JOURNAL OF GEOPHYSICAL RESEARCH, VOL. 116, C12046, doi:10.1029/2011JC007310, 2011

Three-dimensional structure of a swarm of the salp *Thalia democratica* within a cold-core eddy off southeast Australia

J. D. Everett,[1,2] M. E. Baird,[3,4] and I. M. Suthers[1,2]

Received 19 May 2011; revised 27 October 2011; accepted 27 October 2011; published 31 December 2011.

[1] Swarms of the salp *Thalia democratica* periodically occur off southeast Australia following the austral spring bloom of phytoplankton. In October 2008 a filament of upwelled water was advected south by the adjacent East Australian Current and formed a 30 km diameter cold-core eddy (CCE). The three-dimensional structure of a subsurface swarm of *T. democratica* within the eddy was examined using both oblique and vertical hauls and an optical plankton counter (OPC) deployed on a towed body. The CCE displayed distinct uplift of the nutricline and elevated fluorescence. Net samples show the zooplankton community was dominated by *T. democratica*, comprising 73%–88% of zooplankton abundance. The size distribution of *T. democratica* measured from net samples was 0.5–5 mm and was used to interpret the OPC transects, which showed the swarm formed a 15 km diameter disc located 20–40 m deep in the center of the eddy. The maximum salp abundance was in the pycnocline and coincided with the subsurface fluorescence maximum. The mean abundance of *T. democratica* size particles within the disc was 5003 individuals m^{-3} (ind. m^{-3}), contrasted with only 604 ind. m^{-3} at the outer edge of the eddy. The vertically concentrated and horizontally constrained disc-shaped salp swarm occurred at the interface of salp-bearing inner shelf water and nutrient-rich upwelled water in a CCE. The physical processes that formed the CCE on the inshore edge of the western boundary current led to the largest density of salps recorded.

Citation: Everett, J. D., M. E. Baird, and I. M. Suthers (2011), Three-dimensional structure of a swarm of the salp *Thalia democratica* within a cold-core eddy off southeast Australia, *J. Geophys. Res.*, *116*, C12046, doi:10.1029/2011JC007310.

1. Introduction

[2] Salps are gelatinous zooplankton with some of the fastest known growth rates of all metazoans. They are non-selective filter feeders who feed by pumping water across a mucus sieve [*Madin and Deibel*, 1998]. The sieves have some of the smallest diameter mesh elements and mesh spacing of all marine filter feeders [*Bone et al.*, 2003]. By capturing particles less than one micron in size [*Sutherland et al.*, 2010] salps are feeding on particles four to five orders of magnitude smaller than themselves [*Fortier et al.*, 1994], thereby bypassing several trophic levels.

[3] The most common salp off southeast Australia, *Thalia democratica* has published growth rates of between 0.3% [*Deibel*, 1982a] and 28% [*Le Borgne and Moll*, 1986] in length per hour. Salps have life cycle adaptations which involve the obligatory alternation between aggregate sexual and solitary asexual generations, allowing fast population growth rates while maintaining genetic variability [*Alldredge and Madin*, 1982]. This effective reproductive strategy, combined with efficient clearance rates of 250–801 mL mg^{-1} h^{-1} [*Deibel*, 1982b; *Mullin*, 1983] can result in population increases of up to 2.5 times per day [*Heron*, 1972b].While such a population growth rate is common in protozoans, it is exceptional among metazoans.

[4] Oceanographic processes are important in determining the location, duration and size of salp swarms which are often associated with regions of high productivity [*Kremer*, 2002; *Deibel and Paffenhofer*, 2009]. Swarms of *T. democratica* commonly occur within nutrient-rich shelf water and slope water intrusions [*Heron and Benham*, 1984; *Deibel and Paffenhofer*, 2009] and upwelling zones [*Yount*, 1958; *Berner*, 1967; *Blackburn*, 1979]. Rapid increases in salp biomass require a seed population of salps, an appropriate life stage to allow fast asexual reproduction, and nutrient-rich water brought into the photic zone, to permit an increase in phytoplankton productivity [*Deibel and Paffenhofer*, 2009; *Kremer*, 2002].

[5] Cold-core eddies (CCE) offer opportunities for local productivity and growth of species particularly adapted to

---

[1] Evolution and Ecology Research Centre, University of New South Wales, Sydney, New South Wales, Australia.

[2] Sydney Institute of Marine Science, Mosman, New South Wales, Australia.

[3] Plant Functional Biology and Climate Change Cluster, Faculty of Science, University of Technology Sydney, Sydney, New South Wales, Australia.

[4] Also at Sydney Institute of Marine Science, Mosman, New South Wales, Australia.

Copyright 2011 by the American Geophysical Union.
0148-0227/11/2011JC007310

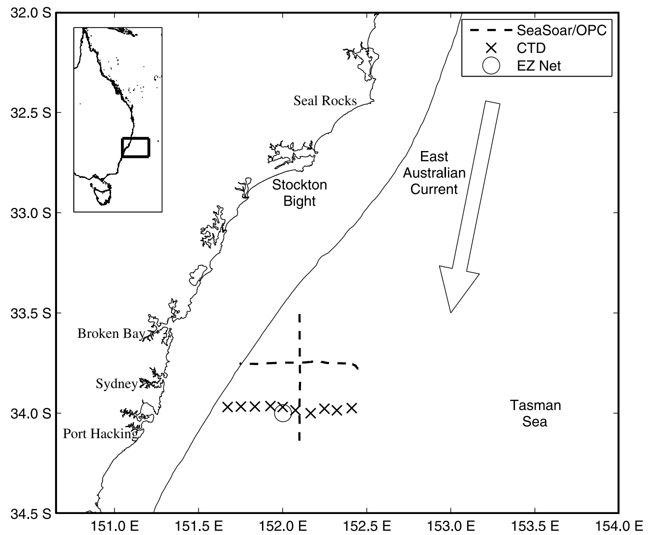

Figure 1. A map of the study region off Sydney, Australia, showing the geographical locations of sampling. The locations of the SeaSoar/optical plankton counter (OPC) (dashed lines), conductivity-temperature-depth (CTD) (crosses), and EZ (open circle) transects are shown. The thin line parallel to the coast is the edge of the continental shelf (200 m isobath). Each transect was targeted to cross the center of the southward moving eddy; hence the sampling locations are offset with time. The general direction and location of the East Australian Current are shown with an arrow.

excelling in such highly productive rapid growth/high-mortality situations [*Bakun*, 2006]. CCEs are characteristic of the coastal side of western boundary currents such as the Agulhas, the Kuroshio, the Gulf Stream and the East Australian Current (EAC), but their biological significance is relatively understudied. When CCEs form close to upwelling zones, mechanisms of enrichment, concentration and retention within a CCE may be arranged in particularly favorable sequences to produce outbursts in biological productivity and reproductive success of organisms capable of using those characteristics to advantage [*Bakun*, 2006; *Deibel and Paffenhofer*, 2009]. Such increases in productivity within CCEs have been described for phytoplankton [*Yoder et al.*, 1981; *Kasai et al.*, 2002] and zooplankton [*Deibel*, 1985; *McGillicuddy et al.*, 1998] as well as increased abundance and survival of larval fish [*Logerwell and Smith*, 2001].

[6] Biogeochemical properties of coastal waters of southeast Australia are dominated by the EAC [*Nilsson and Cresswell*, 1981]. The EAC originates in the warm oligotrophic waters of the Coral Sea and flows southward along the offshore edge of the continental shelf [*Baird et al.*, 2008]. Between 30°S and 34°S the EAC separates from the coast [*Godfrey et al.*, 1980], generating uplift of nutrient-rich slope water onto the continental shelf [*Tranter et al.*, 1986; *Oke and Middleton*, 2000; *Roughan and Middleton*, 2002; *Roughan et al.*, 2003; *Roughan and Middleton*, 2004] resulting in surface phytoplankton blooms [*Cresswell*, 1994; *Baird et al.*, 2006; *Hallegraeff and Jeffrey*, 1993; *Ajani et al.*, 2001]. South of the separation zone the EAC meanders eastward across the Tasman Sea, leaving behind a dynamic southward moving eddy field [*Ridgway and Godfrey*, 1997; *Mata et al.*, 2006], analogous to the frontal eddies of the Gulf Stream [*Mann and Lazier*, 2006]. Swarms of *T. democratica* have commonly been associated with processes such as upwelling or slope water intrusions off southeast Australia, especially during the austral spring and summer [*Thompson*, 1948; *Heron and Benham*, 1984; *Heron*, 1972a; *Deibel and Paffenhofer*, 2009]. High densities of *T. democratica* have also reoccurred in the Californian Current [*Blackburn*, 1979], Gulf Stream [*Deibel and Paffenhofer*, 2009], west Mediterranean [*Licandro et al.*, 2006] and the Agulhas Bank [*Gibbons*, 1997].

[7] CCEs that form from upwelled water are amongst the most productive oceanic waters [*Bakun*, 2006]. In this paper we report observations of the salp, *T. democratica*, within a CCE off southeast Australia and use oceanographic conditions to explain the three-dimensional structure, biomass and size distribution of a salp swarm. The use of high resolution and multiple gear types allows improved quantification of the spatial extent, abundance and physical processes driving an usually dense salp swarm.

2. Methods

2.1. Study Site

[8] A 30 km diameter CCE was sampled during the austral spring (14–16 October 2008) aboard the R/V *Southern Surveyor*. The surveyed area extended off southeast Australia, from Broken Bay in the north (33.5°S) to Port Hacking in the south (34.1°S), extending offshore to 152.5°E (Figure 1). Prior to the cruise, in mid-September 2008, the EAC had relatively weak flow, with temperatures ranging from 20°C to 22°C and a significant retroflection around 35°S (from satellite imagery, not shown). By the commencement of sampling in October 2008, the EAC had warmed to 23°C (Figure 2a). The EAC temperature during this time was approximately 1°S–2°C warmer than the average October SST over the previous 50 years (from CSIRO Atlas of Regional Seas (CARS), version 2006a).

2.2. Physicochemical Sampling

[9] The eddy was first sampled using a SeaSoar (Figure 1), which is a continuously profiling towed body, that undulates between the surface and 120 m. Two deployments of the SeaSoar took place across the CCE on 14–15 October 2008 measuring temperature, salinity and fluorescence. The first transect took place in an east–west direction and the second transect in a south–north direction (Table 1).

