



# The Influence of Tidal Phase on Patterns of Ichthyoplankton Abundance in the Vicinity of an Estuarine Front, Botany Bay, Australia

**M. J. Kingsford and I. M. Suthers<sup>a</sup>**

*School of Biological Sciences A08, University of Sydney, NSW 2006, Australia*

*Received 16 August 1993 and in revised form 24 March 1995*

**Keywords:** ichthyoplankton; plume; fronts; tide; oceanography; transport; Australia; estuary

The influence of oceanography on abundance patterns of ichthyoplankton was compared at different phases of the tide in the vicinity of an estuarine front in Botany Bay, Australia. Fronts were observed at high, ebb, low and flood tides, but the most conspicuous colour discontinuities were found on ebb and flood tides. Greatest differences in water density were found across the frontal region on ebb tides. Because rainfall was low, density differences were primarily due to differences in temperature. There was strong advection of drogues into fronts and along frontal margins on ebb and flood tides. Thus, particles are 'jetted' along fronts. Total ichthyoplankton was always greatest in fronts on low tides (by 1.5–4 times). Rank abundance of ichthyoplankton in the plume, front and ocean, at other phases of the tide (flood, high, ebb), varied among days. Great differences in the composition of ichthyoplankton were found between the plume, front and ocean at all phases of the tide, but differences were most clear on ebb and low tides. Some types of fish were always most abundant in the front (e.g. Exocoetidae), or the plume and front (e.g. Gobiidae, Pleuronectidae, Hemiramphidae, Blenniidae), regardless of the state of the tide. Some pelagic juveniles were only found in tows that contained drift algae, especially in the front. The 'jetting' of larvae along topographically stable fronts on flood tides may influence spatial patterns of recruitment in bays and estuaries. The intensity of differences in water density across the frontal region, between the plume and ocean, did not explain the relative abundance patterns of fish. The authors argue that a combination of physical advection, responses by ichthyoplankton to the biological attributes of fronts (e.g. abundance of food), lag effects (i.e. response of plankton to aggregation), and differences in larval supply (from spawning) were responsible for patterns of abundance in different water masses at scales of less than 15 km. © 1996 Academic Press Limited

## Introduction

There is active debate on the importance of estuaries in Australia as nursery areas for fish from a variety of coastal environments (e.g. rocky reefs, demersal and pelagic fishes from

<sup>a</sup>Present address: School of Biological Sciences, University of New South Wales, Sydney, NSW 2052, Australia.

the continental shelf; Bell & Pollard, 1989; Bell & Worthington, 1993; Gillanders & Kingsford, 1993), as in other parts of the world (e.g. Nyman & Conover, 1988). It is generally accepted that a combination of larval behaviour and oceanography is critical for the retention of, or transport of, young invertebrates and fish out of and back into these areas (Norcross & Shaw, 1984). Although fronts may influence the distribution and movements of ichthyoplankton near estuaries (Kingsford, 1990; Largier, 1993), historically, attention has been given to the role of vertical movements of larvae and their relationship to tidal currents (Rijnsdorp *et al.*, 1985; Epifanio, 1988), direction of the wind (Shanks, 1986), and time of day (Kendall & Naplin, 1981).

Estuaries and adjacent coastal waters are influenced by freshwater runoff. Recent descriptions of nearshore oceanography have focused on low density plumes and how they influence the distribution of ichthyoplankton and other zooplankters (e.g. Govoni *et al.*, 1989; Grimes & Finucane, 1990; Kingsford & Suthers, 1994). The fronts of plumes clearly represent a major demarcation of the relative abundance of zooplankters and they have a potential role in the transport of larvae (Largier, 1993). Although abundances are often highest in frontal regions, this is not always the case (Kingsford & Suthers, 1994). Because of temporal variation in the sharpness of fronts (Yanagi & Takahashi, 1988; Yanagi & Tamaru, 1990), it has been hypothesized that state of the tide, topography, lunar cycle, freshwater input and related differences in the intensity of convergence (Wolanski & Hamner, 1988) may account for different patterns of plankton abundance (e.g. Govoni & Grimes, 1992). Whilst Dustan and Pinckney (1989) found that aggregation of phytoplankton in an estuarine front varied according to state of the tide, no stratified sampling programmes have quantitatively described such patterns for zooplankton.

Flotsam and other particles in fronts off Botany Bay appear to be advected along the frontal margin. On flood tides, these fronts have the potential to advect ichthyoplankton and 'jet' them to different locations in bays (Kingsford & Suthers, pers. obs.). On the ebb tides, plankters may be advected along the frontal margin as the plume extends across the continental shelf and is deformed by coastal currents (Kingsford & Suthers, 1994). The objective of this project was to test the prediction that abundance of ichthyoplankton in fronts would be influenced by differences in water density and related intensity of advection at frontal margins at different states of the tide. Patterns of ichthyoplankton abundance were described and compared with the physical intensity of discontinuities between water masses of the plume and ocean in fronts off Botany Bay on flood, full, ebb and low tides. It was possible that greatest abundances of some taxa would be predictably found where differences in water density were greatest (Le Fevre, 1986), but this is not always the case (Govoni & Grimes, 1992).

## Materials and methods

### *Oceanography*

Botany Bay is partially flushed by the tide on the east coast of New South Wales, Australia, and is fed by two rivers, the Cooks River and the Georges River. These rivers have a mean annual runoff of  $520 \times 10^6 \text{ m}^3$  (Total Environmental Centre, Sydney) which is low compared with the flood tide volume of  $4000 \text{ m}^3 \text{ s}^{-1}$  into the bay (Environmental Protection Authority, unpubl. data). Low density waters in the bay produce plumes that may extend up to 11 km from the entrance to the bay (Kingsford

& Suthers, 1994). Plumes extended 2–6 km on ebb tides, and on the flood tide the frontal region was found within the entrance of the bay.

The Botany Bay plume and associated fronts were examined 12 times during flood, high, ebb and low tidal phases in the austral spring–summer of 1990. The maximum tidal range in Botany Bay is 2 m, but tides ranged between 0.8 and 1.4 m during the study. Observations of each tidal phase took a maximum of 2 h. High or low tides were sampled within 1 h of the predicted tide, and ebb or flood tides were sampled during 2 h of peak flow. Sampling was stopped if the wind was  $>8 \text{ m s}^{-1}$ . Rainfall during the study was low, 16% of the November average for the last 57 years (Bureau of Meteorology, NSW regional office).

Temperature and salinity were determined using a Yeo-kal conductivity, temperature and depth device (CTD) from an inflatable boat; the water density was subsequently calculated using the UNESCO formulation and expressed as  $\sigma_t$ . Fronts were identified by differences in water colour and/or the presence of slick (*sensu*: Kingsford, 1990) which often contained flotsam. Horizontal physical discontinuities were measured by towing the CTD beside the boat and perpendicular to the front for approximately 200 m at  $0.5 \text{ m s}^{-1}$ , carefully avoiding turbulence about the sensors. The vertical profiles of physical measurements at sites 100 m either side of the front were determined by lowering the CTD at  $1\text{--}3 \text{ m s}^{-1}$  to just above the substratum. Depth of the plume was determined from the shallowest isopycnal which did not surface between ocean and plume sites.

Convergence rates into fronts, advection rates along the front, and direction of transport were determined using mini-drogues consisting of a numbered float (10 cm diameter), a weighted  $35 \text{ cm}^2$  square stiff plastic sheet suspended 35–45 cm below the surface. Ten drogues were deployed individually at 10-m intervals (a 10 m rope was trailed astern) perpendicular to the long axis of the front. Three bearings were taken from surrounding landmarks to record the starting position. The relative displacement of drogues was estimated 1–2 min after the initial deployment, and bearings and distances between the floats were recorded after 30–40 min when drogues had accumulated in the front. Mini drogues were deployed on three of three ebb tides and two of three flood tides. Drogues were only released in light winds (i.e.  $<15$  knots).

#### *Ichthyoplankton sampling and sampling design*

Ichthyoplankton were collected from October to December 1990 in Botany Bay (Figure 1). Neustonic ichthyoplankton were sampled using a neuston net with a  $40 \times 40 \text{ cm}$  mouth [as for Sameoto & Jarosznski (1969)] and  $0.28 \text{ mm}$  mesh. The mesh of the square net was organized as a box-pyramid with a filtration efficiency of 1:10. The net allowed rapid sampling of ichthyoplankton in different water masses (cf. purse seine used by Kingsford & Suthers, 1994). A General Oceanics flowmeter was situated at  $0.25\text{--}0.33$  of the width of the net to record average flow and volume filtered. The flowmeter was submerged at all times. The upper edge of the mouth of the net was approximately 2 cm out of the water.

