Size Selective Predation by Rainbow Trout on Two Lacustrine *Oncorhynchus nerka* Populations

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Fisheries Management Report No. 94
1989

Canadian Cataloguing in Publication Data

Parkinson, Eric A. (Eric Arthur), 1950-
Size selective predation by rainbow trout on two lacustrine Oncorhynchus nerka populations

(Fisheries management report, ISSN 0705-5390 ; no. 94)

Issued by Fisheries Branch.
Bibliography: p.
ISBN 0-7726-0969-1

1. Rainbow trout - Food. 2. Rainbow trout - British Columbia - Kootenay Lake. 3. Rainbow trout - British Columbia - Quesnel Lake. 4. Predation (Biology) 5. Sockeye salmon. I. Hume, Jeremy M. B., 1948- . II. Dolighan, Robert. III. British Columbia. Ministry of Environment. IV. British Columbia. Fisheries Branch. V. Title. VI. Series: Fisheries management report (British Columbia. Fisheries Branch) ; no. 94.

QL638.S2P374 1989 597'.55 C89-092165-2

ABSTRACT

Parkinson, E. A., J. M. B. Hume and R. Dolighan. 1989. Size selective predation by rainbow trout on two lacustrine Oncorhynchus nerka populations. B. C. Fisheries Management Report No. 94, 14p.

Size distributions of prey from the lake and in the diet of large (> 350 mm) rainbow trout feeding on O. nerka were compared in two lakes. In both lakes, O. nerka made up over 98% of the fish in both rainbow trout stomachs and midwater trawl catches. In Kootenay Lake, where there were no anadromous sockeye, kokanee (the non-anadromous morph) that were 100-200 mm fork length made up 42% of trawl catches, but in Quesnel lake, which supports both kokanee and a large run of anadromous sockeye, trawl catches consisted of 95% age-0+ O. nerka (< 80 mm fork length). Although the size of prey in Quesnel Lake (104 mm) was smaller than in Kootenay Lake (139 mm), most of this differnce appeared to be due to differences in the size of the trout predators which averaged 540 mm in Quesnel Lake and 713 mm in Kootenay Lake. Few fry (<80 mm) were observed in the stomach samples of rainbow trout caught in either lake. In both lakes, the largest prey taken by rainbow trout predators were less than about 1/3 of the predator length.

Acknowledgements

We thank H. Andrusak and L. Fleck for stomach sample collection on Kootenay Lake, and C. Mueller and H. Enzenhofer for trawl sample collection on Quesnel Lake.

INTRODUCTION

The size of prey consumed by many piscivorous fish increases with the size of the predator (Lawler 1965, Moodie 1972, Timmons and Shelton 1980, Knight et al. 1984). Since most fish swallow their prey whole, an upper size limit is assumed to be set by the gape of the predator and seems to be between 1/3-1/2 of the predator by length (Shelton et al. 1979). Larger predators tend not to utilize small prey (eg. MacClean and Magnuson 1977) perhaps because of decreasing energy gain per unit time (Gillen et al. 1981). A parallel situation in which predators select larger prey is well established for a variety of vertebrate planktivores (Zaret 1980).

In many rainbow populations, larger individuals become increasingly piscivorous after reaching a threshold size of about 25-30 cm (Crossman 1959, Jeppson and Platts 1959, Stoeck and MacCrimmon 1965, Northcote 1973, Marrin and Erman 1982, Andrusak and Parkinson 1984). Prey size of piscivores tends to increase with predator size in both rainbow (Oncorhynchus mykiss) (Crossman and Larkin 1959) and cutthroat trout (O. clarki) (Moodie 1972).

Piscivorous rainbow trout in some of the large steep-sided lakes in south central British Columbia feed almost exclusively on O. nerka (Ward and Larkin 1964, Andrusak and Parkinson 1984), but can encounter very different prey size spectra in different lakes because O. nerka occurs in two forms (Scott and Crossman 1973). In lakes where anadromous sockeye predominate, the O. nerka population consists mostly of age-0+ sockeye fry the majority of which leave the lake in the spring as age-1 smolts at a size of less than 100 mm (Goodlad et al. 1974). In lakes where non-anadromous kokanee predominate, a much higher proportion of the population consists of age-1+ and older individuals which remain in the lake until they mature at sizes of over 200 mm (Vernon 1957, Lorz and Northcote 1965). We refer to the anadromous form as sockeye and the non-anadromous form as kokanee. The two forms are indistinguishable as juveniles and we therefore refer to mixed populations using the species name, O. nerka.

