FOOD HABITS OF PACIFIC WHITING, *MERLUCCIUS PRODUCTUS*, OFF THE WEST COAST OF NORTH AMERICA, 1967 AND 1980

The Pacific whiting, *Merluccius productus*, forms a major groundfish resource off the west coast of North America. According to Nelson and Larkins (1970) it is "one of the most abundant species of fish in the northeastern Pacific Ocean." Fishing effort on the Pacific whiting stock has increased dramatically since 1965 when it became the target of the United States and Soviet fishermen (Grinols and Tillman 1970). The stock is now the basis of a large U.S. joint-venture and domestic fishery. Management of this stock requires more detailed information on the major prey of Pacific whiting throughout its distribution.

Previous studies have shown that Pacific whiting feed primarily on euphausiids, but at certain times commercially important fish or pandalid shrimp may constitute an important item in the diet (Gotshall 1969a, b; Alton and Nelson 1970; Outram and Haegele 1972). Indirect evidence of nocturnal feeding by Pacific whiting has also been presented by Alton and Nelson (1970) and by Outram and Haegele (1972). Although these studies contain useful baseline information, they are not complete enough to describe quantitatively the predatory interactions of Pacific whiting, with the exception of Gotshall's (1969a, b) study which focused only on the impact of whiting predation on the commercially important pink shrimp, *Pandalus jordani.*

The objective of the present study is to provide a quantitative account of the predatory patterns of Pacific whiting by identifying their major prey items, determining whether size-selective predation occurs, examining diel feeding behavior, and calculating daily ration.

Collection and Processing of Samples

Stomachs of adult Pacific whiting were collected in 1967 off the Oregon and Washington coasts (Livingston and Alton 1982) and in 1980 off Oregon, Washington, and Vancouver Island (Fig. 1). Also, samples of juvenile Pacific whiting taken off the California coast in the fall of 1980 were saved for stomach analysis (Table 1). Samples were obtained during resource assessment surveys using either bottom or midwater trawls. Only vessels operating during daylight hours used bottom trawls to survey whiting which were mostly on the sea bottom. Midwater trawls were used on those vessels with both day and night operations so that the net could be set at depths of greatest whiting concentration. Stomach samples were taken opportunistically at standard resource assessment stations. In 1967, most stations were at bottom depths of <100 m, while in 1980 bottom depths ranged from 77 to 298 m. Stomachs were taken randomly from the entire catch in 1967, but were stratified in 1980 by 10 cm whiting length groups.

A 15-h time series of stomach samples was taken in 1967 at a station off the Washington coast to detect

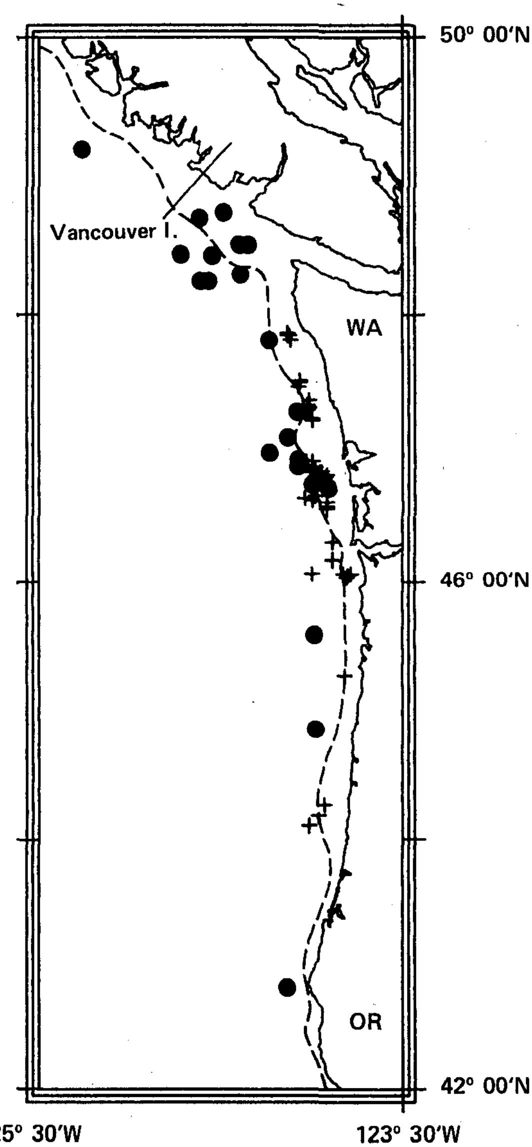

FIGURE 1.—Sampling locations for Pacific whiting, *Merluccius productus*, in 1967 (+) and 1980 (·) in relation to the 100 m depth contour (---).

TABLE 1.—Dates, locations, station information, and sample sizes of stomach samples of Pacific whiting taken from the northwest Pacific Ocean, 1967 and 1980.