[10] Following the SeaSoar deployments, a transect of 10 conductivity-temperature-depth (CTD) casts (Figure 1) was undertaken across the eddy on 15 October 2008 (Table 1). During each CTD cast temperature, salinity and fluorescence were electronically measured, and nutrients (NO_3, PO_4, Si) taken at the surface, and nominal depths of 25, 50, 75, 100, 150, 200, 300 m. The closest bottle depth was adjusted to sample the fluorescence maximum based upon the fluorescence profile on the downcast. Nutrient analysis followed techniques described by *Cowley et al.* [1999] and has an approximate accuracy of 0.02 μM.

[11] Acoustic Doppler Current Profiling (ADCP) data from the R/V *Southern Surveyor* were collected using an RDI vessel mounted Ocean Surveyor with a frequency of 75 kHz. The bin size was 16 m and there were 50 bins per

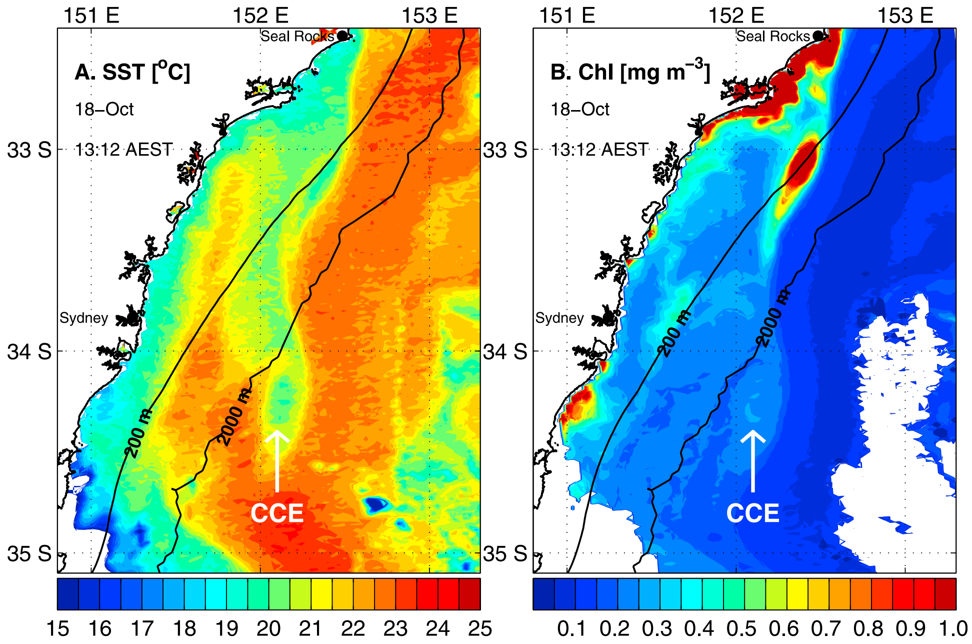

Figure 2. (a) Sea surface temperature (SST) and (b) surface chlorophyll *a* (Chl) concentration on 18 October 2008 derived from Level-2 MODIS-Aqua. The sampled cold-core eddy (CCE) is marked with an arrow and centered at 34.3°S and 152.1°E. Note that the satellite image is 2 days after sampling due to significant amounts of cloud cover 14–16 October. Another billow of cool, high chlorophyll *a* water is visible at ~33°S.

profile with the shallowest bin centered on 30 m. ADCP data was supplemented with velocities from a Surface Velocity Program (SVP) drifter and ADCP's mounted on the IMOS-ANMN Sydney Mooring Array.

2.3. Zooplankton Net Sampling and Analysis

[12] Plankton sampling was conducted with a multiple opening closing net known as an EZ Net, which consisted of multiple 335 μm mesh nets of 1 m^2 which were triggered remotely. The EZ Net was lowered to a depth of 100 m and three oblique tows were performed, centered around 90 m (100–80 m), 50 m (60–40 m) and 10 m (20–0 m). Approximately 250 m^3 of water was filtered through the 90 m net and 100 m^3 was filtered through the 10 and 50 m nets. The ship returned to the same geographic location four times over 18 h (Figure 1). Sampling was targeted at the center of the eddy, although the center was missed due to the eddy moving south at 15–35 km d^{-1}. The actual sampling location relative to the eddy was later determined from temperature profiles to be to the northwest of the eddy center (see section 3). The zooplankton sample from each net was sieved to remove excess water, concentrated into 1 L and preserved in a 5% formalin solution. Where necessary, 1 L was subsampled and the volume of the remaining sample recorded.

[13] To be comparable to previous studies in the region, the methods for calculation of zooplankton abundance were based on those of the M/V *Warreen* cruises 1938–1942 [*Thompson and Kesteven*, 1942]. A 100 mL subsample (i.e., 10%) was taken and filtered through a 200 μm sieve. The 100 mL sample was gently mixed to ensure an even consistency of organisms suspended in the solution before two 1 mL replicate subsamples were taken with a wide-mouth pipette. A minimum of 100 individuals per subsample were counted and identified, with extra 1 mL subsamples examined if necessary. Organisms were classified into the following categories enumerating major taxonomic groups known to frequently occur off southeast Australia, following *Thompson and Kesteven* [1942]: salps, doliolids, pyrosoma, copepods, krill, crustaceans (other), larvaceans, chaetognaths and other zooplankton. The first 60 *T. democratica* individuals, both aggregate and solitary forms, within each subsample were measured and photographed using image analysis software (Image Pro Plus 5.1; Media Cybernetics, Silver Spring, MD, USA). Salp length was measured from oral opening to the posterior ridge of the gut, exclusive of

Table 1. Details of the Instrument Deployments in Chronological Order[a]

Gear Type	Start Time	Finish Time	Start Location	Finish Location
SeaSoar (east–west)	14 Oct 13:01	14 Oct 17:59	33°46.8′S, 152°28.2′E	33°45′S, 152°44.4′E
SeaSoar (south–north)	14 Oct 21:49	15 Oct 03:14	34°8.4′S, 152°6′E	33°29.4′S, 152°6′E
CTD	15 Oct 08:30	15 Oct 23:30	33°58.2′S, 152°24.6′E	33°58.2′S, 151°40.2′E
EZ Nets	16 Oct 05:00	16 Oct 21:40	34°S, 152°E	34°S, 152°E

[a] All deployments occurred in October 2008 aboard the R/V *Southern Surveyor*.

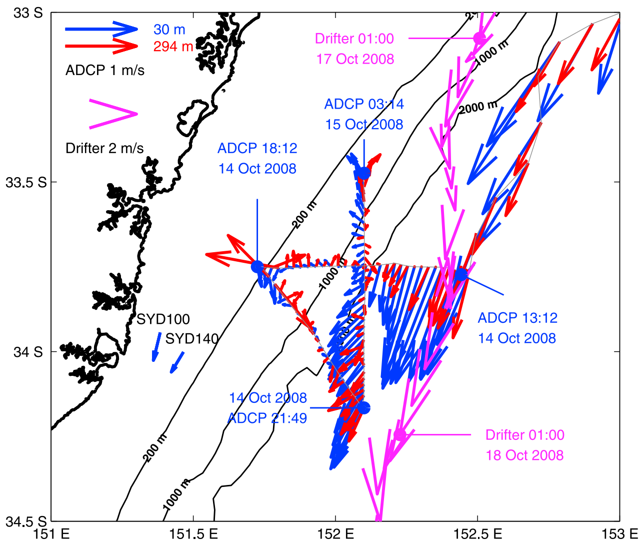

Figure 3. Ship-mounted Acoustic Doppler Current Profiling (ADCP) velocities (m s^{-1}) at the surface (30 m, blue) and depth (294 m, red) overlaid with the velocities from a Surface Velocity Program (SVP) drifter (pink). The mean surface (10 m) velocities measured by the IMOS-ANMN Sydney Mooring Array (SYD100 and SYD140) from 06:00 14 October to 06:00 15 October at ~34°S on the continental shelf are shown as blue arrows.

the outer test [*Foxton*, 1966] and corrected for formalin shrinkage using the equation of *Nishikawa et al.* [1995].

2.4. Optical Plankton Counter Measurements

[14] Size-resolved particulate matter (organic and inorganic) was measured using an optical plankton counter (OPC; Focal Technologies Corporation Model OPC-2 T with a sampling aperture of 20 cm^2) [*Herman*, 1988] mounted on the SeaSoar. The OPC optically measures the projected area of particles to calculate the equivalent spherical diameters (ESD). The size of the particles were allocated to 4096 size bins in the range 400 μm–4 mm. Total biovolume (volume of biological material per m^3) was calculated using the ESD and was based on a running average of the counts in a particular size class over 10 s. The volume of flow through the OPC was based on distance measured over a 10 s interval using a General Oceanic Flowmeter. The choice of time interval was a trade-off between a larger time period to obtain a higher particle count for accurate estimation of the size distribution, and a shorter time period to provide better spatial resolution.

3. Results

3.1. Physical Properties of the Cold-Core Eddy

[15] Satellite imagery indicated a 30 km diameter CCE formed approximately 7–10 days prior to sampling and was made up of inner-shelf and upwelled slope water derived from the shelf around 33°S and the upwelling zone off Seal Rocks (32.5°S). The CCE had been "spun up" by the adjacent EAC and advected south as part of an extended filament (visible as cooler water in Figure 2 south to 34.5°S). The CCE (Figure 2) was moving south at a rate of 15–35 km d^{-1} and was initially sampled east of Sydney (33.9°S). By the completion of sampling, the eddy was located off Port Hacking (34.1°S). Shelf velocities were predominately southward flowing, except in the vicinity of the CCE, where cyclonic (clockwise) rotation was evident (Figure 3).

[16] Between the two SeaSoar transects the eddy moved at 26 km d^{-1} in a direction 195° from north. The 30 km diameter eddy had a tangential velocity at its perimeter of ~0.5 m s^{-1}, giving a period of 2.2 days. The Rossby number, $Ro = U/LF$ was ~0.5, where U and L are characteristic velocity and length scales, and f is the Coriolis parameter. At $Ro \sim 0.5$ the balance between the pressure gradient and Coriolis terms dominate the dynamic balance of the eddy, but the centrifugal force is not negligible.

[17] The CTD transect across the CCE shows decreased temperature at the center of the eddy, uplift of the isotherms and isohalines (Figure 4a), typical of CCEs [*Mann and Lazier*, 2006]. Nitrate, silicate and phosphate were depleted in the surface layer (down to approximately 30 m) of the CCE with elevated subsurface nutrient concentrations near the eddy center (Figures 4c–4e). The coastal side (left side of Figure 4) of the CCE showed nutrient enrichment relative to the EAC edge (i.e., offshore) of the eddy. The fluorescence maximum was located at a potential density of ~1025.8 kg m^{-3} (Figure 4b) and extended toward the coast.

