Quantifying macrodetritus fluxes from a small temperate estuary

Rebecca V. Gladstone-Gallagher*[1], Dean R. Sandwell[1], Andrew M. Lohrer[2], Carolyn J. Lundquist[2,3], Conrad A. Pilditch[1]

[1] School of Science, University of Waikato, Hamilton 3240, New Zealand

[2] National Institute of Water and Atmospheric Research Ltd. (NIWA), Hamilton 3216, New Zealand

[3] Institute of Marine Science, University of Auckland, Auckland 1142, New Zealand

* Corresponding author email: rgladstonegallagher@gmail.com

Table of contents abstract

Hydrodynamics drive the export of estuarine-derived primary production and nutrients to adjacent less productive offshore waters. This study quantified estuary-to-coast fluxes of detritus and nutrients by sampling the water at the mouth of a small temperate estuary. These types of studies are important to determine the ecosystem services provided by temperate estuaries.

Abstract

Empirical measurements of estuary-to-coast material fluxes usually exclude the fraction of primary production that is exported as macrodetritus (marine plant litter), potentially leaving a gap in our understanding of the role of estuaries as outwelling systems. To address this gap, we sampled water and suspended material seasonally from the mouth of Pepe Inlet, Tairua Estuary, New Zealand. From samples collected hourly over 24 h, we calculated the lateral tidal fluxes (import, export, net flux) of macrodetritus,particulate and dissolved forms of nitrogen (N) and phosphorus (P). Annually, the inlet was a net exporter of N and P (5145 kg N and 362 kg P). However, macrodetritus accounted for <13% and <3% of seasonal N and P exports, respectively. Macrodetritus is an obvious and visible source of estuary-to-coast subsidy, but our derived nutrient budgets suggest the dissolved and particulate forms dominate the net export of N and P (>87%). Nevertheless, seasonal pulses in the source and supply of macrodetritus may have consequences for the temporal scales over which this resource subsidy affects receiving ecosystems (e.g. intertidal sandflats). These mensurative investigations are useful to inform estuarine nutrient budgets that quantify the ecosystem services provided by temperate estuaries (e.g. contribution to fisheries foodwebs).

Additional keywords: Estuarine flux; Outwelling hypothesis; Detritus; Spatial subsidies; Macrophyte detritus

Running title: Macrodetritus fluxes from a small temperate estuary

Introduction

Temperate estuaries/lagoons are considered among the Earth's most productive marine ecosystems, containing diverse vegetated (e.g. mangroves, saltmarsh, seagrass) and unvegetated habitats (e.g. intertidal sand and mud flats) (Eyre and Balls 1999; Underwood and Kromkamp 1999; Odum 2000; Valiela *et al.* 2000). Microphytobenthos in unvegetated sediments alone can contribute ~50% of the total estuarine primary production (Underwood and Kromkamp 1999), and marine vegetated habitats constitute hotspots of productivity, producing substantial amounts of leaf litter detritus (e.g. temperate mangroves up to 12.5 t DW ha^{-1} $year^{-1}$; reviewed in Morissey *et al.* 2010). Many estuaries tidally exchange large proportions of their water volume with the coastal ocean. Consequently, these hydrodynamics drive the export of estuarine production to adjacent less productive offshore waters (up to 100's kilometres offshore; i.e. the 'outwelling hypothesis' of Odum 1968; Dame and Allen 1996; Odum 2000). Through outwelling, estuaries contribute to the coastal oceanic food web (Doi *et al.* 2009; Savage *et al.* 2012) and ecosystem services that society values (e.g. fisheries; Barbier *et al.* 2011; Savage *et al.* 2012).

Since the formulation of the 'outwelling hypothesis' (Odum 1968), numerous studies have attempted to test and expand on it (reviewed in Nixon 1980; Odum 2000; Childers *et al.* 2000; Valiela *et al.* 2000). Naturally occurring stable isotopes (e.g. Doi *et al.* 2009; Granek *et al.* 2009; Savage *et al.* 2012) and sediment lignin content analyses (reviewed in Valiela *et al.* 2000) have confirmed that estuarine primary production is transported (often at a scale of kilometres) and incorporated into adjacent coastal food webs. However, these studies reveal little of the magnitude of the subsidy, that is, the amount of organic matter exported from estuarine habitats, as well as the proportion of production that is exported vs. retained and recycled within the estuarine system (i.e. net fluxes).

Direct quantification of estuary-to-coast subsidies to date have mostly focused on fluxes of suspended fine particles and solutes (i.e. particulate and dissolved matter), usually involving temporal water sampling in a tidal creek/channel (e.g. Borey *et al.* 1983; Dankers *et al.* 1984; Baird *et al.* 1987; Boto and Wellington 1988; reviewed in Valiela *et al.* 2000; Sánchez-Carillo *et al.* 2009). However, very few studies have directly measured estuary-to-coast fluxes of macrodetritus (large pieces of plant litter, including leaf, wood, and propagule material), due to the associated logistical challenges. Consequently, macrodetritus fluxes are often excluded from estuarine nutrient/production budgets (e.g. Valiela *et al.* 2000), or instead estimated based on *in situ* production, decay, and consumption rates within the ecosystem (e.g. from a mangrove forest: Boto and Bunt 1981; Robertson 1986; from a seagrass bed: Pergent *et al.* 1997). Since marine plants produce large quantities of leaf litter, estimates of macrodetritus export can be quite large (e.g. in a mangrove-dominated inlet, macrodetritus export of 15.3-19.5 kg DW ha^{-1} day^{-1} is estimated to be 6 × greater than particulate transport; Boto and Bunt 1981; Robertson 1986). Therefore, the exclusion of the macrodetritus fluxes leaves a potentially large gap in our understanding of the contributions of estuarine production to adjacent coastal environments.

The form in which production is exported (i.e. dissolved nutrients, particulate, or macrodetritus) will have consequences for its utilisation by the receiving environment, and influence how quickly this production is incorporated into coastal food webs. Particulate organic carbon (C), nitrogen (N), and phosphorus (P) (which broadly includes organic matter associated with suspended sediment, phytoplankton, and decayed fragmented detritus) are forms that are available to be immediately consumed by macrofaunal consumers, while bacteria, microphytes, and macrophytes can utilise the dissolved inorganic forms. However, because macrodetrital decay is relatively slow (reviewed in Enriquez *et al.* 1993), the temporal scales over which macrodetritus is utilised may be greater than that of particulates and dissolved nutrients, giving it the opportunity to also be transported over greater spatial scales. Accordingly, the main role of this form of production may instead be in structuring macroinvertebrate communities in receiving environments (e.g. Kelaher and Levinton 2003; Bishop and Kelaher 2007), or acting as a primary production source to marine environments with low *in situ* production (e.g. deep subtidal marine environments below the photic zone; Britton-Simmons *et al.* 2009).

Of the studies that have directly quantified net macrodetrital export from estuaries, most have been limited to saltmarsh-dominated lagoon systems in the northern hemisphere (Dame 1982; Dame and Stillwell 1984; Hemminga *et al.* 1996; Bouchard and Lefeuvre 2000), and/or focused on macrodetrital fluxes from just one vegetation type (e.g. macroalgae, Biber 2007; mangrove litter, Woodroffe 1985; Wattayakorn *et al.* 1990; Silva *et al.* 1993 as cited in Ramos e Silva *et al.* 2007 p. 528; Rajkaren and Adams 2007; see summary of macrodetritus flux studies in Table A1 in Appendices). In addition, many of these studies have been conducted in estuarine/lagoon systems that are atypical of temperate mixed habitat estuaries. For example, Tuff Crater (New Zealand) is a mangrove-dominated, enclosed crater that exchanges tidal water through a single break in the crater wall (Woodroffe 1985); Mont Saint-Michel Bay (France) is a macro-tidal bay with a very large average tidal range of 12 m (Bouchard and Lefeuvre 2000); whilst Biscayne Bay (Florida, USA) is a large, open coastal cut separated by coastal islands (Biber 2007; Table A1). Thus, generalisation of the fluxes measured in these study systems to other temperate estuaries is difficult. Dame and colleagues (Dame 1982; Dame and Stilwell 1984; Dame *et* *al.* 1986) constructed export budgets after sampling all of the production size fractions in a South Carolina tidal marsh system (North Inlet), and suggested that macrodetritus constituted a relatively small proportion of the total outwelled production. We took a similar approach here to evaluate estuary-to-coast subsidies in a well-defined part of a small New Zealand estuary.

As the supply and quality of estuarine subsidies are temporally variable (reviewed in Odum 2000), it is important that estuary-to-coast flux studies effectively encompass seasonal variability. In temperate climates, marine plant productivity is highly seasonal, with temporal pulses in the supply of leaf litter associated with seasonal production peaks (usually in summer or spring; e.g. Turner 2007; Imgraben and Dittmann 2008; Gladstone-Gallagher *et al.* 2014). Temporal variation in the supply of terrestrially derived detritus and nutrients is likely to be associated with spring-neap tidal cycles (i.e. spring tides will potentially inundate more terrestrial habitat to mobilise detritus), and seasonal rainfall levels (that can wash terrestrial detritus into the marine system). Further, shallow-water unvegetated benthic habitats rely on light reaching the sediment surface for production (Lohrer *et al.* 2015; Needham *et al.* 2011), and therefore the associated uptake of nutrients (before they can be exported out of the estuary) by the benthos may be tightly coupled with seasonal day length and weather conditions.

Quarterly, at the mouth of a tidally-dominated temperate sub-estuary, we measured the flux of macrodetritus, dissolved and particulate forms of N and P, as well as chlorophyll *a* (chl *a*) to increase understanding of the seasonal variability in the source and quantity of production that is transported across the boundary of a small temperate estuary. The study was designed to: 1) obtain empirical data on the magnitude of macrodetrital fluxes from a mixed habitat estuary that is typical of estuaries in the North Island of New Zealand (i.e.

large intertidal areas, with large tidal water exchange); and 2) increase our knowledge of the magnitude of export of production in a tidal estuary, with particular emphasis on the contribution of macrodetritus to the total exported production, N and P. Studies such as this contribute to understanding of how anthropogenic habitat degradation (e.g. mangrove forest clearances and seagrass bed declines that can change the supply of detritus available to be exported; Inglis 2003; Moore and Short 2006; Orth *et al.* 2006; Harty 2009) may affect the ecosystem services associated with production outwelling from temperate estuaries.

Materials and methods

Site description

Tairua Estuary (37°00’05” S, 175°50’42” E) is located on the east coast of the Coromandel Peninsula (Fig. 1), and is representative of a common type of estuary in the North Island of New Zealand (Hume *et al.* 2007). Tairua Estuary is a 605 ha barrier-enclosed lagoon, of which 71% (of the high tide area) is intertidal (Fig. 1), and the mean water depth at mid-tide is ~2 m (Hume and Herdendorf 1993; Bell 1994). The estuary is well flushed, taking 1.3 tidal cycles to flush the entire tidal prism, and 82% of the water that enters the estuary during each flooding tide is ‘new’ ocean water (Bell 1994). The estuary has spring and neap tidal ranges of 1.63 m and 1.22 m, respectively (Liu 2014). The estuary’s 29,381 ha catchment is occupied by a number of land uses, including forestry, pasture, and small urban settlements, as well as indigenous forest and scrub (O’Donnell 2011).

