Diet, Movement, and Growth of Dolly Varden in Response to Sockeye Salmon Subsidies

KEITH P. DENTON,* HARRY B. RICH JR., AND THOMAS P. QUINN
School of Aquatic and Fishery Sciences,
Box 355020, University of Washington, Seattle, Washington 98195, USA

Abstract.—A large and growing body of literature has documented the transfer of marine-derived nutrients from the ocean to freshwater and riparian systems by semelparous Pacific salmon Oncorhynchus spp. The pathways by which these nutrients reach resident fish are often indirect, and the evidence for direct benefits to the resident fish is not always conclusive. However, the consumption of salmon tissue (in one form or another) by resident fish would constitute a direct and efficient pathway for energy transfer. We studied a population of small-bodied, nonanadromous Dolly Varden Salvelinus malma feeding on the fry and eggs of sockeye salmon O. nerka and blowfly (family Calliphoridae) larvae that had fed on salmon carcasses at a series of spring-fed and otherwise unproductive ponds in southwestern Alaska. The Dolly Varden fed heavily on sockeye salmon fry when available, shifted their diet almost exclusively to eggs after salmon spawning commenced, and then shifted to blowfly larvae toward the end of the season. Dolly Varden large enough to eat eggs moved into ponds where sockeye salmon spawn synchronously with the arrival of the salmon, and Dolly Varden growth rates increased greatly once salmon eggs and blowfly maggots were available. Young-of-the-year Dolly Varden, which were too small to eat eggs and fry, were concentrated in small streams between ponds where fewer sockeye salmon spawn, perhaps to minimize the risk of predation from larger conspecifics. These results indicate the importance of a pulse of salmon-related food resources for this population of resident fish and their adaptations to take advantage of these resources. It is likely that similar dependence occurs in other systems where sockeye salmon produce a suite of temporally predictable energy resources; thus, resident fish may depend on large populations of salmon.

Ecosystems are not independent of each other but are intricately connected by the movement of energy, nutrients, and materials across the landscape. These “spatial subsidies” are fluxes of energy from one habitat to another that can influence the structure and function of recipient food webs (Polis et al. 1997; Polis et al. 2004). Dramatic effects of a subsidy affecting the productivity and function of a recipient system have been demonstrated across the marine–terrestrial boundary in a variety of systems. Nutrients and material moving from highly productive marine environments to less-productive terrestrial habitats subsidize plants (Anderson and Polis 1998; Anderson and Polis 2004) and consumer populations (Polis and Hurd 1995; Polis and Hurd 1996; Rose and Polis 1998). Research on subsidies has emphasized the passive movement of nutrients and material between habitats, but biota can actively transport energy across the landscape (e.g., aquatic macroinvertebrates [Sabo and Power 2002a, 2002b], terrestrial invertebrates [Nakano et al. 1999], and seabirds [Maron et al. 2006]).

In temperate coastal regions, highly productive marine ecosystems may subsidize less-productive freshwaters through the upstream transport of nutrients by anadromous fishes. These fishes typically accumulate most of their biomass while feeding at sea, then return to freshwater to spawn and, if semelparous, die, thereby subsidizing freshwater ecosystems with marine-derived nutrients (MDN). Studies have demonstrated increased productivity of recipient communities from clupeids Alosa spp. (Durbin et al. 1979; Garman and Macko 1998; MacAvoy et al. 2009) and salmonids, including Atlantic salmon Salmo salar (Jonsson and Jonsson 2003), brown trout S. trutta (Lyle and Elliott 1998), and Pacific salmon Oncorhynchus spp. (reviewed by Schindler et al. 2003).

