

Beyond hydrography: daily ichthyoplankton variability and short term oceanographic events on the Sydney continental shelf

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Abstract—Surface ichthyoplankton concentrations along a shore-normal transect across the Sydney continental shelf and upper slope changed between three replicate nights in January and April of 1994. Over 70 families of fish were recorded, which, during January, included: Myctophidae (49% of individuals), Carangidae (14%), Gonostomatidae (11%) and Pomacentridae (8%); and during April included: Gonorhynchidae (43%), Myctophidae (10%), Berycidae (11%) and Serranidae (6%). Multidimensional scaling analysis identified inshore and offshore communities, which nightly moved between the nearshore and mid-shelf stations. During January no distinct near-surface water masses could be identified from the temperature-salinity data, although the shelf waters were under the influence of forcing by the local wind stress and the East Australian Current. Good agreement between the cross-shore transport in the near-surface layer and the temporal variability of the icthyoplankton was nevertheless found. The sampling during April was performed during a period of relatively steady oceanographic conditions, and two water masses were identified from the hydrographic data. Temporal ichthyoplankton variability at any station was correspondingly less during the April period and stable inshore and offshore communities were identified, that shifted with characteristic water masses. The results presented in this paper demonstrate that the large variance often associated with ichthyoplankton distribution within a similar water mass may be interpreted by the dynamics in cross-shelf flows, which has implications for the selection of control sites used when studying environmental impacts of coastal outfalls. © 1997 Elsevier Science Ltd

INTRODUCTION

An interplay of physical and biological processes governs the spatial and temporal variability of larval fish assemblages. Accordingly, a physically and biologically integrated approach in the study of ichthyoplankton communities is necessary (Legendre and Demers, 1984; Mackas et al., 1985; Cowen et al., 1993). Spurious interpretations of ichthyoplankton assemblage structure have been shown to be a consequence of ignoring either physical (Frank and Leggett, 1985) or biological (Kingsford, 1990, 1993) components of variability. Obtaining the data to describe oceanographic events adequately, particularly over large spatial scales, is beyond the scope of many studies (Gray, 1993; Tzeng and Wang, 1993). Consequently, many studies have focused on explaining variability in terms of biological factors and simple hydrographic parameters.

Salinity and temperature are extensively used as indicators of water masses, the distribution of which is then related to spatial and temporal ichthyoplankton patchiness

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(Richardson et al., 1980; Fortier and Leggett, 1985; Tzeng and Wang, 1993; Chiu and Hsyu, 1994). While this approach proves useful where strong, steady hydrographic boundaries exist, it is limited in regions where significant small scale circulation occurs within the same water mass (Cowen et al., 1993). For example, temperature and salinity differences accounted for only 15% of the observed variability of ichthyoplankton assemblages in the Middle Atlantic Bight (Cowen et al., 1993). Clearly, analysis of the regional physical oceanography is required in areas characterised by small scale unsteady flows, for example in the coastal ocean.

Recent studies of the ichthyoplankton of the coastal waters off Sydney have indicated that a diverse larval fish community of over 100 different families inhabits the region (Gray et al., 1992; Gray, 1993). These studies established that large spatial and temporal heterogeneity of ichthyoplankton assemblages exists, although links with water masses or dynamic processes were not established.

Several oceanographic processes are potentially important ichthyoplankton assemblages in the Sydney coastal ocean. The East Australian Current (EAC) streams in a southerly direction approximately following the 200 m isobath along the northern New South Wales continental margin. Around a latitude of 32°S the main EAC stream departs the slope and heads eastward into the Tasman Sea (Nilsson and Cresswell, 1981). Meso-scale, anti-cyclonic eddies which break off from the main EAC stream often continue to move southwards and may intrude upon the Sydney shelf, significantly altering the background stratification and current velocity field (McClean-Padman and Padman, 1991). Persistent local winds also drive upwelling or downwelling events on the Sydney shelf (McClean-Padman and Padman, 1991; Griffin and Middleton, 1992). Coastally trapped waves (CTWs) which propagate northwards along the New South Wales coast also account for a significant amount of the variability in nearshore barotropic currents at Sydney (Griffin and Middleton, 1991).

The aim of this study is to use detailed physical oceanographic data, including currents and hydrographic data, to attempt to account for the night-to-night variability in surface ichthyoplankton assemblages during two cruises on the Sydney shelf and upper slope.

METHODS

Study area and sampling gear

Data were collected from the Sydney coastal ocean (Fig. 1) during two 10-day cruises in January (18–27) and April (3–12) 1994, on the research vessel R.V. Franklin. Biological sampling was conducted at five stations along a shore-normal transect (Fig. 1, Table 1). At each station, two replicate neuston tows were made using a 75×75 cm² mouth plankton net with 330 μ m mesh and a General Oceanic flow meter positioned in the mouth of the net. Tow speeds varied between 1.0 and $1.5 \, \mathrm{m \, s^{-1}}$, and the duration of each tow was approximately 6 min, filtering an average volume of approximately 300 m³. Samples were preserved in 5% formalin/seawater. Sampling was conducted at night to minimise possible net avoidance.

In January a complete transect from stations A to E, commencing at station A (inshore), was conducted on the nights of 22, 23 and 25 January. In April, during the first two nights (5 and 6 April), sampling began at station A, while on the third night (8 April) sampling began at station E and proceeded inshore.

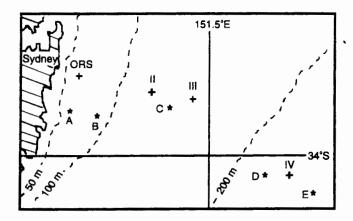


Fig. 1. Map of the study area with sampling stations (A–E) and current meter mooring positions, showing the Ocean Reference Station (ORS) and moorings II, III and IV.

Table 1. Position, latitude, longitude, depth (m) and distance offshore (km) of each sampling station

Station	Position	Latitude	Longitude	Depth	Distance
A	inshore	33°56.7′	151°17.5′	67	2.7
В	inshore	33°57.5′	151°20.0′	83	7.3
C	mid-shelf	33°57.0′	151°26.6′	130	16.4
D	offshore	34°00.0′	151°35.0′	250	32.8
E	offshore	34°02.5′	151°40.0′	600	40.0

Laboratory procedures

Plankton samples were gently rinsed in a 500 μ m mesh sieve (to remove small zooplankton and yolk-sac larvae), before sorting and counting all larval fish. Identifications were made to the family level (except for leptocephali larvae, which were grouped at the order level) using Leis and Rennis (1983), Moser et al. (1984), Ozawa (1986), Smith and Heemstra (1986) and Leis and Trnski (1989). Absolute numbers of fish from each sample were standardised to numbers 100 m^{-3} . All concentrations of families were log-transformed $[\ln(x+1)]$ before using analyses of variance (Underwood, 1981) and multidimensional scaling (MDS, Clarke and Green, 1988). The ANOVA design was month (2), station (5) and night (3, nested within month), with homogeneity of variance tested using Cochran's test (Underwood, 1981). If data were not homogeneous then comparisons were made by inspection only. *Post-hoc* comparisons of means were by the Student-Newman-Kuels test (SNK).

