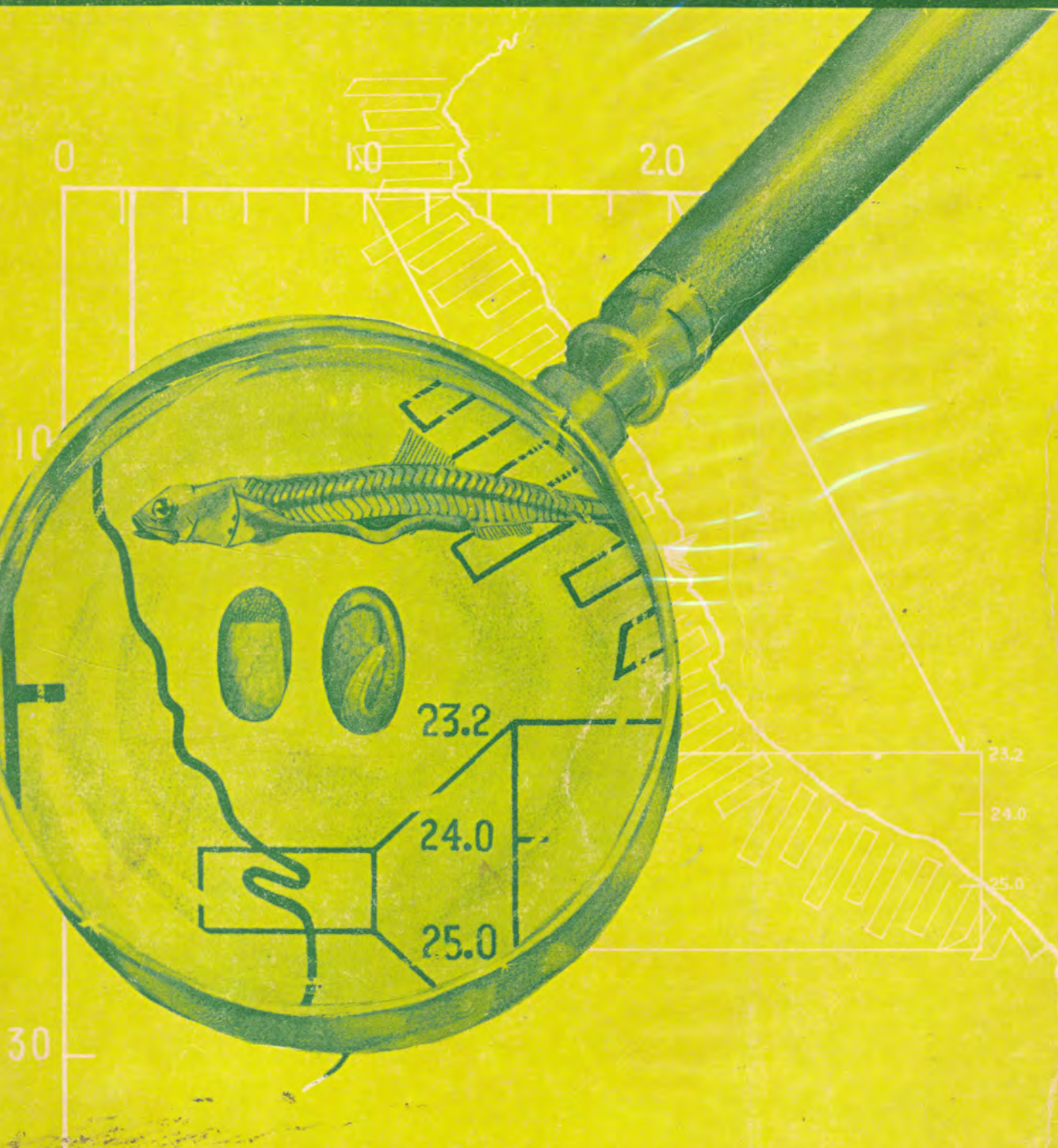




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**INVESTIGACION COOPERATIVA DE LA ANCHOVETA  
Y SU ECOSISTEMA - ICANE - ENTRE PERU Y CANADA  
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## BEHAVIOUR OF FIRST-FEEDING PERUVIAN ANCHOVETA LARVAE, *Engraulis ringens* J\*

