DIEL VARIATIONS IN THE FEEDING HABITS OF PACIFIC SALMON CAUGHT IN GILL NETS DURING A 24-HOUR PERIOD IN THE GULF OF ALASKA

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ABSTRACT

Changes in prey composition and stomach fullness indicate diel variations in feeding behavior of sockeye, pink, and coho salmon caught in surface gill nets set for 2 hours each over a 24-hour period at a station in the Gulf of Alaska. All of these species of salmon switched from feeding primarily on squids, fishes, and amphipods during the day to euphausiids at night. Apparently dense concentrations of euphausiids can be exploited by salmon in surface waters at very low light intensities, even during an overcast night. Day-night changes were less obvious in the food of chum salmon, which fed largely on salps. Total catches of salmon and catches in the near-surface portion of the gill nets were highest between sunset and sunrise, suggesting that diel vertical movements contribute to the higher night than day catches of surface gill nets.

Although many studies have been published on the feeding habits of salmonids in oceanic waters of the North Pacific Ocean (Andrievskaya 1957; Allen and Aron 1958; LeBrasseur 1966; Ito 1964; Manzer 1968; Takeuchi 1972), most studies of daily feeding patterns have been conducted on juvenile salmon in fresh water or in coastal waters. These have generally shown that juvenile pink, sockeye, and chum salmon are diurnal or crepuscular (dawn and dusk) feeders (see Godin 1981 for review). The few studies conducted on diel feeding variations of adult or maturing Pacific salmon in oceanic waters of the northwestern Pacific Ocean have not revealed a consistent pattern (Machidori 1968; Shimazaki and Mishima 1969; Ueno et al. 1969).

To further elucidate the diel feeding patterns of these fishes, we collected and examined stomach contents of four species of Pacific salmon caught in the Gulf of Alaska during one 24-h period.

METHODS

Two gill nets, each 800 m long and 6 m deep, with 300 m of 115 mm, 250 m of 121 mm, and 250 m of 130 mm (stretch) mesh, were alternately fished for about 2-h periods over a 24-h period in the Gulf of Alaska from the *Oshoro Maru*, training ship of the Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido. The first net was set at 1200 h local time (GMT - 9 h) on 13 July; the last set was hauled at 1206 h on 14 July 1981 (Table 1). The time that the gill nets were fishing varied in the first 11 sets from 140 to 152 min (from start of set to start of

TABLE 1.—Summary of gill net sets and catches for salmon, 13-14 July 1981.

Set no.	Start of set and haul (h)	Number of salmon: Sockeye	Chum	Pink	Coho	Steelhead	Total
1	1200 1422	8	4	1	0	0	13
2	1400 1629	2	0	1	5	0	8
3	1600 1821	2	8	4	7	0	21
4	1800 2020	7	1	5	2	0	15
5	1957 2227	15	1	5	3	1	25
6	2158 0025	9	5	11	11	1	37
7	2359 0224	11	7	8	7	0	33
8	0159 0430	17	8	7	8	0	40
9	0358 0627	6	2	11	5	2	26
10	0600 0832	11	3	2	1	2	19
11	0758 1026	7	1	6	1	0	15
12	0957 1206	12	4	7	1	0	24
	Total	107	44	68	51	6	276

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hauling) and 129 min in the last set. Five to eight minutes were required to set the nets, 12-20 min to retrieve them.

The study area was between lat. 54°51.5′ and 54°57.9′N, long. 144°55.1′ and 145°11.3′W. On consecutive sets the gill nets were set 1.5-30 km apart to reduce the possibility of one net influencing the catch of another. Gill nets were set along a ship course of 040°, except for the first two nets which were set along 230°. In general, nets drifted 0.4-6.5 km northeastward during the sets.

The vertical location in the gill net (upper, middle, and lower 2 m) and species of each captured salmon were noted as the gill net was hauled aboard. Fish were removed from the gill nets, measured (fork length), and weighed with a beam balance. Stomachs were removed, weighed to the nearest gram with a beam balance, placed in a tray, and cut open with scissors. The fullness of cardiac and pyloric portions of the stomach was estimated visually as a) empty, b) trace amounts (few individual organisms with cumulative weights of a gram or less), c) <⅓ full, d) ⅓-⅔ full, and e) full (rugae fully distended, stomach lining thin and translucent). The degree of digestion was estimated as a) fresh (prey intact, no obvious digestion; fishes and squids with intact skin, euphausiids translucent), b) partially digested (fishes and squids identifiable, their skin, but not flesh, largely digested; euphausiids opaque, appendages often absent), and c) digested (fishes consisting of pieces of white flesh and vertebrae, crustaceans in pieces, euphausiids sometimes identifiable from fragments, especially their eyes).

