

Growth and survival of larvae of the northern anchovy *Engraulis mordax* (Pisces: Engraulidae) reared under starvation conditions

J.A. Rodríguez Murillo *, Enrique Carrillo-Barrios-Gómez **, Alejandro Chagoya-Guzmán **.

* Universidad Nacional, Heredia, Costa Rica.

** Centro de Investigación Científica y Enseñanza Superior de Ensenada, Baja California, México.

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Abstract: A batch of 2800 larvae of the northern anchovy, *Engraulis mordax* Girard, was maintained up to twelve days after hatching in the laboratory under supposed starvation conditions (20-300 orgs./l) and variable concentrations of the nanoflagellate *Tetraselmis* sp. (5,000-10,000 cells/ml).

In contrast with previous reports, growth and survival under these conditions were comparable to those observed under optimum feeding conditions. This suggests strategies that may be used by marine fish larvae to avoid starvation and be able to grow in an environment characterized by low food densities. We question the existence of a "critical period". The ecological importance of nanoflagellates as a source of food in the marine environment is also suggested.

Key Words: fish larvae, starvation, *Engraulis*.

Food and feeding are important factors in growth and survival of marine fish larvae. Both appear to be intimately related to natural fluctuations in their abundance and hence, to the failure of success of a year class.

In the last seventy years, a growing number of researchers have reviewed the original hypothesis put forward by Hjort (1914), which suggests that fluctuations in the abundance of fish populations are related to the availability of adequate food during the early larval stages (Hunter 1981, Lasker 1981).

Hjort's hypothesis has stimulated many studies on the feeding ecology of marine fish larvae (May 1970, Lasker and Sherman 1981). From these, there is evidence of an apparent contradiction of trophodynamics: average densities of microzooplankton, the major food source of marine fish larvae, seldom exceed 200 organisms/L in the marine environment (Houde 1978, Hunter 1981). Yet, as a rule, minimum food densities of microzooplankton required for marine fish larvae to meet their basic metabolic requirements have been estimated, in the laboratory, at densities 1000 organisms/L

(O'Connell and Raymond 1970, Detwyler and Houde 1970, Wyatt 1972). Thus, to avoid death from starvation, marine fish larvae need 1-2 orders of magnitude more organisms for food than are available in the ocean. Apparently, marine fish larvae live in an environment characterized by theoretical starvation conditions.

Several authors have introduced alternatives to explain this contradiction. For instance, Lasker and coworkers suggest the dependence of marine fish larvae on food patches (Lasker 1975, Lasker and Zweifel 1978, Owen 1981). The results presented in this paper suggest that adequate growth and survival of fish larvae may be possible without the need for a strategy based on the utilization of food patches. Thus, it is based on the premise that fish larvae can feed successfully in the marine environment.

Larvae of the northern anchovy *Engraulis mordax* Girard were chosen because most studies relating larval survival to food patches have been conducted with this species (Hunter and Thomas 1974, Lasker 1975, Lasker and Zweifel 1978, Owen 1981) and this species offers one

of the most objective examples of the theoretical contradiction between the minimum food densities required for survival and those found in the natural environment.

We used nanoflagellates in this study because it has been shown that larvae of *E. mordax* will feed successfully on them (Moffatt 1981, Carrillo-Barrios-Gómez and Solís-Guevara: manuscripts). In addition, they are found in the California current in average densities similar to those used in the laboratory for *E. mordax* (Gaxiola-Castro 1984, F.M. Reid, personal communication). We chose *Tetraselmis* sp. as a representative of marine nanoflagellates because of its small size ($\bar{x} = 15 \mu\text{m}$) and its adaptability for rearing in monoxenic cultures in the laboratory.

MATERIAL AND METHODS

Table 1 summarizes the experimental design. Two series of experiments were conducted under theoretical starvation conditions (1000 microzooplankters/L) through three similarly designated concentrations of food particles, which were designed to encompass similar ranges of microzooplankton densities found in the marine environment. All experiments in Series 1 were characterized by a designated concentration of 5000 cells/mL of *Tetraselmis* sp. All experiments in Series 2 were conducted under designated concentrations of 10000 cells/mL of *Tetraselmis* sp. In addition, one experiment was conducted under real starvation conditions as a control. Every experiment in each Series and in the control group was replicated once.

All the eggs of *E. mordax* utilized in this study were provided by National Marine Fisheries Service, SWFC, La Jolla California.

Fertilized eggs were placed in thermos containers the same day they spawned. Upon arrival, eggs that looked viable were sorted immediately under dissecting microscopes with the aid of a wide mouth dropper.

A total of 3000 eggs were sorted. 2800 were divided, 200 each, into 14 beakers (1 L each, filled with sea water from the same experimental containers where each 200 egg batch was gently emptied immediately afterwards. Additionally, 200 eggs were also sorted, 10 each, into 20 plastic petri dishes, 5 cm in diameter and filled with approximately 20 ml of sea water. These were maintained as controls to easily determine the approximate percent of hatching in the containers (Carrillo-Barrios-Gómez and Solís-Guevara: manuscript).

