

Feeding Behavior, Prey Consumption, and Growth of Juvenile Red Hake¹

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Abstract

Juvenile red hake *Urophycis chuss* were collected while they were inhabiting sea scallops *Placopecten magellanicus*, and the effects of appetite and food availability on prey consumption and growth were examined under laboratory conditions. Fish took increasing amounts of live amphipods *Gammarus annulatus* with increasing periods of food deprivation up to 40–50 hours. The largest portion of a meal was consumed within the first 3 minutes following prey introduction. With longer periods of food deprivation, red hake increased the time their chemosensitive pelvic fins were extended, indicative of a rise in feeding motivation. The average amount of sand shrimp *Crangon septemspinosa* consumed by fish was 7.4% of body weight/day. Under conditions of high prey abundance, fish grew at rates equal to field growth rates, but under conditions of low prey abundance, growth rate was inhibited. Prey availability can influence the growth rate, which might lead to size differentials within a cohort.

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The growth of fishes depends in large measure on the amount of food consumed. The amount consumed, in turn, depends on a variety of factors including food availability (Ivlev 1961; Elliott 1970) and appetite (Beukema 1968; Brett 1971; Elliott 1975). In order to estimate accurately the potential amount of food that may be consumed, it is essential to understand the precise role that food availability and appetite play in feeding behavior. Considering these two factors in this present work, we have examined the food consumption and growth of juvenile red hake *Urophycis chuss* fed live natural prey items under controlled laboratory conditions.

The red hake is a marine gadid that occurs on the continental shelf of the northwest Atlantic Ocean, ranging from Nova Scotia to North Carolina (Musick 1974). The species has an extended spawning period lasting from April until October (Hildebrand and Schroeder 1928; Mu-

sick 1969; Wilk and Morse 1979). The larvae hatch in the plankton, spend 1–2 months as pelagic juveniles, and, after reaching a size of 23–49 mm total length (TL), descend to the bottom where they commonly live symbiotically in the mantle cavity of the sea scallop *Placopecten magellanicus* (Goode 1884; Musick 1969). This association persists for 2–3 months until the fish outgrow the scallops (Steiner et al. 1982). The size of fish found in scallops ranges from 23 to 136 mm TL (Musick 1969; Steiner et al. 1982). Juvenile red hake apparently gain only shelter from this relationship and laboratory studies have shown that the fish will use other types of shelter, such as clam shells, the perimeter of live scallops, and sections of pipe (Steiner et al. 1982). Laboratory observations and field collections made throughout the day and night have shown that juvenile red hake emerge most often from shelter at night when they are most active (Steiner et al. 1982).

In this study we determined, from field collections, the types of prey consumed by red hake while they were associated with sea scallops. Then, under controlled laboratory conditions and using live prey, we described the method of prey capture and measured the amount consumed daily. In addition, we examined the effects of food deprivation on the rate of prey consumed in a meal and the effect of prey abundance on growth rates.

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Methods

Animal Collection and Maintenance

Sea scallops were collected at 40°13'N, 73°48'W with a 1.2-m scallop dredge, then transported immediately to the Sandy Hook Laboratory in aerated seawater held in temperature-insulated containers. Seawater bottom temperatures, at the time of collection, ranged from 4.0 to 4.9 C and the depth ranged from 27 to 35 m. In the transport containers and subsequently in laboratory aquaria, juvenile red hake gradually emerged from the mantle cavities of the scallops. Fish and scallops were held together in 800- and 1,000-liter aquaria provided with running seawater, aeration, and a sand-gravel bottom. Fish were fed, three times each week, live amphipods *Gammarus annulatus*, sand shrimp *Crangon septemspinosa*, or chopped surf clam *Spisula solidissima*. Amphipods and sand shrimp were used as prey in experiments because stomach analysis showed them to occur naturally in the diet. Temperature (\pm SD) and salinity (\pm SD) were held at 10.7 ± 0.76 C and $23.5 \pm 1.55\text{‰}$, respectively. Temperature was comparable to field water temperature at the scallop collection site during the months of peak red hake occupation (Steiner et al. 1982). The photoperiod simulated natural seasonal changes; timers that controlled fluorescent lights were adjusted weekly. Daytime light intensity averaged 400 lux and night intensity 0.5 lux.