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### ABSTRACT

During the prolarval stage *Engraulis ringens* use their yolk reserve to increase proportionally more in body length than in width. Under experimental conditions the prolarval stage lasted 2.75 d at 18°C. First-feeding began, on average, at age 4.4 d or 1.7 d after complete yolk resorption. The age of first-feeding was inversely correlated with the size of the post-larvae. Swimming activity increased from 0 % of the time at hatching to 50 % by age 4.5 d. In the absence of food, maximum activity occurred at age 6 d then declined to 0 % as the larvae weakened and became moribund. With one exception, phytoplankton *Actinocyclus* and *Gymnodinium* formed the principal food on the first day of feeding, regardless of the concentration of zooplankton. At zooplankton concentrations <0.2 individuals/ml phytoplankton continued to dominate the diet, whereas copepod nauplii and small copepodites formed the principal foods at higher zooplankton concentrations. The percentage of larvae feeding and gut fullness increased with age. Food width was also proportional to the size of the larvae, averaging 1-2 % of the body length. These observations are compared with similar findings for *E. mordax*. And the possible significance of Langmuir circulations in generating small-scale food patchiness is discussed in relation to the feeding and survival of anchoveta larvae in nature.

### RESUMEN

Las prolarvas de *Engraulis ringens* usan su reserva vitelina para crecer mas en longitud que en grosor. En condiciones experimentales el estadio prolarval duró 2.75 días a 18°C. La primera alimentación comenzó, en promedio, a la edad de 4.4 días ó a 1.7 días después de la reabsorción completa del vitelio. La edad de la primera alimentación estuvo inversamente relacionada con el tamaño de las post larvas. La actividad natatoria aumentó del 0 % del tiempo al momento de la eclosión hasta el 50 % al cumplirse los 4.5 días de edad. En ausencia de alimento, la actividad máxima se dió a la edad de 6 días después de la cual decayó hasta el 0 % conforme las larvas se debilitaban hasta quedar moribundas. El principal alimento en el primer día de alimentación fue, con una sola excepción, fitoplancton, *Actinocyclus* y *Gymnodinium*, independientemente de la concentración de zooplancton. El fitoplancton continuó dominado la dieta a concentraciones de zooplancton menores de 0.2 individuos por ml pero a mayores concentraciones el principal alimento fueron los nauplios de copépodos y pequeños copépodos. El porcentaje de larvas alimentándose así como el de tractos digestivos llenos aumentó con la edad. La anchura del alimento también fue proporcional al tamaño de las larvas, y en promedio fue del 1 al 2 % de la longitud. Se compara estas observaciones con sus similares para *E. mordax*. En relación a la alimentación y la sobrevivencia de las larvas de anchoveta en su ambiente natural, se ha discutido el posible papel desempeñado por la circulación de Langmuir en la distribución del alimento en pequeñas manchas.

\* Reprinted from: Sherman, K. and G. Hempel, editors, Symposium on Early Life History of Fish, Conseil International pour l'Exploration de la Mer, Rapports et Procès-Verbaux des Reunions. Vol. 178, 1980.

## INTRODUCTION

The reason why the Peruvian anchoveta fishery—once the largest in the world—failed, is of fundamental importance to that country's economy. To date several theories have been advanced to explain the current state of the fishery, and climatic phenomena usually figure prominently. Thus Walsh (1978) suggested that the collapse of most of the world's clupeid stocks may be linked with interactions between overfishing and natural oscillations at the storm scale of variability, which might interrupt the food supply of the larvae.

The development of the feeding response of the northern anchovy (*E. mordax*) has been studied intensively, and linked in a causal way to recruitment variability. In this article we report similar observations for its southern counterpart (*E. ringens*) and draw a comparison between the two species. The work was conducted under field conditions at Samanco Bay—about 300 km north of Lima—in November 1977. So we note in passing that rather than providing any definitive answers, the information presented here is more preliminary in nature, intended to identify promising lines of future research.

## MATERIAL AND METHODS

By November, anchoveta eggs and prolarvae were becoming scarce so we were forced to use all the material that we collected in good condition. The experiments were started with three different combinations of ichthyoplankton. Five batches, each of 100 eggs (groups, A, B, C, D, L), and 7 batches (groups E, F, G, H, I, J, K) of 30 recently hatched prolarvae were transferred to 2 litre glass battery jars filled with sand-filtered sea water. These groups were scheduled for development studies, but there were enough survivors at the end of the prolarval stage in jars A, B, G, I and J to use in the feeding experiments. Groups H and L were held without food to indicate survival under starvation conditions.

Two additional batches, each of 200 eggs, were transferred to 20 litre, yellow plastic buckets (filled with 10 litres of san-filtered water) for more extensive development and feeding work (groups Y1 and Y2). The containers were placed in a flowing sea water bath, where the temperature varied between 17 to 19°C.

