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Characteristic ichthyoplankton taxa in the separation zone of the East Australian Current: Larval assemblages as tracers of coastal mixing

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ABSTRACT

Ichthyoplankton assemblages were compared between regions dominated by the oligotrophic East Australian Current (EAC) and the inner-shelf waters off southeastern Australia, to determine if the early life history of fish was related to the separation of the EAC from the coast, producing different water masses as well as characteristic taxa. Samples were collected at the surface and in sub-surface waters, at 50 and 100 m isobath stations, during two summer research voyages in November 1998 and January 1999. On both voyages the study region was characterized by coastal and EAC waters in the north (~31°S), and in the south by topographically induced upwelling (~31°S), associated with narrowing of the continental shelf and separation of the EAC from the coast. Among the 111 families of larval fish, we observed distinctive assemblages of ichthyoplankton associated with the two different water masses. A greater abundance of the Carangidae, Labridae, Lutjanidae, Microcanthidae, Myctophidae and Scombridae was associated with the nutrient poor EAC water mass, while the Callionymidae, Clupeidae, Platycephalidae and Sillaginidae were mostly found in the cooler and/or fresher inner-shelf water mass. We assessed these patterns with opportunistic samples from an unusual, wind-driven upwelling event in the north (~31°S) earlier in the November voyage. The relative abundance of these 10 characteristic families distinguished this wind-driven upwelling event from the subsequent relaxation and predominance of the EAC assemblage at this location just 6 d later. Distinctive and abundant families such as larval clupeids, relative to larval carangids, could be a useful marker of inner-shelf, EAC and mixed water masses in the absence of robust hydrographic data. This and related studies indicate contrast in early life histories of *Sardinops sagax* and *Trachurus* spp., which appear to spawn respectively in the inner-shelf and outer-shelf waters. The post-flexion stages of *S. sagax* predominate in the outer-shelf and Tasman Front, while post-flexion *Trachurus* spp. predominate in inner-shelf water masses.

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1. Introduction

The assemblages of ichthyoplankton reflect not only early life history strategies, but also could provide characteristic, short-term biological properties of different water masses. Local ichthyoplankton assemblages are dynamic, being advected at least at the scales of days and kilometres across the Sydney shelf (Dempster et al., 1997; Smith et al., 1999). Using detailed current velocity measurements to interpret the assemblage variability, these two studies concluded that larval assemblages functioned as a tracer (or property) of the water masses. It is possible we could generalize these patterns and use characteristic ichthyoplankton taxa as biological markers of water masses, the way *Sagitta* (or arrow worms, Chaetognatha) has long been used to characterise oceanographic events (Ulloa et al., 2000 and references therein).

The passage of the East Australian Current (EAC) along the coast of eastern Australia can cause uplifting of deep nutrient-rich waters, shown by upward tilting the isotherms towards the surface near the coast (Oke and Middleton, 2001). The uplifted water may be brought completely to the surface by poleward, upwelling favourable (northeasterly) winds. Uplifting is also driven by the EAC where the continental shelf off central New South Wales (31°S) narrows by 50%, to around 15 km wide (Rochford, 1984; Roughan and Middleton, 2002, 2004) and is evident at the surface where the EAC separates from the coast between 30° and 33°S (Oke and Middleton, 2001; Roughan and Middleton, 2002, 2004). The behaviour of this western boundary current has many biological-water mass similarities with the Kuroshio extension (Watanabe, 2002), the Agulhas Current (Beckley, 1993), the Brazil Current (Nonaka et al., 2000), the Leeuwin Current (Muhling et al., 2008),

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the Florida Current (Grothues and Cowen, 1999; Pitts, 1999) and the Gulf Stream (Hare et al., 2001; Quattrini et al., 2005).

The separation zone is a key feature for the region (Cresswell, 1994), producing a diversity of water masses and ichthyoplankton assemblages off central New South Wales (Keane and Neira 2008). The production and fate of these water masses is important to assess the effects of an increasing EAC (Hill et al., 2008; Ling et al., 2009) and the water masses themselves may be used for real-time allocation of long-line fisheries permits (Hobday and Hartmann, 2006). South of the separation from the coast and along shore, the upwelled water mass is cooler and/or fresher and was described by Cresswell (1994) as "inner-shelf water". The ichthyoplankton of this water mass so near to the separation has not been sampled before.

The biological significance of upwelling by the EAC is evident in phytoplankton blooms, which may be transported southwards towards the cities of Newcastle (~33°S) and Sydney (~34°S) (Dela-Cruz et al., 2003). Upwelled nutrients could have a dramatic influence on the ichthyoplankton composition, its abundance and success in fish recruitment due to the increased food availability (Cury and Roy, 1989; Agostini and Bakun, 2002). It is possible that reproduction by some species may even be stimulated by upwelling events, producing characteristic taxa of upwelling and the inner-shelf. Upwelling can vary considerably in the mechanism, magnitude and biological response (Cury and Roy, 1989). For example, persistent and strong upwelling can dilute larval fish abundance and diversity (off western Africa (Hamann et al., 1981; Olivar and Shelton, 1993); off northern California (Roughan et al., 2006)) or oceanographically displace ichthyoplankton assemblages (Smith et al., 1999; Smith and Suthers, 1999), or may uncouple the biological response due to advection (Peterson et al., 1988).

This study examines the larval assemblages of the EAC, the inner-shelf and upwelled water masses. Mixed water masses

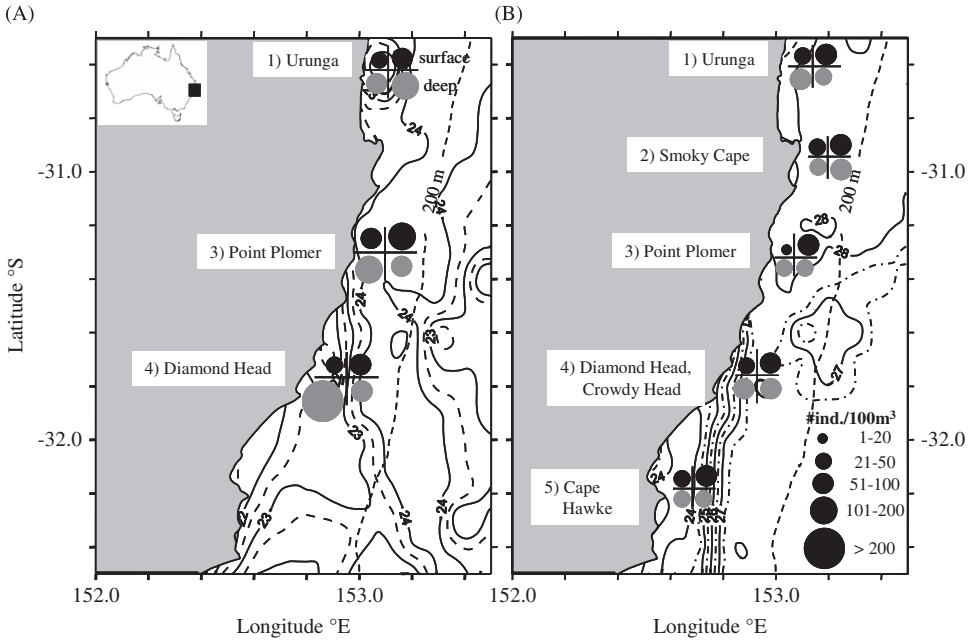

Fig. 1. Contours of remotely sensed sea surface temperature (SST), NOAA 14 on (A) 21 November 1998 and (B) 19 January 1999. The sampling regions are numbered 1–5, as referenced in the text and Table 1. Expanding symbols show the average total larval abundance for the surface and sub-surface nets, at the approximate locations of the inshore and offshore stations.

Table 1
Summary of sampling regions numbered from north to south, location name, stations (inshore, 50 m isobath; offshore, 100 m isobath), latitude, longitude and sampling date in November 1998 and January 1999. Additionally, a separate, local upwelling event was sampled to examine generality of findings (annotated as Region′). *n*-Nov. and *n*-Jan are the number of samples in November and January, respectively (surface, upper mixed layer). Sampling was conducted during the night from 20:00 to 05:30.

