

The Lake Washington Ecosystem: The Perspective from the Fish Community Production and Forage Base¹

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In Lake Washington, fish production through detritus-based food chains is substantially greater than fish production through the grazing food chain. The lack of significant grazing by fish on the zooplankton is a consequence of both piscivore predation and conditions in the planktivore spawning environment. At low planktivore abundance, squawfish may switch to benthos feeding, exploiting the abundant prickly sculpin. At high planktivore abundance, squawfish feed more heavily on planktivores. Thus, even when reproductive success of planktivores is good, swamping of the squawfish population does not occur and compensatory mortality due to squawfish predation prevents planktivore abundance from increasing to the point where zooplankton resource depletion would occur. Benthic-littoral species are vulnerable to predation essentially only as larva and juveniles. They avoid predation by occupying littoral and epibenthic refugia. Recruitment to the adult population from these refugia may be sufficient to account for the greater rate of benthos exploitation by fish relative to the rate of zooplankton exploitation by fish. *Neomysis* is an important component of the Lake Washington fish production, since potentially *Neomysis* is a regulating agent on the zooplankton, and reduction in *Neomysis* predation on zooplankton, due to decreasing abundance and a deeper vertical distribution, may be partly responsible for the recent reappearance of *Daphnia*. The response of the fish community to trophic changes in Lake Washington has been slight. No consistent trends in the growth of fish utilizing zooplankton were observed. However, annual growth increments of consumers utilizing the benthic detrital food chain have declined with sewage diversion. The insights gained from analyzing the Lake Washington fish community structure and the Lake Washington carbon budget corroborate the above response of the fish community to trophic changes. Planktivores are predator-controlled and not able to deplete zooplankton resources, and thus would be insensitive to alterations in standing crop of zooplankton. On the other hand, benthic-littoral fish are more resource-limited and would be expected to respond to alterations in their forage base.

Key words: ecosystem, fish, production, Lake Washington, eutrophication, predation

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Dans le lac Washington, la production de poissons par l'intermédiaire des chaînes alimentaires à base de détritus est beaucoup plus forte que celle que donne la chaîne alimentaire à base de broutage. Le fait que les poissons ne broutent pas à un degré significatif le zooplancton est le résultat tant d'une prédation sur les piscivores que des conditions de l'environnement reproducteur des planctivores. Quand les planctivores sont peu abondants, la sauvagessse peut changer et adopter un mode d'alimentation benthique, se nourrissant de chabots visqueux abondants. Quand les planctivores sont abondants, la sauvagessse mange davantage de planctivores. C'est pourquoi, même quand les planctivores ont une reproduction réussie, il n'y a jamais submersion de la population de sauvagesses et la mortalité anticompensatoire causée par la prédation des sauvagesses empêche les planctivores d'augmenter au point où la ressource zooplanctonique s'épuise. Ce n'est qu'aux stades de larves et de jeunes que les espèces benthio-littorales sont vulnérables à la prédation. Elles évitent les prédateurs en occupant des refuges littoraux et benthiques. Les recrues qui quittent ces refuges pour se joindre à la population adulte peuvent suffire à expliquer le taux plus élevé d'exploitation du benthos par les poissons comparativement à leur taux d'exploitation du zooplancton. *Neomysis* est un composant important de la production de poissons du lac Washington, car l'espèce est un agent possible de régulation du zooplancton et il se peut qu'une diminution de prédation de *Neomysis* sur le zooplancton, par suite d'une abondance moindre et d'une distribution verticale plus en profondeur, soit responsable de la récente réapparition de *Daphnia*. La communauté ichthyologique n'a que très peu réagi aux changements trophiques qui se sont produits dans le lac Washington. Nous n'avons observé aucune tendance régulière dans la croissance des poissons se nourrissant de zooplancton. Cependant, les augmentations annuelles de croissance des consommateurs se nourrissant à même la chaîne alimentaire à base de détritus benthiques ont diminué avec le détournement des eaux usées. L'analyse de la structure de la communauté ichthyologique du lac Washington et du budget du carbone de ce lac est en accord avec cette réponse de la communauté ichthyologique aux changements trophiques. Les planctivores sont contrôlés par les prédateurs et ne peuvent épuiser les ressources zooplanctoniques, et seraient ainsi insensibles aux changements dans la biomasse de zooplancton. D'autre part, les poissons benthio-littoraux sont plus limités par la ressource et l'on s'attendrait qu'ils réagissent à des changements dans la biomasse des organismes fourrage.

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THIS paper presents the Lake Washington ecosystem from the perspective of total fish community production and the respective contributions of forage base groups of zooplankton, mysids, benthos, and fish to this production. The objective is to provide insight into the response of ecosystem components to changes in lake trophic state and into the determinants of fish community structure. This study provides information for comparison with other ecosystems of differing trophic states and perturbational histories. Loftus and Regier (1972) have suggested that comparative approaches are useful because they provide contrasts for drawing and testing inferences regarding fish community response to stressed and unstressed conditions. Lake Washington is particularly suited for ecosystem studies because of its unique perturbation history. Lake Washington is a low-land mesotrophic lake lying adjacent to Seattle and is well known as a case history in eutrophication and subsequent recovery after diversion of treated sewage (Edmondson 1972a, b, 1974a, 1977; Chasan 1971).

Study Area

Lake Washington is a warm monomictic lake. Stratifi-

cation occurs from June through October, and the thermocline is typically located in the 10-20-m interval. Surface water temperatures range from 4 to 6°C in winter to over 20°C in summer. Physical characteristics of Lake Washington are summarized in Table 1.

Two major tributaries flow into Lake Washington. The Cedar River entering the lake at the south end contributes 55% of the inflow, and an additional 35% is furnished by the Sammamish River at the north. Several smaller streams contribute another 10% of the water income. Prior to 1916, the main inflow to Lake Washington was through the Sammamish River and outflow was through the Black River to Puget Sound. With construction of the Chittenden Locks and the Lake Washington ship canal, joining Lake Washington and Puget Sound through Union Bay and Lake Union, additional water was needed for operation of the locks. Accordingly, the Cedar River was diverted into Lake Washington and the original outlet was blocked.

Residential development has occurred along most of the 115-km shoreline. Bulkheads and docks have altered these areas, with the exception of areas designated as parks and the shorelines with wide littoral areas. The lake has shallow areas in bays and river mouths, but most shore areas are relatively steep.

There are 29 resident or transient species of fish found

TABLE 1. Physical characteristics of Lake Washington (from Anderson 1954 unless otherwise indicated).

Maximum depth (m)	65
Mean depth (m)	33
Area (km ²)	87.6
Volume (km ³)	2.88
Length (km)	35.1
Mean width (km)	2.4
Elevation (m)	4.3
Turnover rate of lake volume (yr ⁻¹)	2.9
Net sedimentation rate for 1958-74 (mm·yr ⁻¹) ^a	5.3

^aBirch (1976).

in Lake Washington (Wydoski 1972). Wydoski lists the following 12 resident fish species as either common or abundant: prickly sculpin (*Cottus asper*), juvenile sockeye salmon (*Oncorhynchus nerka*), peamouth (*Mylocheilus caurinus*), northern squawfish (*Ptychocheilus oregonensis*), yellow perch (*Perca flavescens*), longfin smelt (*Spirinchus thaleichthys*), threespine stickleback (*Gasterosteus aculeatus*), largescale sucker (*Catostomus macrocheilus*), brown bullhead (*Ictalurus nebulosus*), black crappie (*Pomoxis nigromaculatus*), largemouth bass (*Micropterus salmoides*), and carp (*Cyprinus carpio*).

The first seven species in this list are the most common and their abundance, annual production, and diet are dealt with here. The last four species are relatively restricted, being found in weedy bays and undeveloped shoreline that constitute only a small portion of the total fish habitat of Lake Washington because of urbanization and shoreline development (Hockett 1975). Suckers are a long-lived, slow-growing species that consume only benthos (Scott and Crossman 1973) and are common throughout the lake. Largemouth suckers are less abundant than squawfish and are a minor component of the total fish production of the lake (Bartoo 1972).

Materials and Methods

All fishing methods were selective with respect to both size of fish and habitat sampled. To obtain comparable population statistics for all age-classes of several species of fish, it was necessary to use several pieces of gear, and to obtain the catchability coefficient, selectivity, and the size or age at which fish were fully recruited for each type of sampling apparatus.

A long-term sampling program was not undertaken specifically to monitor the response of several populations to trophic changes in Lake Washington. Instead, we utilized the results of several diverse studies, most of which were individual efforts, for estimates of the abundance of each age-class of the major fish species in Lake Washington. Then we assessed the fish populations quantitatively in terms of annual production, growth, and prey consumption rates.

This study summarizes and synthesizes the work of many people over the years 1962-76. Three sampling methods were used.

LIMNETIC SAMPLING

Limnetic sampling with midwater trawls and hydro-acoustic gear was targeted at juvenile sockeye salmon, longfin smelt, and threespine stickleback. The limnetic fish populations in Lake Washington have been sampled since 1962 (Dryfoos 1965; Woodey 1971; Dawson 1972; Traynor

1973; Doble 1974; Moulton 1974). Acoustic estimation techniques have evolved over this period (Thorne 1970, 1971, 1972, 1973; Thorne and Lahore 1969; Thorne and Woodey 1970; Thorne et al. 1972, 1974). Also, population estimates can be derived solely from the trawl catch per unit effort (Traynor 1973).