For studies of feeding deprivation and daily food consumption, experimental fish were held and tested under a light regime in which the daily light cycle was reversed; that is, night light intensities occurred during the normal daylight period, and vice versa. This change was made approximately 5 weeks before testing. The fish adapted to this new cycle as evidenced by their greater activity during the subjective night; red hake are normally most active at night (Steiner et al. 1982).

Stomach Analysis

One hundred thirty juvenile red hake (23–93 mm TL) were collected from sea scallops for stomach analysis and were immediately preserved in 5% formalin. All fish were collected between 1000 and 1400 hours eastern standard time at approximately monthly intervals for 1 year (November 1979 to November 1980). Subsequently, the stomachs were dissected and the

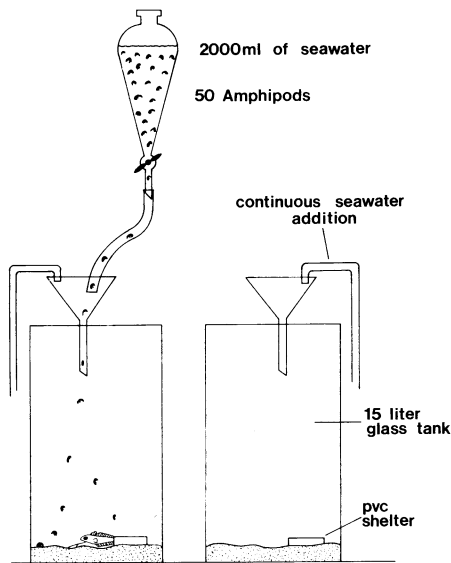
contents identified to the lowest taxon possible under a binocular dissecting microscope. The results are expressed as percent occurrence (number of stomachs containing a particular food item divided by the number of stomachs containing food).

Feeding Deprivation Studies

Four red hake of similar size (86–100 mm TL; 3.3–5.9 g wet weight) were selected from holding aquaria and placed into four 15-liter glass testing aquaria (38 cm \times 25 cm \times 15 cm) with 3 cm of clean sand and a section of polyvinyl chloride pipe (2 cm diameter \times 5 cm long) that afforded shelter. A continuous flow of sea water was supplied to each tank at an average flow rate of 0.8 liter/minute and a mean temperature (\pm SD) of 10.2 ± 0.65 C. Above each aquarium was suspended a 2,000-ml separatory funnel containing sea water and 50 live amphipods *G. annulatus*. To initiate a feeding bout, the stopcock of the separatory funnel was opened and water and amphipods were introduced over a 2-minute period (Fig. 1). Blinds with viewing slits isolated the experimenter from the fish, and blinds also were placed between aquaria so that fish were visually isolated from one another. Light intensity was 42 lux during the day and 1.4 lux during the night, and all feedings were conducted during the night when red hake are normally most active.

Fish were acclimated to test aquaria 3–12 days before they were tested, and fed *G. annulatus* during this period. An experiment began with the introduction of 50 amphipods. After 15 minutes, each fish was transferred to an identical but food-free aquarium. The deprivation interval began at the time of transfer and ended with a subsequent introduction of 50 amphipods. Again, after 15 minutes, each fish was transferred to another food-free aquarium. The number of amphipods taken was recorded during each 15-minute feeding, as was the time since introduction for each ingestion. The number of amphipods eaten was multiplied by the mean wet weight of an amphipod (either 21 or 45 mg) to obtain the wet weight of a meal. Each subsequent deprivation interval began and ended in the same manner.

