

# Entrainment and retention of the coastal larval fish assemblage by a short-lived, submesoscale, frontal eddy of the East Australian Current

Thomas J. Mullaney<sup>1,\*</sup> and Iain M. Suthers<sup>1,2</sup>

<sup>1</sup>School of Biological, Earth & Environmental Sciences, University of New South Wales, Sydney, Australia

<sup>2</sup>Sydney Institute of Marine Science, Building 19, Mosman, Australia

## Abstract

We examined the fate of larval fish assemblages after the East Australian Current (EAC) had separated from the coast and larval fish were advected eastward along the Tasman Front. There was no difference in the assemblages at four stations as the EAC meandered from the continental shelf to 220 km eastward. At a fifth station, we sampled a submesoscale, frontal eddy that had formed at the EAC separation zone 11 d earlier and had entrained shelf water. Zooplankton biomass was greater within the eddy compared to the adjacent shelf. The larval fish assemblage in the eddy was significantly different from all other stations. There was an order of magnitude greater abundance of three species characteristic of the shelf: sardine (*Sardinops sagax*; Clupeidae), blue mackerel (*Scomber australasicus*; Scombridae), and yellowtail scad (*Trachurus novaezelandiae*; Carangidae), which were also significantly larger than larvae from a station on the adjacent shelf. In particular, *S. sagax* in the eddy were ~ 5 mm longer and ~ 10 d older, although growth rates were similar. Larval retention in the eddy was inferred from the co-occurrence of small and large larvae of all three species compared to the adjacent shelf. The EAC is only 20–30 km from the inner-shelf water, where frontal eddies may facilitate three stages of successful recruitment: entrainment, enrichment, and retention. Frontal eddies off southeastern Australia entrain preconditioned shelf water, move slower than the mean flow of the EAC, decreasing transport rates, and may sustain planktonic communities through eddy uplift. These eddies are frequent and short-lived (2 to 4 weeks), and we suspect they are of fisheries importance as their duration is sufficient for fish larvae to complete their early life history and, presumably, recruit back to the coast.

Eddies and gyres produced by ocean boundary currents are often regions of entrainment, retention, enhanced productivity, and transport (Kimura et al. 1997; Hare et al. 2002; Govoni et al. 2010). Eddies produced by disturbance of the frontal edge of a boundary current are a source of enhanced plankton production (Kimura et al. 1997; Logerwell and Smith 2001), where increased concentration and survival of larval fish is often observed (Kendall et al. 1996; Rodríguez et al. 1999). The importance of eddies for fish production was proposed in Bakun's (2006) three stage model of favorable reproductive habitat—enrichment, larval concentration, and retention—providing an explanation for successful fisheries recruitment in boundary current systems (Logerwell and Smith 2001; Kasai et al. 2002; Okazaki et al. 2003). Furthermore, the advection of eddies can be up to 5- to 10-fold less than the boundary current itself (Mooers and Fiechter 2005; Everett et al. 2011), giving the biological community time to grow and become nektonic.

Eddy productivity can result when preconditioned shelf waters are entrained into the eddy (Rodríguez et al. 1999). Cyclonic (cold-core) eddies can further increase primary and secondary productivity through the uplifting and doming of isotherms and nutriclines (Lee et al. 1991; Kimura et al. 1997; Everett et al. 2011).

The East Australian Current (EAC) is an ocean boundary current that drives a cascade of biophysical processes with the narrowing of the shelf off Smoky Cape at ~ 31°S. This includes topographically induced upwelling

(Oke and Middleton 2001), which is manifest as phytoplankton enriched water off Diamond Head (31.7°S) and Port Stephens (32.7°S; Suthers et al. 2011). This process leads to the shelf water being more productive than the EAC. As the EAC separates from the coast, the intervening coastal water is cooler and exhibits a slight northward flow adjacent to the EAC (Syahailatua et al. 2011a). On occasion, the velocity shear between the EAC and the intervening coastal water generates a frontal instability or “billow,” forming a small coastal, cyclonic eddy (Tranter et al. 1986; Everett et al. 2011).

The separation zone of the EAC ranges between 30°S and 34°S (Suthers et al. 2011), making the ensuing frontal eddy formation spatially dynamic. Mesoscale eddies are typically > 100 km diameter and are observed by surface altimetry (Chelton et al. 2011; Everett et al. 2012), which cannot resolve the more frequent submesoscale eddies (Kim et al. 2011). Submesoscale, frontal eddies are therefore not readily observed in altimetry, and their study is difficult and often serendipitous, as in this study.

A submesoscale frontal eddy formed in the western Tasman Front off New South Wales during our voyage in the austral spring of 2006, providing an opportunity to compare the larval fish community of the eddy with that in the EAC. Shelf water in this region is already enriched with phytoplankton, zooplankton, and larval fish (Mullaney et al. 2011) compared to the EAC or Tasman Sea (Baird et al. 2008). Our aim, therefore, was to examine entrainment of preconditioned shelf water into a short-lived, submesoscale frontal eddy of the EAC and determine whether such eddies can emulate longer-lived mesoscale eddies (Bakun 2006) in

\* Corresponding author: t.mullaney@unsw.edu.au

larval fish entrainment, larval retention, and larval survival.

We first compared the water properties and larval fish assemblages of the EAC and western Tasman Front, focusing on the abundance and diversity of coastal species to assess entrainment. Second, we examined the larval fish size distributions of pelagic fish species to assess larval retention (Reiss et al. 2000). Third, we compared the age and growth of larval sardine, *Sardinops sagax*, between the eddy and the adjacent shelf to determine the significance of entrainment into a frontal eddy.

We expected that the eddy's larval assemblage would be similar to the shelf assemblage if significant entrainment had occurred and that there would be a broad range of larval sizes (ages) to indicate larval retention rather than transport. Larval retention or enhanced survival in an eddy would be evident when size classes co-occur, such as when different larval ages occur in the same sample (Reiss et al. 2000). We also expected that larval fish growth rates in the eddy would be greater than on the shelf if significant eddy enrichment occurred.

## Methods

**Study area**—A research voyage was undertaken during October 2006 to sample the larval fish assemblages along the Tasman Front and south of the EAC separation zone. During this period, the EAC separated from the New South Wales coast near Smoky Cape ( $\sim 31^\circ\text{S}$ ) and continued poleward. The continental shelf off Smoky Cape is the narrowest ( $\sim 15$  km) for the region and is where the EAC strengthens before separating from the shelf (Oke and Middleton 2001). The nutrient and plankton regime is dominated by the separation (Suthers et al. 2011), and there are no major rivers discharging into the area. After separation, the EAC bifurcated at  $\sim 33.5^\circ\text{S}$ , where a component of the EAC continued east and the remainder returned toward the coast and flowed southward out of the study area. A cyclonic eddy formed between the EAC and the coast in late September and early October 2006 at approximately  $32.2^\circ\text{S}$  and was located 100 km off the coast ( $33.2^\circ\text{S}$  and  $152.7^\circ\text{E}$ ) during the sampling period (Fig. 1c).

**Sampling methods**—Four stations were located in the EAC at longitudes  $152^\circ\text{E}$ ,  $153^\circ\text{E}$ ,  $154^\circ\text{E}$ , and  $155^\circ\text{E}$  (stations labeled 152, 153, 154, and 155, respectively) and were sampled between 09 and 11 October. A fifth station was located within the cyclonic eddy. There were two sites (a and b) within each station, which were 5.2 km apart (152); 11.5 km apart (153); 7.8 km apart (154); 11.5 km apart (155); and 5.1 km apart (eddy). At each site three replicate 13 min mid-water oblique tows were conducted ( $\sim 90$  min per station). The local sampling times were 01:00 h (152), 12:00 h (153), 03:00 h (154), 19:00 h (155), and 20:00 h (eddy); thus, all stations but 153 were sampled at night. The rectangular mid-water trawl (RMT) was a 1 m<sup>2</sup> net, 1 mm mesh, with a two-point bridle attached to the top spar and a weighted bottom spar. Replicated oblique tows were conducted by the RMT from 40 to 5 m depth over 13 min to sample the upper mixed layer, at approximately

