Rapp. P.-v. Réun. Cons. int. Explor. Mer, 173: 77–84. 1978.

POSITION OF LARVAL FISH IN AN ECOSYSTEM

PAUL E. SMITH and REUBEN LASKER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service, Southwest Fisheries Center
P.O. Box 271, La Jolla, California 92038, U.S.A.

First order estimates of distribution, abundance, growth and survival rate of the northern anchovy larva are used to examine the interactions of the larval stage and its environment and how these regulate the northern anchovy population.

Changes in the degree of spawning of anchovy are compared to the seasonal and annual variations in seawater temperature, vertical temperature gradients, upwelling, California Current speed, flushing rate of the southern California Bight, and secondary production. It appears that the usual habit of the anchovy to spawn heavily in the southern California area in winter, alters radically in some years. The cause for this is not yet known.

Quarterly apparent mortality rates are assembled for the years of greatest environmental changes in the southern California regions for anchovy eggs and larvae (to 6·5 mm in length). Information needed for analysing the causes of anchovy larval mortality has been assembled. For example, first-feeding anchovy larvae require abundant food in a narrow size range (30 to 50 µm). Tests with laboratory-reared larvae have confirmed the need for larval food organisms at proper concentrations (> 30/ml) to insure adequate feeding. In nearshore waters, these are associated with chlorophyll maximum layers at 15 to 30 m depth off California. Upwelling was observed to disperse the food organisms until they were too low in number to support larval anchovy growth.

INTRODUCTION

In the past three decades, 1946 to 1976, the northern anchovy has replaced the Pacific sardine in biomass (Smith, 1972) and in the commercial reduction and baitfish fisheries off the California coast (Baxter, 1967; Messersmith, 1969; Ahlstrom, 1966). The northern anchovy is now the chief forage fish for the sport fishes, large commercial fishes, marine mammals, and marine birds of the California and the northeast Pacific. The disappearance of the Pacific sardine and the appearance of the massive anchovy population has sustained a large research effort to determine the causes of the major fluctuations of the fish populations off the Pacific coast of North America. This report combines results from theoretical, field and laboratory studies of the northern anchovy, particularly the causes of reproductive success. The primary impetus for these studies stems from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) in field and laboratory work begun in 1947.

It now appears that the fishery on the central subpopulation of the northern anchovy (Fig. 65) will increase before we gain a functional understanding of the causes of rapid decline in pelagic stocks. Because of the socio-economic issues involved, a fishery on the anchovy will likely be carefully regulated. We intend to use this period of cautious harvest to study features of the biological and physical environment of the anchovy which are associated with reproductive success. Specifically, we will use a selection of cause and effect relationships in the description of reproductive success. Minimal criteria for that success will be established through theoretical models, designed from and verified by field studies and laboratory experiments.

GENERAL PRODUCTIVITY OF THE ANCHOVY LARVA ENVIRONMENT

Although the ability to measure the primary productivity of a representative area of the California Current exists (see, for example, Owen, 1974), there is no long-term record. However, estimates of secondary production are possible by the observation of zooplankton displacement volume. The absence of adequate descriptions of zooplankton populations which make up this diverse assemblage, does not permit a quantitatively satisfactory model for this area. Therefore, fluctuations are presented as mean seasonal cycles of zooplankton displacement volumes with year-to-year differences.

