

FOOD AND FEEDING OF PACIFIC HAKE LARVAE, *MERLUCCIUS PRODUCTUS*, OFF SOUTHERN CALIFORNIA AND NORTHERN BAJA CALIFORNIA

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ABSTRACT

The diet of larval Pacific hake, *Merluccius productus*, consisted primarily of copepod eggs and calanoid copepod adults, copepodites, and nauplii, based on an examination of material collected in March 1975 off southern California and northern Baja California. In spite of a large mouth, Pacific hake larvae ingested a broad size range of prey, with a concentration of food particles 70-200 μm in width. First-feeding Pacific hake larvae fed upon a wide range of prey (50 to about 400 μm prey width), and the range in prey sizes changed little with larval length from 3.0-10.7 mm. Although copepod eggs, nauplii, and copepodites were a significant portion of the diet in numbers of prey, adult copepods contributed about 74% of prey volume.

Observations of feeding incidence in relation to time of capture revealed a slow rate of gut evacuation. Larvae began feeding at about 1000 hours, and the number of prey items found in the gut increased during the day, reached a maximum after sunset, and thereafter decreased gradually. The comparatively large mouth, slow evacuation rate, and ability to feed on copepod stages from egg to adult seem to form an adaptive strategy for success in the relatively deep and cold strata inhabited by Pacific hake larvae.

RESUMEN

El examen del material colectado en marzo de 1975 en las costas del sur de California y del norte de Baja California indicaría que la dieta de las larvas de merluza del Pacífico, *Merluccius productus*, consiste principalmente de huevecillos de copépodos y adultos copépodos calanoides, copepoditos, y nauplios. Las larvas de merluza del Pacífico, a pesar de tener una boca muy grande, ingirieron presas de muy variados tamaños, con una concentración de partículas de comida que alcanzaba de 70-200 μm de anchura. Las larvas de merluza del Pacífico se alimentaban primero de una amplia calidad de presas (de 50 a 400 μm anchura de presa), y la amplitud de tamaños de presas cambió poco con las larvas de longitudes de entre 3.0 a 10.7 mm. Aunque los huevecillos de copépodos, nauplios, y copepoditos formaron una parte significativa de la dieta en cuanto a su frecuencia como presa, los copépodos adultos formaron aproximadamente 74% del volumen de la presa.

Observaciones sobre las incidencias del alimento en relación con el tiempo de captura presentaron una pro-

porción muy baja de evacuaciones intestinales. Las larvas empezaron a comer alrededor de las 1000 horas, y el número de presas encontradas en el intestino aumentó durante el día, alcanzando un máximo después de la puesta del sol, y disminuyendo después gradualmente. La boca comparativamente grande, una baja proporción de evacuaciones, y la habilidad de alimentarse de todas las fases de desarrollo de los copépodos, desde huevecillo hasta adulto, forman conjuntamente una estrategia de adaptación perfecta al complejo faunístico de los estratos relativamente profundos y fríos habitados por las larvas de merluza del Pacífico.

INTRODUCTION

Pacific hake¹ larvae (*Merluccius productus*) are the second most abundant pelagic fish larvae in the California Current, being surpassed only by larvae of the northern anchovy, *Engraulis mordax* (Ahlstrom 1965; MacGregor 1966). A hake fishery exists off the California-Washington coast, exploited primarily by foreign trawlers (Grinols and Tillman 1970; Pacific Fishery Management Council 1979). Information is available on larval development and distribution and on adult spawning and feeding of *M. productus* (Ahlstrom and Counts 1955; Ahlstrom 1959, 1969; Kramer and Smith 1970; Smith and Richardson 1977; Bailey 1980; Best 1963; Alton and Nelson 1970). In contrast, little is known of the feeding habits of Pacific hake larvae, although studies have been undertaken for larvae of *Merluccius merluccius hubbsi* in the South Atlantic (de Ciechomski and Weiss 1974) and for other kinds of gadoid larvae and juveniles (Marak 1960; Sysoeva and Degtereva 1965; Bainbridge and McKay 1968; Arntz 1974). The present report analyzes data obtained on gut contents, mouth size, and feeding incidence of Pacific hake larvae.

