

Impact of a flood event on benthic and pelagic coupling in a sub-tropical east Australian estuary (Brunswick)

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Abstract

We examined the impact of a 1:3 year return period flood on benthic and pelagic coupling in the river-dominated sub-tropical Brunswick Estuary. The flood had a significant impact on the study site flushing it with freshwater, reducing the flushing time 0.6 days, increasing nutrient concentrations in the water column and scouring the sediment surface. In the three weeks post-flood the benthic and pelagic systems alternated between being coupled and un-coupled via dissolved, particulate and living material pathways. Immediately post-flood benthic and pelagic coupling via the deposition of phyto-detritus and viable algal cells was reduced due to the scouring of the top sediment layers, and benthic respiration and productivity and NH_4^+ effluxes all decreased correspondingly. In contrast, benthic and pelagic coupling was enhanced via the uptake and denitrification of NO_3^- due to elevated NO_3^- concentrations in the water column. Some of the NO_3^- consumed by the sediments may have also been converted to DON. Two weeks post-flood benthic and pelagic coupling was significantly enhanced via the deposition of phyto-detritus and viable algal cells associated with a phytoplankton bloom in the water column. This increased supply of phyto-detritus and viable algal cells rapidly increased benthic respiration and productivity and NH_4^+ efflux. The depletion of water column DIN by the phytoplankton bloom resulted in a de-coupling of the benthic and pelagic systems via the uptake and denitrification of NO_3^- . However, benthic and pelagic coupling was enhanced via the uptake of NH_4^+ by benthic microalgae. Three weeks post-flood the phytoplankton bloom had collapsed and the coupling between the benthic and pelagic systems via the deposition of phyto-detritus and living algal cells had diminished. Again benthic and pelagic coupling was enhanced via the uptake and denitrification of NO_3^- due to elevated NO_3^- concentrations in the water column associated with the recycling of bloom material. Overall the sediments became less heterotrophic (increasing benthic productivity/respiration ratio) following the flood. Floods can cause rapid and complex changes in the coupling between benthic and pelagic systems in sub-tropical estuaries.

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1. Introduction

Benthic and pelagic coupling is central to the nutrient cycling and overall productivity of shallow coastal ecosystems. Sediment heterotrophic processes decompose much of the carbon produced in the water column of shallow coastal ecosystems (Hammond et al., 1985). Nutrients released via carbon decomposition can in-turn provide a large proportion of the nitrogen and phosphorus required by pelagic communities (Boynton and Kemp, 1985; Cowan and Boynton, 1996). Bottom

sediments can also be a sink for nutrients from the water column through burial and CO_2 and N_2 efflux to the atmosphere (Boynton et al., 1995; Eyre and McKee, 2002). Benthic microalgae interact closely with the water column of shallow coastal ecosystems via the uptake, temporary storage and release of nutrients (Rizzo et al., 1996; Sundback and Miles, 2000; Ferguson et al., 2004a). The net balance of sediment productivity and respiration determines if the sediment will be a net sink of carbon and nitrogen from, or a net source to, the water column (Eyre and Ferguson, 2002; Eyre and Ferguson, 2005). Macrofauna can enhance both the uptake (via suspension feeders) and release of carbon and nitrogen (via bioturbation and bioirrigation) (Cloern, 1982; Webb and Eyre, 2004). As well as

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dissolved and particulate pathways benthic and pelagic systems may also be coupled via the exchange of organisms (Marcus and Boero, 1998) and living algae (Widdows et al., 2004).

Episodic events are important drivers of the coupling between benthic and pelagic systems. Field and laboratory studies have demonstrated that episodic inputs of labile organic carbon can rapidly increase sediment respiration, NH_4 and DON efflux and NO_3 uptake (Hansen and Blackburn, 1992; Caffrey et al., 1993; Overnell et al., 1995). Denitrification may be either enhanced or suppressed by episodic inputs of labile organic carbon. For example, narrowing of the oxic zone as the excess labile carbon decomposes and an associated increase in the diffusional supply of NO_3 may enhance denitrification (Risgaard-Petersen, 2003). In contrast, when the increased load of labile organic carbon decomposes it may inhibit nitrification by exposure to sulphide (Joye and Hollibaugh, 1995) or due to a lack of oxygen for nitrification decreasing coupled nitrification–denitrification (Kemp et al., 1990). Both field and laboratory experiments have shown that denitrifiers respond almost immediately to episodically elevated NO_3 concentrations in the overlying water column (Joye and Paerl, 1993; Kana et al., 1998). In Boston Harbour elevated denitrification rates were also associated with episodic increases in the numbers of benthic infauna (Nowicki et al., 1997).

Episodic floods are common events in tropical estuaries and can significantly alter the physical, chemical and biological conditions of these systems (Eyre and Balls, 1999; Eyre, 2000). Floods can fill the entire estuarine basin with freshwater elevating water column nutrient concentrations and increasing light attenuation due to increased suspended sediment concentrations (Eyre, 2000). Increased light attenuation may in-turn result in the loss of seagrass communities (Campbell and McKenzie, 2004). Floods may also remove the upper few centimeters of the sediment column scouring the soft-bottom benthos (Saenger et al., 1988) resulting in long-term (months) changes to the benthic community (Corfield, 2000). As the estuary recovers both pelagic and benthic production may be stimulated due to less rapid flushing and increased light as suspended sediments settle, or are flushed, out and nutrient concentrations remain elevated (Eyre, 2000; Ferguson et al., 2004b). Enhanced production, in particular

pelagic production, may in-turn rapidly increase carbon delivery to sediments. All these flood-induced changes should influence benthic and pelagic coupling in the system, however, to our knowledge the impact of a flood event on benthic and pelagic coupling in a tropical estuary has never been studied in detail. One of the problems with most sampling programs is that flood events are missed because benthic (and in many cases pelagic) sampling is undertaken too infrequently, typically no more often than monthly. In addition, to have a pre-flood record regular sampling must be carried out in anticipation of a flood, as the exact timing of the event cannot be predicted, and then the field program must be able to respond quickly following the event requiring resources to be mobilised at short notice. This study aimed to better capture the influence of a flood event on benthic and pelagic coupling by undertaking both benthic and pelagic sampling immediately before, and at weekly intervals following, a flood event.

2. Study area

The Brunswick River is located on the northern coast of New South Wales (NSW), Australia (Fig. 1), which has a sub-tropical climate controlled by two major influences: the sub-tropical high pressure belt during winter/spring (July–October) bringing clear, mainly dry conditions; and easterly monsoonal tradewinds during summer/autumn (November–May) bringing warm, humid conditions. The region experiences the highest annual rainfall in NSW, with a summer/autumn maximum (wet season), and lowest rainfall occurring during the winter/spring transition (dry season). There is high interannual variation in rainfall due to the influence of the Southern Oscillation on climate in the region: lower than average annual rainfalls occur during El Nino years (atmospheric pressure at Darwin > Tahiti); while greater than average rainfalls occur during La Nina years (atmospheric pressure at Darwin < Tahiti). Freshwater flows to the Brunswick Estuary are dominated by low (20 percentile flow: 6 (4 gauged) $\text{m}^3 \text{d}^{-1}$) to median (50 percentile flow: 24 (17 gauged) $\text{m}^3 \text{d}^{-1}$) flows throughout most of the year interspersed by episodic, short-lived flood events (Eyre, 2000). Large flood events are mostly

