

Kelp and rivers subsidize rocky intertidal communities in the Pacific Northwest (USA)

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ABSTRACT: Rocky intertidal filter feeders couple benthic and pelagic systems by consuming particles in the water column and transferring energy and nutrients to sediments and benthic predators. Less is known about their role as links between terrestrial and marine systems. I explored this link using a dual stable isotope approach to discern the diets and trophic position of 4 common sympatric rocky intertidal filter feeders (*Mytilus californianus*, *Balanus glandula*, *Semibalanus cariosus*, *Pollicipes polymerus*) living near river mouths in the Pacific Northwest (USA). Freshwater particulate organic matter (POM) was assimilated by all filter feeders, though at relatively low levels (5 to 41%). Intertidal macroalgae and seagrass also contributed to filter feeder diets, but the primary resource base was kelp in both summer and winter, accounting for 11 to 88% in filter feeder diets, depending on species and season. Although these species shared a common resource base, they occupied distinct trophic positions. Natural and logging-induced increases in riverine inputs were related to higher trophic position for all species, indicating that riverine carbon may enter the rocky intertidal food web through the microbial loop. I show that filter feeder trophic positions were higher in winter when river discharge is highest, near river mouths (in winter) where river-borne inputs are highest, and downstream of more heavily logged watersheds where river loads of dissolved organic carbon are highest. Rocky intertidal filter feeders do couple land and sea, further emphasizing the need to manage these ecosystems jointly.

KEY WORDS: Logging · Isotopes · Trophic structure · Terrestrial–marine links · Conservation · *Balanus glandula* · *Mytilus californianus* · *Semibalanus cariosus*

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INTRODUCTION

Benthic filter feeders couple benthic and pelagic systems by consuming particles in the water column and transferring energy and nutrients to sediments and benthic predators (Menge 1992, Ricciardi & Bourget 1999). For example, mussels and barnacles in rocky intertidal habitats capture suspended material including phytoplankton, detritus, or zooplankton (Navarrete & Wieters 2000, Wong & Levinton 2006) and are the primary prey of the keystone predator *Pisaster ochraceus* in the Pacific Northwest, USA (MacGinitie 1938). These same invertebrates also produce pelagic larvae that are eaten by larval fish (Hartman et al. 2004), and barnacle molts provide food for juvenile

migrating chinook salmon *Oncorhynchus tshawytscha* in the northeast Pacific (Fisher & Pearcy 1997). Despite their ecological importance, little is known about the dietary composition of many common species of intertidal mussels and barnacles (Sanford & Menge 2001).

Detritus produced by kelp forests may be one of the major components of rocky intertidal filter feeder diets. Kelp beds provide some of the most substantial and far-reaching subsidies in the natural world. Kelp detritus is a major food source for residents of sandy beaches (Zobell 1971, Griffiths et al. 1983), subtidal areas (Duggins et al. 1989), offshore surface waters (Kingsford 1992), submarine canyons (Harrold et al. 1998), and other regions of the deep ocean (Lawson et al. 1993). Kelp-derived material has also been identi-

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fied as a major food source for some rocky intertidal filter feeders in Alaska, USA (*Mytilus edulis*; Duggins et al. 1989) and South Africa (*M. galloprovincialis*, *Aulacomya ater*, *Gunnarea capensis*; Bustamante & Branch 1996). However, no generality exists about the importance of kelp-derived subsidies to adjacent rocky intertidal communities, and this potentially major diet component has been overlooked in recent hypotheses about the drivers of mussel and barnacle population dynamics (Sanford & Menge 2001, Leslie et al. 2005, Phillips 2005).

In addition, intertidal filter feeders may act as important links between terrestrial and marine systems by consuming detritus from freshwater or terrestrial sources. Sites where kelp subsidies to intertidal and subtidal communities have been documented are near land masses with few large rivers. Yet, many rocky intertidal communities occur near rivers, the potential conduits of subsidies from terrestrial and aquatic systems (Howarth et al. 1991, Rabalais & Turner 2001). The importance of upstream subsidies to nearshore marine systems is critical to understand since rocky intertidal population dynamics can be driven by bottom-up processes (Sanford & Menge 2001, Leslie et al. 2005) and human activities are massively altering the delivery of nutrients (Vitousek et al. 1997, Rabalais & Turner 2001) and carbon (Howarth et al. 1991, Smith & Hollibaugh 1993, Correll et al. 2001) to coastal oceans worldwide. Excess nutrients can stimulate primary production (Rabalais & Turner 2001), and additional dissolved organic carbon can increase heterotrophic bacteria production and the importance of the microbial loop (Howarth et al. 1991, Maranger et al. 2005). Most examples of marine responses to land conversion either come from bays and estuaries with relatively long residence times (Hudson River) or areas that have undergone massive land conversion (Mississippi River watershed). But the question remains: what are the consequences of common, less severe levels of land use for coastal communities other than those in large estuaries, such as rocky intertidal habitats on exposed coasts?

I used stable nitrogen and carbon isotopes to explore the importance of kelp and riverine subsidies to rocky intertidal filter feeder diets and trophic position. Species investigated were the competitive dominant space occupier, the California mussel *Mytilus californianus* and 3 co-occurring barnacle species (*Balanus glandula*, *Semibalanus cariosus*, *Pollicipes polymerus*). Along the Washington coast in the Pacific Northwest, the rocky intertidal lies between extensive kelp beds and intensively logged coastal watersheds. River chemistry varies substantially with logging intensity (Tallis 2006), the predominant human land-based activity in this region, which allows an analysis of the

sensitivity of filter feeder diets and trophic position to major differences in river inputs driven by land use.

