Mobile scavengers create hotspots of freshwater productivity

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Adjacent communities and ecosystems often differ in underlying productivity but are connected by flows of nutrients, energy, and matter. Pacific salmon (*Oncorhynchus* spp.) transport substantial quantities of nutrients from marine ecosystems to coastal freshwater habitats when they return to spawn and die. Nutrients from their carcasses are initially concentrated in spawning streams and lakes, but are subsequently dispersed by abiotic (floods, hyporheic flow) and biotic processes (predators and scavengers). In southwest Alaska, mobile avian scavengers (gulls; *Larus* spp.) breed on small islands within salmon nursery lakes and consume large quantities of spawning salmon during the chick-rearing period. However the role of birds as vectors of salmon-derived nutrients remains unknown. We examined how gulls – by transporting salmon tissues to their chicks – create hotspots of biological productivity in the aquatic habitats surrounding their nesting colonies. We found that algal production was $\sim 10 \times$ higher at islands with high gull densities compared to islands without nesting gulls, but was concentrated within 40 m of island shorelines. Carbon stable isotopes ($\delta^{13}C$) confirmed that gulls enhance primary production in local benthic communities and demonstrated that this production was transferred up the food web to grazers (snails) and carnivores (blackfish). Nitrogen stable isotopes ($\delta^{15}N$) confirmed that salmon dominated the diet of gulls and that nutrients from gull guano were incorporated into algae and passed up the food web. By relocating and concentrating salmon-derived nutrients into new and distant locations, gulls alter and magnify production in local aquatic communities. We offer the first evidence that the avian community can move salmon-derived nutrients great distances, enriching otherwise isolated habitats.

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Adjacent ecosystems can vary greatly in productivity, with unproductive areas juxtaposing highly productive ones. However, abiotic and biotic vectors transport materials and energy across ecosystem boundaries, providing key nutrient subsidies to recipient habitats (Polis et al. 1997, 2004). Examples of abiotic vectors that transfer spatial subsidies across ecosystem or habitat boundaries include gravity (e.g. fruits/feces falling from a forest canopy onto the forest floor), water flow (e.g. fish carcasses being swept down river into a lake), and wind (e.g. insects or seeds being blown from an open grassland into a nearby wetland). Abiotic spatial subsidies move materials down gradients in the direction dictated by the abiotic force, which is often unidirectional (e.g. gravity, prevailing wind). In contrast to abiotic vectors, biotic vectors, namely mobile organisms (consumers), can also move subsidies "up stream" against those same gradients (Polis et al. 1997, Vanni 2002). Mobile consumers can act as vectors of nutrients and energy by feeding in one ecosystem, crossing an ecosystem boundary, and then defecating, excreting, or dying in another (Polis et al. 1997, Vanni 2002). For example, geese feeding in agricultural fields during the day transport nutrients into wetlands when roosting at night (Post et al. 1998). In

whatever form they occur, spatial subsidies are fundamentally important inputs to ecosystems because they have the potential to increase primary and secondary productivity of recipient food webs (Polis et al. 1997, Stapp et al. 1999, Baxter et al. 2004).

Because the spatial extent of any spatial subsidy depends upon transport by its vectors, highly mobile consumers (which are often large-bodied organisms) are especially able to transport nutrients and energy across long distances via their daily or seasonal movement patterns. One well-known example of mobile consumers that transport substantial quantities of nutrients and energy across ecosystem boundaries and pertains directly to our study is the Pacific salmon (*Oncorhynchus* spp.).

Pacific salmon transport marine-derived nutrients and energy vast distances across ecosystem boundaries (reviewed by Gende et al. 2002, Naiman et al. 2002, Schindler et al. 2003). Semelparous and anadromous salmon forage throughout marine ecosystems and then return to their restricted natal freshwaters to spawn and die. Through this spawning migration, Pacific salmon transport enormous quantities of marine-derived nutrients to coastal and inland ecosystems in a seasonal pulse (Larkin and Slaney 1997, Gresh et al. 2000, Moore and Schindler 2004). For example, sockeye salmon (*Oncorhynchus nerka*) carcasses contribute 4×10^5 kg of nitrogen and 5×10^4 kg of phosphorus every year to inland spawning grounds in the Kvichak River, Alaska (Moore and Schindler 2004). In the areas where fish spawn and die, salmon-derived nutrients are incorporated into a wide variety of freshwater and riparian taxa, ranging from primary producers, such as riparian trees and shrubs (Ben-David et al. 1998, Hilderbrand et al. 1999, Helfield and Naiman 2001), to aquatic and terrestrial consumers such as marten (Ben-David et al. 1997) or caddisflies (Winder et al. 2005). Despite the widely recognized importance of salmon-derived nutrients to the ecosystems where fish spawn and die, nutrients from salmon carcasses are in fact restricted to streams and shallow waters associated with spawning habitat, and to the areas connected to those habitats via abiotic (e.g. downstream flow, hyporheic flow, floods) and biotic vectors (e.g. predatory and scavenging organisms).

Most work on vectors of salmon-derived nutrients has emphasized the role of abiotic vectors (Cederholm et al. 1989, Ben-David et al. 1998, O'Keefe and Edwards 2003), and how bears (as biotic vectors) move nutrients from spawning streams/beaches to adjacent riparian/shoreline ecosystems (Ben-David et al. 1998, Hilderbrand et al. 1999, Gende et al. 2004). However, other highly mobile organisms, namely avian scavengers and predators, are also common in salmon spawning areas, although their role as vectors of salmon-derived nutrients remains unknown. These birds consume large

quantities of salmon tissue (Mossman 1958), are extremely mobile, and their daily foraging movements have the potential to redistribute salmon-derived nutrients from localized areas where carcasses accumulate, to areas far beyond the spawning stream or adjacent riparian zone. Hence, avian scavengers such as gulls (*Larus* spp.) have the potential to redistribute and amplify salmon subsidies by spatially connecting salmon-derived nutrients from spawning streams to new areas around gull nesting colonies.

