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INTRODUCTION

A number of salmon-producing watersheds along both the Asian and North American coasts drain into the northern North Pacific Ocean. In spite of their strongly oligotrophic nature, the production of salmon is high, primarily due to the anadromous nature of all Pacific salmon belonging to the genus *Oncorhynchus* sp.

A continuous linkage between the marine environment and any oligotrophic freshwater watershed producing Pacific salmon is accomplished by the annual return of adults from the sea to spawn and die. Almost the entire body weight (e.g. more than 99%) is of marine origin and is delivered to the freshwater system through excretion, gametes, and carcass decomposition. The availability of nutrients from this source varies from year to year and is influenced by the size of the escapement and also by variation in runoff.

Over the years, evidence has accumulated that marine nutrients transported from the sea by a salmon escapement are indeed significant and important to the productivity of the oligotrophic lakes and streams in which they spawn (e.g. Juday et al. 1932; Krokhin 1959, 1967; Donaldson 1967; Brickell and Goering 1970; Richey et al. 1975; Koenings and

Burkett in press). In addition, the productivity of some sockeye salmon-producing lakes has been enhanced by additions of suitable inorganic fertilizers, especially in British Columbia (Stockner 1979, 1981; Stockner and Shortreed 1985). However, the evidence of biogenic enrichment by salmon carcasses has been more of an indirect nature. The situation has changed in recent years with the use of stable isotope tracers to evaluate the importance of nutrients derived from salmon returns to freshwater systems.

The fundamental hypothesis of the RETURNS project is that marine nitrogen is transported from the sea to freshwater by returning salmon in amounts traceable to different trophic levels and that it affects the growth and survival of juvenile sockeye salmon (*O. nerka*) in addition to other resident fish species, e.g. rainbow trout (*Salmo gairdneri*) and char (*Salvelinus* sp.).

STUDY AREA

The primary study site of our investigations is the Kvichak River watershed, the largest sockeye salmon-producing system in Bristol Bay, southwestern Alaska (Figure 1). The annual escapement of sockeye salmon returning to this system to spawn ascend the Kvichak River in late June and July. A counting station at the outlet of Iliamna Lake provides a very accurate estimate of the numerical size of

