

MINIREVIEW

Trophic Transfers from Seagrass Meadows Subsidize Diverse Marine and Terrestrial Consumers

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ABSTRACT

In many coastal locations, seagrass meadows are part of a greater seascape that includes both marine and terrestrial elements, each linked to the other via the foraging patterns of consumers (both predators and herbivores), and the passive drift of seagrass propagules, leaves, roots and rhizomes, and seagrass-associated macroalgal detritus. With seagrasses declining in many regions, the linkages between seagrass meadows and other habitats are being altered and diminished. Thus, it is timely to summarize what is known about the prevalence and magnitude of cross-habitat exchanges of seagrass-derived energy and materials, and to increase awareness of the importance of seagrasses to adjacent and even distant habitats. To do so we examined the literature on the extent and importance of exchanges of biomass between seagrass

meadows and other habitats, both in the form of exported seagrass biomass as well as transfers of animal biomass via migration. Data were most abundant for Caribbean coral reefs and Australian beaches, and organisms for which there were quantitative estimates included Caribbean fishes and North American migratory waterfowl. Overall, data from the studies we reviewed clearly showed that seagrass ecosystems provide a large subsidy to both near and distant locations through the export of particulate organic matter and living plant and animal biomass. The consequences of continuing seagrass decline thus extend far beyond the areas where seagrasses grow.

Key words: seagrass; connectivity; trophic subsidy; consumers.

INTRODUCTION

Ecologists increasingly recognize that ecosystems are open and interconnected. Both the passive and active transport of materials via advective processes,

propagule dispersal, and active foraging migrations inextricably link many ecological assemblages across boundaries. Movement of nutrients, detritus, prey, and consumers between ecosystems can have major effects on food web structure and productivity, especially in places with little or no in situ primary production (for example, caves, mountaintops, central ocean gyres, and the deep sea—see

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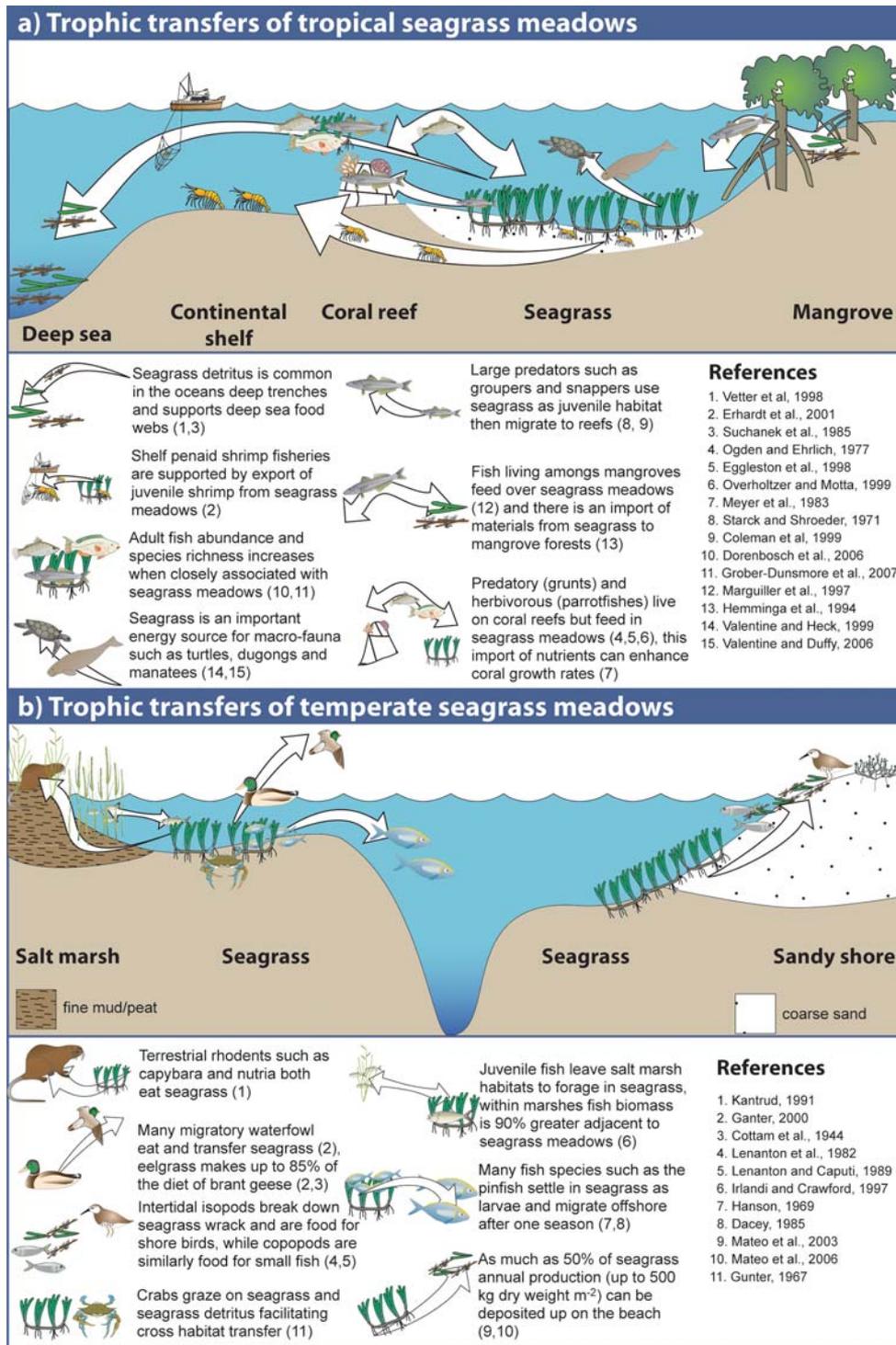