Region #	Locality name	Station	Latitude (°S)	Longitude (°E)	Nov.-98		Jan.-99	
					date	*n*-Nov.	date	*n*-Jan.
1	Urunga	Inshore	30°32.68′	153°09.09′	22/23	4, 2	21/22	4, 2
		Offshore	30°33.79′	153°15.34′	22/23	4, 2	21/22	4, 1
2	Smoky Cape	Inshore	31°00.19′	153°05.68′	–	–	22/23	4, 2
		Offshore	30°59.97′	153°09.90′	–	–	22/23	4, 2
3	Point Plomer	Inshore	31°19.31′	153°01.21′	23/24	4, 2	23/24	4, 2
		Offshore	31°20.04′	153°05.78′	23/24	4, 2	23/24	4, 2
4	Diamond Head	Inshore	31°45.43′	153°00.63′	24/25	4, 2	24/25	4, 2
		Offshore	31°44.62′	152°53.45′	24/25	4, 2	24/25	4, 2
5	Cape Hawke	Inshore	32°10.06′	152°36.88′	–	–	25/26	4, 2
		Offshore	32°10.10′	152°46.77′	–	–	25/26	4, 1
1′	Urunga	Inshore	30°32.68′	153°09.09′	16/17	(2, –)	–	–
		Offshore	30°33.79′	153°15.34′	16/17	(2, –)	–	–
2′	Smoky Cape	Inshore	31°00.19′	153°05.68′	16/17	(2, –)	–	–
		Offshore	30°59.97′	153°09.90′	16/17	(2, –)	–	–
	Total					32, 12		40, 18

Table 2
List of ichthyoplankton taxa (in alphabetical order), the total number of larvae caught over both cruises, their contribution (%) and the rank based on individual number caught at surface and sub-surface in November 1998 and January 1999. 0, refers to $<0.1\%$; –, refers to no larvae caught, numbers and families in **bold** refers to $>1\%$, and were analysed for assemblage structure. If the family abundance is $>5\%$ or contains a commercial species, the dominant species are listed where identification was possible (at least for the larger individuals), but the species abundance is uncertain.

Taxa	November 1998				January 1999			
	Surface		Sub-surface		Surface		Sub-surface	
	n	%	*n*	%	*n*	%	*n*	%
Acanthuridae	9	0.2	31	0.4	14	0.3	87	0.9
Acropomatidae	2	0	13	0.2	–	–	4	0
Ammodytidae	9	0.2	5	0.1	16	0.4	46	0.5
Anguilliformes	4	0.1	9	0.1	17	0.4	**165**	**1.7**
Apogonidae	5	0.1	12	0.1	**43**	**1.0**	53	0.6
Argentinidae	–	–	2	0	–	–	–	–
Arripidae (*Arripis trutta*)	24	0.5	12	0.1	18	0.4	11	0.1
Atherinidae	–	–	9	0.1	2	0	–	–
Aulostomidae	–	–	2	0	–	–	1	0
Balistidae	2	0	3	0	–	–	21	0.2
Belonidae	1	0	–	–	–	–	2	0
Berycidae	1	0	–	–	2	0	8	0.1
Blenniidae	30	0.6	28	0.3	16	0.4	14	0.1
Bothidae	**118**	**2.6**	**228**	**2.8**	**153**	**3.7**	**344**	**3.6**
Bramidae	–	–	1	0	12	0.3	–	–
Bregmacerotidae	–	–	2	0	–	–	12	0.1
Callanthiidae	–	–	3	0	–	–	–	–
Callionymidae	**139**	**3.0**	**1035**	**12.6**	**100**	**2.4**	**454**	**4.8**
Caproidae	1	0	7	0.1	1	0	18	0.2
Carangidae (*Pseudocaranx, Trachurus*)	**768**	**16.6**	**2323**	**28.4**	**221**	**5.4**	**841**	**8.8**
Centrolophidae	2	0	10	0.1	4	0.1	1	0
Cepolidae	–	–	3	0	–	–	66	0.7
Chaetodontidae	5	0.1	8	0.1	12	0.3	**116**	**1.2**
Chandidae	8	0.2	8	0.1	6	0.1	27	0.3
Cheilodactylidae	4	0.1	–	–	1	0	–	–
Chironemidae	4	0.1	7	0.1	–	–	–	–
Cirrhitidae	–	–	–	–	1	0	4	0
Clupeidae (*S. sagax*)	**1380**	**29.9**	**1725**	**21.1**	**368**	**8.9**	**255**	**2.7**
Coryphaenidae	20	0.4	–	–	5	0.1	–	–
Creediidae	4	0.1	16	0.2	3	0.1	9	0.1
Cynoglossidae	29	0.6	54	0.7	**181**	**4.4**	**228**	**2.4**
Dactylopteridae	29	0.6	37	0.5	16	0.4	38	0.4
Diodontidae	1	0	4	0	–	–	4	0
Engraulidae	26	0.6	**86**	**1.1**	27	0.7	25	0.3
Enoplosidae	3	0.1	4	0	6	0.1	3	0
Exocoetidae	15	0.3	–	–	30	0.7	–	–
Fistulariidae	–	–	2	0	–	–	1	0
Gempylidae (*Rexea solandri*)	2	0	–	–	2	0	1	0
Gerreidae	–	–	37	0.5	13	0.3	36	0.4
Girellidae	12	0.3	18	0.2	1	0	6	0.1
Gobiesocidae	7	0.2	22	0.3	–	–	7	0.1
Gobiidae	**185**	**4.0**	**341**	**4.2**	**692**	**16.8**	**1127**	**11.9**
Gonorynchidae	3	0.1	5	0.1	5	0.1	54	0.6
Gonostomatidae	–	–	1	0	1	0	–	–
Haemulidae	3	0.1	9	0.1	1	0	10	0.1
Hemiramphidae	10	0.2	–	–	2	0	1	0
Holocentridae	–	–	–	–	6	0.1	**98**	**1.0**
Kyphosidae	14	0.3	37	0.5	9	0.2	24	0.3
Labridae	29	0.6	**182**	**2.2**	**309**	**7.5**	**412**	**4.3**
Leiognathidae	–	–	8	0.1	1	0	–	–
Leptobramidae	–	–	–	–	2	0	3	0
Leptoscopidae	3	0.1	–	–	–	–	–	–
Lethrinidae	30	0.6	32	0.4	**74**	**1.8**	**150**	**1.6**
Lophotidae	–	–	1	0	–	–	–	–
Lutjanidae	**138**	**3.0**	**100**	**1.2**	**142**	**3.4**	**445**	**4.7**
Malacosteinae	–	–	1	0	–	–	1	0
Melamphaidae	–	–	2	0	–	–	–	–
Menidae	–	–	1	0	–	–	–	–
Microcanthidae (*Atypichthys strigatus*)	**477**	**10.3**	64	0.8	3	0.1	11	0.1
Microdesmidae	3	0.1	3	0.0	**66**	**1.6**	55	0.6
Monacanthidae	12	0.3	20	0.2	14	0.3	45	0.5
Monodactylidae	–	–	–	–	1	0	1	0
Mugilidae	–	–	17	0.2	3	0.1	4	0
Mullidae	**157**	**3.4**	45	0.5	**77**	**1.9**	24	0.3
Myctophidae	16	0.3	38	0.5	**355**	**8.6**	**1655**	**17.4**
Nemipteridae	**52**	**1.1**	50	0.6	31	0.8	**116**	**1.2**
Notacanthidae	–	–	1	0	10	0.2	22	0.2
Odacidae	9	0.2	22	0.3	14	0.3	49	0.5

Table 2 (*continued*)

