Quantifying macrodetritus fluxes from a small temperate estuary

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1 Table of contents abstract

2   Hydrodynamics drive the export of estuarine-derived primary production and nutrients to

3   adjacent less productive offshore waters. This study quantified estuary-to-coast fluxes of

4   detritus and nutrients by sampling the water at the mouth of a small temperate estuary.

5   These types of studies are important to determine the ecosystem services provided by

6   temperate estuaries.

7 Abstract

8   Empirical measurements of estuary-to-coast material fluxes usually exclude the fraction of

9   primary production that is exported as macrodetritus (marine plant litter), potentially

10 leaving a gap in our understanding of the role of estuaries as outwelling systems. To

11 address this gap, we sampled water and suspended material seasonally from the mouth of

12 Pepe Inlet, Tairua Estuary, New Zealand. From samples collected hourly over 24 h, we

13 calculated the lateral tidal fluxes (import, export, net flux) of macrodetritus,particulate and

14 dissolved forms of nitrogen (N) and phosphorus (P). Annually, the inlet was a net exporter

15 of N and P (5145 kg N and 362 kg P). However, macrodetritus accounted for <13% and

16 <3% of seasonal N and P exports, respectively. Macrodetritus is an obvious and visible

17 source of estuary-to-coast subsidy, but our derived nutrient budgets suggest the dissolved

18 and particulate forms dominate the net export of N and P (>87%). Nevertheless, seasonal

19 pulses in the source and supply of macrodetritus may have consequences for the temporal

20 scales over which this resource subsidy affects receiving ecosystems (e.g. intertidal

21 sandflats). These mensurative investigations are useful to inform estuarine nutrient budgets

22 that quantify the ecosystem services provided by temperate estuaries (e.g. contribution to

23 fisheries foodwebs).

24   Additional keywords: Estuarine flux; Outwelling hypothesis; Detritus; Spatial subsidies;

25   Macrophyte detritus

26   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

50 exported from estuarine habitats, as well as the proportion of production that is exported

51 vs. retained and recycled within the estuarine system (i.e. net fluxes).

52 Direct quantification of estuary-to-coast subsidies to date have mostly focused on fluxes of

53 suspended fine particles and solutes (i.e. particulate and dissolved matter), usually

54 involving temporal water sampling in a tidal creek/channel (e.g. Borey *et al.* 1983;

55 Dankers *et al.* 1984; Baird *et al.* 1987; Boto and Wellington 1988; reviewed in Valiela *et*

56 *al.* 2000; Sánchez-Carillo *et al.* 2009). However, very few studies have directly measured

57 estuary-to-coast fluxes of macrodetritus (large pieces of plant litter, including leaf, wood,

58 and propagule material), due to the associated logistical challenges. Consequently,

59 macrodetritus fluxes are often excluded from estuarine nutrient/production budgets (e.g.

60 Valiela *et al.* 2000), or instead estimated based on *in situ* production, decay, and

61 consumption rates within the ecosystem (e.g. from a mangrove forest: Boto and Bunt

62 1981; Robertson 1986; from a seagrass bed: Pergent *et al.* 1997). Since marine plants

63 produce large quantities of leaf litter, estimates of macrodetritus export can be quite large

64 (e.g. in a mangrove-dominated inlet, macrodetritus export of 15.3-19.5 kg DW ha^{-1} day^{-1} is

65 estimated to be $6 \times$ greater than particulate transport; Boto and Bunt 1981; Robertson

66 1986). Therefore, the exclusion of the macrodetritus fluxes leaves a potentially large gap in

67 our understanding of the contributions of estuarine production to adjacent coastal

68 environments.

69 The form in which production is exported (i.e. dissolved nutrients, particulate, or

70 macrodetritus) will have consequences for its utilisation by the receiving environment, and

71 influence how quickly this production is incorporated into coastal food webs. Particulate

72 organic carbon (C), nitrogen (N), and phosphorus (P) (which broadly includes organic

73 matter associated with suspended sediment, phytoplankton, and decayed fragmented

74 detritus) are forms that are available to be immediately consumed by macrofaunal

75 consumers, while bacteria, microphytes, and macrophytes can utilise the dissolved

76 inorganic forms. However, because macrodetrital decay is relatively slow (reviewed in

77 Enriquez *et al.* 1993), the temporal scales over which macrodetritus is utilised may be

78 greater than that of particulates and dissolved nutrients, giving it the opportunity to also be

79 transported over greater spatial scales. Accordingly, the main role of this form of

80 production may instead be in structuring macroinvertebrate communities in receiving

81 environments (e.g. Kelaher and Levinton 2003; Bishop and Kelaher 2007), or acting as a

82 primary production source to marine environments with low *in situ* production (e.g. deep

83 subtidal marine environments below the photic zone; Britton-Simmons *et al.* 2009).

84 Of the studies that have directly quantified net macrodetrital export from estuaries, most

85 have been limited to saltmarsh-dominated lagoon systems in the northern hemisphere

86 (Dame 1982; Dame and Stillwell 1984; Hemminga *et al.* 1996; Bouchard and Lefeuvre

87 2000), and/or focused on macrodetrital fluxes from just one vegetation type (e.g.

88 macroalgae, Biber 2007; mangrove litter, Woodroffe 1985; Wattayakorn *et al.* 1990; Silva

89 *et al.* 1993 as cited in Ramos e Silva *et al.* 2007 p. 528; Rajkaren and Adams 2007; see

90 summary of macrodetritus flux studies in Table A1 in Appendices). In addition, many of

91 these studies have been conducted in estuarine/lagoon systems that are atypical of

92 temperate mixed habitat estuaries. For example, Tuff Crater (New Zealand) is a mangrove-

93 dominated, enclosed crater that exchanges tidal water through a single break in the crater

94 wall (Woodroffe 1985); Mont Saint-Michel Bay (France) is a macro-tidal bay with a very

95 large average tidal range of 12 m (Bouchard and Lefeuvre 2000); whilst Biscayne Bay

96 (Florida, USA) is a large, open coastal cut separated by coastal islands (Biber 2007; Table

97 A1). Thus, generalisation of the fluxes measured in these study systems to other temperate

98 estuaries is difficult. Dame and colleagues (Dame 1982; Dame and Stilwell 1984; Dame *et*

99   *al.* 1986) constructed export budgets after sampling all of the production size fractions in a

100 South Carolina tidal marsh system (North Inlet), and suggested that macrodetritus

101 constituted a relatively small proportion of the total outwelled production. We took a

102 similar approach here to evaluate estuary-to-coast subsidies in a well-defined part of a

103 small New Zealand estuary.

104 As the supply and quality of estuarine subsidies are temporally variable (reviewed in

105 Odum 2000), it is important that estuary-to-coast flux studies effectively encompass

106 seasonal variability. In temperate climates, marine plant productivity is highly seasonal,

107 with temporal pulses in the supply of leaf litter associated with seasonal production peaks

108 (usually in summer or spring; e.g. Turner 2007; Imgraben and Dittmann 2008; Gladstone-

109 Gallagher *et al.* 2014). Temporal variation in the supply of terrestrially derived detritus and

110 nutrients is likely to be associated with spring-neap tidal cycles (i.e. spring tides will

111 potentially inundate more terrestrial habitat to mobilise detritus), and seasonal rainfall

112 levels (that can wash terrestrial detritus into the marine system). Further, shallow-water

113 unvegetated benthic habitats rely on light reaching the sediment surface for production

114 (Lohrer *et al.* 2015; Needham *et al.* 2011), and therefore the associated uptake of nutrients

115 (before they can be exported out of the estuary) by the benthos may be tightly coupled

116 with seasonal day length and weather conditions.

117 Quarterly, at the mouth of a tidally-dominated temperate sub-estuary, we measured the

118 flux of macrodetritus, dissolved and particulate forms of N and P, as well as chlorophyll *a*

119 (chl *a*) to increase understanding of the seasonal variability in the source and quantity of

120 production that is transported across the boundary of a small temperate estuary. The study

121 was designed to: 1) obtain empirical data on the magnitude of macrodetrital fluxes from a

122 mixed habitat estuary that is typical of estuaries in the North Island of New Zealand (i.e.