Differences in river inputs could influence filter feeder trophic position by altering the relative abundance of phytoplankton and microbes. Barnacle and mussel diets are largely determined by the size of particles caught with their gill filaments or cirri. Barnacles can capture phytoplankton (Lewis 1981, Navarrete & Wieters 2000), and mussels may do so preferentially (Ward & Shumway 2004), so land use that elevates nutrient delivery could increase the proportion of phytoplankton available. Some species of mussels (Ward & Shumway 2004) and barnacles (Southward 1955, Bouvy et al. 2006) can also capture bacteria, but it is more likely that they access the microbial loop by consuming ciliates or zooplankton that have fed on bacteria (Gosselin & Qian 1997, Scherwass & Arndt 2005, Bouvy et al. 2006). Feeding through this pathway would place filter feeders at a higher trophic level. Land use that increases the amount of dissolved organic carbon (DOC) delivered to the coastal ocean could thus increase filter feeder trophic level by enhancing the microbial loop and increasing the relative abundance of bacteria and their protozoan predators.

I show that all 4 common rocky intertidal filter feeders act as links between terrestrial, benthic, and pelagic systems by assimilating material derived from freshwater particulate organics, intertidal macroalgae, and kelp. In addition, I provide several lines of evidence suggesting that riverine DOC inputs increase filter feeder trophic position by stimulating the microbial loop.

MATERIALS AND METHODS

Study sites. I studied 5 intertidal sites on the Olympic Peninsula, Washington (USA; Fig. 1). These sites were located around river mouths downstream of watersheds ranging in area from 6 to 1628 km² (Table 1). There are 2 prominent land uses in the region, with at least 99% of each watershed in some combination of forest (Olympic National Park) or land managed for commercial timber harvest. Unpaved road density ranges from 1.2 to 2.3 km road km⁻² in the study watersheds and serves as a useful indicator of logging intensity (Table 1). Nutrient and carbon concentrations are strongly related to logging intensity (Tallis 2006). River DOC concentrations range from 1.45 to 5.37 mg C l⁻¹ in summer and from 1.77 to 7.12 mg C l⁻¹ in winter (Tallis 2006). DOC concentrations increase with watershed road density in summer only (Tallis 2006). Nitrate concentrations range from 38 to 383 µg l⁻¹ in summer and from 39 to 526 µg l⁻¹ in winter (Tallis 2006). Nitrate

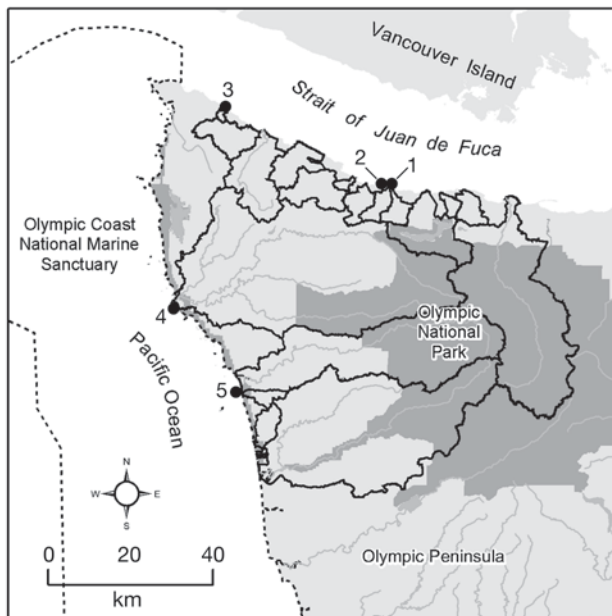


Fig. 1. Study rivers on the Olympic Peninsula, Washington (USA). Rivers, starting from the east, were East Twin Creek (1), West Twin Creek (2), Rasmussen Creek (3), Quillayute River (4), and Cedar Creek (5). Heavy black lines demarcate each river's watershed area

Table 1. Study watershed characteristics. na: not applicable

River	Area (km ²)	Annual average precipitation (mm)	Road density (km road km ⁻²)
Rasmussen	6	na	1.55
Cedar	27	2538	2.34
West Twin	33	1639	1.83
East Twin	36	1505	1.58
Quillayute	1628	2562	1.23

concentrations increase with road density in both seasons (Tallis 2006).

There is a substantial rainfall gradient across the study area, with west coast watersheds receiving an average rainfall of 3.1 m yr⁻¹ (Edmonds et al. 1995) and northeastern watersheds only 1.5 m yr⁻¹ (see Table 1 for rainfall in study watersheds). All rivers empty along exposed coastline, although the west coast (Fig. 1, Rivers 4, 5) is more exposed.

Plume mapping. Invertebrate and macroalgal sampling locations were established in the summer of 2004 to evenly sample rocky intertidal sites affected by river plumes. I mapped plumes on 2 to 4 occasions each season by surveying the surf zone with a handheld YSI temperature and salinity probe (Model 30M or 58) and a handheld GPS unit (Garmin etrex Legend). Mapping always began 1 h after high tide so that river flow was

not impeded by tidal surge. Using this timing, I was able to map the maximum extent of summer plumes during the time when benthic filter feeders would be feeding. I plotted all plumes in ArcView 3.1 and determined the average summer plume extent. For each river, I split the plume on each side of the mouth into 4 equal sections and used the coordinates at the nodes as sampling locations, establishing 10 sampling locations per plume. When rocky intertidal habitat was not continuous, I sampled the closest available rocky substratum. Many river plumes increase in extent and overlap with other plumes during high winter flows, making the extent of individual plumes unclear. Because of my inability to map the full extent of each plume in the winter, sampling locations defined by the summer plume mapping were used in winter as well. This means that winter sampling was no longer representative of each river's full plume area. Rather, sampling the same points in both seasons allowed me to determine whether seasonal changes in freshwater discharge influenced diet composition or trophic level in a set area (as defined by the summer plumes).

Collection of food sources. I assumed possible dietary sources for all consumers to be intertidal and subtidal detritus, marine phytoplankton, and freshwater phytoplankton and detritus. Macroalgal carbon and nitrogen isotope signatures of all likely food sources were determined by collecting macroalgal and seagrass samples (5 to 10 g of each species present) at the 10 sampling locations within each river site. The full set of species collected included *Mastocarpus* spp., *Fucus* spp., *Porphyra* spp., *Ulva* spp., *U. intestinalis*, unidentified filamentous red algae, unidentified filamentous green algae, and the seagrass *Phyllospadix scouleri*. I also collected pieces of drift kelp where present. It was often impossible to identify kelp species, but dominant species in this region are *Nereocystis leutkeana*, *Alaria marginata*, *Laminaria bongardiana*, *L. setchellii*, *Hedophyllum sessile*, *Egregia menziesii*, *Costaria costata*, *Cymathere triplicata*, and *Macrocystis* spp. *N. leutkeana* and *A. marginata* likely contribute the most biomass to the detrital pool since they are both abundant, fast-growing annual species (A. Salomon pers. comm.).

