

## REVIEW

# Production and fate of kelp detritus

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**ABSTRACT:** The flow of detritus between habitats is an important form of connectivity that affects regional productivity and the spatial organization of marine ecosystems. Kelps form highly productive beds or forests that produce detritus through incremental blade erosion, fragmentation of blades, and dislodgement of whole fronds and thalli. Rates of detrital production range from 8 to 2657 g C m<sup>-2</sup> yr<sup>-1</sup> for blade erosion and fragmentation, and from 22 to 839 g C m<sup>-2</sup> yr<sup>-1</sup> for loss of fronds and thalli. The estimated global average rate of detrital production by kelps is 706 g C m<sup>-2</sup> yr<sup>-1</sup>, accounting for 82% of annual kelp productivity. Detrital production rates are regulated by current and wave-driven hydrodynamic forces and are highest during severe storms and following blade weakening through damage by grazers and encrusting epibionts. Detritus settles within kelp beds or forests and is exported to neighboring or distant habitats, including sandy beaches, rocky intertidal shores, rocky and sedimentary subtidal areas, and the deep sea. Exported kelp detritus can provide a significant resource subsidy and enhance secondary production in these communities ranging from tens of meters to hundreds of kilometers from the source of production. Loss of kelp biomass is occurring worldwide through the combined effects of climate change, pollution, fishing, and harvesting of kelp, which can depress rates of detrital production and subsidy to adjacent communities, with large-scale consequences for productivity.

**KEY WORDS:** Kelp bed · Kelp forest · Connectivity · Detritus · Resource subsidy · Local-regional productivity

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## INTRODUCTION

Kelp species have a broad geographic distribution and are a major source of primary production and biogenic habitat in coastal zones of temperate and polar oceans worldwide (Dayton 1985a, Steneck et al. 2002). Kelp productivity is tightly linked to seawater nutrient concentrations (Chapman & Lindley 1980, Gagné et al. 1982), which are regulated by oceanographic processes. Kelps support high secondary productivity in rich and diverse communities of invertebrates, fish, and mammals, including many commercially important species. The sensitivity of kelps to environmental change and increasing fishing pressure is altering kelp productivity and biomass, which can have important follow-on effects on

secondary production and ecosystem function both within kelp beds or forests (Dayton et al. 1992, Steneck et al. 2002) and in adjacent communities that receive kelp detritus.

There is growing recognition that the exchange of detritus is an important form of connectivity among coastal habitats that can influence spatial patterns of primary and secondary productivity (Polis et al. 1997, Loreau et al. 2003, Marczak et al. 2007), and that a significant proportion of energy produced in macrophyte communities enters detrital pathways (Mann 1988, Cebrian 1999). Kelps continuously produce detritus, which is either consumed or decomposed within kelp beds or forests, or exported. Various studies show that kelp detritus is an important resource in adjacent communities (Duggins et al.

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1989, Bustamante et al. 1995, Dugan et al. 2003, Vanderklift & Wernberg 2008), however, a comprehensive understanding of the nature and extent of this subsidy is lacking. Although the production and fate of detritus have been reviewed for other marine macrophyte communities (e.g. seagrass beds: Mateo et al. 2006, Heck et al. 2008; mangrove forests: Kristensen et al. 2008), reviews of kelp ecosystems provide only a cursory description of detrital pathways (Dayton 1985a, Steneck et al. 2002). Other reviews consider detrital production and processing in terrestrial and aquatic ecosystems more broadly, without specific emphasis on kelp communities (Mann 1988, Cebrian & Lartigue 2004). The impact of anthropogenic pressures on kelp detrital production and export has not been considered.

In this review, we summarize estimates of detrital production from kelp populations worldwide for comparison with other macrophyte communities that contribute detritus to coastal habitats. We identify environmental and biological factors that regulate the rate of kelp detrital production and degradation, and examine the consequences of detrital kelp subsidies for community organization and productivity in a variety of marine habitats, including sandy beaches, rocky intertidal shores, rocky and sedimentary subtidal areas, and the deep sea. Finally, we discuss anthropogenic impacts on kelp ecosystems that are causing declines in kelp biomass, and highlight the broader implications of these declines for communities subsidized by kelp detritus.

## PRODUCTION OF KELP DETRITUS

There are 3 morphological groupings of kelp species: canopy, stipate, and prostrate (Dayton 1985a, Steneck et al. 2002). All kelps are attached to the substrate by a root-like structure known as a holdfast. Canopy kelps have flexible stems or stipes that are supported by gas-filled bladders called pneumatocysts. The largest of the canopy kelps, the genus *Macrocystis*, has a primary stipe that gives rise to multiple secondary stipes, each with lateral blades along their extent, referred to as fronds. Other canopy kelps, such as the genus *Nereocystis*, have a single stipe supported by one large pneumatocyst, from which emanate multiple blades. Stipate kelps typically are smaller and have rigid stipes supporting a single blade, while prostrate kelps are the smallest and have blades that lie directly on the substrate. Stipate and prostrate kelps include the genera *Laminaria*, *Saccharina*, *Ecklonia*, *Lessonia*, and *Eisenia*.

Populations of canopy kelps form so-called forests, while prostrate and stipate kelps form beds (Steneck et al. 2002).

Kelp detritus ranges in size from small particles to whole thalli. Whole thalli are lost through breakage at the base of the primary stipe or when holdfasts become detached from the substratum. Frond loss is the result of breakage of the secondary stipe for *Macrocystis* spp.; individual blades also can detach from secondary stipes with multiple blades. Breakage at the junction of the stipe and blade of prostrate and stipate kelps is another form of blade loss. Loss of whole thalli and blade breakage below the basal meristem prevent re-growth of an individual, and are considered fatal. The distal ends of blades can erode rapidly or gradually, producing detrital fragments that range from small particulates to large sections of blade. Dissolved organic matter is released as kelp blades fragment and erode, and is estimated to account for 16 to 35% of annual energy production in kelps (Johnston et al. 1977, Hatcher et al. 1977, Mann et al. 1979, Newell et al. 1980).

Rates of dislodgement (including loss of whole thalli and fronds) and erosion (including blade loss and breakage) have been measured (as dry mass or C) for kelp populations spanning the temperate range of kelps worldwide (Fig. 1, Table 1). Although the range of kelps extends into the high Arctic, erosion rate is recorded for only a single population of *Laminaria solidungula* in the Beaufort Sea, Alaska, USA (Dunton 1984), which was the lowest of all kelp populations studied ( $26 \text{ g m}^{-2} \text{ yr}^{-1}$ ,  $8 \text{ g C m}^{-2} \text{ yr}^{-1}$ ). Erosion rate spans 3 orders of magnitude globally, with the highest rate measured for *Lessonia* spp. in Chile ( $11071 \text{ g m}^{-2} \text{ yr}^{-1}$ ,  $2657 \text{ g C m}^{-2} \text{ yr}^{-1}$ ), reflecting the high blade density of these species (2369 to 3019 blades  $\text{m}^{-2}$ ) (Tala & Edding 2007). Erosion rates of *Ecklonia* spp. were moderately high across all locations, and erosion of *Laminaria* spp., *Saccharina* spp., and *Macrocystis pyrifera* were in the mid to low end of the range. Erosion of *Saccharina latissima* (formerly *Saccharina longicruris*, *Laminaria longicruris* or *Laminaria saccharina*) (McDevit & Saunders 2010) was an order of magnitude greater in Nova Scotia, Canada than in Scotland, indicating high variability among populations of the same species in different geographic locations. Erosion rate of a cultured population of *Undaria pinnatifida* in northern Japan ( $9 \text{ g m}^{-2} \text{ yr}^{-1}$ ,  $3 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) was lower than all naturally occurring kelp populations worldwide (Table 1).

Across all populations, erosion accounted for 17.3 to 111.3% of annual primary productivity (Table 1). Although erosion rate was highest for *Lessonia* spp.

