

Harpacticoid copepods: potential link between inbound adult salmon and outbound juvenile salmon

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ABSTRACT: Stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of estuarine organisms were measured monthly within 2 field seasons in Seldovia Bay, Alaska, USA, to assess the impact of salmon carcass decomposition on estuarine productivity. A hypothesized indirect link between adult and juvenile salmon, with estuarine harpacticoid copepods acting as an intermediary, was supported by the data. Data show an influence of nutrients derived from salmon carcasses on estuarine macroalgal primary production, as nitrogen stable isotope ratio values of *Ulva* sp., an estuarine macroalga, were elevated in late summer following the salmon run. The isotope data also indicate that harpacticoids depend on *Ulva* sp. and possibly its epiphytes. Stomach content data for chum salmon fry (*Oncorhynchus keta*) show that they depend primarily on harpacticoids. Therefore, there is a nutrient link between adult and juvenile chum salmon in Seldovia Bay. Because harpacticoid production in an estuary is thought to control survival of chum fry, the nutrient link may function as a positive feedback mechanism influencing population fluctuations.

KEY WORDS: Harpacticoid copepod · Salmon · Seagrass · *Ulva* · Estuary · Food web · Nutrients · Stable isotope

INTRODUCTION

Each year, large numbers of salmon spawn and die in streams along the Pacific Coasts of Asia and North America. The anadromous behavior of Pacific salmon is one of the unsolved mysteries in marine science. Why do salmon return to their natal stream? What is the advantage for them to die in the stream?

The energy and nutrients transported from the ocean by salmon can be released into aquatic environments such as streams, lakes, and estuaries through carcass decay. If the imported material is sufficient to substantially increase primary or secondary productivity of the systems, anadromous behavior of Pacific salmon can be viewed as an adaptation to provide increased food sources for their offspring. This link, which can function as a feedback mechanism between adult and juve-

nile salmon, has been hypothesized for sockeye salmon *Oncorhynchus nerka* (Juday et al. 1932, Hall 1967, Kline et al. 1990), and numerous observations and experiments support the hypothesis (Eguchi et al. 1954, Nelson & Edmondson 1955, Nelson 1959, Donaldson 1967, Krokin 1968, Barraclough & Robinson 1972, Mathisen 1972, LeBrasseur et al. 1978, Robinson & Barraclough 1978, Stockner 1981, Kline et al. 1993). Brickell & Goering (1970), Sugai & Burrell (1984), and Kline et al. (1990) have shown the strong influence of nutrients derived from adult pink salmon *Oncorhynchus gorbuscha* carcasses on the primary and secondary productions in stream and estuarine systems. These observations suggest the possible existence of a similar link between adults and juveniles for other Pacific salmon species.

Juvenile chum and pink salmon (*Oncorhynchus keta* and *O. gorbuscha*), which are the focus of this study, have estuarine residence periods of up to 3 wk and 2 d, respectively (Neave 1966a, b, Healey 1980, 1982). Food availability in estuaries has been suggested to

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limit their survival (Parker 1965, 1968, 1971, Healey 1979, Sibert 1979, Godin 1981, D'Amours 1987). If adult chum and pink salmon carcasses increase estuarine production, the feedback mechanism between inbound adult salmon and outgoing juvenile salmon may be a major factor in regulating populations of both species.

We hypothesized that organic carbon derived from salmon carcasses can become a seasonally important food source for harpacticoid copepods. This hypothesis was based on the following points:

- (1) A large amount of dissolved organic carbon is released from adult salmon carcasses (Brickell & Goering 1970, Sugai & Burrell 1984).
- (2) Negatively charged dissolved organic matter tends to precipitate as aggregates in an estuary where it encounters positively charged metallic ions (Morris et al. 1978).
- (3) Some epibenthic harpacticoid copepods can assimilate bacterially formed aggregates of dissolved organic carbon (Rieper-Kirchner et al. 1991).
- (4) Stream-transported organic matter is considered to be the major food source for the estuarine copepods when the river transport of dissolved and particulate organic matter increases (Naiman & Sibert 1979).
- (5) Harpacticoid copepods are the major food source of juvenile chum salmon (Feller & Kazynski 1975, Healey 1979, Sibert 1979, Landingham 1982, Cordell 1986, D'Amours 1987, Massa 1995) and juvenile pink salmon (Barnard 1981, Godin 1981, Webb 1991) during their estuarine residence periods.

Our project was designed to test this trophic-link hypothesis. In addition to testing the hypothesis, we also attempted to observe other influences of adult salmon carcasses on an estuary, such as fertilization effects on benthic algae and seagrass.

If the organic matter derived from the adult salmon carcasses actually contributes to increased spring harpacticoid copepod abundance, the anadromous behavior of chum and pink salmon may be an adaptation to increase survival rates of their offspring by nourishing prey organisms in a nursery area. This model would have important implications for the management of salmon populations.

Presently salmon harvesting is regulated so as to allow only enough females to reach nesting areas in streams (escapement) to maintain the population. 'Over-escapement' of adult salmon to a stream is thought to be deleterious to future populations mainly because the offspring would have to compete for limited resources. However, if the carcasses of adult

salmon have significant positive effects on survival of offspring, optimal management plans for salmon should consider implications of this linkage.

Stable isotope ratio analysis is commonly used to reveal food web structures in terrestrial and aquatic environments (Peterson & Fry 1987, Wada & Hattori 1991, Michener & Schell 1994) and is the major tool used in this project. The nitrogen stable isotope ratio, denoted by $\delta^{15}\text{N}$, of a primary producer depends on the $\delta^{15}\text{N}$ of its nitrogen sources and the origin of nutrients. The nitrogen stable isotope ratio of a consumer depends on the $\delta^{15}\text{N}$ of its food sources. At each trophic level step, $\delta^{15}\text{N}$ increases by 3.4‰ on average (Michener & Schell 1994).