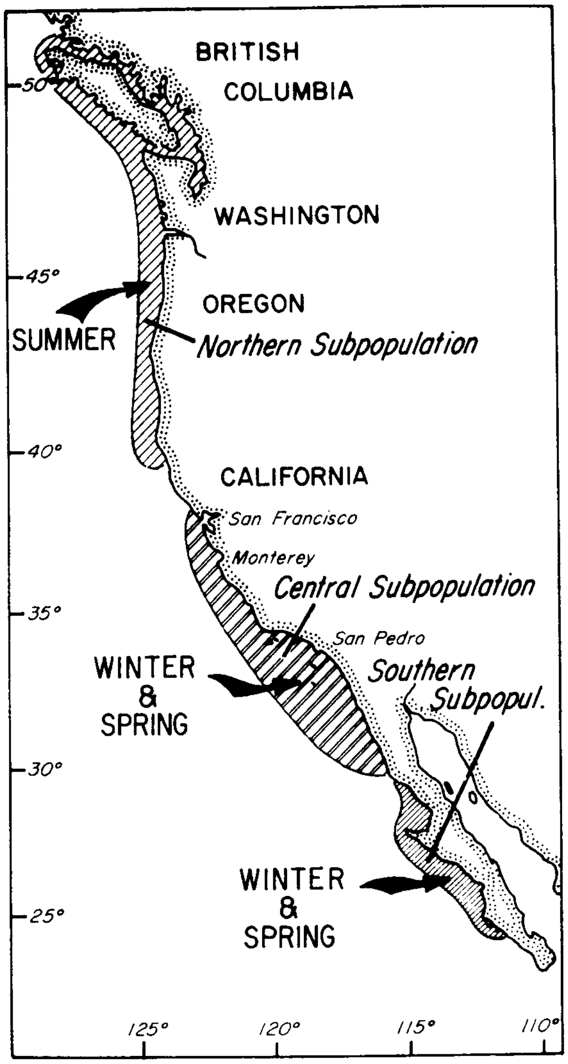

Figure 65. The major spawning seasons and areas of the three sub-populations of the northern anchovy *Engraulis mordax* off the temperate west coast of North America, modified from Vrooman and Smith (1971).

Representative primary production rates (Owen and Sanchez, 1974) for 1969 indicate that the entire habitat of the northern anchovy is probably much less productive than the Peru Current system. In the 80000 n m² (275000 km²) usually occupied by the central sub-population, the annual productivity in 1969 was 490 mg C/m²/day. Values as high as 1300 mg C/m²/day were seen occasionally. The maximum seasonal productivity for the entire region was 800 mg C/m²/day in February–March and the minimum was 260 mg C/m²/day in November–December. Productivity in the area of the Peruvian anchoveta is usually stated in the range of 1000 to 10000 mg C/m²/day (Walsh, 1976) and during the "El Niño" phenomenon of 1972, it fell to 300 mg C/m²/day (Guillen, 1974).

SEASONAL CYCLES

Solar radiation. In Figure 66, it may be seen that the actual average peak in solar radiation is in April because the clear sky solar radiation is strongly modified by cloud cover (Clark et al, 1974). Minimum solar radiation does coincide with the winter solstice. Peak cloud cover coincides with peak upwelling as estimated from the Bakun (1973) barometric pressure model.

Temperature. Temperatures representative of the upper layers of the ocean inhabited by the anchovy commonly vary 4 to 6°C under the influence of water transport from the subarctic water mass, the central water mass, subtropical water mass, upwelling, and seasonal changes in local warming and cooling rate. The 10-m depth peak temperature is commonly attained in August, but a 30-m peak is reached in October–November due to the apparent influence of upwelling. Average minimum temperatures at 30 m occur in July, following the maximum in local upwelling rate. The 10 to 30 m temperature difference indicates two important phenomena for larvae: in January, the temperature difference is minimal, offering the best chances for mixing, and in July, the temperature difference is at a maximum indicating that upwelling and warming are at a joint maximum. Both the minimum and maximum 10 to 30 m temperature difference appear to be detrimental to the formation of feeding layers for larvae and maintenance of patches.

UPWELLING AND CALIFORNIA CURRENT INDICES

Upwelling and the transport offshore of surface waters which it entails (Bakun, 1973) is at a maximum in June and at a minimum in December. One may expect upwelling to add nutrients to the upper layers, to transport nearshore organisms offshore, and to destroy stratification locally. In general, the effect of upwelling should be to favour the adults of a species, but to be inimical to the embryos and larvae.

The California Current rate of flow appears to have a distinct minimum in January and a rather prolonged, but moderate, maximum from March to November. In general, the combined effects of upwelling, offshore transport, and southerly drift would