Rainbow trout over 40 cm in length are capable of consuming most size classes of O. nerka. In this paper, we first compare the size spectrum of prey available to these large rainbow trout in a sockeye- and a kokanee-dominated lake in terms of relative abundance of small and large prey. We then compared the size spectrum of prey in the stomachs of large rainbow trout from the same two lakes. The objective was to determine whether rainbow of similar size shift their size prey size selection toward smaller prey and therefore take advantage of the relatively large numbers of small prey available in the pelagic zone of sockeye-dominated lakes.

Study Area

Kootenay and Quesnel lakes are both large, steep-sided oligotrophic lakes in south-central British Columbia. Some physical and chemical characteristics are given by Zyblut (1970) and Cloern (1976) for Kootenay Lake and by Stockner and Shortreed (1983) for Quesnel Lake. Kootenay Lake is not accessible to anadromous species and the O. nerka population therefore consists entirely of non-anadromous kokanee described by Vernon (1957).

Quesnel Lake supports both kokanee and sockeye salmon populations. The sockeye population has a four-year population cycle similar to that described by Ward and Larkin (1964) on nearby Shuswap Lake. Sockeye populations range from about 500-4,000 spawners in the low years to 270,000-1,300,000 spawners in the dominant years. Our data are from 1987 which was a subdominant brood year with 165,000 spawners. No estimates of kokanee spawner numbers are available.

METHODS

The size spectrum of available prey was estimated from midwater trawl catches. The trawl used in Kootenay Lake had a square opening of 20.25 m^2 and was 11 m long with mesh sizes ranging from 101 mm at the head to 9 mm at the cod end. Oblique tows were made through the entire layer of fish (20-50 m in depth) detected on a Furuno FM-22 echosounder. In Quesnel Lake the trawl had a rectangular opening of 21 m^2 (3 m wide x 7 m deep) and was 18.0 m long with mesh sizes ranging from 102 mm to 3 mm in the body. Horizontal tows were made within the layer of fish (about 15 m in depth) indicated on a Biosonics Model 101 echosounder. In both cases, towing speeds were between 0.9 and 1.1 m/sec. Samples were preserved in 10% formalin before measuring but were corrected to the original length using conversions given by Parker (1963).

Rainbow trout caught by sports anglers were sampled in both lakes by Fish and Wildlife employees and by lodge owners. The rainbow trout fishery occurs exclusively in the limnetic zone of both lakes. Rainbow trout fork lengths and weights were recorded and stomachs were frozen in water. From the stomach contents only fish that were identifiable as O. nerka were measured. In Kootenay Lake, the size of fish prey was measured volumetrically and converted to lengths using a regression generated from the trawl data. In Quesnel Lake, lengths of fish prey were measured directly. Other prey items were classified as either other fish or insects.

In Kootenay Lake stomach samples were collected between April and December 1980, and trawls were made in early October 1987. Because of the large differences in collection dates in Kootenay Lake, we compared the 1987 oblique trawl catches to depth stratified catches made in 1985 and 1986. In Quesnel Lake, stomach samples were collected in June and July 1987, and trawls were made on August 11 and 12, 1987.

Limnetic fish populations were estmated hydroacoustically using methods and equipment similar to those used by Burzcynski and Johnson (1986).