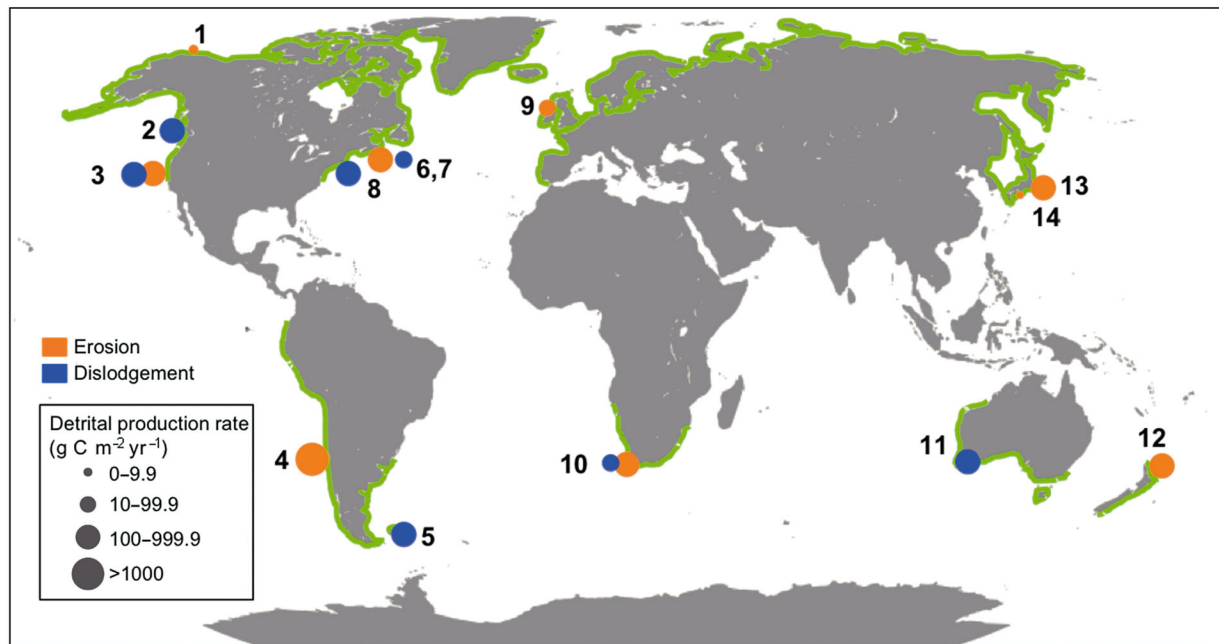


Fig. 1. Global distribution of kelps (green shading) and locations (numbered) where rates of kelp production, erosion (orange circles) and dislodgement (blue circles) have been measured (Table 1). Circle area represents the magnitude of measured rates; overlapping circles indicate locations where erosion and dislodgement rates were measured simultaneously

in Chile, the amount of material eroded accounted for less than half (47.3%) of annual primary production. In contrast, *Ecklonia cava* in southern Japan had the second highest erosion rate (2547 g m<sup>-2</sup> yr<sup>-1</sup>, 774 g C m<sup>-2</sup> yr<sup>-1</sup>) but 91% of biomass produced annually was eroded. Annual erosion exceeded production for populations of *Laminaria digitata* and *Saccharina latissima* in Nova Scotia, indicating that the standing biomass of these species decreased over the measurement period.

Few studies document dislodgement rates for kelp populations (Table 1). Interestingly, measurements from populations of *Laminaria digitata* and *Saccharina latissima* in 2 separate locations represented the minimum (Nova Scotia, Canada) and maximum (Rhode Island, USA) rates of the range recorded (74 to 2798 g m<sup>-2</sup> yr<sup>-1</sup>, 22 to 839 g C m<sup>-2</sup> yr<sup>-1</sup>). Dislodgement accounted for 6.2 to 49.0% of annual productivity, which is lower than the range presented for erosion. Only 2 studies have simultaneously measured erosion and dislodgement rates in a single kelp population (Gerard 1976, Newell et al. 1982). For *Macrocystis pyrifera*, dislodgement rate (50% of annual production) was an order of magnitude greater than erosion rate (17%) (Gerard 1976). The opposite was observed for populations of *Laminaria pallida* and *Ecklonia maxima* in South Africa, where dislodgement accounted for a small portion of biomass pro-

duced annually (6%) compared to erosion (70%) (Newell et al. 1982). Erosion rate also exceeded dislodgement rate in populations of *Laminaria digitata* and *Saccharina latissima* measured in 2 separate studies in Nova Scotia (Chapman 1984, Krumhansl & Scheibling 2011a), and *Ecklonia radiata* in northern New Zealand and Western Australia (Novaczek 1984, Hatcher et al. 1987). The relative importance of erosion and dislodgement to detrital production may be related to kelp morphology, with larger canopy-forming kelps producing more detritus through dislodgement than smaller canopy-forming and prostrate kelps. Spatial and temporal variation in physical processes that cause dislodgement also may account for differences in the relative importance of dislodgement among kelp populations. Erosion is likely to be greater than dislodgement rate in areas less prone to physical disturbance, or during periods when disturbance events are less frequent.

#### FACTORS REGULATING PRODUCTION OF KELP DETRITUS

Kelp detritus is produced through wave and current-driven water motion. Losses of kelp biomass through dislodgement and erosion are greatest during storms that generate high flow rates (Gerard

Table 1. Estimated rates of productivity, blade erosion, dislodgement of whole fronds and thalli ( $\text{g dry mass m}^{-2} \text{ yr}^{-1}$  and  $\text{g C m}^{-2} \text{ yr}^{-1}$ ), and percent of productivity lost to erosion and dislodgement for kelp populations worldwide. One measurement is presented for the combined contribution of all kelp species present in a particular location. The number in the first column indicates the location of measurements in Fig. 1

Location	Species	Productivity ( $\text{g C m}^{-2} \text{ yr}^{-1}$ )	Erosion ( $\text{g C m}^{-2} \text{ yr}^{-1}$ )	% Eroded	Dislodgement ( $\text{g C m}^{-2} \text{ yr}^{-1}$ )	% Dis- lodged	Source
1 Beaufort Sea, Alaska, USA	<i>Laminaria solidungula</i>	28	26	90.7	—	—	Dunton (1984)
2 British Columbia, Canada	<i>Macrocystis integrifolia</i>	—	—	—	774	232	Druehl & Wheeler (1986)
3 Monterey Bay, California, USA	<i>Macrocystis pyrifera</i>	2389	414	17.3	1170	325	Gerard (1976)
4 Tongoy, Chile	<i>Lessonia nigrescens</i> , <i>Lessonia trabeculata</i>	23424	11071	47.3	—	—	Tala & Edding (2007)
5 Falkland Islands	<i>Macrocystis pyrifera</i>	27121	—	—	565	157	Van Tussenbroek (1993)
6 Nova Scotia, Canada	<i>Laminaria digitata</i> , <i>Saccharina latissima</i>	951	1058	111.3	—	—	Krumhansl & Scheibling (2011a)
7 Nova Scotia, Canada	<i>Laminaria digitata</i> , <i>Saccharina latissima</i>	—	—	—	74	22	Chapman (1984)
8 Rhode Island, USA	<i>Laminaria digitata</i> , <i>Saccharina latissima</i>	6152	—	—	2798	839	Brady-Campbell et al. (1984)
9 Loch Creran, Scotland	<i>Saccharina latissima</i>	395	160	40.5	—	—	Johnston et al. (1977)
10 Cape Town, South Africa	<i>Laminaria pallida</i> , <i>Ecklonia maxima</i>	1614	1129	70.0	97	29	Newell et al. (1982)
11 Perth, Australia	<i>Ecklonia radiata</i>	—	—	—	662	201	Hatcher et al. (1987)
12 Goat Island Bay, Leigh, New Zealand	<i>Ecklonia radiata</i>	3000	1500	50.0	—	—	Novaczek (1984)
13 Ostuchi Bay, Japan	<i>Undaria pinnatifida</i> (cultured)	33	9	28.3	—	—	Yoshikawa et al. (2001)
14 Shimizu, Japan	<i>Ecklonia cava</i>	2800	2547	91.0	—	—	Hayashida (1977)

1976, Lüning 1979, Gunnill 1985, Witman 1987, Seymour et al. 1989, Reed et al. 2008, Cavanaugh et al. 2011, Filbee-Dexter & Scheibling 2012). During periods when maximum wave heights exceed 2.5 m, as much as 30% of thalli and fronds of *Macrocystis pyrifera* are lost (Gerard 1976), and losses of density, biomass, and kelp cover can range from 40 to 100% during the largest wave events (5 to 15 m maximum wave height) (Ebeling et al. 1985, Seymour et al. 1989, Reed et al. 2008). Detached fronds and thalli may become entangled with attached kelps, causing substantial increases in drag that lead to further dislodgement (Gerard 1976, Seymour et al. 1989, Brown et al. 1997). Poorly attached kelps, and those that have settled on small cobbles and biogenic structures such as mussels, are more likely to become dislodged from the substratum at higher flow rates (Gunnill 1985, Witman 1987, Scheibling & Gagnon 2009). Erosion occurs continuously, even during relatively calm conditions (Reed et al. 2008, Krumhansl & Scheibling 2011a). Loss of fronds and blade area may actually increase the survivorship of kelps in strong flow by reducing drag on thalli (Gunnill 1985, Thomsen & Wernberg 2005).

