Land–Ocean Coupling of Carbon and Nitrogen Fluxes on Sandy Beaches

Thomas A. Schlacher[1]* and Rod M. Connolly[2]

[1]*Faculty of Science, Health and Education, University of the Sunshine Coast, Maroochydore DC, Queensland 4558, Australia;*
[2]*Australian Rivers Institute - Coast and Estuaries, and School of Environment, Griffith University, Gold Coast Campus, Gold Coast, Queensland 4222, Australia*

ABSTRACT

Rivers link oceans with the land, creating global hot spots of carbon processing in coastal seas. Coastlines around the world are dominated by sandy beaches, but beaches are unusual in that they are thought to rely almost exclusively on marine imports for food. No significant connections to terrestrial production having been demonstrated. By contrast, we isotopically traced carbon and nitrogen pathways leading to clams (*Donax deltoides*) on beaches. Clams from areas influenced by river plumes had significantly different isotope signatures (δ^{13}C: -18.5 to -20.2‰; δ^{15}N: 8.3–10.0‰) compared with clams remote from plumes (δ^{13}C: -17.5 to -19.5‰; δ^{15}N: 7.6–8.7‰), showing that terrestrial carbon and sewage, both delivered in river plumes, penetrate beach food webs. This is a novel mechanism of trophic subsidy in marine intertidal systems, linking the world's largest shore ecosystem to continental watersheds. The same clams also carry pollution signatures of sewage discharged into rivers, demonstrating that coastal rivers connect ecosystems in unexpected ways and transfer contaminants across the land–ocean boundary. The links we demonstrate between terrigenous matter and the largest of all marine intertidal ecosystems are significant given the immense social, cultural, and economic values of beaches to humans and the predicted consequences of altered river discharge to coastal seas caused by global climate change.

Key words: land–ocean coupling; sandy shores; food webs; trophic subsidy.

INTRODUCTION

Ecosystems typically receive materials from outside of their boundaries (sensu Cole and others 2006). Such cross-boundary transfers are ubiquitous, and they can profoundly modify the dynamics of recipient systems in numerous ecosystem types (Cadenasso and others 2003). Fluxes of materials, energy, and organisms that transcend ecosystem boundaries provide a potent conduit for linking landscape elements (Cadenasso and others 2004). Theoretical frameworks of meta-ecosystems that incorporate spatial connectivity integrate perspectives of community and landscape ecology, and provide a useful conceptualization of ecosystem functioning, dynamics, and stability (Loreau and others 2003).

Flows of nutrients and organic matter link production and consumption processes, and recipient systems typically become energetically connected to donor systems via trophic subsidies (Polis and others 1997). Theory indicates that trophic subsidies can strongly influence population dynamics, pred-

Corresponding author; e-mail: tschlach@usc.edu.au

ator–prey interactions, and food webs (Loreau and Holt 2004), and ecologists increasingly recognize their fundamental structuring role (Marczak and others 2007). Significant effects of subsidies span a wide range of ecological organization, including: (a) stimulating primary productivity (Schlacher and others 2008b), (b) modifying vegetation structure (Ellis and others 2006), (c) increasing the abundance and biomass of consumers (Stapp and Polis 2003; Paetzold and others 2006; Marczak and others 2007), (d) modulating predator–prey interactions (Knight and others 2005; Schlacher and Cronin 2007), (e) altering the dynamics of spatially-coupled food webs (McCann and others 2005), and (f) fuelling ecosystems metabolism (Rubbo and others 2006; Pace and others 2007).

Aquatic-terrestrial ecotones are prime examples of discontinuities between physically well-bounded ecosystems (Post and others 2007). Material fluxes do, however, transcend the land–water boundary in numerous settings, and cross-boundary transfers substantially modify ecological processes in lakes (Pace and others 2007), streams (Burdon and Harding 2008), wetland ponds (Rubbo and others 2006), estuaries (Chanton and Lewis 2002), and on marine shores (Polis and Hurd 1996).

The land–sea boundary is a critical transition zone (Levin and others 2001). Fluxes of materials carried in river discharges rank amongst the largest cross-boundary fluxes globally (Schlünz and Schneider 1999). Coastal seas impacted by river discharges are the oceans' hotspots for the processing of terrestrial material transferred from land to the sea. Large quantities of sediment and C are deposited by rivers in coastal margins and these fuel disproportionately high rates of material transformations that account for 90% of modern carbon burial, thereby impacting global bio-geo-chemical cycles (McKee and others 2004). The most important biogeochemical reactions in these systems are associated with the decomposition of terrestrial organic carbon exported to the sea (Schlünz and Schneider 1999).