Vessel	Location	Sampling period	Tows Number[1]	Tows Type[2]	Bottom depth range (m)	No. of stomachs collected[3]
RV *John M. Cobb*	Oregon	Apr.-July 1967	6 (2)	MW	84-126	104 (86)
RV *Commando*	Oregon	June 1967	1 (1)	MW	144	7 (8)
MV *Baron*	Oregon	June 1967	4 (0)	MW	49-77	91 (5)
RV *John M. Cobb*	Washington	May-July 1967	30 (2)	MW	53-156	785(108)
MV *Baron*	Washington	June 1967	8 (0)	MW	62-75	191 (56)
MV *Recruit*	Washington	June 1967	1 (0)	MW	75	9 (2)
MV *St. Michael*	Washington	June-July 1967	9 (0)	MW	55-84	243 (54)
RV *Tikhookeanskiy*	Oregon	Apr.-May 1980	3 (3)	BT	120-200	53 (13)
RV *Miller Freeman*	Washington-Vancouver I., B.C.	Aug.-Sept. 1980	6 (6)	MW	111-298	34 (–)
MV *Pat San Marie*	Washington-Vancouver I., B.C.	Sept. 1980	14(10)	BT	77-293	77 (–)
RV *Poseydon*	California	Oct. 1980	2 (2)	BT	130-160	40 (12)

[1]Number of tows at bottom depths >100 m are given in parentheses.
[2]MW = midwater trawl; BT = bottom trawl.
[3]Stomachs containing food. Number of empties in parentheses.

feeding discontinuity. A total of 258 stomachs were collected at seven different times of day (Table 2).

Fish showing signs of regurgitation were discarded from samples. Lengths were recorded for fish with stomachs containing food. The stomachs of adult fish were then excised and placed in muslin bags with a specimen card containing fish length and station information. Juvenile fish were placed whole in muslin bags for later stomach excision in the laboratory. All samples were preserved in a 10:1 seawater/formaldehyde mixture.

Because of incomplete records of numbers of empty stomachs sampled on two cruises in 1980, that data set could not be used for daily ration calculations. In 1967, however, numbers of empty stomachs at each station were recorded along with corresponding fish lengths.

Fish lengths were converted to weights using the weight-length relationship for Pacific whiting, sexes combined (Traynor[1]):

$$w_g = 0.004774 \quad l_{cm}^{3.0947}.$$

[1]J. Traynor, Fishery Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112, pers. commun. December 1982.

TABLE 2.—Summary of a diel series of Pacific whiting stomach samples obtained on RV *John M. Cobb*, 14-15 July, 1967 off the Washington coast lat. 47° 19′N, long. 124° 33′W at a bottom depth of 65 m.

Time of day (P.S.T.)	No. of stomachs With food	No. of stomachs Empty	Total weight of stomach contents (g)	Mean fish length (mm)
1800	30	1	557.9	486
2100	34	2	474.8	429
2300	36	0	215.6	509
0100	61	1	348.2	524
0300	35	1	373.8	500
0400	17	2	83.9	533
0900	38	0	403.3	484
	251	7		

Stomachs were analyzed individually in the laboratory, with the exception of the fall 1980 samples which were analyzed by composite groups. Prey items were identified to the lowest practical taxon, and damp weight and number of each prey taxon per stomach or composite of stomachs were recorded. In 1967, there was some loss of information on the number of prey in some taxa because no attempt was made to count certain prey items when they showed a fair degree of digestion.

Food of Pacific Whiting

Euphausiids, including *Thysanoessa spinifera* and *Euphausia pacifica*, were the dominant food of Pacific whiting in 1967, constituting 72.2 and 90.2% by weight of the diet of Pacific whiting taken off Oregon and Washington, respectively (Table 3). In 1980, euphausiids were also the predominant item in the diets of Pacific whiting <200 mm in length off California (100% by weight) and of Pacific whiting 350-449 mm long off Oregon (99.6% by weight).

Schooling fish were also important dietary components for Pacific whiting. Northern anchovy, *Engraulis mordax*, comprised 16.4% by weight of the diet of Pacific whiting in summer 1967 off Oregon. In spring 1980 off Oregon, eulachon, *Thaleichthys pacificus*, comprised 22% by weight of the diet of 450-549 mm Pacific whiting and 79.6% by weight of the diet of 550+ mm fish. Pacific herring, *Clupea harengus pallasi*, dominated the diets of Pacific whiting taken in summer 1980 off Washington and Vancouver Island, constituting 54.2 and 67% by weight of the 450-549 mm and 550+ mm whiting size groups, respectively.

Other fish items were predominantly flatfish and rockfish, *Sebastes* sp. Pandalid shrimp, including *Pandalus jordani*, comprised <5% by weight of the

TABLE 3.—Percentage by weight of prey items in the stomachs of Pacific whiting, 1967 and 1980, off the west coast of North America and summary of average stomach content weight (not including empty stomachs)[1].