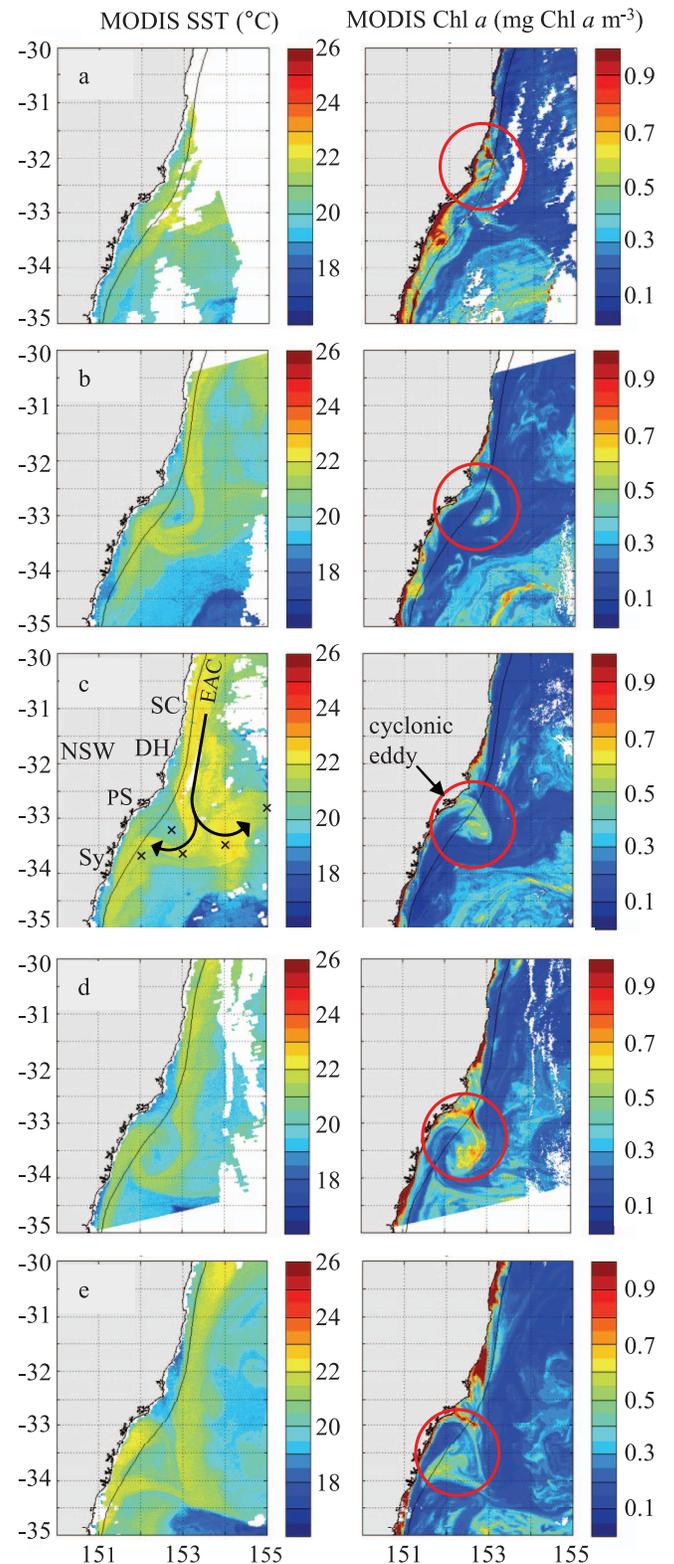


Fig. 1. Remotely sensed images of the sea surface temperature (left) and Chl *a* (right) from 01 to 14 October 2006 showing the EAC (SST  $> 21^\circ\text{C}$ ) off New South Wales and a cyclonic eddy (SST  $< 20^\circ\text{C}$ ) located inshore of the EAC, (a) 01 October, (b) 05 October, (c) 07 October, (d) 12 October, and (e) 14 October. SC, Smoky Cape; DH, Diamond Head; PS, Port Stephens; Sy, Sydney; NSW, New South Wales. Images derived from level-2 MODIS-Aqua.

4–5 km h<sup>-1</sup>. A General Oceanics flow meter recorded the volume of water sampled, and a Vemco Time Depth Recorder recorded temperature and trawl depth. Mounted inside the RMT was a 20 cm diameter, 100  $\mu$ m mesh plankton net. These preserved plankton samples were subsequently processed through a laboratory-based Focal Technologies optical plankton counter (OPC) to determine the biomass size–frequency distribution (*see below*).

The water mass at each tow location was identified by the sea surface temperature (SST) and salinity measured by the vessel's underway thermosalinograph and by the current direction and velocity recorded by the vessel's Acoustic Doppler Current Profiler (ADCP). Water depth at Sta. 152 ranged from 163 m to 220 m and, within the eddy, from 1650 m to 2050 m; at Sta. 153, 154, and 155, it was approximately 4800 m.

All samples were preserved in a 5% formalin:seawater solution, and  $\sim 3$  g of NaCO<sub>3</sub> (buffer) was added to maintain otolith structure. Within 2 weeks all larval fish were removed under a dissecting microscope and stored in 95% ethanol. All fish were identified to family where possible and to species for the more common or commercially valuable taxa. Less than 0.1% of larvae were too damaged to be identified. Concentration was standardized to number of individuals 1000 m<sup>-3</sup>, as the average volume of water sampled with each tow was 1059 m<sup>3</sup>. Families with fewer than three individuals are listed under “other” in the tables.

Fish larvae from Sta. 152 (shelf) and the eddy were measured for standard length (SL) using a dissecting microscope and optical micrometer to the nearest 0.1 mm. The sagittae of *S. sagax* larvae were removed using a dissecting microscope and polarized light (Uehara et al. 2005) and were fixed to microscope slides with Crystal Bond<sup>®</sup>; then the total number of increments were counted. Since increment formation occurs 2–3 d post hatch (Hayashi et al. 1989) we added 2 d to the total increment count to estimate larval age. An integrated growth rate for *S. sagax* was determined by dividing the SL (less a hatch length of 5mm) by age (days). A recent growth index (RGI) was calculated from the otolith increment widths using a compound microscope with a digital camera and Image-Pro Plus 5.1 software. The widest hatch check diameter, subsequent increment widths, including the partial increment to outer edge, were measured along the longest axis. The SL for an individual at the end of each day's growth (or increment) was then calculated from Eq. 1, derived from the allometric relationship between length and otolith radius (Watanabe and Kuroki 1997). The growth for each day was the difference in SL between that day and the previous.

$$L_i = a \times R_i^b \quad (1)$$

where

$$a = L_h / R_h^b \quad (2)$$

and

$$b = \ln(L_h / L_c) / \ln(R_h / R_c) \quad (3)$$

$L_i$  = length at increment  $i$ ,  $R_i$  = radius at increment  $i$ ,  $L_h$  = length at hatch (set at 5 mm),  $R_h$  = otolith radius at hatch,  $L_c$  = length at capture, and  $R_c$  = otolith radius at capture. RGI was calculated as the mean daily growth (mm) of the last three full days of life divided by the natural log of the standard length (Uehara et al. 2005). This removed any relationship between growth and size.

The 100  $\mu$ m zooplankton samples were rinsed of formaldehyde solution before being slowly added to a 50 liter header tank flowing through the sampling tunnel of the OPC at a rate of  $\sim 10$  L min<sup>-1</sup>. To reduce the effect of particle coincidence (more than one particle in the OPC's 4 mS sampling interval), the addition of zooplankton to the header tank was controlled such that counts were maintained between 10 counts s<sup>-1</sup> to 35 counts s<sup>-1</sup> (Moore and Suthers 2006). As a particle passes the 680 nm light beam from seven light emitting diodes, the reduction in light is proportional to the cross-sectional surface area. The particles are assigned to digital (millivolt) size bins calibrated to particles of equivalent spherical diameter (ESD), which are then sorted into 24 size bins between 0.35 mm ESD and 3.35 mm ESD (Moore and Suthers 2006). These particles are converted to a biomass in mg using geometric mean size of each size bin and the formula for the volume of sphere, assuming the density of water. Each size category's biomass is normalized by dividing the biomass by the size category's width, to produce a normalized biomass size frequency distribution (or “spectrum”).