Many rivers discharge turbidity plumes to coastal seas (Figure 1). Plumes enrich coastal waters with inorganic nutrients, they enhance biological production and fisheries yields, and they create a distinct biogeochemical imprint on the seafloor (Gillanders and Kingsford 2002; Dagg and others 2004; Gaston and others 2006). Thus, plumes are the key functional link that couples terrestrial and marine systems in many coastal regions.
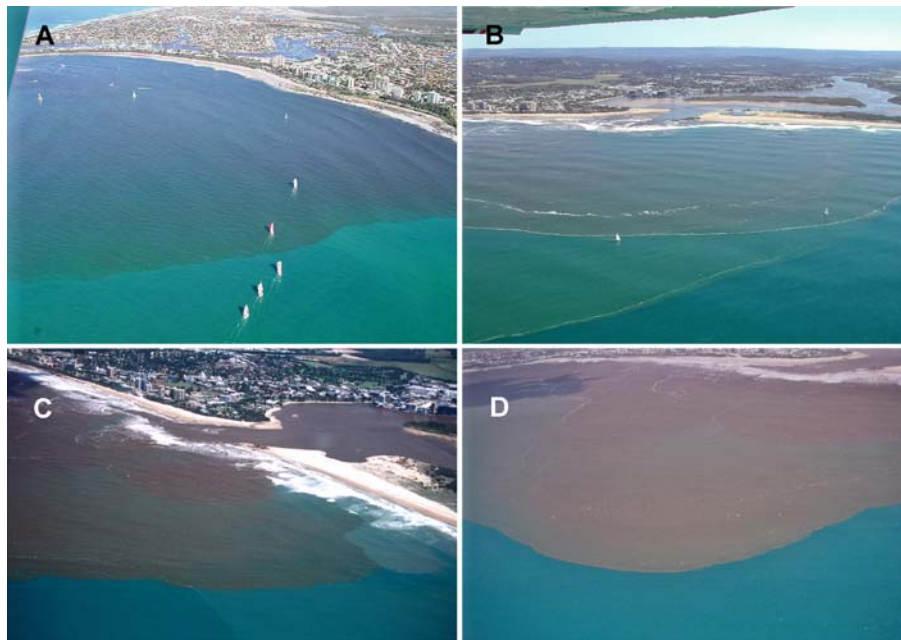

Figure 1. Examples of river plumes exporting large amounts of terrestrial sediment, carbon and nitrogen to coastal oceans. Plumes are created by episodic, strongly pulsed rainfall events, and are characterized by highly distinct and sharply bounded water masses in the nearshore zone. Note that plume waters can impact on sandy beaches adjacent to estuarine inlets, supplying terrigenous material as energetic subsidies to food webs, and transferring estuarine pollutants (sewage) to sandy shores. All aerial images show plumes for the systems investigated in this article in Eastern Australia. (**A**) Mooloolah River, 18 May 2003; (**B**) Maroochy River, 18 May 2003, (**C**) and (**D**) Maroochy River, 07 March 2004).

Sandy beaches are the single largest coastal ecosystem on earth, covering 70% of all continental margins (McLachlan and Brown 2006). Beaches are of immense social and cultural importance to humans as prime recreational assets: more people interact directly with beaches than with any other type of shoreline worldwide (Schlacher and others 2008a). Sandy beaches mostly lack biological structure, are physically controlled environments, and support little in situ primary production; their food webs therefore rely heavily on imports from marine sources (McLachlan and Brown 2006).

Interface regions between aquatic and terrestrial ecosystems are biogeochemical hot spots in the biosphere (McClain and others 2003), and sandy shore ecosystems can support some of the highest metabolic rates measured (Coupland and others 2007). Because beaches are prime examples of terrestrial–aquatic ecotones, they would thus be predicted to play a pivotal role in the processing and transfer of organic matter. In fact, sandy beaches can provide trophic subsidies to terrestrial food webs in situations where marine resources are transferred from the shore to terrestrial consumers (Polis and Hurd 1995, 1996; Anderson and Polis 1998; Stapp and Polis 2003). Conversely, the reverse pathway of material exchange across the land–beach ecotone where terrestrial production is transferred to beaches has not been reported to date.

Studies of material processing through beach food webs have historically ignored the potential role of trophic subsidies from river discharges. Yet, many sandy beaches are either bounded or intersected by estuarine inlets that discharge river plumes (Figure 1). Thus, river plumes can impact on sandy shores and supply terrestrial material to their food webs, thereby coupling the largest of all intertidal ecosystems to continental production. Thus, the specific hypothesis tested in this study was that terrestrial trophic subsidies operate on sandy beaches via the delivery of land-derived production in river plumes.

We investigated the transfer of terrestrial material to beaches by measuring the incorporation of terrestrial C and N isotopic signals (δ^{13}C and δ^{15}N) in wedge clams, *Donax deltoides* (Lamarck, 1818). Stable isotopes provide an effective measure of relative contributions of terrestrial and marine matter because they typically have distinct isotopic ratios (Peterson and Fry 1987). For C, this occurs either because plants have different photosynthetic pathways or because they obtain C from air rather than water. For N, the variation in isotopic signatures usually results from the effects of widespread changes in catchment land-uses, in particular urbanization (McClelland and others 1997). Because the isotope end-members of the broad source categories, terrestrial and marine, are reasonably well known, stable isotope analysis can detect riverine input to coastal waters (Darnaude and others 2004; Wissel and Fry 2005). Nitrogen isotopes are also used to investigate the incorporation of anthropogenic sources of nitrogen from developed catchments into marine food webs (Hansson and others 1997; Waldron and others 2001).