	Summer 1967 Oregon	Summer 1967 Washington	Fall 1980 California	Spring 1980 Oregon			Summer 1980 Wash.-Vancouver I.	
	Mean predator size (mm)		Predator-size group (mm)					
Prey item	491	503	<200	350-449	450-549	550+	450-549	550+
Crustacea								
Euphausiids								
T. spinifera	21.1	35.3	72.5	6.2	9.1	T	19.0	1.7
E. pacifica	1.7	0.3	6.8	93.0	26.9	1.0	4.2	3.0
Unidentified	49.4	54.6	20.7	0.4	23.4	0.2	6.6	2.7
Crab megalops larvae	1.1	0.1						
Mysidacea	T	T	T	—	—	—	—	T
Pandalidae (unidentified)	0.3	0.3	—	—	3.7	4.5	3.0	0.3
Pandalus jordani	—	—	—	—	—	—	0.7	1.7
Sergestes similis	—	T	—	—	—	—	0.1	0.2
Pasiphaea pacifica	—	—	—	—	—	—	—	0.1
Spirontocaris sp.	—	—	—	—	—	—	—	T
Crangon sp.	0.2	0.2	—	—	—	—	0.4	—
Caridea (unidentified)	0.1	0.4	—	—	—	—	0.1	—
Gonatus sp.	—	—	T	—	0.1	0.2	—	—
Pisces								
Engraulis mordax	16.4	0.1	—	—	—	—	—	—
Clupea harengus	—	—	—	—	—	—	54.2	67.0
Thaleichthys pacificus	—	—	—	—	22.0	79.6	3.3	9.4
Osmeridae	0.7	0.8	--	—	7.8	—	1.0	2.3
Sebastes sp.	—	T	—	—	—	—	4.1	0.1
Liparis fucensis (larvae)	—	—	—	—	—	—	0.2	—
Agonidae	—	—	—	—	—	—	0.5	—
Gadidae	—	1.3	—	—	—	—	0.2	—
Pleuronectidae (unid.)	—	T	—	—	6.8	6.3	0.6	—
Citharichthys sp.	—	—	—	—	—	—	0.6	—
Poroclinus rothrocki	—	—	—	—	—	—	0.7	—
Icicthys lockingtoni	—	—	—	—	—	—	—	8.9
Zoarcidae	—	0.5						
Unidentified	8.8	5.7	—	0.4	0.2	8.1	0.5	2.5
Number of Stomachs	202	1,228	40	16	17	20	70	41
Total weight of stomach contents(g)	2,403.8	10,560.8	13.65	133.7	86.74	607.3	849.1	934.6
Mean stomach content weight (g)	11.9	8.6	3.3	8.4	5.1	30.4	12.1	22.8
Mean fish length (mm)	491	503	132	380	506	587	529	591
Percentage body weight of stomach contents	1.46	0.96	23.57	2.27	0.57	2.14	1.18	1.57

[1]T indicates trace amounts of food, i.e. <0.1% by weight of the diet.

Pacific whiting diet in all cases. Other shrimp eaten included *Cragon* sp., *Pasiphaea pacifica*, and *Sergestes similis*. Other invertebrates were predominantly crab megalops larvae.

In terms of general prey categories, Pacific whiting in 1967 off Oregon ate proportionally more fish, especially northern anchovy, than did whiting in 1967 off Washington (Fig. 2). The diets of similar-sized Pacific whiting (450-549 mm) taken in 1980 off Oregon and Washington-Vancouver Island, however, contained an even greater proportion of fish (Fig. 3), but of different species. A shift in major dietary component from euphausiids to fish occurred as the length of Pacific whiting increased during spring and late summer of 1980. Diets of Pacific whiting >550 mm consisted of 90.2% fish by weight.

To illustrate the switch in food from euphausiids to fish as the length of Pacific whiting increased, the percentage frequency of occurrence of Pacific herring in Pacific whiting stomachs was plotted against Pacific whiting length for the late summer 1980 samples (Fig. 4). A steady increase in the occurrence of Pacific herring is noticeable up to the 561-580 mm whiting length interval. Thereafter, the curve

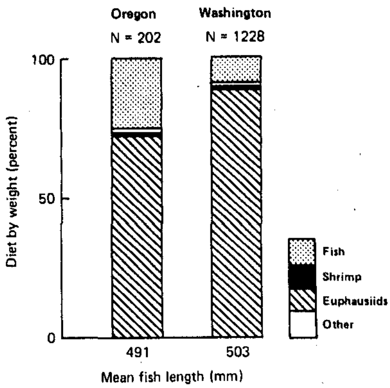

FIGURE 2.—Percentage by weight of major prey categories in the diet of Pacific whiting, *Merluccius productus*, taken off Oregon and Washington, summer 1967.

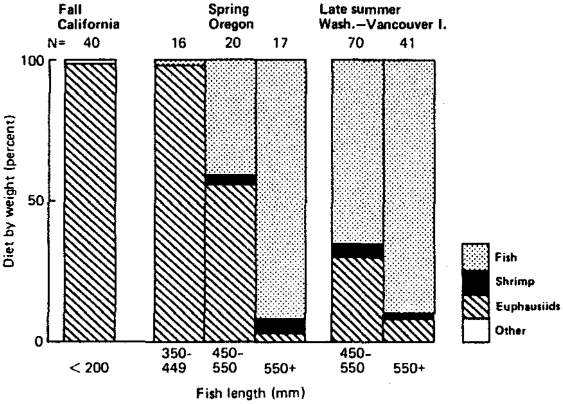

FIGURE 3.—Percentage by weight of major prey categories in the diet of Pacific whiting, *Merluccius productus*, for different length groups of whiting at various locations in 1980.