Figure 1. Conceptual diagram detailing trophic transfers from seagrass meadows as well as connectivity between seagrass meadows and marine and terrestrial habitats in (a) tropical and (b) temperate regions.

Vetter 1994, 1998; Polis and Strong 1996; Persson and others 1996; Rose and Polis 1998).

The high degree of cross-habitat biomass and energy transfer in many marine ecosystems has long been recognized. For example, as Beck and others (2001) noted, some of the earliest examples of

marine cross-habitat transfers were reported nearly a century ago. These studies emphasized taxa with complex life cycles, such as portunid crabs, penaeid shrimp, and a number of species of finfish, whose larvae were transported from offshore spawning areas to estuaries where they subsequently metamorphosed and grew rapidly before returning off-

shore to adult habitats in the fall (Hay 1905; Hildebrand and Schroeder 1928). The concept of the entire estuary as a “nursery” for juvenile finfish and shellfish pervaded the literature for decades and was considered a law (Gunter 1967). As research expanded, especially studies with more detailed and sophisticated investigations of larval transport, habitat use, and predator–prey dynamics, a heightened appreciation for the importance of shallow vegetated habitats such as marshes and seagrass meadows as “nurseries” developed, primarily because of the much greater densities of juvenile finfish and shellfish that vegetated habitats supported (Turner 1977; Orth and others 1984; Minello 1999).

Seagrass meadows have very high levels of primary production, owing to the high turnover of seagrass leaves themselves and their associated epiphytes (Orth and others 2006). In addition, they provide habitat for a diverse assemblage of invertebrates and fishes (Williams and Heck 2001). Thus, there are a variety of potential pathways linking seagrasses and other marine and terrestrial habitats. For example, although living seagrass leaves are commonly consumed, they remain uneaten in many areas, at least in recent times (see below), and directly enter the detrital pool. Seagrass and seagrass-associated macroalgal detritus can then be transported passively by currents and waves (Robertson and Lucas 1983; Hemminga and others 1994), in some cases over extensive distances (Wolff 1980; Suchanek and others 1985). On route, and where ultimately deposited, they provide habitat structure and trophic subsidy (Thresher and others 1992; Ochieng and Erftemeijer 1999; see review by Mateo and others 2006). Accumulations of detritus can support consumers in areas such as deep-sea canyons (Vetter 1994, 1998), where detrital inputs are likely to be most important because primary production is low and habitat structure is limited (Kirkman and Kendrick 1997).

Living seagrass leaves are also an important pathway for habitat linkages, providing an important source of energy for both residents (for example, sea urchins, turtles, dugongs, and manatees) and transients (for example, waterfowl) in coastal food webs in the Caribbean and Mediterranean Seas, as well as in the Indian and Pacific Oceans (summarized in Valentine and Heck 1999; Valentine and Duffy 2006). The abundance and secondary production of small seagrass-associated invertebrates and fishes rival or exceed the highest estimates reported from other marine communities (Valentine and Heck 1993). However, the current understanding is that algal, not seagrass, carbon is the source of energy for most of these small

seagrass-associated animals. This means that the primary production of algae growing on and among seagrass leaves is regularly consumed by small animals and then becomes available for export in the biomass of intermediate trophic levels (for example, isopods, decapods, gastropods, and small fishes, see Orth and others 1984; Greenway 1995; Williams and Heck 2001; Figure 1) that are consumed by larger finfish that visit the seagrass meadows to forage. Thus, the potential for the transfer of secondary production from seagrass meadows to higher-order predators is very high, and we include information on this trophic pathway when possible.