The carbon stable isotope ratio, denoted by $\delta^{13}\text{C}$, of a marine primary producer depends on the $\delta^{13}\text{C}$ values of the carbon sources and their availabilities. Values of $\delta^{13}\text{C}$ are also affected by the rate of primary production, temperature, acidity, and other environmental factors. The carbon stable isotope ratio of a consumer also depends on the $\delta^{13}\text{C}$ of its food sources. At each trophic-level step, little or no change is observed in $\delta^{13}\text{C}$ (Michener & Schell 1994).

Because of the predictable properties of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in food webs, they can be used as tracers for nutrient links. Stable isotopes are especially useful in differentiating marine, terrestrial, and estuarine food sources (Peterson & Fry 1987, Michener & Schell 1994). Kline et al. (1990, 1993), for example, use this technique to trace nutrient input from salmon carcasses to a freshwater food web.

Pacific salmon $\delta^{15}\text{N}$ values (all 5 species) range between +10 and +14‰ (Welch & Parsons 1993). The $\delta^{15}\text{N}$ values of primary producers in salmon-free subarctic streams are close to 0‰ (Kline et al. 1990), and the values for plant tissue are also typically low (below +2‰) (Nadelhoffer & Fry 1994). Kline et al. (1990, 1993) successfully used these differences between $\delta^{15}\text{N}$ of salmon and other potential nitrogen sources to quantify the influence of the salmon carcasses on freshwater primary and secondary productions.

METHODS

Study area. The study site is an intertidal estuary in Seldovia Bay (59° 23' N, 151° 41' W) located on the south side of Kachemak Bay, south-central Alaska, USA (Fig. 1). A small stream, the Seldovia River, flows into the bay. Pink and chum salmon (*Oncorhynchus gorbuscha* and *O. keta*) are the major species of salmon spawning in the river. The escapement of pink salmon into the stream was estimated to be 24 400 in 1994, and the average number of the escapement over 35 yr was estimated to be about 33 500 yr⁻¹ by the

Alaska Department of Fish and Game (ADF&G) (Bucher & Hammarstrom 1994). The head of the bay is an intertidal delta patchily covered with seagrass *Zostera marina* and macroalgae *Ulva* sp. The river and the bay are surrounded by Sitka spruce *Picea sitchensis* forest. Sitka alder *Alnus sinuata*, paper birch *Betula papyrifera*, and ferns are also common vegetation. The maximum tidal range in Seldovia Bay is about 9 m. The river freezes from late December to late February. The salinity of the sampling site (Site B) ranges from 0‰ during low tide to 30‰ at high tide.

Very few people live along the stream. The town of Seldovia, where approximately 350 people live, is located 4 km toward the mouth of the bay from the sampling site (Fig. 1). Therefore, any anthropogenic effects on the study site are very small. The study location is close (ca 17 km by road) to the University of Alaska's Kasitsna Bay Laboratory.

Sampling was conducted in Seldovia Bay, 1994 to 1996. In 1996, sampling was also conducted in Jakolof Bay, Alaska, to assess variability between the 2 bays (Fig. 1). Jakolof Bay is about 10 km east of Seldovia Bay. Chum (*Oncorhynchus keta*), pink (*O. gorbuscha*), and silver salmon (*O. kisutch*) spawn in Jakolof Stream. Adult chums and pinks return to streams in Kachemak Bay from early July to early August and from July to September, respectively.

Sample collection. Sampling in Seldovia Bay was done monthly from 1994 through 1996 during late spring, summer, and early fall. In 1994, surface sediment layers, seagrass *Zostera marina*, and macroalgae *Ulva* sp. were collected from Site B (Fig. 1). In 1995, sediment cores (3 cm in diameter, 3 cm in depth), surface sediment layers, *Z. marina*, and *Ulva* sp. were col-

lected. In 1996, the surface sediment layer (from March through June), *Z. marina*, and *Ulva* sp. were collected from Site B, and macroalgae were also sampled from Site A (Fig. 1). Two locations for sediment layer collection were chosen randomly every sampling month by throwing a marker blindly within a sampling station (approximately 10 × 10 m) of nearly uniform topography. The same sampling station was used every month because the purpose of this project was to characterize time series variations rather than spatial variations. In the same manner, sites for sediment cores were chosen by throwing markers. Similarly, seagrass and macroalgae were chosen randomly by throwing a marker blindly. Only green parts of seagrass leaves were selected. Leaves of terrestrial plants (ferns, paper birch, Sitka alder, Sitka spruce), were also sampled in August 1995 and August 1996.

From May to September 1996, plankton tows were conducted monthly during high tide to collect zooplankton at Site B and at the mouth of Seldovia Bay off Outside Beach (Fig. 1). Two tows were done at each site in each sampling month to obtain 2 isotope measurements. The samples were taken to Kasitsna Bay Laboratory and filtered with 500 and 125 µm mesh sieves. Plankton retained in the 125 µm sieve was immediately frozen for later stable isotope ratio analysis. *Zostera marina* and *Ulva* sp. were also collected during the same period from Jakolof Bay (Fig. 1). In the same year, freshwater algae *Enteromorpha* sp. were also collected in Seldovia River approximately 100 m upstream from the extreme high tide level.

During each of the May and June sampling periods in 1995 and 1996, approximately 10 chum salmon fry were collected in a seagrass bed (Fig. 1) during low