Sampling was done at four states of the tide; high, ebb, low and flood during the day. Each tidal category was separated by at least 1 h. For each state of the tide, sampling was conducted on three random days and ichthyoplankton was collected from waters of the plume, front and ocean on each day. Samples in the plume and ocean were 150–300 m from the front. Three replicate hauls of 5 min duration were taken, filtering an average of  $40 \text{ m}^3$ . Drift algae may influence the types of fish found in different water masses

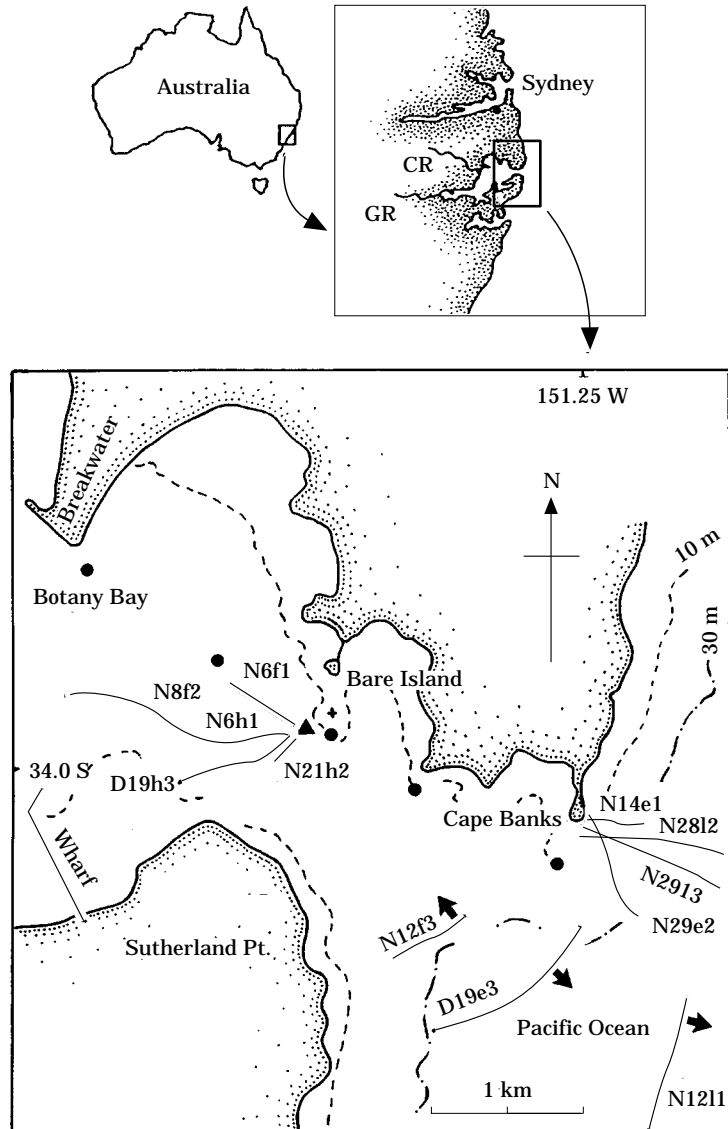


Figure 1. Map of the study area showing the region fronts were sampled at the entrance to Botany Bay, New South Wales, Australia. The position of sections of fronts sampled in this study are shown. Abbreviations for fronts are given as month/day/state of the tide/replicate within state of the tide.

(Kingsford, 1992, 1993), thus all drift algae collected in tows were weighed (wet wt. in grams) and correlated with catches of fish. Terminology of the developmental forms of fish is according to Leis and Rennis (1983).

#### *Relationships between physical oceanography and fish abundance*

The intensity of a discontinuity was related to the abundance patterns of fish as follows. The physical intensity of the frontal discontinuity was expressed as change in water density ( $\Delta D$ );  $\sigma_r$

Relationships between abundance of total ichthyoplankton and density differences in frontal regions were expressed using two methods: (1) abundance of fish in fronts minus that in plumes or the ocean side; these values were then correlated with  $\Delta D$ ; and (2) variation in abundance of total ichthyoplankton across the frontal region at each time was expressed as the variance divided by the mean of average fish abundances in the plume, front and ocean [equation (1)]; these values were also correlated with  $\Delta D$ . Equation (1) gave greater sensitivity than coefficients of variation.

$$\Sigma(\text{mean}-H)^2/\text{mean} \quad (1)$$

Where  $H$  is plume, front or ocean.

#### *Analytical procedures*

Data on concentrations of ichthyoplankton were analysed using ANOVA. State of the tide (Factor Tide) and plume, front, ocean (Factor Hydrology) were treated as fixed factors. Days [Factor Day(Tide)] were nested in the factor tide and all data were  $\ln(x+1)$  transformed to avoid heterogeneity of the data; data were tested for homogeneity using Cochran's tests after transformation.

Canonical discriminant analyses (CDA) were done for each state of the tide to identify differences in species composition among the water masses (i.e. plume, front, ocean). Analyses were done using SYSTAT (Wilkinson, 1990). Ten groups of fish were included in analyses for each state of the tide; groups were chosen based on the results of principal component analysis (PCA).  $\ln(x+1)$  transformations were used to normalize the data. Assemblages of fish were analysed using PCA and individual taxa were selected for CDAs based on the highest 'component loadings'. Component loadings (from PCA) indicated the species that contributed most variation to the data set and, therefore, were the likely candidates for CDA to identify differences in faunal composition between waters of the plume, front and ocean. Canonical plots are presented as Factor (1)  $\times$  Factor (2) and species that contributed most to the canonical loadings and/or had significant univariate  $F$ -tests among groups (i.e. plume, front, ocean).

## **Results**

### *Oceanography*

Physical attributes of the plume, front and ocean varied among states of the tide (Table 1). Highest differences in density were found on ebb tides, while physical measurements in water masses were similar at other states of the tide. Lowest density waters were found in the plume as for Kingsford and Suthers (1994). Temperature differences of up to 0.7 °C were recorded across the frontal boundary, with temperature generally highest in the plume. Differences in salinity were relatively small at the time of sampling (<0.09).

Composite broad-scale profiles (Figure 2) showed that low density water was within 1 km from the breakwater at high tide. These waters pushed out into the Tasman Sea during the ebb tides and facilitated the occurrence of fronts off Cape Banks (where a number of contours reached the surface at 3–4 km). Fronts were further from the entrance to the south-east of Cape Banks on ebb tides. At low tide, the low density anomaly was approximately half the depth of that on ebb tides. During flood and high tides, the low density layer was confined inside the entrance to Botany Bay.

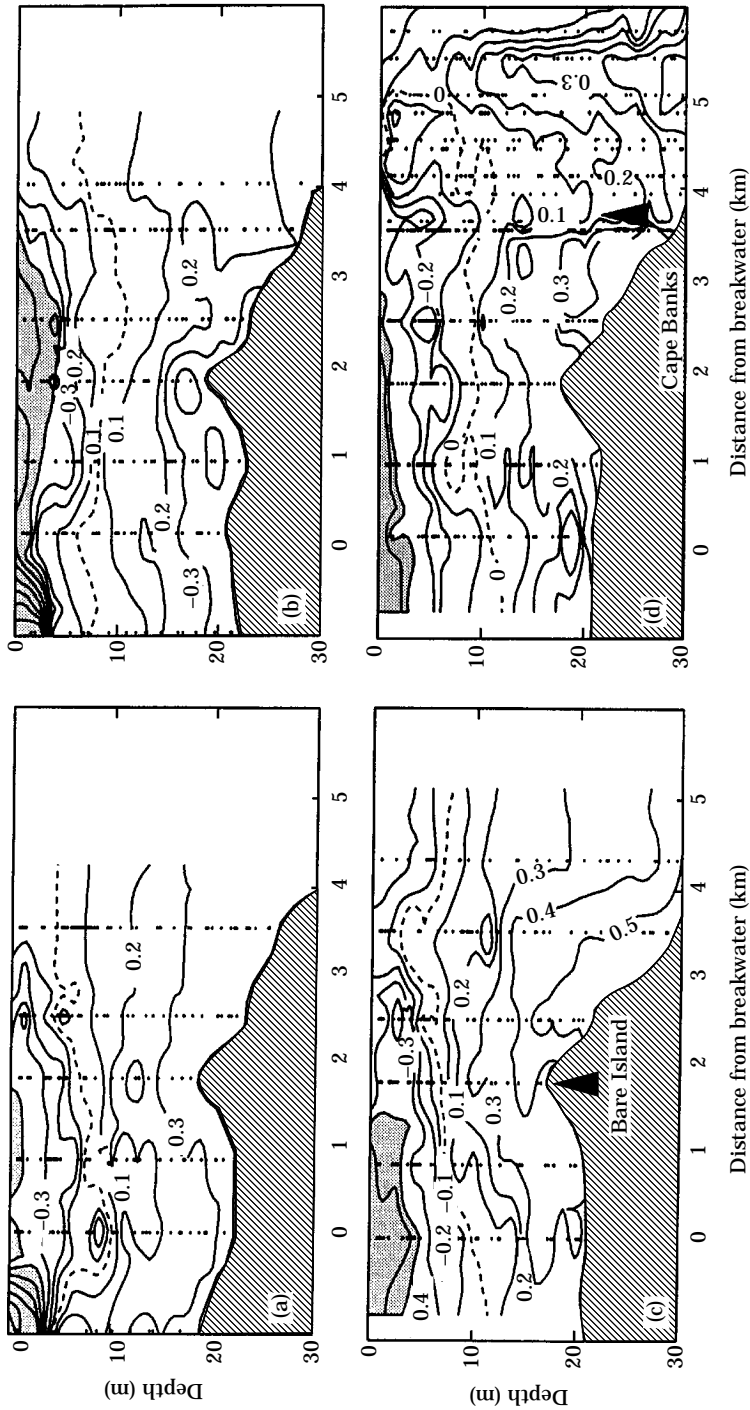


Figure 2. Composite broad-scale vertical profiles of density anomalies for each tidal phase (with dates from which the data were pooled). (a) high tide (21 November), (b) ebb tide (6 November; 19 December); (c) low tide (12, 14, 28 November; 19 December); (d) flood tide (12, 29 November). Density has been standardized for each day by subtracting the average from each datum. The dashed line shows the average contour (0), and stippled region shows density anomaly  $> -0.4 \text{ kg m}^{-3}$ . Location along the vertical profile immediately south of Bare Island (approximate flood tide location) and south of Cape Banks (approximate ebb tide location) is indicated with arrows.