The decline of seagrasses in many regions of the earth (Orth and others 2006), combined with losses of large consumers (Jackson and others 2001), has undoubtedly altered linkages between marine habitats. Thus, it is timely to summarize the prevalence and magnitude of various cross-habitat exchanges, to increase awareness of the importance of seagrasses to adjacent and even distant habitats, and to outline pertinent questions for future research. Whereas many of the examples we discuss are known by seagrass biologists and estuarine ecologists, to date they have not been considered as a whole and their broader implications assessed. Here we examine the magnitude and importance of exchanges of biomass between seagrass meadows and other oceanic habitats and between seagrass meadows and terrestrial habitats, both in the form of exported seagrass biomass as well as transfers of animal biomass between habitats. Habitats for which the best data exist are Caribbean coral reefs, and organisms for which there are quantitative estimates include Caribbean fishes and migratory waterfowl. In addition, a relatively small number of studies have quantified the export of seagrass detritus in other locations around the world and we report the magnitude of these estimates. We also report on the limited number of studies that have estimated the export of dissolved organic matter from seagrass leaves, roots, and rhizomes. Data from the studies we review clearly show that seagrass ecosystems provide a large energy and nutrient subsidy to near and distant locations through the export of particulate and dissolved organic matter and of living plant and animal biomass. The consequences of seagrass decline thus can extend far beyond the areas where seagrasses grow. Surprisingly, this has only recently been recognized by marine conservation biologists who now have begun to argue for the inclusion of seagrass meadows in Marine Protected Areas (MPAs) designed to preserve coral reefs in the Western Atlantic Ocean (Grober-Dunsmore and others 2007).

EXPORT OF SEAGRASS DETRITUS AND DISSOLVED ORGANIC MATTER

Despite abundant qualitative evidence for the trophic importance of detrital export from seagrass meadows, relatively few quantitative estimates of the magnitude of detrital fluxes exist, and these exist primarily for meadows in North America, the Caribbean, and Europe (Figure 2). This is likely due

to the difficulty in quantifying fluxes in open systems such as those in which most seagrass meadows occur (Mateo and others 2006). Existing estimates of export range from 0% to 100% of total production, and from 10% to 60% of leaf production (summarized by Mateo and others 2006; Table 1), depending on physical processes and bottom topography, with a mean value of around 15% of net primary production exported. The

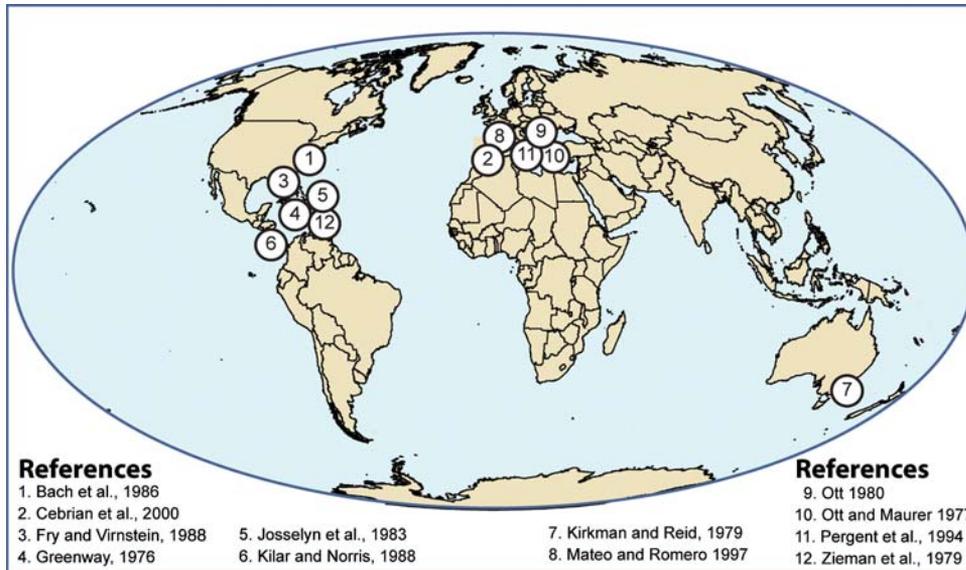


Figure 2. Location of studies in Table 1 that provide quantitative estimates of both the magnitude and percentage of exported seagrass production.

Table 1. References Containing Estimates of both the Amounts ($\text{gCm}^{-2} \text{ year}^{-1}$) and Percentages of Net Primary Productivity (NPP) Exported from Various Types of Seagrass Meadows.

Source	Seagrass species	$\text{gCm}^{-2} \text{ year}^{-1}$ exported	%NPP exported
Bach and others (1986)	<i>Zostera marina</i>	43.80	6.74
Bach and others (1986)	<i>Z. marina</i>	9.12	1.70
Bach and others (1986)	<i>Z. marina</i>	73.00	20.00
Bach and others (1986)	<i>Z. marina</i>	7.30	1.07
Bach and others (1986)	<i>Z. marina</i>	24.45	7.00
Cebrian and others (2000)	<i>Cymodocea nodosa</i>	83.95	29.11
Fry and Virnstein (1988)	<i>Syringodium filiforme</i>	124.10	47.24
Greenway (1976)	<i>Thalassia testudinum</i>	87.60	9.99
Josselyn and others (1983)	<i>T. testudinum</i>	11.68	24.75
Josselyn and others (1983)	<i>T. testudinum</i>	15.33	3.89
Kilar and Norris (1988)	<i>T. testudinum</i>	135.05	48.23
Kirkman and Reid (1979)	<i>Posidonia australis</i>	18.61	11.60
Mateo and Romero (1997)	<i>Posidonia oceanica</i>	24.00	7.32
Mateo and Romero (1997)	<i>P. oceanica</i>	5.00	4.55
Ott (1980)	<i>P. oceanica</i>	682.55	54.92
Ott and Maurer (1977)	<i>P. oceanica</i>	175.20	31.55
Pergent and others (1994)	<i>P. oceanica</i>	40.15	21.09
Zieman and others (1979)	<i>Thalassia testudinum</i>	4.01	1.02
Zieman and others (1979)	<i>Syringodium filiforme</i>	36.50	77.34