*Data analysis*—Total taxa and concentration (individuals 1000 m<sup>-3</sup>) were compared among stations, and significant differences were determined from a two-factor analysis of variance (ANOVA), with “station” being orthogonal and fixed and “site” being nested and random. The Student–Newman–Keuls (SNK) post hoc test identified the differences between stations. Multidimensional Scaling (MDS) on  $\ln(x + 1)$  transformed data, and a Bray–Curtis similarity matrix was used to distinguish patterns in the larval fish assemblages. MDS is an ordination that uses the similarities or dissimilarities of data (in this case the abundance of taxa) within and among groups to assign a nondimensional location to each group and calculate the distance among groups. A nondimensional plot is produced based on those distances, which reflects the similarities or dissimilarities among groups so that similar groups are plotted closer to each other and dissimilar groups are further apart. Monte Carlo  $p$  values, of pairwise comparisons from permutational multivariate analysis of variance (PERMANOVA), identified differences between stations based on overall assemblage. With assemblage data, PERMANOVA usually accompanies MDS plots and provides a statistical probability that groups differ based on permutations of similarity or dissimilarity distances. PERMANOVA is a nonparametric statistical test that does not require the normal distribution of data. This is important when using multiple species (or the assemblage) as multiple variables, as there would be many missing values and a normal distribution would be unlikely. The PERMANOVA was a two-way design, with “station”

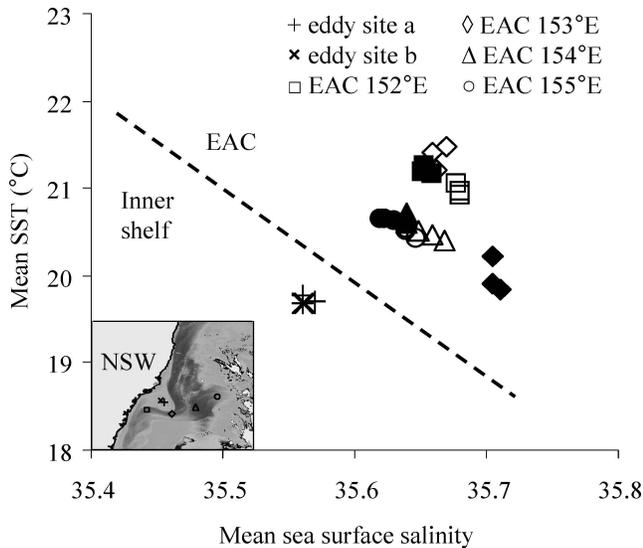


Fig. 2. Water type T-S properties separate the cyclonic eddy sites from the EAC sites (closed symbol = site a, open symbol = site b). Inset shows the location of the sites off New South Wales (NSW) and the extent of the EAC (darker shading). Dashed line separates the EAC and inner-shelf water types previously identified in this region (Henschke et al. 2011; Mullaney et al. 2011).

being crossed and fixed and “site” being nested and random on  $\ln(x + 1)$ -transformed data with a Bray–Curtis similarity matrix and 9999 permutations. Analysis of similarity percentages (SIMPER) on  $\ln(x + 1)$ -transformed data identified the taxon that mostly contributed to each water type assemblage. SIMPER uses a similarity matrix to identify the contribution of each variable (in this case, taxon) to the observed similarity or dissimilarity among groups. SIMPER can therefore identify the taxon that most contributes to the similarity or dissimilarity. Two-way ANOVAs were performed on common or heavily contributing taxa (according to SIMPER) with “station” being orthogonal and fixed and “site” being nested and random and data being  $\ln(x + 1)$  transformed. Differences between stations were identified by the SNK post hoc test. One way ANOVAs were performed on the integrated growth rate and RGI for *S. sagax* from the cyclonic eddy ( $n = 25$ ) and the EAC station over the shelf at 152°E ( $n = 12$ ).

## Results

**Study region and water properties**—During September, altimetry and moderate resolution imaging spectroradiometer (MODIS) imagery indicated that the EAC flowed poleward along the shelf until separation, and there was no evidence of any frontal instability in the region south of Smoky Cape (31°S). By 01 October 2006 (Fig. 1a) MODIS imagery revealed an instability off Seal Rocks and Sugarloaf Point Lighthouse (32.44°S). The instability had formed into a distinctive cyclonic eddy by 05 October (Fig. 1b). It grew over 7 d to form a cyclonic eddy, with a 20 cm negative surface anomaly, 60–80 km in diameter by 07 October. MODIS-aqua imagery of chlorophyll *a* (Chl *a*) indicated

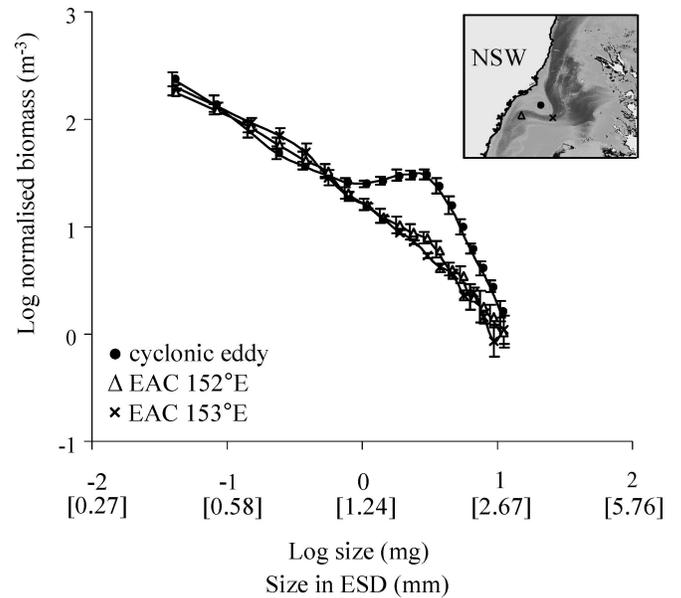


Fig. 3. Zooplankton normalized biomass size spectrum comparing the cyclonic eddy with the EAC on the shelf at Sta. 152°E and off the shelf at Sta. 153°E. The  $x$ -axis is additionally labeled with size in equivalent spherical diameter (ESD). Inset shows the location of the stations off New South Wales (NSW) and the extent of the EAC (darker shading).

entrainment of coastally enriched water into the eddy (Fig. 1b–d). By 09 October the eddy was 75 km diameter and increased to 95 km by 12 October (Fig. 1d). The eddy was sampled on 11 October. By 14 October the distinct eddy shape was no longer evident, and the surface depression was merging with a larger mesoscale eddy in the Tasman Sea (Fig. 1e).

The MODIS image (Fig. 1c) indicated that the EAC bifurcated south of Sta. 153 and 154, where near-surface currents (shipborne ADCP) were flowing south (182° and 188°, respectively) at 0.8 m s<sup>-1</sup>, representing the EAC’s initial southward flow after separation. On the shelf at Sta. 152 the near-surface current was flowing northwest (318°) at 0.7 m s<sup>-1</sup>, representing the partial EAC westward meander and return to the coast. Furthest east, at Sta. 155, the near-surface current was flowing north (9°) at 0.23 m s<sup>-1</sup>, representing an eastward meander of the EAC. At the cyclonic station the surface velocity was 0.19 m s<sup>-1</sup> east (83°), the lowest velocity of all stations.

The cyclonic eddy station was cooler and less saline and separated from all EAC stations by the temperature–salinity (T-S) signatures (Fig. 2). The western EAC sites (152a, 152b, and 153b) were approximately 0.6°C warmer than sites in the eastern EAC stations (154 and 155). However Site 153a was distinctly cooler and more saline than the other three western EAC sites (152a, 152b, and 153b). This most likely related to its closer proximity with the Tasman Sea.

The plankton biomass within the cyclonic eddy and the nearest inshore and offshore EAC stations were similar for plankton < 1.2 mm ESD (Fig. 3). The plankton biomass

Table 1. Mean larval fish concentrations (individuals 1000 m<sup>-3</sup>) from the cyclonic eddy and the EAC stations located at longitudes 152°E, 153°E, 154°E, and 155°E.