METHODS AND MATERIALS

A total of 298 larvae, 3.0-10.7 mm in length, from 18 formaldehyde-preserved samples taken during the March 1975 CalCOFI cruise aboard the R/V *David Starr Jordan* were examined. Stations represented cover a region 33° 25' to 29° 02' N by 115° 18' to 120° 54.5' W, roughly off San Pedro, California, to south of Punta Baja, Baja California. All samples were collected with a 505- μm

¹The common name "pacific hake" has been replaced by "Pacific whiting" for *Merluccius productus* by the marketing and fishing industry, however, the former name is retained in this work.

mesh, 1-m aperture plankton net, towed obliquely from an approximate depth of 210 m to the surface. When samples contained more than 100 hake larvae, subsamples of 25 were randomly selected over a representative size range for dissection.

Body lengths (measured from the tip of the snout to the tip of the notochord) were recorded from the specimen on a glass slide under a stereomicroscope. In order to hold the larva in position for mouth width measurements, a plexiglass plate was etched with a size gradient of grooves, and the larva was placed along its dorsal body edge in the appropriate sized groove with its upper and lower jaws held open at about 90° for the measurement.

The entire gut was removed intact from each specimen and was placed in a drop of glycerin on a glass depression slide (see Arthur 1976). Using probes tipped with pig's eyelashes, the mid- and hindgut walls were carefully slit open, and prey organisms teased out. A drop of lactic acid pigmented with Chlorazol Black E saturated in 70% ethanol was added to the glycerin to stain crustacean cuticle (Judkins and Fleminger 1972), greatly improving the visibility of the prey and facilitating their enumeration and measurement (maximum width). Identifications of food particles were made to the lowest taxa possible with the aid of a compound microscope.

Food volume index was calculated for each food particle by treating copepod eggs as spheres, and nauplii, copepodites, and adults as ellipsoids. The ellipsoidal length for nauplii was generalized as twice the width, and for copepodites and adults, 2.5 times the width. Thus, the general volumetric equation, $V = 4/3 \pi abc$, where a , b , and c are diameters along the three axes, could be used to calculate a food volume index for the principal food components. Singular cases of oddly shaped food items, such as fish and polychaete larvae, were measured and treated individually for volume computations.

RESULTS

Composition of Food

Copepod eggs, calanoid adults, copepodites, and nauplii were the principal components of ingested material (Table 1). The copepods *Clausocalanus*, *Paracalanus*, *Calocalanus*, and the cyclopoid *Oithona* occurred the most frequently. The rather low diversity of food organisms indicates that hake larvae may feed selectively. This problem could not be investigated because the samples were from oblique integrated tows. No significant variations in the composition of diet were indicated in day versus night or inshore versus offshore samples.

One case of cannibalism (common in adults, Best 1963) occurred, in which two yolk-sac larvae were preyed upon by a 5.5-mm hake larva. The two larvae were partially digested in the midgut of the predator hake larva, providing evidence against the possibility of net feeding.

Size of Food

Pacific hake larvae fed on a wide size range of food particles (Figure 1), ingesting prey almost as large as their maximum mouth width (Figure 2) soon after yolk absorption. Larvae ingested an abundance of copepod eggs, nauplii, and copepodites as well as larger organisms such as adult copepods at larval lengths up to 8 mm (Figure 1). However, examination of the cumulative frequency distribution of numbers and volume of prey types (Table 2) reveals that adult copepods constitute the bulk (ca. 74%) of prey volume, and copepod eggs less than 1%. Of 27 yolk-containing larvae examined, 7 had begun feeding before yolk depletion.

TABLE 1
 Food Composition of Pacific Hake Larvae.

Food item	Size range (mm)											
	3.0-3.9	4.0-4.9	5.0-5.9	6.0-6.9	7.0-7.9	8.0-10.9						
	No. %	No. %	No. %	No. %	No. %	No. %						
Copepod adults:												
<i>Clausocalanus</i> spp.	25	51	38	23	8							
<i>Paracalanus</i> spp.	19	39	21	6								
<i>Calocalanus</i> spp.	5	10	17	16	3							
<i>Calanus</i> spp.		1			2							
<i>Mecynocera clausi</i>		6	10	4								
<i>Oithona</i> spp.	2	13	32	10	6	4						
Calanoid- unidentifiable	6	9	14	20	7	1						
Disintegrated	5	7	8	2		3						
Total adults	62	17.7	136	22.0	140	20.4	81	37.3	26	37.7	8	88.9
Copepodites:												
<i>Calanus</i> spp.	1	5	5	5	1							
<i>Oithona</i> spp.	2	13	7	2								
Calanoid (most are <i>Paracalanus</i> / <i>Clausocalanus</i>)	72	84	99	10	4							
Cyclopoid	2	5	6	18	1							
Disintegrated	14	31	15		2							
Total copepodites	91	26.0	138	22.3	132	19.2	35	16.1	8	11.6		
Copepod nauplii:												
Calanoid	102	98	141	39	5							
Cyclopoid	29	20	16									
Disintegrated	1	2										
Total nauplii	132	37.7	120	19.4	157	22.8	39	18.0	5	7.2		
Copepod eggs, single	58	214	251	62	29							
Copepod eggs, clusters	1	5	4									
Total copepod eggs	59	16.8	219	35.4	255	37.1	62	28.6	29	42.0		
Unidentified												
invertebrate eggs	2	0.6	5	0.8								
Polychaete larva				1	0.1							
Hake yolk-sac larvae				2	0.3							
Mollusc larva						1	11.9					
Unidentified crustacean fragment	3	0.9	1	0.2		1	1.4					
Unidentified particles	1	0.3		1	0.1							
TOTAL NUMBER												
FOOD ITEMS	350	619	688	217	69	9						
Number larvae examined ($\Sigma=298$)	86	113	72	16	8	3						
Number larvae empty ($\Sigma=90$)	29 ¹	38	18	3	1	1						