Pepe Inlet is a 26 ha tidally-dominated inlet within Tairua Estuary (Fig. 1). The inlet tidally drains through a single mouth (~37 m wide), and has one main freshwater input at Pepe Stream, which discharges on average 0.23 $m^3 s^{-1}$ of water into the estuary (mean annual discharge; Liu 2014). Pepe Inlet supports diverse marine vegetated habitats, which include mangrove forest (*Avicennia marina* subsp. *australasica;* ~3 ha, ~11% of estuary area), seagrass beds (*Zostera muelleri;* ~2 ha, ~8% of estuary area), and saltmarsh (~10 ha; made up of various rushland, saltwater paspallum, *Spartina* spp., salt meadow, and saltmarsh ribbonwood species, some of which is above mean high water springs; Fig. 1; Graeme 2008; Felsing and Giles 2011). Macroalgae (*Hormosira banksii*) also grow within and outside the mouth of the inlet (Graeme 2008). The unvegetated sediments within Pepe Inlet are comprised mainly of fine to medium sands (Felsing and Giles 2011). Sampling was done at the mouth of Pepe Inlet, and at Pepe Stream (Fig. 1C) to determine the flux of macrodetritus, dissolved and particulate nutrients from this sub-estuary to the wider estuary/coastal system. The well constrained mouth, as well as the mixture of vegetation types within Pepe Inlet make this estuary an ideal place to study material fluxes.

During the study period (May 2014-February 2015), the Coromandel region had maximum and minimum daily air temperatures of 28.9°C and -1.8°C, respectively. Total rainfall over a 48 h period (24 h before, and during each sampling period) was 0.4, 0.2, 12.8, and 6.8 mm, in May, July, November, and February, respectively (climate data obtained from the NIWA CliFlo database at http://cliflo.niwa.co.nz; data from the Whitianga weather station, ~30 km from Tairua).

Sampling regime

To derive material fluxes, we sampled macrodetritus, water column chl *a* (an indicator of phytoplankton and resuspended benthic microphyte biomass), total dissolved N and P (TDN and TDP; includes both inorganic and organic components), as well as total particulate N and P (TPN and TPP) concentrations, over a 24 h period (two ebb and two flood tides). The 24 h sampling was repeated in May (late-autumn = Aut), July (midwinter = Win), November (late-spring = Spr), and February (late-summer = Sum). 24 h sampling periods were chosen during spring tides, and sampling encompassed both midday and midnight high tides to reduce the variability between sampling dates that may be confounded by diurnal uptake of inorganic nutrients (i.e. by microalgae during photosynthesis; Lohrer *et al.* 2015).

Suspended macrodetritus was sampled using nets positioned in the mouth of Pepe Inlet, which were emptied on each slack tide (as the tidal flow direction changed). Three nets (opening: 50 × 100 cm, length: 100 cm, mesh size: 4 × 4 mm) were placed at two positions within the 37 m wide channel (6 nets total; sampling 5.4% of the channel width), with three nets stacked on top of one another (Fig. A1 in Appendices). The bottom and middle nets were kept at a fixed depth, while the top net floated and sunk as the tide rose and fell to sample the surface waters. All nets were attached to a central pole, enabling them to change direction with the water flow.

Preliminary depth profiles (as well as hourly depth profiles during all sampling dates; 0.1 m depth intervals) of salinity, temperature, and dissolved oxygen (DO; Multi-parameter water quality Sonde 600QS; YSI Inc.) indicated that Pepe Inlet channel remained well mixed for most of the tidal cycle (and during times of greatest tidal exchange; see results). Because the channel remained well-mixed, water samples (1 L) were collected half hourly in the centre of the channel using a Van Dorn water sampler (3.2 L, PVC, ENVCO) lowered just below the water surface. To sample the freshwater input into the estuary, a portable vacuum sampler (model: VST, Manning Environmental Inc.) was positioned to collect surface water (0.5 L) in the centre of Pepe Stream half hourly into acid washed containers.

One 100 ml water sample from each half hourly sampling was immediately pressure filtered through two 25 mm Whatman GF/C fibreglass filters, and the filtrate and filters were frozen for later analysis of dissolved nutrients and chl *a*, respectively. The remaining water from each half hour sample was then pooled across 2 h for measurement of particulate N and P (i.e. TPN and TPP), and filtered through pre-weighed 45 mm Whatman GF/C fiberglass filters using a vacuum pump (i.e. particulates include suspended particles, from 0.5-1.75 L water samples, retained on 1.2 µm pore size fiberglass filter; the sample volume depended on the amount suspended content). Filters for TPN and TPP were also frozen awaiting analysis.

During each 24 h sampling period, either a SonTek Triton ADV (averaging interval 1 min, sampling interval 10 min; ~65 cm above seafloor; deployed in Win, Spr, Sum) or a SonTek Argonaut ADCP (XR 3000 kHz; averaging interval 2 min, sampling interval 5 min; 20 cm above seafloor; deployed in Aut) was positioned in the centre of the Pepe Inlet channel to measure current velocity. A Solinist Levelogger (measuring absolute water pressure) was placed in the centre of the channel to measure water depth, and a Solinist Barologger was used to compensate the depth obtained by the Levelogger for barometric pressure (sampling interval 10 min.). The cross-sectional area and water velocity was measured using a SonTek FlowTracker Handheld ADV to calculate discharge (0.6 depth and multipoint methods; Sontek/YSI Inc. 2007), approximately hourly during the daylight hours.

Laboratory analyses

Plant detritus collected by the nets was washed, separated by source (e.g. mangrove, seagrass, terrestrial/marsh, macroalgae), dried to constant weight at 60°C, and weighed (dry weight, DW). Half hourly filtered water samples were pooled in the laboratory across one hour and subsamples taken for measurements of TDN, TDP, and ammonium (NH_4^+) on a LACHAT Quickchem 8500 series 2 Flow Injection Analyser (FIA). NO_x and PO_4^{2-} were also measured, but results were unreliable and data are not presented. TDN consists of dissolved NH_4^+ + NO_x + organic N, and TDP consists of dissolved PO_4^{2-} + organic P, but the proportions of NO_x and PO_4^{2-}, as well as dissolved organic N and P are unknown. Water samples for TDN and TDP, and filters for TPN and TPP (one filter for each two hourly sampling) were first digested (potassium persulphate solution) and autoclaved (30 min at 121°C, 15 psi), before analysis of total N and P on the FIA. Water column particulate chl *a* concentrations were determined by steeping and grinding filters (two filters for each half hour sampling) in 90% buffered acetone, and then pigment concentrations were measured fluorometrically (Turner 10-AU fluorometer) before and after acidification (Arar and Collins 1997).

Data analysis and material flux calculations

A linear correlation between the discrete discharge measurements (Flowtracker ADV during the day) and the continuous water velocity × depth (5-10 min measurement interval) was used to predict discharge over the 24 h sampling period (correlation r^2 = 0.84-0.94; see Fig. A2 in Appendices for correlations). The total discharge volume for each flood and ebb tide was then estimated by summing the predicted discharge rate at 10 min intervals within each tidal stage (Fig. A3, and Table A2).

TDN, TDP, TPN, TPP, and chl *a* concentrations averaged over the 4 h of peak flow (estimated from velocity measurements) were used to calculate the fluxes from Pepe Inlet, where the 4 h average concentration was multiplied by the discharge volume for each ebb and flood tide. Using the mean annual discharge from Pepe Stream (0.23 $m^3 s^{-1}$; Liu 2014; which is <1% of the peak discharge measured at the mouth of Pepe Inlet), we estimated the input of TDN, TDP, TPN, TPP, and chl *a* from Pepe Stream into Pepe Inlet over a tidal cycle (i.e. stream input = stream discharge scaled to a tidal cycle × average solute or particulate concentration measured at Pepe Stream). As all sampling periods fell during periods of low rainfall (i.e. there was <13 mm of rain in the 24 h prior to and during sampling), we consider the mean annual discharge suitable for estimating stream inputs.

Fluxes of macrodetritus were calculated by summing the total detritus DW collected in the nets during each flood and ebb tide, and this total was multiplied by the width of the channel (i.e. macrodetritus flux = total detritus DW × 37 m / 2 m sampling width of nets; similar flux calculations are described in Bouchard and Lefeuvre 2000). This calculation assumes that our nets sample the entire water column throughout the tidal cycle; a reasonable assumption given that just ~0.6 m of the water column was omitted during high tide, but during times of peak flow (mid-tide) the entire water column was sampled by the nets. Further, the top and the bottom nets captured the majority of the macrodetritus (>72%, but usually >90% of the total collected macrodetritus), suggesting that detritus usually either floats or is transported along the seafloor, and little was caught suspended in the middle of the water column. To estimate the flux of macrodetritus N and P, and to allow comparisons with other sources (dissolved and particulate), detrital DW was converted to N and P using the average values (as % of DW) for each detrital source (or similar sources) from the Enriquez *et al.* (1993) review, as well as from N content measured for *Z. muelleri, A. marina,* and *E. radiata* in Gladstone-Gallagher *et al.* (2016).

Results

Across sampling dates, the channel at the mouth of Pepe Inlet remained well mixed for ~75% of the tidal cycle (determined from hourly depth profiles of salinity, temperature and DO in the channel), only becoming stratified for ~3 h at slack low tide when tidal exchange was minimal. The difference in salinity between the bottom and surface waters during this low tide stratification (i.e. channel depth ~0.7-0.9 m) was <14.2 ppt, with temperature and DO differences of <2.9°C and <2.2 mg L^{-1}, respectively. During the remainder of the tidal cycle, when the water column was well mixed (i.e. channel depth ~0.9-2.2 m), salinity differences between the bottom and surface waters were <4.9 ppt (but often <0.5 ppt), with surface vs. bottom water differences in temperature <1.9°C (but often <0.5°C), and DO <0.68 mg L^{-1}. Across the sampling dates, salinity averaged across the tidal cycle ranged from 24.2-31.6 ppt, temperature from 11.4-20.3°C, and DO concentration from 7.5-9.3 mg L^{-1}.

Macrodetritus fluxes

The magnitude of the flood and ebb macrodetritus fluxes varied across seasons, by both weight and source (Fig. 2). Seagrass (*Z. muelleri*) was the dominant detrital source to be transported by flood tides in all seasons (40-92% of flood fluxes). In Spr and Sum, macroalgae (including unidentified green and brown species) were equally dominant, contributing 49 and 36% to the Spr and Sum flood tide fluxes, respectively. Ebb tide macrodetrital transport was highly seasonal and dominated by mangrove litter (*A. marina*) in Spr (61% of the ebb flux), but by seagrass in Aut and Win (39 and 52%, respectively), and macroalgae in Sum (38%). The transport of terrestrial/marsh detritus (broadly grouped and not identified to species level) was consistent across seasons in terms of absolute contribution (0.1-5.3 kg DW $tide^{-1}$ on both flooding and ebbing tides), but varied across seasons in relative contribution to the total macrodetritus fluxes (Ebb fluxes: 50% Aut, 32% Win, 16% Spr, 19% Sum; Flood fluxes: 4% Aut, 33% Win, 6% Spr, 12% Sum; Fig. 2).

The net fluxes of macrodetritus (ebb flux minus flood flux) show that Pepe Inlet acted as a net exporter of macrodetritus on three of the four sampling dates (Aut, Win, and Sum; Fig. 2). The greatest export occurred in Sum, where nearly 10 kg DW tidal cycle^{-1} of macrodetritus was exported from Pepe Inlet. The Sum macrodetritus export was comprised of 43% macroalgae, 33% terrestrial/marsh, 17% seagrass, and 7% mangrove detritus. In Aut, the small net export was largely made up of terrestrial/marsh litter (83%), and in Win, the export was comprised equally of the four sources (i.e. mangrove, seagrass, terrestrial/marsh, and macroalgae all contributed 20-30% of the net export). In Spr there was a net import into the inlet (11 kg DW tidal cycle^{-1}), which was predominantly comprised of seagrass and macroalgae (Fig. 2) and juxtaposed against a small export of mangrove detritus (1.6 kg tidal cycle^{-1}). Using the average of the net fluxes across seasons, it is estimated that ~449 kg DW yr^{-1} of macrodetritus is exported from Pepe Inlet, or 30 kg DW ha^{-1} yr^{-1} when scaled to the area occupied by marine vegetated habitats (~15 ha of mangroves, seagrass and saltmarsh) within Pepe Inlet. In Sum and Win, the net fluxes were relatively small compared to the total ebb or flood fluxes (net fluxes 18-34% and 22-52% of the total flood and ebb flux, respectively).