Catches from midwater trawl hauls were used to determine length (fork length for sockeye, and standard length for stickleback and smelt), weight, and species composition (used in conjunction with acoustic surveys). During the years 1967-71, trawl surveys were incomplete. The catches from those strata not sampled were considered as missing data and were estimated by simple linear regression from those strata sampled. The population estimates presented here are simple averages of all point estimates (from acoustic as well as net sampling) made December through January when the limnetic fish were fully recruited to the gear.

Neomysis awatchensis were caught in substantial numbers during the nocturnal sampling with the Isaacs-Kidd midwater trawl (IKMWT). A 2-m IKMWT was used during the early period May 7, 1962 to October 21, 1964, and a 3-m IKMWT thereafter. To standardize these catch data, an effective cross-sectional area for the two nets was estimated using information from Banse and Semon (1963) and Friedl (1971). The population estimation technique for *Neomysis* was patterned after the net estimation technique for limnetic fish (Traynor 1973). Missing data due to incomplete trawl surveys were similarly estimated.

The diet composition of limnetic fish species in Lake Washington was determined from diel sampling at roughly 2-mo intervals, November 1974-October 1975. Sampling methods and means of determining numerical diet composition are given in Doble and Eggers (1978). The mean body carbon content for each prey species found in the diet was determined by measuring the mean length of each prey species and then converting that length to total body carbon from relationships given by M. L. Perkins (Water and Air Resources, Dept. Civil Engineering, Univ. Washington, Seattle, Wash., personal communication). Using this information, we converted the numeric diet composition to diet composition by prey body carbon content. This analysis was performed on individual fish stomachs. Stomach contents were pooled by fish age-class and sampling date and then averaged to give mean diet composition by prey body carbon content.

GILLNET SAMPLING

Gillnet sampling was targeted at peamouth, squawfish, and yellow perch. The primary gear used for sampling these species was monofilament gill nets. Panels of mesh from 2.54 to 12.70 cm, in 1.27-cm increments, were connected in random order to form the nets. Gill nets were fished in either a horizontal or a vertical mode. Details of the horizontal gillnet construction are given by Nishimoto (1973) and Hansen (1972). Horizontal gill nets sample the stratum within 1.83 m of the bottom. Vertical gill nets sampled the entire water column. Details of the vertical gillnet construction are given in Hansen (1972), Bartoo (1972), and Bartoo et al. (1973). Data collected consisted of standard life history information—length, weight, sex, gonad weight, otolith or scale sample, and stomach sample.

Population estimates based on the horizontal and vertical gillnet sampling were given by Bartoo (1977). The estimated abundance of age 1+ peamouth from limnetic

sampling was extrapolated to population estimates of peamouth, northern squawfish, and yellow perch from information on relative abundance; horizontal, vertical, and regional distribution; age composition; and age structure from gillnet catches. The gillnet catch data were adjusted for selectivity by a procedure modified from Hamly (1975) using data given by Hansen (1972). Abundances of age 0+ peamouth, age 0+ and 1+ squawfish, and 0+ yellow perch, not yet recruited to the gillnet sampling gear, were extrapolated from the abundance of older age-classes based on rate of natural mortality.

BAITED MINNOW TRAP SAMPLING

Sampling with baited minnow traps was targeted at prickly sculpin. Largescale sucker filets were used as bait. Data from this sampling consisted of standard life history information — length, weight, sex, gonad weight, otolith sample, and stomach sample.

Population estimates based on the baited minnow trap sampling are also given by Rickard (1978). Rickard determined the mean trapping area of each trap by an experiment in which strings with traps at various distances apart were fished. The CPUE increased asymptotically as the distance between traps increased allowing estimation of mean trapping area. The catches were adjusted for selectivity using a model described by Rickard (1978) and then extrapolated to a population estimate using the mean trapping area and area of the particular stratus fished.

GROWTH, PRODUCTION, AND BIOMASS

Seasonal growth curves by weight for sockeye, smelt, and stickleback were estimated from limnetic sampling. Sample sizes were insufficient for directly constructing seasonal growth curves for all age-classes of squawfish, peamouth, yellow perch, and prickly sculpin. However, the mean annual growth increments (in length) for all constituent age-classes were determined for peamouth (Nishimoto 1973), squawfish (Olney 1975), yellow perch (Nelson 1977), and sculpin (Rickard 1978) by the back-calculation method of determining mean length at annulus formation from growth zones on scales or otoliths (Tesch 1971; Chugunova 1963). For some year-classes, sample sizes were sufficient for direct estimation of seasonal growth curves by length or weight. The monthly growth increments in length or weight were converted to percentage of the annual growth increment. Bartoo (1977), Rickard (1978), and Nelson (1977) found no difference in the seasonal growth pattern expressed as percentage of annual growth increment for the following groups:

1. All age-classes of peamouth (weight).
2. Age 2–4 squawfish (immature) (length).
3. Age 5 and older squawfish (mature) (length).
4. Age 2 and older yellow perch females (mature) (length).
5. Age 2 and older yellow perch males (mature) (length).
6. Age 1+ yellow perch (immature) (length).
7. All age-classes of prickly sculpin (weight).

The data for each of these groups were pooled to give a curve of monthly growth increments. From this information and the mean annual growth increments a seasonal growth curve for the above age-classes and species was computed.

Seasonal growth curves were not available for age 0+ and 1+ squawfish and age 0+ yellow perch. For those groups growth was assumed to be linear. If the measured monthly growth increments were in units of length, the derived seasonal growth curve (in units of length) was converted to units of weight via length-weight relationships given in Olney (1975) and Nelson (1977). If the measured monthly growth increments were in units of weight, the annual growth increments from scale studies were converted to weight based on the technique of Pienaar and Ricker (1968) and weight-length relationships given by Nishimoto (1973) and Rickard (1978).

Production is defined here as the total amount of tissue elaborated in the population or community under study in a given period of time (Allen 1971). That is,

$$(1) \quad P = \int_{T_1}^{T_2} N_t \frac{dW_t}{dt} dt$$

where P is the production, T_1 is the beginning of the time period, T_2 is the end of the time period, N_t is the number of fish in the population at time t , and dW_t/dt is the instantaneous rate of growth in weight. To compute production, a model is needed for abundance (N_t) and a model for growth (W_t). From analyses of catch curves, Bartoo (1977) found mortality to be an exponential decay function for peamouth, squawfish, and yellow perch. Similar results were found for sculpin (Rickard 1978) and juvenile sockeye (Bryant 1976). Thus,

$$(2) \quad N_t = N_0 \exp(-mt)$$

where m is the instantaneous rate (month⁻¹) of natural mortality. To simplify the computation of annual production, the year was divided into monthly intervals where growth was linear; hence dW_t/dt is constant during those intervals. Substituting equation (2) into equation (1) and integrating yields

$$(3) \quad P = \sum_{i=1}^{12} \Delta W_i N_i \left[\frac{1 - e^{-m}}{m} \right]$$

where ΔW_i is the monthly growth increment and N_i is the population abundance at the beginning of month i . P was computed for each species and constituent age-class. Mean annual biomass (B) was similarly computed for each species and constituent age-classes:

$$(4) \quad B = \frac{\sum_{i=1}^{12} W_i N_i \left[\frac{1 - e^{-m}}{m} \right]}{12}$$

where W_i is the mean weight during month i .

Results

PARTICULATE ORGANIC CARBON BUDGET

To relate the Lake Washington fish community to the trophic economy by the lake, we estimated the dietary components of the annual fish production. To make this estimate we had to construct the annual pattern of abundance, growth, and diet for each major fish species and respective age-class.

Mean annual biomass and production of the limnetic species were computed for the period January 1, 1972

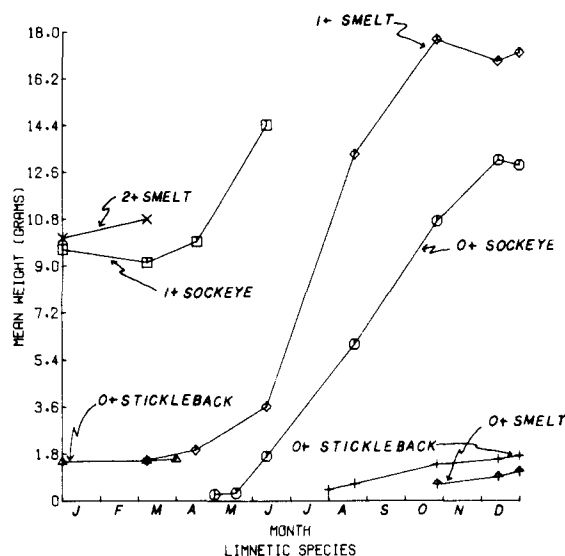


FIG. 1. Seasonal growth trajectories for relevant year-classes of the limnetic fish species in Lake Washington during 1972.

to December 31, 1972. In Lake Washington, threespine stickleback and longfin smelt mature at age 1 and age 2, respectively, and die after spawning. This period encompassed the growth (Fig. 1) of 1970 and 1971 year-classes of juvenile sockeye salmon (migrated spring 1972 and 1973, respectively); 1971 and 1972 year-classes of threespine stickleback (matured spring 1972 and 1973, respectively); and 1970, 1971, and 1972 year-classes of longfin smelt (matured late winter 1972, 1973, and 1974, respectively). Using the respective instantaneous rates of natural mortality (Table 2), the abundances of the limnetic fish species during this period were extrapolated from the winter abundance before maturity or outmigration of the 1970, 1971 year-class of juvenile sockeye salmon; 1971, 1972 year-class of stickleback; and 1970, 1971, 1972 year-classes of longfin smelt.