Immediately before each prey introduction, an event recorder was used to measure, for 180 seconds, the duration of pelvic fin extensions past a 90° angle with the fish's body (Pearson



Apparatus used in deprivation study

FIGURE 1.—The aquarium and apparatus used to deliver 50 live amphipods to juvenile red hake during the food-deprivation and satiation study. After each 15-minute feeding, fish were transferred to an adjacent food-free aquarium for the prescribed deprivation period.

et al. 1980). The pelvic fins of this species have chemoreceptors and function behaviorally in food gathering (Herrick 1904; Bardach and Case 1965).

Daily Food Consumption

Red hake (93–139 mm TL; 5.7–27.3 g wet weight) were chosen randomly from holding aquaria and placed, one per tank, into each of six 116-liter fiberglass aquaria (95 cm × 35 cm × 35 cm) with 3 cm of sand covering the bottom. A sea scallop (125–135 mm valve height) was placed in each tank to serve as shelter. The tanks were arranged so that the fish were visually isolated from one another. Sea water was kept at a flow rate of 2 liters/minute; mean temperature was 10.7 ± 0.79 C. Photoperiod averaged 14 hours light and 10 hours dark during the testing period, and light intensities were the same as for holding aquaria. In order to estimate daily prey consumption, a known number of sand shrimp (mean weight per shrimp = 0.56 g; range 0.49–0.62 g) were introduced in a batch into the test aquaria at the beginning

of each test. After 82 hours (four night periods and three day periods), the number remaining was counted. The number eaten was calculated by difference. Tests were first performed with 10 sand shrimp (combined weight, 4.9–5.9 g), and then repeated with 25 sand shrimp (13.2–15.5 g) per tank. The food intake was estimated as the number of sand shrimp eaten multiplied by the mean weight of a shrimp, which was determined separately for each group of prey that was added. When weights of shrimp were unavailable, but lengths were, wet weights were estimated from a regression of wet weight on length (Luczkovich 1982). The wet-weight estimate of food consumption was converted to a percentage of body weight for each fish, which was divided by 3.42 (the number of 24-hour periods in 82 hours) to gain a daily value.

In order to compare consumption when prey were continuously available with consumption when prey were available only during nighttime, we performed a second set of 82-hour tests. Sand shrimp were introduced at the onset of darkness and removed and counted at the end of each night. These tests were first done with 10 shrimp (4.9–5.9 g) per introduction, then repeated with 15 shrimp (7.4–8.7 g). The difference between initial and final counts was used to calculate food consumption as a percentage of body weight per day, as described above.

Growth

To determine the effects of food availability on the growth of red hake, growth was measured under two different levels of prey abundance, high and low. Similarly-sized red hake were placed, two per tank, in six 290-liter fiberglass tanks (120 cm × 45 cm × 53 cm) with a viewing window, sand bottom, and two large sea scallops (115–147 mm valve heights) for use as shelter. The tanks were supplied with running sea water from the same source and the temperature averaged 11.1 ± 0.48 C. Ten sand shrimp (mean = 0.46 g/shrimp) were placed daily at 1530 hours into each of three tanks. This number was equivalent to an average ratio of 17.8% (9.3–32.1%) of body weight per day. Because the amount of prey available was greater than the amount eaten in our daily-consumption studies, these densities were considered high prey abundance. Into the remaining three tanks, 10 sand shrimp (mean = 0.49

g/shrimp) were placed every fourth day at 1530 hours. This density was equivalent to an average ratio of 4.3% (1.7–8.2%) of body weight per day. Because the amount of prey available was less than the amount eaten in our daily-consumption studies, these densities were considered low prey abundance. Every 8 days over the 24-day experiment, the fish were removed from the tanks, weighed to the nearest 0.01 g, and measured to the nearest millimeter. The absolute increases in length and weight were the difference between initial and final values for any interval. The specific growth rate (G) was calculated for any interval by

$$G = \left[\frac{\log_e(X_f) - \log_e(X_i)}{d} \right] 100;$$

X_f is the final length or weight, X_i is the initial length or weight, and d is the number of days in the interval (Ricker 1975). In addition, the condition factor (K) was calculated on each measurement day by

$$K = 100W/L^3;$$

W is the weight in grams, and L is the length in centimeters (Weatherly 1972).

