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Larval fish assemblages along the south-eastern Australian shelf: linking mesoscale non-depth-discriminate structure and water masses

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ABSTRACT

We present findings of the first mesoscale study linking larval fish assemblages and water masses along shelf waters off south-eastern Australia (southern Queensland-New South Wales), based on vertical, non-depth discriminate data from surveys in October 2002 and 2003 (spring) and July 2004 (winter). Clustering and ordination were employed to discriminate between larval assemblages and, for the first time, to define water masses from water column temperature frequencies. Surveys yielded 18 128 larval fishes comprising 143 taxa from 96 identifiable families, with small pelagics accounting for 53% of the total. Three major recurrent larval assemblages were identified during the study, each of which matched one of three water masses, namely East Australian Current to the north (EAC; 20.5–23.4°C), Tasman Sea to the south (TAS; 14.8–17.5°C), and mixed EAC–TAS water in between (MIX; 18.3–19.9°C). All three assemblages were present in spring, whereas only EAC and MIX occurred in the more northerly constrained winter survey. Furthermore, boundaries between the EAC, MIX and TAS assemblages were found to be dynamic, with locations shifting temporally and spatially depending on EAC extent. Assemblage composition differed significantly between water masses across surveys, with EAC–TAS being most dissimilar. Such contrast was due to the presence of tropical/temperate taxa in EAC, primarily temperate-associated taxa in TAS, and a combination of EAC–TAS taxa within MIX consistent with the convergence of both waters. Results highlight the strength of employing larval assemblages as indicators of water masses, particularly in view of the potential effect of climate change on spawning habitats of shelf fishes.

Key words: East Australian Current, faunal transition, larval fish assemblages, multivariate analyses, pelagic shelf ecosystem, Tasman Sea, *Trachurus*

INTRODUCTION

Linking ichthyoplankton assemblages with oceanographic processes is becoming increasingly important to ecosystem-based fishery management (EBFM) and fishery-independent stock assessments (Legendre and Demers, 1984; Moser and Smith, 1993; Bakun, 2006). Processes such as small- to meso-scale currents, upwelling events, fronts and eddies influence the distribution, abundance and survival of fish eggs and larvae, and consequently define structure and diversity of ichthyoplankton assemblages (Reiss and McConaugha, 1999; Smith and Suthers, 1999; Smith *et al.*, 1999; Hare *et al.*, 2001; Bakun, 2006; Franco *et al.*, 2006). A clear understanding of how such processes define assemblages is particularly relevant to the characterisation of spawning habitats of small pelagic fishes, a key step before the application of egg-based methods to estimate spawning biomass (e.g. van der Lingen *et al.*, 2001, 2005; Castro *et al.*, 2005; Stratoudakis *et al.*, 2006; Neira and Keane, 2008). Ultimately, a thorough integration of ichthyoplankton dynamics and oceanography should underpin any future research on the potential effects of climate change on the distribution and abundance of fish stocks.

Discrete larval assemblages have been strongly linked to water masses in many of the world's major marine shelf ecosystems, including north-eastern North America (Hare *et al.*, 2001), South Africa (Olivar and Shelton, 1993) and southern Western Australia (Muhling *et al.*, 2008), with oceanic fronts often relating to distinct boundaries between such assemblages. By comparison, information on the seasonal mesoscale structure of larval fish assemblages along shelf waters of south-eastern Australia, including

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links to water masses, is scarce and patchy. In fact, most larval community studies in this region have been spatially confined (≤50 km), and have focused on specific local oceanographic processes (e.g. Dempster *et al.*, 1997; Smith *et al.*, 1999; Gray and Miskiewicz, 2000; Gray and Kingsford, 2003). A common finding among these studies is the incidence of larval assemblages characterized by a comparatively rich taxonomic diversity which, to some extent, reflects the convergence of subtropical and temperate habitats in that region. In addition, larvae and juveniles of tropical fishes typically associated with coral reefs are frequently caught in more southern, predominately temperate habitats (Smith and Suthers, 1999; Booth *et al.*, 2007), having been transported southwards by the East Australian Current (EAC). This major western boundary current system carries warm, low-nutrient tropical water southwards along eastern Australia (Boland and Church, 1981; Ridgway and Godfrey, 1997), and has been linked to hydrographic processes responsible for nutrient enrichment and increased primary productivity of shelf waters (Hallegraeff and Jeffrey, 1993; Bax *et al.*, 2001; Oke and Middleton, 2001).

This paper examines linkages between larval fish assemblages and water masses along the continental shelf of south-eastern Australia between southern Queensland (Qld) and New South Wales (NSW), a region regarded as a major faunal transition zone (Kuiter, 2000). Results are derived from non-depth discriminate data collected during three winter/spring surveys which were primarily designed to characterise the spawning habitat of *Scomber australasicus* (Neira and Keane, 2008). We describe along-shelf larval fish assemblages and their respective distributions in relation to water masses, and determine if assemblage structures reflect the complex hydrography of the pelagic shelf ecosystem in the region. We also introduce a novel technique that employs multidimensional analysis of water column temperature frequencies to define water mass interfaces, and discuss the advantages of this approach to similar integrated studies.

MATERIALS AND METHODS

Data collection

Vertical plankton samples and oceanographic data were obtained simultaneously from surveys carried out in shelf waters off south-eastern Australia between 25.8°S (Wide Bay) and 37.5°S (Cape Howe) in October 2002 and 2003 (spring), and between 24.6°S (Bundaberg) and 32.9°S (Newcastle) in July 2004 (winter) (Table 1; Fig. 1). Spring surveys consisted of 15 across-shelf transects (labelled 1–15) located 50 nm apart, each with four stations. Additional along-shelf transects (labelled A1–A14), each with three stations, were added between all 15 across-shelf transects in October 2002 (n = 14) and along the upper six across-shelf transects in October 2003 (n = 5). The winter survey comprised 21 across-shelf transects (labelled 1–21) located 25 nm apart, each with 3–7 across shelf stations (85 stations in total). Across-shelf stations during spring surveys were located 10 and 5 nm inshore from the shelf break, at the break, and 5 nm past the break, whereas in the winter survey stations were located at the break and then every 5 nm shoreward to the coast (10 nm in transects 1 and 3–5 due to the large shelf width). Five stations in October 2002 and one in October 2003 were omitted due to bad weather.

Samples were collected continuously day and night using a bongo sampler equipped with 300 and 500 μm mesh, 3 m long plankton nets enclosed in a purpose-built, weighted stainless steel frame to facilitate vertical drops. The mouth of each net (0.6 m diameter) was fitted with a General Oceanics flowmeter to estimate total volume of water filtered during each vertical haul. Haul speed was ca. 0.5 ms^{-1}. A Scanmar unit was fitted to the frame to measure instantaneous sampling depth, thus allowing the sampler to be lowered to within ~5 m of the sea floor or to a maximum depth of 200 m. A Seabird Electronics SBE 19 CTD profiler, also fitted to the frame, recorded salinity, temperature and depth simultaneously with each plankton sample. Damage to the CTD prevented data from being taken south of transect 13 during October

Table 1. Details of the spring and winter larval fish surveys conducted along shelf waters of south-eastern Australia in 2002–2004. Length of coastline (nautical miles; nm) covered between southern Queensland (Qld) and New South Wales (NSW) during each survey is approximate.

Survey dates (Season)	Shelf region sampled (States)	Latitudinal range (°S)	Length of coastline (nm)	Transects	Samples
12–22 October 2002 (Spring)	Wide Bay – Cape Howe (Qld-NSW)	25.8–37.5	775	29	97
1–8 October 2003 (Spring)	Wide Bay – Cape Howe (Qld-NSW)	25.8–37.5	775	20	74
19–28 July 2004 (Winter)	Bundaberg – Newcastle (Qld-NSW)	24.6–32.9	450	21	85