We examined the role of avian scavengers as vectors of salmon-derived nutrients, fertilizing novel areas – and thereby influencing recipient communities with salmon-derived nutrients. Although presumably all colonial waterbirds contribute nutrient inputs to local aquatic food webs around their nesting sites, it is not always possible to measure this effect. Our study offered a unique opportunity to trace these nutrient inputs due to the marked difference in salmon-derived nutrients (enriched in ^{15}N) compared to other freshwater N sources. We present evidence that glaucous-winged gulls (*Larus glaucescens*) redistribute and concentrate salmon-derived nutrients into freshwater areas surrounding nesting islands in an Alaskan lake, and show that these subsidies subsequently enrich three trophic levels of the nearshore food webs.

Methods

Study system

We studied breeding gulls and benthic communities associated with nine small islands in a freshwater lake system (Wood River lakes) in southwestern Alaska. The largest of five interconnected lakes, Nerka (59°30′N, 158°50′W) has a 201 km² surface area and averages 80 m deep. Lake Nerka is relatively oligotrophic (as are the other Wood River lakes), with average epilimnetic chlorophyll concentrations of 0.9 µg l^{-1}, and total phosphorus and nitrogen concentrations of 6.5 and 310 µg l^{-1}, respectively (Schindler et al. 2005). The 5-lake system flows into Bristol Bay and is an important spawning and nursery system for anadromous sockeye salmon. An average of 1 million adult sockeyes return to spawn in the streams, rivers, and lake beaches of the Wood River lakes every year, of which ~4.8×10^5 spawn and die along the lake beaches, creeks and rivers draining into Lake Nerka (Schindler et al. 2005). This biological phenomenon represents a massive, annual nutrient pulse that continues from June through October, when the last spawners die and decay.

During the summer months (June–Sept), seabirds nest on dozens of small islands located throughout the Wood River lakes. We surveyed nine of these islands spanning a natural gradient in seabird density (Fig. 1, Table 1). As
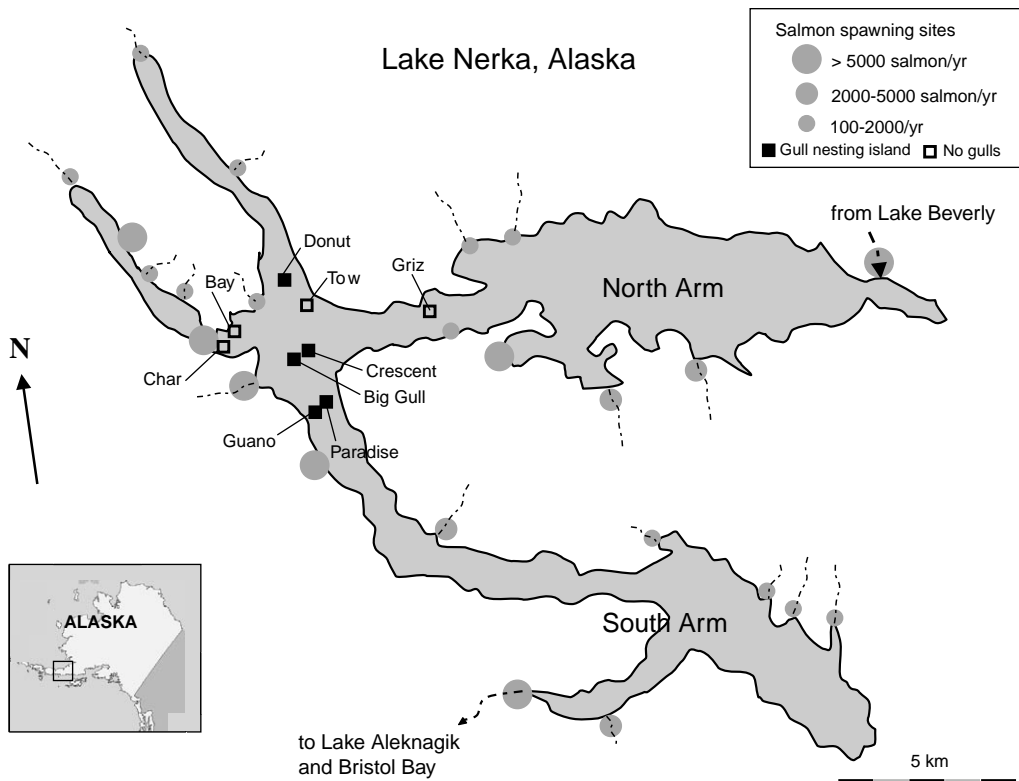
Fig. 1. Map of study location (Lake Nerka, Alaska), including gull nesting islands and salmon spawning streams and beaches.

glaucous-winged gulls were the dominant seabird and most common gull in the area, we selected five islands with nesting colonies of glaucous-winged gulls and four others with few to no gulls.

Study islands range from 0.095 to 0.72 ha in size (measured with a Global Positioning System device), with a median area of 0.32 ha; the only exception is Donut Island, which measured 6.03 ha. The vegetation on the islands included grasses (Gramineae), ferns (Polypodiaceae), willows (Salicaceae), *Spirea* (Rosaceae), and alder shrubs (Betulaceae), with occasional spruce trees (Pinaceae) on several islands.

Glaucous-winged gulls raise a single clutch every summer, laying three eggs per clutch (and 1–3

Table 1. Summary of island physical characteristics, and per-island estimates of gull attendance.

Island	Area (m^2)	Perimeter (m)	Gulls
Bay	3332	225	0
Big Gull	7209	340	165
Char	946	117	0
Crescent	3160	292	280
Donut	60361	983	140
Griz	5566	291	0
Guano	1121	172	160
Paradise	1414	143	60
Tow	2627	188	5

replacement eggs, if nest is predated early in the season). The incubation period is 27–29 d and fledging occurs between 42 and 54 d after hatch (L. X. Payne, unpubl., Verbeek 1993). In addition to glaucous-winged gulls, other waterbirds nest along the lakeshores of these islands, including mew gulls (*Larus canus*), Arctic terns (*Sterna paradisaea*), red-breasted mergansers (*Mergus serrator*), and common loons (*Gavia immer*), however they occur at much lower densities (<3 pairs per island) so we excluded them from our analyses.