The percentage composition by volume of prey taxa (euphausiids, amphipods, squids, fishes, salps, pteropods, copepods) was visually estimated for the cardiac and pyloric portions of each stomach. Stratification of food taxa in the cardiac portion was noted. Stomachs with diverse prey taxa were flushed into a petri dish to facilitate identification and estimation of prey compositions. Samples of prey organisms were preserved in Formalin[4] for verification and identification to lower taxa. Stomachs with more than trace amounts of food were then rinsed with water to remove adhering food items, blotted, and reweighed to the nearest gram.

The data were all obtained during the 2-h periods after setting one gill net and hauling the other.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Catches of Salmon

A total of 107 sockeye, 68 pink, 51 coho, and 44 chum salmon and 6 steelhead trout were caught in the 12 sets (Table 1). In general, the catches of each species were highest between sunset (2113 h) and sunrise (0420 h). This trend is clearly shown in Table 1. Catches were several times larger during night sets (1957-0627 h, sets 5-9) than sets that fished during daylight periods.

To illustrate diel trends in the vertical distribution of the salmon captured in the gill net, catches of a species were combined (because of the low numbers of individual species caught per set in each vertical section of the net) for afternoon (sets 1-5), night (sets 6-8), and morning (sets 9-12). Figure 1 shows that the average percentage of all species of salmon caught in the upper 2 m of the gill net was highest at night. Moreover, as the lower part of Figure 1 illustrates, peak catches of all species combined occurred at night.

Length-frequency distributions of the four species of salmon from the catches at all sets combined are shown in Figure 2. Fish of several ocean

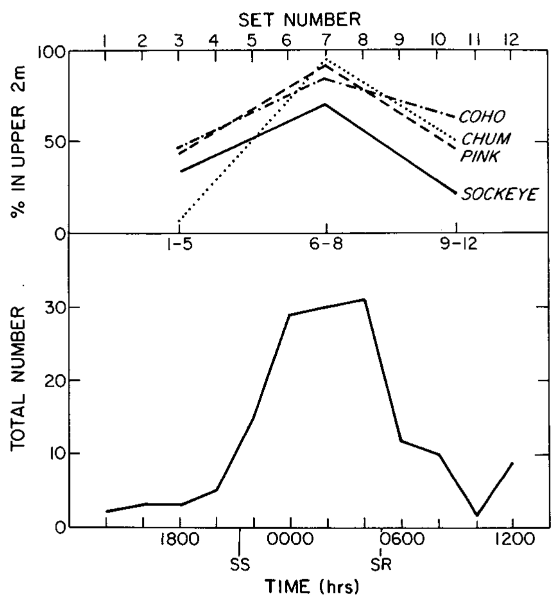

FIGURE 1.—Average percent of the total catch of the four species of salmon caught in the upper 2 m of the gill net during afternoon (sets 1-5), nighttime (sets 6-8), and morning hours (sets 9-12) (upper panel), and the total number of all species of salmon caught in the upper 2 m of the gill nets per set during the 24-h period (lower panel).

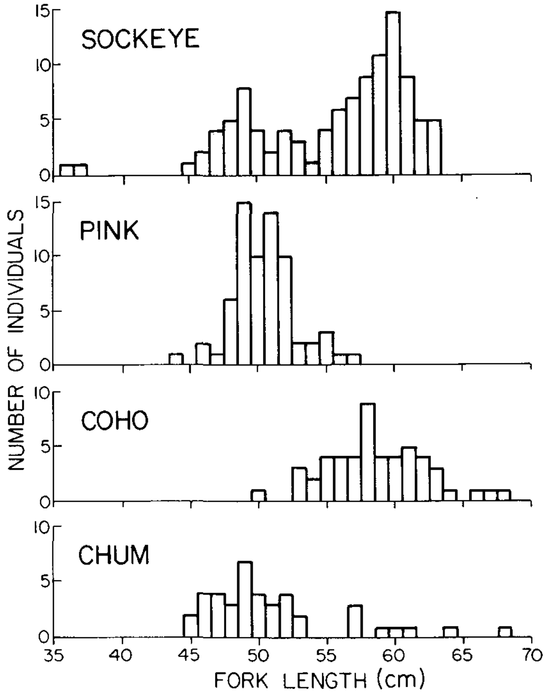

FIGURE 2.—Length-frequency histograms for the four species of salmon caught in the 24-h study.

ages are represented for sockeye and chum salmon. All pink and coho salmon were probably beginning their second year of ocean life. Comparisons of length-frequencies between day (sets 1-4 and 10-12) and twilight and night (sets 5-9) were not significantly different for sockeye, pink, and chum salmon, but were significant for coho salmon (Kolmogorov-Smirnov test, $P < 0.05$). Coho salmon were 2.4 cm larger in the twilight-night sets.