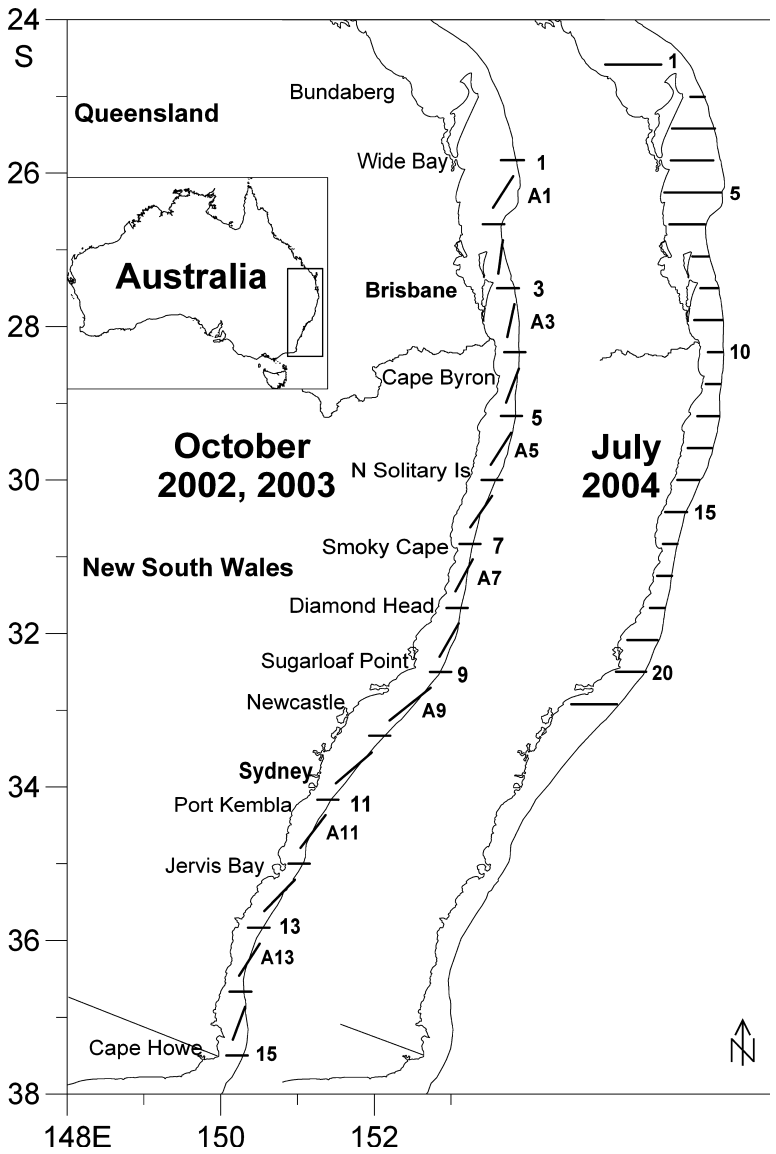


Figure 1. Map of south-eastern Australia showing the locations of transects sampled in October 2002, 2003 and July 2004. Solid line next to coast corresponds to the 200 m shelf break contour.

2003. Samples were immediately preserved in 98% ethanol.

All larvae caught were identified to the lowest possible taxon primarily using the guides of Fahay (1983), Moser *et al.* (1984), Ozawa (1986), Okiyama (1988), Moser (1996), Neira *et al.* (1998), Moser and Watson (2001), Leis and Carson-Ewart (2004) and Richards (2006). The term 'larva' is defined as the developmental stage from hatching to the attainment of full external meristic characters (fins and scales), and includes yolk sac through to postflexion stages (Neira *et al.*, 1998). Given the high number of taxa identified, we list only those families and taxa which contributed ≥0.2% to the total caught during the study. Larvae which contributed <0.2% as well as those that could not be identified (including damaged specimens and/or yolk-sac larvae) were classified as 'others.' Classification of larval fish taxa as either tropical, sub-tropical or temperate was based on the adult distribution (Gomon *et al.*, 1994; Kuiter, 2000).

Identification of water masses

Water masses present in the sampling area during each survey were identified by a combination of sea surface imagery (obtained from CSIRO Marine and Atmospheric Research, Hobart, Tas., Australia), CTD recorded temperature/salinity data and multivariate analyses of water column temperature frequencies. For the latter, hierarchal clustering (not shown) and non-metric multidimensional scaling (nMDS) ordination

of transects were based on 0.5°C increment-temperature frequency matrices for each survey. Frequency matrices were constructed form pooled frequency distributions of water column temperatures at all 1 m depth bins sampled on each transect, with transect and temperature being the matrix dimensions. The individual matrix elements thus represented the frequency of water column temperatures sampled on each transect. Matrix data were then standardised (converted to a percentage) to account for variable number and depths of stations along transects before being square root transformed to construct the Bray–Curtis similarity matrix. The rationale for using temperature to separate water masses was based on preliminary analyses that showed negligible variability in salinity within surveys, and the fact that the Tasman Front, which separates warmer EAC water from cooler Tasman Sea water, is primarily a thermal front (Nilsson and Cresswell, 1981). Transect 1 in July 2004 was omitted from all analyses as it was geographically separated from the rest and appeared as an outlier. Major splits between water masses indicated by clustering are shown in ordination plots for each survey. Ordinations of temperature frequencies were also performed on data pooled across all surveys to examine variability between water masses and surveys. All multivariate analyses were performed using PRIMER® v.6.1 (PRIMER-E Ltd, Plymouth, UK). One way ANOVA was performed to test whether mean sea surface and water column temperatures and salinities differed significantly between water masses across all surveys. When factors were found to be significant, the Bonferroni procedure was applied to ascertain which levels were different (Sokal and Rohlf, 1995).

Larval assemblages

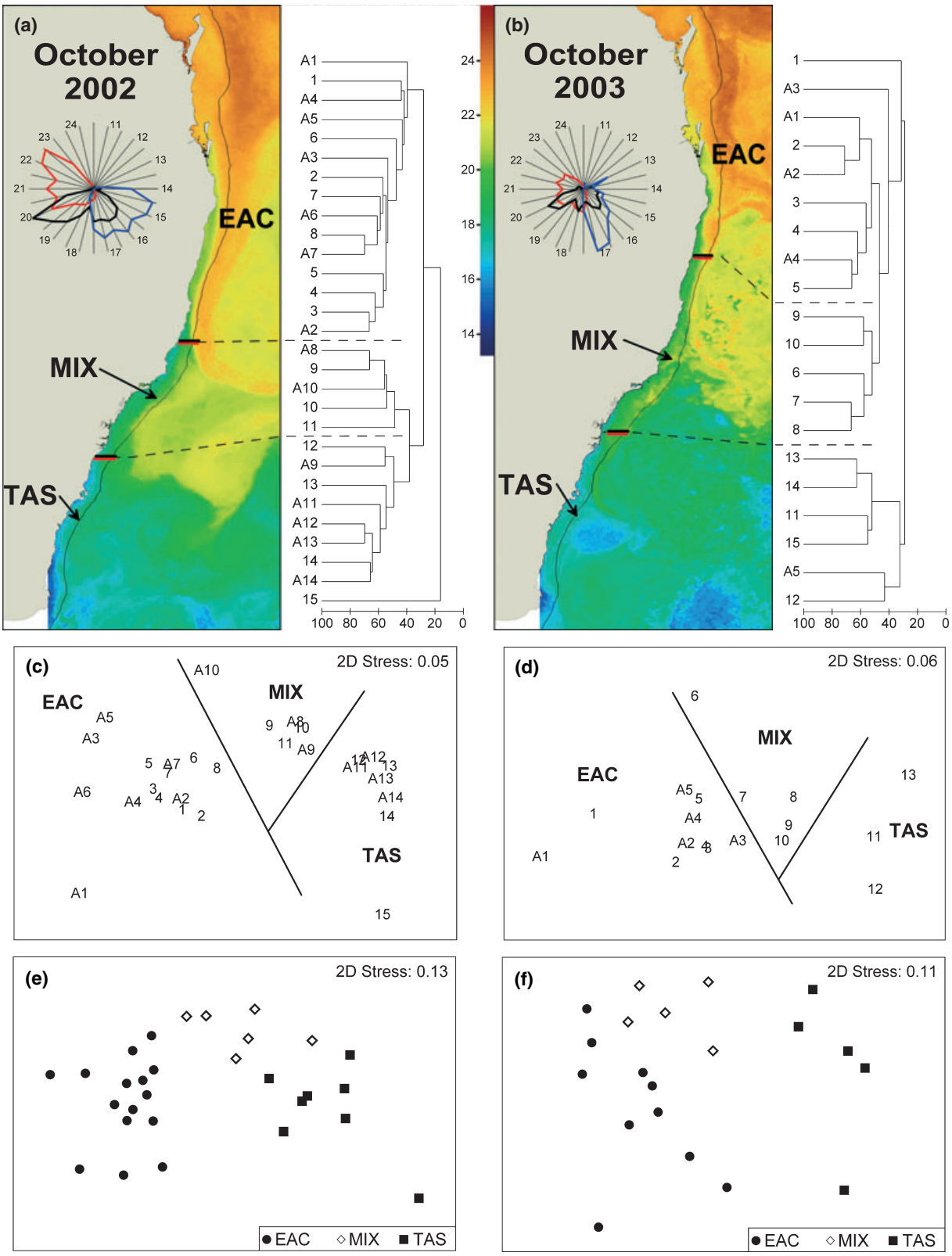
All classification and ordination analyses are based on the average abundance of larvae (number/10 m^2) of each taxon across each transect in each survey. Assemblages for each survey were defined using classification and nMDS ordination of mean $\log(x+1)$-transformed abundances based on a Bray–Curtis similarity matrix (Field *et al.*, 1982). Ordinations of transects (excluding 1 in July 2004) were compared to those of temperature frequencies to determine how close assemblages represented specific water masses in each survey. Ordinations were also performed on data pooled across all surveys to examine variability between water masses and surveys.