Semelparous Pacific salmon are especially important for nutrient transfer because they accumulate more than 99% of their final mass while feeding at sea and then return, spawn, and inevitably die in freshwater ecosystems (Quinn 2005). Their decaying carcasses release vast quantities of MDN to freshwater ecosystems (Kline 1991). In addition, they typically spawn at much higher densities than iteroparous fishes, increasing the magnitude of their subsidy (Quinn 2005). Researchers have long recognized the potential effect of this subsidy on the nutrient dynamics of freshwater communities (Juday et al. 1932; Donaldson 1967; Krohkin 1967; Richey et al. 1975). Through the use of stable isotopes, researchers have traced salmon-derived

* Corresponding author: kdenton2@u.washington.edu
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nitrogen and carbon in periphyton communities (Yanai and Kochi 2005), macroinvertebrates (Chalonier et al. 2002), riparian vegetation (Helfield and Naiman 2002), and juvenile salmonids (Kline et al. 1990; Bilby et al. 1996). While it is important to document the presence of salmon-derived nutrients in recipient communities, studies that link salmon presence to a change in diet and movement patterns or increased growth rates in communities and organisms are especially compelling (Bilby et al. 1998; Minakawa and Gara 1999; Wipfli et al. 2003; Scheuerell et al. 2007; Moore et al. 2008).

Salmon can fertilize recipient food webs through bottom-up processes, as nitrogen and phosphorous leached from decaying carcasses are utilized in primary production and indirectly transferred to higher trophic levels. However, MDN can also enter the food web by direct consumption of salmon tissue and eggs. Caddisflies (order Trichoptera; Winder et al. 2005), terrestrial blowflies (family Calliphoridae; Meehan et al. 2005), juvenile salmon (Bilby et al. 1996), resident fish (Eastman 1996; Scheuerell et al. 2007), and a wide variety of terrestrial vertebrates (Willson and Halupka 1995) all consume salmon flesh and eggs. Organisms directly consuming salmon products may be more strongly affected than those receiving salmon nutrients through indirect pathways because of the efficiency of passing energy through fewer trophic levels (Johnson and Ringler 1979).

Despite the availability of food resources from salmon, the connection to movements of resident fish is poorly understood. Radio-tracking studies of large resident rainbow trout *Oncorhynchus mykiss* in watersheds of southwest Alaska containing high densities of spawning salmon revealed distinct ecotypes of trout based on movement patterns, but the temporal and spatial scales were not designed to document movement in response to salmon subsidies (Burger and Gwartney 1986; Meka et al. 2003). At smaller scales, two studies used changes in juvenile salmon densities in response to artificial carcass addition as a proxy for movement, but they reached conflicting conclusions (Bilby et al. 1996; Lang et al. 2006).

Perhaps most importantly, the direct consumption of salmon nutrients, particularly their energy and lipid-rich eggs, may increase the growth rates of resident fish. The positive effect of salmon subsidies on the growth of young-of-the-year (age-0) salmonids has been investigated using artificially planted salmon carcasses, but the pathway through which the resident fish incorporated salmon-derived nutrients was not documented (Wipfli et al. 2003; Wilzbach et al. 2005). Furthermore, the effect of feeding on salmon-derived nutrients by larger fish remains unknown.

Building on previous studies that investigated the effect of salmon subsidies on the diet, movement, and growth of resident fish, our goal was to assess the effect of salmon on all of these processes at once. Specifically, we tested the hypotheses that resident Dolly Varden *Salvelinus malma* would (1) directly feed on salmon products when available, (2) move to areas where they could take advantage of these subsidies, and (3) exhibit increased growth when consuming salmon products.

**Methods**

*Study site.*—We examined interactions between anadromous sockeye salmon *O. nerka* and resident (nonanadromous) Dolly Varden in a series of seven small ponds and creeks that comprise a wetland complex near the village of Pedro Bay, in the northeast part of Iliamna Lake, in the Bristol Bay region of southwest Alaska (outlet: 59°47'38"N, 154°07'60"W; Figure 1). The ponds (~100 to almost 2,000 m²) are relatively uniform in depth (~0.2–0.4 m; Quinn and Kinnison 1999), and water temperatures are low and stable throughout the summer at approximately 5°C (Table 1). The substrate is dominated by sand (approximately 1 mm in diameter; Quinn et al. 1995), over a bed of medium sized cobble (~15–25 cm in diameter). The ponds are connected by a series of small streams approximately 1 m wide and 0.2 m deep, flowing 1–2 km to a deeper slough (3 m wide and 1.5 m deep) that enters Iliamna Lake in 0.5 km (Table 1).