Five larvae were removed from each group every morning, and examined in a fresh state under a microscope to determine their length, body width, jaw development, amount of eye pigmentation and gut contents. A yolk index: length of yolk-sac/total length of gut, was also calculated. The groups were studied until all the individuals had been removed by sampling, or had died from natural causes. The larvae were fixed in a 5% solution of buffered formalin, and selected specimens were remeasured 3 months later to determine the amount of shrinkage during preservation.

Wild plankton, which served as food in the ex-

periments, was collected with a 40µm mesh net. The raw material was washed gently through a 153 µm mesh screen and trapped on a 40µm screen. Hence the nominal width of the food organisms varied between 40 to 153µm. However, it was practicably impossible to obtain a perfect size separation without damaging the plankton, so some particles as small as 20µm were retained on the 40µm screen. This material was concentrated in one litre of filtered sea water, examined for species composition and abundance, and used as a stock food concentrate.

Plankton was added to the appropriate containers one day before complete yolk resorption. Following Lasker (1975), a gentle air stream was directed over the surface of the water in the jars to promote mixing. But this did not stop some particles from settling, so a 5 ml water sample was taken periodically to establish the abundance and species composition of the suspended material. All the food concentrations given here are based on average suspended particle counts.

Similarly all references to age are reckoned from the hatching time, or beginning of the prolarval stage, Hence the true age is equal to the stated age plus 2.3 days.

## RESULTS

### Development

**Egg development and mortality.** Eggs collected in the morning were invariably in late stages of development (about 24 to 40 hr old). This is consistent with Santander and Castillo's (1973) finding that spawning occurs at night, and that the incubation period lasts about 48 to 60 hr at 18°C.

On one occasion we were fortunate enough to video tape an individual hatching. It took 6 hr from the time the tail had penetrated the chorion until the larvae was finally free. We have no way of knowing whether this isolated observation is typical or not.

In the groups started with eggs the pre-hatching mortality due to handling and other causes averaged 50 % to 60 %.

**Morphogenesis of prolarvae.** Figure 1 gives a composite representation of the developmental sequence and growth of the larvae during the yolk-sac stage. Note that the yolk index decreased linearly with time, whereas the total length increased according to the Von Bertalanffy function:

$$L = 4.17 (1 - \text{EXP} [-0.036 (t + 30.06)])$$

where

L = Length (mm) and t = time after hatching (hrs).

The duration of the prolarval stage averaged 64 hours, by which time the eyes were fully pigmented and the mouth functional.

We noticed that there was a marked diversity in the amount of yolk in relation to larval size (Fig. 2). Undoubtedly some of the variability was due to human errors in measurement. But the scatter is so great that either there was a wide range in

Fig. 1 Group composite indicating the change in mean yolk index (open circles) and total length (solid circles) after hatching at 18°C. The sequence of developmental events and time of first feeding are shown. Note that the shrinkage in length after day 4 did not occur in groups A, Y2 or Y1. In the latter group, the survivors began growing on day 8, averaging 4.8 mm by day 9.

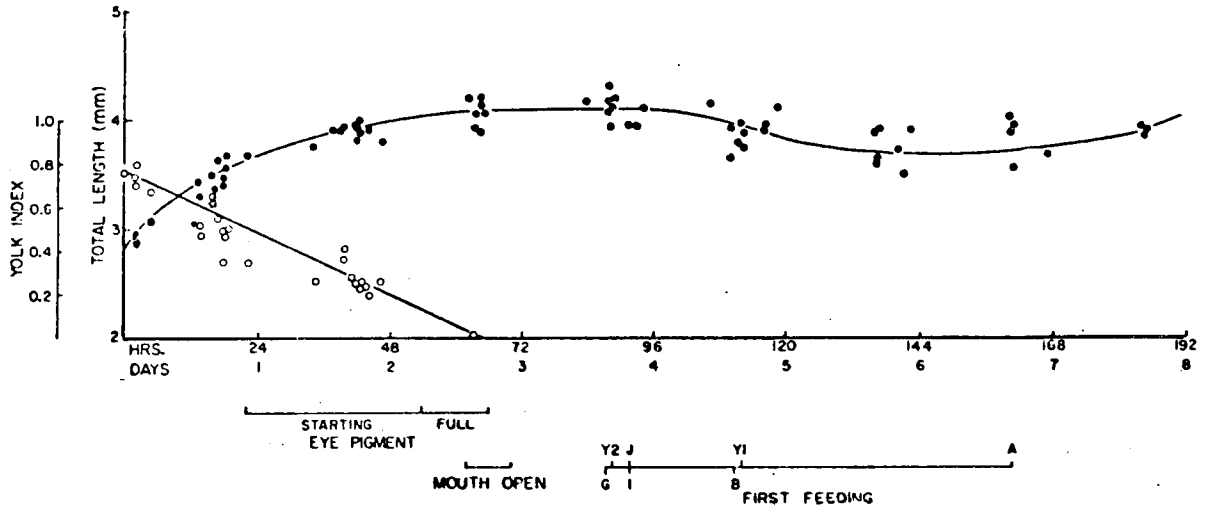
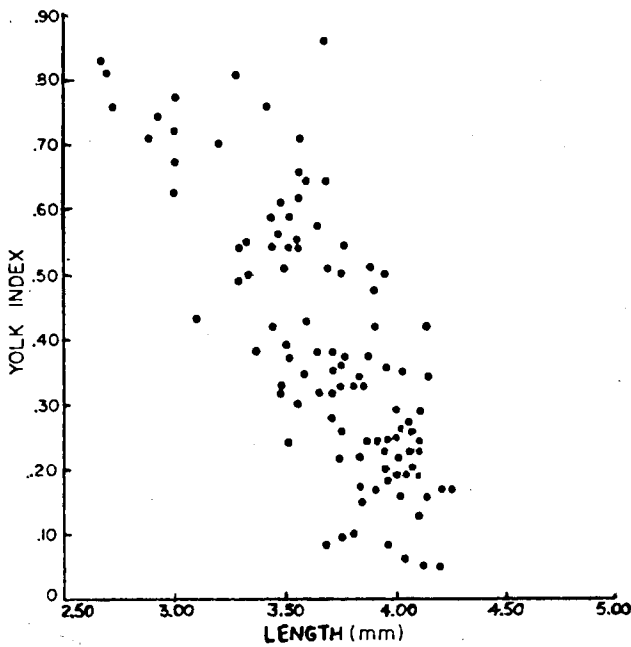