TABLE 1. Physical characteristics of the frontal discontinuity in Botany Bay, New South Wales, Australia

Tidal phase	Variable				Front abbreviations
	$\Delta\sigma_t$	$\Delta$ Salinity	$\Delta$ Temperature (°C)	$\Delta$ Plume depth (m)	
High	0.013 (0.056-0.187)	0.045 (0.015-0.06)	0.364 (0.18-0.5)	4 (0-7)	N6h1,N2h2,D19h3
Ebb	0.233 (0.181-0.26)	0.088 (0.023-0.0124)	0.64 (0.6-0.7)	7.7 (7-8)	N14e1,N29e2,D19e3
Low	0.11 (0.005-0.2)	0.028 (0.016-0.051)	0.351 (0.028-0.709)	2.3 (0.3)	N1211,N2812,N2913
Flood	0.057 (0.014-0.12)	0.037 (0.005-0.095)	0.113 (0.019-0.194)	4 (3-5)	N6f1,N8f2,N12f3

Changes indicate the physical differences between waters of the plume and ocean. Mean (range) of values from 3 days. Front abbreviations, month/day/state of the tide/replicate day for each state of the tide.  
 $\sigma_t$ , water density.

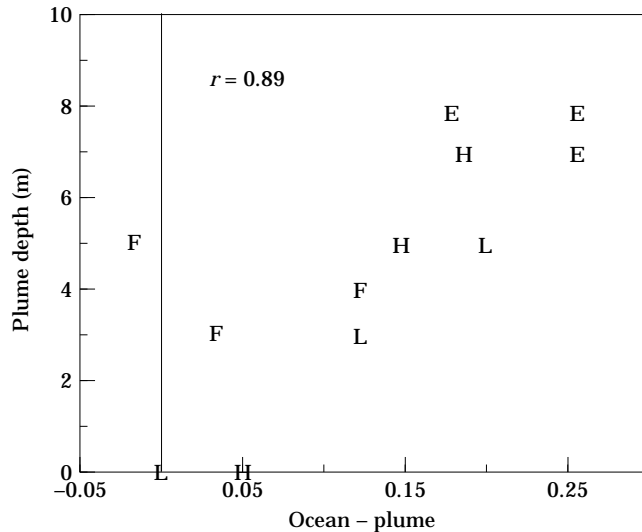


Figure 3. Correlation between plume depth and horizontal difference in water density. E, ebb; H, high; F, flood; L, low tide.

Most plumes were 2–8 m deep within 100 m of the front. Differences in  $\sigma_t$  between the ocean and the plume correlated with depth of the plume (Figure 3); greatest differences in  $\sigma_t$  and greatest plume depths were found on ebb tides (Figure 3). Differences in  $\sigma_t$  across fronts did not correlate with the range in tidal heights (0.8–1.5 m; i.e. change in lunar tides) when all states of the tide were considered ( $r=0.03$ ,  $n=12$ , n.s.). Single fronts at both high and low tides (when water movement was minimal) showed no clear profile of differences in physical structure, despite being associated with a visible front.

On both ebb and flood tides, Lagrangian drogues were advected into and transported along the front within minutes of deployment (Figure 4). Net movement of the drogues along the front was about 0.38–0.42 m s<sup>-1</sup> into Botany Bay. Flood tide fronts exhibited convergence rates of 0.33 m s<sup>-1</sup> from the incoming ocean and 0.17 m s<sup>-1</sup> from the plume side, even when drogues were moving against a 8 m s<sup>-1</sup> wind. Initial advection along the front was 0.58–0.65 m s<sup>-1</sup> on the ocean side and 0.3–0.38 on the plume side. Strongest shear at the front on flood tides was observed in the vicinity of Bare Island where topography appeared to influence the position of fronts.

The net movement of the 10 drogues over the 30–40 min study was 0.18–0.33 m s<sup>-1</sup> along the frontal margin. Drogues on the ocean side (19 December) appeared to be ‘run into’ by the plume as it was advected out of Botany Bay. Maximum convergence from both sides of ebb tide fronts was approximately 0.17 m s<sup>-1</sup>. Initial advection rates along the front was up to 0.1–0.5 m s<sup>-1</sup>.

#### *Distribution of fish*

Total abundance of larvae was always highest in fronts at low tides (Figure 5), but the patterns of abundance were variable for flood, high and ebb tides. On flood tides, highest concentrations of larvae were found in the plume, while the front generally ranked second in abundance (2 of 3 days). Total abundance varied considerably among days (e.g. flood tide Day 2 vs. Day 3); this resulted in a significant day effect [Day(tide),



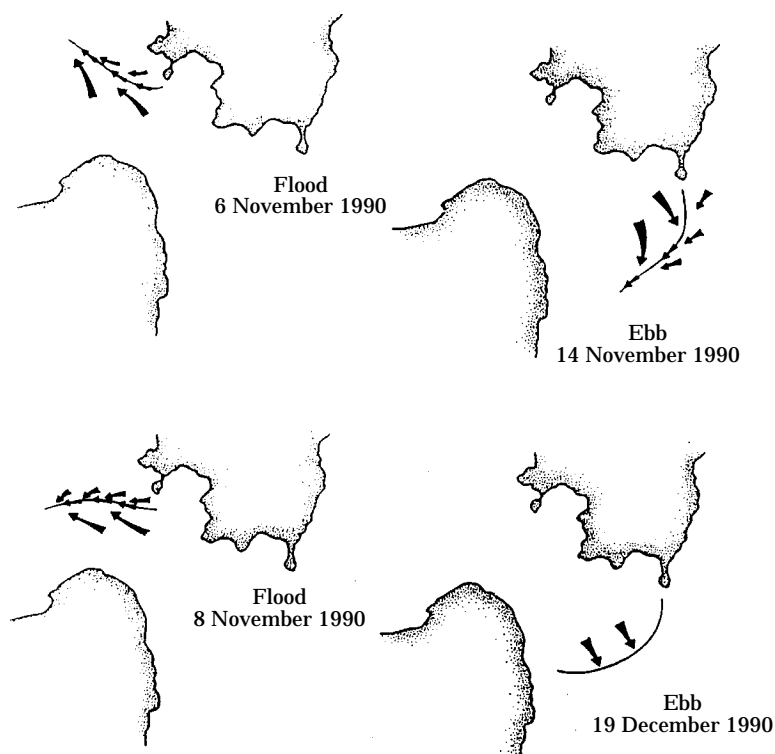


Figure 4. Schematic diagram showing the advection of mini-drogues into and along ebb and flood fronts in Botany Bay. The size of arrows indicates relative velocity.

Table 2]. Variable rank abundance of larvae in plume, front and ocean on different days resulted in a significant Hydrology \* Day(Tide) interaction.

Small larvae (preflexion and flexion) showed changes in rank abundance in the plume, front and ocean at all states of the tide and patterns varied among days (Figure 6). This resulted in a significant Hydrology \* Day(Tide) interaction. Highest concentrations of larvae were generally captured in the plume (e.g. high, Day 3; ebb, Day 1; low, Day 1; flood, Day 2). The variable input of small larvae to the area (e.g. from spawning) probably resulted in large differences among days (Table 2). With few exceptions (i.e. ebb, Day 3; high, Day 2), abundance of small larvae was always highest in the plume or front, as Kingsford and Suthers (1994) found for fish eggs. This would suggest that many fish reproduce in Botany Bay, and that larvae from estuarine (e.g. gobies) and coastal spawnings (e.g. exocoetids) are advected into and aggregate in fronts.

When postflexion and juvenile fish were abundant, they were generally found in highest abundance in fronts, or occasionally in plumes (e.g. high, Day 3; low, Days 1 & 3; Figure 7). Variation in rank abundance in waters of plumes, fronts and the ocean resulted in a significant Hydrology \* Day(Tide) interaction (Table 2). For example, at high tide, most fish were found in the front on 2 of 3 days, but highest abundances were found in the plume on Day 3.

There were major differences in the taxonomic composition of larvae collected in the plume, front and ocean on ebb and low tides (Figure 8). There was little or no overlap in taxonomic composition of samples from the front with other water masses. A high number of atherinids, exocoetids, mullids and hemiramphids characterized fronts at