The seven ponds we sampled were divided into four pond complexes based on connectivity. Ponds connected by the same tributary to the main slough were considered to be in the same complex; thus, the complexes were Trail, Pond 1, Grass, and Bear (Figure 1). Densities of adult sockeye salmon (the only salmonid other than Dolly Varden regularly seen) vary among years and ponds, but range from 0 to approximately 1 fish/m². Based on observations since 1994 (T. P. Quinn, unpublished data), the sockeye salmon arrive and begin spawning at the end of July (little variation occurring among years), but they consistently arrive earlier at some ponds than others.

*Field protocols.*—Dolly Varden were sampled prior to and during the period of sockeye salmon spawning in the ponds and associated creeks from 2005 to 2007. Initial sampling in 2005 was designed to ascertain general patterns of density and habitat use as a function of fish size. In 2006 and 2007, Dolly Varden were caught with a stick seine in each of seven ponds and their connecting streams every 3 d from late June until early September (16 sampling events in 2006 and 20 in 2007). In 2006, all captured fish were weighed to the nearest 0.1 g, measured to the nearest 1-mm fork length, sampled for stomach contents using gastric
lavage, and those longer than 65 mm had a passive integrated transponder (PIT) tag inserted into their body cavity. Passive integrated transponder tags reveal a unique code when energized by an auxiliary sensor and do not adversely affect the growth, survival, or behavior of fish longer than 65 mm (Prentice et al. 1990). All fish were weighed and measured in 2007, but due to increased catches in that year, only a subset...
from representative time periods and size-classes were tagged and sampled for diet. Stomach contents were preserved in ethanol and analyzed in the laboratory. After Dolly Varden capture events in each pond, systematic visual surveys by three observers were conducted to enumerate any additional Dolly Varden present that were not captured. The shallow, exceptionally clear water and modest size of the ponds facilitated these surveys. Over the course of the study, approximately 95% of the Dolly Varden present in a pond during any given sampling event were captured during seining. Concurrent with Dolly Varden captures, live and dead salmon were counted. After each survey, all dead salmon were removed from each pond and its immediate vicinity to avoid double counting on subsequent surveys. The number of sockeye fry present in each pond was also recorded every 3 d between June 24 and July 27, 2007, based on the average of independent visual counts made by two observers.

**Laboratory protocols.**—Preserved diets were processed in the laboratory to determine their overall mass and the relative contribution of specific taxa, emphasizing the comparison between salmon-related items (eggs, fry, blowfly larvae) and items not directly related to salmon (aquatic and terrestrial macroinvertebrates). Macroinvertebrates were classified to order, and into one of three life history stages (larvae, pupae, and adult) and three size-classes within each life history stage. Ten items from each order, life history stage, and size-class were then dried at 60°C to a constant mass, and the average mass of each item was used for further analysis. The dry mass of salmon fry in the Dolly Varden diets was derived using 10 sacrificed fry from each site because most fry in the Dolly Varden stomachs were partially digested. Salmon eggs from different time periods and ponds (n = 11) did not differ in dry mass; therefore, the average value was used. Finally, diet masses were standardized for different sizes of Dolly Varden by dividing them by the mass of the fish.

**Data analyses: delineation of salmon resource periods.**—Live counts of adult sockeye salmon in 2006 and 2007, and counts of fry in 2007 were recorded every 3 d throughout the sampling season to determine when salmon fry and eggs were available for Dolly Varden consumption. Fry counts had tapered off to a consistently low level (30% of their peak) by 12 July, and adult salmon arrived in the pond complex as a whole on 27 July (Figure 2). Therefore, in 2007, the period of fry availability was defined from the first sampling date, 24 June through 12 July. In both years, the before-salmon-arrival period was from 12 to 27 July, and the after-salmon period was from 28 July until the last sampling date (2 September 2006 and 4 September 2007). Sockeye salmon spawn within a few days of arrival on the breeding grounds (e.g., McPhee and Quinn 1998), so these dates represent the period when at least some eggs would be available for consumption. There was no “fry period” in 2006 because few fry were seen in the ponds, presumably because sampling began 2 weeks later than in 2007. In addition, far fewer sockeye salmon spawned in 2005 than in 2006, so fewer fry were presumably present in 2006 compared with 2007. The cumulative number of dead salmon plus the live counts on 25 August (our index of overall abundance) was 298 in 2005; 3,151 in 2006; and 4,381 in 2007.