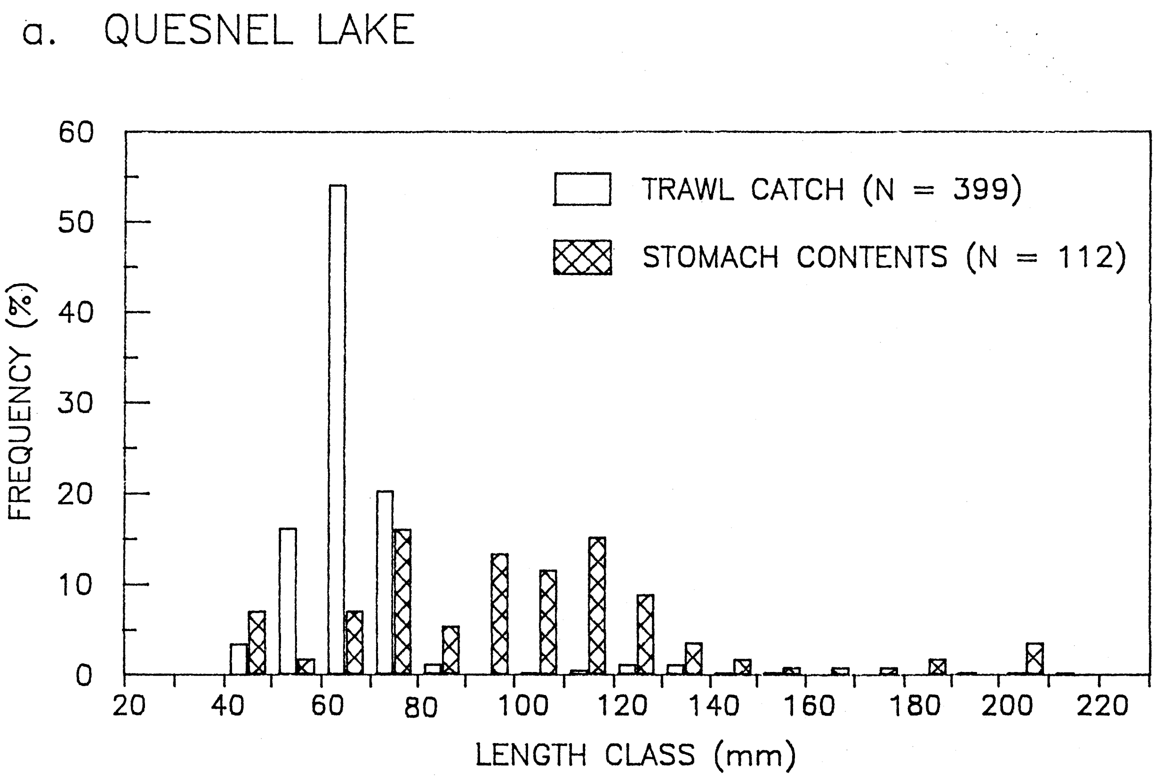
RESULTS

Hydroacoustic estimates indicated that densities of fish in the pelagic zone were much higher in Quesnel Lake than in Kootenay Lake. In Kootenay Lake, September population estimates were 265 and 396 fish/ha in 1985 and 1986, respectively, but no estimates were made in 1980. The August, 1987 estimate for Quesnel Lake was 2,240 fish/ha.

Trawl catches indicated that O. nerka was the dominant fish species in the pelagic zone and there was a large difference in the size spectrum of prey available in the two lakes. In Quesnel Lake, trawl catches consisted of 95% age-0+ O. nerka (<80 mm) and 5% older kokanee (80-210 mm) (Fig. 1a). The only other fish caught in Quesnel Lake was a 62 mm whitefish. In Kootenay Lake 99% of the 1987 catch from oblique hauls consisted of a mixture of various kokanee age classes ranging in size from 42 mm to 198 mm (Fig. 1b). The only other fish captured were a burbot, Lota lota (450 mm), a Dolly Varden, Salvelinus malma (750 mm), and a pygmy whitefish, Prosopium coulteri (66 mm). Depth stratfied trawl catches from 1985 and 1986 were similar in length frequency distribution and species composition but there tended to be a higher frequency of larger kokanee in deeper trawls (Parkinson 1988). Quesnel Lake trawls were concentrated in the main, upper layer of fish and may have sampled larger kokanee less effectively.

O. nerka formed an important part of the diet of rainbow trout caught in the offshore fishery in both lakes. In Quesnel Lake 104 rainbow trout stomachs contained fish (55% of stomachs with food). In 55 of these stomachs the fish were not identifiable due to digestion. Of the 113 identifiable fish 112 were O. nerka. In Kootenay Lake 93 (87%) rainbow trout stomachs contained fish, 13 of these contained unidentifiable fish. Of the 96 identifiable fish 95 were O. nerka. Some of these stomachs also contained terrestrial origin insects while another 85 (45%) from Quesnel Lake and 14 (13%) from Kootenay Lake contained only insects. There were 44 and 64 empty stomachs from Quesnel and Kootenay lakes, respectively.