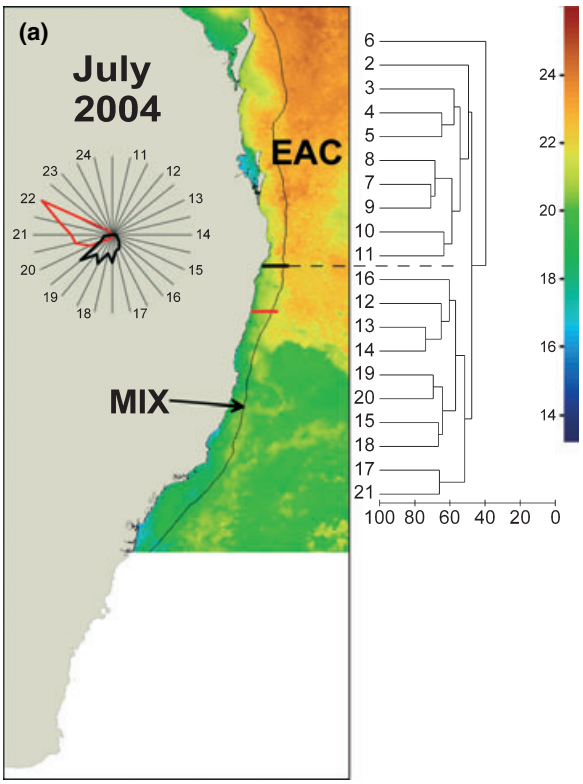
One-way non-parametric analysis of similarities (ANOSIM; Clarke, 1993) was performed on transects associated with each water mass to determine whether larval assemblages differed between water masses both by individual survey and combined; R values from pairwise comparisons and significance are provided when appropriate, where 1 represents complete segregation and 0 no segregation. Taxa which accounted for the groupings from combined data across all surveys were identified using analysis of similarity percentages (SIMPER), which calculates the contribution of each taxon to the dissimilarity between different groups, i.e. discriminating species (Clarke, 1993).

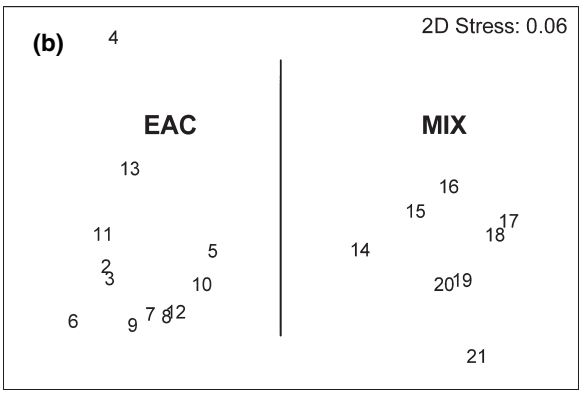
Taxa were regarded as 'representative' and 'discriminators' of water masses if they contributed to the top 60% of each the average similarity ($\bar{S}$) within an assemblage and dissimilarity ($\bar{\delta}$) between assemblages, respectively. Representative and discriminating taxa were further deemed as robust if the ratios $\bar{S}_i/\mathrm{SD}(S_i)$ and $\bar{\delta}_i/\mathrm{SD}(\delta_i)$ were ≥1.4, respectively. The use of the arbitrary 1.4 value derives from the lack of a formal statistical basis to set cut-off thresholds since similarity/dissimilarity contributions from each taxon are not independent. If contributions were independent, such ratio would be significant if it was above ~1.4 (K.R. Clarke, personal communication).

Classification of the most abundant taxa (n = 35) belonging to shelf fishes across all three surveys was performed on a log-transformed Bray–Curtis dissimilarity matrix to examine taxa groupings and their association with water masses; mesopelagic taxa were omitted from these analyses since they showed no consistent association with water masses after preliminary classification on individual surveys. The along-shelf change in assemblage structure was illustrated by plotting the mean rela-

Figure 2. Composite SST images of south-eastern Australia during (a) 14–19 October 2002 and (b) 4–9 October 2003, showing boundaries between EAC, MIX and TAS water masses (red lines) and main splits in larval fish assemblages (black lines); radar plots (inserts) show distribution of water column temperature frequencies of EAC (red), MIX (black) and TAS (blue). Bray–Curtis similarity classification of transects based on mean larval fish abundances are shown next to corresponding SST images, with dashed lines indicating transects where assemblages split. Ordinations below (a) and (b) depict water masses defined from temperature frequencies by transect (c, d), and larval fish assemblages overlaid with respective water masses (e, f). Notations (1, A1, 2, etc.) in classification and ordinations refer to transect number.


(a)
October 2002
EAC
MIX
TAS
(b)
October 2003
EAC
MIX
TAS
(c)
2D Stress: 0.05
EAC
MIX
TAS
(d)
2D Stress: 0.06
EAC
MIX
TAS
(e)
2D Stress: 0.13
EAC MIX TAS
(f)
2D Stress: 0.11
EAC MIX TAS





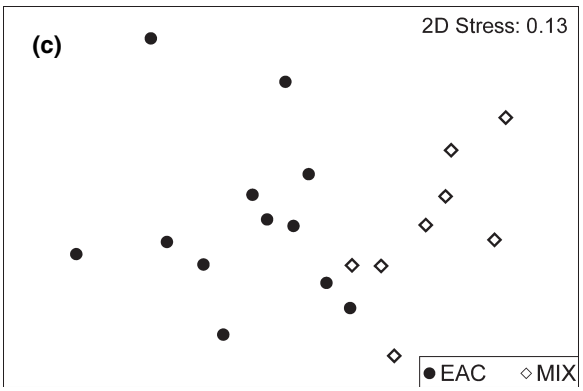


Figure 3. Composite SST image of south-eastern Australia during 22–27 July 2004 (a), showing boundaries between EAC and MIX water masses (red line) and the main split in larval fish assemblages (black line); radar plot (insert) shows distribution of water column temperature frequencies of EAC (red) and MIX (black). Bray–Curtis similarity classification of transects based on mean larval fish abundances is shown next to SST image, with dashed line indicating transects where assemblages split. Ordinations below depict water masses defined from temperature frequencies by transect (b), and larval fish assemblages overlayed with respective water masses (c). Notations (1, 2, 3, etc.) in classification and ordinations refer to transect number.

tive abundance of key taxa by transect using the data visualization program JColorGrid (Joachimiak *et al.*, 2006).

RESULTS

Oceanographic conditions

The south-flowing EAC constituted the main oceanographic feature of the surveyed area during the study. Warm (~21–24°C) EAC water covered almost the entire south-eastern Australian shelf to 28°S (southern Qld) in October 2002 and 2003, extending to 35°S in 2002 and 33°S in 2003, and meeting cooler (<18°C) Tasman Sea water that prevailed over southern NSW during these surveys (Fig. 2a,b). Surface currents were strong (0.6–0.8 m s^{-1}) within the main EAC body but weaker (0.2–0.3 m s^{-1}) south of 31°S, the region where the current separates from the coast and deflects offshore. By contrast, the EAC was less advanced in July 2004, only extending to ~30°S (Fig. 3a).

Upwelling of cooler water was evident around 31.6°S (Diamond Head) and 30.9°S (Smoky Cape) in October 2002 and 2003, respectively, in association with the EAC separation point. While only the 2002 upwelling event was evident in the SST image, both events were evident in CTD-measured profiles that show temperatures at 50–70 m being as much as 5°C cooler than at the surface.

Water masses

Clustering and ordination of water column temperature frequencies distinguished three water masses between 25.8°S (Wide Bay, Qld) and 37.5°S (Cape Howe, NSW) both in October 2002 and 2003, namely EAC to the north, Tasman Sea water (TAS) to the south, and a composite mixed water mass (MIX) in between (Fig. 2c,d). The EAC–MIX and MIX–TAS interfaces were located at about 31.8°S (Diamond

Head) and 34.3°S (Coalcliff) in October 2002, whereas in October 2003 they were located some 110 and 50 nm further north near 29.9°S (North Solitary Is) and 33.7°S (Broken Bay), respectively, reflecting the weaker EAC conditions at that time. Both EAC and MIX were also present in the more northern survey area between 24.6°S (Bundaberg) and 32.9°S (Newcastle) in July 2004, with the interface identified at about 29.8°S (Fig. 3b). Ordinations from data pooled across all surveys clearly showed transects grouping in accordance to their respective water mass as opposed to survey (Fig. 4a,b).