Nitrogen fluxes

The dominant form of N transported by both flooding and ebbing tides was TDN, which comprised >94% of the total fluxes in Aut, Win and Spr. In Sum, TDN was lower and comprised 80 and 85% of N on ebb and flood tides, respectively (Fig. 3). TDN fluxes consisted of 6-28% NH_4^+ (compare Fig. 3C with D), with the proportion of NO_x and organic N unknown. Across seasons, macrodetritus contributed <3% to the total N flux on both flood and ebb tides. In Aut, Win, and Spr, TPN contributed <5% to the total N fluxes, whereas, in Sum, when TDN fluxes were lower, the TPN comprised 13 and 17% of flood and ebb tide fluxes, respectively (Fig. 3).

Across seasons, Pepe Inlet was a net exporter of N (dissolved and particulate N exports offset macrodetritus imports in Spr), exporting a total of 2-12 kg N tidal cycle^{-1}. The dominant form of N exported in Aut, Win and Spr was dissolved (TDN >93% of the total net N exports). Macrodetritus and particulate matter contributed relatively little to the total net N export (<7%), except for in Sum where dissolved fluxes were low, and macrodetritus and particulate N contribution were 13 and 66% of the net N export, respectively (Fig. 3). Annual estimates of net N fluxes are 6 kg N yr^{-1} imported as macrodetritus, 467 kg N yr^{-1} exported as particulates, and 4684 kg N yr^{-1} exported as dissolved (total annual N export = 5145 kg N).

Phosphorus fluxes

In Aut and Spr, P fluxes transported by both flood and ebb tides were dominated by TDP (TDP contribution in Aut = 74-82%, and Spr = 82-87% of total P fluxes). Whereas, in Win and Sum, P fluxes transported in both flood and ebb tides were dominated by TPP (TPP contribution in Win = 51-55%, and Sum = 87% of total P fluxes). Across seasons, macrodetritus contributed relatively little to the total P fluxes of both flood and ebb tides (<13%; Fig. 4).

In Win, Spr, and Sum, Pepe Inlet acted as a net exporter of P (macrodetritus imports in Spr were offset by TDP and TPP exports), exporting a total of 0.5-1.5 kg P tidal cycle^{-1}, but in Aut, Pepe Inlet imported 0.5 kg P tidal cycle^{-1}. In Win (when all forms of P were exported from Pepe Inlet), macrodetritus, TDP, and TPP represented 2.3, 57.2, and 40.4% of the total net export of P, respectively (Fig. 4). Annual estimates of net P fluxes are 8 kg P yr^{-1}

imported as macrodetritus, 164 kg P yr^{-1} exported as particulates, and 206 kg P yr^{-1} exported as dissolved material (total annual export = 362 kg P).

Chlorophyll *a* fluxes

Pepe Inlet was a net exporter of chl *a* (i.e. particulate chl *a* captured on filters), where 35-146 kg tidal cycle^{-1} of chl *a* was exported from the inlet (except in Spr where 14 kg tidal cycle^{-1} of chl *a* was imported; Fig. 5). Annually, it is estimated that Pepe Inlet exports 39,145 kg particulate chl *a*.

Stream contribution to net fluxes

The contribution of nutrients and chl *a* from Pepe Stream was seasonally variable, and contributed 10-42% of the total N, and 10-19% to the total P exports at the mouth of Pepe Inlet (Table 1). In Aut, the stream contributed 20-55% to the exports of TDN, TDP, TPN, TPP, and chl *a* measured at the mouth of the Inlet, but in Win, the stream contributed less to these material exports (just 6-19% of the net exports were from the stream). In Spr, the stream inputs of TDN and TDP were low (8 and 4%, respectively), while inputs of TPN and TPP were relatively high (51 and 74%, respectively). In Sum, Pepe Stream inputs accounted for 10-44% of the material exports from Pepe Inlet, except for TDN, where the input from the stream was almost double the net export out of Pepe Inlet (Table 1).

Discussion

As empirical measurements of macrodetritus fluxes from temperate estuaries are rare and often excluded from estuarine nutrient budgets, this study was designed to quantify the relative contribution of macrodetritus to the overall estuary-to-coast flux of primary production, N and P. We found that across most seasons, Pepe Inlet was a net exporter of macrodetritus, chl *a*, as well as total N and P. The dissolved and small particulate fractions dominated the net fluxes of total N and P from Pepe Inlet. Given that coastal marine primary production is regulated by both N and P, with dissolved N often being the limiting nutrient (Herbert 1999; Tyrell 1999), estuaries including Pepe Inlet potentially play an important role as exporters of nutrients, supporting production in the open coastal ocean. Whilst the contribution of macrodetritus to the N and P export out of the inlet was small (<13% and <3% of N and P exports, respectively, across seasons, except for spring where macrodetritus was imported), macrodetritus flux was relatively large in terms of DW. As macrodetritus is an obvious and visible source of estuarine primary production, its degradation and accumulation in receiving habitats (e.g. coastal soft-sediments, seagrass beds and other vegetated habitats) has the potential to alter ecosystem structure and function (e.g. by structuring macrofaunal communities; Kelaher and Levinton 2003; Rossi 2006; Bishop *et al*. 2010).

Scaling up the macrodetritus weights to estimate the amount of litter that is exported annually from Pepe Inlet yields ~30 kg DW ha^{-1} of vegetated area within the inlet (~15 ha of seagrass, mangroves and marsh habitat). This estimate is comparable to the macrodetritus export that was measured in the mangrove basin, Tuff Crater, New Zealand (7-42 kg DW ha^{-1} yr^{-1} when converted to area of vegetation; Woodroffe 1985), and although hydrodynamically different, Tuff Crater is similar in area to Pepe Inlet. In addition, our estimated annual export of macrodetritus is also comparable to that of North Inlet (USA), which was found to export 27 kg DW ha^{-1} of saltmarsh annually (annual export scaled to saltmarsh area; Dame and Stilwell 1984; Dame *et al.* 1986). Others have found lower macrodetritus exports than Pepe Inlet, which is likely related to the specific hydrodynamics of the systems in question, being temperate marsh systems that have high water residence times and less frequent tidal inundation (Table A1; Hemminga *et al.* 1996; Bouchard and Lefeuvre 2000).

In their review of estuary-to-coast flux studies, Childers *et al.* (2000) used regression analysis (n = 20 studies) to identify the physical factors regulating dissolved and particulate material transport across estuarine to open ocean boundaries. Tidal range explained 40% of the variation in dissolved nutrient flux, where systems switched from importers to exporters at tidal ranges >1.2 m (similar results were also found by Adame and Lovelock 2011, when reviewing the hydrological factors that affect nutrient export from mangrove forests). The extensive review also found that smaller estuaries (<54 ha) showed greater exports of particulate organic matter. Tairua Estuary not only has a high tidal exchange (82% of water exchanged each tide; Bell 1994) and range (1.2-1.6 m), but is regarded as a small estuary (<54 ha). Further, the majority of vegetated habitats in Pepe Inlet (seagrass and mangroves, as well as some of the marsh) occur below the mean high water spring tide mark, which is likely to increase the opportunity for material exports out of these systems. These hydrodynamic properties will undoubtedly influence the exchange of macrodetritus, and to some extent limit the generalisability of our results to other temperate estuaries (i.e. larger salt marsh systems that have more limited tidal exchange). However, Pepe Inlet represents a common estuary type, at least in the New Zealand context (Hume *et al.* 2007), in that it is a largely intertidal, ebb-dominated (Fig. A3 in Appendices), mixed habitat estuary.

Whilst Pepe Inlet annually exported macrodetritus in terms of total DW, it was found to be a net importer of macrodetritus N and P on an annual basis (imports = 6 kg N yr^{-1} and 8 kg P yr^{-1}; Table A1). The N and P content of macrodetritus depends on the plant species; macroalgae are 1.0-3.9% N and 0.2-0.4% P, while mangrove litter contains 0.7-1.2% N and 0.1% P, and seagrass litter is 1.3-4.0% N and 0.6-2.5% P (Enriquez *et al.* 1993). The total macrodetritus flux in terms of total DW does not distinguish between the differences in detrital species composition on the ebbing and flooding tides, where the imports into Pepe Inlet were generally dominated by macroalgae and seagrass, and exports were dominated by mangrove and terrestrial/marsh leaf litter. Thus, the resulting annual flux of macrodetritus N and P were imports (i.e. imports of relatively N and P rich macrodetritus offset exports of relatively N and P poor macrodetritus). On an annual basis, Pepe Inlet acts as a net importer of macrodetritus N and P (albeit minimal), but an exporter of other forms of N and P (particulates and dissolved), suggesting the potential role of these estuaries as organic matter transformers. It is also worth noting that, in Pepe Inlet, the individual flood and ebb macrodetritus fluxes were often much higher than net fluxes (net fluxes 18-52% of the total flood/ebb flux in summer and winter), suggesting that some of the macrodetritus transported out of the estuary probably returns with the subsequent flooding tide (i.e. macrodetritus is transported in large volumes, but the net export is relatively small by comparison). This returning detritus can also become trapped within the vegetated habitats in the estuary (e.g. seagrass beds and mangrove forest), increasing retention and limiting export out of the estuarine system (Gillis *et al*. 2014).

Fluxes of all forms of N and P varied across seasons. Most markedly was the difference in summer (compared to other seasons), where macrodetritus and chl *a* transport (and export) peaked, and dissolved N and P dropped. The summer peak in macrodetritus transport is not surprising given that many marine plants show seasonal peaks in growth and production in summer, which could also promote dissolved inorganic nutrient uptake by macrophytes (potentially explaining the lower dissolved nutrient exports in summer). New Zealand mangroves produce 77% of their total litter production between November and February (Gladstone-Gallagher *et al.* 2014). In addition, macroalgae senescence and erosion, and seagrass growth and production, can also be greatest in summer (Brown *et al.* 1997; Turner 2007). However, when organic matter is imported into the estuary (e.g. macrodetritus in spring), or when exports are low (i.e. high retention of macrodetritus), decay and remineralisation processes will occur within the estuary. If *in situ* decay and organic matter transformations are high, then outwelled production may be in the form of dissolved inorganic nutrients rather than organic detritus.

Organic matter transformations that occur within the estuary are likely to modify the form in which production and nutrients are outwelled, and they may help to explain some of the seasonal fluctuations in N and P fluxes. In Pepe Inlet, the contribution of the stream was seasonally variable, contributing between 10-55% of the estuary's total N, P and chl *a* exports. Analysing each form of N and P separately revealed some interesting results, for example, the summer input of TDN from Pepe Stream was 1.5 × greater than the TDN exported from Pepe Inlet. However, for total N (i.e. TDN + TPN + macrodetritus N), Pepe Stream only contributed 42% to the total N exported (Table 1). This further indicates that processes within the estuary transform and utilise some of this dissolved N before it can be exported at the estuary mouth. As the net export of chl *a* was also highest in summer, the dissolved inorganic N may be utilised by *in situ* phytoplankton and microphytobenthos during summer, exporting N as particulate organic N.

Our study design did not detail within-estuary processes, and instead focused on the differences between measured inputs (at Pepe Stream) and outputs (at the mouth of Pepe Inlet). Nevertheless, processes within the estuary can be discussed, in an attempt to illuminate the simple 'black box' model (depicted in Fig. 6). In summer and winter, >67% of the net exports of macrodetritus were from marine sources, and therefore it is likely that this production mostly occurred within the inlet itself, rather than transported by the stream (although the terrestrial/marsh sources were important in autumn). Other processes within the estuary, including the solute fluxes across the sediment-water interface, are likely to contribute to the export of nutrients from the inlet. In temperate estuaries, sediment-water effluxes of dissolved inorganic N (NO_x and NH_4^+) and P (PO_4^{2-}) occur through nutrient remineralisation processes in the benthos (e.g. Lohrer *et al.* 2004; Pratt *et al*. 2014). It is estimated that up to 50% of global organic matter remineralisation occurs in the coastal soft-sediments (Middelburg *et al.* 1997), and therefore these sediments may supply dissolved N and P to the water column that is available to be outwelled to the adjacent coastal waters.

