

DOI: 10.1002/iroh.200711050

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Research Paper

Coupling between Marine Plankton and Freshwater Flow in the Plumes off a Small Estuary

key words: land-ocean coupling, zooplankton, size spectra, freshwater flow

Abstract

Freshwater discharge from rivers is a powerful forcing agent in coastal ecosystems. It not only generates strong ecological effects in estuaries, but also drives the dynamics of nearshore marine waters where prominent river plumes form biogeochemical hot spots in coastal seas worldwide. Large plumes from major rivers exert important controls on pelagic processes. The majority of estuaries are smaller, however, and the importance of the smaller plumes they generate is unknown. We measured the degree of coupling between freshwater flow and inshore zooplankton in such a plume from a subtropical estuary on the east coast of Australia. Flow regimes encompassed long periods of low freshwater input, punctuated by pulsed freshets that initiated the formation of buoyant, lower-salinity plumes in the nearshore marine zone. Plumes stimulated phytoplankton biomass in the receiving waters, and ultimately changes in zooplankton assemblages. Zooplankton responded strongly to river discharge: (1) in the absence of substantial freshwater flows and plumes, zooplankton was broadly similar in density and biomass across the estuarine-marine gradient; (2) freshets that generated significant plumes strongly modified hydrological conditions and lowered zooplankton in the estuarine and nearshore waters, and (3) after the initial freshet, zooplankton in the residual plume was at a higher density in nearshore than shelf waters. We demonstrate that coupling between riverine and coastal pelagic systems operates in small plumes, but that there is substantial temporal variance linked to fluctuations in freshwater delivery.

1. Introduction

Freshwater inflow is one of the fundamental drivers of coastal ecosystems. The amount and temporal modes of freshwater discharge profoundly influence a wide range of biological processes at multiple levels of ecological organisation in estuaries, ranging from shifts

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in species distributions to enhanced fisheries landings (SCHLACHER and WOOLDRIDGE, 1996; GILLANDERS and KINGSFORD, 2002). Ecological effects of freshwater discharge are, however, not confined to estuaries: they cross ecosystem boundaries in situations where river discharge enters coastal seas to produce prominent plumes over the continental shelf. In fact, river plumes extending into the sea create global hot spots of biogeochemical processes and biological activity in marine waters and link catchments with oceans (DAGG and BREED, 2003; MCKEE *et al.*, 2004). Some of the strongest ecological responses to freshwater inflow are manifested in the pelagos of estuaries. Estuarine phytoplankton biomass and primary productivity is highly variable at multiple, nested spatial and temporal scales (MALONE *et al.*, 1988). Numerous factors have been identified that regulate estuarine phytoplankton, including temperature, nutrient concentrations and recycling, irradiance, grazing and hydrodynamic regimes (CLOERN, 2001; HOWARTH and MARINO, 2006; SMITH, 2006). Freshwater inflow strongly modifies environmental conditions that control phytoplankton growth and can therefore be an important forcing agent for primary production in estuaries. Freshwater inflow has been linked to inter-annual variations in primary productivity in estuaries (HOWARTH *et al.*, 2000), the timing and intensity of seasonal blooms (MALONE *et al.*, 1988; HARDING, 1994), elevated phytoplankton biomass and productivity (MALLIN *et al.*, 1993) and shifts in assemblage composition and diversity (VINCENT *et al.*, 2002; ALBAINA and IRIGOIEN, 2004; CHÍCHARO *et al.*, 2006).

Changes to environmental conditions and primary productivity caused by variations in freshwater discharge to estuaries can propagate to higher trophic levels, affecting the abundance, distribution and species composition of both zooplankton and nekton (SCHLACHER and WOOLDRIDGE, 1996). Numerous examples exist of positive correlations between freshwater discharge and population responses of either estuarine invertebrates (WOOLDRIDGE and CALLAHAN, 2000; REAUGH *et al.*, 2007) or fish (HOUDE and RUTHERFORD, 1993; CHÍCHARO *et al.*, 2006). In some circumstances, however, the dynamics of plankton in relation to freshwater flow are decoupled from that of shrimp and fish (KIMMERER, 2002), and freshwater inflow can produce mixed species responses that differ between systems (ROSE, 2000). Exports of freshwater to coastal seas create a unique environmental milieu in continental shelf seas where they form turbid, nutrient-rich and buoyant plumes that overlay the more saline oceanic water masses (WOLANSKI *et al.*, 1999; DAGG *et al.*, 2004; DEVLIN and BRODIE, 2005; CRAVO *et al.*, 2006; GASTON *et al.*, 2006).

Plumes produced by low-salinity water that is discharged from estuaries provide favourable conditions for phytoplankton growth chiefly because of high nutrient concentrations (DAGG *et al.*, 2004). Consequently, river discharge plumes rank amongst the most productive regions of the world's oceans (GRIMES and KINGSFORD, 1996; DAGG and BREED, 2003).

Plume and frontal waters typically support phytoplankton biomass several fold higher than the adjacent shelf waters (DUSTAN and PINCKNEY, 1989; GRIMES and FINUCANE, 1991; GRIMES and KINGSFORD, 1996; MALLIN *et al.*, 2005). Patterns of phytoplankton biomass and production are, however, spatially complex and temporally variable (WYSOCKI *et al.*, 2006), or indicate small plume effects (MORGAN *et al.*, 2005; VARGAS *et al.*, 2006). Part of this complexity stems from the differential growth response of phytoplankton to the turbid but nutrient-rich plume waters (CLOERN, 2001). This usually results in peak productivity at intermediate salinities where growth is enhanced by increased nutrient availability but no longer limited by turbidity (LOHRENZ *et al.*, 1999; LIU and DAGG, 2003).

The increased phytoplankton biomass and production in river plumes can be mirrored by elevated densities of zooplankton, including larval fish, that are generally more abundant in the vicinity of plumes and frontal regions compared with the surrounding shelf waters (GOVONI and GRIMES, 1992; GRIMES and KINGSFORD, 1996; KINGSFORD and SUTHERS, 1996; MORGAN *et al.*, 2005). Plumes are sites of intense zooplankton grazing (LIU and DAGG, 2003), and zooplankton forms a key link in the trophic architecture of nearshore waters influenced by river discharges (BREED *et al.*, 2004). Concentrations of larval fish in frontal

regions and plume waters may also enhance recruitment of marine fish to coastal, inshore regions (GOVONI *et al.*, 1989; GRIMES and KINGSFORD, 1996).