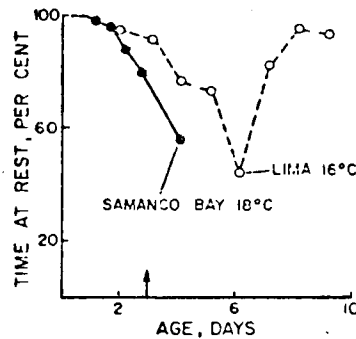
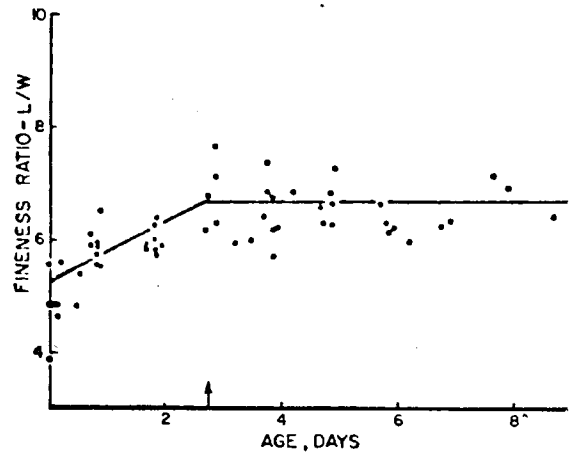
Fig. 2 Variation in relative size of the yolk sac (see text) with length of prolarvae.



egg size, or else the eggs and prolarvae taken from Samanco Bay had been developing under different environmental conditions. This inconsistency in the yolk reserves consequently led to notable differences in the size of the post-larvae in the different groups.

One measure of the change in form during morphogenesis is the fineness ratio: the length/maximum width, including the finfold. Figure 3 shows that anchoveta increase proportionally more in length than width during the prolarval stage. The fineness ratio reached a maximum on day 2.7 by which time the average length of the larvae

Fig. 3 Change in fineness ratio (total length/maximum width), and per cent of time larvae are inactive, with age. Arrows indicate end of the prolarval stage (age 2.7d).



had increased by a factor of 1.55 times, whereas the corresponding increase in width was only 1.17 times. Presumably, the unusual anguilliform-like swimming mode of anchovy, analyzed by Vlymen (1974), is one manifestation of these changes.

Casual observations of the activity pattern in *E. ringens* indicated it to be remarkably similar

to *E. mordax* (Hunter, 1972). In the early prolarval stages both species orient vertically with the head down and remain motionless except for passive transport by turbulent motions in the water. Over the next 48 hours this behaviour gradually evolves to one of intermittent swimming so that by the time the larvae begin feeding (age 4-5 days) they are actively moving about half the time (Fig. 3).