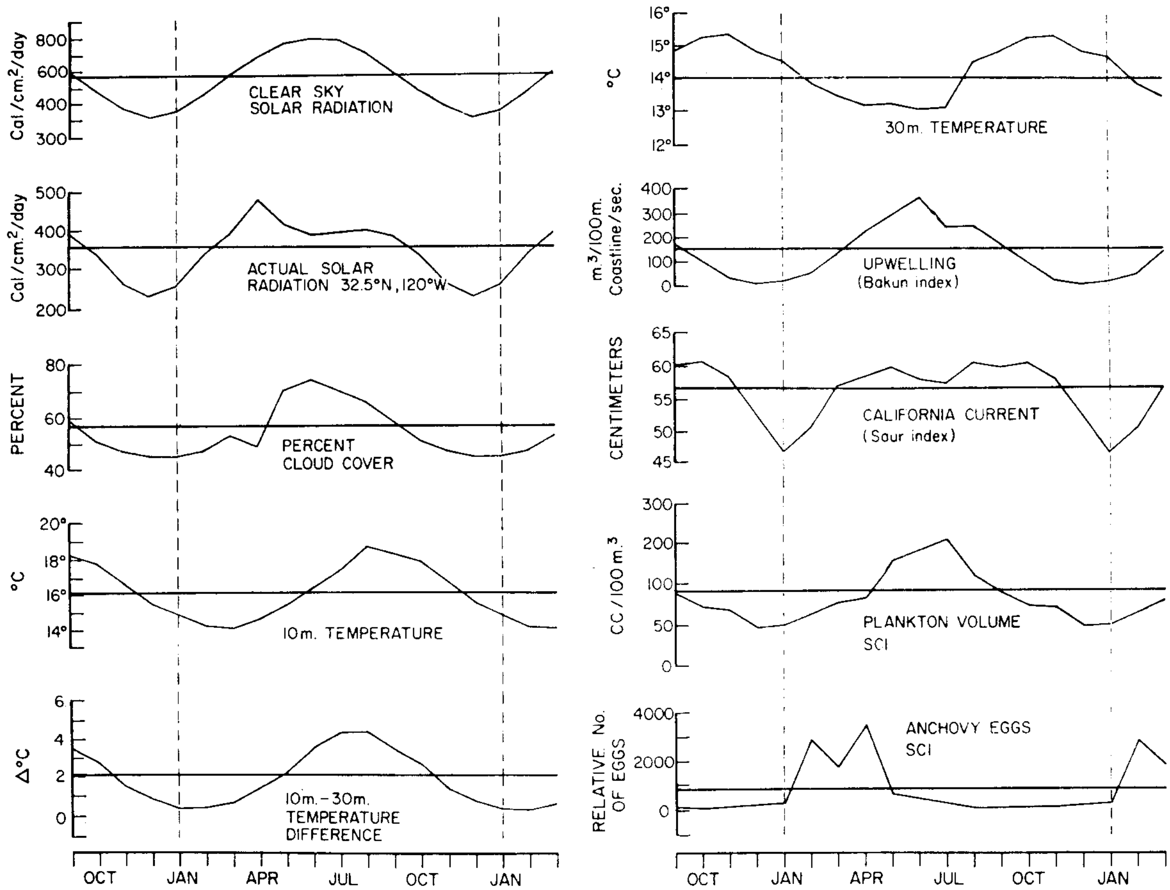

Figure 66. Seasonal cycles of solar radiation cloud cover, temperature, upwelling index, California Current strength, plankton volume and anchovy eggs from various sources and over various periods, modified from Lasker and Smith (in press).

carry the planktonic stages of larvae offshore and south of the places where spawning occurs.

ZOOPLANKTON

The plankton volume cycle indicates a mass surplus of production over consumption from December to July with a maximum rate of increase in the standing stock of zooplankton from April to May and the maximum rate of decrease from July to August. The maximum rate of increase coincides with rapidly increasing day length and elevation of the sun, while the maximum rate of decrease of the plankton would be likely to reflect continued high primary productivity with a greatly increased consumption by fishes and other consumers spawned in the spring and summer. The gradual decline in zooplankton which follows, probably indicates a declining general production rate with decreasing day length and elevation of the sun, and a decrease in upwelled nutrients: this all takes place in the continued high consumption of the spring cohorts of various consumer species.

SPAWNING

The incidence of anchovy eggs is at a maximum in February, March and April. This coincides with the maximum weight of gonads at about 6% of the mature anchovy's body weight (Fig. 66). The minimum gonad index of about 1% is attained in July and August. The maximum rate of increase in fat deposits is in the summer which probably reflects the minimum elaboration of spawning products, the maximum zooplankton standing stock as well as the maximum rate of decrease in standing stock. Anchovy produce smaller, as well as fewer, eggs in summer.

ANNUAL CHANGES

Proportionate changes from year to year in solar radiation, upwelling, and flow of the California Current appear to be relatively small, relative to seasonal changes. It appears that while the annual and seasonal averages are rather regular, there are important changes in timing and short-term maxima in upwelling. Net zooplankton display large changes in standing stock from year to year. Annual changes of 15-fold have been observed while the seasonal cycle is of the order of 5-fold or less. Spawning appears to be a simple function of the biomass of adults in the northern anchovy and the annual record reflects little more complexity than the rapid increase of anchovy over the past 25 years.