123   large intertidal areas, with large tidal water exchange); and 2) increase our knowledge of

124   the magnitude of export of production in a tidal estuary, with particular emphasis on the

125   contribution of macrodetritus to the total exported production, N and P. Studies such as

126   this contribute to understanding of how anthropogenic habitat degradation (e.g. mangrove

127   forest clearances and seagrass bed declines that can change the supply of detritus available

128   to be exported; Inglis 2003; Moore and Short 2006; Orth *et al.* 2006; Harty 2009) may

129   affect the ecosystem services associated with production outwelling from temperate

130   estuaries.

131   Materials and methods

132   Site description

133   Tairua Estuary (37°00'05" S, 175°50'42" E) is located on the east coast of the Coromandel

134   Peninsula (Fig. 1), and is representative of a common type of estuary in the North Island of

135   New Zealand (Hume *et al.* 2007). Tairua Estuary is a 605 ha barrier-enclosed lagoon, of

136   which 71% (of the high tide area) is intertidal (Fig. 1), and the mean water depth at mid-

137   tide is ~2 m (Hume and Herdendorf 1993; Bell 1994). The estuary is well flushed, taking

138   1.3 tidal cycles to flush the entire tidal prism, and 82% of the water that enters the estuary

139   during each flooding tide is 'new' ocean water (Bell 1994). The estuary has spring and

140   neap tidal ranges of 1.63 m and 1.22 m, respectively (Liu 2014). The estuary's 29,381 ha

141   catchment is occupied by a number of land uses, including forestry, pasture, and small

142   urban settlements, as well as indigenous forest and scrub (O'Donnell 2011).

143   Pepe Inlet is a 26 ha tidally-dominated inlet within Tairua Estuary (Fig. 1). The inlet

144   tidally drains through a single mouth (~37 m wide), and has one main freshwater input at

145   Pepe Stream, which discharges on average 0.23 $m^3 s^{-1}$ of water into the estuary (mean

146   annual discharge; Liu 2014). Pepe Inlet supports diverse marine vegetated habitats, which

147   include mangrove forest (*Avicennia marina* subsp. *australasica;* ~3 ha, ~11% of estuary

148   area), seagrass beds (*Zostera muelleri;* ~2 ha, ~8% of estuary area), and saltmarsh (~10 ha;

149   made up of various rushland, saltwater paspallum, *Spartina* spp., salt meadow, and

150   saltmarsh ribbonwood species, some of which is above mean high water springs; Fig. 1;

151   Graeme 2008; Felsing and Giles 2011). Macroalgae (*Hormosira banksii*) also grow within

152   and outside the mouth of the inlet (Graeme 2008). The unvegetated sediments within Pepe

153   Inlet are comprised mainly of fine to medium sands (Felsing and Giles 2011). Sampling

154   was done at the mouth of Pepe Inlet, and at Pepe Stream (Fig. 1C) to determine the flux of

155   macrodetritus, dissolved and particulate nutrients from this sub-estuary to the wider

156   estuary/coastal system. The well constrained mouth, as well as the mixture of vegetation

157   types within Pepe Inlet make this estuary an ideal place to study material fluxes.

158   During the study period (May 2014-February 2015), the Coromandel region had maximum

159   and minimum daily air temperatures of 28.9°C and -1.8°C, respectively. Total rainfall over

160   a 48 h period (24 h before, and during each sampling period) was 0.4, 0.2, 12.8, and 6.8

161   mm, in May, July, November, and February, respectively (climate data obtained from the

162   NIWA CliFlo database at http://cliflo.niwa.co.nz; data from the Whitianga weather station,

163   ~30 km from Tairua).

164   Sampling regime

165   To derive material fluxes, we sampled macrodetritus, water column chl *a* (an indicator of

166   phytoplankton and resuspended benthic microphyte biomass), total dissolved N and P

167   (TDN and TDP; includes both inorganic and organic components), as well as total

168   particulate N and P (TPN and TPP) concentrations, over a 24 h period (two ebb and two

169   flood tides). The 24 h sampling was repeated in May (late-autumn = Aut), July (mid-

9

170 winter = Win), November (late-spring = Spr), and February (late-summer = Sum). 24 h

171 sampling periods were chosen during spring tides, and sampling encompassed both

172 midday and midnight high tides to reduce the variability between sampling dates that may

173 be confounded by diurnal uptake of inorganic nutrients (i.e. by microalgae during

174 photosynthesis; Lohrer *et al.* 2015).

175 Suspended macrodetritus was sampled using nets positioned in the mouth of Pepe Inlet,

176 which were emptied on each slack tide (as the tidal flow direction changed). Three nets

177 (opening: 50×100 cm, length: 100 cm, mesh size: 4×4 mm) were placed at two positions

178 within the 37 m wide channel (6 nets total; sampling 5.4% of the channel width), with

179 three nets stacked on top of one another (Fig. A1 in Appendices). The bottom and middle

180 nets were kept at a fixed depth, while the top net floated and sunk as the tide rose and fell

181 to sample the surface waters. All nets were attached to a central pole, enabling them to

182 change direction with the water flow.

183 Preliminary depth profiles (as well as hourly depth profiles during all sampling dates; 0.1

184 m depth intervals) of salinity, temperature, and dissolved oxygen (DO; Multi-parameter

185 water quality Sonde 600QS; YSI Inc.) indicated that Pepe Inlet channel remained well

186 mixed for most of the tidal cycle (and during times of greatest tidal exchange; see results).

187 Because the channel remained well-mixed, water samples (1 L) were collected half hourly

188 in the centre of the channel using a Van Dorn water sampler (3.2 L, PVC, ENVCO)

189 lowered just below the water surface. To sample the freshwater input into the estuary, a

190 portable vacuum sampler (model: VST, Manning Environmental Inc.) was positioned to

191 collect surface water (0.5 L) in the centre of Pepe Stream half hourly into acid washed

192 containers.

193   One 100 ml water sample from each half hourly sampling was immediately pressure

194   filtered through two 25 mm Whatman GF/C fibreglass filters, and the filtrate and filters

195   were frozen for later analysis of dissolved nutrients and chl *a*, respectively. The remaining

196   water from each half hour sample was then pooled across 2 h for measurement of

197   particulate N and P (i.e. TPN and TPP), and filtered through pre-weighed 45 mm Whatman

198   GF/C fiberglass filters using a vacuum pump (i.e. particulates include suspended particles,

199   from 0.5-1.75 L water samples, retained on 1.2 µm pore size fiberglass filter; the sample

200   volume depended on the amount suspended content). Filters for TPN and TPP were also

201   frozen awaiting analysis.

202   During each 24 h sampling period, either a SonTek Triton ADV (averaging interval 1 min,

203   sampling interval 10 min; ~65 cm above seafloor; deployed in Win, Spr, Sum) or a

204   SonTek Argonaut ADCP (XR 3000 kHz; averaging interval 2 min, sampling interval 5

205   min; 20 cm above seafloor; deployed in Aut) was positioned in the centre of the Pepe Inlet

206   channel to measure current velocity. A Solinist Levelogger (measuring absolute water

207   pressure) was placed in the centre of the channel to measure water depth, and a Solinist

208   Barologger was used to compensate the depth obtained by the Levelogger for barometric

209   pressure (sampling interval 10 min.). The cross-sectional area and water velocity was

210   measured using a SonTek FlowTracker Handheld ADV to calculate discharge (0.6 depth

211   and multipoint methods; Sontek/YSI Inc. 2007), approximately hourly during the daylight

212   hours.

213   Laboratory analyses

214   Plant detritus collected by the nets was washed, separated by source (e.g. mangrove,

215   seagrass, terrestrial/marsh, macroalgae), dried to constant weight at 60°C, and weighed

216   (dry weight, DW). Half hourly filtered water samples were pooled in the laboratory across

217 one hour and subsamples taken for measurements of TDN, TDP, and ammonium (NH_4^+)

218 on a LACHAT Quickchem 8500 series 2 Flow Injection Analyser (FIA). NO_x and PO_4^{2-}

219 were also measured, but results were unreliable and data are not presented. TDN consists

220 of dissolved NH_4^+ + NO_x + organic N, and TDP consists of dissolved PO_4^{2-} + organic P,

221 but the proportions of NO_x and PO_4^{2-}, as well as dissolved organic N and P are unknown.

222 Water samples for TDN and TDP, and filters for TPN and TPP (one filter for each two

223 hourly sampling) were first digested (potassium persulphate solution) and autoclaved (30

224 min at 121°C, 15 psi), before analysis of total N and P on the FIA. Water column

225 particulate chl a concentrations were determined by steeping and grinding filters (two

226 filters for each half hour sampling) in 90% buffered acetone, and then pigment

227 concentrations were measured fluorometrically (Turner 10-AU fluorometer) before and

228 after acidification (Arar and Collins 1997).