Plumes from small estuaries are common on exposed coasts worldwide, where estuaries discharge directly on high-energy, open coastlines. Unlike the plumes produced by very large systems such as the Amazon or Mississippi (CALEF and GRICE, 1967; GREEN *et al.*, 2006), small estuaries generate small plumes (<10 km), and these are generally ephemeral as a result of strongly pulsed discharge events (GASTON *et al.*, 2006). Our underlying conceptual premise is that coupling between freshwater discharge and biological responses of marine plankton in small plumes may not scale linearly from that reported in larger systems, and may be highly variable over time. We therefore measured the numerical and biomass response of nearshore zooplankton influenced by strongly pulsed plume events. Specifically, we tested predictions that zooplankton would be: 1) similar in nearshore and offshore waters when freshwater discharge is low (baseflow), 2) less abundant nearshore than offshore during peak discharges because of low salinity and flushing (plume event), and 3) more abundant inshore than offshore as the plume subsides and productivity is stimulated by plume nutrients (residual plume).

2. Methods

2.1. Study Area

The response of mesozooplankton to pulsed river discharge events was measured in the Mooloolah Estuary on the east coast of Australia (Fig. 1). The estuary is small (catchment area 194 km²), shallow (average water depth 1–5 m) and short (tidal reaches ~13 km; GASTON *et al.*, 2006). Landuse in most of the upper and middle watershed is mainly grazing, agriculture (*e.g.*, cane fields) and remnant natural vegetation including mangroves. By contrast, the lower section has been transformed into urbanised canal estates, marinas and artificially stabilised embankments from which riparian vegetation has been removed (SCHLACHER and CARUTHERS, 2002). The mouth of the estuary (width 100 m) is trained by two artificial rock walls extending into a high-energy coastline.

Three sites predicted to differ in the relative strength of river plume influence were sampled: (1) the estuary 3 km upstream from the tidal inlet, (2) a nearshore site, located 1 km seawards from the estuary mouth, where plumes develop, and (3) an offshore reference site, 2.5 km seaward from the estuary, outside the influence of river plumes (GASTON *et al.*, 2006).

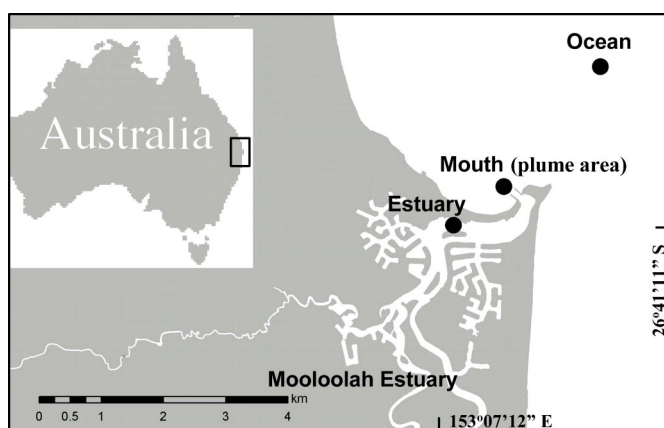


Figure 1. Map of the study system (Mooloolah Estuary) in Eastern Australia where the response of zooplankton to pulsed freshwater discharge events was quantified at three sites (Estuary, Mouth, Ocean) influenced to different degrees by river plumes.

Rainfall in the region is strongly seasonal, with dry periods during the Austral winter (July–September) alternating with a wet season during the austral spring and summer (November–March; SCHLACHER *et al.*, 2005). Because our principal aim was to capture plume events and contrast these with baseflow conditions, sampling extended from the dry winter period in August 2003 into the rainy season in February 2004 (Fig. 2). During baseflow conditions, when no significant rainfall events and river plumes occurred, we sampled at fortnightly intervals. Rainfall events triggered response sampling within 24 hr, followed by higher frequency sampling (2–7 days intervals) to track plume trajectories.

2.2. Field Collections

Mesozooplankton was collected in horizontal net tows using modified WP2-nets (200 μm mesh aperture, mouth diameter 0.5 m, cone length 2.6 m) fitted with General Oceanics flowmeters (model 20/30R). Tows were made from a small (6 m) boat at 3–4 knots for 7 min, the average volume of water filtered per tow being 61.3 m^3 . Two depths, surface (0–0.6 m) and subsurface (2 m in estuary and 5 m outside the estuary), were sampled, with 2 replicate tows per depth. All sampling was conducted at night (~ 2–4 hr after sunset) on ebbing tides. Samples were preserved in 5% formalin. CTD casts were made with a Hydrolab Datasonde 4a, fitted with a submersible fluorometer, taking recordings at 0.1 m depth intervals of salinity, temperature, turbidity, ph, dissolved oxygen and chlorophyll-*a*.

2.3. Laboratory Processing

Size spectra and abundance of mesozooplankton were determined with an optical plankton counter (Focal Technologies), detecting particles in the size range 0.225–1.521 mm. Particle size was calculated from the cross sectional area, reported as equivalent spherical diameter (ESD). Sample volume was adjusted to achieve a minimum count of ca. 10000 individuals over 40 min, adding samples slowly to maintain a count rate of <10 counts per second (CPS) and to avoid coincidence (SPRULES *et al.*, 2001). Biomass values (wet weight) were obtained by converting body volumes (V), based on spheres at $V = 4/3 \times \pi \times r^3$, where r is ESD/2, and assuming neutral buoyancy of the plankton at a density of 1 mg/mm^3 .

