VARIOUS SPECIES OF PHYTOPLANKTON AS FOOD FOR LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, AND RELATIVE NUTRITIONAL VALUE OF THE DINOFLAGELLATES *GYMNODINIUM SPLENDENS* AND *GONYAULAX POLYEDRA*

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ABSTRACT

First feeding northern anchovy larvae were presented with a variety of phytoplankters common to coastal waters of southern California to determine which species are acceptable as food. Most of the larvae ate the four species of dinoflagellates tested in feeding experiments but did not feed on diatoms or small flagellates. Larval rearing experiments were conducted to compare the nutritional value of *Gymnodinium splendens* and *Gonyaulax polyedra*, two species of dinoflagellates readily eaten by anchovy larvae and known to predominate in the chlorphyll maximum layers off the southern California coast. *Gymnodinium splendens* was a nutritional food for the first 10 days of larval life, but *Gonyaulax polyedra* was judged to be inadequate. Supplementing the *G. polyedra* diet with microzooplankton increased larval survival comparable to survival on a microzooplankton diet alone. When the *Gymnodinium splendens* diet was supplemented with microzooplankton, the larvae grew faster but survival did not increase. Results are discussed in relation to studies on larval survival in the Southern California Bight during 1974 and 1975.

The strength of a year class of fish may depend on availability of food organisms during the early larval stages (May 1974). Consequently, there have been attempts to assess the abundance of planktonic organisms in larval feeding areas as a step towards predicting year class success (Shelbourne 1957; Bainbridge and Forsyth 1971; Lasker 1975, in press). For this approach to be successful, additional information is also necessary concerning: 1) selection of prey by the fish larvae, 2) concentration and size of food organisms necessary to initiate feeding by the fish larvae, 3) nutritional value of the food that the larvae select, and 4) temporal and spatial distribution of the food organisms in the feeding area.

The northern anchovy, *Engraulis mordax*, larva has been studied in the laboratory and many criteria for successful feeding have been determined (Lasker et al. 1970; O'Connell and Raymond 1970; Hunter 1972, 1976; Hunter and Thomas 1974). Results of these studies indicate that first feeding anchovy larvae require small particles (<100 μm in smallest dimension) at relatively high densities to initiate feeding and to insure moderate survival. O'Connell and Raymond (1970) found in laboratory experiments that anchovy larvae reared in seawater containing 1 copepod nauplius/ml or less experienced heavy mortalities during the sixth and seventh days after hatching. To date such a high concentration has not been found in the nearshore region of the California Current (Beers and Stewart 1967, 1969). However, the possibility does exist that anchovy larvae could survive on some of the larger phytoplankters during early stages of development (Hunter and Thomas 1974). Lasker et al. (1970) found that anchovy larvae would feed and grow to a length of 5 to 6 mm in the laboratory on a diet of the naked dinoflagellate, *Gymnodinium splendens*. With this in mind, Lasker (1975) used laboratory-spawned anchovy larvae to test for feeding activity in seawater pumped from the surface and chlorophyll maximum layer in the nearshore region of the Southern California Bight. Lasker found that during March and April 1974 there were sufficient numbers of *G. splendens* (>20 organisms/ml) in the chlorophyll maximum layer for initiation of feeding by anchovy larvae. During 1974 and 1975, Lasker (in press) monitored the plankton distribution off the southern California coast in an effort to establish a

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relationship between oceanographic conditions and larval anchovy food organisms. In 1975 he found that *G. splendens* was replaced as the dominant organism in the chlorophyll maximum layer by the armored dinoflagellate, *Gonyaulax polyedra,* and later by a variety of small diatoms. In an effort to assess effects that this succession might have on survival of anchovy larvae, we have conducted feeding experiments with some of the phytoplankters common in the Southern California Bight to determine which species are acceptable as food by anchovy larvae. In addition, we have examined the relative nutritional value of *Gymnodinium splendens* and *Gonyaulax polyedra.*

METHODS AND MATERIALS

Phytoplankton Cultures

The phytoplankters chosen for feeding experiments are common to southern California coastal waters, and most were major components of the chlorophyll maximum layers during 1974 and 1975 (Lasker in press). Also, they were of an appropriate size for ingestion by first feeding anchovy larvae (Table 1). Axenic cultures of the selected phytoplankters were supplied by James Jordan of the Food Chain Research Group at Scripps Institution of Oceanography. Culture techniques were described by Thomas et al. (1973).