The importance of hydrodynamic forces in determining kelp survivorship and biomass is corroborated by morphological variation in kelps along spatial gradients of wave and current exposure. Kelps in areas of high flow are typically more streamlined or strap-like, less crenulated or undulate, have thicker stipes and blades, and are more firmly attached at the holdfast than kelps in low-flow environments (Gerard & Mann 1979, Koehl et al. 2008, Wernberg & Vanderklift 2010, Miller et al. 2011). Never-

theless, dislodgement and erosion are typically greater at sites with high wave exposure than at more protected sites (Duggins et al. 2003, Krumhansl & Scheibling 2011a). The measured force to break kelp stipes and blades often exceeds the predicted hydrodynamic force acting on kelps (Utter & Denny 1996, Denny et al. 1997, Mach et al. 2007), suggesting that breakage and dislodgement are uncommon. For example, Utter & Denny (1996) showed that the breaking strength of stipes of *Macrocystis pyrifera* (2.82 MPa) greatly exceeds the stress experienced by stipes (0.04 to 0.68 MPa) under normal wave conditions (0.85 to 2.71 m significant wave height). Thomsen & Wernberg (2005) calculated a mean dislodgement force of 93.5 N for 48 populations of kelp encompassing 10 species. The actual hydrodynamic force acting on kelps is dependent on the size, shape, and buoyancy of macroalgal thalli (Denny 2006), and therefore is species- and location-specific. However, *in situ* measurements of these forces on kelps are lacking.

High erosion and dislodgment rates occur as a result of damage to kelp holdfasts, stipes, and blades. Fatigue from repetitive loading, abrasion, epiphytism, and grazing generate nicks, holes, and flaws in kelp tissues that concentrate stress when the thallus is in tension, and lead to crack formation and propagation at lower force applications than required to break undamaged tissues (Black 1976, Koehl & Wainwright 1977, Biedka et al. 1987, Duggins et al. 2001, Krumhansl et al. 2011). For example, grazing damage by snails and sea urchins on kelp stipes and holdfasts is linked to stipe breakage and holdfast dislodgement (Koehl & Wainwright 1977, Biedka et al. 1987, Duggins et al. 2001). Perforations generated by snails reduce the strength of kelp blade tissues (Black 1976, Krumhansl et al. 2011), which accounts, in part, for seasonal variation in erosion rate (Krumhansl & Scheibling 2011a) and loss of kelp biomass during storms (Krumhansl & Scheibling 2011b). Encrustation of kelp blades and stipes by bivalves and bryozoans also increases drag and induces flaws in blade tissues that lead to dislodgement and breakage (Brady-Campbell et al. 1984, Brown et al. 1997, Krumhansl & Scheibling 2011a, Krumhansl et al. 2011). In particular, encrustation of kelp blades by the bryozoan *Membranipora membranacea* in its native (Europe) and invaded range (east and west coasts of North America) causes quantifiable reductions in blade strength (Krumhansl et al. 2011), resulting in widespread defoliation of kelp beds during periods of high wave action (Scheibling et al. 1999, Scheibling & Gagnon 2009).

Water temperature and nutrient availability can affect the quality of kelp blade tissue and, in turn, erosion rate. Low nitrate in summer corresponds to a seasonal minimum in kelp growth rate (Mann 1973, Gagné et al. 1982, Brown et al. 1997). During this period, temperature, irradiance and sedimentation on blades are high (Gunnill 1985, Brown et al. 1997), causing tissue degradation and increasing the susceptibility of blades to breakage (Gunnill 1985, Brown et al. 1997). Older thalli may erode more rapidly than juvenile kelps (Brown et al. 1997, Krumhansl & Scheibling 2011a).

### COMPARISON OF DETRITAL PRODUCTION RATES AMONG MACROPHYTE COMMUNITIES

The annual rates of erosion and dislodgement averaged among kelp populations measured globally (Table 1) are  $448 \pm 455$  (unadjusted mean  $\pm$  95% confidence interval) and  $257 \pm 206$  g C m<sup>-2</sup> yr<sup>-1</sup> respectively. Summing these quantities yields an estimated average detrital production rate of 705 g C m<sup>-2</sup> yr<sup>-1</sup> (Fig. 2). The average productivity of these kelp populations is 864 g C m<sup>-2</sup> yr<sup>-1</sup>, indicating that detrital production accounts for the large majority of kelp primary production (81.7%) (Fig. 2). Similar global estimates of detrital production exist for other macrophyte communities. Seagrass ecosystems produce on average 817 g C m<sup>-2</sup> yr<sup>-1</sup> (including above and below ground production), of which 650 g C m<sup>-2</sup> yr<sup>-1</sup> (79.5%) enters detrital pathways (Mateo et al. 2006) (Fig. 2).

Mangrove forests contribute a significant amount of detritus in the form of leaf litter to coastal marine communities. Productivity of mangroves (1788 g C m<sup>-2</sup> yr<sup>-1</sup>) typically exceeds that of seagrass or kelps, but annual leaf litter estimates (456 g C m<sup>-2</sup> yr<sup>-1</sup>) represent only 25.5% of primary production (Kristensen et al. 2008) (Fig. 2). Salt marshes are also highly productive and produce a significant quantity of detritus annually. Bouchard & Lefeuvre (2000) estimated productivity of marsh grasses (*Puccinellia maritima*, *Suaeda maritima*, *Aster tripolium*, *Salicornia* spp., *Atriplex portulacoides*, *Elytrigia aetherica*, and *Festuca rubra*) in France at 4370 g C m<sup>-2</sup> yr<sup>-1</sup>, of which 3330 g C m<sup>-2</sup> yr<sup>-1</sup> (76.2%) entered detrital pathways. Haines (1977) presents a more moderate estimate of detrital production (648 g C m<sup>-2</sup> yr<sup>-1</sup>) from a salt marsh in Georgia, USA composed of *Spartina alterniflora*, which is similar to detrital production rates from salt marshes in Argentina composed of *S. alterniflora* (788 g C m<sup>-2</sup> yr<sup>-1</sup>) and *Spartina densiflora* (862 g C m<sup>-2</sup> yr<sup>-1</sup>) (Montemayor et al. 2011). Averaging

