed by individuals counted (e.g.: n = 7 stations; 1696 individuals)

Euphausia pacifica size structure

The size structure of *Euphausia pacifica* was more variable over the middle shelf than over the inner shelf and in offshore waters. Mean size of *E. pacifica* ranged from 8.48 to 19.46 mm in water 50 to 100 m deep and from 10.88 to 18.11 mm in water 100 to 150 m deep during June 2000 and May and June 2001 (Fig. 7A–D). In contrast, the size of *E. pacifica* showed little variation in water >250 m deep (range of mean = 7.49 to

9.95 mm) and in water <50 m deep (range of mean = 3.03 to 7.62 mm) (Fig. 7A–D).

Seasonally, the mean size of *Euphausia pacifica* decreased from 10.04 ± 0.06 mm in summer to 3.41 ± 0.02 mm in winter ($U = 18081950$, $n_1 = 2297$, $n_2 = 8592$, $p < 0.001$) (Fig. 7). Interannual differences in average euphausiid size were slight (June 2000 = 9.16 ± 0.06 mm and May and June 2001 = 11.19 ± 0.01 mm), but were significantly different ($U = 10204007$, $n_1 = 3721$, $n_2 = 4871$, $p < 0.001$) (Fig. 7A–D).

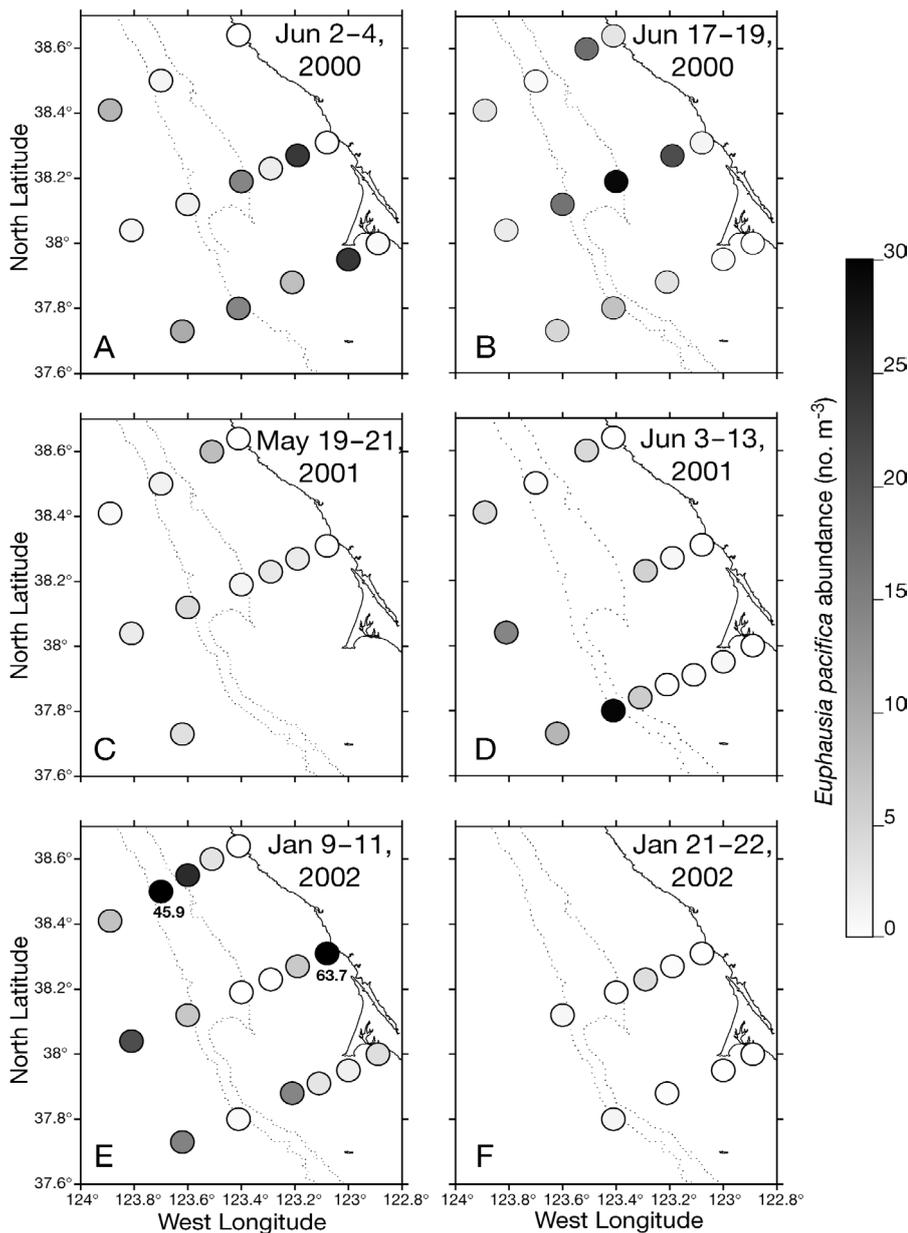


Fig. 6. *Euphausia pacifica*. Abundance for (A) June 2 to 4, 2000, (B) June 17 to 19, 2000, (C) May 19 to 21, 2001, (D) June 3 to 13, 2001, (E) January 9 to 11, 2002, (F) January 20 to 22, 2002. Numbers below black circles in (E) indicate abundance at relevant stations

Reproductive effort

Abundance of euphausiid eggs (eggs m^{-3} ; mean \pm SE) was significantly greater after relaxation wind events (1217 ± 412) than after periods of increased wind strength (234 ± 63.2) ($U = 702$, $n_1 = 24$, $n_2 = 37$, $p < 0.001$) (Fig. 8A,B). The total number of *Euphausia pacifica* oocytes (oocytes $ovary^{-1}$; mean \pm SE) was significantly lower ($U = 993$, $n_1 = 38$, $n_2 = 39$, $p < 0.01$) after relaxation events (1232 ± 52.5) than after upwelling events (1431 ± 53.4) (Fig. 9A–D).