In a previous study, we measured summertime sediment-water solute fluxes of NH_4^+ in Pepe Inlet (Gladstone-Gallagher *et al.* 2017), and since NH_4^+ is the dominant form of dissolved inorganic N that is moved out of the sediments (>88% of inorganic N efflux; Thrush *et al.* 2006; Jones *et al*. 2011; Pratt *et al.* 2014; Gladstone-Gallagher *et al.* 2016), these fluxes can be used to estimate the contribution of the unvegetated sediments to the export of N. Using the summertime measurements in Pepe Inlet, we estimate that on average ~0.7 kg of N tidal cycle^{-1} comes from the sediments in the form of NH_4^+, accounting for ~40% of the total N exported (Fig. 6). To explore this same N budget model for the other seasons, we used the NH_4^+ flux values from Pratt *et al.* (2014), who measured benthic ecosystem function across nine estuaries in different seasons (Table 2). Based on maximum benthic NH_4^+ fluxes documented in Pratt *et al.* (2014; scaled to the area of Pepe Inlet), it is plausible that in autumn and summer, the benthic fluxes could account for the differences in inputs and outputs of N in Pepe inlet (0.46 kg and 0 kg N unaccounted for in autumn and summer, respectively). However, in winter and spring some N is unaccounted for by this budget (3.29 and 5.67 kg N tidal cycle^{-1}, respectively; Table 2). The sources of N contributing to this shortfall remain unknown, but could be associated with seasonal differences in rainfall and groundwater discharge (Santos *et al.* 2012; Santos *et al.* 2014). Benthic NH_4^+ fluxes may be outwelled as NH_4^+, but may also be utilised within the estuary (e.g. by *in situ* phytoplankton production) and exported in another form. This has been suggested for dissolved C and N in the North Inlet estuary (saltmarsh-dominated inlet), where it is thought that dissolved nutrients are rapidly utilised within the estuary and instead exported as particulates (Dame *et al.* 1986). Whilst our calculations do not account for the contribution of NO_x or PO_4^{2-} from the sediments, the analysis highlights that the benthos is likely to represent a significant source of outwelled nutrients (Fig. 6; Table 2).

Seasonal flux differences may be confounded by differences in the lunar cycle stage during times of sampling (i.e. some variability in the tidal amplitude was inevitable; Table A2), which has particular consequences for overestimating the transport of terrestrial and marsh production. Other limitations of our flux estimates include the simplification of macrodetritus flux estimates to omit variability in flow conditions across the channel width; small differences in the accuracy of the model used to predict discharge between the different sampling dates (Fig.A2); the omission of storm/flood conditions from sampling (i.e. such conditions would result in increased transport of materials particularly from the terrestrial habitat); and the potential effects of the small-scale temporal variability in abiotic factors (e.g. wind speed/direction and stream flow conditions) confounding the perceived seasonal variability in detrital transport.

This study provides real-world quantification of the magnitude of macrodetritus fluxes, as well as the simultaneous measurements of other forms of production exported from a typical temperate New Zealand estuary. Data of this type can be useful to inform studies of estuarine food webs, nutrient budgets, and the ecosystem services provided by temperate estuaries, which are important when predicting ecosystem effects of anthropogenic degradation of marine habitats. Whilst macrodetritus represents a relatively minor source of N and P, its transport (here up to 10 kg net tidal cycle^{-1}) and accumulation in large patches will have important effects on receiving ecosystems. Examples include its effects in structuring benthic infaunal communities (e.g. Kelaher and Levinton 2003; Bishop and Kelaher 2007), or its role in modifying ecosystem function in receiving habitats (e.g. Gladstone-Gallagher *et al.* 2016). Because detritus is transported in relatively large quantities, and it decays slowly, it may represent an important source of primary production to offshore, deeper food webs that have low *in situ* productivity (e.g. sediments below the photic zone; Britton-Simmons *et al.* 2009). Our results also emphasise the role of temperate estuaries as sites of efficient organic matter transformation, where there is a net export of total N and P, but when broken down into the various components of material transport, some materials are imported (e.g. macrodetritus in spring), but processed within the estuary and exported in a different form (e.g. dissolved N).

Acknowledgements

We thank Dudley Bell, Warrick Powrie, Chris Morcom, Bradley Monahan, Emily Douglas, Clarisse Niemand, Ryan Hughes, Catherine Kelly, Holly Bredin-Grey, Katie Brasell, and Mathew Bennion for helping with field work, Ronald Ram for laboratory assistance, Ben Norris, Bradley Monahan, and Berengere Dejeans for data analysis advice, and Hazel Needham for providing helpful advice during sampling design planning. We also acknowledge and thank an anonymous reviewer who greatly improved the manuscript.

This project was supported by a University of Waikato Doctoral Scholarship, Shirtcliffe Fellowship, Waikato Graduate Women Charitable Trust Merit Award for Doctoral Study, and New Zealand Coastal Society PhD scholarship to RVGG.

The authors declare no conflicts of interest.

References

Adame, M. F., and Lovelock, C. E. (2011). Carbon and nutrient exchange of mangrove forests with the coastal ocean. *Hydrobiologia* **663**, 23-50.

Arar, E. J., and Collins, G. B. (1997). Method 445.0: *In vitro* determination of chlorophyll *a* and pheophytin *a* in marine and freshwater algae by fluorescence. (U.S. Environmental Protection Agency: Cincinnati, Ohio, USA)

Baird, D., Winter, P. E. D., and Wendt, G. (1987). The flux of particulate material through a well-mixed estuary. *Continental Shelf Research* **7**, 1399-1403.

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., and Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs* **81**, 169-193.

Bell, R. G. (1994). Behaviour of dissolved silica, and estuarine/coastal mixing and exchange processes at Tairua Harbour, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **28**, 55-68.

Biber, P. D. (2007). Hydrodynamic transport of drifting macroalgae through a tidal cut. *Estuarine, Coastal and Shelf Science* **74**, 565-569.

Bishop, M. J., Coleman, M. A., and Kelaher, B. P. (2010). Cross-habitat impacts of species decline: response of estuarine sediment communities to changing detrital resources. *Oecologia* **163**, 517-525.

Bishop, M. J., and Kelaher, B. P. (2007). Impacts of detrital enrichment on estuarine assemblages: disentangling effects of frequency and intensity of disturbance. *Marine Ecology Progress Series* **341**, 25-36.

Borey, R. B., Harcombe, P. A., and Fisher, F. M. (1983). Water and organic carbon fluxes from an irregularly flooded brackish marsh on the upper Texas coast, U.S.A. *Estuarine, Coastal and Shelf Science* **16**, 379-402.

Boto, K. G., and Bunt, J. S. (1981). Tidal export of particulate organic-matter from a Northern Australian mangrove system. *Estuarine, Coastal and Shelf Science* **13**, 247-255.

Boto, K. G., and Wellington, J. T. (1988). Seasonal-variations in concentrations and fluxes of dissolved organic and inorganic materials in a tropical, tidally-dominated, mangrove waterway. *Marine Ecology Progress Series* **50**, 151-160.

Bouchard, V., and Lefeuvre, J. C. (2000). Primary production and macro-detritus dynamics in a European salt marsh: carbon and nitrogen budgets. *Aquatic Botany* **67**(1), 23-42.

Britton-Simmons, K. H., Foley, G., and Okamoto, D. (2009). Spatial subsidy in the subtidal zone: utilization of drift algae by a deep subtidal sea urchin. *Aquatic Biology* **5**, 233-243.

Brown, T. M., Nyman, A. M., Keogh, A. J., and Chin, M. N. K. (1997). Seasonal growth of the giant kelp *Macrocystis pyrifera* in New Zealand. *Marine Biology* **129**, 417-424.

Childers, D. L., Day, J. W. J., and McKellar, H. N. J. (2000). Twenty more years of marsh and estuarine flux studies: revisiting Nixon (1980). In ‘Concepts and controversies in tidal marsh ecology’. (Eds M. P. Weinstein and D. A. Kreeger) pp. 391-423. (Springer Netherlands.)

Dame, R., Chrzanowski, T., Bildstein, K., Kjerfve, B., McKellar, H., Nelson, D., Spurrier, J., Stancyk, S., Stevenson, H., Vernberg, J., and Zingmark, R. (1986). The outwelling hypothesis and North Inlet, South-Carolina. *Marine Ecology Progress Series* **33**, 217-229.

Dame, R. F. (1982). The flux of floating macrodetritus in the North Inlet estuarine ecosystem. *Estuarine, Coastal and Shelf Science* **15**, 337-344.

Dame, R. F., and Allen, D. M. (1996). Between estuaries and the sea. *Journal of Experimental Marine Biology and Ecology* **200**, 169-185.

Dame, R. F., and Stilwell, D. (1984). Environmental factors influencing macrodetritus flux in North Inlet estuary. *Estuarine, Coastal and Shelf Science* **18**, 721-726.

Dankers, N., Binsbergen, M., Zegers, K., Laane, R., and Vanderloeff, M. R. (1984). Transportation of water, particulate and dissolved organic and inorganic matter between a salt-marsh and the Ems-Dollard Estuary, The Netherlands. *Estuarine, Coastal and Shelf Science* **19**, 143-165.

Doi, H., Matsumasa, M., Fujikawa, M., Kanou, K., Suzuki, T., and Kikuchi, E. (2009). Macroalgae and seagrass contribution to gastropods in sub-tropical and temperate tidal flats. *Journal of the Marine Biological Association of the United Kingdom* **89**, 399-404.

Enriquez, S., Duarte, C. M., and Sandjensen, K. (1993). Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia* **94**, 457-471.

Eyre, B., and Balls, P. (1999). A comparative study of nutrient behavior along the salinity gradient of tropical and temperate estuaries. *Estuaries* **22**, 313-326.

Felsing, M., and Giles, H. (2011). Tairua Estuary shellfish and benthic habitat mapping and assessment of sediment contamination (2009/10). Waikato Regional Council Technical Report 2011/31, Hamilton, New Zealand.

Gillis, L. G., Bouma, T. J., Kiswara, W., Ziegler, A. D., and Herman, P. M. J. (2014). Leaf transport in mimic mangrove forests and seagrass beds. *Marine Ecology Progress Series* **498**, 95-102.

Gladstone-Gallagher, R. V., Lundquist, C. J., and Pilditch, C. A. (2014). Mangrove (*Avicennia marina* subsp. *australasica*) litter production and decomposition in a temperate estuary. *New Zealand Journal of Marine and Freshwater Research* **48**, 24-37.

Gladstone-Gallagher, R. V., Lohrer, A. M., Lundquist, C. J., and Pilditch, C. A. (2016). Effects of detrital subsidies on soft-sediment ecosystem function are transient and source-dependent. *PLoS ONE* **11**, e0154790.

Gladstone-Gallagher, R. V., Needham, H. R., Lohrer, A. M., Lundquist, C. J., and Pilditch, C. A. (2017). Site dependent effects of bioturbator-detritus interactions alter soft-sediment ecosystem function. *Marine Ecology Progress Series* **569**, 145-161.

Graeme, M. (2008). Estuarine Vegetation Survey - Tairua Harbour. Environment Waikato Technical Report 2008/52, Hamilton, New Zealand.

Granek, E. F., Compton, J. E., and Phillips, D. L. (2009). Mangrove-exported nutrient incorporation by sessile coral reef invertebrates. *Ecosystems* **12**, 462-472.

Harty, C. (2009). Mangrove planning and management in New Zealand and South East Australia – A reflection on approaches. *Ocean & Coastal Management* **52**, 278-286.

Hemminga, M. A., Cattrijsse, A., and Wielemaker, A. (1996). Bedload and nearbed detritus transport in a tidal saltmarsh creek. *Estuarine, Coastal and Shelf Science* **42**, 55-62.