Taxon	Eddy	152°E	153°E	154°E	155°E
Myctophidae	120.8	56.9	47.0	19.8	76.2
Phosichthyidae	1.7	26.8	9.1	6.1	26.3
Clupeidae	38.3	3.6	—	—	—
Scombridae	32.6	0.3	—	—	—
Gonostomatidae	—	5.5	3.3	12.0	11.4
Carangidae	19.7	3.1	—	—	—
Bothidae	8.4	1.0	0.3	2.2	0.5
Anguilliformes	—	2.0	—	3.7	2.2
Paralepididae	0.1	2.6	0.8	1.1	3.2
Champsodontidae	0.1	5.7	1.6	—	0.3
Gempylidae	0.1	2.2	2.5	0.1	0.4
Bramidae	—	—	0.5	2.8	1.2
Howellidae	1.6	1.3	1.4	0.1	0.2
Melanostomiinae	0.3	0.8	1.6	0.4	0.4
Labridae	0.3	1.2	0.7	0.3	1.0
Notosudidae	0.8	0.5	0.2	—	1.8
Macroramphosidae	0.3	1.0	—	1.1	0.6
Mullidae	1.4	1.0	—	0.1	—
Serranidae	0.4	0.7	0.3	1.1	—
Bregmacerotidae	0.6	1.1	0.7	—	0.3
Ophidiidae	—	1.2	0.6	—	0.4
Evermannellidae	—	0.5	0.5	0.3	0.6
Gobiidae	0.5	0.8	0.2	0.1	0.3
Scorpaenidae	—	0.7	0.3	—	0.6
Stromateoidei	—	0.5	0.6	—	0.5
Chaetodontidae	—	1.3	—	—	—
Tetraodontidae	0.1	0.2	0.1	0.3	0.5
Triglidae	0.7	0.5	—	—	—
Monacanthidae	0.7	0.2	—	—	0.1
Scaridae	0.1	—	0.2	—	0.8
Astronesthinae	—	—	0.2	0.6	0.1
Callanthiidae	0.1	0.4	—	0.1	0.3
Synodontidae	0.2	0.3	—	0.4	—
Idiacanthinae	0.4	0.4	—	—	—
Nomeidae	—	0.6	0.2	—	0.2
Trachichthyidae	0.2	0.2	0.3	—	0.1
Microcanthidae	0.3	0.3	—	—	—
Scopelarchidae	—	0.2	0.1	0.3	—
Trachipteridae	—	0.4	0.3	—	—
Acropomatidae	0.4	—	—	—	—
Ammodytidae	—	0.5	—	—	—
Cirrhitidae	—	—	0.2	0.1	0.1
Melamphaidae	—	0.2	0.3	—	—
Pomacentridae	—	0.4	0.2	—	—
Stomiinae	—	—	0.4	—	—
Other	1.0	2.1	1.2	0.4	0.3
Unknown	—	0.7	—	—	—

size spectrum, however, showed a distinct increase (represented by doming in Fig. 3) in plankton > 1.2 mm ESD within the eddy. This trend continued up to approximately 2.7 mm ESD.

*Larval fish distributions in the Tasman Front and eddy*—Seventy-two larval fish families and 4113 individual fish larvae were identified from all stations. Myctophidae composed over 50% of the larval fish community, and Phosichthyidae, Clupeidae, Scombridae, Gonostomatidae, and Carangidae composed a further 30% (Table 1). The

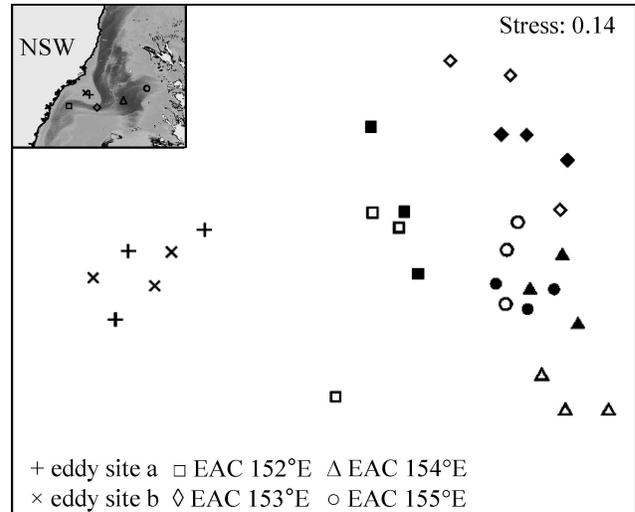


Fig. 4. MDS plot of larval fish assemblages grouped by dissimilarities of family abundance. Greater distance between symbols indicates greater dissimilarity. Closed symbols = site a and open symbols = site b, for the EAC sites. Inset shows the location of the sites off New South Wales (NSW) and the extent of the EAC (darker shading).

Phosichthyidae were all *Vinciguerria* spp. Clupeidae were *S. sagax* (97%) and *Etrumeus teres* (3%). Scombridae were > 99% *Scomber australasicus* and < 1% *Thunnus* spp. Carangidae were *Trachurus novaezelandiae* (> 99%) and *Seriola* spp. (< 1%).

There was a significant difference in larval fish concentration among stations (ANOVA,  $p = 0.01$ ) owing to the high abundance of clupeids, scombrids, and carangids found in the eddy (Table 1). Larval fish concentrations were significantly higher within the eddy than all EAC stations (from pairwise comparisons in ANOVA), with a mean concentration of 233 individuals 1000 m<sup>-3</sup>. None of the EAC stations significantly differed from each other in larval fish concentration (from pairwise comparisons in ANOVA). The mean number of taxa (families) within each station did not differ (ANOVA,  $p = 0.19$ ) and ranged from 12 to 26. However, in shelf site 152a there was a high presence of reef and inner-shelf families that were found in low numbers ( $\leq 3$ ) at this station and nowhere else (such as Ammodytidae, Callionymidae, Malacanthidae, and Hoplichthyidae; mostly listed as “Other” in Table 1).

The eddy larval fish assemblage was significantly different from the EAC assemblages (Fig. 4; PERMANOVA,  $p = 0.0013$ ), with Monte Carlo  $p$  values of pairwise comparisons being 0.003, 0.003, 0.007, and 0.003 for the eddy vs. Sta. 152, 153, 154, and 155, respectively. The western EAC stations (152 and 153) were only different from the eastern EAC station at 154°E ( $p = 0.029$  and 0.049) and not at Sta. 155 ( $p = 0.065$  and 0.054). The larval fish assemblages among the western EAC stations (152 and 153) differed ( $p = 0.043$ ), whereas the eastern stations (154 and 155) did not ( $p = 0.167$ ).

Myctophidae were common at all stations and contributed relatively evenly to all assemblages (Table 2; Fig. 5e). Clupeidae, Scombridae, Carangidae, and Bothidae were

Table 2. Contributions (% similarity) of common families to the cyclonic eddy and EAC stations at longitudes 152°E, 153°E, 154°E, and 155°E.

Taxon	Eddy	152°E	153°E	154°E	155°E	Assemblage description
Myctophidae	25.3	23.9	37.6	23.3	29.6	Widespread
Scombridae	17.7	<1	<1	0	0	Eddy
Clupeidae	17.1	6.7	0	0	0	Eddy
Carangidae	15.6	4.2	0	0	0	Eddy
Bothidae	9.8	1.7	<1	7.8	<1	Eddy
Phosichthyidae	1.7	19.3	19.0	14.8	22.2	All EAC
Paralepididae	<1	1.6	1.6	3.9	6.5	All EAC
Gempylidae	<1	4.1	12.0	<1	<1	Western EAC
Champsodontidae	<1	4.2	5.8	0.0	<1	Western EAC
Gonostomatidae	0	7.8	8.6	22.5	16.2	Eastern EAC
Anguilliformes	0	5.3	0	8.6	6.8	Eastern EAC

the main contributors to the cyclonic eddy assemblage (Table 2). These families were distinctly more common in the cyclonic eddy than any EAC station (Fig. 5a–d). Clupeidae, Scombridae, and Carangidae were present at only one other station, being the EAC station on the shelf (Sta. 152, Fig. 5a–d; Table 1). Phosichthyidae (Fig. 5f) and Paralepididae (Table 1) were distributed across all EAC stations, and concentrations were an order of magnitude less within the eddy. Phosichthyidae and Paralepididae were therefore representative of an EAC assemblage (Table 2). Gempylidae (Fig. 5g) and Champsodontidae (Table 1) were primarily found in the western EAC stations, 152 and 153, and were representative of a western EAC assemblage (Table 2). Alternatively, Gonostomatidae (Fig. 5h) were not present in the cyclonic eddy and were approximately three times more abundant in the eastern, offshore EAC Sta. 154 and 155 than either western station and were representative of the EAC assemblage located furthest off shore.