Multidimensional scaling is an ordination technique which reduces a swarm of multivariate data (species × stations matrix) to fewer dimensions to identify patterns in the data structure. In this paper, stations with similar larval fish communities are grouped together, while stations with different communities are separate. The stress value indicates the degree to which the data are distorted in order to fit the required number of dimensions. A stress value above 0.2 is unacceptable and a value below 0.15 indicates a good fit (Clarke, 1993). There are no values on the axes as an MDS scatter can be arbitrarily rotated.

Oceanographic data

The physical data collected during the study consists of current velocity data, wind velocity data and hydrographic data. Measurements of temperature and salinity at a depth of 4 m were taken during each replicate tow from the ship's in situ instruments. During daylight hours a Neil-Brown CTD was deployed along a shore-normal transect to obtain cross-shore hydrographic data. Current velocity data were obtained from four current meter moorings. The innermost mooring is a permanent facility operated by Australian Water Technologies Ensight, known as the Ocean Reference Station (ORS). The ORS is positioned at 33°59'.25S, 151°18'.48E and lies in a depth of 65 m of water. The ORS also provided temperature data, recorded by a thermistor string, and wind velocity data from an anemometer positioned 5 m above the sea surface. Three other current meter moorings, known hereafter as II, III and IV, were also deployed across the shelf and upper slope during the first research cruise at depths of 98, 104 and 337 m respectively. All the current meter moorings, including the ORS, were aligned in an approximately shore-normal direction, and the biological and physical data were collected along the same general transect (Fig. 1). The top current meters on each mooring were positioned to remain within the near-surface mixed layer at depths of 17, 22, 22 and 44 m for the ORS and moorings II, III and IV respectively. Current meter moorings II, III and IV were recovered prior to the April cruise; hence only current velocities from the ORS were available during the April sampling period.

Pre-processing of the current meter data involved firstly resolving the currents into principle along-shore and across-shore directions. The currents from the current meters on the ORS and moorings II, II and IV were rotated by 11, 13, 17 and 29°, respectively, to align them with the bathymetry which runs in an approximately northeast—southwest direction. The principle currents were then lowpass filtered using a Lanczos-cosine filter with a cutoff period of 2 h to remove high frequency contributions. The lowpassed currents were then decimated to hourly records.

Estimates of the of the near-surface cross-shore flow were obtained from the current meter data. Currents on the Sydney shelf are directed primarily along-shore and therefore, the magnitude of the across-shore components is significantly smaller than the along-shore components. As a result, caution must be exercised when resolving the across-shore and along-shore components, as a small error in the principle directions will contaminate the small across-shore components.

A time series of wind stress data was calculated from the wind velocities obtained from the ORS using the method of Large and Pond (1981). The filtering and decimating routines applied to the currents were used to prepare the wind stress data for further analyses. Conventions used in all figures are oceanographic — the vector sticks point in the direction in which the wind or current was flowing.

RESULTS

Larval fish assemblages in January and April

A total of 6948 fish larvae belonging to 70 families were caught over the two sampling periods, with 59% of larvae sampled during January and 41% sampled in April (Table 2). A shift in the dominant taxa occurred between the two sampling periods. In January myctophids (48.5%) dominated the samples, with high numbers of carangids (13.9%), gonostomatids (11.4%) and pomacentrids (8.2%). The myctophids were predominantly

Table 2. Total abundance and percentage abundance of families and species of fish larvae captured during January and April 1994

CLUPEIFORMES C SALMONIFORMES C STOMIIFORMES C	Family Leptocephali larvae Clupeidae Engraulidae Gonorhynchidae Gonostomatidae	Genus Sardinops Hyperlophus Etrumeus Engraulis Gonorhynchus	Species neopilchardus terres australis	Total January 12 25 36	% January 0.29 0.61	Total April 94	% April 3.30 0.11
CLUPEIFORMES C SALMONIFORMES C STOMIIFORMES C	Clupeidae Engraulidae Gonorhynchidae	Hyperlophus Etrumeus Engraulis	terres	25	0.61		
SALMONIFORMES COSTOMIIFORMES CO	Engraulidae Gonorhynchidae	Hyperlophus Etrumeus Engraulis	terres			3	0.11
SALMONIFORMES C	Gonorhynchidae	Engraulis		36	0.00		
SALMONIFORMES C	Gonorhynchidae		austratis	30	II XX	5	0.18
STOMIIFORMES C	-	Gonorhynchus			0.00	,	0.10
	Gonostomatidae		greyii	13	0.32	1219	42.83
N		Cyclothone	•	468	11.38	79	2.78
	Melanostomiidae			6	0.15	1	0.04
AULOPIFORMES A	Aulopodidae	Aulopus	purpurissatus	1	0.02	6	0.21
S	ynodontidae	Synodontus		39	0.95	5	0.18
P	aralepididae	•		1	0.02	0	0.00
MYCTOPHIFORMES M	Ayctophidae			1995	48.49	289	10.15
OPHIDIIFORMES C)phidiidae			1	0.02	2	0.07
	Carapodidae			0	0.00	4	0.14
LOPHIIFORMES A	Antennariidae			3	0.07	2	0.07
ATHERINIFORMES E	Exocoetidae			2	0.05	2	0.07
В	Bellonidae			0	0.00	1	0.04
S	comberesocidae			11	0.27	2	0.07
LAMPRIDIFORMES T	rachipteridae	Trachipterus		3 *	0.07	0	0.00
BERYCIFORMES T	rachichthyidae			1	0.02	0	0.00
В	Berycidae	Centroberyx	affinis	52	1.26	304	10.68
. H	Iolocentridae			1	0.02	0	0.00
ZEIFORMES C	Caproidae		•	0	0.00	4	0.14
GASTERO- M STEIFORMES	Macroramphosidae	Macroramphosus		0	0.00	82	2.88
SCORPAENIFORMES D	Dactylopteridae	Dactyloptena	orientalis	10	0.24	7	0.25
	corpaenidae	•		12	0.29	63	2.21
	riglidae		•	8	0.19	5	0.18
	latycephalidae			56	1.36	15	0.53
	mbassidae			19	0.46	0	0.00
	erranidae	Type 1, Anthiinae		0	0.00	159	5.59
	Apogonidae			7	0:17	0	0.00
	cropomatidae	~···		2	0.05	4	0.14
	illaginidae	Sillago	bassensis; flindersi	101	2.46	33	1.16
	Malacanthidae			0	0.00	2	0.07
C	Coryphaenidae	Coryphaenus	hippurus	5	0.12	0	0.00

Table 2 (Cont.).