These data are the actual values used to plot Figure 3(c and d) of Mateo and others (2006)

largest fluxes measured have been between seagrass meadows and nearby sandy beaches. Supply rates of seagrass detritus have been estimated by Ochieng and Erftemeijer (1999) and Coupland and others (2007) to range from 30 to 400 kg wet weight per meter of beach per year. In the Spanish Mediterranean deposits ranged from 18 to 500 kg DW m⁻², which, depending on the time required for detrital decomposition, could represent as much as 50% of the meadow's annual dry weight production (Mateo and others 2003, 2006). Export of seagrass detritus occurs in other areas as well, and has been documented in temperate eelgrass beds in North Carolina (USA) by Bach and others (1986) and in Caribbean seagrass meadows by Zieman and others (1979), who found that only a small amount of turtlegrass (*Thalassia testudinum*) was exported from the study site, whereas more than 75% of manatee grass (*Syringodium filiforme*) was exported (Table 1). Although these studies did not quantify the contribution of seagrass detritus to destination habitats in the way Mateo and others (2003, 2006) did, they nevertheless showed substantial export of seagrass production from source meadows. In addition, quantitative monthly estimates of seagrass export from a Panamanian back reef of approximately 1.5 ha ranged from 37 to 294 kg mo⁻¹ over a 15-month period (Kilar and Norris 1988), indicating a large export from shallow water to the open waters of the Caribbean Sea (Table 1).

Seagrass detrital export also plays an important role in the global ocean carbon cycle. Although seagrass carbon contributes only around 20% of the total amount of carbon buried by marine vascular plants, the absolute mass represents an enormous transfer of organic carbon and nutrients to the coastal ocean that can and does fuel the growth and reproduction of a wide array of consumers (Duarte and others 2005).

Seagrasses excrete dissolved organic carbon (DOC) from living leaves, rhizomes, and roots, and leach DOC from decomposing tissues. A review of what little is known about rates of DOC release from seagrasses by Marba and others (2006) showed that DOC release varies seasonally, and reaches a maximum in summer (Ziegler and Benner 1999). Most studies indicate that seagrass meadows are net sources of DOC to both the water column and sediment pore waters (Marba and others 2006), and that microbial activity is enhanced in both the water column and in the rhizosphere (Holmer and others 2001) by DOC released from seagrass tissues. However, the relative importance of seagrass-derived DOC in nutrient cycling and secondary production has not yet

been quantified, although it seems likely to play an important role in coastal biogeochemistry (Marba and others 2006).

SEAGRASS MEADOWS HAVE STRONG LINKS TO OTHER COASTAL HABITATS

In assembling information on the frequency and magnitude of biomass transfers between seagrass meadows and other coastal habitats, we first reviewed studies in Gillanders and others (2003), which focused on connections between juvenile and adult habitats of mobile marine fishes and invertebrates. To gather recent papers we also searched the Web of Science from 2000 to 2006 using the key words provided in Gillanders and others (2003) as well as seagrass connectivity, seagrasses-(other habitat). In addition, we relied heavily on our collective library resources to supplement our literature searches. Although many qualitative examples of connectivity between seagrass meadows and other habitats are reported in the literature, it is somewhat surprising that there are only a few quantitative estimates of the transfer of consumer biomass from seagrass meadows to other habitats (Gillanders 2006). The global loss of seagrass meadows dictates that efforts to develop such estimates should be a priority for seagrass researchers.

Coral Reefs

The structure and function of coral reef communities is enhanced when they are adjacent and connected to seagrass beds. Early studies of coral reef ecosystems found that most reef fishes were carnivores whose biomass was 3–4 times greater than that of herbivorous fishes (Bakus 1969; Goldman and Talbot 1976; Polunin 1996). Such inverted food webs suggested that predators must have foraged in other habitats to meet their nutritional needs. Early studies of the feeding habits of fishes demonstrated the trophic connectivity between reefs and seagrass meadows, which has been best documented in the western Atlantic (for example, Randall 1965, 1967); however, similar connectivity is also known from other areas, suggesting it might be a general phenomenon. For example, many coral reef fish species have long been known to forage daily on seagrasses, algae, and small invertebrates and fishes in adjacent seagrass meadows (Ogden 1980). Many reef herbivores that shelter on western Atlantic coral reefs forage on algae and seagrasses in the adjacent seagrass meadows, and many predatory fishes leave