*Larvae of small pelagic fish species on the shelf and in the eddy*—The larvae of *S. sagax*, *S. australasicus*, and *T. novaezelandiae* were only present in the eddy and at Sta. 152 on the shelf in EAC water, although at a much lower abundance. In the eddy, *S. sagax* larvae ranged from 8 to 24 mm SL and were only 7 to 13 mm SL at Sta. 152 (Fig. 6a). Similarly, *S. australasicus* larvae ranged from 7 to 20 mm SL in the eddy, and there were only two individuals of 8 mm SL at Sta. 152 (Fig. 6b). *T. novaezelandiae* larvae were 5 to 17 mm SL in the eddy and 4 to 8 mm at Sta. 152 (Fig. 6c).

Importantly, there was evidence of larval retention by all three species in the eddy, from the overlap of a range of size classes from preflexion or flexion, to postflexion. Size of *S. sagax* was linearly related to age (Fig. 7;  $SL = 2.424 + 0.713 \times \text{age}$ , adjusted  $R^2 = 0.69$ ). By applying the above growth regression to the size distribution (Fig. 6a), the distribution of ages in the eddy for *S. sagax* was from 7 to 30 d post hatch (PH; modal age = 18 d PH) and on the shelf at Sta. 152 was from 6 to 14 d PH (modal age = 12 d PH). The 1 mm<sup>2</sup> mesh of the RMT precluded capturing newly hatched larvae, i.e., smaller than 8 mm SL. We

estimate that the modal ages for *T. novaezelandiae* were 23 d in the eddy and 14 d on the shelf, using larval *T. novaezelandiae* growth rates from the region (Syahailatua et al. 2011b). For larval *S. australasicus* (using length-age of larvae sampled in October 2004, A. Fowler and I. M. Suthers pers. comm.), the modal ages were 19 d in the eddy and 14 d on the shelf. The length frequencies of all three species were unimodal (Fig. 7).

There was no significant difference in the mean integrated growth rate for *S. sagax* between the eddy (0.54 mm d<sup>-1</sup>) and the EAC over the shelf at 152°E (0.50 mm d<sup>-1</sup>; ANOVA,  $p = 0.17$ ). The same result was obtained for recent growth between the eddy (RGI = 0.237) and the shelf (RGI = 0.258; ANOVA,  $p = 0.26$ ).

## Discussion

A region of mixed EAC, Tasman Sea, and coastal water exists off the coast of Sydney and over 100 km offshore (Keane and Neira 2008), known as the western Tasman Front (wTF; Mullaney et al. 2011). The cyclonic eddy observed here is part of the same process forming the wTF and its mixture of water types. This eddy entrained and retained a larval fish assemblage of shelf origin into the wTF. Our study reveals the importance of this relatively small and short-lived frontal eddy to the ichthyoplankton assemblage.

*Eddy formation and enrichment*—The precise origin of the eddy is difficult to determine due to cloud cover over the region during late September 2006. There was no evidence of a frontal instability in the advanced very high resolution radiometer (AVHRR) SST on 24 September or earlier. The next available image on 01 October reveals a frontal instability at 32.2°S and ~ 40 km in diameter. This was clearly evident with a core SST ~ 18°C (~ 3°C cooler than the surrounding EAC). From 01 to 12 October, quasi-daily MODIS-Aqua images revealed flow lines of chlorophyll, suggesting entrainment of inner-shelf water into the eddy.

The inner-shelf water in this region has previously been shown to be distinctively enriched in nitrate (Suthers et al.

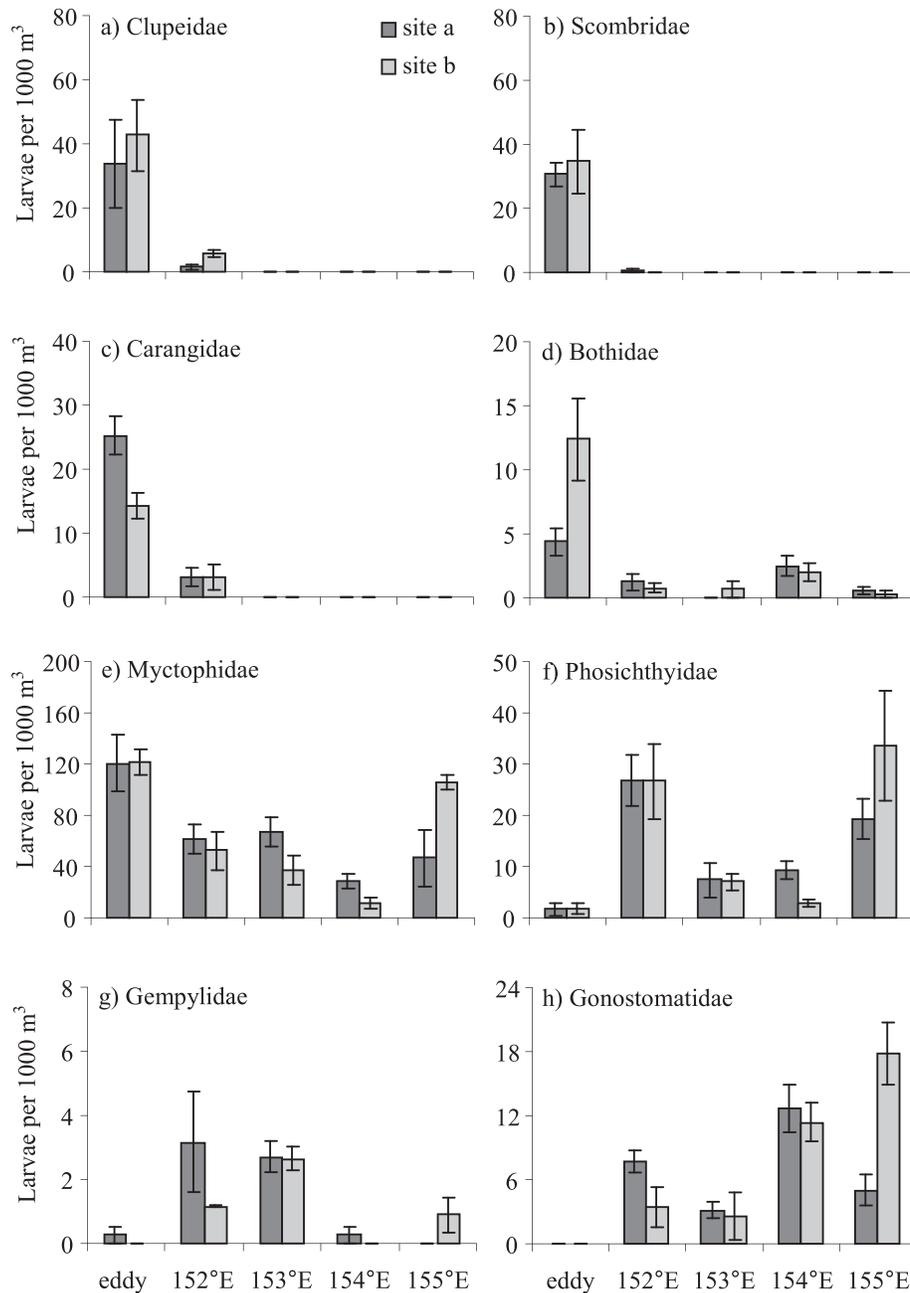


Fig. 5. The concentration of common larval fish families within the cyclonic eddy and the EAC stations at 152°E, 153°E, 154°E, and 155°E, darker shading = site a, lighter shading = site b. Note different scales on the y-axis.

2011), phytoplankton (Condie et al. 2011), zooplankton (Everett et al. 2011), and larval fish (Mullaney et al. 2011; Syahailatua et al. 2011a). In this study, satellite imagery showed the inner-shelf water to have enhanced levels of Chl *a* ( $> 1 \mu\text{g L}^{-1}$ ). Together, the MODIS image and the T-S signatures indicate that the inner-shelf water was entrained into the frontal instability off Seal Rocks (32.45°S) during early October.

The cyclonic eddy grew in diameter to over 90 km by the time of sampling on 11 October. The area of the eddy more than doubled over 2 weeks, from  $\sim 3000$  to  $\sim 8000$  km<sup>2</sup>.