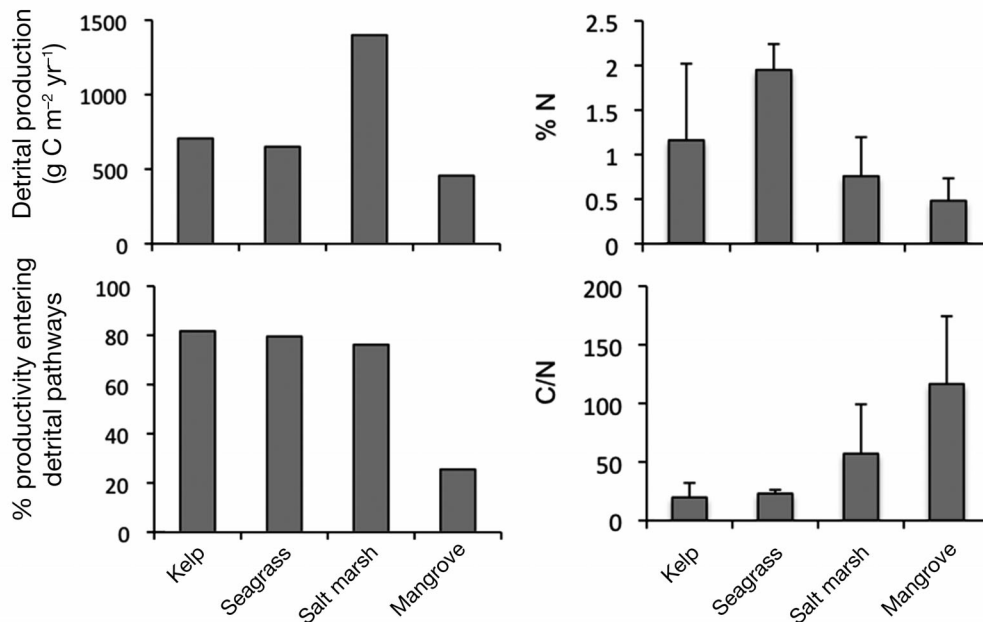


Fig. 2. Average detrital production rates ( $\text{g C m}^{-2} \text{yr}^{-1}$ ), the percentage of primary productivity entering detrital pathways, the average percentage of nitrogen and C/N ratio (+1 SD) for kelp (% N:  $n = 184$ , C/N:  $n = 190$ ), seagrass (% N:  $n = 770$ , C/N:  $n = 813$ ), salt marsh (% N:  $n = 37$ , C/N:  $n = 120$ ), and mangrove communities (% N:  $n = 153$ , C/N:  $n = 141$ ). % N and C/N were calculated from a range of species within each macrophyte type. Kelp sources: Hurd et al. (1994), Henley & Dunton (1995), Wakefield & Murray (1998), Van Alstyne et al. (2001), Norderhaug et al. (2003), Dean & Hurd (2007), Hepburn et al. (2007), Cerda et al. (2009), McDonald & Bingham (2010), Schaal et al. (2010), Krumhansl & Scheibling (2012); seagrass sources: Fourqurean et al. (1997), Fourqurean & Zieman (2002), Touchette et al. (2003), Papadimitriou et al. (2005), Johnson et al. (2006), Smit et al. (2006), Vinther et al. (2008), Campbell & Fourqurean (2009), Kowalski et al. (2009), Mascaro et al. (2009), MacArthur et al. (2011), Prado & Heck (2011); salt marsh sources: Buchsbaum et al. (1991), Burke et al. (2002), Dai et al. (2005), Sanmarti & Menendez (2007), Menendez (2008), Canepuccia et al. (2010), Montemayor et al. (2011), Simoes et al. (2011), Chen et al. (2012), Jimenez et al. (2012); mangrove sources: Giddins et al. (1986), Poovachiranon et al. (1986), Robertson (1988), Camilleri (1989), Rao et al. (1994), Feller et al. (1999), Skov & Hartnoll (2002), Thongtham & Kristensen (2005), Nordhaus et al. (2011)

these values yields an estimate of detrital production from salt marsh communities of  $1399.5 \text{ g C m}^{-2} \text{yr}^{-1}$  (Fig. 2).

Few studies directly quantify detrital production from macroalgal communities other than kelp beds or forests, and these measurements are primarily for other large brown algae. Fucales form extensive beds in intertidal and shallow subtidal habitats, and are often a dominant component of beach wrack (Josselyn & Mathieson 1980, Yatsuya et al. 2007). Josselyn & Mathieson (1980) estimated that *Ascophyllum nodosum* and *Fucus vesiculosus* in an estuarine system produce detritus at rates of 540 and  $414 \text{ g C m}^{-2} \text{yr}^{-1}$  respectively, although these estimates were based on wrack deposited on shore. The rate of detrital production from a population of *Sargassum muticum* in a Danish estuary is estimated at  $136 \text{ g C m}^{-2} \text{yr}^{-1}$ , while *Halidrys siliquosa* produce substantially less detritus ( $6.3 \text{ g C m}^{-2} \text{yr}^{-1}$ ) in the same area (Pedersen et al. 2005).

A comparison of these studies indicates that detrital production accounts for a similar percentage of

primary production in kelp, seagrass, and salt marsh communities (76 to 82%) (Fig. 2). This represents the majority of primary production, whereas most of the primary production in mangrove communities accumulates as standing stock biomass (Lugo & Snedaker 1975, Lee et al. 1990, Kristensen et al. 2008) (Fig. 2). The decomposition rate and ability of organisms to consume plant and algal material is related to its nutritional quality and palatability, specifically to the C/N ratio, % N, content of fibrous material (cellulose, lignin), and concentration of deterrent chemicals (Mann 1988, Cebrian & Lartigue 2004, Hladysz et al. 2009, Krumhansl & Scheibling 2012). Based on the % N or C/N ratio, kelp on average is more nutritious than salt marsh grass and mangrove leaves (senescent), and less nutritious than seagrass (Fig. 2). Lower consumption, assimilation, and degradation rates of vascular plants relative to kelps and other macroalgae are likely related to a higher content of fibrous material (or lower labile fraction) (Smith & Foreman 1984, Tenore et al. 1984, Mann 1988, Cebrian 1999, Hladysz et al. 2009). Consumers often

prefer kelp and other macroalgal detritus to vascular plant detritus (Smit et al. 2006, Doropoulos et al. 2009), and more refractory material accumulates in vascular plant than macroalgal communities (Cebrian & Lartigue 2004).

## DEGRADATION OF KELP DETRITUS

The rate of kelp degradation depends on the chemical and physical characteristics of detritus, and the environmental conditions under which degradation is occurring. Degradation occurs more rapidly at higher water temperatures (Bedford & Moore 1984, Rothausler et al. 2009), and under high flow conditions where mechanical breakdown occurs (Tenore et al. 1984, Alkemade & van Rijswijk 1993). Physical processes also play a role in regulating the environmental conditions within detrital accumulations. Resuspension exposes a greater surface area of detritus to microbial colonization (Stahlberg et al. 2006) and increases the concentration of dissolved oxygen (Tenore et al. 1984, Kristensen 1994, Okey 1997, 2003). Smaller detrital particles degrade at a faster rate than larger fragments because they have a higher surface area relative to their volume for microbial colonization (Smith & Foreman 1984). Microbial respiration is reduced when algal material is dried onshore, resulting in slower degradation rates compared to wet material (Newell et al. 1985).

Nutritional quality increases throughout the course of kelp degradation (Smith & Foreman 1984, Mann 1988, Duggins & Eckman 1997, Norderhaug et al. 2003, Krumhansl & Scheibling 2012). Microbial colonization and transformation increase the % N in kelp tissues, leading to a gradual decrease in the C/N ratio (Mann 1988, Duggins & Eckman 1997, Norderhaug et al. 2003, Krumhansl & Scheibling 2012). Phlorotannins occur in varying concentrations among kelp species and are known to deter grazing (Johnson & Mann 1986, Iken et al. 2009), reduce growth in filter feeders by decreasing assimilation efficiency (Duggins & Eckman 1997), and deter colonization by microbes (Ragan & Glombitza 1986). Phlorotannin concentration decreases rapidly during degradation, and the largest increases in nitrogen occur in species that undergo the greatest reduction in phlorotannins (Duggins & Eckman 1997). Assimilation efficiency, survival, and growth of several species of polychaetes, mussels, scallops, and amphipods are reduced when fed a single diet of fresh kelp, but are enhanced when fed aged kelp particles (Cranford & Grant 1990, Duggins & Eckman 1997,

Norderhaug et al. 2003). Species with different nutritional preferences and physiological tolerances colonize algal material at varying times over the course of degradation in response to changing environmental conditions and nutritional quality of the detritus (Fauchald & Jumars 1979, Bedford & Moore 1984, Okey 2003, Mamouridis et al. 2011, Krumhansl & Scheibling 2012).

## EXPORT OF KELP DETRITUS: PHYSICAL TRANSPORT

The extent of detrital export from kelp beds and forests and transport to other habitats is regulated by the interaction between physical characteristics of detritus, physical transport processes, topography, and substratum characteristics (Witman et al. 2004, Kotta et al. 2008, Britton-Simmons et al. 2012). The size of detritus influences its settling and resuspension rates across flow velocities (Norton & Fetter 1981, Watanabe et al. 2009), while buoyancy determines whether detritus is transported at the surface (positive buoyancy), in the water column (neutral buoyancy), or near-bottom (negative buoyancy), where it is subject to different transport mechanisms. Currents are altered by topographic features, such as submarine canyons, sills, embayments, rocky pinnacles, and depressions, which accelerate or decelerate flow and generate eddies and internal waves (Witman et al. 2004). Detrital kelp accumulates on sandy beaches (Stenton-Dozey & Griffiths 1983, Dugan et al. 2011), in submerged rocky depressions (Witman 1987, Vetter 1995, Britton-Simmons et al. 2012), and in embayments (Vetter 1995, Bustamante & Branch 1996) where flow is reduced. The movement of detritus across habitat boundaries is influenced by boundary permeability; topographic features (e.g. cliffs) and biogenic structures (e.g. macrophytes) can act as barriers to transport (Witman et al. 2004). The softness and penetrability of the substratum influences the likelihood that detritus is trapped and buried (Kristensen et al. 2008, Montemayor et al. 2011), and substratum roughness increases turbulence in the benthic boundary layer, delivering suspended detrital particles to benthic consumers (Witman et al. 2004).

