

The Behavior and Ecology of Pacific Salmon and Trout

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Contents

Preface	vii
Acknowledgments	x
1 Introduction	3
2 Homeward Migration of Adults on the Open Ocean	37
3 Migrations in Coastal and Estuarine Waters	53
4 Upriver Migration and Energetics	67
5 Homing and Patterns of Straying	85
6 Mating System and Reproductive Success	105
7 The Ecology of Dead Salmon	129
8 Incubation Rate and Mortality of Embryos	143
9 Alevin Movements, Emergence, and Fry Migrations	159
10 Sockeye Salmon and Trout in Lakes	167
11 Juvenile Salmonids in Streams	185
12 Downstream Migration: To Sea or Not to Sea?	209

Contents

13	Estuarine Residence and Migration	229
14	Marine Migration Patterns	241
15	Survival in the Marine Environment	253
16	Feeding and Growth at Sea	269
17	Age and Size at Maturity	283
18	The Evolution and Structure of Salmon Populations	299
19	The Abundance and Diversity of Pacific Salmon: Past, Present, and Future	317
	References Cited	329
	Index	363

Preface

Pacific salmon are a remarkable group of animals, and the connections to their ecosystems and to humans may be more complex and profound than any other group of animals, and certainly more than any other group of fishes. First, though perhaps not foremost, they are collectively among the most valuable commercial fishery resources of the United States, with annual landed values that averaged \$390 million from 1992 to 2001 according to U.S. Department of Commerce statistical reports. This is matched only by taxa such as crabs and shrimp that are taken from both oceans and include many diverse species. The finfish species that dominate the tonnage landed, walleye pollock and Atlantic menhaden in recent years, are lower in value than salmon despite their volume.

In addition to their commercial value, salmon are the target of recreational fisheries with significant value to local economies. Perhaps more important than the amount of money spent in pursuit of salmon is the psychological uplift (often mixed liberally with frustration) that comes with time spent outdoors fishing alone or in the company of family and friends. Salmon also hold a special place in the culture, nutrition, and economy of peoples native to the coast of the North Pacific Ocean. They were traditionally important for food and for barter, and they continue to be a very important component of the culture and commerce of many groups. The salmon have been adopted as the region's icon by non-native peoples as well. One need only visit the gift shops in San Francisco, Portland, Seattle, Vancouver, Anchorage, and many smaller communities to see that salmon are readily embraced by modern society. Certainly, large trees and snow-capped mountains are also icons of the region, but somehow we do not connect with them as strongly as we do with salmon. The image of the salmon, leaping a waterfall in its heroic

but tragic effort to get home, reproduce, and die, is among the most recognizable in the natural world, and it strikes a chord with us.

Salmon are not only important for cultural and consumptive purposes, but their conservation and management presently pervade the regulatory environment of their ecosystem. Past and present human activities, including but not limited to mining, agriculture, hydroelectric production, flood control, forestry, shoreline development, and urbanization, all affect salmon. Increasingly, these activities are regulated because of their effects on salmon. One cannot understand water management in the Columbia River system or forestry on the Oregon coast without understanding salmon. Salmon have also been at the heart of many conceptual and technological advances in fisheries science and management.

Besides the complex roles that salmon play for people, they play equally important and complex roles for other organisms. Most streams they inhabit are nutrient-poor, and the annual return of salmon to spawn and die provides a pulse of food that directly and indirectly enriches the plants and animals in nearby aquatic and terrestrial ecosystems. Finally, the salmon's influence on their ecosystem is not limited to natural processes but they have indirect effects through humans as well. Because salmon are so important, people will modify land-use practices to benefit them when they would have done nothing for amphibians or less charismatic fishes. The northern spotted owl was granted protection under the U.S. Endangered Species Act and was vilified in a way that salmon never will be. Put simply, salmon are special.

The natural history of salmon is important for people seeking to understand these fishes, the North Pacific ecosystems in Asia and North America, and their management by humans. I hope this book will provide insights into the basic biology of salmon to a range of people, including university students and faculty, biologists working in agencies, nongovernmental organizations, and companies devoted to salmon or to some aspect of the natural or human world that interacts with them. In addition to these people with a direct need to know about salmon, I hope the book will also interest members of the public who wish to learn about these fishes or become involved in their conservation. However, this book is not designed for advocacy. My goal is not to sway opinion but to inform and excite the reader. I will have succeeded if I have conveyed some of my enthusiasm for salmon and if I have stimulated readers to question my ideas, formulate and test their own hypotheses, and expand our knowledge of salmon.

The book is entitled *The Behavior and Ecology of Pacific Salmon and Trout*. As will be explained more fully later, the term "Pacific salmon" has traditionally been applied to five species of fishes in the genus *Oncorhynchus* that are native to the North American and Asian coasts of the Pacific Ocean, and to two (or one) species native only to Asia. Trout, notably rainbow (and their sea-run form, known as steelhead) and cutthroat but also lesser-known species such as Apache, golden, and Gila trout, have been included in the genus *Oncorhynchus* since 1989. The fishes of the genus *Oncorhynchus* are the subjects of the book. In addition to this genus, there are two other major genera in the family Salmonidae: *Salmo* (including Atlantic salmon and brown trout, both native only to Atlantic drainages) and *Salvelinus* (the char, including species in all continents around the north temperate and boreal regions). The introductory chapter provides thumbnail sketches of the common fishes in the family found in western North America and Asia.

The rest of the book is focused on the traditional salmon species and steelhead and cutthroat trout, though there are some references to other species. This scope reflects my own knowledge and the richness of the published literature (both of which thin out greatly after the five North American salmon and two trout species). However, I believe that the major points in behavior and ecology of the groups are amply demonstrated in these species and my focus on them is not misleading.

Just the seven principal species of Pacific salmon and trout (often, for convenience, referred to collectively as salmon) are described by a truly vast scientific literature. It is impossible to do justice to the tremendous volume and variety of excellent work that has been done. If I tend to cite my own research it is only because it is familiar to me, not because it is superior to the work of others. It is equally impossible to present all the unusual life-history patterns, habitats, and other ecological circumstances of salmon. I have tried to give both the general patterns and some exceptions that seem instructive, but there will always be some population or site that does not fit the patterns I described. In the interests of a readable book, some compromises were needed.

I have used data from primary, secondary, and unpublished sources, and have made graphs and tables to illustrate important points and highlight selected studies. However, readers are strongly advised to seek out the primary sources when doing their own analyses and should then give credit to those authors rather than to me. In a few cases, such as the compilation of data on fecundity and survival of salmon populations, it is impractical for me to cite every source of information and note every adjustment needed to make my tables comprehensible. I trust that readers will accept my efforts as honest. Finally, I have largely avoided statistical analyses in the text. Unless otherwise stated, patterns that I present as significant meet the general professional standard; there is a less than 5 percent chance that the apparent pattern arose by chance. In a number of the graphs depicting the relationship between two variables, such as body size and number of eggs, I show a value designated r^2 . This value indicates the proportion of the variation in the dependent variable (in this case, number of eggs) that is explained in a statistical sense by the independent variable (body size). Thus $r^2 = 0.45$ means that 45 percent of the variation in fecundity can be explained by female size.

10

Sockeye Salmon and Trout in Lakes

Most juvenile sockeye salmon rear in lakes for the first year or two of their lives before migrating to sea (though there are also river-type and ocean-type sockeye). Lakes are also typical habitat for many species of trout and char, and coho salmon may inhabit lakes in winter (e.g., Quinn and Peterson 1996) or as a primary rearing area (e.g., Ruggerone and Rogers 1992). In addition, some populations of pink, chum, and chinook migrate through lakes on their way to the ocean. It is not possible to do justice to the myriad patterns of all these species, so this chapter focuses on sockeye and, to a lesser extent, trout.