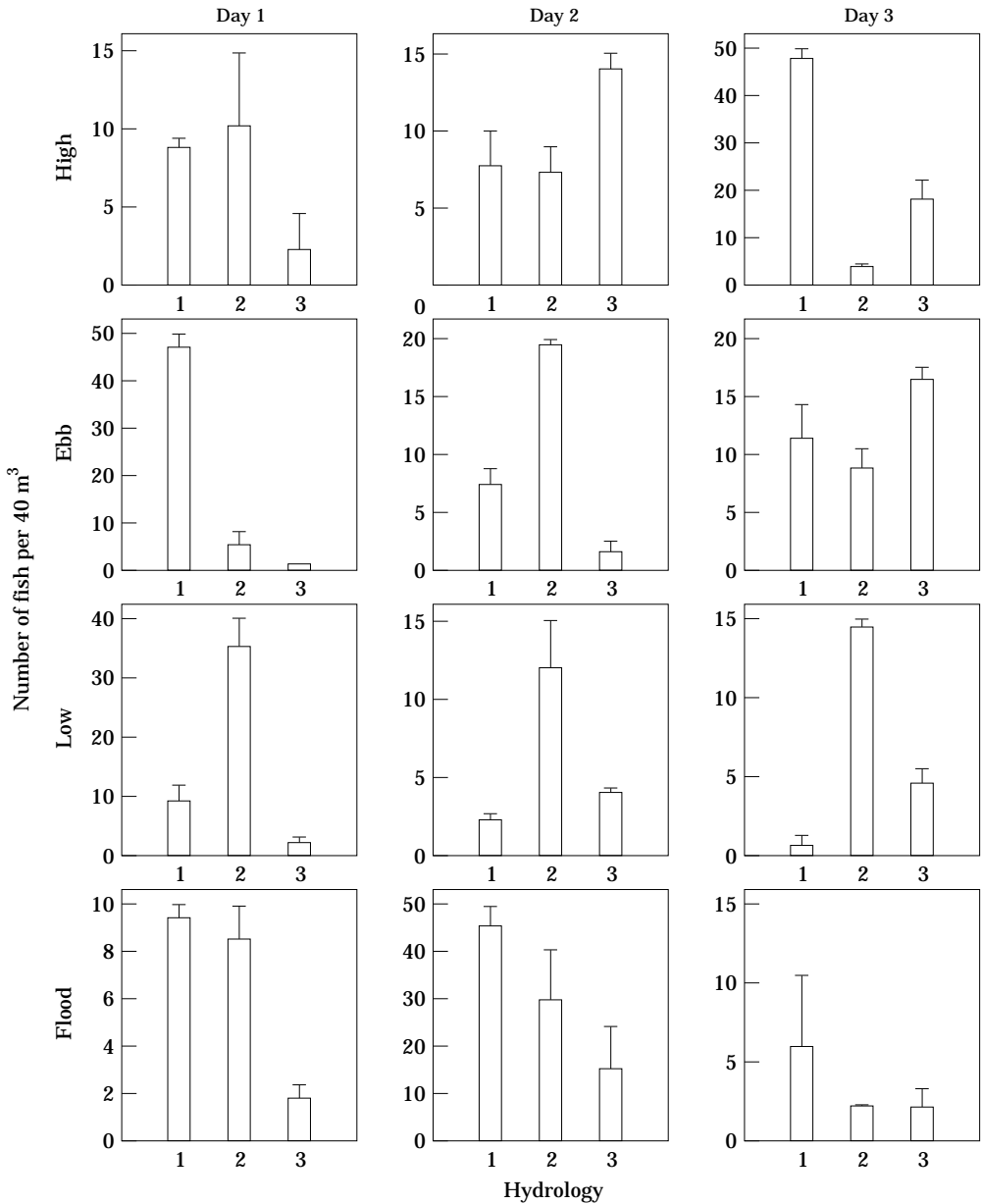


Figure 5. Total abundance of fish sampled at 200–300 m from the estuarine front in the plume (1), front (2) and ocean (3) on three different days and four phases of the tide; mean+SE.

these stages of the tide. Exocoetids, scorpaenids, 'other carangids' and scorpidids were rarely found outside of the front at any state of the tide (Figure 5, Table 3). Partly as a result of this, species diversity was greatest in the front (Table 3). Most individuals of many taxa were in the plume and front and were, therefore, rare or absent in 'ocean' waters; e.g. hemiramphids, gerriids, atherinids and blennies (Table 3). On the ebb, low tide, highest numbers of blennies and pleuronectids were found in the plume. Although

TABLE 2. Analyses of variance for fish collected at four states of the tide (Factor Tide), in plume, front and ocean (Factor Hydrology) on three replicate days (Factor Day)

Category of fish		Total	BF	PJ
Cochran's <i>C</i>		0.17 n.s.	0.13 n.s.	0.11 n.s.
Source of variation	df	MS	MS	MS
Tide	3,8	0.8	6.4	4.2
Hydrology	2,16	5.0	7.2	5.5 <sup>a</sup>
T*H	6,16	2.8 <sup>b</sup>	1.1	2.4
Day (Tide)	8,72	3.7 <sup>b</sup>	4.4 <sup>b</sup>	2.9 <sup>b</sup>
H*D(T)	16,72	1.7 <sup>b</sup>	2.1 <sup>b</sup>	1.1 <sup>b</sup>
Residual	72	0.4	0.4	0.2

$n=3$  replicate tows. Tide (T) and Hydrology (H) were treated as fixed factors and Day (D) as random. Cochran's *C* was used to test for homogeneity of the data (degrees of freedom 2, variances 36).

<sup>a</sup> $P<0.05$ ; <sup>b</sup> $P<0.001$ ; BF, preflexion and flexion fish; PJ, postflexion and pelagic juveniles (terminology Leis & Rennis, 1983); df, degrees of freedom; MS, mean squares; n.s., not significant.

gobies were usually characteristic of the plume, some individuals were also found in the ocean (Figure 9). Concentrations of pleuronectids (Figure 10) and gobiids dropped quickly outside of the plume. Low numbers of these fish found in the ocean may have been exported from the bay on a previous ebb tide (Kingsford & Suthers, 1994).

Although the abundance of some species varied among states of the tide and days in different water masses, similar total numbers were caught in waters of the plume, front and offshore after pooling (Table 3). Mullids (120/121 were postflexion fish), for example, were most abundant in the front and ocean at times [plume, front, ocean; mean(SE)]: low, Day 1, 0.3(0.3), 3.3(1), 0; low, Day 2, 1(0.6), 3.6(1), 3.3(3); and the plume at other times: high, Day 3, 8(2), 0, 3(2); ebb, Day 2, 3.3(1), 1.3(1), 1.3(1). This variation in abundance from day to day between plume, front and ocean may relate partly to movements or transport of small fish to and from the enclosed bay.

Significant quantities of drift algae were collected in tows at three times of sampling (mean 50–800 g per tow) and it was always most abundant in fronts. Because only certain taxa and developmental forms of fish associate with drift algae (Kingsford, 1992), there was no significant relationship between abundance of fish and amount of algae in tows; i.e. large numbers of some fish were found in the absence of algae which destroys this relationship ( $n=108$  tows): total fish  $r=0.002$ , n.s.; preflexion and flexion fish  $r=0.04$ , n.s.; postflexion and juvenile fish  $r=0.072$ , n.s.; mullids  $r=0.037$ , n.s.; Exocoetidae  $r=0.041$ , n.s. Some pelagic juveniles, however, were only found in tows that contained drift algae including: *Coryphaena*, *Seriola*, *Stigmatophora*, *Petroscirtes*, *Plagiotremus*, Diodontidae and Antennariidae (Table 3). Most of the monacanthids caught were preflexion (17/21); only postflexion and juvenile monacanthids associate with algae.

The magnitude of differences in water density between the plume and ocean did not explain the relative abundance patterns of fish. There was a poor relationship between the total number of fish in the front vs. that of the plume and the difference in water density ( $r=0.39$ ,  $n=12$ , n.s. @  $P=0.05$ ). Although the greatest differences in water

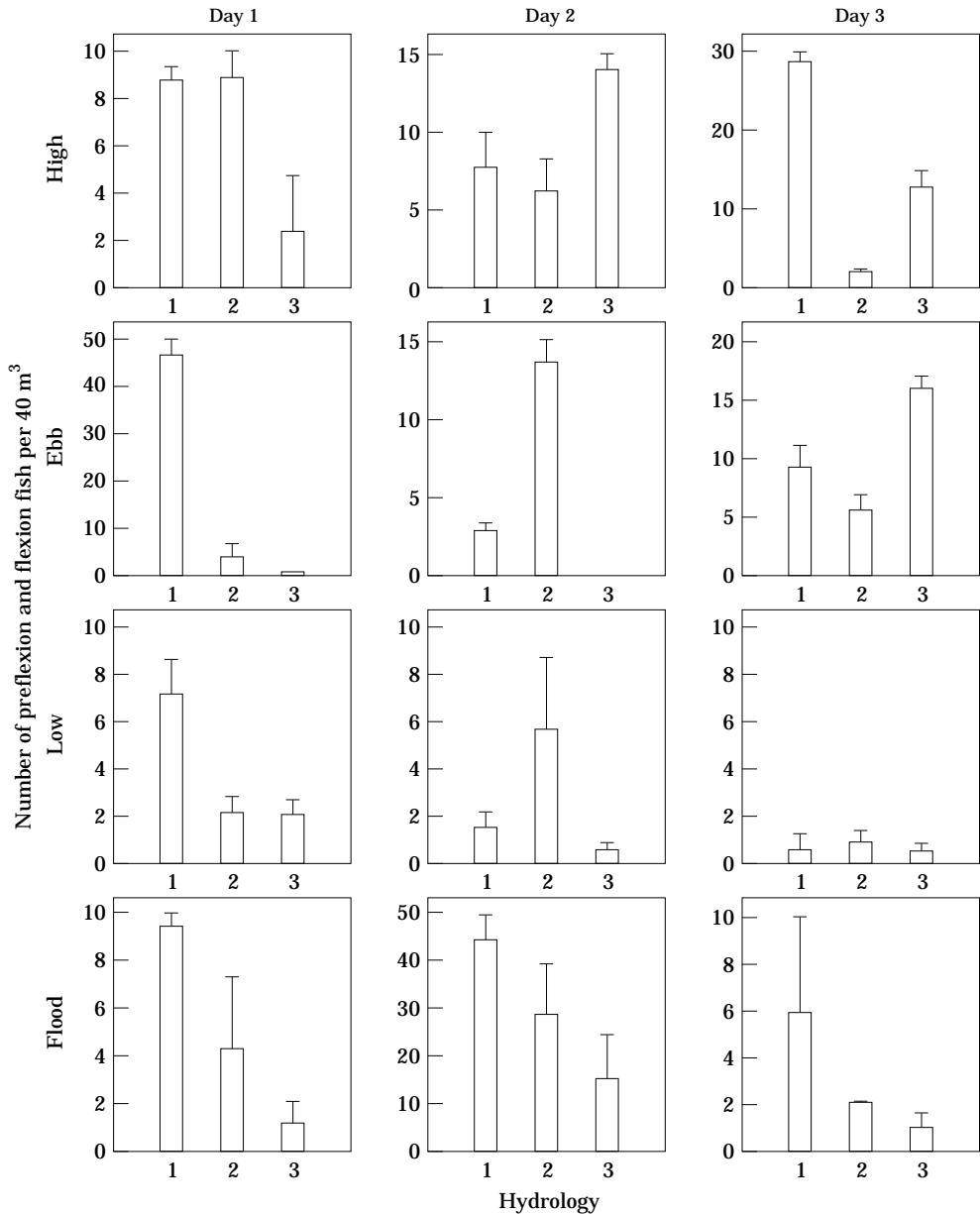


Figure 6. Preflexion and flexion fish sampled at 200–300 m from the estuarine front in the plume (1), front (2) and ocean (3) on three different days and four phases of the tide; mean+SE.