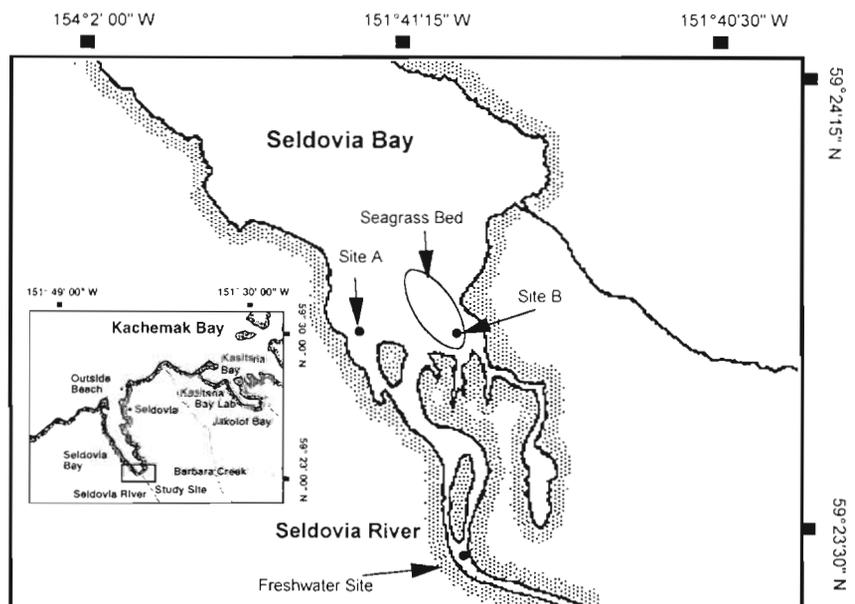


Fig. 1. Study sites in Jakolof Bay and Seldovia Bay, Alaska, USA

tide using a 3 mm mesh dip net. The fish were collected from different schools as much as possible by sampling from different locations within the seagrass bed. The captured fish were placed on a blue ice pack in a plastic bucket and transported to Kasitsna Bay Laboratory. The fish were dissected immediately. Stomachs were preserved in 10% formalin, and their contents were observed later. The rest of the body was rinsed with distilled water and frozen for later stable isotope ratio measurements.

The surface layer of the sediment was sieved through 125 μm mesh, and harpacticoid copepods (mixture of several species) were separated from the detritus and sediment under a dissecting microscope. Approximately 1500 copepods were collected for each stable isotope ratio ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) measurement. Phytoplankton harpacticoid copepods (*Harpacticus uniremis*) were also separated from the seagrass. Because *H. uniremis* is a large species, approximately 300 individuals were sufficient for each isotope ratio measurement. This species was rarely found in sediment and was not included in the benthic copepod samples. For seagrass and macroalgae, a mixture of several leaves were used for each measurement. They were rinsed with distilled water immediately after the samples were brought to Kasitsna Bay Laboratory. After the above procedures, all samples were frozen for later stable isotope ratio measurements. In each sampling month, 2 to 3 measurements for each type of organism were done.

Adult chum ($n = 2$) and pink salmon ($n = 5$) were also sampled from Seldovia Bay and Jakolof Bay in 1995 and 1996. Muscle from the dorsal part just behind the head was used for stable isotope measurements.

Stable isotope ratio measurements. Two sediment cores from each sampling date in 1995 were thawed and rinsed through a 1 mm sieve, 63 μm sieve, and 0.8 μm Millipore filter. The material retained by the 63 μm sieve and Millipore filter (scraped from the filter) was used for stable isotope ratio measurements. Both types of material contain living matter such as bacteria, Protista, and small metazoans. However, the contribution of the living matter to the stable isotope ratios of these materials was assumed to be small, and they are called detrital material in the rest of this paper. All the other frozen samples were thawed, rinsed with distilled water, and dried in an oven overnight at 60°C. Prior to drying the copepods, zooplankton, and detrital material, a few drops of 10% HCl were added to eliminate carbonate. The dried seagrass and macroalgae were ground into powder and weighed prior to analysis. Other dried samples were weighed but not ground. Lipids tend to have lower $\delta^{13}\text{C}$ values than other organic molecules (Parker 1964, DeNiro & Epstein 1977, O'Leary 1981). Our calculation, based on lipid contents of copepods measured by

Hobson & Welch (1992) and the difference in $\delta^{13}\text{C}$ values between lipid and non-lipid material measured by DeNiro & Epstein (1977), shows that a large change in lipid contents of copepods will cause a change in $\delta^{13}\text{C}$ of less than 1.4‰. Because this value is small for our purpose, lipid extraction from harpacticoid copepods was not done prior to isotope ratio measurements. The stable isotope ratios were determined with a continuous flow stable isotope ratio mass spectrometer ('Europa 20/20') at the Institute of Marine Science, University of Alaska Fairbanks. The determinations of stable isotope ratio values were done as described in Goering et al. (1990). $\delta^{13}\text{C}$ values are reported as

$$\delta^{13}\text{C} = \frac{[^{13}\text{C}]/[^{12}\text{C}]_{\text{sample}} - [^{13}\text{C}]/[^{12}\text{C}]_{\text{standard}}}{[^{13}\text{C}]/[^{12}\text{C}]_{\text{standard}}} \times 1000\text{‰}$$

where standard is Peedee Belemnite (PDB limestone). Similarly, $\delta^{15}\text{N}$ values are reported as

$$\delta^{15}\text{N} = \frac{[^{15}\text{N}]/[^{14}\text{N}]_{\text{sample}} - [^{15}\text{N}]/[^{14}\text{N}]_{\text{standard}}}{[^{15}\text{N}]/[^{14}\text{N}]_{\text{standard}}} \times 1000\text{‰}$$

where standard is atmospheric nitrogen.

RESULTS

Nitrogen stable isotope ratios of adult chum and pink salmon were $+10.62 \pm 0.02\text{‰}$ ($\pm\text{SE}$) and $+10.90 \pm 0.42\text{‰}$, respectively. These values are similar to sockeye salmon values ($+11.6 \pm 0.15\text{‰}$) ($\pm\text{SE}$) for the Kvichak River, Alaska (Kline et al. 1993), and to all 5 species of Pacific salmon sampled in the central North Pacific ($+10$ to $+14\text{‰}$) (Welch & Parsons 1993). The chum and pink salmon $\delta^{15}\text{N}$ values were higher than terrestrial plant, which ranged from -2.37 ± 0.09 to $+0.81 \pm 0.23\text{‰}$, indicating nutrients derived from the decomposition of salmon carcasses and plant litter would have quite distinct nitrogen isotopic signatures.

Table 1 shows carbon and nitrogen stable isotope ratios of chum salmon fry in 1995 and 1996. Their carbon stable isotope ratios differed between May

Table 1 Mean stable isotope ratios, associated standard errors, and sample sizes (N) for chum salmon fry *Oncorhynchus keta* sampled in Seldovia Bay (Alaska, USA)

Date	$\delta^{13}\text{C}$ ‰	$\delta^{15}\text{N}$ ‰	N
May 1995	-20.22 ± 0.23	$+11.94 \pm 0.16$	10
Jun 1995	-16.84 ± 0.33	$+11.43 \pm 0.12$	14
May 1996	-22.43 ± 0.47	$+11.08 \pm 0.06$	5
Jun 1996	-18.20 ± 0.86	$+10.52 \pm 0.15$	10

and June in both years, indicating their main carbon sources were probably different between the 2 months.