3.2. Depth-Stratified Zooplankton Community Composition

[18] The only salp species found was *T. democratica*, which dominated the zooplankton community to a depth of 50 m (Table 2 and Figure 5), making up 73%–88% of zooplankton abundance. The deeper samples (90 m) were dominated by copepods during the night when *T. democratica* made up only 9% of zooplankton abundance, however during the day *T. democratica* dominated with 74% (Figure 5). Other gelatinous zooplankton (Pyrosomas and Doliolids) were collected, but in relatively low abundance. Pyrosomas were present in only one sample (90 m, 11:30) with an abundance of 50 individuals m^{-3} (ind. m^{-3}), while doliolids were more abundant at dusk and night (0–62.5 ind. m^{-3}) compared to dawn and day (0–18.7 ind. m^{-3}).

[19] Aggregate forms of *T. democratica* were always more abundant than the solitary forms in the ratio of 3.7:1 up to 44:1 (data not shown). There was little evidence of diel vertical migration (DVM), with *T. democratica* being present at all sampled depths and times. Numbers of *T. democratica* were reduced at 90 m depth at night (Table 2), with a corresponding increase at the surface, although there was also a reduction at 90 m depth at dawn, with no corresponding increase at the surface. The lowest surface abundance occurred at dawn with the maximum in the midday haul.

3.3. Zooplankton Size Distribution and Abundance

[20] The size distribution of *T. democratica* from EZ net samples showed a range of lengths between 0.5–5 mm with the peak of the histogram varying between 1.5–3 mm length (Figure 6). Increased proportion of smaller sizes, suggesting reproduction, was evident at 50 and 90 m depth at dawn, however there was no recorded evidence that this cohort grew through the size distribution in the following 18 h.

[21] The size distribution of particles from the OPC mounted on the SeaSoar showed a lower abundance and

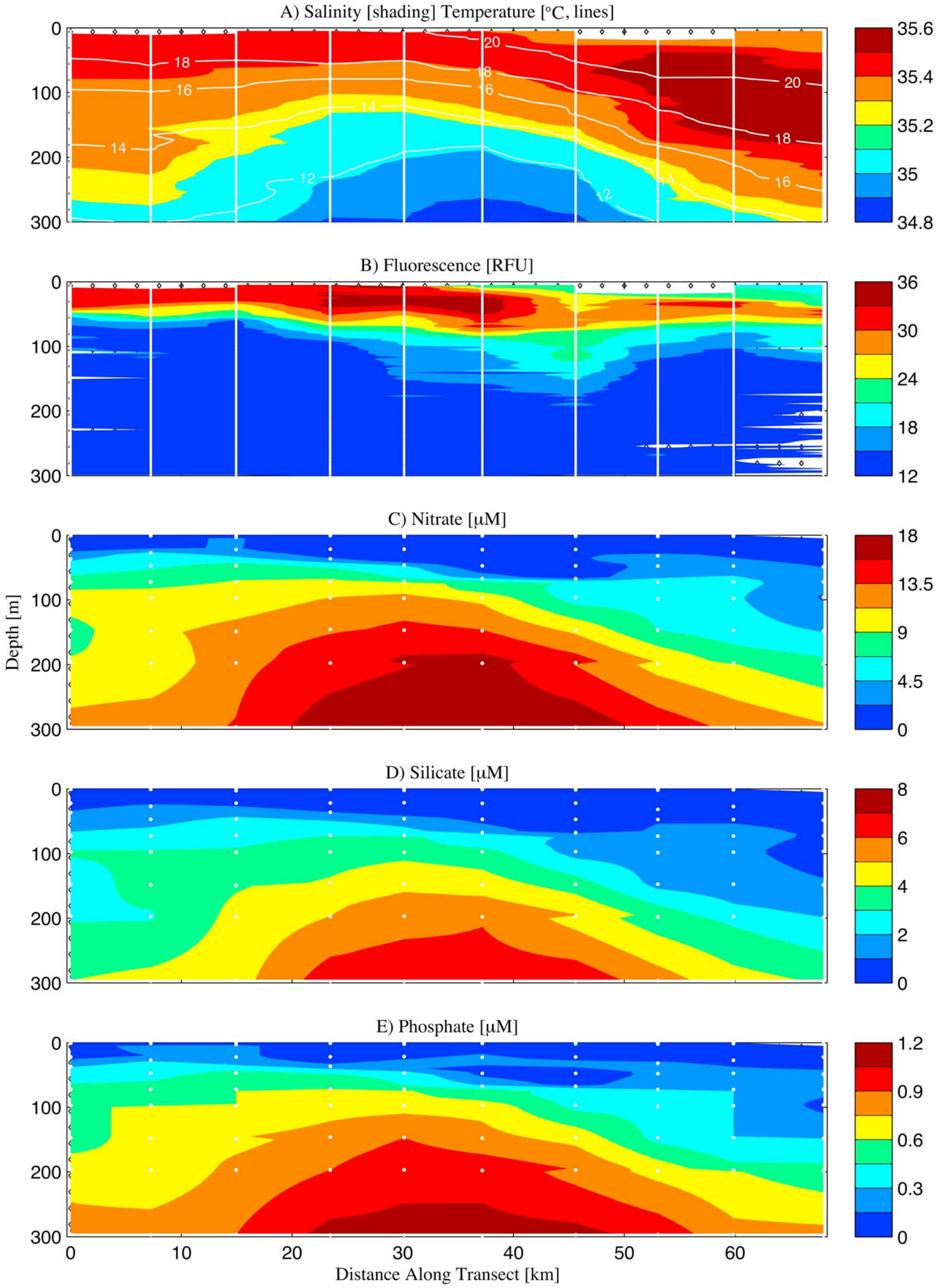

Figure 4. CTD transect from the coastal waters off Sydney (west) through the cold-core eddy to the East Australian Current (east), showing (a) salinity (color shading) and temperature (lines), (b) fluorescence, (c) nitrate, (d) silicate, and (e) phosphate. The thin white lines indicate the electronic CTD casts with measurements taken each meter. The nitrate, phosphate, and silicate concentrations were obtained from bottle samples from the location indicated by a white dot. The transect was undertaken in an easterly direction from 08:30 to 23:50 on 15 October 2008 (Figure 1). The black diamonds near the surface represent missing data.

proportion of large (≥680 μm) particles at the edge of the eddy (Figure 7a), relative to the center (Figure 7b). ESDs from the OPC were converted to body lengths of *T. democratica* by maintaining the OPC-measured projected area, and adjusting the length to width ratio of the particle to be 2.37:1 as measured from the EZ samples (n = 4465; data not shown). Using $Length = ESD\sqrt{2.37}$ (where Length is mm and ESD is μm) a 680 μm ESD particle is equivalent to a salp of ≈1 mm length. These OPC-measured large particles (≥680 μm ESD) corresponded with the net-sampled size of *T. democratica* (Figure 6). Net samples show that *T. democratica* comprised 73%–88% of the zooplankton community

Table 2. Mean Abundance (and Standard Deviation) of *T. democratica* (ind. m^{-3}) for Three Depths at the Northwestern Edge of the Eddy[a]

Depth (m)	Dawn 05:00	Day 11:30	Dusk 18:00	Night 21:15
10	280 (80)	780 (299)	1287 (460)	2103 (43)
50	1263 (50)	1056 (0)	1791 (0)	no data
90	466 (10)	1514 (880)	1093 (1149)	162 (82)

[a] Sampling occurred over an 18 h period on 16 October 2008 using the EZ net.

composition in the region (Figure 5). The community composition and size measurements of the *T. democratica* population obtained from the EZ net samples indicate that the abundant large zooplankton at the center of the eddy recorded by the OPC was *T. democratica*.

[22] Temperature and salinity from the SeaSoar (Figures 8a and 9a) show similar uplift as the CTD transect (Figure 4a). The fluorescence maximum (Figures 8b and 9b) was located at a depth of 30–40 m, between the 1025.5 and 1026 kg m^{-3} potential density contours. Mean zooplankton counts (Figures 8c and 9c) in the center of the eddy (5863 ind. m^{-3}) were more than 5 times those at the edge of the eddy (1104 ind. m^{-3}). Mean counts of large zooplankton (ESD $\geq$ 680 μm), were much higher at the eddy center (5003 ind. m^{-3}) relative to the edge (604 ind. m^{-3}). The maximum biovolume of zooplankton (Figures 8d and 9d) was 25480 mm^3 m^{-3} at the center of the eddy compared to 1148 mm^3 m^{-3} at the edge of the eddy. A similar pattern of total and large zooplankton increases was seen in both the south–north and east–west transect indicating that even though the eddy was at the head of the filament (Figure 2), the highest zooplankton biomass and abundance, was constrained to the center of the eddy as a subsurface disc.

4. Discussion

4.1. Physical Influences on Biological Processes

[23] The physical processes that formed the CCE also led to the large biomass and determined the spatial distribution of the salp swarm. The processes leading to the formation of the eddy north of Seal Rocks (Figure 2) were investigated using temperature and salinity properties from the same cruise detailed by *Henschke et al.* [2011]. In the vicinity of the formation, inner shelf water (mean properties in the top 50 m; T = 19°C, S = 35.55, σ = 1025.45 kg m^{-3}) and upwelled water (T = 17.2°C, S = 35.42, σ = 1025.80 kg m^{-3}) were present [*Henschke et al.*, 2011]. At the center of the CCE during the sampling period, the SeaSoar transects (Figures 8 and 9) show the inner shelf water above 20 m (19°C) and upwelled water below 40 m (17°C).

