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Mechanisms and ecological role of carbon transfer within coastal seascapes

Glenn A. Hyndes[1,*], Ivan Nagelkerken[2,3], Rebecca J. McLeod[4], Rod M. Connolly[5], Paul S. Lavery[1] and Mathew A. Vanderklift[1,6]

[1]*Centre for Marine Ecosystems Research, School of Natural Sciences, Edith Cowan University, Perth 6027, Australia*
[2]*Department of Animal Ecology and Ecophysiology, Radboud University Nijmegen, Institute for Water and Wetland Research, Nijmegen, 6500, The Netherlands*
[3]*Southern Seas Ecology Laboratories, School of Earth and Environmental Sciences, The University of Adelaide, Adelaide 5005, Australia*
[4]*Department of Chemistry, University of Otago, PO Box 56, Dunedin, New Zealand*
[5]*School of Environment and Australian Rivers Institute, Griffith University, Brisbane 4222, Australia*
[6]*CSIRO Marine and Atmospheric Research, Wembley 6913, Australia*

ABSTRACT

Worldwide, coastal systems provide some of the most productive habitats, which potentially influence a range of marine and terrestrial ecosystems through the transfer of nutrients and energy. Several reviews have examined aspects of connectivity within coastal seascapes, but the scope of those reviews has been limited to single systems or single vectors. We use the transfer of carbon to examine the processes of connectivity through multiple vectors in multiple ecosystems using four coastal seascapes as case studies. We discuss and compare the main vectors of carbon connecting different ecosystems, and then the natural and human-induced factors that influence the magnitude of effect for those vectors on recipient systems. Vectors of carbon transfer can be grouped into two main categories: detrital particulate organic carbon (POC) and its associated dissolved organic and inorganic carbon (DOC/DIC) that are transported passively; and mobile consumers that transport carbon actively. High proportions of net primary production can be exported over meters to hundreds of kilometers from seagrass beds, algal reefs and mangroves as POC, with its export dependent on wind-generated currents in the first two of these systems and tidal currents for the last. By contrast, saltmarshes export large quantities of DOC through tidal movement, while land run-off plays a critical role in the transport of terrestrial POC and DOC into temperate fjords. Nekton actively transfers carbon across ecosystem boundaries through foraging movements, ontogenetic migrations, or 'trophic relays', into and out of seagrass beds, mangroves or saltmarshes. The magnitude of these vectors is influenced by: the hydrodynamics and geomorphology of the region; the characteristics of the carbon vector, such as their particle size and buoyancy; and for nekton, the extent and frequency of migrations between ecosystems. Through a risk-assessment process, we have identified the most significant human disturbances that affect the integrity of connectivity among ecosystems. Loss of habitat, net primary production (NPP) and overfishing pose the greatest risks to carbon transfer in temperate saltmarsh and tropical estuaries, particularly through their effects on nekton abundance and movement. In comparison, habitat/NPP loss and climate change are likely to be the major risks to carbon transfer in temperate fjords and temperate open coasts through alteration in the amount of POC and/or DOC/DIC being transported. While we have highlighted the importance of these vectors in coastal seascapes, there is limited quantitative data on the effects of these vectors on recipient systems. It is only through quantifying those subsidies that we can effectively incorporate complex interactions into the management of the marine environment and its resources.

Key words: landscape ecology, spatial subsidy, food webs, ecosystem functioning, coastal ecosystems, fjords, reefs, mangroves, saltmarshes, seagrasses.

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* Address for correspondence (Tel: ++61 8 6304 5798; Fax ++61 8 6304 5509; E-mail: g.hyndes@ecu.edu.au)

I. INTRODUCTION

Ecosystem functioning relies on the supply and cycling of energy and nutrients. It has long been recognised that, while energy transfer in shallow aquatic ecosystems can occur through direct grazing on autochthonous primary producers, the main supply of organic matter to many ecosystems can be externally derived detritus (Valiela *et al.*, 1997; Dobson & Frid, 1998). The cross-habitat movement of carbon from donor to recipient habitats can be important in shaping food webs and productivity in the recipient systems (Polis, Anderson & Holt, 1997; Marczak, Thompson & Richardson, 2007) and has led to the conceptualisation of coastal seascapes as heterogeneous habitats linked through carbon (and other) exchanges.

Coastal ecosystems constitute proportionately small areas on a global scale, but are amongst some of the most productive in both aquatic and terrestrial environments, with net primary production (NPP) of algal reefs, seagrass beds, mangroves and saltmarshes often exceeding $1 \, kg \, C.m^{-2} \, year^{-1}$ (Valiela, 1995). As a consequence of this high productivity, they often provide important ecosystem functions. For example, mangroves, saltmarshes and seagrass beds in estuaries and bays provide refuge and feeding areas for juvenile fish and crustaceans, many of which are economically important (Polunin, 2008). Like seagrasses in more sheltered environments, kelp forests in more open, temperate coasts provide habitat for numerous mammal, fish, crustacean and mollusc species (Andrew & Jones, 1990; Estes & Duggins, 1995). By contrast, sandy shores often contain little *in situ* productivity, but play a significant role in recycling nutrients from marine detritus (Colombini & Chelazzi, 2003). Fjords are another prominent coastal (estuarine) system that receive large quantities of detritus from nearby highly productive forests (Glasby, 1978; Naiman & Sibert, 1978; McLeod, Wing & Skilton, 2010*b*).

With over half of the world's coastal vegetated ecosystems being lost through human activities (Lotze *et al.*, 2006), these ecosystems are amongst the most threatened systems (Polunin, 2008). These systems provide important ecosystem services, which require management across seascapes (Barbier *et al.*, 2011). Effective management of coastal systems, therefore, requires an understanding of the processes driving biodiversity and productivity in these systems, yet the synthesis of such processes occurring across coastal seascapes has been limited, e.g. ocean to island (Polis *et al.*, 1997). In this review, we examine the processes of large-scale connectivity mediated by vectors in a variety of globally occurring coastal seascapes. We focus on the supply and movement of carbon, representing organic matter, across coastal seascapes, since carbon is a major nutrient and its cycling is closely linked to energy flow through ecosystems (Dickinson & Murphy, 1998). We discuss the supply and movement of carbon in the form of vectors, which describe magnitude and direction. While Polis *et al.* (1997) defined both biological and physical vectors, we have defined vector in the biological and nutrient context, where the vector is the vehicle that transports carbon from one place to another, in a similar way to an organism transporting a pathogen (epidemiological vector) or gametes (dispersal vector). In our discussions, we consider physical processes such as hydrodynamics as the forces that move those vectors. Thus, in our review, carbon can be transported in the form

of dissolved organic and inorganic carbon (DOC and DIC), and as particulate organic carbon in the form of living organisms (e.g. phytoplankton, grazers or predators), and particulate organic carbon (POC), which represents detrital particles that are larger than molecules through to dislodged macrophyte material including dislodged mangrove leaves and kelp.

High *in situ* primary production in many coastal ecosystems provides large sources of autochthonous organic matter that contributes to secondary production either directly or indirectly. Detritus derived from those primary producers (and other organisms) provides one vector of POC. The movement of this vector may occur between terrestrial and marine systems, for example, when litter is moved by land run-off from the forest system into coastal ecosystems, it can contribute to the carbon sources for those coastal (recipient) systems (Valiela, 1995). Similarly, detrital carbon can move among marine ecosystems. For example, up to 80% of a seagrass meadow's production can be exported annually into a range of other ecosystems, including beaches and submarine canyons (Heck *et al.*, 2008), providing a vector of POC to those recipient systems. The migration of fish and other consumers across habitat boundaries has long been recognised (Beck *et al.*, 2001) and represents another vector for carbon. Once in the recipient habitat, their ingested and assimilated organic carbon is available to predators and scavengers. Alternatively, both plants and animals crossing boundaries may leak or excrete DOC (Valiela, 1995), forming another vector that may be advected by water movement (e.g. Wild *et al.*, 2004) and/or taken up by phytoplankton or algae (e.g. Hyndes, Lavery & Doropoulos, 2012). The availability and type of those vectors, as well as their interactions with the forces that move them between systems, will determine the level of influence they have on the food webs of recipient ecosystems.

As food webs frequently encompass multiple habitats (Polis *et al.*, 1997), linkages within food webs can be both trophic (i.e. flow of energy from one organism to another) and spatial (i.e. flow of energy from one place to another, resulting in a trophic subsidy). Throughout this review, we focus on food-web linkages among different ecosystems within the coastal environment that create spatially subsidised food webs (Polis *et al.*, 1997). These linkages encompass multiple spatial scales, from a few metres (Guest, Connolly & Loneragan, 2004) to thousands of kilometres (Naiman *et al.*, 2002). Furthermore, the linkages are controlled by the strength and direction of the forces that move the vectors. For example, marine-derived detritus is transported by advection, and thus relies on the strength and direction of water movement, but also depends on the processes that create wrack, such as dislodgement or mortality (Vanderklift & Wernberg, 2008). Alternatively, the strength of recruitment pulses of nekton species to different habitats over their life cycles (Beck *et al.*, 2001) will influence the strength of carbon supply to recipient systems. Thus, the numerous vectors of carbon, and the numerous ways in which they move around seascapes, create complex spatial linkages among food webs in coastal systems.

In this review, we examine the processes of connectivity in coastal seascapes using four case studies that vary markedly in carbon cycling and represent coastal seascapes in different latitudes/regions: (*i*) tropical estuaries and bays; (*ii*) temperate saltmarsh-dominated estuaries; (*iii*) forested temperate fjords; and (*iv*) open temperate coasts. Since a number of reviews have discussed sea-to-land transfer of material (e.g. Polis *et al.*, 1997; Colombini & Chelazzi, 2003), our discussions focus mainly on the transfer of carbon across subtidal ecosystems or from land to sea. The main vectors of carbon transfer, in two broad forms (detritus and its associated dissolved material, and consumers), are discussed for each of the four case studies, which reflect different types of carbon vectors (e.g. nekton *versus* plant detritus, terrestrial *versus* marine) and different cross-shelf scales (e.g. estuaries *versus* open coast). We then use these four case studies to address the following questions. What are the main vectors of carbon connecting different ecosystems? What scales of connectivity do different vectors provide? What factors influence the effectiveness of those vectors as donors of carbon to recipient systems? Finally, we discuss the implications of carbon flow across ecosystem boundaries in terms of management and future trajectories for connectivity based on anthropogenic disturbances (e.g. agriculture, urbanisation and climate change).

II. TROPICAL ESTUARIES AND BAYS

(1) Definition and distribution of the system

A myriad of different tropical inshore areas exist, such as estuaries, deltas, bays, lagoons, and tidal wetlands, and a variety of definitions have been used for these shallow-water ecosystems (Wolanski, 2007). For simplicity, the term tropical estuaries and bays is used here for inshore or semi-enclosed bodies of shallow water that are protected from ocean currents and waves and that are largely dominated by soft bottoms. Estuaries and bays are catchment areas that often receive significant amounts of nutrients from land through run-off, leading to high primary and secondary production. In clear tropical waters, submerged aquatic vegetation such as macroalgae and seagrasses can produce up to $0.5 \, kg \, C.m^{-2} \, year^{-1}$ (Table 1). This abundance of food resources and the protection from predation afforded by the structure-rich habitat (Nagelkerken, 2009) leads to high densities of macrofauna and nekton associated with the habitat (Adams *et al.*, 2006). The intertidal vegetation along sheltered coastlines is often dominated by mangroves, which can produce up to $1 \, kg \, C.m^{-2} \, year^{-1}$, much of which falls down as litter and forms a source of carbon in the intertidal zone. The fate of primary productivity in tropical estuaries and bays is highly variable, with some vegetation types showing a relatively large degree of consumption (e.g. macroalgae) while others are mainly decomposed (e.g. seagrasses) or exported (e.g. mangrove and macroalgae) (Table 1). This case study focuses on the main vectors of

carbon that contribute to the flow of energy across ecosystems in the tropical coastal seascape. It uses examples from across the globe and from estuaries as well as marine embayments.