the reef and forage on the very large secondary production in nearby structurally simpler seagrass meadows (Meyer and others 1983; Zieman and others 1984; McAfee and Morgan 1996; Figure 1a). Most common are predatory species in the family Haemulidae (grunts) and herbivores in the family Labridae (parrotfishes), but many other taxa, including those not usually thought of as relying on seagrass meadows, such as moray eels (Muraenidae) and squirrelfish (Holocentridae), forage in seagrass meadows at night (Heck and Weinstein 1989). These migrations of foraging animals thus constitute a major energetic linkage between coral reefs and seagrass meadows and contribute to maintaining high fish biomass on coral reefs adjacent to seagrass meadows.

The fish-mediated connectivity between seagrass meadows and coral reefs can also result in a significant enhancement of the growth rates of dominant reef-building corals. Caribbean grunts, upon return to their resting spots on the reef, provide an important trophic subsidy to corals, whose growth is increased by nutrients deposited in the form of feces from grunts (see Meyer and Schultz 1985a, b). It is likely that green turtles, which feed in seagrass meadows but move to coral reefs to sleep between foraging bouts, also mediate a similar enhancement, although this has not yet been documented.

In addition, there are many species of larger predators, including the gray (*Lutjanus griseus*), lane (*L. synagris*), and dog (*L. jocu*) snappers, as well as groupers such as the Nassau (*Epinephelus striatus*) and gag (*Mycteroperca microlepis*) that often use western Atlantic seagrass meadows as juvenile habitat, and after reaching sizes of around 0.3 m standard length (SL) take up residence on reefs, thereby transferring the biomass they have accumulated from seagrass meadows to reefs (Starck and Schroeder 1971; Coleman and others 1999; Figure 1a).

These examples demonstrate that coral reefs are strongly linked trophically to seagrass meadows when they exist in proximity. This trophic connectivity was verified by Nagelkerken and colleagues, who used stable isotope analyses supplemented by visual censuses to show that near several islands in the southern Caribbean juvenile coral reef fish foraged in seagrass meadows as well as mangrove channels (Nagelkerken and van der Velde 2004a, b). In addition, they showed that adult fish abundances, species richness and composition were positively associated with this connectivity and the presence of adjacent seagrass meadows (Nagelkerken and others 2001, 2002;

Figure 1a). Similar patterns also appear to hold for reefs adjacent to seagrass meadows in East Africa (Dorenbosch and others 2005, 2006; Lugendo and others 2005). Thus, as Randall (1965) noted more than four decades ago, and Grober-Dunsmore and others (2007) recently confirmed, reefs in close contact with seagrass meadows support predatory fish biomasses far in excess of those reefs that are isolated from seagrass meadows.

Mangrove Forests, Marshes, Mud Flats, and Oyster Reefs

Similar to their strong association with coral reefs, seagrass meadows are also linked through foraging fishes to other coastal wetlands such as mangroves in tropical regions and salt marshes in temperate regions. For example, Marguillier and others (1997) used stable isotope analyses to assess the food resources of a suite of carnivorous fishes and concluded that even though mangrove creeks in Kenya are rich in detritus and secondary production, creek-dwelling animals were doing the bulk of their foraging on prey in seagrass meadows seaward of the mangrove creek mouths. Seagrass carbon was also identified isotopically in mangrove forests in Eastern Africa, indicating a reverse flux of materials from the subtidal seagrass meadows to the intertidal mangrove forest (Hemminga and others 1994).

Although less well studied than some tropical regions, temperate seagrass beds are connected to a variety of habitats through animal migrations and trophic subsidies of seagrass detritus. For example, juvenile fish leave temperate intertidal salt marshes to forage in subtidal seagrass meadows, and when seagrass meadows are adjacent to salt marshes, fish biomass is 90% greater than when unvegetated mud flats are adjacent to salt marshes (Irlandi and Crawford 1997; Figure 1b). Similarly, oyster reefs adjacent to seagrass meadows supported higher piscivorous fish biomass than oyster reefs isolated on mud flats (Grabowski and others 2005), and Micheli and Peterson (1999) found that predation rates on clams associated with oyster reefs were greater when reefs were adjacent to seagrass meadows, which provided a protected corridor for crabs to move between oyster reefs and salt marshes. In addition, the commercially important blue crab, *Callinectes sapidus*, settles in U.S. Atlantic and Gulf coast seagrass meadows as post-larvae, and subsequently migrates to other estuarine habitats in early juvenile stages, but returns to seagrass meadows to mate and molt as adults (Orth and van Montfrans 1990). In this way, carbon is exchanged

among seagrass meadows and other habitats as blue crabs forage, grow, and reproduce.