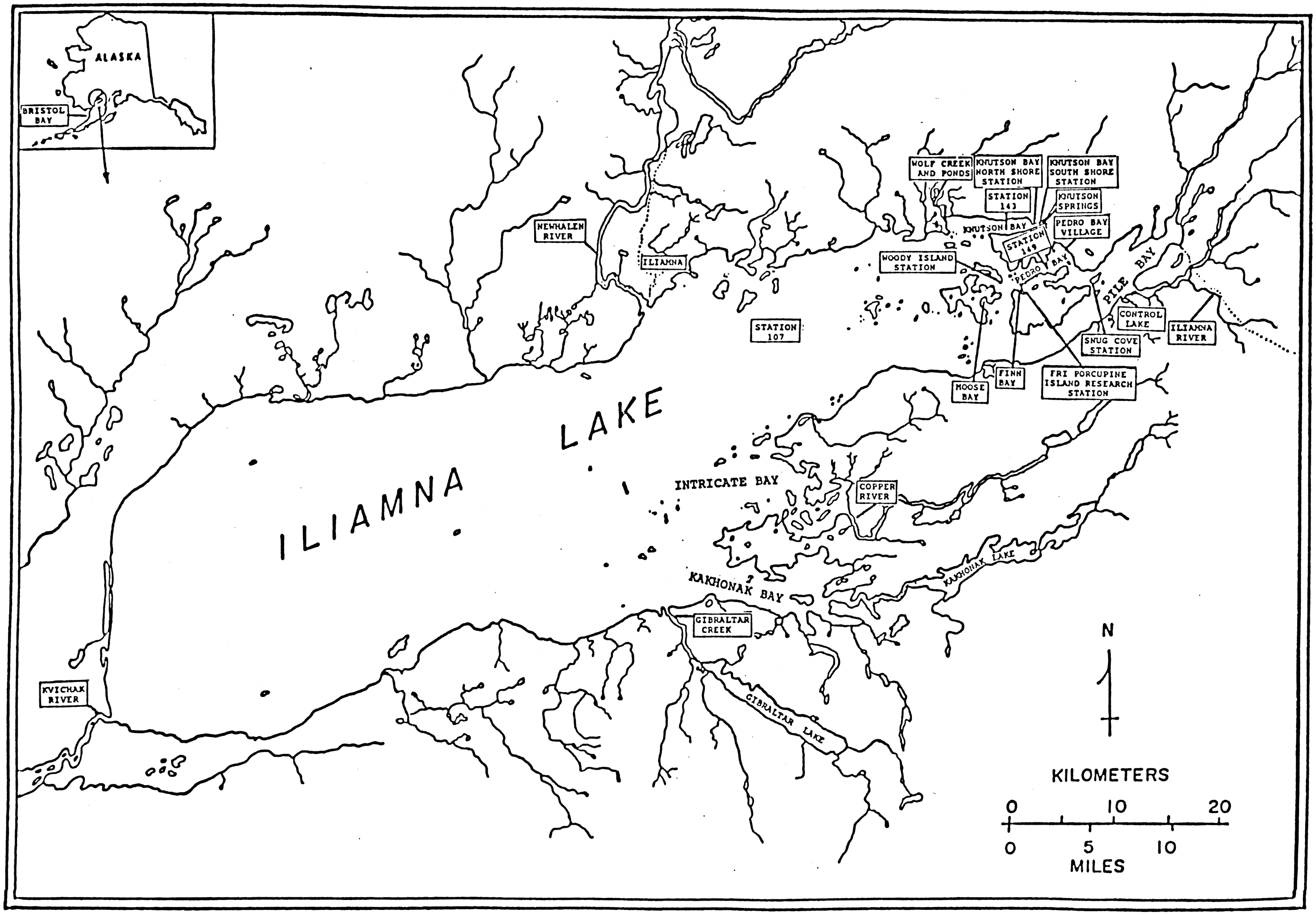

Figure 1.--RETURNS project sampling stations in the Iliamna Lake system, Kvichak River watershed, Bristol Bay region, southwestern Alaska.

the escapement. Most spawning occurs from early August to late September. Spent fish die off rapidly, and most of the carcasses decompose rapidly.

Juvenile salmon produced in the Kvichak River system spend from 1 to 2 year feeding in the limnetic zone of the nursery lakes before they migrate to sea as smolts. The major portion mature and return after 2 or 3 years in saltwater. Thus, there are four principal age classes among the spawners.

Since 1955, escapements of sockeye salmon to the Kvichak system have ranged from 225,000 to 24 million. Therefore, it is an ideal system for studying the effects of different levels of marine nutrients transported by salmon from the sea into a freshwater lake system.

METHODS AND MATERIALS

The average chemical composition of both unspawned and spawned-out, or spent, sockeye salmon that returned to the spawning grounds of the Kvichak watershed in 1985 was determined. The methods of chemical analysis are detailed in Table 1. Because there are two size groups of sockeye salmon spawners, depending on whether they have spent 2 or 3 years in the ocean, and the two sexes differ in size within each ocean age group, chemical analyses were made separately for the four age-sex groups.

To examine and determine the importance of additions of nutrients derived from salmon returns, we used stable

Table 1.--Chemical analyses performed[1] and methods.

Instrumental measurements	
Wet/dry ratio	Gravimetric
Ash content	Gravimetric
Lipid content	Solvent extraction
Protein content	Electrophoresis
C, H, N analysis	CHN analyzer
Cl, Br, I, S	Ion Chromatography
Metal analysis	
Major elements: Ca, Mn, Mg, P, Fe, Na, K, B	Inductively coupled plasma (ICP)
Tracer elements: Al, As, Se, Mo, V, Zn, Cm, Ag	Neutron activation analysis (NAA)
Pl, Co, Ni, Cu	AA graphite furnace
Hg	Cold vapor, AA