density sometimes corresponded with differences in abundance of fish between fronts and plumes (Figure 11), this did not appear to relate to phase of the tide. No significant relationship was found between total fish in the front and ocean, and how these compared with the difference in water density ( $r = -0.569$ ,  $n=12$ , n.s.@ $P=0.05$ ). Furthermore, there was no consistent relationship between variation in fish abundance among water masses [according to equation (1)] in the vicinity of fronts and differences

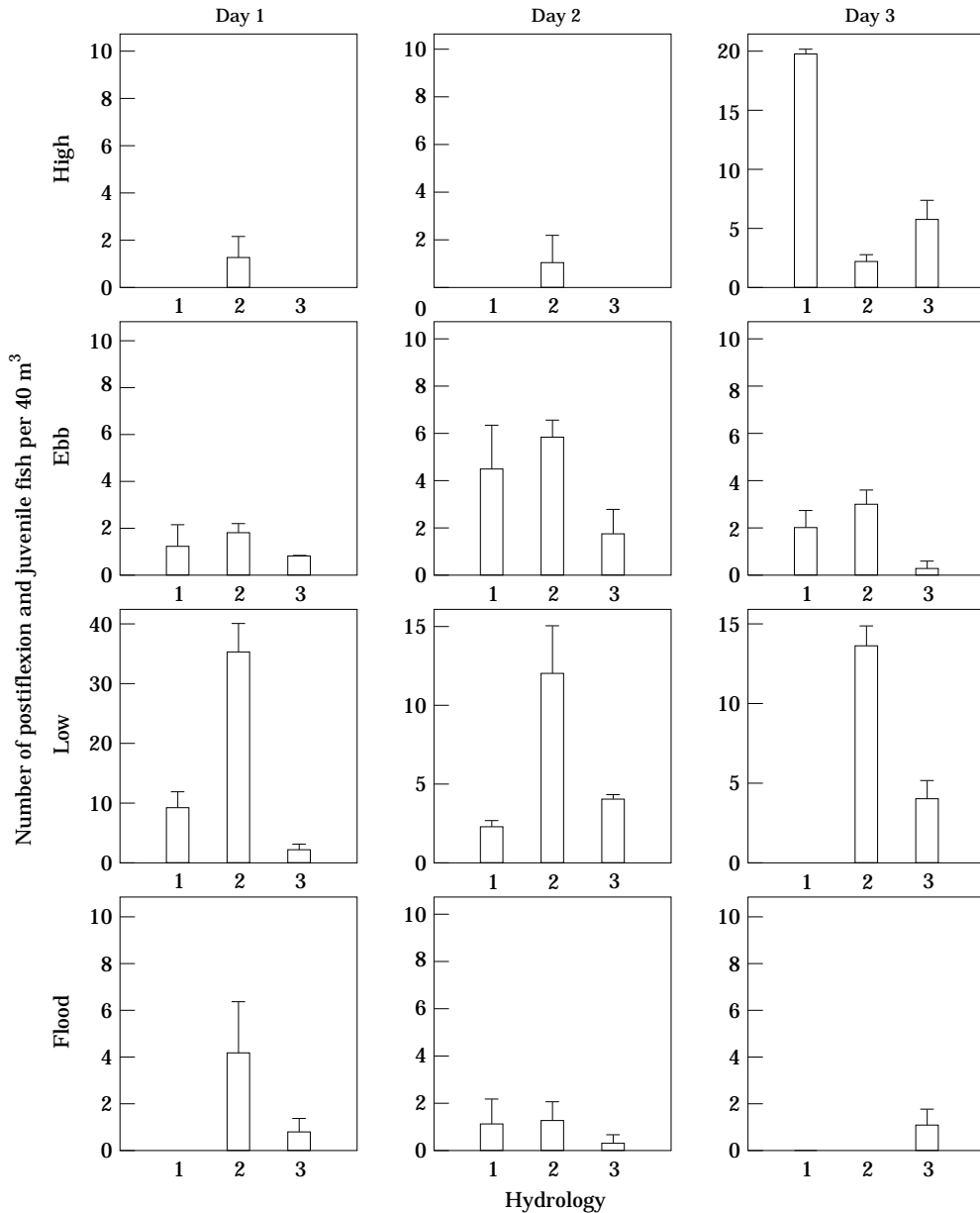


Figure 7. Postflexion and juvenile fish sampled at 200–300 m from the estuarine front in the plume (1), front (2) and ocean (3) on three different days and four phases of the tide; mean+SE.

in water density. Variances greater than 15 times the mean were recorded at low and high differences in water density. Convergence rates alter with water density and other factors (Govoni & Grimes, 1992). Greatest differences in density, movement of the plume (1–1.25 kph; Chick, 1993) and interaction with mainstream currents, which flow perpendicular to the movement of the plume (Kingsford & Suthers, 1994), were found on ebb tides. Drogues indicated high convergence rates on flood tides, but patterns of

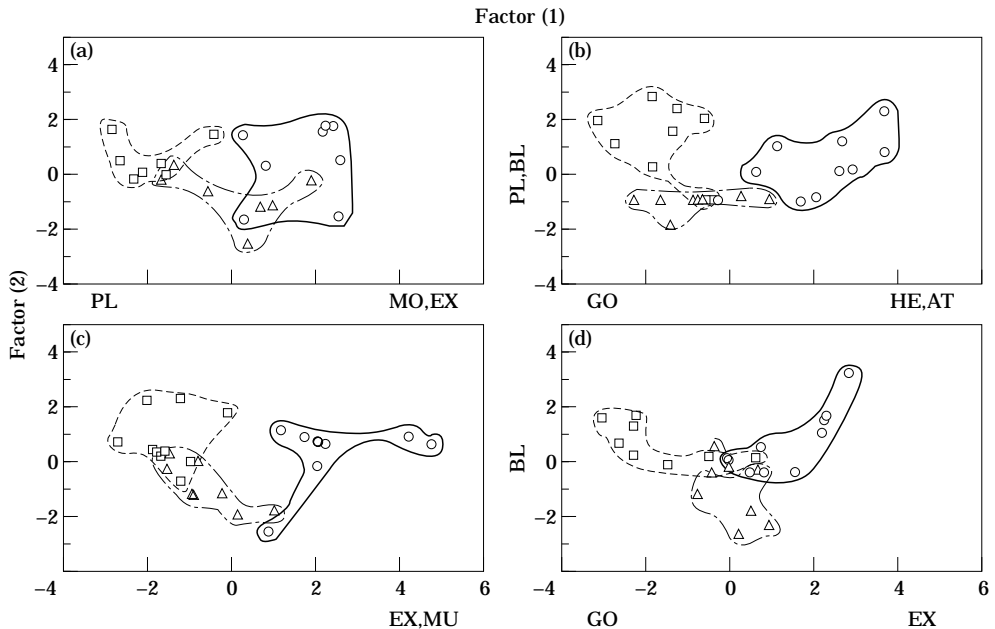


Figure 8. Canonical discriminant analyses on ichthyoplankton from waters of the plume, front and ocean at different phases of the tide. (a) high, (b) ebb, (c) low, (d) flood tides.  $\square$ , plume;  $\circ$ , front;  $\triangle$ , ocean; PL, Pleuronectidae; BL, Blenniidae; Mo, Monacanthidae; GO, Gobiidae; He, Hemiramphidae; AT, Atherinidae; EX, Exocoetidae; MU, Mullidae.

abundance of ichthyoplankton were not predictably highest in fronts at ebb or flood tides.

It was hypothesized that the abundance of very small larvae (preflexion and flexion) was more likely to vary according to differences in water density (and potentially the intensity of convergence) than abundance of postflexion and juvenile fish. However, no significant relationships were found between the abundance of preflexion and flexion larvae and water density for comparisons between front and plume ( $r=0.263$ ,  $n=12$ , n.s. @  $P=0.05$ ) as well as front and ocean ( $r=0.09$ ,  $n=12$ , n.s. @  $P=0.05$ ; Figure 11).