Order	Family	Genus	Species	Total January	% January	Total April	% April
	Carangidae	Trachurus					
		Pseudocarynx	dentex	571	13.89	83	2.92
	Gerreidae	Gerres	subfasciatus	11	0.27	0	0.00
	Sparidae	Pagrus	auratus	1	0.02	1	0.04
	Lethrinidae			1	0.02	0	0.00
	Sciaenidae			31	0.76	0	0.00
	Mullidae			46	1.12	38	1.37
	Chaetodontidae			2	0.05	0	0.00
	Monodactylidae	Schuettea	scalaripinnis	2	0.05	0	0.00
	Kyphosidae			0	0.00	I	0.04
	Girellidae			11	0.27	0	0.00
	Scorpididae	Scorpis	lineolata	7	0.18	U	0.00
	Atypicthyidae	Atypicthys	strigatus	3	0.07	0	0.00
	Terapontidae			I	0.02	0	0.00
	Ap lodactylidae			i	0.02	0	0.00
	Cheilodactylidae			0	0.00	79	2.78
	Mugilidae			24	0.58	5	0.18
	Pomacentridae	Chromis	hypsilepsis	337	8.19	77	2.71
	Labridae			6	0.15	2	0.07
	Scaridae			3	0.07	3	0.11
	Mugiloididae			2	0.05	0	0.00
	Creedidae			1	0.02	3	0.14
	Callionymidae			2	0.05	7	0.25
	Gobiidae			7	0.17	16	0.57
	Schindleriidae	Schindleria		l	0.02	0	0.00
	Tripterygidae			1	0.02	0	0.00
	Sphyraenidae	Sphyraena		2	0.05	0	0.00
	Gempylidae			2	0.05	1	0.04
	Scombridae			15	0.36	2	0.08
	Nomeidae			4	0.10	1	0.04
PLEURONECT!-	Bothidae			28	0.68	15	0.64
FORMES	Cynoglossidae			4	0.10	0	0.00
	Soleidae			2	2.05	i)	9.00
	Pleuronectidae			1	0.02	!	0.04
	Paralychthiidae	Pseudorhombus		2	0.05	9	0.33
TETRAODONTI-	Monacanthidae	20 to 10 to		l	0.02	0	0.00
FORMES	Ostracidae			0	0.00	1	0.04
	Tetraodontidae			3	0.07	10	0.35
Unknown Type A				9	0.24	0	0.00
Unknown Type B				0	0.00	3	0.12
Unknown Type C				0	0.00	41	1.44
Damaged				79	1.92	43	1.61
TOTAL				4114	190.00	2834	100.00

Abundance data of different genera are not recorded.

Hygophum sp., gonostomatids were Cyclothone sp. and carangids were predominantly Pseudocaranx dentex (85%) and Trachurus sp. (13%). Pomacentrids were invariably Chromis sp. (A. G. Miskiewicz, personal communication, 1994) and were most probably C. hypsilepsis.

In April the most abundant taxa were gonorhynchids (42.8%), myctophids (10.2%), berycids (10.7%) and serranids (5.6%). Carangids (2.9%), gonostomatids (2.8%) and pomacentrids (2.7%) were also present in April. Several species of myctophids were grouped into the family Myctophidae (including *Lampadena* and *Lampanyctes*). Gonorhynchids were represented by the single species, *Gonorynchus greyi*. All berycids in April were the common redfish, *Centroberyx affinis* (A. G. Miskiewicz, personal communication, 1994). Serranids occurring in the samples were all one type of the subfamily Anthiinae.

Trends in cross-shelf ichthyoplankton

In January total average abundances of larval fish were relatively uniform across the shelf (45.100 m^{-3}) , with slightly lower abundances at stations B and E on 25 January compared to previous nights [Fig. 2(a)]. Family diversity (\pm standard error, S.E.) was highest at midshelf station C (18.7 ± 1.7) and the two inshore stations [A = 15 ± 1.7 , B = 14 ± 1.8 , Fig. 2(b)]. A dramatic decrease in family diversity occurred between the mid-shelf and offshore stations (D = 7.7 ± 1.5 , E = 7.2 ± 0.8).

In April there was a distinct inshore/offshore increase in total abundance [Fig. 2(c)], particularly between stations B and C, to peak abundance at station E. The nearshore stations had a far lower family diversity (A = 5.5 ± 0.6 , B = 7.5 ± 2.1) than offshore [D = 16.3 ± 1.7 , E = 16.3 ± 2.3 , Fig. 2(d)].

MDS reduced the January community data of 65 taxa to two dimensions [stress value 0.069, Fig. 3(a)]. The analysis showed a gradual cross-shelf gradient in the ichthyoplankton community, with the most inshore station (A) having a different community to the mid-shelf and offshore stations (B–E). Between-night variability was significant, as replicate samples from station A on 23 January [points a3, a4, Fig. 3(a)] indicated a different ichthyoplankton community to that sampled on 22 and 25 January.

In April the community data of 49 taxa were reduced to two dimensions with a stress value of 0.114 [Fig. 3(b)]. The MDS plot indicates the presence of two separate community groupings over the April sampling period, with the communities present at stations A and B tightly grouped and clearly separated from the communities at stations C, D and E, which were more loosely grouped. A notable exception is the community that occurred at station B on 8 April [points b5, b6, Fig. 3(b)], placed by the analysis as more similar to communities at stations C and D. The community at station E was highly variable between nights, with the community sampled on 6 April (e3, e4) being more closely related to stations A–D than on 5 April (e1, e2) and 8 April (e5, e6).

Between-night ichthvoplankton variability

During January pomacentrid distribution was clearly defined by a peak abundance inshore at station A (average $100 \text{ m}^{-3} = 16$) and comparatively few found elsewhere [Fig. 4(a)]. Carangid larvae also decreased with increasing distance offshore [Fig. 4(b)], with similar abundances at stations A–C (11) and very few at D and E.

