

# Seasonal variations in a deep aggregation of *Calanus pacificus* in the Santa Barbara Basin

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**ABSTRACT:** A deep aggregation of fifth copepodid (C5) *Calanus pacificus* in the Santa Barbara Basin (SBB) was mapped over 1½ yr with zooplankton net tows, an optical plankton counter, and a moored acoustic Doppler current profiler. High concentrations of diapausing C5 *C. pacificus* built up in the deep waters of the SBB during the summer and into the fall. During the buildup, the deep aggregation moved up from the bottom as oxygen became depleted in the basin's deep waters. The deep aggregation apparently builds up due to the basin trapping C5s that migrate below the sill depth from water advected over the basin. C5s are retained within the basin until they swim, or are forced, above the sill depth. Possible mechanisms responsible for the dispersal of the deep aggregation are migration to the surface waters with subsequent dispersal by surface currents, advection over the basin's sill due to the buildup of oxygen-deficient water, or flushing of the basin's deep water.

**KEY WORDS:** *Calanus pacificus* · Deep aggregation · Santa Barbara Basin · Diapause

## INTRODUCTION

Many calanoid copepod species have a dormant phase where the majority of the population stays at depth during months of low primary productivity in order to survive long periods of food shortage (e.g. Miller et al. 1984, Conover 1988). *Calanus pacificus* Brodsky is a common marine planktonic copepod which displays this pattern to varying degrees throughout its range. In the waters off southern California the basic seasonal cycle for *C. pacificus* is hypothesized to be as follows (Fleminger 1985): a portion of the *C. pacificus* population remains active in the surface 100 m of the water column throughout the year. Starting in late spring, however, some individuals arrest their development at the fifth copepodid (C5) stage, migrate to deeper waters (300 to 600 m) and enter diapause. The diapausing C5s remain dormant through the fall, becoming active and rejoining the surface population sometime in winter. The factors controlling the triggering and termination of diapause in *Calanus* are not yet known (Hirche 1996).

Deep dwelling, diapausing individuals are obviously important to the survival of species which have this resting stage, and to the entire ecosystem, because the diapausing individuals are a source for repopulation of the surface waters the following year. Basins adjacent to the continental shelf, such as the Santa Barbara Basin (SBB), may be especially important to local plankton dynamics because these basins' deep waters can contain intense aggregations of the resting stages of copepods. To understand the importance of these deep aggregations it is necessary to know their temporal and spatial extent, the degree to which the copepods are concentrated within the basins compared to the surrounding areas, and the processes controlling the aggregations' formation, maintenance, and dissipation.

High concentrations of diapausing C5 *Calanus pacificus* have been observed in the deep waters of the SBB (Alldredge et al. 1984, Osgood & Checkley in press). Based on the size and concentration of the basin's deep C5 *C. pacificus* aggregation compared to the concentrations outside the basin, Osgood & Checkley (in press) inferred the aggregation to be important to the regional *C. pacificus* population. This was based only on measurements made during fall and on the hypothesis that the basin aggregation is

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not static but, rather, at some time, the individuals leave the deep waters of the basin and are advected throughout the region. They also hypothesized that concentrations of diapausing C5s could build up within the basin, relative to the concentrations outside the basin, during the time when some of the *C. pacificus* population is in diapause (i.e. summer-fall) by being trapped and then retained within the SBB due to its bathymetry. To test these hypotheses, we now describe the temporal changes in the basin C5 *C. pacificus* population through the year and compare these to the changes that occurred in the population outside the basin.

## METHODS

The SBB is located off the coast of southern California, USA (Fig. 1). Its maximal depth is just over 600 m while its western sill, extending down to 472 m in a narrow region, is its deepest opening to the surrounding waters. We employed 3 types of sampling to describe the temporal variability of the deep C5 *Calanus pacificus* aggregation, a MOCNESS (Multiple Opening and Closing Net and Environmental Sensing System, Wiebe et al. 1976), an OPC (optical plankton counter, Herman 1988, 1992), and an ADCP (acoustic Doppler current profiler).

The vertical distributions of the copepodid stages of *Calanus pacificus* were quantified with vertically stratified zooplankton samples obtained with a MOCNESS on 4 cruises (Table 1). Details of the MOCNESS sampling and sample analysis are provided in Osgood & Checkley (in press). Briefly, a double, 1 m<sup>2</sup> MOCNESS, equipped with 20 nets of 333  $\mu$ m mesh, was

Table 1. Dates and types of sampling conducted in this study. For CalCOFI, standard CalCOFI sampling was conducted in the SBB area (see Fig. 1)

Dates	Sampling conducted
<b>1994</b>	
15–16 Aug	CalCOFI
20–21 Aug	5 station transect of OPC/CTD stations
10–11 Oct	CalCOFI
14 Oct	5 station transect of OPC/CTD stations
20–22 Nov	MOCNESS and extensive OPC/CTD mapping
<b>1995</b>	
16–17 Jan	CalCOFI
21 Jan	5 station transect of OPC/CTD stations
25–27 Feb	MOCNESS and extensive OPC/CTD mapping
16–17 Apr	CalCOFI
21–23 Jun	MOCNESS and extensive OPC/CTD mapping
17–18 Jul	CalCOFI
22 Jul	5 station transect of OPC/CTD stations
7–9 Sep	MOCNESS and extensive OPC/CTD mapping

used to obtain 10 pairs of zooplankton samples per tow, 8 of which were obtained during the retrieval of the net (near bottom to 515, 515 to 475, 475 to 450, 450 to 400, 400 to 200, 200 to 100, 100 to 50, 50 to 0 m). A 333  $\mu$ m mesh net quantitatively retains C3 and larger *C. pacificus*. During the November, February, and June cruises, daytime and nighttime MOCNESS tows were made at a central station within the SBB and a single tow was conducted at a station southwest of Santa Rosa Island (Fig. 1). In September, however, the only samples obtained were from a tow taken at a station within the basin. In addition to counting the copepodid stages of *C. pacificus* in the samples, we also measured the wet displacement volume of some of the samples, using the procedure outlined by Kramer et al. (1972).