Analysis of covariance was used in the daily-consumption and growth experiments in order to compare treatment groups comprised of fish of different initial sizes.

Results

Stomach Analysis

Juvenile red hake associated with sea scallops fed predominantly on crustaceans (Table 1). Decapods (sand shrimp) were the most frequently occurring crustaceans, followed by gammaridean amphipods *Unciola irrorata*, *Lep-*

tocheirus pinguis, *Monoculodes edwardsi*, *Eriethonius rubricornis*, and *Phoxocephalus holbolli* and copepods *Centropages* sp., amphipods and copepods occurring with equal frequency. Mysids and cumaceans contributed little to the diet. Unidentifiable noncrustacean material occurred frequently, but never in large quantities.

Feeding Behavior

Typically, before prey were introduced to aquaria, some fish were swimming slowly over the substrate while others were inactive, sheltered either within or under scallops, or next to tank walls. When fish searched for food, they swam just above the substrate with pelvic fins extended in front and to the side of the head, lightly touching the substrate (Herrick 1904; Bardach and Case 1965; Pearson et al. 1980).

Upon introduction of live sand shrimp or amphipods, some of the red hake immediately chased and attempted to capture prey still in the water column. Inactive fish became active and exhibited characteristic food-searching behavior. Fish often did not appear to detect an inactive sand shrimp or amphipod, even when close to or swimming over one. However, if contact were made (usually with the extended pelvic fins) and the prey moved, the red hake attempted a capture. Some prey were small enough to be ingested whole. Others, too large to be ingested whole, were held in the fish's jaws and eventually swallowed head or tail first, this taking as long as 15 minutes to complete.

Attacks were not always successful. The sand shrimp were able to spring from the substrate into the water column with a rapid flexure of the abdomen, then swim to another location and resettle. Amphipods swam away rapidly, changing the direction of their escape continually. Some captures occurred after little or no pursuit, but others followed many repeated escapes and pursuits.

Effects of Food Deprivation

The mean weight of amphipods consumed in each 15-minute feeding bout increased with the duration of food deprivation, and reached an apparent asymptote at 7–9% of body weight after 40–50 hours of deprivation (Fig. 2). The largest percentage of each 15-minute meal was always ingested in the first 3 minutes regardless of the length of deprivation, although the number of amphipods eaten during this interval in-

TABLE 1.—*Stomach contents of juvenile red hake collected in association with sea scallops. Values are percentages of the 83 stomachs with food that contained each item. Mean fish total length was 48 mm (range 23–93 mm).*

Food category	Occurrence (%)
Total Crustacea	79.6
Unidentifiable	28.9
Decapoda	26.7
Amphipoda	10.8
Copepoda	10.8
Mysidacea	6.0
Cumacea	1.2
Unidentifiable noncrustacean material	20.5

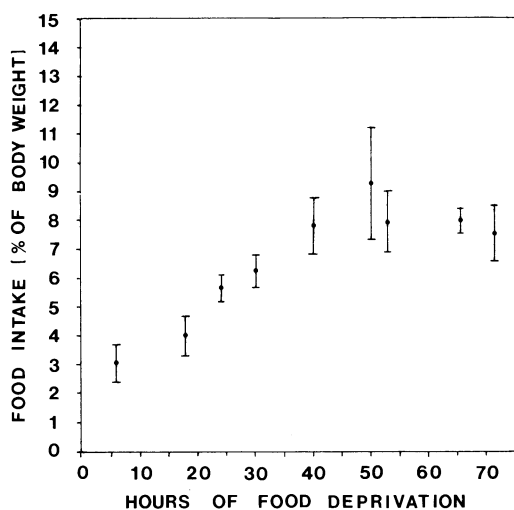


FIGURE 2.—Fifteen-minute food intake (% of body weight) of juvenile red hake versus the hours of prior food deprivation. Points are means (± 1 SE) for four fish, and values at 6, 18, 24, and 30 hours of food deprivation were pooled from more than one feeding after similar deprivation periods.

creased with deprivation (Table 2). In each 30-minute interval that followed, the mean number consumed was not significantly affected by deprivation.