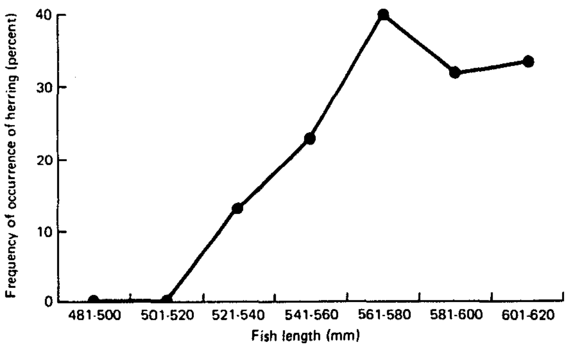

FIGURE 4.—Percent frequency of occurrence of Pacific herring, *Clupea harengus pallasi*, in stomachs of different length groups of Pacific whiting, *Merluccius productus*, taken late summer 1980 off Washington and Vancouver Island.

appears to level off at a 30% occurrence of Pacific herring.

The difference in Pacific whiting diets between the years 1967 and 1980 is mainly seen as a greater percent consumption of fish in 1980 by whiting >450 mm. No clear explanation is available because sample size in 1980 was small and samples were obtained further offshore than in 1967. The most distinct relationship noted in these results is the tendency of Pacific whiting to consume prey species which occur in patches or schools, usually euphausiids and pelagic fishes such as eulachon, northern anchovy, and Pacific herring which also prey on euphausiids (Wailes 1936; Barraclough 1964; Barraclough et al. 1968). Likewise, the majority of the invertebrate prey of Pacific whiting (e.g., pandalid, sergestid, and pasiphaeid shrimp) are documented predators of euphausiids (Renfro and Pearcy 1966; Pearcy 1970; Judkins and Fleminger 1972). Thus, euphausiids appear to be the unifying factor, their presence attracting not only the Pacific whiting but also other organisms which then become available prey for Pacific whiting.

Alton and Nelson (1970) reported the main food items of Pacific whiting off northern Oregon and Washington to be euphausiids, eulachon, and pandalid shrimp. Similarly, Outram and Haegele (1972) found euphausiids, pandalid shrimp, and schooling fish (such as Pacific sand lance, *Ammodytes hexapterus*; Pacific herring; and eulachon) most frequently in stomachs of Pacific whiting sampled off Vancouver Island. They also found Pacific herring to be a more important component in the diet of large Pacific whiting. Off California, Gotshall (1969a) discovered pandalid shrimp, euphausiids, flatfish, and schooling fish constituted most of the whiting's food. Although Gotshall (1969a, b) showed that on the average pandalid shrimp dominated the Pacific whiting diet, in some months fish or euphausiids were found to be the primary food items. This seasonal change in diet may have resulted from the changing size composition of the Pacific whiting population in the study area due to northward migration of adults in spring.

Predator-Prey Size Relationship

An examination of the relationship between a fish predator's size and its choice of prey sizes may aid in understanding, interpreting, and quantifying a predator's feeding habits (Ursin 1973; Werner 1974; Agger and Ursin 1976; Werner and Hall 1977; Hahm and Langton 1980). Calculation of the frequency distribution of predator weight to prey weight ratios, as described by Ursin (1973), quantifies a predator's food size preference through central tendency measures of its distribution. These measures can then be used directly as input parameters to models such as Andersen and Ursin's (1977) multispecies Beverton and Holt model or the various multispecies VPA models (Helgason and Gislason 1979; Sparre 1980).

The basic method of calculating predator-prey size ratios utilizes the total weight in grams (W_j) and total number (ΣN_j) of each prey type j in a collection of predator stomachs. The individual mean weight of each prey type ($\bar{w}_j$) is calculated and compared with the mean predator weight ($\bar{w}_i$). Ursin (1973) discovered that for benthic-feeding fish the frequency distribution of the ratios of predator weight to prey weight ($\bar{w}_i/\bar{w}_j$) was approximately log-normal in shape. Therefore, a plot of ln ($\bar{w}_i/\bar{w}_j$) vs. ΣN_j should be a normally shaped curve.

This methodology was applied to the 1980 Pacific whiting stomach data. There was a total of 204 Pacific whiting in this sample, ranging in length from 116 to 645 mm, with $\bar{w}_i$ of 862 g. These Pacific whiting consumed a total of 8,940 food items $[\Sigma(\Sigma N_j)]$ with individual $\bar{w}_j$ ranging from 0.002 g for amphipods to 83 g for a medusafish, *Icicthys lockingtoni*.

The solid lines in Figures 5-7 represent the shape of the predator-prey size curves resulting from the analysis of 1980 data when separated into three predator size groups. However, these curves do not necessarily represent the prey-size preference of Pacific whiting. Lawlor (1980) stated that the proportion of a food item in the diet of a predator is a function not only of the predator's choice for that item but also of the item's availability. Only when abundances of all prey items are equal, do the observed proportions of prey items in a predator's stomach reflect the predator preference.