Between August 1994 and September 1995 the OPC was used to map the spatial extent of the C5 *Calanus pacificus* deep aggregation during 8 cruises (Table 1). At each station occupied, the OPC was lowered vertically from the surface to near the bottom at a rate of 1 m s<sup>-1</sup>, providing data at 0.5 s, hence 0.5 m, intervals. During the November cruise, triplicate OPC profiles were made at each station. During the other cruises, only single OPC profiles were conducted except at MOCNESS stations, where triplicate profiles were made. A Sea-Bird CTD (conductivity, temperature, depth) was deployed along with the OPC on each cast. During the 4 cruises when MOCNESS samples were collected, we obtained along- and cross-basin transects of OPC stations, as well as having

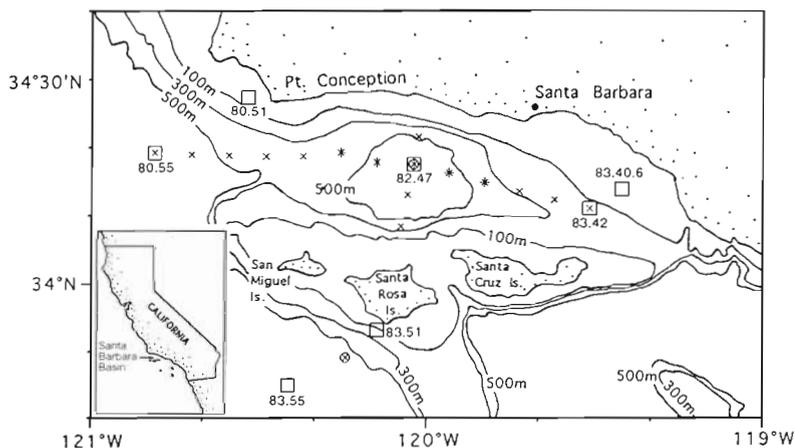


Fig. 1 Santa Barbara Basin and station locations. (○) MOCNESS stations, (×) OPC/CTD stations occupied during MOCNESS cruises, (□) CalCOFI stations, (+) OPC/CTD stations occupied during CalCOFI cruises (\* shows superimposed × and +)

an OPC station at the MOCNESS tow location southwest of Santa Rosa Island (Fig. 1). An oxygen sensor was connected to the CTD during these 4 cruises. During the September cruise, the along-basin transect did not extend as far west, but more extensive mapping was done inside the basin (see Osgood & Checkley in press for details).

The cruises without MOCNESS tows were California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises. During CalCOFI cruises a host of oceanographic measurements are made at a regular series of stations, including 7 stations in the Santa Barbara Channel region (Fig. 1). In this paper we present oxygen concentration data from CalCOFI Stn 82.47. CalCOFI investigators determine dissolved oxygen from water samples by the Winkler method, as modified by Carpenter (1965), using the equipment and procedure outlined by Anderson (1971). We also analyzed CalCOFI bongo net samples, from the stations shown in Fig. 1, for concentrations of *Calanus pacificus*. The bongo nets used by the CalCOFI program are 71 cm diameter, 505  $\mu\text{m}$  mesh nets which are towed obliquely from 0 to 210 to 0 m, bottom permitting. A 505  $\mu\text{m}$  mesh net quantitatively retains C5 and larger *C. pacificus*. In addition, during the August and October 1994 and January and July 1995 CalCOFI cruises we were able to obtain an along-basin (W-E) transect of 5 OPC/CTD stations (Fig. 1).

The OPC counts and sizes particles ranging from 250  $\mu\text{m}$  to 15 mm equivalent spherical diameter. Therefore, we needed to be able to identify which particles are C5 *Calanus pacificus* based upon their size and depth distribution. Details about the methods we used to approach this problem are in Osgood & Checkley (in press); but, briefly, live C5 *C. pacificus* were brought into the laboratory and passed through an OPC to obtain their size-frequency distributions as sensed by an OPC. The mean  $\pm$  1 SD from this distribution was taken to represent C5 *C. pacificus*-sized particles. In comparisons between estimates of C5 *C. pacificus* concentrations from MOCNESS tows and OPC profiles, the OPC was found to effectively represent C5 abundance patterns, though it generally overestimated C5 concentrations, except in the deep aggregation within the SBB, where it seriously underestimated their concentrations. The OPC was able to clearly delineate the deep C5 layer and was thus useful for mapping its spatial extent.

To monitor the deep currents within the SBB, and to attempt to qualitatively follow the appearance/disappearance of the deep C5 *Calanus pacificus* aggregation between cruises, a broadband, 150 kHz ADCP was used. It was moored near the bottom at the central station in the SBB, oriented upwards, from 25 February 1995 to 12 January 1996. During this time period it

obtained vertical profiles of the current velocities and echo intensity from 562 m (20 m above the bottom) to 310 m, with a depth bin size of 4 m. The data collected were averages from 20 pings spaced evenly through each hour. The range-corrected, relative backscatter intensity (Flagg & Smith 1989) was calculated from the echo intensity data by first subtracting the noise level from the signal counts for each of the ADCP's 4 beams. The noise level for each beam was taken to be the echo intensity for that beam from depths far away from the transducer when the echo intensity was at low and constant values and the correlation magnitude had decreased. The average corrected echo intensity data for the 4 beams was then calculated and converted to relative backscatter intensity (dB) using the conversion factor supplied by RD Instruments (San Diego, CA, USA). Finally, the range correction described by Flagg & Smith (1989) was applied. This procedure generally follows that outlined by Heywood et al. (1991). There were times when some of the data above 400 m were meaningless due to decreases in the correlation magnitudes. Therefore, we only present data extending up to 400 m.