Herbert, R. A. (1999). Nitrogen cycling in coastal marine ecosystems. *FEMS Microbiology Reviews* **23**, 563-590.

Hume, T. M., and Herdendorf, C. E. (1993). On the use of empirical stability relationships for characterising estuaries. *Journal of Coastal Research* **9**, 413-422.

Hume, T. M., Snelder, T., Weatherhead, M., and Liefting, R. (2007). A controlling factor approach to estuary classification. *Ocean & Coastal Management* **50**, 905-929.

Imgraben, S., and Dittmann, S. (2008). Leaf litter dynamics and litter consumption in two temperate South Australian mangrove forests. *Journal of Sea Research* **59**, 83-93.

Inglis, G. J. (2003). Seagrasses of New Zealand. In ‘World atlas of seagrasses’. (Eds E. P. Green and F. T. Short) pp. 148-157. (University of California Press: Berkeley, California)

Jones, H.F.E., Pilditch, C.A., Bruesewitz, D.A., Lohrer, A.M. (2011). Sedimentary environment influences the effect of an infaunal suspension feeding bivalve on estuarine ecosystem function. *PloS ONE* **6**, e27065.

Kelaher, B. P., and Levinton, J. S. (2003). Variation in detrital enrichment causes spatio-temporal variation in soft-sediment assemblages. *Marine Ecology Progress Series* **261**, 85-97.

Liu, Z. (2014). Hydrodynamic and sediment transport numerical modelling and applications at Tairua Estuary, New Zealand. PhD thesis, University of Waikato, Hamilton, New Zealand.

Lohrer, A. M., Thrush, S. F., and Gibbs, M. M. (2004). Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* **431**, 1092-1095.

Lohrer, A.M., Thrush, S.F., Hewitt, J.E., and Kraan, C. (2015). The up-scaling of ecosystem functions in a heterogeneous world. Scientific Reports **5**, 10349.

Middelburg, J. J., Soetaert, K., and Herman, P. M. J. (1997). Empirical relationships for use in global diagenetic models. *Deep Sea Research Part I: Oceanographic Research Papers* **44**, 327-344.

Moore, K. A., and Short, F. T. (2006). *Zostera:* Biology, ecology and management. In ‘Seagrasses: Biology, ecology and conservation’. (Eds A. W. D. Larkum, R. J. Orth and C. M. Duarte) pp. 363-380. (Springer: Dordrecht, The Netherlands)

Morrisey, D. J., Swales, A., Dittmann, S., Morrison, M., Lovelock, C. E., and Beard, C. M. (2010). The ecology and management of temperate mangroves. *Oceanography and Marine Biology: An Annual Review* **48**, 43-160.

Needham, H. R., Pilditch, C. A., Lohrer, A. M., and Thrush, S. F. (2011). Context-specific bioturbation mediates changes to ecosystem functioning. *Ecosystems* **14**, 1096-1109.

Nixon, S.W. (1980). Between coastal marshes and coastal waters - A review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. In ‘Estuarine and Wetland Processes’. (Eds P. Hamilton and K. B. Macdonald) pp. 437-525. (Springer US)

O'Donnell, E. (2011). Tairua Harbour and catchment management plan. Waikato Regional Council Technical Report 2011/40, Hamilton, New Zealand.

Odum, E.P. (1968). A research challenge: evaluating the productivity of coastal and estuarine water. In '2nd Sea Grant Conference'. pp. 63-64. (University of Rhode Island, Kingston)

Odum, E. P. (2000). Tidal marshes as outwelling/pulsing systems. In ‘Concepts and Controversies in Tidal Marsh Ecology’. (Eds M. P. Weinstein and D. A. Kreeger) pp. 3-7. (Springer Netherlands)

Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Olyarnik, S., Short, F. T., Waycott, M., and Williams, S. L. (2006). A global crisis for seagrass ecosystems. *BioScience* **56**, 987-996.

Pergent, G., Rico-Raimondino, V., and Pergent-Martini, C. (1997). Fate of primary production in *Posidonia oceanica* meadows of the Mediterranean. *Aquatic Botany* **59**, 307-321.

Pratt, D. R., Lohrer, A. M., Pilditch, C. A., and Thrush, S. F. (2014). Changes in ecosystem function across sedimentary gradients in estuaries. *Ecosystems* **17**, 182-194.

Rajkaran, A., and Adams, J. B. (2007). Mangrove litter production and organic carbon pools in the Mngazana Estuary, South Africa. *African Journal of Aquatic Science* **32**, 17-25.

Ramos e Silva, C. A., Oliveira, S. R., Rêgo, R. D. P., and Mozeto, A. A. (2007). Dynamics of phosphorus and nitrogen through litter fall and decomposition in a tropical mangrove forest. *Marine Environmental Research* **64**, 524-534.

Robertson, A. I. (1986). Leaf-burying crabs: their influence on energy-flow and export from mixed mangrove forests (*Rhizophora* spp) in Northeastern Australia. *Journal of Experimental Marine Biology and Ecology* **102**, 237-248.

Rossi, F. (2006). Small-scale burial of macroalgal detritus in marine sediments: Effects of *Ulva* spp. on the spatial distribution of macrofauna assemblages. *Journal of Experimental Marine Biology and Ecology* **332**, 84-95.

Sánchez-Carrillo, S., Sánchez-Andrés, R., Alatorre, L. C., Angeler, D. G., Álvarez-Cobelas, M., and Arreola-Lizárraga, J. A. (2009). Nutrient fluxes in a semi-arid microtidal mangrove wetland in the Gulf of California. *Estuarine, Coastal and Shelf Science* **82**, 654-662.

Santos, I. R., Bryan, K. R., Pilditch, C. A., and Tait, D. R. (2014). Influence of porewater exchange on nutrient dynamics in two New Zealand estuarine intertidal flats. *Marine Chemistry* **167**, 57-70.

Santos, I. R., Eyre, B. D., and Huettel, M. (2012). The driving forces of porewater and groundwater flow in permeable coastal sediments: A review. *Estuarine, Coastal and Shelf Science* **98**, 1-15.

Savage, C., Thrush, S. F., Lohrer, A. M., and Hewitt, J. E. (2012). Ecosystem services transcend boundaries: estuaries provide resource subsidies and influence functional diversity in coastal benthic communities. *PloS ONE* **7**, e42708.

Silva, C. A. R., Mozeto, A. A., and Ovalle, Á. R. C. (1998). Distribution and fluxes as macrodetritus of phosphorus in red mangroves, Sepetiba Bay, Brazil. *Mangroves and Salt Marshes* **2**, 37-42.

Sontek/YSI Inc., (2007). ‘FlowTracker Handheld ADV technical manual, firmware version 3.3, software version 2.20.’ (Sontek/YSI Inc.: San Diego, USA)

Thrush, S.F., Hewitt, J.E., Gibbs, M., Lundquist, C., Norkko, A. (2006). Functional role of large organisms in intertidal communities: Community effects and ecosystem function. *Ecosystems* **9**, 1029-1040.

Turner, S. J. (2007). Growth and productivity of intertidal *Zostera capricorni* in New Zealand estuaries. *New Zealand Journal of Marine and Freshwater Research* **41**, 77-90.

Tyrrell, T. (1999). The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature* **400**, 525-531.

Underwood, G. J. C., and Kromkamp, J. C. (1999). Primary production by phytoplankton and microphytobenthos in estuaries. *Advances in Ecological Research* **29**, 93-153.

Valiela, I., Cole, M. L., McClelland, J., Hauxwell, J., and Cebrian, J. (2000). Role of salt marshes as part of coastal landscapes. In ‘Concepts and controversies in tidal marsh ecology’. (Eds M. P. Weinstein and D. A. Kreeger) pp. 23-39. (Kluwer Academic Publishers: Dordecht)

Wattayakorn, G., Wolanski, E., and Kjerfve, B. (1990). Mixing, trapping and outwelling in the Klong Ngao mangrove swamp, Thailand. *Estuarine, Coastal and Shelf Science* **31**, 667-688.

Woodroffe, C. D. (1985). Studies of a mangrove basin, Tuff Crater, New Zealand: III. The flux of organic and inorganic particulate matter. *Estuarine, Coastal and Shelf Science* **20**, 447-461.

Figures:

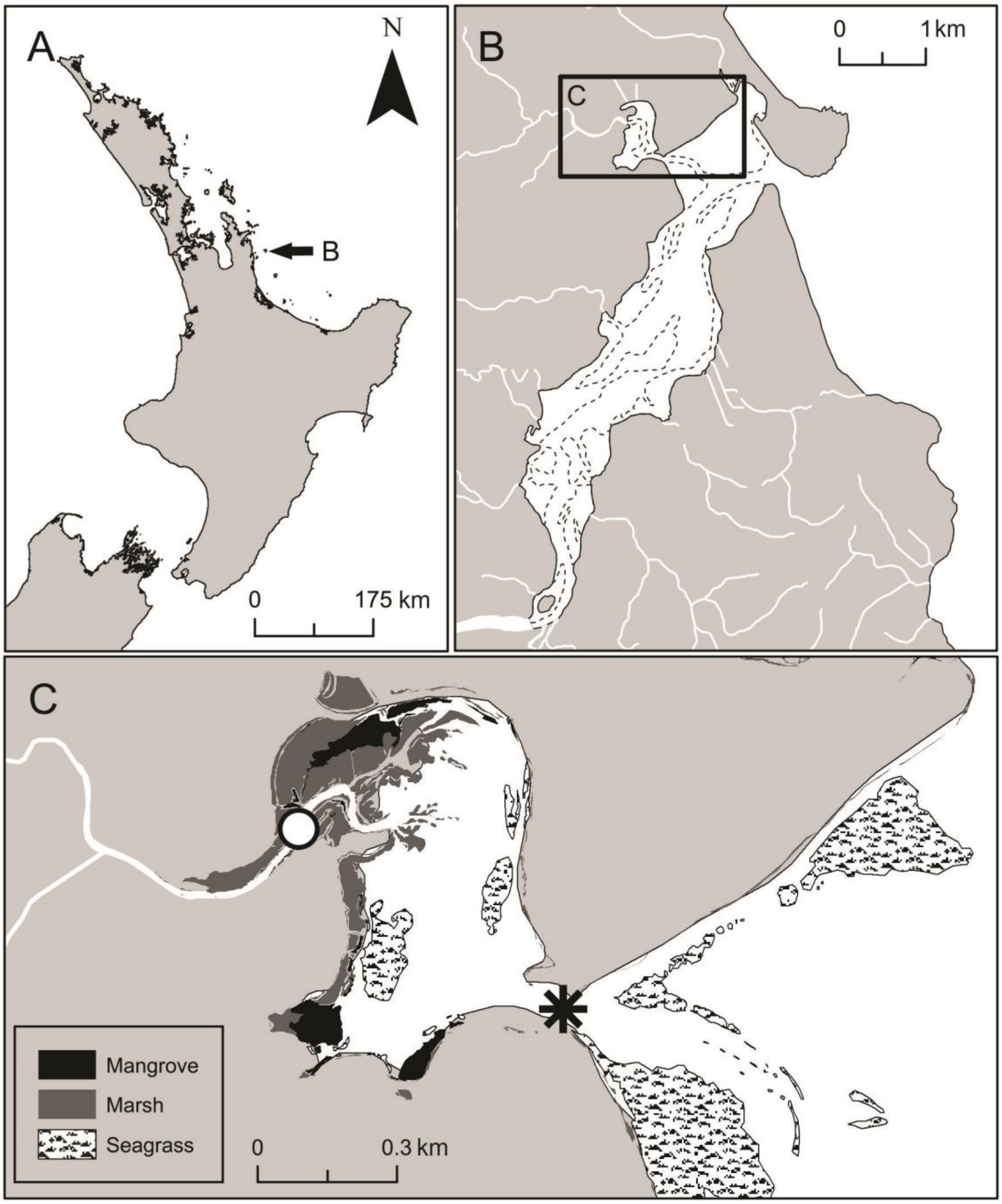

Fig. 1. Map of North Island, New Zealand (**A**), Tairua Estuary with the intertidal boundary shown by dashed lines (**B**), and Pepe Inlet showing the distribution of vegetated habitats (**C**). Water sampling for dissolved and particulate N and P, and chlorophyll a was carried out at both '○' and '*', and sampling of macrodetritus only at '*'. Data source: Waikato Regional Council, Hamilton, New Zealand (GIS vegetation layers).