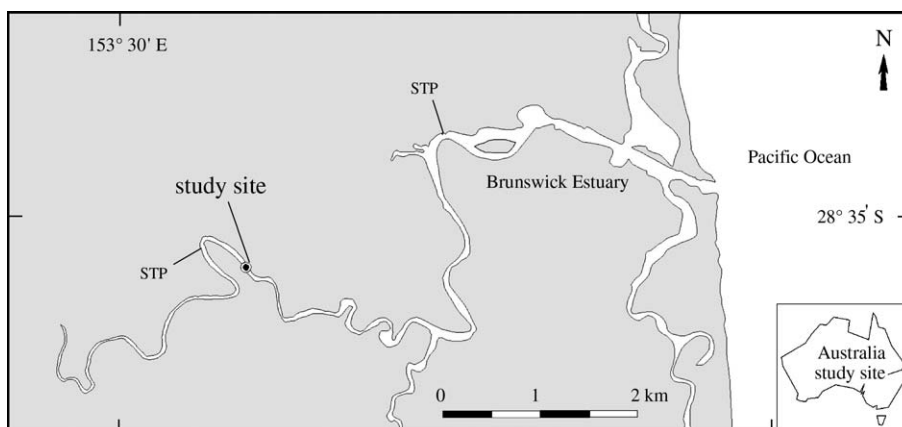


Fig. 1. Location of the Brunswick Estuary, the study site and the sewage treatment plants (STPs) (modified from Eyre and Ferguson, 2005).

in response to rainfall associated with either tropical cyclones (which may affect the region between January and April); or intense low-pressure systems off the NSW coast (East Coast Lows), which occur predominantly during winter or the transition seasons. Cyclone genesis tends to move east during El Niño years resulting in generally less cyclonic influence on the region's climate.

3. Methods

3.1. Selection of sample site

One site was selected in the upper Brunswick Estuary (Fig. 1). The site was the same as the upper estuary site (site RW) sampled by Ferguson et al. (2003) and the site sampled by Eyre and Ferguson (2005) allowing long-term comparisons. This site was chosen to represent the upper extent of extensive sub-tidal shoals (and hence organic matter deposition) within the Brunswick Estuary. Upstream of this site the sediments are dominated by coarse gravel beds and rock substrate. The site was located on sub-tidal littoral shoals with a mean depth of $1\text{ m} \pm 0.75\text{ m}$, and was therefore euphotic for most of the year except during and immediately following floods when suspended sediment loads were high. The study site is situated approximately 1 km downstream of the Mullumbimby sewage treatment plant (STP) and therefore was heavily influenced by elevated nutrients and phytoplankton blooms associated with effluent discharges. Peak phytoplankton biomass along the estuary generally occurs within 1 km upstream or downstream of the STP discharge at high tide. It was therefore expected that the study site would represent the area of maximum phyto-detritus deposition along the estuary. This site is fairly representative of the upper sections of other sub-tropical east Australian and some temperate estuaries where similar zones of maximum phytoplankton biomass occur at the head of the estuary (Schuchardt and Schirmer, 1991; Eyre, 2000; Holmes et al., 2000) making the findings from this study broadly applicable to other systems.

3.2. Sample collection, core incubations solid phase sampling, analytical techniques and flux calculations

A detailed description of the sample collection, core incubations, solid phase sampling, analytical techniques and flux calculations can be found in Eyre and Ferguson (2005) and are only briefly summarised below. The flood event of interest occurred on the 1st February 2001. Sampling was undertaken (fortuitously) at one site (Fig. 1) on the 30th January immediately before the flood and weekly for three weeks (7th, 14th and 22nd February 2001) following the flood. Additional sampling was also undertaken in December 2000 and every one to two months between May 2001 and December 2002, however, this work is reported by Eyre and Ferguson (2005). Three to five undisturbed cores (95 mm i.d.) were collected using a surface operated hand corer. Waters samples for nutrients and chlorophyll-*a* were also collected and physico-chemical

parameters were also measured mid-water column during each sampling. Following a 24 h pre-equilibrium period the cores were incubated at in situ light ($\pm 5.0\%$) and temperature ($\pm 2\text{ }^\circ\text{C}$) conditions over a 24 h dark–light cycle. Dissolved oxygen concentrations ($\pm 0.01\text{ mg L}^{-1}$) were measured electro-chemically and nutrient and N_2 samples were collected at 0, 3, 6 and 13 h during the dark cycle and 0, 4, and 8 h during the light cycle. Dissolved oxygen typically only decreased about 20% over the course of the dark incubation. Nutrient and alkalinity samples were withdrawn with a plastic syringe, filtered ($0.45\text{ }\mu\text{m}$) and transferred to 10 ml acid-rinsed and sample-rinsed polyethylene vials. As a sample was withdrawn, an equal amount was replaced from a gravity-feed reservoir of estuary water. To minimise the introduction of bubbles, N_2 samples were collected in triplicate by allowing water to flow, driven by the reservoir head, directly into 7 ml gas-tight glass vials with glass stoppers filled to overflowing. All nutrient samples were immediately frozen at $-20\text{ }^\circ\text{C}$. N_2 samples were poisoned with $20\text{ }\mu\text{l}$ of 5% HgCl_2 and stored submerged at about $1\text{--}2\text{ }^\circ\text{C}$ below ambient temperature. One core (blank) with only water was pre-incubated and incubated and sampled as above. At completion of the flux incubations the top 2 cm of each sediment core was sampled for total organic carbon and total nitrogen, and the top 2 mm of each sample core was sampled for chlorophyll-*a* analysis. The sediment samples were placed in a 30 ml polyethylene vial and these were immediately frozen at $-20\text{ }^\circ\text{C}$. The chlorophyll-*a* samples were immediately extracted in 90% acetone in 10 ml polyethylene vials, wrapped in aluminum foil, and frozen at $-20\text{ }^\circ\text{C}$. All nutrient analyses were carried out colourmetrically using Lachat™ Flow Injection Analysis. Di-nitrogen gas was measured using a modified membrane inlet mass spectrometer with O_2 removal (Eyre et al., 2002). Solid phase carbon and nitrogen concentrations were measured using high temperature combustion (LECO) and sediment chlorophyll-*a* concentrations were measured spectrometrically following 90% acetone extraction (Strickland and Parsons, 1972).

Fluxes across the sediment–water interface were calculated by linear regression of the concentration data, corrected for the addition of replacement water and changes in the blank, as a function of incubation time, core water volume and surface area. Dark flux rates were calculated using concentration data from the first 12 h of the incubation and light flux rates were calculated using concentration data from the second 12 h of the incubation. Net flux rates are the average of the dark and light flux rates. Benthic production was calculated as: benthic oxygen production (+ve, efflux) = light O_2 flux (+ve) – dark O_2 flux (–ve, uptake). Error bars represent the standard deviation between the replicate core ($n = 3\text{--}5$) measurements.