For display purposes, we filtered the range-corrected backscatter data with a 38 h, low-pass filter (pl64 filter, Limeburner 1985) for plots of several months' duration. Data for shorter time periods were also plotted without filtering to demonstrate the higher frequency fluctuations that occurred.

Sound with a frequency of 150 kHz reflects more efficiently off particles larger than 10 mm than it does off smaller particles, given similar compositions. Therefore, individual C5 *Calanus pacificus* with a prosome length of  $\sim$ 2 mm will not reflect the sound from our ADCP very efficiently, and only if they are in high concentrations will they appear as a strong backscatter signal.

## RESULTS

A layer with high C5 *Calanus pacificus* concentration in the deep waters of the SBB was indicated by the OPC transects from August, October, and November 1994 (Fig. 2). The layer was closer to the bottom at the central OPC station in August than in October and November. MOCNESS samples obtained from the central station during November confirmed that the deep layer sensed by the OPC was composed of C5 *C. pacificus*, with a maximal concentration close to 7000 C5  $\text{m}^{-3}$  (Fig. 3). In fact, C5s accounted for 95 to 97% of all zooplankton collected between 507 and 475 m during the day and between 521 to 478 m at night. The C5s in the deep layer showed no evidence of diel vertical migration. In the November OPC cross-

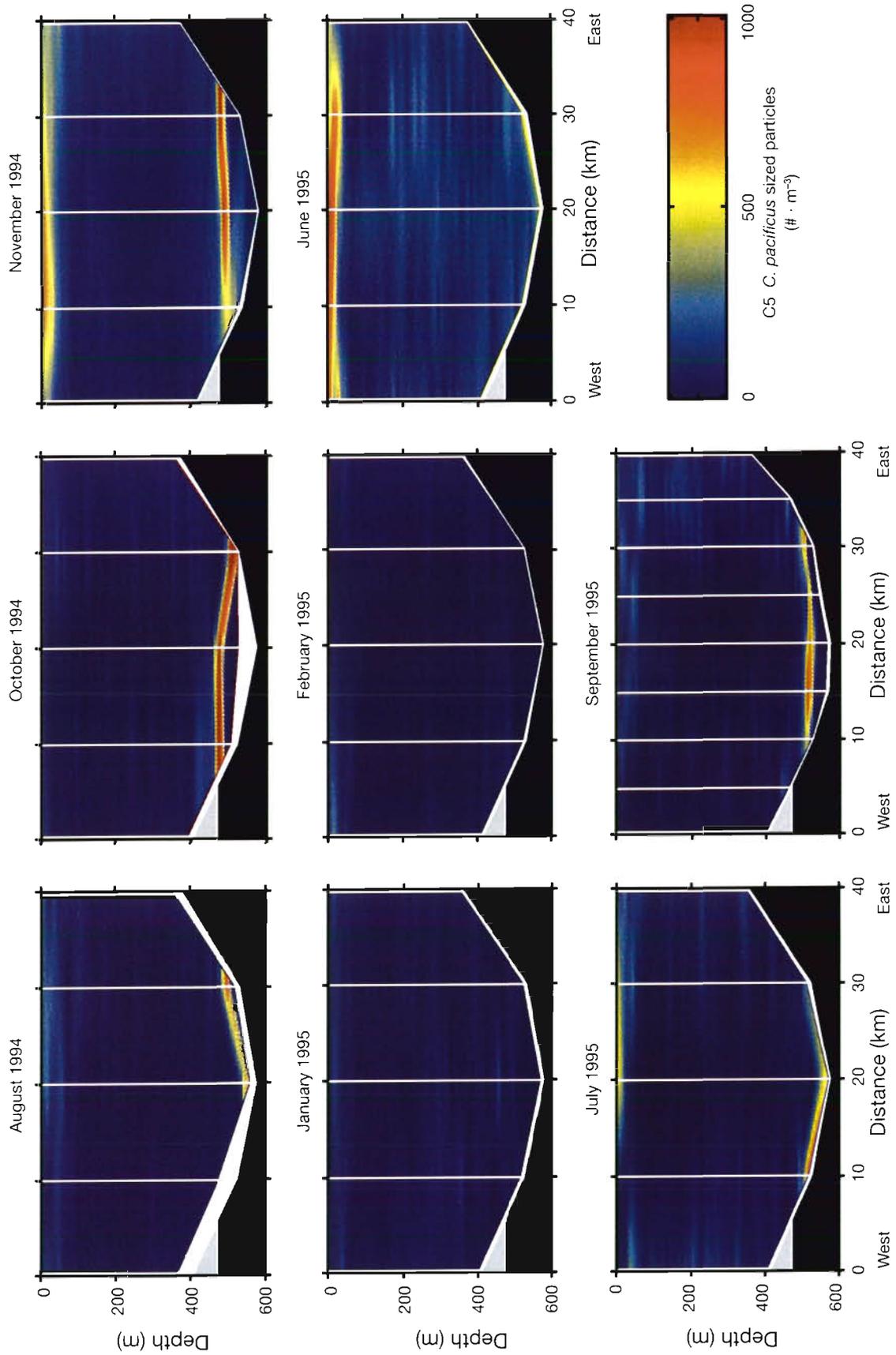


Fig. 2. OPC-measured distribution of C5 *Calanus pacificus*-sized particles in the SBB along the west-east transect composed of the 5 OPC profiles obtained during CalCOFI and MOCNESS cruises. September transect composed of 9 OPC profiles. Verticle white lines indicate profile locations. White areas near base of plots represent regions with no data. Black and gray shaded areas together represent the bottom as encountered along the transects. Bottom of the gray area represents the maximal depth of the basin's western sill