Taxa	November 1998				January 1999			
	Surface		Sub-surface		Surface		Sub-surface	
	n	%	*n*	%	*n*	%	*n*	%
Ophidiidae	1	0	–	–	1	0	13	0.1
Opistognathidae	–	–	–	–	–	–	8	0.1
Ostraciidae	3	0.1	4	0	4	0.1	72	0.8
Paralepididae	–	–	1	0	–	–	6	0.1
Paralichthyidae	6	0.1	15	0.2	5	0.1	11	0.1
Pegasidae	2	0	–	–	2	0	2	0
Pempheridae	1	0	–	–	2	0	–	–
Percophidae	1	0	5	0.1	5	0.1	3	0
Pinguipedidae	27	0.6	31	0.4	23	0.6	55	0.6
Platycephalidae	**72**	**1.6**	**377**	**4.6**	**47**	**1.1**	**226**	**2.4**
Plesiopidae	1	0	12	0.1	2	0	11	0.1
Pleuronectidae	2	0	6	0.1	–	–	8	0.1
Poecilopsettinae	–	–	–	–	1	0	–	–
Polynemidae	3	0.1	8	0.1	2	0	3	0
Pomacanthidae	14	0.3	13	0.2	8	0.2	32	0.3
Pomacentridae	39	0.8	6	0.1	**43**	**1.0**	**98**	**1.0**
Pomatomidae (*Pomatomus saltrix*)	8	0.2	19	0.2	5	0.1	9	0.1
Priacanthidae	1	0	17	0.2	2	0	21	0.2
Psettodidae	–	–	3	0	–	–	–	–
Pseudochromidae	–	–	2	0	1	0	22	0.2
Samaridae	–	–	–	–	3	0.1	–	–
Scaridae	7	0.2	15	0.2	9	0.2	1	0
Scatophagidae	–	–	–	–	6	0.1	–	–
Schindleriidae	9	0.2	19	0.2	42	1.0	50	0.5
Scianidae	–	–	13	0.2	32	0.8	46	0.5
Scomberesocidae	3	0.1	–	–	–	–	–	–
Scombridae (*Scomber australasicus*)	**62**	**1.3**	**82**	**1.0**	**159**	**3.9**	**336**	**3.5**
Scorpaenidae	37	0.8	52	0.6	29	0.7	**271**	**2.8**
Scorpididae	20	0.4	10	0.1	–	–	2	0
Serranidae	30	0.6	25	0.3	38	0.9	53	0.6
Siganidae	–	–	–	–	–	–	1	0
Sillaginidae (*Sillago* spp.)	**221**	**4.8**	**389**	**4.8**	**128**	**3.1**	**266**	**2.8**
Soleidae	–	–	3	0	–	–	5	0.1
Sparidae	**109**	**2.4**	**101**	**1.2**	**178**	**4.3**	**128**	**1.3**
Sphyraenidae	5	0.1	4	0	18	0.4	28	0.3
Synodontidae	22	0.5	27	0.3	**56**	**1.4**	**177**	**1.9**
Terapontidae	**79**	**1.7**	52	0.6	**82**	**2.0**	**104**	**1.1**
Tetraodontidae	1	0	3	0	–	–	2	0
Toxotidae	1	0	1	0	–	–	2	0
Trachichthyidae	–	–	–	–	–	–	3	0
Trichiuridae	1	0	2	0	1	0	2	0
Trichonotidae	–	–	–	–	–	–	2	0
Triglidae	1	0	31	0.4	12	0.3	82	0.9
Tripterygiidae	–	–	1	0	–	–	1	0
Unidentified	22	0.4	88	1.1	70	1.7	132	1.4
Total no. of individuals	4616		8183		4125		9509	
Total no. of families	78		89		82		92	

predominate off the Sydney coast (Keane and Neira, 2008) and are difficult to identify by usual temperature–salinity properties. Larval assemblages based on many distinctive families are a novel method to examine the degree of mixing between EAC and Tasman Sea water masses (Keane and Neira, 2008). We use this approach to examine in finer spatial resolution (10 s of km), the characteristic taxa of EAC and inner-shelf water masses. Our aims are

(1) to compare the ichthyoplankton abundance, diversity and assemblages among water masses of the separation zone, and to identify the characteristic families of those assemblages;
(2) to assess the water mass discrimination of these characteristic taxa from opportunistic sampling of an unusual wind driven upwelling event, immediately preceding the November voyage.

We conclude with inferences on the early life history of two predominant species of the region, bringing together local studies of the contrasting distribution and larval growth rates of *S. sagax* (Uehara et al., 2005) and *Trachurus* spp (Syahailatua et al., 2011).

2. Methods

2.1. Study area

Episodic upwelling of cold, nutrient-rich waters off eastern Australia is usually attributed to the flow of the East Australian Current (EAC) in conjunction with poleward wind stress (Jeffrey et al., 1990; Gibbs et al., 1998) or with topographic features (Oke and Middleton, 2000; 2001; Roughan and Middleton, 2002, 2004). Upwelling is typically observed between 30 and 33°S where the EAC separates from the coast, forming the Tasman Front (Cresswell, 1983, 1994; Roughan and Middleton, 2002, 2004). Several upwelling sites have been identified along the coast from 28° to 33°S in spring and summer (Rochford, 1984),

associated with headlands and the narrowing of the continental shelf, occurring episodically 2–3 times per summer when the EAC flows stronger adjacent to the coast and upwelling favourable winds are more frequent (Griffin and Middleton, 1991).

Two voyages conducted aboard the Research Vessel Franklin, in the austral summer November 1998 and January–February 1999, focused on the upwelling zone off the coast of southeastern Australia at the edge of northwestern Tasman Sea (Fig. 1, Table 1), with sampling along the coast between 30.50°S, 153.25°E and 32.05°S, 152.60°E. Sampling was conducted along four shore normal transects: Urunga, Smoky Cape, Point Plomer and Diamond Head (referred hereafter to Regions 1–4, north to south, Fig. 1). In January, additional sampling was also conducted further south off Crowdy Head and South Crowdy Head (close to Region 4) and Cape Hawke (Region 5, Fig. 1). The continental shelf varies in width in this region (Region 1—30 km, Region 2—17 km, Region 3—22 km and Region 4—32 km from the coast to the 200 m isobath), contributing to acceleration of the current where the shelf narrows and a pooling of uplifted nutrients in the wider downstream regions (Roughan and Middleton, 2002).

2.2. Ichthyoplankton sampling

At each region plankton sampling was conducted at two stations (inshore at the 50 m isobath and offshore at the 100 m bathymetric contours). A neuston net (0.75×0.75 m^2 mouth) with 500 μm mesh and an EZ-net (a multiple depth, opening/closing net with 1 m^2 mouth) with 500 μm mesh were deployed to collect ichthyoplankton. Here we only analysed ichthyoplankton from the upper depth stratum of the EZ-net, i.e. 10–20 m depth stratum at the 50 m station or 10–30 m at the 100 m station. The neuston and EZ nets are hereafter referred to as "surface" and "upper mixed layer", respectively. These nets were deployed from the vessel cruising at 2–3 knots for up to 10 min, where a General Oceanic flow meter indicated the volume of water filtered (200–400 m^3). All net tows were made at night to reduce net avoidance.

At each station, 4 surface and 2 sub-surface tows were conducted (Table 1). Where possible repeated sampling was conducted depending on cruise schedule and weather, although Smith and Suthers (1999) found that within night variation was considerably less than between night variation. A regularly calibrated thermosalinograph recorded temperature, salinity and fluorescence continuously from an intake at 4 m depth. The thermosalinograph data was used to compare with the simultaneous neuston data.

To produce an along-shore vertical profile of temperature, a Neil–Brown conductivity–temperature–depth cast (CTD, with 12 Niskin bottle rosette) was conducted prior to each plankton tow (Roughan and Middleton, 2002). At times due to logistical constraints, a CTD cast before the plankton tow was not possible and we used the nearest CTD cast at that station within at least 12 h of the plankton sample. Fluorescence from a WetLabs fluorometer was converted to chlorophyll *a* concentration (Chl *a*, μg L^{-1}) after Dela-Cruz et al. (2003).

All ichthyoplankton samples were preserved in 5% formaldehyde/seawater, buffered with sodium carbonate to preserve the otoliths. Some bleaching of melanophores occurred with this buffer if samples were not transferred to 95% alcohol within 2 months. In the laboratory, samples were gently rinsed before sorting to separate fish larvae from the zooplankton using a binocular microscope. Fish larvae were then preserved in 95% ethyl alcohol and zooplankton was preserved in 5% formaldehyde. Fish larvae were identified to as low a taxon as possible, following Leis and Carson-Ewart (2000); Neira et al. (1998) and Moser et al. (1993, 1994). For analysis, the abundance of taxa was identified to the family level, except the order Anguilliformes.