(2) Main vectors of carbon

Due to the presence of multiple habitat types that occur relatively close to one another, and due to their strong connectivity through movement of water and nekton, flow of energy is an important process in the tropical coastal seascape (Ogden, 1997). The main pathways of cross-ecosystem carbon flow are through riverine and tidal transport of POC (including detritus), release of DOC from the vegetation, and feeding migrations of nekton that forage in donor habitats and release carbon through defecation in shelter habitats (Fig. 1; Bouillon & Connolly, 2009).

In the tropics, terrestrial coastal landscapes supply carbon to adjacent marine ecosystems predominantly through river run-off containing organic matter from terrestrial soil and catchment vegetation (in estuarine environments) and through litterfall from intertidal mangrove vegetation (in non-estuarine environments). Rough estimates of global riverine carbon fluxes to the tropical coastal zone are 0.1×10^9 kg C.year^{-1} POC, 0.1×10^9 kg C.year^{-1} DOC, and 0.2×10^9 kg C.year^{-1} DIC (Ludwig, Probst & Kempe, 1996; Bouillon & Connolly, 2009), part of which is transported to the open ocean and part of which is retained in estuaries and bays (Fig. 1) where it contributes to primary and secondary production. Mangroves have an average NPP of about 0.9 kg C.m^{-2}.year^{-1} (Table 1), of which litterfall accounts for approximately $0.3-1.2$ kg C.m^{-2}.year^{-1} (Bouillon *et al.*, 2008*a*). Newly fallen mangrove leaves leach large amounts of DOC during the first $10-14$ days, after which they are partly consumed and reworked to smaller particles by resident gastropods and crabs (Table 1; Kristensen *et al.*, 2008). Most carbon is retained and recycled through the sedimentary microbial food web and only some mangrove-derived carbon is transported to adjacent systems through tidal exchange, often referred to as 'outwelling' (Lee, 1995). Total export of organic carbon is on average 20% (0.2 kg C.m^{-2}.year^{-1}) of total litterfall, partitioned about equally between DOC and POC. Export through detrital POC is higher in regions with low precipitation and high temperatures, while export of finer POC is higher in areas with low temperature (Adame & Lovelock, 2011). Reliable estimates for DIC export are missing, but one study suggested that it could be up to eight times higher than for DOC (Bouillon *et al.*, 2008*a*). Mangrove carbon is only incorporated to some degree into food webs of adjacent habitats up to just a few hundred meters away (e.g. Hemminga *et al.*, 1994; Granek, Compton & Phillips, 2009; Kruitwagen *et al.*, 2010) and some mangroves even experience a net influx of DOC (Bouillon & Connolly, 2009). Riverine mangroves, systems with large tidal amplitudes, and more open mangrove systems tend to export carbon across larger spatial scales (Adame & Lovelock, 2011). Contribution of mangrove carbon to directly adjacent faunal communities has been estimated to be up to 58%, but the exact contribution remains ambiguous (Bouillon, Connolly & Lee, 2008*b*).

Aquatic vegetation, consisting mainly of macroalgae, microphytobenthos, periphyton, and seagrasses, can be highly productive and an important source of carbon for adjacent ecosystems. Average NPP for tropical seagrasses and for macroalgae in estuaries and bays is about 0.5 kg C.m^{-2}.year^{-1} (Table 1). Seagrass beds can accumulate significant quantities of carbon (up to 0.3 kg C.m^{-2}.year^{-1}) through deposition of phytoplankton onto the substratum (Hemminga, Harrison & van Lent, 1991). Export through leaching is about $2-10\%$ of their daily production, released as DOC to the surrounding water column (Robertson, Mills & Zieman, 1982; Velimirov, 1986; Ziegler & Benner, 1999*b*). Export rates of seagrass leaves and/or detritus range up to 0.1 kg C.m^{-2}.year^{-1} in the Caribbean region, and depending on the seagrass species, export varies from 1% to as much as 77% of NPP (Heck *et al.*, 2008). Seagrass leaves can be exported, for example, to the deep sea where they contribute significantly to the diet of Echinodermata (Suchanek *et al.*, 1985), or to intertidal habitats such as mangroves, mudflats and sandy beaches (Bouillon & Connolly, 2009).

Consumers of seagrass, mainly in the form of marine meso- and macro-grazers (Valentine & Heck, 1999; Heck *et al.*, 2008), transfer carbon daily across large spatial scales and neighbouring ecosystems (Fig. 1). Many herbivorous fish, such as parrotfishes (Scaridae), surgeonfishes (Acanthuridae) and sea breams (Sparidae) feed on aquatic vegetation during daytime and migrate to rocks, ledges, corals and channels in adjacent areas at dusk (Ogden & Buckman, 1973; Nagelkerken *et al.*, 2000), where they release carbon in sheltered habitats through defecation. Sea urchins (*Diadema antillarum*) that shelter on patch reefs in seagrass beds can create conspicuous bare 'halos' around their home reefs through their grazing activity (Ogden, Brown & Salesky, 1973). However, seagrass leaves are generally considered to be of little nutritional importance (Kitting, Fry & Morgan, 1984). Consumption of seagrass leaves is on average 20% of NPP, much smaller than that of macroalgae (58%) or microphytobenthos (42%, including periphyton) (Table 1). Significant transfer of carbon can occur through offshore macrograzers, such as dugongs, manatees, and green turtles, which rest in deeper waters and migrate to shallow inshore areas where they consume large quantities of seagrass and macroalgae (Thayer *et al.*, 1984). Dugongs, for example, create foraging scars where they can remove up to 86% of the seagrass biomass (Heinsohn, Wake & Marsh, 1977). Few quantitative data are available on transfer rates of consumed aquatic vegetation by migratory organisms, and it remains inconclusive to what degree consumption and defecation affects productivity in donor and recipient habitats.

Carnivores also act as important vectors of carbon transfer across ecosystem boundaries. Mesopredators that are permanent or temporary residents of estuaries and bays, such as snappers (Lutjanidae), grunts (Haemulidae) and squirrelfishes (Holocentridae), undergo diurnal migrations in microtidal systems (Verweij & Nagelkerken, 2007). These

Table 1. Net primary production (NPP) and fate of primary production (kg C.m^{-2}.year^{-1}) of aquatic vegetation for different autotrophs in different coastal environments

	NPP	Fate			
		Decomposition	Consumption	Export	Detrital accumulation
Tropical estuaries and bays					
Macroalgae	0.54 (0.63)	—	0.32 (0.24)	0.25 (0.53)	—
Mangroves	0.94 (0.59)	0.21 (0.22)	0.04 (0.03)	0.18 (0.17)	0.10 (0.09)
Microphytobenthos	0.19 (0.16)	0.05 (0.03)	0.08 (0.08)	—	—
Seagrasses	0.61 (0.40)	0.36 (0.20)	0.16 (0.19)	0.06 (0.04)	—
Temperate estuaries					
Seagrasses	0.46 (0.34)	0.23 (0.16)	—	—	—
Saltmarshes	1.38 (1.69)	0.33 (0.38)	0.23 (0.19)	0.06 (0.04)	0.57 (0.77)
Microphytobenthos	0.30 (0.64)	0.03 (0.03)	0.13 (0.13)	0.04 (0.04)	0.04 (0.09)
Temperate open coasts					
Macroalgae	0.97 (0.62)	0.53 (0.39)	0.05 (0.06)	0.35 (0.38)	0.06 (0.04)
Seagrasses	0.44 (0.37)	0.12 (0.07)	0.03 (0.04)	0.22 (0.26)	0.04 (0.04)
Temperate fjords					
Phytoplankton (including picoplankton)	0.03–1.40*	—	—	—	—
Macroalgae	0.12–1.75[†]	—	—	—	—
Microphytobenthos	0.01–0.40[‡]	—	—	—	—
Forest	0.65[§]	—	—	—	—

*Note that this estimate is for gross primary production from a single Chilean fjord over the course of 1 year.
[†]Note that the available surface area for macroalgal colonisation in fjords is restricted to the photic zone of fringing reefs. The volume of habitat for phytoplankton therefore far exceeds that for macroalgae.
[‡]From Montero *et al.* (2011).
[§]From Waring & Schlesinger (1985).
Data are means (1 S.D.) of different studies, recalculated from online appendix 1 of Cebrian (2002) using relevant studies for each group. Note that the sum of the values for each category will not equal NPP due to data being derived from a subset of studies. Decomposition includes detritivory. Export is across habitat boundaries. Ranges of primary production for temperate fjords are from Burrell (1988) unless otherwise indicated.

predators feed on resident invertebrates and small prey fish in sand, seagrass or algal beds at night, and migrate up to 1 km to daytime shelter sites in mangroves, rocks and crevices, and patch reefs (Nagelkerken *et al.*, 2008*a*; Krumme, 2009). While opportunistic feeding in shelter habitats does occur (Nagelkerken & van der Velde, 2004; Verweij *et al.*, 2006), most daily carbon transfer is likely to be from feeding to shelter sites, and these migrations may fuel recipient food webs (Layman *et al.*, 2011). For example, Meyer, Schultz & Helfman (1983) found that nutrient excretion from grunts that fed on seagrass beds and rested over coral heads enhanced growth rates of corals in patch reefs. Compared to microtidal systems, tidal feeding migrations are more typical for macrotidal coasts, although such migrations result from interactive effects of diurnal and tidal cycles, and carbon transfer is usually across larger spatial scales of up to a few kilometers (Krumme, 2009). During high tide, many species of fish and decapods colonise and feed in high-intertidal habitats such as mangroves, or move from (deeper) adjacent habitats to feed in seagrass beds (Krumme, 2009). Top predators such as sharks (Carcharhinidae), dolphins (Delphinidae) and barracudas (Sphyraenidae) that irregularly or opportunistically visit inshore feeding areas from offshore waters or adjacent habitats (Blaber, 2000; Nagelkerken *et al.*, 2008*a*; Krumme, 2009) can have considerable local effects on the resident fauna through short but significant predation

(Blaber, 2000). Also various swimming, diving and wading bird species prey significantly on nekton in shallow waters (Blaber, 2000; Torres, 2009) and cause transfer of carbon from sea to land. However, quantitative data on carbon transfer by migrating animals are generally lacking.