229 Data analysis and material flux calculations

230 A linear correlation between the discrete discharge measurements (Flowtracker ADV

231 during the day) and the continuous water velocity × depth (5-10 min measurement

232 interval) was used to predict discharge over the 24 h sampling period (correlation r^2 =

233 0.84-0.94; see Fig. A2 in Appendices for correlations). The total discharge volume for

234 each flood and ebb tide was then estimated by summing the predicted discharge rate at 10

235 min intervals within each tidal stage (Fig. A3, and Table A2).

236 TDN, TDP, TPN, TPP, and chl a concentrations averaged over the 4 h of peak flow

237 (estimated from velocity measurements) were used to calculate the fluxes from Pepe Inlet,

238 where the 4 h average concentration was multiplied by the discharge volume for each ebb

239 and flood tide. Using the mean annual discharge from Pepe Stream (0.23 $m^3 s^{-1}$; Liu 2014;

240 which is <1% of the peak discharge measured at the mouth of Pepe Inlet), we estimated

241   the input of TDN, TDP, TPN, TPP, and chl *a* from Pepe Stream into Pepe Inlet over a tidal

242   cycle (i.e. stream input = stream discharge scaled to a tidal cycle × average solute or

243   particulate concentration measured at Pepe Stream). As all sampling periods fell during

244   periods of low rainfall (i.e. there was <13 mm of rain in the 24 h prior to and during

245   sampling), we consider the mean annual discharge suitable for estimating stream inputs.

246   Fluxes of macrodetritus were calculated by summing the total detritus DW collected in the

247   nets during each flood and ebb tide, and this total was multiplied by the width of the

248   channel (i.e. macrodetritus flux = total detritus DW × 37 m / 2 m sampling width of nets;

249   similar flux calculations are described in Bouchard and Lefeuvre 2000). This calculation

250   assumes that our nets sample the entire water column throughout the tidal cycle; a

251   reasonable assumption given that just ~0.6 m of the water column was omitted during high

252   tide, but during times of peak flow (mid-tide) the entire water column was sampled by the

253   nets. Further, the top and the bottom nets captured the majority of the macrodetritus

254   (>72%, but usually >90% of the total collected macrodetritus), suggesting that detritus

255   usually either floats or is transported along the seafloor, and little was caught suspended in

256   the middle of the water column. To estimate the flux of macrodetritus N and P, and to

257   allow comparisons with other sources (dissolved and particulate), detrital DW was

258   converted to N and P using the average values (as % of DW) for each detrital source (or

259   similar sources) from the Enriquez *et al.* (1993) review, as well as from N content

260   measured for *Z. muelleri, A. marina,* and *E. radiata* in Gladstone-Gallagher *et al.* (2016).

261 ## Results

262   Across sampling dates, the channel at the mouth of Pepe Inlet remained well mixed for

263   ~75% of the tidal cycle (determined from hourly depth profiles of salinity, temperature and

264   DO in the channel), only becoming stratified for ~3 h at slack low tide when tidal

265 exchange was minimal. The difference in salinity between the bottom and surface waters

266 during this low tide stratification (i.e. channel depth ~0.7-0.9 m) was <14.2 ppt, with

267 temperature and DO differences of <2.9°C and <2.2 mg L^{-1}, respectively. During the

268 remainder of the tidal cycle, when the water column was well mixed (i.e. channel depth

269 ~0.9-2.2 m), salinity differences between the bottom and surface waters were <4.9 ppt (but

270 often <0.5 ppt), with surface vs. bottom water differences in temperature <1.9°C (but often

271 <0.5°C), and DO <0.68 mg L^{-1}. Across the sampling dates, salinity averaged across the

272 tidal cycle ranged from 24.2-31.6 ppt, temperature from 11.4-20.3°C, and DO

273 concentration from 7.5-9.3 mg L^{-1}.

274 Macrodetritus fluxes

275 The magnitude of the flood and ebb macrodetritus fluxes varied across seasons, by both

276 weight and source (Fig. 2). Seagrass (*Z. muelleri*) was the dominant detrital source to be

277 transported by flood tides in all seasons (40-92% of flood fluxes). In Spr and Sum,

278 macroalgae (including unidentified green and brown species) were equally dominant,

279 contributing 49 and 36% to the Spr and Sum flood tide fluxes, respectively. Ebb tide

280 macrodetrital transport was highly seasonal and dominated by mangrove litter (*A. marina*)

281 in Spr (61% of the ebb flux), but by seagrass in Aut and Win (39 and 52%, respectively),

282 and macroalgae in Sum (38%). The transport of terrestrial/marsh detritus (broadly grouped

283 and not identified to species level) was consistent across seasons in terms of absolute

284 contribution (0.1-5.3 kg DW tide^{-1} on both flooding and ebbing tides), but varied across

285 seasons in relative contribution to the total macrodetritus fluxes (Ebb fluxes: 50% Aut,

286 32% Win, 16% Spr, 19% Sum; Flood fluxes: 4% Aut, 33% Win, 6% Spr, 12% Sum; Fig.

287 2).

14

288 The net fluxes of macrodetritus (ebb flux minus flood flux) show that Pepe Inlet acted as a

289 net exporter of macrodetritus on three of the four sampling dates (Aut, Win, and Sum; Fig.

290 2). The greatest export occurred in Sum, where nearly 10 kg DW tidal cycle^{-1} of

291 macrodetritus was exported from Pepe Inlet. The Sum macrodetritus export was comprised

292 of 43% macroalgae, 33% terrestrial/marsh, 17% seagrass, and 7% mangrove detritus. In

293 Aut, the small net export was largely made up of terrestrial/marsh litter (83%), and in Win,

294 the export was comprised equally of the four sources (i.e. mangrove, seagrass,

295 terrestrial/marsh, and macroalgae all contributed 20-30% of the net export). In Spr there

296 was a net import into the inlet (11 kg DW tidal cycle^{-1}), which was predominantly

297 comprised of seagrass and macroalgae (Fig. 2) and juxtaposed against a small export of

298 mangrove detritus (1.6 kg tidal cycle^{-1}). Using the average of the net fluxes across seasons,

299 it is estimated that ~449 kg DW yr^{-1} of macrodetritus is exported from Pepe Inlet, or 30 kg

300 DW ha^{-1} yr^{-1} when scaled to the area occupied by marine vegetated habitats (~15 ha of

301 mangroves, seagrass and saltmarsh) within Pepe Inlet. In Sum and Win, the net fluxes

302 were relatively small compared to the total ebb or flood fluxes (net fluxes 18-34% and 22-

303 52% of the total flood and ebb flux, respectively).

Nitrogen fluxes

305 The dominant form of N transported by both flooding and ebbing tides was TDN, which

306 comprised >94% of the total fluxes in Aut, Win and Spr. In Sum, TDN was lower and

307 comprised 80 and 85% of N on ebb and flood tides, respectively (Fig. 3). TDN fluxes

308 consisted of 6-28% NH_4^+ (compare Fig. 3C with D), with the proportion of NO_x and

309 organic N unknown. Across seasons, macrodetritus contributed <3% to the total N flux on

310 both flood and ebb tides. In Aut, Win, and Spr, TPN contributed <5% to the total N fluxes,

311   whereas, in Sum, when TDN fluxes were lower, the TPN comprised 13 and 17% of flood

312   and ebb tide fluxes, respectively (Fig. 3).

313   Across seasons, Pepe Inlet was a net exporter of N (dissolved and particulate N exports

314   offset macrodetritus imports in Spr), exporting a total of 2-12 kg N tidal cycle^{-1}. The

315   dominant form of N exported in Aut, Win and Spr was dissolved (TDN >93% of the total

316   net N exports). Macrodetritus and particulate matter contributed relatively little to the total

317   net N export (<7%), except for in Sum where dissolved fluxes were low, and macrodetritus

318   and particulate N contribution were 13 and 66% of the net N export, respectively (Fig. 3).

319   Annual estimates of net N fluxes are 6 kg N yr^{-1} imported as macrodetritus, 467 kg N yr^{-1}

320   exported as particulates, and 4684 kg N yr^{-1} exported as dissolved (total annual N export =

321   5145 kg N).