4. Results

4.1. Hydrology, salinity and flushing characteristics

A 1:3 year return period flood peaked at $10\,300\text{ (7107 gauged) m}^3\text{ d}^{-1}$ in the Brunswick River on the 1st of February, 2001 (Fig. 2a). The river stage rose sharply from a base flow of

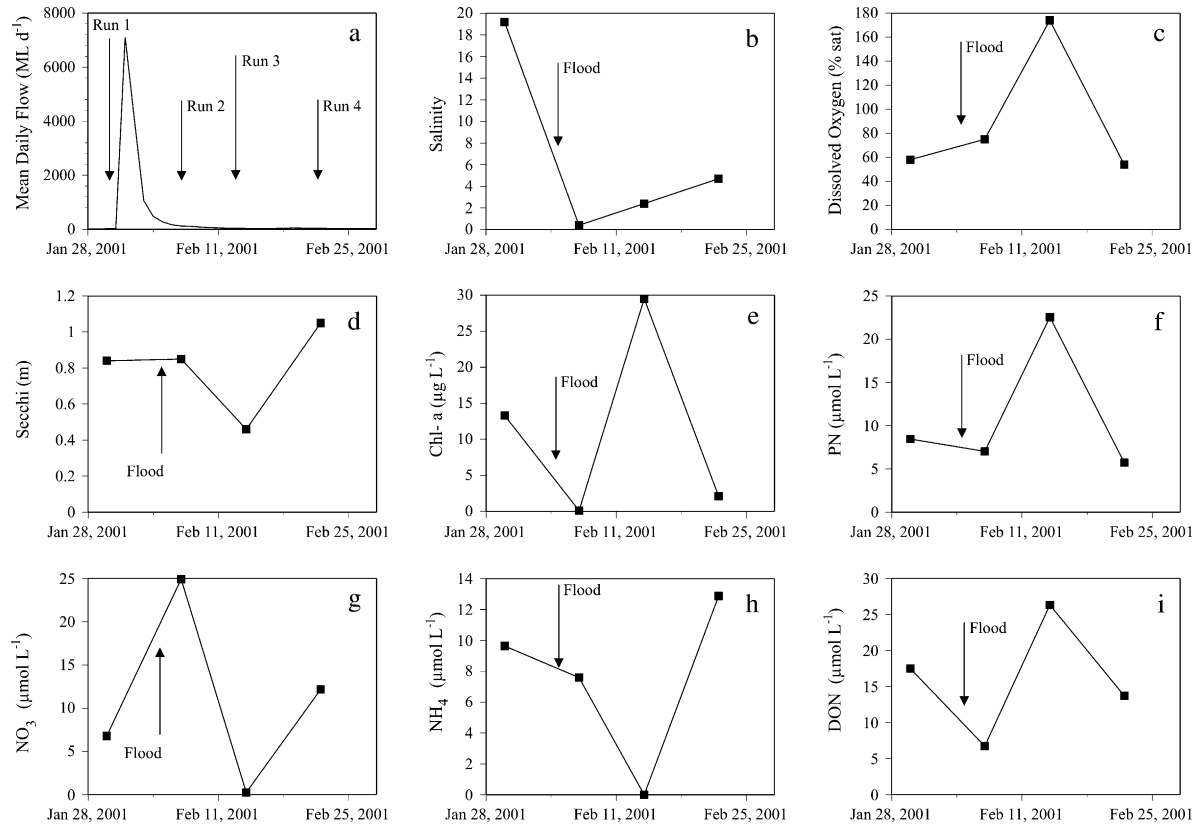


Fig. 2. Temporal variability in physico-chemical parameters over the three-week study period.

26 (18 gauged) $\text{m}^3 \text{d}^{-1}$ during sample run 1 (pre-flood) on the 30th January, 2001. The flood was short-lived and by the time the second sample run was undertaken on the 7th February river flow had already dropped to 175 (121 gauged) $\text{m}^3 \text{d}^{-1}$. River flow continued dropping and was back to near the pre-flood base flow during sample runs 3 and 4 (46–51 (32–35 gauged) $\text{m}^3 \text{d}^{-1}$). Salinity was strongly related to river flow and the study site was flushed fresh during the flood peak (data not shown), from a pre-flood salinity of 19.2, and remained near-fresh (salinity of 0.4) during the first sample run (Fig. 2b). Salinity recovered slowly reaching only 4.7 by sample run 4. Flushing times (fraction of freshwater method; see Eyre, 2000) were also strongly related to river flow. The flood reduced flushing times at the study site from a pre-flood rate of 3 days during sample run 1 to an immediate post-flood rate of 0.6 day during sample run 2. The study site remained rapidly flushed post-flood only increasing to 2 days during sample run 3 (13 days post-flood) and 3 days during sample run 4 (21 days post-flood).

4.2. Water column parameters

Flooding caused water column temperatures to drop from a pre-flood high of 29.0 °C during sample run 1 to an immediate post-flood low of 24.7 °C during sample run 2 as the study site was flushed with colder river water. Temperatures had increased to 27.4 °C by sample run 4 three weeks after the flood. Dissolved oxygen concentrations were depressed

pre-flood (58% saturation) due to sediment oxygen demand associated with the decomposition of phyto-detritus in the upper Brunswick Estuary (Eyre, 2000; Ferguson et al., 2003) (Fig. 2c). The flood waters were also oxygen deficient (i.e. 75% saturation during sample run 2) most likely due to the oxygen demand of dissolved and particulate organic material typically mobilised and carried by floods in sub-tropical river/estuaries (Eyre, 1997; Eyre and Twigg, 1997). Dissolved oxygen was super-saturated during sample run 3 two weeks after the flood and then decreased to pre-flood concentrations by sample run 4. Except for immediately following the flood (i.e. sample run 2), dissolved oxygen concentrations were strongly influenced by phytoplankton production as illustrated by the positive correlation between dissolved oxygen and secchi depth ($r^2 = 0.996$; $n = 3$; $p < 0.05$) and chlorophyll-*a* ($r^2 = 0.86$; $n = 3$; not significant); increased phytoplankton production results in decreased secchi depth due to shading by phytoplankton biomass in the water column (Fig. 2d). Although the sample size is small (i.e. $n = 3$) these patterns are consistent with those seen in a much larger data set over 2 years at the same site in the Brunswick Estuary (Eyre and Ferguson, 2005). Immediately following the flood dissolved oxygen concentrations and secchi depth are more likely controlled by material carried in the flood waters.

Chlorophyll-*a* decreased from a pre-flood concentration of 13.3 $\mu\text{g L}^{-1}$ during sample run 1 (pre-flood) to the detection limit (0.1 $\mu\text{g L}^{-1}$) immediately following the flood during sample run 2 (Fig. 2e). Concentrations of chlorophyll-*a* had