## EXPORT OF KELP DETRITUS: SINKS

Kelp detritus can settle within kelp beds and forests, where it serves as food for local benthic invertebrates (Dunton & Schell 1987, Tutschulte &

Connell 1988, Norderhaug et al. 2003, Schaal et al. 2009), or be advected to adjacent or distant habitats. The transfer of resources across habitat boundaries plays a central role in shaping ecological patterns and processes (Huxel et al. 2004, Heck et al. 2008, Lamberti et al. 2010). Resource subsidies influence almost all levels of ecology, from behavior (Harrold & Reed 1985, Rodriguez 2003) and species interactions (Spiller et al. 2010), to productivity (Bustamante & Branch 1996, Polis & Hurd 1996), food web stability (Huxel & McCann 1998, Huxel et al. 2002, Marleau et al. 2010), and population dynamics (Bustamante et al. 1995, Barrett et al. 2005). Nutrients and detritus subsidize lower trophic levels, while carrion and prey subsidize higher trophic levels. Subsidies have a larger effect when they occur at lower trophic levels where species are more specialized than consumers at higher trophic levels (Polis & Hurd 1996, Huxel & McCann 1998, Marczak et al. 2007), and when productivity or the amount of an equivalent resource is lower in the recipient community than in the source community (Polis & Hurd 1996, Marczak et al. 2007). Subsidies can be reciprocal (Nakano & Murakami 2001); for example, when imported kelp detritus is processed and nutrients are returned to the source kelp bed or forest (Gravel et al. 2010). The proportion of detritus that is exported from kelp beds and forests is unknown, but the consequences of detrital subsidies for recipient populations and communities are documented in a variety of habitats.

### Onshore transport and deposition

#### Sandy beaches

Kelp detritus plays a significant role in shaping community dynamics on sandy beaches, and is perhaps the most well-known example of kelp detrital subsidy to an adjacent community. Sandy beaches have very low local primary productivity ( $0$  to  $50 \text{ g C m}^{-2} \text{ yr}^{-1}$ ; Brown 1964, Munro et al. 1978, Griffiths et al. 1983, Colombini & Chelazzi 2003), largely because sandy sediments are highly mobile and thus unsuitable for attachment by macrophytes or formation of benthic diatom assemblages (Griffiths et al. 1983). Imported detritus is the primary food source for resident fauna and microbes. Rates of kelp deposition (as wet

mass) range from  $1200$  to  $2200 \text{ kg m}^{-1} \text{ yr}^{-1}$  for *Laminaria pallida* and *Ecklonia maxima* in South Africa (Koop & Field 1980, Stenton-Dozey & Griffiths 1983), from  $450$  to  $548 \text{ kg m}^{-1} \text{ yr}^{-1}$  for *Macrocystis pyrifera* in California, USA (Hayes 1974, Dugan et al. 2011), and from  $180$  to  $1450 \text{ kg m}^{-1} \text{ yr}^{-1}$  for *Ecklonia radiata* in Western Australia (Hansen 1984). Deposition of kelp detritus varies by season in response to changing water temperatures and wave conditions (Koop & Field 1980, Stenton-Dozey & Griffiths 1983). For example, deposition is highest following storms in spring (April–May) and fall (October–November) in Maine, USA (Witman 1987). Kelp is estimated to account for  $55$  to  $66\%$  of total macrophyte biomass on sandy beaches in California (Lastra et al. 2008, Dugan et al. 2011) and  $14$  to  $52\%$  in Patagonia (Piriz et al. 2003).

Detrital processing by microbes and meio- and macrofauna on sandy beaches plays a key role in coastal nutrient cycling (Pearse et al. 1942, Dugan et al. 2011). Bacteria and protozoans rapidly colonize detrital kelp deposits on beaches (Fig. 3), causing surficial lesions and cell lysis that release dissolved and particulate organic matter into the sediments (Koop et al. 1982). Carbon in this leachate is converted to microbial biomass and remineralized (Koop et al. 1982), directly absorbed by meiofauna (Koop & Griffiths 1982, McLachlan 1985), or returned to the sea via tidal forcing or rainwater run-off. Nitrogen in the leachate is rapidly remineralized and nitrified, and accumulated as dissolved inorganic nitrogen (DIN) in sediments beneath kelp deposits (Dugan et

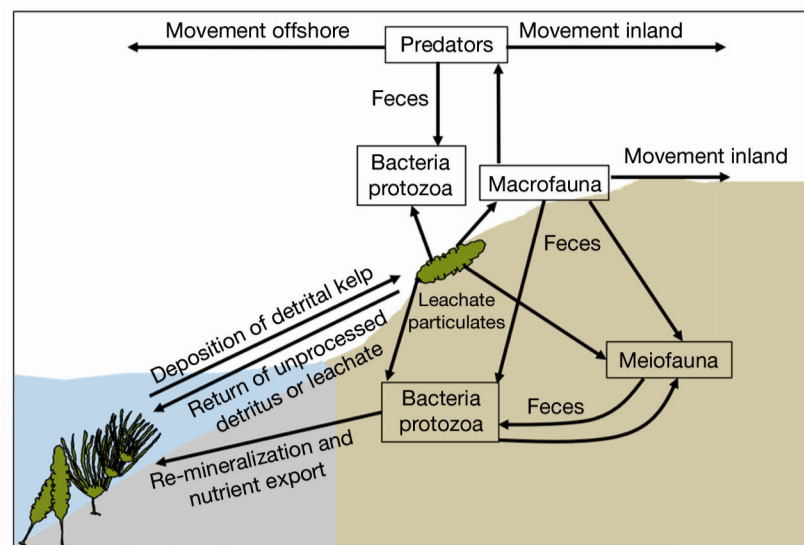


Fig. 3. Energy flow associated with faunal and microbial processing of kelp detritus in sandy beach ecosystems



al. 2011). Koop et al. (1982) found that very little DIN is returned to the sea following remineralization in beach sands in South Africa. In contrast, Dugan et al. (2011) showed that DIN in surf-zone water in California was positively correlated with DIN in intertidal sediments, suggesting export from beach sediments. Beaches can act as sources or sinks of nitrogen depending on the rate of erosion of beach sediments (Colombini & Chelazzi 2003, Dugan et al. 2011). Dissolved organic matter (DOM) may also return to the sea before bacterial processing (Dugan et al. 2011).

Deposits of kelp detritus on beaches also are readily colonized by meio- and macrofauna (Hayes 1974, Koop et al. 1982, Griffiths et al. 1983, McLachlan 1985, Inglis 1989, Dugan et al. 2003). Species distributions are tightly linked to kelp deposition, with the highest microbial and faunal abundance, biomass, and diversity occurring in the vicinity of detritus (Griffiths et al. 1983, McLachlan 1985, Dugan et al. 2003). Amphipods, isopods, dipterans, and coleopterans are the predominant macrofaunal consumers of kelp detritus (Griffiths & Stenton-Dozey 1981, Griffiths et al. 1983, Lavoie 1985, McLachlan 1985, Dugan et al. 2003). Their grazing activity releases particulates, leachates, and fecal pellets (Fig. 3), which stimulate the growth of bacteria and infaunal invertebrates, such as bivalves, nematodes, and oligochaetes (Newell et al. 1982, Griffiths et al. 1983, McLachlan 1985). Meiofauna in sediments directly absorb DOM and consume bacteria associated with kelp leachate and fecal pellets (Griffiths et al. 1983). Invertebrates can consume up to 75% of the biomass of detrital kelp in some beach systems (Griffiths & Stenton-Dozey 1981, Griffiths et al. 1983, Lastra et al. 2008), or as little as 5 to 9% in others (Koop et al. 1982, Inglis 1989), indicating large variability in the importance of these consumers in detrital processing. Macrofauna can slow the process of degradation in some systems by preferentially consuming highly degraded material, which retards microbial colonization and breakdown (Bedford & Moore 1984). The extent of microbial and meio- and macrofaunal colonization and processing of detritus are determined by the residence time of detrital deposits, which in turn is regulated by physical factors, such as beach morphology, weather, and tides, and characteristics of the detritus (e.g. buoyancy) (Orr et al. 2005). Long-term deposition of kelp detritus may have detrimental effects on species distribution and abundance on beaches by creating areas of anoxia, low pH, or high hydrogen sulfide concentration (McLachlan 1985, Colombini & Chelazzi 2003), or by providing a physical barrier to burrowing (Soares et al. 1996).

Kelp deposition on beaches and the associated accumulation of meio- and macrofauna attract predators such as birds, carnivorous isopods and coleopterans, crustaceans, and arachnids (Griffiths et al. 1983, Bradley & Bradley 1993, Anderson & Polis 1998, Dugan et al. 2003, Mellbrand et al. 2011). Consumption of kelp-associated fauna can account for a significant portion of the diets of these predators (Griffiths et al. 1983, Mellbrand et al. 2011), which then act as vectors for the landward transport of marine-derived material (Anderson & Polis 1998, Mellbrand et al. 2011). In particular, islands with low terrestrial relative to marine productivity are heavily influenced by the input of marine detritus (Polis & Hurd 1996, Anderson & Polis 1998).