[24] There are two possible processes which may have occurred around the time of CCE formation to explain this. Either the upwelled filament never reached the surface and was advected south with inner shelf water overlying it, or a 20 m layer of lighter inner shelf water flowed over the top of the eddy after formation. In either case, the pycnocline between 20 and 40 m, shown by the density gradient between 1025.5–1026.0 kg m^{-3} (Figures 8 and 9), represents a mixing zone between the nutrient-rich upwelled

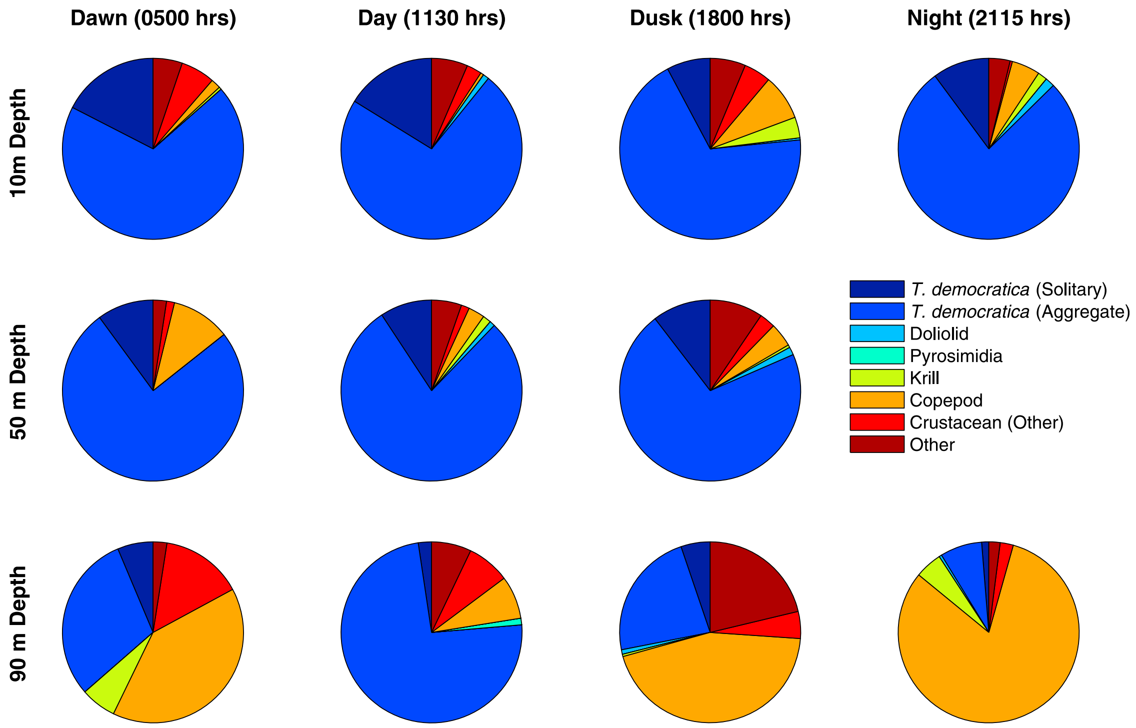

Figure 5. Zooplankton community composition (percent of individuals) for three depths over an 18 h period on 16 October 2008. The colors represent zooplankton groups with *T. democratica* split into aggregate and solitary form. Only the dominant taxonomic groups are plotted, with the remaining groups making up "Other." No data are available for the 50 m night tow because of equipment malfunction.

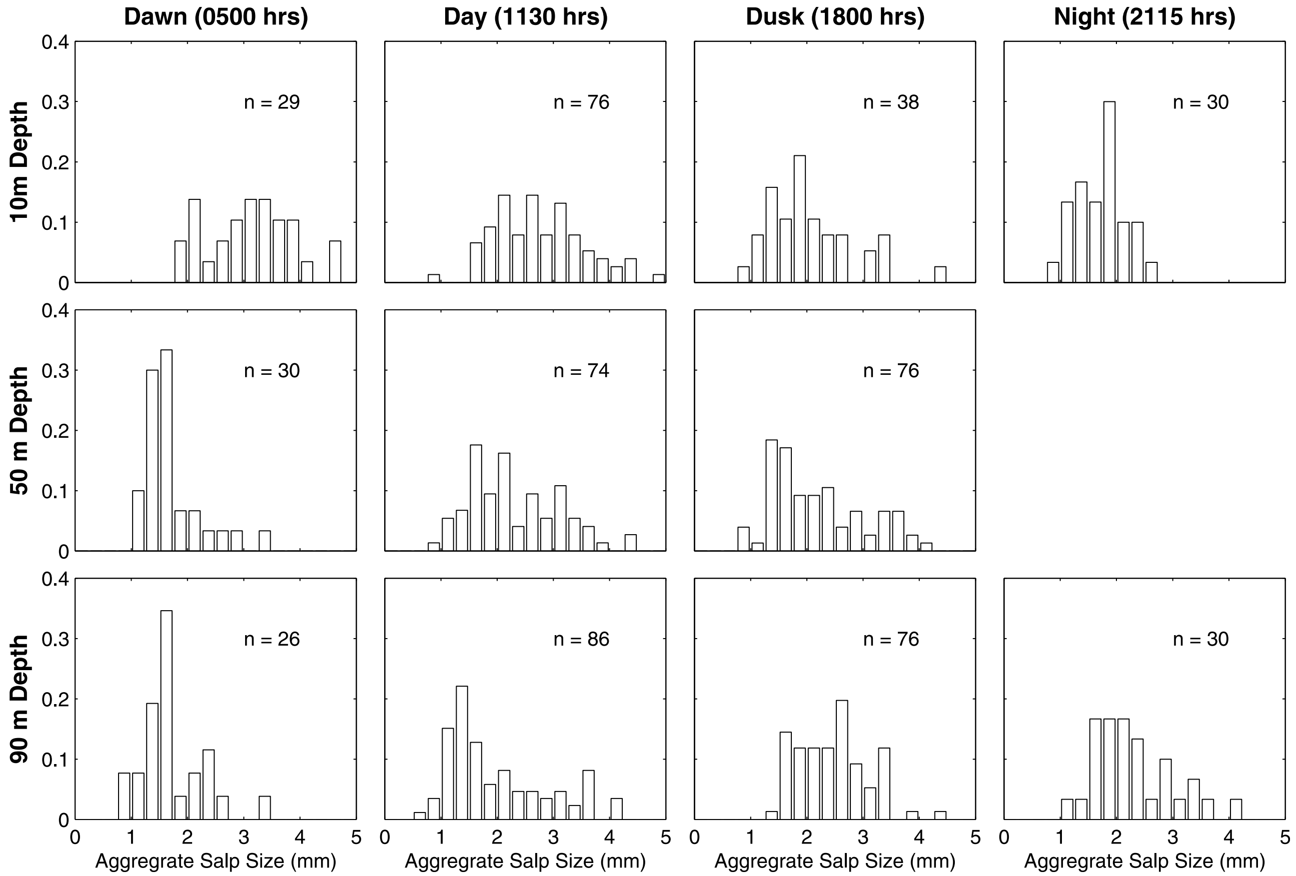

Figure 6. Size distribution (as a proportion) of length (mm) of the aggregate form of *T. democratica* from the EZ net. Data for three depths over an 18 h period on 16 October 2008. The number of individuals used to create the size distribution is shown as *n*. No data are available for the 50 m night tow because of equipment malfunction.

water and the inner shelf surface water, with potential seed populations of both phytoplankton and zooplankton. Both the fluorescence maximum and the OPC-measured biovolume maximum occurred in this thin mixing zone. During its advection south, the filament transforms into a closed circulation. This is seen by the elliptical shape of surface temperature and chlorophyll *a* concentration fields (Figures 2a and 2b) and the cyclonic rotation (Figure 3).

4.2. Inferring the Abundance of *Thalia democratica*

[25] The OPC provides a high spatial resolution of particle size and abundance, unachievable through net sampling. A key question is whether in this application the OPC accurately quantifies the abundance of the transparent salps. Previous studies have shown OPC observations of gelatinous organisms to be problematic [*Remsen et al.*, 2004; *Gonzalez-Quiros and Checkley*, 2006]. In order to assess the

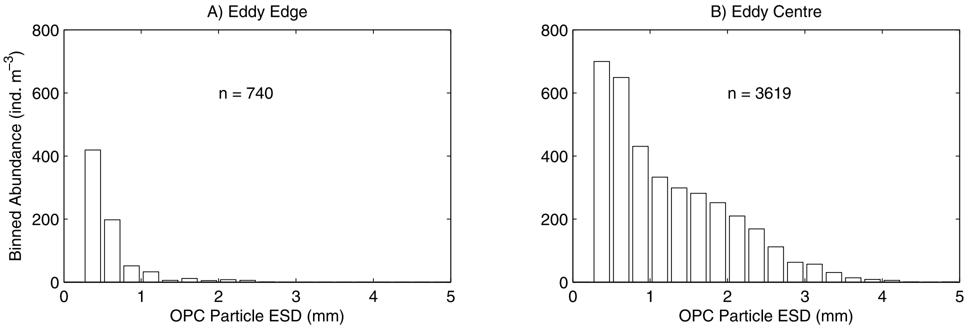

Figure 7. Size-resolved abundance of zooplankton from the OPC (a) at the edge of the eddy and (b) in the center of the eddy. Data are extracted from 25–35 m depth to coincide with the subsurface salp swarm and are the total size distribution of a 5 km transect. For comparison to Figure 6, 1 mm salp length ≈680 μm equivalent spherical (ESD).