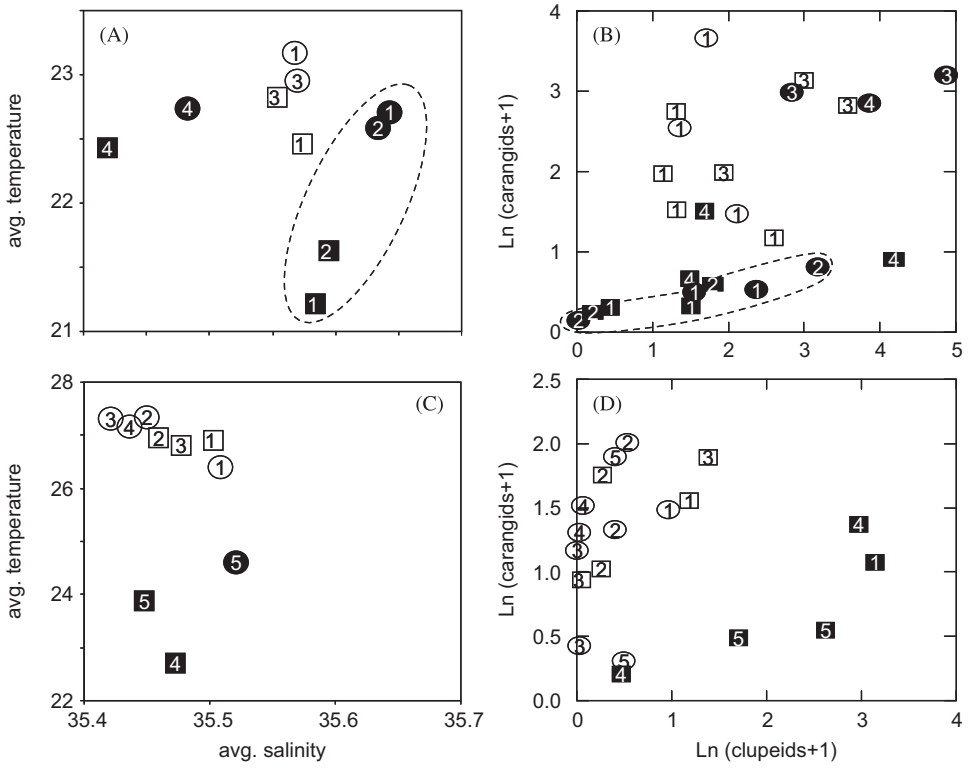

Fig. 2. Surface *T–S* plots from underway thermosalinograph with the intake at 4 m depth, during the plankton tows at each of the regions and stations in (A) November 1998 and (C) January 1999. Scatterplot of the concentrations of clupeids versus carangids (transformed ln(x+1)) for (B) November surface; (D) January surface. Numbers inside symbols refer to the region numbers; square symbols (50 m isobath); circles (100 m isobath); filled symbols dominated by the inner-shelf assemblages N2 or J4 (Figs. 3 and 4); and open symbols other assemblages. Dashed line in (A) and (B) encloses initial samples from a wind-driven coastal upwelling event (Regions 1' and 2'), which subsequently reverted to the usual non-upwelled assemblage (Regions 1 and 2).

2.3. Analysis

Total larval counts were standardized to volume (abundance, numbers per 100 m^3) and were separately analysed for each voyage. Assemblages were determined from cluster dendrograms of the Bray–Curtis similarity matrix using standardized data of the station average and ordinated by non-metric multi-dimensional scaling (MDS). Only those taxa $>1\%$ of the total abundance were included (Table 2). Standardised (or compositional data) are calculated as the percentage composition of each family. For each month we compared the total abundance of larvae and the Shannon diversity index among the orthogonal and fixed effects of region ($n=3$), station ($n=2$) and depth ($n=2$) in a 3 factor ANOVA ($n=2$ replicate tows, using 2 averages of the 4 surface tows to produce balanced data). Three regions were sampled in November (Regions 1, 3 and 4, Table 1), whereas in January our sampling was not balanced due to logistic constraints. In January only 3 regions were analysed by ANOVA (Regions 2, 3 and 4), but for both voyages the analysis bracketed the upwelling region (Fig. 1). Homogeneity of variance was tested by Cochrans test, and if necessary was transformed successfully (except where noted). Cluster and MDS plots were used to detect the effects of region, station and depth differences in the ichthyoplankton assemblage structure (Primer,V5.0). SIMPER (similarity percentage analysis) was used to examine the contribution of taxa to the various clusters.

The temperature–salinity (T–S) plot was calculated for the abundant families revealed by the SIMPER analysis. Each family's weighted mean T or S ($\bar{x}$) was determined from the average T or S during each sub-surface tow (from tow i to n, x_i), weighted by the family's larval density in each tow (w_i, nos. 100 m^{-3}) by the following formula:

$$\bar{x} = \frac{\sum_{i=1}^{n} w_i x_i}{\sum_{i=1}^{n} w_i}$$

The weighted variance (S^2) was determined for each family from the summed differences of the observed T or $S(x_i)$ at each station and $\bar{x}$:

$$S^2 = \sum((x_i - \bar{x})^2 w_i))/\sum w_i$$

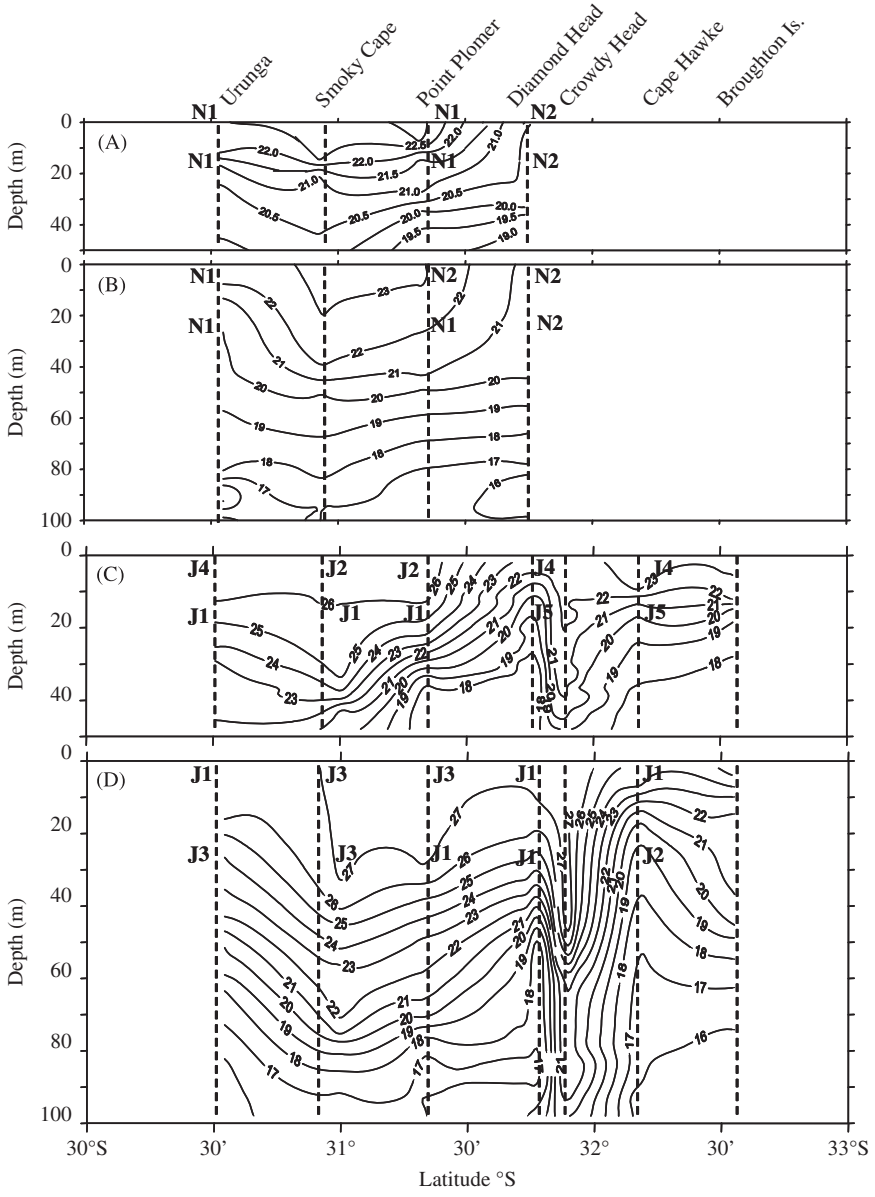

Fig. 3. Temperature profiles along the inshore (A, C; 50 m contour) and offshore (B, D; 100 m contour) stations in (A, B) November 1998 and (C, D) January 1999. Dashed lines show the location of the CTD cast (after Uehara et al., 2005). The ichthyoplankton assemblages subsequently identified (N1, N2, J1–J6, Fig. 4) are included.