Research on sockeye salmon in lakes has emphasized three related processes: spatial distribution and movements (horizontal and vertical) within the lake, growth, and predator avoidance. Sockeye could grow faster in the ocean than in a lake, but they emerge from the gravel so small that the mortality they would experience at sea apparently counters the higher growth potential. Sockeye are the smallest, on average, of the North American salmon as eggs (Beacham and Murray 1993), and fry average 28.4 mm (based on the average of thirty-four populations, ranging from 23.5 to 31.4 mm: Ruggerone 1989; photo 10-1). So, sockeye stay in the lake for a year or two, grow slowly, try to avoid being eaten, and then take their chances at sea when they are bigger.

Distribution and horizontal movements

Sockeye emerge, often at high densities, and migrate to lakes that are usually very oligotrophic (unproductive). Sockeye fry generally feed on aquatic insects and crustacean zooplankton in the nearshore (littoral) zones of lakes and on zooplankton species in the offshore (limnetic) zone. How might sockeye fry orient their movements upon entering their lake? Do they move at random, move in response to proximate stimuli such as

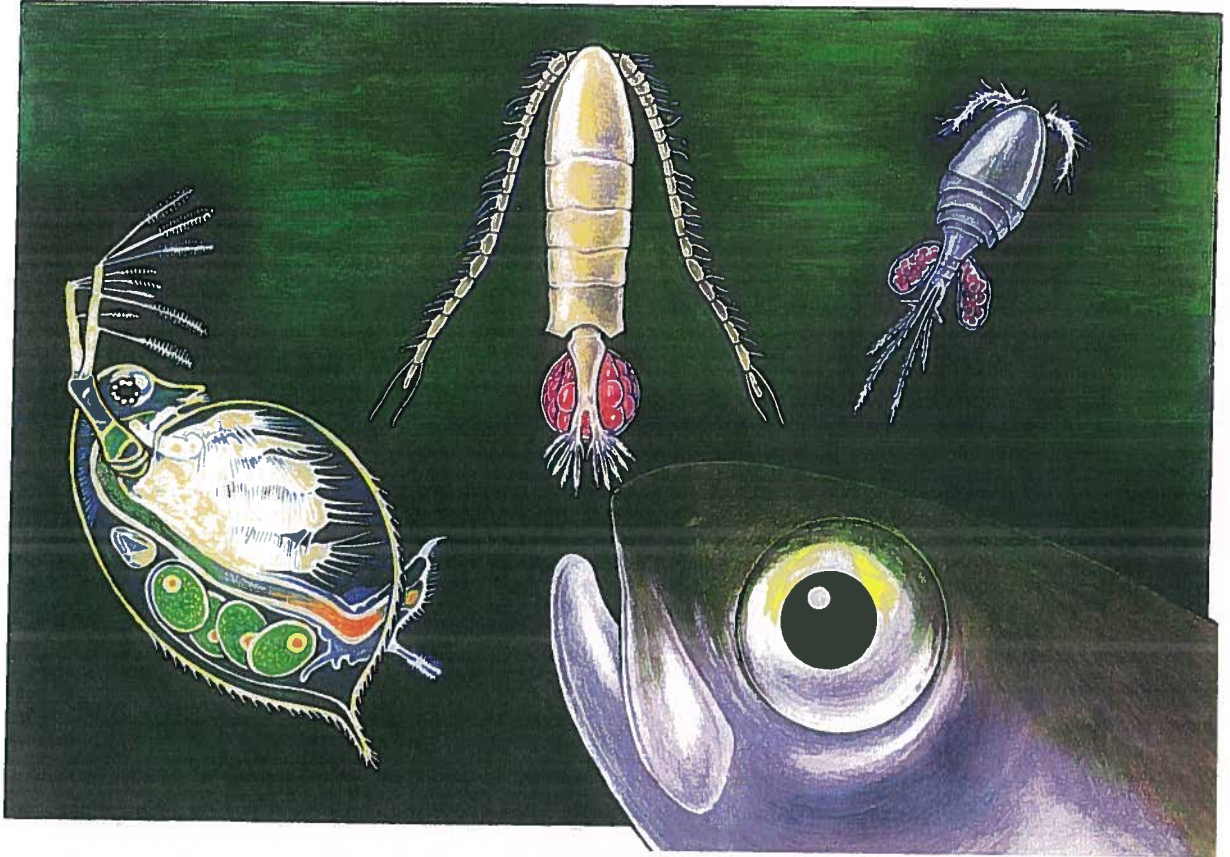


PLATE 13. Close-up of the head of a juvenile sockeye salmon and three of its common crustacean zooplankton prey: *Daphnia* (on the left; note the prominent eye and developing embryos), *Diaptomus* (in the center; note the cylindrical body, long antennae and single egg cluster), and *Cyclops* (on the right; note the more tear-drop shaped body, shorter antennae, and two clusters of eggs). Copyright: Charles D. Wood, Ph.D.

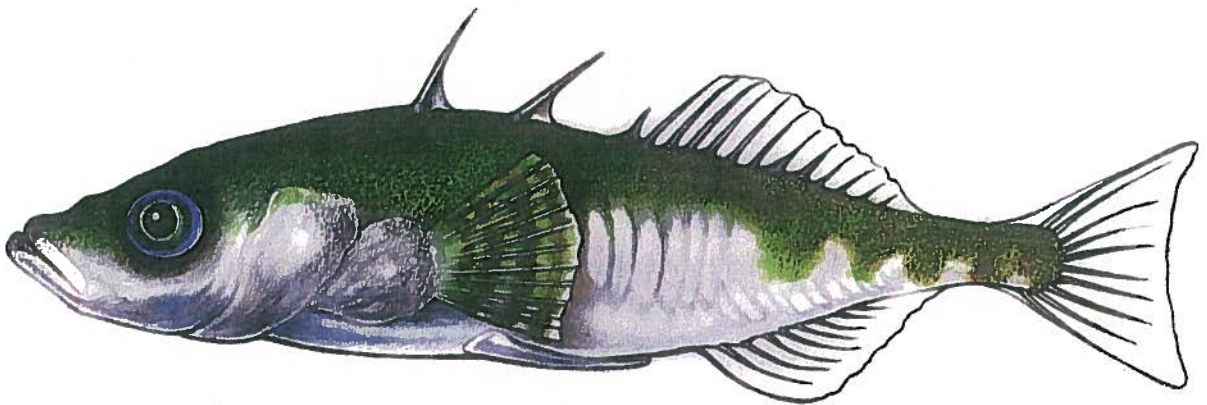
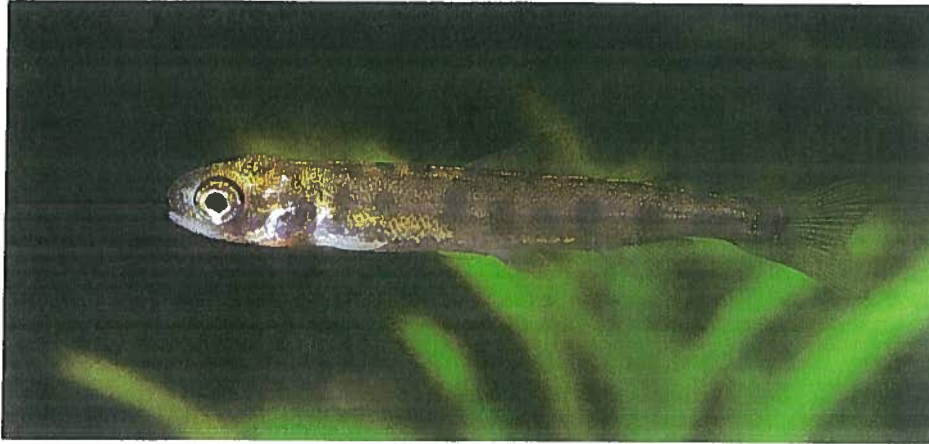


PLATE 14. Illustration of a threespine stickleback, *Gasterosteus aculeatus*, a common competitor with juvenile sockeye salmon in lakes. The development of lateral plates and spines varies among populations, and the colors change in the breeding season. Copyright: Charles D. Wood, Ph.D.