ANCHOVY MORTALITY

The major causes of larval mortality now being investigated are starvation, predation and their interrelationships. The primary interrelation appears to be that sublethal shortages of food, slow growth and development rates, leave the larvae vulnerable to predation for extended periods. Among the density-dependent forms of these mortality features are:

1) Starvation:
   a. the adults produce more larvae and juveniles than can be supported by the carrying capacity of the stock's environment.
   b. crowded adults invest eggs with deficient yolk and the resultant larvae starve at a rate which does not permit unit replacement of the spawning biomass.
   c. crowded adults are forced to spawn outside optimum areas for larval and juvenile survival and growth, or in seasons in which eggs and larvae are swept out to such areas.

2) Predation:
   a. feeding activities of adults kill so many eggs and larvae by ingestion that unit replacement of the spawning biomass is precluded; for example, crowded adult anchovy may switch from a preponderance of feeding by biting, which can be avoided by larval stages of anchovy, to feeding chiefly by filtration which cannot be avoided by the embryonic stages of anchovy.
   b. spawning rate of the stock becomes so high that population growth or aggregation of predatory species on any single stage of the anchovy life cycle increases mortality and does not permit unit replacement of the spawning biomass.

Density-independent sources of mortality such as mixing and cooling of the ocean below physiological thresholds or an influx of predators can be important as well. Predation on anchovy embryos has been measured for copepods (Lillelund and Lasker, 1971) and for euphausiids (Theilacker and Lasker, 1974) and has been observed in samples by Alvariño (1976)[1] by chaetognaths over a wider range of sizes of anchovy. Presumably, too, the filtering organisms, the abundant thaliaceans and larvaceans, and the passive paralytic predators, the coelenterates and cnidarians, are all important. This means that the anchovy larvae, always a small proportion of the plankton volume, are continuously vulnerable to a vast majority of the zooplankton organisms which are captured in the same net. It is doubtful that any of these predators depend on anchovy for a large proportion of their metabolic requirements, but the effect of their predation is part of the density independent causes of mortality for anchovy.

LABORATORY EXPERIMENTS

Basic measurements on metabolic requirements, food capture ability, and search behaviour (Hunter, 1972) of the larvae have outlined the required density and quality of food to be furnished by the environment. An early conclusion from this series of laboratory experiments was that the requirements were seldom met on the average in the anchovy spawning area. Very few systematic or quantitative samples of anchovy larval food had been taken or analysed by species in the anchovy spawning area. This led Lasker (1975) to conduct a direct larval bioassay of ocean waters in which first-feeding larvae spawned and reared in the laboratory were provided with water collected at sea to test their ability to feed. This led to the discovery of a large horizontal area which contained thin strata of dense aggregations of *Gymnodinium* and demonstrated the need for development of theory on the relationship of larval anchovy survival and growth to prey microdistribution and larval behaviour.

THEORETICAL MODELS

One theoretical model uses all the survival, growth and behaviour information available to assemble a comprehensive simulation of growth through the early larval stage (4–20 mm) for 1 or 2 months, depending on temperature (13·5°–17·5°C). A startling result of this simulation was that if the mean abundance of food was not adequate, the variance/mean ratio index[2]

[1] Reported in monthly reports of the National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California.

[2] Several methods of describing contagion use sample parameters of variance and mean to express the significance and intensity of patchiness.

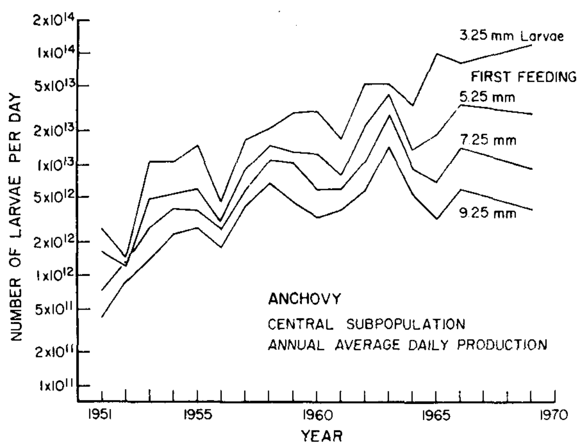

Figure 67. Time series of larval production by the central subpopulation of northern anchovy. Ordinate is expressed as the number entering the size category per day. Distance between adjacent lines is the first approximation to larval mortality within the interval. The 3·25 mm stage is a continuation of the embryonic stage following hatching since yolk persists, no functional mouth or eye has developed and feeding has not yet commenced.