Rearing system: anchovies. All experiments were conducted in black plastic cylindrical rearing tanks, similar to those used by Lasker *et al.* (1970). Each tank was filled with 10 L of filtered sea water from Todos Santos Bay, Ensenada, Baja California. All the sea water utilized was filtered to $3 \mu\text{m}$ through a series of Hytrex eartridges and disinfected through a UV system (Hamilton and Carlucci 1966). Two hundred eggs were introduced into each tank, following similar

stocking densities used previously for this species (Laske *et al.* 1970).

In general, static rearing conditions were maintained throughout the duration of the experiments; no aeration was provided (Lasker *et al.* 1970). Semi-static rearing conditions resulted only for those containers where it became necessary to adjust the densities of nanoflagellates or microzooplankton by adding or removing water from them.

Illumination was provided through two 75 watts "cool white" fluorescent lights kept approximately 30 cm above the surface of the rearing tanks (Scura and Jerde 1977). A 12 hour diel period of illumination was kept throughout the experiment; it was started and finished approximately at the same time every day.

Temperature was maintained approximately constant at $17 \pm 1^\circ\text{C}$ through an air conditioned system equipped with electrostatic filtration. This temperature is within the range of spawning and rearing for this species (Kramer and Zweifel 1970). Salinity was kept around $33\text{‰} \pm 1\text{‰}$.

Food for anchovy larvae. Several combinations of microzooplankton and the nanoflagellate *Tetraselmis* sp. were used as food for anchovy larvae. The densities are within the natural ranges reported for nanoflagellates (Gaxiola-Castro 1984) and microzooplankton. (Arthur 1977, Beers *et al.* 1982).

Tetraselmis sp. was added to the tanks at least two days before the introduction of *E. mordax* eggs, to minimize the wide fluctuations that have been observed for this nanoflagellate during the initial days after its inoculation into the rearing tanks (Carrillo-Barrios-Gómez and Solís-Guevara: manuscript). Microzooplankton was added two days after hatching, at the approximate time of yolk absorption (Lasker *et al.* 1970). It consisted mainly of copepod nauplii in the 50-100 μm (O'Connell and Raymond 1970, Houde 1973).

The microzooplankton used as food was sorted from wild plankton tows from Todos Santos Bay. It was collected with a 30 cm ring net equipped with a 0.239 mm mesh. Upon arrival at the laboratory the plankton samples were diluted into pyrex trays filled with precooled sea water.

The densities of microzooplankton in the larval rearing tanks were determined from a homogenized sample resulting from three 25 ml aliquots obtained by sampling the surface the bottom and the middle portions of each tank with a modified syringe. All measurements were determined twice each day for every tank: in the morning, before turning on the lights and in the afternoon, approximately one hour before turning them off.

Monoxenic strains of *Tetraselmis* sp. were maintained in the laboratory following standard techniques for rearing (Guillard 1972).

The densities of *Tetraselmis* sp. in the larval rearing tanks were determined three times each day.

From a homogenized sample resulting from three 5 ml aliquots obtained with a procedure similar to the one used for microzooplankton. Densities were determined by counting samples on haemocytometer slides (Fuchs-Rosenthal ruling). All necessary adjustments

TABLE 1

Experimental design. Effect of several below minimum food densities (theoretical starvation conditions) in the growth and survival of larvae of the northern anchovy Engraulis mordax.

Experimental Series ¹	Stocking density (eggs/l) ²	Designated density of microzooplankton (organisms/l) ³	Designated concentration of <i>Tetraselmis</i> sp. (cells/ml)
1A	20	40	5,000
1A'	20	40	5,000
1B	20	100	5,000
1B'	20	100	5,000
1C	20	400	5,000
1C'	20	400	5,000
2A	20	40	10,000
2A'	20	40	10,000
2B	20	100	10,000
2B'	20	100	10,000
2C	20	400	10,000
2C'	20	400	10,000
Control	20	*	*
Control	20	*	*

1. Each experiment within each Series and the control group was replicated once.
 2. Total stocking density per experiment: 200 eggs per each 10 liter container.
 3. Below minimum food densities (< 1000 organisms per liter): theoretical starvation conditions.
- * real starvation conditions.

were done in each tank after these determinations, to maintain the designated densities of microzooplankton and *Tetraselmis* sp.

All dead larvae in each tank were counted and removed twice every day with a suction pipette. In addition, three live larvae were removed randomly every day from each tank, from the day of hatching through the end of the experiment. Standard length was determined for each larvae by placing it immediately after removal under a dissecting microscope equipped with an ocular micrometer.

All experiments were terminated at day 12 after hatching with the exception of those that ended prematurely due to the total mortality of the larvae. At the end of each experiment surviving larvae were counted and measured.

Growth. Length increments of larvae in each tank were determined daily. A linear model of growth was used because it fitted well during the first days of growth (Kramer and Zweifel 1970, Lasker *et al.* 1970).

Survival. The daily percent of survival was estimated for each experiment following a procedure used by O'Connell and Raymond (1970). In addition, survival at the end of each experiment was adjusted to include the larvae that were sampled.

RESULTS

Rearing of *E. mordax*. Table 2 summarizes basic information on the rearing of *E. mordax* larvae. Fluctuations in temperature were minimal; as an average it was kept approximately at 16.6° C. On the other hand, differences in the initial number of larvae were more pronounced, ranging from 156 to 199. These were the result of hatching success in each series of experiments: an average of 96 % hatching for Series 1 and for the control experiments and 81% hat-

TABLE 2

Summary of basic data for larvae of the northern anchovy *Engraulis mordax* reared under theoretical starvation conditions.