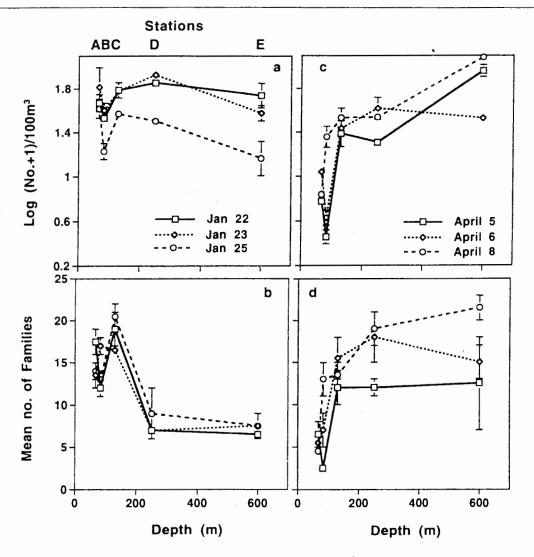
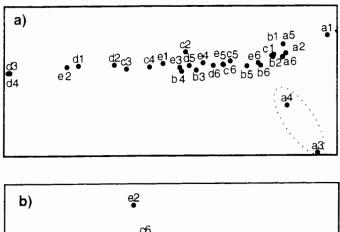


Fig. 2. Average total abundance of larval fish (number 100 m⁻³) and mean number of families per sample, with respect to bathymetry, observed on each night during January (a), (b); and April (c), (d) cruises. Locations of stations A-E are indicated for (a). Error bars are standard error.

On the night of 23 January stations A and B had significantly more pomacentrids (average = 45) than the other two nights [I and 2, respectively, p < 0.01, Fig. 4(a)], while on 23 January station A had significantly fewer carangids (5) than the other two nights [28 and 24, respectively, p < 0.01, Fig. 4(b)]. Stations B and C had significantly more carangids on 22 January (15) than on either 23 or 25 January (2 and 1, respectively, p < 0.01). There were no significant differences between nights in pomacentrids or carangids at the offshore stations C-E.

In contrast, gonostomatids and myctophids were rare inshore at stations A–B (average = 1 and 8, respectively) and were found mostly at stations D and E [10 and 36, respectively, Fig. 4(c) and 4(d)]. On 22 January there were more gonostomatids at station D (22) than on 23 or 25 January [8 and 7, respectively, Fig. 4(c)], while at station E, there were less on 25 January (2) than on 22 or 23 January (9 and 12, respectively). Myctophid abundance did not vary significantly between sampling nights at stations A, C, D and E [Fig. 4(d)]. At station B, however, there were significantly more myctophids on 23 January (26) than on the other two nights (4 and 6, p < 0.01).



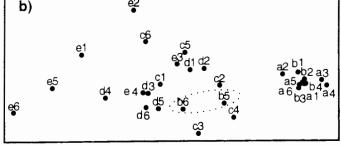


Fig. 3. Multidimensional scaling plot of family abundances during (a) January and (b) April. Each sample is labelled by their station and night (1), (2): 22 January or 5 April; (3), (4): 23 January or 6 April; (5), (6): 25 January or 8 April. Unusual samples at station A on 23 January (a3), (a4) and at station B on 8 April (b5), (b6) are circled.

During the April sampling period berycids and serranids and were generally rare or absent at station A and occurred offshore C–E [Fig. 5(a) and 5(b)]. On 8 April at station B, berycids (6) appeared and were absent on the previous two sampling nights. At station C significantly more berycids were found on 6 April (9) than on 5 and 8 April (3 and 2, respectively, p < 0.01). At station D significantly fewer occurred on 5 April (1) than on 6 and 8 April (6 and 7, respectively, p < 0.01). Highest numbers of berycids were present at station E, with significantly more on 8 April (13) than the other two nights (2 and 4, respectively, p < 0.01).

Serranids were found in similar numbers between 5 and 6 April at stations C–E across the shelf [1, Fig. 5(b)]. Significantly higher numbers of serranids occurred on 8 April at stations B (4), C (4) and E (9) than the other nights (p = 0.05).

Gonorhynchid abundance increased 100-fold from the inshore to the offshore stations, with an average of $50 \times 100 \text{ m}^{-3}$ at station E [Fig. 5(c)]. At stations C and E significantly fewer gonorhynchids were present on 6 April (1 and 15, respectively) than on 5 April (10 and 60, respectively) or on 8 April (6 and 71, respectively, p < 0.01). At station D significantly more gonorhynchids occurred on 5 and 6 April (9 and 12, respectively) than on 8 April (3, p < 0.01).

Myctophids tended to increase across the shelf in April [Fig. 5(d)], with low numbers at the two inshore stations (A and B). At station C significantly fewer myctophids were found on 5 and 6 April (0 and 1, respectively) than on 8 April (13, p < 0.01). Myctophid abundance was similar at station D on all three nights (5). At station E significantly more occurred on 5 April (18) than on the following two nights (2 and 2, p < 0.01).

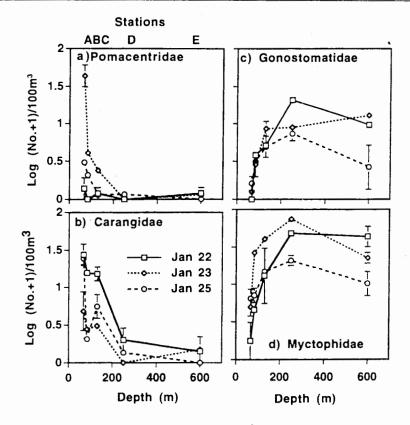


Fig. 4. Average larval abundance (numbers 100 m⁻³) of the four dominant families observed during each night of the January cruise: (a) Pomacentridae, (b) Carangidae, (c) Gonostomatidae, (d) Myctophidae. Error bars are standard error.

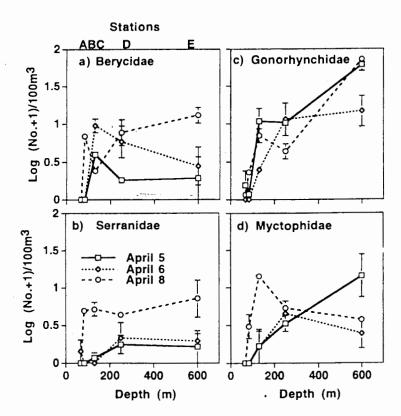


Fig. 5. Average larval abundance (numbers 100 m⁻³) of the four dominant families observed during each night of the April cruise: (a) Berycidae, (b) Serranidae, (c) Gonorhynchidae, (d) Myctophidae. Error bars are standard error.

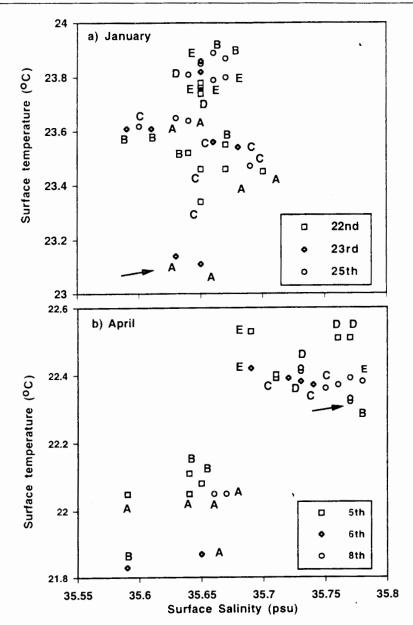


Fig. 6. Near-surface temperature—salinity diagrams during (a) January and (b) April, using two replicate observations at each station during each neuson tow from the vessel's thermosalinograph, with water taken from 4 m depth. Note station A on 23 January and station B on 8 April (arrowed).