3. Results

3.1. Environmental conditions

The East Australian Current (EAC) dominated the study area, flowing swiftly poleward adjacent to the coast with velocities greater than 1 ms^{-1} (Roughan and Middleton, 2004). The current separated from the coast at approximately 31.5°S, although the exact separation point fluctuated as the current moved on and off the continental shelf (Fig. 1). Winds were light and variable with a mean wind speed of 3 $m\ s^{-1}$ (Roughan and Middleton, 2004), except when a significant upwelling favourable wind event occurred from 12 to 14 November where wind stress reached 0.4 Pa poleward (Roughan and Middleton, 2002). This event was 2 days prior to our first sampling period and increased sub-surface nitrate concentrations to 14 $\mu M\ L^{-1}$ (which was 50% greater than average concentrations).

In November the sea surface temperature ranged between 21 and 23 °C (Figs. 1A and 2A), compared to January when it ranged between 22 and 28 °C (Fig. 1B and 2C). The sea surface temperature (SST) images showed the EAC flowing southward past Regions 1 and 2 and separating from the coast near Region 3. Intrusion of cooler, less saline Tasman Sea waters was detected near shore at Region 4 in November and 2–3 °C cooler water in January off Regions 4 and 5 (22–24 °C). Upwelling was clearly evident off Region 4 (and to the south) at the 100 m and especially 50 m stations during both sampling periods (Fig. 3). Isotherms shoaled with depth south of Region 2, but cooler surface waters were only manifested at Region 4. Our main sampling of this region was on 22–23 November (Table 1) with additional sampling on 16–17 November when strong upwelling favourable winds temporarily caused uplift to be observed off Regions 1 and 2. The SST image (Fig. 1A) also reveals a small patch of cooler water (22.5 °C) off Region 1 on 21 November, remnant of the wind driven upwelling event (4 days prior).

3.2. Abundance and diversity

A total of 25,438 individual larvae were identified comprising 112 taxa (111 families and 1 order, Table 2) across both sampling periods. The Anguilliformes consisted of at least three families including the Anguillidae, Congridae and Ophichthidae. Most larvae were at the flexion or post-flexion stages, and larval length ranged from 1.6 mm (Carangidae) to more than 20 mm (Anguilliformes). During November we observed an order of magnitude greater larval abundance and slightly less diversity (Table 2). We also found fewer larvae in the surface nets than sub-surface nets. In both nets during November and January voyages we found 101 and 103 taxa, respectively, and the most abundant 10 families accounted for 81% and 58% of the total abundance of larvae, respectively. The 10 dominant taxa in November were the carangids (trevally), clupeids (herrings), callionymids (dragonets), sillaginids (whiting), microcanthids (stripeys), gobies, platycephalids (flatheads), bothids, lutjanids (snapper) and sparids (bream). In January the 10 dominant taxa were gobies, carangids, clupeids, callionymids, labrids (wrasses), bothids, lutjanids, cynoglossids, sillaginids and scombrids (Table 2).

During the November sampling there was no significant difference in the total abundance of larvae among regions, stations or depths (Table 3a, ANOVA, $p > 0.2$), but there was a significant Region × Station interaction with diversity (Table 3b, ANOVA, $p = 0.05$), where Region 4 offshore had a slight, but significantly lower diversity than the other regions and stations (SNK test). The total abundance in January was significantly greater at Region 2 compared to the other 2 southern regions (Table 3c, ANOVA, $p = 0.001$). The diversity in January could not be satisfactorily transformed (Table 3d), but it tended to decline from north to south.

3.3. Comparisons of the assemblage

The MDS ordinations of samples revealed two separate assemblages from the November sampling period (N, November), defined at the 50% similarity level (N1, N2; Fig. 4A and B). N2 represents all the Region 4 samples (i.e. surface and upper mixed layer, inshore and offshore off Diamond Head) and the surface-offshore (Region 3). Typically, the Region 4 assemblages were found in water < 21 °C (Fig. 3A and B) and we identify this as an inner-shelf community. The EAC assemblage (N1) was distinguished by a greater representation of carangids, clupeids, callionymids, sillaginids and microcanthids (Table 4, SIMPER analysis) and was found in water > 20.5 °C (Fig. 3A and B). The inner-shelf community (N2) was distinguished by clupeids, gobiids, sillaginids and callionymids

Table 3
Summary table of analysis of variance, comparing (a, c) the total abundance of larvae and (b, d) the Shannon diversity index among regions, stations and sampling depths (Fig. 5), of the cruises in (a, b) November 1998 and (c, d) January 1999. In January, only Regions 2–4 were compared with balanced data. In (d), no transformation could stabilise the variance so significance levels (**) are interpreted with caution.

Source	SS	DF	MS	F	P	SS	MS	F	P
(a) Nov.-98, total abundance						(b) Nov.-98, ln(diversity index)			
Region (R)	5546	2	2772.9	0.41	NS	0.30	0.15	2.50	NS
Station (S)	1449	1	1448.5	0.22	NS	0.01	0.01	0.17	NS
Depth (D)	2099	1	2099.0	0.31	NS	0.04	0.04	0.62	NS
R*S	11,631	2	5815.5	0.87	NS	0.48	0.24	3.99	*
R*D	10,503	2	5251.3	0.78	NS	0.19	0.10	1.59	NS
D*S	10,891	1	10,890.5	1.62	NS	0.21	0.21	3.39	NS
R*S*D	8601	2	4300.3	0.64	NS	0.09	0.04	0.73	NS
RES	80,600	12	6716.6			0.73	0.06		
TOT	131,318	23				2.05			
(c) Jan.-99, total abundance						(d) Jan.-99, diversity index			
Region (R)	16,020	2	8009.9	11.95	**	0.02	0.01	0.43	NS
Station (S)	1039	1	1039.4	1.55	NS	0.02	0.02	1.09	NS
Depth (D)	536	1	535.5	0.80	NS	0.23	0.23	10.25	(**)
R*S	3347	2	1673.6	2.50	NS	0.33	0.16	7.16	(**)
R*D	310	2	155.0	0.23	NS	0.11	0.05	2.36	NS
D*S	50	1	50.3	0.08	NS	0.03	0.03	1.52	NS
R*S*D	1231	2	615.6	0.92	NS	0.02	0.01	0.49	NS
RES	8041	12	670.1			0.27	0.02		
TOT	30,574	23				1.04			

NS = not significant; * = $0.01 < p < 0.05$; ** $p < 0.01$.

(Table 4). The two assemblages shared many taxa (particularly clupeids and carangids), but differed in the proportions of the characteristic taxa (Table 5).

During the January sampling there were five assemblages at the 50% similarity level, with two major assemblages evident (J, January): J1 and J3 (EAC assemblage) and J4 and J5 (from regions of upwelling, Fig. 4C and D). J1 and J3 were distinguished by a greater representation of carangids, labrids, myctophids and scombrids (Table 4, SIMPER analysis) and generally found >25 °C, upstream of Region 4 (Fig. 3C and D). J4 and J5 assemblages were distinguished by clupeids, callionymids, platycephalids, terapontids and sillaginids, and found inshore at Regions 4 and 5, in water temperatures <24 °C (Fig. 3C). Assemblage J5 was sub-surface and J4 was surface (although J4 was also identified at the surface, Region 1 inshore at >26 °C, Fig. 3C). J2 assemblage was characterized by a general paucity of families (Table 5). The EAC (N1, J1, J2, J3) and inner-shelf (N2, J4, J5) assemblages shared clupeids, callionymids and carangids but in different proportions (Table 5).

Over both seasons, the SIMPER analysis revealed 10 families that were important in distinguishing assemblages (Table 4). Six