TABLE 1.—Average dimensions of phytoplankters offered as food to first feeding anchovy larvae.

BACILLARIOPHYCEAE:	
Ditylum brightwellii (25 × 150 μm, single cells)	
Chaetoceros affinis (4 μm wide in chains to 200 μm)	
Thalassiosira decipiens (8 × 10 μm, single cells)	
Leptocylindrus danicus (5 μm wide in chains to 75 μm)	
DINOPHYCEAE:	CHLOROPHYCEAE:
Gymnodinium splendens (51 μm)	*Chlamydomonas* sp. (10 μm)
Gonyaulax polyedra (40 μm)	*Dunaliella* sp. (6 μm)
Prorocentrum micans (27 × 38 μm)	
Peridinium trochoideum (20 μm)	

Feeding Experiments

To determine which phytoplankters are preyed upon by anchovy larvae, feeding experiments were conducted using methods similar to those of Lasker (1975). Cylindrical 8-liter battery jars, wrapped with dull black cardboard, were filled with approximately 5 liters of filtered seawater (filter pore size, 5 μm) and inoculated from a dense culture of the phytoplankton to be tested. The densities were determined by counting organisms in 1-ml alilquots in a Sedgwick–Rafter[3] counting chamber and/or with a Coulter Counter Model Ta, and the size was measured with an ocular micrometer. Experiments were conducted at temperatures ranging from 16.9° to 19.6°C, and the test jars were illuminated from above with a bank of four 40-W fluorescent lamps. Light intensity at the surface of the test jars was approximately 2,400 lx. Because anchovy larvae readily feed on *Gymnodinium splendens* (Lasker 1975), at least one container in each series of experiments contained only this food organism as a control to test the feeding ability of each batch of larvae.

Diatoms were maintained in suspemsion during the feeding trials by a gentle stream of bubbled air in each test jar. To evaluate the effect of such agitation on the ability of larvae to feed, experiments were conducted with and without bubbled air using *G. splendens* as food. Little effect on feeding ability could be detected (Table 2, Trial 1).

Anchovy eggs were obtained from adult anchovies maintained in spawning condition at the Southwest Fisheries Center Laboratory. Spawning techniques were described by Leong (1971). Anchovy eggs and larvae were allowed to develop in 1-liter jars (100 eggs/jar) containing filtered seawater (filter pore size, 5 μm). First feeding larvae (2.5 days after hatching at 17°C) were placed in the experimental containers with the test organism for approximately 8 h before being siphoned from the containers and quickly immobilized on a membrane filter (pore size, 8 μm) by vacuum filtration. This technique helped to prevent the larvae from defecating (Lasker 1975). The larvae remained somewhat transparent after air drying so that the presence of food in the gut could be determined by microscopic examination of the intact animal.

Larval Rearing Experiments

Anchovy larvae were reared for 10 days in 10-liter circular containers immersed in a temperature-controlled bath in an air-conditioned room (Lasker et al. 1970). The containers were filled with membrane filtered seawater (pore size, 0.45 μm), the salinity was 33.4‰, and the temperature was maintained at 16.0° ± 1.1°C. Lighting

[3]Mention of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Laboratory feeding experiments showing the percentage of anchovy larvae that fed on: 1) diatoms—*Ditylum brightwellii, Chaetoceros affinis, Thalassiosira decipiens,* and *Leptocylindrus danicus*; 2) dinoflagellates—*Gymnodinium splendens, Gonyaulax polyedra, Prorocentrum micans,* and *Peridinium trochoideum*; and 3) flagellates—*Chlamydomonas* sp. and *Dunaliella* sp.