Feeding Habits

Stomach fullness of the four species of salmon, calculated as a percentage of body weight, were usually variable, ranging from 0% (empty) to a maximum of 4% for sockeye, 3.0% for chum, 3.3% for coho, and 2.3% for pink salmon (Fig. 3). Some individuals of all species had empty stomachs during most sets, regardless of time of day. Although ranked differences of the stomach weight:fish weight ratio were not significantly different between day (sets 1-4 and 10-12) and night-twilight (sets 5-9) for each of the four species of salmon (Mann-Whitney U-test, $P > 0.05$), the highest percentages of stomach weight to body weight for sockeye (>3%) and coho and pink salmon (>2%) were obtained from nighttime sets (Fig. 3). Moreover, our visual estimates of stomachs also indicated that full, distended stomachs of sockeye, coho, and pink salmon occurred only at night. There were no suggestions of diel periodicity of stomach fullness for chum salmon, however.

The frequency of occurrence and percent composition of the most common prey taxa (euphausiids, amphipods, squids, fishes) in the cardiac portions of salmon stomachs containing more than trace amounts of food are summarized in Table 2. All species of salmon consumed all of the four major categories of food. The most frequently occurring major taxa was euphausiids in sockeye and coho salmon, amphipods in pink salmon, and "other taxa" (mainly salps, but often unidentified material and sometimes pteropods and polychaetes) in chum salmon stomachs. Amphipods were the second most frequent taxa in

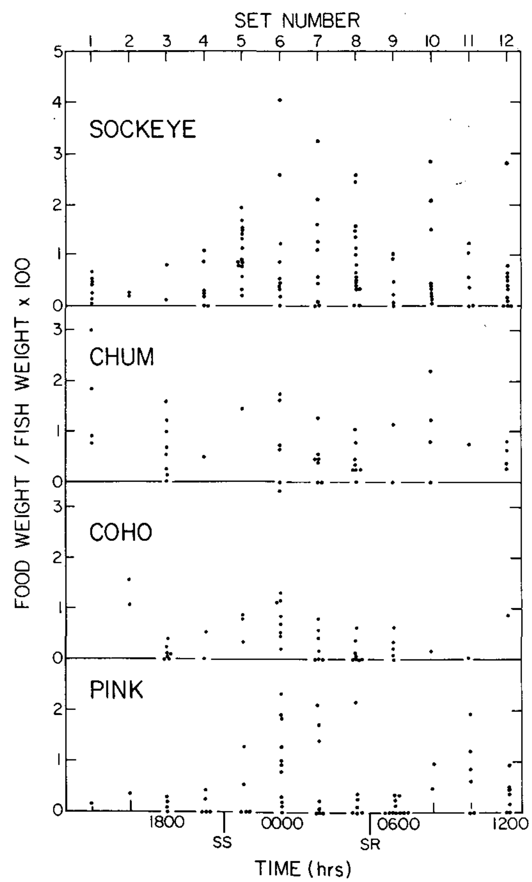

FIGURE 3.——Stomach fullness, expressed as a ratio of food weight to fish weight, for the four species of salmon caught in each of the 12 gill net sets during the 24-h period.

TABLE 2.—Frequency of occurrence and mean percent composition of major prey taxa in the gastric portions of salmon stomachs containing more than trace amounts of food.

		% occurrence					% volume				
	No. of stomachs	Euphausiids	Amphipods	Squids	Fishes	Other	Euphausiids	Amphipods	Squids	Fishes	Other
Sockeye	92	73	40	17	18	17	53	18	9	14	5
Pink	35	49	63	17	17	11	37	35	9	14	4
Chum	27	41	37	4	7	78	29	10	2	4	56
Coho	30	63	33	43	3	0	54	3	39	4	0

sockeye, euphausiids in pink and chum salmon, and squids in coho salmon stomachs.

The same taxa that ranked first and second on a frequency of occurrence basis usually ranked first and second on the basis of mean percent volume. Euphausiids (mainly *Euphausia pacifica* and *Thysanoessa longipes*) were most important for sockeye, pink, and coho salmon; "other taxa" were most important for chum salmon. Amphipods (mainly *Parathemisto pacifica* and *Hyperia medusarum*) ranked second in sockeye and pink salmon. Gonatid squids ranked second in coho stomachs and euphausiids ranked second in chum salmon stomachs. Thus sockeye fed primarily on euphausiids and secondarily on amphipods and myctophid fishes. Pink salmon fed mostly on euphausiids and amphipods. Coho fed mainly on euphausiids and squids, and chum on salps and euphausiids (see Table 2). Squids comprised only 2% of the volume of the stomach contents of chum salmon, and fishes comprised only 4% of the volume for chum and coho salmon. Copepods were not important (<1% of volume) for any species of salmon captured during the study.

Dietary overlap, based on the sum of minimum percentage volumes (percent similarity index, PSI, Sanders 1960) of the four main prey taxa, was 78% between sockeye and pink, 69% between sockeye and coho, and 53% between pink and coho. Because chum salmon had the most unique diet of the four species consuming mainly salps and gelatinous zooplankton, they had overlap values of only 45% with sockeye and pink and 38% with coho.