Replicate summer freshwater particulate organic matter (POM) samples were collected at the mouth of each river (0.0 salinity) 3 to 4 times between June and September 2004. During the same period, I also collected replicate marine POM samples 4 to 8 times from points closest to the river mouths with salinity >30. This was repeated for replicate freshwater POM (2 to 5 times per river) and replicate marine POM samples (2 to 4 times per river) in winter between February and March, 2005. For all POM samples, a known volume of seawater or freshwater sample was filtered through

precombusted Whatman G/F filters, iced for less than 24 h, and frozen. The total volume varied by river and season and was always sufficient to collect enough material for isotope analysis.

Collection of consumers. Invertebrate samples were collected twice in a 1 yr period. The first sampling (September 2004) represented summer conditions characterized by periodically intense upwelling off the Washington coast (Hickey & Banas 2003) and minimal rainfall (Edmonds et al. 1995). The second sampling (March 2005) represented typical winter conditions of frequent storms and maximal rainfall (Edmonds et al. 1995). During each collection, I used the biological assemblage to identify the middle of the upper midlittoral zone (~1.7 m above mean lower low water, MLLW) where acorn barnacles *Balanus glandula* are most common (Kozloff 1993). At each sampling location (n = 10 per river site), I gathered 10 *B. glandula* (n = 100 per river site per season) that represented the size distribution of individuals present in 1 m². When present, I also collected individuals (n = 5 per sampling location, 50 per river site per season) of thatched barnacles *Semibalanus cariosus*, gooseneck barnacles *Pollicipes polymerus*, and California mussels *Mytilus californianus*. These were collected from the middle of the lower midlittoral zone (~0.6 m above MLLW; Kozloff 1993). All samples were placed on ice, frozen within 1 d of collection, and returned to the laboratory.

Pre-processing of samples for isotope analysis. In the lab, average basal diameters and heights of all *Balanus glandula* and *Semibalanus cariosus* were measured. I considered body volume the best estimate of size for these barnacles, since their shape changes dramatically with space competition. Body volume was calculated with an equation that relates the cylindrical volume derived from barnacle measurements to actual volume. The equation was derived by regressing shell measurements with shell volume determined by filling barnacles (n = 50) with plastic beads of known volume ($F = 621$, $p < 0.0001$, $r^2 = 0.93$; C. Harley unpubl. data). *Pollicipes polymerus* was measured across the base of the caudal plates just above the peduncle, and I recorded the longest length of each *Mytilus californianus*.

Whole bodies of *Balanus glandula* (n = 5) and *Semibalanus cariosus* were removed from their shells, soaked in 1 N HCl to remove remnant calcium carbonate for ~2 min, rinsed in deionized water, and freeze dried. The muscular stalks of *Pollicipes polymerus* and the adductor and byssal retractor mussels of *Mytilus californianus* were prepared in the same way. I rinsed approximately 1 g of each algal sample in deionized water and removed all visible epiphytes. These samples were also acid washed and rinsed. All prepared samples were freeze dried, homogenized, packed in

tin capsules, and sent to the isotope facility of the University of California, Davis, for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic analysis.

River plume trends in diet contributions and trophic level. I calculated diet contributions and trophic level for rocky intertidal filter feeders separately for 2 sets of analyses: river plume trends and community trends. First, I was interested in spatial patterns within each area adjacent to river mouths. Filter feeders were collected along the gradient from fresh to salt water at each river mouth, and therefore, I expected the relative contribution of freshwater and marine food sources to change along these transects. Logging has changed the amount of nitrogen and carbon in fresh water among these sites (Tallis 2006), so I also expected different patterns along the fresh–salt gradient among watersheds. For these analyses, I only used *Balanus glandula*, because it was the only filter feeder found at all sampling locations (n = 10) within each river site (n = 5).

I used the SOURCE mixing model (Lubetkin & Simenstad 2004) in S-PLUS to identify discrete food sources, calculate their contributions to filter feeder diets, and estimate the trophic level of each consumer. Fractionation values of carbon and nitrogen in barnacles are not known, so I used literature values based on other invertebrates. For nitrogen fractionation, I used the value of +2.1‰ from the most recent meta-analysis of nitrogen trophic fractionation for analyses of whole organisms (McCutchan et al. 2003). This value is very similar to the suggested trophic fractionation for marine mussels of +2.0‰ (Minagawa & Wada 1984). I assumed no trophic fractionation for carbon, and justify this in the following section.

I identified discrete food sources for each river in each season using the nearest neighbor distance (NND) analysis in the SOURCE code (Lubetkin & Simenstad 2004). Macroalgal/seagrass and marine POM samples with NND scores <0.1 were combined into 1 food source. Consumer inputs were the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the 5 barnacles collected at each sampling location. The SOURCE model determines center of mass estimates for the contribution of each discrete source to a given consumer and its trophic position.

Statistics. I used an information theory-based model selection approach (Burnham & Anderson 1998) to ask whether the relative contribution of each possible food source, or the trophic level of *Balanus glandula*, changed with distance from each river mouth, and whether any relationship with distance changed with logging intensity in the contributing watershed. The main effects considered were barnacle size, distance from river mouths, road density, and the interaction between distance and road density. The response vari-

ables were diet contributions of kelp in summer or winter, freshwater POM in summer or winter, marine POM in winter (marine POM was not distinguishable from freshwater POM at any rivers in summer), macroalgae/seagrass in summer, and summer and winter trophic level. For each response variable, I considered several linear mixed effects models. All possible models (including the null model) included a random effect associated with the intercept to account for unmeasured variance among sites.