Large (>40cm) rainbow trout selected prey that were larger than average in both lakes. In Kootenay Lake only 18.6% of kokanee in rainbow trout stomachs were less than 100 mm (Fig. 1), whereas 58% of the trawl catch was less than 100 mm. In Quesnel Lake, few



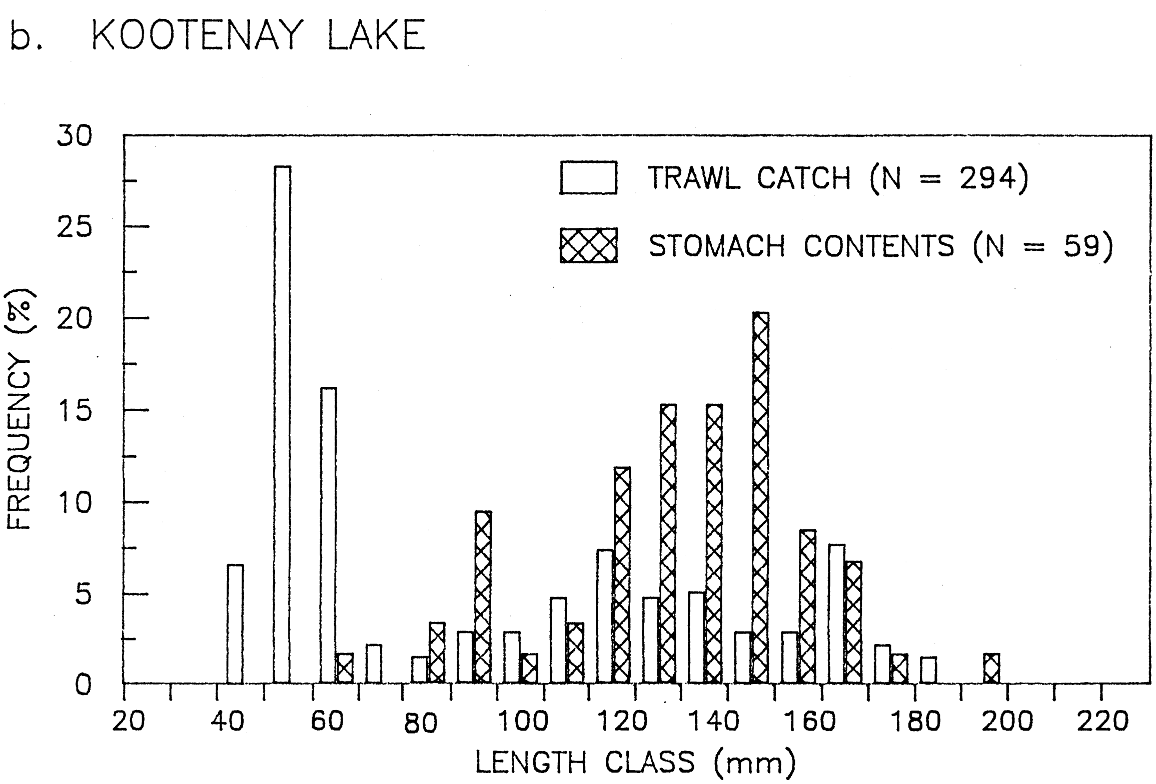


Figure 1. Length frequency of O. nerka in a)the August 1987 trawl catches and the June and July stomach samples from Quesnel Lake and b)the October 1987 trawl catches and April to December 1980 stomach samples from Kootenay Lake.

rainbow trout had fed on the abundant age-0+ population; only 42 of 112 (37.5%) of the O. nerka in trout stomachs were within the size range of age-0+ sockeye.

Both O. nerka in rainbow trout stomachs and rainbow trout in angler catches were larger in Kootenay Lake than in Quesnel Lake. The size of ingested prey covered approximately the same range in both lakes but the frequency distribution was skewed toward smaller sizes in Quesnel Lake. Average length of ingested prey was 139 mm and 104 mm in Kootenay and Quesnel lakes, respectively. Rainbow trout averaged 713 ± 28 mm (5.3 kg) in Kootenay Lake and 540 ± 30 mm (2.1 kg) in Quesnel Lake.