10-1 Newly emerged sockeye salmon fry. Photograph by Richard Bell, University of Washington.

food and competition, or move in a directed manner that has evolved to facilitate growth and predator avoidance? Extensive sampling in Lake Aleknagik, Alaska, revealed that newly emerged sockeye salmon (about 26–28 mm long) occupy the littoral zone from early June through mid-July, growing to about 50 mm long as the waters of the lake warm (Rogers 1973). They then move offshore and remain in the open water of the lake until they leave as smolts the following spring. It is not clear whether the fry move offshore after food becomes scarce in the littoral zone or if they move in anticipation of better feeding offshore, but they tend to move offshore earlier in years when the ice leaves early and the lake is warm.

Some populations show highly directed migrations. For example, sockeye fry enter Babine Lake (a very long, narrow lake in the Skeena River system, British Columbia) from a number of tributaries, including the Fulton River, near the lake's middle. Fulton River fry enter in late May and early June and have largely left the littoral zone by mid-July. McDonald (1969) found a very strong tendency for fry to move southward, along the shore and in open water, rather than to the north. Simulations by Simms and Larkin (1977) also indicated a highly oriented, southward migration for the first few months. The movements were more random from late in the first summer until the following spring, when a highly directed northward migration took the smolts to the outlet and down to the ocean.

Foraging opportunities (and perhaps also predator avoidance) may provide the ecological motivation for migration, but how do the fish know which way to go? In the 1960s there was a blossoming of research on the orientation abilities of animals, including homing pigeons, a variety of migratory birds, fishes, honeybees, reptiles, intertidal invertebrates, and others. In many cases, migratory animals released in the middle of radially symmetrical areas (round tanks or platforms, cages, or multi-armed apparatus) will move in the direction that is appropriate for their migration in open space. Cognizant of this work and that of Groot (1965) on sockeye salmon smolts leaving Babine Lake, Brannon (1972) released sockeye salmon fry from the Chilko River population in the middle of tanks with six arms and recorded the directions of movement. The fry

TABLE 10-1. Numbers of Chilko River sockeye salmon fry trapped in the four cardinal compass directions when the sky was clear and visible or obscured by clouds or covers, and in the normal magnetic field of the earth or in a field in which south was shifted to the east (Quinn 1980).

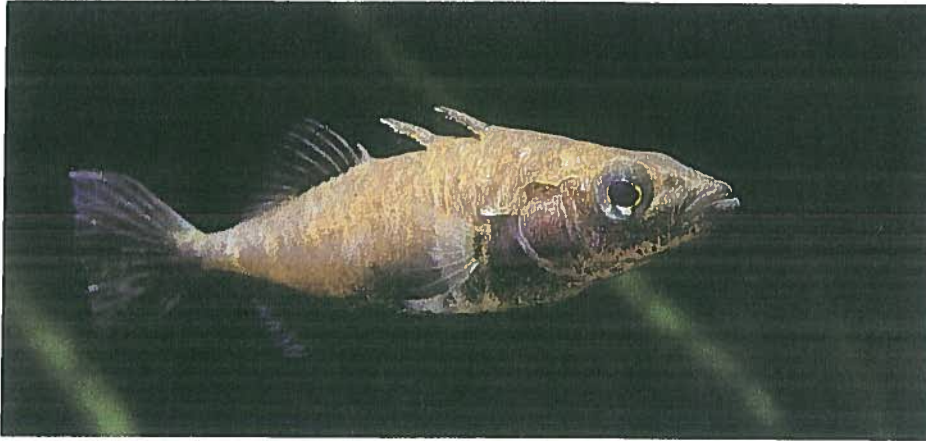
<i>Sky</i>	<i>Field</i>	<i>North</i>	<i>South</i>	<i>East</i>	<i>West</i>	<i>Mean direction</i>
Visible + obscured	normal	488	916	662	617	155°
Visible	S in the E	83	229	162	154	177°
Obscured	S in the E	166	147	231	151	77°

tended to move southward, as would be appropriate for migration because they enter at the north end of this long, narrow lake.

I built smaller, four-armed versions of Brannon's arenas, captured fry migrating to lakes, released them in the center of the tanks, and then counted the numbers trapped in the north, south, east, and west arms after 45-minute trials (Quinn 1980). Some tests were conducted with a view of the sky (clear or cloudy, as the weather determined), others under covers that allowed light but obscured the image of the sun (during the day), or were fully opaque (at night). In addition, a direct current of electricity running through coils of wire around the tanks rotated the horizontal component of the earth's magnetic field 90° counterclockwise (moving north to the west, south to the east, etc.).

The fry were denied the water current and odors that so strongly control migration to the lake and were in a highly artificial environment, so the absence of directional movement would not have been surprising. However, Lake Washington fry (in Washington State) tended to move northward when tested at night, and this is the compass direction that they migrate from the spawning grounds to the lake and in the lake itself (Quinn 1980). Chilko River fry, tested in the day as appropriate for their migration, oriented to the south, as they would in the lake. They showed this response on both clear and cloudy days and when the tanks were covered. An alteration in the magnetic field did not affect their orientation when they could see the sky but when tested under cloudy skies or covers, their orientation shifted from south-southeast to east-northeast, as predicted (table 10-1). These results indicated that the primary orientation mechanism was visual, probably the position of the sun or polarized light patterns, but that in the absence of such clues the earth's magnetic field gave the salmon directional information.

These orientation abilities are impressive but not unique. Many kinds of aquatic and terrestrial animals migrate in fixed compass directions by linking their circadian rhythm (internal clock) to the apparent movement of the sun across the sky (at 15° of arc per hour). The animals shift their direction of movement, relative to the sun, to compensate for the changing position of the sun in order to move in a fixed direction. Many kinds of animals, including salmonids, can also detect and orient to the plane of polarized light (Parkyn et al. 2003), and this can indicate the position of the sun when it is obscured by clouds or is low on the horizon. The ability to detect earth-strength magnetic field has been documented in many animals, including nudibranchs, bees, salamanders, sea



10-2 Threespine stickleback, a common competitor for food with sockeye salmon in lakes. Photograph by Richard Bell, University of Washington.