Although all species of salmon fed on a variety of taxa, individual fish usually contained only a few prey taxa. Only two major prey taxa were found in 85%, 89%, 93%, and 89% of the cardiac portions of sockeye, pink, coho, and chum salmon stomachs, respectively, containing more than trace amounts of food. Most sockeye and pink salmon had only one taxon of food in their stomachs. When salmon had only one food type in their stomachs, it was euphausiids in 65%, 52%, 85%, and 28% of the individual sockeye, pink, coho, and chum salmon, respectively. Euphausiids were obviously the most important prey for sockeye, pink, and coho salmon during this study. They were often the exclusive prey.

Sometimes the contents of the cardiac portion of sockeye and pink salmon stomachs were clearly divided with one type of prey in the anterior and one in posterior portion of the stomach. Generally this "stratification" involved euphausiids and amphipods, or euphausiids and squid. Usually, however, the cardiac and pyloric portions of the stomach had similar percentage compositions of major taxa (excluding empty stomachs and stomachs with trace amounts). Cardiac and pyloric contents were similar for 70% of the sockeye, 72% of the pink, and 60% of the coho and chum salmon. When sockeye and coho had the same prey composition in cardiac and pyloric stomachs, both portions usually contained only euphausiids. When pink salmon had the same prey composition, amphipods or euphausiids were found.

The relative composition of major prey taxa in the stomachs of each species caught in the 12 gill net sets is illustrated in Figure 4 and is discussed below. Open circles in Figure 4 indicate when fresh prey were common, except for amphipods which usually showed little evidence of being digested.

Sockeye Salmon

Prey composition of sockeye salmon had a distinctive diel pattern. Sockeye caught at night (2158-0430 h) contained a high percentage of euphausiids compared with the afternoon and morning sets (Fig. 4). In these night sets, euphausiids averaged over 80% of the volume of the stomach contents, and about 90% of the sockeye contained only euphausiids. Fish caught during and after sunset (1957-0224 h) also contained large numbers of freshly ingested euphausiids. Some fish in set 5 (1957-2227 h) had a clear division between euphausiids in the fore portion and amphipods in the posterior portion of the cardiac

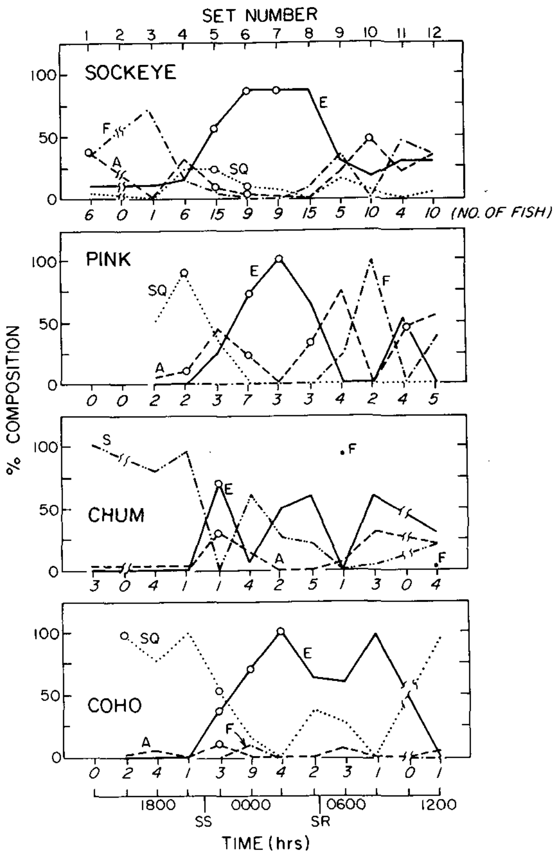

FIGURE 4.—Diel variations in the percent composition of major prey taxa in the stomachs of the four species of salmon containing more than trace amounts of food. E = euphausiids, A = amphipods, F = fishes, SQ = squids, S = salps. Open symbols show when fresh prey was common. The number under each figure indicate the number of fish with more than trace amounts of food in their stomachs. SS = sunset; SR = sunrise.

stomach, indicating a switch from amphipods to euphausiids during dusk. Euphausiids comprised <30% of the food in sets before sunset and after sunrise, and no fresh euphausiids were noted during these daytime periods. Amphipods and fishes formed the highest percentage of the food during daytime. Squids were also eaten by sockeye salmon and were most important during late afternoon and sunset (1800-2227 h) and during sunrise (0350-0627 h). Fresh squids were noted in stomachs of fish caught in sets that fished from 1957 to 0025 h.

Pink Salmon

As with sockeye salmon, euphausiids attained peak importance as prey for pink salmon after sunset (2158-0430 h), when they comprised over 65% of the food and were often in fresh condition. All three fish with over trace amounts of food in the set that fished from 2359 to 0224 h contained 100% euphausiids. Squids and amphipods are most important in the afternoon (1600-2020 h), and fresh squids were found in stomachs of pink salmon caught from 1800 to 2020 h, just before sunset. Fishes and amphipods were the most important prey during the morning daylight period.