The model set contained all possible combinations of the main effects. I used Akaike's information criterion corrected for small sample size (AICc) to compare the ability of each model to explain variance in each response variable (Burnham & Anderson 1998) AICc values were standardized to the best fit model to produce ΔAICc values. In each exercise, the best fit model has a $\Delta\text{AICc} = 0.00$, and only models with $\Delta\text{AICc} \leq 3.00$ are reported (Burnham & Anderson 1998). The importance of individual parameters can be compared by AICc weights ($w\text{AICc}$), the sum of the normalized likelihood of all models that include that parameter (Burnham & Anderson 1998). All statistical analyses were done in S-PLUS.

Community trends in diet contributions and trophic level. Not all species of filter feeders were present at all sample locations and sites. I averaged all samples within a river to allow comparison of diet contributions and trophic level among species. To most clearly represent the uncertainty of the mixing model outputs, I input average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each consumer at each river, and report the center of mass estimates and standard deviations generated by the SOURCE code (Lubetkin & Simenstad 2004) for source contributions and trophic level.

I used the same discrete sources and trophic fractionations for *Balanus glandula* described above. The stalk of *Pollicipes polymerus* is largely muscular, but includes the ovaries (Darwin 1851), so the nitrogen fractionation values for whole body analyses were used for this species as well. Since only muscle tissue of *Mytilus californianus* was used, I assumed a trophic nitrogen shift of +2.9‰ (McCutchan et al. 2003).

I assumed no trophic fractionation for carbon, as McCutchan et al. (2003) suggested that the current best estimate of carbon trophic fractionation for the analysis of whole organisms is +0.3‰, and +1.3‰ for muscle tissue. Since the SOURCE model solves for trophic level and source contributions simultaneously, the 2 estimates are highly correlated if any trophic fractionation is assumed for carbon. Since I was explicitly interested in the 2 parameters (source contributions and trophic level) independently, I assumed no trophic fractionation for carbon, but tested the sensitivity of source contribution and trophic level estimates

using other values of carbon fractionation (+0.3‰ for whole organisms, +1.3‰ for muscle).

Average source contributions for all organisms were only slightly different when carbon fractionation was included. Summer whole organism estimates of each source's contribution to consumer diet was $0.0001\% \pm 0.09$ (mean \pm SD) higher with carbon fractionation, and $0.0002\% \pm 0.12$ lower for muscle tissue. The difference in winter analyses was also small, with estimates of source contributions to whole organisms being $0.0001\% \pm 0.05$ lower with carbon fractionation, and estimates for muscle tissue being $0.0002\% \pm 0.17$ higher. Trophic level was slightly more sensitive, but differences were still small for all calculations. Including carbon trophic fractionation decreased summer trophic level estimates by 0.01 ± 0.04 for whole organisms and by 0.08 ± 0.11 for muscle tissue. Summer trophic level increased by 0.07 ± 0.02 for whole organisms and decreased by 0.2 ± 0.3 for muscle tissue. All patterns of relative source contributions and trophic position were conserved. I only report SOURCE estimates calculated with no trophic fractionation of carbon.

RESULTS

River plume trends

I identified relationships between logging intensity (as represented by road density) and both the contribution of macroalgae/seagrass to *Balanus glandula* diets and *B. glandula* trophic level in summer (Table 2). Summer macroalgal/seagrass diet contribution declined dramatically with increasing road density, while summer trophic level increased (Table 3).

Trophic level declined with barnacle size in both seasons. I did not attempt to representatively sample

Table 2. Models that best describe patterns in barnacle *Balanus glandula* diet and trophic level. AICc: Akaike's information criterion corrected for small sample sizes; k : number of parameters in model

Variable Model	n	k	AICc	ΔAICc
Summer % macroalgae				
Roads	54	8	-205.56	0.00
Distance + Roads	54	9	-202.77	2.79
Summer trophic level				
Size	47	8	30.61	0.00
Size + Roads	47	9	33.59	2.99
Winter trophic level				
Size + Distance	47	9	15.81	0.00
Size	47	8	17.19	1.37

Table 3. Parameter weights for response variables that were well explained by selected models based on *Balanus glandula*. A small sample size corrected Akaike's information criterion weight (wAIC_c) value = 1.00 indicates that a factor is present in all models that describe variance in the response variable well. Variables with wAIC_c ≥ 0.50 are considered strong predictors and are shown in **bold**. Symbols represent the sign of the regression coefficients and are only included for strong predictor variables

Variable	Summer % macroalgae	Summer trophic level	Winter trophic level
Roads	0.92 (-)	0.19	0.23
Size	0.00	0.96 (-)	0.99 (-)
Distance	0.28	0.19	0.68 (-)
Roads × Distance	0.10	0.01	0.07

the size distribution of barnacles at each sampling location, but rather included size in the model selection to account for variance in isotopic signatures associated with size. I will not interpret the parameter weights for this predictor.

Winter trophic level was the only response variable that showed a spatial pattern with distance from river mouths (Table 2). In winter, *Balanus glandula* trophic level was lower farther from river mouths (Table 3). I was unable to detect relationships between any model

parameters and diet contributions of kelp in summer or winter, freshwater POM in summer or winter, or marine POM in winter.

Community trends

The mussel *Mytilus californianus* had the most depleted ¹⁵N signature, while the gooseneck barnacle *Pollicipes polymerus* was the most enriched (Fig. 2, Table 4). Carbon signatures were more similar among filter feeders, but *M. californianus* was the most enriched in ¹³C and *P. polymerus* was the most depleted (Fig. 2, Table 4). The potential food sources I considered had a wide range of ‰¹⁵N values, ranging across ~4‰ in summer from freshwater POM (most depleted) to the red algae *Porphyra* spp. (most enriched) and across ~8‰ in winter from freshwater POM (again most depleted) to the intertidal surf grass *Phyllospadix scouleri* (most enriched; Table 4). Carbon isotope signatures also varied widely among possible food sources. Kelp was always the most enriched source, ~10‰ higher in ¹³C than freshwater POM (Table 4).