increased rapidly to $29.5 \mu\text{g L}^{-1}$ by sample run 3 (13 days post-flood) and decreased almost as rapidly to $2.1 \mu\text{g L}^{-1}$ by sample run 4 (21 days post-flood). NO_3^- concentrations showed an opposite pattern to chlorophyll-*a* with a dramatic increase immediately post-flood to $26.5 \mu\text{mol L}^{-1}$ from a pre-flood concentration of $6.8 \mu\text{mol L}^{-1}$ (Fig. 2e). Concentrations of NO_3^- then decreased rapidly to near the detection limit by sample run 3 (13 days post-flood) ($0.3 \mu\text{mol L}^{-1}$) and then increased rapidly to $12.2 \mu\text{mol L}^{-1}$ by sample run 4 (21 days post-flood). Removal of NO_3^- during sample run 3 (13 days post-flood) corresponded with increased chlorophyll-*a* concentrations suggesting uptake by phytoplankton (Eyre, 2000). In contrast to NO_3^- , NH_4^+ concentrations decreased slightly immediately post-flood to $7.5 \mu\text{mol L}^{-1}$ from a pre-flood concentration of $9.6 \mu\text{mol L}^{-1}$ due to dilution of STP effluent in the estuary by the flood waters (Fig. 2g). However, similar to NO_3^- , NH_4^+ concentrations then decreased rapidly to the detection limit by sample run 3 (13 days post-flood) ($0.4 \mu\text{mol L}^{-1}$) and then increased rapidly to $12.2 \mu\text{mol L}^{-1}$ by sample run 4 (21 days post-flood). Excluding sample run 2 immediately following the flood, dissolved inorganic nitrogen concentrations (DIN) were negatively correlated ($r^2 = 0.991$; $n = 3$; $p < 0.05$) with chlorophyll-*a* concentrations which is consistent with uptake by phytoplankton. Dissolved organic nitrogen (DON) concentrations (Fig. 2h) were negatively correlated with DIN concentrations ($r^2 = 0.999$; $n = 3$; $p < 0.05$) and positively correlated with chlorophyll-*a* concentrations ($r^2 = 0.990$; $n = 3$; $p < 0.05$) if sample run 2 is excluded. Particulate nitrogen (PN) concentrations were positively correlated ($r^2 = 0.930$; $n = 3$; not significant) with chlorophyll-*a* concentrations, if sample run 2 is excluded, indicating that the main source of PN was algal biomass. Particulate nitrogen concentrations immediately post-flood during run 2 are similar to run 1 (pre-flood) concentrations despite much lower chlorophyll-*a* concentrations most likely reflecting flood water derived PN.

4.3. Sediment parameters

Sediment chlorophyll-*a* decreased dramatically from a pre-flood concentration of 3.8 mg m^{-2} during sample run 1 (pre-flood) to an immediate post-flood concentration of 0.8 mg m^{-2} during sample run 2 (6 days post-flood) (Fig. 3). Sediment chlorophyll-*a* concentrations then increased rapidly to 5.9 mg m^{-2} by sample run 3 (13 days post-flood) and then decreased slightly to 4.4 mg m^{-2} by sample run 4 (21 days post-flood). Sediment organic carbon decreased from a pre-flood concentration of 42.3 mg g^{-1} to an immediate post-flood concentration of 29.6 mg g^{-1} (Fig. 3). Concentrations of sediment carbon during sample run 3 (13 days post-flood) (27.2 mg g^{-1}) remained similar to sample run 2 (6 days post-flood), but then increased to the highest concentration recorded by sample run 4 (21 days post-flood) (46.6 mg g^{-1}). Sediment nitrogen concentrations show a similar pattern to sediment carbon with a decrease from sample run 1 (pre-flood) (2.9 mg g^{-1}) to 2 (2.1 mg g^{-1}), similar concentrations during sample runs 2 (6 days post-flood) and 3 (13

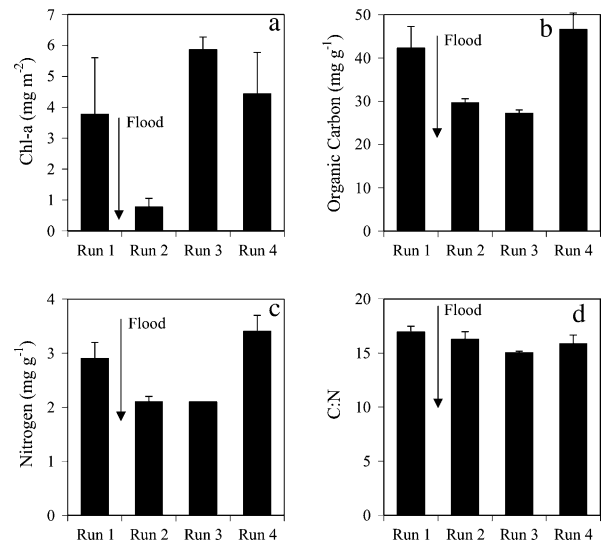


Fig. 3. Temporal variability in average \pm SD ($n = 3-5$) sediment parameters over the three-week study period.

days post-flood) (2.1 mg g^{-1}), and an increase to the highest concentrations recorded by sample run 4 (21 days post-flood) (3.4 mg g^{-1}) (Fig. 3). Sediment molar C:N ratios decreased from pre-flood ratio of 17.0 to an immediate post-flood ratio of 16.2 and continued to decrease to run 3 (13 days post-flood) (15.0) and then increased to 15.9 by run 4 (21 days post-flood) (Fig. 3).

4.4. Benthic metabolism

Dark O_2 fluxes (respiration) decreased from a pre-flood rate of $3072 \mu\text{mol m}^{-2} \text{ h}^{-1}$ during sample run 1 (pre-flood) to an immediate post-flood rate of $1819 \mu\text{mol m}^{-2} \text{ h}^{-1}$ during sample run 2 (6 days post-flood) (Fig. 4). Respiration rates then increased rapidly to $3137 \mu\text{mol m}^{-2} \text{ h}^{-1}$ by sample run 3 (13 days post-flood) and then decreased to $2374 \mu\text{mol m}^{-2} \text{ h}^{-1}$ by sample run 4 (21 days post-flood). There was a distinct diurnal variation in dark O_2 fluxes with a reduced efflux in the light due to benthic productivity. Benthic productivity showed a similar pattern to respiration with a decrease from a pre-flood rate of $1956 \mu\text{mol m}^{-2} \text{ h}^{-1}$ during sample run 1 (pre-flood) to an immediate post-flood rate of $1152 \mu\text{mol m}^{-2} \text{ h}^{-1}$ during sample run 2 (6 days post-flood) (Fig. 4). However, the rapid increase to $3060 \mu\text{mol m}^{-2} \text{ h}^{-1}$ by sample run 3 (13 days post-flood) was larger than the corresponding increase in respiration. The decrease to $2196 \mu\text{mol m}^{-2} \text{ h}^{-1}$ by sample run 4 (21 days post-flood) was similar to the corresponding decrease in respiration.

4.5. Nitrogen fluxes

For the first three sample runs dark NH_4^+ fluxes mirrored dark O_2 fluxes decreasing from a pre-flood rate of $205 \mu\text{mol m}^{-2} \text{ h}^{-1}$ during sample run 1 (pre-flood) to an immediate post-flood rate of $108 \mu\text{mol m}^{-2} \text{ h}^{-1}$ during sample run 2 (6 days post-flood) and then increasing again to nearly

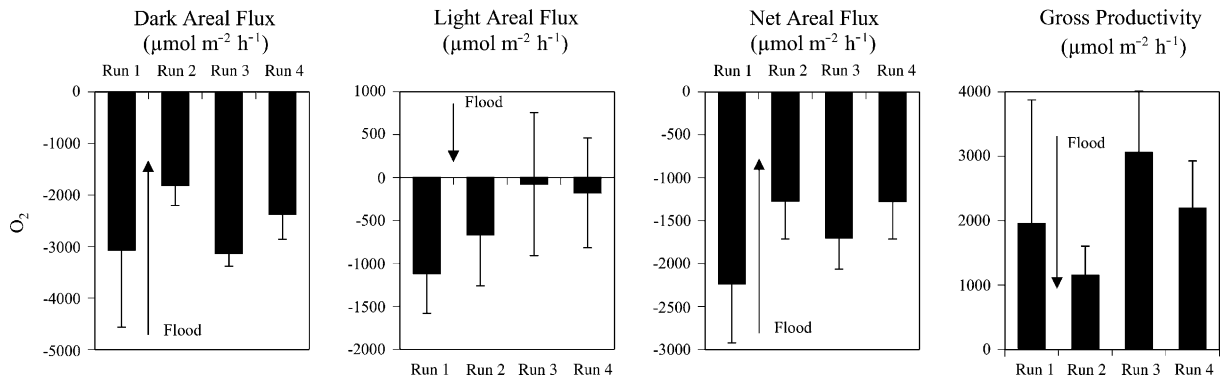


Fig. 4. Temporal variability in average \pm SD ($n = 3-5$) benthic O_2 fluxes over the three-week study period.