Net tows of zooplankton from the subtropical estuaries and sheltered, inshore waters of the region are usually dominated (~80% of total abundance) by copepods, with typical genera including *Pseudodiaptomus*, *Stephos*, *Pseudocalanus*, *Ridgewayia*, *Acartia*, *Oithona*, and *Parvocalanus* (GREENWOOD, 1981; JACOBY and GREENWOOD, 1989). Other common, but less abundant members of the mesozooplankton in the study region typically comprise a diversity of larval forms from many taxa (*e.g.*, zoea, veligers, megalopa, anomuran polychaetes-, and fish larvae), as well as mysids, larvaceans, and chaetognaths. Demersal, benthic-pelagic taxa such as various peracarids (isopods, cumaceans, amphipods, tanaids) and ostracods are present in net samples but less common (GREENWOOD, 1981; JACOBY and GREENWOOD, 1989).

2.4. Data Analysis

Biomass and abundance of zooplankton were compared among sites (*i.e.*, ocean, mouth, estuary) using a generalised additive model (GAM; HASTIE and TIBSHIRANI, 1990). The primary purpose of the GAM model was to partition out the effects of the shape of the size distribution to allow spatial contrasts between sites that were not confounded by body size. This technique is conceptually analogous to including a co-variate in a generalised linear model (GLM) to partition out the effects of a co-variate (body size in our situation) before testing for the effects of a treatment (site in our application). We also used GAMs because the nature of relationships between body size and abundance and biomass were not necessarily linear. In these situations, GAMs allow the simultaneous fit of non-parametric and semi-parametric models.

The general form of the model used was:

$$y = \alpha_0 + \beta_1 \times \text{size} + f_1 \times \text{size} + \beta_2 \times \text{location} ,$$

where β_1 and β_2 are linear estimators and f_1 is a linear adjusted non-parametric estimator of the effects; hence, the model is described as semi-parametric (SAS, 2004). For the non-linear component we fitted a spline function (CRAVEN and WAHBA, 1979). This step used generalized cross validation (WAHBA, 1990) to maximise the tightness of the spline fit. A spline function fits a series of polynomials to the data and can have different degrees of freedom, depending on the complexity of the data. Analysis of deviance was used to determine the significance of the spline function in each equation, and we report the degrees of freedom to assist in interpreting the complexity of the relationships. The parameter estimates and standard errors were used to compare spatial contrasts for each model combination using t-tests with $\alpha = 0.01$ to reduce the likelihood of type I errors from multiple comparisons.

Because freshwater discharge is primarily driven by local rainfall events in the catchment, which modify multiple chemical and physical properties of the water column in the receiving water body, we used a multivariate ordination technique (PCA – Principal Component Analysis) to delineate phases of plume development (CLARKE and GORLEY, 2006).

3. Results

3.1. Physico-Chemical Variables and Chlorophyll-*a*

Our sampling captured both low-flow periods and plume events. Two rainfall events during the study produced two distinct plumes: the first in early Dec (5–8) 2003, and the second on 4 Feb 2004 (Figs. 2 and 3). Based on rainfall intensity and physico-chemical properties (*i.e.*, turbidity, salinity, stratification) of the water column, three distinct phases could be identified: (1) baseflow conditions (no plumes) leading up to the wet season in December, (2) strong plume events, and (3) residual plume conditions between the pulsed events (Fig. 3).

The plumes were small, extending approximately 1500 m offshore and 1200 m alongshore (estimated from aerial overflights). The life span of the plumes was around 1 week, after which salinity values at the estuarine entrance returned to baseflow values (~35 psu). The visible plume was usually less pronounced on the flood tide, typically alternating between distinct fronts forming during ebb-tides and advection of oceanic water masses into the plume area on rising tides.

Freshwater discharge pulses profoundly changed the physico-chemical structure of the water column, producing buoyant plumes off the estuarine inlet (Fig. 2, Table 1). The estuary and the mouth area became strongly stratified after heavy freshwater discharges, with surface salinities dropping to 7 psu. Plume waters were generally confined to the top 2–3 m of the water column, where a lens of turbid and low-salinity water overlay denser and clearer oceanic water (Table 1). Plumes did not propagate to the ocean site located 2.5 km offshore; here salinity values remained uniform at ~36 psu irrespective of estuarine discharge. Plume events produced peaks in water-column phytoplankton biomass that were most pronounced in the estuary and the mouth area (Fig. 2, Table 1). These elevated chlorophyll-*a* levels persisted for several weeks after the main discharge event in the estuary and off the entrance, suggesting that nutrients delivered by the river plumes enhanced local primary production.

3.2. Zooplankton

River discharge and the formation of plumes off the estuarine entrance profoundly influenced the spatial distribution of zooplankton abundance and biomass. Both the direction and magnitude of the hypothesized 'plume effect' on zooplankton assemblages concurred with our *a priori* prediction that flow regimes structure spatial patterns of zooplankton abundance and biomass according to the strength of hydrodynamic forcing (*i.e.*, baseflow, plume event and residual plume) and the spatial scale of plume influence (Figs. 4–6).