The potential food sources discernable by carbon and nitrogen isotope signatures varied with site and season (Table 5). Kelp and intertidal macroalgae had discrete signatures at all sites in summer, and were the

Table 4. Average carbon and nitrogen isotopic signatures for rocky intertidal invertebrate filter feeders, macroalgal species, and particulate organic matter (POM) in summer and winter 2004–2005. All isotope values are ‰. na: not applicable

Species	Summer					Winter				
	δ ¹⁵ N	SD	δ ¹³ C	SD	n	δ ¹⁵ N	SD	δ ¹³ C	SD	n
Filter feeders										
<i>Mytilus californianus</i>	8.64	0.78	-15.67	0.45	25	9.39	0.55	-15.73	0.39	17
<i>Balanus glandula</i>	9.11	0.89	-16.23	0.35	54	9.38	0.93	-16.70	0.62	53
<i>Semibalanus cariosus</i>	9.56	0.78	-15.79	0.49	13	9.59	1.35	-16.45	0.69	11
<i>Pollicipes polymerus</i>	10.84	1.35	-16.24	0.44	7	11.02	0.37	-17.70	0.42	5
Macroalgae										
<i>Ulva</i> spp.	6.57	0.81	-17.20	1.61	15	5.83	0.49	-17.87	1.55	6
Drift						5.51	1.07	-18.32	1.07	3
<i>Mastocarpus</i> spp.	6.91	0.70	-16.06	1.62	10	6.34	0.51	-16.72	1.24	12
<i>Ulva intestinalis</i>	6.28	2.05	-16.69	1.25	7	1.90	0.93	-18.86	1.23	6
<i>Fucus</i> spp.	6.08	0.86	-16.86	1.70	10	5.28	1.00	-18.11	1.98	16
Drift						5.92	na	-17.90	na	1
<i>Porphyra</i> spp.	7.21	0.93	-19.47	2.20	23	5.03	1.96	-20.12	2.46	16
Filamentous red algae (unident. spp.)	6.84	0.40	-23.36	4.44	3	6.96	0.79	-22.62	1.50	5
Filamentous green algae (unident. spp.)					5.15	1.07	-19.94	3.06	7	
Kelp (unidentified spp.)	6.13	2.99	-13.68	0.28	2	5.82	na	-15.90	na	1
Drift						5.25	0.72	-14.16	1.17	2
Seagrass										
<i>Phyllospadix scouleri</i>	4.32	1.85	-14.52	1.38	4	7.92	na	-17.37	na	1
Drift						6.46	1.27	-14.45	0.90	4
POM										
Freshwater POM	3.48	4.92	-24.67	2.76	36	-0.25	1.42	-25.93	0.69	16
Marine POM	6.72	3.23	-20.24	3.21	46	2.74	0.82	-21.95	0.75	14

Fig. 2. *Balanus glandula*, *Semibalanus cariosus*, *Mytilus californianus*, and *Pollicipes polymerus*. Average stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope signatures (‰) of 4 rocky intertidal filter feeders and several of their possible food sources. Although grand averages are shown here, independent averages for each food source and consumer from each river were used in the mixing models. FW POM: freshwater particulate organic matter, SW POM: saltwater particulate organic matter. Macroalgae values include the sea-grass *Phyllospadix scouleri*. Error bars are SD

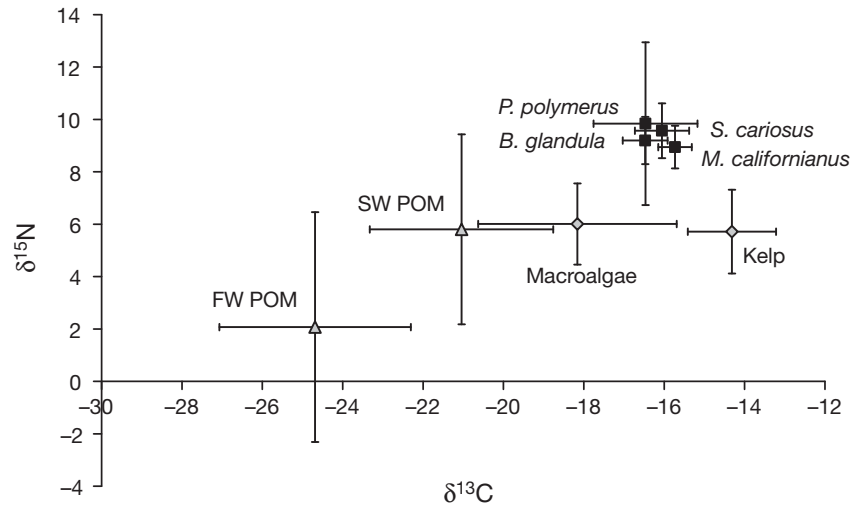


Table 5. Percent contributions of potential food sources assimilated by intertidal filter feeders and their trophic levels at 5 rivers on the Olympic Peninsula. Values are center of mass estimates and their SD, as calculated by the SOURCE mixing model. POM: particulate organic matter