1 Chemical analyses performed under the supervision of Dr. A. E. Nevissi, Laboratory of radiation and ecology, University of Washington.

isotope tracers. The stable isotope ratios reported here are written as a del values $\delta^{Y}X$ where X is the elements carbon or nitrogen and Y is the heavy isotope mass number. The $\delta^{13}C$ is relative to the Pee Dee Belimite limestone standard, and $\delta^{15}N$ is relative to atmospheric nitrogen. The purpose and guideline of the sampling program was established around the use of stable isotope tracers at the natural abundance level to quantify the transport of these elements from the sea to a freshwater system. Synoptic sampling of periphyton, net plankton, sediments, and resident fish species in salmon-producing Iliamna Lake and a non-salmon-producing lake, designated Control Lake, was performed, and values of $\delta^{13}C$ and $\delta^{15}N$ from the various biota were determined in the laboratory

RESULTS

Chemical Analysis of Sockeye Salmon Carcasses

The chemical constituents examined did not reveal any significant difference between either males and females or between two- and three-ocean fish. Therefore, all data were combined. For ease of comparison, they have been expressed in grams per average-sized fish.

A comparison of selected chemical data for unspawned fish collected at their entrance into Iliamna Lake and spawned-out sockeye salmon collected on the spawning ground when the fish were ready to die off is presented in Table 2. The table includes three important chemical parameters

Table 2.--Comparison of selected chemical measurements for unspawned and spawned-out sockeye salmon from the Kvichak River system, 1985

Measure	Unit	Adult Sockeye Salmon Unspawned (n=4) (a)	Spawned-out (n=16) (b)	% Difference ((100-[a/b])100
Carbon	g/fish	350.0	159.0	-54.6
Nitrogen	g/fish	94.2	49.2	-47.8
Phosphorus	g/fish	13.1	9.2	-29.8
Potassium	g/fish	8.7	4.7	-46.0
Sulfur	g/fish	3.6	2.4	-33.3
Sodium	g/fish	2.6	1.8	-30.8
Magnesium	g/fish	0.7	0.5	-28.6
Heat	kcal/fish	4,388.7	1,785.0	-61.1
Protein	g/fish	423.3	291.7	-31.1
Lipid	g/fish	173.5	20.4	-88.2
C/N	g/fish	3.7	3.2	-13.5
Lipid/N	g/fish	1.8	0.4	-77.7
Calories/N	cal/g mg/g	46.4	34.6	-25.4

expressed as ratios of nitrogen content. The C/N ratio for the two groups is almost identical, indicating that carbon and nitrogen are expended at nearly the same rate. However, the lipid content (lipid/N) and calories per gram ($cal \cdot g^{-1}/N$) differ significantly between the two groups. These results, together with other data presented in Table 2, indicate that sockeye salmon rapidly burn lipids and lose calories during the migration and approach to the spawning grounds and that there is a lot of leaking going on from metabolic activities during this process.

A profile of nutrient and temperature data from the Knutson Bay monitoring station (station 143) in the eastern portion of Iliamna Lake is shown in Figure 2. We speculate that the high concentrations of ammonium and urea are related to living adult sockeye salmon, which contribute significant amounts of nitrogen to Iliamna Lake through excretion. Upon entering freshwater, Pacific salmon no longer feed but continue to metabolize lipids, carbohydrates, and proteins of marine origin. This metabolic activity results in the release of nitrogen-containing excretion products such as ammonium, urea, and creatin. This is corroborated by the salmon carcass analysis data presented in Table 2 that shows adult sockeye salmon losing substantial amounts of marine nitrogen (i.e. 48%) and other important biogenic nutrients after being in freshwater for over 1 month. Therefore, it appears that important amounts of marine nutrients are introduced into