the pre-flood rate ($183 \mu\text{mol m}^{-2} \text{h}^{-1}$) by sample run 3 (13 days post-flood) (Fig. 5). However, in contrast to dark O_2 fluxes which decreased during sample run 4 (21 days post-flood), dark NH_4^+ fluxes ($183 \mu\text{mol m}^{-2} \text{h}^{-1}$) were similar to dark NH_4^+ fluxes during sample run 3 (13 days post-flood) ($183 \mu\text{mol m}^{-2} \text{h}^{-1}$). There was a distinct diurnal variation in NH_4^+ fluxes with an efflux in the dark and an uptake or reduced efflux in the light (Fig. 5). The decrease in NH_4^+ efflux was most notable during sample runs 3 (13 days post-flood) and 4 (21 days post-flood). Net NH_4^+ fluxes decreased immediately post-flood mostly due to decreased dark NH_4^+ effluxes during sample run 2 (6 days post-flood) and increased light NH_4^+ uptakes during sample runs 3 (13 days post-flood) and 4 (21 days post-flood). The changes in NH_4^+ fluxes between runs are not significant ($p > 0.05$) due to high variability between replicates.

Dark NO_3^- fluxes were always directed into the sediments (uptakes) but the uptake rates changed dramatically (Fig. 5) reflecting changes in NO_3^- concentrations in the overlying water column (Fig. 2). Dark NO_3^- uptakes increased from a pre-flood rate of $-4 \mu\text{mol m}^{-2} \text{h}^{-1}$ during sample run 1 (pre-flood) to an immediate post-flood rate of $-152 \mu\text{mol m}^{-2} \text{h}^{-1}$ during sample run 2 (6 days post-flood) (Fig. 5). Dark NO_3^- uptakes then decreased rapidly to $-2 \mu\text{mol m}^{-2} \text{h}^{-1}$ by sample run 3 (13 days post-flood) and then increased rapidly again to $-94 \mu\text{mol m}^{-2} \text{h}^{-1}$ by sample run 4 (21 days post-flood). There was a distinct diurnal variation in dark NO_3^- fluxes with a reduced uptake in the light resulting in lower net uptakes compared to the dark.

Dark DON fluxes increased from a pre-flood rate of $12 \mu\text{mol m}^{-2} \text{h}^{-1}$ during sample run 1 (pre-flood) to an immediate post-flood rate of $60 \mu\text{mol m}^{-2} \text{h}^{-1}$ during sample run 2 (6 days post-flood) (Fig. 5). Dark DON fluxes then decreased to $48 \mu\text{mol m}^{-2} \text{h}^{-1}$ by sample run 3 (13 days post-flood) and then decreased again to $37 \mu\text{mol m}^{-2} \text{h}^{-1}$ by sample run 4 (21 days post-flood). There was a distinct diurnal variation in dark DON fluxes with an increase in the light during sample runs 1 (pre-flood) and 2 (6 days post-flood) and a decrease during sample runs 3 (13 days post-flood) and 4 (21 days post-flood). Net DON fluxes increased immediately post-flood due to the increase in dark DON fluxes and little change during the light but net DON fluxes were similar during the other three runs.

The changes in DON fluxes between runs are not significant ($p > 0.05$) due to very high variability between replicates, particularly immediately post-flood.

The pattern of N_2 fluxes closely reflected water column NO_3^- concentrations and benthic NO_3^- fluxes with an increase from the pre-flood rate of $9 \mu\text{mol m}^{-2} \text{h}^{-1}$ during sample run 1 (pre-flood) to an immediate post-flood rate of $19 \mu\text{mol m}^{-2} \text{h}^{-1}$ during sample run 2 (6 days post-flood) (Fig. 5). Dark N_2 fluxes then decreased rapidly to $6 \mu\text{mol m}^{-2} \text{h}^{-1}$ by sample run 3 (13 days post-flood) and then increased again to $26 \mu\text{mol m}^{-2} \text{h}^{-1}$ by sample run 4 (21 days post-flood). There was a distinct diurnal variation in dark N_2 fluxes with a reduced uptake in the light during sample runs 1 (pre-flood) and 4 (21 days post-flood) and increased efflux in the light during sample runs 2 (6 days post-flood) and 3 (21 days post-flood). Overall the net N_2 fluxes showed a similar pattern to the dark N_2 fluxes.

5. Discussion

5.1. Immediate (one week) post-flood response

Elevated nutrient concentrations immediately post-flood (Fig. 2) reflect the erosion and leaching of material from the catchment, much of which (75%) has been cleared for agriculture and grazing (Eyre, 2000). Six days post-flood (i.e. sample run 2) most of the nitrogen in the water column at the study site was in dissolved forms, mainly NO_3^- . However, these concentrations were much less than those measured during the flood peak at a site just above the tidal limit about 5 km upstream from the study site (unpublished data). Particulate nitrogen showed the largest change decreasing from $73.6 \mu\text{mol L}^{-1}$ during the flood peak to $7.0 \mu\text{mol L}^{-1}$ during sample run 2 (6 days post-flood). As such, secchi and PN at the study site showed little change immediately post-flood (i.e. sample run 2) because most of the flood-derived particulate material had already settled out of the water column or had been flushed out of the system by the time sampling was undertaken. NO_3^- concentrations remain elevated immediately post-flood only dropping to $24.9 \mu\text{mol L}^{-1}$ from a flood peak high of $39.2 \mu\text{mol L}^{-1}$. However, despite elevated DIN concentrations and similar light conditions (secchi) to