**Diets.**—Qualitative and quantitative characterization of diet compositions were conducted in 2006 and 2007 to determine if Dolly Varden prey and ration size varied over the season with respect to the availability of a sockeye salmon subsidy. The occurrence of empty stomachs necessitated a three-step approach to the analysis of variation in diet mass across salmon subsidy periods. First, for both years of diet data, a chi-square test was performed to determine if the proportion of empty stomachs differed among periods. Then, in 2006, a t-test was used to compare the log-normalized masses of nonempty Dolly Varden diets (standardized for body mass) from the periods before and after salmon arrived. In 2007, analysis of variance was used to compare the log-normalized masses of nonempty Dolly Varden diets (standardized for body mass) of all three salmon subsidy periods with each other (fry, before salmon arrival, and after salmon arrival).

**Movement.**—The movements of Dolly Varden with respect to salmon were examined on two scales: changes in Dolly Varden abundance in the pond complex as a whole, and on a pond-by-pond basis. Data on Dolly Varden catches from the entire pond complex for each sampling event in 2006 and 2007

### Table 1.—Physical features of the Pedro Bay ponds, in which salmon subsidies were studied; values are means with SDs in parentheses. Temperatures were recorded every 90 min in 2006 and 2007. The July temperatures represent the period before the arrival of sockeye salmon, the August temperatures the period after arrival. Ponds 1, 1A, and 2 form a complex, as do Trail and Berg’s ponds.

<table>
<thead>
<tr>
<th>Pond</th>
<th>Area (m²)</th>
<th>Depth (cm)</th>
<th>Jul</th>
<th>Aug</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bear</td>
<td>1,820</td>
<td>41.6 (7.6)</td>
<td>4.8 (0.8)</td>
<td>5.3 (1.2)</td>
</tr>
<tr>
<td>Grass</td>
<td>1,070</td>
<td>19.9 (6.6)</td>
<td>5.5 (1.4)</td>
<td>6.5 (1.4)</td>
</tr>
<tr>
<td>Pond 1</td>
<td>1,350</td>
<td>26.0 (6.5)</td>
<td>4.4 (0.5)</td>
<td>5.1 (0.9)</td>
</tr>
<tr>
<td>Pond 1A</td>
<td>165</td>
<td>13.5 (3.9)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pond 2</td>
<td>355</td>
<td>16.5 (3.7)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trail</td>
<td>1,135</td>
<td>38.5 (8.6)</td>
<td>4.9 (0.8)</td>
<td>4.9 (0.9)</td>
</tr>
<tr>
<td>Berg’s</td>
<td>300</td>
<td>26.7 (5.7)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
were grouped into the same periods as the diets for statistical analysis (before and after salmon in 2006, plus the fry period in 2007), and the means of each period were compared. However, before the mean catches of each time period could be compared, their confidence intervals were adjusted according to Bence’s (1995) method because of significant lag 1 autocorrelation coefficients (0.654 in 2006 and 0.581 in 2007).

Salmon entered individual ponds asynchronously within a year, allowing us to compare Dolly Varden movement with available egg subsidies on a pond-by-pond basis. Dolly Varden catches in specific ponds that received salmon up to 10 d apart were compared to determine if the timing of increased Dolly Varden abundance was correlated with the timing of salmon arrival. Finally, individual fish movement was investigated by analyzing the tagging and recapture locations of PIT-tagged fish to determine if individuals moved between pond complexes. Only fish recaptured at least 6 d (two sampling events) later were included in the analysis.

Size distributions and growth.—Separate length frequency histograms were made for Dolly Varden caught in creeks and in ponds during the salmon spawning seasons in 2005–2007. These were then qualitatively evaluated to investigate habitat segregation by size.

Instantaneous daily growth rates of individually tagged fish from 2006 and 2007 were calculated using the equation

\[ g = \frac{\log_e (M_2/M_1)}{\Delta t}, \]  

where \( g \) is the instantaneous growth rate, \( M_1 \) is the fish’s mass at capture event one, \( M_2 \) is the fish’s mass at capture event two, and \( \Delta t \) is the number of days between the two capture events.