Extension of pelvic fin rays during the 3 minutes before prey introduction, a measure of feeding motivation, was of short duration after 6 and 18 hours of food deprivation (Fig. 3). Fin extension became most pronounced after 24–40 hours, and again after 72 hours of deprivation, but occurred for shorter periods of time after 40–50 hours of deprivation.

Daily Food Consumption

Red hake ate 1–7 sand shrimp during 82 hours; their average daily consumption was 7.4% (1.4–16.3%) of body weight. This percentage decreased as the weight of the fish increased (Fig. 4). There were no significant differences among the mean amounts of shrimp consumed daily under any of the four conditions of prey availability: 10 or 25 sand shrimp available continuously; 10 or 15 sand shrimp available during the night only (analysis of covariance, fish weight used as a covariate: $F = 1.45$; $df = 3.18$; $P > 0.25$). Thus, the mean daily consumption was not affected by either the shrimp densities used

TABLE 2.—Mean numbers of amphipods eaten by juvenile red hake during 3-minute intervals of a 15-minute bout, related to the time of prior food deprivation, based on at least three replicates of four fish. Within the column with a significant F value (analysis of variance), means with a letter in common are not significantly different (least significant differences; $P < 0.05$).

Hours of food deprivation or statistic	Intervals in a feeding bout (minutes)				
	0–3	3–6	6–9	9–12	12–15
6	1.1 a	0.1	0.5	0.2	0.3
18	2.6 b	0.7	0.2	0.1	0.2
24	3.6 b	0.9	0.2	0.3	0.3
>40	5.2 c	1.0	0.6	0.5	0.6
F (3,57 df)	20.897	2.265	1.311	1.954	2.185
P	<0.01	NS	NS	NS	NS

or the amount of time the predator and the prey were held together.

Prey Abundance and Growth

Over 24 days, red hake fed 10 sand shrimp daily (high prey abundance) grew significantly faster than those fed 10 sand shrimp every 4 days (low prey abundance) whether the measure was absolute or specific daily increase in length or weight (Table 3). Condition factors (K), not

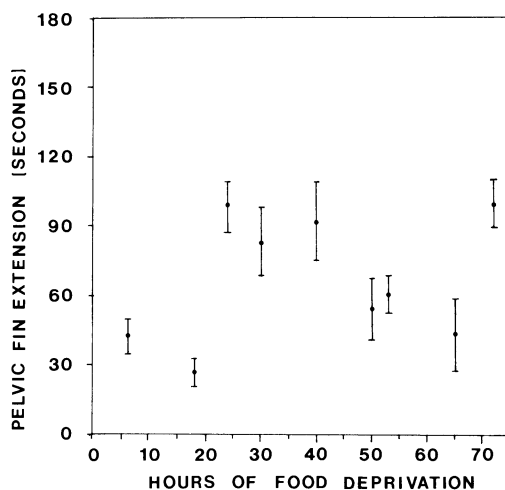


FIGURE 3.—Mean time (seconds) juvenile red hake extended their modified pelvic fins in a 3-minute pre-feeding observation period, versus the hours of prior food deprivation. Means (± 1 SE) are based on four fish, and values at 6, 18, 24, and 30 hours of food deprivation were pooled from more than one feeding after similar deprivation periods.