Beach clams of the genus *Donax* are ideal model organisms to measure C and N transfers into beach food webs: the clams are highly efficient primary consumers (Matthews and others 1989), comprise a significant portion of biomass on beaches (McLachlan and others 1996), are instrumental in nutrient cycling (Soares and others 1997) and occupy a pivotal role in the trophic architecture of sandy shores (Ansell 1983).

METHODS

Field Sampling

We sampled wedge clams, *Donax deltoides*, on two exposed sandy beaches in southern Queensland on the East Coast of Australia. The first beach borders the Maroochy River which discharges highly turbid and nutrient-rich plumes through its estuarine inlet located at the southern end of the beach from which clams were collected (26.65°S, 153.10°E). These river plumes occur as distinctly pulsed events and are usually confined close inshore. From aerial surveys and ship-based tracking of plume fronts (Gaston and others 2006), we determined that plumes disperse mostly in an offshore direction, but also impact on the adjacent sandy beach, either as part of the main plume or as lateral eddies that recurve and transport plume waters onshore. The watershed of the estuary is largely cleared for agriculture and housing. Substantial loads of wastewater enter the estuary, with sewage nitrogen (47 t y^{-1}) amounting to 65% of the total nitrogen load (Schlacher and others 2005). Matching sets of clams were collected from an ocean beach remote from freshwater discharge. This marine-reference site (26.01°S 153.15°E) was 70 km north of the plume-impacted beach and 42 km from the nearest estuary, which is a small system that discharges only very small plumes not extending for more than 2 km alongshore.

Rainfall and river discharge in the region is strongly bimodal, with most of the annual precipitation falling during the austral summer which

contrasts with dry conditions during the austral winter. To test for temporal variation in the strength of land–ocean coupling driven by fluctuating river discharge, we collected clams before the main river discharge in early January 2004, after the wet season (May 2004), and at the end of the low-flow period in September 2004.

Clams (*Donax deltoides*) were hand-collected from the lower intertidal zone of the exposed beach during low tides; about 50–200 individuals were obtained per trip. The across-shore distribution of this species extends from the mid-intertidal to the swash and shallow parts of the surf zone seawards (James and Fairweather 1995; Schlacher and Thompson 2007). As for other species of the genus *Donax*, the clams can actively adjust their position across the beach through swash riding (Donn 1990; Ellers 1995). Abundances are spatially heterogeneous in an along-shore direction: dense patches of 100–200 m length often alternate with sparse stretches along the beach, and this pattern can be related to variations in beach morphology (James and Fairweather 1996; James 2000). Donacid clams dominate the biomass on many sandy beaches worldwide, and constitute an important prey category for numerous invertebrates (for example, crustaceans, gastropods), fishes and shorebirds (Ansell 1983; Salas and others 2001; Peterson and others 2006).

Laboratory Analysis

To encompass the full size spectrum of the sampled clam population, we selected for isotope analysis the smallest and largest individual plus 8–12 additional specimens at equal size steps in between. A total of 233 clams were analyzed, giving a sample size (*n*) for each time × site combination of 10–14. Body size in the sampled population ranged from 10 to 54 mm shell length (mean 31.8 ± 12.9 SE). From each individual, the foot tissue, adductor muscle, and gills were excised. Tissues were rinsed twice in deionized water, decalcified (immersion in 1 M HCl for 40 min), followed by four rinses in deionized water and drying at 65°C for 48 h. Stable isotope ratios were measured in the Isotope Analytical Facility of Griffith University on an automated Isoprime Isotope-Ratio Mass Spectrometer. Stable isotope ratios are expressed in ‰ using the conventional delta (δ) notation: δX (‰) = $[(R_{sample}/R_{standard}) - 1] \times 1000$; where X is $\delta^{13}C$ or $\delta^{15}N$, and R is the $^{15}N/^{14}N$ (nitrogen) or $^{13}C/^{12}C$ (carbon) ratio in the sample and standards (Pee Dee Belemnite equivalent for carbon and the IAEA international standard of atmospheric N_2 for nitrogen).

Data Analysis

The main test of interest was the magnitude of isotopic differences between clams from areas impacted by river plumes versus those remote from plumes. Because the three tissue types analyzed originate from the same individual, they are multiple dependent variables. We therefore used a Multivariate Analysis of Variance (MANOVA) as the GLM model to partition variance in the full data set. This analysis included the terms: (i) site (plume-impacted vs. marine-reference site), (ii) time (low, medium, and high river discharge), and (iii) the time × site interaction. The MANOVA was complemented by univariate ANOVAs for individual tissue types to assess whether effects are consistent amongst tissue types. To remove any possible confounding of body size on isotope ratios (that is, independent of site and time), we standardized isotope ratios to the median length (32 mm) of clams using the slopes derived from regressions of size versus $\delta^{13}C$ or $\delta^{15}N$; slopes were computed for each tissue × site × time combination separately.