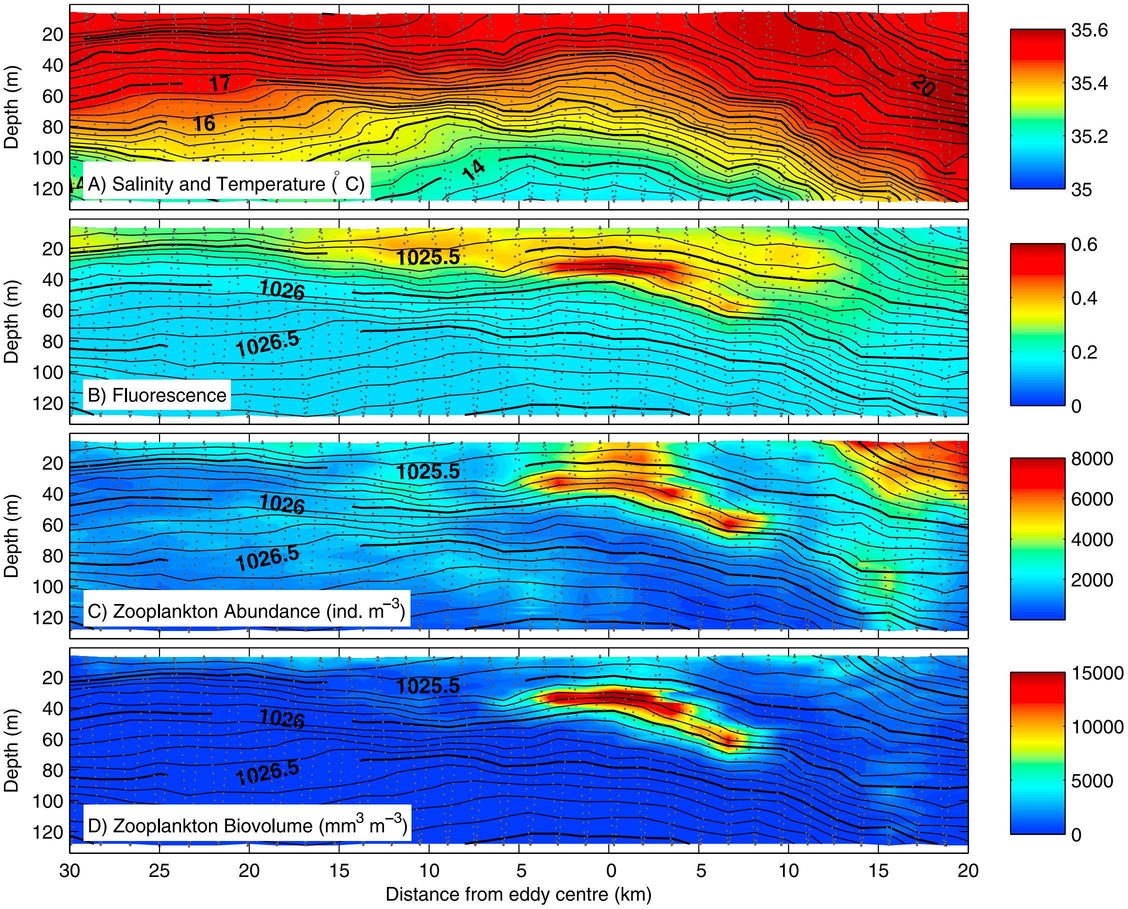

Figure 8. SeaSoar transect showing a vertical slice of (a) salinity (color shading) and temperature (°C; contour lines), (b) fluorescence (RFU), (c) zooplankton counts (ind. m^{-3}) between the surface and 120 m depth, and (d) zooplankton biovolume (mm^3 m^{-3}). The black contours on Figures 8b–8d show potential density (kg m^{-3}). The grey dots represent the SeaSoar track through the water column. Figure 8 is oriented from west or coastal (left) to east or offshore (right).

OPC for this application, we compare the in situ abundance and size distribution of samples from the EZ nets (this study) and N70 nets [*Henschke et al.*, 2011] with OPC determined values. The N70 net is a 70 cm diameter net which was used extensively during the 1938 to 1942 M/V *Warreen* cruises to sample zooplankton off southeast Australia [*Thompson and Kesteven*, 1942]. The N70 net was designed for the capture of medium and smaller size organisms [*Kemp and Hardy*, 1929] and was modified to suit modern materials (for a full description see *Henschke et al.* [2011]).

[26] Despite the different times of deployment, and the various limitations and artifacts inherent in each of the different gear types (N70 net, EZ net and OPC), a comparison of abundance shows consistency of estimation between both net types and the OPC at the edge of the eddy (Table 3). N70 vertical haul nets (0–50 m) and oblique EZ tows had similar abundances of zooplankton, with mean (and standard deviation) values of 1547 (985) and 1750 (932) ind. m^{-3}, respectively. The zooplankton abundance measured by the OPC at the edge of the eddy has an abundance (1684 ind. m^{-3}) which is between the values from the different nets. The consistency among gear types allows confidence in using nearby net samples to interpret the high-resolution OPC transects, without which the three-dimensional structure of *T. democratica* at the center of the eddy could not be determined.

[27] The taxonomic composition of the subsurface zooplankton community sampled by the OPC during the two SeaSoar transects across the CCE can only be inferred. However, the CTD transect 12–24 h after the SeaSoar transects included 0–50 m vertical haul nets (detailed by *Henschke et al.* [2011]) in the center of the eddy. The mean abundance (and standard deviation) of *T. democratica* in the top 50 m of the CCE determined from net samples was 2444 (502) ind. m^{-3} (Table 3). *T.* democratica made up 78% of all zooplankton counted, with aggregates exceeding solitaries by a factor of 14 [*Henschke et al.*, 2011]. The OPC recorded a mean abundance of 3243 ind. m^{-3} (ESD $\geq$ 680 μm) in the top 50 m of the eddy (Table 3). Given that the surface waters are the likely source of the subsurface zooplankton community, and the quantitative agreement between net and OPC estimates, the OPC-measured subsurface zooplankton maximum is almost certainly an accurate spatially resolved quantification of a dense *T. democratica* population.

[28] The mean abundance of particles in the *T. democratica* size range (ESD $\geq$ 680 μm; Figure 10) formed a 15 km diameter circular disc located 20–40 m deep in the center of

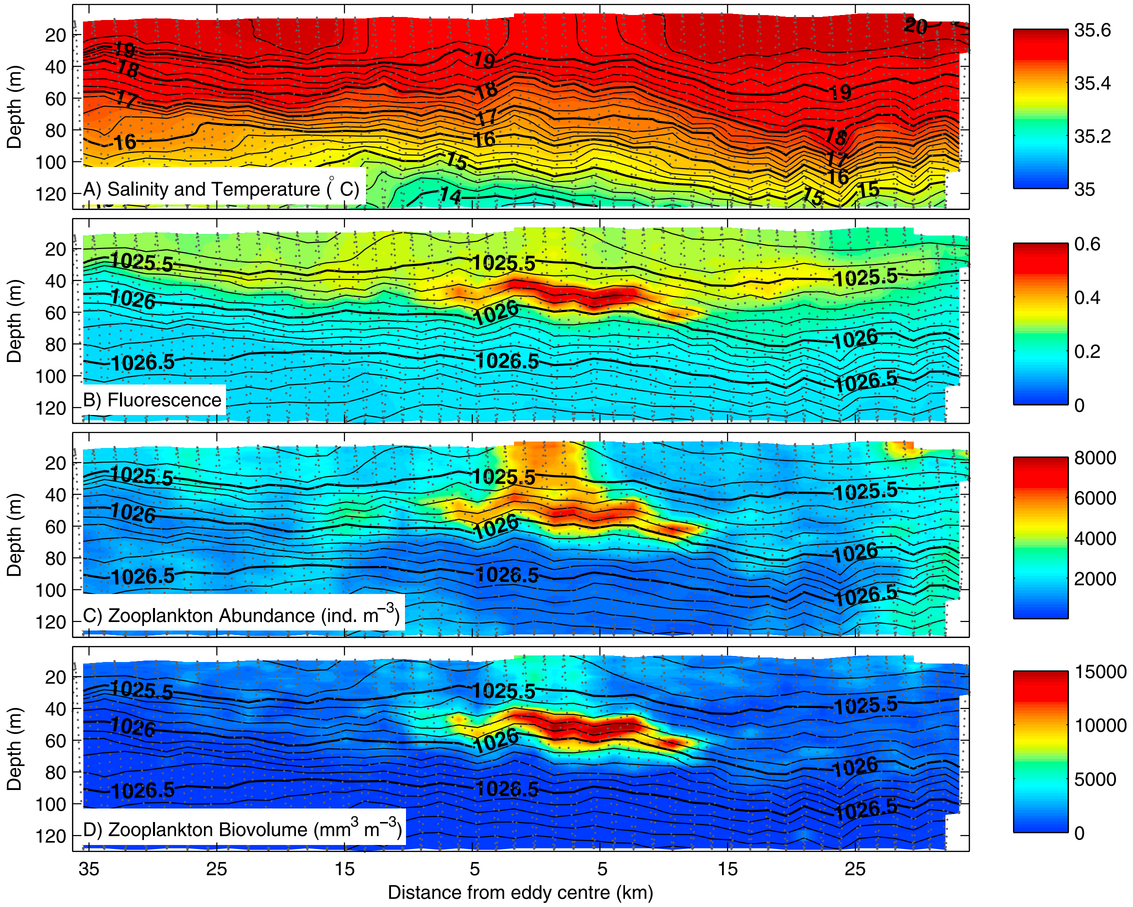

Figure 9. SeaSoar transect showing a vertical slice of (a) salinity (color shading) and temperature (°C; contour lines), (b) fluorescence (RFU), (c) zooplankton counts (ind. m^{-3}) between the surface and 120 m depth, and (d) zooplankton biovolume (mm^3 m^{-3}). The black contours on Figures 9b–9d show potential density (kg m^{-3}). The grey dots represent the SeaSoar track through the water column. Figure 9 is oriented from north (left) to south (right).

the eddy and was 8 times higher than the equivalent depth at the edge. The maximum abundance of these inferred salps in the center of the eddy was 6162 ind. m^{-3} and occurred within the pycnocline, coinciding with the subsurface fluorescence maximum. The maximum abundance at the edge was 974 ind. m^{-3}, which is similar to the highest values recorded globally (1000 ind. m^{-3} [*Andersen*, 1998]).

[29] The maximum abundance of net-sampled *T. democratica* in the austral spring of 2008 (2115 ind. m^{-3} [*Henschke et al.*, 2011]) was found to be approximately an

Table 3. Mean Abundance (and Standard Deviation) of Zooplankton and *T. democratica* From the Three Gear Types Considered in This Study (ind. m^{-3})[a]

	Mean (SD) Zooplankton Abundance	Number/Area of Sites	Mean (SD) *T. democratica* Abundance	Reference
		Eddy Edge		
EZ Nets (10, 50, 90 m)	1750 (932)	11 nets	1072 (614)[b]	this study
Vertical hauls (0–50 m)	1547 (985)	6 hauls	797 (255)[b]	*Henschke et al.* [2011]
OPC (0–50 m)	1684 (N/A)	10 km × 50 m	1019[c]	this study
		Eddy Center		
Vertical hauls (0–50 m)	3078 (663)	4 hauls	2444 (502)[b]	*Henschke et al.* [2011]
OPC (0–50 m)	4222 (N/A)	10 km × 50 m	3243[c]	this study
		OPC Comparison: Eddy Edge Versus Eddy Center		
Edge (OPC: 25–35 m)	1104 (N/A)	10 km × 10 m	604[c]	this study
Center (OPC: 25–35 m)	5863 (N/A)	10 km × 10 m	5003[c]	this study

[a] The depth bins from which the samples were taken are shown in parentheses. A comparison of OPC counts between the edge and the center of the eddy for the depth range 25–35 m is also shown. This depth range represents the core of the swarm.

[b] Calculated from community composition analysis from the respective nets.

[c] Inferred values. See section 4.2.