(a) Summer		POM		Algae			Trophic level	
River	Species	Freshwater	Combined ^a	Intertidal macroalgae 1 ^b	Intertidal macroalgae 2 ^c	Kelp		
East Twin	<i>Balanus glandula</i>	41 ± 58		48 ± 68		11 ± 11	1.6 ± 1.1	
West Twin	<i>B. glandula</i>	11 ± 15		27 ± 39		62 ± 24	1.2 ± 0.5	
Rasmussen	<i>B. glandula</i>	15 ± 22		38 ± 53		47 ± 31	1.6 ± 0.4	
Quillayute	<i>Mytilus californianus</i>		13 ± 15	43 ± 49	23 ± 36	22 ± 35	0.9 ± 0.4	
	<i>B. glandula</i>		10 ± 16	57 ± 52	17 ± 33	16 ± 31	1.8 ± 0.4	
	<i>Semibalanus cariosus</i>		11 ± 16	59 ± 54	16 ± 32	15 ± 31	1.8 ± 0.4	
Cedar	<i>M. californianus</i>		9 ± 13	18 ± 26		73 ± 13	1.6 ± 0.1	
	<i>B. glandula</i>		12 ± 16	23 ± 33		66 ± 17	1.9 ± 0.1	
	<i>S. cariosus</i>		9 ± 13	19 ± 27		72 ± 14	1.6 ± 0.1	
	<i>Pollicipes polymerus</i>		9 ± 18	26 ± 36		62 ± 19	2.2 ± 0.2	
(b) Winter		POM		Algae			Trophic level	
River	Species	Freshwater	Marine	Filamentous red	Intertidal macroalgae ^d	Intertidal + kelp		
East Twin	<i>B. glandula</i>	9 ± 13			18 ± 25		73 ± 12	1.9 ± 0.4
West Twin	<i>B. glandula</i>	1 ± 1	1 ± 2			97 ± 1		1.6 ± 0.04
Rasmussen	<i>M. californianus</i>	2 ± 4	3 ± 6		7 ± 12		88 ± 8	1.2 ± 0.1
	<i>B. glandula</i>	5 ± 9	8 ± 14		17 ± 30		70 ± 19	1.7 ± 0.3
	<i>S. cariosus</i>	4 ± 7	6 ± 10		12 ± 21		78 ± 14	1.3 ± 0.2
Quillayute	<i>M. californianus</i>	0 ± 0	0.2 ± 0.2	0.2 ± 0.4		99 ± 0.1		1.5 ± 0.01
	<i>B. glandula</i>	3 ± 4	4 ± 7	5 ± 9		88 ± 4		2.5 ± 0.2
Cedar	<i>M. californianus</i>	2 ± 5	3 ± 6	3 ± 5	6 ± 11		86 ± 6	1.5 ± 0.1
	<i>B. glandula</i>	6 ± 12	9 ± 17	7 ± 14	15 ± 31		63 ± 17	2.6 ± 0.4
	<i>S. cariosus</i>	5 ± 9	7 ± 13	5 ± 11	12 ± 23		72 ± 12	2.5 ± 0.3
	<i>P. polymerus</i>	7 ± 14	10 ± 19	8 ± 16	17 ± 34		58 ± 19	2.8 ± 0.5

^aQuillayute: freshwater and marine POM; Cedar: freshwater POM, marine POM, filamentous red algae (FR)
^bEast Twin: *Mastocarpus* spp. (MA), *Phyllospadix scouleri* (PH), *Ulva* spp. (UL), *Porphyra* spp. (PO), marine POM; West Twin: *Fucus* spp. (FU), UL, PO, marine POM; Rass: *U. intestinalis* (UI), FU, MA, PH, PO, UL, marine POM; Quillayute: FU, MA, UL, UI; Cedar: FU, MA, UL
^cQuillayute: PH
^dEast Twin: filamentous green algae (FG), FR, MA, UL, marine POM; Rasmussen: FU, Drift FU, MA, PH, PO, UL; Cedar: MA, PO, FU

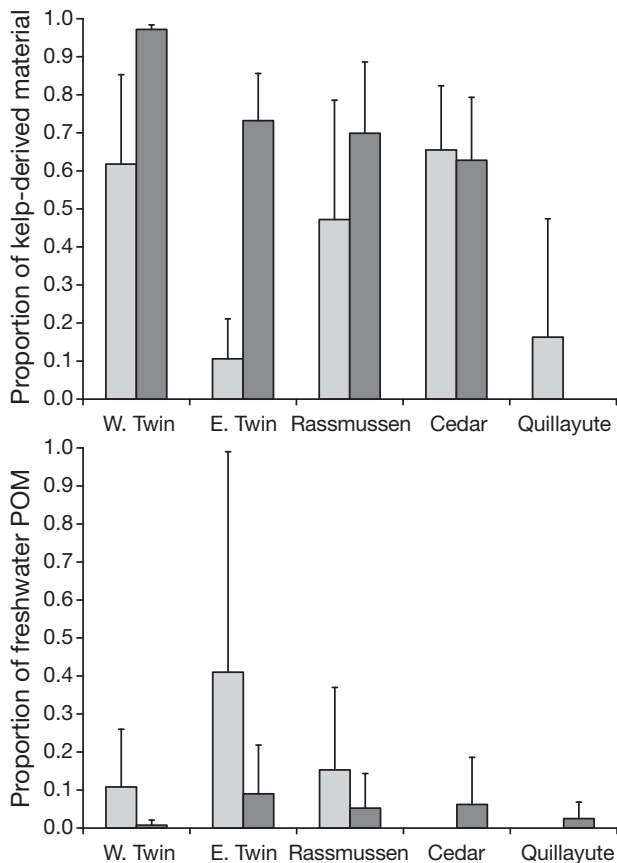


Fig. 3. *Balanus glandula*. Center of mass estimates of the proportion of kelp-derived material and freshwater particulate organic matter (POM) assimilated in summer (light gray) and winter (dark gray). Error bars are SD of the center of mass estimates. Kelp was not a discernable source at the Quillayute River in winter, and freshwater POM was not discernable at Cedar Creek or Quillayute River in summer

2 sources assimilated most by all filter feeders. These 2 sources were again distinct at 3 sites in winter. Kelp contributed ~30% more to *Balanus glandula* diet and ~40% more to *Mytilus californianus* diet during this season (Table 5). This shift in contributions appears large relative to the SOURCE output variability at the 2 north coast sites (East Twin and Rasmussen), but not at the west coast site (Cedar, Fig. 1).

Freshwater POM had a discrete isotope signature at 3 sites during summer. *Balanus glandula* assimilated the most freshwater POM at East Twin River in the summer, although the contribution estimate was quite variable (Table 5a). I was able to calculate freshwater POM contribution at all sites in winter, when it was generally ~15% lower for *B. glandula* (Fig. 3). All other filter feeders assimilated ~3% freshwater POM in winter (Table 5b). Although the error around these estimates was large in both seasons, all filter feeders appeared to assimilate some freshwater POM.