Across their range, glaucous-winged gulls are omnivorous, eating a wide variety of prey including fish, marine invertebrates, and carrion (Verbeek 1993). However, as do many other scavengers, gulls often consume prey in proportion to its availability. In the Wood River system, breeding gulls feed almost exclusively on the super abundant salmon (Mossman 1958, L. X. Payne, unpubl.). Gulls primarily scavenge for bear-killed and senescent salmon (Mossman 1958), but will also peck salmon to death in very shallow water (Quinn and Buck 2001). We examined chick diet during a separate study on chick growth rates (as chicks often regurgitate their stomach contents when disturbed); content was established by a visual check of a subset (n =34) of the boluses; items were readily identifiable (namely salmon eggs, salmon flesh, whole smolts and

maggots). In late summer, after most gull chicks have fledged, gulls can also be seen foraging in blueberry patches on surrounding mountains overlooking (and ≥ 0.2 km from) the lake shore, and we encounter their blue-stained guano along streams and on beaches.

Gulls fly varying distances to find food in the Wood River system. In June, while gulls are incubating eggs (and before adult salmon return from the ocean to spawn), gulls appear to make daily migrations to Bristol Bay (~ 80 km away) to feed on the offal from commercial salmon processing operations (D. E. Rogers, pers. comm.). During July to September, when gulls are actively raising chicks, salmon have returned to spawn in streams and along lake beaches and are readily available for local consumption by gulls (Table 2). Depending upon the availability of salmon at any given spawning site, the required daily commuting distance between gull nesting islands and salmon carcasses can vary from 3 km to 10 or more (Fig. 1, Table 2). Overall, salmon are extremely abundant, with $\geq 200\,000$ carcasses within 20 km of gull nesting colonies during Jul–Aug (Table 2).

Study design and lab analyses

To examine the role of gulls as vectors of salmon-derived nutrients, we conducted visual counts of adult gulls (i.e. attendance) at nesting islands, by boat, several times during the study period. Per-island attendance was highly correlated with number of active nests ($r = 0.98$ for 4 islands); therefore, we chose to use attendance as our index of gull abundance, because it was much less disruptive to the nesting birds. Direct counts of gull attendance were made twice per island; once during hatch (early July) and once during chick-rearing (early Aug). Using average attendance, we computed densities of adult gulls m^{-2} of island area, and gulls m^{-1} of island shoreline (Statistical analyses).

Table 2. Location and timing of availability of sockeye salmon, the major food source of glaucous-winged gulls, during the chick-rearing phase (Jul–Aug).

Locations of sockeye salmon[1]	Distance to gull colony[2]	Dates when salmon are present[3]	Average no. of salmon[3]
Lake Nerka (adults)[4]	≤ 26	$Jun_{mid}-Oct_{mid}$	480 000
Lake Nerka (smolts)[5]	≤ 26	$Jun_{mid}-Jul_{mid}$	>10 million
Bristol Bay (fishery)[6]	80	$Jun_{mid}-Jul_{mid}$	>2 million
Cottonwood Creek	9	$Jul_{mid}-Oct_{mid}$	100
Rainbow Creek	16	$Jul_{mid}-Aug_{mid}$	100
Pick Creek	3	$Jul_{mid}-Aug_{late}$	10 000
A' Creek	6	$Jul_{late}-Aug_{early}$	150
C' Creek	8	$Jul_{late}-Aug_{early}$	150
Little Togiak Creek	13	$Jul_{late}-Aug_{early}$	500
Fenno Creek	22	$Jul_{late}-Aug_{mid}$	5000
Across-Griz beach	6.5	$Jul_{late}-Aug_{late}$	2000
Joe Creek	9	$Jul_{late}-Aug_{late}$	3000
Lynx Creek	10	$Jul_{late}-Aug_{late}$	3000
Sam Creek	11	$Jul_{late}-Aug_{late}$	3000
Hidden Lake Creek	14	$Jul_{late}-Aug_{late}$	5000
Kema Creek	18	$Jul_{late}-Aug_{late}$	4500
Teal Creek	18.5	$Jul_{late}-Aug_{late}$	1500
Bear Creek	23.5	$Jul_{late}-Aug_{late}$	1500
Stovall Creek	25	$Jul_{late}-Aug_{late}$	5000
Pike Creek	27	$Jul_{late}-Aug_{late}$	2500
Elva Creek	3	$Aug_{early}-Aug_{late}$	500
Little Togiak River	5	$Aug_{early}-Sep_{early}$	10 000
N-6 beaches	7	$Aug_{early}-Sep_{mid}$	4000
N-4 beaches	10	$Aug_{early}-Sep_{mid}$	3000
Agulowak River	19	$Aug_{early}-Sep_{mid}$	110 000
Agulukpak River	26	$Aug_{early}-Sep_{mid}$	120 000
Little Togiak beaches	10	$Aug_{early}-Sep_{late}$	10 000
Anvil Bay beach	9	$Aug_{mid}-Sep_{mid}$	20 000

[1]All spawning sites are for Lake Nerka and Little Togiak Lake (except Bristol Bay fishery). See Fig. 1 for spatial configuration
[2]Distance (km) to Crescent Island, the most centrally located of the gull nesting islands we studied (Fig. 1)
[3]Information taken from Alaska Salmon Program, Univ. of Washington
[4]Beginning in late June, adult sockeye are present in lake Nerka. Although not yet spawning, some salmon become available to gulls when they are killed by bears, which fish on the large schools of sockeye that hold in shallow waters at the creek mouths (prior to the fish entering their spawning grounds)
[5]For 2–3 weeks in early spring, smolts migrate out of small tributary lakes into Lake Nerka, and concentrate in large numbers near the water's surface, becoming susceptible to predation by terns and gulls. Although smolts are present throughout the summer, they are more spatially dispersed and lower in the water column after this period (hence, less susceptible to gull predation)
[6]Nushagak fishing district processed out of Dillingham, AK