## Discussion

The effect of tidal phase on estuarine plumes had a major influence on patterns of ichthyoplankton abundance and species composition. Differences in abundance in the vicinity of estuarine/riverine plumes have previously been found at small scales (10 s of m, Govoni & Grimes, 1992; Kingsford & Suthers, 1994) and mesoscales (1–100 km, e.g. Govoni *et al.*, 1989; Grimes & Finucane 1991). Abundance of ichthyoplankton, in these studies, was sometimes highest in fronts, yet states of the tide can influence rank abundance of plankters in water masses around frontal boundaries (Dustan & Pinckney, 1989; Pinckney & Dustan, 1990). Previous studies on ichthyoplankton around fronts have not stratified sampling according to phase of the tide. In the present study, ichthyoplankters were consistently (i.e. on all days) most abundant in fronts at low tide, largely due to high abundance of postflexion and juvenile fish. The species composition of fish in fronts was conspicuously different from the plume on ebb and low tides, while

TABLE 3. The taxonomic composition of small fish collected from plumes (P), fronts (F) and ocean (O) in Botany Bay

Family	Specific	P	F	O
Clupeidae	<i>Sardinops neopilchardus</i>	11	8	6
	<i>Spratelloides robustus</i>	5	4	1
Engraulididae	<i>Engraulis australis</i>	4	3	2
Gobiesocidae		0	5	0
Antennariidae		0	2	0
Exocoetidae	<i>Cypselurus</i> spp.	1	73	0
Hemiramphidae		27	23	7
Atherinidae		92	73	20
Macroramphosidae	<i>Macroramphosus</i> sp.	0	1	1
Syngnathidae		0	2	0
Scorpaenidae		0	21	0
Triglidae		2	1	2
Pegasidae		0	2	0
Teraponidae	<i>Pelates quadrilineatus</i>	9	0	0
Ambassidae	<i>Velambassis jacksoniensis</i>	1	0	4
Sillaginidae		0	1	3
Pomatomidae	<i>Pomatomus saltator</i>	2	1	0
Carangidae	Other carangids	0	9	0
	<i>Trachurus</i> spp.	2	3	2
Corphaenidae	<i>Corphaena hippurus</i>	1	0	0
Sparidae	<i>Acanthopagrus australis</i>	4	0	3
	<i>Pagrus auratus</i>	1	0	0
Gerreidae	<i>Gerres ovatus</i>	11	3	0
Mullidae		41	41	39
Monodactylidae	<i>Monodactylus argenteus</i>	0	1	1
Girellidae	<i>Girella tricuspidata</i>	3	10	5
Kyphosidae		5	1	3
Scorpididae	<i>Microcanthus strigatus</i>	1	9	1
Enoplosidae	<i>Enoplosus armatus</i>	0	3	1
Pomacentridae	Other pomacentrids	0	1	0
	<i>Chromis</i> sp	3	1	4
Cheilodactylidae		1	1	3
Mugilidae	Other mugilids	0	1	0
	<i>Liza argentea</i>	2	3	1
Labridae		2	0	1
Blenniidae	Other blennies	13	8	2
	<i>Omobranchus anolius</i>	19	13	6
	<i>Petroscirtes lupus</i>	3	9	0
	<i>Plagiotremus</i> sp	0	1	0
Tripterygiidae/Clinidae		21	17	10
Dactylopteridae		1	0	0
Gobiidae		154	40	39
Siganidae		0	2	0
Pleuronectidae		143	57	32
Monacanthidae		10	7	5
Ostraciidae	<i>Lactoria</i> sp.	0	0	1
Diodontidae		0	1	0
Yolk sac larvae		21	8	30
Unidentified		11	10	17
Total taxa		31	39	29

Data are total numbers pooled for each state of the tide.

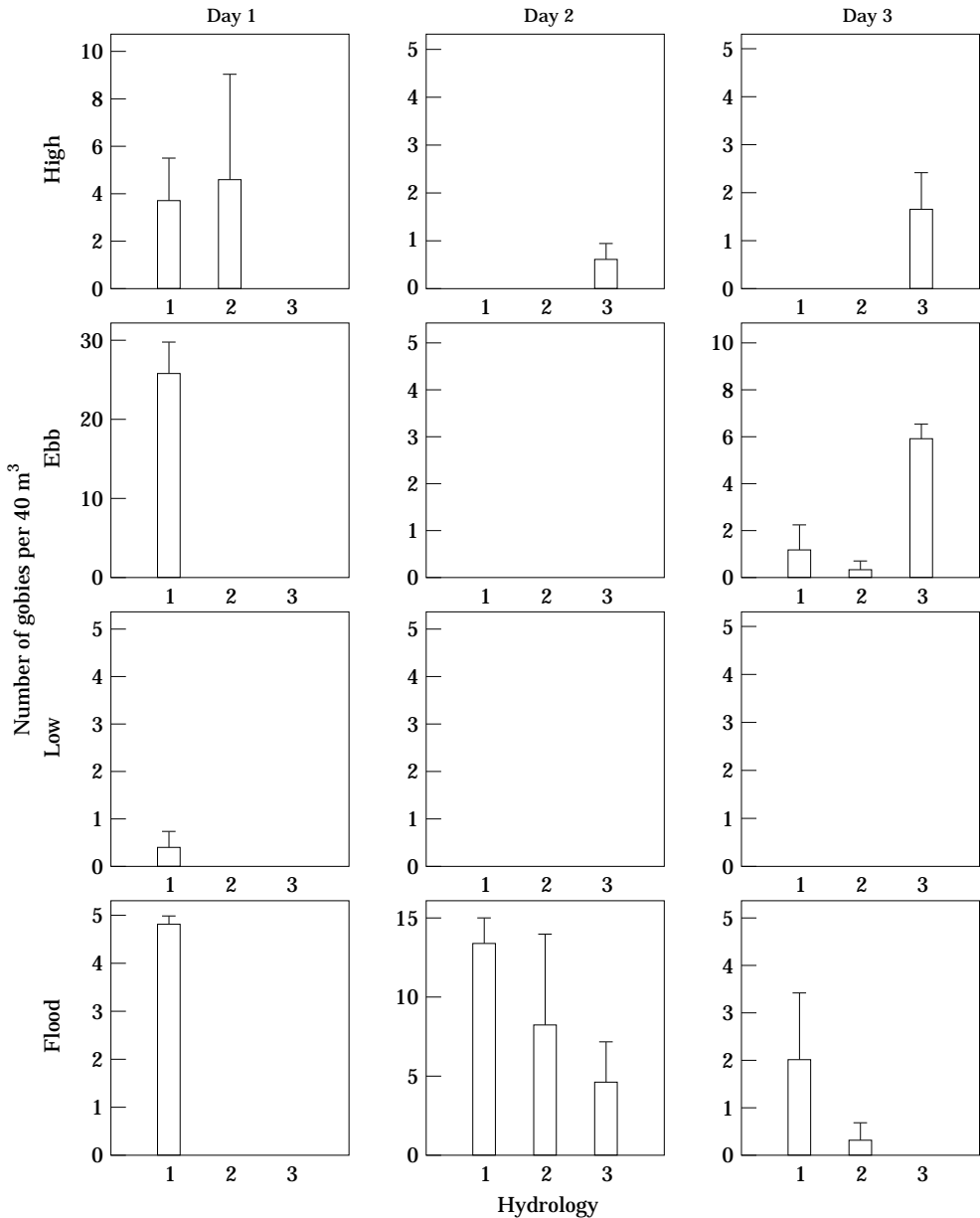


Figure 9. Gobiidae sampled at 200–300 m from the estuarine front in the plume (1), front (2) and ocean (3) on three different days and four phases of the tide; mean + SE.

some ‘overlap’ in sample composition was found on flood and high tides. Greatest convergence rates have been found at ebb and low tides in the Mississippi plume (Govoni & Grimes, 1992), but in the present study, fish were not consistently more abundant in fronts at these stages of the tide. High convergence rates were recorded on flood tides, with drogues, which may be related to the influence of topography near Bare Island (Figure 1; Wolanski & Hamner, 1988). Total abundance of ichthyoplankton was