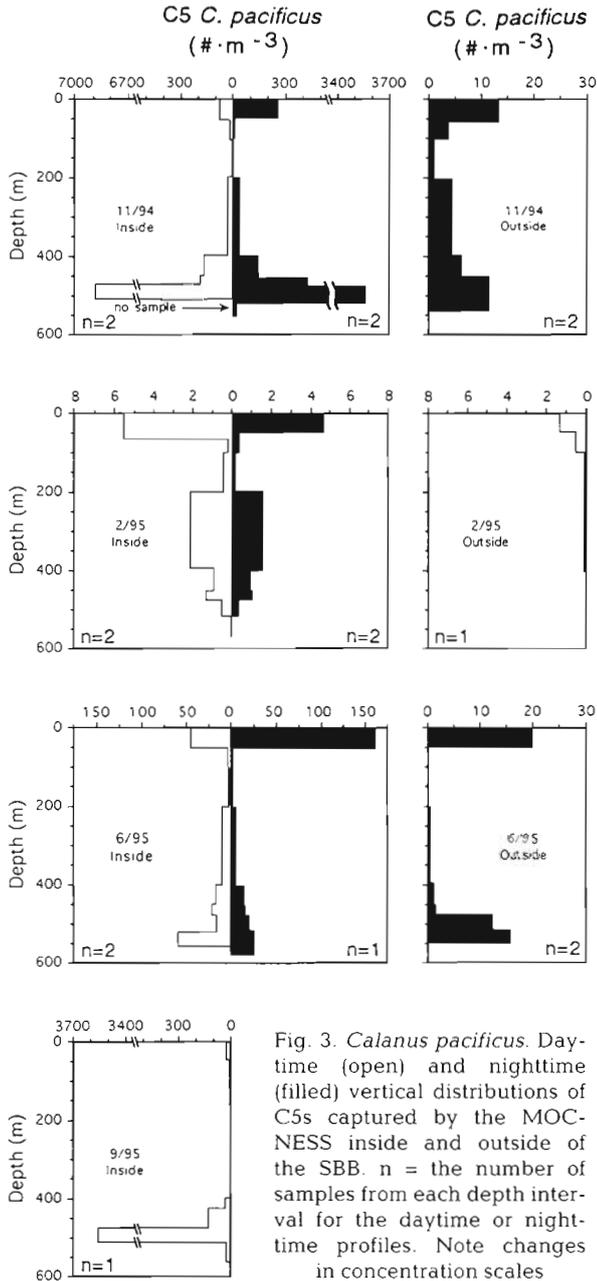


Fig. 3. *Calanus pacificus*. Daytime (open) and nighttime (filled) vertical distributions of C5s captured by the MOCNESS inside and outside of the SBB. n = the number of samples from each depth interval for the daytime or nighttime profiles. Note changes in concentration scales

section, there also appeared to be high C5 concentrations in the surface waters. However, only a fraction of the zooplankton counted by the OPC in the surface waters during November was actually C5s.

In January and February 1995 there was no indication of the deep C5 *Calanus pacificus* aggregation (Fig. 2). Maximal concentrations of C5s obtained with MOCNESS tows in February were found in the surface 50 m and were merely 5 C5 m<sup>-3</sup> (Fig. 3). The drastic reduction in the numbers of C5 *C. pacificus* within the SBB between the fall of 1994 and early 1995 was not due to simple maturation to adulthood. The total

water column abundance of C5s at the central station dropped dramatically between November 1994 and February 1995, yet there was only a small increase in the adult abundance (Table 2). In addition, although there were some moderate increases in the surface water concentrations of C5s and/or adults between the fall of 1994 and early 1995 at some of the stations in the SBB region (Fig. 4), large numbers of *C. pacificus* did not appear near the surface at any station.

In June 1995 the OPC indicated elevated concentrations of C5 *Calanus pacificus* in the surface waters and near the bottom at the 20 and 30 km stations (Fig. 2). The June MOCNESS samples revealed that the C5s were, in fact, bimodally distributed, with concentrations similar to those present in the surface waters the previous November (Fig. 3). The aggregation in the deep layer grew and moved away from the bottom throughout the summer so that by September 1995 the distribution appeared similar to that recorded the prior fall (Figs. 2 & 3).

There were also seasonal changes in the oxygen concentrations in the deep waters of the SBB (Fig. 5). During the summer and fall of 1994 a bottom layer of oxygen-deficient water built up within the SBB (note the shoaling of the shoulder in the profiles). In January and February of 1995 the deep waters were still depleted of oxygen, though the upper range of this layer had not continued to shoal. In April the bottom waters contained elevated concentrations of oxygen while the water near 500 m was still very depleted of oxygen, indicating the basin's deep waters were being flushed at this time. Homogenization of oxygen concentrations in the waters below 500 m occurred by June and concentrations in June and July were higher than those recorded for the previous late summer through winter. By September 1995, though, the deepest basin waters were once again very depleted of oxygen.

At the MOCNESS station southwest of Santa Rosa Island the C5 *Calanus pacificus* population went through a cycle similar to that observed in the SBB,

Table 2. *Calanus pacificus*. Total water column abundance (no. ind. m<sup>-2</sup>) from MOCNESS tows at the SBB central station. Values are means of all the profiles from the central station for each cruise (November and February n = 4, June n = 3, September n = 1)

Stage	Nov 1994	Feb 1995	Jun 1995	Sep 1995
M	409	800	350	221
F	442	1064	731	129
C5	221317	792	10497	135287
C4	1984	154	3823	452
C3	3458	92	2860	704