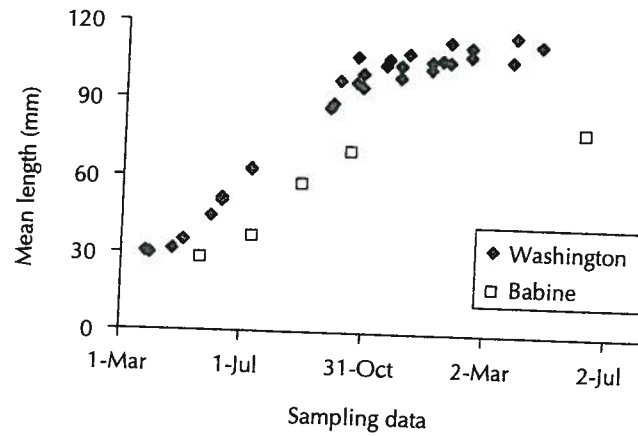
turtles, birds, and tuna, as well as salmon. The actual mechanism by which organisms detect the field has been a subject of much research and controversy over several decades. Single-domain sized crystals of magnetite are apparently an essential component of this sense (e.g., research on rainbow trout by Walker et al. 1997; Diebel et al. 2000).

Feeding and growth

Once the sockeye fry enter the lake, regardless of the mechanisms orienting their movements, they are occupied with two goals: to grow and to avoid being eaten. These two goals are not entirely compatible, as we will see shortly. The lakes that they rear in are generally oligotrophic, meaning that primary production rates are low, relative to most lakes. These lakes often have rather simple communities (i.e., few species) of fishes. Sockeye salmon are often the most abundant fish species feeding on crustacean zooplankton in the open water of the lake, though there may be sticklebacks (threespine: *Gasterosteus aculeatus*, photo 10-2; ninespine: *Pungitius pungitius*), smelt (e.g., pond smelt, *Hypomesus olidus*, or longfin smelt, *Spirinchus thaleichthys*), and whitefish (e.g., least cisco, *Coregonus sardinella*) competing for the zooplankton as well. Some lakes have freshwater shrimp (e.g., *Neomysis mercedis* or *Mysis relicta*) that may be prey for the sockeye salmon but can also compete with them for zooplankton. In addition to these species in the open waters of the lake, there are typically sculpins (e.g., *Cottus asper*) on the bottom and various invertebrates including insects near the edges. Larger salmonids are the main predatory fishes, foraging in nearshore and open-water areas.

Growth is fastest in late spring and summer and very slow in winter (fig. 10-1). Growth results from the interactions of food and temperature, because water temperature controls fish metabolism. Brett et al. (1969) conducted controlled feeding trials of sockeye salmon at different temperatures and demonstrated clearly that the maximum scope for growth is at about 15°C. That is, if fed a high or excess ration, this is the temperature at which they grow most rapidly. At lower temperatures, food is digested too slowly for maximum growth, and at higher temperatures the metabolic

FIGURE 10-1. Growth of sockeye salmon in Lake Washington, Washington (from Woodey 1972), and Babine Lake, British Columbia (from McDonald 1969).



rate is so high that much of the food is required to maintain the fish and little remains for growth (fig. 10-2). Food conversion was relatively efficient from 5–17°. Such curves are typical of fishes, but the optimal temperature varies greatly among species. However, if the fish are fed a reduced ration (as might occur in oligotrophic lakes), the optimal temperature for growth shifts downward because at 15° the metabolic demand is higher than at 10°, for example, and if the fish is not satiated then some of the

FIGURE 10-2. Growth of juvenile sockeye salmon as a function of food ration (percentage of body weight per day) and temperature (from Brett et al. 1969). Note that growth peaks at intermediate temperatures, and as ration is reduced, the optimal temperature for growth is lower.

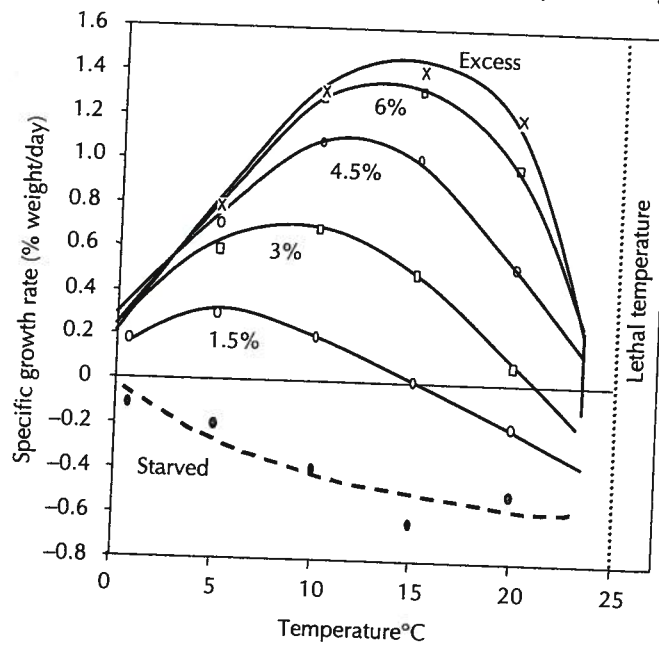
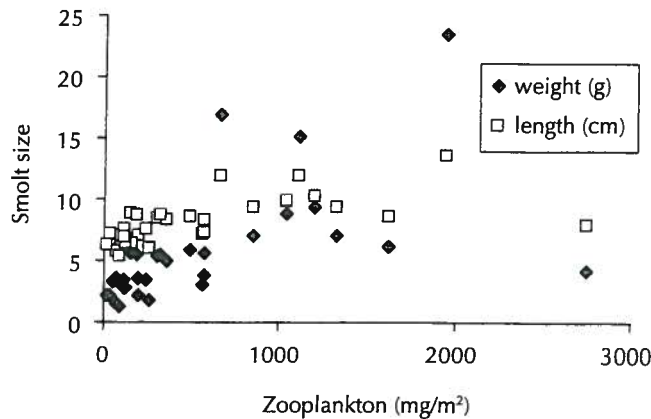


FIGURE 10-3. Average length and weight of age-1 sockeye salmon smolts from thirty-six lakes in Alaska differing in zooplankton density (Edmundson and Mazumder 2001).



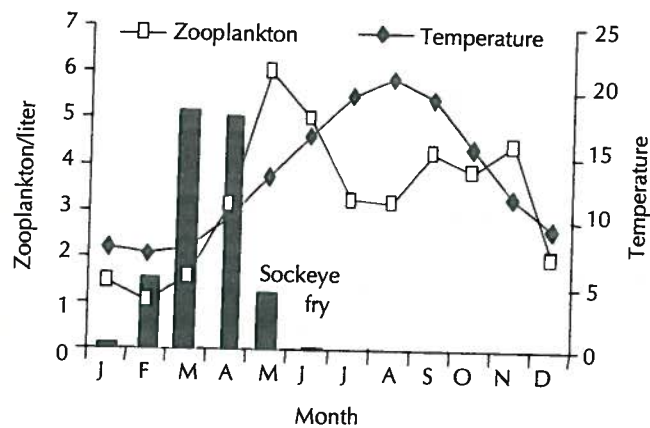
higher metabolism comes at a cost to growth. This can be understood by the extreme case; if fish do not feed at all, they lose weight most slowly in the coldest water because their metabolism is so slow.

Sockeye salmon occupy lakes with a wide range of thermal regimes and other physical attributes, including coastal lakes in Washington that stratify in summer with surface temperatures near 20° and that remain mixed without freezing in winter, to lakes in the interior and in northern latitudes that are covered by ice for at least half the year and have summer surface temperatures barely above 10°. These lakes range in elevation from essentially sea level to 2000 m, in area from 1 to 2600 km², and include coastal lakes from Washington to Alaska and lakes in the interior of the Columbia, Fraser, and Skeena river systems. The mean length of age-1 smolts varies among lakes from about 50 to 140 mm (a more than fifteenfold range in weight), but the mode is between 60 and 90 mm, based on data from Burgner (1991), Gustafson et al. (1997), Edmundson and Mazumder (2001), and K. D. Hyatt (personal communication).