Feeding trial no. (duration in hours)	Temp (°C)	Air-stone	Food organism	Concentration of food particles (organisms/ml)	Number of larvae per experiment	Feeding by anchovy larvae		
						% of larvae with ¼ to full gut	% of larvae with <8 particles in gut	% of larvae with empty gut
1 (7.25)	18.2		*G. splendens*	162	65	65	7	28
	18.2	X	*G. splendens*	162	54	48	9	43
	18.2	X	*G. splendens*	162	70	53	16	31
2 (8.0)	18.2		*G. splendens*	180	70	33	16	51
	18.5	X	*D. brightwellii*	164	59	0	0	100
	19.6	X	*D. brightwellii*	164	46	0	0	100
3 (8.0)	17.0		*G. splendens*	240	67	67	16	17
	17.0	X	*C. affinis*	127 chains	59	0	0	100
	17.0	X	*C. affinis*	127 chains	80	0	0	100
	17.0	X	*T. decipiens*	154	73	0	0	100
	17.0	X	*T. decipiens*	205	69	0	0	100
4 (8.0)	17.1		*G. splendens*	195	60	55	7	38
	16.9	X	*L. danicus*	197 chains	75	0	0	100
	16.9	X	*L. danicus*	780 chains	57	2	0	98
5 (8.0)	17.4		*G. splendens*	208	62	34	10	56
	17.7		*P. trochoideum*	56	65	67	22	11
	17.7		*P. trochoideum*	97	54	65	7	28
	17.7		*P. trochoideum*	210	46	50	26	24
	17.7		*Chlamydomonas* sp.	211	46	0	0	100
	17.7		*P. micans*	201	38	45	21	34
6 (8.0)	18.2		*G. splendens*	193	26	58	23	19
	18.2		*G. polyedra*	102	58	78	7	15
	18.2		*G. polyedra*	60	48	60	10	30
	17.7		*Dunaliella* sp.	303	67	0	0	100
	17.7		*Dunaliella* sp.	242	31	0	0	100

was provided for 14 h/day by 40-W fluorescent lamps as described earlier.

Eight rearing containers were inoculated with *G. splendens* and eight with *Gonyaulax polyedra* at a concentration of 100 organisms/ml. As a supplement to these food organisms, some containers were also stocked with a combination culture of the rotifer, *Brachionus plicatilis,* and the harpacticoid copepod, *Tisbe holothuriae,* with final concentrations of 0.0, 0.1, 1.0, and 5.0 organisms/ml (Table 3). Duplicate experiments were run simultaneously for all treatments including two containers without dinoflagellates but stocked with *B. plicatilis* and *T. holothuriae,* at a concentration of 5 organisms/ml.

The relative proportions of *B. plicatilis* and *T. holothuriae* (hereafter also referred to as microzooplankton) in the larval rearing containers

TABLE 3.—Survival and growth of anchovy larvae reared for 10 days on different diet regimes.

Stocking density of larvae on day 0 (no./liter)	Concentration of dinoflagellate (organisms/ml)	Concentration of microzooplankton (organisms/ml)	Survival		Standard length (mm)		Average weight (mg)
			Number	Percent	Mean	S_x	
	Gymnodinium splendens						
3.3	100	5.0	11	33.3	4.24	0.359	0.039
3.4	100	5.0	15	44.1	4.87	0.671	0.048
2.2	100	1.0	5	22.7	4.30	0.480	0.061
2.5	100	1.0	12	48.0	4.73	0.677	0.047
3.1	100	0.1	13	41.9	4.46	0.355	0.046
3.9	100	0.1	6	15.4	3.57	0.314	0.046
2.8	100	0.0	9	32.1	4.23	0.485	0.042
3.6	100	0.0	8	22.2	4.03	0.413	0.056
	Gonyaulax polyedra						
3.3	100	5.0	5	15.2	4.02	0.403	0.065
3.9	100	5.0	14	35.9	4.82	0.710	0.059
3.8	100	1.0	5	13.2	4.54	0.796	0.077
3.7	100	1.0	7	18.9	4.41	0.219	0.057
2.8	100	0.1	1	3.6	3.7	—	(1)
2.9	100	0.1	1	3.5	4.0	—	(1)
3.5	100	0.0	1	2.9	3.0	—	(1)
3.9	100	0.0	0	0.0	—	—	—
4.2	0	5.0	8	19.1	4.51	0.669	0.050
2.3	0	5.0	0	0.0	—	—	—