Experimental Series	Mean temperature (°C)	Stocking density (eggs/l) ¹	Hatching (%)	Number of larvae stocked	DENSITY OF MICRO-ZOOPLANKTON (Organisms/l)		CONCENTRATION OF <i>Tetraselmis</i> (Cells/ml)		Length of experiment (days) ⁴
					Designated	Actual (\bar{x}) ²	Designated	Actual (\bar{x}) ³	
1A	17.0	20	99	198	40	37	5,000	3,800	9
1A'	16.8	20	96	192	40	30	5,000	3,600	8
1B	16.4	20	95	190	100	83	5,000	4,000	9
1B'	16.5	20	94	187	100	82	5,000	3,900	9
1C	16.7	20	99	199	400	299	5,000	3,700	12
1C'	16.7	20	94	178	400	260	5,000	3,400	12
2A	16.7	20	83	165	40	37	10,000	9,900	10
2A'	16.7	20	83	165	40	31	10,000	10,200	11
2B	16.4	20	78	156	100	94	10,000	9,300	10
2B'	16.6	20	82	163	100	80	10,000	9,200	11
2C	16.8	20	79	157	400	211	10,000	9,500	12
2C'	16.7	20	83	165	400	197	10,000	9,400	12
Control	16.9	20	95	190	*	*	*	*	9
Control	17.0	20	98	196	*	*	*	*	9

1. Calculated initially with 100 eggs in each Series. Adjusted at the end of each experiment when necessary.
2. Mean value based on two determinations per day.
3. Mean value based on three determinations per day.
4. Computed as days after hatching.

* real starvation conditions.

ching for Series 2. It must be pointed out that eggs used in each Series of experiments came from different spawnings.

The designated densities of microzooplankton and *Tetraselmis* sp. fluctuated throughout the duration of the experiment.

Nevertheless, they were kept close to the nominal densities of the experimental design (Table 2). Table 2 also shows the differences in the duration of experiments: from a biological maximum of 8-9 days after hatching under starvation conditions or low densities of microzooplankton-nanoflagellates (1A-A' and 1B-1B'), to a designated maximum of 12 days after hatching under higher densities of microzooplankton-nanoflagellates (1C-1C' and 2C-2C').

Growth. Standard length and daily growth rate of *E. mordax* larvae are shown in Table 3. There is no clear correlation between an in-

crease in the density of microzooplankton-nanoflagellates and a corresponding increment in the length or in the growth rate of the larvae during the first week after hatching, whereas the opposite seems to be true from the second week on. For example, the maximum recorded values of an increment in length and in the growth rate of *E. mordax* are evident from day seven, after hatching in experiments characterized by higher microzooplankton densities in both series (1C-1C' and 2C-2C') and in those experiments with the higher concentrations of nanoflagellates (2C-2C').

The same pattern emerges when considering the mean daily growth rates of the larvae throughout the duration of the experiments (Figs. 1-2). A non-parametric analysis (Kruskal-Wallis, 95%) of these means shows there were no significant differences between them during the first week after hatching for both Series of

TABLE 3

Summary of growth data for larvae of the northern anchovy *Engraulis mordax* reared under theoretical starvation conditions.

Experimental Series	Number of larvae Stocked	Number of larvae preserved	Length of experiment (days) ¹	Day 0 ²	STANDARD LENGTH (mm)				DAILY GROWTH RATE (mm)		
					S \bar{x}	Day 7 ³	S \bar{x}	End of exp. ⁴	S \bar{x}	Days 0 - 7	Days 7 - end of exp.
1A	198	24	9	3.03	—	3.67	0.11	3.68	0.19	0.107	0.061
1A'	192	25	8	3.03	—	3.55	0.20	4.00	—	0.111	0.148
1B	190	27	9	3.03	—	3.48	0.15	4.10	0.29	0.186	0.002
1B'	187	24	9	3.03	—	3.65	0.15	3.83	0.67	0.112	0.001
1C	199	36	12	3.03	—	4.31	0.30	5.97	0.30	0.040	0.439
1C'	178	36	12	3.03	—	4.51	0.46	5.96	0.11	0.133	0.410
2A	165	33	10	3.39	0.28	4.14	0.10	4.40	0.42	0.110	0.102
2A'	165	30	11	3.39	0.28	4.24	0.05	4.64	0.05	0.134	0.062
2B	156	31	10	3.39	0.28	4.28	0.72	4.60	—	0.125	0.245
2B'	163	33	11	3.39	0.28	3.90	0.26	5.79	0.08	0.182	0.333
2C	157	36	12	3.39	0.28	4.00	0.17	7.70	1.54	0.128	0.524
2C'	165	36	12	3.39	0.28	5.05	0.48	8.00	0.17	0.162	0.608
Control	190	23	9	3.03	—	3.67	0.21	3.41	0.32	0.040	0.001
Control	196	22	9	3.03	—	3.72	0.04	3.33	—	0.072	0.001

1. Computed as days after hatching (day 0 indicates day of hatching)

2. Mean value computed from ten larvae in each Series

3. Mean value computed from three larvae in each experiment.

4. Mean value computed from all survivors in each experiment.

experiments. A similar analysis for the second week shows that the mean daily growth rates in both Series were significantly greater in experiments conducted with higher densities of microzooplankton.