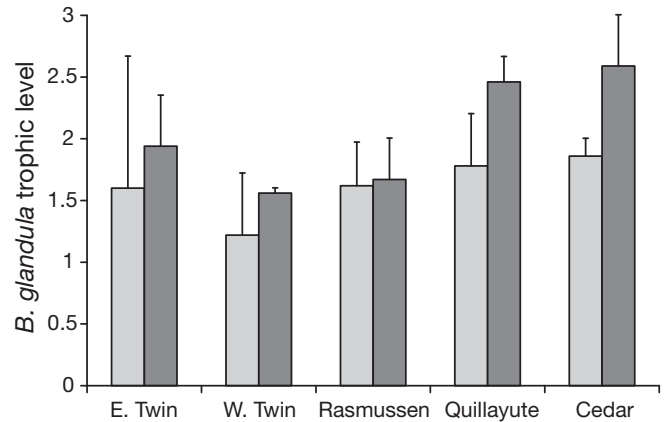


Fig. 4. *Balanus glandula*. Summer (light gray) and winter (dark gray) center of mass estimates of trophic level. Quillayute River and Cedar Creek are on the west coast of the Olympic Peninsula, while all other rivers are on the north coast. Error bars are SD of the center of mass estimates

As with diet contributions, I found no large geographic variation in *Balanus glandula* trophic level in summer. The average summer trophic level for this species was ~1.6, indicating that *B. glandula* were not solely acting as primary consumers (Table 5a). The average winter trophic level of *B. glandula* was approximately half a step higher, suggesting some consumption of other primary consumers. This seasonal shift was large relative to calculation error at the 2 west coast sites (Quillayute and Cedar; Fig. 4). All 4 species of filter feeders co-occurred at one of these sites, Cedar Creek. Although kelp was the main contributor to the diets of all species, trophic partitioning was evident. *Mytilus californianus* was a full trophic level lower than the largest barnacle, *Pollicipes polymerus* (Fig. 5). *Semibalanus cariosus* and *B. glandula* held equivalent, intermediate trophic positions. All species showed a seasonal trophic shift, occupying a higher position in winter (Fig. 5). The fact that I was able to identify seasonal shifts in *B. glandula* source contributions on the north coast and trophic level shifts on the west coast indicates that this species turns over enough tissue within 6 mo to make isotopes a useful tool for exploring sub-annual diet variability.

DISCUSSION

Kelp subsidy to rocky intertidal filter feeders

Kelp is a major part of many species' diets, spanning entire food webs in some parts of the world (Duggins et al. 1989, Fredriksen 2003), but relatively few cases have been made for the role of kelp in rocky intertidal

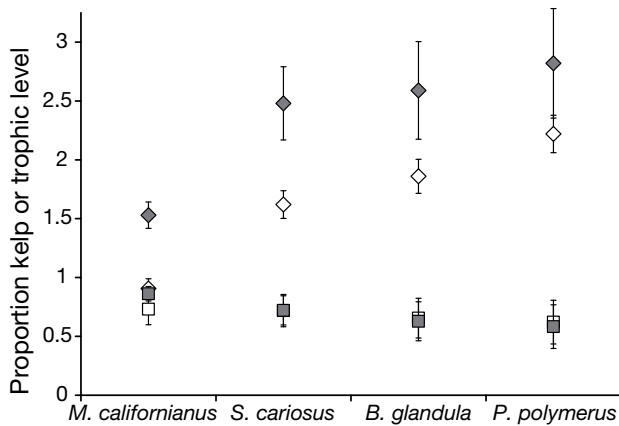


Fig. 5. *Mytilus californianus*, *Semibalanus cariosus*, *Balanus glandula*, and *Pollicipes polymerus*. Seasonal patterns in kelp contribution (squares) and trophic level (diamonds) from Cedar Creek, Washington. White symbols: summer; gray symbols: winter. Error bars are SD of center of mass estimates

filter feeder diets. Here, I add 3 intertidal barnacles and an intertidal mussel to the list of species that rely heavily on kelp as a food source. Carbon and nitrogen stable isotope analyses showed that all 4 filter feeders primarily assimilated kelp and intertidal macroalgae (Figs. 2 & 3) at multiple sites up to 150 km apart in the Pacific Northwest (Fig. 1).

Kelp isotopic values used in these analyses were within the range of other reported values from the US west coast and other regions ($\delta^{13}\text{C} = -23.59$ to -11.12% , $\delta^{15}\text{N} = 2.79$ to 6.98% ; Raven et al. 2002, Fredriksen 2003, M. Foley pers. comm). Average freshwater POM $\delta^{15}\text{N}$ values (Table 4) used in these analyses were similar to those in another ecosystem with native N-fixing alder and anadromous salmon populations ($2.97 \pm 0.18\%$ [SD] in Alaskan non-salmon lakes, Finney et al. 2000; $5.35 \pm 0.68\%$ in Alaskan lakes with salmon, Schindler et al. 2005) but were highly variable. Although I cannot account for this variation, enriched values are likely associated with fertilizer applied to timber plantations. Marine POM $\delta^{13}\text{C}$ values from this region (Table 4) were similar to published values (-20.0% , Monteiro et al. 1991; $-20.54 \pm 0.2\%$, Bushula et al. 2005) as were the $\delta^{15}\text{N}$ values ($\sim 5.6\%$, Owen 1987; -1.09 to -3.59% , Bushula et al. 2005).

On average, *Semibalanus cariosus* assimilated 15 to 72% kelp-derived material in summer and 72 to 78% in winter (Table 5). Similarly, *Balanus glandula* assimilated 11 to 66% kelp-derived material in summer and 63 to 73% in winter (Table 5). Another study in this region found that a subtidal relative of this species, *B. nubilus*, assimilated 80% kelp-derived material when growing near subtidal kelp beds in summer (Duggins et al. 1989). In this study, *Pollicipes polymerus* was

found only at one site, where kelp contributed 62% to its summer diet and 58% in winter (Table 5).

I found similar, but slightly higher kelp contributions to the diet of *Mytilus californianus* (22 to 73% of diet assimilated in summer, 86 to 88% in winter) than those reported elsewhere for its congeners. Further north in the Pacific Northwest, *M. edulis* assimilated 30% kelp-derived material near areas with extensive subtidal kelp beds (Duggins et al. 1989). In South Africa, *M. galloprovincialis* relied primarily on kelp-derived material that accounted for 50% of assimilated nitrogen and 65% of assimilated carbon (Bustamante & Branch 1996).