Data on abundance, growth, and diet of the benthic-littoral fish species were collected from 1971 to 1975. Population abundances were essentially point estimates (Fig. 2). Because these species are long-lived, and, except for squawfish, show no extensive variation in year-class strength (Fig. 2), the bias due to annual variation in abundance is negligible. The abundance of the youngest age-classes of peamouth, squawfish, and yellow perch not yet recruited to the gill nets was estimated by extrapolating from the abundance of the older age-classes, taking into account the instantaneous rates of natural mortality (Table 2). Growth was estimated by extrapolating size at annulus formation (Table 3) by monthly values of mean annual growth increments. Most of the production and biomass of fish in Lake Washington is prickly sculpin (Table 4).

TABLE 2. Instantaneous (day^{-1}) rate of natural mortality for Lake Washington fish populations.

Population	Mortality	Source
Juvenile sockeye		
1970 year-class	-0.00290	Bryant (1976)
1971 year-class	-0.00274	Bryant (1976)
Smelt	-0.00282	Avg of the sockeye mortality rates
Stickleback	-0.00282	Avg of the sockeye mortality rates
Peamouth	-0.00397	Bartoo (1977)
Squawfish	-0.00074	Bartoo (1977)
Yellow perch	-0.00156	Bartoo (1977)
Prickly sculpin	-0.00295	Rickard (1978)

TABLE 3. Mean weight (grams) at annulus formation for various species of fish in Lake Washington.

Age	Peamouth	Squawfish	Prickly sculpin	Yellow perch males	Yellow perch females
1	9	—	1.0	8.8	10
2	38	26	7.2	52	65
3	81	94	16	125	171
4	132	187	26	188	281
5	190	293	41	242	376
6	240	408	60	282	454
7	303	528	81	328	502
8	352	650	110		
9	408	773			
10		897			
11		1,021			
12		1,145			
13		1,269			
14		1,393			
15		1,517			
16		1,641			
17		1,765			
18		1,889			
19		2,013			
20		2,137			
21		2,261			
22		2,385			

A great number of prey items are available to Lake Washington fishes. To provide a simple picture of carbon flow through water column and benthic communities, as well as to avoid a confusing presentation involving tens of prey species, the prey items in the diet were grouped according to zooplankton, benthos, mysids, and fish (Fig. 3 and 4). The diet of age 2+ peamouth is strictly benthos (Nishimoto 1973; Shanbhogue 1976).

The relative contribution of the zooplankton, mysids, benthos, and fish prey items to fish production was estimated by grouping fish according to similar feeding habitat and diet composition (Table 5). These functional groups ranged from strictly limnetic fish feeding on zooplankton and emergent insects to strictly benthic

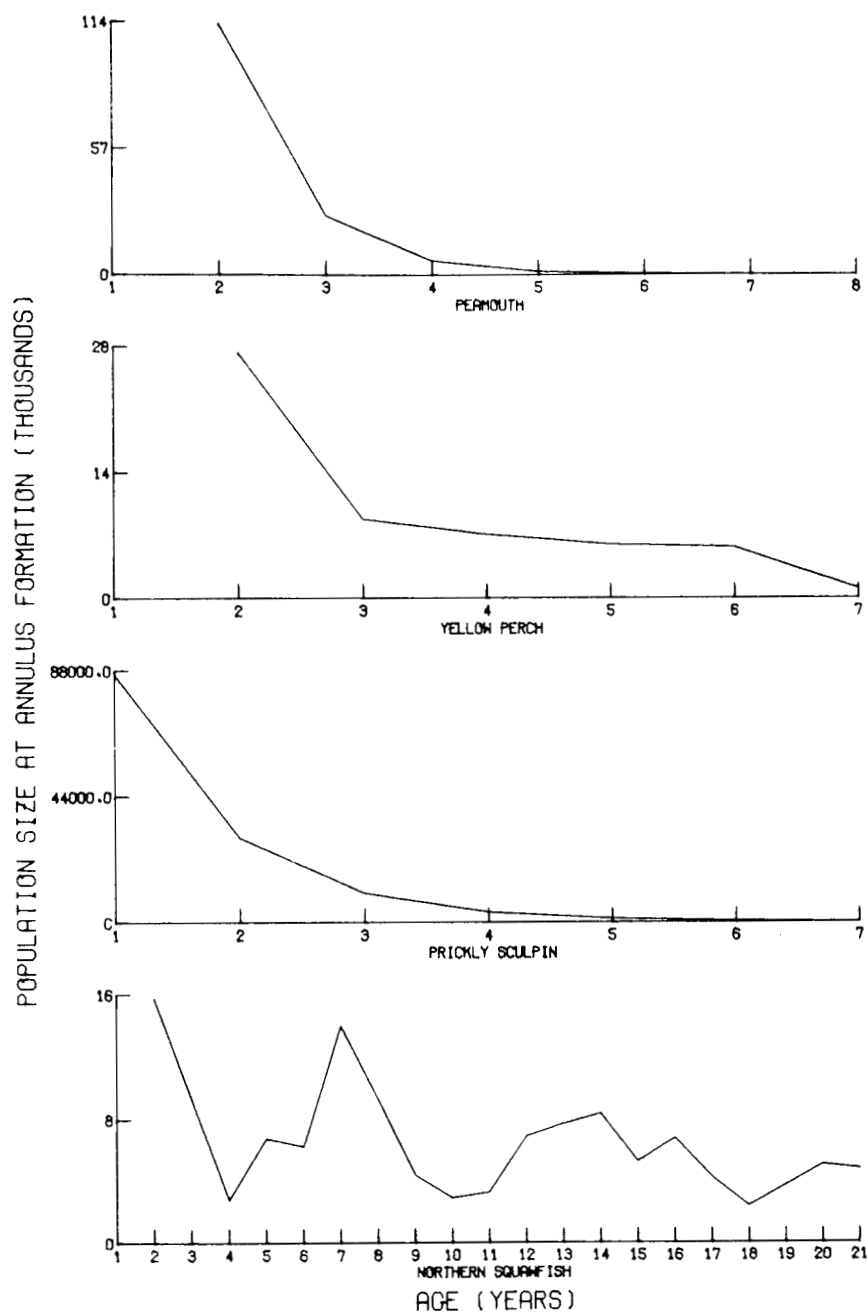


FIG. 2. Abundance at annulus formation for constituent age-classes of peamouth, yellow perch, prickly sculpin, and northern squawfish in Lake Washington.

feeding fish as evidenced by a diet of benthos, mysids, and bottom fish (sculpin). Older age-classes of sculpin were cannibalistic and can be considered piscivores as well as benthic feeders. The facultative piscivores (older

age-classes of yellow perch and squawfish) feed in the water column as well as on the bottom.

The relative contribution of each prey group to fish production was estimated by partitioning the production

TABLE 4. Annual production and mean annual biomass of Lake Washington fishes.

Species	Annual production (kg wet wt/yr)	Percent of total production	Mean annual biomass (kg wet wt)	Percent of total biomass	Turnover rate $\frac{P}{B}$
Prickly sculpin	6.56×10^5	83.8	5.95×10^5	72.7	1.41
Juvenile sockeye salmon	4.88×10^4	6.2	4.07×10^4	5.0	1.19
Peamouth	2.65×10^4	3.4	1.98×10^4	2.4	1.34
Longfin smelt	2.68×10^4	3.4	3.07×10^4	3.8	0.87
Northern squawfish	1.55×10^4	2.0	1.16×10^5	14.2	0.13
Yellow perch	5.51×10^3	0.7	1.14×10^4	1.4	0.48
Threespine stickleback	3.42×10^3	0.4	4.53×10^3	0.6	0.75

of each constituent age-species class in the functional group by its respective diet composition and summing (Table 6). Of the prey groups, benthos contributed most (74.3%) and fish contributed least (6.4%) to fish production.

A particulate organic carbon budget incorporating the dietary components of fish production and ration was constructed for Lake Washington (Table 7). The Lake Washington carbon budget is incomplete because of the lack of data on littoral primary production and on allochthonous inputs to the lake. Data are also inadequate for estimating production, respiration, and diet

of the *Neomysis* population. Values presented in parentheses reflect only the population cropped by fish and therefore serve as a minimum estimate.

The carbon budget shows that the benthic food chain is as important as water column processes to the trophic dynamics of Lake Washington, which is surprising for a deep lake where the littoral area is <20% of the lake surface area. However, fluvial and direct sedimentation inputs of carbon to the sediments appear insufficient to fuel the benthic production (Table 7). This deficiency was most likely due to unaccounted-for inputs of littoral production by periphyton and attached macrophytes.

In Lake Washington, cold littoral water sinking down the steep sides of the lake basin causes winter thermal convection currents (Syck 1964). These convection currents have been described as sufficient in magnitude to have eroded the original U-shaped Lake Washington basin to its present W shape (Gould and Budinger 1958). Thus, detrital material produced in littoral regions could be transported to profound regions of the lake.