¹20 with yolk

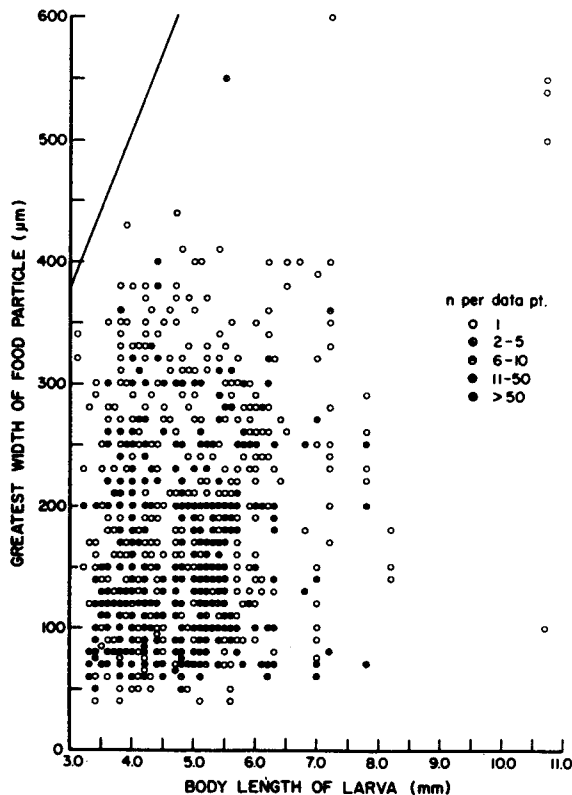


Figure 1. Food size of 208 Pacific hake larvae. Diagonal line indicates maximum mouth width.

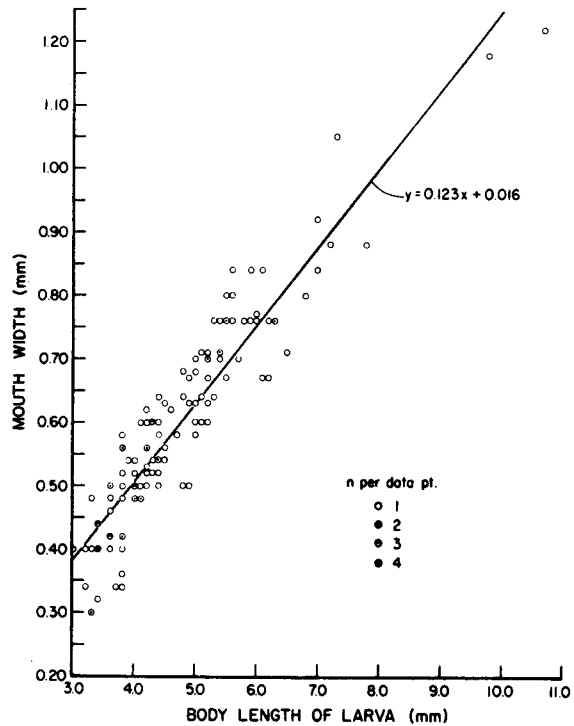


Figure 2. Mouth width of Pacific hake larvae. The correlation with body length is $r = 0.93$.