An analysis of the total growth, from the day of hatching to the end of each experiment is summarized in Table 4. The data suggest a pattern similar to the one described above: the student "t" test indicates that under starvation conditions or under low densities of microzooplankton-nanoflagellates (1A-1A') the daily growth rate may be considered as being equal to zero. For the remaining experimental conditions there is a clear correlation between food density and growth rate: maximum growth occurs under conditions of higher microzooplankton densities (1C-1C') and (2C-2C') and between these, the best growth is found under the higher concentrations of nanoflagellates in Series 2 (2C-2C').

Survival. Throughout the durations of this study, *E. mordax* larvae were maintained under theoretical starvation conditions (1000 organisms/L). Under similar conditions, larvae of this species have been kept alive for a maximum of nine days after hatching (Lasker *et al.* 1970, O'Connell and Raymond 1970). For this reason, an experiment was considered successful whenever survival extended beyond nine days after hatching. Figures 3 and 4 summarize survival data for both Series. Under the stated premise, the most successful survival was found under the highest concentrations of microzooplankton in both Series (1C-1C') and (2C-2C'); the only larvae alive at 12 days were those reared under these feeding conditions. Survival of *E. mordax* larvae, although low, extended beyond nine days in all experiments of Series 2, characterized by the higher concentrations of nanoflagellates (Fig. 4).

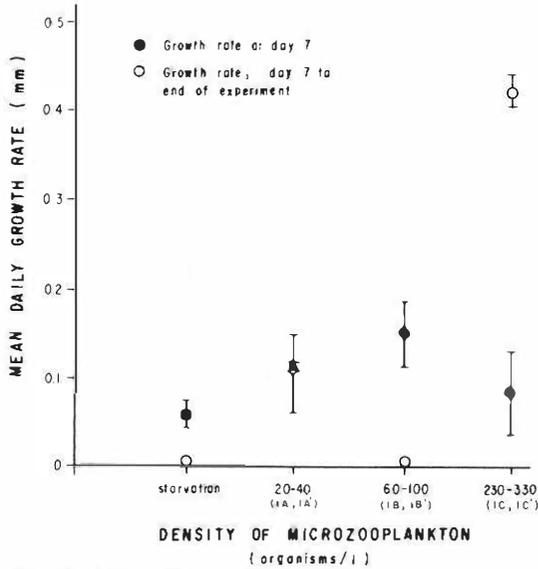


Fig. 1. Effect of several below minimum densities of microzooplankton (theoretical starvation conditions) in the growth rate of larvae of the northern anchovy *Engraulis mordax*. A background concentrations of approximately 3,800 cells ml^{-1} of the nanoflagellate *Tetraselmis* sp. was used in all experiments, excluding those under starvation conditions. Vertical lines indicate the range of data for each experiment.

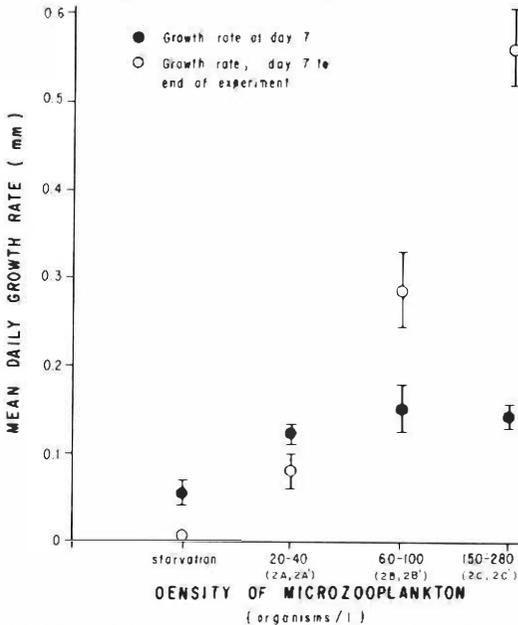


Fig. 2. Effect of several below minimum densities of microzooplankton (theoretical starvation conditions) in the growth rate of larvae of the northern anchovy *Engraulis mordax*. A background concentrations of approximately 9,000 cells ml^{-1} of the nanoflagellate *Tetraselmis* sp. was used in all experiments, excluding those under starvation conditions. Vertical lines indicate the range of data for each experiment.

DISCUSSION

Assuming that the quantitative data on zooplankton densities in the ocean adequately represent food availability in the marine environment, it seems evident that food densities in the ocean are two orders of magnitude below those that have been estimated as minimum to meet the metabolic requirements of most marine fish larvae. Under this premise, the potential utilization of food patches as a survival strategy for marine fish larvae is attractive: food would tend to be concentrated in a relatively small area, increasing the possibilities of food aggregations in densities high enough to reduce or avoid starvation conditions for the larvae.

Several field and laboratory studies conducted with larvae of *E. mordax* add strength to the importance of food patches for the survival of marine fish larvae (Lasker 1975, Lasker and Zweifel 1978, Owen 1981). However, it seems paradoxical that marine fish larvae would have developed survival mechanisms that would favor a feeding strategy based upon an unstable resource (food patches), that is randomly distributed in a subutilized habitat and where adequate food densities of another potential food organisms may be available.