We estimated the relative contribution of terrestrial and marine carbon to clams using the Iso-Error mixing model (Phillips and Gregg 2001). For the terrestrial (including estuarine) source we used the $\delta^{13}C$ of suspended particulate organic matter (SPOM) collected in the mid estuary (−25.15‰ in summer, −25.92‰ in winter). For the marine source, we considered that the tissue of clams at the reference (non-plume) site provided a more reliable isotope value, after making a 0.5‰ adjustment for trophic fractionation (−19.20‰ in summer, −19.95‰ in winter). Direct isotope measurements of marine SPOM were not used because the composition and isotopic signature of suspended particles in coastal waters vary markedly over short periods. Fluctuations in the mixing between onshore and offshore waters and changing inputs from a broad spectrum of allochthonous sources and autochthonous production are the main cause of this variability (Megens and others 2001; Hill and others 2006). This temporal variance in the chemical properties of suspended matter in coastal seas means that spot measurements of isotopic signatures in particulate matter extracted from water samples are generally unrepresentative of the actual carbon available to consumers, such as bivalves, over longer time periods. Given this mismatch in the temporal integration of isotopic signals (minutes to days for suspended particles vs. weeks to months for animal consumers), isotopic signals in SPOM samples generally do not track

changes in the tissues of filter-feeding bivalves (Lorrain and others 2002; Hill and others 2006; Gustafson and others 2007).

RESULTS AND DISCUSSION

Clams exposed to river plumes had isotope ratios that were significantly depleted in ^{13}C and enriched in ^{15}N, an isotopic shift consistent with the incorporation of terrestrial C and N (Figures 2, 3, 4; Table 1). Isotopic variation among beach clams was chiefly driven by spatial differences between clams from the marine reference and those from the plume-impacted area (MANOVA; site effect: df = 3,62; $P < 0.001$; Table 1). The magnitude of the contrast (effect size) between plume and reference sites varied subtly through time, evident as a weak, but significant, interactive effect of time × site (MANOVA; site × time: df = 6,124; $P < 0.001$; Table 1), but the direction of the isotopic shift between sites never changed. Carbon isotope ratios were always significantly lower in clams from the plume area and N ratios always significantly higher (Figures 3 and 4); this is in close agreement with a stronger terrestrial signal present in clams exposed

Figure 2. Shifts in carbon and nitrogen stable isotope ratios in three tissue types of wedge clams (*Donax deltoides*) exposed to river plumes on a sandy beach abutting an estuarine inlet. Clams from the marine reference area were collected from an ocean beach not affected by river plumes. Data are seasonal means (3 sampling periods corresponding to low, medium and high river discharge; compare Figure 5) with 95% confidence intervals.

to plume waters. Furthermore, this isotopic shift, indicating greater incorporation of terrestrial C and N by clams in the plume area, was highly consistent across the three tissue types analyzed (that is, foot, adductor muscle, gills; ANOVA: df = 1,64; $P < 0.001$ for all tissues and elements). Based on carbon isotopic mixing models (Phillips and Gregg 2001), clams in plume areas obtain a sizeable fraction of their body carbon from terrestrial sources; values of terrestrial carbon assimilation average 15% (CI: 3–28%) across seasons, with a maximum of 18% (CI: 4–32%) at the end of the rainy season.

The global flux of riverine organic carbon to the oceans of 434×10^6 tC y^{-1} (Schlünz and Schneider 1999) is about 6% of coastal primary production at $6,900 \times 10^6$ tC y^{-1} (Wollast 1991). Assuming that (i) 10% of the exported TOC is buried (Schlünz and Schneider 1999), (ii) particulate organic carbon (POC) represents 46% of the total terrestrial load (Ludwig and others 1996), and (iii) 65% of the POC load is refractory (Ittekkot 1988), about 62.9×10^6 tonnes of labile POC with a terrestrial provenance are available for biological processing in the oceans worldwide. This 'bioavailable' fraction of the total terrestrial C export from rivers represents about 1% of coastal production on a global scale.

Although there are many uncertainties in the estimates of global C fluxes, it is remarkable that our estimate of terrestrial C uptake (~15%) by consumers on a sandy beach is an order of magnitude greater than the global average projected above. However, spatial heterogeneity in the energetic importance of plume subsidies is likely to be pronounced. Plume subsidies are predicted to be more important at local and regional scales along coastlines where river discharges are large, but much less so in arid regions with low river run-off or few plume areas. We hypothesized that the magnitude of terrestrial C delivery and trophic assimilation is higher in coastal regions impacted by river plumes than in areas not influenced by freshwater influence. Indeed, the uptake of terrestrial material we measured in marine consumers demonstrates the existence of an energetic link between coastal ecosystems and continental C sources. Importantly, the amount of terrestrial material assimilated by sandy beach animals that feed in plume areas is broadly consistent with predictions about the putative strength of land–ocean coupling based on global estimates of terrestrial C flux to coastal seas and the biological processing of this material in marine systems affected by river plumes.