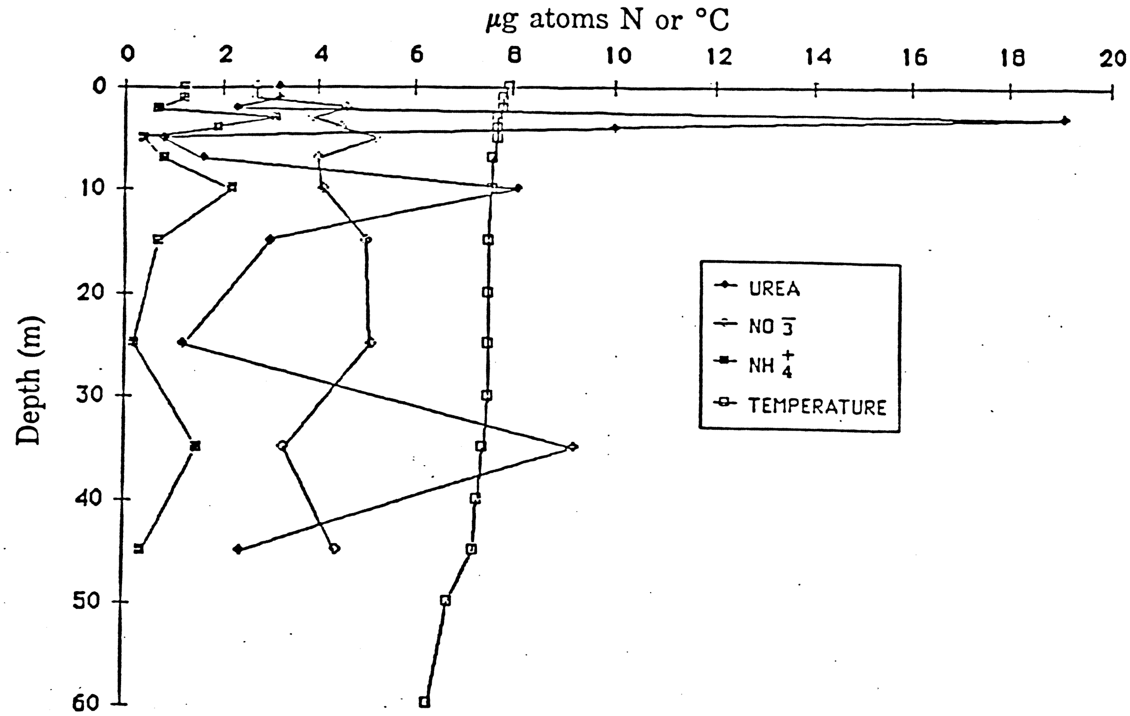

Figure2.--Knutson Bay, Iliamna Lake (station 143) nitrogen and temperature profile, 18 August 1985.

the open water limnetic zone of Iliamna Lake by salmon before they die, which provide an immediate nutrient source for limnetic production.

Isotope Studies of Freshwater Food Chains

The data obtained confirm the proposed hypothesis (Figure 3). Adult salmon which have migrated to Iliamna Lake and are about to spawn and die have an average $\delta^{15}N$ value of +11.2, with a range of +10.4 to +12.2. This +11.2 nitrogen reservoir, highlighted in Figure 3, is absent in Control Lake because salmon are not able to navigate a waterfall and enter the lake. Several nitrogen reservoirs, including sculpins (*Cottus* spp.), sticklebacks (*Gasterosteus aculeatus*), char, and rainbow trout, are enriched in $\delta^{15}N$ and are shifted toward the +11 adult salmon in Iliamna Lake as compared with Control Lake. The sediment and periphyton in Iliamna Lake also appear enriched in $\delta^{15}N$ over those found in Control Lake, but additional data are still being gathered and evaluated. The overlapping range shown for the $\delta^{15}N$ sediment data may be better resolved when analyses are completed.