For instance, most coastal marine fishes occupy a small portion (1%) of its adult habitat (Smith 1981). Under these conditions, larvae of those species would significantly reduce their potential to find and utilize food patches in most of their distributional range. In addition, the utilization of food patches by marine fish larvae requires of spatial and temporal stability of the patches (Lasker 1981). Yet, one of the most striking characteristics of food patches lies precisely on their unstable nature (Lasker 1975, 1981). Finally several authors have shown that larvae of *E. mordax* species will feed successfully on other food sources available in the marine environment (Moffatt 1981, Quiñónez-Velázquez 1985, Gil-Hernández 1986) but previously disregarded as inadequate because of its type, size and concentration (May 1970, Scura and Jerde 1977, Hunter 1981).

Our results suggest that contrary to what may be expected, larvae of *E. mordax* could grow and survive in an environment characterized by low food densities. For instance, the growth rates obtained in this study under theoretical starvation conditions ($\bar{x} = 0.13$ mm/day

TABLE 4

Growth equations (\hat{Y} estimated length after X days from hatching), growth rates (\hat{b} and $\pm S_{\hat{b}}$), student "t" value for the test ($b = 0$; $b \neq 0$) and correlation coefficients for larvae of the northern anchovy *Engraulis mordax* reared under theoretical starvations conditions.

Experimental Series	Equation	\hat{b} and $\pm S_{\hat{b}}$	Degrees of freedom	"t"	Correlation coefficient
1A	$\hat{Y} = 3.52 + 0.043 X$	0.043 ± 0.032	8	1.35*	0.29*
1A'	$\hat{Y} = 3.44 + 0.070 X$	0.070 ± 0.037	8	2.00*	0.50*
1B	$\hat{Y} = 3.14 + 0.160 X$	0.160 ± 0.030	6	5.32	0.89
1B'	$\hat{Y} = 3.60 + 0.006 X$	0.006 ± 0.006	8	0.18*	0.06*
1C	$\hat{Y} = 2.85 + 0.206 X$	0.206 ± 0.035	11	5.84	0.86
1C'	$\hat{Y} = 2.89 + 0.225 X$	0.225 ± 0.030	11	7.36	0.90
2A	$\hat{Y} = 3.55 + 0.085 X$	0.085 ± 0.017	10	5.07	0.83
2A'	$\hat{Y} = 3.64 + 0.068 X$	0.068 ± 0.022	10	3.15	0.67
2B	$\hat{Y} = 3.52 + 0.097 X$	0.097 ± 0.035	7	2.78	0.68
2B'	$\hat{Y} = 2.96 + 0.192 X$	0.192 ± 0.032	10	6.00	0.87
2C	$\hat{Y} = 2.71 + 0.337 X$	0.337 ± 0.047	11	7.10	0.90
2C'	$\hat{Y} = 2.58 + 0.354 X$	0.354 ± 0.047	11	7.57	0.91
Control	$\hat{Y} = 3.55 + 0.022 X$	0.022 ± 0.039	7	0.57*	0.21*
Control	$\hat{Y} = 3.58 + 0.013 X$	0.013 ± 0.043	7	0.30*	0.11*

* Not significant at 95 %C.L.

during the first week after yolk absorption; $\bar{x} = 0.50$ mm/day from day 7-12) are very similar to those found by Kramer and Zweifel (1970) and Lasker *et al.* (1970) with larvae of the same species reared under optimum feeding conditions (0.14 mm/day during the first week after yolk absorption; 0.3-0.5 mm/day during the second week).

Our results also agree with studies conducted with fish larvae of several species. For instance, Moffatt (1981) found that larvae of *E. mordax* can grow and survive in an environment with low densities of microzooplankton and a dense bloom of *Chlorella* sp. Houde (1977, 1978) and Houde and Schekter (1981) obtained good growth and survival with fish larvae of several subtropical species reared on a combination of below minimum (< 100 organisms/L) food

densities and a bloom of phytoplankton in the rearing container.

Current literature on the feeding ecology of *E. mordax* larvae shows contrasting results obtained when rearing larvae of this species with or without the addition of nanoflagellates. In the presence of these phytoplankters: a) below minimum feeding conditions seem to be adequate for succesful growth and survival (Moffatt 1981); b) survival is extended significantly beyond the estimated "point of no return" (Carrillo-Barrios, Gómez and Solís -Guevara: manuscript); c) better growth and survival than that found under real starvation conditions can be obtained on a diet composed exclusively of nanoflagellates (Carrillo-Barrios, Gómez and Solís-Guevara: manuscript), and d) survival can also be extended significantly be-