Concordance of temporal changes in mean stable isotope ratios of benthic harpacticoid copepods, *Ulva* sp., and seagrass in 1995 and 1996 was analyzed by pairwise comparisons of differences in monthly mean stable isotope ratios (i.e. benthic harpacticoids vs *Ulva* sp. and benthic harpacticoids vs seagrass). These analyses were done with Bonferroni multiple comparison tests and by constructing Bonferroni 95% confidence intervals consisting of 13 intervals. Standard deviations of stable isotope ratio values were assumed to be constant for the duration of the study. The results of the tests show that there were no significant differences over time among the monthly differences between the stable isotope ratios (both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of macroalgae and harpacticoid copepods in 1995 ($p > 0.05$), indicating trends in mean stable isotope ratios for the 2 organisms remained the same (Fig. 2). However, the differences between harpacticoid and *Zostera marina* values changed between months in 1995 ($p < 0.05$), indicating trends in mean stable isotope ratios for the 2 organisms varied independently over time (Fig. 2).

The differences in stable isotope ratios (both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) between benthic harpacticoid copepods and *Ulva* sp. did not change ($\alpha = 0.05$) in 1996 except for $\delta^{15}\text{N}$ in May (Fig. 3). The 2 harpacticoid $\delta^{15}\text{N}$ measurements in May differed considerably (difference of 1.75‰), suggesting a possible outlier. If the higher value is eliminated, the difference in mean harpacticoid and macroalgae $\delta^{15}\text{N}$ values in May would be within the confidence intervals for other months. We conclude that trends in monthly mean stable isotope ratios of harpacticoid copepods and *Ulva* sp. were the same over 2 yr, suggesting a trophic relationship between them.

Peterson & Fry (1987) reported that carbon stable isotope ratios generally increase between 0.0 and +1.0‰ per trophic level. Michener & Schell (1994) found a similar range of +0.5 to +1.0‰ for ^{13}C enrichment per trophic level. Nitrogen stable isotope ratios show a mean increase of +3.4‰ per trophic level on average (Michener & Schell 1994). All monthly confidence intervals for differences between harpacticoid and *Ulva* sp. $\delta^{13}\text{C}$ values overlap with the conservative 0.0 to +1.0‰ range; however, the confidence intervals for harpacticoids and seagrass do not always overlap with the expected range and would not even if the range was extended to -1.5 to +1.5‰. Furthermore, all monthly confidence intervals for differences between harpacticoid copepod and *Ulva* sp. $\delta^{15}\text{N}$ values overlap with the $+3.4 \pm 1.0$ ‰ range. However, the values for harpacticoids and seagrass do not always overlap with

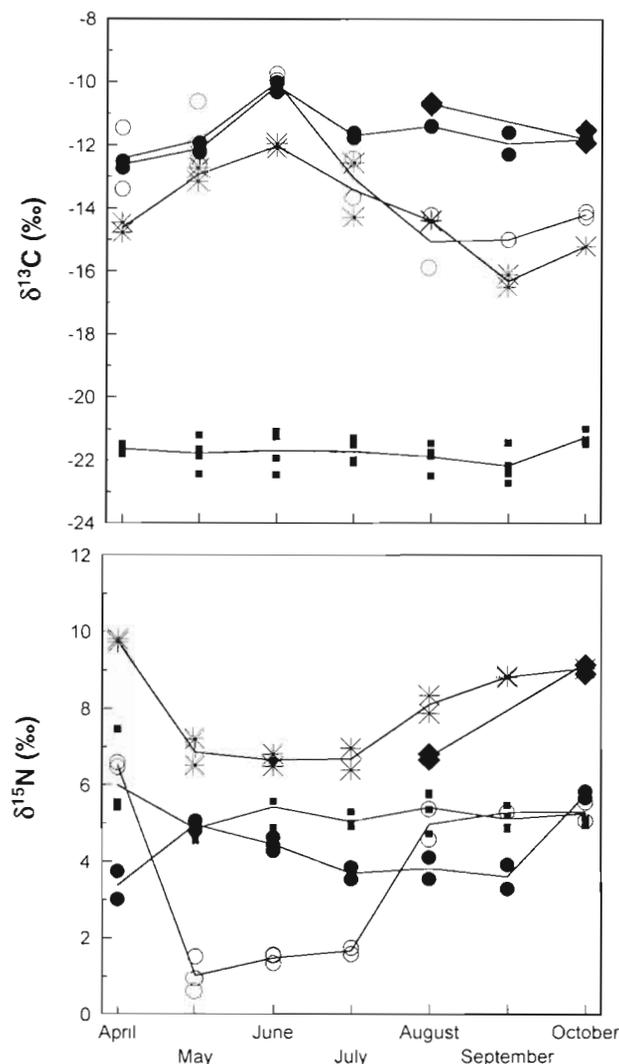


Fig. 2. Carbon and nitrogen stable isotope ratios of (O) estuarine macroalgae *Ulva* sp., (●) seagrass *Zostera marina*, (■) detritus, (*) benthic harpacticoid copepods, and (◆) *Harpacticus uniremis* in 1995. Lines connect monthly mean values of each type of organism

the range. Therefore, the limited magnitude of the differences between the stable carbon isotope ratios of benthic harpacticoid copepods and *Ulva* sp. also supports a trophic relationship between the 2 organisms.

Nitrogen stable isotope ratios of *Ulva* sp. collected at Site B in 1996 showed a similar trend (low values during the summer months and high values during spring and fall) to samples collected in 1995 (Fig. 3). Furthermore, similar trends were also observed among *Ulva* sp. collected at Site A (different location in Seldovia Bay) and in Jakolof Bay (Fig. 4). Compared with *Ulva* sp., seagrass did not show large monthly changes in $\delta^{15}\text{N}$ (Fig. 4).