Dolly Varden were only included in this analysis if they were caught twice before or twice after salmon arrived, and if the capture events were at least 6 d apart within a given season. Analysis of covariance (ANCOVA) analyses were used to compare Dolly Varden growth rates between before- and after-salmon arrival periods across a range of sizes. The dependant variable was the instantaneous growth rate \( g \), the independent variable was the initial mass \( M_1 \) and the fixed-grouping factor was initially year and then salmon period. First, we determined if data from both years, within either the before- or after-salmon arrival period, could be pooled. To accomplish this, a linear model that included the interaction term of the year effect was run for each period. Since the interaction term was not significant, it was dropped from the model and the test was run again to determine if the intercepts differed. The slopes and intercepts did not differ from each other, indicating no year effect, so the data from 2006 and 2007, within the same salmon subsidy period, were pooled and tested for differences in growth rates between periods. This was done by performing the same ANCOVA analysis as above with the pooled data, but defining salmon period as the interaction term. The interaction term was not significant, it was dropped from the model and the test was run again to determine if the intercepts differed. The slopes and intercepts did not differ from each other, indicating no year effect, so the data from 2006 and 2007, within the same salmon subsidy period, were pooled and tested for differences in growth rates between periods. This was done by performing the same ANCOVA analysis as above with the pooled data, but defining salmon period as the interaction term. The interaction term was not significant, indicating that the slopes were the same, so the model was run again without it to determine if the intercepts were different. If the intercepts were different, then we concluded that growth rates of Dolly Varden during the two periods differed, and during the period with the higher intercept Dolly Varden grew faster. These are
standard procedures for removing the effects of a covariate (Huitema 1980).

Results
A total of 2,194 Dolly Varden were caught during the course of this study: 603 of these were tagged and released, and 148 of these were subsequently recaptured at least once. Diets were collected from 978 fish. Of the 148 recaptured fish, 116 fit the criteria for growth analysis.

Diets
Dolly Varden diets were dominated by macroinvertebrates during the 2 weeks prior to salmon arrival in both years (Figure 3). In 2007, sockeye salmon fry (30–35 mm, depending on the pond and date) were also consumed between the first sampling period, 24 June, until 8 July. During this period, 47% of nonempty diets contained fry. After the arrival of adult salmon, on 27 July in both years, Dolly Varden diets consisted almost entirely of sockeye salmon eggs. During the salmon spawning period in 2006, 98% of all Dolly Varden greater than 65 mm in length had eggs in their diets, as did 81% in 2007. In 2006, the proportion of empty stomachs in the period before salmon was significantly higher than the period after salmon (0.17 versus 0.02; \( \chi^2 = 8.79, P = 0.003 \)). In 2007, the proportion of empty stomachs was significantly different in all three periods. In the earliest period, when salmon fry were available, 0.19 of the stomachs were empty. The proportion increased to 0.42 during the period before salmon arrived, followed by a decrease to 0.06 in the

![Figure 3](image.png)
period after salmon arrived (fry, before: $\chi^2 = 10.28, P = 0.013$; fry, after: $\chi^2, P < 0.0001$; before, after: $\chi^2, P < 0.0001$). Average ration size before the salmon arrived, excluding the period of fry consumption (24 June to 12 July in 2007), was similar in 2006 and 2007, at 0.66 and 0.63 mg/g Dolly Varden, respectively. Ration sizes during the after salmon arrival period were approximately 30 times higher than the before salmon period of the same year, and similar in 2006 and 2007, at 27.3 and 22.1 mg/g Dolly Varden, respectively (2006: df = 190, $t = -14.9, P < 0.0001$; 2007: df = 404, $t = -9.31, P < 0.0001$, Figure 3). Fry consumption was only observed in 2007 and was evident when sampling began on 24 June, lasting until 15 July, although fry appeared in only 10% of the diets after 8 July. The average ration size during this period, 4 mg/g Dolly Varden, was higher than the ration size before adult salmon arrived, but lower than the period after salmon arrived (df = 537; $F = 84.5; P < 0.0001$). In summary, Dolly Varden feeding rates were about five times higher when feeding on sockeye fry and 30 times higher when feeding on salmon eggs, compared with presalmon conditions.