Phosphorus fluxes

323   In Aut and Spr, P fluxes transported by both flood and ebb tides were dominated by TDP

324   (TDP contribution in Aut = 74-82%, and Spr = 82-87% of total P fluxes). Whereas, in Win

325   and Sum, P fluxes transported in both flood and ebb tides were dominated by TPP (TPP

326   contribution in Win = 51-55%, and Sum = 87% of total P fluxes). Across seasons,

327   macrodetritus contributed relatively little to the total P fluxes of both flood and ebb tides

328   (<13%; Fig. 4).

329   In Win, Spr, and Sum, Pepe Inlet acted as a net exporter of P (macrodetritus imports in Spr

330   were offset by TDP and TPP exports), exporting a total of 0.5-1.5 kg P tidal cycle^{-1}, but in

331   Aut, Pepe Inlet imported 0.5 kg P tidal cycle^{-1}. In Win (when all forms of P were exported

332   from Pepe Inlet), macrodetritus, TDP, and TPP represented 2.3, 57.2, and 40.4% of the

333   total net export of P, respectively (Fig. 4). Annual estimates of net P fluxes are 8 kg P yr^{-1}

334 imported as macrodetritus, 164 kg P yr^{-1} exported as particulates, and 206 kg P yr^{-1}

335 exported as dissolved material (total annual export = 362 kg P).

Chlorophyll *a* fluxes

337 Pepe Inlet was a net exporter of chl *a* (i.e. particulate chl *a* captured on filters), where 35-

338 146 kg tidal cycle^{-1} of chl *a* was exported from the inlet (except in Spr where 14 kg tidal

339 cycle^{-1} of chl *a* was imported; Fig. 5). Annually, it is estimated that Pepe Inlet exports

340 39,145 kg particulate chl *a*.

Stream contribution to net fluxes

342 The contribution of nutrients and chl *a* from Pepe Stream was seasonally variable, and

343 contributed 10-42% of the total N, and 10-19% to the total P exports at the mouth of Pepe

344 Inlet (Table 1). In Aut, the stream contributed 20-55% to the exports of TDN, TDP, TPN,

345 TPP, and chl *a* measured at the mouth of the Inlet, but in Win, the stream contributed less

346 to these material exports (just 6-19% of the net exports were from the stream). In Spr, the

347 stream inputs of TDN and TDP were low (8 and 4%, respectively), while inputs of TPN

348 and TPP were relatively high (51 and 74%, respectively). In Sum, Pepe Stream inputs

349 accounted for 10-44% of the material exports from Pepe Inlet, except for TDN, where the

350 input from the stream was almost double the net export out of Pepe Inlet (Table 1).

Discussion

352 As empirical measurements of macrodetritus fluxes from temperate estuaries are rare and

353 often excluded from estuarine nutrient budgets, this study was designed to quantify the

354 relative contribution of macrodetritus to the overall estuary-to-coast flux of primary

355 production, N and P. We found that across most seasons, Pepe Inlet was a net exporter of

356   macrodetritus, chl *a*, as well as total N and P. The dissolved and small particulate fractions

357   dominated the net fluxes of total N and P from Pepe Inlet. Given that coastal marine

358   primary production is regulated by both N and P, with dissolved N often being the limiting

359   nutrient (Herbert 1999; Tyrell 1999), estuaries including Pepe Inlet potentially play an

360   important role as exporters of nutrients, supporting production in the open coastal ocean.

361   Whilst the contribution of macrodetritus to the N and P export out of the inlet was small

362   (<13% and <3% of N and P exports, respectively, across seasons, except for spring where

363   macrodetritus was imported), macrodetritus flux was relatively large in terms of DW. As

364   macrodetritus is an obvious and visible source of estuarine primary production, its

365   degradation and accumulation in receiving habitats (e.g. coastal soft-sediments, seagrass

366   beds and other vegetated habitats) has the potential to alter ecosystem structure and

367   function (e.g. by structuring macrofaunal communities; Kelaher and Levinton 2003; Rossi

368   2006; Bishop *et al*. 2010).

369   Scaling up the macrodetritus weights to estimate the amount of litter that is exported

370   annually from Pepe Inlet yields ~30 kg DW ha^{-1} of vegetated area within the inlet (~15 ha

371   of seagrass, mangroves and marsh habitat). This estimate is comparable to the

372   macrodetritus export that was measured in the mangrove basin, Tuff Crater, New Zealand

373   (7-42 kg DW ha^{-1} yr^{-1} when converted to area of vegetation; Woodroffe 1985), and

374   although hydrodynamically different, Tuff Crater is similar in area to Pepe Inlet. In

375   addition, our estimated annual export of macrodetritus is also comparable to that of North

376   Inlet (USA), which was found to export 27 kg DW ha^{-1} of saltmarsh annually (annual

377   export scaled to saltmarsh area; Dame and Stilwell 1984; Dame *et al.* 1986). Others have

378   found lower macrodetritus exports than Pepe Inlet, which is likely related to the specific

379   hydrodynamics of the systems in question, being temperate marsh systems that have high

380   water residence times and less frequent tidal inundation (Table A1; Hemminga *et al.* 1996;

381   Bouchard and Lefeuvre 2000).

382   In their review of estuary-to-coast flux studies, Childers *et al.* (2000) used regression

383   analysis (n = 20 studies) to identify the physical factors regulating dissolved and

384   particulate material transport across estuarine to open ocean boundaries. Tidal range

385   explained 40% of the variation in dissolved nutrient flux, where systems switched from

386   importers to exporters at tidal ranges >1.2 m (similar results were also found by Adame

387   and Lovelock 2011, when reviewing the hydrological factors that affect nutrient export

388   from mangrove forests). The extensive review also found that smaller estuaries (<54 ha)

389   showed greater exports of particulate organic matter. Tairua Estuary not only has a high

390   tidal exchange (82% of water exchanged each tide; Bell 1994) and range (1.2-1.6 m), but

391   is regarded as a small estuary (<54 ha). Further, the majority of vegetated habitats in Pepe

392   Inlet (seagrass and mangroves, as well as some of the marsh) occur below the mean high

393   water spring tide mark, which is likely to increase the opportunity for material exports out

394   of these systems. These hydrodynamic properties will undoubtedly influence the exchange

395   of macrodetritus, and to some extent limit the generalisability of our results to other

396   temperate estuaries (i.e. larger salt marsh systems that have more limited tidal exchange).

397   However, Pepe Inlet represents a common estuary type, at least in the New Zealand

398   context (Hume *et al.* 2007), in that it is a largely intertidal, ebb-dominated (Fig. A3 in

399   Appendices), mixed habitat estuary.

400   Whilst Pepe Inlet annually exported macrodetritus in terms of total DW, it was found to be

401   a net importer of macrodetritus N and P on an annual basis (imports = 6 kg N yr^{-1} and 8 kg

402   P yr^{-1}; Table A1). The N and P content of macrodetritus depends on the plant species;

403   macroalgae are 1.0-3.9% N and 0.2-0.4% P, while mangrove litter contains 0.7-1.2% N

404   and 0.1% P, and seagrass litter is 1.3-4.0% N and 0.6-2.5% P (Enriquez *et al.* 1993). The

405   total macrodetritus flux in terms of total DW does not distinguish between the differences

406   in detrital species composition on the ebbing and flooding tides, where the imports into

407   Pepe Inlet were generally dominated by macroalgae and seagrass, and exports were

408   dominated by mangrove and terrestrial/marsh leaf litter. Thus, the resulting annual flux of

409   macrodetritus N and P were imports (i.e. imports of relatively N and P rich macrodetritus

410   offset exports of relatively N and P poor macrodetritus). On an annual basis, Pepe Inlet

411   acts as a net importer of macrodetritus N and P (albeit minimal), but an exporter of other

412   forms of N and P (particulates and dissolved), suggesting the potential role of these

413   estuaries as organic matter transformers. It is also worth noting that, in Pepe Inlet, the

414   individual flood and ebb macrodetritus fluxes were often much higher than net fluxes (net

415   fluxes 18-52% of the total flood/ebb flux in summer and winter), suggesting that some of

416   the macrodetritus transported out of the estuary probably returns with the subsequent

417   flooding tide (i.e. macrodetritus is transported in large volumes, but the net export is

418   relatively small by comparison). This returning detritus can also become trapped within the

419   vegetated habitats in the estuary (e.g. seagrass beds and mangrove forest), increasing

420   retention and limiting export out of the estuarine system (Gillis *et al*. 2014).