Seasonally, there were a significantly lower number of total oocytes ($U = 1617$, $n_1 = 21$, $n_2 = 77$, $p < 0.001$) and mature oocytes ($U = 1201$, $n_1 = 21$, $n_2 = 77$, $p < 0.01$) in *Euphausia pacifica* ovaries during winter (Fig. 9). Interannually, there was no significant difference in egg abundance or *E. pacifica* ovarian oocyte composition between June 2000 and May and June 2001 (Fig. 8).

DISCUSSION

Short time-scale

Short time-scale changes in wind stress, physical water characteristics, euphausiid egg abundance and *Euphausia pacifica* abundance were observed over the course of this study. Sampling took place during both upwelling and relaxation periods in all 3 years, allowing a comparison of the effects of differing upwelling states on the *E. paci-*

fica population of the Northern California coast. In general, SST decreased during active upwelling and increased during relaxation (Fig. 3A–C). Peaks in chlorophyll *a* abundance were observed at the onset and during periods of relaxation, while during extended upwelling, chlorophyll *a* levels were typically lower (Fig. 3A–C). However, not all periods of relaxation led to increases in chlorophyll *a*, and slight increases in chloro-

phyll *a* were observed during extended upwelling. Other factors which were beyond the scope of this study, such as grazing, transport into the study area, and local retention of chlorophyll *a*, probably impact chlorophyll *a* levels. Similar to previous studies in the region (Steger et al. 2000), the surface mixed layer moved offshore during upwelling events and onshore during relaxation events (Dever pers. comm.).