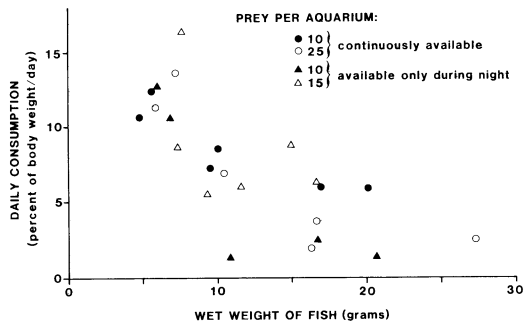


FIGURE 4.—Daily consumption (% of fish body weight/day) of sand shrimp by individual juvenile red hake versus the wet weight of each fish under different conditions of prey availability.

significantly different between the two groups on day 1, were greater for the group with high prey abundance by day 24.

Discussion

The predominance of crustaceans in the diet of juvenile red hake generally agrees with what has been reported by others. For example, red hake collected on the continental shelf between Nova Scotia and North Carolina (Bowman 1981)

and off the coast of Maine (Garman 1983) showed a diet dominated by sand shrimp and amphipods.

Chemoreception plays an important role in food detection and localization by red hake (Herrick 1904; Bardach and Case 1965; Pearson et al. 1980). In our experiments, however, fish ingested prey in the water column, but were stimulated to pursue prey along the bottom only when the prey were active, which often occurred after the prey had been contacted by a fish searching for food. This suggests that vision, at least under certain conditions, plays a role in mediating feeding behavior.

The amount of food taken by red hake in a meal increased with the length of time they were deprived of food, until an apparent asymptote was reached. Similar patterns have been observed in other species: for example, sockeye salmon *Oncorhynchus nerka* (Brett 1971); brown trout *Salmo trutta* (Elliott 1975); sweetlip *Parapristipoma trilineatum*, jack *Trachurus japonicus*, puffer *Fugu vermicularis porphyreus*, filefish *Stephanolepis cirrifer*, and rainbow trout *Salmo gairdneri* (Ishiwata 1968a). If the maximum amount of food eaten voluntarily by a fish in a single meal is a measure of stomach capacity

TABLE 3.—Twenty-four-day growth and condition of red hake fed sand shrimp at two rates.

Fish	Total length (mm)		Weight (g)		Condition (K) ^a		Absolute 24-day increase ^b		Specific growth rate (%/day) ^c	
	Day 1	Day 24	Day 1	Day 24	Day 1	Day 24	Length (mm)	Weight (g)	Length (mm)	Weight (g)
	High prey availability (10 sand shrimp/day)									
1	92	125	5.79	13.71	0.74	0.70	33	7.92	1.28	3.59
2	107	143	8.45	22.00	0.69	0.76	36	13.64	1.21	4.00
3	116	142	9.56	20.67	0.61	0.72	26	11.11	0.84	3.21
4	125	153	12.18	28.04	0.62	0.78	28	15.86	0.84	3.47
5	127	152	11.33	26.49	0.55	0.75	25	15.16	0.75	3.54
6	133	157	15.00	27.02	0.64	0.70	24	12.02	0.69	2.45
Mean					0.642	0.735	28.7	12.62	0.935	3.38
Low prey availability (10 sand shrimp every 4th day)										
1	104	124	7.18	11.92	0.64	0.63	20	4.74	0.73	2.11
2	108	126	7.76	11.91	0.62	0.60	18	4.15	0.64	1.78
3	114	142	9.68	19.12	0.65	0.67	28	9.44	0.92	2.84
4	121	143	12.20	20.11	0.69	0.69	22	7.91	0.70	2.08
5	152	169	23.72	31.43	0.68	0.65	17	7.71	0.44	1.17
6	178	194	37.72	48.96	0.67	0.67	16	11.24	0.36	1.09
Mean					0.658	0.652	20.2	7.53	0.632	1.85

^a (K) = 100(weight)/length³. Day-24 means were significantly different between feeding groups (Student's *t*-test; *P* < 0.01).
^b Feeding groups were significantly different by analysis of covariance: length, *P* < 0.02; weight, *P* < 0.01.
^c Specific growth rate = 100(log_eX₂₄ - log_eX₁)/24; X = length or weight. Feeding groups were significantly different by analysis of covariance: length, *P* < 0.05; weight, *P* < 0.01.