On a larger time scale, ontogenetic migration by nekton leads to permanent transfer of carbon across ecosystems (Fig. 1). Nekton such as fishes, shrimp, and crabs function as vectors of carbon when they settle from the open ocean into shallow-water coastal habitats (Pollux *et al.*, 2007; Adams & Ebersole, 2009), show ontogenetic movements among these habitats (Lugendo *et al.*, 2006), and leave these inshore nurseries as (sub) adults to take residence on coral reefs or in offshore waters (Nagelkerken, 2007, 2009; Haywood & Kenyon, 2009). Similarly, diadromous species energetically connect freshwater, estuarine and marine habitats through spawning migrations by adults and life-cycle migrations by their larvae or juveniles (Milton, 2009). However, since many fish species in tropical estuaries and bays are estuarine residents (Blaber, 2009), export of carbon through life-cycle migrations is probably lower than that of other pathways. The exact degree of offshore carbon flux has not been quantified, but for some species of fish it has been estimated that 36–98% of the adults found on coral reefs have passed through mangrove and seagrass nurseries (Nagelkerken, 2009). In addition, strong correlations between mangrove abundance
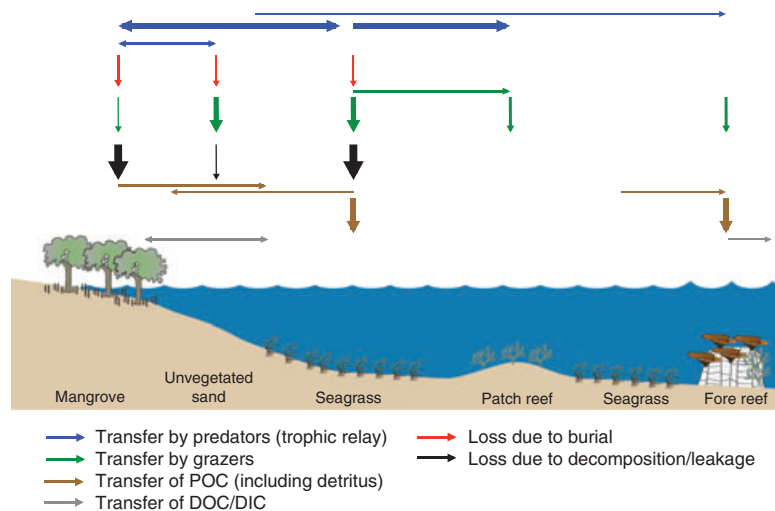
Fig. 1. Conceptual diagram of the relative magnitude and direction of the transfer of different carbon vectors across ecosystems in tropical estuaries and bays. The colour of each line indicates the type of vector, while its thickness represents the relative importance of the vector. The arrow indicates the direction of flow of each vector. DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; POC, particulate organic carbon.

and offshore catches of shrimp or estuarine-dependent fishes (Blaber, 2009) suggest that 20–90% of offshore commercial fisheries may be explained by the presence of mangroves or estuaries (Nagelkerken *et al.*, 2008*a*) further suggesting connectivity between these ecosystems through fish as a vector of carbon.

III. TEMPERATE SALTMARSH ESTUARIES

(1) Definition and distribution of the system

Saltmarshes dominate the world's temperate estuaries on all continents except Antarctica. It was in these estuaries that the original theory of 'outwelling' was developed to explain unusually high secondary production in coastal waters adjacent to marshes (Teal, 1962; Odum, 1968). Primary production in saltmarshes can be high, often exceeding $1\,\mathrm{kg\,C.m^{-2}.year^{-1}}$, while other autotrophs in temperate estuaries have lower levels of production (Table 1). Around one third of the productivity within the marsh is by benthic microalgae (Vernberg, 1993). A wide diversity of invertebrates and fishes utilise the flooded marsh. Fish penetrate far into marshes with the flooding tide (Kneib & Wagner, 1994; Rozas & Zimmerman, 2000; Thomas & Connolly, 2001), but our knowledge of carbon consumption comes mostly from studies focusing on the narrow strip of marsh edge fringing open estuarine waters (e.g. Connolly, Dalton & Bass, 1997; Minello *et al.*, 2003; Crinall & Hindell, 2004; Bloomfield & Gillanders, 2005). We focus on carbon transfer from temperate saltmarshes, but draw on information from subtropical estuaries where appropriate. Although seagrass beds are also common in temperate estuaries, where their rates of primary production are high with average levels of $0.5\,\mathrm{kg\,C.m^{-2}.year^{-1}}$ (Table 1), this case

study focuses on the vectors that specifically transport carbon from saltmarshes, rather than the broader estuarine systems.

(2) Main vectors of carbon

In the case of saltmarshes, the main vectors for carbon flow across ecosystem boundaries are through tidal transport of DOC released from the vegetation and detritus, POC (including detritus), and the feeding migrations of nekton (Fig. 2). More carbon is exported as DOC than as POC. Of 11 studies that measured both, DOC comprised 18% in one case but 50–100% in all other cases [percentages computed from raw data in table 3 in Taylor & Allanson (1995)]. POC export, in particular, can be restricted by the height of the marsh in the intertidal zone and marsh size (Guest & Connolly, 2006). Furthermore, crab burrowing activity returns buried POC to the surface (Gutierrez *et al.*, 2006), making it available once again for transport to adjacent ecosystems. The fraction of total annual primary production exported from saltmarshes thus varies enormously, ranging from 3 to 63% (Taylor & Allanson, 1995). Once exported, the most commonly reported fate of saltmarsh POC is burial in estuarine sediments, where it comprises a significant fraction of the detrital carbon (South African estuaries, Schlacher & Wooldridge, 1996; Western Australian estuaries, Svensson, Hyndes & Lavery, 2007). It apparently does not make a major contribution to DIC pools in estuarine waters (Schlacher *et al.*, 2009).

Carbon from the dominant macrophytes, such as *Spartina* spp., and from algae is available to consumers, with close to 20% of mean NPP taken up by consumers (Table 1), yet direct consumption of living saltmarsh macrophytes is rare. *Spartina* spp. is typically consumed as detritus (Currin, Newell & Paerl, 1995). It has been shown experimentally that amphipods consuming detrital rather than living *Spartina* spp. have higher survival and faster growth and sexual development
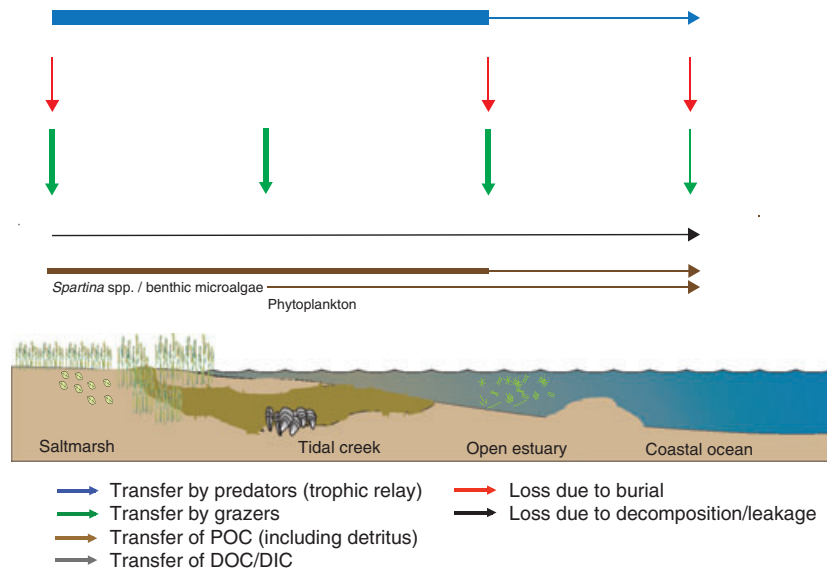
Fig. 2. Conceptual diagram of the relative magnitude and direction of the transfer of different carbon vectors across ecosystems in temperate saltmarshes. The colour of each line indicates the type of vector, while its thickness represents the relative importance of the vector. The arrow indicates the direction of flow of each vector. DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; POC, particulate organic carbon.

(Parker, Montoya & Hay, 2008). Macrophytes, however, are rarely the dominant source of carbon for animals living on the marsh (Haines, 1976). Rather, microalgae on the marshes seem to be more important (Sullivan & Moncreiff, 1990), but the relative contributions of saltmarsh macrophytes and microalgae to consumers vary among locations within estuaries and among taxa with different feeding modes (Peterson & Howarth, 1987).

Fish and crustacean migration from intertidal feeding areas in saltmarshes to deeper estuarine and offshore waters is an important vector for carbon transfer (Fig. 2). Transport can occur either through migration of nekton to offshore waters or through what is known as 'trophic relay', a series of predator-prey interactions that results in a net flow of carbon from marsh to estuary to coastal waters (Kneib, 1997). Migration commonly occurs in penaeid shrimps that reside in marshes in early juvenile stages and migrate to offshore waters for spawning (Kneib, 2003). There are numerous examples of potential trophic relay. On the Atlantic coast of the USA, killifish (*Fundulus* spp.) prey upon amphipods that have grazed on saltmarsh detritus, and are themselves eaten by larger piscivorous fish entering the marsh at high tide (Kneib, 1997; Parker *et al.*, 2008). In Australia, glassfish (*Ambassis* spp.) enter the marsh at high tide and eat large numbers of crab larvae produced by female shore crabs that gain their nutrition from the marsh (Hollingsworth & Connolly, 2006; Mazumder, Saintilan & Williams, 2006). Considerably more work is needed to quantify accurately the extent of export in different places, but it is already clear that export *via* vectors such as fish is important in these systems. Of the total annual fish production in a saltmarsh lagoon in Florida, it was estimated that 29% was directly exported by emigrating fish. Another 20% was consumed by piscivorous

fish, although because only a fraction (estimated at 10%) of that is converted to biomass in this next trophic level, this equates to about 2% transported from the lagoon as the piscivorous fish depart (Stevens, Montague & Sulak, 2006). The remainder of the fish production was either recycled within the lagoon (38%) or consumed by avian predators (13%). From an energy-budget perspective, the cycle is one of incoming fish larvae of low total biomass expanding in size by consuming intertidal primary production, and then exiting the marsh as a major stock of marsh carbon.

The extent of subsidy of estuarine food webs by saltmarsh carbon has not been precisely quantified because the large number of potential sources in estuaries makes tracing carbon pathways difficult. Carbon isotope studies of animals from open estuarine waters in USA and Korea have shown detectable but minor contributions of saltmarsh macrophytes, and a greater reliance on carbon from microalgae, originating either from the marsh flats or in the water column in the open estuary (Haines & Montague, 1979; Choy, An & Kang, 2008). However, a stronger contribution of carbon from fringing marsh vegetation was evident in the food web of a South African estuary, but only where terrestrial carbon from the river catchment was not flushed into the estuary by river flow (Vorwerk & Froneman, 2009). Whether saltmarsh carbon subsidises food webs in coastal waters beyond the estuary is less clear. We know from carbon budgets that carbon production in saltmarshes is enough to subsidise secondary production in coastal food webs (Lee, 1995). However, river plumes in coastal zones also include catchment and estuarine matter including POC, DOC and, perhaps more importantly, inorganic nitrogen, which potentially stimulates *in situ* carbon production by phytoplankton in the plume (Schlacher *et al.*, 2009). This is an active area

of research but is yet to result in definitive quantification of saltmarsh contributions (e.g. Darnaude, 2005).