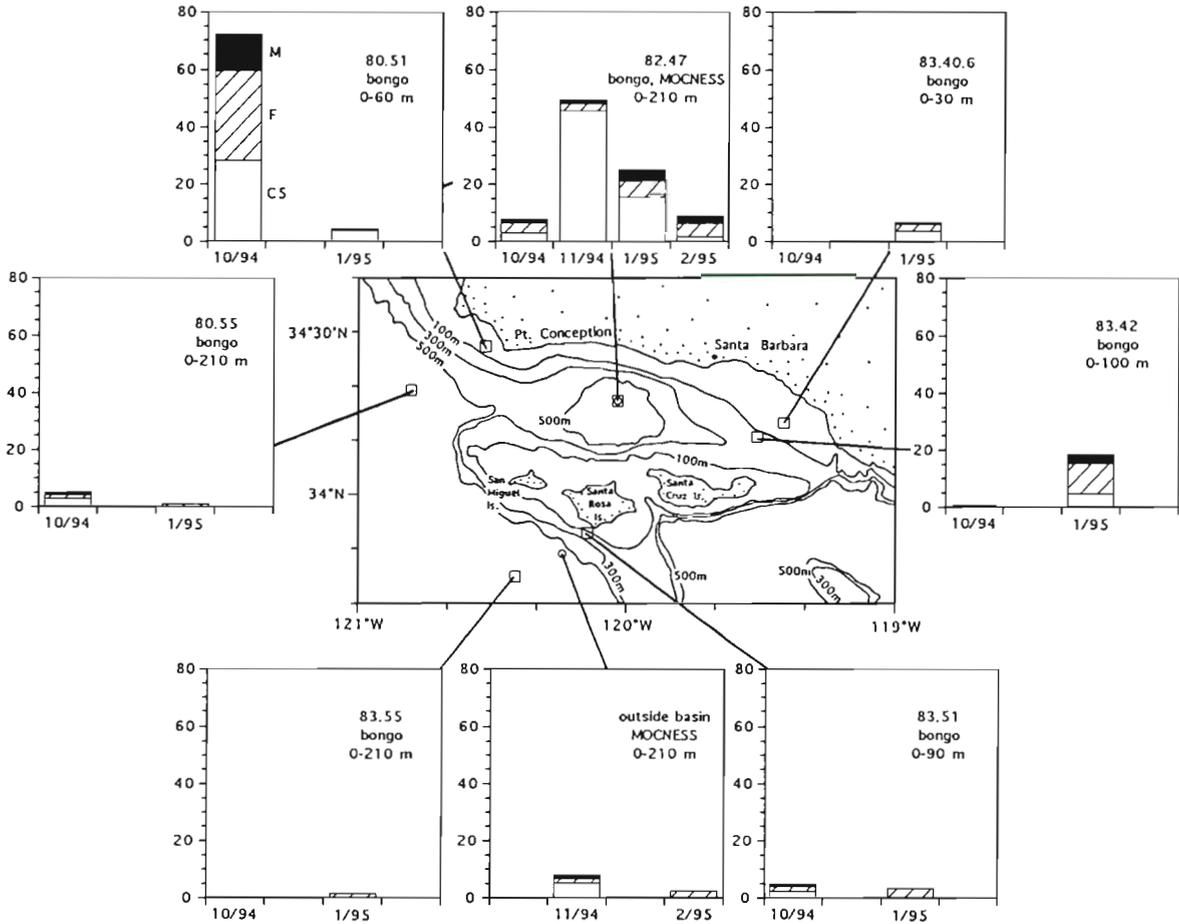


Fig. 4. *Calanus pacificus*. Concentrations (no. ind. m<sup>-3</sup>) of C5s (open), adult females (striped), and adult males (filled) in the surface 210 m (or the entire water column if shallower than 210 m). Data from 10/94 and 1/95 are from single CalCOFI bongo net tows. Data from 11/94 and 2/95 are means from MOCNESS tows

though during the fall the deep dwelling C5s did not accumulate in concentrations nearly as high as those in the SBB (Fig. 3). In November 1994, C5s were bimodally distributed outside the SBB, with approximately equal concentrations present in the shallow and deep waters. By February 1995, C5 *C. pacificus* were rare at this station and the few C5s present were located in the top 100 m. Then by June 1995, the C5s had increased to concentrations similar to those pre-

sented the previous November, and there were once again approximately equal concentrations present in the shallow and deep waters. We were not able to obtain a MOCNESS tow at this station during September 1995; however, the OPC profile from this station at this time appeared very similar to the OPC profiles obtained during the previous November and June. At this station, oxygen concentrations were fairly low in the deep waters, but never below 0.2 ml l<sup>-1</sup>.

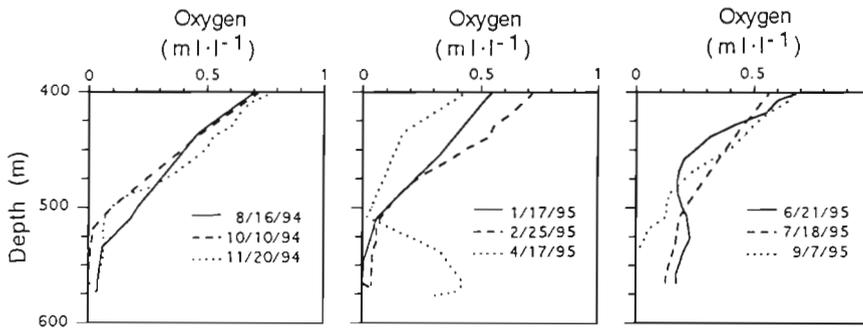


Fig. 5. Oxygen profiles below 400 m from the SBB central station. Sampling dates shown as mo/d/yr. Profiles obtained with an *in situ* oxygen sensor on 11/20/94, 2/25/95, 6/21/95, and 9/7/95, other profiles obtained from titration of water samples

Since the ADCP backscatter signal is a log value, the differences between the backscatter at different depths (Fig. 6) should appear similar to the differences between the wet displacement volumes at different depths, when the volumes are plotted on a log scale (Fig. 7). When collection of ADCP data began in February 1995, the water below about 500 m had very low oxygen concentrations, as discussed above. The ADCP measured low levels of backscatter from this stratum (Fig. 6), indicating there were few zooplankton in the oxygen-deficient water. Above this low oxygen water, moderate and fairly constant levels of backscatter were sensed up to 400 m. This is in good agreement with the wet displacement volumes from our MOCNESS samples at this time (Fig. 7). The intrusions of moderate backscatter levels below 500 m at the end of March indicate the commencement of flushing of the basin's deep waters. The flushing continued through April so that by early May moderate backscatter levels were present throughout the waters below 400 m.