421   Fluxes of all forms of N and P varied across seasons. Most markedly was the difference in

422   summer (compared to other seasons), where macrodetritus and chl *a* transport (and export)

423   peaked, and dissolved N and P dropped. The summer peak in macrodetritus transport is not

424   surprising given that many marine plants show seasonal peaks in growth and production in

425   summer, which could also promote dissolved inorganic nutrient uptake by macrophytes

426   (potentially explaining the lower dissolved nutrient exports in summer). New Zealand

427   mangroves produce 77% of their total litter production between November and February

428   (Gladstone-Gallagher *et al.* 2014). In addition, macroalgae senescence and erosion, and

429 seagrass growth and production, can also be greatest in summer (Brown *et al.* 1997;

430 Turner 2007). However, when organic matter is imported into the estuary (e.g.

431 macrodetritus in spring), or when exports are low (i.e. high retention of macrodetritus),

432 decay and remineralisation processes will occur within the estuary. If *in situ* decay and

433 organic matter transformations are high, then outwelled production may be in the form of

434 dissolved inorganic nutrients rather than organic detritus.

435 Organic matter transformations that occur within the estuary are likely to modify the form

436 in which production and nutrients are outwelled, and they may help to explain some of the

437 seasonal fluctuations in N and P fluxes. In Pepe Inlet, the contribution of the stream was

438 seasonally variable, contributing between 10-55% of the estuary's total N, P and chl *a*

439 exports. Analysing each form of N and P separately revealed some interesting results, for

440 example, the summer input of TDN from Pepe Stream was $1.5 \times$ greater than the TDN

441 exported from Pepe Inlet. However, for total N (i.e. TDN + TPN + macrodetritus N), Pepe

442 Stream only contributed 42% to the total N exported (Table 1). This further indicates that

443 processes within the estuary transform and utilise some of this dissolved N before it can be

444 exported at the estuary mouth. As the net export of chl *a* was also highest in summer, the

445 dissolved inorganic N may be utilised by *in situ* phytoplankton and microphytobenthos

446 during summer, exporting N as particulate organic N.

447 Our study design did not detail within-estuary processes, and instead focused on the

448 differences between measured inputs (at Pepe Stream) and outputs (at the mouth of Pepe

449 Inlet). Nevertheless, processes within the estuary can be discussed, in an attempt to

450 illuminate the simple 'black box' model (depicted in Fig. 6). In summer and winter, >67%

451 of the net exports of macrodetritus were from marine sources, and therefore it is likely that

452 this production mostly occurred within the inlet itself, rather than transported by the stream

453   (although the terrestrial/marsh sources were important in autumn). Other processes within

454   the estuary, including the solute fluxes across the sediment-water interface, are likely to

455   contribute to the export of nutrients from the inlet. In temperate estuaries, sediment-water

456   effluxes of dissolved inorganic N (NO_x and NH_4^+) and P (PO_4^{2-}) occur through nutrient

457   remineralisation processes in the benthos (e.g. Lohrer *et al.* 2004; Pratt *et al*. 2014). It is

458   estimated that up to 50% of global organic matter remineralisation occurs in the coastal

459   soft-sediments (Middelburg *et al.* 1997), and therefore these sediments may supply

460   dissolved N and P to the water column that is available to be outwelled to the adjacent

461   coastal waters.

462   In a previous study, we measured summertime sediment-water solute fluxes of NH_4^+ in

463   Pepe Inlet (Gladstone-Gallagher *et al.* 2017), and since NH_4^+ is the dominant form of

464   dissolved inorganic N that is moved out of the sediments (>88% of inorganic N efflux;

465   Thrush *et al.* 2006; Jones *et al*. 2011; Pratt *et al.* 2014; Gladstone-Gallagher *et al.* 2016),

466   these fluxes can be used to estimate the contribution of the unvegetated sediments to the

467   export of N. Using the summertime measurements in Pepe Inlet, we estimate that on

468   average ~0.7 kg of N tidal cycle^{-1} comes from the sediments in the form of NH_4^+,

469   accounting for ~40% of the total N exported (Fig. 6). To explore this same N budget

470   model for the other seasons, we used the NH_4^+ flux values from Pratt *et al.* (2014), who

471   measured benthic ecosystem function across nine estuaries in different seasons (Table 2).

472   Based on maximum benthic NH_4^+ fluxes documented in Pratt *et al.* (2014; scaled to the

473   area of Pepe Inlet), it is plausible that in autumn and summer, the benthic fluxes could

474   account for the differences in inputs and outputs of N in Pepe inlet (0.46 kg and 0 kg N

475   unaccounted for in autumn and summer, respectively). However, in winter and spring

476   some N is unaccounted for by this budget (3.29 and 5.67 kg N tidal cycle^{-1}, respectively;

477   Table 2). The sources of N contributing to this shortfall remain unknown, but could be

478   associated with seasonal differences in rainfall and groundwater discharge (Santos *et al.*

479   2012; Santos *et al.* 2014). Benthic NH_4^+ fluxes may be outwelled as NH_4^+, but may also be

480   utilised within the estuary (e.g. by *in situ* phytoplankton production) and exported in

481   another form. This has been suggested for dissolved C and N in the North Inlet estuary

482   (saltmarsh-dominated inlet), where it is thought that dissolved nutrients are rapidly utilised

483   within the estuary and instead exported as particulates (Dame *et al.* 1986). Whilst our

484   calculations do not account for the contribution of NO_x or PO_4^{2-} from the sediments, the

485   analysis highlights that the benthos is likely to represent a significant source of outwelled

486   nutrients (Fig. 6; Table 2).

487   Seasonal flux differences may be confounded by differences in the lunar cycle stage during

488   times of sampling (i.e. some variability in the tidal amplitude was inevitable; Table A2),

489   which has particular consequences for overestimating the transport of terrestrial and marsh

490   production. Other limitations of our flux estimates include the simplification of

491   macrodetritus flux estimates to omit variability in flow conditions across the channel

492   width; small differences in the accuracy of the model used to predict discharge between

493   the different sampling dates (Fig.A2); the omission of storm/flood conditions from

494   sampling (i.e. such conditions would result in increased transport of materials particularly

495   from the terrestrial habitat); and the potential effects of the small-scale temporal variability

496   in abiotic factors (e.g. wind speed/direction and stream flow conditions) confounding the

497   perceived seasonal variability in detrital transport.

498   This study provides real-world quantification of the magnitude of macrodetritus fluxes, as

499   well as the simultaneous measurements of other forms of production exported from a

500   typical temperate New Zealand estuary. Data of this type can be useful to inform studies of

501   estuarine food webs, nutrient budgets, and the ecosystem services provided by temperate

502   estuaries, which are important when predicting ecosystem effects of anthropogenic

503   degradation of marine habitats. Whilst macrodetritus represents a relatively minor source

504   of N and P, its transport (here up to 10 kg net tidal cycle^{-1}) and accumulation in large

505   patches will have important effects on receiving ecosystems. Examples include its effects

506   in structuring benthic infaunal communities (e.g. Kelaher and Levinton 2003; Bishop and

507   Kelaher 2007), or its role in modifying ecosystem function in receiving habitats (e.g.

508   Gladstone-Gallagher *et al.* 2016). Because detritus is transported in relatively large

509   quantities, and it decays slowly, it may represent an important source of primary

510   production to offshore, deeper food webs that have low *in situ* productivity (e.g. sediments

511   below the photic zone; Britton-Simmons *et al.* 2009). Our results also emphasise the role

512   of temperate estuaries as sites of efficient organic matter transformation, where there is a

513   net export of total N and P, but when broken down into the various components of material

514   transport, some materials are imported (e.g. macrodetritus in spring), but processed within

515   the estuary and exported in a different form (e.g. dissolved N).