IV. TEMPERATE FJORDS

(1) Definition and distribution of the system

The term fjord applies to glacially carved coastal estuaries that have been inundated with sea water since the last glacial maximum. In the Southern Hemisphere, temperate fjords occur predominantly in southern Chile, southern New Zealand and many of the sub-Antarctic islands, while in the Northern Hemisphere they occur in western Canada, Alaska (USA), Scotland, southern Norway and Denmark. Fjords are typically long and narrow, and characterised by steep topography, deep bathymetry, and the presence of a moraine-deposited sill at the entrance. These features, combined with the wave-sheltered environment and the presence of multiple sills within most fjords, promote retention of organic matter (Pickrill, 1980, 1987; Stanton & Pickard, 1981; Nuwer & Keil, 2005), resulting in most fjords being net carbon sinks (Pickard & Stanton, 1980; Nuwer & Keil, 2005). In addition, high rainfall of up to $8 \, \mathrm{m \, year^{-1}}$ (Naiman & Sibert, 1978; Sansom, 1984; Silva & Prego, 2002) provides optimum conditions for temperate rainforest production, and the subsequent flow of forest-derived organic matter into the fjord marine environment (Glasby, 1978; Nuwer & Keil, 2005; Sepúlveda *et al.*, 2009). Data on rates of primary production are limited, but temperate rainforests that cover the often extensive catchments of fjords can often exceed $0.65 \, \mathrm{kg \, C.m^{-2}.year^{-1}}$, while productivity of aquatic autotrophs can range up to nearly $2 \, \mathrm{kg \, C.m^{-2}.year^{-1}}$ (Table 1). This case study is concerned primarily with carbon flow in forested temperate fjords, and so will focus on those in New Zealand, Canada and Chile where extensive native forest remains (Scott, Mark & Sanderson, 1964; Silva & Prego, 2002; Vargas *et al.*, 2011)

(2) Main vectors of carbon

POC and DOC released from the forest vegetation form the main vectors for carbon flow across ecosystem boundaries between temperate forests and fjords (Fig. 3). Forest organic matter enters the fjords via fluvial transport of particulate and dissolved organic matter (Nuwer & Keil, 2005; Sepúlveda *et al.*, 2009; Silva, Vargas & Prego, 2011; Vargas *et al.*, 2011), and sudden deposition events such as landslides (St-Onge & Hillaire-Marcel, 2001; Timothy, Soon & Calvert, 2003). POC settles rapidly and is thus retained in fjord marine sediments in close proximity to the source (Fig. 3). Rates of sedimentation for temperate fjords range between 0.25 and $0.74 \, \mathrm{cm \, year^{-1}}$ (organic carbon sedimentation rate $30–35 \, \mathrm{g.m^{-2}.year^{-1}}$) in Chilean fjords (Sepúlveda *et al.*, 2005) and $0.08–0.43 \, \mathrm{cm.year^{-1}}$ in New Zealand fjords (Glasby, 1978). Although the composition of the organic component of these sediments is biased towards less biologically available sources, it is most likely that terrestrial organic matter is the largest source of organic carbon, particularly for sediments in close proximity to the head rivers of fjords (Peake, 1978; Pickrill, 1980; Nuwer & Keil, 2005; McLeod *et al.*, 2010*b*; Montero *et al.*, 2011; Sepúlveda, Pantoja & Hughen, 2011, Silva *et al.*, 2011). Alternatively, this over-representation of terrestrial organic matter in the sedimentary record could be due to preferential use of algal matter by marine microbes and invertebrates, due to its higher nutritional quality (Tenore, 1977, 1983; McCallister, Bauer & Canuel, 2006). Indeed, recent food-web studies using chemical approaches have demonstrated that production of phytoplankton and macroalgae typically support the majority of secondary production (Rodgers & Wing, 2008; Jack, Wing & McLeod, 2009; McLeod & Wing, 2009). Pelagic mean gross primary production in fjords in northern Patagonia has been estimated at $311 \, \mathrm{g \, C.m^{-2}.year^{-1}}$ (Sepúlveda *et al.*, 2011), with high seasonal variability due to spring and autumn blooms (Iriarte *et al.*, 2007). There is a paucity of data on the rates of macroalgal productivity in temperate fjords.

The extent of the subsidy of terrestrial POC to the fjord ecosystem is unknown, but there is evidence that it becomes available to higher trophic levels in the fjord food webs through direct consumption by zooplankton (Vargas *et al.*, 2011) and *via* bacterial assimilation (McLeod & Wing, 2007, 2009; McLeod, Wing & Davis, 2010*a*). In the Chilean fjords, terrestrial carbon can account for 20–50% of total carbon assimilation in copepods, during periods of low autochthonous algal production (Vargas *et al.*, 2011). While an increasing number of studies are demonstrating that heterotrophic marine bacteria preferentially assimilate marine algae over terrestrial organic matter (e.g. McCallister *et al.*, 2004), there is evidence that in the heads of the New Zealand fjords where terrestrial inputs of organic matter far outweigh autochthonous primary production, a fraction of this organic source pool is assimilated by heterotrophic bacteria (McLeod & Wing, 2009). This organic matter then becomes available to invertebrate consumers including deposit-feeding urchins and polychaetes (McLeod & Wing, 2009; McLeod *et al.*, 2010*b*). In anoxic sediments, fermentation of organic matter produces methane and hydrogen sulfide gases (Schlesinger, 1997) that are oxidized by free-living and endosymbiotic methanotrophic and chemoautotrophic bacteria to gain energy required to fix dissolved organic carbon (Cavanaugh, 1983; Zhang *et al.*, 2005). The source of the dissolved carbon is determined by the organic composition of the sediment, which in fjords with high sedimentation of terrestrial POC and relatively low marine algal sedimentation, is primarily of terrestrial origin (McLeod & Wing, 2007). In one of New Zealand's fjords, Doubtful Sound, invertebrate-chemoautotrophic bacterial symbioses are represented mostly by bivalve species in the families Solemyiidae and Manzanellidae (Brewin, Probert & Barker, 2008; McLeod *et al.*, 2010*a*). This chemosynthetically fixed carbon has been shown to supplement the diet of larger consumers within this fjord including fishes (McLeod &
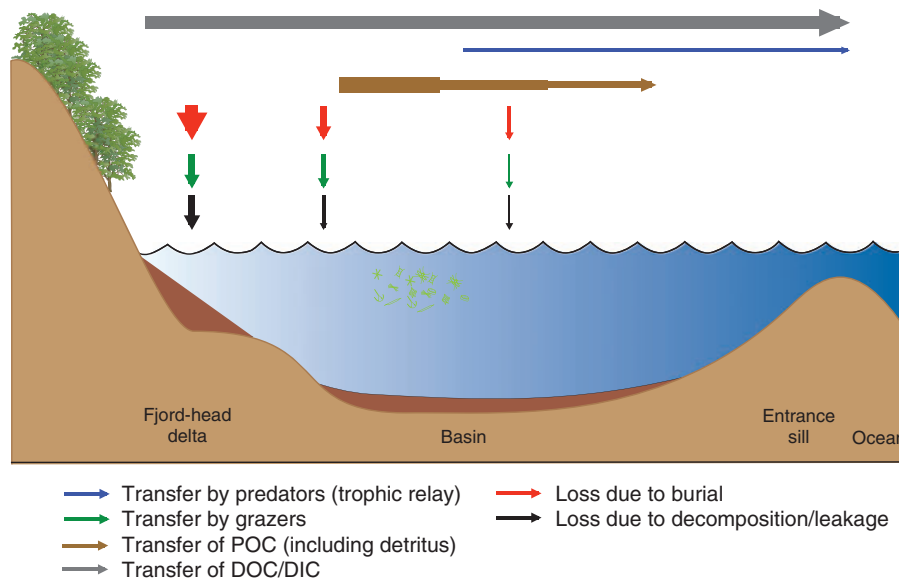
Fig. 3. Conceptual diagram of the relative magnitude and direction of the transfer of different carbon vectors across ecosystems in temperate fjords. The colour of each line indicates the type of vector, while its thickness represents the relative importance of the vector. The arrow indicates the direction of flow of each vector. DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; POC, particulate organic carbon.

Wing, 2007; Rodgers & Wing, 2008; McLeod *et al.*, 2010*a*) and rock lobsters (Jack *et al.*, 2009).

DOC, the other main vector of carbon flow from forests to fjords, is leached from soils and is often evidenced by tannin staining in surface waters. This dissolved organic matter comprises a significant form of terrestrial organic matter in temperate fjords surrounded by forest, and is considered to far outweigh POC inputs in temperate fjords in Canada (Naiman, 1982). However, there is limited evidence that this vector contributes to production in fjords, indicating a need for further research in this area. In highly stratified waters, DOC is constrained to the low-salinity surface layer, which flows seawards, suggesting that this terrestrial input is not retained within the fjord environment over long temporal scales. However, there is evidence that terrestrial DOC is absorbed by microbes and algae (McCallister *et al.*, 2004), thus potentially contributing to higher trophic levels in temperate fjords, but this influence is likely to be restricted to the upper reaches of the fjords (Cornelisen, Russell & Catriona, 2007).

There is scarce knowledge of the extent of exchange of organic carbon between fjords and adjacent coastal and oceanic ecosystems. Whilst there is evidence of high retention of terrestrial POC within the sheltered fjord environment (Silva *et al.*, 2011), larger floating pieces of wood are exported from fjords (Hinojosa, Rivadeneira & Thiel, 2011). Animals that migrate among terrestrial and marine environments, including some insect, fish, and seabird taxa, may also act as vectors of organic carbon across ecosystem boundaries. Whilst such carbon flux is increasingly well documented in the wider literature (e.g. Harding *et al.*, 2004; Heintz *et al.*, 2004; Romanuk & Levings, 2005), there appear to

be no fjord-specific studies. Movement of animals and algae between fjords and neighbouring habitats is likely to provide additional vectors for carbon flow and connectivity between ecosystems, although these vectors do not appear to have been quantified.

V. OPEN TEMPERATE COASTS

(1) Definition and distribution of the system

Temperate, open coasts are defined here as marine waters where light penetrates to the seabed allowing growth of vegetation (up to 30 m depth and up to 10 km from shore) but are not protected by land masses that surround other coastal systems such as estuaries and coastal lagoons. These ecosystems are typically dominated by algal reefs and seagrass meadows (Dayton, 1985). These reef and seagrass habitats are among the most productive ecosystems in the world, although they often occur in relatively exposed coastlines which otherwise have little *in situ* productivity. Productivity of macroalgae averages nearly 1 kg C.m^{-2}.year^{-1} (Table 1), but that of laminarian brown algae (kelp) can be as high as 3.5 kg C.m^{-2} year^{-1} (Kirkman, 1984; Krumhansl & Scheibling, 2012). Similarly, productivity of seagrasses averages nearly 0.5 kg C.m^{-2}.year^{-1} (Table 1), and when including epiphytes, can be as high as 1–6 kg C.m^{-2}.year^{-1} (Cambridge & Hocking, 1997; Kendrick *et al.*, 2002). Seagrass beds and algal reefs provide habitats for a high diversity of fauna, with macroalgae, including seagrass epiphytes, providing important food sources for primary consumers (Valentine & Duffy, 2006). However, the importance

of those high levels of productivity extends beyond the borders of each of those ecosystems. On average, export of macroalgae and seagrass is 0.35 and 0.22 kg C.m^{-2}.year^{-1}, respectively, compared to relatively negligible consumption and detrital deposition within reef systems (Table 1). Exported macroalgal and seagrass detritus has been detected in a range of marine ecosystems, including surf zones and beaches (e.g. Crawley, Hyndes & Ayvazian, 2006) and submarine canyons (e.g. Josselyn *et al.*, 1983), and beaches (Koop, Newell & Lucas, 1982; Ince *et al.*, 2007). In this case study, we focus particularly on detached macrophytes as a means of carbon transfer across ecosystem boundaries in open coasts of temperate regions of the world.