We investigated the impact of gull-transported nutrients on the nearshore aquatic communities surrounding each island. At the local extent, within ~ 20 m of each island shoreline, we quantified the relationship between gull density and nearshore periphyton production. We measured the isotopic signatures of primary producers (periphyton), herbivores (snails), and consumers (Alaska blackfish, Umbridae, *Dallia pectoralis*) around each island. We estimated periphyton biomass (chlorophyll-a cm^{-2}) in the nearshore area around each island. To provide a uniform surface for algal growth, we placed four unglazed ceramic tiles (11×11 cm) on the lake bottom in shallow (1 m deep) water. Tiles were spaced at least 30 m from adjacent tiles, spaced at even intervals around each island and incubated there for 45 days. After incubation we removed the substrate on the tiles by scrubbing them with a small brush and rinsing vigorously with filtered lake water. We filtered a known volume of the rinsed solution through 47 mm GF/F filters (pore size of 0.7 μm) and froze the filters at $-10°$C for chlorophyll-a analysis. We repeated this procedure with pre-ashed filters for isotopic analysis. For the chlorophyll-a analysis, we extracted filters in methanol and used fluorometry to determine chlorophyll-a concentrations (Marker et al. 1980). To calculate the amount of chlorophyll-a by area (μg cm^{-2}), we divided chlorophyll-a mass by the surface area of each tile.

Second, we quantified the relationship between gull density and nearshore (aquatic) enrichment at a broader extent (0–60 m from island shorelines). Specifically, we investigated the spatial extent of the 'enriched footprint' of each island for a subset of the study islands: two islands with high gull densities (Big Gull and Guano), and two with few to no gulls (Tow and Griz). On each of these islands, we established three transects, each running perpendicular to the island shoreline. Along each transect, we suspended four tiles from tethered buoys at 10, 20, 40 and 60 m away from the shoreline. The tiles were suspended 1 m below the lake surface, and incubated for 16 days. We harvested and measured algal biomass as described above.

Isotopic analyses

We used stable isotopes to trace gull-transported nutrients through nearshore aquatic assemblages surrounding each island. Stable isotopes represent an integration over time of accumulated elements of an organism (Kling et al. 1992, Schindler and Lubetkin 2004), and can be used to trace flows of salmon-derived nutrients through the nearshore food web of each island (Kline et al. 1990, 1993). We used ^{13}C in periphyton to estimate relative primary productivity (Hecky and Hesslein 1995) and to trace this source of organic matter to consumers

(Peterson and Fry 1987, Finlay et al. 2002). Because salmon have an enriched δ^{15}N relative to watershed sources of N (Schindler et al. 2005), we used δ^{15}N to trace the inputs of salmon-derived nutrients through the food webs around islands. This technique has enabled other researchers to estimate the relative contribution of salmon-derived nutrients to various components of freshwater food webs (Kline et al. 1990, 1993, Finney et al. 2000).

We collected periphyton from incubated tiles as described above. We collected the dominant herbivore, snails, by visually searching for up to an hour in <2 m water around each island. We sampled the nearshore fish community with unbaited minnow traps placed in <3 m water. We caught several fish species, but selected Alaskan blackfish as representative consumers because they were the numerically dominant species and were caught at all study islands. Fish were identified, measured, and weighed, and up to three fish per island were preserved in 70% ethanol for subsequent isotopic analyses. We examined the stomach contents of the sampled blackfish by dissecting preserved specimens. In our samples, blackfish diet was dominated by snails and larval caddisflies (Tricoptera), both of which graze algae (Merritt and Cummins 1984). However, blackfish are known to eat aquatic insects and other small invertebrates, and occasionally small fish (Morrow 1980). In addition, we took samples of fresh gull guano (by attaching a Ziploc bag around the gull's hind end), body feathers from juvenile gulls, and sockeye salmon tissue for isotope analysis. We ran isotopic analyses on gull guano, gull feathers, salmon flesh, salmon eggs, salmon smolts, and three trophic levels (primary producers, snails and blackfish) from the nearshore aquatic communities of the nine study islands. Stable isotopes were analyzed by comparing the isotopic signatures of the samples to standards (atmospheric nitrogen and Pee Dee Belemnite carbon; Peterson and Fry 1987).

Statistical analyses

We calculated two estimates of gull densities per island: gulls m^{-1} of island perimeter, and gulls m^{-2} of island area. Because the statistical relationships using either estimate were virtually identical, here we present the densities as gulls m^{-1} of shoreline. We think this density estimate is more relevant for our study because we are interested in how the nearshore habitat (island perimeter) is impacted by nutrients washed off the islands, rather than the impact of gull-transported nutrients on the entire terrestrial zone (island area).

To investigate the shape of the relationship between gull density and response variables, we used likelihood methods assuming normally distributed errors, and compared the performance of alternative models with

the Akaike information criterion corrected for small sample sizes (AIC$_c$; Burnham and Anderson 2002). When we had multiple estimates of a response variable for an island (for example, isotope signature of periphyton), we used the average value for the island in these analyses; thus, each island represents a single data point. We compared three models: a non-linear saturating function, a standard linear model, and a null model of no relationship between the variables. We investigated the relationships between the stable isotope signatures of different trophic levels using correlations and linear regressions (SYSTAT 1998). We used two-way analysis of variance (ANOVA SYSTAT 1998) to examine the spatial extent of enrichment, using distance and island as effects. In addition, we ran post-hoc ANOVAs on all islands individually to examine how distance from the island impacted algal biomass at each island.

Results

Densities of adult glaucous-winged gulls varied by island, ranging from 0.0 to 0.14 gulls m^{-2} of island area, and 0.0 to 0.96 gulls m^{-1} of island shoreline. Gull diet was dominated by salmon, and observations of gulls foraging throughout the breeding season were consistent with their diet. During a separate study on chick growth rates, we noted that of 327 chicks handled, at least 50% of chicks regurgitated upon capture, with regurgitate dominated by salmon flesh and eggs, and no non-salmon material detected in any diet, except (rarely) maggots in combination with decaying salmon flesh (Table 3, L. X.