More extensive observations in Lima under similar conditions indicated that maximum activity in the absence of food occurred 6 days after hatching, but then diminished as the larvae weakened and became moribund (Fig. 3). We suggest that this regressive change in the swimming frequency denotes the point-of-no-return (Blaxter and Hempel, 1963). If so, then death is an inevitable consequence if feeding is not initiated within 48 to 72 hours after the beginning of the post-larval stage, at temperatures between 16-18°C.

### First Feeding Behaviour

**Food Concentration and Feeding intensity.** The food concentrations and other characteristics of the feeding experiments are summarized in Table 1. The zooplankton fraction consisted mainly of copepod nauplii and small copepodites notably *Oithona* and *Oncaea* sp. — whereas the dominant phytoplankton genera included: *Actinocyclus*, *Skeletonema*, *Chaetoceros*, *Nitzschia*, *Asterionella*, *Coscinodiscus*, and a few *Gymnodinium* and *Thalassiosira*. Examination of 127 post-larvae, including a few wild-caught individuals, indicated that they fed on only 5 of the 12 or so phytoplankton genera available: *Actinocyclus*, *Mesodinium*, *Gymnodinium*, *Thalassiosira*, and *Coscinodiscus*, and primarily on the first three. This list compares favourably with previous findings by Rojas de Mendiola (1975), but contrast with Lasker's (1975) observation that *E. mordax* would not eat *Thalassiosira*.

The age of first-feeding for *E. ringens* varied between 3.5 to 6.8 days, with a mean time of 4.4 day after hatching (Fig. 1). A closer examination of the data indicated that the timing was inversely related to the size of the post-larvae one day after yolk absorption (day 3.7)  $r = -0.76$ ,  $N = 7$ ,  $P \sim 0.05$ . Hence the groups with large individuals began feeding about 1 day later than those with

smaller post-larvae (Table 1).

Groups Y1 and Y2 contained the largest populations, so the development of their feeding response was followed for more than a week. Figure 4 shows that in both cases the incidence of feeding rose to a maximum 9 or 10 days after hatching. Concurrently, there was also a marked increase in the mean gut fullness.

In terms of the composition of the diet, the groups with less than 0.2 zooplankton/ml fed almost exclusively on phytoplankton. By contrast, at higher zooplankton concentrations — with the exception of the first day — the larvae fed mainly on zooplankton, particularly groups Y1 and Y2 (Fig. 5).

Contrary to similar studies we were surprised to find that there was no relationship between the proportion of larvae with food and the concentrations of either zooplankton, or *Actinocyclus* and *Gymnodinium* for the first 48 hours after yolk absorption. By the third day a relation was apparent but only with the concentration of zooplankton (Fig. 5). Over the duration of each experiment, however, the proportion of post-larvae sampled after day 3.7 that had fed ( $Pf_{3.7}$ ) was significantly correlated with the total concentration of suspended particles, and particularly the number of zooplankton:  $Pf_{3.7} = 0.125 (Zoo/ml) + 0.169$  ( $r = 0.83$ ,  $P \sim 0.02$  Table 1).

In total, 33% of the post-larvae sampled contained food but only those from Y1 and Y2 can be considered to have consumed significant rations. To some extent the reason for this was a result of our decision to sample early in the morning. Although this was the best time from a logistical

Fig. 4 Increase in per cent of larvae feeding, and mean proportion of posterior gut containing food, with age. Groups Y1 (open circles) and Y2 (solid circles) only. Arrows as before (Fig. 3).

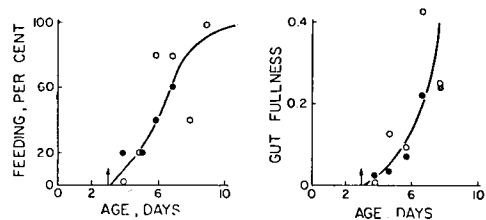


TABLE 1: FOOD CONCENTRATIONS, FIRST-FEEDING CHARACTERISTICS AND DEATH RATES OF THE EXPERIMENTAL GROUPS.  $Pf_{3.7}$  indicates the proportion of larvae feeding after day 3.7