To determine the prey-size preference of Pacific whiting, we may examine a theoretical situation in which equal numbers of each prey size are offered to the Pacific whiting. Assuming the numbers of each prey type in the environment to be inversely proportional to the prey type's weight (Ursin 1973), this situation can be created by multiplying total ΣN_j by $\bar{w}_j$. To adjust for predator size, this quantity is divided by $\bar{w}_i$. The dashed lines in Figures 5-7 depict the theoretical results of offering equal numbers of each prey size to the whiting.

Pacific whiting <200 mm, whose diet consisted mainly of euphausiids, have a very narrow prey-size selection curve (Fig. 5) which reflects their choice of a narrow size range of food. The dashed line of the pre-

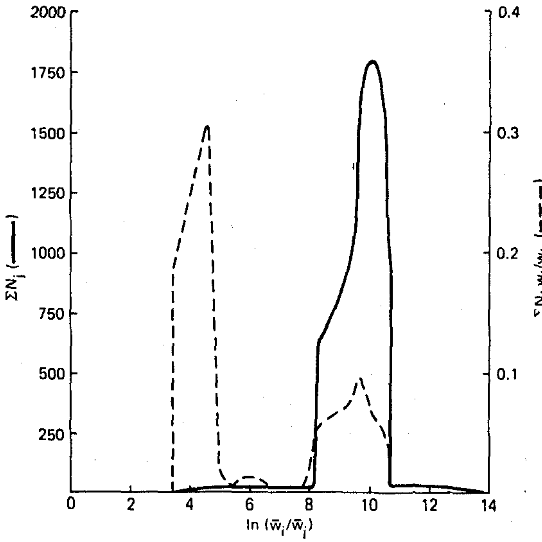

FIGURE 6.—Frequency distribution of predator-prey size scores for Pacific whiting, *Merluccius productus*, predators 350-549 mm long with an average weight ($\bar{w}_i$) of 876.2 g, under natural (—) and simulated (---) conditions.

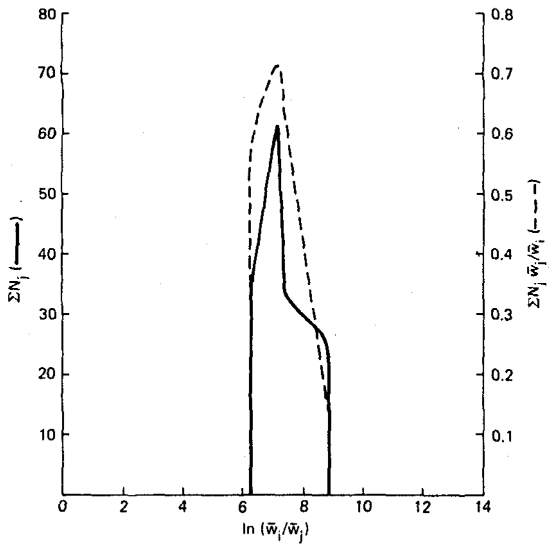

FIGURE 5.—Frequency distribution of predator-prey size scores for Pacific whiting, *Merluccius productus*, predators <200 mm long with an average weight ($\bar{w}_i$) of 13.2 g, under natural (—) and simulated (---) conditions.

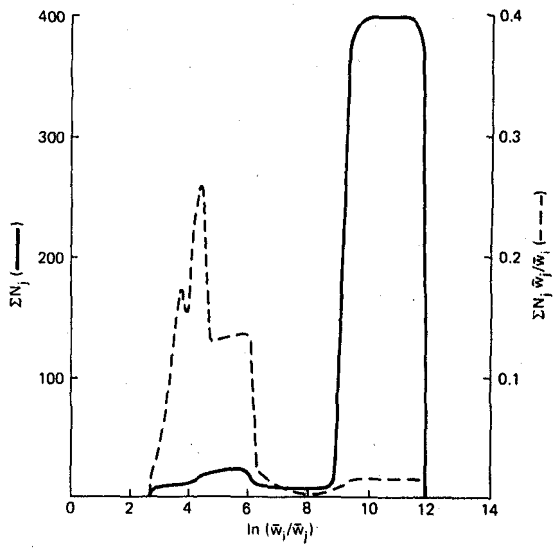

FIGURE 7.—Frequency distribution of predator-prey size scores for Pacific whiting, *Merluccius productus*, predators 550+ mm long with an average weight ($\bar{w}_i$) of 1,441.3 g, under natural (—) and simulated (---) conditions.

ference curve for the small Pacific whiting closely follows the selection curve in which euphausiid-sized prey dominated.

The selection curve for the middle-sized group of Pacific whiting, 350-549 mm, also peaks sharply but with long, trailing ends indicating that euphausiids dominated the diet in numbers although small numbers of prey items, both smaller and larger than euphausiids, were eaten (Fig. 6). The preference curve is bimodal with the largest mode corresponding to a predator-prey size ratio of about 100:1, while the second mode reflects a continuing preference for euphausiid-sized items.