(Fänge and Grove 1979), we would conclude that stomach capacity of juvenile red hake averages 7–8% of body weight.

The tendency of juvenile red hake to eat the bulk of a meal early in a feeding bout also is typical of other species studied in this regard. Rainbow trout and jack mackerel ate the bulk of a meal in 10 minutes, and puffers and filefish in about 2 minutes (Ishiwata 1968b), sockeye salmon in 8 minutes (Brett 1971), and threespine sticklebacks *Gasterosteus aculeatus* in 9 minutes (Tugendhat 1960). Threespine sticklebacks, like red hake, increased their food-consumption rate with increasing periods of food deprivation.

The rapidity with which juvenile red hake consume a meal leads us to conclude that they are time-minimizers (Schoener 1971); that is, they capture as much food as possible in a short period of time. In addition, their consumption of food in discrete meals would classify them as discontinuous feeders (Brett 1971; Elliott 1975). Feeding in this way would enable these fish to take advantage of resources distributed transiently in space and time, and would be of selective value since it would shorten the time spent foraging away from shelter.

The mean daily consumption by juvenile red hake (7.4% of body weight for 5–22 g fish) falls within a range of values obtained in laboratory studies on other fishes of similar size: threespine sticklebacks, 12.1% of wet body weight (Beukema 1968); black acaras *Cichlasoma bimaculatum*, 14% of dry body weight (Davis and Warren 1968); sockeye salmon, 6.9% of dry body weight (Brett 1971); and *Micropogon opercularis*, 3.3–4.6% of wet body weight (DeCiechowski 1981). Daily consumption for a 5-g red hake (11–12% of body weight) was higher than the single-meal consumption (8% of body weight) for a similar-sized red hake, indicating that the fish could take more than one meal per day.

The amount of sand shrimp consumed in a day relative to body weight decreased as the size of a fish increased, similar to what has been shown previously for other species (for example, Brett 1971). However, because density of prey was held constant, the ration decreased as the fish size increased. This makes it impossible to separate the effect of fish size from ration size.

The increase in the duration of pelvic fin ex-

tension with increased food deprivation apparently was associated with an increase in feeding motivation. The decrease in fin extension between 50 and 60 hours of food deprivation probably was due to a change in the red hake's food searching strategy rather than a decrease in the feeding motivation, because food consumption remained high over this range. The result of this decrease in food searching may be a saving in energy expenditure in environments where food may be scarce.

Differences in growth rate between different year classes in both yearlings and older fish have been observed for red hake by Rikhter (1973), who speculated that such differences could be caused by changes in the food supply. Although there was no evidence to support this, our own laboratory data suggest that the availability of food could play a role in modifying yearly growth rate so that fish of the same age could be different sizes. When the possibility of an overlap exists in the sizes of different aged fish, the practice of using an age-length distribution from one year to determine age structure in subsequent years may lead to spurious conclusions about the age composition of the population (Westrheim and Ricker 1978).

The mean specific growth rate in length (0.94% TL/day) for fish in the high-prey-abundance groups was very close to values given for laboratory (1.00% TL/day) and field (0.93% TL/day) growth rates at similar temperatures by Steiner et al. (1982), whereas fish in the low prey abundance grew at a much slower rate (0.63% TL/day). Steiner et al. (1982) found a positive correlation between temperature and specific growth in length. However, in the study reported here, temperature was constant for fish in both high and low prey abundance, and could not have caused the observed differences in growth rates.

Similar studies, conducted on winter flounder *Pseudopleuronectes americanus* (Tyler and Dunn 1976) and plaice *Pleuronectes platessa* (Jobling 1982) showed that when food rations were limited, the growth rate decreased. Our study differed in that two different densities of live prey were offered as food and thus rations for the fish in these densities were different. Although the rations were somewhat variable due to our attempt to regulate prey densities, our results do show a decrease in growth rate due to the

decreased prey density. Thus, juvenile red hake of the same age could be different sizes due to prey availability in the environment.

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