Detritus-Based Food Webs: Exploitation by Juvenile Chum Salmon (*Oncorhynchus keta*)

Abstract. *Harpacticoid copepods are the principal food of chum salmon during the first critical weeks of estuarine life. Heterotrophic food sources are preferentially ingested by harpacticoids. A commercially valuable fisheries resource, usually considered to be planktivorous, is related to a detritus-based, benthically derived food web.*

Detritus and its associated microflora are important sources of energy and organic carbon in estuarine food chains (*1*). However, its importance to commercial fisheries is often difficult to establish. We report evidence from multidisciplinary studies of juvenile salmon ecology of the Strait of Georgia that food resources derived from organic detritus by bacterial activity contribute to a commercially important fishery.

Moderate populations of three species of Pacific salmon spawn in the Nanaimo River (49°10′N, 123°54′W) and juveniles of one or more of these species exploit the estuarine resources of the river from March through September (*2, 3*). In 1975, a mark-and-recapture experiment was conducted to determine the size of the downstream migrating chum (*Oncorhynchus keta*) fry population and the length of time they spend in the estuary. Approximately 5.3×10^7 fry migrated from the river between March and the end of May. In March and April, individual fish stayed in the shallow, mudflat areas of the estuary for an average of 13 to 18 days. This period of residence decreased to approximately 1.5 days in May. The biomass of fry on the mudflat reached a maximum of 2.3×10^6 g (fresh weight) at the end of April. From 7 March to 24 May, the relative increase in weight of these fish averaged 4 percent per day. The amount of food required to support the observed growth of the fry population during their residence on the mudflat is estimated (*4*) to be approximately 3.85×10^6 g. Analysis of the stomach contents of these fish indicated that their primary food source was epibenthic and interstitial harpacticoid copepods (*5*).

The harpacticoid population was assessed by coring at seven stations on the intertidal flat. The mean density of harpacticoids in the top 1 cm of sediment at one of the stations between March and June was 411 animals per 10 cm^2 (N = 13, standard error = 67). The average dry weight of harpacticoids was 2.7 μg, and with a wet-to-dry ratio for copepods (*6*) of 8.4, the harpacticoid biomass is 9.4 g m^{-2} (wet weight). If this biomass is representative of the 9.0 km^2 of mudflat, the total biomass of harpacticoids is roughly 22 times the calculated food requirement of the chum fry from March to May.

The feeding of harpacticoid copepods was investigated through the use of a radioisotope technique (*7*). Mixed assemblages of harpacticoids were collected from the estuary. Several hundred animals were presented a food mixture labeled with $NaH^{14}CO_3$ and [^{3}H]glucose. The uptake of both isotopes was followed and found to be linear for as long as 8 hours. Harpacticoid copepods ingest heterotrophically processed carbon sources about nine times as rapidly as autotrophic sources (Table 1).

The potential food resources of harpacticoids have been studied at four stations on the Nanaimo estuary. Autotrophic activity (primary productivity) of the mud surface was estimated according to an in situ $^{14}CO_2$ uptake technique. Heterotrophic activity was estimated by measuring the rate of incorporation of [^{14}C]glucose in sediment slurries. Autotrophic and heterotrophic biomasses and detritus were estimated from chlorophyll, adenosine 5′-triphosphate (ATP), and total organic carbon measurements (*8*). The results from one station, averaged over the period of chum fry residence, are shown in Table 2. The biomass and activity of the heterotrophic populations are much greater than those of the autotrophic population. There is, in addition, a large pool of organic carbon. These results agree well with those reported by Ferguson and Murdock (*9*) for detritus and heterotrophic biomass for the Newport River estuary in southeastern United States. The results for autotrophic biomass are higher than reported by Pamatmat (*10*) for a shallow bay in the Pacific Northwest.

The diversity of techniques used in this study preclude a simple estimate of the overall error in the carbon budget of the estuarine food web. The 95 percent confidence limits for these techniques ranged from less than 2 percent of the mean for some of the chemical and isotopic procedures to more than 50 percent of the mean for some of the population estimates. The overall error will be a complex function of the constituent errors and will, further, depend on the model used to link the constituents. Although we cannot estimate overall rates of carbon cycling through detritus and salmon, this is an important

Table 1. Feeding of harpacticoid copepods on heterotrophic and autotrophic food sources. Uptake rate of algal and bacterial carbon is given as micrograms of carbon per milligram of dry weight of the feeding animal per hour. All calculations are rounded to two significant figures.