Steele (1974) and Mills (1975) encountered imbalances in their analysis of the trophic economy of the North Sea ecosystem. They were unable to account for the observed demersal fish production from inputs to the demersal food web due to sedimentation of zooplankton fecal material if consideration was given to possible losses of bacteria respiration, metabolism of meiobenthos, and metabolism of carnivorous epifauna. At this time there are not enough studies of benthos and

TABLE 5. Definition of the functional groups of fish used to compute the relative contribution of zooplankton, benthos, mysids, and fish prey items to fish production.

Functional group	Fish species and age composition	Feeding behavior	Diet
Obligate planktivores	Age 0+ sockeye Age 1+ sockeye Age 0+ stickleback	Limnetic	Zooplankton and emergent insects
Smelt	Age 0+, 1+, and 2+ longfin smelt	Limnetic epibenthic	Zooplankton mysids, emergent insects
Facultative benthic	Age 0 to 2+ peamouth Age 0 to 1+ squawfish Age 0 to 1+ yellow perch	Benthic epibenthic limnetic	Benthos, mysids, zooplankton
Obligate benthic	Age 2+ to 8+ peamouth Age 0 to 7+ sculpins	Benthic epibenthic	Benthos, mysids, sculpins
Facultative piscivores	Age 1+ to 6+ yellow perch Age 1+ to 21+ squawfish	Limnetic benthic	Benthos, mysids, fish

TABLE 6. Dietary components of fish production (numbers in parentheses are percentage total production).

Group	Biomass (kg wet wt)	Production (kg wet wt per year)	Production due to forage items			
			Zooplankton	Benthos	Mysids	Fish
Obligate planktivores	45 200	52 200	47 640 (91.3)	4 110 (7.9)	450 (0.9)	0 (0)
Smelt	30 680	26 800	9 740 (36.3)	4 200 (15.7)	12 530 (46.8)	330 (1.2)
Facultative benthic feeders	19 610	24 460	12 000 (49.0)	11 890 (48.6)	580 (2.4)	0 (0)
Obligate benthic feeders	571 800	658 584	0 (0)	510 837 (77.6)	91 630 (13.9)	56 117 (8.5)
Facultative piscivores	127 700	19 420	0 (0)	2 790 (14.4)	2 060 (10.5)	14 570 (75.0)
Total	794 500	718 464	69 380 (8.9)	533 827 (68.3)	107 250 (13.7)	71 017 (9.1)

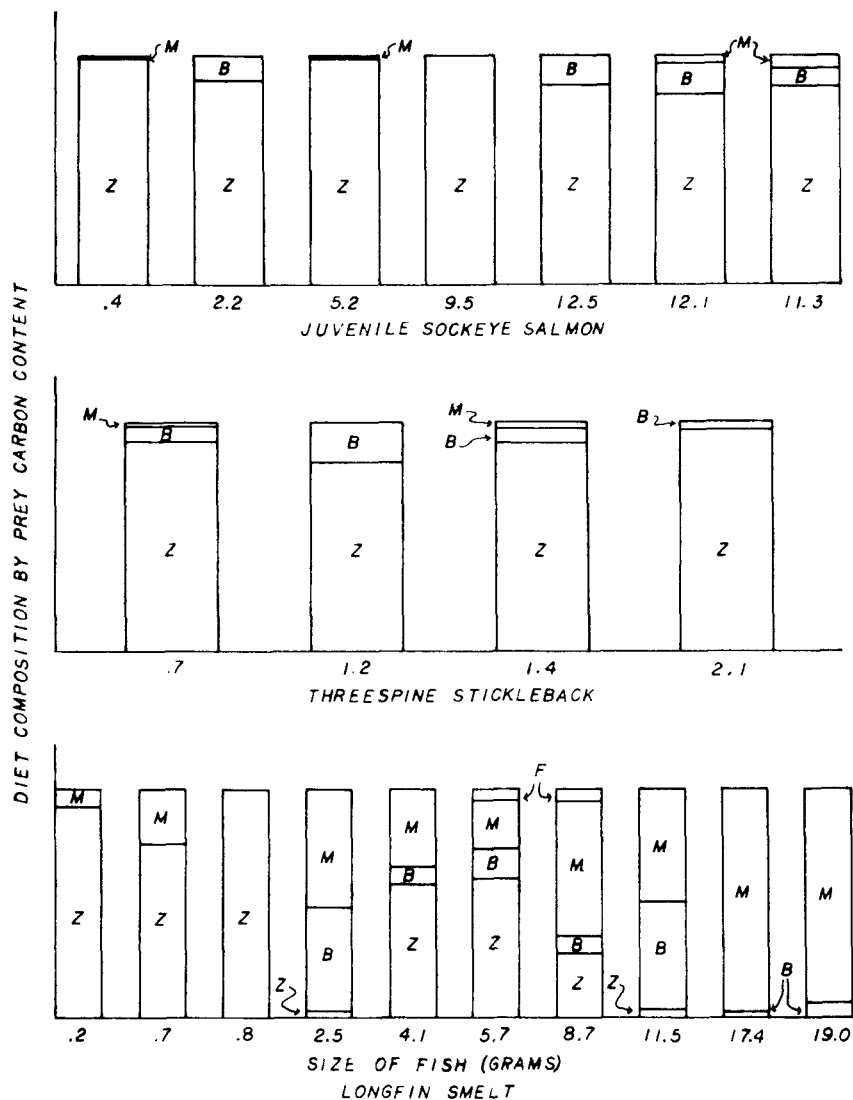


FIG. 3. Diet composition (by prey carbon content) for various sizes of juvenile sockeye, threespine stickleback, and longfin smelt in Lake Washington. These data reflect seasonal trends in diet as sampling was conducted over the period of limnetic residence for each species. The diet of sockeye (0.4–11.3 g) was collected February through February. Similarly, the diet of stickleback, (0.7–2.1 g) was collected August through February; age 0+ smelt (0.2–2.5 g) was collected August through February; and age 1+ smelt (4.1–19 g) was collected June through February. The component dietary items include zooplankton (Z), mysids (M), benthos (B), and fish (F).

zooplankton paralleling studies of fish production for generalization.

In Lake Washington the fish community is dominated by benthos feeders. The limnetic fish population was estimated to use only 1.7% of the annual zooplankton production. *Neomysis*, an organism that seemed unimportant in the catches from zooplankton sampling

gear and midwater trawls, is potentially an important component of the water column food chains. In the limnetic zone of Lake Washington, *Neomysis* has declined in abundance since 1962 (Fig. 5). Abundance during 1968–71 was less than during 1974–75. The estimated mean biomass for *Neomysis* during the period November 5, 1974 to October 13, 1975 was 0.0144 g

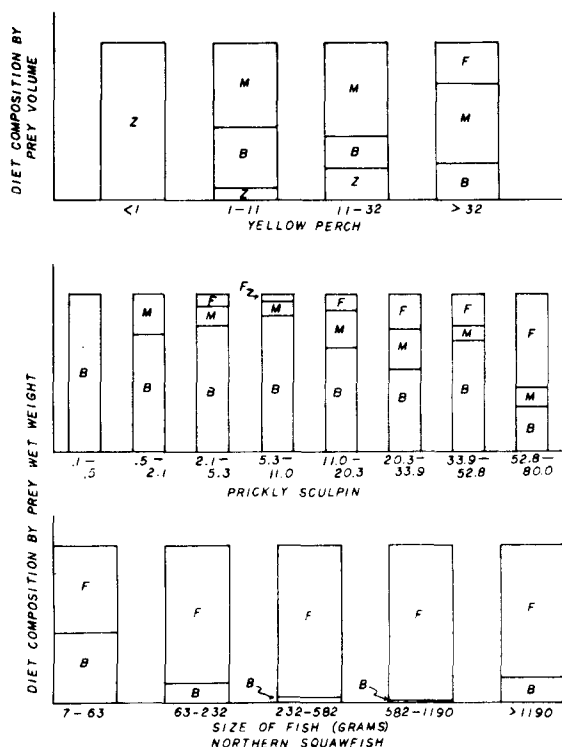


FIG. 4. Diet composition for various sizes of yellow perch (by prey volume), prickly sculpin, and northern squawfish (by prey wet weight) in Lake Washington. Data were pooled by size and do not reflect seasonal trends. The component dietary items include zooplankton (Z), mysids (M), benthos (B), and fish (F).

C·m⁻². If it is assumed that the amount of *Neomysis* consumed by fish was the minimum *Neomysis* production during 1974, then the production/biomass (P/B) ratio was at least 90.3, an unreasonably high figure. The calculated P/B for Lake Washington zooplankton is 12.66. Mean zooplankton biomass during 1974 was estimated using unpublished zooplankton density (W. T. Edmondson, Dept. Zoology, Univ. Washington, Seattle, Wash., personal communication), mean length (Eggers and Doble unpublished data), and a conversion from length to body carbon content (Perkins personal communication). The high P/B for *Neomysis* indicates that we are underestimating the abundance of *Neomysis*. Accordingly, there may be sizable inshore and littoral populations not available to the sampling gear (Nelson 1977). Also, only a part of the population may be migrating from the bottom into the water column at night.