Payne, unpubl.). Throughout the field season, we also observed gulls feeding on salmon carcasses, gulls flying between nesting islands and salmon spawning habitats, and gulls regurgitating salmon for their young on nesting islands. We occasionally noted prey items encountered at or in gull nests during the first week of chick-rearing; of 16 items noted, salmon eggs were most prevalent (n =9), followed by salmon flesh (n =3), salmon smolts (n =3) and once, a single red squirrel carcass (noted due to its rarity). Finally, during Jun-Aug, gull nesting islands are littered with salmon (especially eggs and flesh), in various stages of decay, as well as a few dead chicks and adults (L. X. Payne, unpubl.).

Periphyton accumulation on ceramic tiles was $\sim 10 \times$ higher around islands with high gull densities than around islands with few or no gulls (Fig. 2). A saturating function ($r^2 = 0.91$) described these data significantly better than a linear or null model. The spatial extent of this enrichment, quantified using periphyton biomass collected at different distances from islands with and without gulls, varied as follows (Fig. 3). Both gull density and distance from island significantly influenced variation in periphyton biomass (ANOVA, island: $F_{3,31} = 25.9$, $P < 0.001$; distance: $F_{3,31} = 12.8$, $P < 0.001$). In addition, distance influenced periphyton biomass differently on the different islands, as indicated by a significant interaction between distance and island (ANOVA, $F_{9,31} = 3.0$, $P < 0.05$). More specifically, distance was a significant factor in influencing periphyton biomass near the two islands with high densities of gulls (ANOVA, $F_{3,7} = 16.3$, $P < 0.005$; $F_{3,8} = 4.2$, $P < 0.05$, for Big Gull and Guano, respectively), but distance did not
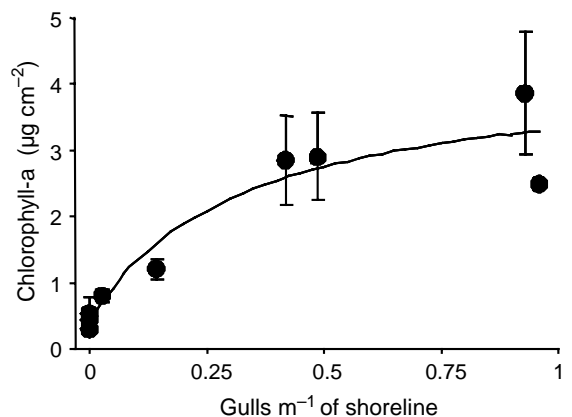
Table 3. Stable isotope (δ^{15}N) values for glaucous-winged gull feathers, fresh gull guano, and for items that we also encountered in gull chick diet (regurgitate). All salmon are sockeye.

Item	Stable isotope (δ^{15}N): [mean $\pm$ 1 SD (n)]	Source
Gull feather	14.9 $\pm$ 0.4 (15)	this study[1]
Fresh gull guano	12.06 $\pm$ 0.58 (4)	this study[2]
Blowfly maggot	12.8 $\pm$ 1.1 (8)	this study[3]
Salmon eggs	11.3 $\pm$ 1.3 (13)	this study[3]
Salmon tissue	11.2 $\pm$ 0.45	Schindler et al. 2005
Salmon smolts	7.9 $\pm$ 0.74 (7)	this study[3]
Blueberry	−2.54 $\pm$ 0.74[5]	Ben-David et al. 1998[4]

[1]Feather samples were taken from juveniles from three study islands in Lake Nerka
[2]Guano samples were collected from four juveniles captured swimming near two study islands in Lake Nerka
[3]All samples are from Lake Nerka; maggot samples were taken from sockeye carcasses along a spawning stream; sockeye salmon eggs and tissue were collected from freshly dead fish along spawning streams, and sockeye smolts were captured with a beach seine in the surface waters of Lake Nerka
[4]Data are from elsewhere in southwestern Alaska. Note that, although we did not record blueberries in chick regurgitate, we observed gulls visiting blueberry patches in late summer
[5]Values refer to mean $\pm$ 1 SE

Fig. 2. Scatter plot of the relationship between periphyton biomass (chlorophyll-a cm^{-2}) and gull density. Each point represents the mean $\pm$ one standard error (SE) of periphyton biomass for a single island. All points represent the mean of 3 or 4 samples except for Griz and Donut (2 samples each). The curved, increasing line represents the saturating function that best fits the data.

Fig. 3. Scatter plots of periphyton biomass (chlorophyll-a cm^{-2}) at different distances from (a) two islands with high densities of gulls, and (b), two islands with few to no gulls. Each point represents the mean ± 1 SE of periphyton biomass at a given distance from island shore, for a given island. All points represent the mean of three samples.
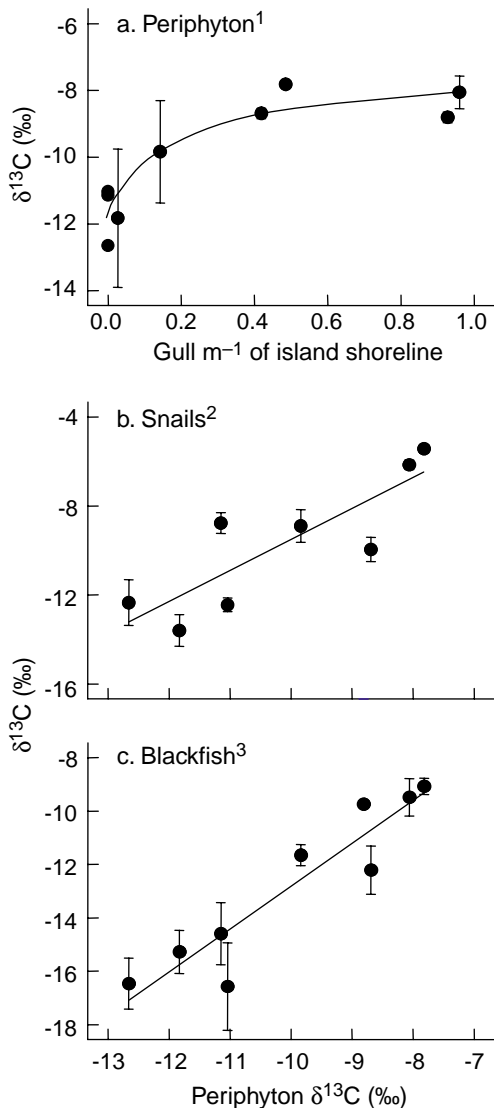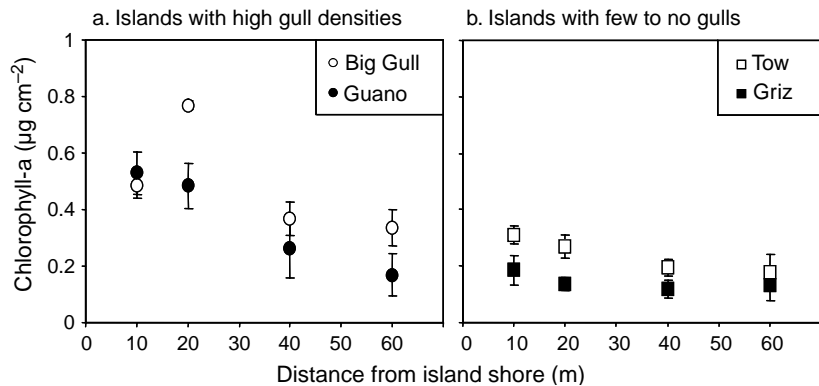
significantly affect periphyton at islands with few or no gulls (ANOVA, $F_{3,8} = 2.1$, $P = 0.18$; $F_{3,8} = 0.48$, $P = 0.71$, for Tow and Griz, respectively). The spatial extent of this enrichment ranged between 20–40 m from gull islands, whereas on the islands without gulls, nearshore areas were not significantly enriched compared to off-shore areas (Fig. 3).