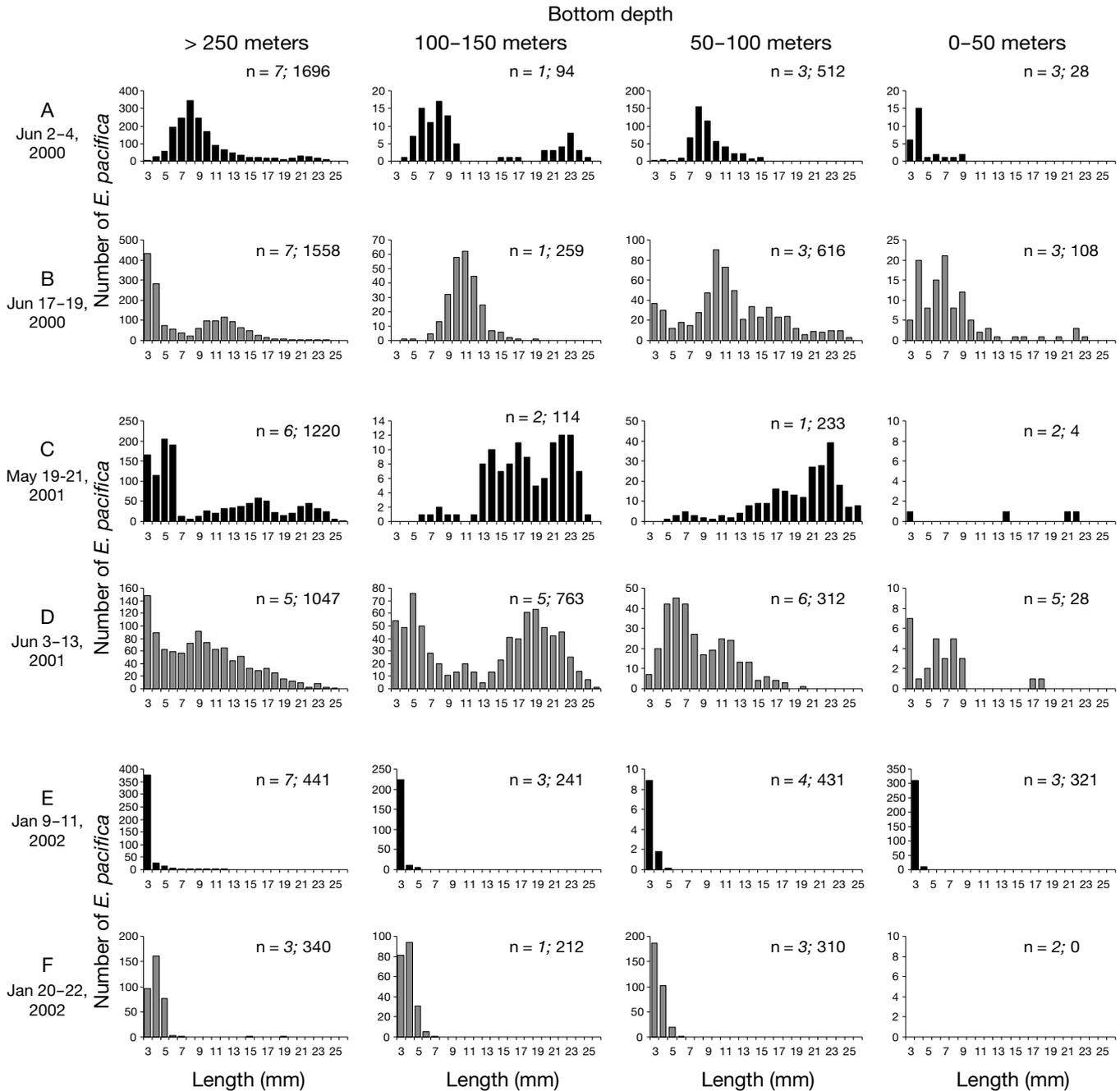


Fig. 7. *Euphausia pacifica*. Size structure for (A) June 2 to 4, 2000, (B) June 17 to 19, 2000, (C) May 19 to 21, 2001, (D) June 3 to 13, 2001, (E) January 9 to 11, 2002, (F) January 20 to 22, 2002. n presented as in Fig. 5