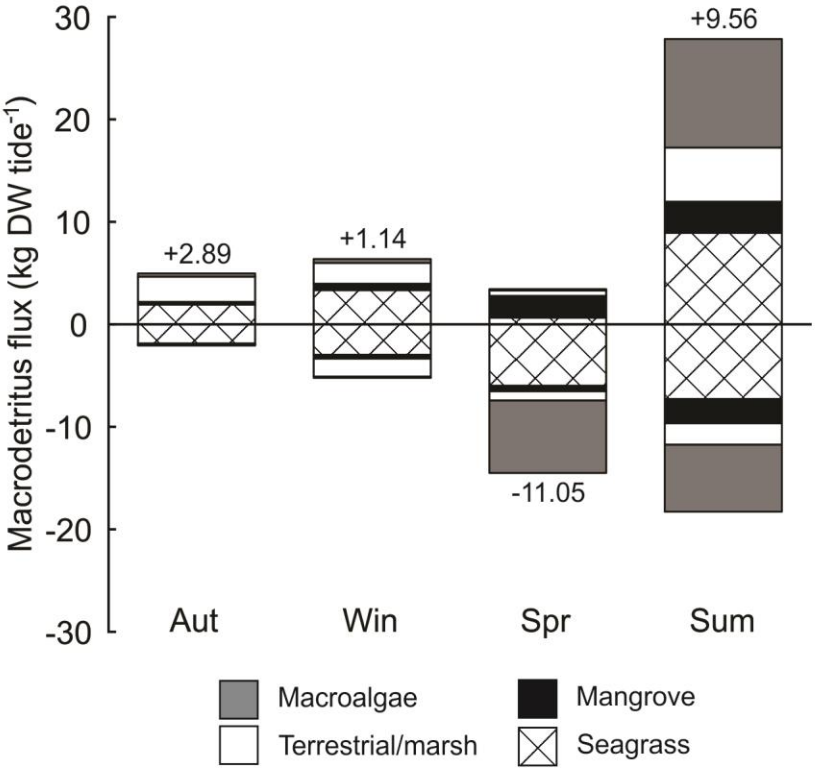

Fig. 2. Fluxes of macrodetritus from Pepe Inlet, Tairua Estuary, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015) and tidal direction (ebb tide fluxes are indicated by positive numbers, and flood tide fluxes are negative; fluxes are the mean of two flood or ebb tides). The net flux (ebb minus flood) is given above/below the bar (in kg DW tidal cycle^{-1}) for each season, and fluxes are separated by source.

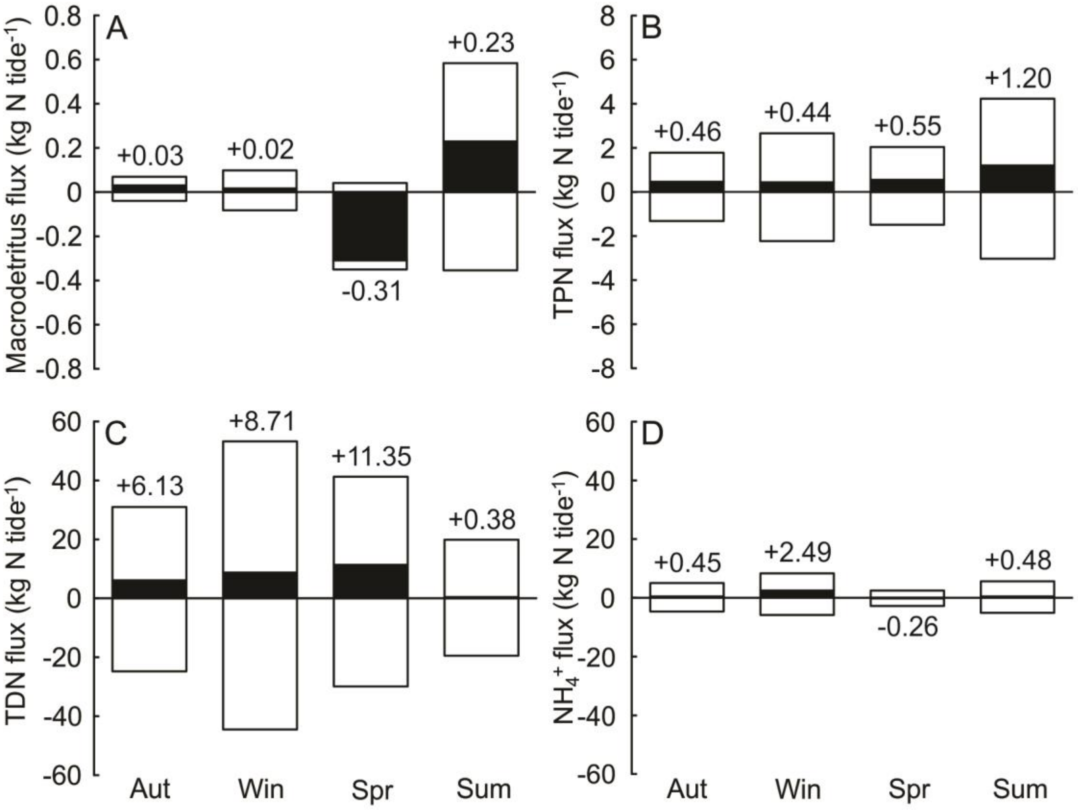

Fig. 3. Nitrogen flux as macrodetritus (**A**), particulate (TPN; **B**), and dissolved (TDN, **C**, and ammonium NH_4^+, **D**), from Pepe Inlet, Tairua Estuary, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015) and tidal direction (ebb tide fluxes are indicated by positive numbers, and flood tide fluxes are negative; fluxes are the mean of two flood or ebb tides). White bars indicate the total flux for each tide, and the net flux (ebb minus flood) is indicated with black bars and given as kg N tidal cycle^{-1} below/above bars. The scale of the y-axes differ between sub-plots.

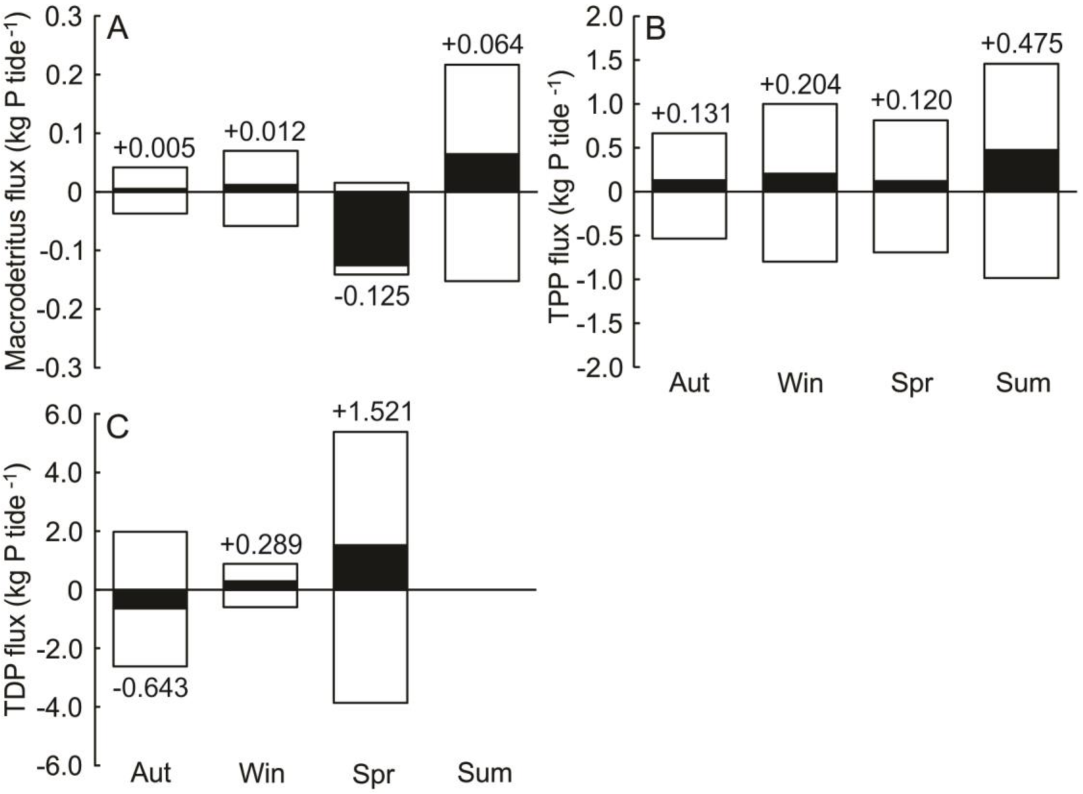

Fig. 4. Phosphorus flux as macrodetritus (**A**), particulate (TPP; **B**), and dissolved (TDP; **C**), from Pepe Inlet, Tairua Estuary, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015) and tidal direction (ebb tide fluxes are indicated by positive numbers, and flood tide fluxes are negative; fluxes are the mean of two flood or ebb tides). White bars indicate the total flux for each tide, and the net flux (ebb minus flood) is indicated with black bars and given as kg P tidal cycle^{-1} below/above bars. In Sum, TDP was below detection limit. The scale of the y-axes differ between sub-plots.

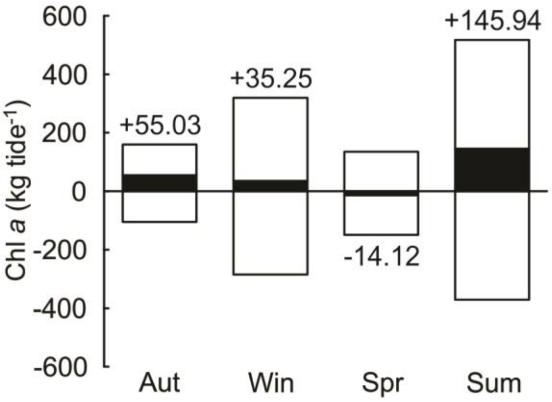

Fig. 5. Particulate chlorophyll *a* (chl *a*) flux from Pepe Inlet, Tairua Estuary, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015) and tidal direction (ebb tide fluxes are indicated by positive numbers, and flood tide fluxes are negative; fluxes are the mean of two flood or ebb tides). White bars indicate the total flux for each tide, and the net flux (ebb minus flood) is indicated with black bars and given in kg tidal cycle^{-1} below/above bars.