Physical oceanography, 22–25 January

No overall distinct surface water masses were apparent during January, with the exception of the temperature–salinity relationship at station A on 23 January, driven by water approximately 0.5°C cooler [Fig. 6(a)]. Station B on 25 January had slightly warmer water, characteristic of the offshore stations at D and E.

The near-surface currents at the ORS and mooring II were northward during 21 and 22 January [Fig. 7(b) and 7(c)]. These currents were probably forced by the strong (0.4 Pa) northward blowing winds [Fig. 7(a)] as nearshore (defined here as the first 10 km from the coast) currents in the Sydney coastal ocean are often forced by the local wind stress (Gibbs *et al.*, 1997). The CTD section from 21 January [Fig. 8(a)] shows the nearshore isotherms dipping down in a downwelling configuration which is consistent with the downwelling, favourable, northward winds during 21 and 22 January.

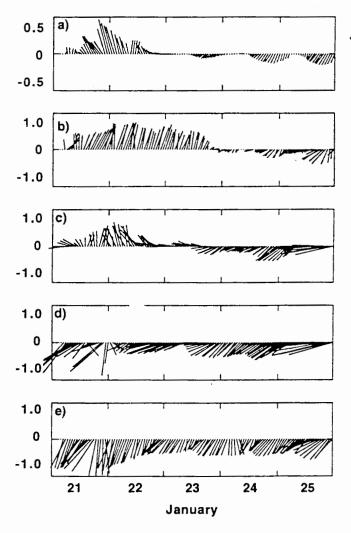


Fig. 7. Physical data recorded during 22-25 January 1994 showing (a) hourly wind stresses (Pa) at the ORS (one of the primary forcing mechanisms on the Sydney shelf); and lowpassed, near-surface current velocities (m s⁻¹) represented in vector stick form at (b) the ORS and (c) moorings II (between stations B and C), (d) III (near station C), and (e) IV (near station D). A vector stick pointing directly up the page represents a near-surface current flowing in an along-shore (northbound) direction.

The near-surface currents at offshore moorings III and IV were southward between 21 and 25 January [Fig. 7(d) and 7(e)]. These currents were probably associated with a mesoscale, warm-core eddy which was evidenced in Advanced Very High Resolution Radiometer (AVHRR) remote sea surface temperature images for the period (not shown). The CTD sections for 22, 23 and 25 January (Fig. 8) show the isotherms over the outer shelf and upper slope to be tilting up towards the surface at the coast, which is common during periods when EAC eddies infringe upon continental slope waters (Gibbs *et al.*, 1997).

The combination of nearshore downwelling tilting isotherms and offshore upwelling tilting isotherms on 22 January [Fig. 8(a)] created a complex frontal region centred around 7 km offshore. These fronts are often unstable and the offshore component of the near-surface currents at the ORS and the onshore component at moorings II, III and IV, indicate that a temporary convergence occurred within the front on 22 and 23 January (Fig. 7).

The nearshore downwelling evidenced in Fig. 8(a) relaxed in response to the weakening of

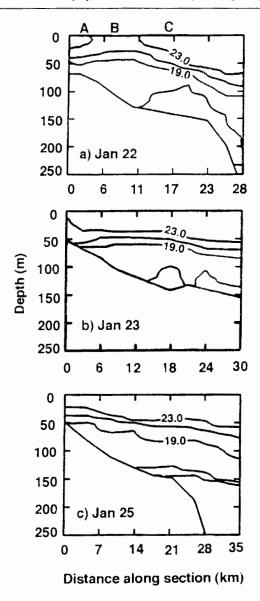


Fig. 8. Section plots of temperature recorded off Sydney during (a) 22 January, 10:00–19:00 h (based on 10 CTD stations), (b) 23 January, 15:00–19:00 h (eight stations), (c) 25 January, 11:00–16:00 h (nine stations), in relation to the wind and current data shown in Fig. 7. Oscillations in the deeper isotherms in (b) are probably a result of internal waves, or bottom boundary dynamics. The nightly surface ichthyoplankton stations A–C are indicated, located <2 km radius of the nearest CTD station.

the downwelling favourable wind stress during 23 January [Fig. 7(a)] and near-surface currents at mooring II developed a strong onshore component [Fig. 7(c) and 8(b)].

The nearshore winds recorded at the ORS during 23–25 January were governed by a sea breeze regime, which is characterised by southwest blowing winds that strengthen and rotate to south blowing during the afternoons before abating overnight [Fig. 7(a)]. The currents at the ORS appeared to respond to these winds by flowing in a southwesterly direction during 24 and 25 January [Fig. 7(b)]. No CTD or biological data were collected on 24 January. By 25 January the nearshore isotherms were horizontal, which is common during these periods of relatively weak local wind forcing.

Surface cross-shelf flow prior and during sampling on 22 January showed an eastwards (offshore) flow of around 0.17–0.25 m s⁻¹ at the ORS, that decreased during the night [Fig.

7(b)]. The near-surface current direction at moorings II and III indicated westward (onshore) transport in the surface layer at stations B, C, D and E over the entire 3-day sampling period, varying in intensity from around 0.20 to 0.70 m s⁻¹, indicating that a convergence zone formed in between stations A and B on 22 January.

Physical oceanography, 5-8 April

The near-surface temperature–salinity (T–S) signatures of each replicate tow at each station in April show the presence of two distinct water masses [Fig. 6(b)]. The T–S signatures of station A on all three nights and station B on 5 and 6 April were similar, with temperatures between 21.8°C and 22.0°C, and salinities between 35.59 and 35.67. The second water mass (22.3–22.0°C, 35.69–35.78 salinity) encompassed stations C, D and E on all three nights and also included station B on 8 April [Fig. 6(b)].

Moorings II, III and IV were retrieved prior to the April sampling period; hence, wind and near-surface current data were only available from the ORS. The near-surface currents at the 17 m ORS current meter were strong and persistent southwest-southeast flowing during 4–8 April [Fig. 9(b)]. These currents may have been in response to the characteristic sea breezes [Fig. 9(a), as observed in January], which occurred during 4–7 April, however, the significant strength of the predominantly along-shore currents ($\approx 0.5 \text{ m s}^{-1}$) suggests that they may also have been associated with the EAC. The tilting up of the isotherms over the outer shelf and upper slope also suggests that the EAC was probably impinging into slope and shelf waters (Fig. 10).