The difference between lakes in the size of ingested prey is apparently due to the difference in the size of the predators in each sample rather than a response to a difference in the size of potential prey. The size of ingested prey was related to the size of the predator in both Kootenay Lake ($r = 0.29$, $P < .01$) and Quesnel Lake ($r = 0.61$, $P < .01$). Regressions of prey size versus predator size differed for the two lakes ($P < 0.05$), but the distributions overlap broadly (Fig. 2). The regression produced by the combined samples does not differ significantly from the Quesnel regression (Fig. 2). Using this combined regression, the length of prey predicted from the predator size distribution in the samples is 134 and 103 mm in Kootenay and Quesnel lakes, respectively. This implies that most of the observed difference in size of ingested prey (139 vs 104 mm) is due to a corresponding difference in the size of the predators (713 vs 540 mm), rather than a response to the smaller average size of prey available in Quesnel Lake.

DISCUSSION

Our results are consistent with other studies which show that large piscivorous fish often do not feed on the smallest individuals of the prey species (Timmons and Shelton 1980, Knight et al. 1984). Age-0+ yellow perch, for example, are ignored during early summer but grow into the size range of prey consumed by adult walleye in Oneida Lake between July and August (MacLean and Magnuson 1977). For both rainbow trout (Crossman and Larkin 1959) and cutthroat trout (Moodie 1972) prey size of piscivores increased with predator size . However, our results also suggest that large changes in the size distribution of prey may have little effect on the size of prey consumed by a piscivore.

The lower than expected frequency of age-0+ O. nerka in the diet of large rainbow trout contrasts with data which suggest that smaller fish are more vulnerable to predation. In enclosure experiments, juvenile coho (110-120 mm) selectively preyed on small (48-50 mm) rather than large (51-54 mm) chum salmon fry (Hargreaves and LeBrasseur 1986). Similar results are reported by Bams (1967)