The largest size group of Pacific whiting, 550+ mm, have an actual prey-size curve which depicts the numerical dominance of euphausiids in their food by the sharp peak at ln $(\bar{w}_i/\bar{w}_j)$ value of about 10.5 (Fig. 7). There is also a pronounced hump in the left tail of the curve in the region of a predator-prey weight ratio corresponding to a large Pacific whiting predator and a Pacific herring-sized prey. The preference curve shifts completely away from the selection curve for these Pacific whiting. The mode for euphausiid prey is dampened almost completely and the most prevalent predator-prey size ratio is about 130:1, equivalent to the ratio of a large Pacific whiting predator to a Pacific herring-sized prey.

Thus, it appears that the diets of Pacific whiting <200 mm long reflect a preference for euphausiid-sized prey. Although the 350-549 mm size group of Pacific whiting shows a dominant prey-size preference of 100:1, the calculated preference curve deviates from the predicted normal shape due to a second mode in the region corresponding to euphausiid-sized prey. Deviations from normality can be caused when the abundance of a naturally occurring prey item is not inversely proportional to its weight as assumed or when the prey occur in such dense patches that the predator consumes more than one prey item at a time (Ursin 1973). The latter case is a likely description of Pacific whiting predation on euphausiids, though this would have to be verified through direct observation. The largest size group of Pacific whiting shows a preference for Pacific herring-sized prey with a median predator-prey size ratio of about 130:1. This is similar to Ursin's (1973) calculation of an average predator-prey size ratio of 160:1 for Atlantic cod, *Gadus morhua*.

The prey-size preference of Pacific whiting is reasonably described by Ursin's model. The major parameters which define the shape of the prey-size preference curve are the mean ($\bar{x}$) and variance (s^2) of the frequency distribution of predator-prey size scores (Table 3) when equal numbers of prey sizes are offered to the predator. These parameters are $\bar{x} = 7.16, s^2 = 0.42$ for <200 mm fish; $\bar{x} = 6.48, s^2 = 7.18$ for 350-549 mm fish; and $\bar{x} = 4.88, s^2 = 2.40$ for 550+ mm fish.

Diel Feeding Pattern

A total of 258 Pacific whiting stomachs (7 of which were empty) were taken at 7 different times of day during a 15-h period at a location off the Washington coast in July 1967. To detect any discontinuity in feeding during this period, a one-way analysis of covariance was performed using the model

$$y = \mu + a_i + bx_i,$$

where y is the weight of the stomach contents and x is the Pacific whiting weight. If the stomachs are grouped by time, i, then the test of among-time variation in the weight of stomach contents after adjustment for Pacific whiting weight is the test of the equality of the intercepts, a_i, given a common slope, b (Jenkins and Green 1977). The F-ratio for this test is the among-group variance estimate divided by the within-group variance estimate.

Figure 8 plots mean stomach content weight as a percentage of Pacific whiting weight for samples taken during the 15-h period in July 1967. Stomach content weight per fish weight is highest at 1800 h, with a value of 2.5%, and slightly increases between 0100 and 0300 h and between 0400 and 0900 h. Despite the great variability among all time periods, the analysis of covariance of the data rejects the null hypothesis of no difference between group means of stomach content weight at the 0.01 level of significance [$F(6{,}243 \text{ df}) = 7.83$]. Therefore, feeding by Pacific whiting was discontinuous during the sampling period.

Stomach fullness was highest in early evening (1800 P.S.T.), with some increases after midnight (0300 P.S.T.) and morning (0900 P.S.T.). These fullness peaks coincide with the times of euphausiid, *Thysanoessa spinifera*, concentration in the same portion of the water column where the Pacific whiting are concentrated—nearbottom at evening and morning and nearsurface after midnight (Alverson and Larkins 1969; Alton and Blackburn 1972).

Hickling (1927) noted that stomachs of European hake, *Merluccius merluccius*, were fullest at midnight. He also suggested that European hake migrate vertically in search of euphausiids. Silver hake, *Merluccius bilinearis*, of the northwest Atlantic also feed nocturnally, starting their feeding activity after dusk and actively feeding until midnight (Bowman and Bowman 1980). Thus, fish of the genus *Merluccius*