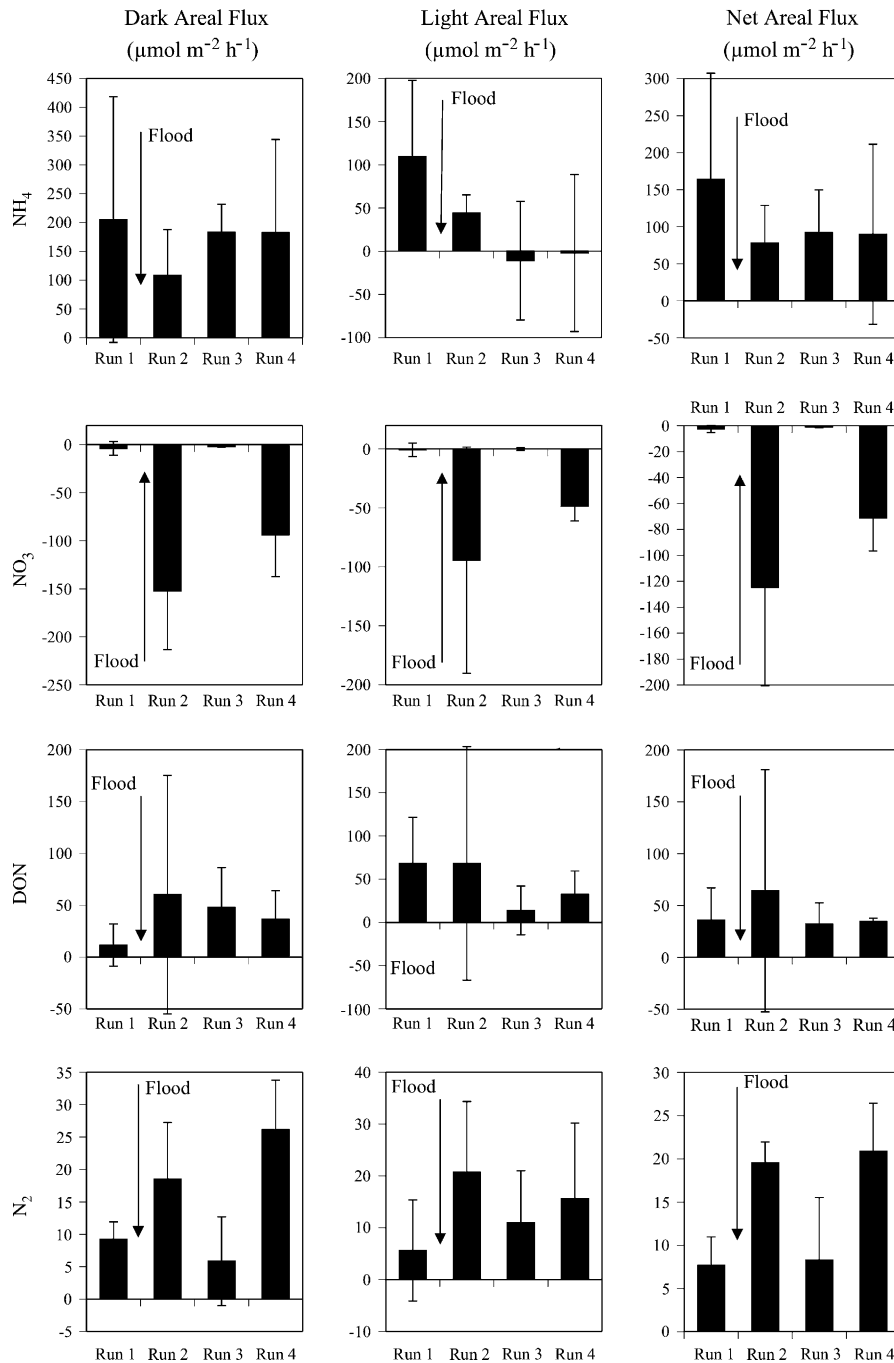


Fig. 5. Temporal variability in average \pm SD ($n = 3-5$) benthic NH₄, NO₃, DON, and N₂ fluxes over the three-week study period.

pre-flood, chlorophyll-*a* was significantly reduced immediately post-flood most likely due to rapid flushing of the study site (0.6 day) which would limit the accumulation of algal biomass (Cloern, 1996; Eyre, 2000; Ferguson et al., 2004b); doubling time for phytoplankton diatoms is typically 1–2 days (Eppley, 1972).

Sediment respiration and productivity and NH₄⁺ effluxes all decreased immediately post-flood most likely due to scouring of the top surface of the sediment by the flood. Sediment cores from the study site typically have a “fluffy” organic rich surface layer of phyto-detritus with a cover of benthic microalgae. However, the surface layer of cores collected

immediately post-flood consisted of fine sandy mud and the “fluffy” layer was absent (visual observation). Consistent with the loss of the “fluffy” layer was a large decrease in the sediment chlorophyll-*a* content and a decrease in the carbon and nitrogen content of the surface sediment immediately post-flood (Fig. 3).

In contrast to oxygen and NH₄⁺ fluxes, N₂ effluxes and NO₃⁻ uptakes increased immediately post-flood in response to elevated NO₃⁻ concentrations in the overlying water column. The NO₃⁻ uptake was the largest previously recorded in the Brunswick Estuary (Ferguson et al., 2004a; Eyre and Ferguson, 2005). An almost immediate response of denitrifiers to

elevated NO_3^- concentrations in the overlying water column has been shown in other field and laboratory studies (Joye and Paerl, 1993; Kana et al., 1998). Because denitrifiers can respond almost instantaneously to increased NO_3^- in the water column (Kana et al., 1998) denitrification rates were probably higher during the flood peak when water column NO_3^- concentration was higher. Applying the relationship between water column NO_3^- concentration and N_2 efflux established for the Brunswick Estuary (Eyre and Ferguson, 2005) to the NO_3^- concentration during the flood peak suggests that D_w rates may have been as high as $66 \mu\text{mol N m}^{-2} \text{h}^{-1}$. However, this D_w rate still does not exceed previously measured D_n rates in the Brunswick Estuary (Eyre and Ferguson, 2005). In addition, these episodically high D_w rates would have little impact on the annual nitrogen budget of sub-tropical estuaries because of the large nitrogen loads transported during floods (see McKee et al., 2000; Eyre and Pont, 2003).

Net denitrification ($39 \mu\text{mol N m}^{-2} \text{h}^{-1}$) cannot account for the entire net uptake of NO_3^- ($125 \mu\text{mol N m}^{-2} \text{h}^{-1}$) from the water column. Uptake by BMA can be excluded because BMA biomass and productivity decreased immediately post-flood and NO_3^- uptakes are lower in the light. Lower NO_3^- uptakes in the light suggest that an increase in the thickness of the oxic zone by benthic production decreases the diffusional supply of NO_3^- to the zone of denitrification. The NO_3^- may have been reduced to NH_4^+ via dissimilatory nitrate reduction to ammonium (DNRA). However, using the dark oxygen efflux and the sediment C:N ratio the decomposing carbon should have produced $111 \mu\text{mol NH}_4^+ \text{m}^{-2} \text{h}^{-1}$ (assuming a $\text{CO}_2:\text{O}_2$ of 1) which is very similar to the measured efflux ($108 \mu\text{mol m}^{-2} \text{h}^{-1}$) leaving no excess NH_4^+ to indicate DNRA is occurring. However, the assumption of a $\text{CO}_2:\text{O}_2$ ratio of 1 may be invalid because the scouring of the surface sediment appeared to have exposed the reduced sediment layers (personal observation) and oxidation of sulphides would decrease the $\text{CO}_2:\text{O}_2$ ratio and associated amount of NH_4^+ efflux from carbon decomposition allowing for some DNRA which has previously been implicated for this site (Ferguson et al., 2004a). DON effluxes increase dramatically immediately post-flood suggesting some of the excess NO_3^- uptake (i.e. not denitrified) may have been converted to DON (see Eyre and Ferguson, 2005 for full discussion). This still leaves a deficit of $21 \mu\text{mol N m}^{-2} \text{h}^{-1}$ which can be accounted for by errors in the mass balance calculations and/or DNRA and bacterial assimilation (see Eyre and Ferguson, 2005 for discussion).