During May through early August the ADCP indicated generally higher backscatter levels from the upper portion of the profiles and the backscatter intensities generally increased during this time (Fig. 6). It is unclear from our zooplankton samples from June (Fig. 7), or OPC data from June and July, why the backscatter intensities from the upper portion of the ADCP profiles would be higher than those from the lower portion. By mid-August a continuous layer of high backscatter intensity appeared just above the bottom of the ADCP profile. A few days later, this layer shoaled a little, and just below it a layer of low backscatter appeared. This layer of high backscatter was the deep aggregation of C5 *Calanus pacificus*, and the area of low backscatter below it was the oxygen-deficient zone. From mid-August through September all 4 beams of the ADCP routinely indicated the presence of the deep C5 layer. The backscatter data also indicated high amounts of zooplankton in the upper portions of the ADCP profiles during much of this time, with backscatter intensities similar to those observed for the C5 layer (Fig. 6). MOCNESS samples from September indicated a low volume of zooplankton in the oxygen-deficient zone and a high volume of zooplankton in the C5 *C. pacificus* layer (Fig. 7), in agreement with the ADCP data. However, the MOCNESS samples did not indicate volumes of zooplankton in any of the water between 400 and 475 m to be similar to the volumes of zooplankton present in the C5 layer.

Besides these long time scale fluctuations seen in the 38 h, low-pass filtered data (i.e. flushing of the deep waters and appearance of the deep C5 *Calanus pacificus* layer and the oxygen-deficient zone) the ADCP backscatter data also show how the C5 layer moved up and down at a single location on a continuous basis

due to the fluid motions in the SBB. In the bottom panel of Fig. 6, higher frequency fluctuations, caused by tidal and inertial motions, are apparent. The extreme events caused the C5 layer to move vertically 40 m in less than half a day!

## DISCUSSION

A complete cycle of the seasonal variation in the deep C5 *Calanus pacificus* aggregation in the SBB was documented. The movement of the deep C5 layer away from the bottom during the summer and into the fall mirrored the movement of the upper extent of the oxygen-deficient waters within the SBB. Vinogradov et al. (1992) found *Calanus euxinus* (their *Calanus ponticus*) stopped swimming and had limited survival duration in experiments when the oxygen concentration was lowered to  $0.06 \text{ ml l}^{-1}$ . If such concentrations apply to *C. pacificus* in the field, then the oxygen concentrations in the SBB's deep oxygen-deficient waters were too low for the survival of the C5s during the late summer and fall of 1994 and during September 1995. At these times the C5s were aggregated right above the oxygen-deficient waters. However, in June and July of 1995, there was sufficient oxygen in the deepest waters of the SBB for the survival of C5 *C. pacificus*, due to the spring flushing, and the C5s were present in highest concentrations near the bottom.

The ADCP did not sense the deep C5 layer within the SBB until mid-August because the deepest ADCP bin was 20 m above the bottom. Therefore, even though we noticed the formation of the deep C5 aggregation in June and July with the MOCNESS and OPC, it was mid-August before the oxygen had been sufficiently depleted in the deep waters of the SBB to force the C5s up into the range of the ADCP. Also, it is unlikely that the low-frequency ADCP would have sensed concentrations of C5s similar to those present in the deep waters during June.

Determining what caused the high backscatter from ~400 to 450 m for much of the ADCP mooring period is problematic. High range-corrected backscatter from more distant depth bins will occur as the limit of the ADCP range is reached. That is, the signal received by the ADCP from bins far away from the instrument is noise and remains constant, so when the signal in this region is range corrected, the farther away the bin, the higher the corrected backscatter. However, for our data below 400 m, the echo intensity was always well above the noise level and the correlation magnitudes of all 4 beams were always high. Thus, we found no good reason to exclude data from any bins below 400 m. Another possibility is that we made too large a range correction, making the more distant bins have