If the nutrients that gulls transport enhance benthic primary productivity, we would expect enriched levels of ^{13}C in periphyton (Hecky and Hesslein 1995). Indeed, periphyton from islands with high densities of gulls were more enriched in ^{13}C than periphyton from islands with low gull densities (Fig. 4a). A positive saturating relationship between gull density and periphyton $\delta^{13}C$ described these data better than a linear or null model, and explained 87% of the variance in the data. Carbon isotope signatures were propagated to higher trophic levels (Fig. 4b, 4c), such that islands with higher periphyton $\delta^{13}C$ values also had snails with higher ^{13}C values ($\delta^{13}C_{snail} = 0.51(\delta^{13}C_{periphyton}) - 5.15$, $F_{1,6} = 15.1$, $P < 0.01$, $r^2 = 0.67$). Snail $\delta^{13}C$ values were more enriched on islands with enriched periphyton, as evidenced by the strong positive correlation between snail and periphyton $\delta^{13}C$ values (Pearson correlation $= 0.85$). We obtained similar results for blackfish, which demon-

Fig. 4. (a) Scatter plot of the relationship between periphyton ^{13}C stable isotope signature and gull density. Each point represents the mean ± 1 SE of the carbon stable isotope signature ($\delta^{13}C$) of the taxa for a given island. The curved solid line represents the best model (saturating function) describing the relationship between the variables. All points represent the mean of 3 samples unless otherwise indicated. (b and c) Scatter plots of the relationship between ^{13}C stable isotope signature of periphyton and snails (b) or periphyton and blackfish (c). Each point represents the mean ± 1 SE of the carbon stable isotope signature ($\delta^{13}C$) of the taxa for a given island. The solid line indicates the linear relationship between the variables. All points represent the mean of 3 samples unless otherwise indicated. Note the different scales for all graphs. [1] Periphyton sample sizes are 3 per island except for Bay, Char, Guano and Tow (2 each) and Griz (1 sample). [2] Snail sample sizes are 3 per island except for Guano, where no snails were found. [3] Blackfish sample sizes were three per island except for Guano and Paradise (2 each).

strated a similarly high correlation with periphyton $\delta^{13}C$ values (Pearson correlation $=0.93$).

Nitrogen stable isotopes provided evidence of two additional factors: 1) that the nutrients fueling enhanced near-shore production around islands with high gull densities were salmon-derived, and 2) that salmon-derived nitrogen was incorporated into nearshore periphyton and propagated up through the food web. In the first case, the mean $\delta^{15}N$ value of feathers from 15 fledgling gulls was $14.9 \pm 0.4\%_0$ (error is 1 SD; Table 3, L. X. Payne, unpubl.), $3.7\%_0$ (i.e. approximately one trophic level; Hobson and Welch 1992, Post 2002) above salmon, which have an average $\delta^{15}N$ of 11.2 ± 0.3 (Schindler et al. 2005). Additionally, fresh gull guano had an average $\delta^{15}N$ of $12.06 \pm 0.58\%_0$ (n $=4$), very similar to the $\delta^{15}N$ of salmon tissue. These results are consistent with our direct and indirect observations that juvenile gulls are fed a salmon-dominated diet during the feather growth period, and that the nutrients in gull guano are dominated by salmon.

Second, periphyton from islands with higher densities of gulls were also more enriched in ^{15}N (Fig. 5a). Linear and saturating relationships were indistinguishable, and both gave better fits than the null model in describing the relationship between gull density and $\delta^{15}N$ of periphyton ($r^2 = 0.41$ for linear model, shown in Fig. 5a). This ^{15}N signal propagated up through the food-web (Fig. 5b, 5c), although correlations with periphyton and higher trophic levels were not quite as strong as those seen for $\delta^{13}C$. Specifically, the Pearson correlation between snail and periphyton $\delta^{15}N$ was 0.73, whereas the correlation between blackfish and periphyton $\delta^{15}N$ values was 0.64.

The average difference between $\delta^{15}N$ values of snails and periphyton on islands was $2.09 \pm 0.34\%_0$ (this and the following are mean ± 1 SE). For a given island, the average difference between the $\delta^{15}N$ value of blackfish and snails was $5.89 \pm 0.28\%_0$. Individual blackfish isotopic signatures were not influenced by their mass for $\delta^{13}C$ (linear regression, $F_{1,23} = 2.05$, $P = 0.17$, $r^2 = 0.04$) or $\delta^{15}N$ (linear regression, $F_{1,23} = 2.07$, $P = 0.16$, $r^2 = 0.04$), demonstrating a surprising lack of trophic ontogeny.