If anything, our estimate of terrestrial carbon incorporation by sandy beach bivalves may be
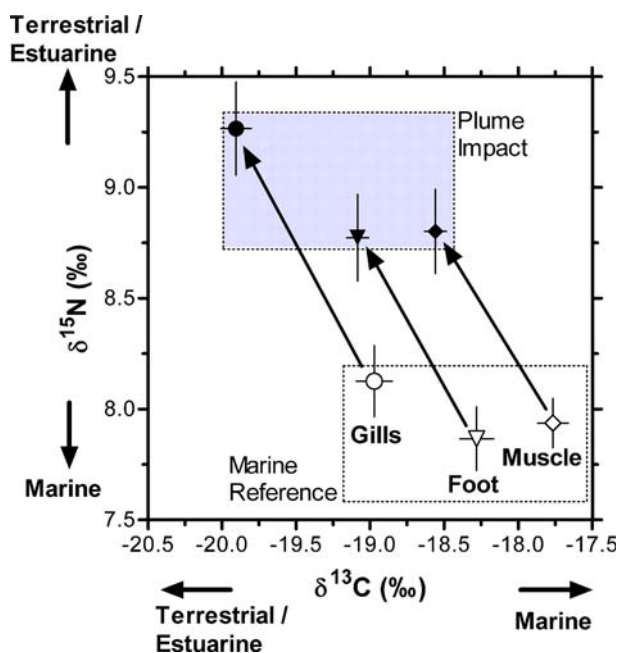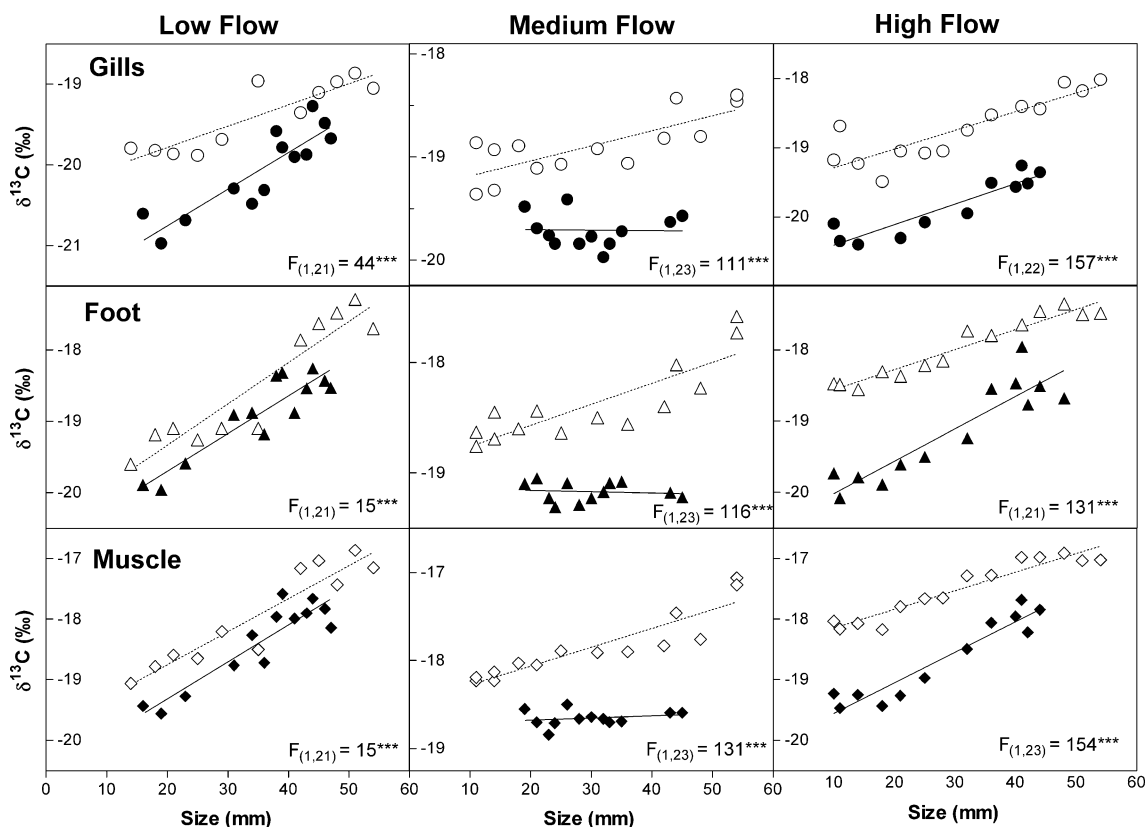
Figure 3. Spatial contrasts in stable carbon isotope ratios (δ^{13}C) in three tissue types of wedge clams (*Donax deltoides*) between a sandy beach impacted by river plumes (solid symbols) and a marine-reference site (open symbols) remote from the influence of river plumes. Contrasts are shown for three different periods of low river discharge (*left* column, Sep. 2004), medium discharge (*center* column, Jan. 2004) and high river discharge (*right* column, May 2004). All site-to-site differences in carbon signals are significant (Analysis of Covariance—ANCOVA, where body size is the co-variate, irrespective of time; ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$).

conservative. Water-borne organic carbon particles with a depleted isotopic signature (that is, material from terrestrial C_3-plants and mangroves) can settle closer to their source, whereas isotopically enriched carbon (that is, C_4-grasses, such as sugarcane) is transported further offshore because of their smaller sizes (Goni and others 1997; Bianchi and others 2007). In situations where significant amounts of terrestrial C_4-carbon mix with marine sources due to the hydrodynamic sorting of fluvial particles that differ in their isotopic signatures, the amount of terrestrial C incorporated by marine consumers may be underestimated. Thus, animals on beaches may assimilate greater amounts of terrestrial material than shown in an isotopic tracer study such as ours.