The results of the 2-factor ANOVA (month and size factors) indicate that the $\delta^{13}\text{C}$ values of detrital mater-

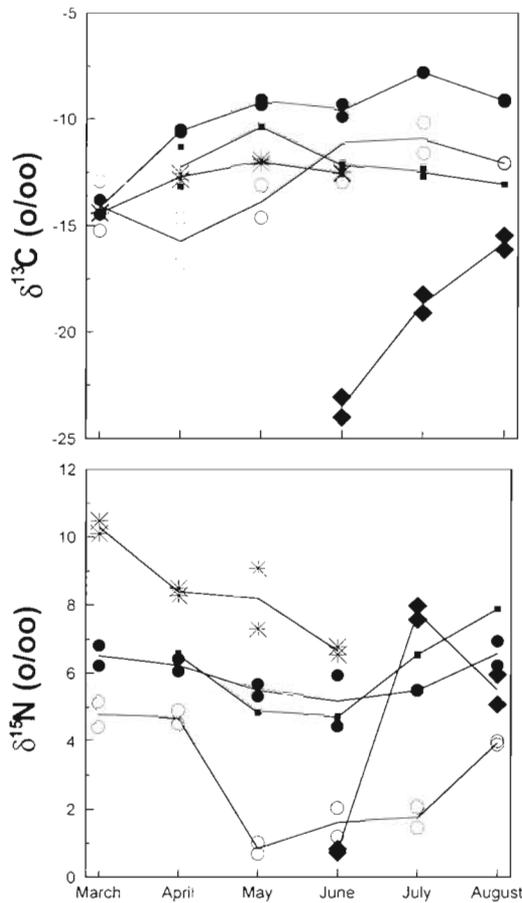


Fig. 3. Carbon and nitrogen stable isotope ratios of (O) estuarine macroalgae *Ulva* sp., (◆) freshwater algae *Enteromorpha* sp., (●) seagrass *Zostera marina*, (*) benthic harpacticoid copepods, and (■) phytoplankton harpacticoid copepods in 1996. Lines connect monthly mean values of each type of organism

ial did not differ significantly among months (2-factor ANOVA: $p = 0.157$). Furthermore, $\delta^{13}\text{C}$ values of detrital material did not differ between the 2 size fractions (2-sample t -test: $p = 0.280$). Nitrogen stable isotope ratios of detrital material also did not differ significantly among months or between the 2 size fractions (2-factor ANOVA: $p = 0.185$, $p = 0.213$).

$\delta^{13}\text{C}$ values of zooplankton, primarily calanoid copepods, at Site B in Seldovia Bay ranged from $-18.39 \pm 0.30\text{‰}$ in March to $-21.16 \pm 0.30\text{‰}$ in June and August in 1996. These values are different from seagrass values, which ranged from -9.12 ± 0.17 to $-14.13 \pm 0.17\text{‰}$, and *Ulva* sp. values, which ranged from -10.95 ± 0.84 to $-15.71 \pm 0.84\text{‰}$ in 1996 (Fig. 5).

Data for 1995 and 1996 stable isotope ratios were pooled, and the $\delta^{15}\text{N}$ values of groups were plotted against their $\delta^{13}\text{C}$ values (Fig. 5). Estuarine, marine, and terrestrial production can be clearly distinguished. Pairwise comparisons of isotope ratios for estuarine

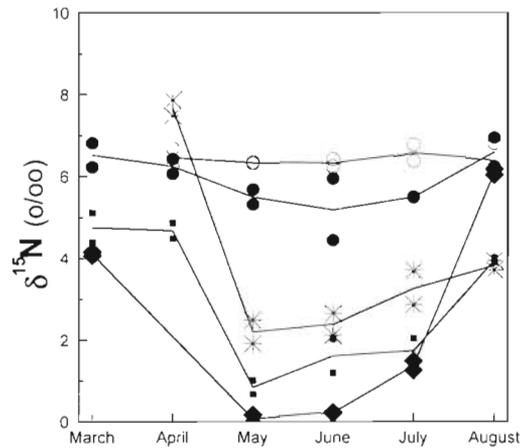


Fig. 4. Monthly mean nitrogen stable isotope ratios of macroalgae *Ulva* sp. (* = Jakolof Bay, ◆ = Site A, ■ = Site B) and seagrass *Zostera marina* (O = Jakolof Bay, ● = Site B) in 1996

(seagrass and *Ulva* sp.), marine (zooplankton), and terrestrial (alder, birch, fern, marsh grass, and spruce) organisms were done. Marine and terrestrial (2-sample t -test: $p = 0.00$), estuarine and marine (2-sample t -test: $p = 0.00$), and estuarine and terrestrial (2-sample t -test: $p = 0.00$) organisms had significantly different $\delta^{13}\text{C}$ values.

Stomach contents of chum salmon fry are shown in Figs. 6 & 7. In both years, the fry depended primarily on harpacticoid copepods (Fig. 6). Among the harpacticoid copepods, *Harpacticus uniremis* was the most abundant species by number in the stomachs (Fig. 7).

DISCUSSION

Nutrient sources for primary producers

Nitrogen stable isotope ratios of major terrestrial plants (alder, birch, and spruce) observed in this study ranged from -2.37 ± 0.09 (\pm SE) to $+0.81 \pm 0.23\text{‰}$. A value close to or lower than $+1\text{‰}$ often indicates that there is a large contribution of nutrients originating from nitrogen fixation (Gu & Alexander 1993). Alder has symbiotic nitrogen-fixing bacteria, so its nitrogen isotope ratio is usually close to atmospheric values ($\delta^{15}\text{N} \approx 0\text{‰}$) (Gu & Alexander 1993). Plants with deeper rooting systems, such as spruce and birch, in the sub-arctic and arctic can also have low $\delta^{15}\text{N}$ relative to other plants because they access nutrients in deeper soil where nutrient nitrogen has a lower $\delta^{15}\text{N}$ (Gu & Alexander 1993, Nadelhoffer & Fry 1994). Because all 3 major plants around Seldovia Bay have low $\delta^{15}\text{N}$ values, terrestrially derived nutrient nitrogen is also expected to have a very low $\delta^{15}\text{N}$.