Seagrass meadows have also been shown to be connected to mudflats in South Australia, where isotopic evidence demonstrated that on inshore mudflats shrimp and polychaetes assimilated seagrass carbon (Connolly and others 2005). Also in Australia, Thresher and others (1992) found isotopic evidence that seagrass detritus was a common and important source of carbon for larvae of the blue grenadier (*Macruronus novaezealandiae*) off the coast of Tasmania. Thus, evidence from tropical and temperate regions and from three continents provides a multitude of examples of trophic transfers and faunal interactions between seagrass meadows and adjacent shallow water habitats.

Continental Shelves

Seagrass meadows also export large amounts of animal and plant biomass to offshore areas, and these subsidies have important consequences for some major fisheries. For example, commercially valuable penaeid shrimp populations annually transfer very large amounts of biomass from seagrass meadows, when large juveniles leave seagrass nursery grounds for the adjacent continental shelf in tropical and subtropical latitudes (Figure 1a). A good example is the pink shrimp (*Farfantepenaeus duorarum*), whose fishery in south Florida (USA) is based almost entirely on the export of shrimp from the 14,622 km² of seagrass nursery grounds in Florida Bay (Erhardt and others 2001). The export of juvenile shrimp results in an annual commercial harvest on the offshore Tortugas shrimp ground of between 2300 and 4500 metric tons. This translates to an estimate of from 0.16 to 0.31 metric tons km⁻² of shrimp produced by the juveniles exported from the seagrass meadows of Florida Bay to the commercial fishery. The harvest of this single species not only supports a commercial fishery, but must be only a small portion of the total export from the Florida Bay seagrass meadows. Also well known are the annual migrations of a number of species of young-of-the-year fish, such as the southern U.S. seagrass dominant, the pinfish (*Lagodon rhomboides*), that are spawned on the shelf, move inshore as larvae to settle in seagrass meadows and later move offshore in truly vast numbers at the end of the growing season (Hansen 1969; Dacey 1985; Figure 1b).

In another example, the migrations of anadromous Pacific salmon (*Oncorhynchus* spp.) form a 'conveyor belt' of nutrients between freshwater and the ocean (Schindler and others 2003). During

their migrations, different species of salmon spend variable amounts of time in estuaries, where feeding during both the in- and out-bound parts of their journey can be critical to their survival. Juvenile chum (*O. keta*), pink (*O. gorbuscha*), and chinook (*O. tshawytscha*) salmon are particularly linked to shallow subtidal areas of estuaries where they are caught in eelgrass (*Zostera marina*) beds and feed heavily on epibenthic crustaceans. These crustaceans in turn derive nutrition from eelgrass and associated epiphytes and macroalgae, as determined by their carbon and nitrogen isotopic signatures (Simenstad and Wissmar 1985; Simenstad and others 1982; Fujiwara and Highsmith 1997).

Deep Sea

A large biomass of seagrass detritus can make its way to the deep sea, and in this vast area of low food and shelter availability, constitutes a permanent, major source of food and domicile for consumers in otherwise uniform surroundings (reviewed by Wolff 1980; Figure 1a). Although algae are also exported from seagrass and other nearshore communities, they have more labile organic matter than seagrasses and decompose before reaching the deep sea. In contrast, many photographs of the deep-sea floor reveal seagrass detritus, indicating that an abundance of seagrass detritus reaches these depths. Although seagrass detritus is highly refractory by the time it reaches the deep sea, it is still consumed by deep-sea benthos, as confirmed by carbon isotope signatures (Suchanek and others 1985). Although not yet identified, specialized gut microbiota in deep-sea benthos might break down the cellulose and/or fix nitrogen, thereby enriching the nutritional value of the seagrass detritus (Waterbury and others 1983; Distel and Roberts 1997). The contribution of seagrass detritus to deep-sea food webs has been quantified papers by Vetter (1994, 1998). Although the connectivity between nearshore seagrass meadows and the deep sea is not widely recognized, it is a compelling example of how environmental impacts on coastal seagrasses can have far-reaching consequences.

SEAGRASS MEADOWS ALSO HAVE STRONG LINKS TO TERRESTRIAL HABITATS

Beaches and Near-Shore Areas

Seagrass detritus that washes up on the shore not only provides habitat and food for invertebrate consumers, but also may indirectly support fish,