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Figures:
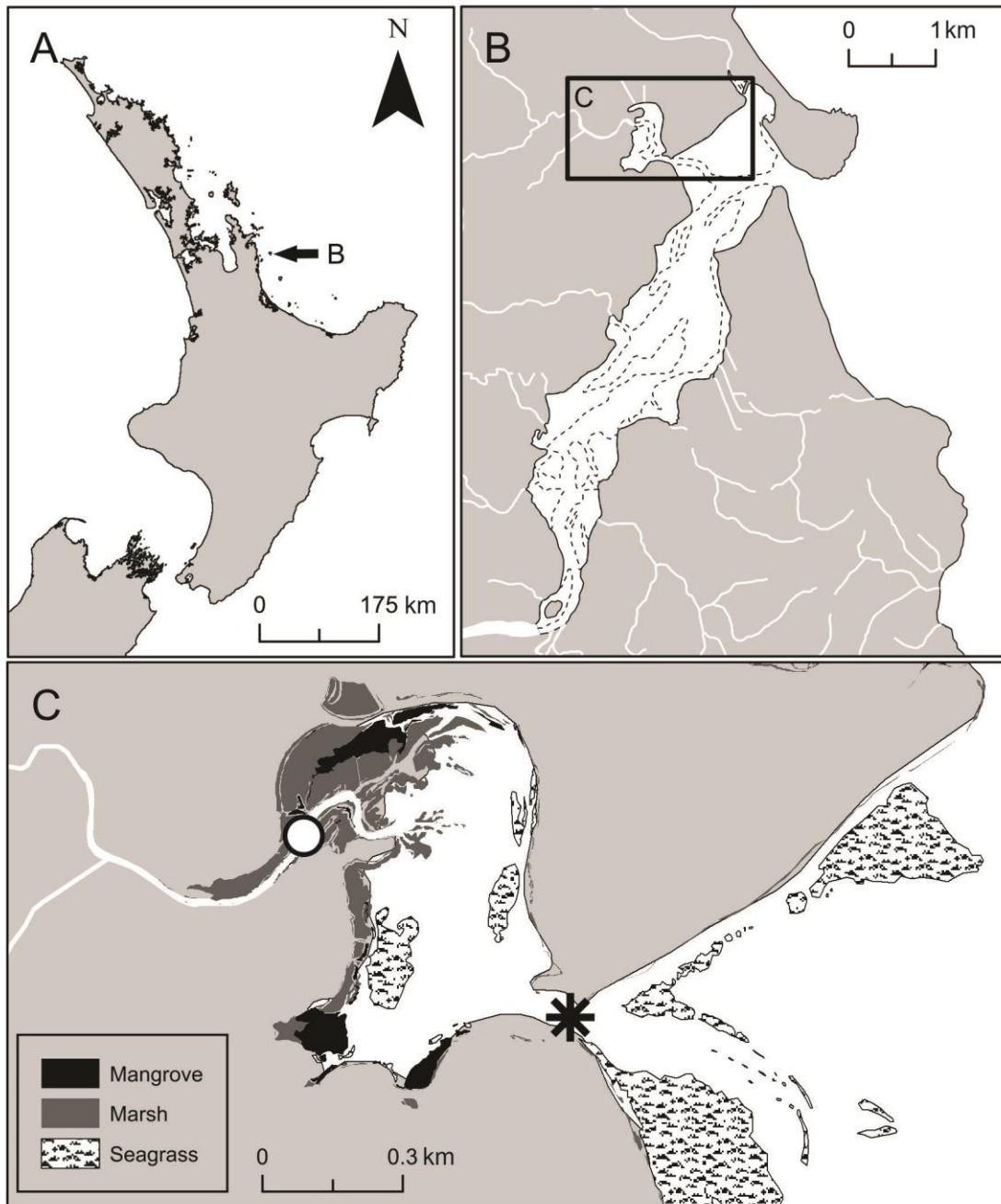
Fig. 1. Map of North Island, New Zealand (**A**), Tairua Estuary with the intertidal boundary shown by dashed lines (**B**), and Pepe Inlet showing the distribution of vegetated habitats (**C**). Water sampling for dissolved and particulate N and P, and chlorophyll a was carried out at both '○' and '*', and sampling of macrodetritus only at '*'. Data source: Waikato Regional Council, Hamilton, New Zealand (GIS vegetation layers).
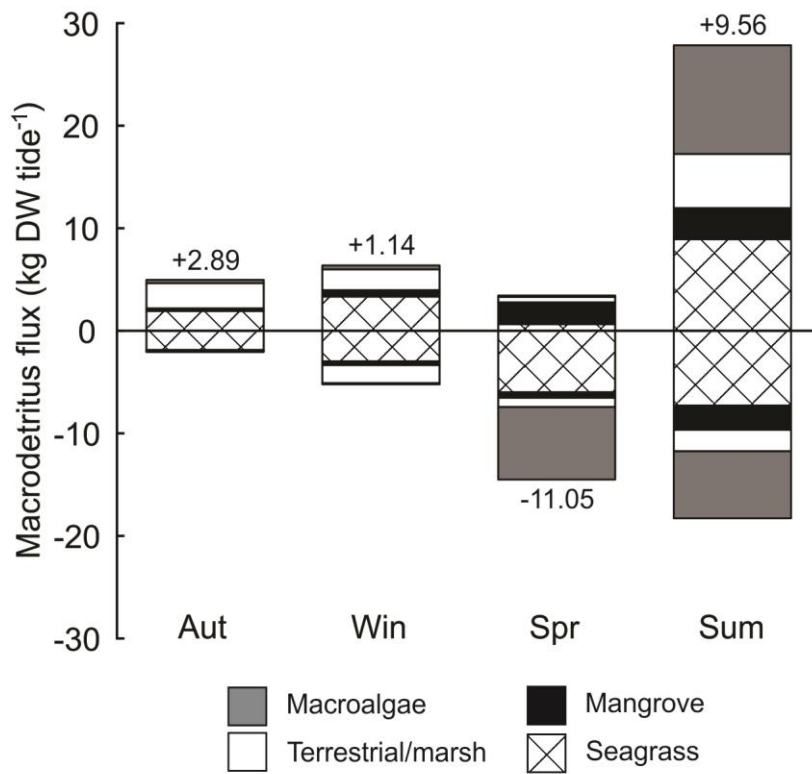
Fig. 2. Fluxes of macrodetritus from Pepe Inlet, Tairua Estuary, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015) and tidal direction (ebb tide fluxes are indicated by positive numbers, and flood tide fluxes are negative; fluxes are the mean of two flood or ebb 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.
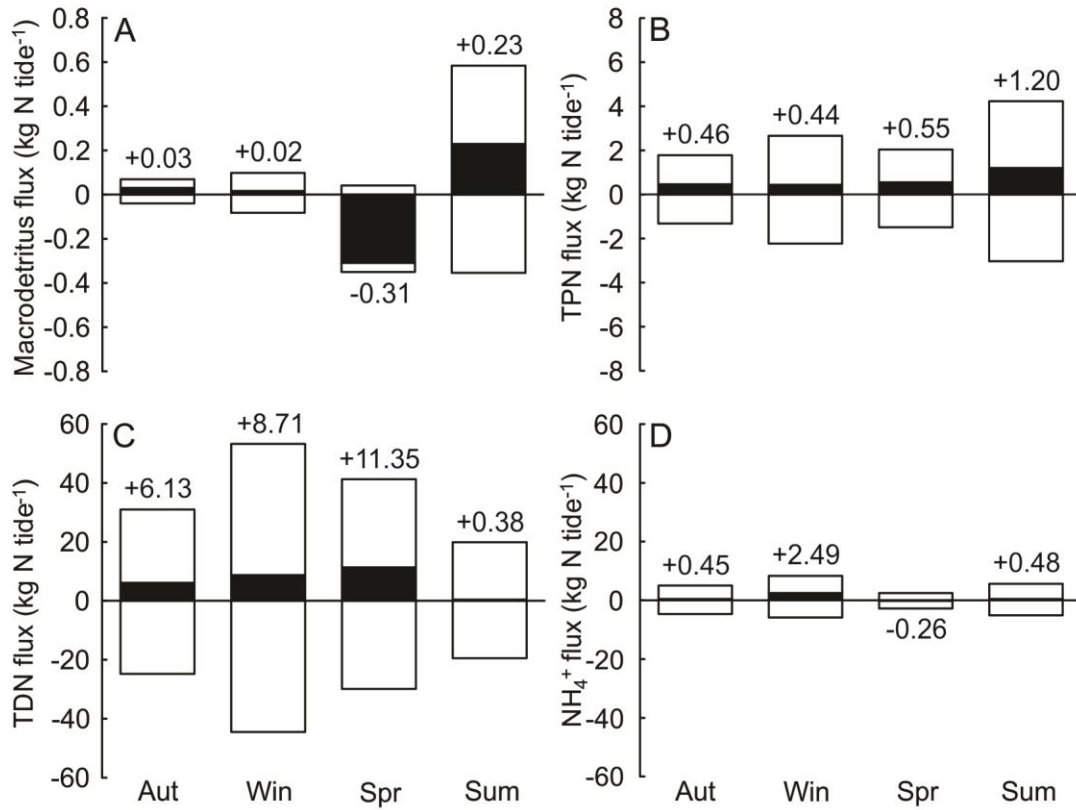
Fig. 3. Nitrogen flux as macrodetritus (**A**), particulate (TPN; **B**), and dissolved (TDN, **C**, and ammonium NH_4^+, **D**), from Pepe Inlet, Tairua Estuary, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015) and tidal direction (ebb tide fluxes are indicated 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.