Short time-scale changes in reproductive effort of the euphausiid community were observed as an increase in euphausiid egg abundance following relaxation events and increases in chlorophyll *a*. This trend was most evident during June 2000, when egg abundance increased by an order of magnitude approximately 2 wk after a large phytoplankton bloom. Adult female euphausiid abundance doubled over approximately the same time period, but the increase was not enough to explain the 10-fold increase in egg abundance. Prior to the high euphausiid egg abundance observed during May 23 to 24, 2001, high levels of chlorophyll *a* (10 to 30 $\mu\text{g l}^{-1}$) were also observed (May 7 to 17) via a moored fluorometer at Stn D2 (Dever & Largier pers. comm.). Changes in *Euphausia pacifica*'s reproductive effort over an annual cycle are variable in the Eastern Pacific, but generally correspond to the annual peak in chlorophyll *a* concentration (Smiles & Percy 1971, Brinton 1976, Ross et al. 1982). Euphausiid spawning, and the resultant increases in abundance, have been related to chlorophyll *a* levels in Southern California (Brinton 1976) and British Columbia (Tanasichuk 1998). Just as chlorophyll *a* concentrations can influence the timing and magnitude of spawning on an annual scale, our data suggest that short time-scale changes in chloro-

phyll *a*, as a result of changes in upwelling state, can similarly affect changes in number of eggs spawned.

Abundance of total *Euphausia pacifica* also changed on a short time-scale during January 2002, decreasing by 1 order of magnitude during an upwelling event. However, change in total abundance of *E. pacifica* on a short time-scale was not observed during either June 2000 or May and June 2001, both of which periods included upwelling and relaxation events. Even during June 2000, when upwelling and relaxation events were most severe, the difference in total *E. pacifica* abundance was nominal. Differences in population size structure during January 2002 (almost entirely larval) and ontogenetic vertical migration patterns of late-stage *E. pacifica* may explain, in part, why short time-scale change in abundance was evident in January 2002 but not in June 2000 or May and June 2001.

Euphausia pacifica adults, juveniles and late furcilia larvae typically exhibit diel vertical migration (Brinton 1962, 1967, Youngbluth 1976, Bollens et al. 1992), while metanauplius, nauplius and early furcilia larvae tend to remain in surface waters both day and night (Brinton 1967, Youngbluth 1976, Bollens et al. 1992, Taki 1998). Variations in migration patterns of early larvae based on geographic location (Brinton 1967,