[1]Sample too small to weigh.

varied during the course of the experiment. Initially, approximately 90% of the microzooplankters in the containers were *T. holothuriae*, but by the end of the rearing experiment, *B. plicatilis* was the dominant organism (97%). We were unable to determine if the anchovy larvae were selectively feeding on the copepods because the combination culture of microzooplankton which was used to stock the larval rearing containers also experienced a similar succession in species dominance during the experimental period.

Brachionus plicatilis and *T. holothuriae* were cultured together in the same vessel using techniques described by Hunter (1976). The cultures were filtered through 105-μm screening to remove the largest organisms before inoculating the larval rearing containers. Microscopic examination of the filtrate revealed a predominance of small rotifers and copepod nauplii.

Fifty anchovy eggs were added to each container the day after spawning and the appropriate dinoflagellate was also introduced at this time. Hatching occurred on the next day, which corresponds to day 0 of the experiment. The number of dead embryos on the container bottom was counted at this time and the percentage hatch was calculated. On day 2, most of the yolk sac was absorbed, the eyes were pigmented, and the larvae initiated feeding. At this time, the microzooplankton were added. The experiments were terminated on day 10; standard lengths were measured for each animal; average dry weight for larvae in each container was determined; and the percent survival in each container was calculated.

Each larval rearing container was sampled daily to monitor the concentration of food organisms. Because *Gymnodinium splendens* and *Gonyaulax polyedra* tend to form patches, 1-ml samples were taken from three different locations in the tank outside of a patch; the numbers were averaged and an appropriate amount of a dense dinoflagellate culture was added daily to maintain a concentration of 100 organisms/ml. The density of *B. plicatilis* and *T. holothuriae* was maintained in a like manner except that the volume sampled was larger (from 10- to 100-ml samples/container, depending on the stock density of microzooplankton). Also, we were careful to sample a few centimeters away from the container surfaces because *T. holothuriae* copepodids and adults are thigmotactic. We stocked the rearing containers with nauplii (which are less thigmotactic than the older stages). However, during the course of the experiments, surviving *T. holothuriae* developed beyond the naupliar stages and tended to settle out on container surfaces becoming less available to anchovy larvae. These stages were not included in our counts.

RESULTS

Feeding Experiments

A total of 518 larvae were presented with four species of diatoms (Table 2). Only one larva fed on diatoms. This single individual ate a narrow (5 × 50–75 μm) chain-forming diatom, *Leptocylindrus danicus*.

Most larvae fed on the dinoflagellates *Gymnodinium splendens, Gonyaulax polyedra, Prorocentrum micans,* and *Peridinium trochoideum.* There was no apparent preference by larvae for a particular species of dinoflagellate. Between 72 and 89% of the larvae tested fed on *P. trochoideum* (20 μm), which are as small as the smallest sized particles known to be ingested by first feeding anchovy larvae (Arthur 1976). *Peridinium trochoideum* is a darkly pigmented dinoflagellate. Perhaps this characteristic makes it more visible to the larvae than other particles of a similar size. Lasker (1975) concluded that first feeding anchovy larvae required a particle greater than 40 μm to fill their gut in 8 h.

Anchovy larvae did not feed on the smallest prey used in the feeding experiments, the flagellates *Chlamydomonas* sp. (10 μm) and *Dunaliella* sp. (6 μm).