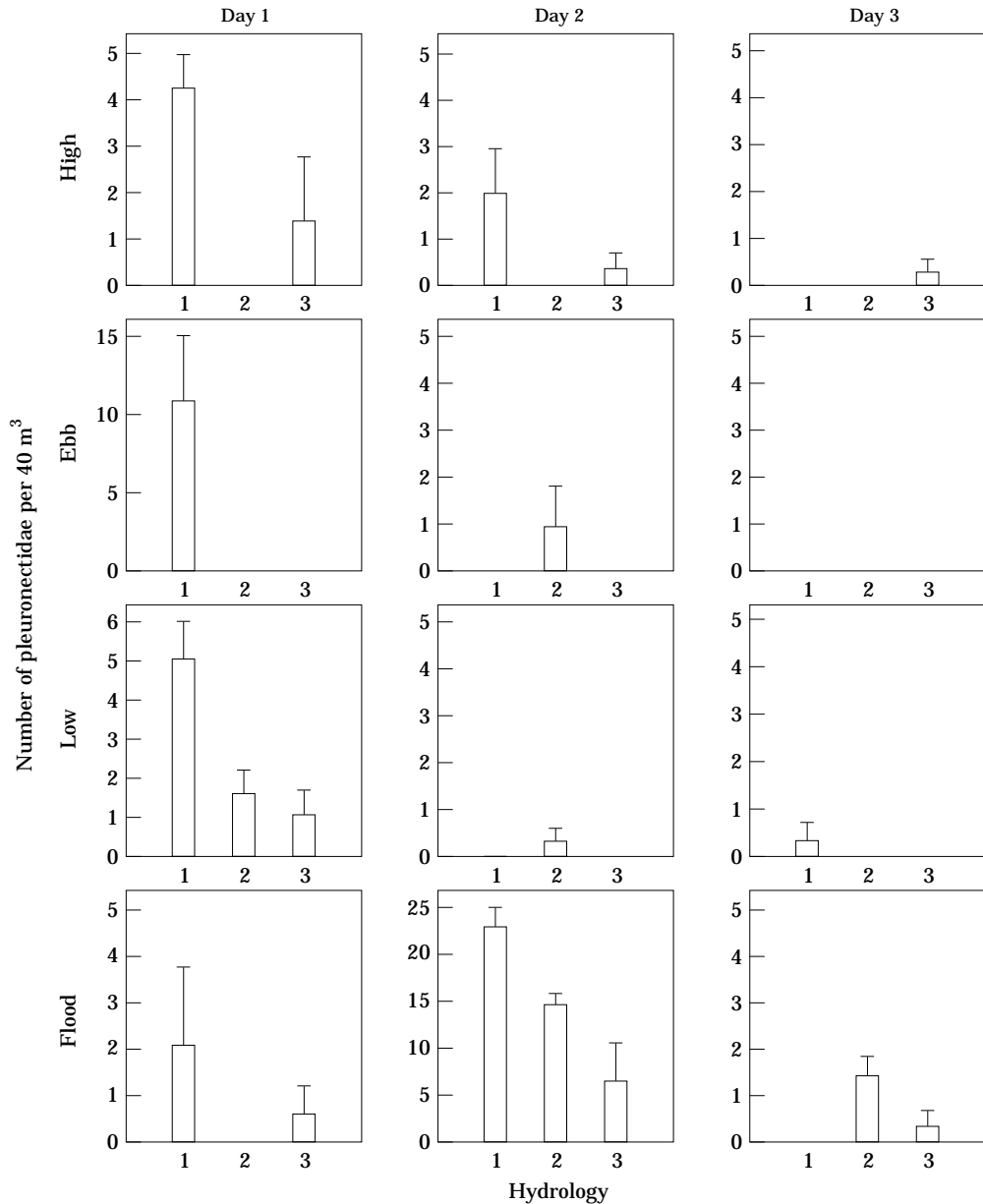


Figure 10. Pleuronectidae sampled at 200–300 m from the estuarine front in the plume (1), front (2) and ocean (3) on three different days and four phases of the tide; mean+SE.

not consistently more abundant in fronts on flood tides. Some fish were only found in fronts, regardless of state of the tide (e.g. Exocoetidae). Thus, fronts were important and importance did not vary with state of the tide for these groups of fish. Pelagic juveniles of some species were only found in tows that contained drift algae, which was generally in fronts, as for other convergences (Kingsford & Choat, 1986; Davenport & Rees, 1993). Although the presence of flotsam and algae may confound comparisons between

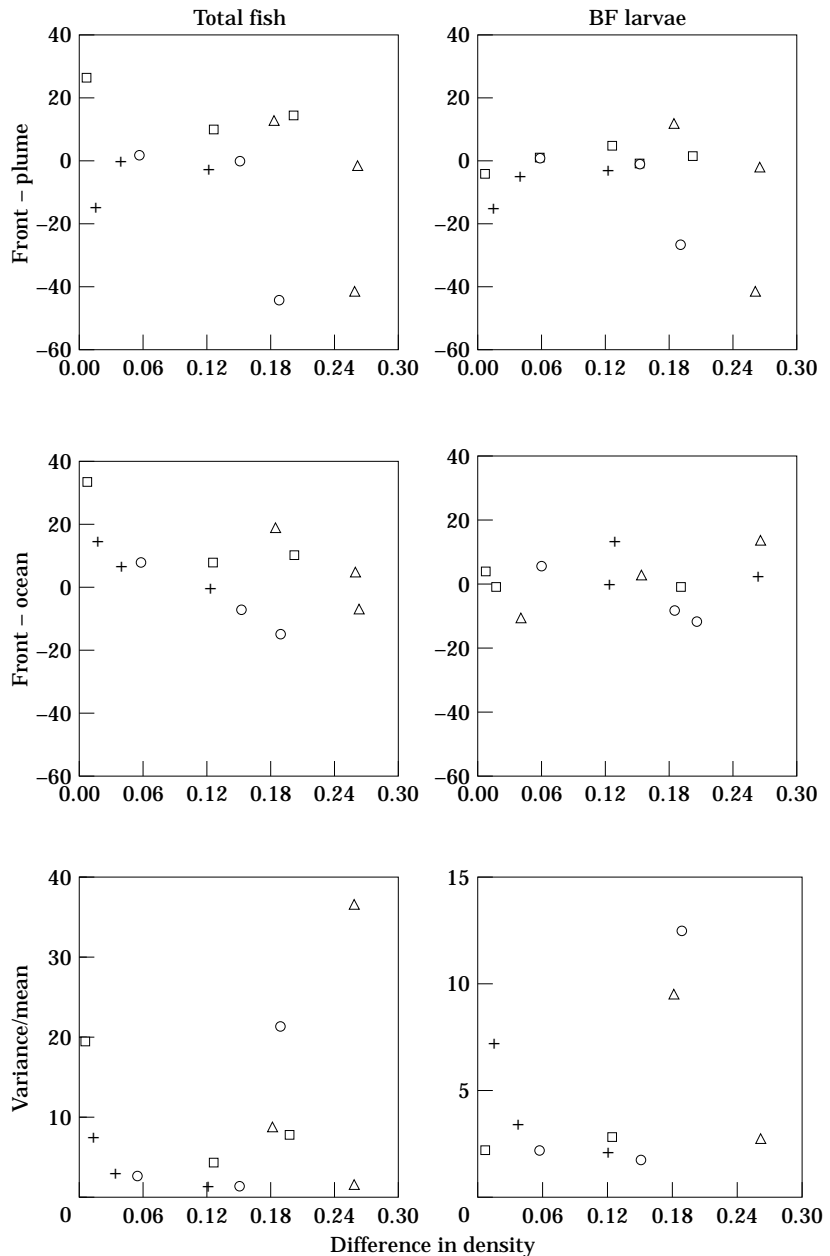


Figure 11. Relationships between differences in water density at the frontal discontinuity and abundance of fish.  $\circ$ , high;  $\triangle$ , ebb;  $\square$ , low;  $+$ , flood; BF, preflexion and postflexion larvae. Front-plume, front-ocean=mean abundance of fish in front minus that of the plume or ocean. Variance/mean, see equation (1).

water masses (Kingsford, 1993), drift algae were only found in fronts on three occasions, and relationships between quantity of algae and number of fish were poor.

On flood tides, particles from the ocean side are quickly advected into fronts and are transported into Botany Bay along the long axis of fronts. Fish that accumulate in fronts

may be 'jetted' to predictable areas of estuaries and shallow bays when fronts are topographically stable in position, as for some other types of fronts (Wolanski & Hamner, 1988). Recruitment 'hot spots' that have been identified in bays and fronts may contribute to such spatial variation in recruitment (e.g. McNeill *et al.*, 1992). Fish that recruit into bays (e.g. Worthington *et al.*, 1992; Hair *et al.*, 1994) and have been collected in high abundance in fronts include scorpidids, mullids, mugillids, girellids (Kingsford & Suthers, 1994; present study). These taxa are largely neustonic during the day (e.g. Kingsford, 1988; McCormick, 1994). A variety of other taxa which rise to the surface during the night (e.g. labrids) were not collected in the present study, and would also be subject to transport in fronts. Although the 'guiding' of larvae by fronts has been suggested (Largier, 1993), and 'axial fronts' move considerable distances into estuaries on flood tides (Nunes & Simpson 1985; Brown *et al.*, 1991), this aspect of fronts has been little explored.

The penetration of plumes across the continental shelf on ebb tides (Kingsford & Suthers, 1994), and advection of coastal waters into fronts on flood tides, appears to result in the concentration of some types of ichthyoplankton in fronts (e.g. Exocoetidae) that are absent or in low concentrations in adjacent waters of the plume and ocean.

It has been hypothesized that intensity of convergence at frontal margins can explain the degree to which fish are concentrated (e.g. Govoni & Grimes, 1992). In the present study, differences in water density were used as a measure of the intensity of the frontal discontinuity, and therefore convergence. No significant relationships were found between abundance of fish in fronts, compared to that of the plume and ocean. This was true for total ichthyoplankton and very small fish (pre- and postflexion) that are more likely to be advected by simple advective processes. The lack of a relationship is not considered surprising given the following: (1) there may be lag effects relating physical processes of advection to the aggregation of plankton; (2) fish may not only remain in fronts due to advective processes, but their residence time may relate to the availability of food (Kingsford, 1990); (3) variation in spawning in the estuary and ocean will alter the magnitude of ichthyoplankton variance between waters of the plume, front and ocean (Kingsford & Suthers, 1994); (4) different types of fish are more prone to advection or respond to fronts in different ways, and this may vary according to the developmental form of larvae; and (5) quantities of flotsam and biological aggregates may alter the attractiveness of fronts and associated fauna (Kingsford, 1993).

Although abundance of larvae did not correlate with the intensity of frontal discontinuities, clearest differences in species composition were found between waters of the plume, front and ocean on ebb tides (Figure 5) when the discontinuity was most intense (Table 1). On ebb tides, the frontal margin moves rapidly seaward (Kingsford & Suthers, 1994). Discontinuities weakened at low tide in the present study, but great differences in species composition were still found between the water masses. It is possible that this pattern is a remnant of advective processes on the ebb, low tides. Physical convergence that facilitates aggregation, and behavioural mechanisms that maintain aggregation in the absence of a physical process, would further explain why linear correlations of fish abundance with the intensity of physical discontinuities are unlikely to adequately describe spatial variation in abundance of zooplankters on spatial scales <10 km. There are clearly potential trophic advantages to ichthyoplankton that maintain their position in patches of food. Recent evidence indicates that some fish change their pattern of swimming to 'foraging mode' when they detect high concentrations of food (Doving

*et al.*, 1994). Hence aggregations facilitated by a physical mechanism may maintain biological integrity for some time after the physical mechanism dissipates.