We detected a greater isotopic shift towards terrestrial C influence following peak river discharges (Figure 5). This shows that after larger quantities of organic C were exported from the estuary, bivalves on the adjacent sandy beach had assimilated sig-

nificantly more terrestrial C than during low-flow periods (Figure 5). Conversely, during baseflow conditions, most of the N in the estuary originates from discharges of sewage that is enriched in ^{15}N (Schlacher and others 2005). Nitrogen isotope ratios of clams on the adjacent beach tracked the export of this elevated sewage signal following low river discharge. This enriched sewage signal becomes diluted by run-off from the watershed during major rainfall events, producing a ^{15}N-depleted isotope signal in the river discharge (Schlacher and others 2005), which resulted in correspondingly lower enrichment factors in the clams (Figure 5).

Detection of an isotopic change symptomatic of land–ocean coupling depends partly on the rates at which C and N are replaced in target consumers. Tissue turnover times in filter-feeding bivalves are species-specific and depend on tissue type, growth rates, and metabolic activity of the animals; measurements range from 80 days in stomach glands of freshwater mussels (Raikow and Hamilton 2001) to
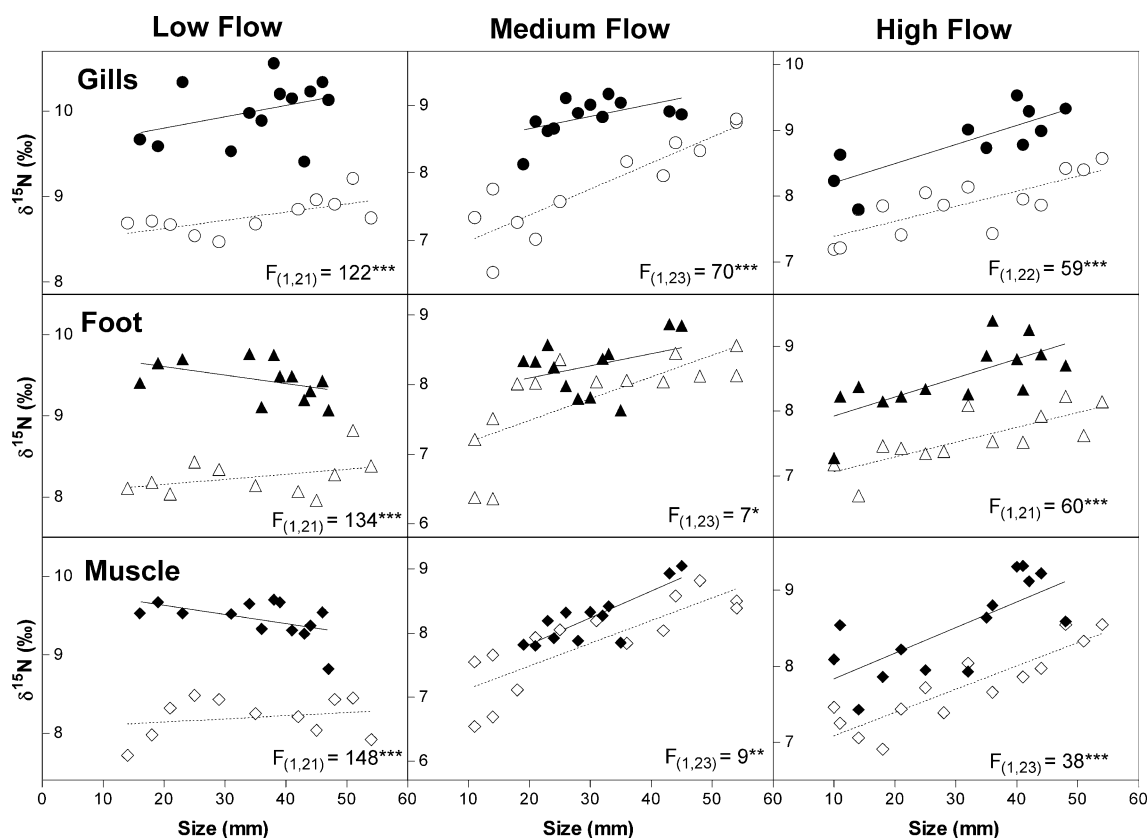
Figure 4. Spatial contrasts in stable N isotope ratios (δ^{15}N) in three tissue types of wedge clams (*Donax deltoides*) between a sandy beach impacted by river plumes (solid symbols) and a marine-reference site (open symbols) remote from the influence of river plumes. Contrasts are shown for three different periods of low river discharge (*left* column, Sep. 2004), medium discharge (center column, Jan. 2004) and high river discharge (*right* column, May 2004). All site-to-site differences in N signals are significant (Analysis of Covariance—ANCOVA, where body size is the co-variate, irrespective of time; ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$).