What controls the variation in growth among lakes? Edmundson and Mazumder (2001) found that water temperature alone explained 24% of the variation in smolt length among thirty-six Alaskan lakes (warmer water being linked to bigger fish), consistent with the physiological role of temperature. However, most (52%) of the variation in smolt size was explained by the density of zooplankton, especially at densities up to 1000 mg/m² (fig. 10-3). Beyond that point, lakes with more zooplankton did not produce larger smolts. The density of juvenile sockeye salmon explained little of the variation in smolt size. Hyatt and Stockner (1987) also reported that the size of sockeye smolts in coastal British Columbia lakes was related to the concentration of zooplankton per fish (including sockeye and their main competitor, threespine sticklebacks).

The zooplankton that the sockeye salmon eat are crustaceans, primarily calanoid and cyclopoid copepods and cladocerans. They vary considerably in size, visibility, and mobility (including escape responses), and these all affect their ease of capture and desirability for sockeye. Zooplankton are not taken by filter feeding but rather are located, pursued, and consumed one at a time, and the stomach of a juvenile sockeye might

FIGURE 10-4. Monthly mean surface water temperature, density of the primary zooplankton species eaten by sockeye salmon (*Daphnia* and *Diaptomus*; data from Daniel Schindler, University of Washington) and the relative abundance of sockeye salmon fry entering Lake Washington (from Seiler 1995 and Seiler and Kishimoto 1997).



contain dozens, hundreds, or even more than a thousand such individual prey items, eaten within a day. Planktivores, including sockeye, tend to eat large prey more often than would occur by chance (Eggers 1982; O'Neill and Hyatt 1987).

All other things being equal, larger prey will be easier to see (think about trying to spot individual zooplankters 1 mm long or smaller, at twilight, 10 m below the surface of a murky or tea-colored lake). However, encounter rate is not the only factor affecting diet. Larger prey provide the predator with a bigger meal than smaller prey, assuming it does not take much longer to catch, subdue, and consume the larger ones. Thus under the principles of optimal foraging theory, a predator should eat the larger of two prey items available to it. The optimal size of prey also increases as the predator gets larger because the gape of its mouth allows it to handle larger prey. The morphology, presence of eggs, and other features of zooplankton make some more easily caught than others. However, prey do not passively accept their fate but are more or less actively trying to evade the fish. Eggers (1982) concluded that the diets of Lake Washington sockeye indicated an active preference (i.e., more than just differential encounter rate) for large, nonevasive prey and a selective avoidance of small prey. However, he pointed out that zooplankton communities are dynamic, thus sockeye diets shift over the seasons with the relative abundance of more or less desirable prey.

The biology of the zooplankton species varies greatly but in general they are herbivores, grazing on phytoplankton. Phytoplankton abundance depends on light, hence there is a marked seasonal pattern in primary production in lakes. The zooplankton often pass the winter as eggs or in some other resting stage and are thus quite scarce as prey to salmon. In spring, as days lengthen and the lake thaws, wind mixes the water column and brings inorganic nutrients to the surface where photosynthesis takes place once the lake warms up and begins to develop thermal stratification. At this time, a phytoplankton bloom usually occurs, followed by an increase in zooplankton density. The emergence of sockeye salmon and their entry into lakes can precede the peak density of zooplankton (fig. 10-4). Zooplankton are preyed upon by the sockeye, and the

TABLE 10-2. Responses of coastal British Columbia lakes to fertilization in primary production (mg carbon per square meter of lake area per day), zooplankton biomass (mg ash-free dry weight/m³), and sockeye salmon smolt weight (g) based on average August and September values in years before and after treatment; see Stockner and MacIsaac (1996) for details.

<i>Variable</i>	<i>Before treatment</i>	<i>After treatment</i>	<i>% increase</i>
Primary production	68	167	146
Zooplankton biomass	5	18	260
Sockeye smolt weight	2.12	3.5	68

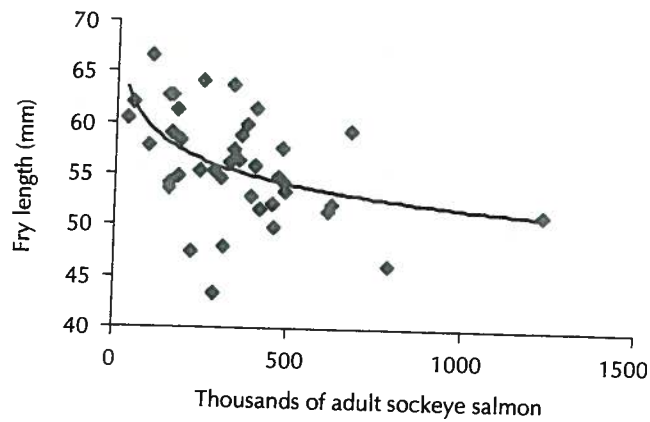
abundance, size distribution, and species composition of zooplankton can be strongly affected by the selective feeding of sockeye and sticklebacks (O'Neill and Hyatt 1987).

Growth depends on the quality as well as the quantity of food, and there are substantial differences among zooplankton in the highly unsaturated fatty acids that are important for growth. For example, Ballantyne et al. (2003) concluded that sockeye growth in Lake Washington was more constrained by food quality (as measured by the fatty acid DHA) than quantity or temperature. Nutritional quality varies among zooplankton species, and it might also vary among lakes, depending on the phytoplankton they eat.

The abundance of phytoplankton, combined with temperature, thus fuels the growth of sockeye. Phytoplankton production depends largely on inorganic nutrients, chiefly nitrogen and phosphorus, and it has long been recognized that the lakes inhabited by sockeye salmon are often nutrient-poor (Stockner 1987). Therefore, the growth of sockeye, especially in some of the coastal lakes of British Columbia and southeast Alaska, is exceptionally poor (barely reaching 2–3 g in a year). Experiments to enhance primary production, hence zooplankton, hence sockeye salmon growth (and hence, it was hoped, survival at sea and adult returns) were initiated more than 50 years ago (P. R. Nelson 1959). A much larger-scale program was undertaken in British Columbia, starting with Great Central Lake in 1969 and growing to include many control and treated lakes (Stockner 1987; Hyatt and Stockner 1987; Stockner and MacIsaac 1996). Considerable research went into determining the appropriate ratio of ammonium polyphosphate and urea ammonium nitrate to encourage the growth of phytoplankton edible by zooplankton (rather than the often inedible cyanobacteria) for each lake, the appropriate concentration, timing of release, and so on (Stockner and MacIsaac 1996). In most cases, application of fertilizers from airplanes to large lakes resulted in striking changes that propagated through the trophic links to juvenile sockeye salmon (table 10-2).

Thus the variation in sockeye growth among lakes is primarily related to the availability of food, which is a consequence of the intrinsic productivity of the lake (i.e., flushing rate and inorganic nutrients from local geology) and the lake's temperature. However, growth also varies considerably within lakes among years, as temperature and food availability vary. In northern lakes, the earlier the ice leaves the lake and the warmer the spring conditions, the larger the fry at the end of the summer (e.g., Iliamna Lake, Alaska; Quinn, unpublished data). This probably reflects both the energetics of the salmon and the ecology of the lake itself. In addition, the density of fry can reduce zooplankton

FIGURE 10-5. Relationship between number of adult sockeye salmon spawning in tributaries of Lake Aleknagik, Alaska, and the mean length of their fry on September 1 of the next year (Schindler et al., forthcoming).



density in some lakes, and growth is often reduced at high fish densities (fig. 10-5). Results reported by Mazumder and Edmundson (2002) based on extensive experimental fertilization and stocking in Packers Lake, Alaska, confirm the connections between food, density, and growth. Before fertilization, sockeye were scarce and grew slowly, and *Daphnia* were also scarce and small. Fertilization increased the density and size of *Daphnia*, and the growth of sockeye, but high densities of sockeye resulting from stocking reversed these effects. These relationships are true for kokanee as well as sockeye, as shown by the positive effects of lake productivity and negative effects of density on growth in Idaho lakes and reservoirs (Rieman and Myers 1992).