wading and migratory birds and some mammals (Figure 1b). In some locations, vast amounts of seagrass detritus wash up upon beaches. Eventually much of this detritus is returned to the water with subsequent tides or storms, and is ultimately deposited elsewhere (see Kirkman and Kendrick 1997; Hyndes and Lavery 2005). Thus, the same mass of seagrass detritus can contribute nutrients and energy to multiple habitats. While on the beaches, seagrass wrack provides an important refuge from predation for highly vulnerable macroinvertebrates (Lenanton and others 1982; Lenanton and Caputi 1989). Smaller invertebrates, including a diverse group of flies, beetles, amphipods, and isopods, help breakdown and process the seagrass detritus and are in turn prey for shore birds such as the Australian silver gull, hooded plover, and ruddy turnstone (Kirkman and Kendrick 1997). The link between subtidal primary production and populations of coastal and wading birds can be strong, as demonstrated by the positive correlation between the quantity of beach wrack and the abundance of two species of shore birds in California (Bradley and Bradley 1993). Although more targeted research is needed to better quantify the scale of the seagrass subsidy to beach food webs, we do know that seagrass wrack deposits are metabolic hot spots. For example, CO₂ fluxes in Western Australia wrack deposits may reach 19 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (with mean fluxes in wrack of nearly 3 \times that of the adjacent beach sand without wrack), owing to the activity of dense assemblages of microbes and invertebrates (Coupland and others 2007). In addition, isotopic analyses conducted in several Western Australian locations revealed that seagrass carbon is also present in shallow sandy substrates where it is assimilated by harpacticoid copepods that are, in turn, ingested by small shore-zone fishes (Lenanton and others 1982; Lenanton and Caputi 1989).

A number of semi-aquatic and terrestrial mammals are known to feed on detrital seagrass accumulations in the intertidal zone (see review by Carlton and Hodder 2003). For example, ground squirrels have been observed visiting eelgrass wrack and removing leaf material (Roest 1993), and quokkas, small western Australian marsupials, have been observed to feed on *Posidonia* spp. seeds that become stranded on the shore (G. Kendrick personal observation). Another example of the transfer of seagrass production to terrestrial mammals is stable isotope evidence that bears (*Ursos arctica*) in Alaska fed on crabs that in turn had fed on seagrass tissues (McConnaughey and McRoy 1979).

Of perhaps greater significance are the semi-terrestrial animals that live on land for much of the time but forage in coastal waters. Creed (2004) documented the consumption of widgeongrass (*Ruppia maritima*) by capybara, a South American rodent, and found that nearly 20% of the widgeongrass meadow being observed showed evidence of capybara grazing. Another rodent, the nutria (*Myocaster copyu*) has also been reported to consume widgeongrass in the southern U.S. (Kantrud 1991). Quantification of the role of semi-aquatic seagrass herbivores from more areas needs to be done, but it is likely that consumption rates will be large in areas where these mammals have not been hunted or trapped extensively.

Inland Areas

Inbound salmon can transfer marine nutrients far into terrestrial ecosystems, sometimes reaching bears, eagles, and trees (Schindler and others 2003). However, the best documented and most extensive ocean-to-inland transfers of seagrass biomass involve migratory waterfowl. Seagrasses provide forage for enormous numbers of geese, ducks, and swans, which increase their energy reserves by feeding heavily on seagrasses in preparation for their flight to breeding grounds that may be half a continent away (see review by Ganter 2000).

Among the best known examples are brant geese (*Branta bernicla*), which occur in both North America and Northern Europe, and have been studied extensively, but many other species, including coots (*Fulica atra*), swans (*Cygnus* spp.), and dabbling ducks (*Anas* spp.) also feed heavily on seagrasses (Ganter 2000; Figure 1b). Waterfowl provide connectivity between seagrass and inland areas along flyways that span both the Atlantic and Pacific coasts of North America. The significance of this linkage became very evident after the massive mortality of eelgrass during the 1920s 'wasting disease' epidemic. Data on the ecology of brant geese, whose diets were predominantly eelgrass (approximately 85% of stomach contents), were available from many study areas before the disease-induced disappearance of most eelgrass from North America and Europe. After the eelgrass decline geese were forced to begin foraging in upland areas, behavior that had never before been observed (Cottam and others 1944; Ganter 2000). After eelgrass recovery in the 1950s many Brant geese populations returned to feeding on eelgrass and according to Ganter (2000) it is clear that eelgrass "...is of outstanding importance to this species."

Existing evidence suggests that brant geese can remove a large proportion of intertidal eelgrass biomass, but they appear to have relatively minor effects on subtidal eelgrass (Ganter 2000).

Movement of seagrass and animal propagules on the feet or in the guts of animals that forage in seagrass meadows is one pathway for transfer of organisms from seagrass meadows that has yet to be measured. In freshwater, Figuerola and Green (2002) showed that bird-mediated transport of invertebrate propagules can be important in structuring assemblages of benthic invertebrates in the recipient habitat. Whether this happens in marine systems is unknown, but large seagrass-associated animals (for example, waterfowl, turtles, manatees and dugongs, and large fish) could be vectors for such dispersal.