The larval form of terrestrial blowflies (i.e., maggots), which colonize salmon carcasses, were also evident in Dolly Varden diets after the arrival of salmon, particularly in age-0 Dolly Varden, whose gape may be insufficient for consumption of salmon eggs. Nineteen out of 34 (55%) age-0 Dolly Varden (average length = 52 mm) had prey in their stomachs, and of these, 92% of their diet consisted of larval blowflies and the other 8% was insects (none had eaten eggs), for an average standardized diet mass of 0.65 mg/g fish.

**Movement**

In both years of intensive sampling (2006 and 2007), catches of Dolly Varden in the pond complex as a whole were high early in the season, followed by a period in mid-July when catches diminished to about 25% of the previous level. During this period, sockeye salmon fry were not available and spawning adults had not yet arrived. After sockeye salmon arrived and began to spawn, catches increased for consumption of salmon eggs. Nineteen out of 34 (55%) age-0 Dolly Varden (average length = 52 mm) had prey in their stomachs, and of these, 92% of their diet consisted of larval blowflies and the other 8% was insects (none had eaten eggs), for an average standardized diet mass of 0.65 mg/g fish.

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levels of fry or eggs. Of the 29 that moved, 13 (45\%) moved from an area of no fry or eggs to a pond complex where they were recorded feeding on these resources. The other 16 moved between areas of similar resource availability; none left areas with salmon resources and moved to areas without such resources.

**Size Distribution and Growth**

Qualitative analysis of length frequency histograms of Dolly Varden caught in creeks and ponds revealed clear patterns of site-specific habitat segregation. Generally, small Dolly Varden (<110 mm) were captured in the narrow, shallow creeks of the pond system, whereas larger (>110-mm) Dolly Varden were captured in the ponds (Figure 6). Most notably, age-0 Dolly Varden (<60 mm) were seldom found in the ponds in any of the 3 years, and with the exception of 2005, 1-year-old Dolly Varden (60–110 mm) were also rarely caught in the pond habitats.

Dolly Varden growth rates were significantly higher after the arrival of spawning salmon in both years (Figure 7). The year interaction term for each of the two salmon subsidy periods, across years, was not significant (before: df = 3 and 38, F = 2.189, P = 0.42; after: df = 3 and 70, F = 5.305, P = 0.97), indicating a consistent effect of spawning salmon between years. The intercepts of the 2 years, within each salmon period, also did not differ (before: df = 2 and 39, F = 2.981, P = 0.25; after: df = 2 and 71, F = 8.07, P = 0.87). Therefore, both years of data were pooled within each period. The slopes of the pooled models did not differ (df = 3 and 112; F = 37.5; P = 0.83), so the interaction term was eliminated from the model. The intercepts of the simplified model were significantly different (df = 2 and 113; F = 56.7; P < 0.0001), indicating that Dolly Varden grew more than three times faster when spawning salmon were present. In addition, the initial mass effect was significant (df = 2 and 113; F = 52.8; P < 0.001), indicating that, in both salmon periods, growth rate covaried with initial mass; smaller fish grew faster than larger fish.