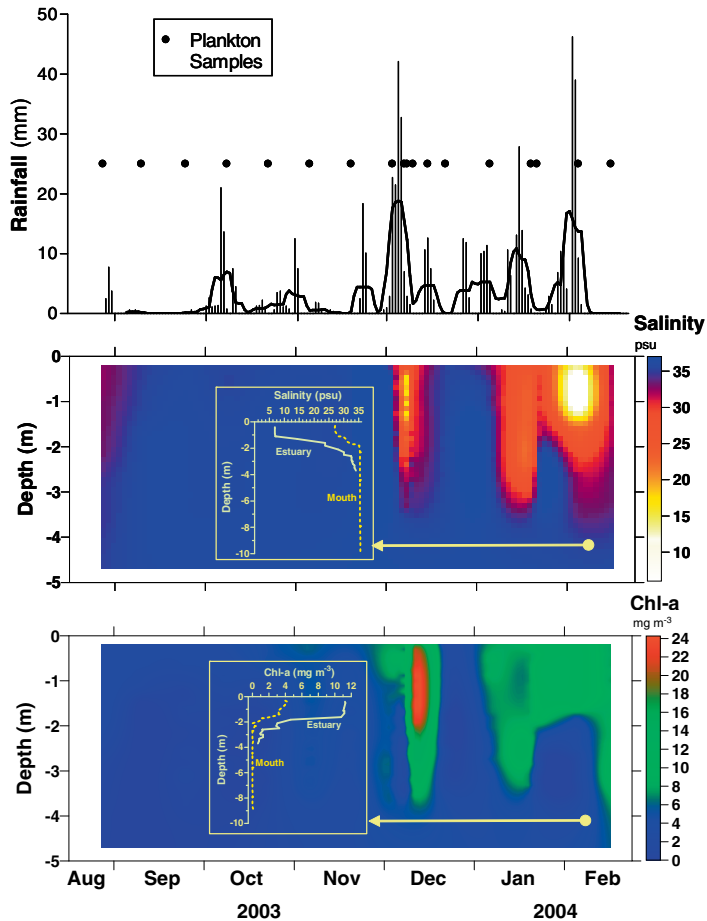


Figure 2. Variability in rainfall, and its effect on the salinity and chlorophyll-*a* biomass in the lower estuary. Solid line in top panel is a 7 day moving average of daily rainfall, which is shown by individual bars. Inserts in middle and bottom panel show CTD casts made during the strongest discharge event of 4-Feb-04 inside the estuary and *ca.* 1 km offshore from the mouth where a buoyant plume had developed.

The linear and non linear components of the generalised additive model were significant for every modelled zooplankton response. The relationships tended to behave very differently amongst plume phases – in terms of the overall response patterns – indicated by spline functions that used markedly different degrees of freedom for each phase (Table 2). Conversely, spline functions were similar between depth layers sampled during the same plume phase (Table 2), the only exception being the biomass response during residual plumes which was more complex near the surface (spline $df = 11.49$) than in deeper layers (spline $df = 3.91$).

During river baseflows when no distinct plumes were present in the nearshore marine zone, abundance and biomass of zooplankton in surface waters were broadly comparable across all sites, albeit with slightly lower values in the estuary than at both marine sites

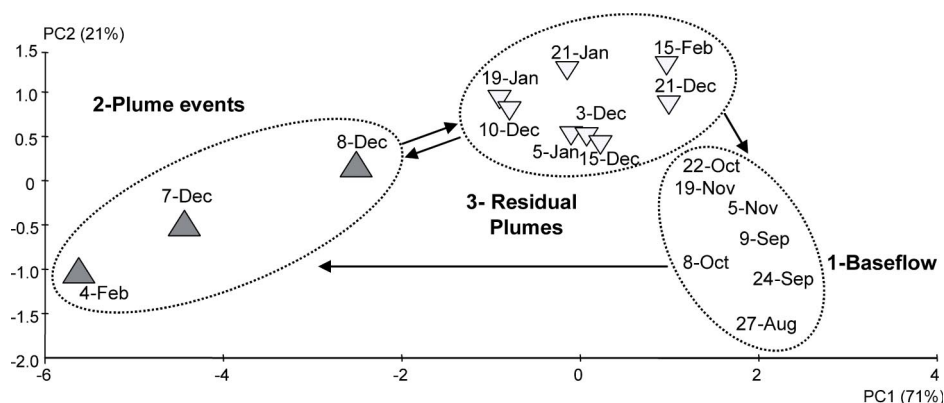
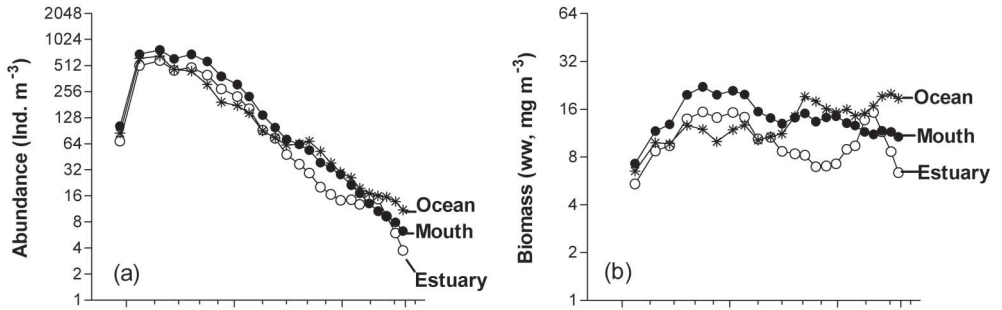


Figure 3. Ordination (PCA) of sampling dates based on similarities (normalised Euclidean distance) in rainfall intensity and physico-chemical properties of the water column in the lower estuary, illustrating phases of plume development, that progress from low freshwater inputs during the austral winter (1-Baseflow), punctuated by heavy precipitation bouts at the onset of summer (2-Plume events), which are in turn followed by moderate freshwater effects in the weeks after the pulsed rainfall events (3-Residual Plumes).

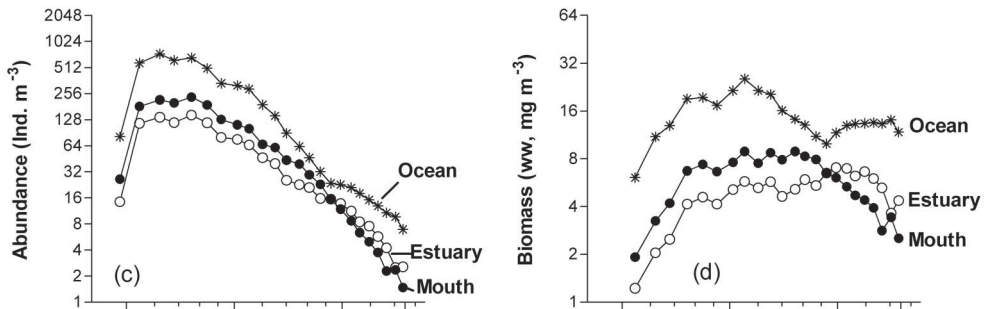
Table 1. Summary of spatio-temporal changes in water-column chlorophyll-*a*, turbidity and salinity in two depth layers (surface and subsurface), at three sites affected to varying degrees by river plumes and during three phases of plume development.