The tilting up of the nearshore isotherms [Fig. 10(a) and (c)] indicates that small scale nearshore upwelling occurred between 4 and 8 April, which is consistent with the shift in the water masses at station B [Fig. 6(b)]. The particular dynamical process or combination of processes which forced this upwelling cannot, however, be determined from the limited data available. Gibbs *et al.* (1997) showed that upwelling in the Sydney coastal ocean is often the result of upwelling favourable winds combining with the EAC in a process called "preconditioning".

Cross-shelf flow at the ORS showed a westward (onshore) flow during the entire sampling period, varying in intensity from 0 to 0.23 m s^{-1} .

DISCUSSION

Effects of spawning location on larval distribution

Spawning time and location contribute significantly to the broad cross-shelf patterns and temporal occurrence of the dominant species (Leis and Miller, 1976; Richardson *et al.*, 1980; Young *et al.*, 1986; Sabates, 1990; Boehlert and Mundy, 1993; Leis, 1993). Gonostomatids and myctophids are widely distributed pelagic/meso-pelagic taxa (Smith and Heemstra, 1986; Bonecker and Hubold, 1990) and their presence in higher numbers on the outer shelf (station D) and off the continental shelf-break [station E, Fig. 4(c), 4(d) and 5(d)] reflects adult distributions and, presumably, spawning.

At the inshore stations pomacentrids and carangids were abundant in January [Fig. 4(a) and 4(b)], which mirrors the distribution and spawning locations of the adults (Hutchins

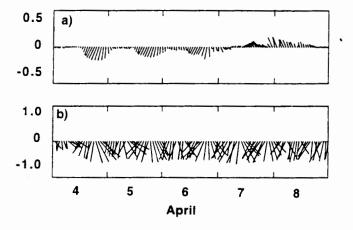


Fig. 9. Hourly wind stresses (Pa) and near-surface currents (m s⁻¹) at the ORS during 5–8 April 1994.

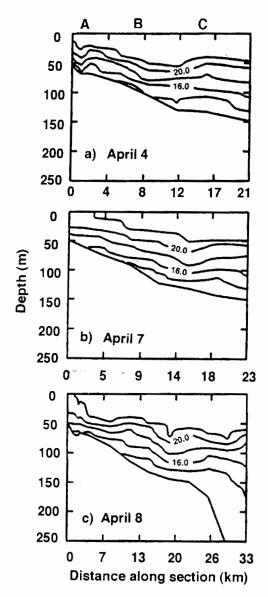


Fig. 10. Section plots of temperature recorded off Sydney during (a) 4 April, 15:00–23:00 h (based on 10 CTD stations), (b) 7 April, 08:00–12:00 (seven stations), and (c) 8 April, 07:00–14:00 (13 stations). Fluctuations due to internal tide are evident (Cresswell and Boland, 1981).

and Swainston, 1986). These pomacentrids (probably the one-spot puller, *Chromis hypsilepsis*) are common on the coastal reefs of New South Wales'and spawn demersal eggs in protected coves and inshore rocky reefs (Gomon *et al.*, 1994). Larvae from demersal eggs are typically more spatially persistent nearshore than larvae from pelagic spawned eggs (Leis and Miller, 1976; Suthers and Frank, 1991).

Carangids (predominantly silver trevally, *Pseudocaranx dentex*) are found as juveniles in estuaries, bays and shallow shelf waters during late summer and adults in spawning condition are found in estuaries and shelf waters (Kailola *et al.*, 1993), consistent with the distribution of larvae.

During April the dominant berycid, *Centroberyx affinis*, inhabit shallow shelf waters to 150 m depth as adults, with juveniles found on the inner shelf and in estuaries (Hutchins and Swainston, 1986; Gomon *et al.*, 1994). Spawning occurs in late summer and early autumn (Kailola *et al.*, 1993), as shown by the spatial and temporal distribution of larvae [Fig. 5(a)]. *Gonorynchus greyi*, or beaked salmon, is an offshore benthic species, preferring sandy substrates (Gomon *et al.*, 1994) where the larvae were observed.

Effects of cross-shelf hydrographic differences in January

Substantial between-night variability in the ichthyoplankton community occurred during January in nearshore waters. A significant amount of the variability is associated with crossshelf advection of the near-surface waters. In January the temperature and salinity signatures of stations across the shelf revealed no distinct water masses, except slightly cooler water at station A on 23 January [Fig. 6(a)]. On 25 January station B had a temperature-salinity signature more similar to the offshore stations [Fig. 6(a)]. Offshore near-surface transport around the ORS (near station A) on 21–23 January, inferred from the currents measured at the ORS, advected slightly cooler nearshore water out to station A [Fig. 11(a)]. Consequently, there was a conspicuous pulse of larval pomacentrids from the rocky subtidal spawning area into station A on 23 January [and partially into station B, Fig. 4(a) and 11(b)] and a concomitant decrease in larval carangids at station A, compared to 22 or 25 January. The cross-shore component of the currents measured at moorings III and IV indicates that the warmer offshore EAC water was being advected onshore at moorings II-IV (stations B-E) at the same time. Thus, an unstable near-surface convergence zone formed on 22–23 January until onshore flow persisted across all stations, transporting slightly warmer water to station B on 25 January [Fig. 11(c)]. This advection pushed the pomacentrids back to the coast, restoring the larval community at station A [MDS plot, Fig. 3(a)]. Larval carangids may well have accumulated at the convergence zone between stations A and B, reflecting their decrease at stations B and C, and high abundance at station A on 25 January [Fig. 4(b)].

Onshore transport of gonostomatid and myctophid larvae from stations D and E occurred on 23 January, increased their abundance at stations B and C, and reducing their abundance at station E by 25 January [Fig. 4(c) and (d)]. Onshore advection of oceanic waters pushing myctophids and gonostomatids into Lake Macquarie has been previously noted (Miskiewicz, 1986). The continuous onshore advection, which may be seen in the currents [Figs 7 and 11(c)] suggests that the high numbers of gonostomatids present at station D on 22 January should have appeared further inshore at station C by 25 January. Although no corresponding increase occurred, it is possible that longshore patchiness may be responsible.