(2) Main vectors of carbon

The main vectors of carbon transfer in the open, temperate coastal seascapes are marine wrack (dead or dislodged macrophytes) and their consumers. The importance of seagrass and macroalgae as vectors of carbon flow across ecosystem boundaries (Fig. 4) is highlighted by the high deposition rates of this material, known as wrack, onto temperate beaches throughout the world. Estimates of deposition rates range from 140 to 520 kg.m^{-1}.year^{-1} in Canada, Chile and South Africa (Griffiths, Stenton-Dozey & Koop, 1983; Wildish, 1988; Piriz, Eyras & Rostagno, 2003; Orr *et al.*, 2005) to over 2000 kg.m^{-1}.year^{-1} in south-western Australia (Kirkman & Kendrick, 1997). Nearly 20% of marine primary production has been estimated to deposit on beaches in south-western Australia (Kirkman & Kendrick, 1997), and up to 7% of seagrass production on beaches in Spain (Mateo, 2010).

The direct flow of seagrass carbon into higher trophic levels through grazing is limited, at least under present conditions that lack the large vertebrate grazers through overharvesting (Valentine & Duffy, 2006). Instead, the transfer of seagrass-derived carbon is likely to be dependent on the detrital path or through DOC leakage of living seagrass. DOC is released from living or dead seagrass through leaching or cell lysis. Indeed, seagrasses can release 2–10% of their daily production to the water column as DOC (Robertson *et al.*, 1982; Velimirov, 1986; Ziegler & Benner, 1999*b*). Whole-system studies suggest that DOC fluxes from seagrass beds can account for almost all water column DOC, with one study suggesting this may be through direct leaching from seagrasses (Ziegler & Benner, 1999*a*) and another indicating that the majority is likely to originate from the sediment within the seagrass bed rather than living seagrass (Velimirov, 1986). It has been estimated that the DOC released from detritus in seagrass ecosystems can account for 71% of the total community production (Barrón & Duarte, 2009). Typically detritus releases greater levels of DOC than living tissue, presumably due to the additional contribution from cell lysis and mechanical degradation (Velimirov, 1986). An estimated 20–50% of the seagrass leaf carbon is lost per month during this decay phase (Newell, 1984; Harrison, Parslow & Conway, 1989; Peduzzi & Herndl, 1991; Pedersen, Berntsen & Lomstein, 1999).

Typically, there is a rapid loss of relatively bio-available DOC in the first few weeks following detachment of leaves (Maie *et al.*, 2006). The movement of seagrass leaves into other ecosystems and release of DOC will, therefore, provide a mechanism for carbon transfer to higher trophic levels in those systems, presumably *via* microbial processes.

Our understanding of the uptake of carbon from seagrass (and macroalgae) by microbial assemblages is limited, providing an important focus for future research. At the seagrass-bed scale, leached DOC is free to contribute to water column production, and can be rapidly assimilated by bacteria in the water column (Moriarty & Pollard, 1982; Moriarty, Iverson & Pollard, 1986; Chin-Leo & Benner, 1991; Ziegler & Benner, 1999*a,b*) with much of it being incorporated into bacterial aggregates that are then rapidly consumed by ciliates and flagellates (Robertson *et al.*, 1982). Seagrass-derived carbon can then flow to higher trophic levels (Fry *et al.*, 1982; Ziegler & Benner, 1999*a*), despite relatively minor amounts of direct grazing in modern seagrass systems (Valentine & Duffy, 2006). The role of microbes in the decomposition of seagrass and macroalgae is perhaps best known in beach-cast wrack, where several studies have examined their importance (see Colombini & Chelazzi, 2003). On a South African beach, bacteria have been estimated to account for nearly 90% of production (Koop & Griffiths, 1982), and for converting approximately 25% of carbon from stranded *Ecklonia maxima*. Bacteria will then support food webs on the beaches, or be returned to the sea to support surf-zone food webs. However, our understanding of the transfer of carbon from allochthonous seagrass or macroalgae material to other ecosystems *via* microbial processing clearly requires greater research effort.

With their high levels of primary production, erosion and dislodgement rates, various kelp taxa act as a major vector for the movement of organic matter from reefs to other systems. Particulate kelp can be removed from reefs through the erosion of thalli or dislodgement of whole thalli during storm events at average rates of 0.45 and 0.26 kg.m^{-1}.year^{-1}, respectively (Krumhansl & Scheibling, 2012). Dislodged material then forms either rafts on the ocean's surface (e.g. Hobday, 2000) or becomes deposited as wrack along shorelines (Orr *et al.*, 2005; Crawley *et al.*, 2009), in inshore subtidal habitats (Wernberg *et al.*, 2006), or in deep-sea canyons (Vetter & Dayton, 1998). Erosion rates of *Saccharina longicruris* and *Laminaria digitata* can reach 0.5 kg C.m^{-2}.year^{-1} and exceed phytoplankton production off the Atlantic coast near Novia Scotia (Krumhansl & Scheibling, 2011). Furthermore, since degradation rates of kelp can be high (Kirkman & Kendrick, 1997; Pederson *et al.*, 2005), the release of nutrients into the water column can be similarly high (Valiela *et al.*, 1997). In California, rafts of *Macrocystis pyrifera* have been estimated to provide local pulses of 0.5 kg C.m^{-2} to adjacent pelagic and benthic ecosystems (Hobday, 2000). Similarly, particulate *Ecklonia radiata* moving along the benthos in south-western Australia could provide up to 0.4–2.7 kg C.m^{-2}.year^{-1} to nearby shoreline systems based on annual estimates of 1.3–7.8 kg dry mass.m^{-2} of
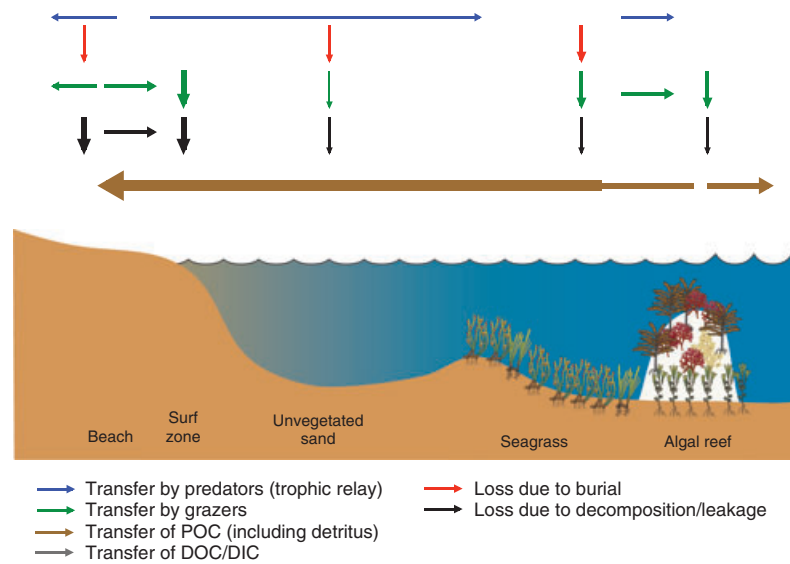
Fig. 4. Conceptual diagram of the relative magnitude and direction of the transfer of different carbon vectors across ecosystems in temperate open coasts. The colour of each line indicates the type of vector, while its thickness represents the relative importance of the vector. The arrow indicates the direction of flow of each vector. DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; POC, particulate organic carbon.

kelp wrack by Kirkman & Kendrick (1997). Since Kirkman & Kendrick (1997) also estimated kelp to take 15–23 days to travel from reefs to the shore, it would travel through a range of subtidal ecosystems, such as seagrass beds and unvegetated sand, prior to accumulating along the shoreline. Indeed, the uptake of dissolved organic nitrogen/dissolved inorganic nitrogen (DON/DIN) from *Ecklonia radiata* has been demonstrated for *Posidonia sinuosa* and its ephiphytes (Hyndes *et al.*, 2012), and both algae-derived DON and DIN can be taken up by other seagrass species (Van Engeland *et al.*, 2011). Through this process, nutrients released from allochthonous kelp would be available for consumption by mesograzers in those ecosystems, and potentially contribute to primary production in those benthic systems. A distinct difference between *M. pyrifera* and *E. radiata* is the absence of pnuematocysts on the latter kelp species, thereby producing a negative to neutrally buoyant vector flowing through benthic ecosystems. By contrast, the positive buoyancy of *M. pyrifera* leads to a greater flow, and possibly a faster dispersal, of nutrients through the pelagic ecosystem.

Inflow of kelp to shorelines strongly subsidises secondary production in surf-zones and lower beaches, particularly for isopods and amphipods (Griffiths *et al.*, 1983; Robertson & Lucas, 1983; Marsden, 1991; Bustamente, Branch & Eekhout, 1995; Crawley & Hyndes, 2007) which often are the dominant group of fauna in those recipient systems (50–90% of the surf-zone fauna in terms of abundance: Griffiths *et al.*, 1983; Robertson & Lucas, 1983; Pennings *et al.*, 2000; Crawley & Hyndes, 2007) and exhibit strong feeding preferences for kelp (Pennings *et al.*, 2000; Dugan *et al.*, 2003; Crawley & Hyndes, 2007). Insects, including beetles and flies, also consume kelp on beaches (e.g. Griffiths & Stenton-Dozey, 1981; Ince *et al.*, 2007; Mellbrand *et al.*,

2011). Less is known about the role of detrital kelp in sub-tidal ecosystems, but urchins and abalone on reefs appear to select drifting algae over their surrounding autochthonous resources (Vanderklift & Kendrick, 2005; Cornwall, Phillips & McNaught, 2009). Furthermore, particulate and/or dissolved organics from kelp have been shown to provide important food sources for filter and suspension feeders (Stuart, Field & Newell, 1982; Duggins, Simenstad & Estes, 1989), while particulate kelp can form a part of the diet for gastropod species in seagrass beds (Doropoulos *et al.*, 2009; Hyndes *et al.*, 2012). Mesograzers, therefore, play a pivotal role in transferring kelp-derived carbon to higher level consumers in a range of marine ecosystems, as well as in the coastal, terrestrial environment.

Nekton in surf zones and sub-tidal systems, and carnivorous beetles, spiders and birds form the main vectors for the transfer of kelp-derived carbon to other ecosystems (Fig. 4). In the surf zones of south-western Australia, amphipods contribute 80–90% of the diet of two dominant fish species (*Cnidoglanis macrocephalus* and *Pelsartia humeralis*; Lenanton, Robertson & Hansen, 1982; Crawley *et al.*, 2006). Since these species use the wrack in the surf zone as a nursery habitat prior to migrating to offshore habitats (Lenanton *et al.*, 1982), they constitute a major vector for carbon transfer among ecosystems. Unfortunately, since there is no quantification of the magnitude of those migrations offshore, the magnitude of subsidies *via* this vector is unknown. In terrestrial systems, abundances of shorebirds, such as plovers, sandpipers and turnstones, are strongly linked to biomass of beach-cast wrack and wrack-associated invertebrates (Colombini & Chelazzi, 2003). The high level of mobility of these avian predators would provide a vector for the transfer of marine-derived carbon to other terrestrial

ecosystems. Scorpions, spiders and mammalian scavengers also consume wrack-associated invertebrates (Colombini & Chelazzi, 2003) and would act as vectors for inland carbon transfer. Similarly, mobile consumers such as lobster (e.g. Phillips, 1983; Follesa *et al.*, 2011) can move large distances from their juvenile foraging habitats (e.g. rocky reefs) to distant habitats in open coasts, providing an additional pathway of carbon transfer across coastal seascapes.