Char and rainbow trout in Iliamna Lake are slightly more positive than salmon, which suggests that they consume salmon eggs and/or salmon fry and that they carry out the documented trophic nitrogen isotope fractionation ($\Delta\delta^{15}N =$ +1 to +3). The match between juvenile and adult salmon and sticklebacks in Iliamna Lake is striking. It has been shown

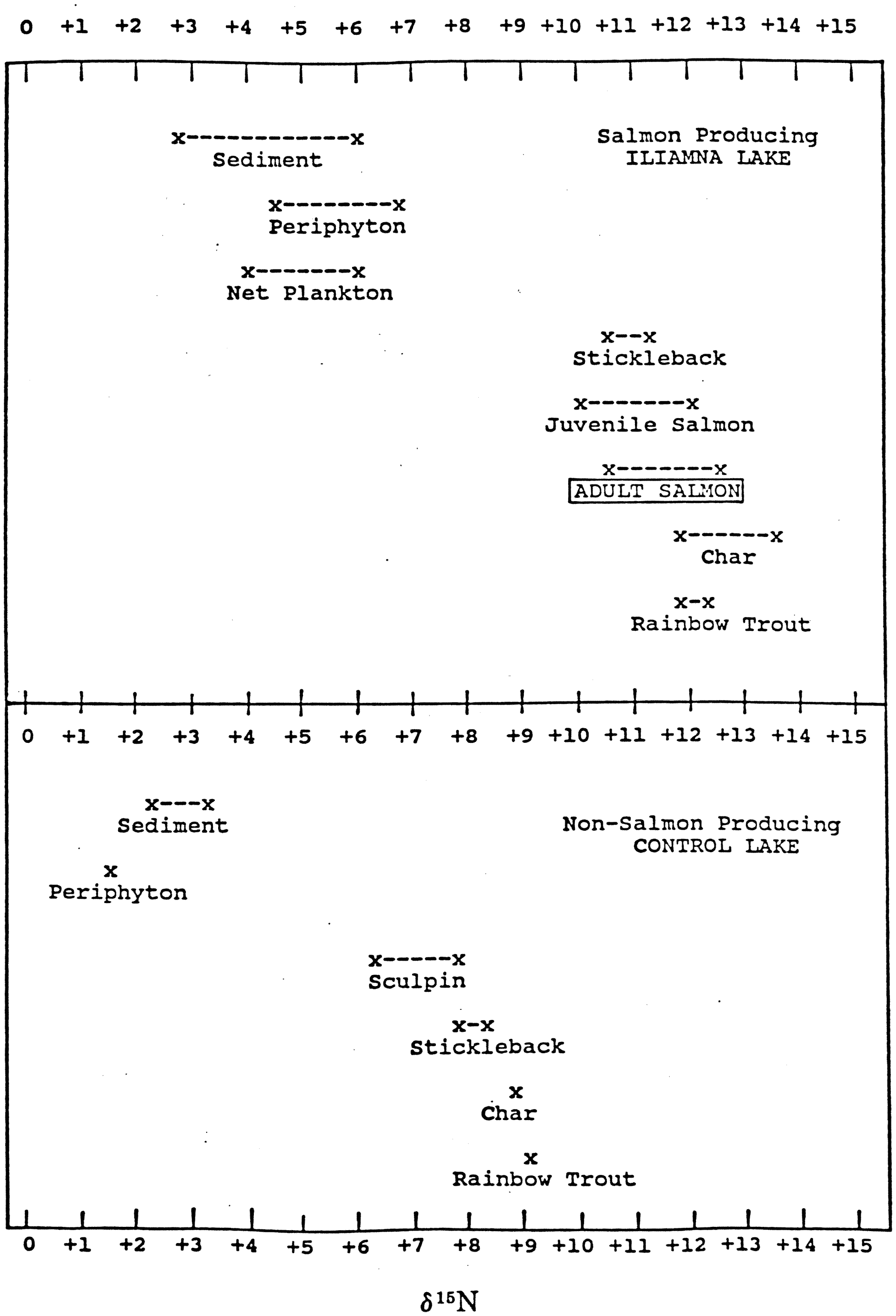

Figure 3.--Values of $\delta^{15}N$ of biota and sediments in salmon- and non-salmon producing lakes.

that juvenile sockeye salmon and sticklebacks compete for the same food base in the sockeye salmon-producing lakes of Bristol Bay (Rogers 1968). At present, the mechanism of this nitrogen flow is unknown, but the difference between the two lakes is taken as strong evidence that migrating salmon play a major role in the nitrogen dynamics of this lake-ocean-coupled system.