Feeding Incidence

Feeding incidence is defined by Arthur (1976) as the percentage of larvae containing at least one food item in the gut for a given sample. This term refers to presence of food in the gut and does not necessarily reflect recent feeding activity. Analysis of feeding incidence of Pacific hake larvae at time of capture (Figure 3) shows presumptive diurnal feeding activity followed by a slow digestion rate with complete gut evacuation occurring between 0600 and 0800 hours PST. That evacuation rates were slow was supported by the extent of digestion and decomposition of prey organisms in larval hake stomachs; food

items from specimens collected between 0400 and 0930 hours showed progressive disintegration over the time range, whereas larvae captured after 1000 hours contained prey in the freshest condition, indicative of first feeding in their diurnal feeding rhythm.

Plots of the mean number of prey and mean food volume index for larvae per sample (Figure 4) are dissimilar in shape. The number curve indicates an increasing accumulation of prey after 1000 hours towards a peak after sunset, whereas the volume index curve is variable and does not show such a trend.

TABLE 2
 Cumulative Frequency Distribution of Numbers and Volume for Major Prey Types Found in *M. productus* Larvae.

Prey	Range max. width (μm)	Mean food volume (10 ³ μm ³)	Standard deviation (10 ³ μm ³)	Frequency	Frequency × volume (10 ³ μm ³)	% of total volume
Copepod eggs	50-100	0.364	0.083	674	0.24534	0.7
Copepod nauplii	40-300	4.013	5.148	441	1.76973	5.3
Copepodites	80-450	14.698	24.308	393	5.77631	17.4
Adult copepods	110-600	57.418	54.850	426	24.46007	73.8
Other	40-550	49.401	107.783	18	0.88922	2.7
					Σ = 33.14067	

DISCUSSION

Much attention has been given to feeding of marine fish larvae as a factor in larval survival and its effect on population dynamics of fishes. May (1974) and Hunter (1976; in press) provide excellent reviews and discussion of gut content studies in the literature. De Ciechomski and Weiss (1974) showed that hake larvae (*Merluccius merluccius hubbsi*) off Argentina have a very high incidence of feeding (94% during spring) that contrasted sharply with the low feeding incidence (28%) of anchovy (*Engraulis anchoita*) larvae. Feeding incidence is as

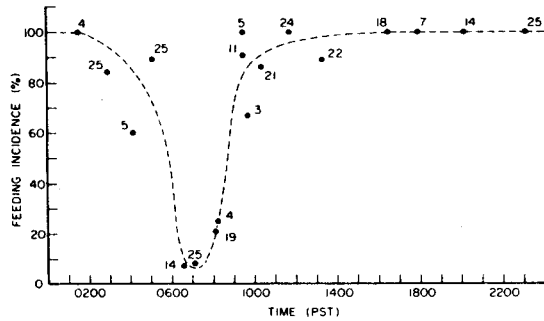


Figure 3. Feeding incidence of Pacific hake larvae in relation to time of capture. Values of data points indicate sample size of larvae. Feeding yolk-sac larvae were excluded from percentage calculations.

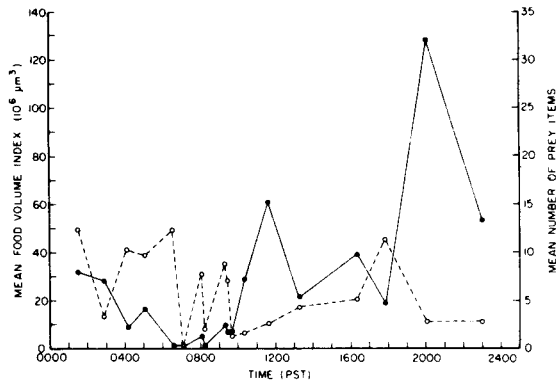


Figure 4. Mean food volume index (dashed line) and mean number of prey (solid line) of hake larvae. Asterisk indicates volume for small sample at 0944 hours when it includes a 7.2-mm hake larva that preyed on a single, unusually large copepod, which was the largest prey encountered in this study.

great or greater for small samples of Pacific hake larvae (up to 100%), but feeding incidence for larvae of the northern anchovy (*Engraulis mordax*) averages less than 10% (Arthur 1976). This disparity in the feeding incidence of two dominant spring ichthyoplankters off California and off Argentina is partly explained by defecation by larvae at time of capture and preservation, especially those with straight guts as found in clupeoid larvae (see Arthur 1976). Hake larvae, however, have folds and a pronounced loop in the gut, which would aid in food retention during capture.