5.2. Two-week response

Two weeks after the flood there was a large phytoplankton bloom as demonstrated by the large increase in chlorophyll-*a*, PN and dissolved oxygen concentrations, the decrease in secchi depth, and the almost complete removal of DIN. This bloom had the fourth highest chlorophyll-*a* concentrations observed in the Brunswick Estuary between the years 1996 and 2002 (Eyre, 2000; Ferguson et al., 2004b; Eyre and Ferguson, 2005). The bloom is probably near its maximum at this stage

as DIN is depleted (Engel et al., 2002). Based on concentration changes in the water column, only about 45% of the DIN uptake appears as biomass (PN) during this stage of the bloom with the remaining appearing in the DON pool. At this stage of the bloom most of the DON would probably have been released via heterotrophic processes (Meersche et al., 2004), most likely grazing (Glibert et al., 1991). The bloom would have been stimulated at this stage due to the decrease in flushing of the study site (2 days) allowing algal biomass to accumulate.

Sediment respiration and dark NH_4^+ effluxes increase at this stage due to the deposition and decomposition of phyto-detritus. A 1 cm thick layer of phyto-detritus had accumulated above the flood scour in cores collected at this stage and was already being actively turned over by macro-fauna (personal observation). Carbon production in the water column can be estimated using a primary productivity/chlorophyll-*a* relationship developed for the Brunswick Estuary (Gay, 2002). Based on dark sediment oxygen consumption and assuming a sediment $\text{CO}_2:\text{O}_2$ ratio of 1 about 25% of the carbon produced in the water column two weeks post-flood was being decomposed in the sediments. Benthic productivity also increased most likely due to the deposition of viable algal cells from the water column. Consistent with this was the 6-fold increase in sediment chlorophyll-*a* concentrations between one and two weeks post-flood (Fig. 3). The increase in benthic productivity resulted in an uptake of NH_4^+ in the light. The increase in benthic productivity exceeded the increase in respiration at this stage as illustrated by the increase in the sediment p/r (Fig. 6).

NO_3^- uptake decreased to almost zero at this stage reflecting the depletion of NO_3^- in the water column by phytoplankton production. N_2 effluxes also decreased due to a decrease in the direct uptake and denitrification of water column NO_3^- (D_w). Only about 20% of the denitrification could be accounted for by the uptake of water column NO_3^- indicating a switch to coupled nitrification–denitrification. Consistent with this was a doubling of N_2 effluxes in the light due to the enhancement of nitrification by benthic productivity (An and Joye, 2001). Enhancement of coupled nitrification–denitrification by benthic production under similar conditions of low water column NO_3^- and high productivity and respiration

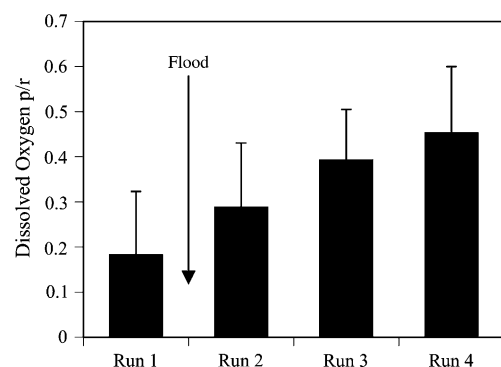


Fig. 6. Temporal variability in average \pm SD ($n = 3-5$) sediment productivity/respiration (p/r) over the three-week study period.

has previously been seen in the Brunswick Estuary (Eyre and Ferguson, 2005).

5.3. Three-week response

By week three post-flood the phytoplankton bloom had collapsed as illustrated by the low chlorophyll-*a*, PN and dissolved oxygen concentrations and the increase in secchi depth in the water column. About 80% of the decrease in PN and DON can be accounted for by the increase in DIN (after accounting for benthic DIN fluxes) indicating that much of the recycling of the phytoplankton bloom during this stage occurred in the water column. Consistent with this is the slight decrease in sediment respiration indicating that no additional phyto-detritus had been deposited and decomposed between two and three weeks post-flood. Benthic productivity also decreased despite better light (i.e. increased secchi) and higher water column nutrient concentrations. The decrease in benthic productivity may be related to a decrease in BMA biomass as illustrated by the decrease in sediment chlorophyll-*a* (Fig. 3). BMA biomass may have decreased due to degradation, burial, resuspension or grazing (Overnell et al., 1995; Ferguson et al., 2004a; Widdows et al., 2004). However, the decrease in benthic productivity between two and three weeks post-flood was less than the decrease in respiration resulting in an overall increase in the sediment p/r (Fig. 6).

NO_3^- uptakes increased in response to elevated NO_3^- concentrations in the overlying water column. Denitrification (net N_2 effluxes) can account for about 59% of the NO_3^- uptake with the remaining uptake ($29 \mu\text{mol m}^{-2} \text{h}^{-1}$) reasonably accounted for by the efflux of DON ($34 \mu\text{mol m}^{-2} \text{h}^{-1}$). The difference ($5 \mu\text{mol m}^{-2} \text{h}^{-1}$) could easily be accounted for by coupled nitrification–denitrification as the NO_3^- uptake being assigned to denitrification would be too high if nitrification was occurring or may simply represent the error in the calculations. A switch to D_w again results in a decrease in N_2 effluxes in the light due to a decrease in the diffusional supply of NO_3^- as the benthic oxic layer thickness increases.

5.4. Summary and synthesis

The major stages of change in the coupling between benthic and pelagic systems associated with flooding in a river-dominated sub-tropical estuary are summarised in Fig. 7. This conceptual model builds on a number of previous models of nutrient cycling in sub-tropical estuaries (Eyre, 2000; Ferguson et al., 2004b; Eyre and Ferguson, 2005) by focusing specifically on the period immediately post-flood which was possible due to the better temporal resolution in the sampling program (weekly) compared to previous work (monthly to three-monthly). This study has not only allowed a more complete understanding of nutrient cycling and phytoplankton growth in the water column in response to a flood, but also a better understanding of the impact of a flood on the coupling between the pelagic and benthic systems. The exact timing of each of these stages post-flood will depend on the size of the flood event; Fig. 7 reflects a 1:3 year return period flood.