Exact measurements of convergence at fronts are difficult to measure. Convergence rates can be influenced by wind, shear with mainstream currents, topography, water density (Garvine & Monk, 1974), rainfall (which was very low during the present study) and tidal regime (O'Donnell, 1993). Moreover, these influences may vary in importance depending on position along the frontal bulge. Based on all of these variables, greatest convergence rates would still be expected on ebb and flood tides, but highest abundances of ichthyoplankton were not always found in fronts at these states of the tide. The authors consider it unlikely, therefore, that improved synoptic views of convergence will fully explain abundance patterns of fish in dynamic estuarine fronts. Because of the multiple physical factors that influence patterns of fish abundance, orthogonal or mixed model sampling designs, as in the present study, are necessary to determine their relative contribution to variation in fish numbers.

In conclusion, great differences in the abundance of ichthyoplankton and species composition were found in the vicinity of fronts off Botany Bay. Greatest differences were found on the ebb, low tides and ichthyoplankton were predictably most abundant in the front at low tide. Physical differences between waters at the frontal discontinuity did not explain differences in abundance of total ichthyoplankton or preflexion and flexion fish in conditions of low rainfall. The authors argue that a combination of physical advection, responses of fish to biological attributes of fronts (i.e. lag effects), and differences in larval supply (from spawning in different water masses) were responsible for this pattern. Some fish were only found in fronts. An important consequence of aggregation in fronts, for fish that recruit to estuaries, is that topographically stable fronts on the flood tide may 'jet' potential settlers to predictable parts of bays and estuaries, thus influencing patterns of recruitment. Frontal transport should be incorporated into models of physical transport of larvae into estuaries.

### Acknowledgements

Thanks to Nicole Gallahar for assistance in the field, and Ben Druce, Karen Tricklebank and Bronwyn Gillanders for assistance in the laboratory. This research was supported by an ARC grant to M. J. Kingsford and an ARC Fellowship to I. M. Suthers. C. Grimes provided much constructive criticism of the manuscript.

### References

- Bell, J. D. & Pollard, D. A. 1989 Ecology of fish assemblages and fisheries associated with seagrasses. In *Biology of Seagrasses* (Larkum, A. W. D., McComb, A. J. & Shepard, S. A., eds). Elsevier, Amsterdam.
- Bell, J. & Worthington, D. 1993 Links between estuaries and coastal rocky reefs in the life of fishes from South eastern Australia. In *Proceedings of the Second International Temperate Reef Symposium* (Battershill, C. N., Schiel, D. R., Jones, G. P., Creese, R. G. & MacDiarmid, A. B., eds). NIWA, Wellington, pp. 85–92.
- Brown, J., Turrell, W. R. & Simpson, J. H. 1991 Aerial surveys of axial convergent fronts in UK estuaries and the implications for pollution. *Marine Pollution Bulletin* **22**, 397–400.
- Chick, R. 1993 *The Influence of Oceanography on the Vertical Distribution of Plankton*. Hons. Thesis, University of Sydney, 90 p.
- Davenport, J. & Rees, E. I. S. 1993 Observations on neuston and floating weed patches in the Irish Sea. *Estuarine, Coastal and Shelf Science* **36**, 395.
- Doving, K. B., Marstol, M., Anderson, J. R. & Knutsen, J. A. 1994 Experimental evidence of chemokinesis in newly hatched cod larvae (*Gadus morhua*). *Marine Biology* **120**, 351–358.

- Dustan, P.O. & Pinckney, J. J. L. 1989 tidally induced estuarine phytoplankton patchiness. *Limnology and Oceanography* **34**, 410–419.
- Epifanio, A. J. 1988 Transport of invertebrate larvae between estuaries and the continental shelf. *American Fisheries Society Symposium* **3**, 104–114.
- Garvine, R. W. & Monk, J. D. 1974 Frontal structure of a river plume. *Journal of Geophysical Research* **79**, 2251–2259.
- Gillanders, B. & Kingsford, M. J. 1993 Abundance patterns of *Achoerodus viridis* (Labridae) on estuarine and exposed rocky reefs: possible linkages. In *Proceedings of the 2nd International Temperate Reefs Symposium* (Battershill, C. N., Schiel, D. R., Jones, G. P., Creese, R. G. & MacDiarmid, A. B., eds). NIWA Marine, Wellington, pp. 93–98.
- Govoni, J. J. & Grimes, C. B. 1992 The surface accumulation of larval fishes by hydrodynamic convergence within the Mississippi River plume front. *Continental Shelf Research* **12**, 1265–1276.
- Govoni, J. J., Hoss, D. E. & Colby, D. R. 1989 The spatial distribution of larval fishes about the Mississippi River Plume. *Limnology and Oceanography* **34**, 178–187.
- Grimes, C. B. & Finucane, J. H. 1991 Spatial distribution and abundance of larval and juvenile fish, chlorophyll and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. *Marine Ecology Progress Series* **75**, 109–119.
- Hair, C., Bell, J. & Kingsford, M. J. 1994 Effects of position in the water column, vertical movement and shade on settlement to artificial habitats. *Bulletin of Marine Science* **55**, 434–444.
- Kendall, J. A. W. & Naplin, N. A. 1981 Diel-depth distribution of summer ichthyoplankton in the middle Atlantic Bight. *Fishery Bulletin U.S.* **79**, 705–726.
- Kingsford, M. J. 1988 The early life history of fish in coastal waters of northern New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research* **22**, 463–479.
- Kingsford, M. J. 1990 Linear oceanographic features: a focus for research on recruitment processes. *Australian Journal of Ecology* **15**, 391–401.
- Kingsford, M. J. 1992 Drift algae and small fish in coastal waters of northeastern New Zealand Marine Ecology Progress Series **80**, 41–55.
- Kingsford, M. J. 1993 Biotic and abiotic structure in the pelagic environment: importance to small fish. *Bulletin of Marine Science* **53**, 393–415.
- Kingsford, M. J. & Choat, J. H. 1986 Influence of surface slicks on the distribution and onshore movements of small fish. *Marine Biology* **91**, 161–171.
- Kingsford, M. J. & Suthers, I. M. 1994 Dynamic estuarine plumes and fronts: importance to small fish and plankton in coastal waters of NSW, Australia. *Continental Shelf Research* **14**, 655–672.
- Largier, J. L. 1993 Estuarine fronts: how important are they? *Estuaries* **16**, 1–11.
- Le Fevre, J. 1986 Aspects of the biology of frontal systems. *Advances in Marine Biology* **23**, 164–281.
- Leis, J. & Rennis, D. S. 1983 *The larvae of Indo-Pacific Coral Reef Fishes*. New South Wales University Press, Sydney.
- McCormick, M. I. 1994 Variability in age and size at settlement of the tropical goatfish *Upeneus tragula* (Mullidae) in the northern Great Barrier Reef Lagoon. *Marine Ecology Progress Series* **103**, 1–15.
- McNeill, S. E., Worthington, D. G., Ferrell, D. J. & Bell, J. D. 1992 Consistently outstanding recruitment of five species of fish to a seagrass bed in Botany Bay, NSW. *Australian Journal of Ecology* **17**, 359–365.
- Norcross, B. L. & Shaw, R. F. 1984 Oceanic and estuarine transport of fish eggs and larvae: a review. *Transactions of the American Fisheries Society* **113**, 153–165.
- Nunes, R. A. & Simpson, J. H. 1985 Axial convergence in a well-mixed estuary. *Estuarine, Coastal and Shelf Science* **20**, 637–649.
- Nyman, R. M. & Conover, D. O. 1988 The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York. *Fishery Bulletin U.S.* **86**, 237–250.
- O'Donnell, J. 1993 Surface fronts in estuaries: a review. *Estuaries* **16**, 12–39.
- Pinckney, J. & Dunstan, P. 1990 Ebb-tidal fronts in Charleston harbor, South Carolina: physical and biological attributes. *Estuaries* **13**, 1–7.
- Rijnsdorp, A. D., Van Stralen, M. & Van der Veer, H. W. 1985 Selective tidal transport of North Sea Plaice larvae *Pleuronectes platessa* in coastal nursery areas. *Transactions of the American Fisheries Society* **114**, 461–470.
- Sameoto, D. D. & Jaroszynski, L. O. 1969 Otter surface sampler: a new neuston net. *Journal Fisheries Research Board of Canada* **25**, 2240–2244.
- Shanks, A. L. 1986 Vertical migration and cross shelf dispersal of larval *Cancer* spp. and *Randallia ornata* (Crustacea: Brachyura) off the coast of southern California. *Marine Biology* **92**, 189–199.
- Wilkinson, L. 1990 *SYSTAT: The System for Statistics*. SYSTAT, Evanston, IL.
- Wolanski, E. & Hamner, W. M. 1988 Topographically controlled fronts in the ocean and their biological influence. *Science* **241**, 177–181.

- Worthington, D. G., Ferrell, D. J., McNeill, S. E. & Bell, J. D. 1992 Effects of the shoot density of sea-grass on fish and decapods—are correlations evident over large spatial scales? *Marine Biology* **112**, 139–146.
- Yanagi, T. & Takahashi, S. 1988 A tidal front influenced by river discharge. *Dynamics of Atmospheres and Oceans* **12**, 191–206.
- Yanagi, T. & Tamuru, H. 1990 Temporal and spatial variations in a tidal front. *Continental Shelf Research* **10**, 615–627.