Mean SST of EAC water (21.2–21.8°C) was distinctly warmer than that recorded in MIX (19.0–20.0°C) and TAS (16.7°C) waters (Table 2). The minimum SST of 17.0°C recorded within EAC in October 2002 was a result of coastal upwelling in the area nearby 31.7°S (Diamond Head). Excluding stations influenced by this event, the lowest SST of EAC in October 2002 was 19.7°C. Mean SSTs differed significantly between water masses across all surveys ($F_{2,234}$ = 365.08; $P < 0.005$), as did and mean water column temperatures ($F_{2,234}$ = 396.71; $P < 0.005$). In contrast, the only significant difference in salinities was between EAC and TAS water column values ($F_{2,234}$ = 4.90; $P < 0.01$). No significant differences were observed in sea surface salinities.

Depth profiles based on mean CTD-measured temperatures clearly distinguished water masses in all surveys, with the largest vertical temperature gradients occurring in MIX water (Fig. 5). Water column temperature frequencies (Figs 2a,b and 3a – inserts) showed a clear separation between EAC and TAS both in October 2002 and 2003, and between EAC and MIX in July 2004. Temperature frequencies of MIX water overlapped those of EAC and TAS in October 2002 and 2003, with a clear bimodal distribution occurring in 2002. The SSTs at the water mass boundaries across all three surveys were ~20°C and 18°C for the EAC–MIX and MIX–TAS interfaces, respectively, i.e. EAC >20°C, MIX 18–20°C and TAS <18°C.

Larval fish composition

A total of 18 128 larval fishes, comprising 143 identifiable taxa from 96 families, occurred in the 256 plankton samples collected during the three surveys. Larvae from Carangidae (30.2%), Clupeidae (19.2%), Myctophidae (7.7%), Scombridae (4.4%), Bothidae (3.6%), Macroramphosidae (2.2%) and Triglidae (2.0%) accounted for 69.3% of the total caught (Table 3). The remaining 89 identified families (23.5%) each individually contributed <2% to the total, of which 10 were represented by only one larva. The most abundant taxa were *Trachurus* spp. (30.0%), *Sardinops sagax* (17.7%), *S. australasicus* (4.3%), *Lophonectes gallus* (2.6%), *Macroramphosus* spp. (2.2%), *Diaphus* spp. (2.1%), *Lepidotrigla* spp.

Figure 4. Ordinations of transects across all surveys from water column temperature frequencies (top) and larval fish abundances (bottom) overlayed with survey (a, c) and water mass (b, d), respectively.

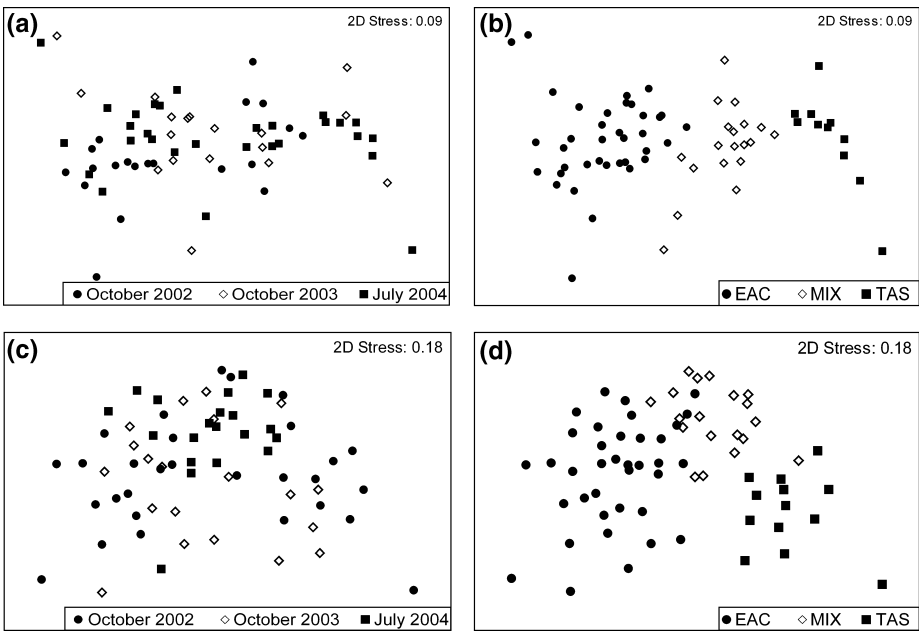


Table 2. Mean sea surface and water column (WC) temperatures and salinities (±SD) of the three water masses identified from the surveys in October 2002 and 2003, and July 2004.

	October 2002		October 2003		July 2004	
	Surface	WC	Surface	WC	Surface	WC
Temperature						
EAC	21.77 ± 1.21 (16.97 – 23.65)	20.66 ± 1.20 (15.78 – 23.14)	21.66 ± 1.13 (19.55 – 23.69)	20.20 ± 1.35 (18.00 – 22.95)	21.18 ± 0.92 (19.73 – 22.10)	20.81 ± 0.77 (19.70 – 21.78)
MIX	19.25 ± 0.97 (16.81 – 20.45)	17.85 ± 1.18 (15.75 – 19.76)	20.01 ± 0.82 (18.30 – 21.52)	17.77 ± 1.23 (15.71 – 20.20)	19.00 ± 0.80 (17.89 – 20.96)	17.91 ± 0.94 (16.04 – 19.82)
TAS	16.71 ± 0.98 (14.58 – 18.09)	15.54 ± 0.73 (14.23 – 17.00)	16.74 ± 0.50 (15.88 – 17.49)	15.54 ± 0.83 (14.10 – 16.23)		
Salinity						
EAC	35.50 ± 0.13 (35.15 – 35.84)	35.57 ± 0.07 (35.36 – 35.80)	35.34 ± 0.09 (35.11 – 35.47)	35.38 ± 0.04 (35.31 – 35.46)	35.47 ± 0.14 (35.07 – 35.63)	35.54 ± 0.10 (35.47 – 35.66)
MIX	35.60 ± 0.10 (35.34 – 35.76)	35.52 ± 0.07 (35.43 – 35.66)	35.27 ± 0.13 (34.91 – 35.41)	35.32 ± 0.08 (35.16 – 35.44)	35.44 ± 0.12- (35.16 – 35.85)	35.52 ± 0.07 (35.34 – 35.61)
TAS	35.55 ± 0.09 (35.32 – 35.68)	35.48 ± 0.04 (35.39 – 35.57)	35.34 ± 0.05 (35.29 – 35.45)	35.34 ± 0.08 (35.19 – 35.41)		

Values in parentheses correspond to ranges. EAC, East Australian Current; MIX, mixed; TAS, Tasman Sea.

(2.0%), myctophids (2.0%), *Apogonops anomalus* (1.9%) and *Etrumeus teres* (1.6%), which combined made up 66.4% of the total caught. About 7.2% of all larvae caught could not be identified.

Classification of assemblages

Clustering and ordination of transects revealed three major assemblages each in October 2002 and 2003, and two in July 2004, with transects generally grouping into discrete latitudinal sections (Figs 2 and 3). Main boundaries between the October 2002 assemblages occurred at 31.8°S (Diamond Hd) and 34.3°S (Coalcliff), whereas in October 2003 they occurred some 110 and 50 nm further north at 29.9°S (North Solitary Is) and 33.7°S (Broken Bay), respectively. The split between the July 2004 assemblages occurred near 29.1°S (Evans Hd). Transects that did not cluster discretely via classification (including A9 in October 2002, A3 and A5 in October 2003, as well as transect 6 in July 2004) were generally characterized by low larval abundances, although they grouped close to respective adjacent transects in ordinations (Figs 2 and 3).

Each of the three larval assemblages present in October 2002 and 2003 mirrored one of each of the EAC, MIX and TAS water masses (Fig. 2). The same was true with the July 2004 assemblages, which matched EAC and MIX waters (Fig. 3). Furthermore, the latitudinal boundaries of the assemblages corresponded almost exactly to those of the water masses except in July 2004, when the split was located ~50 nm north of the EAC–MIX interface.