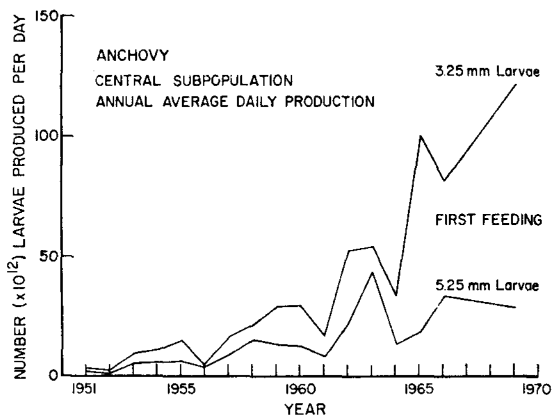

Figure 68. The time series of Figure 67 at the 3·25 mm and 5·25 mm embryo to larva transition is emphasized by plotting on the arithmetic scale rather than the logarithmic scale.

of patchiness had to be above 6, was optimum at about 14, and was favourable, but declining slowly over a wide range of patchiness indices up to 1000 (Vlymen, 1977). This interesting result will allow simple multiple sampling of a site and the setting of absolute threshold criteria regarding the number of organisms ranging in size from dinoflagellates to nauplii and their distribution patterns.

Another theoretical model uses all the sized-larva collections from the sea to estimate mortality rate (Zweifel and Smith, 1976) of anchovy larvae. In general, they show that only one larva survives from a thousand anchovy eggs after a month, with a mortality of about 53% per day in the embryonic period and about 13% per day in the early larval period. This means that the stringent set of conditions set by the Vlymen model with the predation by adults of the same species, predation by all others, drift into unsuitable areas, and all other forms of mortality need to be surpassed by at least one larva from a thousand eggs after a month. In the series under consideration (1951–1969) (Fig. 67), there was no evidence of density dependence in the mortality of embryos. In the past 14 years of population increase, the early larva mortality rate averaged less than 12% per day, but at the population maximum, mortality shifted to 21% per day for the first 8 to 17 days after spawning (Fig. 68). In each year, the larval mortality rate was less than the embryonic survival rate (Fig. 69) suggesting that predation of the embryos is a regular feature of spawning and that the mortality and vision which accompanies the onset of feeding also functions to reduce drastically the overall mortality rate to an even greater extent than the food requirement is accelerating mortality.

Events in the development of anchovy larvae are being examined (Hunter, 1976) for impact on the survival of larvae and for the effect on sampling. Hatching occurs at about 2·4 days at a temperature of 16·2°C. At hatching, larvae are unpigmented and have no functional eye or mouth, and are inactive

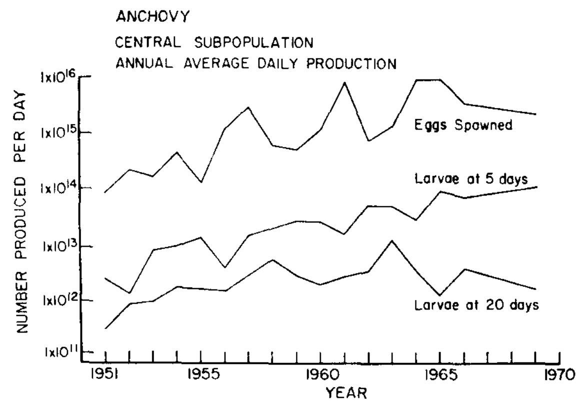

Figure 69. Back projections of spawning rate, assumed to be proportional to spawning biomass as compared with forward projections of the number of larvae near the end of the early larva phase before air bladder filling and schooling behaviour begins (adjusted for 16·2°C). A 5-days-old larva is just beginning to feed at this temperature.