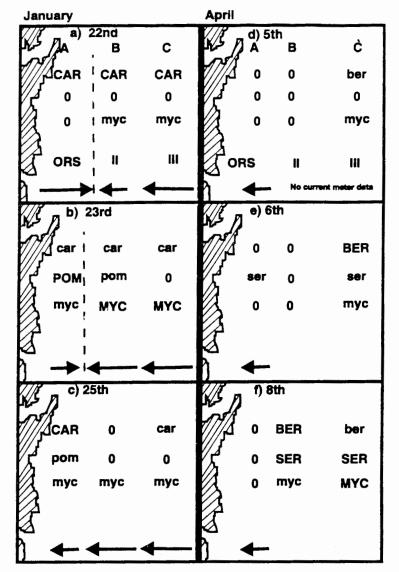


Fig. 11. Summary of the major biological and physical interactions observed off Sydney during January and April 1994, at the inshore stations A, B and C, and at the corresponding current meter stations ORS, II and III. For January three dominant larval fish taxa were carangids (CAR), pomacentrids (POM) and myctophids (MYC). For April the three dominant taxa were berycids (BER), serranids (SER) and myctophids (MYC). The change between uppercase, lowercase and 0 corresponds to >50%, 5-50% and <5% of the maximum larval concentration of that taxon observed. The large and small current vector arrows correspond to a cross-shelf velocity >0.2 m s⁻¹ and <0.2 m s⁻¹ respectively. The dashed line between stations A and B in January represents the probable convergence zone.

Effects of cross-shelf hydrographic differences in April

The cross-shelf temperature and velocity fields displayed considerably less variability during the April sampling period than during the January sampling period. Local wind stress during the April sampling period was weak and offshore the EAC was strong and relatively steady over the four days (Fig. 9). Little change in the average abundance of the four dominant families was observed between 5 and 6 April (Fig. 5). This agrees with the lack of change of oceanographic conditions observed over these two days.

The temperature and salinity data recorded by the ship's in situ instruments during the

sampling tows show that the temperature–salinity signatures across the shelf are split into two distinct groups: inshore (A, B) and offshore [C, D, E, Fig. 6(b)], with the single exception of station B on 8 April. The shift in the T–S signature at station B on 8 April was associated with a concomitant increase in berycids, serranids and myctophids [Figs 5 and 11(f)]. The onshore water mass shift at station B on 8 April is consistent with the weak onshore near-surface drift [Fig. 11(f)]. The temperature difference between these groups is only approximately 0.3°C in magnitude, with a minimal but consistent salinity difference (0.05–0.1). These differences are not able to be resolved in the temperature sections shown in Fig. 10. It is unclear why the overall abundance of serranids increased on the night of 8 April.

Importance of a dynamic approach to ichthyoplankton variability

Mass transport has been previously identified as an important modifier of the spatial distribution of ichthyoplankton near Lizard Island (Leis, 1986; Leis and Goldman, 1987) in the Coral Sea (Leis, 1993) and in the Banda Sea, Indonesia (Soewito and Schalk, 1990). Cowen et al. (1993) concluded that "without more sophisticated data describing actual flow, we are relegated to the same old exercise of attempting to correlate highly variable and dynamic larval fish distributions with average flow/hydrographic conditions" (p. 584). Off Sydney, a significant amount of variability in surface ichthyoplankton was accounted for by considering transport in the near-surface layer. In April a more traditional comparison between temperature–salinity signatures and biological distributions was able to account for the between-night changes in abundance of the four dominant families. This water mass approach would not, however, have been successful during the January period when cross-shore advection in the near-surface layers could not be readily identified by changes in temperature or salinity.

Longshore currents were not considered in the present authors' interpretation as no along-shore replication of ichthyoplankton sampling was undertaken. Gray (1993) found no consistent along-shore trends for the abundant taxa occurring on the Sydney shelf in both April–May and August–September 1990. Intrinsic along-shore patchiness in the abundance of individual taxa (e.g. serranids on 8 April) was beyond the scope of this study. Nevertheless, the processes described in this paper are derived from gross changes in abundance and generally for more than one taxon. Along-shore ichthyoplankton variability may be minimal as the Sydney shelf lacks significant topographic discontinuities. In summary, it is assumed that the nightly cross-shelf trends observed are persistent throughout each night. It should be noted that the day CTD profiles were 6–12 h prior to the night ichthyoplankton sampling. Therefore, slight discrepancies between day CTD profiles (Figs 8 and 10) and night T–S diagrams (Fig. 6) occurred.

It has also been assumed in this study that the larvae behaved as passive particles — active larval swimming has not been accounted for (Leis, 1991). Vertical migration by larval fish may have specific consequences relating to the cross-shelf current comparisons made in this study, as fish larvae may be capable of migrating from the surface waters to depths where a different current regime may exist. The low passed currents shown in Figs 7 and 8 are representative of gross currents in the near-surface mixed layer, which varied in depth between 30 and 80 m during the sampling periods. Subsequently, for this analysis to become invalid, larvae must migrate to depths greater than 30–80 m for extended periods.

The Sydney shelf is remarkably dynamic for a relatively straight coast. This is a

consequence of the complex forcing processes which drive the circulation of the shelf and slope waters, which are primarily local wind, the EAC, remotely forced CTWs and smaller scale processes such as the baroclinic tide (McClean-Padman and Padman, 1991; Griffin and Middleton, 1992; Gibbs and Middleton, 1997). This study has shown that quantifying these processes is crucial when determining baseline ichthyoplankton assemblages, necessary for the environmental impact assessment of Sydney's former coastal sewage outfalls (e.g. Gray et al., 1992). Sampling could be stratified with regard to temperature and salinity, rather than bathymetry or geographic location alone. Sporadic cross-shelf flows are probably also important in the transport of larvae from shelf spawning to coastal and estuarine nurseries.

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REFERENCES

- Boehlert, G. W. and Mundy, B. C. (1993) Ichthyoplankton assemblages at seamounts and oceanic islands. *Bulletin of Marine Science*, 53, 336-361.
- Bonecker, A. C. T. and Hubold, G. (1990) Distribution and abundance of larval gonostomatid fishes in the southwest Atlantic. *Meeresforsch*, 33, 38–51.
- Chiu, T.-S. and Hsyu, Y.-H. (1994) Interannual variation of ichthyoplankton density and species composition in the waters off northeastern Taiwan. *Marine Biology*, **119**, 441–448.
- Clarke, K. R. and Green, R. H. (1988) Statistical design and analysis for a biological effect study. *Marine Ecology Progress Series*, **46**, 213–226.
- Clarke, R. H. (1993) Non-parametric analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.
- Cowen, R. K., Hare, J. A. and Fahay, M. P. (1993) Beyond hydrography: can physical processes explain larval fish assemblages within the middle Atlantic Bight? *Bulletin of Marine Science*, **53**, 567–587.
- Cresswell, G. R. and Boland, F. M. (1981) Internal waves detected with a continental shelf array. Australian Journal of Marine and Freshwater Research, 32, 1-8.
- Fortier, L. and Leggett, W. C. (1985) A drift study of larval fish survival. *Marine Ecology Progress Series*, 25, 245-257.
- Frank, K. T. and Leggett, W. C. (1985) Reciprocal oscillations in densities of larval fish and potential predators: a reflection of present or past predation? *Canadian Journal of Fisheries and Aquatic Science*, **42**, 1841–1849.
- Gibbs, M.T. and Middleton, J.H. (1997) Barotropic and baroclinic tides on the Sydney continental shelf. *Continental Shelf Research*, 17, 1005–1027.
- Gibbs, M. T., Middleton, J. H. and Machesiello, P. (1997) Baroclinic response of Sydney shelf waters to local wind and deep ocean forcing. *Journal of Physical Oceanography*, in press.
- Gomon, M. F., Glover, J. C. M. and Kuiter, R. H. (1994) *The Fishes of Australia's South Coast.* State Print, Adelaide, 992 pp.
- Gray, C. (1993) Horizontal and vertical trends in the distributions of larval fishes in coastal waters off central New South Wales, Australia. *Marine Biology*, **116**, 649–666.
- Gray, C. A., Otway, N. M., Laurenson, F. A., Miskiewicz, A. G. and Pethebridge, R. L. (1992) Distribution and abundance of marine fish larvae in relation to effluent plumes from sewage outfalls and depth of water. *Marine Biology*, 113, 549-559.
- Griffin, D. A. and Middleton, J. H. (1991) Local and remote wind-forcing of New South Wales inner shelf currents and sea level. *Journal of Physical Oceanography*, 21, 304-322.
- Griffin, D. A. and Middleton, J. H. (1992) Upwelling and internal tides over the inner New South Wales continental shelf. *Journal of Geophysical Research*, 97, 14389–14405.