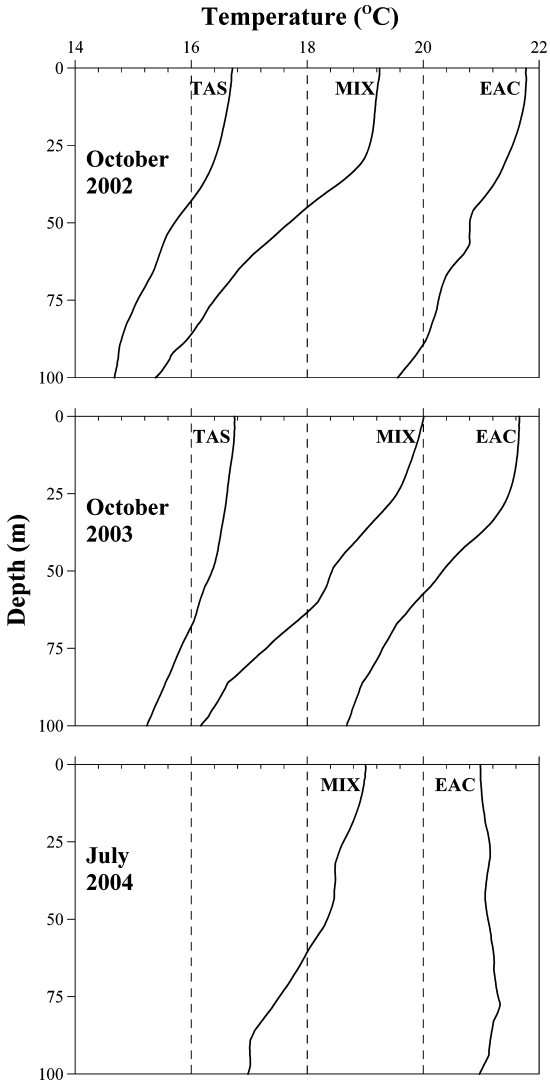
Ordination of transects combined across all three surveys produced groupings linked to their respective associated water masses as opposed to surveys (Fig. 4c,d). This was reflected in $R \geq 0.420$ between water masses compared to $R \leq 0.275$ between surveys (ANOSIM; Table 4). Larval compositions differed significantly between the three water masses across all surveys, with near complete separation between EAC and TAS ($R = 0.888$), and least segregation between EAC and MIX ($R = 0.420$).

Representative and discriminating taxa

The total number of taxa identified across all surveys comprised 124 in EAC, 103 in MIX and 61 in TAS. Representative taxa, i.e. those found to contribute to the top 60% of average similarity within an assemblage, equalled 12 in EAC, 9 in MIX and 7 in TAS (Table 5). *Trachurus* spp. and *Lepidotrigla* spp. were robust representatives of all water masses (i.e. $\bar{S}_i/SD(S_i) \geq 1.4$), with *Trachurus* accounting for 10.4–16.2% of average similarity across all water masses. Other robust representative taxa included labrids (EAC), callionymids (EAC, MIX), *Macroramphosus* spp. (MIX), *L. gallus* (MIX, TAS) and Anthiinae serranids (TAS). The MIX-associated assemblage contained predominantly EAC and TAS taxa, with *S. australasicus* being the only representative taxa solely associated with MIX (Table 5).

The EAC and TAS larval assemblages were the most dissimilar ($\bar{\delta} = 76.3$, Table 4), with robust discriminators including labrids and callionymids in

Figure 5. Mean temperature (°C) profiles of the upper 100 m in the EAC, MIX and TAS water masses identified along shelf waters of south-eastern Australia during October 2002, 2003 and July 2004.



EAC, and *L. gallus* and morids in TAS (Table 6). Robust discriminators between EAC and MIX comprised labrids (EAC) and *L. gallus* (MIX), as well as bothids (EAC) and *Macroramphosus* spp. (MIX). The TAS assemblage was best distinguished from MIX by the high abundances of *Helicolenus percoides* and morids (Table 6).

Classification of the most abundant shelf taxa across all surveys revealed three distinct groups at the 29% similarity level (Fig. 6). Furthermore, these groups were generally associated with EAC (E1-3), MIX or TAS water. Taxa within subgroup E-1 were more prevalent in the northern EAC region, e.g. synodontids and lethrinids, while E-2 taxa occurred throughout EAC and MIX, albeit were relatively more abundant in the former, e.g., *E. teres*, *E. australis* and labrids. Taxa within subgroup E-3 had the highest abundances and widespread distribution, and included *Trachurus* spp., *S. sagax* and *S. australasicus* which abound within MIX, especially in the vicinity of the EAC separation point. Taxa primarily associated with MIX included *Atypichthys strigatus* and *Scorpis* sp., while TAS-associated taxa included *H. percoides*, *E. nitidus* and *L. caudatus* (Fig. 6).

The composition and abundance of larval fishes within each survey varied markedly with latitude, matching a southwards decline in SSTs, which was most evident in spring (Fig. 7). In addition, there was a gradual decline in the prevalence of EAC-associated taxa within MIX, while TAS-associated taxa increased. For example, primarily EAC-associated taxa, such as labrids, lethrinids and synodontids, were regularly caught in MIX waters but rarely south of the MIX–TAS interface. Similarly, TAS-associated taxa such as *E. nitidus*, morids and *H. percoides* also occurred in MIX waters but were seldom caught north of the EAC–MIX interface (Fig. 7).

DISCUSSION

Water masses

This constitutes the first mesoscale study to link discrete larval fish assemblages and water masses along the south-eastern Australian shelf using multivariate techniques. Three discrete water masses were identified based on water column temperatures in the survey area during the winter–spring study period, namely East Australian Current to the north (EAC; 20.5–23.4°C), Tasman Sea to the south (TAS; 14.8–17.5°C), and a mixed mass containing EAC–TAS water (MIX; 18.3–19.9°C). Both the EAC and TAS are well known in south-eastern Australia (Rochford, 1957), whereas MIX has not been described in similar studies within the region (Gray and Miskiewicz, 2000). Interfaces between these masses were delineated using temperature frequencies from CTD-derived profiles, an approach that departs from the traditional method based primarily on temperature/salinity (TS) structure and/or satellite imagery (e.g. Gray and Miskiewicz, 2000; Hare *et al.*, 2001; Quattrini *et al.*, 2005), and which often results in subjective boundaries. As water mass interfaces diverge from sharp fronts to less-defined gradients, precise boundaries become increasingly difficult to delineate. However, our novel multivariate approach

Table 3. Families and taxa of larval fishes identified from samples collected along shelf waters of south-eastern Australia in spring (October 2002 and 2003) and winter (July 2004). Percentage contributions of families and taxa (%) were calculated after adding adjusted numbers, i.e. larvae/10 m^2. Listed families and taxa comprise only those that contributed ≥0.2% to the total caught across all surveys, and are arranged in decreasing order of contribution. Values in parentheses next to each family correspond to total number of taxa identified per family; in cases of families comprising a single taxon, the total number (*n*) and percentage contribution (%) are given for both in the same row.

		Spring		Winter		Total study	
Family	Taxon	*n*	%	*n*	%	*n*	%
Carangidae (3)		2321	26.9	2908	32.6	5229	30.2
	Trachurus spp.	2280	26.6	2908	32.6	5188	30.0
Clupeidae (4)		784	8.2	2520	27.4	3304	19.2
	Sardinops sagax	601	6.5	2384	26.0	2985	17.7
	Etrumeus teres	181	1.7	136	1.4	317	1.6
Myctophidae (13)		753	9.0	626	6.6	1379	7.7
	Diaphus spp.	329	4.1	67	0.6	396	2.1
	Myctophids	81	0.9	246	2.7	327	2.0
	Hygophum spp.	88	0.9	190	2.0	278	1.5
	Lampanyctus spp.	102	1.3	70	0.7	172	1.0
	Myctophum spp.	69	0.7	12	0.1	81	0.4
	Benthosema spp.	23	0.2	21	0.2	44	0.2
	Symbolophorus spp.	27	0.4	1	<0.05	28	0.2
Scombridae (4)		554	7.4	188	2.1	742	4.4
	Scomber australasicus	539	7.2	188	2.1	727	4.3
Bothidae (2)		360	3.9	282	3.4	642	3.6
	Lophonectes gallus	163	1.9	252	3.1	415	2.6
	Bothids	197	1.9	30	0.3	227	1.0
Macroramphosidae (1)	*Macroramphosus* spp.	223	2.4	177	2.0	400	2.2
Triglidae (2)		326	3.4	99	1.0	425	2.0
	Lepidotrigla spp.	320	3.4	99	1.0	419	2.0
Acropomatidae (1)	*Apogonops anomalus*	52	0.5	304	2.9	356	1.9
Labridae (1)	Labrids	233	2.1	104	1.1	337	1.5
Callionymidae (1)	Callionymids	195	2.0	98	1.1	293	1.5
Notosudidae (1)	Notosudids	14	0.2	239	2.4	253	1.4
Serranidae (4)		180	2.1	75	0.9	255	1.4
	Anthiines	174	2.0	75	0.9	249	1.3
Engraulidae (1)	*Engraulis australis*	223	2.2	36	0.3	259	1.1
Scorpaenidae (3)		109	1.4	59	0.6	168	1.0
	Scorpaenids	46	0.6	49	0.5	95	0.5
	Helicolenus percoides	40	0.5	6	0.1	46	0.3
Synodontidae (1)	Synodontids	202	1.9	15	0.1	217	0.9
Kyphosidae (4)		108	0.9	76	0.8	184	0.9
	Scorpis spp.	35	0.3	55	0.6	90	0.5
	Atypichthys strigatus	72	0.6	17	0.2	89	0.4
Platycephalidae (2)		98	1.1	60	0.7	158	0.8
	Platycephalus spp.	84	0.9	42	0.5	126	0.7
	Platycephalus fuscus	14	0.2	18	0.2	32	0.2
Gobiidae (1)	Gobiids	125	1.2	50	0.4	175	0.7
Mullidae (1)	Mullids	180	1.4	25	0.3	205	0.7
Monacanthidae (1)	Monacanthids	27	0.3	86	0.9	113	0.7
Sillaginidae (1)	*Sillago* spp.	42	0.4	80	0.8	122	0.6
Astronesthidae (2)		64	1.1	19	0.2	83	0.6
	Astronesthids	61	1.1	8	0.1	69	0.5
Cepolidae (1)	*Cepola australis*	25	0.2	78	0.8	103	0.6
Bregmacerotidae (1)	*Bregmaceros* spp.	77	0.7	33	0.3	110	0.5

Table 3. Continued.