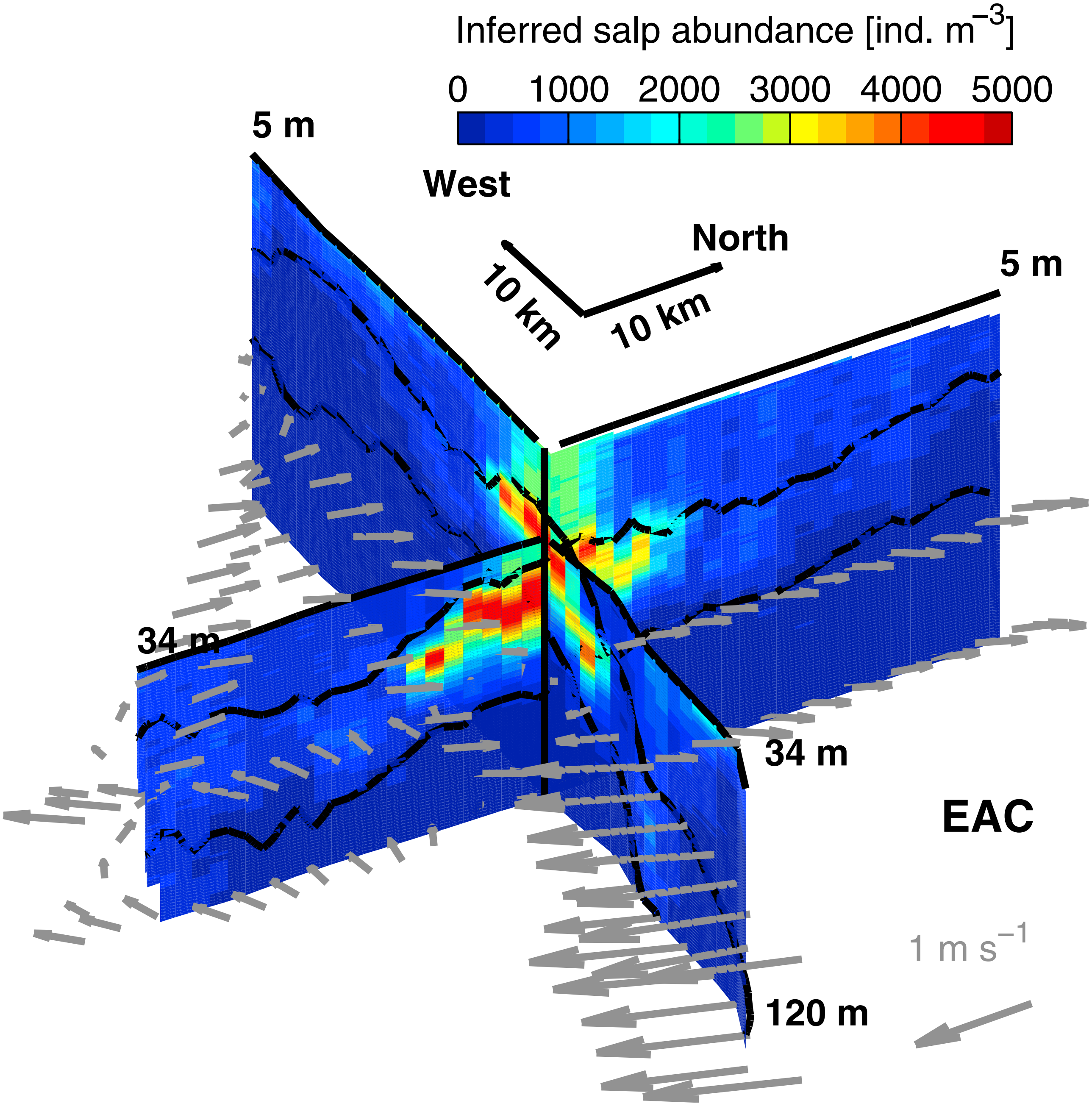

Figure 10. Three-dimensional view of combined north–south and east–west SeaSoar transect. Colors represent inferred salp abundance (ind. m^{-3}), black lines are potential density, and grey arrows are ADCP vectors (m s^{-1}) relative to the eddy center. Inferred salp abundance is derived from the OPC size distribution where salp length is ≥1 mm (≥680 μm ESD). The location of the transects is relative to the center of the eddy, which had a velocity of 0.30 m s^{-1} at 195°. Velocity vectors are located along the transect, with arrows shown on the visible side of each vertical plane. The top 34 m of the easterly and southerly planes have been omitted to allow better viewing of the westerly and northerly planes.

order of magnitude greater than the highest values found off southeast Australia using similar sampling procedures between 1938 and 1942 [*Thompson*, 1948; *Baird et al.*, 2011] and of a similar magnitude to the highest values recorded globally (1000 ind. m^{-3} [*Andersen*, 1998]). Isolated observations of salp swarms off southeast Australia may have been of a similar size to that found by *Henschke et al.* [2011] on the continental shelf and slope, however zooplankton biomass rather than individual counts were recorded. For example, *Tranter* [1962] observed large swarms of *T. democratica* in 1959 and 1960, with the total zooplankton biomass (dominated by salps) reaching 1187 and 2399 mg m^{-3} (wet weight).

Table 4. Estimated Daily Nitrogen Demand (mmol N m^{-3} d^{-1}) of the *T. democratica* Community and Water Column Nitrogen Turnover (Days) Within the Center of the Cold-Core Eddy Given Growth Rates for 0.5%, 2%, and 5%

Initial Biomass (mmol N m^{-3})	Growth Rate (% Length h^{-1})	Daily Nitrogen Demand (mmol N m^{-3} d^{-1})	Water Column Nitrogen Turnover (Number of Days)
0.565	0.5	0.17	103.67
0.565	2	0.45	40.39
0.565	5	2.55	7.07

4.3. Biochemical Transformation

[30] The carbon:nitrogen (C:N) ratio of *T. democratica* is variable depending on the life history stage. *Heron et al.* [1988] found a C:N ratio of between 3.81 mol mol^{-1} (solitary adult) and 9.5 mol mol^{-1} (aggregate embryo), while *Madin et al.* [1981] recorded ratios between 4.0 mol mol^{-1} (aggregate; n = 12) and 4.4 mol mol^{-1} (solitary; n = 12). There is general agreement for a C:N ratio around 4 mol mol^{-1} for mature *T. democratica*, although it appears likely that there is a rapid change over the early life stages. ESDs from the OPC were converted to body lengths of *T. democratica* by maintaining the OPC-measured projected area and adjusting the ratio of length to width to be 2.37 using $Length = ESD\sqrt{2.37}$ (see section 3.3). The size distribution can then be converted to carbon content (μg $ind.^{-1}$) using $1.62Length^{1.93}$ [*Heron et al.*, 1988] and nitrogen content using a C:N ratio of 4.0 mol mol^{-1} [*Madin et al.*, 1981]. The maximum biovolume (10 s sampling rate) reached was 25480 mm^3 m^{-3}, which results in a nitrogen concentration held as *T. democratica* being equivalent to 0.30 mmol N m^{-3} (for the measured size distribution).

[31] Due to their gelatinous test around a hollow atrial and pharyngeal cavity, a low nitrogen biomass for salps relative to other zooplankton of a similar size was expected. In spite of their low nitrogen requirements, the extraordinary growth rates of salps, and the size of the swarm, mean that their daily nitrogen demand would therefore be significant. Assuming the swarm is mature, the number of individuals is constant (births = deaths) and using growth rates of 0.5%, 2%, and 5% of length h^{-1} (within the range of *Heron* [1972a] and *Deibel* [1982a]), the population would have had a daily nitrogen demand up to 0.17, 0.45, and 2.55 mmol N m^{-3} d^{-1}, respectively (Table 4). The uplift of slope water at the center of the CCE (Figure 4) had a maximum concentration of 18 mmol N m^{-3}. The measured population of *T. democratica* growing at 2% length h^{-1} would take 40 days to account for all nitrogen from the water column whereas if they were growing at 5% length h^{-1}, it would take just 7.1 days.

[32] Published growth rates of *T. democratica* are highly variable, ranging from 0.3% [*Deibel*, 1982a] to 28% of length h^{-1} [*Le Borgne and Moll*, 1986]. These upper growth rates seem extraordinary and are impossible in the circumstances of this swarm. A growth rate of even 10% [*Heron*, 1972a] for the center of the eddy would result in a nitrogen demand of 24.22 mmol N m^{-3} d^{-1} accounting for the upwelled slope water nitrogen within just 0.75 days.

[33] Previous studies have used cohort tracking to estimate the growth rates of *T. democratica* by measuring the change in position of the peak of the size distribution over a fixed time period [*Tsuda and Nemoto*, 1992; *Heron*, 1972a, 1972b]. An increased proportion of smaller sizes (≤1.5 mm) are visible in this data set at 50 and 90 m depth at dawn (Figure 6). These peaks at dawn are likely the result of synchronized mating aggregations and release of buds which occur at dawn and dusk [*Heron*, 1972a, 1972b; *Heron and Benham*, 1984; *Miller and Cosson*, 1997]. A similar peak in the distribution would be expected after dusk but was not visible in the current data set (Figure 6). Cohort tracking was not possible with the current data set as the peak at dawn did not grow through the sampled size distribution in the following 18 h.

[34] By comparison, if this maximum biovolume comprised copepods, with a carbon:volume ratio of 0.126×10^6 g C m^{-3} (Table 1) [*Hansen et al.*, 1997] and a C:N ratio of 6.3 mol mol^{-1} [*Sterner and Elser*, 2002], the maximum biovolume at the center of the eddy (25480 mm^3 m^{-3}) would correspond to 41.6 mmol N m^{-3}. This is more than double the slope water concentration of nitrogen (18 mmol N m^{-3}) further illustrating that for the given size distribution, the zooplankton within the eddy center is dominated by zooplankton with a low nitrogen content per size, such as *T. democratica*. Due to their low nitrogen content and high growth rates, *T.democratica* are able to reach high densities, outcompeting other zooplankton for limited resources.

4.4. The Fate of Salp Organic Material

[35] When salps occur in such large aggregations as seen in this study, there are significant implications for biogeochemical cycling and fluxes to the seafloor [*Madin*, 1982; *Morris et al.*, 1988]. Many studies document the growth, feeding and fecundity of *T. democratica* [*Heron*, 1972a, 1972b; *Heron and Benham*, 1984; *Deibel*, 1982a, 1982b]; however, little is known about the fate of their fecal pellets or carcasses relative to larger species such as *Salpa fusiformis*. Due to the episodic nature of these swarms, quantifying the annual contribution of salps to the downward flux of organic material is difficult. Salp fecal pellets composed up to 90% of the organic matter in sediment traps in the California Current [*Coale and Bruland*, 1985] during a swarm of *S. fusiformis*. *T. democratica* swarms within the Mediterranean Sea have been shown to alter sediment fluxes at a shallow site (80–85 m), with maximum ammonification rates occurring during and after a swarm [*Fernex et al.*, 1996]. Sediment traps deployed in the Mediterranean Sea during a swarm of the same species showed a major increase in the flux of organic material. Chemical analysis suggests the flux was made up primarily of discarded mucus material from the salp's feeding mesh [*Morris et al.*, 1988].