Harpacticoid species	Uptake rate (μg mg^{-1} hour^{-1})		Ratio of bacterial carbon to algal carbon	
	Algal	Bacterial	Food	Uptake rate
Tisbe furcata, *Harpacticus uniremis*	.37	3.3	1.6	8.8
H. uniremis, *H. spinulosus*	.39	4.1	0.93	10.
Dactylopodia crassipes	5.0	45.	0.52	9.0

Table 2. Potential food resources for harpacticoid copepods. Production is given as grams of carbon per square meter per day. Biomass and detritus are given as grams of carbon per square meter. Autotrophic biomass was calculated from chlorophyll by using a ratio of carbon to chlorophyll of 30 : 1. Heterotrophic biomass was calçulated from ATP by using a ratio of carbon to ATP of 280 : 1 and subtracting autotrophic biomass. Detritus was calculated from total organic carbon by subtracting autotrophic and heterotrophic biomasses. All calculations are rounded to two significant figures.

Depth in sediment (cm)	Primary production (g m^{-2} day^{-1})	Autotrophic biomass (g m^{-2})	Heterotrophic activity per hour	Heterotrophic biomass (g m^{-2})	Detritus (g m^{-2})
0 to 1	0.079	3.2	0.12	10	160
1 to 2		1.8	0.13	10	240
2 to 5		3.9	0.063	10	580
Total	0.079	9.0	0.088*	31	980

*Depth-weighted average.

and hitherto unrecognized process in the ecology of salmon.

Salmonids have usually been considered to be strictly planktivorous, and the importance of benthic food resources has only recently been recognized (*3, 11*). Harpacticoid copepods are of particular importance to chum fry (*12*). These fish spend the first critical weeks of their sea life in river mouths and along beaches feeding on harpacticoids and other small benthos. The food of the harpacticoids is the bacterial flora associated with organic detritus. The estuary receives pulsed inputs of detritus from several sources: (i) *Zostera* spp. meadows from the seaward areas, (ii) algae from the intertidal areas, (iii) *Carex* spp. marsh from the landward areas, and (iv) downstream transport from the upland areas of the watershed.

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2. The numbers of salmon spawning in the Nanaimo River range are as follows: *Oncorhynchus keta*, 22,000 to 70,000; *O. kisutch*, 800 to 6,000; and *O. tshawytscha*, 850 to 1,950 [K. V. Aro, *Fish. Res. Board Can. Manuscr. Rep. 1178* (1972)].
3. *An Environmental Assessment of Nanaimo Port Alternatives* (Lands Directorate, Canadian Department of Environment, Ottawa, 1974); J. Sibert, *Fish. Res. Board Can. Tech. Rep. 537* (1975); unpublished data.
4. The amount of food required to increase weight by a rate of 4 percent per day is 9 percent of the body weight per day [R. J. LeBrasseur, *J. Fish. Res. Board Can.* **26**, 1631 (1969)]. The daily food requirement of the estuarine population equals number of fish × mean weight of fish × 0.090.
5. Analysis of the stomach contents of approximately 50 chum fry collected from March through June 1975 agreed with the results of more extensive samples (approximately 500) collected in previous years (*3*). Individual fry contained as many as 1000 harpacticoid copepods; the species present, in order of abundance, were *Harpacticus uniremis*, *Huntemania jadensis*, and *Tisbe furcata*.
6. J. Fulton, *Fish. Res. Board Can. Tech. Rep. 313* (1972).
7. T. J. Brown and J. Sibert, *J. Fish. Res. Board Can.*, in press.
8. Primary productivity was estimated by injecting 500 μc of $Na_2H^{14}CO_3$ into 3.4 liters of water enclosed over the sediment surface by light and dark plexiglass chambers. After a 4-hour incubation period, sediment cores were taken and the ^{14}C activity determined in the nitric acid extract [C. Van Raalte, *Bot. Mar.* **17**, 186 (1974)]. Heterotrophic activity was estimated by adding 0.15 μc of [^{14}C]glucose (specific activity 310 μc/μmole) to 0.6 ml of sediment slurried in 30 ml of filtered estuarine water and incubated for 1 hour in the dark. This addition of glucose was less than 0.3 μg/liter, low enough to avoid stimulatory effects [J. Sibert and T. J. Brown, *J. Exp. Mar. Biol. Ecol.* **19**, 97 (1975)]. Chlorophyll, corrected for phaeopigments by acidification, was determined by the fluorometric technique of J. D. H. Strickland and T. R. Parsons [*Bull. Fish. Res. Board Can. 167* (1972)]. The ATP was determined by the technique of O. Holm-Hansen and C. R. Booth [*Limnol. Oceanogr.* **11**, 510 (1966)] and D. M. Karl and P. A. LaRock [*J. Fish. Res. Board Can.* **32**, 599 (1975)]. The total organic carbon was determined in a carbon-hydrogen analyzer (Coleman model 33).
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Galilean Satellites of Jupiter: 12.6-Centimeter Radar Observations