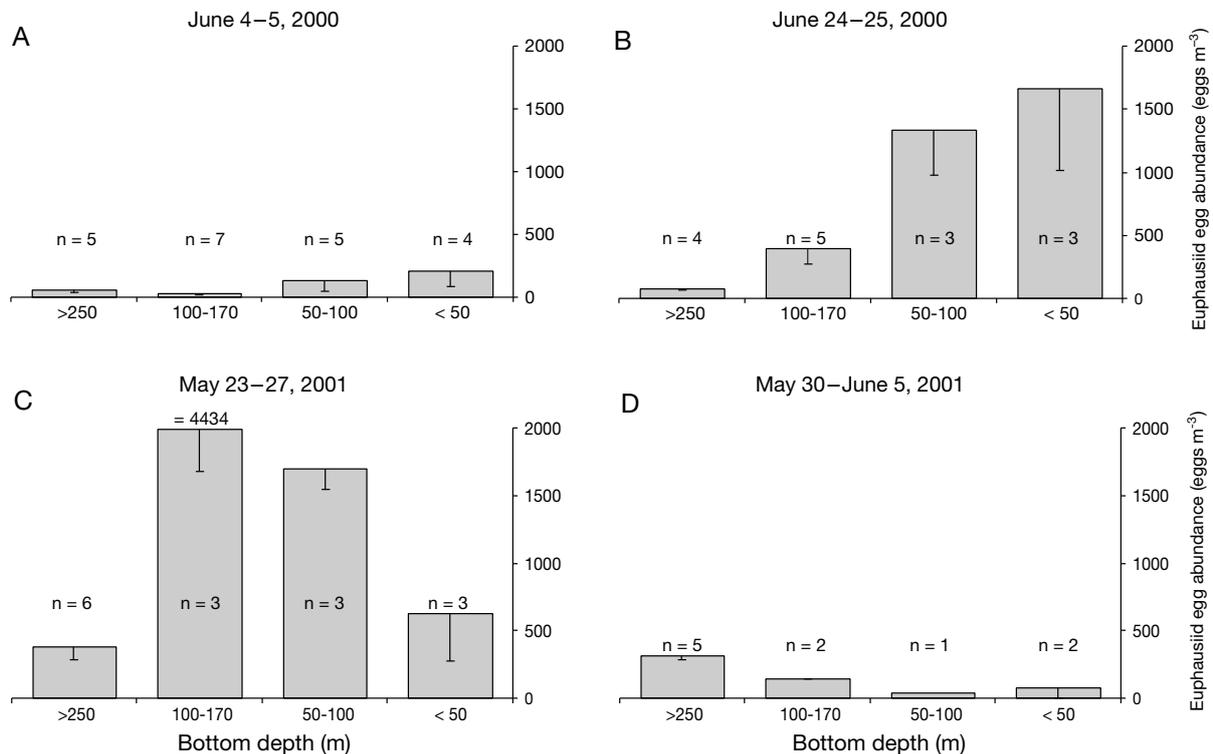


Fig. 8. Mean \pm SE abundance of euphausiid eggs cross-shelf for (A) June 4 to 5, 2000, (B) June 24 to 25, 2000, (C) May 24 to 27, 2001, (D) May 30 to June 5, 2001. (A) and (D) represent periods following or during upwelling, (B) and (C) periods following or during relaxation. Number above second bar in (C) shows actual abundance

Youngbluth 1976) and season (Bollens et al. 1992) have been reported, but larval *E. pacifica* are generally considered weakly or non-migratory. Given that we observed almost the entire winter population to be larval and presumably residing in surface waters, an upwelling event with offshore flow of surface water, as observed prior to and during our late January 2002 sampling, would reduce abundance over the shelf due to advection. Similarly, abundance of larval (3 to 5 mm) *E. pacifica* in June 2000, when upwelling and relaxation events were prolonged and distinct, was significantly lower during upwelling. No significant difference in larval abundance was observed during May and June 2001, however, when the difference between upwelling and relaxation events was less pronounced.

In addition, the movement of *Euphausia pacifica* adults and juveniles out of the offshore-flowing Ekman layer during daytime, via diel vertical migration, would reduce advective losses from the study area. This would result in little change in total abundance, despite strong upwelling and offshore surface flow, during May and June 2000 and 2001, for example. Studies of migratory copepod species in upwelling environments support the idea that diel vertical migration enhances retention during active upwelling (Peterson et al. 1979, 1988, Verheye et al. 1992, Peterson 1998). Similar conclusions have also been drawn in studies of euphausiids (primarily *E. lucens*, *E. hanseni*, and *Nyctiphanes capensis*) of the Benguela upwelling system (Pillar et al. 1992). In the Southern Benguela upwelling region, Pillar & Stuart (1988) found that older, vertically migrating stages of *E. lucens* were more abundant inshore while non-migratory stages were more abundant offshore. In the Northern Benguela, those stages of both *E. hanseni* and *N. capensis* that reside in the advective surface layer were more abundant offshore during active upwelling (Barange & Boyd 1992, Barange & Pillar 1992), while those stages capable of vertical migration were retained further inshore. In the northern California region, meroplankton studies found that those organisms that vertically migrated during active upwelling were retained due to their interaction with both onshore (at depth) and offshore (at the surface) flows (Wing et al. 1998).