**Discussion**

This study demonstrated that sockeye salmon provided an important subsidy to resident fish. Early in the growing season, Dolly Varden fed heavily on sockeye salmon fry, and after the arrival of spawning adults, Dolly Varden fed almost exclusively on salmon eggs. The only other significant diet item during that period was larval blowflies, a byproduct of decaying salmon carcasses. Furthermore, Dolly Varden did not await the arrival of these subsidies but actively moved into areas where salmon resources became available. Most importantly, we also demonstrated increased growth rates of Dolly Varden after the arrival of spawning sockeye salmon and the associated appearance of salmon eggs in Dolly Varden diets. Previous studies of stream fish diets indicated the direct pathway of energy transfer from salmon to resident fish that we found. Juvenile salmon and resident nonanadromous fish ingested salmon eggs and flesh associated with carcass addition (Johnson and Ringler 1979; Bilby et al. 1998; Lang et al. 2006), and adult resident fish consumed salmon eggs and carcasses in natural settings (Scheuerell et al. 2007; Moore et al. 2008). We did not detect direct consumption of salmon carcasses, perhaps because the abundant eggs and maggots were more readily consumed by the small Dolly Varden. It is also possible that had we not removed the salmon carcasses every third day (a necessary part of our surveying methods), they might have decomposed and become more readily consumed by the Dolly Varden. Such consumption would have been further evidence of a
direct subsidy of the Dolly Varden by the sockeye salmon. In addition to these direct pathways, salmon can also indirectly pass nutrients to stream fish communities via the insects that scavenge salmon carcasses. Up to 35,000 larval blowflies can feed on a single carcass (Meehan et al. 2005), and thereafter become prey for resident fish if they move from the skeletonized carcass and fall into the water. Additionally, a diverse community of aquatic macroinvertebrates, which resident fish also eat, can consume salmon carcasses, including mayflies (order Ephemeroptera), stoneflies...
(order Plecoptera), caddisflies and true flies (order Diptera) (Wipfli et al. 1998; Winder et al. 2005). Bears (in the present study, brown bears Ursus arctos) often determine whether salmon carcasses are deposited on land, where they can be consumed by terrestrial insects, or remain in the water to be consumed by aquatic insects (Meehan et al. 2005; Quinn et al. 2009). Our removal of carcasses from the ponds during surveying increased their availability for colonization by maggots and so might have elevated this resource. However, predation by bears in these ponds is heavy, and many carcasses are available for maggot colonization (Quinn and Kinnison 1999; Quinn et al. 2009). Thus, at most, our survey methods might have affected the proportional use of carcass tissue and maggots, but the overall importance of the subsidy seems clear.

This study was carried out in an area famous for its prolific salmon runs, but still provides important insights for other areas with smaller salmon populations. By demonstrating the importance of healthy salmon runs to resident fish populations, it can be inferred that resident fish in areas with depressed salmon returns could benefit from more robust salmon populations. That being said, in areas currently experiencing depressed salmon returns (e.g., Puget Sound, Washington; Ellings 2003; Lowery 2008), studies indicate that the ecological connection between salmon and resident fish exists even at low salmon densities.

The availability of nutrients from salmon depends, in this case and elsewhere, on two returning cohorts of salmon: the current and the previous. The lack of fry in Dolly Varden diets in 2006 was probably due to the later start of the sampling season than in 2007. Fry abundance in Dolly Varden diets had declined to almost zero by 9 July in 2007, the first day of sampling in 2006 (Figure 3). However, far fewer adult salmon spawned in 2005 than in 2006; therefore, fewer fry were produced for consumption in 2006. Fry consumption also appears to depend on more than mere availability. In 2007, fry consumption had declined to almost zero by 9 July, even though some fry remained in the ponds after that date, presumably because as fry sizes increased through time, it becomes more difficult for Dolly Varden to prey upon them. In terms of Dolly Varden population dynamics, a poor run of salmon fails to provide eggs and maggots as prey in the summer when the Dolly Varden are preparing to spawn and then overwinter, and it also fails to produce fry for them to consume the following spring. Some effect on Dolly Varden dynamics might be expected, and over the past decade we have documented years in which no salmon at all spawned in several of these ponds, and the entire pond complex had very few salmon (Quinn, unpublished survey data).

Few studies have attempted to link the movement of resident stream fishes to the availability of salmon subsidies; most have dealt with juvenile salmon and have reached mixed conclusions. Bilby et al. (1998) recorded increased densities of age 0+ and 1+ coho salmon O. kisutch and steelhead O. mykiss in response to artificial carcass addition in a western Washington stream, but Lang et al. (2006) reported decreased juvenile coho salmon catches after the arrival of spawning coho salmon and artificial carcass additions. Our results suggested that Dolly Varden moved towards areas where salmon subsidies were available. However, this movement was almost entirely composed of Dolly Varden large enough to eat eggs. The young of the year (~40–60 mm) were caught in the very shallow streams between ponds but not in the ponds themselves. This probably reflects both their inability to consume the eggs and also the risk of being preyed upon by older Dolly Varden in the ponds.