We presume this is from the horizontal entrainment of shelf water based on the increase in Chl *a* shown in the satellite images. Within the eddy, the plankton normalized biomass size spectrum (NBSS) had a distinct bump or nonlinearity, which may indicate earlier enrichment being transferred through a food web, sustained by the eddy uplift. Typically, an NBSS should be approximately linear with a slope of  $-1$  (Suthers et al. 2006). Instead, the eddy samples had a bulge of biomass in the 1–2.5 mm ESD region, and inspection of the sample indicated an abundance of juvenile krill (Taylor et al. 2010) and small salps (Everett et al. 2011). This

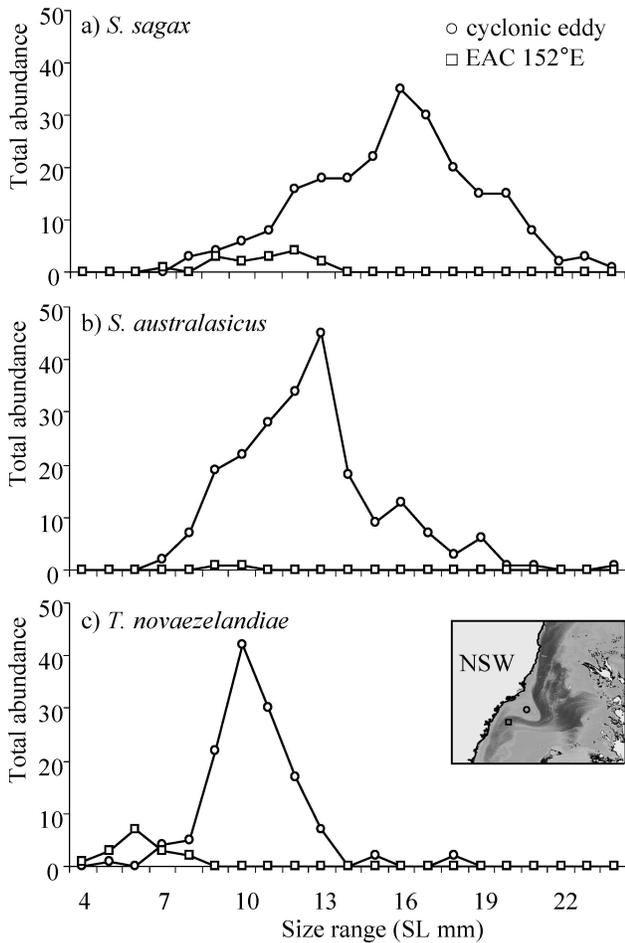


Fig. 6. Size distribution of *Sardinops sagax*, *Scomber australasicus*, and *Trachurus novaezelandiae*, comparing the cyclonic eddy with the EAC on the shelf at 152°E. Total abundance is all individuals across all samples within each water type. Inset shows location of the stations off New South Wales (NSW) and the extent of the EAC (darker shading).

suggests that a pulse of entrained preconditioned shelf water was sustained during the eddy's formation, with optimal growth conditions and little predation from fish.

A similar 40 km diameter frontal eddy in the region (October 2008; Everett et al. 2011) remained associated with the EAC and gained its vorticity from the tangential velocity of the EAC. Everett et al. (2011) reported that doming of the isotherms, uplifting them from 60 m to 40 m from the surface, was likely responsible for a localized bloom of salps (*Thalia democratica*). Shallowing of the mixed layer was also evident toward the end of our study and likely sustained a planktonic food chain to support larval fish. Lee et al. (1991) estimated that upwelling raised the density structure of a frontal eddy approximately 10 m d<sup>-1</sup>, bringing with it nutrients for biological uptake. Similarly, coastal water from the Enshu-nada Sea is entrained into frontal meanders of the Kuroshio and is sustained by cyclonic upwelling processes (Kimura et al. 1997; Kasai et al. 2002). Upwelling, therefore, likely sustains the planktonic community in the EAC frontal eddies.

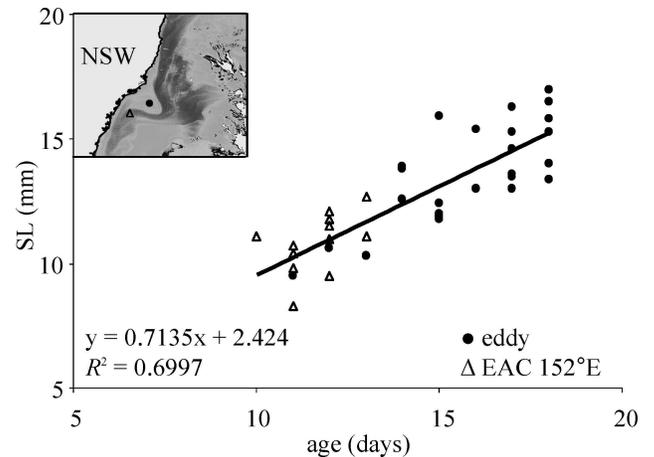


Fig. 7. Size (standard length) on age for *Sardinops sagax* comparing the cyclonic eddy with EAC-influenced shelf water at 152°E. Age = number of otolith increments + 2. Line of best fit and equation calculated on all fish. Inset shows the location of stations off New South Wales (NSW) and the extent of the EAC (darker shading).

It was significant that over the ~ 14 d of the eddy's life, the approximate center had only moved south from 32.5°S to 33.5°S (approximately 100 km), whereas the surrounding EAC was flowing at 0.2 ms<sup>-1</sup> to 0.5 ms<sup>-1</sup> and was potentially transporting plankton well over 500 km south and then east. The physical nature of the eddy suggested not only entrainment of coastal larval fish, but also spatial persistence and retention of the larval fish. We explore the evidence of entrainment and retention in the following sections.

*The western Tasman Front and entrainment into the frontal eddy*—The larval fish assemblages of the wTF were dominated by the EAC in October 2006, except for the eddy which was comprised of shelf water. The eddy was distinguished by a larval abundance of taxa that are known to spawn on the continental shelf (Ward et al. 2003; Syahailatua et al. 2011a,b). Larval Clupeidae, Scombridae, Carangidae, and Bothidae have been previously described as coastal or shelf families off eastern Australia (Keane and Neira 2008), and Clupeidae and Bothidae are particularly characteristic of the inner-shelf water type (Mullaney et al. 2011). *S. sagax* spawn off northern New South Wales from June to October at inner-shelf < 50 m isobath (Ward et al. 2003), whereas *S. australasicus* spawns on the outer shelf between 25°S and 35°S (Neira and Keane 2008) and is readily entrained into the EAC (Mullaney et al. 2011). *T. novaezelandiae* is more associated with EAC water than *S. sagax* and is likely to have a spring spawning distribution similar to *S. australasicus* (Syahailatua et al. 2011a,b). Together these species occur as larvae during spring on the continental shelf and are observed in near-shore upwelling zones (Uehara et al. 2005; Syahailatua et al. 2011b) or 200 km offshore in the Tasman Front (Condie et al. 2011; Mullaney et al. 2011). The co-occurrence of these species within the eddy indicates mixing of shelf and EAC water prior to eddy formation.

There was an abundance of Myctophidae in the eddy; however, Myctophidae are widespread across all water types in the wTF region (Mullaney et al. 2011). Otherwise, there was a paucity of the deep-sea larval fish assemblage in this offshore eddy, such as Gonostomatidae, Phosichthyidae, and Gempylidae (Mullaney et al. 2011), indicating that the frontal eddy had entrained and encircled shelf water. Simpson and Lynn (1990) considered lateral entrainment of nutrient-rich, near-surface coastal water into offshore eddies off the California Current as the basis for offshore productivity, rather than local (endogenous) nutrient loads. Therefore, lateral entrainment of shelf water appears to be as important as eddy uplift for production within frontal eddies.

*Retention of larval fish*—We inferred that the eddy habitat had promoted larval retention, using the Reiss et al. (2000) definition, based on overlapping size and age classes compared to the adjacent shelf water (i.e., Sta. 152). The presence of small, younger sardine larvae (8 mm SL and 7 d old) along with large, older larvae (24 mm and 30 d old) in the eddy suggests enhanced survival rates and reduced dispersion of larvae (i.e., larval retention). Modal ages for *S. sagax* (sardine), *T. novaezealandiae* (yellowtail scad), and *S. australasicus* (blue mackerel) in the eddy were 5 to 9 d older than those on the shelf. It is likely that the eddy received and retained the older and then the younger larvae as they arrived from the shelf. It is also possible that a progressive spawning wave along the coast, from north to south, introduced younger larvae into the older drifting cohort, before the simultaneous entrainment of both size classes into the eddy. Perhaps sardine spawned within the eddy to produce the mixture of size classes, although the species is believed to spawn only in coastal waters (Keane and Neira 2008); nor did we observe in the eddy many larvae < 12 mm in length. It is also possible that the eddy's broad size distribution could be produced by a much lower mortality rate, allowing the large larvae to co-occur with the small, despite using the same gear type and same sample volume. Nevertheless, the eddy was essential to restrict any further eastward dispersal.