Discussion

The benthic habitats of islands with higher gull densities had higher levels of primary production, consistent with our hypothesis that gulls move salmon-derived nutrients to their nesting islands, where nutrients enter the surrounding aquatic zone and enhance local primary production. Specifically, islands with the highest gull densities had approximately 10x more periphyton than islands with few gulls, and gull density explained over 90% of the substantial variation in periphyton biomass among islands (Fig. 2). This local enrichment of algal
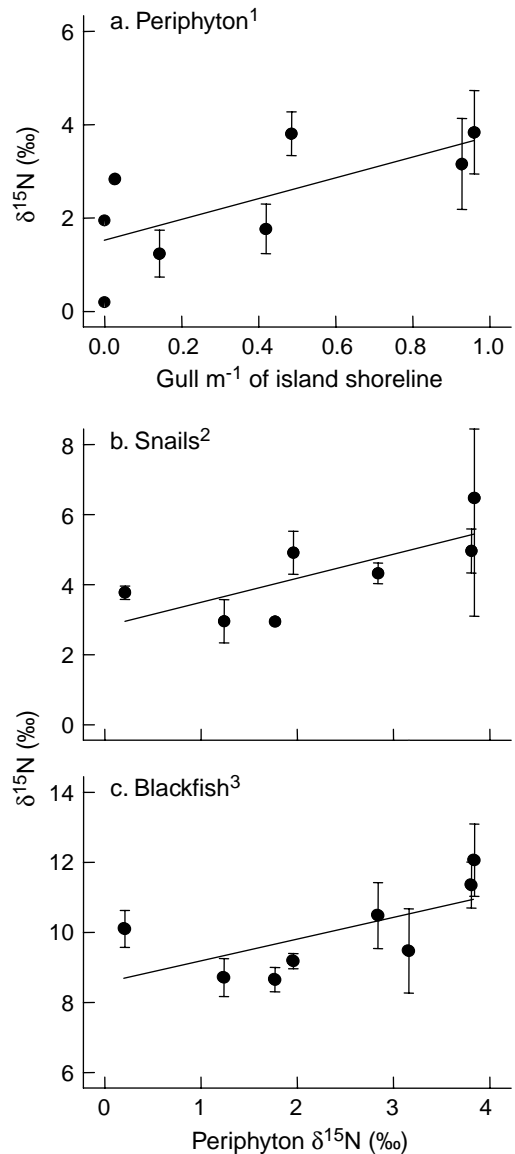

Fig. 5. (a) Scatter plot of the relationship between periphyton ^{15}N stable isotope signature and gull density. Each point represents the mean ± 1 SE of the nitrogen stable isotope signature ($\delta^{15}N$) of the taxa for a given island. The solid line represents the best model (linear function) describing the relationship between the variables. All points represent the mean of 3 samples unless otherwise indicated. (b and c) Scatter plots of the relationship between ^{15}N stable isotope signature of periphyton and snails (b) or periphyton and blackfish (c). Each point represents the mean ± 1 SE of the nitrogen stable isotope signature ($\delta^{15}N$) of the taxa for a given island. The solid line indicates the linear relationship between the variables. All points represent the mean of 3 samples unless otherwise indicated. Note the different scales for all graphs. [1] Periphyton sample sizes are 3 per island except for Guano (2 samples), Bay, Char and Tow (1 each), and Griz (no sample). [2] Snail sample sizes are 3 per island except for Guano, where no snails were found. [3] Blackfish sample sizes were three per island except for Guano and Paradise (2 each).

biomass extended up to 20–40 m from islands with high densities of gulls, whereas there was no significant nearshore enrichment around islands with few or no gulls (Fig. 3). Periphyton $\delta^{13}C$ values were substantially more enriched around islands with high densities of gulls (Fig. 4), providing additional evidence that periphyton productivity was higher near gull islands. Enriched $\delta^{13}C$ and $\delta^{15}N$ values surrounding gull islands were propagated up several trophic levels, demonstrating that gull-transported salmon-derived nutrients fuel the nearshore aquatic community, and that the relatively low mobility of aquatic consumers (i.e. snails and blackfish) results in localized hotspots of productivity surrounding these islands.

Link between gulls and salmon

Several lines of evidence demonstrate that the nutrients that fuel freshwater productivity surrounding islands with gull colonies are dominated by salmon-derived nutrients. In addition to the many direct observations of adult gulls scavenging salmon in the Wood River system (L. X. Payne and J. W. Moore, pers. obs., Mossman 1958, Quinn and Buck 2001), and the observed contents of chick regurgitate, stable isotope analyses confirm this link. The mean $\delta^{15}N$ value of juvenile gull feathers was ~3.7‰ (approx. one trophic level; Post 2002) above salmon, consistent with our observations that salmon is the dominant food source of these young gulls. In addition, the similarity between the $\delta^{15}N$ values of gull guano and salmon flesh are consistent with the other evidence. Although ammonification of guano can lead to a greatly enriched N signal over dietary signals when accumulated in soils at seabird rookeries, fresh guano does not show this effect (Mizutani et al. 1986, 1991). However, this process may lead to enriched $\delta^{15}N$ of nitrogen taken up by algae near gull colonies, although the magnitude of this effect has not been quantified.

Tracing production through food webs

Stable isotope data provide evidence that algal production driven by gull guano is propagated through the food web yet retained at localized sites (Fig. 4). The increased enrichment of periphyton $\delta^{13}C$ around gull islands, indicative of increased primary productivity, explained 67% of the variation in $\delta^{13}C$ of the grazers (snails) around those islands. Similarly, the $\delta^{13}C$ values of snails explained 79% of the variation in $\delta^{13}C$ values of blackfish (consumers of snails). Therefore, the primary production fueled by gull-transported salmon-derived nutrients propagates up to at least two trophic levels of the nearshore community at islands used by nesting gulls. Thus, gull foraging behavior creates hotspots of

biological productivity by subsidizing three trophic levels of the local nearshore communities associated with nesting islands.