In 2006, Dolly Varden abundance in the pond complex as a whole was higher after the arrival of sockeye salmon, although not significantly so, mostly because there were also high catch rates on the first three sampling events of the season (Figure 4). This early period was not considered a period of salmon subsidy (fry), as it was in 2007, because few fry were seen in the ponds and none were found in Dolly Varden diets. The Dolly Varden may have entered the ponds during this time period in search of fry but encountered few, because few sockeye salmon spawned in 2005. In 2007, Dolly Varden abundance at the whole-pond complex level was clearly linked to the availability of sockeye salmon subsidies. During the fry and after-salmon-arrival periods, Dolly Varden catches were similar and almost four times higher than they were during the intervening before salmon period. We conclude that Dolly Varden moved into the ponds when fry and eggs were available, perhaps attracted to the odors from these salmon resources. Furthermore, sockeye salmon arrival differed among ponds by 10 d, and Dolly Varden catches in individual ponds mirrored this asynchronous arrival of salmon. It is unclear where the Dolly Varden were in the intervening period of low salmon subsidy. It is likely that they were in deep sloughs downstream of the ponds, but our efforts to locate them were not successful.

The effect of salmon on Dolly Varden growth observed in our study is particularly important as it corroborates carcass addition experiment results in mesocosms (Wipfli et al. 2003) and stream channels (Bilby et al. 1998). In fact, Wipfli et al. (2003) found that juvenile coho salmon actually lost 16% of their...
body mass in control reaches without carcasses. Wipfli et al. (2003) also noted an increase in the growth rate of juvenile coho salmon and Dolly Varden. Lang et al. (2006) saw increased growth of juvenile coho salmon in beaver ponds due to both artificial carcass addition and natural spawning. We found that Dolly Varden growth rates more than tripled after the arrival of spawning salmon in the pond system (Figure 7). We also documented a significant increase in growth rates over a broad range of age-classes. Furthermore, diet data indicated that the increased growth rate was due to the direct consumption of salmon eggs and maggots.

Management Implications

Artificial carcass addition has been implemented in some areas to mitigate for declining salmon returns and the associated loss of MDN to freshwater ecosystems (Compton et al. 2006). The present study illustrates the importance of the direct consumption of salmon products, especially eggs, by resident fish, highlighting the value of live, naturally spawning salmon to freshwater ecosystems. Thus, in areas with large commercial salmon fisheries, there is a potential conflict between recreational fisheries for species that benefit from the salmon subsidy and the commercial fisheries that capture the salmon in salt water before they can return to freshwater and provide the subsidy.

This study was carried out in Bristol Bay, Alaska, which has one of the largest runs of sockeye salmon in the world and also a very valuable recreational fishery. In 2005, the value of the commercial sockeye salmon fishery was estimated at over US$91 million, and in recent years the fishery has captured over 70% of the returning salmon while meeting escapement goals (Alaska Department of Fish and Game, unpublished data). The value of the recreational sport fishery in the same year was recently estimated at $61 million and relies heavily on resident species such as Dolly Varden Salvelinus spp. and rainbow trout (Duffield et al. 2007). In addition, a significant subsistence fishery for Dolly Varden exists in parts of Bristol Bay, providing a valuable food source for the area’s residents (Crane et al. 2003).

While they both depend on healthy runs of sockeye salmon, the commercial and recreational fisheries of Bristol Bay are managed independently. Escapement goals for the commercial fishery are designed to produce the maximum sustainable yield of salmon, and the Alaska Department of Fish and Game has proven very successful at achieving this goal. The recreational fishery is managed under the premise that the only factor affecting population size is exploitation by humans. Therefore, the role that “surplus” spawning salmon play as a subsidy for the freshwater ecosystem is not considered in the management plans of the commercial or recreational fisheries, and indeed the fisheries are managed by different divisions within the agency. Moore et al. (2008) found that the relationship between the magnitude of egg subsidies and the number of spawning sockeye salmon was not linear. At low densities, few eggs are available because they are successfully buried by the females. Only at high salmon densities are eggs mobilized by redd superimposition and become available as food for resident fish. Thus, the escapement goals may maximize salmon production but restrict the natural delivery of surplus eggs to resident fish. Producing specific management goals that recognize the value of salmon as both a commercially harvestable product and a subsidy to upstream ecosystems will be a challenge, but our study, and others, illustrate that these fisheries have strong ecological links.

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