For anadromous sockeye, the negative effect of fry density on growth may be offset, to some extent, by the possible positive, fertilizing effect of the carcasses of the parents that spawned them (Donaldson 1967; Schmidt et al. 1998; Finney et al. 2000). In general, however, large escapements tend to give rise to numerous but slow-growing fry. Clear evidence of the effects of density was provided by Koenings and Burkett (1987), reporting on the experimental stocking of Leisure Lake, Alaska. As they increased the density of fry, the growth rate (to smolt stage) decreased dramatically. The proportion leaving the lake after a single year decreased and more fish remained for 2 full years (table 10-3), and the combination of poorer growth and mortality reduced the overall biomass almost threefold after a fourfold increase in number of fry stocked. In general this effect seems to be restricted to a single year (that is, the growth of fry in one year is affected by their own density). However, in cases of exceptionally large escapements, as occurred in 1989 when concern about salmon contaminated by oil from the *Exxon Valdez* tanker spill greatly reduced commercial fisheries, the competition seems to affect growth in the following year as well (Ruggerone and Rogers 2003).

Sockeye salmon not only compete with each other but sometimes also with threespine and ninespine sticklebacks (Rogers 1973), as these fishes also feed on zooplankton (O'Neill and Hyatt 1987). Sticklebacks breed in spring in the lake's littoral zone or in slow-moving streams, and the males guard nests containing fertilized eggs. The larval sticklebacks are too small to effectively compete with sockeye fry but later in the summer they may be

TABLE 10-3. Relationship between the number of sockeye salmon fry stocked in Leisure Lake (otherwise devoid of sockeye) and the average size (g), age, and biomass (kg) of smolts (Koenings and Burkett 1987).

<i>Fry stocked</i>	<i>Age-1 smolt weight</i>	<i>Age-2 smolt weight</i>	<i>% age-1 smolts</i>	<i>Smolt biomass</i>
0.5 million	8	13.2	97	2009
1 million	4	7	77	1894
1.5 million	2.2	3.6	87	888
2 million	1.8	3.4	58	771

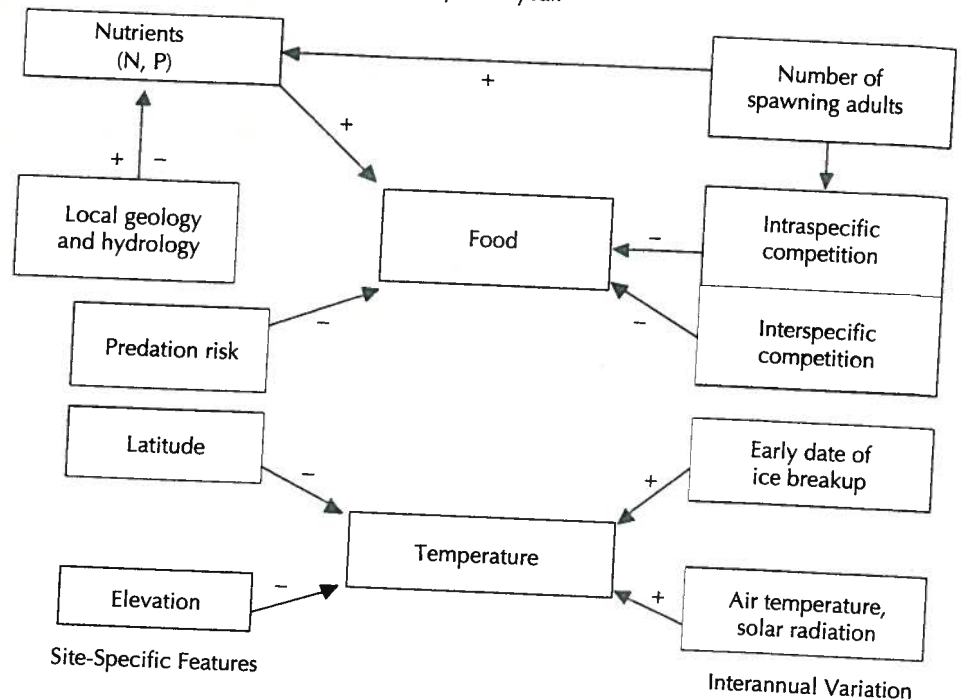
large enough to compete, and age-1 sticklebacks certainly overlap in diet with sockeye. In some lakes the sticklebacks primarily inhabit the littoral zone and so do not compete extensively with the sockeye offshore. However, in other lakes the sticklebacks are common offshore and more competition may occur. Because they are spawned in spring, stickleback abundance may be related to different factors than juvenile sockeye, such as perhaps the date of ice breakup or lake level. Overall, growth of sockeye (and other fishes) in lakes is most directly controlled by temperature and food, and these reflect a series of site-specific features including the lake's location, morphology, and nutrient inputs, climatic factors, and levels of competition (fig. 10-6).

Diel vertical migration

The zooplankton consumed by sockeye concentrate near the surface of lakes, feeding on phytoplankton. The sockeye might be expected to spend all their time near the surface, where there is enough light to see and catch the zooplankton. However, in most lakes the sockeye spend the day in deep water, ascending toward the surface near dusk and back down around dawn (e.g., Narver 1970; reviewed by Levy 1987). Rhythmic behavior patterns such as this, displayed every day, are termed "diel," hence this is a diel vertical migration (DVM). DVM is a very common phenomenon among organisms in lakes and oceans, and it has intrigued biologists for decades. In Babine Lake, for example, sockeye are found at 20–40 m depth during the day in summer. They move to the upper 5–10 m at dusk, down to the thermocline at night, briefly up to surface at dawn, and then down again during the day. In Lake Washington, they stay deep during the day, followed by a brief ascent to about 10 m below the surface at dusk (Eggers 1978). They go back down during night and do not ascend again at dawn. In Great Central Lake, they are 70–120 m deep during the day, ascend to about 10–20 m at night, stay in this upper range all night, and descend at dawn (Levy 1987). In Lake Tustumena (a glacially turbid lake in Alaska), they show the reverse pattern: near the surface in the day and deep at night (Thorne 1983).

How, then, do we explain the general pattern and the variations among lakes? Three main hypotheses have been proposed, related to prey capture, bioenergetic efficiency, and predator avoidance. From the perspective of prey capture, perhaps the sockeye vertically migrate because the zooplankton also migrate. Although this is plausible and may occur in some cases, it does not seem to be a general pattern. Levy (1990) examined

FIGURE 10-6. Conceptual representation of the factors with positive (+) and negative (-) effects on each other, and eventually on the two factors (food and temperature) most strongly affecting growth of salmonids in lakes, with an effort to distinguish factors that primarily vary among lakes from factors that primarily vary from year to year.



data from four lakes where sockeye vertically migrate (Cultus, Babine, Quesnel, and Shuswap) and in no case was there a clear vertical migration by the prey. In contrast, zooplankton showed vertical migration in Nimpkish Lake where the sockeye and sticklebacks did not consistently migrate. Levy (1990) concluded that this reciprocal pattern of migration by prey or predator but not both was inconsistent with the hypothesis that sockeye migrate simply to follow their prey. Moreover, the sockeye in Great Central Lake spend the day far below the zone of maximum food density. Thus though the distribution of sockeye and their food must sometimes overlap, prey movements are not sufficient to explain sockeye vertical migrations.