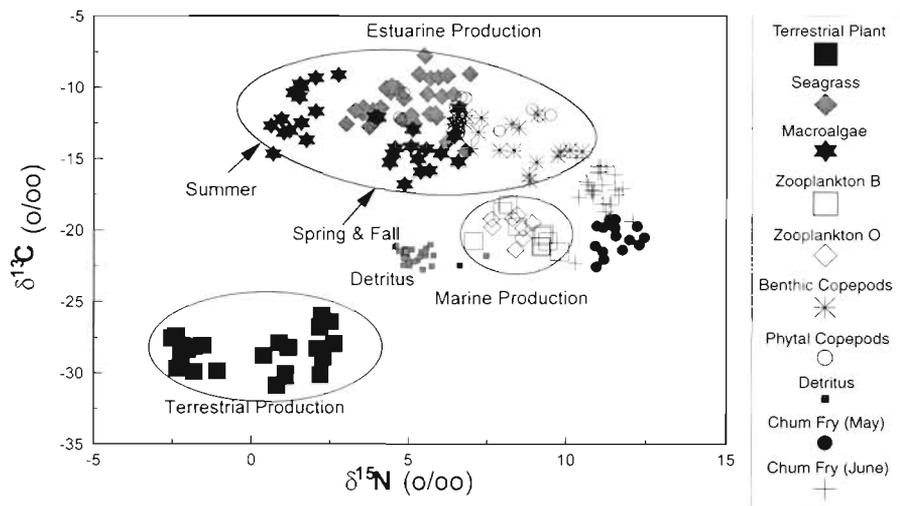


Fig. 5. Pooled carbon and nitrogen stable isotope ratios of benthic copepods, phytal copepods, detritus, macroalgae, seagrass, terrestrial plants (alder, birch, spruce, and marshgrass), and zooplankton (B = Site B, O = Outside Beach) in 1995 and 1996. Circles show data clusters for estuarine, marine, and terrestrial organisms

Nitrogen stable isotope ratios of *Ulva* sp. changed seasonally. *Ulva* sp. absorbs nutrients from the surrounding water in which the isotopic values of the dissolved nitrogen can change depending on its form (i.e. nitrate, nitrite, and ammonium) and source (i.e. recycled, terrestrial, or marine). During summer months (May, June, and July), $\delta^{15}\text{N}$ values of *Ulva* sp. were low ($+1.38 \pm 0.19\text{‰}$ in 1995 and $+1.40 \pm 0.18\text{‰}$ in 1996), indicating a possible contribution of nutrients originating from nitrogen fixation. There is no report of *Ulva* sp. having nitrogen-fixing capabilities or associated symbionts with nitrogen-fixing capability. Therefore, the low $\delta^{15}\text{N}$ values suggest an input of nutrient nitrogen with a low $\delta^{15}\text{N}$ to the study site. The nitrogen stable isotope ratio of *Enteromorpha* sp. sampled in the Seldovia River in June was also low ($+0.78 \pm 0.28\text{‰}$) and, as with *Ulva* sp., increased in summer (Fig. 3). This suggests that nutrients utilized by *Enteromorpha* sp. and *Ulva* sp. during the summer months came primarily from an upstream source. Nitrogen from sewage can have a low $\delta^{15}\text{N}$ (Rau et al. 1981). However, very few people live in the area near the stream so sewage cannot be a major nutrient source. Nutrient nitrogen with low $\delta^{15}\text{N}$ (near 0‰) can be derived from nitrogen-fixing bacteria or decomposition of terrestrial plant material in soil. We were unable to distinguish between these potential sources, but decomposition of plants definitely occurs at least seasonally in the area.

On the other hand, the increased $\delta^{15}\text{N}$ values of *Ulva* sp. observed after July in 1994, 1995, and 1996 were likely due to nutrients derived from salmon tissues, which have high $\delta^{15}\text{N}$ values, $+10.62 \pm 0.02$ and $+10.90 \pm 0.42\text{‰}$ for chum and pink salmon, respectively. This conclusion is based on the following 5 points. (1) The

increase in $\delta^{15}\text{N}$, which occurred in August in both 1995 and 1996, closely followed the adult salmon run, which began in early July and continued through September. (2) All other major nitrogen sources above the estuary (spruce, alder, birch, and nitrogen-fixing bacteria) have very low $\delta^{15}\text{N}$ values (-2 to $+2\text{‰}$). (3) A high standing stock of *Enteromorpha* sp. and *Ulva* sp. appeared in the stream and the bay from late July to August (authors' pers. obs.), indicating that extra nutrients probably became available around this time.

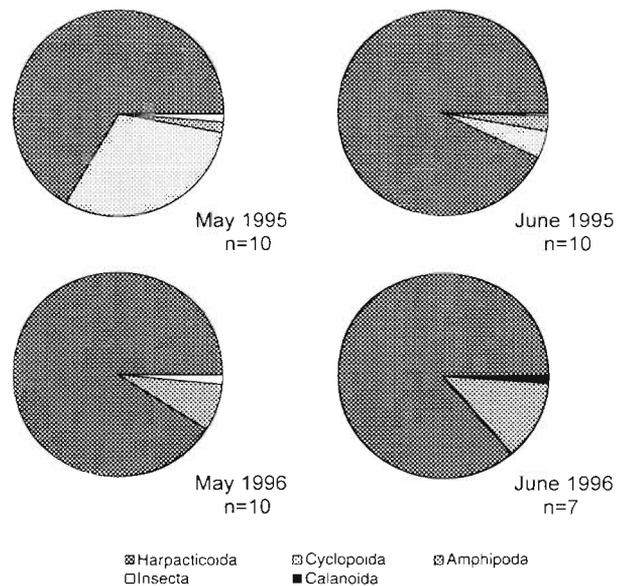


Fig. 6. Relative proportion by number of total invertebrates found in the stomachs of chum salmon fry (*Oncorhynchus keta*) in Seldovia Bay