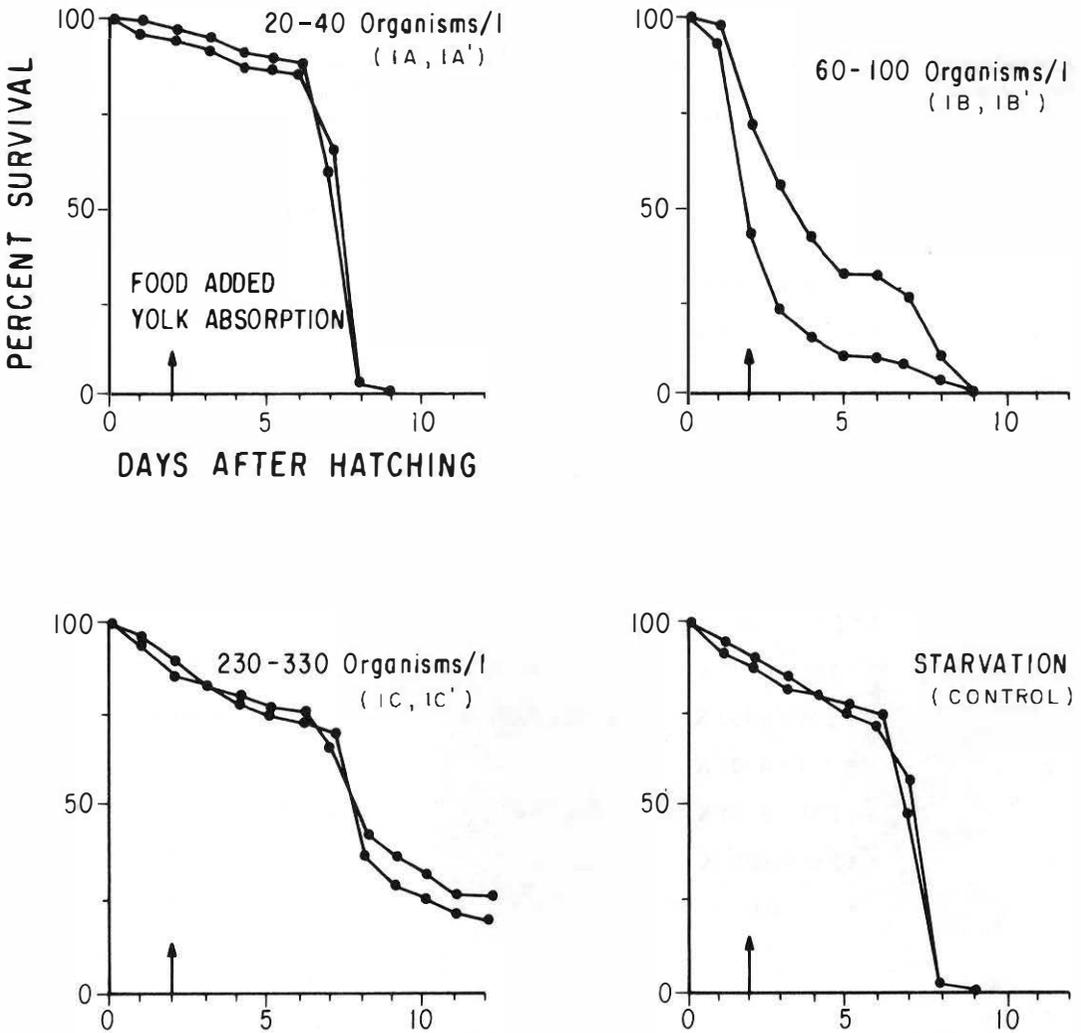


Fig. 3. Percent survival of larvae of the northern anchovy *Engraulis mordax* reared under theoretical starvation conditions. Vertical line at day 2 indicates time when food was added and approximate time of yolk absorption. A background concentrations of approximately 3,800 cells ml⁻¹ of the nanoflagellate *Tetraselmis* sp. was added at day 0 and maintained in all experiments, excluding those under starvation conditions.

yond maximum periods reached without nanoflagellates (Quiñónez-Velázquez 1985, Gil-Hernández 1986). The results presented here, together with those reported by Houde (1977, 1978), Houde and Schekter (1981) and Moffatt (1981), emphasize the importance of flagellates in the feeding ecology of fish larvae.

Recent studies have shown that larvae of *E. mordax* can use particulate organic matter as a source of food during the first week after yolk absorption, and that the utilization of that food source extends significantly the survival of these larvae during the second week (Quiñónez-

Velázquez 1985). Similar studies have also shown that dissolved organic matter extends significantly the survival of larvae of this species beyond its range of survival under real starvation conditions (Gil-Hernández 1986).

Our results suggest that fish larvae of some species can grow and survive successfully in the theoretical starvation conditions of the marine environment. They also suggest the availability of other sources of food as well as the potential for additional ones, and thus, the existence of successful feeding strategies that do not require of food patches to avoid starvation.