[36] The eventual fate of *T. democratica* below the euphotic zone is relatively unknown. There is no evidence of diel vertical migration of *T. democratica* in this study

(Table 2) or previous studies [*Gibbons*, 1997; *Tsuda and Nemoto*, 1992; *Heron*, 1972a]. Some movement occurred between depths but there was no significant evidence of a diel pattern. In this case, unlike vertically migrating species, the mechanisms for transfer of salp biomass below the euphotic zone are limited to sinking following death or grazing by migrating predators. Sinking of salp carcasses is thought to occur reasonably slowly, due to their specific gravity being close to that of seawater [*Tsukamoto et al.*, 2009], presumably increasing their chance of being consumed by predators if they are preferred prey. Salps have been found in the stomachs of 47 fish species belonging to 23 families, indicating they play a major role in the diet of many fish species in the mesopelagic region [*Kashkina*, 1986]. Unfortunately the species of salps are often unable to be determined [*Yount*, 1958]. Salps have been found in the stomachs of deepwater fish [*Dunn et al.*, 2010] but it is unclear if live salps are being grazed at depth, or the carcasses of mesopelagic salps are being consumed while sinking to the seafloor.

4.5. Quantifying the 3-D Structure and Origin of the Salp Swarm

[37] The 3-D structure of the swarm (Figure 10) is revealed from a composite of SeaSoar transects in east–west (Figure 8) and south–north (Figure 9) orientations. The disc shape of the abundance contours generally follow the isopycnals. A circular disc of 20 m thickness, with a diameter of 15 km, has a volume of 1.4×10^{10} m^3. With an average salp concentration of 3000 ind. m^{-3}, this represents a total of 4×10^{13} individuals. Assuming a constant length of 2 mm (and using the equations in section 4.3) this equates to 246 t of carbon and 72 t of nitrogen held within the salp swarm. Additionally, the fluorescence maximum is limited to the pycnocline, while the salp swarm is more dispersed and reaches the surface in a 5 km diameter region at the center of the CCE.

[38] A seed population of salps and favorable growth conditions are required for the development of a salp swarm. *Paffenhofer and Lee* [1987] suggested that shelf break upwellings are a likely location for swarms due to increased phytoplankton abundance in the presence of elevated nutrients. Reproduction of the solitary *T. democratica* has been shown to occur as soon as phytoplankton becomes abundant [*Paffenhofer and Lee*, 1987], with a similar response by doliolids [*Deibel*, 1985; *Paffenhofer and Lee*, 1987]. *Deibel and Paffenhofer* [2009] suggest that Moreton Bay, in southern Queensland, is a possible source of seed populations of salps for the southeast Australian continental shelf, although for the CCE examined in this study a more local source is likely.

[39] *Thompson* [1948] and *Baird et al.* [2011] show salp populations are present across the continental shelf and slope for all seasons from 1938 to 1942. The origin of the CCE in this study can be traced using satellite SST and in situ temperature and salinity to the upwelling zone off Seal Rocks (∼32.5°S) in the EAC separation zone. The closed circulation of the CCE ensures retention of the blooming plankton populations. Thus, the vertically concentrated and horizontally constrained disc-shaped salp swarm (Figure 10) likely occurred due to the stratification at the interface of the seed-bearing inner shelf water and nutrient-rich upwelled waters and retention in a small CCE that formed from an upwelled filament.

4.6. Concluding Thoughts

[40] This study is the first to explore the three-dimensional structure of a subsurface *T. democratica* swarm within a CCE. The productivity of the CCE was evident through distinct uplift of the nutricline and elevated fluorescence. The abundance of salps within the center of the CCE was 8 times higher than at the edge. Further work to examine the fate of these zooplankton communities as they are advected off the shelf is crucial. With a strengthening EAC predicted in future years [*Cai et al.*, 2005], current driven upwelling and eddy production in this region are likely to change and understanding the role of eddies in regional biogeochemistry will become increasingly important.

[41] **Acknowledgments.** This research was funded by ARC Discovery Projects DP0881182 and DP0880078 held by M.E.B., I.M.S., and P. Oke. The authors wish to thank the crew of R/V *Southern Surveyor* 05/2008 and the scientists involved with the cruise: P. Brodie, D. Mills, L. Pender, and L. Macdonald (CSIRO); M. Taylor, A. Richardson, H. Macdonald, N. Henschke, and B. Harris (UNSW); C. Hassler and R. Djajadikarta (UTS); and W. Figuiera (Sydney University). We thank P. Oke and D. Griffin (CSIRO), who provided satellite images during the cruise, as well as K. Taylor and B. Harris for the community composition and salp length measurements. ADCP Mooring data in Figure 3 was sourced from the Integrated Marine Observing System (IMOS), an initiative of the Australian Government being conducted as part of the National Collaborative Research Infrastructure Strategy and the Super Science Initiative. We thank Don Deibel for fruitful discussions and four anonymous reviewers, whose comments greatly improved the manuscript.

References

Ajani, P., R. Lee, T. Pritchard, and M. Krogh (2001), Phytoplankton patterns at a long-term coastal station off Sydney, Australia, *J. Coastal Res.*, *34*, 60–73.

Alldredge, A. L., and L. P. Madin (1982), Pelagic tunicates: Unique herbivores in the marine plankton, *BioScience*, *32*(8), 655–663.

Andersen, V. (1998), Salp and pyrosomid blooms and their importance in biogeochemical cycles, in *The Biology of Pelagic Tunicates*, edited by Q. Bone, pp. 125–138, Oxford Univ. Press, New York.

Baird, M. E., P. G. Timko, I. M. Suthers, and J. H. Middleton (2006), Coupled physical–biological modelling study of the East Australian Current with idealised wind forcing. Part I: Biological model intercomparison, *J. Mar. Syst.*, *59*(3–4), 249–270.

Baird, M. E., P. G. Timko, I. M. Suthers, J. H. Middleton, T. J. Mullaney, and D. R. Cox (2008), Biological properties across the Tasman Front off Southeast Australia, *Deep Sea Res., Part I*, *55*, 1438–1455.

Baird, M. E., J. D. Everett, and I. M. Suthers (2011), Analysis of southeast Australian zooplankton observations of 1938–42 using synoptic oceanographic conditions, *Deep Sea Res., Part II*, *5*, 699–711.

Bakun, A. (2006), Fronts and eddies as key structures in the habitat of marine fish larvae: Opportunity, adaptive response and competitive advantage, *Sci. Mar.*, *70*(S2), 105–122.

Berner, L. (1967), Distributional atlas of Thaliacea in the California Current region, *Calif. Coop. Oceanic Fish. Invest. Atlas 8*, State of Calif. Mar. Res. Comm., La Jolla.

Blackburn, M. (1979), Thaliacea of the California Current region: Relations to temperature, chlorophyll, currents, and upwelling, *Calif. Coop. Oceanic Fish. Invest. Rep. 20*, pp. 184–193, CalCOFI Comm., La Jolla, Calif.

Bone, Q., C. Carre, and P. Chang (2003), Tunicate feeding filters, *J. Mar. Biol. Assoc. U. K.*, *83*, 907–919.

Cai, W., G. Shi, T. Cowan, D. Bi, and J. Ribbe (2005), The response of the Southern Annular Mode, the East Australian Current, and the southern mid-latitude ocean circulation to global warming, *Geophys. Res. Lett.*, *32*, L23706, doi:10.1029/2005GL024701.

Coale, K. H., and K. W. Bruland (1985), ^{234}Th:^{238}U Disequilibria within the California Current, *Limnol. Oceanogr.*, *30*(1), 22–33.

Cowley, R., G. Critchley, R. Eriksen, V. Latham, R. Plaschke, M. Rayner, and D. Terhell (1999), Hydrochemistry operations manual, *Rep. 236*, 106 pp., CSIRO Mar. Lab., Hobart, Tasmania, Australia.

Cresswell, G. R. (1994), Nutrient enrichment of the Sydney continental shelf, *Mar. Freshwater Res.*, *45*, 677–691, doi:10.1071/MF9940677.

Deibel, D. (1982a), Laboratory determined mortality, fecundity and growth-rates of *Thalia democratica* Forskal and *Dolioletta gegenbauri* Uljanin (Tunicata, Thaliacea), *J. Plankton Res.*, *4*, 143–153, doi:10.1093/plankt/4.1.155.

Deibel, D. (1982b), Laboratory-measured grazing and ingestion rates of the salp, *Thalia democratica* Forskal, and the doliolid, *Dolioletta gegenbauri* Uljanin (Tunicata, Thaliacea), *J. Plankton Res.*, *4*, 189–201, doi:10.1093/plankt/4.2.189.

Deibel, D. (1985), Blooms of the pelagic tunicate, *Dolioletta gegenbauri*: Are they associated with Gulf Stream frontal eddies?, *J. Mar. Res.*, *43*, 211–236.

Deibel, D., and G. Paffenhofer (2009), Predictability of patches of neritic salps and doliolids (Tunicata, Thaliacea), *J. Plankton Res.*, *31*, 1571–1579.

Dunn, M. R., L. Griggs, J. Forman, and P. Horn (2010), Feeding habits and niche separation among the deep-sea chimaeroid fishes *Harriotta raleighana*, *Hydrolagus bemisi* and *Hydrolagus novaezealandiae*, *Mar. Ecol. Prog. Ser.*, *407*, 209–225, doi:10.3354/meps08580.

Fernex, F. E., J. Braconnot, S. Dallot, and M. Boisson (1996), Is ammonification rate in marine sediment related to plankton composition and abundance? A time-series study in Villefranche Bay (NW Mediterranean), *Estuarine Coastal Shelf Sci.*, *43*, 359–371, doi:10.1006/ecss.1996.0075.

Fortier, L., J. Le Fèvre, and J. Legendre (1994), Export of biogenic carbon to fish and to the deep ocean: The role of large planktonic microphages, *J. Plankton Res.*, *16*, 809–839, doi:10.1093/plankt/16.7.809.