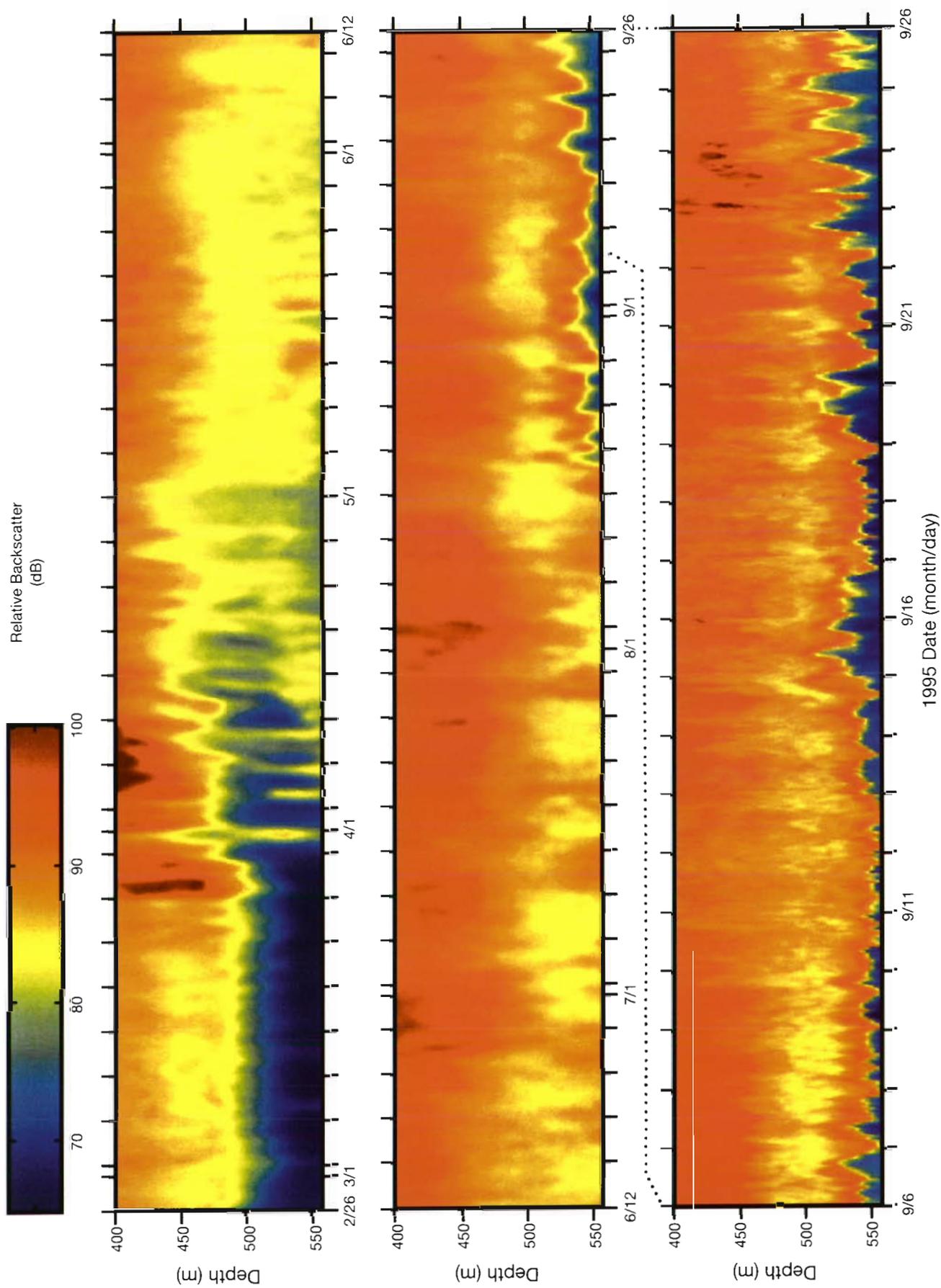


Fig. 6. Range-corrected, relative backscatter intensity measured by the ADCP at the SBB central station. Data in the top 2 panels (26 Feb to 26 Sep 1995) have been filtered with a 38 h, low-pass filter and date ticks are 4 d apart, unless otherwise labeled. Data in the bottom panel (6 to 26 Sep 1995) have not been filtered and date ticks are 1 d apart

higher corrected backscatter. However, engineers at RD Instruments independently processed some of our data and obtained range-corrected backscatter values consistent with our results. This leaves the possibility that the high backscatter from ~400 to 450 m is real, but due to organisms not efficiently sampled by the MOCNESS or OPC. Mesopelagic fish are one such possibility. However, there was no diel variability in this backscatter as would be expected for mesopelagic fish which vertically migrate on a diel cycle.

Osgood & Checkley (in press) remarked about the continuity of the deep C5 *Calanus pacificus* layer within the SBB. The ADCP backscatter data further testify to the continuity of the layer, in both time and space. The backscatter data also demonstrate the dynamics of the deep layer at a single location. Not only was the gradual shoaling of the C5 layer apparent, such as was observed with the OPC data from successive cruises, but rapid and extensive fluctuations in the depth of the layer were also observed. It is important to keep these rapid fluctuations in mind when the deep C5 layer or other properties are observed at different times. Profiles obtained with instruments such as a CTD, OPC or MOCNESS may show significant depth variation on the scale of hours.

Two questions arise, the answers to which are important to our understanding the dynamics of the *Calanus pacificus* populations in this region. The first question is: how does the deep C5 aggregation within the SBB build up to such high concentrations? The second question is: what happens to the individuals of the deep aggregation between fall and early winter?

### How does the deep aggregation build up?

There are 2 possible mechanisms for the build up of high concentrations of diapausing C5 *Calanus*

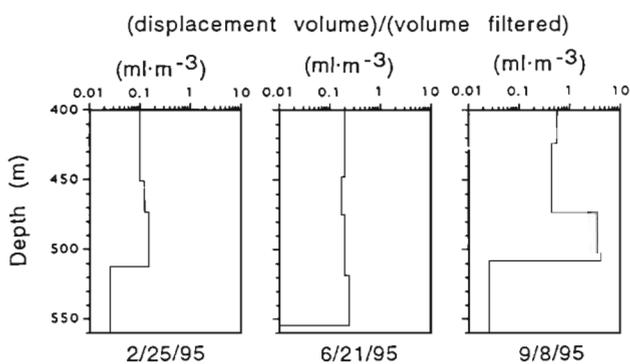


Fig. 7. Wet displacement volume/volume filtered of MOCNESS samples. Each profile is comprised of data obtained from all the daytime samples obtained for the shown depth intervals on that date. Dates shown as mo/d/yr

*pacificus* in the SBB. These are local high reproduction in the surface waters above the SBB or, as hypothesized by Osgood & Checkley (in press), accumulation of the C5s due to advection over the SBB of C5s that are entering diapause (or are in diapause but from shallower surrounding areas) and migrating below the basin's sill. To determine which of these mechanisms is most important, we compare the dynamics of the SBB deep aggregation to the changes in the deep dwelling C5 concentrations outside the basin.

At both MOCNESS stations during June, approximately equal C5 concentrations were observed in the surface 50 m and near the bottom, with slightly higher concentrations being found within the basin. By June, a portion of the *Calanus pacificus* population have arrested their development at the C5 stage and migrated to deeper waters for diapause while the rest of the population is still active in the surface waters. However, it has not been long since the entire population was in the surface waters (Fleminger 1985) and, hence, the deep population has not had much time to accumulate individuals from anywhere other than the presently overlying surface waters.

In contrast, during the fall, approximately equal C5 concentrations were observed in the surface and deep layers outside the SBB, but the C5 concentrations had built up substantially in the deep waters inside the basin. By fall, a portion of the *Calanus pacificus* population has been in diapause as deep-dwelling C5s for a long time. During this time they could have been trapped and accumulated below the basin's sill. There is no such concentrating mechanism outside the basin. The lack of below-sill-depth flushing during this period allows the C5s to be retained within the basin and also allows the oxygen-deficient waters to build up within the basin.