VI. SYNTHESIS OF MECHANISMS FOR CARBON VECTORS

The four case studies above highlight a number of generalisable aspects of carbon transfer among coastal ecosystems, as well as some unique aspects. Biological vectors of carbon transfer can be grouped into two main categories: (*i*) detrital POC and its associated DOC, and DOC from living autotrophs in donor systems, that are transported passively through tidal or wind-generated currents or land run-off; and (*ii*) consumers (mainly nekton) that actively transport carbon through their feeding migrations or ontogenetic shifts in habitats associated with migratory patterns over their life histories.

The export of detrital POC provides an important vector for carbon transfer among ecosystems in coastal seascapes, with high proportions of NPP exported from seagrass beds, algal reefs and some mangroves (Table 1; Cebrian, 2002; Heck *et al.*, 2008; Bouillon & Connolly, 2009; Krumhansl & Scheibling, 2012) as POC. Wind- and tide-generated water movement can transport carbon over distances of tens to hundreds of meters (Wernberg *et al.*, 2006) to tens to hundreds of kilometers (Kirkman & Kendrick, 1997; Krumhansl & Scheibling, 2012). In comparison, movement of POC through tidal exchange can be limited in many mangroves (Granek *et al.*, 2009) or absent in saltmarsh systems (Taylor & Allanson, 1995), whereas transport of DOC from decomposition of material can be high. However, data on the export of DIC, and on the scale of movement of both DOC and DIC, are limited or lacking in all the systems we examined. Land run-off also plays a critical role in the transport of terrestrial POC and DOC into coastal systems, particularly in fjords (Sansom, 1984; Burrell, 1988; Silva & Prego, 2002), but the extent of the influence of these vectors is likely to be limited. Once imported into a recipient system, POC influences productivity *via* mesograzers (Crawley & Hyndes, 2007; Ince *et al.*, 2007), which are consumed by higher trophic levels, or the release of DOC from macrophytes that becomes available to microbial activity and uptake by microalgae or macrophytes (Berg & Jorgensen, 2006; Vonk *et al.*, 2008). Unfortunately, the relative magnitude of these fates and their effects on a recipient system is poorly understood due to their complexity, and requires further investigation.

Consumers form the second main group of vectors that actively transfer carbon across ecosystem boundaries, through their movement from one system to another for foraging activities or transition into different life-history phases. Movements can be through diurnal or tidal-cycle foraging migrations (e.g. Hollingsworth & Connolly, 2006; Heck *et al.*, 2008; Nagelkerken *et al.*, 2008*b*), or opportunistic foraging movements of macrograzers (Heinsohn *et al.*, 1977), over spatial scales of meters to thousands of meters (e.g. Guest *et al.*, 2004; MacArthur *et al.*, 2008; Nagelkerken *et al.*, 2008*b*). In comparison, the transfer of carbon through ontogenetic movements of nekton from 'nursery' to offshore adult habitats occurs over larger spatial scales of kilometers or more (Gillanders, 2006). Alternatively, the flow of carbon across systems can rely on a 'trophic relay' from systems such as saltmarshes, mangroves and seagrass beds based on a series of predator-prey interactions. However, the paucity of data on the magnitude of these movements, the predation rates on those vectors, or the uptake of DOC/DIC released through excretion in the recipient systems, makes it difficult to determine the size of any subsidy to neighbouring ecosystems.

VII. NATURAL FACTORS AFFECTING MAGNITUDE OF CARBON TRANSFER

In terms of natural factors, variation in the rates of primary production and in the proportion of this exported, consumed, decomposed, and accumulated material within each system will influence the rate and mechanism that leads to a subsidy in other systems. The NPP for a range of autotrophs in coastal systems is high, but also highly variable (Table 1). Relative levels of *in situ* consumption are high mainly for macroalgae (Poore *et al.*, 2012), whereas decomposition rates are high for several autotrophs including macroalgae, seagrasses, saltmarshes and mangroves (Table 1). Similarly, export rates of POC (including detritus) are high for macroalgae and seagrasses and can be high for mangroves (Table 1). In comparison to all other systems, saltmarshes have very high rates of detrital accumulation, with an average rate of $0.57 \, \mathrm{kg \, C.m^{-2} \, year^{-1}}$, although this is likely comparable to river deltas at the heads of forested fjords.

(1) Export

The magnitude of export of POC is highly variable (Table 1; Cebrian, 2002). Hydrodynamics and geomorphology play major roles in determining the magnitude of export of POC and DOC/DIC and the movement of nekton across coastal seascapes (Table 2, Fig. 5), although the relative importance of different hydrodynamic and geomorphological process varies among systems. For saltmarshes and mangroves, carbon transfer through POC or DOC/DIC depends heavily on river discharge, tidal amplitude, geomorphology and hydrodynamics of the estuary or bay, distance to and surface areas of adjacent or offshore habitats, and age of the wetland (Dame & Allen, 1996; Gattuso, Frankignoulle & Wollast, 1998). In seagrass beds and macroalgal reefs, storms and other severe weather events play a critical role in the removal and transport of POC in the form of living and detached seagrass leaves and other macrophyte material (Dame, 1982;

Table 2. Principal physical and biological factors that affect the magnitude of carbon vectors in recipient ecosystems

Factor	Impact on carbon vectors
Hydrodynamics	Increased river flow and tidal amplitude increases POC and/or DOC/DIC export from mangroves and saltmarshes.
	Storm events increase flow of POC export from algal reefs and seagrass beds.
	Increased rainfall (plus gravity) increases POC and/or DOC/DIC from land to coastal ecosystems, e.g. fjords.
Geomorphology	Increased size and decreased entrance of estuary decreases movement of POC and/or DOC/DIC to adjacent marine ecosystems.
Form of vector	DOC/DIC will advect into water column.
	Increased particle size of POC will lead to greater retention of POC in donor ecosystem, e.g. saltmarsh.
	Higher buoyancy of POC will increase transportation through water flow, e.g. different forms of kelp.
	Increased abundance of palatable plant sources (e.g. macroalgae) increases consumption by grazers.
Timescale	More rapid transport of POC from donor system will increase amount of DOC/DIC from POC in recipient systems.
Consumers	Increased microbial activity increases uptake of DOC, and subsequent release of DIC to autotrophs and consumption by consumers.
	Increase in abundance of grazers increases consumption of primary producers and transport of carbon.
	Increased nekton recruitment increases carbon consumption and export from donor system.
	Increase in foraging excursions by fish in donor system increases carbon export.

DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; POC, particulate organic carbon.
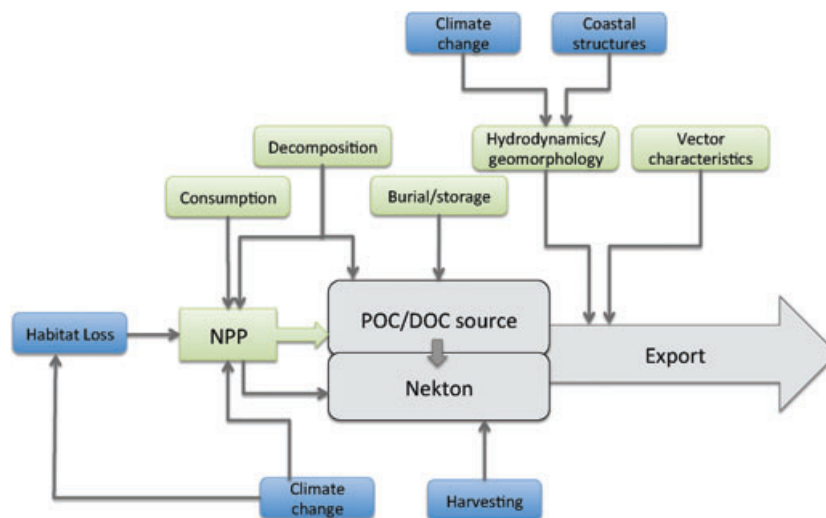

Fig. 5. Flow diagram of the main vectors (grey rectangles) exporting transporting carbon from one ecosystem to another, with the main natural processes (green) and human activities (blue) influencing the magnitude of those vectors transferring carbon from one system to another. DOC, dissolved organic carbon; NPP, net primary productivity; POC, particulate organic carbon.

Ochieng & Erftemeijer, 1999; Balestri, Vallerini & Lardicci, 2006). In forest–fjord systems, rainfall and catchment gradient affect the flow of forest detritus into fjords, with POC and DOC inputs varying in response to rainfall patterns and riverine discharge (Naiman & Sibert, 1978; Gonsior et al., 2008). While the export of POC in these systems is limited, the export of DOC may be much higher and appears to be influenced by stratification and density-driven circulation patterns driven by the amount of surface freshwater discharge into the fjord (Farmer & Freeland, 1983; Gonsior et al., 2008).

Export of carbon will also be influenced by the characteristics of the carbon vector (Table 2, Fig. 5). Dissolved carbon will freely advect into the water column (Wild et al., 2004) and move with tides or currents as discussed above. However, the transport of POC away from its source will be partly related to particle size and buoyancy. For example, since coarser POC

settles to the benthos close to its source in fjords (Glasby, 1978; Burrell, 1988; McLeod & Wing, 2009; McLeod et al., 2010b), it is unlikely that there is significant export of terrestrial POC from temperate fjords to the adjacent coastal zone, with the exception of floating wood (Hinojosa et al., 2011). In this case, the retention of terrestrial POC is likely to be a function of sill characteristics and exposure to ocean currents and swells for each fjord. Alternatively, the movement of large particles (e.g. seagrass or kelp) will depend on the buoyancy of detrital material once it is removed from the donor system. Seagrass propagules (fruits) can be highly buoyant and move large distances (Kendrick et al., 2012) before being consumed (Orth, Kendrick & Marion, 2007). Similarly, the kelp Macrocystis and Durvillaea are positively buoyant allowing them to be transported along the ocean surface (Fraser, Nikula & Waters, 2011), before sinking to benthic habitats (Harrold, Light &

Lisin, 1998). In comparison, *Ecklonia* is neutrally to negatively buoyant, restricting the movement of this detrital material to the benthic region. Thus, at least in the early stages after detachment, *Macrocystis* and *Durvillaea* are likely to play a greater role in providing nutrients and subsidising productivity in pelagic systems, while *Ecklonia* will influence benthic ecosystems until they become stranded along shorelines.

The relative rates of physical transport of POC, and the rates of biogeochemical transformation of that material will strongly influence the transport of DOC/DIC across ecosystem boundaries (Table 2, Fig. 5). For example, it is clear that high rates of DOC loss through leaching occur rapidly following detachment of macrophyte leaves or thalli (Maie *et al.*, 2006; Hyndes *et al.*, 2012). Thus, leaching of DOC will be greatest during the initial phase for detached macrophytes, followed by a phase of low release rates, and possibly of different compounds. How this timescale interacts with the timescale of transport will dictate the magnitude and type of DOC that adjacent habitats may receive. This relationship between the rate of the chemical/biological process and the transport rate has been examined elsewhere through the Damkholer number or similar approaches (rate of reaction/rate of transport), ranging from cases where transport processes dominate, to those where biogeochemical transformations dominate (Ocampo, Oldham & Sivapalan, 2006; Loveless & Oldham, 2010). In our case studies, this relationship among timescales of reaction and transport may be crucial in determining whether effective transport of carbon occurs and the form of carbon transferred. For example, when rates of transport of POC (e.g. seagrass leaves and macroalgae) exceed typical leaching rates, we might expect POC to pass through large spatial scales and release DOC over multiple ecosystems, whereas low transport rates are likely to result in larger quantities of DOC being released in fewer ecosystems closer to the source of POC. This also has implications on the release of DOC from systems such as saltmarshes, where rates of throughflow are likely to affect the advection of DOC into the water column and, therefore, the magnitude being exported. Unfortunately, there is almost no work documenting the rates of export and transport and relating these to the carbon chemistry of detritus or other biological processes.