Bathymetric features, such as Point Reyes, may also enhance retention of planktonic organisms by their

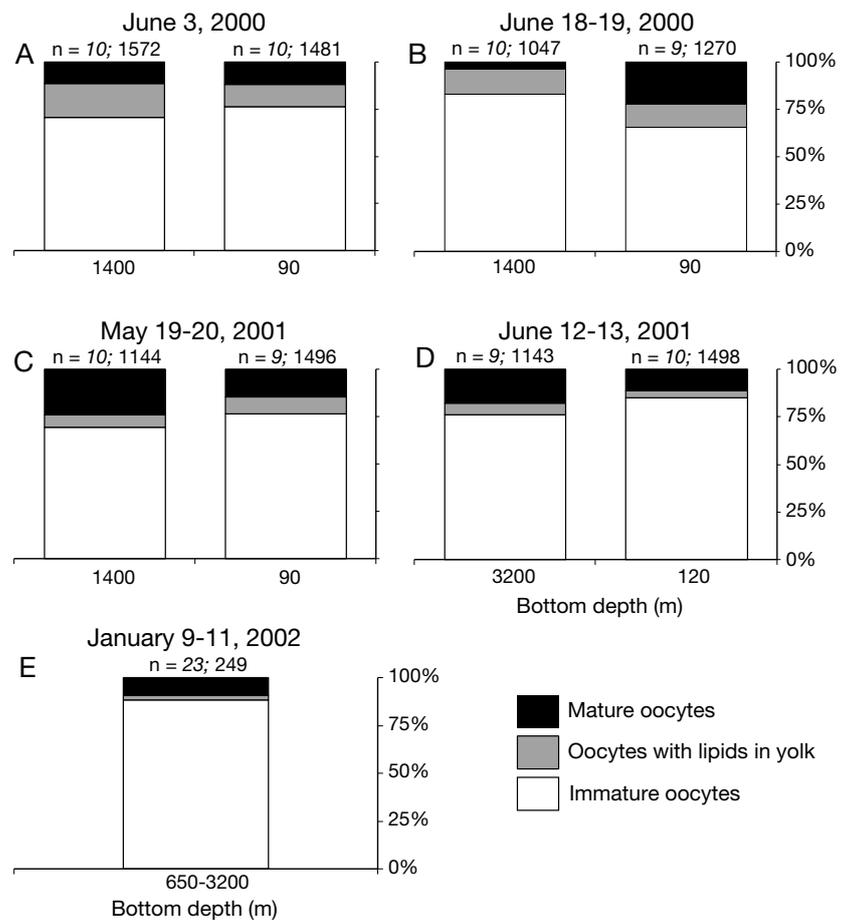


Fig. 9. *Euphausia pacifica*. Oocyte composition across continental shelf for (A) June 3, 2000, (B) June 18 to 19, 2000, (C) May 19 to 20, 2001, (D) June 12 to 13, 2001, (E) January 9 to 11, 2002. n presented as in Fig. 5

effects on the flow of shelf currents. Wing et al. (1995a) found increased crab settlement to the south of Point Reyes during periods of upwelling. This is an exception to the general observation that greater settlement of meroplankton on the Northern California coast is correlated with relaxation events (Farrell et al. 1991, Roughgarden et al. 1991, Wing et al. 1995b), suggesting that this area may serve as a plankton retention zone during upwelling. Upon relaxation of winds, surface flows can quickly shift from southerly to northerly (Send et al. 1987, Wing et al. 1998), providing a means of advection of zooplankton back up around Point Reyes. Indeed, surface drifters placed to the south of Point Reyes at the onset of relaxation events during June 2000 and May and June 2001 moved to the north of Point Reyes within a few days (Largier pers. comm.). However, if this were the case, no change in larval abundance of *Euphausia pacifica* would have been observed on a short time-scale, such as was seen in June 2000 and January 2002. While this area may retain some plankton, the observed change in larval

abundance points to a significant amount lost due to advective surface currents as well. Thus, behavioral mechanisms, such as diel vertical migration, are more likely to enhance retention of late-stage *E. pacifica* on the Northern California continental shelf during strong upwelling events than bathymetric features.