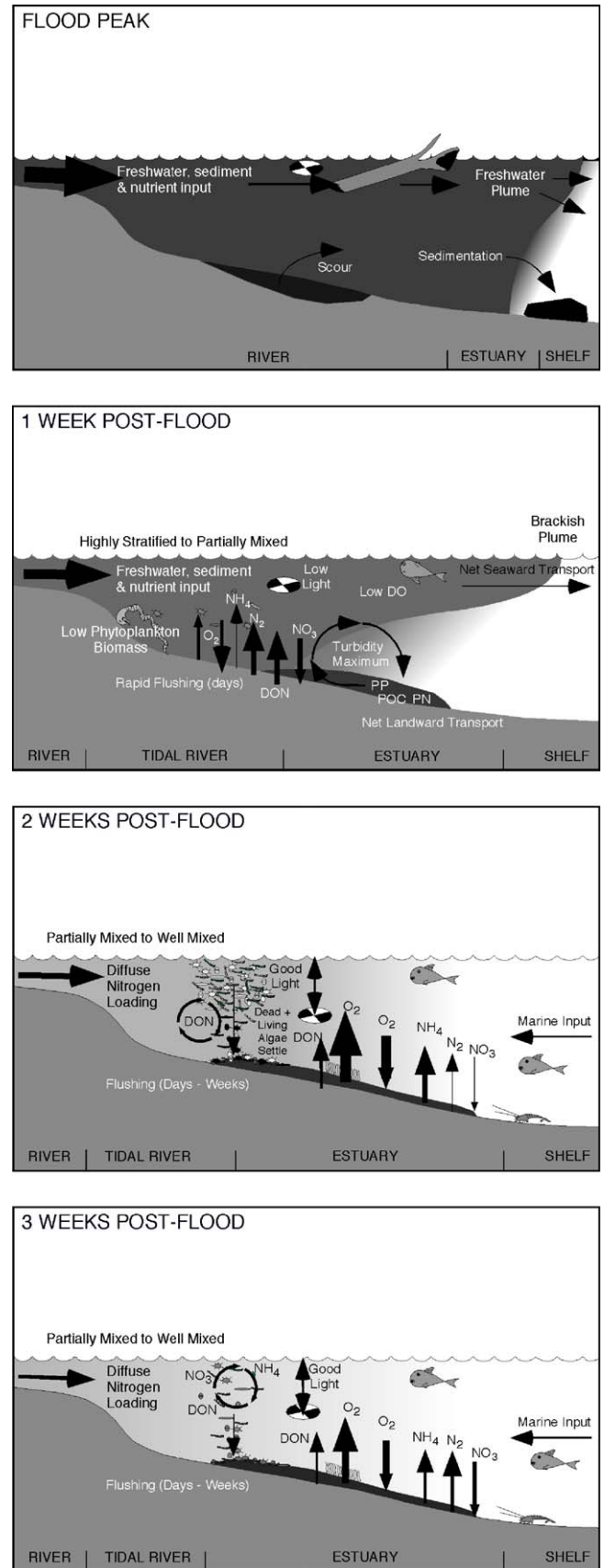


Fig. 7. Conceptual model of the impact of a 1:3 year return period flood event on benthic and pelagic coupling in the upper Brunswick Estuary. Arrow thickness represents the relative magnitude of the flux rates.

5.4.1. Flood peak

Changes in the estuary associated with the flood event were consistent with previous studies. The estuarine basin was filled with freshwater, dissolved and particulate nutrient concentrations were elevated, and internal biological processes were mostly bypassed due to rapid flushing (Eyre, 2000; Ferguson et al., 2004b). The flood was large enough to scour the sediment surface suggesting most of the catchment load of sediment and nutrients would have been delivered to the near-shore coastal waters (McKee et al., 2000; Hossain et al., 2001). Elevated NO_3^- concentrations during the flood peak may have resulted in denitrification rates as high as $66 \mu\text{mol N m}^{-2} \text{h}^{-1}$. The flood event was short-lived and within 2–3 days following the flood peak the estuary would have started to recover by way of a salt-wedge intruding along the channel bottom (Eyre and Twigg, 1997; Eyre, 2000). These short-lived episodic flood events contrast with the more extended spring freshets, and large flood events associated with storms, seen in many temperate systems the effect of which can typically last up to months (Fisher et al., 1988; Ramus et al., 2003).

5.4.2. One week post-flood

Despite elevated DIN concentrations and similar light conditions (secchi) to pre-flood, there is little accumulation of phytoplankton biomass due to rapid flushing. A flood event in the temperate Parker River Estuary resulted in a similar decrease in algal biomass due to a decrease in residence time (Holmes et al., 2000). Algal biomass also decreased following a number of flood events in the temperate Cape Fear Estuary, but the decrease was attributed to elevated light attenuation (Mallin et al., 2002). Benthic and pelagic coupling via the deposition of phyto-detritus and viable algal cells is reduced due to the scouring of the top sediment layers by the flood, and benthic respiration and productivity and NH_4^+ effluxes all decrease correspondingly. In contrast, benthic and pelagic coupling is enhanced via the uptake and denitrification of NO_3^- due to elevated NO_3^- concentrations in the water column. Some of the NO_3^- consumed by the sediments may also be converted to DON. A rapid increase in denitrification associated with increased NO_3^- concentrations in a runoff event was also seen in microbial mats in Tomales Bay (Joye and Paerl, 1993).

5.4.3. Two weeks post-flood

Two weeks after the flood an increase in residence times results in large phytoplankton blooms that can assimilate most of the water column DIN. The bloom is probably near its maximum at this stage as DIN is depleted. Although there is an increase in algal biomass (i.e. particulate nitrogen), much of the DIN uptake is recycled into the DON pool via heterotrophic processes. A large proportion of this DON may be exported to the ocean (Ferguson et al., 2004b) as the estuary still rapidly flushed (2 days). A post-flood increase in phytoplankton biomass associated with an increased nitrogen load appears to be a fairly typical response in a number of different types of systems (Rudek et al., 1991; Kristiansen, 1998; Pennock

et al., 1999; Eyre, 2000; Chan and Hamilton, 2001; Peierls et al., 2003). Benthic and pelagic coupling is significantly enhanced via the deposition of phyto-detritus and viable algal cells associated with the phytoplankton bloom in the water column. This increased supply of phyto-detritus and viable algal cells rapidly increases benthic respiration and productivity and NH_4^+ efflux. Although we know of no other studies that have linked increased benthic respiration and NH_4^+ efflux to an increased rain of phyto-detritus from post-flood phytoplankton blooms, an increase in benthic respiration and NH_4^+ efflux associated with the episodic inputs phyto-detritus is well established (Caffrey et al., 1993; Overnell et al., 1995). This almost immediate response contrasts with the lag between delivery of phyto-detritus and remineralisation seen in some temperate systems (Cowan and Boynton, 1996; Cowan et al., 1996). The differences between the sub-tropical and temperate systems reflect the higher temperatures in the sub-tropical estuaries; blooms can occur anytime of the year in sub-tropical estuaries in response to hydrological events (Eyre, 2000). Depletion of water column DIN by the phytoplankton bloom results in a de-coupling of the benthic and pelagic systems via the uptake and denitrification of NO_3^- . However, benthic and pelagic coupling is enhanced via the uptake of NH_4^+ by benthic microalgae.

5.4.4. Three weeks post-flood

Three weeks after the flood the phytoplankton bloom collapses and is recycled into the water column as DIN. It appears that the post-flood phytoplankton blooms are short-lived compared to during more stable pre-flood conditions where phytoplankton growth is sustained by constant STP inputs (Eyre, 2000; Ferguson et al., 2004b; Eyre and Ferguson, 2005). However, our previous sampling has limited our understanding of phytoplankton dynamics to three-monthly and monthly time scales (i.e. Eyre, 2000; Ferguson et al., 2004b; Eyre and Ferguson, 2005) which may have obscured these rapid bloom-bust scenarios. No additional phyto-detritus is deposited and sediment respiration decreases. Benthic productivity also decreases despite better light and higher water column nutrient concentrations due to a decrease in BMA biomass. However, the decrease in benthic productivity is less than the decrease in respiration resulting in an overall increase in the sediment p/r. NO_3^- uptakes increase in response to elevated NO_3^- concentrations in the overlying water column and denitrification (D_w) accounts for about 59% of the NO_3^- uptake. The remaining uptake ($29 \mu\text{mol m}^{-2} \text{h}^{-1}$) is accounted for by the efflux of DON ($34 \mu\text{mol m}^{-2} \text{h}^{-1}$). A switch to D_w results in a decrease in N_2 effluxes in the light due to a decrease in the diffusional supply of NO_3^- as the benthic oxic layer thickness increases.

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