(2) Grazing

The ability of carbon from autotrophs to enter the food web directly through grazing will influence the magnitude of carbon flow through the movement of consumers (nekton) from the donor system or the flow of POC to recipient systems where consumers assimilate carbon from the donor system (Table 2, Fig. 5). Macroalgae is readily consumed by a number of mesograzers, but direct consumption of saltmarsh, mangrove and seagrass by mesograzers is more limited, possibly due to the lower nutrient concentrations and higher levels of phenolics and lignin in these vascular plants (Tenore *et al.*, 1982). The food webs in coastal systems such as seagrass beds and saltmarshes are, therefore, often based on macroalgae or microalgae (Sullivan & Moncreiff, 1990;

Hyndes & Lavery, 2005) or the detrital pathway (Cebrian, 2002). However, the flow of carbon from POC will also enter the food web indirectly through microbial activity. For example, the strength of the flux of terrestrial organic matter to higher trophic levels in some New Zealand fjords is determined by the abundance of free-living bacteria and invertebrate-bacterial symbioses (McLeod & Wing, 2007, 2009; McLeod *et al.*, 2010*b*).

(3) Nekton movement

Since seagrass beds, mangroves and saltmarshes are often considered important nursery habitats for juvenile fish (Beck *et al.*, 2001), the subsequent movement of those fish to other coastal ecosystems can provide a major vector for carbon transfer within coastal seascapes. The magnitude of that vector will depend on the frequency of foraging excursions between ecosystems, and the number and size of individuals undertaking any habitat shifts for foraging or ontogenetic movements. Those excursions will also depend on the time of tidal inundations, which seems to determine the degree to which fish utilise resources in intertidal habitats such as mangroves, with the extremes ranging from no to complete dietary dependence on mangrove resources (Lugendo *et al.*, 2007). The extent of carbon transfer from seagrass beds, mangroves and saltmarshes in estuarine environments to other coastal systems appears highly variable and could depend on a few species. For example, many fish species in tropical estuaries and some temperate estuaries spend their entire life cycles in those systems (Potter & Hyndes, 1999; Blaber, 2009), which would limit the export of carbon through these vectors. However, some fish species display clear migrations from estuarine to open coastal systems (Gillanders, 2006; Verweij *et al.*, 2008), leading to export of carbon to those recipient systems. The extent of carbon transfer will therefore depend on the life-cycle characteristics of the nekton, particularly whether species that utilise the donor system undergo migrations to other coastal systems, as well as the mobility of the species which determines the distance of carbon transport from the donor to recipient system. Unfortunately, there has been no quantification of carbon export of this vector, despite the fact that several species of nekton are known to migrate from estuarine systems to other coastal systems and contribute significantly to the fisheries in those systems (Blaber, 2009).

VIII. ANTHROPOGENIC FACTORS AFFECTING MAGNITUDE OF CARBON TRANSFER

Human disturbances are likely to affect the direction and magnitude of detrital vectors, mainly through: (*i*) loss of habitat and NPP; (*ii*) climate change; (*iii*) coastal development, including structures that interfere with connectivity and habitat alteration; and (*iv*) fisheries overharvesting (Table 3, Fig. 5). It must, however, be recognised that these four broad types of disturbances are not mutually exclusive, and one can

Table 3. Principal anthropogenic stressors and their predicted impacts on vectors of carbon transfer across coastal seascapes

Stressor	Impact on carbon vectors
Habitat loss and alteration	Decrease in NPP decreasing the amount of POC and DOC/DIC exported to other ecosystems. Moderate fragmentation increasing edge effects and increasing some species abundances and increasing export through nekton emigration. Increased fragmentation reducing magnitude of nekton vectors.
Eutrophication	Alteration of type of autotroph, shifting the type of carbon vector from POC/DOC/DIC to nekton.
Construction of barriers to hydrodynamics	Dam construction reduces flow of fresh water through intertidal systems, decreasing nekton immigration and emigration, terrestrial carbon inputs, and degree of DOC/POC dispersal by riverine flow.
Climate change	
Increased temperature and CO$_2$	Reduction of geographic distribution for autotrophs with limited temperature range, reducing the magnitude of POC/DOC/DIC transported to other ecosystems. Increase in NPP due to elevated CO$_2$?
Increased storm events	Initially increasing transport of POC to other ecosystems, until donor system depleted due to more frequent storm events.
Sea level rises	Reduction in creek channels in intertidal ecosystems, reducing the immigration and emigration of nekton.
Increased rainfall	Increasing flow of terrestrial POC/DOC/DIC into coastal ecosystems.
Overfishing	Reduction in abundances of consumers, reducing the magnitude of nekton vectors among ecosystems.

DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; NPP, net primary productivity; POC, particulate organic carbon.

Table 4. Categories and values for consequence, likelihood and risk used in the risk assessment of human impacts on the magnitude of vectors within different coastal seascapes in Table 5

Consequence	Likelihood	Risk
0—Negligible	6—Likely; expected to occur	0; Negligible
1—Minor; rapid recovery if threat removed	5—Occasional; may occur sometimes	1–6; low
2—Moderate; recovery in months to years if threat removed	4—Possible	7–12; Moderate
3—Severe; recovery in years if threat removed	3—Unlikely	13–20; high
4—Major; recovery in years to decades if threat removed	2—Rare; may occur in exceptional circumstances	20–30; extreme
5—Catastrophic; recovery longer than decades or not at all	1—Remote; never heard of, but not impossible	—

Based on Fletcher (2005), consequence and likelihood were each assigned one of six ordinal levels depending on the severity of the consequence and the probability of that consequence occurring, respectively. The value for risk was calculated by multiplying the consequence and likelihood, allowing for the risk to be categorised into levels of risk from 'negligible' to 'extreme'.

exacerbate the impact of one or more of the others. To examine the effect of these human impacts on carbon transfer, we have adopted a qualitative risk-assessment process adapted from a formal approach used in a decision-making process for sustainable fisheries management (Fletcher, 2005). This process is based on identifying the risk (issue), consequence (impact) of that risk, and the likelihood (probability) of that consequence occurring on the main vectors for carbon transfer across coastal seascapes, namely nekton, POC and DOC/DIC. For each risk, the consequence and likelihood were assigned six ordinal levels, ranging from 0 (negligible) to 5 (catastrophic) for consequence, and 1 (remote) to 6 (likely) for likelihood. The value for each risk was calculated by multiplying the consequence and likelihood values, resulting in risk values (0–30) that were then categorised into 'negligible' to 'extreme' risk (Table 4; Fletcher, 2005).

(1) Loss of habitat

Anthropogenic-induced changes to NPP within particular regions are likely to affect the magnitude of export of NPP across ecosystem boundaries and, therefore, its potential to subsidise adjacent ecosystems (Fig. 5). There are numerous examples of direct and indirect removal of autotrophs through human disturbance, including massive losses of kelp forests (e.g. deforestation, Steneck *et al.*, 2002), seagrasses (e.g. eutrophication; Green & Short, 2003), mangroves (e.g. deforestation; Dodd & Ong, 2008), saltmarshes (Adam, 2002) and forests (e.g. timber harvesting/forest clearance; Ewers *et al.*, 2006), and this will influence a range of carbon vectors (Table 3). In the case of mangroves, 50% of the world's mangroves have been lost due to human pressure, and it has been predicted that mangrove forests will be rare by 2025 under current rates of decline (Dodd & Ong, 2008). Loss of mangrove forests would have high to extreme consequences on the export of carbon through a range of vectors, including POC and nekton (Table 5). Similarly, the loss or major alteration of NPP/habitat in temperate saltmarsh estuaries would have high to extreme negative consequences on nekton, but also on DOC/DIC since dissolved nutrients form a significant vector in these systems. In comparison, NPP/habitat loss in temperate fjords and open coasts is likely to have an extreme impact mainly on POC and/or DOC/DIC (Table 5) through the loss of the source of detrital material.

Table 5. Risk assessment of human impacts on the magnitude of vectors (nekton, POC and DOC/DIC) transferring carbon within different coastal seascapes, based on the consequence, likelihood and risk determined using criteria in Table 4

	Habitat/NPP loss and alteration	Eutrophication	Construction of barriers to hydrodynamics	Climate change	Overfishing
Tropical estuaries					
Nekton	E: C=4/L=5	M: C=2/L=5	M: C=3/L=3	M: C=3/L=4	E: C=4/L=6
POC	H: C=3/L=5	M: C=2/L=5	L: C=2/L=3	M: C=3/L=4	M: C=2/L=4
DOC/DIC	M: C=2/L=4	M: C=2/L=4	M: C=3/L=4	M: C=3/L=4	M: C=2/L=4
Temperate saltmarsh estuaries					
Nekton	E: C=4/L=5	M: C=2/L=5	M: C=2/L=5	M: C=3/L=4	E: C=4/L=6
POC	L: C=1/L=5	L: C=1/L=4	L: C=2/L=3	M: C=3/L=4	M: C=2/L=4
DOC/DIC	H: C=3/L=5	M: C=2/L=4	M: C=2/L=5	M: C=3/L=4	M: C=2/L=4
Temperate fjords					
Nekton	M: C=2/L=4	L: C=1/L=3	L: C=1/L=3	M: C=2/L=4	M: C=3/L=4
POC	E: C=4/L=5	L: C=1/L=3	L: C=1/L=3	E: C=5/L=4	L: C=0/L=4
DOC/DIC	E: C=4/L=5	L: C=1/L=3	L: C=1/L=3	E: C=5/L=4	L: C=0/L=4
Temperate open coasts					
Nekton	L: C=2/L=3	L: C=3/L=2	L: C=1/L=3	M: C=2/L=4	H: C=3/L=5
POC	E: C=4/L=5	M: C=4/L=2	L: C=1/L=3	E: C=5/L=4	L: C=2/L=3
DOC/DIC	M: C=2/L=4	M: C=2/L=4	L: C=1/L=3	H: C=4/L=4	L: C=2/L=3

Consequence (C): 0–5. Likelihood (L): 1–6. Risk: E = extreme; H = high; M = moderate; L = low/negligible. DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; POC, particulate organic carbon.

Of the causes of habitat loss and associated changes in NPP, eutrophication is noteworthy since it can influence both the magnitude of vectors and their form, with consequences for recipient habitats and the magnitude of subsidies. Eutrophication tends to shift the carbon base towards microalgae and macroalgae. For example, eutrophication of Oyster Harbour in Australia led to over 80% of the seagrass being lost since the late 1960s and replaced with the macroalgae *Cladophora albida* (Cambridge, Bastyan & Walker, 2002). Such changes also alter the associated animal communities, e.g. benthic to pelagic fish (Table 3) (Cloern, 2001) and are likely to change the use or fate of carbon within the altered region. Thus, excluding the anoxic and toxic effects of algal blooms in eutrophic systems, increased algal growth in these systems is likely to benefit some resident and migratory nekton, since macroalgae exhibits higher consumption rates than seagrass (Table 1). Eutrophication is likely to have a moderate to high impact on carbon flow in estuarine systems particularly (Table 5). However, through the increased food availability, nekton undertaking feeding migrations are likely to increase the proportion of carbon flow to recipient systems *via* their movements to other systems.