Fish consumed by yellow perch and prickly sculpin were small fish, mostly small prickly sculpin (Nelson 1977; Rickard 1978). Northern squawfish consumed both planktivorous fish (smelt, stickleback, and sockeye) as well as prickly sculpin.

RESPONSE OF THE FISH COMMUNITY TO TROPHIC CHANGES IN LAKE WASHINGTON

There were two periods of sewage input to Lake Washington. During the early part of this century, the lake received untreated sewage until diversion of the untreated effluent to Puget Sound was completed in 1936. This diversion was in response to health concerns as some communities used the lake for drinking water. Beginning in 1941, secondary sewage treatment plants dispersed effluent into Lake Washington. Because of public concern for the deterioration of the lake, diversion of the secondary treatment plant effluent began in 1963 and was completed by 1966. The phytoplankton community responded rapidly to the reduced nutrient loadings (Edmondson 1972a).

Specific components of the eutrophication history thus far documented are:

1. Nutrient loadings were 108 000 kg phosphorus in 1957; 231 000 kg in 1962; and 41 000 kg in 1974 (Edmondson 1977).

2. The summertime chlorophyll *a* concentration reached maximum levels (40 µg/L) in 1964, but were high from 1962 to 1966 (20–40 µg/L). Summertime Secchi disk readings were low (<1.5 m), 1962–67 (Edmondson 1972a).

3. Species composition of the algae has changed markedly since the period of maximum nutrient loading when filamentous blue-green algae constituted as much as 98% by volume of the phytoplankton. The percentage of blue-green algae has decreased sharply in recent years, constituting 44% of the phytoplankton in 1973 and 1974 (Edmondson 1977).

4. Zooplankton had shown no major changes in species composition until 1972 when *Daphnia* reappeared in the lake (Edmondson 1977). *Daphnia* had been observed in the 1930s (Sheffer and Robinson 1939) but not in the years 1950–72 (Edmondson personal communication). Some changes in abundance have occurred over the years but none that can be attributed to trophic changes in Lake Washington (Edmondson 1972b).

There was no consistent change in the size of juvenile sockeye at the end of the summer–fall growing season, 1966–75, that might be associated with change in the trophic condition of Lake Washington (Fig. 6). In stickleback, there was no consistent change between 1971 and 1975 in the size reached by December, even though stickleback increased greatly in abundance during the period 1967–76 while sockeye declined in abundance (Fig. 7).

Smelt exhibited cyclic abundance patterns for 1966–71 year classes, the even-numbered year-classes being more abundant than the odd-numbered year-classes. During these years, smelt exhibited density-dependent growth, the less abundant odd-numbered year-classes showing a higher growth rate (Fig. 6) than the even-numbered more abundant year-classes (Moulton 1974), a pattern that has disappeared in recent years. This pat-

tern of growth may be related to the long-term trends in abundance of *Neomysis* (Fig. 5), which is the major prey item of smelt older than age 1. During the period of density-dependent growth (1968–71), *Neomysis* abundance was very low.

Long-term patterns of growth were estimated for peamouth (Nishimoto 1973) and for squawfish (Olney 1975) by back-calculation techniques. Nishimoto showed that back-calculated annual growth increments increased from 1962 to 1967–68 when they peaked (Fig. 8). In subsequent years, a progressive decline in growth occurred. The maximum growth rates for peamouth were observed approximately 2 yr after maximum primary production resulting from cultural eutrophication (Edmondson 1972a). Olney (1975) compared the back-calculated total length at each annulus as well as annual growth increments during the first 5 yr of growth for 1955–71 year-classes of squawfish (Fig. 9). Annual growth increments during the first 3 yr of growth increased from 1955 to 1966–68 and declined thereafter. This pattern did not hold for the 4th and

5th yr of growth. Age 0–2+ squawfish feed primarily on benthos. The historical trends in growth of squawfish correlate with those of peamouth which also feed primarily on benthos.

Although there were trends of decreasing growth in fish utilizing benthos as food following sewage diversion, comparisons of size at annulus formation for squawfish (Olney 1975), peamouth (Nishimoto 1973), and yellow perch (Nelson 1977) show that the growth achieved by these Lake Washington fishes is greater than or equal to that in other lakes.

Although growth of Lake Washington planktivores has not changed during the period following sewage diversion, abundance has. Stickleback have increased greatly in abundance during 1967–76 while sockeye have declined (Fig. 2). The decline in sockeye abundance has been attributed to high incidence of mid-winter floods during the last 7 yr in the Cedar River, washing the eggs out of the gravel (Bryant 1976; Miller 1976). The increase in stickleback abundance may be due to changes in littoral environment accom-

TABLE 7. Particulate organic carbon budget for Lake Washington. (All values are given in $\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. See footnote for explanation of source data.^a)

Water column			Benthic-littoral		
Inputs	Value	Source	Inputs	Value	Source
Allochthonous			Water column		
Fluvial	20.0	1	Sedimentation	53.0	3
Precipitation	ND		Autochthonous		
Litter	ND		Periphyton	ND	
Autochthonous			Macrophytes	ND	
Phytoplankton production	157.0	2	Total inputs	53.0	
Total inputs	177.0				
Losses			Losses		
Outflow	0.5	1	Benthic respiration	52.0	8
Sedimentation	53.0	3	Fish respiration	2.0	6
Microplankton respiration	59.0	4	Burial	35.0	9
Zooplankton respiration	48.0	5	Emergence	ND	
<i>Neomysis</i> respiration	ND (2.4)	7	Macrophyte and periphyton respiration	ND	
Planktivorous fish respiration	0.5	6	Total losses	104.9	
Piscivorous fish respiration	0.03	6			
Total losses	163.0				
Internal transformations			Internal transformations		
Ingestion			Ingestion		
Material ingested by zooplankton	97.0	5	Material ingested by macroinvertebrates	113	10
Material ingested by <i>Neomysis</i>	ND (4.0)	7	Macroinvertebrates ingested by fish	3.1	6
Zooplankton ingested by fish	0.33	6	Fish ingested by fish	0.5	6
<i>Neomysis</i> ingested by fish	0.6	6	Production		
Fish ingested by fish	0.04	6	Microbial	ND	
Production			Macroinvertebrates	16.9	10
Microbial	ND		Fish production supported by macroinvertebrates	0.8	6
Zooplankton	19.0	5	Fish production supported by fish	0.1	6
<i>Neomysis</i>	ND (0.6)	7			
Fish production supported by zooplankton	0.10	6			
Fish production supported by <i>Neomysis</i>	0.15	6			
Fish production supported by fish	0.01	6			

panying trophic changes in Lake Washington. Stickleback are territorial and compete for suitable spawning substrate (Scott and Crossman 1973). During periods of peak nutrient loading, littoral areas of Lake Washington had mats of blue-green algae growing on the substrate (Chasan 1971). Possibly suitable spawning substrate or rearing habitat limited the Lake Washington stickleback population before 1970.

Zooplankton showed no consistent change in abundance or species composition from 1962 (Edmondson 1972b) until 1972 when *Daphnia* sp. appeared (Edmondson 1977). Large zooplankters present in Lake Washington include *Epischura nevadensis* and *Diaphanosoma* sp. before 1972, and *Epischura*, *Diaphanosoma*, and *Daphnia* after 1972.

Planktivorous fish in Lake Washington show extreme size-selective predation, but are not sufficiently abundant to regulate the large zooplankters. The reappearance of *Daphnia* in Lake Washington may have been a response to phytoplankton succession accompanying sewage diversion. However, in addition to planktivorous fish, there is another potential zooplankton predator, *Neomysis*, that is an important contributor to fish production in Lake Washington. Its biomass ingested by fish is twice that of zooplankton ingested.

The information we have on *Neomysis* is based on nighttime midwater trawls, and indicates that since 1962 *Neomysis* abundance has decreased and that the nocturnal vertical distribution has shifted to lower strata

(Fig. 6). From 1962 to 1964, when lake water transparency was much lower than at present, substantial numbers of *Neomysis* were found in the water column during the day. Although we have no information on the present daytime vertical distribution, *Neomysis* must be near the bottom because they constitute a significant portion of the diet of prickly sculpin. This is because cottids are ambush predators, with no swim bladder, and therefore can feed effectively only near the bottom. The apparent downward shift in the vertical distribution of *Neomysis* may be a response to the changing ambient light conditions in Lake Washington as a consequence of sewage diversion.

The vertical distribution of *Neomysis* in Lake Washington is consistent with the behavior of a similar species, *Mysis relicta*. The vertical distribution of *M. relicta* in Lake Huron and Lake Michigan was strongly influenced by ambient light intensity (Beeton 1960). Beeton also found that *Mysis* were deeper in the water column on moonlit nights than on dark nights. Additionally, the introduction of *Mysis* into Lake Tahoe caused a virtual disappearance of *Daphnia* from that lake (Richards et al. 1975). Lasenby and Langford (1972) found that *Mysis* in Stony Lake was a benthic detritivore by day and a voracious carnivore preying on *Daphnia* by night.

These two pieces of evidence, the vertical distribution and the apparent decline in abundance of *Neomysis*, along with the information on *M. relicta*, suggest a second cause of the reappearance of *Daphnia* in Lake

*1. Representative particulate organic carbon measurements in the Cedar and Sammamish rivers extrapolated from U.S.G.S. flow data (J. E. Richey, Fisheries Research Institute, Univ. Washington, Seattle, Wash., personal communication).