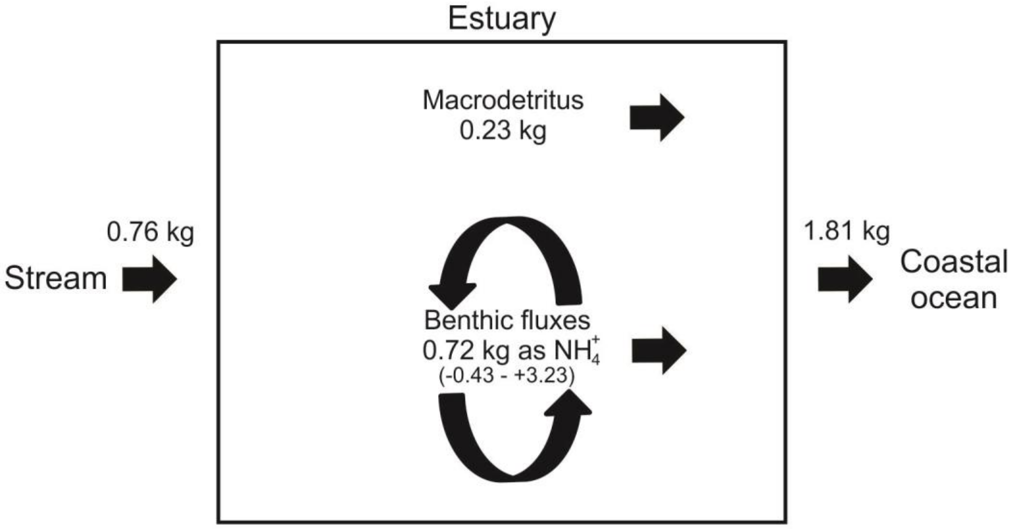

Fig. 6. Conceptual diagram of simplified total nitrogen fluxes (in kg N tidal cycle^{-1}) in summer, including inputs of total N from Pepe Stream, N as NH_4^+ from the benthos, and total N exported at the mouth of Pepe Inlet. Benthic fluxes are the night and day average of those measured in Pepe Inlet in Gladstone-Gallagher *et al.* (2017; n = 16, with adult crab densities of 12-108 ind. m^{-2}), and are scaled up to the estuary area (259,909 m^2 calculated using analysis of aerial photographs), and approximate time that the majority of the intertidal flat area is covered by water (~6 h, personal observation) (range for benthic fluxes is shown in brackets; positive benthic fluxes indicate an efflux of NH_4^+ out of the sediment and into the water column, and negative indicates uptake by the sediments).

Tables:

Table 1. Input of dissolved nitrogen and phosphorus (TDN, TDP), ammonium (NH_4^+), particulate nitrogen and phosphorus (TPN, TPP), and chlorophyll a (chl *a*), from Pepe Stream into Pepe Inlet, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015).

Values are the mean of two tidal cycles, and given in brackets is the percentage contribution of the stream to the net exports from Pepe Inlet (a percentage is not given in the case of a net import into Pepe Inlet). The total N (TDN + TPN) and P (TDP + TPP) contributed by Pepe Stream are also given.

Source	**Aut**		**Win**		**Spr**		**Sum**	
TDN (kg N tidal cycle^{-1})	1.228	(20%)	1.006	(12%)	0.870	(8%)	0.568	(149%)
NH_4^+ (kg N tidal cycle^{-1})	0.248	(55%)	0.155	(6%)	0.218		0.213	(44%)
TDP (kg P tidal cycle^{-1})	0.096		0.037	(13%)	0.068	(4%)	0.041	
TPN (kg N tidal cycle^{-1})	0.136	(30%)	0.084	(19%)	0.279	(51%)	0.188	(16%)
TPP (kg N tidal cycle^{-1})	0.042	(32%)	0.028	(14%)	0.090	(74%)	0.050	(10%)
Chl *a* (kg tidal cycle^{-1})	30.210	(55%)	3.609	(10%)	90.727		43.957	(30%)
Total N (kg N tidal cycle^{-1})	**1.364**	**(21%)**	**1.090**	**(12%)**	**1.149**	**(10%)**	**0.756**	**(42%)**
Total P (kg P tidal cycle^{-1})	**0.136**		**0.065**	**(13%)**	**0.158**	**(10%)**	**0.091**	**(19%)**

Table 2. Nitrogen (N) budget model for Pepe Inlet across seasons (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015).

Values are in kg N tidal cycle^{-1}. N supplied to the water column from the benthos for Pepe Inlet are the night and day average of those measured in Pepe Inlet (Gladstone-Gallagher *et al.* 2017; n = 16, with adult crab densities of 12–108 ind. m^{-2}), and benthic fluxes from Pratt *et al.*(2014) are measured in nine estuaries across a comprehensive seasonal range (n = 143; the maximum and minimum values reported here represent the average of values above the 90th percentile and below the 10th percentile). NH_4^+ fluxes (from Gladstone-Gallagher *et al.* 2017 and Pratt *et al.* 2014) are scaled up to the estuary area (259,909 m^2 calculated using analysis of aerial photographs), and approximate time that the majority of the intertidal flat area is covered by water (~6 h, personal observation) (positive benthic fluxes indicate an efflux of NH_4^+ out of the sediment and into the water column, and negative indicates uptake by the sediments).

					NH_4^+ from benthos		**N unaccounted for using range of benthic fluxes from Pratt *et al.* (2014)**
Season	**Stream**	**Macro-detritus**	**Total export**	**Unaccounted N**	**Pepe Inlet: Gladstone-Gallagher *et al.* (2017)**	**Pratt *et al.* (2014)**	
Aut	1.36	0.03	6.62	5.23	Mean 0.72	Mean 1.23	0.46
Win	1.09	0.02	9.17	8.06	Min -0.43	Min -0.19	3.29
Spr	1.15	-0.31	11.59	10.44	Max 3.23	Max 4.77	5.67
Sum	0.76	0.23	1.81	0.82			0

Appendices:

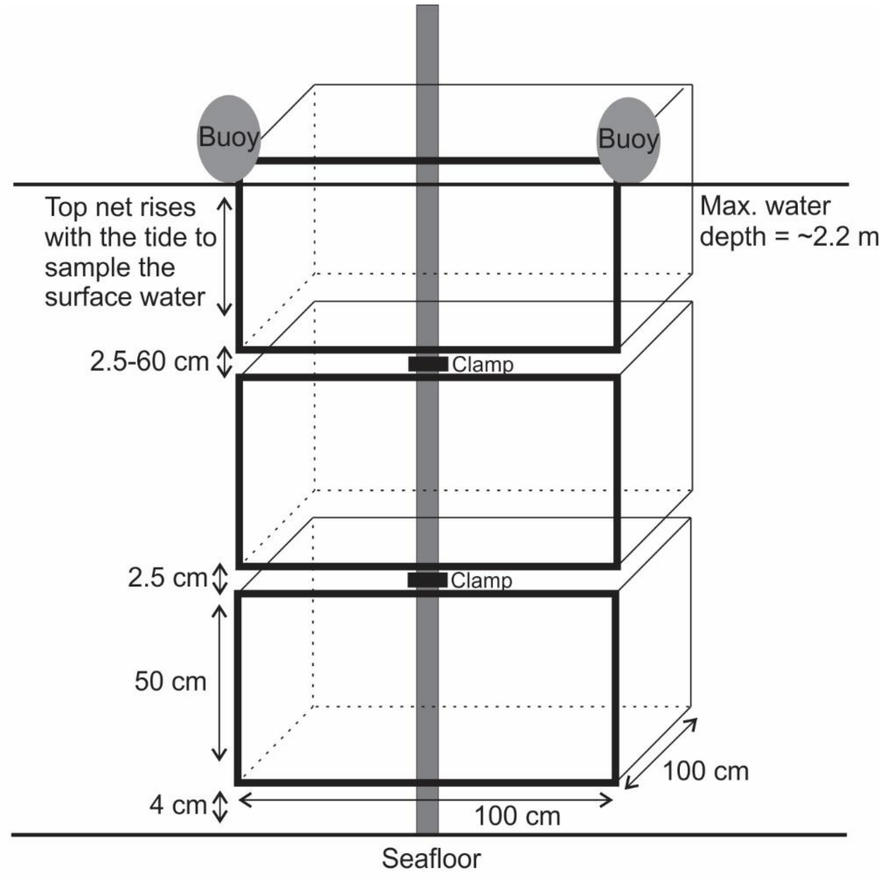

Fig. A1. Diagram of one of the two sets of macrodetritus nets positioned in the main channel at the mouth of Pepe Inlet, Tairua Estuary (diagram is not to scale).

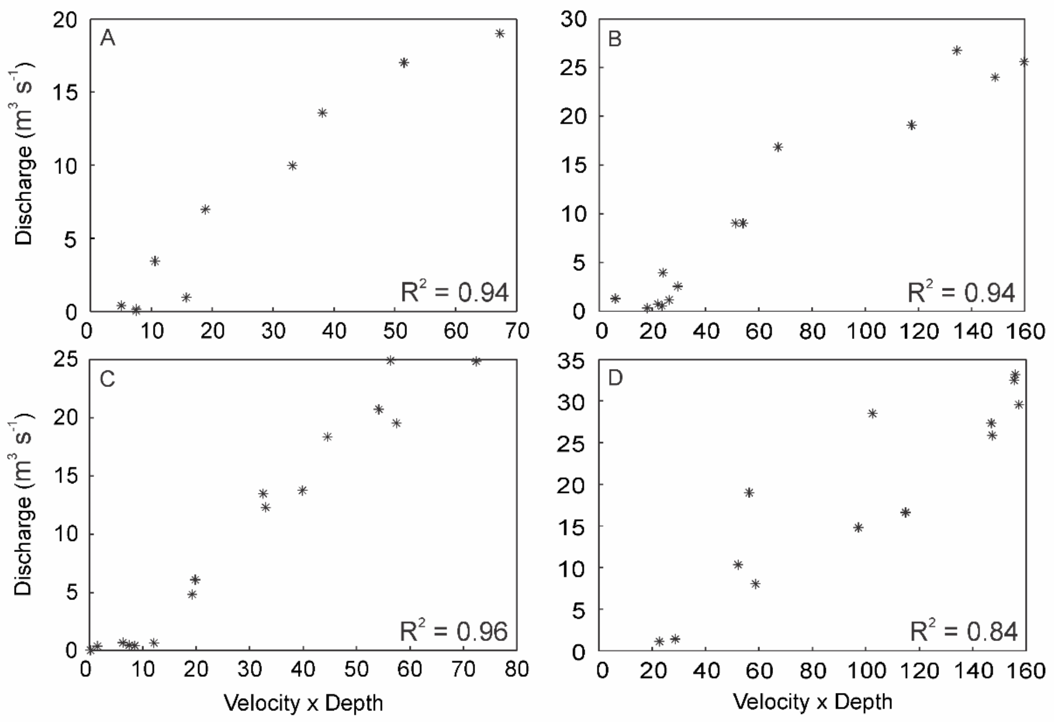

Fig. A2. Correlations used to predict discharge, between velocity × depth (ADV/ADCP measurement interval = 10 min) and discrete discharge measurements (Flowtracker ADV) on each sampling date (**A** = May 2014 - Aut, **B** = Jul 2014 - Win, **C** = Nov 2014 - Spr, **D** = Feb 2015 - Sum).