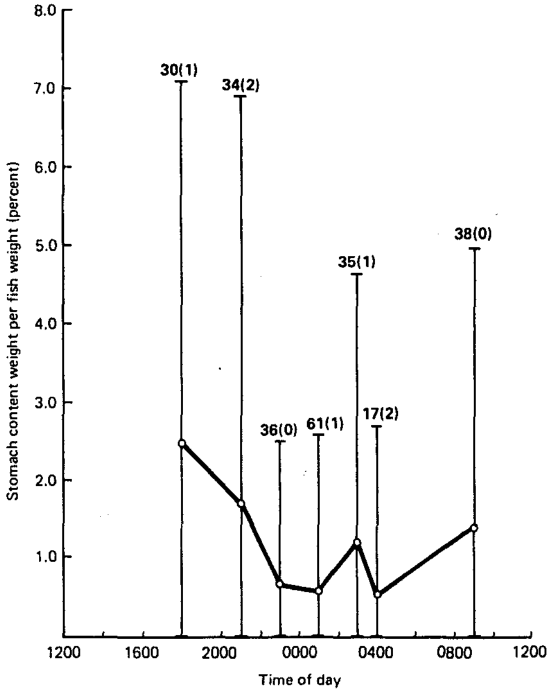

FIGURE 8.—Mean stomach content weight as a percentage of Pacific whiting, *Merluccius productus*, weight over part of a 24-h period at a diel sampling location off the Washington coast in July 1967 (vertical bars indicate the range of values in a given time period). Numbers of stomachs containing food are noted above each time period, with numbers of empty stomachs in parentheses.

have similar nocturnal feeding habits, although the timing of peaks in stomach fullness is not identical.

Daily Ration

An estimate of the average food intake by a fish predator is needed to evaluate predation mortality rates of prey species in some models (Majkowski and Waiwood 1981). Daily ration is a useful measure of food intake and can be calculated from field data if there exists an estimate of the gastric evacuation rate (Eggers 1977; Elliott and Persson 1978). The total 1967 Pacific whiting data set, containing 1,749 stomach samples, is used here to compute daily ration, since it includes a large number of samples taken at many different times of day and records of the number of empty stomachs present in the samples which is necessary for daily ration calculation.

The Elliott and Persson (1978) model which assumes an exponential, temperature-dependent evacuation rate, R, is applied to the data set for the daily ration computations. If stomach samples are collected at intervals of t hours, the mean stomach content weight as a percentage of fish weight, S_i, in each interval i is calculated for a total of m intervals over the 24-h period. According to Elliott and Persson (1978) the daily ration in terms of percentage body weight, ΣC_t, can then be evaluated by the following expression:

$$\Sigma C_t = \frac{Rt}{1 - e^{-Rt}} \sum_{i=1}^{m} S_i \, (1 - e^{-Rt}) = 24\bar{S}R \qquad (1)$$

where $\bar{S} = \Sigma S_i/\mathrm{m}$. Durbin and Durbin (1980) found that the relationship between R and water temperature T for marine fish eating small food organisms was

$$R = 0.416e^{0.105T}. \qquad (2)$$

This Equation (2) was used to calculate R here, since most prey eaten by Pacific whiting in 1967 were small organisms, mainly euphausiids. Some error is introduced at this point because part of the diet consisted of fish which are evacuated at a slower rate than small crustaceans (Durbin et al. 1980). Water temperature was assumed to be 8.2°C, the approximate monthly mean temperature for July at 60 m below surface in the Washington-Oregon coastal region (Robinson 1976) where most of the fish were collected.

The calculated daily ration of Pacific whiting, using Equations (1) and (2) on the 1967 data, is equal to 2.5% body weight/d for an average Pacific whiting size of 500 mm. Although this estimate is probably high, due to the use of the evacuation rate only for small crustaceans, it is comparable to other estimates. Daily ration estimates for a similar fish—adult silver hake in the northwest Atlantic—range between 0.6 and 2.7% body weight/d (Durbin et al. 1980; Cohen and Grosslein 1981; Pennington 1981). The present estimate is reasonable but should be verified further before it is used in calculating energy budgets for Pacific whiting.

Literature Cited

AGGER, P., AND E. URSIN.
1976. Food and food preference of the grey gurnard. Int. Counc. Explor. Sea, ICES C.M. 1976/F:41, 8 p.

ALTON, M. S., AND C. J. BLACKBURN.
1972. Diel changes in the vertical distribution of the euphausiids, *Thysanoessa spinifera* Holmes and *Euphausia pacifica* Hansen, in coastal waters of Washington. Calif. Fish Game 58:179-190.

ALTON, M. S., AND M. O. NELSON.
1970. Food of Pacific hake, *Merluccius productus*, in Washington and northern Oregon coastal waters. *In* Pacific hake, p. 35-42. U.S Fish Wildl. Serv., Circ. 332.