Surface Layer (0–0.6 m)		Chl- <i>a</i> (mg m ⁻³)		Turbidity (NTU)		Salinity (psu)	
Site	Phase	Mean	SE	mean	SE	Mean	SE
Estuary	Baseflow (no plumes)	3.60	0.47	1.76	1.17	35.36	0.48
	Plume event ('first flush')	8.72	1.49	28.93	7.99	15.33	4.90
	Post plumes (1–5 weeks)	9.20	1.85	4.87	1.16	31.56	1.37
Mouth	Baseflow (no plumes)	1.22	0.73	0.65	0.65	36.22	0.08
	Plume event ('first flush')	3.64	0.29	6.67	0.88	31.24	1.68
	Post plumes (1–5 weeks)	2.71	0.70	1.37	0.91	35.45	0.53
Ocean	Baseflow (no plumes)	0.07	0.05	0.00	na	36.29	0.09
	Plume event ('first flush')	2.09	1.68	6.00	2.00	35.77	0.66
	Post plumes (1–5 weeks)	0.56	0.54	1.75	1.18	35.93	0.32
Sub-surface Layer (2–5 m)		Chl- <i>a</i> (mg m ⁻³)		Turbidity (NTU)		Salinity (psu)	
Site	Phase	Mean	SE	mean	SE	Mean	SE
Estuary	Baseflow (no plumes)	1.75	0.69	1.71	1.13	35.88	0.35
	Plume event ('first flush')	3.14	0.39	19.27	4.51	29.94	2.02
	Post plumes (1–5 weeks)	7.14	1.71	4.30	1.19	33.06	1.28
Mouth	Baseflow (no plumes)	0.89	0.57	0.40	0.40	36.23	0.07
	Plume event ('first flush')	1.53	0.98	3.39	1.78	35.45	0.46
	Post plumes (1–5 weeks)	1.02	0.54	1.24	0.73	36.09	0.17
Ocean	Baseflow (no plumes)	0.01	0.00	<0.01	<0.01	36.28	0.08
	Plume event ('first flush')	0.16	–	4.00	–	36.42	–
	Post plumes (1–5 weeks)	0.16	0.15	1.70	1.14	36.28	0.23

1-Baseflow Conditions



2-Plume Events



3-Residual Plumes

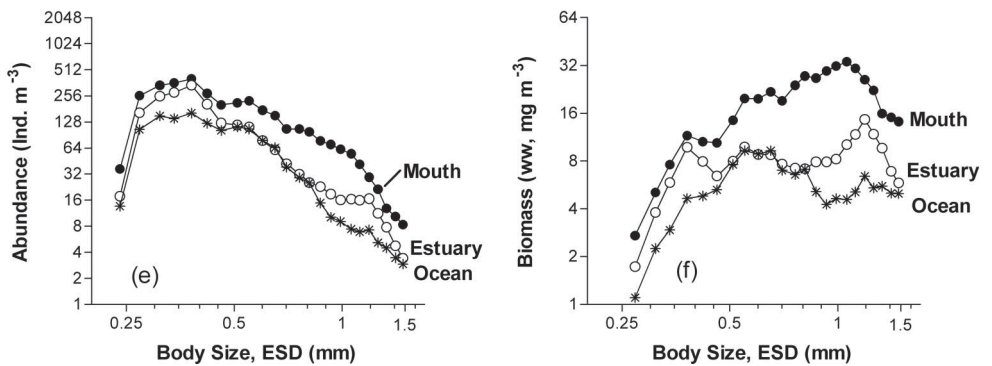
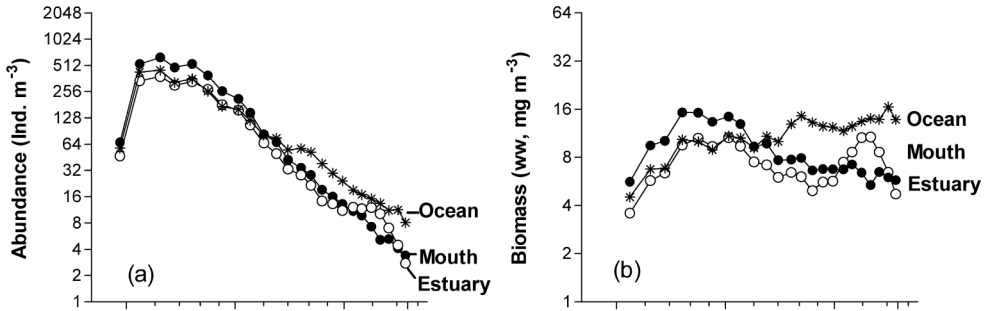
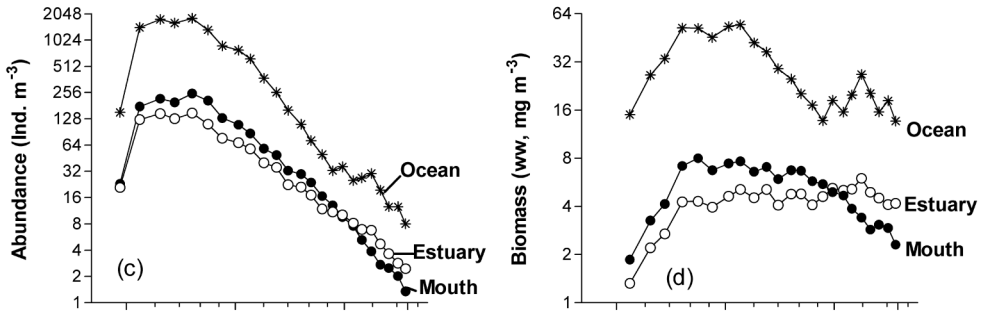


Figure 4. Abundance (left column) and biomass (right column) size spectra for mesozooplankton in surface layers (0–0.6 m) at three sites subjected to different degrees of river plume influence (estuary ○, mouth ●, and offshore ocean site *) during three phases of plume development (*cf.* Fig. 3 for definition of plume phases).