According to de Ciechomski and Weiss (1974), larvae of *M. merluccius hubbsi* feed almost exclusively on copepodites and adult copepods, with calanoids dominating the diet. Average prey width increases from about 500 μm at first feeding to 800 μm at 8-mm larval length. Copepods, particularly calanoids, also dominate the diet of Pacific hake larvae; however, copepod eggs and nauplii

constitute about half of the diet items throughout the size range studied (Table 1). Despite their high incidence in the diet, these small-sized prey items contribute only about 6% of the total food volume of prey (Table 2). Hake larvae may be dependent on the successful capture of copepodites and adult copepods to provide the required nutritive level for survival and growth.

First-feeding Pacific hake larvae are capable of feeding on a large size range of prey (50- to about 400-μm prey width), and the propensity to exploit prey organisms throughout this size range persists even in the largest larvae examined in our study. In contrast, clupeoid larvae tend to have relatively small and restricted prey size ranges that are more closely correlated with mouth size (Arthur 1976). Larvae of jack mackerel (*Trachurus symmetricus*) are intermediate between clupeoids and Pacific hake with respect to prey size range. According to Arthur (1976), first-feeding jack mackerel larvae contain prey items in the 50- to 200-μm size range (mostly copepodites and adult copepods). Maximum prey size increases with larval size (to about 400 μm at 7-mm larval length), and larvae tend to exploit prey over a wide size range, although to a lesser extent than do larvae of Pacific hake. Availability of prey organisms is an important factor contributing to prey sizes consumed. Examination of the spawning periods and the distribution and abundance of major prey items in the region would be helpful in understanding these observations on larval feeding.

In *M. productus* larvae, the number of prey items in the gut increases during the day, reaches a maximum after sunset, decreases during the night, and reaches a minimum at dawn (Figure 4). Bainbridge and McKay (1968) showed a similar sequence for cod (*Gadus morhua*) larvae in the north Atlantic, where the number of identifiable copepod nauplii peaked after sunset. Their data for redfish (*Sebastes marinus*) larvae show a pre-sunset peak for number of nauplii in the gut. Arthur (1976) showed a gradual increase in feeding incidence in Pacific sardine (*Sardinops sagax*) during the day, reaching a peak before sunset, followed by a gradual decline during the night. Last (1978) found that the number of prey items of three species of flatfish larvae (plaice, flounder, and sole) reached a peak after sunset, whereas a fourth species, the dab, reached a pre-sunset peak. The disparity between the curves for mean volume and mean number of prey in hake larvae could be due to a longer digestion rate for large prey such as adult copepods, which would be retained in the gut longer and would be reflected in the variable peaks in mean volume despite a low number of prey organisms (Figure 4). The curve for number of prey may then reflect greater temporal sensitivity to feeding activity on smaller prey such as copepod eggs and nauplii.

Since marine fish larvae, including hake, are primarily

visual feeders (see review by Hunter, in press), the post-sunset feeding peak shown by hake and some other species is intriguing. One would expect that feeding success would diminish markedly at sunset, providing they do not switch over to another sensory modality at dusk. Initial speculation that hake larvae, unlike most fish larvae, develop rods in their retina early in life, thereby allowing greater visual perception in diminishing light, proved unfounded. A lack of rod development in hake larvae through 8 mm and the formation of rods in a 13.4-mm larva were observed in histological sections of the eye (O'Connell, personal communication). The development of rods in hake larvae between 8 and 13.4 mm indicates that they are similar to anchovy larvae (O'Connell in press), which initiate retinal rod formation at 10-12 mm and which are visual feeders and probably representative of most pelagic fish larvae. Another explanation may be that possible vertical migration of prey after sunset increases the probability of encounters for feeding success. A further possibility is that the general metabolic level of hake larvae declines at sunset, producing a decline in gut evacuation rate and consequently an apparent post-sunset feeding peak. Perhaps the post-sunset feeding peak may result from a combination of these suggested causes.

Adult and juvenile Pacific hake are considered to be opportunistic feeders owing to the variety and availability of their prey organisms (Best 1963; Alton and Nelson 1970). In addition to a host of invertebrates and fish species, adult hake stomachs have contained smaller hake (Best 1963). The propensity to cannibalize is expressed early in ontogeny. The finding of cannibalism by a small hake larva in this study raises the possibility that this could be an important mortality factor when patches of yolk-sac larvae are spatially contemporary with larger larvae and juveniles. If cannibalism is a characteristic of hake larvae, one could speculate that the comparatively short spawning period of this species, late January to late March (Smith and Richardson 1977), enhances survival by reducing size heterogeneity within the larval population and consequently reducing the proportion of potential cannibals. It would be of interest to investigate further the degree of cannibalism by Pacific hake larvae, whether opportunistic or deliberate, and to determine its role in the ecology and density-dependent dynamics of hake populations.

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