2. Phytoplankton production from ^{14}C uptake during 1974 (Devol and Packard 1978).

3. Losses of algal, fecal, and allochthonous material from the water column measured by sediment trap, March 1974 to March 1975 (Birch 1976).

4. Sum of euphotic and aphotic microplankton respiration during 1974 (Devol and Packard 1978). Respiration was measured by the activity of the respiratory electron transport system (ETS activity) (Packard 1971).

5. Net zooplankton respiration measured by ETS activity (Devol 1977). Based on summary data presented in Parsons and Takahashi (1973) and Edmondson (1974b), amount of material ingested assumed to be 2 times the respiration, and egestion was assumed to be 30% of ingestion.

6. Fish. The organic material ingested and respiration losses were estimated by simple energy budgets ($I = R + P + E$). All of the budget components are specified by gross conversion efficiency ($K = P/I$), the assimilation coefficient (α , $E = (1 - \alpha)I$), and the production (P); α was assumed to be 0.8 (Winberg 1956). Total body carbon was assumed to be 12.5% of wet weight. In the obligate planktivore, smelt, and facultative benthic functional groups, as well as age 0-1 sculpin (Table 5), K was assumed to be 0.3 (Eggers 1975). Because larger, older fish are less efficient in converting ingested material to growth (Winberg 1956), K for the obligate benthic (except age 0-1 sculpin) and facultative piscivores (except age 1+ to 21+ squawfish) was assumed to be 0.20. Squawfish are large, slow-moving top carnivores with even lower K . Age-specific respiration and egestion for squawfish were estimated using production (Table 4) and relationship of total metabolism to body size and ambient temperature given for cyprinids by Winberg (1956). These age specific estimates of I , R , and E for piscivores were attributed to water-column supported fish and benthos-supported fish based on diet composition. The whole lake production figures were converted to a per hectare basis by dividing by the surface area of the lake.

7. Minimum estimates (shown in parentheses) of ingestion, respiration, and egestion to support the production of *Neomysis* cropped by fish assumed that $I = 5I$, $E = 0.3I$, $K = 0.5I$. This budget is the same as that used for zooplankton.

8. Benthic respiration was measured for several profundal stations during September 1972 by Pamatmat and Bhagwat (1973). Since these samples were incubated at 10°C, it is necessary to convert to in situ temperature (mean annual water column temperature 15-58 m is approximately 8°C). The mean measured value of 600 kg C·ha⁻¹·yr⁻¹ was converted to 520 kg C·ha⁻¹·yr⁻¹ assuming a Q_{10} of 2.3 (Pamatmat 1971).

9. Permanent sediment burial given by Birch (1976).

10. Bissonnette (1975) gave production for Chironomidae, March 1973-March 1974. These numbers were converted from grams dry weight to kilograms carbon and multiplied by 2, since Thut (1969) found Chironomidae to constitute approximately one half of the benthos biomass. We assumed a 15% gross conversion efficiency to estimate the required food base of 1,130 kg C·ha⁻¹·yr⁻¹.

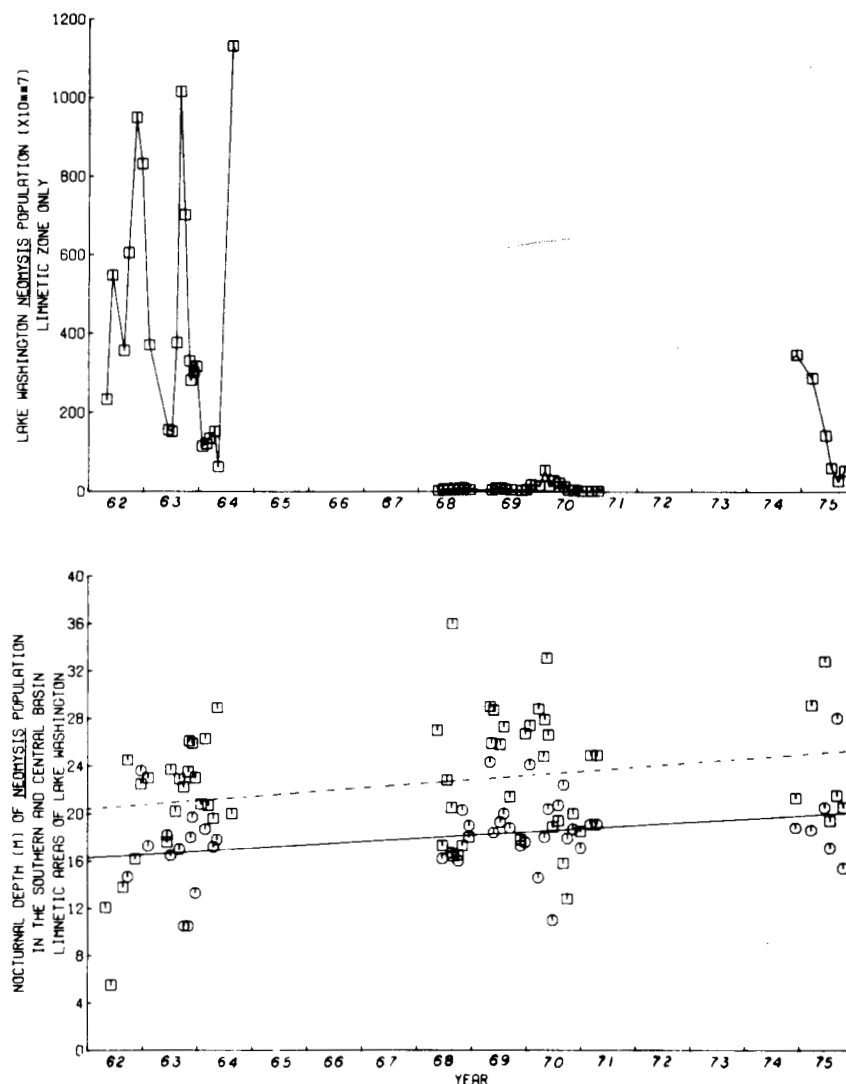


FIG. 5. Long-term trends in limnetic zone abundance (A) and the nocturnal mean depth of occurrence (B) of *Neomysis* in Lake Washington. Fitted linear regression line and data are plotted for the southern (○ solid line) and central (□ dashed line) basins. For the southern basin, $Y = 16.3 + 0.25X$, $R = 0.316$. For the central basin, $Y = 20.4 + 0.33X$, $R = 0.252$.

Washington. After the sewage diversion and subsequent decline in primary production, the amount of algae cropped by herbivorous zooplankton apparently remained constant because there was no decrease in zooplankton abundance associated with sewage diversion. Therefore, more organic material may have been reaching the sediments during past periods of high phytoplankton production than at present. Wissmar and Wetzel (1978) in a comparison of five temperate North American lakes showed that as primary production

increased, a higher fraction was available to benthic and detrital food chains. If a decrease in benthos production resulted from sewage diversion, then the decline in *Neomysis* abundance may have resulted from fish switching from benthos to *Neomysis*. This decline in abundance coupled with the downward shift of the *Neomysis* distribution may create a "refuge" in the upper water column strata for prey organisms such as *Daphnia*. *Daphnia*, like other zooplankters, are much more abundant in the upper 20 m of the lake (W. T.

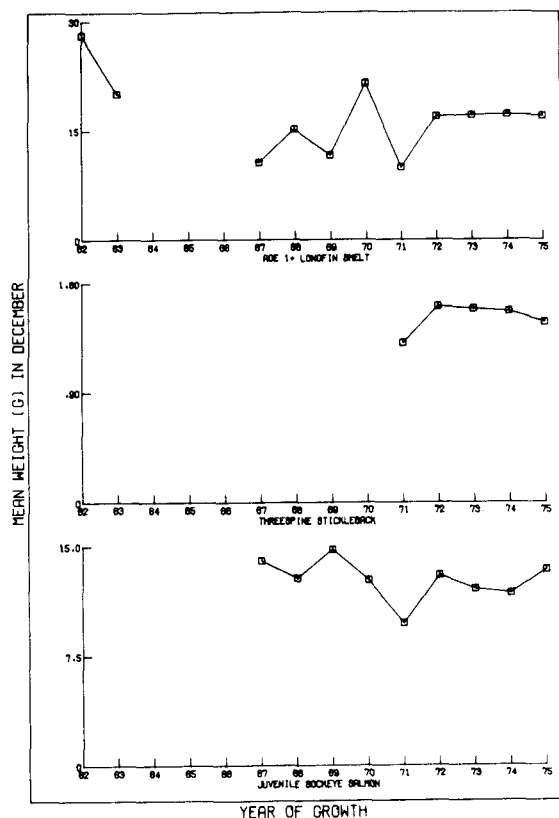


FIG. 6. Long-term trends in the mean weight in December for age 1+ longfin smelt, threespine stickleback, and juvenile sockeye salmon in Lake Washington.

Edmondson personal communication). Thus, the limited evidence we have on both vertical distribution and abundance suggests that the magnitude of predation by *Neomysis* on the zooplankton community has declined since the early 1960s.