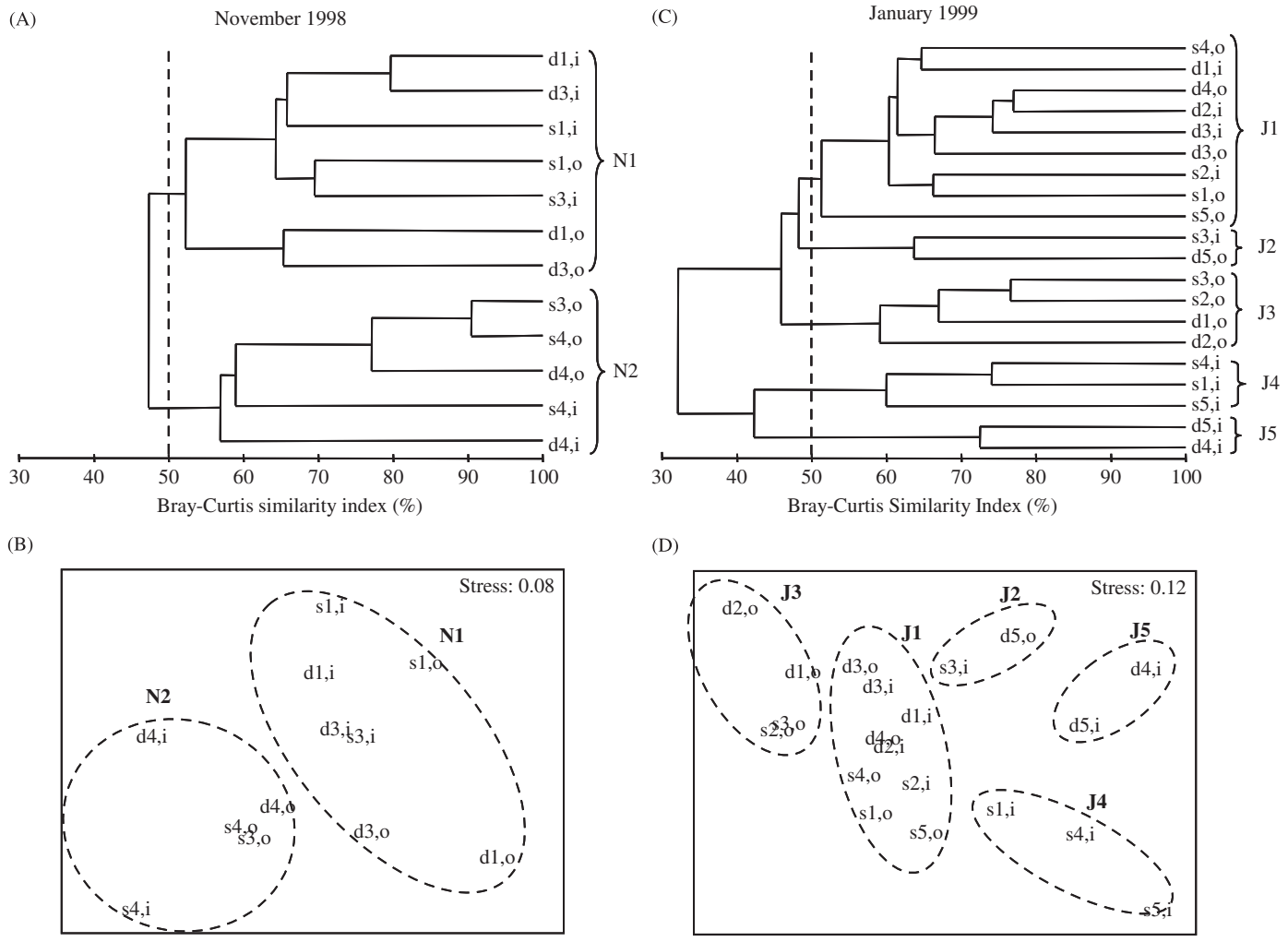

Fig. 4. Cluster dendrogram and two-dimensional MDS ordinations of Bray–Curtis similarities, based on standardised average family abundances of ichthyoplankton at each station/depth, which contributed $\geq 1\%$ of the total abundances in (A, B) November 1998 and (C, D) January 1999. The assemblages (N1, N2 and J1–J5) are defined at the 50% Bray–Curtis similarity level with a dashed line. The data labels refer to sampling depth (s, surface neuston net; d, deeper or upper mixed layer by the EZ net); Regions (1–5 as defined in Table 1), and distance offshore (i, inshore, at the 50 m isobath; o, offshore at the 100 m isobath).

Table 4
The ichthyoplankton assemblages from the MDS ordinations (Fig. 4) and the average similarity (%) of each assemblage from the similarity percentages (SIMPER) procedure (Clarke and Warwick, 1994). The first five most influential families/taxa are listed.

Month/year	Assemblage	Average similarity (%)	Dominant families
Nov.-98	N1	60	Carangidae, Clupeidae, Callionymidae, Sillaginidae, Microcanthidae
	N2	64	Clupeidae, Carangidae, Gobiidae, Sillaginidae, Callionymidae
Jan.-99	J1	61	Gobiidae, Carangidae, Labridae, Lutjanidae, Bothidae
	J2	64	Carangidae, Clupeidae, Gobiidae, Callionymidae, Bothidae
	J3	65	Myctophidae, Gobiidae, Labridae, Carangidae, Clupeidae, Scombridae
	J4	65	Clupeidae, Sparidae, Sillaginidae, Carangidae, Terapontidae
	J5	73	Callionymidae, Platycephalidae, Clupeidae, Sillaginidae, Carangidae

Table 5
The average abundance (numbers 100 m^{-3}) in the EAC associated assemblages N1, J1, J2, J3) and the inner-shelf (IS) or upwelling associated assemblages (N2, and J4, J5, as identified in Fig. 4). The table is derived from the dominant families identified in the SIMPER analysis (Table 4), with at least one abundance >1.2 per standardized tow. The assemblage is classified as EAC or inner-shelf on the relative abundance between the two groups. Classification of terapontids, bothids, gobiids and sparids is unclear (see text).

Family	EAC/IS	N1	J1	J2	J3	N2	J4	J5
Carangidae	EAC	27.7	5.0	4.8	4.7	12.2	1.6	2.5
Labridae	EAC	0.0	3.6	0.7	6.2	0.0	0.0	0.0
Lutjanidae	EAC	0.0	3.9	0.5	2.4	0.0	0.0	0.0
Microcanthidae	EAC	6.3	0.0	0.0	0.0	1.2	0.0	0.0
Myctophidae	EAC	0.0	1.5	0.0	31.8	0.0	0.0	0.0
Scombridae	EAC	1.2	2.6	0.0	3.2	0.0	0.0	0.0
Callionymidae	IS	4.6	0.0	0.5	0.0	12.7	0.0	9.5
Clupeidae	IS	8.4	0.0	1.9	0.0	41.7	13.3	3.8
Platycephalidae	IS	2.2	0.0	0.0	0.0	4.3	0.0	4.2
Sillaginidae	IS	3.7	1.5	0.0	0.0	4.8	1.6	3.8
Terapontidae	–	0.0	0.0	0.0	0.0	0.0	2.0	0.0
Bothidae	–	2.1	3.6	0.4	0.0	3.1	2.2	1.6
Gobiidae	–	2.5	7.6	1.5	11.3	5.6	1.2	1.3
Sparidae	–	0.0	2.5	0.0	1.1	0.0	2.7	0.0

families were indicative of EAC waters (Carangidae, Labridae, Lutjanidae, Microcanthidae, Myctophidae and Scombridae), four families indicated upwelled and inner-shelf waters (Callionymidae, Clupeidae, Platycephalidae and Sillaginidae) and three families represented neither (Bothidae, Gobiidae or Sparidae).

The weighted temperature–salinity (TS) plot for each family reveals the two main larval assemblages for both voyages (Fig. 5A and B). In January especially, it may be seen that Clupeidae (mostly *S. sagax*), Callionymidae, Platycephalidae and Sillaginidae occupy slightly cooler and fresher water along the coast ("inner-shelf water", Cresswell, 1994), while the other families are in the relatively warmer and saltier waters of the EAC. In November the SE ellipses overlap but the same 4 families are in the same inner-shelf water.

The most abundant family from each assemblage was the Clupeidae (inner-shelf) and Carangidae (EAC). A scatter plot of these two taxa for each surface tow revealed them to be significantly correlated in November ($r=0.47$, $p<0.02$, Fig. 2B) and not in January ($r=-0.07$, Fig. 2D). When the data points were identified as being the inner-shelf assemblage (i.e. assemblage N2 or J4, Figs. 3 and 4), the separation is particularly evident in January (Fig. 2D), and similar to the *T*/*S* plot from the thermosalinograph (Fig. 2C). In November the inner-shelf sampled stations (Region 4, and Region 3 offshore) tended to have more clupeids, and this was especially evident during upwelling in early November (Fig. 2B). Upwelling favourable (poleward) winds (>7.5 ms^{-1}) were present for 2–3 days prior to sampling on 16 November (Roughan and Middleton, 2002). The 20 °C isotherm was uplifted by >50 m (Fig. 6), and cooler surface waters (<22 °C) were apparent inshore up to 4 days later (Fig. 1A). The surface net samples from Regions 1 (inshore) and 2, revealed 3 larval assemblages that grouped with N2 at the 50% similarity level, which were subsequently found off Region 4 (Fig. 7A and B). The scatter plot of carangids on clupeids during this event (Fig. 2B) showed uniformly few carangids and often populated by clupeids.