Larval retention was invoked by Iles and Sinclair (1982) as a larval behavior to explain reduced dispersal and, possibly, enhanced recruitment of larval herring in coastal areas of the Gulf of Maine. Short-term larval retention (days) was also evident in larval gadoids on the Scotian Shelf (Western Bank), and Reiss et al. (2000) concluded that no convergence or larval behavior was necessary to explain the observed distributions. Reduced dispersal is important for coastal marine populations for the formation of metapopulations and life-cycle closure (Reiss et al. 2000). Our quantitative measurement of larval retention in a cyclonic feature beside a dynamic boundary current is novel and important for the region. Relatively low larval retention rates are estimated for southeastern Australia compared to the Leeuwin Current, or compared to the Great Australian Bight (Condie et al. 2011). They estimated that less than 1% of particles are retained for 28 d on the shelf in the separation zone off southeastern Australia. Therefore, any process that could slow dispersion and

enhance retention until fish larvae are active swimmers would be advantageous.

Sardine larvae were not growing significantly faster in the eddy compared to the shelf—they were only older and larger on average. However, growth rates can be a function of the slower growing larvae being removed by differential mortality (Tian et al. 2007). Perhaps predation on larval fish was less in the eddy compared to the shelf waters.

*Comparisons with other ocean boundary currents*—The occurrence of a cyclonic eddy caused by a frontal instability (Okazaki et al. 2002) is typical on the coastal side of western boundary currents such as the Kuroshio and the Gulf Stream (Lee et al. 1991; Kimura et al. 1997). Coastally spawned anchovy eggs and larvae in the Enshu-nada Sea, as well as nauplii, are entrained into a frontal eddy of the Kuroshio, where they are provided with favorable growing conditions (Nakata et al. 2000). Frontal eddies of the Kuroshio can occur 18 times per summer (Kimura et al. 1997), and this process may be the basis for anchovy recruitment in the Kuroshio system (Kasai et al. 2002).

The cyclonic eddies of the Charleston Gyre entrain and retain larval fish from both the Gulf Stream and shelf assemblages, and eddy duration of weeks to months matches the larval duration of most fishes (Govoni and Hare 2001; Govoni et al. 2010). In particular, coastal eddy formation is observed further south and “upstream” of most Gulf Stream studies, near this current's separation from the shelf around Cape Canaveral during autumn. In this region, nutrients and phytoplankton are entrained into frontal eddies of the Florida Current and transported north of Cape Canaveral, alternating between onshore and offshore transport with the onshore and offshore velocities of the eddies (Fiechter and Mooers 2007). Additionally, a southward flowing countercurrent can form adjacent to the Florida and Georgia coast and export carbon offshore (Lee et al. 1991). This recirculation, leading to entrainment and retention, may explain identification of the Georgia shelf as a larval retention zone (Hare and Walsh 2007). It is possible that the Stockton Bight region of New South Wales, between Sugarloaf Point (or Seal Rocks, 32.45°S) and the city of Newcastle (32.92°S) may also be a significant larval retention zone.

Our sampling of this eddy was fortuitous; it was only detected because of clear skies allowing for satellite imagery to be available during the voyage. We expect that similar, and even smaller, cyclonic eddies may be more common and yet go undetected. Inspection of the AVHRR-SST imagery (<http://oceancurrent.imos.org.au/>) from 2008–present reveals that submesoscale cyclonic eddies ~ 60 km in diameter form off Sydney approximately once per week, similar to occurrence in the Florida Current. At the separation of the Gulf Stream off Florida, Lee et al. (1991) observed that frontal eddies typically occurred about once per week and lasted 1 to 3 weeks. We also observed that many small frontal eddies (< 30 km diameter) initially form in the separation zone but quickly disappear within days.

Off eastern Australia, short-lived, submesoscale frontal eddies likely play the role similar to the long-lived, mesoscale eddies of other western boundary currents, in larval fish entrainment, retention, and survival (Bakun

2006). Frontal instabilities are to be expected south of Diamond Head, where the EAC strengthens locally and therefore creates a greater velocity shear with respect to the inner-shelf water (Suthers et al. 2011). If the small frontal eddies described in this study occur frequently, then their importance to fisheries recruitment would be significant. The key to this particular eddy's larval assemblage is the source water—immediately south of the separation zone—and the entrainment of the preconditioned, inner-shelf water.

#### Acknowledgments

We thank the crew of R/V *Southern Surveyor* (voyage SS09/2006) and the scientists from the cruise: Jason Middleton, Greg Nippard, and Debbie Cox (University of New South Wales), Lindsay Pender, Mark Underwood, Drew Mills, and Neale Johnstone (Commonwealth Scientific and Industrial Research Organisation), and Melanie O'Byrne (Australian National University). David Griffin (Commonwealth Scientific and industrial Research Organisation) and Jason Everett (University of New South Wales) supplied the satellite images. We thank the anonymous reviewers, Rob Stephenson, and associate editor, James J. Leichter, for providing valuable comments that substantially improved the manuscript. This research was funded by the Australian Research Council Discovery Projects to IMS.