Lake Washington is unique as an experiment in eutrophication and subsequent oligotrophication with diversion of treated sewage. The response of the phytoplankton to the changing nutrient loading is well documented, but the response of Lake Washington higher consumers has not previously been documented. Detrimental effects of cultural eutrophication on salmonid communities occur at much higher nutrient loadings or more severe perturbations than occurred in the Lake Washington drainage basin (Colby et al. 1972). Detrimental effects result from depletion of hypolimnion oxygen or deforestation, erosion, damming, and pollution on the spawning tributaries.

Determinants of Limnetic and Benthic Fish Community Structure

The most significant result of this study is the de-

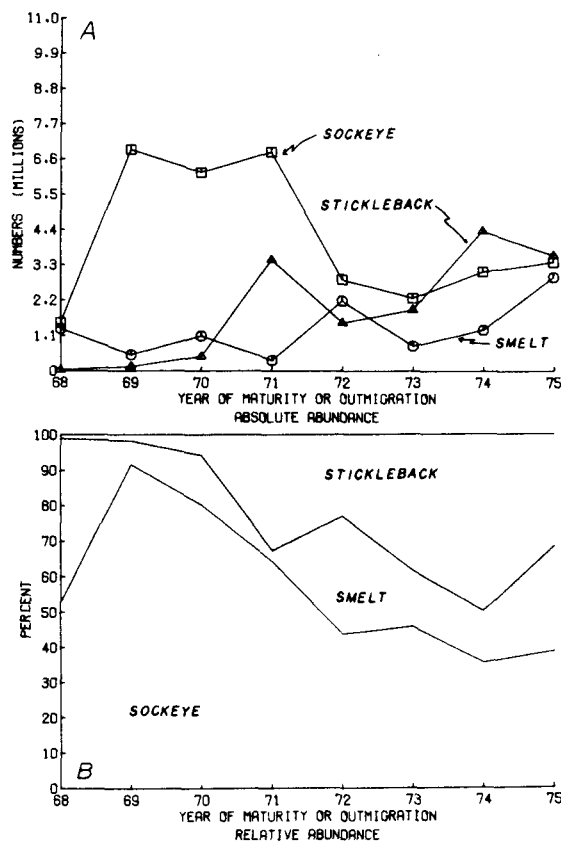


FIG. 7. Long-term trends in absolute (A) and relative (B) abundance of limnetic fish species in Lake Washington.

termination that the fish community is dominated by benthos-consuming fish. This is surprising in a large deep lake where the area of the littoral zone is much smaller than the area of the limnetic zone. Furthermore, the magnitudes of benthos and zooplankton production are comparable (Table 7). If the prey resources were strictly limiting the fish populations, one would expect the magnitudes of benthos- and zooplankton-supported fish production to be more similar than observed in Lake Washington.

It is perhaps a truism to say that competition for resources and effects of piscivorous predation are the determinants of fish community structure. However, the structural manifestations of competition and predation are quite different and the structure of the Lake Washington fish community cannot be explained without consideration of the interaction of competition and predation.

Studies of morphological differences, habitat utilization, diet, and timing of feeding among cohabiting fish species in Lake Opinicon (Keast and Webb 1966; Keast 1970) and Lawrence Lake (Werner et al. 1977; Hall

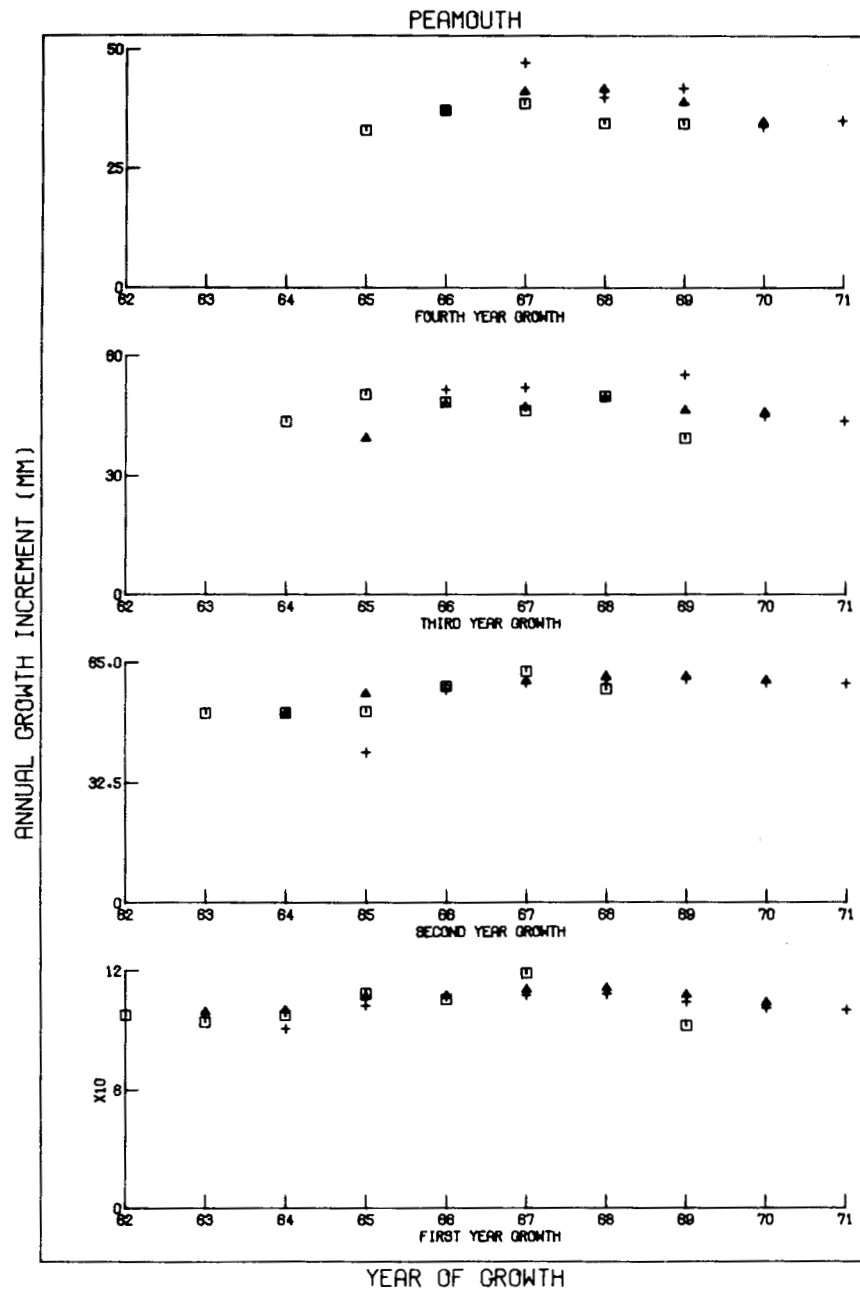


FIG. 8. Mean annual growth increments (mm) for each of the first four years of growth for peamouth caught in 1970 (\square), 1971 (\blacktriangle), and 1972 (+). The 1962–69 year-classes were sampled in 1970, the 1963–70 year-classes were sampled in 1971, and the 1964–71 year-classes were sampled in 1972. Data from Nishimoto (1973).

and Werner 1977) demonstrated substantial diet overlap among cohabiting fish species. However, these fish communities were highly differentiated according to

habitat utilized and timing of feeding. In Lawrence Lake, co-occurring largemouth bass and bluegill sunfish utilized different sized prey (Werner et al. 1977), which