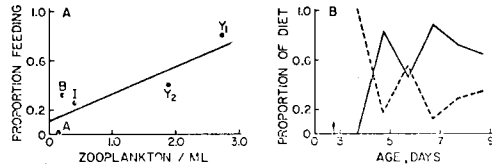
GROUP	PARTICLE CONCENTRATION (N/ML)			MEAN TEMPERATURE (°C)	DENSITY POST LARVAE DAY 3.7 ( $N_0/L$ )	DURATION OF EXPERIMENT (d)	FIRST-FEEDING			MEAN SIZE POST-LARVAE DAY 3.7 (mm)	DEATH RATE ( $N/N_0, d$ )	PRINCIPAL FOOD
	ZOOPLANKTON	ACTINOCYCLUS GYMNODINIUM	OTHER PHYTOPLANKTON				AGE (d)	LENGTH (mm)	$Pf_{3.7}$			
H	0	0	0	17.5	9.5	6	-	-	-	4.16	0.07	-
L	0	0	0	17.7	15.5	9	-	-	-	4.14	0.09	-
A	0.15	4.3	14.6	17.9	16.5	8	6.8	4.04	0.08	4.27	0.02	Phytoplankton
G	0.20	1.0	15.3	18.0	7.5	4	3.5	4.16	0.22	4.11	0.20	Phytoplankton
B	0.21	9.4	10.8	17.7	16.0	6	4.8	3.68	0.27	4.20	0.09	Phytoplankton
I	0.40	11.0	74.9	17.6	17.0	4	3.8	4.0	0.33	3.95	0.24	Both
J	0.80	18.0	63.3	17.6	12.5	4	3.8	4.4	0.17	3.92	0.21	Zooplankton
Y <sub>2</sub>	1.9	1.4	91.8	17.9	7.1	8	3.7	4.12	0.36	4.06	0.12	Zooplankton
Y <sub>1</sub>	2.8	2.1	133.8	17.8	9.4	11	4.7	3.68	0.56	4.19	0.07	Zooplankton

viewpoint, it meant that the larvae had only had sufficient light to feed for 3 hours (0600-0900 hrs).

**Food size vs larval size.** As expected, food

Fig. 5 A. relation between proportion of larvae feeding on the third day (72 hrs) after yolk resorption ( $Pf_{72}$ ) and the concentration of zooplankton/ml:  $Pf_{72} = 0.216 (Zoo/ml) + 0.121$  ( $r = 0.88, p = 0.05$ ). Letters designate groups still extant at that time.

B. Proportion of diet consisting of phytoplankton (dashed line) and zooplankton (solid line) with time. Groups Y1 and Y2 only. Arrows as before.



size increased as the larvae grew (Fig. 6). Considering the wide size range of food particles available, it appears that the preferred particle width for 3.5 mm larvae is about 10% of the body length, which increases to about 20% by 5.5 mm. At this rate, it follows that the natural transition from small, predominantly phytoplankton cells, to copepod nauplii ought to occur at a length of about 4.3 mm. Hence according to the growth rate of group Y1, zooplankton can be expected to form an increasing larger proportion of the diet between 5 to 6 days after complete yolk resorption.

**Survival.** Survival in the different groups varied considerably. Certainly the largest source of mortality was the sampling procedure itself which eliminated 5 groups within 2 days after the pro-larval stage. In the remaining 9 groups, the death rate ( $D_r$ , expressed as the proportion of the initial number of individuals dying per day) was lower, when the post-larvae (L, day 3.7) were large (Table

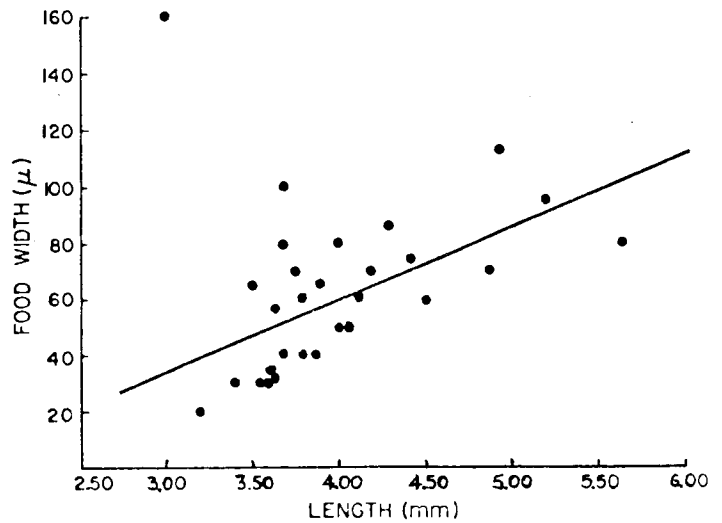
1):

$$D_r = 2.51 - 0.58 \bar{L},$$

$$(r = -0.89, N = 9, P \sim 0.001).$$

By contrast, there was no apparent correlation

Fig. 6 Relation between mean food width and larval size:  $Food\ width\ (\mu m) = 25.21 L(mm) - 40.64$  ( $r = 0.62, p < 0.001$ ). One individual containing a large *coesmodoncus* cell 160  $\mu m$  in diameter (upper left of figure) was not included in the regression.



between the death rate and either the concentration of zooplankton, or *Actinocyclus* and *Gymnodinium*. Compared with similar studies of *E. mordax* (e.g., Lasker et al., 1970; Scura and Jeroe, 1977), the death rate in our experiments was 2 to 3 times higher. However, the concentration of suitable food organisms (notably *Actinocyclus* and *Gymnodinium*) was 15 to 20 times lower.