1-Baseflow Conditions



2-Plume Events



3-Residual Plumes

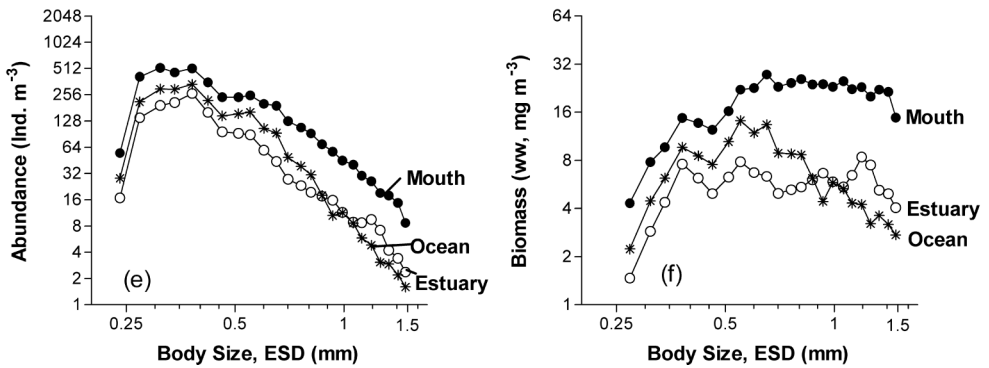


Figure 5. Abundance (left column) and biomass (right column) size spectra for mesozooplankton in sub-surface layers (2–5 m) at three sites subjected to different degrees of river plume influence (estuary ○, mouth ●, and offshore ocean site *) during three phases of plume development (*cf.* Fig. 3 for definition of plume phases).

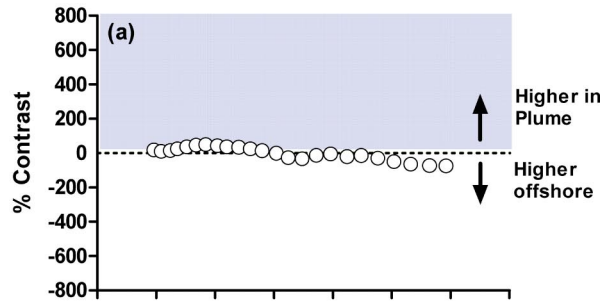
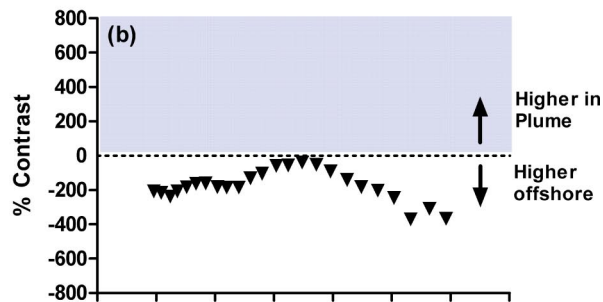
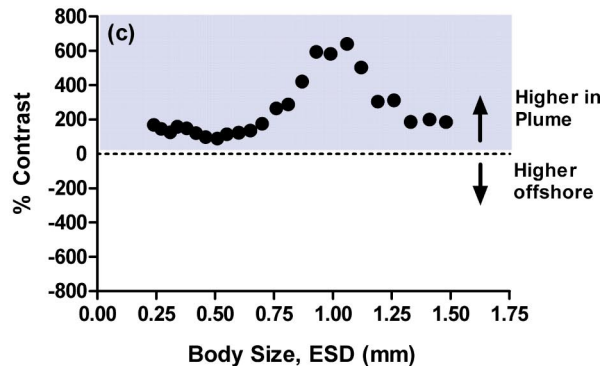
1-Baseflow Conditions**2-Plume Events****3-Residual Plumes**

Figure 6. Contrasts in zooplankton abundance by body size (ESD) between the mouth (plume) and ocean, reference site. Contrast is calculated as: $\% \text{ Contrast} = (\text{Abu}_{\text{mouth}} - \text{Abu}_{\text{ocean}}) / (\text{Abu}_{\text{mouth}}) \times 100$, where Abu is mean surface abundance in units of Ind. m^{-3} .

(Fig. 4, Table 2). By contrast, the pulsed discharge events substantially lowered densities of zooplankton in the estuary and adjacent nearshore waters; both sites recorded significantly lower values than the offshore, oceanic reference site (Fig. 4, Table 2). The short-term effect of pulsed discharge events thus resembles a “first-flush” impact on the zooplankton in water masses of lower salinity. Following this first-flush effect, which was detectable for 1–3 days after the strong discharge events, zooplankton reached significantly higher abundance and biomass values in the plume area compared with both the estuary and offshore waters

Table 2. Summary of generalised additive model (GAM) results used to compare abundance and biomass spectra of zooplankton among three sites that differed in the intensity of plume influence (*i.e.*, ocean, mouth, estuary). Spatial contrasts are made separately for surface and sub-surface layers and for each phase of plume development (*i.e.*, baseflow: $n = 7$; plume event: $n = 3$; and post/residual plumes $n = 8$). Results of multiple comparison tests are denoted by capital letters (A, B, C), where different numerals denote sites that differ significantly ($P < 0.01$); in each of these contrasts, 'A' refers to the highest value and C to the lowest site value.

Surface Layer (0–0.6 m)		Smoothing Spline Analysis of deviance results			Spatial Contrasts Multiple comparison tests		
Phase		Spline $DF^{(a)}$	Chi-Square ^(b)	P -value	Ocean	Mouth	Estuary
Abundance	1 – Baseflow	7.25	124.88	<0.001	A	A	B
	2 – Plume Event	8.35	39.98	<0.001	A	B	B
	3 – Post/Residual Plumes	12.68	34.43	0.001	B	A	B
Biomass	1 – Baseflow	7.67	30.29	<0.001	A	A	B
	2 – Plume Event	5.39	59.94	<0.001	A	B	B
	3 – Post/Residual Plumes	11.49	39.30	<0.001	B	A	B
Sub-surface Layer (2–5 m)		Smoothing Spline Analysis of deviance results			Spatial Contrasts Multiple comparison tests		
Phase		Spline $DF^{(a)}$	Chi-Square ^(b)	P -value	Ocean	Mouth	Estuary
Abundance	1 – Baseflow	6.95	91.70	<0.001	A	B	B
	2 – Plume Event	8.07	47.39	<0.001	A	B	B
	3 – Post/Residual Plumes	11.53	26.42	0.007	B	A	C
Biomass	1 – Baseflow	7.05	27.06	<0.001	A	B	B
	2 – Plume Event	6.59	22.66	0.002	A	B	B
	3 – Post/Residual Plumes	3.91	46.77	<0.001	B	A	B

^{a)} The spline df is the amount of information used to explain the non-linear component in the equation (see methods).