Abstract. *Observations of the Galilean satellites with the radar system at the Arecibo Observatory, Puerto Rico, show that their surfaces are highly diffuse scatterers of radio waves of length 12.6 centimeters; spectra of the radar echoes are asymmetric and broad. The geometric radar albedos for the outer three satellites—0.42 ± 0.10, 0.20 ± 0.05, and 0.09 ± 0.02 for Europa, Ganymede, and Callisto, respectively—show about the same relative decreases as do the optical albedos, although the latter presumably bear only on material much nearer the surface. Radii of 1420 ± 30, 2640 ± 80, and 2360 ± 70 kilometers for Europa, Ganymede, and Callisto were determined from the radar data and are in good agreement with the corresponding optically derived values. Io, observed successfully only once, appears to have an albedo comparable to Ganymede's, but no radius was estimated for it.*

Interest in the Galilean satellites of Jupiter has heightened in recent years as the result of an avalanche of new observations. The Pioneer 10 and Pioneer 11 spacecraft have photographed all four of these planet-sized satellites at resolutions substantially better than those obtainable in earth-based observations and have provided important information on the magnetic and plasma environment of Jupiter within which these satellites move (*1*). Ground-based observations have shown that large portions of the surfaces of Europa and Ganymede appear to be covered with water frost, whereas Callisto's surface seems to be covered mostly with darker material, perhaps siliceous in composition (*2*). Most surprising of all are the findings of substantial amounts of hydrogen, potassium, sodium, and sulfur in the environment of Io, the innermost of the Galilean satellites (*3*). The flow of new information has been so rapid that no review article is recent enough to encompass it all.

Attempts to study the Galilean satellites by radar began in 1970 with an unsuccessful effort (*4*) to detect echoes of 3.8-cm signals directed at Callisto. In 1974, an

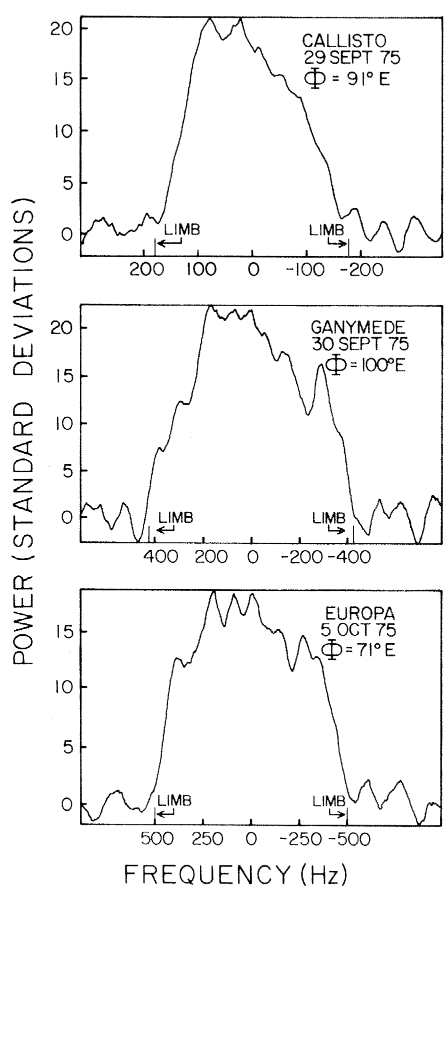

Fig. 1. Radar scattering spectra taken in same-sense polarization (see text) for Europa, Ganymede, and Callisto. Positions of the limbs are shown under the assumption of synchronous rotation and an optically derived value for the radius (see Table 1). The spectra have been smoothed by using a resolution of 10 percent of the calculated limb-to-limb bandwidth. The ordinate is given in units of the standard deviation of the noise accompanying the signal. Variations in the spectra of amplitudes of the order of 3 standard deviations are probably not significant.