Larval Rearing Experiments

Growth and survival of anchovy larvae reared for 10 days on different diet regimes are shown in Table 3. The survival rate of larvae reared on the *Gymnodinium splendens* diet was higher than on the *Gonyaulax polyedra* diet. The relationship between larval survival and supplementation of the dinoflagellate diet with microzooplankton was described with linear regressions (Figure 1). The survival of larvae reared in seawater containing 100 *Gymnodinium splendens*/ml did not significantly increase (t for the slope of the regression = 0.1, $P<0.20$) when microzooplankton were added to their diet as a supplement (Figure 1). Supplementation of the *Gonyaulax polyedra* diet with microzooplankton did result in a significant increase (t for the slope of the regression = 3.24,

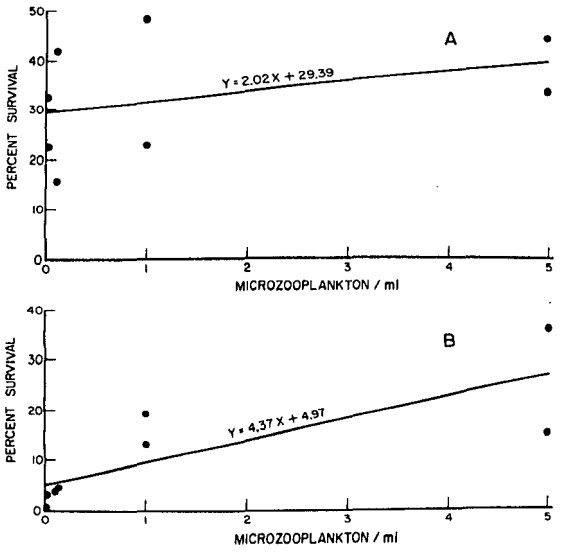

FIGURE 1.—Percent survival of *Engraulis mordax* at 10 days in relation to supplementation of a dinoflagellate diet with microzooplankton. A) *Gymnodinium splendens* diet. B) *Gonyaulax polyedra* diet.

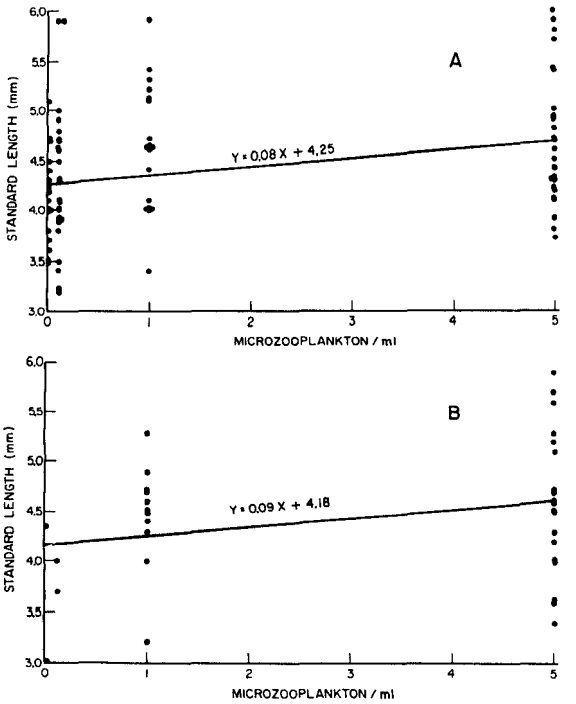

FIGURE 2.—Standard lengths of *Engraulis mordax* at 10 days in relation to supplementation of a dinoflagellate diet with microzooplankton. A) *Gymnodinium splendens* diet. B) *Gonyaulax polyedra* diet.

$P<0.025$) in larval survival. Larvae reared on a *G. polyedra* diet required at least 1 microzooplankton/ml in order to have survival rates that were comparable to larvae reared on a diet of *Gymnodinium splendens*. These results were comparable to the survival rates recorded by O'Connell and Raymond (1970) for anchovy larvae fed copepod nauplii at various concentrations. They found that larvae did not survive for 12 days in containers with less than 1 nauplius/ml.

Although anchovy larvae grow slowly during the first several days of feeding, a slight but significant increase ($t = 2.67$, $P<0.05$) in standard length occurred in larvae fed *G. splendens* when their diets were supplemented with microzooplankton (Figure 2), but no differences in dry weight were detected. Larvae fed *Gonyaulax polyedra* also appeared to increase in standard length when their diets were supplemented (Figure 2), but because the increase was slight and the number of data points was small due to the low survival rates on this diet, no significant increase was detected ($t = 1.50$, $P>0.20$).