1 year in whole body and adductor muscle of marine and freshwater mussels (Hawkins 1985; Raikow and Hamilton 2001). Bivalves exposed to plume waters would therefore integrate isotopic signals of terrestrial exports over periods of months to a year. Moreover, isotopic signals in consumer tissues are the product of metabolic replacement in combination with the addition of new C and N during growth. Tissue turnover in faster-growing juveniles is mainly driven by growth, with only a minor contribution of metabolic replacement (Zuanon and others 2006). Juvenile clams should therefore show higher rates of isotopic change in their tissues and respond more readily and strongly to major inputs of new terrestrial carbon supplied by the high river discharge during the austral summer and autumn (Jan to May; Figure 6). This explains why the degree of isotopic shift between animals from the marine-reference station and those from the plume was inversely related to body size (Figure 4; OLS: $\Delta\delta^{13}C = 1.50 + \text{Size} \times$

-0.0116; $F_{(1,16)} = 7.386$, $P = 0.01$). Juveniles had incorporated significantly more terrestrial C at the end of the rainy season compared to larger individuals, which had slower rates of C replacement. This differential response of juvenile and adult clams further supports our conclusion that isotopic patterns result from the uptake of terrestrial matter.

Conventional wisdom holds that food webs of sandy beaches are supported almost exclusively by marine imports (McLachlan and Brown 2006). Here we document for the first time that consumers on beaches can be linked to terrestrial C delivered by river plumes. This is a novel mechanism of trophic subsidy in marine intertidal systems. Marine bivalves play a pivotal role in carbon cycling in the coastal oceans. Dense populations of bivalves, common on sandy beaches, process large amounts of suspended carbon, regenerate nutrients, enhance the flux of organic matter to the seafloor and mediate the trophic routing of pelagic primary production (Dame 1996).

Table 1. Summary of GLM Model Results to Partition the Total Variance in C and N Isotope Ratios in Wedge Clams Between Sites and Times Using (A) Multivariate Analysis of Variance (MANOVA) as the Main Test, Complemented by (B) Univariate Tests for Individual Tissue Types

(A) Multivariate (MANOVA)

	Wilks' Lambda	F	Effect df	Error df
$\delta^{13}C$				
Time	0.24	23.3***	6	134
Site	0.12	156.5***	3	67
Time × Site	0.71	4.2***	6	134
$\delta^{15}N$				
Time	0.19	27.14***	6	124
Site	0.15	118.28***	3	62
Time × Site	0.63	5.34***	6	124

(B) Univariate (ANOVA)

	df	Foot		Gills		Muscle	
		MS	F	MS	F	MS	F
$\delta^{13}C$							
Time	2	1.09	24.1***	2.74	67.8***	1.01	24.6***
Site	1	10.76	238.2***	14.54	359.5***	10.73	260.4***
Time × Site	2	0.55	12.1***	0.16	3.9*	0.36	8.7***
Error	69	0.05		0.04		0.04	
$\delta^{15}N$							
Time	2	4.78	44.1***	7.75	100.8***	3.60	39.0***
Site	1	12.90	119.2***	20.03	260.2***	12.61	136.7***
Time × Site	2	1.09	10.1***	0.15	2.0 ns	1.24	13.5***
Error	69	0.11		0.08		0.09	

Site comparisons are between plume impacted and reference sites. Times include three discharge periods (compare Figure 5).
***P < 0.001, **P < 0.01, *P < 0.05, $^{ns}P > 0.05$.

We used wedge clams (*Donax deltoides*) as a model system to test the strength of trophic coupling between terrestrial primary production and sandy beach food webs. Wedge clams were chosen because they are the dominant macroscopic consumer of suspended organic matter in the benthos of many beaches worldwide (Ansell 1983; Soares and others 1997), are highly efficient filter feeders (Matthews and others 1989), mineralize organic matter on beaches (Soares and others 1997) and form a critical energetic link to higher trophic levels such as shorebirds and fishes (Ansell 1983). Importantly, the clams can access the terrestrial C and N delivered by plumes via several routes: (1) uptake of phytoplankton production that has been stimulated by nutrients outwelled in plumes; (2) direct uptake of particulate organic matter (POM) exported by river discharge; (3) assimilation of carbon originally delivered in dissolved form and subsequently converted to particulate form in the prominent microbial loop of the surf zone and interstitial sediments (Cockcroft and McLachlan 1993), and (4) direct uptake of DOC, although this pathway may be inconsequential for marine species (Pan and Wang 2004). Based on the multiple roles that bivalves play in the processing of matter in benthic systems, we predict that the isotopic shifts of clams measured in this study will be detectable in other consumers, and that they will propagate through most of the food web on sandy beaches impacted by river plumes.