Our finding that blackfish from different islands have different $\delta^{13}C$ values, yet similar enrichment relative to within-island community members (snails and algae), also provides some interesting evidence regarding the behavior of blackfish in the Wood River system. Namely, blackfish populations must be relatively localized and sedentary, staying close to each island and not foraging substantially in other areas. Were blackfish more mobile, ranging further to feed, they would have shown similar $\delta^{13}C$ values among all islands.

The nitrogen stable isotope data indicate a strong correlation between ^{15}N enrichment of algae and island gull density (Fig. 5), evidence that gull guano is fertilizing algae. Additionally, the average difference between $\delta^{15}N$ values of snails and periphyton was consistent with what one would expect if snails were grazing on periphyton (i.e. values suggest approximately one trophic level difference between periphyton and snails, i.e. ~3.4‰; Post 2002). However, the difference between snail and blackfish $\delta^{15}N$ values was higher but also within the range reported from the literature (Post 2002), suggesting that blackfish feed on snails, and therefore benefit indirectly from guano-enhanced algal production transmitted via snails. Additional variation in this relationship may be accounted for by omnivory by blackfish (Morrow 1980) that we did not quantify in this study.

Mobile consumers as vectors of salmon-derived nutrients

Because Pacific salmon return from the ocean to spawn and die in freshwaters, they represent a massive flux of marine-derived nutrients to coastal ecosystems (Gende et al. 2002, Naiman et al. 2002, Schindler et al. 2003). These nutrients are initially deposited in spawning locations where salmon die and their carcasses accumulate, but the nutrients are subsequently dispersed by both abiotic and biotic vectors. Different vectors disperse salmon-derived nutrients in different ways, moving distinct quantities of nutrients variable distances and to different habitats. Mobile consumers that feed on salmon in one area and then feed, defecate, urinate, or die in another actively move salmon-derived nutrients to habitats that the nutrients may otherwise not reach (Gende et al. 2002). Mammalian consumers such as bears, raccoons, river otters, mink and marten have been identified as vectors of salmon-derived nutrients because they drag partially consumed carcasses into riparian ecosystems and excrete salmon-derived nutrients in their urine and feces (Cederholm et al. 1989, Ben-David et al. 1997, 1998, Hilderbrand et al. 1999, Gende et al. 2004).

In general, these consumers transport carcasses only short distances (<20 m) from streams (Cederholm et al. 1989, Gende et al. 2004), although on the Kenai Peninsula, some bears may transport salmon-derived nutrients up to 1 km from streams (Hilderbrand et al. 1999). In a different southwestern Alaskan stream, isotopic enrichment of vegetation extended to 100–200 m from salmon streams (Ben-David et al. 1998). Not surprisingly, mammalian consumers do not distribute nutrients evenly across the landscape, but rather they disperse and redistribute carcasses away from spawning habitats to other areas determined by their behavior, such as to riparian banks adjacent to prime fishing spots or resting locations (Ben-David et al. 1998, Hilderbrand et al. 1999).

In addition to mammals, aquatic insects – spending their juvenile stages in streams but emerging and moving into terrestrial areas as adults – are also potential vectors of salmon-derived nutrients. Aquatic insect larvae can both directly and indirectly incorporate salmon-derived nutrients while in streams (Bilby et al. 1996, Wipfli et al. 1999, Winder et al. 2005). During the dispersal period, when they disperse up to 50 m from stream edges (Francis et al., unpubl.), these insects may suffer predation from insectivores or natural mortality, thus transporting salmon-derived nutrients short distances into riparian habitats.

Our study demonstrates that birds, due to their extreme mobility as consumers and their high densities on nesting islands, are key vectors of salmon-derived nutrients. In contrast to previously described biological vectors, gulls can transport nutrients much greater distances to distinct habitats, not only downstream or into adjacent riparian habitats. Additionally, whereas mammals and invertebrates tend to redistribute salmon-derived nutrients by diffusing nutrients away from already existing nutrient hotspots (e.g. spawning areas littered with carcasses), avian consumers can actively create new hotspots of biological productivity in distant areas, by moving and then re-concentrating those nutrients. Finally, although other birds have been shown to influence productivity around their nesting islands within particular ecosystems (e.g. seabirds in the marine environment, Bosman and Hockey 1986; and blackbirds and geese in freshwater systems, Hayes and Caslick 1984, Kitchell et al. 1999), we offer new evidence demonstrating how birds can indirectly link marine with freshwater systems (see also Harding et al. 2004).

Summary

Anadromous salmon represent a widely described case study of how mobile species can transport nutrients and energy across great distances, coupling distinct ecosystems (Willson et al. 1998, Gende et al. 2002, Naiman et al. 2002, Schindler et al. 2003). However, there is a growing realization that salmon are only the initial vector of these marine-derived nutrients, and that mobile consumers of salmon play key roles in distributing these nutrients further, into novel habitats. We offer the first evidence that the avian community can move salmon-derived nutrients great distances, enriching otherwise isolated habitats. Unlike other vectors that diffuse salmon nutrients away from spawning areas, or generate small patches of enhanced production, gulls redistribute and concentrate these nutrients in areas that would otherwise receive dilute salmon-derived nutrients only through passive processes, such as hydrologic mixing. In other words, salmon connect marine ecosystems to coastal spawning areas, and gulls connect salmon spawning areas to gull-nesting islands, indirectly connecting the marine ecosystem with freshwater island ecosystems. These complicated chains of nutrient movement and resultant habitat coupling alter landscape-level patterns in productivity.

In ecosystems with intact consumer assemblages, nutrients can be redistributed across the landscape into novel habitats. These redistributed nutrients impact local productivity in different habitats, localities, and species (Polis et al. 1997, 2004). Through these processes, the presence and movement patterns of mobile consumers impacts landscape-level patterns of productivity. Human activities that alter the abundance or movement of mobile consumers disrupt habitat coupling by changing spatial subsides of critical allochthonous inputs.

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