Chum Salmon

A diel trend for this species, which fed on a variety of prey taxa, was less obvious than for other species of salmon (Fig. 4). Salps composed over 75% of the stomach contents during the afternoon (1200-2020 h). Euphausiids were the most common prey taxa from sunset to the last set at midday, with the exception of a single chum salmon caught at 2158-0025 h whose stomach contained many salps and a salmon caught at 0358-0627 h whose stomach contained 95% fish. Most euphausiids in the stomachs of fish caught about the time of sunset (1957-2227 h) appeared to be recently ingested. Squids, which were only a minor part of the stomach contents, are not indicated in Figure 4.

Coho Salmon

Coho salmon fed mainly on euphausiids during the night and on squids during the day. Euphausiids were not observed in stomachs of coho salmon during the afternoon but increased in importance from 0 to 100% of the stomach volumes between 1800 and 0240 h (Fig. 4). Most of the euphausiids during this period were in fresh condition. Euphausiids also comprised most (>60%) of the stomach contents during the morning hours (0159-0832 h) but were never fresh. Squids were the most important prey of coho salmon caught during the afternoon-daylight period and in the last set in late morning. Amphipods and fishes were of minor importance.

DISCUSSION

The larger catches of salmon in surface gill nets during twilight-night periods than in daytime periods have three possible explanations: Avoidance of nets during the daytime when visual acuity of salmon is highest, increased swimming activity in surface water at night compared with daytime, and diel vertical ascent of salmon into near-surface waters at night. The higher catches in the upper 2 m of the gill net at night than day lend support to the last possibility, but not to the exclusion of the other possibilities.

Most other authors favor vertical migration as an explanation for diel peaks in gill net catches (Taguchi 1963; Manzer 1964; Mishima et al. 1966). Birman (1964) noted visual avoidance of "sweep nets" by day, but concluded that salmon migrate into upper waters primarily as a response to vertical movements of their zooplanktonic prey which they feed on during periods of low light intensity, chiefly before dawn.

Swimming activity could also influence catchability, but neither Ichihara et al. (1975) nor Ichihara and Nakamura (1982) found large differences in day-night swimming speeds of chum salmon tagged with ultrasonic transmitters.

The most interesting finding of our study is the distinct diel change in composition of major prey. Stomach contents of sockeye, pink, and coho salmon were comprised largely of euphausiids after sunset and during the night (Fig. 4). The largest number of full stomachs, usually containing only fresh euphausiids, were also found during the nighttime. These three species of salmon preyed intensively on euphausiids at night, often to the exclusion of other types of prey.

This change to feeding on euphausiids was first observed in the salmon caught during the time that the 24-kHz sonic scattering layer ascended into surface waters (Fig. 5). We assume that euphausiids were an important component of this scattering layer (see Suzuki and Ito 1967).

A 1.8 m Isaacs-Kidd midwater trawl collection (three mesh sizes: 70, 11, and 4 mm stretch) in the upper 10 m at night at the 24-h gill net station caught mainly salps and medusae, but euphausiids were abundant (19g/1,000 m^3). Euphausiids were also abundant in a 1.3 m ring net (1.0 mm mesh) towed at the surface after sunset at this station. The most common euphausiids caught were *Euphausia pacifica* and *Thysanoessa longipes*, the same species common in salmon stomachs. *Euphausia pacifica* were found to undertake diel vertical migrations at the Canadian Weather Station located at lat. 50°N, long. 145°W (Marlowe and Miller 1975). Frost and McCrone (1974) also found evidence for diel vertical migration of *E. pacifica* at this location but not for *T. longipes*. The intense predation on euphausiids at night is therefore thought to be related to their dense concentration and increased vulnerability in surface waters after dark.

Most of the studies of the diel periodicity or chronology of feeding in salmon have been juveniles in fresh or coastal waters (Godin 1981). In general, these indicate diurnal or crepuscular feeding patterns for juveniles of pink salmon (Ali 1959; LeBrasseur and Barner 1964; Bailey et al. 1975; Parker and Vanstone 1966; Parker 1969; Godin 1981), chum salmon (Bailey et al. 1975; M. C. Healey as cited in Godin 1981), sockeye (Narver 1970; McDonald 1973; Doble and Eggers 1978), and coho salmon (Mundie 1971). Bailey et al. (1975) concluded that pink and chum salmon fry did not feed during cloudy moonless nights. Nighttime feeding by sockeye apparently occurs during moonlight but not on cloudy or moonless nights in Babine Lake (Narver 1970). Experiments conducted by Brett and Groot (1963) and Ali (1959) indicated that juvenile pink salmon changed their mode of capturing prey below 10^0 mc (meter candle), an intensity where the change from phototopic to scotopic vision apparently occurs, and their feeding activity decreased between intensities of 10^0 to 10^{-4} mc and most ceased between 10^{-3} and 10^{-5} mc. Experiments by Bailey et al. (1975) showed almost no feeding by pink salmon fry at light intensities below 10^1 mc.