Given the ecological importance of wedge clams, the incorporation of C and N from river plumes, which we document here as a novel mechanism of ecotonal coupling, is predicted to have several consequences that extend beyond the ecological organization of the filter-feeding guild. (1) Energetic subsidies of keystone prey species by river discharge may profoundly influence ecosystem energetics on sandy shores, including trophic effects that cascade upwards to affect populations of threatened vertebrates on beaches. (2) River discharge has been linked to higher fisheries yields in coastal seas (Gillanders and Kingsford 2002); beach
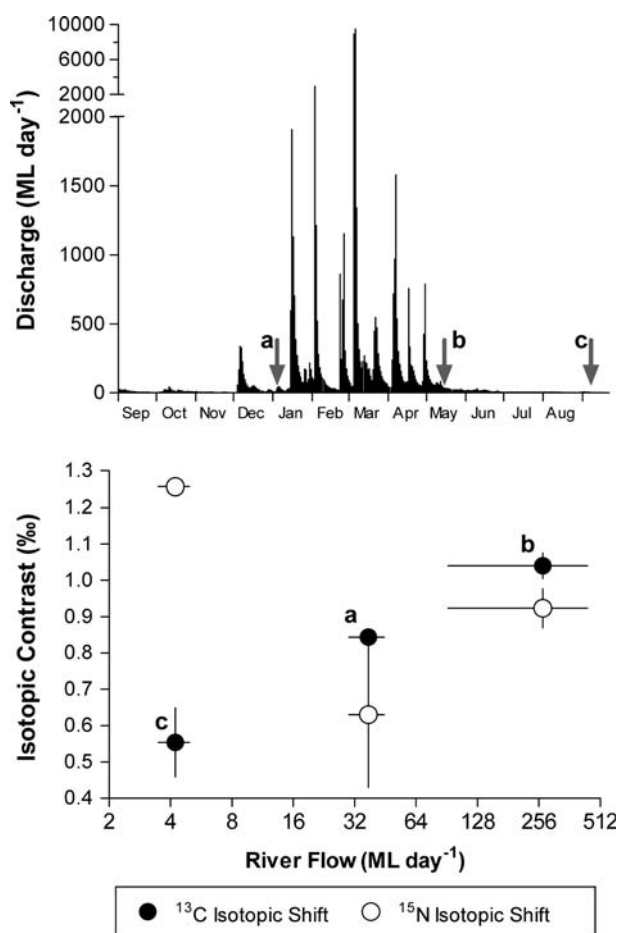
Figure 5. Variation in river discharge and sampling times for beach clams (*top* panel, letters **a–c**), and isotopic contrast between clams from marine-reference and plume-impacted beaches ($\Delta_{\text{plume effect}} = |\delta_{\text{marine ref}} - \delta_{\text{plume}}|$) as a function of discharge (*lower* panel). Letter symbols in *lower* panel correspond to sampling events (**a–c**) shown in *top* panel.

Figure 6. Contrasts in C isotope ratios (δ^{13}C) between clams from a sandy beach impacted by river plumes and clams from ocean beaches without plumes ($\Delta\delta^{13}$C = $|\delta^{13}C_{\text{marine ref}} - \delta^{13}C_{\text{plume}}|$) after peak river discharge (May 2004) in relation to body size (*F*-tests for regression slopes—Gills: $F = 7.9$, $P = 0.07$; Foot: $F = 1.7$, $P = 0.25$; Muscle: $F = 4.5$, $P = 0.10$; All tissues—$F = 7.39$, $P < 0.01$).

clams are an important fisheries resource (McLachlan and others 1996), and extra C and N from river plumes may enhance fisheries yields of sandy beach invertebrates. (3) Rivers are exporting higher amounts of nutrients and pollutants, resulting mainly from burgeoning population growth and development in coastal watersheds, and the detrimental effects of nutrient enrichment and toxicants on coastal ecosystems are numerous, widespread and well-documented (Schlacher and others 2005; Howarth and Marino 2006). The assimilation of the sewage-derived N that we measured in beach organisms highlights a serious environmental issue of pollutant transfer across ecosystem boundaries. This pollutant transfer impacts on sandy beaches, which are the prime recreational resource for humans on ocean shores
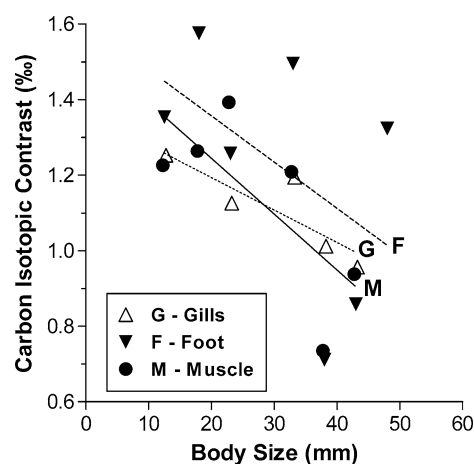
worldwide and are already under threat from a plethora of human pressures (Schlacher and others 2006, 2007a, b). (4) Finally, global climate change is predicted to modify the volume and pattern of river flows (Meehl and others 2007), altering the amount of organic matter delivered to the coastal oceans globally. Our data show that marine intertidal ecosystems can be energetically linked to river inputs, suggesting that key properties of C and N cycling on ocean shores worldwide are vulnerable to impacts arising from climate change.

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