#### Rocky intertidal habitats

A strong linkage also can occur between subtidal kelp beds or forests and adjacent rocky intertidal communities through the transfer of detritus. While detrital deposition tends to be low in rocky intertidal areas with high wave exposure, deposition on semi-exposed and sheltered rocky shores can be substantial (Bustamante et al. 1995, Bustamante & Branch 1996, Rodriguez 2003). For example, Bustamante et al. (1995) showed that, on average,  $960 \text{ g m}^{-2} \text{ d}^{-1}$  (wet mass) was deposited in a sheltered rocky bay in South Africa, exceeding local estimates of kelp productivity. Orr et al. (2005) estimated that kelps (*Macrocystis integrifolia*, *Nereocystis luetkeana*, and *Egregia menziesii*) account for 18 to 32% of macrophyte biomass accumulating on rocky and gravel beaches in British Columbia, Canada.

Invertebrate grazers on rocky shores may depend more on imported kelp detritus than intertidal micro- and macroalgae (Bustamante et al. 1995, Rodriguez 2003). On the central Chilean coast, sea urchins emerge from cryptic habitats in response to kelp deposition (Rodriguez & Farina 2001), forming aggregations that rapidly consume detritus (Rodriguez 2003). Sea urchins receiving this subsidy develop larger gonads than those consuming only autochthonous production (Rodriguez 2003). On rocky shores in South Africa, the limpet *Patella grenatina* traps and consumes detrital kelp when submerged at high tide (Bustamante et al. 1995). Kelp is a major component of the diet of these limpets, whose spatial distribution is correlated with the biomass of deposited kelp (Bustamante et al. 1995). Experimentally restricting access to detrital kelp reduced survival and biomass of limpets, indicating that this subsidy is a major

determinant of the distribution and abundance of this intertidal grazer (Bustamante et al. 1995).

Particulate detritus produced during erosion of kelp blades is utilized by intertidal and subtidal benthic filter feeders (Bustamante & Branch 1996, Kaehler et al. 2006). Kelp particulates are the dominant form of particulate organic matter (POM) within kelp beds and forests (Bustamante & Branch 1996) and can occur in concentrations exceeding that of phytoplankton across an offshore range of >14 km (Kaehler et al. 2006). In South Africa, kelp constitutes the largest proportion of the diets of intertidal filter-feeding mussels and barnacles, and spatial variation in filter-feeder biomass is related to near-shore concentrations of particulate kelp (Bustamante & Branch 1996). Duggins et al. (1989) linked high rates of secondary production in intertidal mussels and barnacles in Alaska to subsidy by nearby subtidal kelps. More recently, Tallis (2009) demonstrated that kelp constitutes 10 to 88% of the diets of filter feeders inhabiting intertidal areas near river mouths in Washington, USA, generally exceeding the dietary contribution of intertidal macroalgae and seagrasses.

### Offshore and alongshore transport and deposition

#### Rocky subtidal habitats

Barren habitats occur in the rocky subtidal zone and are generated through the grazing action of sea urchins, which denude the substratum of erect fleshy macroalgae. Barrens are characterized by low local productivity (Breen & Mann 1976, Chapman 1981, Miller 1985), but receive macroalgal subsidies from adjacent kelp beds and forests (Dayton 1985b, Basch & Tegner 2007, Britton-Simmons et al. 2009, Filbee-Dexter & Scheibling 2012). Basch & Tegner (2007) found that up to 250–400 g m<sup>-2</sup> of *Macrocystis pyrifera* (wet mass) accumulates at depths of 8 to 18 m off California. Similarly, Britton-Simmons et al. (2009) recorded an average of 514 g m<sup>-2</sup> of detrital kelp (*Laminaria* spp., wet mass) at 23 m depth in Washington. Kelp is the dominant component of macrophyte detritus accumulating in these rocky habitats above 30 m depth, accounting for ~50% of detrital biomass in California (Gerard 1976, Harrold & Reed 1985) and 71% in Washington (Britton-Simmons et al. 2009).

When detritus is abundant within kelp forests and adjacent areas, sea urchins do not graze attached kelps, but instead form sedentary aggregations or hide within cryptic habitats where they trap detritus as it is transported along-bottom or accumulates

(Mattison et al. 1977, Dean et al. 1984, Harrold & Reed 1985, Rogers-Bennett et al. 1995, Vanderklift & Kendrick 2005, Basch & Tegner 2007, Vanderklift & Wernberg 2008, Britton-Simmons et al. 2009). When detrital supply becomes limited, sea urchins increase their rate of movement and form grazing fronts that rapidly consume stands of attached kelps (Dayton 1985b, Ebeling et al. 1985, Harrold & Reed 1985). Low detrital supply, therefore, triggers the transition from a highly productive kelp forest to a low-productivity sea urchin barren.

The onshore advance of grazing fronts of sea urchins is generally limited by wave action, either directly or via the whiplash effect of kelps (Velimirov & Griffiths 1979, Dayton 1985b, Scheibling et al. 1999, Konar & Estes 2003, Siddon & Witman 2003, Lauzon-Guay & Scheibling 2007). In Nova Scotia, this wave-mediated upper limit of destructive grazing enables kelp beds to persist in shallow bands along the coast (Brady & Scheibling 2005), while dense populations of sea urchins in adjacent barrens subsist in part on the supply of kelp detritus from the shallows (Kelly et al. 2012). Sea urchins supplied with detrital kelp develop larger gonads than those without access to this food resource (Rogers-Bennett et al. 1995, Basch & Tegner 2007, Britton-Simmons et al. 2009). Detrital kelp is less abundant along exposed coastlines relative to more sheltered coastlines or bays (Dayton 1985b, Filbee-Dexter & Scheibling 2012). As a result, sea urchins in barrens on exposed coasts are of lower nutritional condition than those feeding directly on kelps in the shallow subtidal zone, whereas sea urchins in deep depositional areas in protected bays are well nourished (Dayton 1985b, Brady & Scheibling 2006, K. Filbee-Dexter & R. E. Scheibling unpubl. data). Detrital subsidy to sea urchins decreases with distance from the kelp bed or forest (Mattison et al. 1977, Rogers-Bennett et al. 1995, Kelly et al. 2012), but is documented for sea urchins on reefs up to 8 km from the kelp source (Vanderklift & Wernberg 2008).

Kelp particulates and fecal pellets from sea urchins and other grazers are transported offshore where they are consumed by filter- and deposit-feeding macroinvertebrates, meiofauna and microbes, enhancing secondary production across a range that can extend >14 km from the kelp source (Duggins et al. 1989, Kaehler et al. 2006). Along the Atlantic coast of Nova Scotia, sea urchins form dense grazing fronts that advance onshore consuming kelp at a rate of 454 to 530 g d<sup>-1</sup> (dry mass) across 1 m of front. This translates to an estimated fecal production rate of 74 to 81 g yr<sup>-1</sup> per linear meter of front, or 20720 kg

$d^{-1}$  across an estimated 280 km of coastline spanned by these grazing fronts in the mid to late 1990s (Sauchyn & Scheibling 2009a, Sauchyn et al. 2011). The small (~2 mm diameter) fecal pellets are a highly nutritious food source relative to live kelp, and nitrogen, lipid, and available energy content increase rapidly during degradation (Sauchyn & Scheibling 2009b).

#### Soft-sediment habitat

Kelp detritus is transported alongshore or offshore via tidal, bottom, or surface currents to unvegetated soft-sediment habitats ranging from the surf zone to bathyal and abyssal depths. Submarine canyons trap submerged detritus as it is transported by alongshore currents, accumulating massive quantities of material and acting as conduits for detrital transport to the deep sea (Josselyn et al. 1983, Vetter 1995, 1996, Harrold et al. 1998, Vetter & Dayton 1998, Okey 2003). *Macrocystis pyrifera* accounted for 12 to 22% of drift 'parcels' in Carmel Canyon, off California, and 53% of drift parcels on the adjacent continental shelf (Harrold et al. 1998). Kelp detritus transported over the continental shelf is more likely to be consumed or buried before arrival at the deep sea, compared to that transported via submarine canyons (Vetter & Dayton 1999). However, the abundance of detrital kelp can decrease by 95% between 30 and 900 m depth in submarine canyons off California (Vetter & Dayton 1999); detrital kelp is sparse ( $2.5 \times 10^{-2}$  g C  $m^{-2}$ ) at depths of >1 km (Smith 1983). Long-distance transport of kelp detritus offshore is more likely to occur via surface dispersal of floating rafts, which ultimately lose buoyancy and sink to the deep sea (Smith 1983, Bernardino et al. 2010). Detrital accumulations (mats) in shallow habitats and submarine canyons are expansive during periods of calm wave action in spring and summer, while wave surge associated with fall and winter storms causes detrital flushing or mat compaction in deeper regions (Vetter 1995, Vetter 1998, Okey 2003).