The carbon-isotope data collected in Iliamna Lake and Control Lake are both interesting and informative. Within the Iliamna Lake system, three sources of organic matter with overlapping $\delta^{13}C$ values are evident: (1) higher-plant detritus, value -26; (2) net plankton, -25.4 to -29.4; and (3) periphyton, -3.5 to -28.4. Whatever causes the periphyton variability is probably an indirect cause of the wide range of $\delta^{13}C$ values for sediment.

The -20 $\delta^{13}C$ value of the mature salmon is interesting because of its constancy but probably is not a major factor in the carbon isotope chemistry of the Iliamna Lake system.

The power of dual isotope tracers is evident in Control Lake sculpins. At ~$\delta^{13}C$ of -20, they appear to be related to salmon, but there are no salmon in this lake. These same sculpins had $\delta^{15}N$ values of +6.3 to +7.8, not at all like +11 salmon (Figure 3). Probably, the sculpins reflect some minor specialized food web or a species-specific biochemistry. The salmon fry ($\delta^{15}N$ of +10) reflect the $\delta^{15}N$

of mature salmon (+11) but not the $\delta^{13}C$. This is probably due to the fact that nitrogen is more conservative, and carbon is more labile in oligotrophic Iliamna Lake.

Sulfur Studies

During the first year of RETURNS, time commitments did not allow us to measure $\delta^{34}S$ of the biota and inorganic sulfur in these lake systems. However, we have isolated barium sulfate from Iliamna Lake water (which required the processing of 6 liters for an adequate sample) and are in the process of analyzing it for $\delta^{34}S$. The amount of sulfur in mature sockeye salmon (~5 $mg \cdot g^{-1}$ dry weight) indicates that sufficient sulfur is present in salmon and probably also in other biota for $\delta^{34}S$ analysis by the usual Parr-bomb technique. The low level of sulfur in the Iliamna Lake system leads one to speculate that $\delta^{34}S$ may indeed be a useful tracer. Testing this idea will be a major goal for the 1986 summer field sampling and subsequent isotope analyses.

DISCUSSION

The sockeye salmon runs to the Kvichak River have a pronounced cyclic nature with a period of 4-5 years, depending upon the average length of freshwater residence of the juveniles. Escapements have ranged from 225,000 to 24 million, and the numbers of juveniles reflect the same variations. Whereas the biogenic enrichment through the salmon carcasses cannot explain the establishment of cyclic salmon runs, they do provide a feedback loop which sustains the variable amount of juvenile biomass.

The probable sequence is from carcass to periphyton, especially in the littoral zone to feeding fry next spring. The fry enter the limnetic zone in late July. Whereas their food requirements are less during the first year of lake residence, it increases drastically during the second year. The principal food item, *Cyclops scutifer*, has a 2-year lifespan which is largely synchronized with the freshwater residence of the juvenile sockeye salmon.

Eventually, the biogenic nutrients are lost through discharge from the system or deposited as sediments at the deeper parts of Iliamna Lake. The focus of future investigations is directed toward an understanding of the residence time of the transported biogenic nutrients in the production cycle of salmon.

ABSTRACT

Реки и озера,прилегающие к северной части Тихого океана, в которых воспроизводится тихоокеанский лосось, в высшей ствпени олиготрофны. Однако, они поддерживают высокую продуктивность, благодаря уникальному притоку питательных веществ морского происхождения, извлеченных из каркасов погибших рыб нерестового хода.

Все виды тихоокеанского лосося погибают после нереста. Почти целиком их общий вес тела - морского происхождения.

Потребность в питательных веществах, привнесенных в озеро Илиамна, Бристольский залив, Аляска, неркой Oncorhynchus nerka, была установлена при помощи детального химического анализа рыб.

Включение этих питательных веществ морского происхождения в разные трофические уровни изучалось при помощи постоянного соотношения изотопов - N,C,S .

Значительная часть азота морского происхождения высвобождается в лимнетическую зону в результате метаболической деятельности перед нерестом. Перифитон является первым главным получателем морских элементов из каркасов погибших рыб.

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