- Hutchins, B. and Swainston, R. (1986) Sea-fishes of Southern Australia. Swainston Publishing, Daglish, Western Australia, 180 pp.
- Kailola, P. J., Williams, M. J., Stewart, P. C., Reichelt, R. E., McNee, A. and Grieve, C. (1993) Australian Fisheries Resources. Bureau of Resource Sciences, Canberra, Australia, 422 pp.
- Kingsford, M. J. (1990) Linear oceanographic features: a focus for research on recruitment processes. *Australian Journal of Ecology*, **15**, 391–401.
- Kingsford, M. J. (1993) Biotic and abiotic structure in the pelagic environment: importance to small fishes. *Bulletin of Marine Science*, **53**, 393–415.
- Large, W. S. and Pond, S. (1981) Open ocean momentum flux measurements in moderate to strong winds. Journal of Physical Oceanography, 11, 324-336.
- Legendre, L. and Demers, S. (1984) Towards dynamical biological oceanography and limnology. Canadian Journal of Fisheries and Aquatic Science, 41, 2-19.
- Leis, J. M. (1986) Vertical and horizontal distribution of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. *Marine Biology*, 90, 505-516.
- Leis, J. M. (1991) Vertical distribution of fish larvae in the Great Barrier Reef lagoon, Australia. *Marine Biology*, 106, 1-10.
- Leis, J. M. and Goldman, B. (1987) Composition and distribution of larval fish assemblages in the Great Barrier Reef lagoon, near Lizard Island, Australia. *Australian Journal of Marine and Freshwater Research*, 38, 211–223.
- Leis, J. M. and Miller, J. M. (1976) Offshore distributional patterns of Hawaiian fish larvae. *Marine Biology*, 36, 359-367.
- Leis, J. M. and Rennis, D. S. (1983) *The Larvae of Indo-Pacific Coral Reef Fishes*. New South Wales University Press, Sydney and University of Hawaii Press, Honolulu. 269 pp.
- Leis, J. M. and Trnski, T. (1989) The Larvae of Indo-Pacific shorefishes. New South Wales University Press, Sydney. 371 pp.
- Leis, L. M. (1993) Larval fish assemblages near Indo-Pacific coral reefs. *Bulletin of Marine Science*, **53**, 362–392.
- Mackas, D. L., Denman, K. L. and Abbott, M. R. (1985) Plankton patchiness: biology in the physical vernacular. Bulletin of Marine Science, 37, 652-674.
- McClean-Padman, J. and Padman, L. (1991) Summer upwelling on the Sydney inner continental shelf: the relative roles of local wind forcing and mesoscale eddy enroachment. *Continental Shelf Research*, 11, 321–345.
- Miskiewicz, A. G. (1986) The season and length at entry into a temperate Australian estuary of the larvae of Acanthopagrus australis, Rhabdosargus sarba and Chrysophrys auratus (Teleostei: Sparidae). In Proceedings of the 2nd International Conference on Indo-Pacific Fishes, ed. T. Uyeno, R. Arai, T. Taniuchi and K. Matsura. Ichthyological Society of Japan, Toyko, pp. 740-747.
- Moser, H. G., Richards, W. S., Cohen, D. M., Fahay, M. P., Kendall, A. W. and Richardson, S. L. (eds.) (1984) Ontogeny and Systematics of Fishes. Vol. 1, pp. 1-760. Special Publication of the American Society of Ichthyologists and Herptologists, Allen Press, Lawrence, KS, U.S.A.
- Nilsson, C. S. and Cresswell, G. R. (1981) The formation and evolution of East Australian Current eddies. *Progress in Oceanography*, 9, 133–183.
- Ozawa, T. (1986) Studies on the Oceanic Ichthyoplankton in the Western North Pacific. Kyushu University Press, Japan, 430 pp.
- Richardson, S. L., Laroche, J. L. and Richardson, M. D. (1980) Larval fish assemblages and associations in the north-east Pacific Ocean along the Oregon coast, winter-spring 1972-1975. Estuarine and Coastal Marine Science, 11, 671-699.
- Sabates. A. (1990) Changes in the heterogeneity of mesoscale distribution patterns of larval fish associated with a shallow coastal haline front. Estuarine, Coastal and Shelf Science, 30, 131-140.
- Smith, M. M., Heemstra, P. C. (1986) Smiths' Sea Fishes. Southern Book Publishers, Grahamstown, 1047 pp. Soewito, J. J. and Schalk, P. H. (1990) Spatial and seasonal patterns in fish larvae distribution in the Banda Sea (Indonesia). Netherlands Journal of Sea Research, 25, 591-600.
- Suthers, I. M. and Frank, K. T. (1991) Comparative persistence of marine fish larvae from pelagic versus demersel eggs off southwestern Nova Scotia, Canada. *Marine Biology*, **108**, 175–184.
- Tzeng, W. N. and Wang, Y. T. (1993) Hydrography and distribution dynamics of larval and juvenile fishes in the coastal waters of the Tanushi River estuary, Taiwan, with reference to estuarine larval transport. *Marine Biology*, 116, 205-217.

Underwood, A. J. (1981) Techniques of analysis of variance in experimental marine biology and ecology.

Oceanography and Marine Biology Annual Review, 19, 513-605.

Young, P. C., Leis, J. M. and Hausfeld, H. F. (1986) Seasonal and spatial distribution fish larvae in waters over the North West continental shelf of Western Australia. *Marine Ecology Progress Series*, 31, 209–222.