^{b)} The Chi-squared is an analysis of deviance, testing the null hypothesis that there is no relationship between body size and the non-linear component of the model.

(Fig. 4; Table 2). Zooplankton responses in sub-surface layers generally mirrored those near the surface; densities and biomass were mostly lower in estuarine and plume regions in the first days after a pulsed discharge event, but this pattern reversed in the residual plumes, which supported significantly more zooplankton than either the estuary or offshore waters (Fig. 5, Table 2). These positive effects of plumes on zooplankton were most pronounced for size classes between 0.75 and 1.25 mm (Fig. 6).

5. Discussion

5.1. Phytoplankton

The occurrence and temporal dynamics of elevated phytoplankton biomass in the estuary and in plume waters corresponded closely with freshwater pulses (Fig. 2). Such concord-

ance between freshwater inflow and higher phytoplankton biomass in the receiving estuary has been linked to higher nutrient loads exported from watersheds and the creation of more stable (*i.e.*, stratified) hydrological conditions (MALLIN *et al.*, 1993; GILLANDERS and KINGSFORD, 2002). In the local situation, plume waters have nutrient levels 2–4 times higher than the surrounding shelf water (GASTON *et al.*, 2006), and the distinct stratification of the water column following freshets is likely to have created favourable conditions for phytoplankton growth and retention within the plume area.

Although elevated nutrient levels in coastal waters are commonly reported to result mainly from river discharge, additional inputs can occur by direct deposition of nutrients in rainfall which promotes localised phytoplankton production (PAERL *et al.*, 1990; WILLEY and CAHOON, 1991). Plumes off the Mooloolah Estuary are created by the discharge of a river that drains a narrow (<50 km) and steep watershed, and very heavy precipitation fell over the plume area and the estuary during peak river discharge. Thus, localised rainfall events coincide spatially with upland inputs from the watershed and could, themselves, provide additional nutrient loads to coastal waters where plumes form. This aspect of small plumes is worthy of further investigation.

The magnitude of increase in pelagic production in riverine plumes may be scale-dependent. Enhanced production increases with the size of the discharge plume, suggesting that a distinct “plume effect” on planktonic organisms may be more pronounced in large plumes such as the Mississippi and Amazon (GRIMES and KINGSFORD, 1996; LIU and DAGG, 2003; WYSOCKI *et al.*, 2006). Part of this suggested scale dependence may be related to the residence time of plume waters and the longevity of the plumes itself. On a global scale, the plumes we studied are very small (<1 km) and ephemeral (longevity days to weeks), but nevertheless produced distinct and strong responses in the plankton.

The balance between residence time and flushing is an important parameter in the control of phytoplankton production in estuaries (LUCAS *et al.*, 1999; HOWARTH *et al.*, 2000). Despite the apparently strong flushing effect during peak discharge events, phytoplankton biomass responded rapidly to increased freshwater inflow – and presumably nutrient loading – and continued to be elevated for several weeks after the discharge events. Flushing effects on phytoplankton thus appear to be very short-lived in the case of small river plumes on exposed coastlines.

5.2. Zooplankton

Zooplankton assemblages in nearshore waters responded strongly to river discharge plumes, with abundance and biomass distribution being closely linked to the strength of freshwater flow. These flow variations resulted in density and biomass shifts across the plankton size spectrum that matched *a priori* predictions about putative plume effects: (1) broadly similar density and biomass values across the estuarine-marine gradient in the absence of substantial freshwater flows, (2) freshets that lowered zooplankton in the estuarine and nearshore zone where river discharge strongly modified hydrological conditions, and (3) significantly elevated zooplankton associated with plumes developing in nearshore waters after the initial freshets had passed.

The dynamics and temporal trajectories of zooplankton assemblages in plumes are complex (Table 3). The principal external drivers and internal mechanisms that influence the abundance, biomass, and secondary production of zooplankton include: a) advection/transport mechanisms (UEDA *et al.*, 2004); b) trophic effects (LIU and DAGG, 2003); c) movement of animals (PAGANO *et al.*, 1993); d) physical entrainment (GAUDY *et al.*, 1996), e) osmotic stress including mortality (KAARTVEDT and AKSNES, 1992) and f) predation on plume plankton (GRIMES and KINGSFORD, 1996).

Table 3. Summary of the principal processes and mechanisms that influence abundance and biomass of zooplankton associated with river discharge plumes in marine waters.

Mechanism / Process	Comments	References
Flushing Seawards displacement of estuarine plankton to marine waters. ("outwelling").	Likely to depend on strength of hydrodynamic forcing; Perhaps more significant for larger systems, but also affects plankton in small estuaries when discharge is strongly pulsed.	(CALEF and GRICE, 1967; Howarth <i>et al.</i> , 2000; Ueda <i>et al.</i> , 2004)
Trophic Effect Growth within plume that is underpinned by enhanced food concentrations.	Requires transfer of plume primary production to higher trophic levels; Duration of enhanced food concentrations at least equals time from stimulation of egg production to development of first larval instars; Predators of larva not significantly more abundant in plume waters.	(DAGG and WHITLEDGE, 1991; ZHAOLI <i>et al.</i> , 1995; LIU and DAGG, 2003)
Migration Active movement of zooplankton in relation to plume water masses.	Positive effects on abundance if zooplankton respond to enhanced food concentrations in plumes by stronger vertical upwards migration into buoyant surface plumes; Negative effects on abundance if a) low-salinity plume waters that override oceanic water masses block upwards migration, and/or b) zooplankton emigrate from low-salinity plumes into more saline near-bottom layers.	(ORTNER <i>et al.</i> , 1989; PAGANO <i>et al.</i> , 1993; SCHLACHER and WOOLDRIDGE, 1994; SCHLACHER and WOOLDRIDGE, 1995; UEDA <i>et al.</i> , 2004)
Entrainment Accumulations of plankton by hydrodynamic forces in frontal convergence zones.	Effects generally confined to narrow zone of fronts, not necessarily extending to bulk of plume water masses; Complex transport processes across and along frontal boundaries interact with species-specific responses to food availability, salinity, or recruitment clues.	(MACKAS and LOUITT, 1988; GRIMES and FINUCANE, 1991; GOVONI and GRIMES, 1992; KINGSFORD and SUTHERS, 1994; GAUDY <i>et al.</i> , 1996; MORGAN <i>et al.</i> , 2005)
Osmotic Stress Physiological effects of low-salinity plume waters, including mortality.	Likely to be more severe for marine taxa than more euryhaline estuarine plankton; Impact likely to be pulsed in situations of strongly spiked discharge events.	(KAARTVEDT and AKSNES, 1992; WEBB <i>et al.</i> , 1997)
Predation Stronger predation pressure on zooplankton associated with plumes.	Higher abundances of predators that prey on zooplankton in plumes when these are concentrated by hydrodynamic forces and/or actively congregate near increased prey availability in plumes.	(GOVONI <i>et al.</i> , 1989; GRIMES and FINUCANE, 1991; GRIMES and KINGSFORD, 1996)