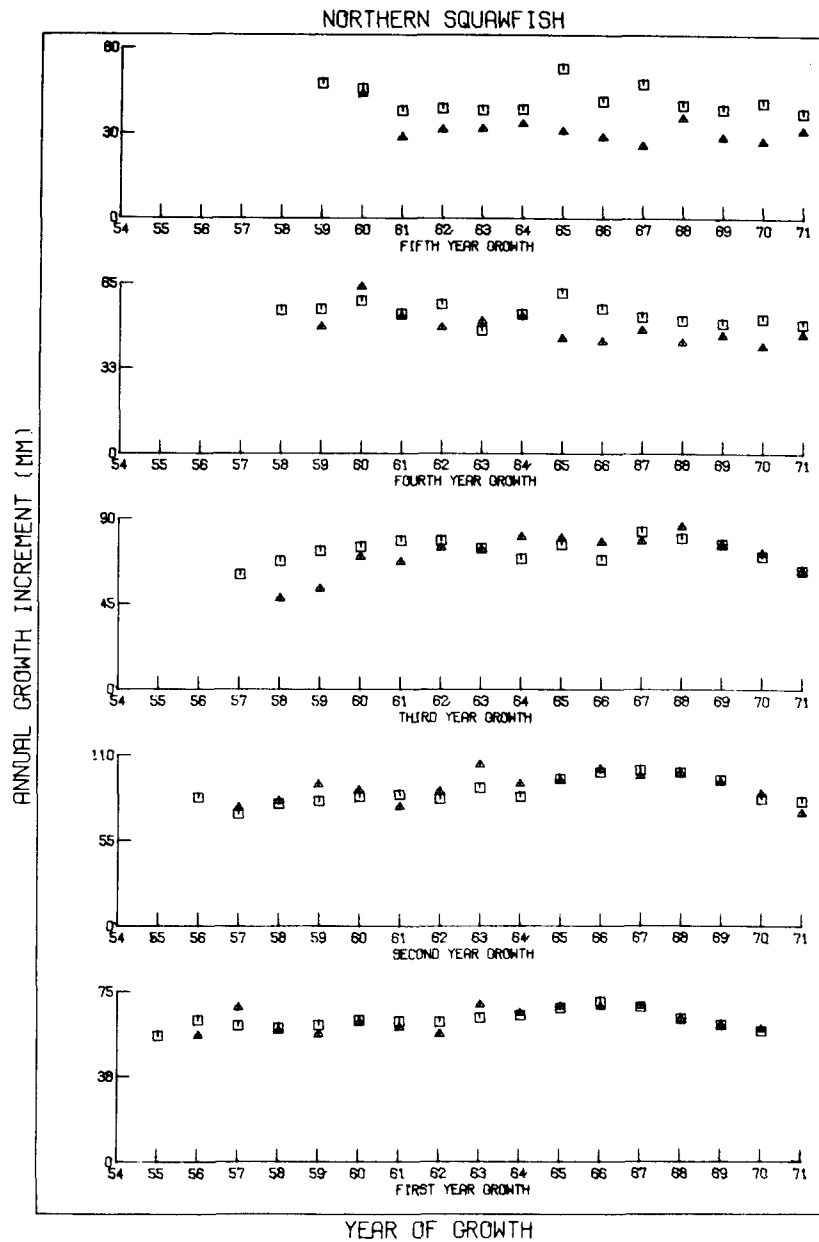


FIG. 9. Mean annual growth increments (length, mm) for each of the first 5 yr of growth (1954-72) for female (\square) and male (\blacktriangle) northern squawfish. Samples were collected 1971-73 for the 1955-70 year-classes. Data from Olney (1973).

reflected differences in functional morphology allowing bass to feed more efficiently on larger prey items (Werner 1977). These studies suggest that ecological segregation in fish communities is by habitat and reflects manifestation of competition.

Alternatively, it has been demonstrated that piscivor-

ous fish predators can greatly affect the structure of fish communities. Introduction of peacock bass (*Cicla ocellaris*) in Lake Gatun, Panama, resulted in virtual extinction of the planktivorous fish population in wide areas of the lake (Zaret and Paine 1973). Introduction of largemouth bass into Lake Atitlan, Guatemala, re-

sulted in similar destruction of the native fish populations (Dorris and Summerfelt 1968, cited in Paine and Zaret 1975).

Piscivorous fish predators have an important role in determining community structure of African lakes. In African lakes having the large piscivorous predators, tigerfish (*Hydrocyon vittatus*) and Nile perch (*Lates* sp.), small fish are restricted to areas with submerged vegetation or to very shallow areas where large predators cannot maneuver (Jackson 1961). Jackson speculated that the most common reproductive behaviors of fishes in African lakes (mouth brooding, the universal reproductive strategy among African cichlids, and anadromy, in which adults migrate to riverine spawning areas) are adaptations against piscivorous predation.

Lowe-McConnell (1975), in her monograph analyzing tropical freshwater fish communities, suggested that evolution in benthic-littoral and pelagic fish communities leads to two different ends that are largely explained by the different manifestations of piscivorous predation. Benthic-littoral fish communities are characterized by a large number of cohabiting fish species with complex trophic and habitat specializations. In the benthic-littoral environment, predation restricts fish to areas of cover, effectively preventing movement between habitats and acting as an isolation mechanism (Fryer 1959). Competition for resources within this habitat further increases diversity and trophic specialization.

Pelagic environments are characterized by a uniform prey resource of small individuals. There is no cover and the only effective refuge is behavioral — that is, remaining in areas of low light intensity, schooling, and feeding briefly (Eggers 1978). Piscivorous predation in the pelagic environment does not isolate populations, rather it forces a more or less uniform behavioral response. Pelagic fish communities are characterized by few species and uniform genotype (small body size necessary to exploit zooplankton) and feeding behavior.

Northern squawfish have significant impact on juvenile sockeye salmon, the most abundant planktivore of Lake Washington. To estimate the number of juvenile sockeye eaten by squawfish, monthly values of material ingested (see footnote 6 of Table 7) were transformed into number of fish by multiplying the ration (kilograms of carbon) by the proportion of sockeye in the squawfish, then dividing by the mean body carbon content of an individual sockeye, and summing over each month of the year. This estimate applies to June 1972–May 1973 or period of lacustrine residence for the 1971 year-class of sockeye salmon, which outmigrated in 1973.

During this period, northern squawfish consumed three million juvenile sockeye salmon. The expected seasonal abundance curve, assuming northern squawfish were the agents of all sockeye mortality, seems to be consistent with observed seasonal abundance (Traynor 1973). However, sockeye were a minor (10–30%) dietary item of northern squawfish and prickly sculpin

the major item (70%). If sockeye were the major dietary item, squawfish could potentially consume 22 million sockeye.

Bryant (1976) showed that in years of high sockeye abundance, sockeye experienced much higher rates of mortality during their lacustrine residence than in years of low sockeye abundance. The abundance of juvenile sockeye from the 1971 year-class was much lower than earlier year-classes that experienced much greater mortality.

These observations suggest that northern squawfish feed heavily on sockeye when sockeye are abundant and switch to prickly sculpin (the most abundant and productive species in the lake) when sockeye abundance is low. Thus, predation by northern squawfish may be a compensatory process except at very high sockeye abundance (previously not observed in the lake).

Juvenile sockeye salmon show complex feeding behavior that seems to minimize vulnerability to predation by the visual piscivore, northern squawfish, while achieving energy requirements (Eggers 1978). Longfin smelt and threespine stickleback, also planktivores, show similar feeding behavior. Northern squawfish, because of their high biomass (Table 4) and respiratory requirements, hence high ration requirement, exert significant mortality on the planktivorous fish community in Lake Washington. To avoid predators, juvenile sockeye limit the time engaged in foraging and generally occur in regions of low light intensity that are removed from regions of high zooplankton abundance. Finally, sockeye engage in schooling behavior which reduces foraging efficiency (Eggers 1976) to minimize further risk of predation. The consequences of this antipredator behavior is that planktivores exploit only a part of the total zooplankton-containing habitat in the lake.

The available information, although not as well developed as information on planktivores, implies that piscivorous predation has a substantial impact on benthic-littoral fishes in Lake Washington. Mature benthic-littoral fishes exploit prey items much larger than zooplankton, and consequently have larger body sizes than planktivores. Their large body size effectively reduces piscivorous predation. However, larval and juvenile benthic-littoral fishes are extremely vulnerable to predators. In addition to northern squawfish, yellow perch and prickly sculpin commonly feed on larval and juvenile benthic-littoral fishes (Fig. 4). Thus, this group has more potential predators than do Lake Washington planktivores.

There are three types of reproductive strategies found in the Lake Washington fish community. The eggs of sockeye salmon and longfin smelt are deposited in the Cedar River. Young-of-the-year sockeye and smelt are limnetic upon entering the lake during the spring. Prickly sculpin construct nests in littoral and profundal areas of the lake (Rickard 1978) and young-of-the-year are epibenthic. All other major species — stickleback, peamouth, squawfish, yellow perch, and suckers — are substrate spawners in littoral regions (Scott and Cross-

man 1973). Their young-of-the-year occur in a narrow band near shore in exposed littoral zones with few macrophytes. In regions with macrophyte growth, the distribution of these young-of-the-year fish is more widespread (Dykeman 1978). Cover, shallowness, and low light intensity of these habitats provide effective refugia.

Werner et al. (1977) and Hall and Werner (1977) also showed similar patterns for small fish—shiners (*Notemigonus* sp. and *Notropis* sp.), and fry and juveniles of species that are large as adults—in Lawrence Lake. DiCostanzo (1957) found year-class strength of sunfish in some Iowa lakes positively correlated with amount and distribution of macrophyte growth.

Are the abundances of benthic-littoral fish species in Lake Washington limited by resources exploited by larval and juvenile forms within these littoral and epibenthic refugia, or by the resources exploited by the less vulnerable maturing and older juvenile community? It is not clear how fry and juvenile species cohabiting in available refugia can give rise to resource partitioning among older fish not vulnerable to predation. For this to occur, the number of fish surviving the refugia must be sufficient for the resulting population, not vulnerable to predation, to deplete resources outside the refugia. In this case resource depletion would limit reproductive potential and consequently limit the input of fry to available refugia below levels that would deplete resources of the refugia. Conversely, resource limitation in the refugia would weaken the competitive interaction of adult cohabiting species.

The recruitment to the adult benthic-littoral and northern squawfish population from refugia inhabited by larvae and juveniles of these species is probably sufficient for these forms to dominate the Lake Washington fish community.

The Lake Washington planktivorous fish community depends on recruitment from the Cedar River spawning area, and on the littoral refugia in the case of stickleback. However, recruitment from these areas has not been sufficient to swamp the squawfish population. Compensatory mortality of juvenile sockeye due to northern squawfish predation has offset positive population increases in years of good survival of eggs in the Cedar River. The limnetic environment offers limited refuge from piscivore predation.

One would expect the production of planktivorous fish to be low in a system like Lake Washington where the piscivores are relatively insensitive to planktivore abundance. This is because of the age structure of the squawfish population and availability of the abundant prickly sculpin as alternative prey.

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