BROKEN CONNECTIONS

Seagrass meadows are under increasing pressure from human activities (Orth and others 2006), and several lines of evidence suggest that the important connections between seagrass beds and other marine and terrestrial habitats have been or are undergoing alterations. It seems likely that the current rate of waterfowl grazing is dramatically lower today than it was before extensive hunting greatly reduced all types of waterfowl (see Valentine and Duffy 2006 for a review). For example, nearly a century ago it was estimated that waterfowl grazing removed approximately 20% of the eelgrass biomass from a Danish eelgrass bed (Peterson 1918; see also Thayer and others 1975), even though a hundred years ago European waterfowl populations might well have been substantially lower than they were before harvest by humans. The eelgrass wasting disease epidemic in the 1930s resulted in a reduction of 90% of the populations of two North American Atlantic brant subspecies, and lack of recovery of eelgrass forced this species to shift its foraging to salt marshes and agricultural vegetation (Cottam and others 1944). Along the eastern Pacific flyway, combined populations of brant subspecies have been reduced dramatically since the 1950s and their wintering feeding grounds have shifted from the U.S. Pacific Northwest to Baja California, concomitant with a reduction in eelgrass habitat along the U.S. coast (Pacific Flyway Council 2002; Moore and others 2004).

The effects of human fishing and hunting in reducing the number of large vertebrate grazers such as waterfowl, turtles, and mammals can in part explain the spatial variability in seagrass grazing (Jackson 1997; Valentine and Duffy 2006).

The loss of major grazers means that large amounts of seagrass detritus are often available for export to other habitats, although the amount of export is also a function of the coastal geomorphology and hydrodynamics of any given location. This is supported by the only quantitative estimates of the effect of large herbivores on detrital abundance, which appear in Thayer and others (1984). They show nearly a 100-fold difference in the amount of detrital nitrogen in ungrazed seagrass meadows in St. Croix, U.S. Virgin Islands, compared to nearby meadows that were regularly grazed by green turtles.

As with most ecological data compilations, the majority of studies considered here were carried out in North America, Europe, and Australia. Thus, there is an obvious need for studies to be done in Africa, South America, and the Indo-Pacific region. However, it is clear that in the tropical and temperate regions that have been studied, seagrass meadows are tightly connected to many other habitats and that exports from seagrass meadows elevate the productivity of other habitats, as noted for the Western Atlantic coral reefs, temperate Australian beaches, and the deep sea. Although quantification of materials exported from seagrass meadows is relatively rare and highly variable, available estimates indicate that, on average, some 15% of seagrass production is exported from meadows (Mateo and others 2006). In terms of the seagrass carbon that is buried, estimates are on the order of $111 \text{ Tmol C year}^{-1}$, a value that represents about 20% of the marine vascular plant carbon buried in the ocean (Duarte and others 2005).

Other points that come through clearly are that preserving single habitat types that are strongly connected to others is unlikely to produce the desired results. This is especially true for Caribbean coral reefs, whose ability to support diverse and abundant consumers is greatly enhanced by exports from nearby seagrass meadows (Nagelkerken and others 2001, 2002; Nagelkerken and van der Velde 2004b; Valentine and Heck 2005). Thus, establishing Marine Protected Areas (MPAs) that contain only coral reefs without including the adjacent seagrass meadows will not successfully sustain the reef-associated fishes or the rest of the coral reef flora and fauna (see Grober-Dunsmore and others 2007).

It is also important to recognize that modern day seagrass beds are likely exporting much more energy in the form of detritus than in the past, when a great deal more export was in the form of animal biomass produced by the consumption of living seagrass and algal tissues. This hypothesis

needs further testing, which could be done by comparing the detrital dynamics in similar seagrass meadows that still contain macroherbivores, such as manatees, green turtles, and dugongs, with those that do not. However, it is also likely that the regional and global flux of detritus from seagrass meadows to other habitats has been substantially reduced by the widespread loss of seagrass meadows (Orth and others 2006).

Finally, although we have focused on seagrass exports to neighboring systems, it is clear that seagrass meadows also receive inputs from adjacent habitats such as salt marshes, mangroves, and rocky shores. Such inputs can be large, as most clearly shown for seagrass meadows in temperate Western Australia, which receive large amounts of drifting algae that has broken loose from rocky reefs (Wernberg and others 2006). Although it is possible that seagrass systems are merely transmitting a subsidy received from elsewhere, our opinion is that seagrass meadows are indeed exporting excess biomass. However, quantitative data regarding both inputs into and exports out of seagrass meadows are needed to evaluate more fully the interconnections between seagrasses and other habitats. Furthermore, such data would allow us to compare the relative importance of seagrass meadow exports with exports from other coastal systems (for example, salt marshes; Valiela and others 2004).

In summary, we have provided examples of how seagrass meadows are part of a greater seascape that contains both marine and terrestrial elements, each linked to the other via the foraging of consumers (both predators and herbivores), and the drift of seagrass and seagrass-associated algal detritus. Where grazing of seagrass is low, export of detrital seagrass leaves can be seasonally high (Harrison 1989; Cebrian and Duarte 1998). Trophic subsidies from seagrass meadows especially assist in maintaining the abundance of coral reef fishes (Valentine and Heck 2005), and seem to be of great importance in the food- and habitat-poor deep sea, although they also are of importance in a variety of other habitats. The on-going global decline of seagrass meadows (Orth and others 2006) means that the linkages between seagrass meadows and other habitats are being altered and diminished, and that the consequences of seagrass decline extend far beyond the seagrass meadows themselves.

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