4. Discussion

Despite the distinct change in nutrient levels that occurred as the EAC moved offshore, there was no consistent effect on the total abundance or diversity of ichthyoplankton in either sampling period. A comparison of larval abundance in Florida Current upwellings also found no significant difference in abundance or diversity (Pitts, 1999). We did find two major larval assemblages at the 50% Bray–Curtis similarity level across both sampling periods, such that assemblages could be identified with water masses as "inner-shelf", "EAC" or a mixture. During both sampling periods the inner-shelf assemblage was distinguished by a greater abundance of clupeids, callionymids, platycephalids and sillaginids, while the EAC assemblage was distinguished by carangids, labrids, lutjanids, microcanthids, myctophids and scombrids. These two assemblages were similar between November and January, with a similar relative location in the weighted temperature–salinity (*T*–*S*) diagram. These two assemblages were characterized at relatively fine spatial (10 s km) and temporal (within 6 day) scales.

4.1. Oceanographic features and ichthyoplankton assemblage structure

During the summer of 1998/1999, the EAC flowed strongly poleward along the coast of southeastern Australia, separating from the coast at the "typical" separation point near Region 3 (31.5°S, Roughan and Middleton, 2002, 2004). Associated with the separation of the EAC was an upwelled, cooler water mass, inshore of the EAC front. This was particularly evident in the SST imagery, revealing a near-coastal water mass off Region 4 and to the south that was up to 2 °C cooler than EAC waters, described as "inner-shelf water" by Cresswell (1994). Velocity profiles were in excess of 2 m s^{-1} (Roughan and Middleton, 2002) southward in the core of the EAC, whereas inshore of the EAC front, currents were weakly northward, consistent with that observed by Cresswell (1983), inshore of the EAC jet. Shore-normal temperature transects at each region revealed upward sloping isotherms, indicating that the upwelling was induced off Smoky Cape (Roughan and Middleton, 2002) and the nutrient concentrations were 3–10 fold greater off Diamond Head (Region 4) than off Urunga (Region 1) and Smoky Cape (Region 2, particularly during the January sampling).

The surface hydrographic data (Fig. 2) provided little assistance in interpreting the water masses and their history. The range in weighted surfaces *T* and *S* is surprisingly small, particularly during November, and resolution of these patterns could only be achieved with the vessel's carefully calibrated thermosalinograph. In November, the narrow range in temperature (2.5 °C) and salinity (0.3) did not distinguish the wind induced upwelling of Regions 1 and 2 offshore, compared to the assemblage analyses. Most important was the finding of the inner-shelf assemblage at Regions 1 and 2 on 16 November, which was replaced once the wind-driven upwelling had relaxed and was returned to the EAC community within 6 days.

The weighted *T*/*S* plot provides a useful means to compare other bio-physical relationships in relative terms. For example the absolute *T*/*S* differed between November and January, but the relative location remained the same. Not surprisingly, the myctophids despite being a diverse family are consistently located in

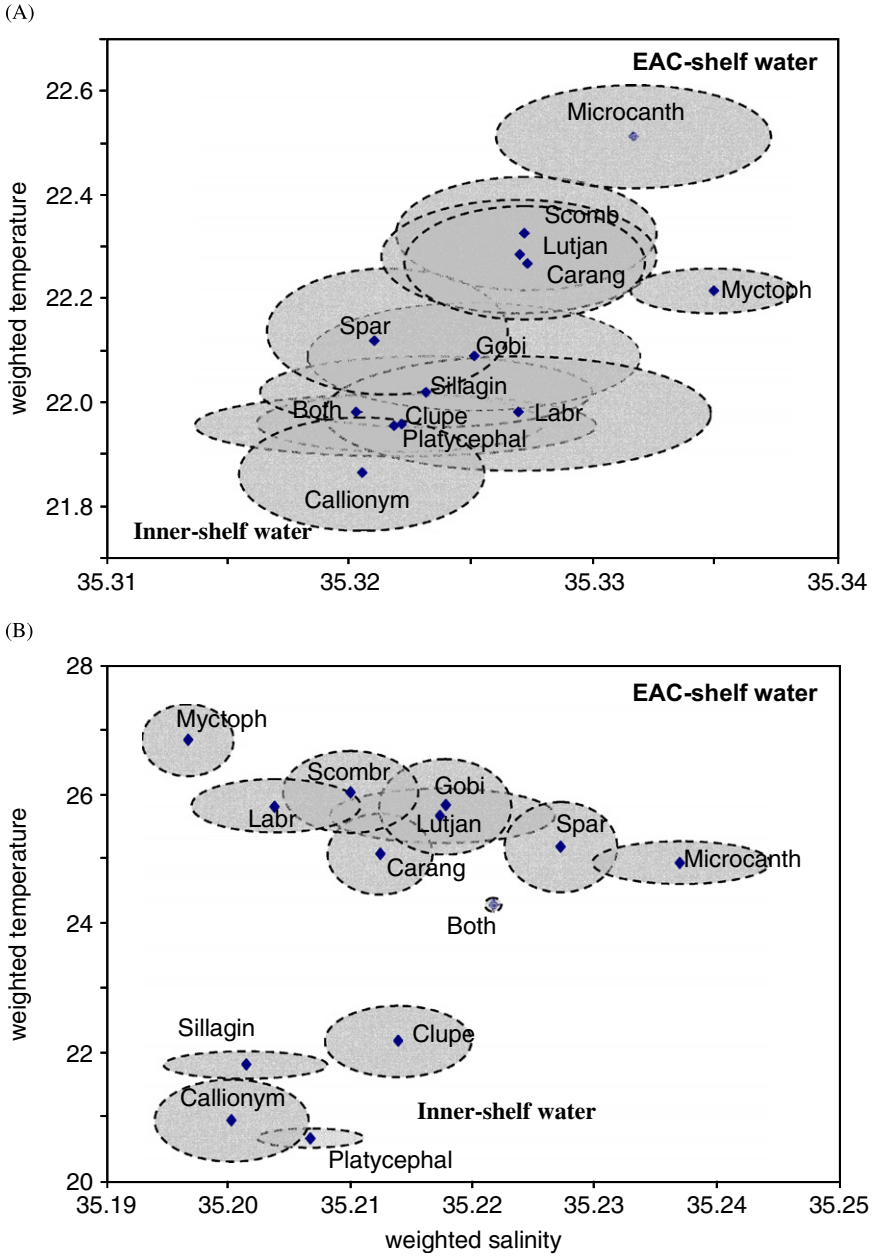

Fig. 5. (A) November and (B) January average temperature–salinity plot from the underway thermosalinograph, weighted by the tow-specific abundance of key families from the upper mixed layer (EZ) net. Abbreviated family names listed in Tables 4 and 5. Ellipses around each weighted average are SE.

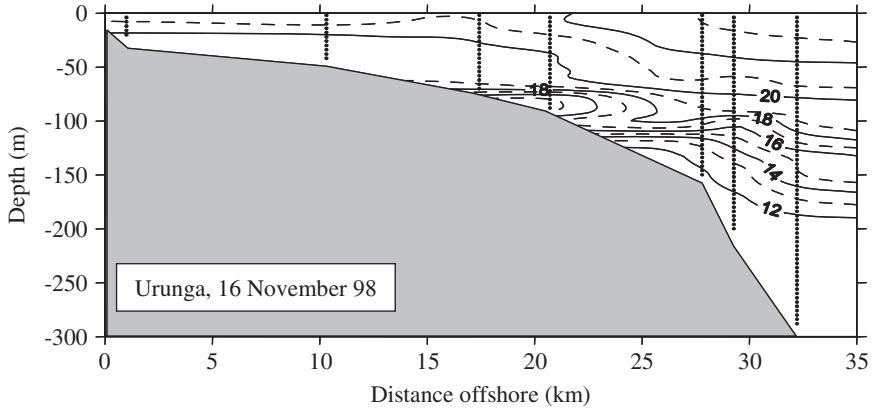

Fig. 6. Vertical profile of water temperature off Region 1' on 16 November 1998, showing the wind-driven upwelling. Dotted lines show the location of the CTD casts.