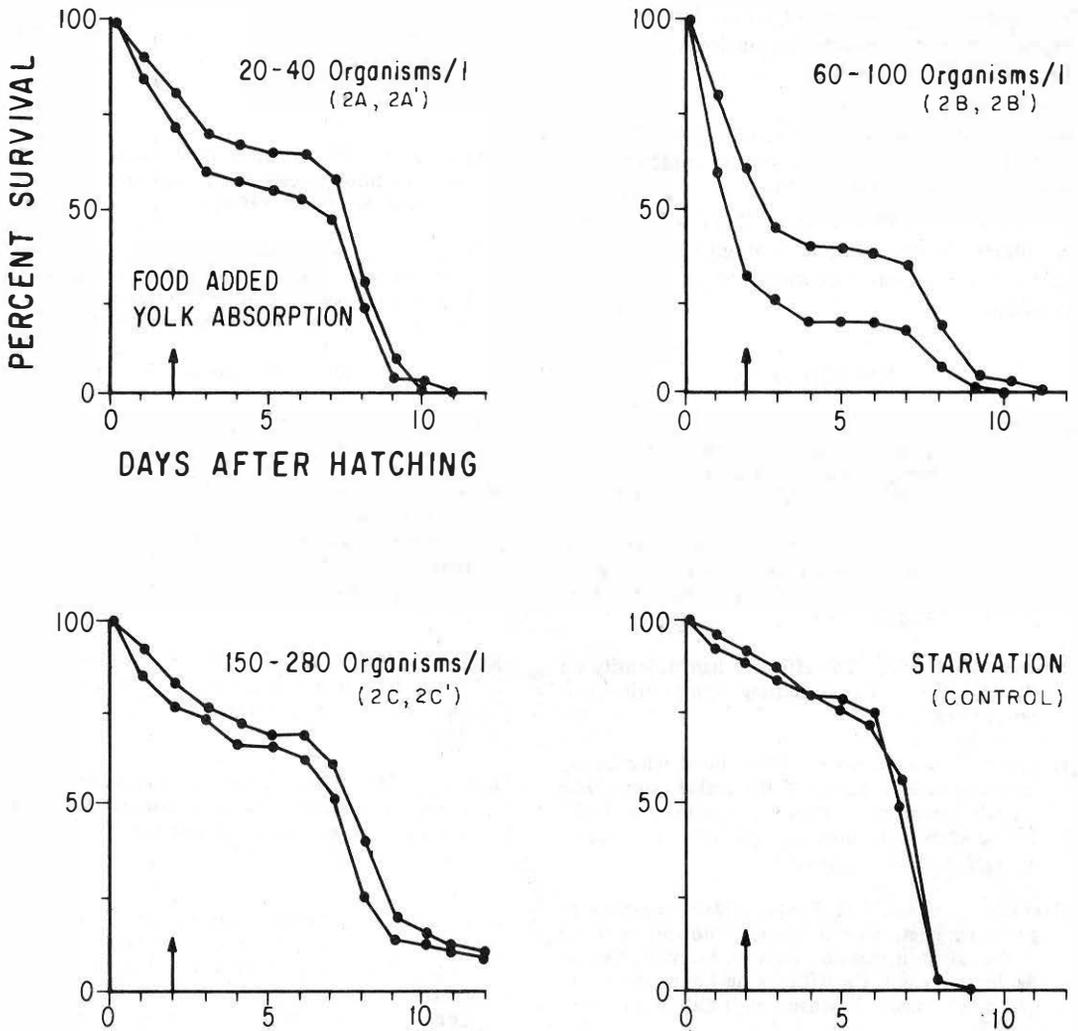


Fig. 4. Percent survival of larvae of the northern anchovy *Engraulis mordax* reared under theoretical starvation conditions. Vertical line at day 2 indicates time when food was added and approximate time of yolk absorption. A background concentration of approximately 9,000 cells ml^{-1} of the nanoflagellate *Tetraselmis* sp. was added at day 0 and maintained in all experiments, excluding those under starvation conditions.

The results presented in this paper suggest that larval mortality due to feeding conditions may not be as significant as previously thought. It is then possible, that predation may indeed be, one of the most important factors regulating mortality in eggs and early larval stages (Hunter 1981), though the importance of other factors is not disregarded (Vladimirov 1975). Thus, the existence of a critical period in the original context proposed by Hjort (1914) can be questioned.

RESUMEN

Un conjunto de 2800 larvas de la anchoveta *Engraulis mordax* Girard fueron mantenidas hasta 12 días después de la eclosión en condiciones de laboratorio, en la presencia de una concentración variable del nanoflagelado *Tetraselmis* sp. (5,000 y 10,000 cels/ml) y en condiciones hipotécnicas de inanición (20-300 orgs./L). Contrario a lo esperado, el crecimiento y la supervivencia encontrados son comparables a

los hallados por otros autores para larvas de esta especie, pero en condiciones óptimas de alimentación. Nuestros resultados sugieren la existencia de otras alternativas que pueden ser utilizadas por larvas de peces marinos para evitar la inanición y crecer en un ambiente caracterizado por bajas densidades de alimento. Se cuestiona por tanto la existencia de un "período crítico". Se sugiere la importancia ecológica de nanoflagelados como fuente de alimento en el ambiente marino.