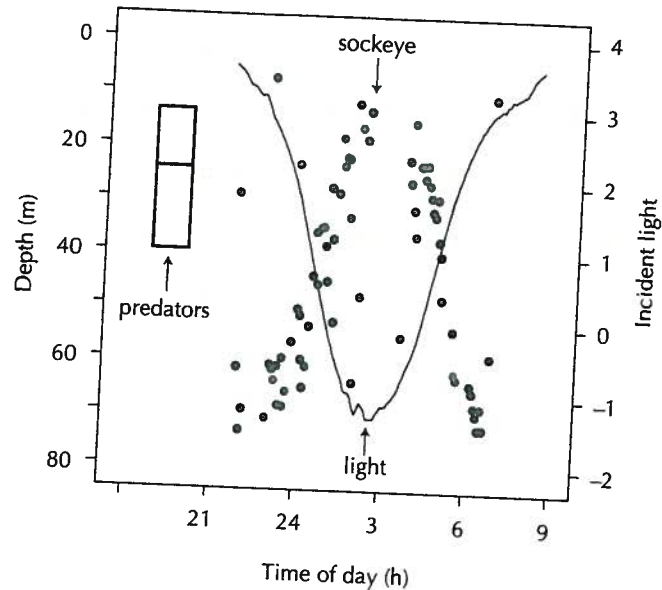
Another hypothesis was presented by Brett (1971), who developed the relationship between growth, temperature, and ration size (Brett et al. 1969; see fig. 10-2). In the summer, if sockeye were to feed at the surface at dusk and remain there all night (when it is too dark to forage successfully), the water would be too warm for optimal digestion efficiency. If the fish moved below the lake's thermocline, they could digest the food more efficiently and then either rise to the surface again at dawn or descend directly to the deep water during the day. Laboratory feeding trials with live zooplankton showed that at moderate rations (similar to what might be experienced in lakes), sockeye grew faster under a temperature regime simulating diel vertical migration than under constant temperature regimes (Biette and Geen 1980). Modeling based on observed patterns of temperature and zooplankton experienced by kokanee in a North Carolina reservoir

also indicated a significant increase in growth for vertically migrating sockeye when the optimal temperature is below the depth where prey are concentrated (Bevelhimer and Adams 1993). However, Steinhart and Wurtsbaugh (1999) documented diel vertical migrations among three populations of *O. nerka* during the winter. The 3–5°C isothermal environment under the ice led them to propose that foraging was more important than temperature in structuring the observed vertical distribution patterns.

Energetic efficiency might explain why juvenile sockeye do not remain at the surface all night (though Levy 1987 pointed out that there is an energetic cost to migrating up and down, and also some cost to maintaining neutral buoyancy during the migration), but what determines the depth to which they go in the day? The most plausible explanation is that they are trying to avoid predation from birds (near the surface) and from larger fishes that feed by sight. The safest place is at the bottom of the lake but there is little to eat there, and the surface is the best place to feed but it is hazardous. Eggers (1978) reported that sockeye in Lake Washington seem to avoid predators by forming schools in darker, deeper water by day and only venturing up to feed in the late afternoon and dusk, when the schools dispersed. There is sufficient food in this lake (based on both zooplankton density and sockeye growth) for the sockeye to minimize vulnerability to predation by feeding to satiation at dusk and then descending until the next evening, rather than reascending to the surface again at dawn to feed again as occurs elsewhere.

Clark and Levy (1988) sought to unify the different hypotheses and proposed that each population strikes an appropriate trade-off between maximizing the opportunity for growth (based on food and temperature) and the risk of predation (based on light levels), given the prevailing local conditions. The sockeye should feed near the surface during an “antipredation window” when it is light enough for them to feed but dark enough to reduce predation risk. Levy (1990) gathered data from a number of lakes in support of this hypothesis. He concluded that visual range, affected by water clarity and light level, affects predator efficiency. Daytime depth is regulated by water clarity; sockeye go as deep as they have to in order to reduce light levels, minimizing risk of predation. The fish ascend to feed during the crepuscular periods but at night it is too dark for them to feed or for the predators to eat them. Thus sockeye move up to feed in the evening in most lakes but can also do so during the day in highly turbid water. The higher the productivity or higher the predation risk, the less time the sockeye should spend near the surface. At night they are found at or near the thermocline (in summer), at temperatures where they can efficiently process their food. Thus the nighttime depth is regulated by temperature, and the vertical pattern varies with the season. Therefore, the conditions of water clarity, predation pressure, food availability, and temperature seem to control variation in vertical migration among lakes and among seasons at a given lake. Recently, Scheuerell and Schindler (2003) provided strong empirical evidence supporting this integrated model to explain DVM. The vertical movement of sockeye was tightly linked to light levels; the predators were suspended in the water column, feeding on the passing sockeye each day; and the sockeye went deeper in the lake than would be needed for energetic efficiency (fig. 10-7). Thus the model by Clark and Levy (1988) explains a great deal about the DVM patterns of sockeye, though sockeye movements in winter are much less well known than those in summer, and the winter patterns are not always consistent among lakes (Steinhart and Wurtsbaugh 1999).

FIGURE 10-7. Vertical distribution of sockeye salmon fry (scattered dots) and predatory fish (the box indicates the depth range of 50% of the predators and the line within the box indicates the median depth), determined by hydroacoustic surveys, and light levels (continuous line: $\log_{10} [W \text{ m}^{-2}]$) from evening to morning in July in Little Togiak Lake, Alaska (modified from Scheuerell and Schindler 2003).



Predation, mortality, and trout in lakes

The subject of predation raises the issue of mortality. Among six populations (Chilko, Babine, Lakelse, Karluk, Washington, and Port John lakes), the average survival of sockeye fry to the smolt stage was 25.8% (see table 15-1). This is probably much higher than they would experience in a year if they went to sea as fry, but the losses call for some explanation. West and Larkin (1987) determined that the mortality in Babine Lake was size selective. They developed a relationship between the lengths of sockeye fry and the radius of their otolith (ear bone). They then measured the otoliths of juveniles at the end of their first summer in the lake, and of smolts leaving the lake, and estimated how large the fish had been when they entered the lake by measuring the mark on the otoliths made when the fry entered the lake. Only 27.2% of the fry from the lower half of the length-frequency distribution survived the year, compared to 43.3% for the larger half of the population. McGurk (1999) proposed that the mortality rate of sockeye and kokanee in lakes decreases as they grow, and he estimated the relationship as annual mortality = $1.38 \times \text{weight}^{-0.19}$. This is the equivalent to mortality decreasing from 90% to 80, 70, 60, and 50% as fish grow from 1.2 g to 2.3, 4.7, 10.6, and 27.8 g.

In most sockeye lakes, the primary predators seem to be other salmonids, especially trout and char. With the exception of lake trout (that spawn in lakes) and juvenile coho salmon rearing in the lake before migrating to sea, these species are generally represented by adfluvial populations. This term refers to fish that were spawned in streams, reared there (often for a few years), and then migrated to the lake to feed. Adfluvial trout may remain in the lake during the whole year, leaving only to spawn in streams, but some



10-3 Arctic tern, Lake Aleknagik Alaska, a predator on sockeye salmon. Photograph by Gregory Buck, University of Washington.

populations also make feeding migrations to streams to feed on insects, salmon eggs, and other prey (e.g., Eastman 1996; Meka et al. 2003). However, sockeye are also eaten by birds, including Arctic terns (photo 10-3), loons, mergansers, gulls, and other species.