Family	Taxon	Spring		Winter		Total study	
		n	%	*n*	%	*n*	%
Emmelichthyidae (1)	*Emmelichthys nitidus*	63	1.1			63	0.5
Moridae (1)	Morids	34	0.5	24	0.3	58	0.4
Nemipteridae (1)	Nemipterids	85	0.9	3	<0.05	88	0.4
Microstomatidae (1)	*Bathylagus* sp.			47	0.6	47	0.4
Gonostomatidae (2)		25	0.3	41	0.4	66	0.3
Pomacentridae (1)	Pomacentrids	57	0.5	17	0.1	74	0.3
Photichthyidae (3)		38	0.4	12	0.1	50	0.2
	Vinciguerria sp.	34	0.4	12	0.1	46	0.2
Terapontidae (1)	*Pelates sexlineatus*	50	0.4	7	0.1	57	0.2
Lethrinidae (1)	Lethrinids	55	0.4	8	0.1	63	0.2
Cynoglossidae (1)	Cynoglossids	44	0.4	7	0.1	51	0.2
Sparidae (3)		12	0.2	23	0.2	35	0.2
Trichiuridae (2)		27	0.5	2	<0.05	29	0.2
	Lepidopus caudatus	25	0.4			25	0.2
Percichthyidae (1)	*Howella* sp.	13	0.2	23	0.2	36	0.2
Nomeidae (2)		20	0.2	17	0.1	37	0.2
Others (58 families, 67 taxa)		1116	12.9	746	7.9	1862	10.0
Total families		89		77		96	
Total taxa		128		102		143	
Total number		8914		9,214		18 128	

Table 4. Pairwise comparisons of larval fish assemblages between water masses and between surveys. Values correspond to *R*-statistics and respective significance levels (first column) and dissimilarity (%) (second column) derived from ANOSIM and SIMPER analyses.

Between water masses	EAC vs. MIX		EAC vs. TAS		MIX vs. TAS	
October 2002	0.724***	66.56	0.943***	77.85	0.604***	63.71
October 2003	0.324*	57.91	0.858***	74.34	0.828**	68.49
July 2004	0.456***	53.43				
All surveys	0.420***	62.56	0.888***	76.24	0.618***	66.25
Between surveys	Oct 02 vs. Oct 03		Oct 02 vs. Jul 04		Oct 03 vs. Jul 04	
	0.032	64.13	0.275***	65.69	0.264***	61.03

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

proved to be an effective and objective method of defining boundaries. In addition, this approach allows for interannual and seasonal variation to be quantified in regions where appropriate data exist and could be applied to alternative variables (e.g. salinity, density, fluorescence). Furthermore, the multivariate approach outlined in this study adds to the expanding array of multivariate applications ranging from age-based fishery assessments (Smith, 2003) to sediment particle size analyses (Chazottes *et al.*, 2004; K.R. Clarke, personal communication).

The fact that the EAC–MIX and MIX–TAS interfaces were identified further south in October 2002 than in October 2003 reflects the less-advanced EAC during the latter survey. This was not unexpected given the significant variability in the EAC extent and strength with time of year (Ridgway and Godfrey, 1997). Moreover, both interfaces during October 2002 coincided with major transitional zones depicted in satellite SST imagery of south-eastern Australia. However, neither of the two could be easily defined in the October 2003 imagery, yet both were clearly evi-

Table 5. Taxa regarded as representative of each EAC, MIX and TAS water mass from data combined across all three surveys, i.e. those that contributed to the top 60% of average similarity ($\bar{S}$) from SIMPER analysis. Taxa are listed in decreasing order of percentage contribution ($\%\bar{S}_i$) to overall $\bar{S}$ per assemblage; those in bold correspond to robust representatives for each water mass, i.e. taxa in which $\bar{S}_i/SD(S_i) \geq 1.4$ (see text for details).

EAC assemblage $\bar{S}$ = 45.1			MIX assemblage $\bar{S}$ = 47.2			TAS assemblage $\bar{S}$ = 46.2		
Taxon	$\%\bar{S}_i$	$\bar{S}_i/SD(S_i)$	Taxon	$\%\bar{S}_i$	$\bar{S}_i/SD(S_i)$	Taxon	$\%\bar{S}_i$	$\bar{S}_i/SD(S_i)$
***Trachurus* spp.**	**10.4**	**2.0**	***Trachurus* spp.**	**14.5**	**3.8**	***Trachurus* spp.**	**16.2**	**2.1**
***Lepidotrigla* spp.**	**6.2**	**1.9**	***L. gallus***	**9.1**	**3.5**	***Lepidotrigla* spp.**	**9.5**	**1.9**
Callionymids	**5.9**	**2.0**	*S. sagax*	7.8	1.3	*Macroramphosus* spp.	9.2	1.2
Labrids	**5.7**	**1.5**	***Macroramphosus* spp.**	**7.1**	**1.8**	**Anthiines**	9.1	**1.8**
Bothids	**5.4**	**1.5**	*S. australasicus*	5.8	1.1	***L. gallus***	8.7	**1.4**
Diaphus spp.	4.6	1.0	**Callionymidae**	**5.7**	**3.3**	**Morids**	6.4	**1.4**
***Bregmaceros* spp.**	**4.6**	**1.8**	***Lepidotrigla* spp.**	**5.5**	**3.2**	*H. percoides*	6.2	1.1
S. sagax	4.3	0.8	Anthiines	4.0	1.3			
E. teres	4.2	1.1	*Hygophum* spp.	3.1	1.1			
Myctophids	3.9	1.1						
Gobiids	3.7	1.3						
Hygophum spp.	3.7	1.1						

dent in multivariate analyses. Such results highlight the capacity of this technique to define interfaces through identification of the location where greatest dissimilarity occurs.

Larval fish diversity and assemblage structure

The shelf-based surveys carried out during this study, by far the most extensive ever undertaken in eastern Australia in terms of area covered, revealed three major recurrent larval assemblages comprising a mixture of 143 taxa from 96 identifiable families. The combined taxonomic diversity recorded across all three surveys resembles the 173 taxa from up to 119 families reported from across the Sydney shelf, where assemblages were likewise dominated by larvae of small pelagics (e.g. carangids and clupeoids) and myctophids (Gray, 1993; Dempster *et al.*, 1997; Smith and Suthers, 1999; Gray and Miskiewicz, 2000). The presence of such taxonomically diverse larval fish assemblages reflects the fact that this region of south-eastern Australia is regarded as a major sub-tropical to temperate faunal transition zone (Kuiter, 2000). Furthermore, assemblages are enriched by the southwards advection of larvae and early juveniles of many tropical species into temperate waters via the EAC (Smith and Suthers, 1999; Booth *et al.*, 2007). Similarly, the overall decline in taxa richness towards TAS waters could be attributed to the sub-tropical to temperate habitat change, similar to that described for the northern Benguela region where larval diversity was higher in warm Angolan waters than in the more southern, cooler Atlantic waters (Olivar, 1990).