Seasonal scale

Community composition changed significantly during winter, as *Thysanoessa spinifera* comprised a much smaller proportion of the community and *Stylocheiron longicorne* and *Nematoscelis difficilis* comprised a larger proportion of the euphausiid community. The abundance of *T. spinifera* decreased significantly during winter, while abundance of *S. longicorne* and *N. difficilis* did not change significantly. This difference in community structure may be the result of the seasonal differences in shelf water origins. Summer flow of the coastal surface waters tends to come from the north (Steger et al. 2000), where *T. spinifera* along with *Euphausia pacifica* dominate the euphausiid community (Simard & Mackas 1989, Tanasichuk 1999, Mackas et al. 2001). During winter, the Davidson Current flow from the south is much stronger and shelf waters tend to originate from the south (Steger et al. 2000), where *T. spinifera* is present but not as a dominant euphausiid (Brinton & Wyllie 1976, Gomez-Gutierrez et al. 1995, Gomez-Gutierrez & Robinson 1997). Predation may also play a role in the reduction of *T. spinifera*, as this species is larger than *E. pacifica*, and predators such as Pacific hake *Merluccius productus* (Tanasichuk 1999) and Cassin's auklet *Ptychoramphus aleuticus* (Ainley et al. 1996) prey selectively on *T. spinifera*.

The size structure of *Euphausia pacifica* also changed seasonally, from one comprised of adults, juveniles, and larvae during May and June to one almost entirely comprised of larvae during January. The drastic reduction of adults and juveniles is surprising, as adults and juveniles have previously been found year-round to the north (Smiles & Pearcy 1971) and to the south (Brinton 1976) of our study area. This suggests that the maximum age of *E. pacifica* in this region may be less than 1 yr, as few adults appeared to overwinter on the shelf. Evidence of this short a life span for *E. pacifica* has been presented off Southern California (Brinton 1976). Also surprising is the high abundance of larval *E. pacifica* during wintertime, when chlorophyll *a* levels were much lower than during summer. Using oceanic juvenile growth rates from Smiles & Pearcy (1971) of 0.095 mm d^{-1} , we estimate the approximate time of spawning for this January 2002 cohort of 3 to 5 mm *E. pacifica* to be late Novem-

ber or early December of 2001. A similar estimate of spawning time is arrived at by incorporating information from Suh et al.'s (1993) study on *E. pacifica* growth rates in the Yellow Sea and Ross' (1981) *E. pacifica* laboratory culture and development experiments. Wind data from November and December 2001 indicate that a significant upwelling event occurred during early November, followed by a 2 wk relaxation. Fluorometry data from a mooring in the study area showed increased chlorophyll *a* concentrations during this relaxation period (Dever & Largier pers. comm.). Thus, the strong larval cohort observed in January 2002 might have been caused by upwelling-induced high egg production, and ultimately high larval recruitment during late autumn, similar to the increase in egg production observed during June 2000 and May and June 2001.