Duggins et al. (1989) suggested that kelp contributions to filter-feeder diets should be highest in winter in this region since phytoplankton production is highest in summer and kelp senescence is highest in winter. I show a trend towards higher kelp contributions for all species in winter, but this difference is only large relative to variation in model estimates for *Balanus glandula* on the north coast (Fig. 3a).

In addition to kelp, intertidal macroalgae/seagrass was also an important component of rocky intertidal filter feeder diets (Table 5). Intertidal macroalgae/seagrass contributed 38% to barnacles in summer and 15% in winter (Table 5). Mussels assimilated similar proportions of this food source (summer 42%, winter 7%; Table 5). Production of most intertidal macroalgal/seagrass species declines sharply in winter (Kozloff 1993), and lower contributions to filter feeder diets during that season may simply mirror lower representation of macroalgae in the detrital pool.

Trophic partitioning

I have shown that 4 species of intertidal filter feeders rely heavily on the same basal food resource, i.e. kelp. All species also overlap spatially (Kozloff 1993), extract all of their food from a homogenous resource pool of suspended particles, and can be food-limited (Sanford et al. 1994). I show that these species do occupy different trophic levels (Fig. 5), possibly reducing food competition. Although I can provide no direct evidence that food competition drives the observed trophic partitioning, the following hypothesis can be considered in light of current knowledge, or tested with future work: filter feeders relying on a single energy source (in this case kelp) minimize food competition through specialized filtration mechanisms that allow them to access different size particles and occupy different trophic levels.

Leg length varies among barnacle species, allowing them to capture different food items, but the explicit link to trophic level previously has not been made.

Marchinko et al. (2004) showed that leg length increases from *Balanus glandula* to *Semibalanus cariosus* to *Pollicipes polymerus*. Within barnacle species, larger individuals with longer legs catch more copepods, the larger food item, while smaller individuals catch more phytoplankton, introducing the potential for larger barnacles to feed at higher trophic levels by capturing larger particles (Lewis 1981). This pattern was repeated at the species level in Chinese waters, where larger barnacle species captured more zooplankton, while smaller species captured more phytoplankton (Jianping et al. 1996). If this same trend holds among the species in this study, trophic position should increase from *B. glandula* to *P. polymerus*, as my isotopic data show (Fig. 5). No studies have compared mussel and barnacle particle capture, but there is evidence that mussels can capture smaller particles than barnacles (Ward & Shumway 2004). *Mytilus californianus* occupied the lowest trophic position in this study, as predicted under my hypothesis. Regardless of the mechanism driving the trophic differentiation among these 4 filter feeders, they clearly feed at different trophic levels, providing one of the first examples of trophic partitioning among sessile species. Most examples of trophic partitioning show mobile predators, such as snails (Kohn 1971) and seals (Field et al. 2005), differentially exploiting spatially patchy resources.

Riverine subsidy to rocky intertidal filter feeders

All 4 species of filter feeders did assimilate some freshwater POM (Table 5, Fig. 3), providing the first evidence that these species not only couple benthic and pelagic marine systems, but also link land and sea. *Balanus glandula* assimilated up to 41% freshwater POM in summer (Table 5), but all barnacles only assimilated on average 5% freshwater POM in winter (Table 5). This food source likely consisted of riverine periphyton detritus, freshwater phytoplankton, and terrestrial detritus. The concentrations of freshwater POM and aquatic chlorophyll *a* were lower at river mouths in winter (unpubl. data), so lower assimilation is again likely representative of lower supply.

Isotope analyses only allowed the consideration of the direct use of terrestrial subsidies (in the form of POM) by filter feeders. However, dissolved nutrients or carbon delivered by rivers can subsidize coastal populations through primary and heterotrophic production (Howarth et al. 1991, Rabalais & Turner 2001, Maranger et al. 2005). I present several lines of evidence suggesting that higher delivery of river-borne dissolved organic carbon (DOC) where freshwater inputs are naturally greatest or where land use is most

intense stimulates the microbial loop, leading to higher trophic status of intertidal filter feeders.

Rainfall is 2 times higher on the west coast of the Olympic Peninsula (Fig. 1, Quillayute and Cedar sites), and most rainfall occurs in winter (Edmonds et al. 1995). *Balanus glandula* trophic level was highest at west coast sites in winter (Fig. 4), corresponding to the time and place of highest river-borne DOC delivery (Edmonds et al. 1995, Tallis 2006). All filter feeders were present at one west coast site, Cedar Creek, where they were all ~0.7 trophic level higher in winter (Fig. 5). The extent of several river plumes was small in summer when rainfall and discharge were naturally lower, with salinity reaching full ocean values within several hundred meters of the river mouth. However, the winter extent of these plumes was much larger as a result of higher discharge rates (Tallis 2006). *B. glandula* trophic level decreased with distance from river mouths, but only in winter when a larger portion of the sample area was influenced by river water (Table 3).

Finally, DOC concentrations at river mouths were 5 times higher downstream of logged watersheds in summer, but unrelated to logging intensity in winter (Tallis 2006). *Balanus glandula* trophic level increased with logging intensity in upstream watersheds in summer only (Table 4). Nutrient inputs are also highest under these 3 conditions, so primary production may be elevated. However, the fact that filter feeders occupy higher trophic levels in areas with greater riverine inputs suggest that the stimulation of the microbial loop by river-borne DOC is relatively more important than nutrient inputs for rocky intertidal trophic structure.

I have shown that rocky intertidal filter feeders living near rivers on exposed coastlines can couple terrestrial and freshwater systems with benthic and pelagic marine systems. It is now essential to understand the importance of seasonal and spatial variation in material derived from kelp and adjacent watersheds for filter feeder population dynamics. Existing hypotheses that coastal phytoplankton production, wave exposure, or sea surface temperature drive variation in rocky intertidal communities often fail to fully explain variation observed in mussel (Phillips 2005) and barnacle growth (Sanford & Menge 2001), possibly because they overlook these 2 important cross-system linkages. Further exploration of these linkages will also improve the understanding of how marine management actions that affect kelp, like sea otter protection or sea urchin fishery regulation, and land management actions that influence river chemistry, like timber harvest regulations, will affect rocky intertidal communities and benthic-pelagic coupling.

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