**Comparison of *E. ringens* and *E. mordax*.** Table 2 shows that the developmental and behavioral characteristics of the Peruvian Anchoveta and its northern counterpart are remarkably similar. Indeed, the only difference appears to be in the maturation of the activity pattern, which may

Table 2. Light saturation parameters for experiments listed in Table 1.

Station	$P_s^B$ (*)	$\alpha$ (**)	$10^3 \cdot \beta$ (**)	$P_m^B$ (*)	$I_m$ (†)	$L_k$ (†)	$I_s$ (†)	$I_b$ (†)
P71	10.1	0.25	11.0	8.4	130	33	40	930
P204	9.60	0.20	0.61	9.40	280	47	48	1600
DAW-4	3.80	0.091	1.9	3.4	160	38	42	2000
DAW-6a	8.33	0.16	0	8.3	-(++)	51	52	-(††)
SC83(5m)	1.05	0.041	0.50	0.98	110	24	26	2100
SC83(36m)	0.81	0.038	2.2	0.64	61	17	21	370
P242	15.6	0.95	3.7	15.3	92	16	17	4200
P244	6.37	0.24	3.6	5.9	110	25	26	1800
P245	1.02	0.082	2.7	1.04	50	13	12	380
P248	1.04	0.064	2.3	0.90	55	14	16	450
P250	2.14	0.086	0.84	2.02	120	24	25	2600

\*mg C (mg Chl  $\alpha$ )<sup>-1</sup>h<sup>-1</sup>

\*\*mg C (mg Chl  $\alpha$ )<sup>-1</sup>h<sup>-1</sup>(Wm<sup>-2</sup>)<sup>-1</sup>

† Wm<sup>-2</sup>

††  $I_m$  and  $I_b$  are defined for  $\beta=0$

develop more slowly in *E. ringens* (Fig. 3). On the other hand, we caution that these results may not be directly comparable if activity depends on larval size or food concentration.

### DISCUSSION

Our observations and similar findings for *E. mordax* indicate that the first 5 or 6 days after yolk resorption is a significant stage in the early life history of anchoveta. During this time a number of remarkable changes are occurring: the activity pattern, which is a major component of the feeding response is beginning to develop, while the success of the larvae in capturing food — particularly zooplankton — is also maturing (Hunter, 1972). So the numbers of individuals feeding and their ration, as indicated by the fullness of the gut, rise markedly.

Given adequate food resources the development of these two processes, however, seems to strike a balance so the ration is just sufficient to meet maintenance metabolic requirements. Consequently, the larvae do not gain a significant amount of mass until age 7 d (Fig. 1 above; Zweifel and Lasker, 1976, Fig. 2). At this point the feeding response has matured and the growth rate increases rapidly.

In laboratory experiments, survival of *E. ringens* and *mordax* during the first week depends primarily upon the size of the post-larvae and the supply of small (30 to 60  $\mu\text{m}$  width) food particles. It is tempting to speculate, though, that the evolution of successful feeding behaviour might be stimulated by the presence of microzooplankton. In some species the feeding drive is heightened by motion receptors in the retina (Blaxter, 1969). But anchoveta larvae seem to have difficulty in capturing actively moving organisms so their first rations consist of small, more quiescent particles.

Though we suspect that survival could have been enhanced by providing more *Actinocyclus* and *Gymnodinium*, dense concentrations of these organisms are not required to initiate feeding. Indeed, groups Y1 and Y2 quickly made the transition from phytoplankton to zooplankton after the first day (Fig. 5), and there were signs that the remnants of Y2 were beginning the rapid growth phase as the experiment ended. However, the death rate in these groups was similar to the controls, so the higher feeding rates did not measurably improve survival. This was an obvious limitation of our experiments since, by analogy with other studies, we expected the death rate to decline at the higher food concentrations (cf. Laurence, 1974; Scura and Jerde, 1977).

Field observations show that the accelerated growth phase in anchoveta is accompanied by an increasing proportion of zooplankton in the diet. Mendiola (1973) and Arthur (1976) found that wild post-larvae fed predominantly on micro-zooplankton — 56% by number for *E. mordax* and 80% for *E. ringens*, hence considerably more for both in terms of mass. By contrast, the proportion of phytoplankton in the diet decreases with size, reaching a minimum by the 5 to 7 mm stage.