Predation is presumably responsible for most of the mortality of sockeye in lakes, and of salmonids in general, though we may be too quick to ignore the role of disease. Pathogens of various sorts can weaken or even kill young salmon. For example, a cestode, *Eubothrium salvelini*, infects young sockeye salmon when they eat copepods, especially *Cyclops*, that contain the parasite. Smaller sockeye (26–35 mm) were more than three times as likely to get infected as larger fish (56–65 mm) in experiments (Boyce 1974), and there was indirect evidence that the parasite might reduce growth and survival. However, the proximate cause of mortality is usually predation. The lakes inhabited by sockeye often contain one or more species of predatory salmonid, including cutthroat or rainbow trout, Dolly Varden, Arctic char, lake trout, and bull trout. Ruggerone and Rogers (1992) conducted an especially thorough study of predation by juvenile coho salmon on sockeye in Chignik Lake, Alaska, and estimated that the coho ate 24–78 million sockeye, or about 59% of the sockeye, per year.

Sockeye salmon nursery lakes from the Columbia River to the Nass River, British Columbia, may also contain a large, piscivorous cyprinid, the northern pikeminnow

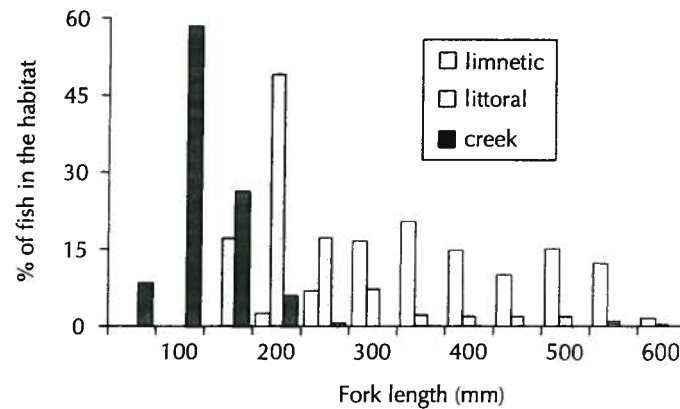


10-4 Rainbow trout in Iliamna Lake, Alaska, known for its large adfluvial trout. Photograph by Gregory Ruggerone, Natural Resources Consultants, Inc.

(*Ptychocheilus oregonensis*). Foerster's (1968) review of the Cultus Lake and Lakelse Lake predation studies indicated that pikeminnow (formerly known as squawfish) were the most numerous piscivore in the lake. They consumed considerable quantities of sockeye, but their per capita predation was lower than that of salmonids. By comparison, the per capita predatory effects of cutthroat trout, coho salmon, and Dolly Varden were estimated to be fivefold, fourfold, and threefold greater than those of pikeminnow, respectively. Similarly, Beauchamp et al. (1995) estimated that each pikeminnow ate about 5.6 fry per year, compared to 138.9 eaten by each cutthroat trout in Lake Ozette, Washington. Though they do not seem to be heavy predators in these lakes, pikeminnow are blamed for much of the juvenile salmonid mortality in the Columbia River system reservoirs (see chapter 12).

The biology of salmonids with adfluvial rather than anadromous life cycles (photo 10-4) is diverse but they tend to be generalist predators, foraging in the littoral zone on emerging insects, benthic invertebrates, and small fishes such as sculpins; and in the limnetic zone on fishes, including smaller salmonids, sticklebacks, smelt and other planktivores, and on zooplankton. These habitats may be used daily on an opportunistic basis but there may also be seasonal or ontogenetic habitat shifts. For example, Lake Washington's cutthroat trout typically spend 2 years in streams before migrating to the lake at a length of about 150 mm (fig. 10-8). They remain in the littoral zone, feeding mainly on insects until they reach about 250 mm. They then move to the limnetic zone and feed much more heavily on fishes (Nowak and Quinn 2002; Nowak et al. 2004).

FIGURE 10-8. Fork length distributions of cutthroat trout sampled in a tributary of Lake Washington (Quinn, unpublished data) and in the lake's littoral and limnetic zones (Nowak et al. 2004). The timing of sampling in the creek results in underrepresentation of young-of-the-year trout, which would be less than 50 mm in spring.



They do so by remaining just below the thermocline in summer, apparently moving slowly and intercepting the sockeye salmon and longfin smelt (*Spirinchus thaleichthys*) that vertically migrate (e.g., see fig. 10-7). However, individual trout move throughout the lake, tending to forage in the littoral zone most often in spring. Adfluvial bull trout also prey heavily on fish (almost exclusively so in Flathead Lake in Montana; Fraley and Shepard 1989), including both benthic and pelagic species.

Like the sockeye, trout seek depths that balance physiologically efficient temperatures, sufficient prey, and light to catch them. They are visual predators, and their encounter rates with prey depend on prey density, water clarity, and ambient light conditions (Beauchamp et al. 1999). Henderson and Northcote (1985) found that Dolly Varden reacted to prey from a greater distance at low light levels, but at higher light levels cutthroat trout showed a greater reactive distance. This is consistent with the higher density of cones in the retina of cutthroat trout (Henderson and Northcote 1988) and the tendency for char to reside deeper in the water column than trout, especially when they are sympatric. In addition to light, the vertical distributions may be constrained by other physical factors, notably temperature and dissolved oxygen (e.g., Rowe and Chisnall 1995).

Besides these physical influences on trout, there is considerable evidence that their distributions reflect interspecific competition. Nilsson and Northcote (1981) obtained information on rainbow and cutthroat trout distributions and diets in a series of lakes, including some containing both species (sympatry) and others where the species existed alone (allopatry). Both species were broadly distributed and fed on a wide variety of prey but differences between the species seemed to be magnified in sympatry. Cutthroat trout were more piscivorous than rainbows, especially when they were found together. Most striking were the patterns of growth. In allopatry, rainbow grew faster than cutthroat but when they were found together the cutthroat grew much faster. Further research on competition in lacustrine trout populations revealed that cutthroat trout tended to dominate Dolly Varden and exclude them from productive littoral feeding areas (though cutthroat were dominated by rainbow; Hindar et al. 1988).

Summary

For juvenile sockeye, the 1 or 2 years spent in the lake are a period of slow growth and low mortality compared to the years at sea. The sockeye often show diel vertical migrations, spending the day in deep water and moving up near the surface at dusk to feed. Such movements seem to balance the need to feed near the surface with the risk of predation there and the energetic efficiency of digesting their meal at moderate temperatures. Sockeye feed on insects in the littoral zone and in the limnetic zone they feed selectively on the largest crustacean zooplankton available (often *Daphnia* or large copepods). Growth is influenced by temperature or length of the growing season and the availability of food. Food is, in turn, influenced by intrinsic features of the lake (chemistry, depth, temperature, etc.) and by the density of planktivores, including both sockeye salmon and other fish species. Adfluvial trout migrate to lakes, often after rearing for a few years in the natal stream. They commonly feed on insects and other invertebrates in the littoral zone and on zooplankton and fish in the limnetic zone. Trout may move back and forth between the lake and streams as food becomes available (e.g., in fall when they eat eggs from spawning salmon). Their diet is increasingly composed of fish as they grow, and they are often the most important predators on young sockeye salmon.