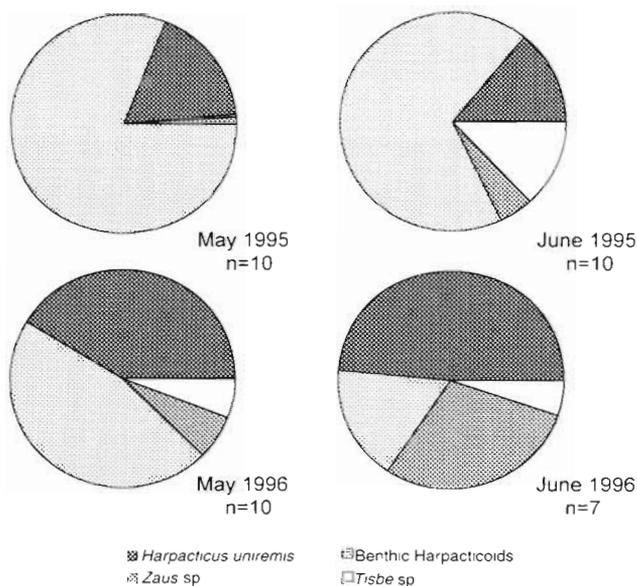


Fig. 7 Relative proportion by number of harpacticoid copepod species found in the stomachs of chum salmon fry (*Oncorhynchus keta*) in Seldovia Bay

(4) Precipitation, which is often correlated with decomposition rates of terrestrial organic material, is at a minimum during the summer months in this area (Watson et al. 1971). (5) Zooplankton collected at Site B and Outside Beach did not show a significant monthly change in $\delta^{15}\text{N}$ between June, July, and August samples (single-factor ANOVA. $p = 0.16$. $p = 0.17$), indicating that phytoplankton $\delta^{15}\text{N}$ values did not change significantly during the summer months.

A high $\delta^{15}\text{N}$ for *Ulva* sp. was found in April 1995 and again in March and April 1996. Furthermore, $\delta^{15}\text{N}$ values of *Ulva* sp. were also high in February 1997 ($+6.92 \pm 0.28\text{‰}$ in Seldovia Bay, $+7.07 \pm 0.42\text{‰}$ in Jakolof Bay), indicating that *Ulva* sp. collected in spring was likely produced in the previous fall. Therefore, the nutrient nitrogen derived from salmon carcasses could have a strong influence on the organisms at the study site from fall to early spring

Ulva sp. collected from Site A and Jakolof Bay in 1996 also showed low $\delta^{15}\text{N}$ during the summer ($+0.56 \pm 0.41$ and $+2.61 \pm 0.32\text{‰}$) and high $\delta^{15}\text{N}$ in spring and fall ($+5.11 \pm 0.81$ and $+5.75 \pm 1.56\text{‰}$). Therefore, the trend found at Site B is a spatially and temporally general phenomenon for the study region.

Compared with *Ulva* sp., seagrasses did not show large monthly changes in $\delta^{15}\text{N}$, indicating they probably had different nitrogen sources. Seagrass can absorb nutrients through leaves and roots (Izumi & Hattori 1982, Short & McRoy 1984, Pederson & Borum 1993) and also recycle nutrients internally (Pederson & Borum 1993). The difference in the trends between

Ulva sp. and seagrass isotope ratios suggests the seagrass at the study site primarily utilized nitrogen from the sediment and internal recycling.

Estuarine detrital material

The carbon stable isotope ratio value of detritus, which ranged from $-22.43 \pm 0.31\text{‰}$ ($\pm\text{SE}$) to $-21.17 \pm 0.31\text{‰}$, was more negative than those of macroalgae, which ranged from $-15.07 \pm 0.84\text{‰}$ to $-10.03 \pm 0.68\text{‰}$, and seagrass, which ranged from -12.62 ± 0.17 to $-10.14 \pm 0.14\text{‰}$ (Fig. 2). Because bacterial decomposition causes small or no changes in $\delta^{13}\text{C}$ (Coffin et al. 1989, 1990), the data suggest that detrital carbon was mostly allochthonous with a possible small contribution of autochthonous material.

The data do not, however, show whether the allochthonous material is of freshwater, marine, or terrestrial origin because they all have more depleted $\delta^{13}\text{C}$ values than autochthonous material. Most identifiable detrital material (i.e. large material) found in the Seldovia River estuary was terrestrial plant parts (authors' pers. obs.). However, the maximum tidal range in Seldovia Bay is large, reaching 9 m during spring tides, and large volumes of water over the intertidal estuary are exchanged with Kachemak Bay. Therefore, phytoplankton can also be a potential source of detrital material at the study site.

Food sources for harpacticoid copepods

Carbon stable isotope ratios of benthic and epiphytic harpacticoid copepods *Harpacticus uniremis* ranged from -16.31 ± 0.28 to $-12.04 \pm 0.28\text{‰}$ and from -11.80 ± 0.33 to $-10.70 \pm 0.40\text{‰}$, respectively, in 1995. Similarly, they ranged from -14.41 ± 0.28 to $-12.01 \pm 0.28\text{‰}$ and from -13.04 ± 0.57 to $-10.37 \pm 0.57\text{‰}$, respectively, in 1996. They were more enriched in $\delta^{13}\text{C}$ than freshwater algae (-16 to -24‰), terrestrial and marsh plants (around -29‰), and zooplankton (around -20‰). Seagrass and estuarine macroalgae were enriched in $\delta^{13}\text{C}$ and available as a food source in the estuary. Therefore, we conclude that both types of harpacticoid copepods primarily fed on these materials.

Trends in monthly means of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for benthic harpacticoid copepods and *Ulva* sp. are very similar to each other. However, trends in monthly means of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for benthic harpacticoid copepods and seagrass are different (see 'Results'). These results suggest that *Ulva* sp. is a potential food source, but seagrass is not a major food source for harpacticoid copepods. *Ulva* sp. and *Zostera marina* were the only noticeable vegetation at the sampling site in 1995 and

1996, and *Ulva* sp. has been experimentally shown to be a good food source for some harpacticoid copepods (Miliou & Moraïtou-Apostolopoulou 1991). Therefore, a likely explanation of the data is that the harpacticoid copepods depended primarily on *Ulva* sp. and possibly associated epiphytes, which were not measured but presumed to have similar isotopic signatures to *Ulva* sp. because the epiphytes are exposed to the same carbon and nitrogen sources.