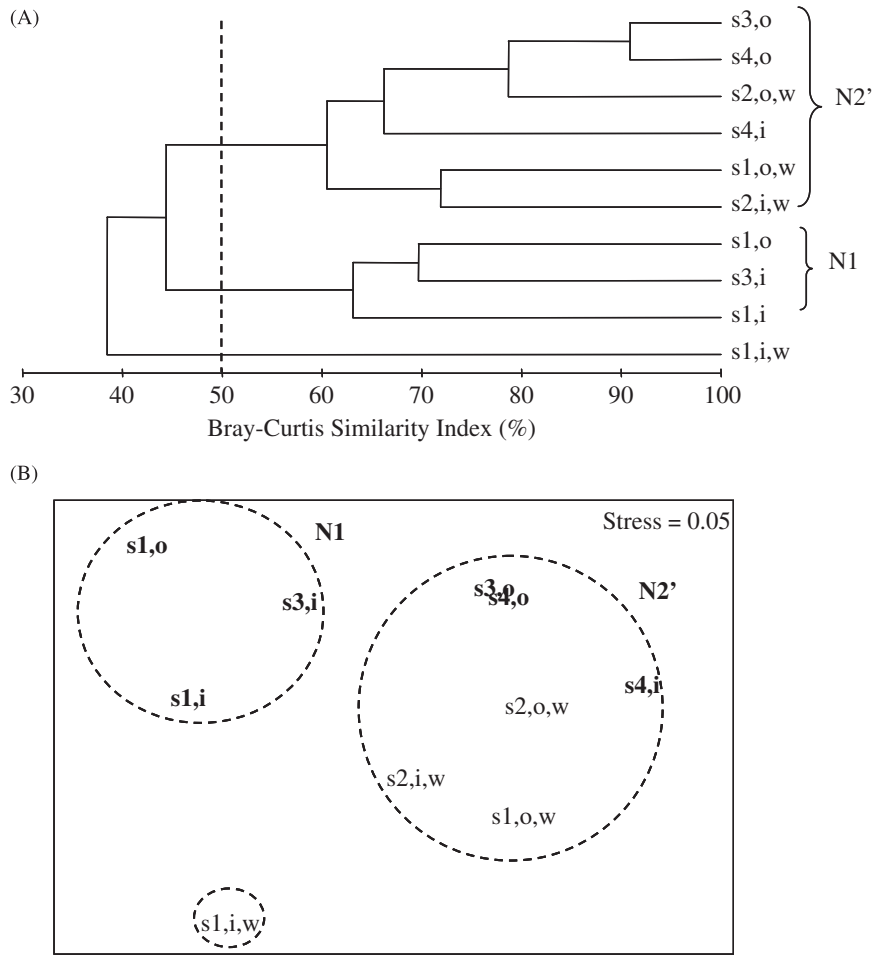

Fig. 7. (A) Cluster dendrogram and (B) two-dimensional MDS ordinations of Bray–Curtis similarities of all the surface, neuston net samples during November and including the initial neuston samples taken during wind-driven upwelling 16–17 November off Regions 1' and 2'; Urunga and Smoky Cape (labels in normal font, with a "w"). Labels in bold are the surface assemblages identified from Fig. 4 (s, surface neuston net; Region #, i, inshore and o, offshore). Assemblages are defined at the 50% similarity level with a dashed line. Note that the EAC assemblage N1 (Fig. 4) is clearly separate from the upwelling assemblage N2', which groups wind-driven upwelling assemblages at Regions 1' and 2', and the topographically upwelled (inner-shelf) assemblage off Regions 3 and 4 (in bold).

oceanic water masses, along with other taxa such as Gonostomatidae (e.g. Smith et al., 1999; Quattrini et al., 2005; Suthers et al., 2006). Under very strong upwelling the lantern fish (myctophid) abundance could occur on the shelf when deep oceanic water may entirely displace coastal water communities (Smith et al., 1999).

The cause of these water mass specific distributions is related to their adult habitat and spawning behaviour (e.g. Doyle et al., 1993; Ward et al., 2003), and indeed, abundances are heavily weighted by the preflexion (early larval) stages. Species and size-specific weighted *T–S* plots could indicate ontogentic habitat shifts (such as for pre- and post-flexion larval trevally, Syahailatua, 2004, see next section). The water mass specific distributions are possibly maintained by differential mortality of some taxa within the assemblage, witj exposure to a new predator or prey field after a mixing event. It is possible that these water mass relationships are conservative or more imprecise by collecting the samples at night than during the day. At night ichthyoplankton is comparatively less stratified, particularly above the thermocline (Leis, 1991).

4.2. *The dominant taxa of Trachurus and Sardinops and their early life histories*

The carangids, dominated by *Trachurus novaezelandiae* and *Pseudocaranx dentex*, were also more abundant in the EAC waters, as were blue mackerel *Scomber australasicus*. *S. australasicus* spawn on the outer shelf waters in this region (Neira and Keane, 2008), so their presence in the EAC-shelf water mass, along with oceanic taxa like larval myctophids, is not surprising. Both carangids have a protracted spawning in spring and early summer off the east Australian coast (Neira et al., 1998). The abundance of both carangid species was significantly correlated in both months and were two to three fold more abundant in November than in January, and in subsurface than surface nets (Syahailatua et al., 2011). As adults, both genera occur in estuaries and coastal regions and both have similar maximum sizes and growth coefficients. The shelf abundance of these larvae in early summer, on the shelf, is consistent with that observed off Sydney (Smith and Suthers, 1999; Smith, 2003), and from the Celtic sea and west of Ireland (Fives et al., 2001). Furthermore, Syahailatua (2004) observed more small larvae (preflexion, <5 mm body length and <10 days old) in EAC dominated water, particularly during November, and proportionally more, larger and older larvae in the inner-shelf (mostly post-flexion, ≥ 5 mm and ≥ 10 days old, Syahailatua, 2004). Larval growth of both species was faster in the inner-shelf water (Syahailatua et al., 2011). Therefore their preflexion abundance indicates both species spawn in warmer shelf waters, but mixing into the inner-shelf may be necessary for faster growth in the post-flexion stage (e.g. *Trachurus trachurus*, Santos et al., 2001).

Both *S. sagax* and callionymids may serve as an abundant and general marker of inner-shelf waters, although the early life history and distribution of the *Callionymidae* is otherwise unknown. The abundance of clupeids (dominated by larval sardines *S. sagax*, Table 2) on the inner-shelf is well documented (Cole and McGlade, 1998), and their co-occurrence with callionymids in coastal and shelf waters (Jenkins, 1986; Leis, 1991; Olivar and Sabates, 1997; Gray and Miskiewicz, 2000; Quattrini et al., 2005) is not surprising. Spawning by *S. sagax* in late winter not only occurs in the coastal waters of southern Queensland and northern NSW (Ward et al., 2003), but our study also indicates spawning may actually occur in the inner-shelf water. Nevertheless, larval growth is slower in the inner-shelf waters, and faster offshore (Uehara et al., 2005 and references therein). The early life history of Australian sardine therefore appears opposite to that of the two local carangids. The relationship between sardines and carangids is complex and warrants further investigation, but there may be parallels with sardine versus engraulid early life history as observed in the California Current (Rykaczewski and Checkley, 2008). The roles of coastal Ekman upwelling versus offshore wind stress curl (Rykaczewski and Checkley, 2008) in the pelagic ecology off eastern Australia, and in comparison with offshore eddies (Logerwell and Smith, 2001), remains unresolved.

In conclusion, the EAC separation zone ($\sim$30–32°S) represents a transition between temperate and tropical systems (Baird et al., 2011), which causes the remarkable diversity (Smith and Suthers, 1999). The eastern seaboard diversity is particularly enhanced during the summer by transport of larvae from the Great Barrier Reef. The importance of transition zones has also been recognized elsewhere (northern Benguela region, Olivar, 1990; Cape Hatteras, Grothues and Cowen, 1999; Abrolhos Bank region off eastern Brazil, Nonaka et al., 2000). Larval fish assemblages on the continental shelf and slope off the northern Benguela region varied dramatically due to the intrusion of Angolan waters to this region (Olivar, 1990). From Cape Hatteras, larval diversity corresponded to the mixed water mass between the Middle Atlantic Bight and South Atlantic Bight, indicating larvae act as a water mass property during spring (Grothues and Cowen, 1999). In the Abrolhos Bank region off eastern Brazil, a mixture of larval assemblages of coral-reef fish and mesopelagic fish was found in the shelf break area, due to the tropical Brazil Current meeting the south Atlantic Central water mass (Nonaka et al., 2000). The origin and mixture of these different water masses would be difficult to determine from hydrographic traits and even current vectors alone. On the other hand, this study has shown that a known affiliation between larval fish taxa and a water mass can provide a measure of origin and water mass mixing, even at the relatively fine 10 km spatial scale of this study.

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