Estuarine zooplankton has evolved behavioural mechanisms to maintain position within the estuary against the net seaward advective forces. The principal method for such position maintenance is selective vertical migration between water masses in vertically-stratified flows (SCHLACHER and WOOLDRIDGE, 1995, 1996; KIMMERER *et al.*, 1998, 2002), and zooplankton may behave similarly during heavy discharge events (UEDA *et al.*, 2004). It is, however, unknown whether such behaviour is sufficient to reduce seaward displacement of estuarine populations. We observed a substantial reduction in zooplankton density in the estuary in the first days after the freshets. These decreases in zooplankton probably resulted from advective losses beyond the plume boundaries, but might also result from downward movement of organisms into the hyperbenthic layer.

Enhanced food concentrations can provide favourable conditions for zooplankton growth in plumes (DAGG and BREED, 2003). Such trophic effects can only operate efficiently if primary production in the plumes is transferred to zooplankton consumers, and demographic responses of consumers are faster than the lifespan of the plumes. Zooplankton grazing can indeed be instrumental in controlling phytoplankton stocks in plumes (LIU and DAGG, 2003), suggesting stimulation of secondary production in plume waters (ZHAOLI *et al.*, 1995). In small, short-lived plumes, this trophic effect might have been expected to be curtailed, but we recorded significantly higher density and biomass values in the plume area compared to surrounding shelf waters in such a small system.

Movement of matter and nutrients across ecosystem boundaries can have significant effects on the structure and dynamics of food webs in the recipient habitat (MARCZAK *et al.*, 2007). Plumes are prime examples of resource-subsidized ecosystems and, conceptually, nutrition of zooplankton in plumes is therefore predicted to be a mixture of marine and terrestrial sources. It is, however, not known to which extent carbon produced *in situ* in the plumes or allochthonous matter support consumers. Resolution of this important question will require the application of biochemical and isotopic tracing techniques, and remains one of the major, unresolved issues for these ecotonal systems.

Spatial and temporal heterogeneity at multiple scales is a key trait of coastal zooplankton (SCHLACHER and WOOLDRIDGE, 1994). Much of this heterogeneity arises from complex movement patterns of plankters, particularly vertical migration (PAGANO *et al.*, 1993; SCHLACHER and WOOLDRIDGE, 1994). In riverine plumes, migration responses of zooplankton can encompass at least three types of behaviour: (1) active and amplified downward movement of plankton that emigrate from surface plumes due to osmotic stress, (2) low-salinity waters blocking the upwards component of the daily vertical migrations, and (3) conversely, enhanced upwards migrations into surface plume waters to exploit richer food resources. The actual behaviour will differ between species, requiring detailed studies of movement patterns to predict which role vertical migration plays in plume zooplankton.

Physical entrainment can concentrate zooplankton at plume fronts via hydrodynamic convergence (GRIMES and FINUCANE, 1991; GRIMES and KINGSFORD, 1996). Such hydrodynamic effects are multi-directional and comprise at least three processes: (1) offshore transport in the plume, counterbalanced by onshore advection in sub-plume waters, (2) transport along fronts, and (3) retention within plume waters and frontal convergence zones (GRIMES and KINGSFORD, 1996). We did not specifically target the narrow (<5 m) frontal convergence zones of the plumes because frontal zones were often not well-defined in the small plumes, particularly during rough sea conditions. Also, the fronts only cover a small fraction of the total plume area and may therefore not contribute greatly to overall ecosystem energetics.

The same processes which concentrate zooplankton in plumes and fronts can also increase the abundance of predators (GOVONI *et al.*, 1989; GOVONI and GRIMES, 1992). In addition, small nekton may actively move into plumes to exploit abundant food resources, although this does not appear to be the case for juvenile salmonids (DE ROBERTIS *et al.*, 2005). Thus, positive "plume effects" on zooplankton may be partly off-set by higher predation pressure in these waters. Negative effects of plumes on zooplankton can also operate via osmotic

stress to the point of direct mortality caused by low-salinity waters (KAARTVEDT and AKSNES, 1992). Estuarine zooplankton can cope physiologically with varying salinities (WEBB *et al.*, 1997), and osmotic effects are likely to be more severe for stenohaline marine taxa, particularly as a pulse disturbance during freshets.

6. Conclusions

In the present study major flow events from a small estuary initially depressed zooplankton populations in the coastal plume area, but this was followed by a significant increase in zooplankton abundance and biomass. Small estuarine discharges on open, exposed coasts are the most common form of plume on many coastlines. The effects of these small plumes are short-lived, and thus the overall pattern is one of higher temporal variability than for larger plumes. This, and the swell conditions at inshore sites, makes studying such plumes particularly difficult. Conversely, the small size of the plumes means that it is easier to access control sites outside any plume influence. This was a feature of the current study, and one that would also be useful in future studies of trophic dynamics of zooplankton in plumes.

7. Acknowledgements

Our special thanks go to W. BARRON for help in collecting the zooplankton samples and I. SUTHERS from the University of New South Wales who kindly provided us with his plankton counter and access to his lab. This project was funded through an Australian Research Council grant (LP0219421) to TS and RC, in partnership with the Moreton Bay Waterways and Catchments Partnership.

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Manuscript received December 11th, 2007; revised April 24th, 2008; accepted April 30th, 2008