Each larval fish assemblage identified during this study matched corresponding EAC, MIX and TAS waters, with EAC and TAS assemblages showing almost complete segregation. Moreover, interfaces between the EAC, MIX and TAS assemblages were found to be dynamic, with locations shifting temporally and spatially depending on the EAC extent. This shifting was reflected both in interannual differences between larval assemblages and associated water mass boundaries in spring, as well as in seasonal variation, with EAC–MIX assemblages located further south in spring matching the southwards EAC advancement at that time (Godfrey *et al.*, 1980; Tilburg *et al.*, 2001). While these results highlight the strength of employing assemblages as proxies of water masses, a similar albeit finer-scale study along the Sydney shelf found no link between seasonal larval assemblages and either EAC or TAS water, possibly as a result of the broad classification of water masses which did not include MIX (Gray and Miskiewicz, 2000). However, our study demonstrated the close affinity between recurrent assemblages and discrete water masses in this region of south-eastern Australia, similar to that described for regions elsewhere in the world (Moser *et al.*, 1987; Doyle *et al.*, 2002; Aceves-Medina *et al.*, 2004). Moreover, mesoscale boundary currents similar to the EAC have been found to drive assemblage change in other major marine ecosystems including the Gulf Stream (Grothues and Cowen, 1999; Hare *et al.*, 2001), Benguela Current (Olivar and Shelton, 1993) and Californian Current (Loeb *et al.*, 1983; Moser *et al.*, 1987; Franco-Gordo *et al.*, 2002).

Table 6. Taxa regarded as discriminators between the EAC, MIX and TAS water masses from data combined across all surveys, i.e. those that contributed to the top 60% of average dissimilarity ($\bar{\delta}$) from SIMPER analysis. Taxa are listed in decreasing order of percentage contribution ($\%\bar{\delta}_i$) to overall $\bar{\delta}$ amongst water mass; those in bold correspond to robust discriminators between water masses, i.e. taxa in which $\bar{\delta}_i/\mathrm{SD}(\delta_i) \geq 1.4$ (see text for details). The water mass in which each taxon was more abundant is provided for each comparison.

EAC & MIX				EAC & TAS				MIX & TAS			
Taxon	$\%\bar{\delta}_i$	$\bar{\delta}_i/\mathrm{SD}(\delta_i)$	Water mass	Taxon	$\%\bar{\delta}_i$	$\bar{\delta}_i/\mathrm{SD}(\delta_i)$	Water mass	Taxon	$\%\bar{\delta}_i$	$\bar{\delta}_i/\mathrm{SD}(\delta_i)$	Water mass
L. gallus	**4.2**	**2.6**	**MIX**	***Macroramphosus* spp.**	**3.2**	**1.4**	**TAS**	***S. sagax***	**5.1**	**1.7**	**MIX**
S. sagax	3.8	1.3	MIX	*S. sagax*	3.1	1.3	EAC	***S. australasicus***	**4.3**	**1.5**	**MIX**
S. australasicus	3.3	1.3	MIX	**Labrids**	**3.0**	**2.0**	**EAC**	**Callionymids**	**3.1**	**2.4**	**MIX**
***Macroramphosus* spp.**	**3.1**	**1.7**	**MIX**	***L. gallus***	**2.9**	**1.7**	**TAS**	*Trachurus* spp.	2.9	1.1	MIX
Trachurus spp.	2.8	1.2	MIX	**Bothids**	**2.8**	**1.9**	**EAC**	*E. nitidus*	2.5	1.0	TAS
Diaphus spp.	2.5	1.3	EAC	**Callionymids**	**2.7**	**2.1**	**EAC**	Astronesthids	2.4	1.3	TAS
Bothids	**2.5**	**1.7**	**EAC**	*Trachurus* spp.	2.6	1.2	EAC	***H. percoides***	**2.4**	**1.4**	**TAS**
Myctophids	2.2	1.3	EAC	***E. teres***	2.5	**1.5**	**EAC**	*E. teres*	2.3	1.2	MIX
E. teres	2.2	1.3	EAC	***H. percoides***	**2.5**	**1.4**	**TAS**	*Macroramphosus* spp.	2.3	1.2	MIX
E. australis	2.1	1.2	EAC	*Diaphus* spp.	2.5	1.3	EAC	Myctophids	2.3	1.1	MIX
A. anomalus	2.1	1.2	EAC	Astronesthids	2.4	1.3	TAS	*A. strigatus*	2.3	1.1	MIX
Labrids	**2.1**	**1.5**	**EAC**	*E. australis*	2.3	1.2	EAC	*L.gallus*	2.2	1.2	MIX
A. strigatus	2.0	1.1	MIX	**Morids**	**2.3**	**1.7**	**TAS**	**Morids**	**2.2**	**1.4**	**TAS**
Notosudids	1.9	1.0	EAC	*E. nitidus*	2.2	1.0	TAS	Anthiines	2.1	1.2	TAS
Anthiines	**1.8**	**1.4**	**MIX**	***Bregmaceros* spp.**	**2.1**	**1.9**	**EAC**	Mullids	2.1	1.2	MIX
Hygophum spp.	1.8	1.3	EAC	**Gobiids**	**2.0**	**1.5**	**EAC**	*Scorpis* sp.	2.0	1.0	MIX
C. australis	1.8	1.1	MIX	Anthiines	2.0	1.2	TAS	*Lampanyctus* spp.	2.0	1.3	TAS
Scorpis sp.	1.8	1.0	MIX	Myctophids	1.9	1.3	EAC	*C. australis*	1.9	1.1	MIX
Mullids	1.7	1.3	MIX	*A. anomalus*	1.9	0.9	EAC	*Hygophum* spp.	1.9	1.3	MIX
Platycephalus spp.	1.7	1.3	MIX	*S. australasicus*	1.8	0.8	EAC	*L. caudatus*	1.9	1.1	TAS
***Bregmaceros* spp.**	**1.6**	**1.4**	**EAC**	Notosudids	1.8	0.9	EAC	*Platycephalus* spp.	1.8	1.3	MIX
Sillago spp.	1.6	1.2	MIX	*Lampanyctus* spp.	1.7	1.3	TAS	**Labrids**	**1.8**	**1.4**	**MIX**
Gobiids	1.6	1.3	EAC	*Hygophum* spp.	1.7	1.3	EAC	*Symbolophorus* spp.	1.8	1.0	TAS
Synodontids	1.5	0.9	EAC	*L. caudatus*	1.7	1.1	TAS	Scorpaenids	1.7	1.1	TAS
Lampanyctus spp.	1.5	1.3	EAC	*Lepidotrigla* spp.	1.7	1.2	EAC	*Lepidotrigla* spp.	1.6	1.3	TAS
Lepidotrigla spp.	1.4	1.3	EAC	*Symbolophorus* spp.	1.6	1.0	TAS	*Sillago* spp.	1.5	1.0	MIX
Scorpaenids	1.4	1.2	EAC	Synodontids	1.5	0.9	EAC				
Myctophum spp.	1.4	1.2	EAC								
Callionymids	1.4	1.3	MIX								

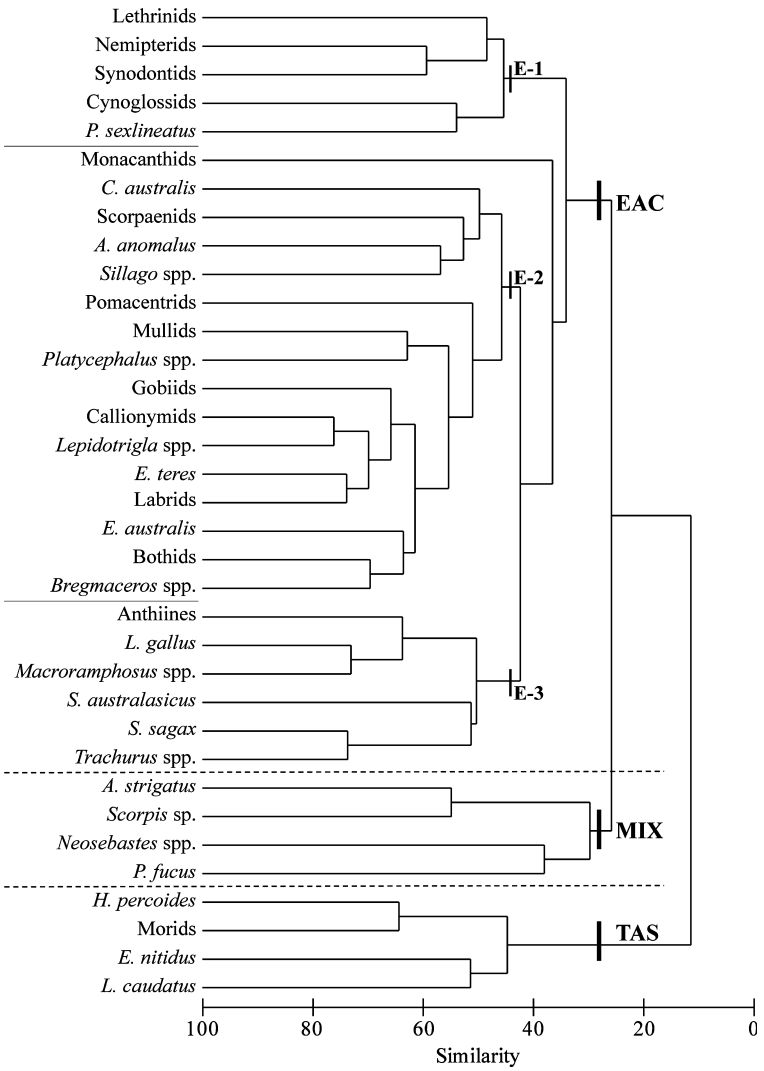


Figure 6. Bray–Curtis similarity classification of the 35 most abundant larval fish taxa (excluding mesopelagic taxa such as myctophids) across all surveys, showing the three main assemblages primarily associated with East Australian Current (EAC), mixed (MIX) and Tasman Sea (TAS) water masses; the EAC assemblage was further divided into three subgroups, namely E-1, E-2 and E-3.