In our study, salmon fed intensively on euphausiids at night under an obscured, overcast sky. From the general data given by Brown (1952) and Blaxter (1970) we estimated that the light intensities on this night were between 10^{-3} and about 10^{-5} mc. But, despite these low light intensities, with attendant reduction in contrast of prey and sighting range to prey (Eggers 1977; Anthony 1981), salmon were capable of actively feeding on small, euphausiid-sized prey. At night, larger prey such as squids and fishes are probably encountered less frequently than euphausiids and evade capture more easily because of reduced sighting and tracking ranges of salmon. Euphausiids may not be as capable of active predator evasion and, when abundant in near-surface aggregations at night, are encountered frequently and actively selected. Bioluminescense produced by euphausiids may facilitate detection and capture by salmon. Thus, escape responses and sighting ranges at different light intensities may influence the size and type of prey selected at different times of a diel period.

Machidori (1968) reported that the indices of stomach:body weight of sockeye and chum salmon caught in gill nets that fished different depths

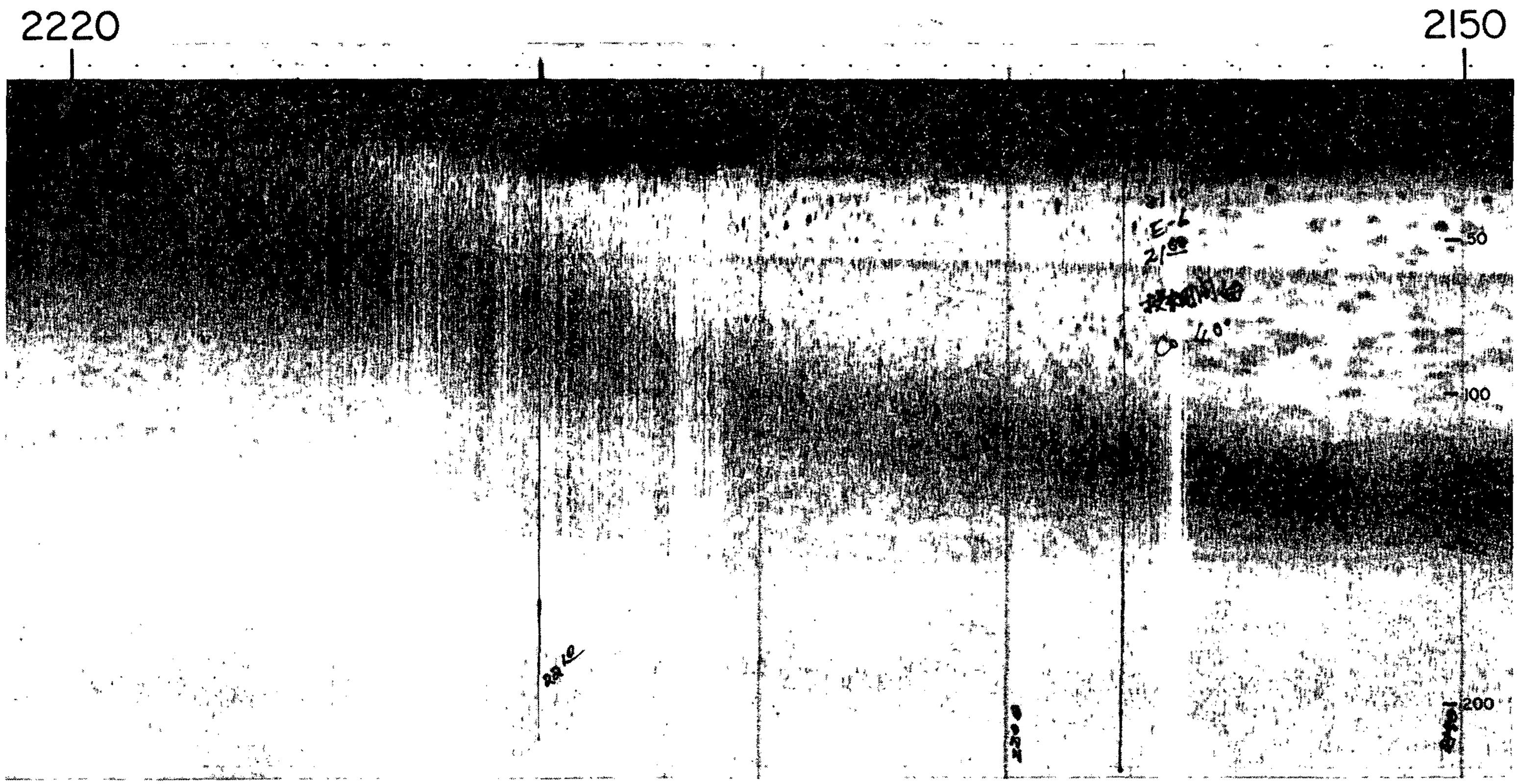

FIGURE 5.—24-kHz echogram from 2150 to 2220 h on 13 July 1981 showing the ascent of a sonic scattering layer into near-surface waters.