Kelp detritus is a primary source of food in subtidal soft-sediment habitats, as it is for sandy beaches, attracting diverse assemblages of detritivores, predators, and microbes, whose distribution and secondary production are largely determined by the availability of detritus (Lenanton et al. 1982, Bedford & Moore 1984, Kim 1992, Vetter 1995, 1996, Okey 1997, Harrold et al. 1998, Vetter & Dayton 1998, 1999, Hyndes & Lavery 2005, Bernardino et al. 2010, Krumhansl & Scheibling 2012). Secondary production rates in de-

trital mat communities in submarine canyons exceed those of most other natural systems (Vetter 1995). Juvenile fish use mats of kelp detritus as nursery habitat, feeding on associated amphipods, leptostraceans, and copepods (Lenanton et al. 1982, Vetter 1998, Hyndes & Lavery 2005). Vetter (1998) experimentally demonstrated that predation rate on these crustaceans decreases with mat thickness, indicating that detrital mats also provide structural protection. During calm conditions, thick bacterial mats colonize the surface of detrital deposits, causing crustaceans to move into open patches where they are more susceptible to predators (Vetter 1998). Bacterial mats are unable to form during periods of frequent wave disturbance (Vetter 1998).

Community dynamics within mats of detrital kelp and underlying sediments are largely dependent on the size and residence time of deposits, which in turn are determined by physical processes and the rate of consumption by large herbivores, such as sea urchins (Scheibling & Raymond 1990, Kim 1992, Okey 1997, 2003, Norkko et al. 2000). In small deposits with short residence times, or in ephemeral deposits in wave- or current-swept locations, faunal abundance and diversity are locally enhanced relative to the surrounding sediments (Lenanton et al. 1982, Vetter 1995, 1996, Harrold et al. 1998, Vetter & Dayton 1998, 1999, Hyndes & Lavery 2005). In larger and more persistent deposits, hypoxic conditions can develop in the bottom layers of detrital mats. In some cases this leads to widespread anoxia and decreased microbial and faunal abundances within the deposit and underlying sediments (Scheibling & Raymond 1990, Tzvetlin et al. 1997, Mokievsky et al. 2005). Local hypoxia also can occur in sediments beneath small deposits with relatively short residence times (Thrush 1986, Vetter 1996, Vetter & Dayton 1998, Okey 2003, Bernardino et al. 2010). Opportunistic species that tolerate low oxygen and high sulfide conditions, such as capitellid and dorvellid worms, can occur in high abundance beneath deposits (Levin & Smith 1984, Thrush 1986, Vetter 1996, Okey 2003, Bernardino et al. 2010). More diverse faunal assemblages may accumulate in the vicinity of detritus, where the adverse effects of organic enrichment are less severe (Thrush 1986). In large, persistent deposits, a greater diversity of fauna can occur on the surface and edges of mats, where detrital material is freshly deposited and turns over more rapidly than material in lower layers (Tzvetlin et al. 1997).

Kelp detritus also is deposited in intertidal surfgrass and subtidal seagrass beds, where it subsidizes multiple trophic levels (Hori 2006, Wernberg et al.

2006). Wernberg et al. (2006) documented large deposits of detrital kelp within seagrass beds hundreds of meters from a kelp source in southwestern Australia. Seagrasses and seagrass epiphytes assimilate kelp-derived nitrogen that is leached during detrital breakdown (Hyndes et al. 2012). Kelp deposits also attract assemblages of herbivores, which in some locations consume most of the detritus within days (Wernberg et al. 2006). When given a choice, herbivores and detritivores that inhabit temperate seagrass beds preferentially consume kelp and other macroalgae over seagrasses (Smit et al. 2006, Doropoulos et al. 2009). Stable isotope analysis shows that seagrass is a less important dietary source than imported and autochthonous macroalgae, periphyton, and epiphytic algae in seagrass food webs (Stephenson et al. 1986, Smit et al. 2006, Hyndes et al. 2012). Doropoulos et al. (2009) suggest that the importance of macroalgal subsidies to seagrass consumers varies seasonally in response to changing levels of production by autochthonous macroalgae and periphyton.

#### Long distance sea-surface transport

Kelps and other macroalgal species with pneumatocysts are buoyant after dislodgement from the substrate, and can accumulate in rafts that drift with surface currents and winds (Helmuth et al. 1994, Hobday 2000a, Hinojosa et al. 2010). The estimated wet biomass of floating rafts of giant kelp *Macrocystis pyrifera* in California and Chile can range from 100 to 1500 kg km<sup>-2</sup> (Hobday 2000a, Hinojosa et al. 2010). In South Africa, rafts of *M. pyrifera* can be up to 6 m in diameter and 1 m deep, and contain as many as 200 individual thalli (Helmuth et al. 1994). Dispersal of rafts is low when prevailing winds are onshore (Harrold & Lisin 1989) or in areas with large freshwater input such as fjords (Hinojosa et al. 2010). Kelp rafts may disperse hundreds of kilometers in areas with strong unidirectional currents (Helmuth et al. 1994, Fraser et al. 2010). The dispersal and spatial distribution of kelp rafts vary seasonally in response to changing wind and current patterns (Harrold & Lisin 1989, Hobday 2000a, Hinojosa et al. 2010).

The dispersal of a kelp raft is also dependent on environmental and biological factors that affect buoyancy (Rothausler et al. 2009). Rothausler et al. (2009, 2011a,b) tested the interactive effects of temperature, UV, and grazing by amphipods on the photosynthesis, growth, and reproduction of floating *Macrocystis pyrifera*. *Macrocystis pyrifera* is able to withstand a wide range of UV conditions by adjust-

ing photosynthetic pigments and photochemical reactions (Rothausler et al. 2011a,b), but photosynthesis, growth, and reproduction are greatly reduced in water temperatures above 20°C, which causes degradation and loss of buoyancy (Rothausler et al. 2009, 2011a). The effect of grazing amphipods on biomass and buoyancy is highest at moderate water temperatures (15 to 20°C) where grazing rate exceeds kelp growth (Rothausler et al. 2009). At low temperatures (<15°C), kelp growth can compensate for biomass lost to grazers (Rothausler et al. 2009). These results indicate that raft dispersal is greatest in waters below 15°C. Low seawater nitrate levels may also reduce buoyancy (Hobday 2000a).

Kelp rafts accumulate diverse communities of invertebrates while drifting (Edgar 1987, Hobday 2000b, Thiel & Gutow 2005). Some organisms remain attached to kelps following dislodgement from the substrate, while others settle or become attached to rafts they encounter during drifting. It is hypothesized that rafting is an important mechanism of long-distance dispersal for invertebrates (Highsmith 1985, Edgar 1987, Helmuth et al. 1994, Fraser et al. 2010), particularly for species that have a short larval phase or brood their young to a benthic stage (Highsmith 1985, Helmuth et al. 1994). Evidence for this includes genetic linkages between broadly distributed populations of brooding species (Fraser et al. 2009), and the discovery of individuals brooding young on kelp rafts (Helmuth et al. 1994). Holmquist (1994) proposed that dispersal via rafting is more effective than larval dispersal because of a lower risk of mortality. Kelps remain reproductive while drifting (Rothausler et al. 2009), and propagules of other algal and plant species have been collected from kelp rafts (Edgar 1987), indicating that dispersal via kelp rafts is not limited to invertebrates.

#### HUMAN IMPACTS ON KELP BIOMASS AND DETRITAL SUBSIDY

Anthropogenic pressures on natural systems have mounted over the past centuries, resulting in profound changes in the marine environment (Worm et al. 2005, Lotze et al. 2006, Jackson 2008). Kelp ecosystems are no exception to this trend, and may be particularly sensitive given their proximity to human populations. A suite of anthropogenic factors causes declines in kelp biomass and population size, which reduces rates of detrital production (Krumhansl & Scheibling 2011a). Fishing high-level predators releases sea urchin populations and leads to the

destructive grazing of kelp beds and forests (Steneck et al. 2002). Climate change is expected to cause large-scale losses in kelp biomass and decrease the resilience of kelp beds and forests due to warming sea surface temperatures, changes in the nutrient dynamics of the water column, and increases in storm frequency and intensity (Steneck et al. 2002, Martinez et al. 2003, Springer et al. 2010, Wernberg et al. 2010). Large-scale kelp canopy loss is linked to warm water temperatures associated with the disruption of upwelling cycles during El Niño years (Gunnill 1985, Steneck et al. 2002, Martinez et al. 2003, Vasquez et al. 2006, Foster & Schiel 2010, Springer et al. 2010). Storms that cause large wave events and reduce kelp biomass (Gerard 1976, Luning 1979, Gunnill 1985, Seymour et al. 1989, Reed et al. 2008) are likely to have greater long-term effects as the incidence of severe storm events increases (Easterling et al. 2000, Byrnes et al. 2011). Declines in kelp biomass also have occurred in response to coastal pollution (Steneck et al. 2002, Connell et al. 2008, Foster & Schiel 2010) and development and extraction activities that disrupt subtidal habitat (Pulfrich et al. 2003) and cause run-off of toxic materials, warm water, and sediments (Medina et al. 2005, Springer et al. 2010). The introduction and spread of non-native algal species can replace kelps, altering the species composition and nutritional quality of detritus (Bishop et al. 2010, Krumhansl & Scheibling 2012).