(2) Climate change

Climate change is likely to lead to spatial shifts in primary producers, but the potential impacts are complex and difficult to predict. For example, changes in CO_2 and temperature could increase or decrease productivity and distribution of seagrasses and saltmarshes, depending on the species (Table 3; Duarte *et al.*, 2008; Adam, 2002). By contrast, kelps are restricted to cold-water coastal zones, and global warming along with associated changes in dissolved CO_2 could shift the depth and geographic range of species within this group of macroalgae (Steneck *et al.*, 2002; Hepburn *et al.*, 2011). Climate change was considered to have an extreme impact on POC in open coasts (Table 5) since POC forms the major vector for carbon transport in this system. Imported kelp POC can play a critical role in the productivity of reef and adjacent ecosystems (Colombini & Chelazzi, 2003), and predicted changes in the latitudinal distribution of these and other primary producers (Hawkins *et al.*, 2009; Müller *et al.*, 2009; Brown *et al.*, 2010) is likely to have a profound negative effect on the magnitude of this carbon vector subsidising recipient systems in some regions. In addition, shifts in the distribution of some algal grazing species from tropical/warm temperate to cooler temperate regions (Johnson *et al.*, 2011), suggest that the flow of carbon through the grazing pathway could become more common.

Climate change is also expected to alter precipitation and the frequency and intensity of storm events (IPCC, 2007). Predicted increases in rainfall in higher latitude regions (IPCC, 2007) is likely to lead to increased terrestrial POC entering fjords and estuaries. The risk of an impact on subsidies to temperate fjords could be extreme (Table 5), in this case by increasing POC and DOC/DIC to recipient systems. In comparison, decreases in rainfall in mid latitudes (IPCC, 2007) are likely to decrease POC entering coastal systems. Through increased frequency and intensity of storm events, our risk assessment indicated a high to extreme impact on POC and DOC/DIC (Table 5) *via* effects on the dislodgement of seagrass leaves and kelp from the substrata and their subsequent transport to other ecosystems. This form of POC can be transported in large amounts to adjacent ecosystems (e.g. Mateo, Sanchez & Romero, 2003; Orr *et al.*, 2005; Wernberg *et al.*, 2006) where it is an

important base food source (Thresher *et al.*, 1992; Polis & Hurd, 1996; Crawley & Hyndes, 2007; Ince *et al.*, 2007). Changes in the magnitude of these vectors will likely impact on the productivity of many adjacent ecosystems. Initially, greater levels of POC could be transported to recipient systems, but the source of POC is likely to be depleted over time with continued frequency and intensity of storms.

Vectors in estuarine systems are likely to experience moderate effects of greenhouse gas emissions and climate change (Table 5). Rising sea levels and ocean acidification due to greenhouse gas emissions (IPCC, 2007) are likely to affect the migration of nekton into donor systems such as saltmarshes, potentially reducing the outflow of carbon *via* this vector. For example, rising sea levels may alter the creek systems present in saltmarshes that are utilised by fishes and reduce access to their nursery areas, thereby reducing the export of carbon. However, the timeframe and magnitude of this impact are difficult to predict due to the uncertainty about the long-term response of saltmarshes to rising sea levels. Ocean acidification negatively affects olfactory capabilities of larval fish by disrupting avoidance behaviour to predators and inhibiting attraction to cues from adult reef habitat (Munday *et al.*, 2009, 2010). This could lead to lower survival and recruitment of larval fish, which would impact on the ability of fish to export carbon derived from those nursery systems to other coastal ecosystems.

(3) Construction of barriers to hydrodynamics

Construction of barriers that alter hydrodynamic conditions present a variety of impacts on potential carbon exchanges, with moderate risk on nekton and DOC/DIC in estuarine systems (Table 5). Damming and channelisation of rivers affect river outflow (total load, amplitude and timing) and therefore the magnitude particularly of DOC/DIC vectors from terrestrial to coastal systems (Table 3). Similarly, changes to estuary openings (as well as habitat fragmentation) could lead to a loss of dispersal corridors (Layman *et al.*, 2011), altering the magnitude of carbon transfer beyond the estuarine system (Tables 3 and 5). In comparison, habitat fragmentation can initially increase the magnitude of carbon flow from donor systems, but continued fragmentation beyond a critical point is likely to reduce that flow. For example, in saltmarshes of the Gulf of Mexico, changed river flow, sediment subsidence and sea-level rise, have shifted continuous saltmarsh habitat into fragmented patches. Modeling by Haas *et al.* (2004) predicts that abundances of juvenile penaeid shrimp will increase, since they preferentially use only the marsh edge, and any fragmentation will initially increase edge habitat. Such an increase in shrimp abundances will presumably transport more carbon from intertidal marshes to offshore coastal waters, mostly through direct ontogenetic migration. However, with further subsidence and/or sea level rise, the total marsh area may become so small that shrimp numbers decline (Haas *et al.*, 2004), at which point carbon flow to offshore waters by nekton migration will be much reduced.

(4) Overharvesting

Overharvesting of fish has occurred at a global scale (Jackson *et al.*, 2002), and this will have a extreme to moderate risk of a negative impact particularly on the nekton vector of carbon transfer predominantly in estuarine systems (Tables 3 and 5). First, reduction in total biomass of some key species (e.g. penaeid shrimp) is likely to reduce trophic transfer by reducing the magnitude of emigration from saltmarshes (see example by Kneib, 2003, in Section III). Second, harvesting of larger piscivores that form the later stages of trophic relays (e.g. Sheaves & Molony, 2000) is likely to interrupt the links in those trophic relays of carbon from saltmarsh, mangrove or seagrass systems. Additionally, overharvesting of high-level predators leads to top-down effects increasing grazing rates and loss of kelp beds (Krumhansl & Scheibling, 2012) or a reduction of risk effects (Heithaus *et al.*, 2008), where mesoconsumers alter their shelter-seeking behaviour leading to changes in feeding migration patterns. Both will affect the magnitudes or directions of carbon transfer. Alternatively, declines in the abundances of large grazers such as turtles and dugongs through over-hunting (Jackson *et al.*, 2001) has almost certainly affected the amount of carbon ingested and transported from tropical seagrass beds to other coastal ecosystems *via* this vector. Thus, overharvesting of consumers is likely to have an extreme negative impact on nekton vectors, and therefore, subsidies in recipient systems, particularly in estuaries (Table 5). However, the magnitude of, and mechanism for, the impact will depend on the trophic level and movement patterns of the consumers being harvested. The growth of intensive aquaculture presents a similar risk. Naylor *et al.* (2000) described the strong relationship between intensive aquaculture production and the increased pressure this places on lower trophic level fish, for use as fishmeal in food pellets. This is fundamentally altering the food-web structure but also depleting pelagic species that are capable of long-distance movement and transfer of carbon.

IX. CONCLUSIONS

(1) Particulate and dissolved carbon, along with nekton, provide major vectors of carbon transfer across ecosystems within seascapes, and water movement plays a major role in facilitating the transfer of carbon regardless of the vector (including nekton). However, the relative importance of those vectors differs among systems and the main types of primary producers present in those systems. POC and DOC/DIC are the main vectors for open coastal systems and temperate fjords, relying on storm surges to transport kelp and sometimes seagrasses to other open coastal ecosystems, and land run-off to import forest POC into temperate fjords. In comparison, nekton appears to provide the main form of carbon transfer from mangroves and saltmarshes in bays and estuarine systems, where tidal movement is pivotal to the movement of that vector. Unfortunately, there is limited capacity to quantify the relative importance of these vectors

of carbon transfer to recipient ecosystems, as estimates of carbon exchange between systems are limited in mangrove and saltmarsh systems (see Taylor & Allanson, 1995; Bouillon *et al.*, 2008*a*) and absent in temperate fjords and open coastal systems. In the case of nekton, carbon transfer has generally been inferred through stable isotope approaches for a range of systems (Hyndes & Lavery, 2005; Kruitwagen *et al.*, 2010). While these provide valuable insight into the direction of carbon flow and the relative importance of different sources of production to consumers, they provide limited insight into the amount of carbon being transferred.

(2) Being able to quantify the movement of carbon across ecosystems is pivotal to gaining an understanding of the level of influence that carbon from one system (e.g. mangrove or kelp forest) has on productivity in other ecosystems in the seascape. However, a recent review by Marczak *et al.* (2007) showed that out of 28 studies that had quantified a subsidy, almost all were based on vectors moving from freshwater to other freshwater systems, freshwater to terrestrial systems or marine to terrestrial systems, and only two examined vectors between marine systems. Our broad ecological understanding of resource subsidies will benefit from a closer inspection of processes in marine seascapes, as our review demonstrates a range of vectors (nekton and dissolved carbon) and mechanisms that influence potential subsidies (water and nekton movement).

(3) Barbier *et al.* (2011) demonstrated the value of the ecosystem services provided by seagrasses, saltmarshes and mangroves. Amongst other services, those systems play significant roles in coastal protection, carbon sequestration and fisheries production in many regions of the world and contribute significantly to the economies in those regions (Barbier *et al.*, 2011). We argue that the value of those habitats, as well as other habitats we examined (e.g. kelp forests and temperate terrestrial forest adjacent to fjords), extends well beyond the ecosystem boundaries and can influence production in other ecosystems tens to hundreds of kilometers away. Barbier *et al.* (2011) recognised that assessments of ecosystem services often ignore important services such as cross-ecosystem transfer of nutrients. This cross-ecosystem service is often recognised in discussions regarding fish utilisation of nursery habitats and their subsequent recruitment into coastal fisheries further offshore, yet our review highlights their role as a major vector of carbon transfer to sustain other systems. POC and DOC/DIC form other important vectors of carbon transfer from coastal systems. For example, up to 80 and 50% of seagrass and kelp production, respectively, is transported from seagrass meadows or kelp beds as POC to a range of coastal systems (Heck *et al.*, 2008; Krumhansl & Scheibling, 2012), where it can provide a multitude of ecosystem services including shoreline stabilisation (Mateo *et al.*, 2003) and shelter from predation for nekton (Crawley *et al.*, 2006).

(4) Through our review, we have been able to identify the most significant risks to the integrity of the transfer of carbon and subsequent subsidies to other ecosystems, but our risk assessment suggests different risk profiles for different ecosystem types. For tropical estuaries, loss of habitat and its associated NPP, and overfishing, have been identified as the greatest risks to carbon transfer, with nekton the most likely vector to be severely affected. The same threats are most significant for temperate saltmarsh estuaries, but in this case, both nekton and dissolved nutrients are likely to be the main vectors affected. By contrast, habitat/NPP loss and climate change are likely to be the major risks to carbon transfer in temperate fjords, albeit with different trajectories. Loss of forest in their catchments will have obvious negative effects on detrital (POC) and dissolved nutrient (DOC/DIC) inputs to the systems, whereas the strong association between climate change and increased precipitation in temperate fjords suggest that detritus and dissolved nutrients will increase with climate change. Finally, the greatest risks for temperate open coasts are habitat/NPP loss and climate change, with the greatest risks to the POC vector through negative impacts on the source of detrital material (seagrass and macroalgae). Clearly, in order to mitigate any anthropogenic impacts on coastal systems and the ecosystem services they provide, there is a need to understand those processes that provide connectivity and subsidies across coastal seascapes, yet there is limited quantification of the effects of these vectors on recipient systems. It is only through quantifying those subsidies, that we can effectively incorporate complex interactions into the management of the marine environment and its resources.

X. ACKNOWLEDGEMENTS

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