between 0 and 50 m in the northwestern Pacific were usually highest in near-surface depths by day and below 10 m at night. Euphausiids were an important food taxa only in salmon caught below 10 m during the day. Since average stomach fullness indices were higher during the day than the night, Machidori concluded that light was necessary for salmon to feed. Takagi (1971) reported that surface longlines and gill nets caught salmon during morning and evening, but during the night salmon were caught in gill nets but not by longlines. These observations indicate reduced feeding activity of salmon at night.

Shimazaki and Mishima (1969) concluded from diel trends in the feeding of maturing pink and chum salmon at two locations in the Sea of Okhotsk that feeding activity was high in the evening before and after sunset and low in daytime. They found peak stomach fullness values after sunset. In three of four instances these peak values were the first values after sunset, and may have been the result of crepuscular feeding. In one instance involving pink salmon, however, stomach fullness increased from 1917-2040 h to a peak at 2119-2245 h, indicating active feeding at night. Amphipods, squids, and fishes were the dominant food on a wet weight basis.

Additionally, Ueno et al. (1969) found that pink and chum salmon had full stomachs during the late afternoon as well as after dark in waters off Kamchatka. Suzuki (1970) compared the volume of food in stomachs of chum salmon caught in gill nets off the Kamchatka Peninsula during night (2100-2330 h) and morning daylight hours (0330-0610 h) and concluded that no major differences existed. He found that myctophid fishes always comprised a larger percentage of the stomach contents during the morning and pteropods usually comprised a larger percentage at night.

Thus the above studies plus our own clearly document that salmon are capable of feeding during both day and night periods in oceanic waters. Their feeding behavior is flexible and variable, permitting opportunistic exploitation of a profitable food resource regardless of when it is encountered.

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LITERATURE CITED

ALI, M. A.
1959. The ocular structure, retinomotor and photobehavioral responses of juvenile Pacific salmon. Can. J. Zool. 37:965-996.

ALLEN, G. H., AND W. ARON.
1958. Food of salmonid fishes of the western North Pacific Ocean. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 237, 11 p.

ANDRIEVSKAYA, L. D.
1957. Pitanie tikhookeanskikh lososei v severo-zapadnoi chasti tikhovo okeana (The food of Pacific salmon in the northwestern Pacific Ocean). [In Russ.] From: Materialy po biologii morskovo perioda zhizni dalnevostochnykh lososei, p. 64-75. Publ. by: Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO), Moscow. [Translation: Fish. Res. Board Can. No. 821.]

ANTHONY, P. D.
1981. Visual contrast thresholds in the cod *Gadus morhua* L. J. Fish Biol. 19:87-103.

BAILEY, J. E., B. L. WING, AND C. R. MATTSON.
1975. Zooplankton abundance and feeding habits of fry of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *Oncorhynchus keta*, in Traitors Cove, Alaska, with speculations on the carrying capacity of the area. Fish. Bull., U.S. 73:846-861.

BIRMAN, I. B.
1964. Vertical migrations and vertical distribution of salmon in the sea. Dokl. Biol. Sci. Proc. Acad. Sci. USSR 156:346-349.

BLAXTER, J. H. S.
1970. Light. Animals. Fishes. *In* O. Kinne (editor), Marine ecology, Vol. 1, No. 1, p. 213-320. Wiley-Interscience, Lond.

BRETT, J. R., AND C. GROOT.
1963. Some aspects of olfactory and visual responses in Pacific salmon. J. Fish. Res. Board Can. 20:287-303.

BROWN, D. W. E.
1952. Natural illumination charts. Dep. Navy, Bur. Ships Rep. 371-1, 11 p., 43 plates.

DOBLE, B. D., AND D. M. EGGERS.
1978. Diel feeding chronology, rate of gastric evacuation, daily ration, and prey selectivity in Lake Washington juvenile sockeye salmon (*Oncorhynchus nerka*). Trans. Am. Fish. Soc. 107:36-45.

EGGERS, D. M.
1977. The nature of prey selection by planktivorous fish. Ecology 58:46-59.

FROST, B. W., AND L. E. MCCRONE.
1974. Vertical distribution of zooplankton and myctophid fish at Canadian Weather Station P, with a description of a new multiple net trawl. IEEE International Conference on Engineering in the Ocean Environment, p. 159-165.

GODIN, J-G. J.
1981. Daily patterns of feeding behavior, daily rations, and diets of juvenile pink salmon (*Oncorhynchus gorbuscha*) in two marine bays of British Columbia. Can. J. Fish. Aquat. Sci. 38:10-15.