Direct removal of the kelp canopy through harvesting also can have severe repercussions for kelp biomass and detrital production. Kelp is primarily used for human consumption (Rothman et al. 2006, Peteiro & Freire 2011), alginic acid extraction (Vasquez 2008, Veá & Ask 2011), and as feed for cultured abalone (Troell et al. 2006, Macchiavello et al. 2010). Canopy harvesting has increased dramatically in recent decades (Rothman et al. 2006, Vasquez 2008, Thompson et al. 2010, Veá & Ask 2011). Kelp is currently harvested in many countries worldwide (including the USA, Canada, Mexico, South Africa, Chile, Australia, New Zealand, Japan, China, Taiwan, Ireland, Norway, the UK, and Iceland) and markets continue to expand (Adams et al. 2009, 2011). Historically, kelp harvesting involved collection of beach-cast material; however, since the 1960s this has been replaced by direct harvesting in response to increasing demand (Vasquez 2008, Veá & Ask 2011). With growing concern that wild populations of kelp cannot sustain harvesting at the current rate, the harvest potential of currently unexploited areas, such as the Arctic, is being investigated (Sharp et al. 2008) and

suspended culture of kelps has been developed in some bays and offshore areas (Troell et al. 2006, Macchiavello et al. 2010, Peteiro & Freire 2011, Radiarta et al. 2011). Kelp mariculture may relieve some of the pressure on natural populations, but little is known about its ecological impact. Cultured kelp is a source of detritus (Yoshikawa et al. 2001), but at high density, suspended kelps can reduce current speeds (Shi et al. 2011) and may cause organic enrichment of local sediments and anoxia.

The negative effects of kelp biomass loss may extend well beyond the local kelp community to areas subsidized by kelp detritus. We have demonstrated that kelp detritus is transported to a wide range of habitats that extend from tens of meters to hundreds of kilometers from the source of production. Patterns of secondary production and community organization in these communities are tightly linked to detrital resources, indicating that kelp productivity fuels regional-scale productivity. A loss of detrital resources can therefore be predicted to have broad-scale ecological consequences. This has been demonstrated in beach systems, where a reduction kelp detrital input due to a decline in subtidal kelp cover or the removal of beach-cast material causes declines in the richness, abundance, and biomass of macrofauna and shorebirds (Bradley & Bradley 1993, Kirkman & Kendrick 1997, Dugan et al. 2003). Similar effects of subtidal kelp removal can be expected in other habitats subsidized by kelp detritus.

## CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

Although most of the primary production of kelp beds and forests flows through detrital pathways, detrital production is quantified for relatively few kelp populations. These measurements are sparsely distributed throughout the temperate range of kelps and are highly variable within and among kelp species, underscoring the need for more location- and species-specific measurements. There is only 1 estimate for an Arctic kelp population, and detrital production rates are missing entirely for many kelp genera (e.g. *Nereocystis*, *Agarum*, *Alaria*, *Costaria*, and *Pterogophora*). Variation in detrital production rates and the relative importance of erosion versus dislodgement as production processes may be related to characteristics of particular kelp species or populations (e.g. morphotype, density), or to the physical environment (e.g. wave exposure, temperature regime, latitude). Understanding the mechanisms that

regulate detrital production at large spatial scales would provide insight into the potential response of communities to environmental change, which may be greatest at the lower and higher latitudinal limits of kelps. A more complete quantification of detrital production throughout the geographic range of kelps and simultaneous measures of erosion and dislodgement are required to address these hypotheses and to improve our ability to model energy flow through coastal systems.

The extent of detrital subsidy by kelps is determined by the magnitude and direction of detrital export. The proportion of detrital production exported or retained is well quantified for seagrass (Heck et al. 2008), salt marsh (Gallagher et al. 1980, Dame & Stillewell 1984, Bouchard & Lefeuvre 2000), and mangrove communities (Kristensen et al. 2008), likely because these macrophyte assemblages typically occur in semi-enclosed bays or estuaries where exported material can be readily trapped and measured. Kelp communities, on the other hand, generally occur on semi-protected or exposed coasts where trapping and quantifying material flows is considerably more difficult. Less detritus may be retained in kelp beds and forests relative to seagrass meadows, salt marshes, and mangrove forests because kelps grow only on rocky substrata in areas with moderate to high wave exposure, where trapping and burial are unlikely. Export rates in kelp ecosystems can be estimated as the difference between simultaneous measures of detrital production and accumulation within kelp beds or forests. Residence time of kelp fragments or thalli manually deposited within these habitats can provide insight into environmental factors that govern detrital export rates and seasonal variation. The relative importance of inshore versus offshore transport can be estimated by relating detrital production rates to arrival rates in habitats along an onshore-offshore gradient. Transport direction and distance also can be measured by tracking labeled detrital fragments and thalli (e.g. with flagging tape) using diver surveys, towed video, or ROVs.

Kelps are a dominant component of detrital accumulations in a variety of intertidal and subtidal habitats, although few studies quantify the composition of these deposits and the proportional contribution of kelps. The relative contribution of kelps and other macrophytes to the detrital pool will depend on their abundance in coastal habitats, physical characteristics of detritus that affect transport, and physical transport mechanisms that can vary across habitat types. A comprehensive understanding of energy flow in coastal systems requires consideration of all

local sources of macrophyte detritus. The composition of detrital deposits affects their turnover rate and patterns of colonization by microbes and meio- and macrofauna on the surface of detritus and in underlying sediments. Future research should emphasize comparisons of subtidal abundance and distribution, detrital production rates, transport, and depositional dynamics between kelps and other dominant macrophytes. Examining the species composition of macrophytes in detrital deposits across broad scales within regions could indicate the relative importance of different detrital sources to macrofaunal communities in various habitat types. The link between spatial patterns of production and deposition of different macrophyte species may be clearer when these species occupy different physical environments.

Kelp detritus subsidizes consumers across a wide range of marine and terrestrial habitats, acting as a major form of connectivity in coastal systems, which enhances species abundance, diversity, productivity, and reproductive output. Most studies focus primarily on kelp subsidies to consumers. The potential for kelp to subsidize primary producers was only recently demonstrated (Hyndes et al. 2012). Kelps rapidly leach nutrients during microbial breakdown (Koop et al. 1982), contributing to the nutrient pool available to nearby primary producers. This nutrient input may be particularly important in oligotrophic systems, and where kelp is degrading in the direct vicinity of other primary producers, such as seagrasses and dune grasses.

Most studies examining the consequences of detrital subsidies in receiving communities have been conducted over relatively short time scales. Seasonal dynamics in some detritus-based communities (e.g. in submarine canyons or on sandy beaches) are related to variation in physical factors that determine the size and residence time of detrital deposits. In many habitats the deposition of kelp detritus is a sporadic occurrence. Receiving communities may be adapted to protracted periods of low food abundance punctuated by detrital food pulses that occur over short time scales (Sears et al. 2004, Filbee-Dexter & Scheibling 2012). These pulsed depositional events may play an important role in maintaining gamma diversity, especially in the deep sea (Bernardino et al. 2010). Long-term environmental changes and reductions in kelp populations may have different and more pronounced consequences for detritus-based communities than changes resulting from short-term environmental variability.

Many of the species that consume detritus within kelp beds and forests and in adjacent systems (e.g.

sea urchins, abalone, sea cucumbers, and mussels) are the basis of valuable coastal fisheries. These species also are prey for higher trophic level consumers (e.g. lobsters, ground fish, and sea otters) that have commercial or ecological importance (Dayton et al. 1998, Steneck et al. 2002). Consequently, the provisioning of detrital food webs is a major ecosystem service provided by kelp beds and forests. Loss of kelp biomass threatens this important function through reduction or elimination of detrital production. Kelp populations require more than 6 yr to recover from canopy harvesting (Lorentsen et al. 2010), and declines in the order of decades are documented following overfishing of apex predators and trophic cascades, repeated El Niño events, or freshwater and sewage run-off (Mann 1977, Dayton et al. 1998, Steneck et al. 2002, Foster & Schiel 2010). Dire ecological and economic consequences can be expected as a result of long-term declines in kelp canopy. Effective management of coastal ecosystems and resources demands a broader consideration of the role of detrital flows from kelp and other marine macrophytes in determining overall productivity on regional scales.

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