Arthur (1976) also noted that a ration solely of *Gymnodinium splendens* will not sustain the normal growth pattern of *N. anchovy* for more than 10-12 days.

These findings suggest that whereas a mixed diet may provide an adequate maintenance ration during the first week of life, the transition to the rapid growth phase, and presumably better survival, depends on the ability of the larvae to find an adequate supply of zooplankton. This requirement is quite understandable since copepod nauplii (68  $\mu\text{m}$  x 134  $\mu\text{m}$ ) contain about 23 times the energy of a 60  $\mu\text{m}$  diameter diatom cell. Consequently, the role of phytoplankton during the very early life history can perhaps be viewed as an adaptation by the larvae to meet maintenance metabolic requirements while they learn to feed on zooplankton. Evidently some individuals fail to make the transition, with obvious consequences.

Perhaps the most enigmatic finding of laboratory studies, including ours, is the poor feeding and survival rates of fish larvae at natural food levels — mean of 0.01 to 0.04 microzooplankton/ml (Arthur, 1977). It is generally believed that survival in the sea is enhanced by small-scale patchiness of the plankton. Indeed, Lasker (1975) found that first feeding anchovy larvae were associated with a chlorophyll maximum layer, which occurred at 15 m under light wind conditions.

Unfortunately, the microdistribution of the plankton field has received little attention largely because of the difficulties in measuring it. Nonetheless, the literature is replete with anecdotal observations of patches on a wide range of spatial scales (Brainbridge, 1957). At distances less than 0.5 km, it occurs to us that much of the horizontal variability is probably associated with helical roll vortices, or Langmuir circulations. In reviewing this extensive phenomenon, Pollard (1977) concluded that wind and consequently surface waves are necessary conditions for the existence of Langmuir circulations. As a rule, the spacing between adjacent convergence zones in the mixed layer increases linearly with wind speed, and varies between 2 to 300 m in the sea.

We observed "windrow" formations in Samanco Bay on many occasions, and recall that they usually appeared as the offshore winds freshened in the afternoon. Langmuir circulations, and still smaller scale thermal convection cells (Pollard, 1977), therefore, raise some interesting possibilities as to how larval fish might have adapted to live in a seemingly dilute medium:

Whenever the plankton layers at depth are stable, the greatest variability in particle concentration probably occurs vertically. So a fish larvae ought to put more emphasis on moving in this plane to locate suitable food supplies. On the other hand, if the layers are dispersed by wind mixing (Lasker, 1975; Walsh, 1978), then the horizontal variability of the plankton field is likely to increase at length scales coherent with Langmuir circulations. Walsh (1978) proposed that more frequent

wind events in El Niño years may lead to a recurring dilution of the food supply and poorer survival of larval anchoveta. Although this may happen to some extent, we note that "windrows" are commonly observed off Peru and that Langmuir circulations have been observed elsewhere over almost the entire range of wind speeds reported by Walsh (1978, Fig. 163). Hence we suggest that atmospheric and wave driven vortices will often restructure the plankton, so particles are no longer concentrated in horizontal layers, as they are under light wind conditions, but rather in lateral rows resembling elongated, vertical "curtains" of organisms (see Bainbridge, 1957, Fig. 4).

By observing the behaviour of *Daphnia* in a current, Stavn (1971) concluded that whether zooplankton tend to accumulate in convergence or divergence zones depends on the strength of the respective downwellings or upwellings. In either case, adjacent rows of organisms will be less than 300 m apart. From the viewpoint of a larval fish this length scale is important because, if it is not passively drawn into the same concentration zone as the plankton, the "windrows" are within the daily cruising range of first-feeding larvae. They swim at about 1 body length/s or 350 m/d (Hunter, 1972), so by either passive drift or active searching some individuals ought to be able to locate concentrations of food organisms within the vortices, and maintain contact by using a mechanism similar to the one proposed by Stavn (1971).

The significant point is that, although the growth

and mortality of anchoveta may indeed be influenced by the distribution of suitable food organisms—and hence atmospheric events—storms are not necessarily harbingers of catastrophes. In fact, in view of the potentially dynamic re-alignment of the plankton field in response to wind stress, perhaps it is not surprising that standard "vertical" or oblique hauls over tens of metres, in both the vertical and horizontal plane, usually yield mean particle concentrations below the survival level of laboratory reared larvae.

Insofar as this phenomenon is related to recruitment variability, we believe that a wider understanding of larval growth and mortality in nature may be achieved by identifying the stimuli which lead to a successful feeding response, including the small-scale spatial associations between fish larvae and the plankton under various hydrographic conditions. We recognize that this important problem will not be resolved easily.

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