ICHIHARA, T., AND A. NAKAMURA.
1982. Vertical movement of mature chum salmon contributing to improvement of set net structure on the Hokkaido coast. Proc. North Pac. Aquaculture Symp., p. 39-50. Univ. Alaska Sea Grant Rep. 82-2.

ICHIHARA, T., T. YONEMORI, AND H. ASAI.
1975. Swimming behavior of a chum salmon, *Oncorhynchus keta*, on the southern migration off Etorofu Island, the southern Kurile Islands. Bull. Far Seas Fish. Res. Lab. 13, p. 63-77.

ITO, J.
1964. Food and feeding habit of Pacific salmon (Genus *Oncorhynchus*) in their oceanic life. Bull. Hokkaido Reg. Fish. Lab. 29, p. 85-97. (Fish. Res. Bd. Canada Transl. Ser. 1309, 1969.)

LEBRASSEUR, R. J.
1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. J. Fish. Res. Board Can. 23:85-100.

LEBRASSEUR, R. J., AND W. BARNER.
1964. Midwater trawl salmon catches in northern Hecate Strait November, 1963. Fish. Res. Board Can. Manuscr. Rep. Ser. 176, 1-7.

MACHIDORI, S.
1968. Vertical distribution of salmon (Genus *Oncorhynchus*) in the Northwestern Pacific. III. Hokkaido Reg. Fish. Res. Lab. Bull. 34, p. 1-11.

MANZER, J. I.
1964. Preliminary observations on the vertical distribution of Pacific salmon (Genus *Oncorhynchus*) in the Gulf of Alaska. J. Fish. Res. Board Can. 21:891-903.
1968. Food of Pacific salmon and steelhead trout in the Northeast Pacific Ocean. J. Fish. Res. Board Can. 25:1085-1089.

MARLOWE, C. J., AND C. B. MILLER.
1975. Patterns of vertical distribution and migration of zooplankton at Ocean Station "P". Limnol. Oceanogr. 20:824-844.

MCDONALD, J.
1973. Diel vertical movements and feeding habits of underyearling sockeye salmon (*Oncorhynchus nerka*), at Babine Lake, B.C. Fish. Res. Board Can. Tech. Rep. 378, 55 p.

MISHIMA, S., S. SAITO, AND K. SHIMAZAKI.
1966. Study on the daily vertical movement of salmon - I. On the tendency of netting by the gill-net (I). Bull. Jpn. Soc. Sci. Fish. 32:922-930.

MUNDIE, H.
1971. The diel drift of Chironomidae in an artificial stream and its relation to the diet of coho salmon fry, *Oncorhynchus kisutch* (Walbaum). Can. Entomol. 103:289-297.

NARVER, D. W.
1970. Diel vertical movements of feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Board Can. 27:281-316.

PARKER, R. R.
1969. Foods and feeding of juvenile pink salmon in Central British Columbia waters. I. 1966 diel series. Fish. Res. Board Can. Manuscr. Rep. 1017.

PARKER, R. R., AND W. E. VANSTONE.
1966. Changes in chemical composition of Central British Columbia pink salmon during early sea life. J. Fish. Res. Board Can. 23:1353-1384.

SANDERS, H. L.
1960. Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. Limnol. Oceanogr. 5:138-153.

SHIMAZAKI, K., AND S. MISHIMA.
1969. On the diurnal change of the feeding activity of salmon in the Okhotsk Sea. Bull. Fac. Fish. Hokkaido Univ. 20:82-93.

SUZUKI, T.
1970. Swimming behaviour of chum salmon in the southeastern area off Kamchatka Peninsula. Bull. Jpn. Soc. Sci. Fish. 36:19-25.

SUZUKI, T., AND J. ITO.
1967. On the DSL in the northwestern area of the North Pacific Ocean - I. Relationship between vertical migration of DSL, submarine illumination and plankton biomass. Bull. Jpn. Soc. Sci. Fish. 33:325-337.

TAGUCHI, K.
1963. Some factors having effects on the behavior of salmon in the time of gill-netting. Bull. Jpn. Soc. Sci. Fish. 29:434-440.

TAKAGI, K.
1971. Information on the catchable time period for Pacific salmon obtained through simultaneous fishing by longlines and gillnets. Bull. Far Seas Fish. Res. Lab. 5, p. 177-194.

TAKEUCHI, T.
1972. Food animals collected from the stomachs of three salmonid fishes (*Oncorhynchus*) and their distribution in the natural environments in the northern North Pacific. Hokkaido Reg. Fish. Res. Lab. Bull. 38:1-119.

UENO, M., S. KOSAKA, AND H. USHIYAMA.
1969. Food and feeding behavior of Pacific salmon - II. Sequential change of stomach contents. Bull. Jpn. Soc. Sci. Fish. 35:1060-1066.