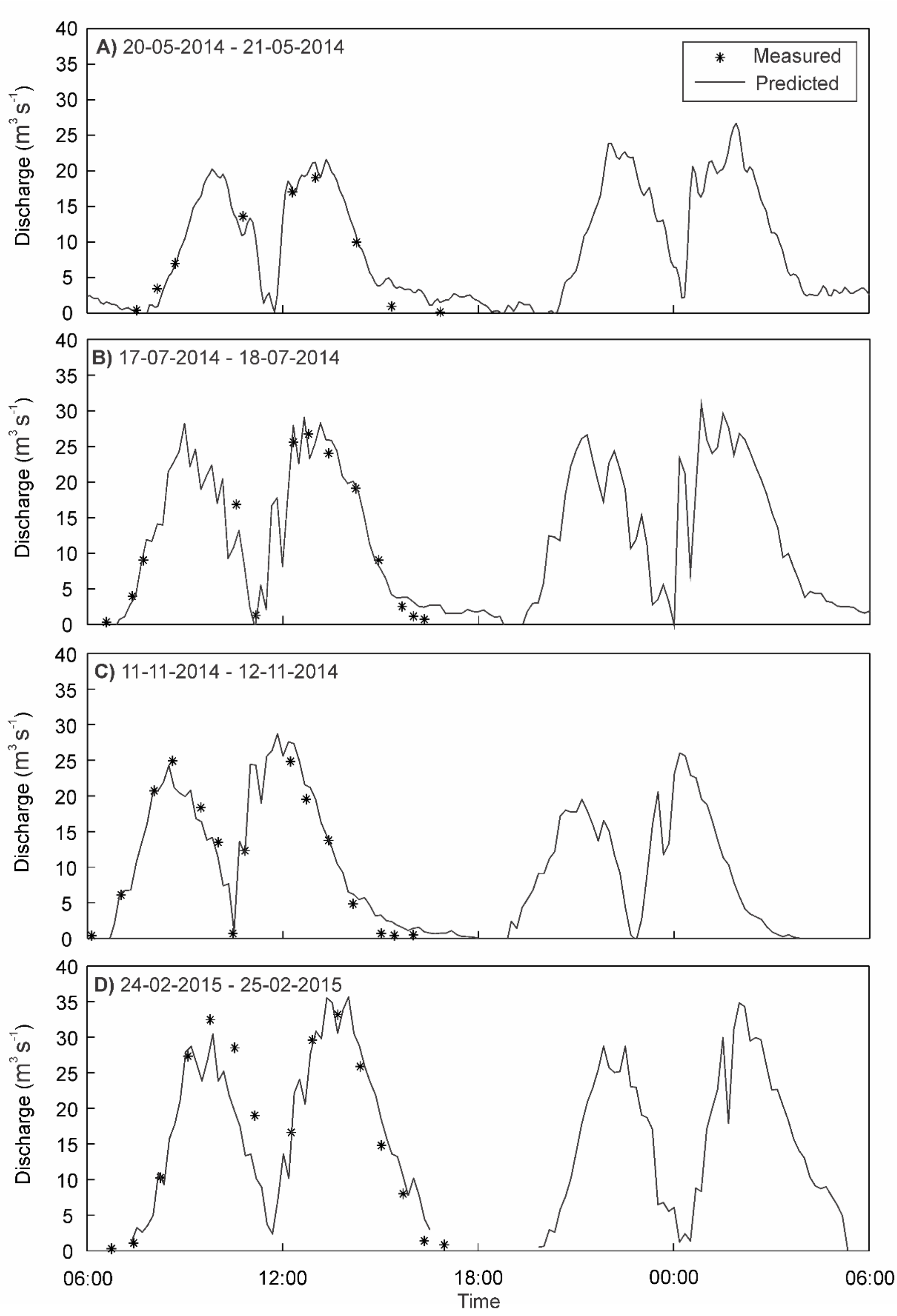

Fig. A3. Predicted and measured discharge as a function of time, on each sampling date (**A** = May 2014 - Aut, **B** = Jul 2014 - Win, **C** = Nov 2014 - Spr, **D** = Feb 2015 - Sum). Discharge is predicted using a correlation between velocity × depth (ADV/ADCP measurement interval = 10 min), and discrete discharge measurements in the first half of the tidal cycle (using Flowtracker ADV; i.e. measured; see Figure A1 for correlations).

Table A1. Summary of estuary-to-coast macrodetritus flux studies.

Only studies that infer direction (i.e. import or export) of macrodetritus fluxes, across a semi-enclosed estuary or bay to open coast boundary are included in the summary. Fluxes of other forms of production (dissolved and particulates) are only included when they were measured simultaneously with macrodetritus fluxes. The source of the data is given as superscripted numbers in the ‘location’ column that correspond to references listed in the table footnotes. Abbreviations are defined in the table footnotes.

Location	Estuary description	Location of measurements	Estuary area	Form	Season/ Annual estimate	Position	Direction	Fluxes
North Inlet South Carolina USA (33° N)[1-3]	Bar-built estuary Ebb-dominated Small freshwater input Tidal flushing = 55% water replaced per tide Spr tidal range = 2.2 m Mean tidal range = 1.6 m 3 major tidal creeks Current velocities = max. 2.3 m s^{-1}	In the 3 main tidal channels (up to 180 m each)	3200 ha 21% tidal creeks 73% saltmarsh 5% mudflats 1% oyster reef	Md	Annual	S (60 cm)	E	63257 kg DW 21000 kg C 240 kg N 24 kg P
				Par		S,M,B	E	3000000 kg C (as POC)
				Dis		S,M,B	E	7800000 kg C (as DOC) 171000 kg N (as $NH_4^+ + NO_x$) 40000 kg P (as PO_4)
Tuff Crater Auckland New Zealand (36° S)[4]	Mangrove basin Tidally drained by breach in the crater wall Minimal freshwater input Spr tidal range = 2.69 m Neap tidal range = 1.99 m (in Waitemata Harbour, but the ranges in the crater are much less)	In the single tidal creek	21.6 ha entirely mangroves	Md	Nov Dec Annual	S (50 cm)	E	0.035-0.036 kg DW tidal cycle^{-1} 0.3-1.5 kg DW tidal cycle^{-1} 162-915 kg DW
Klong Ngao Estuary, Thailand (9° N)[5]	Mangrove swamp drained from a single tidal channel Annual rainfall = 4 m Rains for 190 d per year Spr tidal range = 4.4 m Mean tidal range = 2.4 m Mangroves are only totally submerged 1-2 times per month	In mouth of Tidal channel (47 m width)	1150 ha almost entirely mangroves	Md	Annual	S	E	0.06-0.25 kg DW ha^{-1} day^{-1}
				Dis	Dry season		E	26 kg N day^{-1} (as NO_x) (other forms of N, P and C were not measured during the dry season)
					Wet season		E	15 kg N day^{-1} (TDN) (of which 4 kg N day^{-1} as NO_x) 13 kg P day^{-1} (TDP) (of which 0.2 kg P day^{-1} as PO_4) 5600 kg C day^{-1} (TOC incl. Dis and Par)

Table A1 continued.

Location	**Estuary description**	**Location of measurements**	**Estuary area**	**Form**	**Season/ Annual estimate**	**Position**	**Direction**	**Fluxes**
Sepetiba Bay Brazil (23° S) Silva et al. 1993 as cited in[6,7]	Mangrove-dominated bay enclosed by two tidal creeks Peak tidal range = 2.0 m Freshwater input minimal	Not reported	4 ha mangroves	Md	Annual	Not reported	E	420 kg DW ha^{-1}
Saeftinge marsh Westerschelde Estuary Netherlands (51° N)[8]	Tidal marsh with many tidal creeks Upper marsh is relatively closed to the tide (above mean neap tide level)	In one of the many tidal creeks (36 m width)	2800 ha saltmarsh	Md	Annual	B	E	550 kg DW
Mont Saint-Michel Bay Brittany France (48° N)[9]	Macro-tidal estuary Mean tidal range = 12 m Spr tidal range = 16 m Marsh infrequently inundated (<16% of tides)	In one channel draining 5 ha watershed (3 m width)	19000 ha mudflat 4000 ha saltmarsh	Md	Annual	S (40 cm)	E	33 kg DW 14 kg C 0.5 kg N
Biscayne Bay Florida USA (25° N)[10]	Coastal cut separated from the open ocean by Islands (open system) Current velocities = 0.5-0.7 m s^{-1} through the inlet	Entrance of several coastal cuts	NA	Md	Aug Dec May	WC	I I I	109 kg DW tidal cycle^{-1} 104 kg DW tidal cycle^{-1} 424 kg DW tidal cycle^{-1} (measured macroalgae fluxes only)

Table A1 continued.

Location	**Estuary description**	**Location of measurements**	**Estuary area**	**Form**	**Season/ Annual estimate**	**Position**	**Direction**	**Fluxes**
Mngazana Estuary, South Africa (31° S)[11]	Mangrove dominated Estuary, drains to the open ocean through a single mouth River dominated	In mouth of tidal channel	118 ha mangrove	Md	Nov	S (25 cm)	E	1.5 kg DW day^{-1}
					June		E	0.4 kg DW day^{-1}
				Par	Annual	S	E	36000 kg C ha^{-1} (as POC)
Pepe Inlet Tairua Estuary New Zealand (37° S)[12]	Barrier enclosed estuary Ebb-dominated Tidal flushing = 82 % water replaced per tide Spr tidal range = 1.63 m Neap tidal range = 1.22 m Freshwater input from Pepe stream	In the single tidal channel (37 m width)	~26 ha Includes: ~10 ha saltmarsh (some above high tide) ~2 ha seagrass ~3 ha mangroves ~20 ha sandflat	Md	May (Aut)	WC	E	2.89 kg DW tidal cycle^{-1}
							E	0.03 kg N tidal cycle^{-1}
							E	0.005 kg P tidal cycle^{-1}
					Jul (Win)		E	1.14 kg DW tidal cycle^{-1}
							E	0.02 kg N tidal cycle^{-1}
							E	0.011 kg P tidal cycle^{-1}
					Nov (Spr)		I	11.05 kg DW tidal cycle^{-1}
							I	0.31 kg N tidal cycle^{-1}
							I	0.125 kg P tidal cycle^{-1}
					Feb (Sum)		E	9.56 kg DW tidal cycle^{-1}
							E	0.23 kg N tidal cycle^{-1}
							E	0.064 kg P tidal cycle^{-1}
					Annual		E	449 kg DW
							I	6 kg N
							I	8 kg P
				Par	May (Aut)	S	E	0.46 kg N tidal cycle^{-1}
							E	0.13 kg P tidal cycle^{-1}
					Jul (Win)		E	0.44 kg N tidal cycle^{-1}
							E	0.20 kg P tidal cycle^{-1}
					Nov (Spr)		E	0.55 kg N tidal cycle^{-1}
							E	0.12 kg P tidal cycle^{-1}
					Feb (Sum)		E	1.20 kg N tidal cycle^{-1}
							E	0.47 kg P tidal cycle^{-1}
					Annual		E	467 kg N
							E	164 kg P

Table A1 continued.

Location	**Estuary description**	**Location of measurements**	**Estuary area**	**Form**	**Season/ Annual estimate**	**Position**	**Direction**	**Fluxes**
Pepe Inlet (continued)[12]				Dis	May (Aut)	S	E	6.13 kg N tidal cycle^{-1}
							I	0.64 kg P tidal cycle^{-1}
					Jul (Win)		E	8.71 kg N tidal cycle^{-1}
							E	0.29 kg P tidal cycle^{-1}
					Nov (Spr)		E	11.35 kg N tidal cycle^{-1}
							E	1.52 kg P tidal cycle^{-1}
					Feb (Sum)		E	0.38 kg N tidal cycle^{-1}
								P below detection limit
					Annual		E	4684 kg N
							E	206 kg P

Data source: [1]Dame *et al*. 1986; [2]Dame 1982; [3]Dame and Stillwell 1984; [4]Woodroffe 1985; [5]Wattayakorn *et al.* 1990; [6]Ramos e Silva *et al.* 2007; [7]Silva *et al.* 1998; [8]Hemminga *et al.* 1996; [9]Bouchard and Lefeuvre 2000; [10]Biber 2007; [11]Rajkaran and Adams 2007; [12]Current study; **Form**: Md = macrodetritus, Par = particulates, Dis = dissolved; **Direction**: E = export, I = import; **Position**: S = surface waters, M = mid-water column, B = bottom, WC = whole water column; **Fluxes**: scale of fluxes (e.g. annual vs. daily or tidal cycle^{-1}; or whole estuary vs ha^{-1}) are given as they appear in the publications; DW = dry weight; C = carbon; P = phosphorus; N = nitrogen; In the current study[13], annual fluxes are estimated by multiplying the average of the seasonal fluxes by the number of tidal cycles in one year (705 tidal cycles in Tairua Estuary in 2014)

Table A2. Total calculated discharge (used in flux calculations) as a function of sampling date and tidal stage.

Sampling date	**Total discharge (m^3)**
May 2014 (Aut):	
Flood 1	146030
Ebb 1	202860
Flood 2	188820
Ebb 2	230140
Jul 2014 (Win):	
Flood 1	213490
Ebb 1	288120
Flood 2	228060
Ebb 2	298270
Nov 2014 (Spr):	
Flood 1	191160
Ebb 1	271240
Flood 2	153050
Ebb 2	187350
Feb 2015 (Sum):	
Flood 1	247490
Ebb 1	356440
Flood 2	236910
Ebb 2	316850