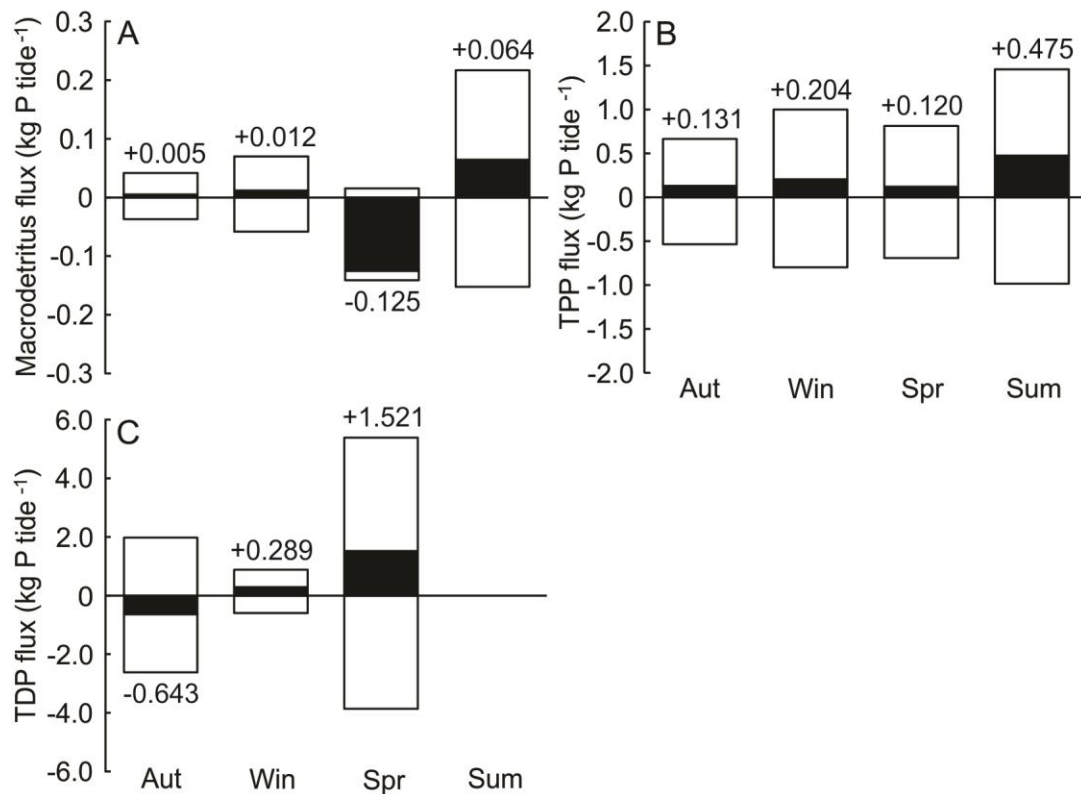
Fig. 4. Phosphorus flux as macrodetritus (**A**), particulate (TPP; **B**), and dissolved (TDP; **C**), from Pepe Inlet, Tairua Estuary, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015) and tidal direction (ebb tide fluxes are indicated by positive numbers, and 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.
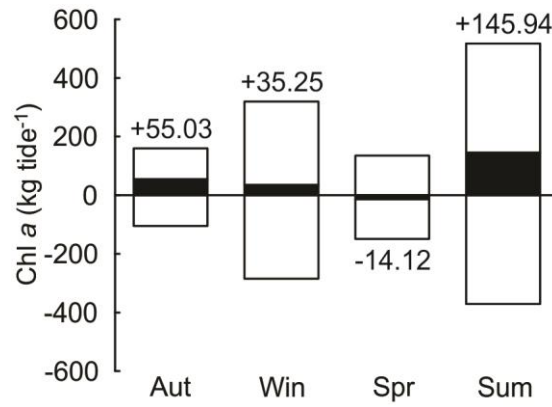
Fig. 5. Particulate chlorophyll *a* (chl *a*) flux from Pepe Inlet, Tairua Estuary, as a function of season (Aut = Feb 2014, Win = Jul 2014, Spr = Nov 2014, Sum = Feb 2015) and tidal direction (ebb tide fluxes are indicated by positive numbers, and flood tide fluxes are negative; fluxes are the mean 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.
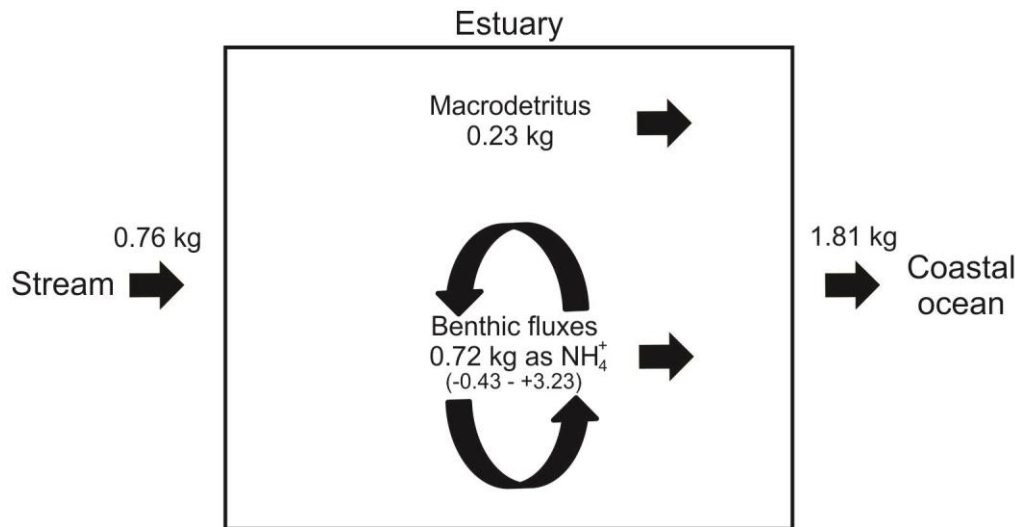
Fig. 6. Conceptual diagram of simplified total nitrogen fluxes (in kg N tidal cycle^{-1}) in summer, including inputs of total N from Pepe Stream, N as NH_4^+ from the benthos, and total N exported at the mouth of Pepe Inlet. Benthic fluxes are the night and day average of those measured in Pepe Inlet 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).