We conclude that the concentration differences observed between the 2 stations' deep waters during June, and surface waters at all times of year, are due to differences in local production. However, the large, deep aggregation of C5s observed in the basin during the late summer and fall is due to an accumulation of C5s from the surrounding waters. This is the same mechanism proposed for the high concentrations of deep-dwelling stages of *Calanus* spp. in basins on the Nova Scotia shelf (Sameoto & Herman 1990). Advection of organisms to an area combined with a concentrating mechanism is also the explanation Wishner et al. (1995) provided for the dense *Calanus finmarchicus* aggregations they observed in surface waters. In their case though, the concentrating mechanism was a fluid convergence zone rather than a bathymetric retention area.

### What happens to the deep aggregation?

There are several ways the deep layer of C5 *Calanus pacificus* could have disappeared from the SBB. The deep waters of the SBB could have been flushed, pushing the C5s out; the C5s could have come out of diapause, migrated to the surface waters, matured to adults, and been dispersed by surface currents; the C5s could have been forced above the sill depth of the basin by the buildup of oxygen-deficient waters and then leaked out of the basin; finally, the C5s could have experienced massive mortality.

The C5s of the deep layer in the SBB were apparently not pushed out of the basin by a flushing event between November 1994 and January 1995 because the oxygen and ADCP data indicate the deep waters of the basin did not flush until April 1995. It also seems unlikely that the deep dwelling C5s experienced massive mortality between November and January: we were able to follow the layer for 3 mo prior to this with no indications of mortality events and we also followed the development of the C5 layer through the next summer and saw no indications of mortality events.

Some of the C5 *Calanus pacificus* in the SBB deep aggregation may have come out of diapause and migrated to the surface waters by November 1994. The surface waters overlying the SBB did have higher concentrations of C5s in November than they did the preceding August or October (Figs. 2 & 4). In addition, C5 concentrations in November were higher in the waters overlying the deep aggregation than they were in the surrounding waters. Even though there was no large signal in the surface waters in November or the following January that a sizable portion of the deep aggregation had migrated to the surface waters, many of the deep-dwelling C5s may have ascended after November and been dispersed from the region by the surface currents before January.

Alternatively, the deep layer of C5 *Calanus pacificus* in the SBB could have been forced above the western sill of the basin by the build up of oxygen-deficient waters and then advected out of the basin at depth between November 1994 and January 1995. In October and November 1994 the C5 layer's upper boundary coincided with the western sill depth (Fig. 2). Given the extent of the vertical motions that the C5 layer experiences, as manifested in the ADCP data, by fall of 1994 the C5 layer was likely above the sill depth at times and would therefore not be efficiently retained within the basin. In November the C5 layer was less concentrated closer to the western sill, consistent with some of the C5 layer having started to leak out over the sill.

We hoped to observe the disappearance of the deep layer of C5 *Calanus pacificus* during the fall of 1995

with the ADCP. However, after early October 1995, the C5 layer became less discrete, as it blended in with the high backscatter values above it. Due to this, it was not possible to follow the C5 layer through October and ascertain its fate. The ADCP data also indicate that a second flushing event of the deep waters of the SBB commenced in late October 1995 and continued through November. Therefore, for the disappearance of the deep C5 layer from the SBB during the fall of 1995, not only did the 2 mechanisms that seemed possible for November 1994 to January 1995 exist, but there was also the confounding effect of the flushing of the basin's deep waters. This flushing may have augmented the advective loss of C5s from the SBB over its sill.

The relative importance of the 3 dispersal mechanisms surely varies between years. Obviously, the deep waters of the basin do not flush every fall. Therefore, in some years, such as the first fall of our study, this does not contribute to the dispersal of the aggregation. The flushing of the SBB deep waters occurs mostly during the spring (Sholkovitz & Gieskes 1971, Reimers et al. 1990). Depending upon the strength and timing of this flushing, oxygen-deficient waters can build up to varying degrees later in the year. Some years they may build up to the sill depth early enough in the fall such that most of the C5s from the deep aggregation within the basin are lost over the sill before they come out of diapause. Other years, the oxygen-depleted water may not build up sufficiently to force the C5s above the sill and the C5s may have time to come out of diapause while still in the SBB. To better determine the fate of the C5s from the deep aggregation a more detailed study centered around late fall/early winter is needed.

### Significance

The diapausing C5 *Calanus pacificus* accumulated within the SBB are available for repopulation of the surface waters upon emerging from diapause. Osgood & Checkley (in press) found that the deep aggregation of C5 *C. pacificus* in the SBB could populate approximately three  $1^{\circ}\text{N} \times 1^{\circ}\text{W}$  blocks at the C5 abundance that was found over the entire water column outside of the basin. How aggregated the *C. pacificus* stay after leaving the deep waters of the SBB depends upon the manner in which they leave the basin, especially the length of time over which the aggregation dissipates and what the prevailing currents are during that period. The copepods from the aggregation may have a large impact in a localized region or a smaller impact over a larger region. We observed no substantial increase of adult *C. pacificus* in the SBB region following the disappearance of the deep aggregation. This

may have been because our few, widely spaced net samples missed high-concentration patches or due to the coarse temporal sampling of our study combined with the length of time over which the aggregation was dispersed and the velocity of the currents into which they were dispersed. Regardless, the SBB and the conditions there are important to the regional *C. pacificus* population. Diapausing C5s trapped in the SBB are retained in waters of relatively low predator abundance (Alldredge et al. 1984) and in a region which is favorable for the growth of the copepods upon their emergence from diapause (Smith et al. 1986, Hendershott & Winant 1996). Interannual variation in the dominant process by which the deep aggregation dissipates, i.e. vertical migration versus horizontal mixing, may cause interannual variation in the dynamics of the surface population, e.g. seeding of waters upwelled off Pt. Conception. More generally, basins in the coastal oceans may be of special importance to some zooplankton by serving as retention areas. Such basin populations may serve as seed populations for larger areas.

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