#### References

- 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. I* **55**: 1438–1455, doi:10.1016/j.dsr.2008.06.011
- 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**: 105–122, doi:10.3989/scimar.2006.70s2105
- CHELTON, D. B., M. G. SCHLAX, AND R. M. SAMELSON. 2011. Global observations of nonlinear mesoscale eddies. *Prog. Oceanogr.* **91**: 167–216, doi:10.1016/j.pocean.2011.01.002
- CONDIE, S. A., J. V. MANSBRIDGE, AND M. L. CAHILL. 2011. Contrasting local retention and cross-shore transports of the East Australian Current and the Leeuwin Current and their relative influences on the life histories of small pelagic fishes. *Deep-Sea Res. II* **58**: 606–615, doi:10.1016/j.dsr2.2010.06.003
- EVERETT, J. D., M. E. BAIRD, P. R. OKE, AND I. M. SUTHERS. 2012. An avenue of eddies: Quantifying the biophysical properties of mesoscale eddies in the Tasman Sea. *Geophys. Res. Lett.* **39**: L16608. doi:10.1029/2011JC007310, doi:10.1029/2012GL053091
- , ———, 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:10.1029/2006JC003576, doi:10.1029/2011JC007310
- FIECHTER, J., AND C. N. K. MOOERS. 2007. Primary production associated with the Florida Current along the East Florida Shelf: Weekly to seasonal variability from mesoscale-resolution biophysical simulations. *J. Geophys. Res.* **112**: C12002. doi:10.1029/2006JC003576, doi:10.1029/2006JC003576
- GOVONI, J. J., AND J. A. HARE. 2001. The Charleston Gyre as a spawning and larval nursery habitat for fishes, p. 123–136. *In* G. R. Sedberry [ed.], *Islands in the stream: Oceanography and fisheries of the Charleston Bump*. American Fisheries Society.
- , ———, E. D. DAVENPORT, M. H. CHEN, AND K. E. MARANCIK. 2010. Mesoscale, cyclonic eddies as larval fish habitat along the southeast United States shelf: A Lagrangian description of the zooplankton community. *ICES J. Mar. Sci.* **67**: 403–411, doi:10.1093/icesjms/fsp269
- HARE, J. A., AND H. J. WALSH. 2007. Planktonic linkages among marine protected areas on the south Florida and southeast United States continental shelves. *Can. J. Fish. Aquat. Sci.* **64**: 1234–1247, doi:10.1139/f07-089
- , AND OTHERS. 2002. Routes and rates of larval fish transport from the southeast to the northeast United States continental shelf. *Limnol. Oceanogr.* **47**: 1774–1789, doi:10.4319/lo.2002.47.6.1774
- HAYASHI, A., Y. YAMASHITA, K. KAWAGUCHI, AND T. ISHII. 1989. Rearing method and daily otolith ring of Japanese sardine larvae. *Nippon Suisan Gakkaishi* **55**: 997–1000, doi:10.2331/suisan.55.997
- 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
- ILES, T. D., AND M. SINCLAIR. 1982. Atlantic herring: Stock discreteness and abundance. *Science* **215**: 627–633, doi:10.1126/science.215.4533.627
- 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, doi:10.1016/S0924-7963(02)00201-4
- KEANE, J., AND F. J. NEIRA. 2008. Larval fish assemblages along the south-eastern Australian shelf: Linking mesoscale non-depth-discriminate structure and water masses. *Fish. Oceanogr.* **17**: 263–280, doi:10.1111/j.1365-2419.2008.00478.x
- KENDALL, JR., A. W., J. D. SCHUMACHER, AND S. KIM. 1996. Walleye pollock recruitment in Shelikof Strait: Applied fisheries oceanography. *Fish. Oceanogr.* **5**: 4–18, doi:10.1111/j.1365-2419.1996.tb00079.x
- KIM, S. Y., AND OTHERS. 2011. Mapping the U.S. West Coast surface circulation: A multiyear analysis of high-frequency radar observations. *J. Geophys. Res.* **116**: C03011, doi:10.1029/2010JC006669
- KIMURA, S., A. KASAI, H. NAKATA, T. SUGIMOTO, J. H. SIMPSON, AND J. V. S. CHEOK. 1997. Biological productivity of mesoscale eddies caused by frontal disturbances in the Kuroshio. *ICES J. Mar. Sci.* **54**: 179–192, doi:10.1006/jmsc.1996.0209
- LEE, T. A., J. A. YODER, AND L. P. ATKINSON. 1991. Gulf Stream frontal eddy influence on productivity of the southeast U.S. continental shelf. *J. Geophys. Res.* **96**: 22191–22205, doi:10.1029/91JC02450
- LOGGERWELL, E. A., AND P. E. SMITH. 2001. Mesoscale eddies and survival of late stage Pacific sardine (*Sardinops sagax*) larvae. *Fish. Oceanogr.* **10**: 13–25, doi:10.1046/j.1365-2419.2001.00152.x
- MOOERS, C. N. K., AND J. FIECHTER. 2005. Numerical simulations of mesoscale variability in the Straits of Florida. *Ocean Dyn.* **55**: 309–325, doi:10.1007/s10236-005-0019-0
- MOORE, S. K., AND I. M. SUTHERS. 2006. Evaluation and correction of subresolved particles by the optical plankton counter in three Australian estuaries with pristine to highly modified catchments. *J. Geophys. Res.* **111**: C05S04, doi:10.1029/2005JC002920
- MULLANEY, T. J., A. G. MISKIEWICZ, M. E. BAIRD, P. T. P. BURNS, AND I. M. SUTHERS. 2011. Entrainment of larval fish assemblages from the inner shelf into the East Australian Current and into the western Tasman Front. *Fish. Oceanogr.* **20**: 434–447, doi:10.1111/j.1365-2419.2011.00594.x
- NAKATA, H., S. KIMURA, Y. OKAZAKI, AND A. KASAI. 2000. Implications of meso-scale eddies caused by frontal disturbances of the Kuroshio Current for anchovy recruitment. *ICES J. Mar. Sci.* **57**: 143–152, doi:10.1006/jmsc.1999.0565

- NEIRA, F. J., AND J. P. KEANE. 2008. Ichthyoplankton-based spawning dynamics of blue mackerel (*Scomber australasicus*) in south-eastern Australia: Links to the East Australian Current. *Fish. Oceanogr.* **17**: 281–298, doi:10.1111/j.1365-2419.2008.00479.x
- OKAZAKI, Y., H. NAKATA, AND S. KIMURA. 2002. Effects of frontal eddies on the distribution and food availability of anchovy larvae in the Kuroshio Extension. *Mar. Freshw. Res.* **53**: 403–410, doi:10.1071/MF01115
- , ———, ———, AND A. KASAI. 2003. Offshore entrainment of anchovy larvae and its implication for their survival in a frontal region of the Kuroshio. *Mar. Ecol. Prog. Ser.* **248**: 237–244, doi:10.3354/meps248237
- OKE, P. R., AND J. H. MIDDLETON. 2001. Nutrient enrichment off Port Stephens: The role of the East Australian Current. *Cont. Shelf Res.* **21**: 587–606, doi:10.1016/S0278-4343(00)00127-8
- REISS, C. S., G. PANTELEEV, C. T. TAGGART, J. SHENG, AND B. DE YOUNG. 2000. Observations on larval fish transport and retention on the Scotian Shelf in relation to geostrophic circulation. *Fish. Oceanogr.* **9**: 195–213, doi:10.1046/j.1365-2419.2000.00139.x
- RODRÍGUEZ, J. M., S. HERNÁNDEZ-LEÓN, AND E. D. BARTON. 1999. Mesoscale distribution of fish larvae in relation to an upwelling filament of Northwest Africa. *Deep-Sea Res. I* **46**: 1969–1984, doi:10.1016/S0967-0637(99)00036-9
- SIMPSON, J. J., AND R. J. LYNN. 1990. A mesoscale eddy dipole in the offshore California Current. *J. Geophys. Res.* **95**: 13009–13022, doi:10.1029/JC095iC08p13009
- SUTHERS, I. M., C. T. TAGGART, D. RISSIK, AND M. E. BAIRD. 2006. Day and night ichthyoplankton assemblages and zooplankton biomass size spectrum in a deep ocean island wake. *Mar. Ecol. Prog. Ser.* **322**: 225–238, doi:10.3354/meps322225
- , AND OTHERS. 2011. The strengthening East Australian Current, its eddies and biological effects—an introduction and overview. *Deep-Sea Res. II* **58**: 538–546, doi:10.1016/j.dsr2.2010.09.029
- SYAHAILATUA, A., M. ROUGHAN, AND I. M. SUTHERS. 2011a. Characteristic ichthyoplankton taxa in the separation zone of the East Australian Current: Larval assemblages as tracers of coastal mixing. *Deep-Sea Res. II* **58**: 678–690, doi:10.1016/j.dsr2.2010.10.004
- , M. TAYLOR, AND I. M. SUTHERS. 2011b. The size-specific response of two larval carangids to upwelling in the separation region of the East Australian Current. *Deep-Sea Res. II* **58**: 691–698, doi:10.1016/j.dsr2.2010.06.009
- TAYLOR, M. D., T. J. MULLANEY, AND I. M. SUTHERS. 2010. Mesoscale distribution of larval *Euphausia similis* in various water masses of the East Australian Current. *Deep-Sea Res. I* **57**: 1295–1303, doi:10.1016/j.dsr.2010.06.010
- TIAN, T., Ø. FIKSEN, AND A. FOLKVORD. 2007. Estimating larval fish growth under size-dependent mortality: A numerical analysis of bias. *Can. J. Fish. Aquat. Sci.* **64**: 554–562, doi:10.1139/f07-031
- TRANTER, D. J., D. J. CARPENTER, AND G. S. LEECH. 1986. The coastal enrichment effect of the East Australian Current eddy field. *Deep-Sea Res.* **33**: 1705–1728, doi:10.1016/0198-0149(86)90075-0
- UEHARA, S., A. SYAHAILATUA, AND I. M. SUTHERS. 2005. Recent growth rate of larval pilchards *Sardinops sagax* in relation to their stable isotope composition, in an upwelling zone of the East Australian Current. *Mar. Freshw. Res.* **56**: 549–560, doi:10.1071/MF04221
- WARD, T. M., J. STAUNTON-SMITH, S. HOYLE, AND I. A. HALLIDAY. 2003. Spawning patterns of four species of predominantly temperate pelagic fishes in the sub-tropical waters of southern Queensland. *Est. Coast. Shelf Sci.* **56**: 1125–1140, doi:10.1016/S0272-7714(02)00318-9
- WATANABE, Y., AND T. KUROKI. 1997. Asymptotic growth trajectories of larval sardine (*Sardinops melanostictus*) in the coastal waters off western Japan. *Mar. Biol.* **127**: 369–378, doi:10.1007/s002270050023

Associate editor: James J. Leichter

Received: 14 November 2012

Accepted: 29 April 2013

Amended: 24 May 2013