Survival was low in larvae fed only 5 microzooplankters/ml without any dinoflagellates (Table 3). One container had no survivors and the other had 19.9% survival. Theilacker and McMaster (1971) found that larval anchovies that were fed only rotifers (*B. plicatilis*) had a lower rate of survival than those fed *Gymnodinium splendens* and *B. plicatilis* in combination. They related this finding to the low feeding success of larvae on the larger sized rotifers during the first few days of feeding. Also, Houde (1973) believes that survival of fish larvae is increased when blooms of phytoplankton are maintained in rearing containers to "condition" the water (presumably by removing metabolites).

DISCUSSION

Anchovy larvae apear to select their prey and it seems as if size is not the only criterion for selection. Larvae did not feed on any of the four species of diatoms tested in this study. The most obvious explanation is that spines and other processes on the diatoms either discouraged the larvae from striking or prevented them from swallowing. On the other hand, most larvae fed on all species of dinoflagellates tested. Visibility might also play an important role in prey selection since the darkly pigmented dinoflagellate, *P. trochoideum*,

was heavily preyed upon by anchovy larvae even though *P. trochoideum* are as small as the smallest particles detected by Arthur (1976) in the guts of larval anchovies.

It appears that prey differ in their nutritional value to anchovy larvae. *Gymnodinium splendens* and *Gonyaulax polyedra* are readily eaten by anchovy larvae, but *G. polyedra* was an inadequate food. Only 1 larva of the 74 that were reared on an exclusive diet of *G. polyedra* survived for 10 days. Larvae reared on a diet of *G. polyedra* supplemented with microzooplankton had survival rates that increased relative to the degree of supplementation. Although certain species of *Gonyaulax* are known to be toxic, it seems unlikely that this was a cause of mortality in our experiments because survival was good when larvae were fed *G. polyedra* supplemented with 5 microzooplankters/ml.

We offer two possible explanations for the difference in the nutritional value of the two dinoflagellates: 1) *G. polyedra* is about 10 μm smaller in diameter than *G. splendens*. Therefore, on the basis of volume alone, *G. splendens* could have twice as many calories as *Gonyaulax polyedra*, because the volume increases as the cube of the radius in a sphere. 2) *G. polyedra* is armored while *Gymnodinium splendens* is not, and, therefore, *G. splendens* is presumably more digestible by anchovy larvae which have an undifferentiated gut during the early stages of their development. Lasker et al. (1970) found that the armored dinoflagellate, *Prorocentrum micans* (27 $\times$ 38 μm), did not sustain life in first feeding anchovy larvae but again, this organism is smaller than *G. splendens*.

Lasker (1975) concluded that the nearshore area of the Southern California Bight was a good feeding ground for first feeding anchovy larvae during the spring of 1974 because of the high concentrations of *G. splendens* found in the chlorophyll maximum layer. In this study, the survival of anchovy larvae fed 100 *G. splendens*/ml was acceptable, and it did not differ from that of larvae fed a *G. splendens* diet supplemented with microzooplankton at concentrations up to 5 organisms/ml. Although larvae grew slightly faster when given the microzooplankton, these results still indicate that a larva could survive until an age of 10 days without the high concentrations of micronauplii that O'Connell and Raymond (1970) found to be necessary. If anchovy larvae survive to a size of 5 to 6 mm on *G. splendens*, their feeding efficiency would be higher than smaller larvae (Hunter 1972), and because of their larger size, the volume of water that larvae could search for food would also be increased. These factors would reduce the concentration of microzooplankton necessary for survival (Vlymen in press).

During several sampling periods in 1975, Lasker (in press) found that the chlorophyll maximum layer in the nearshore region of the Southern California Bight was dominated by *Gonyaulax polyedra* or a variety of small diatoms. Our work indicates that during the time periods when these phytoplankters predominated, feeding conditions for post yolk-sac anchovy larvae would be less suitable than when *G. splendens* was abundant.

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