REFERENCES

- Arthur, D.K. 1977. Distribution, size and abundance of microcopepods in the California Current systems and their possible influence on survival of marine teleost larvae. *Fish. Bull. U.S.* 75(3): 601-611.
- Beers, J.R., F.M.H. Reid & G.L. Stewart. 1982. Seasonal abundance of the microplankton population in the north Pacific Central gyre. *Deep-Sea Res.* 29-2A-: 227-245.
- Blaxter, J.H.S. 1966. The effect of light intensity on the feeding ecology of herring. *Symp. Brit. Ecol. Soc.* 6:393-409.
- Detwyler, R. & E.D. Houde. 1970. Food selection by laboratory-reared larvae of the scaled sardine *Harengula pensacolatae* (Pisces: Clupeidae) and the bay anchovy *Anchoa mitchilli* (Pisces: Engraulidae). *Mar. Biol.* 7: 214-222.
- Gaxiola-Castro, G. 1984. Productividad primaria y algunos parámetros de la relación fotosíntesis-luz en el fitoplancton marino. Tesis de Maestría, Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, Baja California, México. 127 p.
- Gil-Hernández, R.A. 1986. Flujo de aminoácidos disueltos y su efecto sobre el crecimiento y supervivencia de huevos y larvas de la anchoveta norteña *Engraulis mordax* Girard. Tesis de Maestría en Ciencias, Centro de Investigación y de Educación Superior de Ensenada, Ensenada, Baja California, México.
- Guillard, R.K.L. 1972. Culture of phytoplankton for feeding marine invertebrates, p. 24-60. *In:* W.L. Smith & N.H. Chanley (eds.) *Culture of Marine Invertebrate Animals*. Plenum Press., New York. 338 p.
- Hamilton, R.D. & A.F. Carlucci. 1966. Use of ultraviolet irradiated sea water in the preparation of culture media. *Nature* 211 (5048): 483-484.
- Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. *Rapp. P. V. Réun. Cons. Inter. Expl. Mer.* 20: 1-228.
- Houde, E.D. 1977. Food concentration and stocking density effects on survival and growth of laboratory-reared larvae of Bay anchovy *Anchoa mitchilli* and lined sole *Archirus lineatus*. *Mar. Biol.* 43:333-341.
- Houde, E.D. 1978. Critical food concentration for larvae of three species of subtropical marine fishes. *Bull. Mar. Sc.* 28(3): 395-411.
- Houde, E.D. & R.C. Schekter. 1981. Growth rates, relations and cohort consumption of marine fish larvae in relation to prey concentrations. *Rapp. P. V. Réun. Cons. int. Explor. Mer.* 178: 441-453.
- Hunter, J.R. 1981. Feeding ecology and predation of marine fish larvae, p. 33-77. *In:* R. Lasker (ed.). *Marine Fish Larvae Univ. Wash. Press. Seattle.* 131 p.
- Hunter, J.R. & G.L. Thomas. 1974. Effect of prey distribution and density on the searching and feeding behavior of larval anchovy *Engraulis mordax* (Girard), p. 559-574. *In:* J.H.S. Blaxter (ed.) *The Early Life History of Fish*. Springer-Verlag, Berlin. 765 p.
- Kramer, D. & J.R. Zweifel. 1970. Growth of anchovy larvae *Engraulis mordax* in the laboratory as influenced by temperature. *CalCOFI Rept.* 14: 84-87.
- Lasker, R. 1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. *Fish. Bull. U.S.* 73(3): 453-462.
- Lasker, R. 1981. Factors contributing to variable recruitment of the Northern Anchovy *Engraulis mordax* in the California Current: Contrasting years, 1975, through 1978. *Rapp. P. V. Réun. Cons. int. Explor. Mer.* 178: 375-388.
- Lasker, R., H.M. Feder, G.H. Theilacker & R.C. May. 1970. Feeding growth and survival of *Engraulis mordax* larvae reared in the laboratory. *Mar. Biol.* 5: 345-353.
- Lasker, R. & J.R. Zweifel. 1978. Growth and survival of first-feeding Northern Anchovy *Engraulis mordax* in patches containing different proportions of large and small prey, p. 329-353 *In* J.H. Steele. (ed.) *Spatial Pattern in Plankton Communities*. Vol. III. Plenum Press, New York.
- Lasker, R. & K. Sherman (eds). 1981. The early life history of fish: recent studies. *Rapp. P. V. Réun. Cons. int. Explor. Mer.* 178: 607 pp.
- May, R.C. 1970. Feeding larval fishes in the laboratory: a review. *Calif. Coop. Oceanic Fish. Invest. Rep.* 14: 76-83.
- Moffatt, N.M. 1981. Survival and growth of Northern anchovy larvae on low zooplankton densities af-

- ected by the presence of *Chlorella* sp. bloom Rapp. P. V. Réun. Cons. Perm. int. Explor. Mer. 178: 475-486.
- O'Connell, C.P. & L.P. Raymond, 1970. The effect of food density on survival and growth of early post yolk-sac larvae of the Northern Anchovy in the laboratory. J. Exp. Mar. Biol. Ecol. 5: 187-197.
- Owen, R.W. 1981. Microscale plankton patchiness in the larval Anchovy environment, Rapp. P. V. R Réun. Cons. int. Explor. Mer. 178:368.
- Quiñónez-Velázquez, C. 1985. Utilización de material orgánico particulado como fuente de alimento por larvas de la anchoveta norteña *Engraulis mordax* Girard. Tesis de Maestría en Ciencias. Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, Baja California. 91 p.
- Scura, E.D. & C.W. Jerde. 1977. Various species of phytoplankton as food for larval northern anchovy *Engraulis mordax* and relative nutritional value of the dinoflagellates *Gymnodinium splendens* and *Gonyaulax polyedra*. Fish Bull. U.S. 75:577-583.
- Smith, P.E. 1981. Fisheries on Coastal Pelagic Schooling Fish, p. 1-32. In: R. Lasker (ed.). Marine Fish Larvae. Univ. Wash. Press. Seattle, Wash. 131 p.
- Vladimirov, V.I. 1975. Critical periods in the development of fishes. P. Ichtyol. 15: 851-868.
- Wyatt, T. 1972. Some effects of food density on the growth and behavior of plaice larvae. Mar. Biol. 14: 210-216.