The structure of the EAC, TAS and MIX larval assemblages identified during this study differed significantly in terms of taxa diversity and individual abundances. Such clear contrast was due to the presence of tropical/sub-tropical as well as temperate taxa in EAC, primarily temperate-associated taxa in TAS, and a combination of EAC–TAS-associated taxa within MIX. The EAC assemblage contributed the highest number of taxa to the total diversity and TAS the least. Furthermore, the EAC assemblage largely resembled that described for the Sydney shelf during spring/summer when the EAC was the dominant feature, and which included common representative taxa such as *Trachurus* spp., *S. sagax*, callionymids and labrids (Gray and Miskiewicz, 2000). Likewise, the TAS assemblage contained the same abundant taxa recorded off Sydney in winter when Tasman Sea water was present, including *H. percoides*, *L. caudatus*, *Macroramphosus* spp. and morids. Such results combined further reinforce the recurrent nature of larval fish assemblages along this region of south-eastern Australia.

Taxa diversity within the MIX assemblage was consistent with the convergence of EAC and TAS waters, as indicated by the overlap of taxa such as *Trachurus* spp., *S. sagax*, *L. gallus* and *S. australasicus*. Furthermore, the higher prevalence small pelagics in MIX compared to EAC and TAS waters during October 2002 and 2003 is likely to be linked to upwelling events recorded in that region at that time, and which regularly occur in spring as a result of the EAC deflection from the coast (Hallegraeff and Jeffrey, 1993; Oke and Middleton, 2001). Moreover, the fact that *S. australasicus* comprised the only representative taxa that was uniquely associated with MIX is consistent with the occurrence of greater

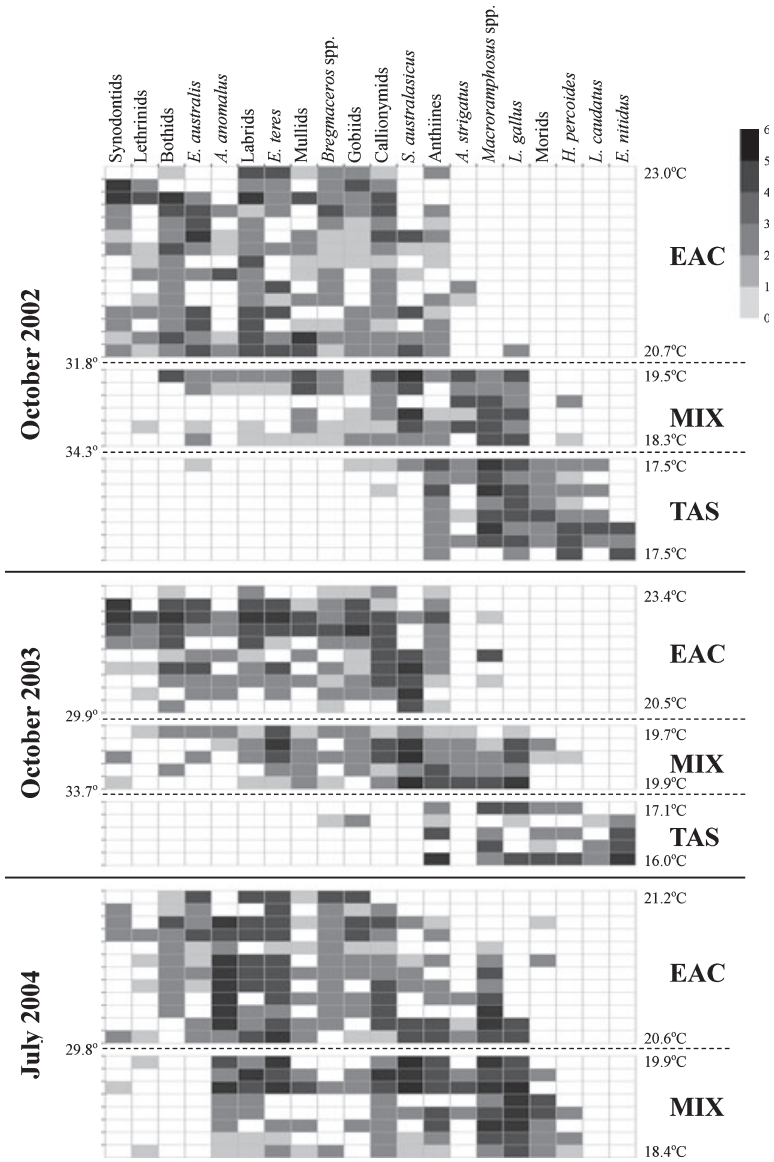


Figure 7. Changes in mean relative abundance (ln(number/m^2)) of key larval fish taxa by transect (rows – north to south) within the EAC, MIX and TAS water masses during the October 2002, 2003, and July 2004 surveys, plotted using the JColorGrid data visualization program. Latitudes (*S*) on the left axis correspond to location of respective water mass interfaces; temperature ranges (°C) on the right axis correspond to mean values across the northern-most and southern-most transects within each respective water mass.

abundances of both eggs and larvae of this scombrid in that region (Neira and Keane, 2008).

Larval *Trachurus* spp. were the most abundant taxa across all water masses and are likely to comprise two common species: namely *T. novaezelandiae* and *T. declivis*. Furthermore, *T. novaezelandiae* is well known in warmer EAC waters while *T. declivis* is confined mostly to cooler TAS waters in south-eastern Australia (Gomon *et al.*, 1994; Kuiter, 2000). The occurrence of these two species along the entire survey area would explain why *Trachurus* spp. was also found to be the most robust representative taxa of EAC and TAS waters, and also of MIX waters where larvae of these carangids more than likely overlap.

The EAC and MIX assemblages were least dissimilar during periods of dynamic, less-defined oceanic conditions, as those identified during the October 2003 survey, when strong currents and EAC-associated mixing processes would have facilitated the southwards transport of tropical/sub-tropical taxa into MIX waters. This observation is consistent with the fact that while EAC-associated taxa were frequent in MIX waters, they were rarely caught past the MIX–TAS interface. Such findings indicate that this temperature front may be a barrier to the southward dispersal of larvae. These results parallel findings off eastern North America where no significant larval exchange occurred between water masses associated

with the Gulf Stream and Middle Atlantic Bight (Grothues and Cowen, 1999).

Recent surveys have suggested that larval fishes along northern NSW coastal waters may become entrained along the EAC deflection front and advected offshore (T. Mullaney, unpublished data). Additionally, as observed in other major ecosystems (e.g. Limouzy-Paris *et al.*, 1997; Chiswell and Roemmich, 1998; Logerwell and Smith, 2001), larvae may also become retained in warm-core mesoscale eddies which periodically pinch off from the EAC and track south along the south-eastern Australia shelf (Nilsson and Cresswell, 1981). The extent to which larvae become associated with and are dependent on these processes could have potential implications for larvae in terms of access to early nursery habitats, as well as transport-related recruitment success and/or genetics diversity.

While this study was limited to data from three surveys, our results highlight the strength of employing larval fish assemblages as indicators of water masses, even in the absence of depth-discriminate data. Such close affinity between assemblages and the regional hydrography could in future be employed to delineate boundaries of pelagic bio-regions in ecosystems such as those along south-eastern Australia, which at present have been primarily defined using physical properties and satellite plankton imagery (Lyne and Hayes, 2005). In addition, results set a foundation for future studies focusing on process-orientated biophysical research in the region, and further emphasise the ongoing need for real-time mesoscale fishery-ecological studies worldwide (Bakun, 2006). Furthermore, a close examination of multispecies assemblages in the context of shifting water masses would help identify alterations in spawning dynamics of fishes resulting from climate (e.g. Ahas, 1999) and/or ecosystem changes (e.g. Neira and Sporcic, 2002). Such alterations could be predicted, for example, using a combination of the multivariate approach applied in this study and SSTs (Greve *et al.*, 2005), and would be reflected in changes in the structure as well as seasonal and spatial occurrence of larval fish assemblages.

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