Foxton, P. (1966), The distribution and life-history of *Salpa thompsoni* Foxton with observations on a related species, *Salpa gerlachei* Foxton, *Discovery Rep. 34*, pp. 1–116, Cambridge Univ. Press, London.

Gibbons, M. J. (1997), Vertical distribution and feeding of *Thalia democratica* on the Agulhas Bank during March 1994, *J. Mar. Biol. Assoc. U. K.*, *77*, 493–505.

Godfrey, J., G. Cresswell, T. Golding, A. Pearce, and R. Boyd (1980), The separation of the East Australian Current, *J. Phys. Oceanogr.*, *10*, 430–440.

Gonzalez-Quiros, R., and D. Checkley Jr. (2006), Occurrence of fragile particles inferred from optical plankton counters used in situ and to analyze net samples collected simultaneously, *J. Geophys. Res.*, *111*, C05S06, doi:10.1029/2005JC003084.

Hallegraeff, G., and S. Jeffrey (1993), Annually recurrent diatom blooms in spring along the New South Wales coast of Australia, *Mar. Freshwater Res.*, *44*, 325–334, doi:10.1071/MF9930325.

Hansen, P., P. Bjørnsen, and B. Hansen (1997), Zooplankton grazing and growth: Scaling within the 2–2,000-μm body size range, *Limnol. Oceanogr.*, *42*, 687–704.

Henschke, N., J. D. Everett, M. E. Baird, M. D. Taylor, and I. M. Suthers (2011), Distribution of life history stages of the salp *Thalia democratica* in shelf waters during a spring bloom, *Mar. Ecol. Prog. Ser.*, *430*, 49–62, doi:10.3354/meps09090.

Herman, A. W. (1988), Simultaneous measurement of zooplankton and light attenuance with a new optical plankton counter, *Cont. Shelf Res.*, *8*, 205–221, doi:10.1016/0278-4343(88)90054-4.

Heron, A. C. (1972a), Population ecology of a colonizing species: The pelagic tunicate *Thalia democratica*. 1. Individual growth rate and generation time, *Oecologia*, *10*, 269–293.

Heron, A. C. (1972b), Population ecology of a colonizing species: The pelagic tunicate *Thalia democratica*. 2. Population growth-rate, *Oecologia*, *10*, 294–312.

Heron, A. C., and E. Benham (1984), Individual growth rates of salps in three populations, *J. Plankton Res.*, *6*, 811–828, doi:10.1093/plankt/6.5.811.

Heron, A. C., P. S. McWilliam, and G. Dal Pont (1988), Length-weight relation in the salp *Thalia democratica* and potential of salps as a source of food, *Mar. Ecol. Prog. Ser.*, *42*, 125–132.

Kasai, A., S. Kimura, H. Nakata, and Y. Okazaki (2002), Entrainment of coastal water into a frontal eddy of the Kuroshio and its biological significance, *J. Mar. Syst.*, *37*, 185–198.

Kashkina, A. (1986), Feeding of fishes on salps (Tunicata, Thaliacea), *J. Ichthyol.*, *3*, 440–447.

Kemp, S., and M. Hardy (1929), The ships, their equipment, and the methods used in research, *Discovery Rep. 1*, pp. 181–189, Cambridge Univ. Press, London.

Kremer, P. (2002), Towards an understanding of salp swarm dynamics, paper presented at the ICES Annual Science Conference and ICES Centenary, Int. Counc. for the Explor. of the Sea, Copenhagen.

Le Borgne, R., and P. Moll (1986), Growth rates of the salp *Thalia democratica* in Tikehau Atoll (Tuamotu is.), *Oceanogr. Trop.*, *21*, 23–29.

Licandro, P., F. Ibanez, and M. Etienne (2006), Long-term fluctuations (1974–1999) of the salps *Thalia democratica* and *Salpa fusiformis* in the northwestern Mediterranean Sea: Relationships with hydroclimatic variability, *Limnol. Oceanogr.*, *51*, 1832–1848.

Logerwell, E. A., and P. E. Smith (2001), Mesoscale eddies and survival of late stage Pacific sardine (*Sardinops sagax*) larvae, *Fish. Oceanogr.*, *10*, 13–25.

Madin, L. P. (1982), Production, composition and sedimentation of salp fecal pellets in oceanic waters, *Mar. Biol.*, *67*, 39–45, doi:10.1007/BF00397092.

Madin, L. P., and D. Deibel (1998), Feeding and energetics of Thaliacea, in *The Biology of Pelagic Tunicates*, edited by Q. Bone, pp. 81–103, Oxford Univ. Press, New York.

Madin, L. P., C. M. Cetta, and V. L. McAlister (1981), Elemental and biochemical composition of salps (Tunicata: Thaliacea), *Mar. Biol.*, *63*, 217–226, 10.1007/BF00395990.

Mann, K. H., and J. R. N. Lazier (2006), *Dynamics of Marine Ecosystems*, 3rd ed., Blackwell Sci., Oxford, U. K.

Mata, M., S. Wijffels, J. Church, and M. Tomczak (2006), Eddy shedding and energy conversions in the East Australian Current, *J. Geophys. Res.*, *111*, C09034, doi:10.1029/2006JC003592.

McGillicuddy, D. J., A. R. Robinson, D. A. Siegel, H. W. Jannasch, R. Johnson, T. Dickeys, J. McNeil, A. F. Michaels, and A. H. Knap (1998), Influence of mesoscale eddies on new production in the Sargasso Sea, *Nature*, *394*(6690), 263–266.

Miller, R. L., and J. Cosson (1997), Timing of sperm shedding and release of aggregates in the salp *Thalia democratica* (Urochordata: Thaliacea), *Mar. Biol.*, *129*, 607–614, 10.1007/s002270050203.

Morris, R. J., Q. Bone, R. Head, J. C. Braconnot, and P. Nival (1988), Role of salps in the flux of organic matter to the bottom of the Ligurian Sea, *Mar. Biol.*, *97*, 237–241.

Mullin, M. (1983), *In situ* measurement of filtering rates of the salp, *Thalia democratica*, on phytoplankton and bacteria, *J. Plankton Res.*, *5*, 279–288, doi:10.1093/plankt/5.2.279.

Nilsson, C., and G. Cresswell (1981), The formation and evolution of East Australian current warm-core eddies, *Prog. Oceanogr.*, *9*, 133–183.

Nishikawa, J., M. Naganobu, T. Ichii, H. Ishii, M. Terazaki, and K. Kawaguchi (1995), Distribution of salps near the South Shetland Islands during austral summer 1990–1991, with special reference to krill distribution, *Polar Biol.*, *15*, 31–39, doi:10.1007/BF00236121.

Oke, P. R., and J. H. Middleton (2000), Topographically induced upwelling off eastern Australia, *J. Phys. Oceanogr.*, *30*, 512–531, doi:10.1175/1520-0485.

Paffenhofer, G., and T. Lee (1987), Development and persistence of patches of Thaliacea, *S. Afr. J. Mar. Sci.*, *5*, 305–318.

Remsen, A., T. L. Hopkins, and S. Samson (2004), What you see is not what you catch: A comparison of concurrently collected net, Optical Plankton Counter, and Shadowed Image Particle Profiling Evaluation Recorder data from the northeast Gulf of Mexico, *Deep Sea Res., Part I*, *51*, 129–151.

Ridgway, K. R., and J. S. Godfrey (1997), Seasonal cycle of the East Australian Current, *J. Geophys. Res.*, *102*, 22,921–22,936, doi:10.1029/97JC00227.

Roughan, M., and J. H. Middleton (2002), A comparison of observed upwelling mechanisms off the east coast of Australia, *Cont. Shelf Res.*, *22*, 2551–2572.

Roughan, M., and J. H. Middleton (2004), On the East Australian Current: Variability, encroachment, and upwelling, *J. Geophys. Res.*, *109*, C07003, doi:10.1029/2003JC001833.

Roughan, M., P. Oke, and J. Middleton (2003), A modeling study of the climatological current field and the trajectories of upwelled particles in the East Australian Current, *J. Phys. Oceanogr.*, *33*, 2551–2564.

Sterner, R., and J. Elser (2002), *Ecological Stoichiometry: The Biology of Elements From Molecules to the Biosphere*, Princeton Univ. Press, Princeton, N. J.

Sutherland, K., L. Madin, and R. Stocker (2010), Filtration of submicrometer particles by pelagic tunicates, *Proc. Natl. Acad. Sci. U. S. A.*, *107*, 15,129–15,134.

Thompson, H. (1948), *Pelagic Tunicates of Australia*, 196 pp., Commonw. Counc. for Sci. and Ind. Res., Melbourne, Austrialia.

Thompson, H., and G. Kesteven (1942), Pelagic tunicates in the plankton of southeastern Australian waters, and their place in oceanographic studies, technical report, Counc. for Sci. and Ind. Res., Melbourne, Australia.

Tranter, D. (1962), Zooplankton abundance in Australasian waters, *Aust. J. Mar. Freshwater Res.*, *13*, 106–142, doi:10.1071/MF9620106.

Tranter, D., D. Carpenter, and G. Leech (1986), The coastal enrichment effect of the East Australian Current eddy field, *Deep Sea Res., Part A*, *33*, 1705–1728.

Tsuda, A., and T. Nemoto (1992), Distribution and growth of salps in Kuroshio warm-core ring during summer 1987, *Deep Sea Res., Part A*, *39*, suppl. 1, S219–S229.

Tsukamoto, K., Y. Yamada, A. Okamura, T. Kaneko, H. Tanaka, M. J. Miller, N. Horie, N. Mikawa, T. Utoh, and S. Tanaka (2009), Positive buoyancy in eel leptocephali: An adaptation for life in the ocean surface layer, *Mar. Biol.*, *156*, 835–846, doi:10.1007/s00227-008-1123-8.

Yoder, J. A., L. P. Atkinson, T. N. Lee, H. H. Kim, and C. R. McClain (1981), Role of Gulf Stream frontal eddies in forming phytoplankton patches on the outer southeastern shelf, *Limnol. Oceanogr.*, *26*, 1103–1110.

Yount, J. (1958), Distribution and ecological aspects of central Pacific Salpidae (Tunicata), *Pac. Sci.*, *12*, 111–130.

M. E. Baird, Plant Functional Biology and Climate Change Cluster, University of Technology Sydney, PO Box 123 Broadway, Sydney, NSW 2007, Australia. (mark.baird@uts.edu.au)

J. D. Everett and I. M. Suthers, Evolution and Ecology Research Centre, University of New South Wales, Sydney, NSW 2052, Australia. (jason.everett@unsw.edu.au; i.suthers@unsw.edu.au)