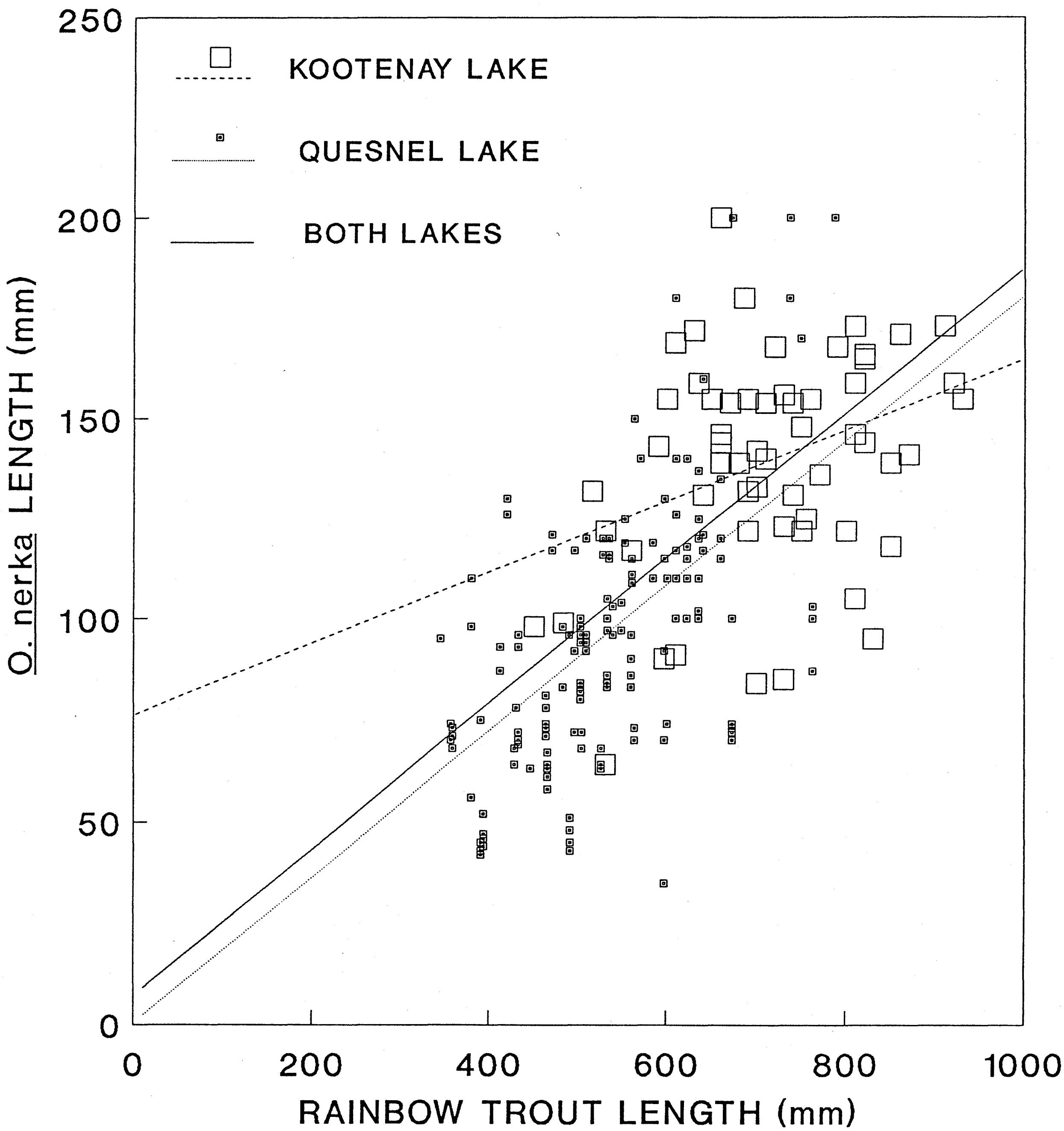


Figure 2. Relationships between the length of *O. nerka* prey and their rainbow trout predators in Kootenay Lake and Quesnel Lake.

for cutthroat trout feeding on newly emerged sockeye fry, Parker (1971) for coho salmon preying on chum and pink salmon fry, and Patten (1977) for torrent sculpins preying on coho fry. Taylor and McPhail (1985) suggest that lower vulnerability of larger fish is a result of an improved ability to accelerate during an escape response. Mortality rates in salmonids are also higher for smaller individuals in some (Healey 1982, West and Larkin 1987) but not all (Fresh and Schroder 1987) natural situations.

One obvious distinction between most of these situations and our study is the much larger size contrasts present in the latter. Rainbow trout from both Kootenay and Quesnel lakes were a minimum of 6 and up to 20 times the length of age-0+ O. nerka fry. The O. nerka prey also span a 5-fold variation in length. Studies of size selection by piscivorous fish have usually involved predators that are 2-3 times the length of the prey. We observed that the largest O. nerka eaten by rainbow trout are about 1/3 the rainbow trout body length (Fig. 2). A similar situation exists in other piscivores (Shelton et al. 1979, Timmons and Shelton 1980, Knight et al. 1984). Fish probably choose an optimum prey size (Wankowski and Thorpe 1979, Gillen et al. 1981) rather than the smallest or largest individuals in the prey population.

Large rainbow trout do not ignore all small food items. Terrestrial insects, particularly flying ants, were an important part of the diet of even the largest trout during June and July in both lakes. The extreme vulnerability and high contrast of these items floating on the surface may account for their importance in the diet.

Explanations of our results, other than simple size selection by piscivorous rainbow trout, include: inconsistency in the methods of data collection, spatial separation of O. nerka sockeye fry and their rainbow trout predators; predator avoidance behaviour by age-0+ O. nerka that is more effective than that of older kokanee; more rapid digestion of smaller fish; and selection by anglers against large rainbow trout that feed on small prey items. These 5 explanations are discussed below.

The most important methodological inconsistencies are differences in: the timing of prey and predator sampling, the processing stomach samples from the two lakes and the trawling technique in the two lakes. Each of these differences may have resulted in misleading data but we believe the only serious problem was the trawling technique in Quesnel Lake which probably resulted in underrepresentation of larger prey. All of these inconsistences are being corrected in an ongoing sampling program.