ALVERSON, D. L., AND H. A. LARKINS.
1969. Status of knowledge of the Pacific hake resource. Calif. Coop. Oceanic Fish. Invest., Rep. 13, p. 24-31.
ANDERSEN, K. P., AND E. URSIN.
1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Medd. Dan. Fisk. Havunders N.S. 7:319-435.
BARRACLOUGH, W. E.
1964. Contribution to the marine life history of the eulachon *Thaleichthys pacificus*. J. Fish. Res. Board Can. 21:1333-1337.
BARRACLOUGH, W. E., D. G. ROBINSON, AND J. D. FULTON.
1968. Number, size composition, weight, and food of larval and juvenile fish caught with a two-boat surface trawl in Saanich Inlet, April 23-July 21, 1968. Fish Res. Board Can. Manuscr. Rep. Ser. 1004, 305 p.
BOWMAN, R. E., AND E. W. BOWMAN.
1980. Diurnal variation in the feeding intensity and catchability of silver hake (*Merluccius bilinearis*). Can. J. Fish. Aquat. Sci. 37:1565-1572.
COHEN, E., AND M. GROSSLEIN.
1981. Food consumption in five species of fish on Georges Bank. Int. Counc. Explor. Sea, ICES C.M. 1981/G:68, 11 p.
DURBIN, E. G., AND A. G. DURBIN.
1980. Some factors affecting gastric evacuation rates in fishes. Int. Counc. Explor. Sea, Biol. Oceanogr. Comm., ICES C.M. 1980/L:59, 15 p.
DURBIN, E., A. DURBIN, R. LANGTON, R. BOWMAN, AND M. GROSSLEIN.
1980. Analysis of stomach contents of Atlantic cod (*Gadus morhua*) and silver hake (*Merluccius bilinearis*) for the estimation of daily rations. Int. Counc. Explor. Sea, Biol. Oceanogr. Comm., ICES C.M. 1980/L:60, 21 p.
EGGERS, D. M.
1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. 34:290-294.
ELLIOTT, J. M., AND L. PERSSON.
1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977-991.
GOTSHALL, D. W.
1969a. Stomach contents of Pacific hake and arrowtooth flounder from northern California. Calif. Fish Game 55:75-82.
1969b. The use of predator food habits in estimating relative abundance of the ocean shrimp, *Pandalus jordani* Rathbun. FAO Fish. Rep. 57, p. 667-685.
GRINOLS, R. B., AND M. F. TILLMAN.
1970. Importance of the worldwide hake, *Merluccius*, resource. *In* Pacific hake, p. 1-21. U.S. Fish Wild. Serv., Circ. 332.
HAHM, W., AND R. LANGTON.
1980. Prey selection based on predator/prey weight ratios for some northwest Atlantic fish. Int. Counc. Explor. Sea, Biol. Oceanogr. Comm., ICES C.M. 1980/L:62, 9 p.
HELGASON, T., AND H. GISLASON.
1979. VPA-analysis with species interaction due to predation. Int. Counc. Explor. Sea, Demersal Fish Comm., ICES C.M. 1979/G:52, 10 p.
HICKLING, C. F.
1927. The natural history of the hake, Parts I and II. Fish. Invest. Minist. Agric. Fish. Food (G. B.), Ser. II, 10(2), 100 p.
JENKINS, B. W., AND J. M. GREEN.
1977. A critique of field methodology for determining fish feeding periodicity. Environ. Biol. Fishes 1:209-214.
JUDKINS, D. C., AND A. FLEMINGER.
1972. Comparison of foregut contents of *Sergestes similis* obtained from net collections and albacore stomachs. Fish. Bull., U.S. 70:217-223.
LAWLOR, L. R.
1980. Overlap, similarity, and competition coefficients. Ecology 61(2):245-251.
LIVINGSTON, P., AND M. ALTON.
1982. Stomach contents of Pacific whiting, (*Merluccius productus*), off Washington and Oregon coasts April-July 1967. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-32.
MAJKOWSKI, J., AND K. G. WAIWOOD.
1981. A procedure for evaluating the food biomass consumed by a fish population. Can. J. Fish. Aquat. Sci. 38:1199-1208.
NELSON, M. O., AND H. A. LARKINS.
1970. Distribution and biology of Pacific hake: A synopsis. *In* Pacific hake, p. 23-33. U.S. Fish Wildl. Serv., Circ. 332.
OUTRAM, D. N., AND C. HAEGELE.
1972. Food of Pacific hake (*Merluccius productus*) on an offshore bank southwest of Vancouver Island, British Columbia. J. Fish. Res. Board Can. 29:1792-1795.
PEARCY, W. G.
1970. Vertical migration of the ocean shrimp, *Pandalus jordani*: A feeding and dispersal mechanism. Calif. Fish Game 56:125-129.
PENNINGTON, M.
1981. Estimating the average food consumption by fish in the field. Int. Counc. Explor. Sea, ICES C.M. 1981/G:69, 12 p.
RENFRO, W. C., AND W. G. PEARCY.
1966. Food and feeding apparatus of two pelagic shrimps. J. Fish. Res. Board Can. 23:1971-1975.
ROBINSON, M. K.
1976. Atlas of North Pacific Ocean monthly mean temperatures and mean salinities of the surface layer. U.S. Dep. Navy, Naval Oceanogr. Off., Ref. Publ. 2, 194 p.
SPARRE, P.
1980. A goal function of fisheries (Legion Analysis). Int. Counc. Explor. Sea, Demersal Fish Comm., ICES C.M. 1980/G:40, 81 p.
URSIN, E.
1973. On the prey size preferences of cod and dab. Medd. Dan. Fisk. Havunders N.S. 7:85-98.
WAILES, G. H.
1936. Food of *Clupea pallasii* in southern British Columbia waters. J. Biol. Board Can. 1:477-486.
WERNER, E. E.
1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Board Can. 31:1531-1536.
WERNER, E. E., AND D. J. HALL.
1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology 58:869-876.

PATRICIA A. LIVINGSTON

Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
2725 Montlake Blvd. E.
Seattle, WA 98112