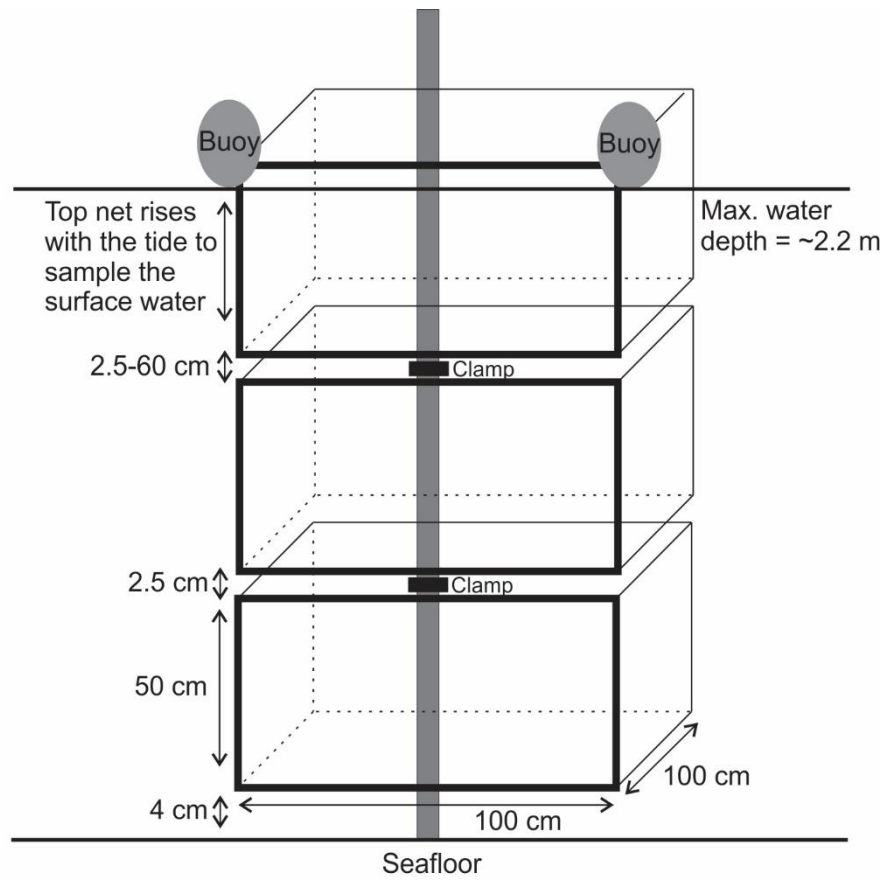| Season	Stream	Macro-detritus	Total export	Unaccounted N	NH_4^+ from benthos Pepe Inlet: Gladstone-Gallagher *et al.* (2017)	Pratt *et al.* (2014)	N unaccounted for using range of benthic fluxes from Pratt *et al.* (2014)
Aut	1.36	0.03	6.62	5.23	Mean 0.72	Mean 1.23	0.46
Win	1.09	0.02	9.17	8.06	Min -0.43	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).
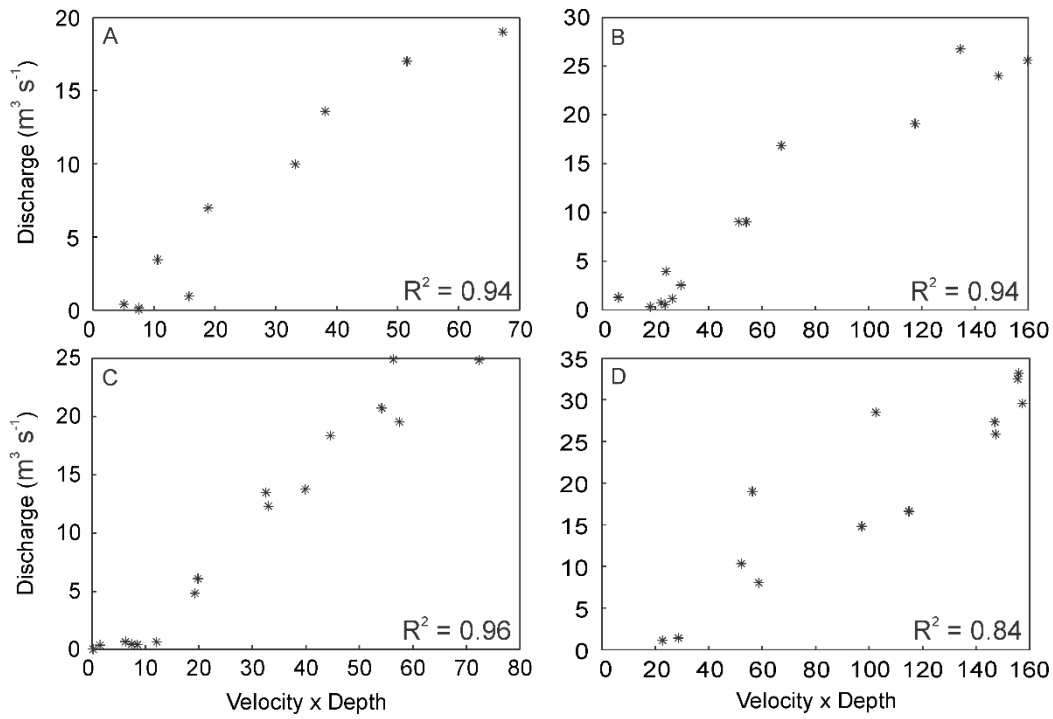
Fig. A2. Correlations used to predict discharge, between velocity × depth (ADV/ADCP measurement interval = 10 min) and discrete discharge measurements (Flowtracker ADV) on each sampling date (**A** = May 2014 - Aut, **B** = Jul 2014 - Win, **C** = Nov 2014 - Spr, **D** = Feb 2015 - Sum).
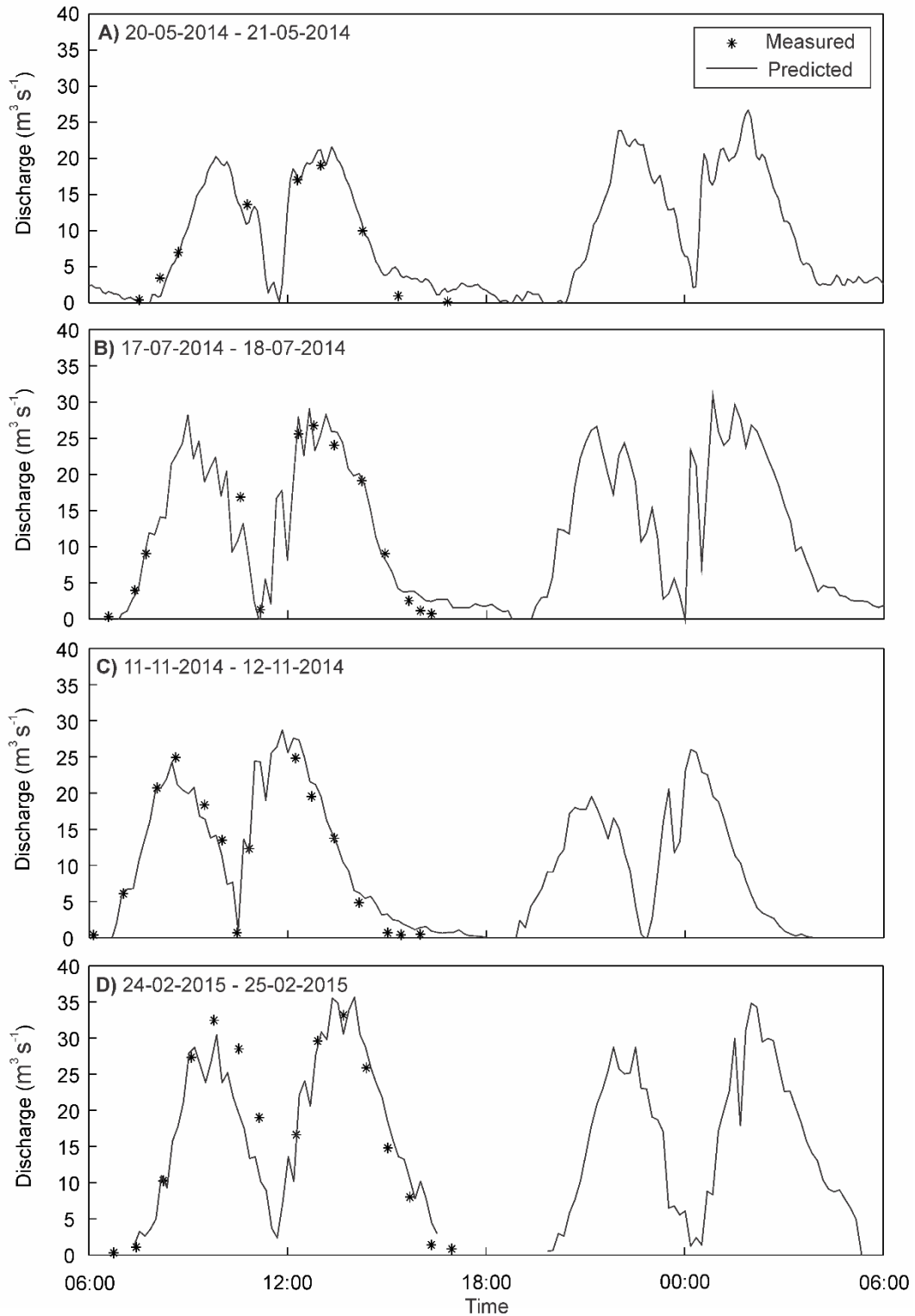
Fig. A3. Predicted and measured discharge as a function of time, on each sampling date (**A** = May 2014 - Aut, **B** = Jul 2014 - Win, **C** = Nov 2014 - Spr, **D** = Feb 2015 - Sum).

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)

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