Alternative interpretations of the data, however, are possible. Unobserved material could have become seasonally available to harpacticoid copepods and their diet composition changed during this study, causing the observed changes in stable isotope ratios. If this is the case, seagrass could be contributing to the diet of benthic harpacticoid copepods and the seasonal trend of seagrass isotopic signature was masked by the changes in their diet composition. However, for this scenario to be true, the similarity of the seasonal trends between harpacticoid copepods and *Ulva* sp. must be dismissed as a mere coincidence. Another possible interpretation of the data is that unobserved material with a similar isotopic signature to *Ulva* sp. was actually the primary food source for the benthic harpacticoids. Benthic microalgae such as diatoms are one type of such potential food material. Schwinghamer et al. (1983) measured $\delta^{13}\text{C}$ of *Ulva* sp. and benthic diatoms in the Bay of Fundy. Their data show that benthic diatoms are more depleted in $\delta^{13}\text{C}$ than *Ulva* sp. Stable isotope ratios of benthic microalgae were not measured in this study, so they cannot be excluded entirely as a potential food source for harpacticoid copepods. However, among the conceivable explanations, benthic harpacticoid copepod utilization of *Ulva* sp. and associated epiphytes seems the most parsimonious interpretation of the data.

Harpacticus uniremis appeared to feed on autochthonous material in the Seldovia Bay estuary, but we were unable to determine the source. Hall & Bell (1993) showed that *Harpacticus* sp. found in a seagrass bed at Egmont Key, Florida, USA, fed on algal epiphytes on seagrass blades. Large numbers of diatom colonies became noticeable in the seagrass bed in Seldovia Bay in 1996 and may have been utilized to some extent by *H. uniremis*. In this study, $\delta^{15}\text{N}$ values of seagrass and *H. uniremis* are very similar. If *H. uniremis* primarily fed on seagrass, it should be more enriched in ^{15}N than seagrass. Therefore, seagrass is not a primary food source for *H. uniremis*.

Food source for chum salmon fry

Chum salmon fry sampled in Seldovia Bay primarily fed on harpacticoid copepods, and *Harpacticus uni-*

remis was the most important among harpacticoid copepod species (Fig. 6). This observation is consistent with other observations in southeast Alaska (Landingham 1982) and British Columbia (Healey 1979, D'Amours 1987) where the major dietary composition of chum salmon fry was also *H. uniremis*. Among benthic harpacticoids, *Microarthridion littorale* was a major species found in the stomachs of chum salmon fry (authors' pers. obs.).

Carbon isotope ratios of chum salmon fry, especially in May of both years, are lower than harpacticoid copepod values (Fig. 5, Table 1). Juvenile chum salmon depend on energy stored in the yolks from winter hatching to emergence from stream gravel in the spring (Neave 1966a, b). Therefore, fry which first appear in the estuary can have isotopic values similar to those of adult salmon, which have more negative ^{13}C values than harpacticoid copepods. The fry population in May was probably composed of younger fish, which still retained isotopic signatures of the eggs, than the population in June, which had had a longer residence time in the estuary where they primarily fed on harpacticoid copepods.

Feedback mechanism

Our hypothesis that organic matter derived from decomposition of salmon carcasses is seasonally important to estuarine harpacticoid copepods is supported by the data with the modification that copepods utilize *Ulva* sp. and its epiphytes rather than dissolved and particulate organic matter derived from salmon carcasses and associated bacteria. The $\delta^{15}\text{N}$ values of *Ulva* sp. indicate that this alga utilizes nutrients derived from adult salmon carcasses during late summer and fall months, and the influence of the salmon derived nutrients remains through early spring. Gravid females of some harpacticoid copepod species overwinter, and their offspring are released in early spring (Webb & Parsons 1992). Because food depletion has been experimentally shown to cause slow development and low fecundity in harpacticoids (Lee et al. 1976, Hicks 1979), the food availability during fall and winter can influence the population size of harpacticoid copepods in spring when juvenile salmon appear in the estuary. In Seldovia Bay, benthic and phytal harpacticoid copepods are the major food source of chum salmon fry (Fig. 6). Because harpacticoid copepods utilized by the salmon fry feed on estuarine algae, there is a nutrient link (temporally indirect link) between adult salmon and juvenile salmon.

Decay of macroalgal detritus can also be a major source of nutrients for seagrass (Williams 1984). As a result, the increased macroalgal production could, in

turn, act as a nutrient trap which enhances seagrass production in an estuary. Because seagrass beds are important nursery locations for juvenile chum salmon, the nutrients derived from adult salmon carcasses could also influence the success of their offspring through increased availability of both food and shelter.

Based on the residence periods and the existence of an alternative nursery area, Healey (1982) concluded that among the 5 species of Pacific salmon, juvenile pink salmon depend least on estuarine resources. However, the length of residence period does not necessarily indicate how important estuarine resources are to future survival of pinks. Pink salmon spend the short, but crucial, first feeding period in an estuary. The mortality rate of juvenile pink salmon during the first 40 d can be as high as 77% (Parker 1965, 1968), and pink salmon have the disadvantage of being smaller than chum salmon when they first emerge (Parker 1971). Therefore, food conditions during the short period in an estuary can be very critical for their future survival and could determine the future population size of pink salmon.

The data support the idea that nutrients derived from inbound adult salmon can have a positive influence on outbound juvenile salmon, suggesting a possible feedback mechanism impacting population size. If a returning population is large, there will be more production in the estuary due to the material available from the carcasses, and, thus, a greater food supply and shelter availability for their offspring. With higher growth and survival rates of salmon fry, more adults could return to the same stream in the future. On the other hand, if only a small number of adult salmon come back to a stream, survival rate of offspring could conceivably be lower because of the reduced food and shelter availability.

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