Reproductive effort decreased during winter compared with summer, as the number of mature oocytes (and total number of oocytes) in *Euphausia pacifica* ovaries were greatly reduced. Brinton (1976) reported year-round spawning, albeit in reduced numbers during winter, in the Southern California Bight, and Smiles & Pearcy (1971) did not observe major concentrations of larvae during either winter or spring, indicating a winter lull in reproduction off the Oregon coast. The large concentration of larvae observed in January 2002 in this study indicates that the spawning season off Northern California extends into late fall, similar to reports from the Oregon upwelling region (Smiles & Pearcy 1971). The reduction in abundance of adult female *E. pacifica* and the decrease in mature oocytes (and total number of oocytes) in the ovaries of *E. pacifica* in January 2002 indicate a lull in reproduction also similar to the findings of Smiles & Pearcy (1971). However, the presence of some mature oocytes in the ovary, as well as observations of female *E. pacifica* with attached spermatophores, indicate possible wintertime spawning off Northern California. Thus, reproductive effort of *E. pacifica* may not cease entirely during winter, but reproductive effort is certainly diminished during January.

Interannual scale

We observed interannual differences in total abundance of *Euphausia pacifica* between June 2000 and May and June 2001, but attribute it to processes different from those of most previous studies. Tanasichuk (1998) examined interannual variability of *E. pacifica* productivity in Barkley Sound, British Columbia, Canada, and concluded that those years with the highest productivity were the result of strong recruitment due to intense upwelling. Brinton (1976) similarly con-

cluded that years of stronger upwelling resulted in greater *E. pacifica* abundance. Yet we found higher abundance of *E. pacifica* during June 2000, a year of less intense upwelling (as measured by the Bakun upwelling index). This difference may be due to differences in study areas. Our study area is not in a coastal bay, as is Barkley Sound, or in a large retention zone, as is the Southern California Bight. The narrow continental shelf off Northern California provides little shelter from the advective surface currents created by intense and extended upwelling. As discussed above, retention zones to the south of headlands, such as Point Reyes, may retain plankton biomass during strong upwelling events, and vertical migratory behavior may also enhance shelf retention of plankton. Nevertheless, presumably some biomass is advected off the shelf during each upwelling event, and an anomalously windy year (e.g. 2001) might be expected to result in lower total biomass on the shelf. The increased chlorophyll *a* levels that help produce strong larval cohorts may also be advected offshore unless interspersed with relaxation events that aid in the retention of plankton. Indeed, higher phytoplankton concentrations during periods of relaxation and lower phytoplankton concentrations during active upwelling events were observed during our study (Dugdale & Wilkerson pers. comm.). Higher abundance of euphausiids (primarily *E. pacifica* and *Thysanoessa spinifera*) during a weak upwelling year is supported by a 15 yr data set collected off the coast of Vancouver Island, Canada, by Mackas et al. (2001). These authors concluded that decreased euphausiid abundance during years of more intense upwelling is most likely due to advective transport off the shelf. Thus, while retention mechanisms are likely to exist in the Northern California region to retain *E. pacifica* biomass on the shelf during upwelling, extended and anomalously strong upwelling probably decreases the abundance of *E. pacifica* in the region.

SUMMARY AND CONCLUSIONS

Strong and prolonged upwelling-favorable winds off Northern California can decrease *Euphausia pacifica* abundance and euphausiid reproductive effort on both a short-time and interannual scale. Decreases in euphausiid egg abundance corresponded to decreases in phytoplankton during upwelling events, while increases in euphausiid reproductive effort corresponded to relaxation events and associated phytoplankton blooms. Upwelling events corresponded to decreased abundance of larval (3 to 5 mm) *E. pacifica*, possibly due to offshore transport, but did not have an effect on overall abundance during summer, due perhaps to behavioral retention mechanisms. Strong per-

sistent upwelling may lead to interannual differences (decreases) in abundance of *E. pacifica* off of Northern California due to advective losses off the shelf. Seasonally, the dominance of larval stages of *E. pacifica* during January indicates a spawning season extending into late autumn off Northern California. As suggested by the recent modeling study of Botsford et al. (2003), our results point to the possibility that there is an optimal level of wind-induced upwelling that provides sufficient nutrients to fuel new primary and secondary production, but is not so strong as to advect plankton off the shelf.

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