Data from previous years showed that fry have entered Quesnel Lake and moved into the area of the rainbow trout fishery by mid-June. In 1982, the previous dominant fry year, about 170 million sockeye fry entered Quesnel Lake starting in early May. By early

June the highest concentration of sockeye fry was in the area of the rainbow trout fishery (Morton and Williams 1989). For the rest of the summer the highest concentrations of fry were always in this area. In 1986, 140 million fry entered the lake approximately 2 weeks earlier than in 1982 (Mueller and Kent 1988). No early distribution data is available for 1987, but it is reasonable to assume that fry had concentrated in the fishery area by mid-June. The August acoustic survey found high fry concentrations in this area in 1987.

Diel vertical migration, a consistent behaviour pattern in many juvenile sockeye populations (Narver 1970, Levy 1987) is thought to be associated with predator avoidance (Eggers 1978, Clark and Levy 1988). There is some evidence the diel vertical migration behaviour is not as well developed and may be reversed in older kokanee (Levy 1987). Older kokanee may therefore be more vulnerable to predation by large rainbow than are age-0+ O. nerka. Bluegill sunfish also show differential predator avoidance by size. Small individuals hide in aquatic vegetation until they have reached a size where they have outgrown most of their gape-limited bass predators (Werner et al. 1983). In both of these cases, small individuals of a prey species may avoid contact with predators because their risk of capture upon contact with a predator is greater than that of a larger individual.

The proportion of age-0+ fry may also be low in the diet because digestion makes them unidentifiable before preservation. Rapid digestion of small, easily digested prey is a problem in many diet comparison studies (Hyslop 1980). Age-0+ fry are probably digested faster than larger fish (eg. Beyer et al. 1988) and therefore the proportion of fry among the unidentified fish remains is probably higher than among the identified fish sample that was used to estimate prey size. Unidentified fish remains are also more common in the lake (Quesnel) where smaller fry make up a larger portion of the prey size spectrum. The size of bones in digested, unidentified fish remains from Quesnel Lake stomachs suggested that all size classes were represented but that the unidentified fish remains contained a higher proportion of age-0+ fry than the identified sample. Unfortunately, the use of angler caught samples exacerbates the problem of differential digestion of large and small prey items because the time between collection and preservation of the sample is longer. Angler catches are the only practical and acceptable means of obtaining a large sample of predator stomachs from the pelagic zone of our study lakes because of low densities of rainbow trout involved.

Arguments for and against angler selection of rainbow trout that are not feeding on age-0+ O. nerka are mostly speculative. Trout do specialize on specific prey types (Bryan and Larkin 1972) and anglers in both lakes usually use silvery lures that are larger than age-0+ O. nerka fry. Many of the rainbow trout stomachs in both lakes, however, contained only insects, indicating that rainbow trout are caught even when they are not feeding on the item that the lure is meant to imitate.

Although rainbow trout and other salmonids do prey extensively on sockeye fry and smolts when they are concentrated in rivers and the inlet or outlet portions of a lake (McCart 1967, Hartman et al. 1967, Ginetz and Larkin 1976, Ruggerone and Rogers 1984), they appear to be less vulnerable after dispersal into the limnetic zone of lakes (McCart 1967, Gilhousen and Williams, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo British Columbia, pers. comm.). Our results suggest that sockeye in Quesnel Lake are not heavily preyed upon by large rainbow once they move into the limnetic zone.

MANAGEMENT IMPLICATIONS

If rainbow predators do prefer kokanee over sockeye prey, strategies for rainbow and sockeye management should be reconsidered. Kokanee and sockeye have very similar diets (eg. kokanee, Rieman and Bowler 1980; sockeye, Narver 1970) and probably compete with each other for food. Enhancement of large piscivorous rainbow may, therefore, produce only a minor increase in predation mortality for sockeye fry and may benefit juvenile sockeye by removing competitors. However, in lakes where sockeye juveniles are large (because of either fast growth rates or a high proportion of 2+ smolts) or in lakes where the rainbow predators are small, there will be a higher risk of increased predation on juvenile sockeye associated with rainbow enhancement. The food base for piscivorous rainbow which specialize on kokanee may also be smaller in sockeye-dominated lakes as a result of kokanee/sockeye competition. If kokanee populations are suppressed through competition from sockeye, expected yields, growth rates and maximum size of rainbow in sockeye-dominated lakes may be lower.

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