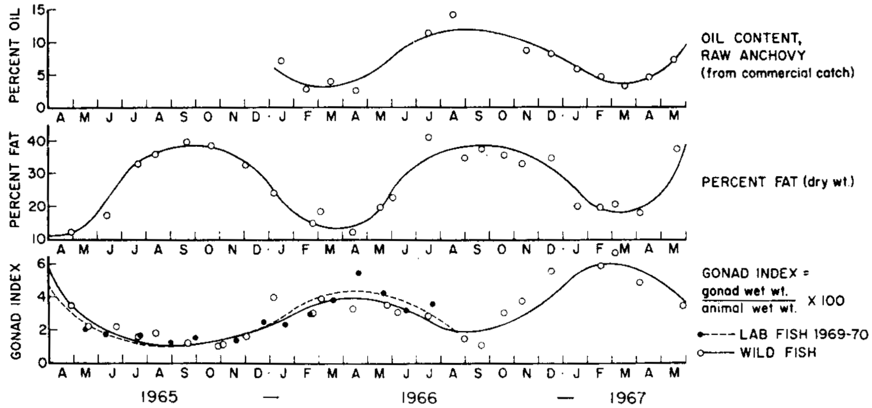

Figure 70. Annual northern anchovy central sub-population fat and gonad cycles for 1965–1967, after Lasker and Smith (in press).

90% of the time. Olfactory and lateral line organs are developed. The major activity is in short bursts of swimming which are likely to be for clearing the larval integument boundary layer of accumulated respiratory and excretory products. Between about 4·1 and 4·2 mm standard length, 7 days after spawning, yolk absorption is nearly complete, functional eyes and mouth exist and locomotor activity is increased. Larval orientation and swimming behaviour have endowed the larva with the ability to remain in patches of dense food particles. Feeding strike success begins at about 10% and increases to 90% at 23 days old. The early larval period discussed here ends with the formation of a functional hydrostatic bladder presumably for energy conservation at night (Hunter and Sanchez, 1977). In the laboratory, when no food is given, starvation is complete before nine days after spawning and total mortality occurs before 11 days. Larvae may survive the early larval period (to 23 days) on only *Gymnodinium* as food, but the larval length never exceeds 6 mm as compared with 10 mm for larvae fed phytoplankton, rotifers and crustacean nauplii.

FIELD STUDIES

Field studies on mortality to date have been totally dependent on laboratory determinations of critical rates as affected primarily by temperature. The quality of the mortality rates, then, is dependent on the comparability of the laboratory and field experiments. Laboratory descriptions of larval food requirements presently exceed, in quality, our ability to describe the feeding environment at sea. This situation is now being remedied by the development and use of pumps, closing bottles, *in situ* particle counters, and ultra-high frequency acoustic probes. The Vlymen patchiness model for larval food describes the mean abundance and variance we are looking for and hopefully one or more of the devices will be efficient enough to deploy over an 80000 n m^2 brood area. Independent age/length tests conducted by embryonic and larval otolith daily rings are now being assembled to confirm or adjust laboratory growth and development rates for direct use in the field (Brothers et al, 1976).

ADULT PHYSIOLOGY

The primary reason for being concerned about adult anchovy physiology in the context of the larval ecosystem is that spawned eggs may not be equally capable from year to year of yielding viable embryos and larvae. It has been observed that eggs sampled in the summer are smaller than eggs sampled in the winter. This size variability raises the possibility that eggs spawned after a low productivity summer, in the following winter, might be different in the quality and quantity of yolk and the size of the hatching larvae (Hunter, in press). Were this to be predictive, the gonad condition and oil content of the early season catch could be used to regulate the fishery on adults so as to avoid low recruitment in an ensuing year. The fat cycle and the gonad cycle are inversely related and the fat cycle is related to the plankton volume cycle (Figs 66 and 70). Valdivia (1974) noted the anomalously low number of adults in the spawning stage prior to the onset of "El Niño" conditions in 1971, and this could have complicated the usual stock-recruit ratio calculation. Both the spawning rate and apparent survival of larvae was low in the El Niño period.

DISCUSSION

Laboratory experiments, theoretical models and field studies used together to study the anchovy through the embryonic and early larval stages lead to important, if tentative, conclusions: 1) larvae have the sensory and motor capacity to remain in patches of dense food and to improve the chances of locating dense food patches when outside them, 2) embryonic mortality appears to be independent of stock size over a wide range of stock sizes of the northern anchovy central sub-population, 3) early larval mortality may become stock size dependent at extremely high stock sizes.

These findings raise the need for combined biological, chemical and physical oceanographic information. We know now that we need more than the usual environmental and biological measurements and that many of the useful parameters cannot be measured efficiently over the broad areas occupied by the anchovy.

PHYSICAL OCEANOGRAPHY

The chief contribution to studies of fish survival in the larval stage in the discipline of physical oceanography is to describe the interaction of wind stress, upwelling and mixing. Pycnocline formation and destruction alternately maintains and destroys layering of larval food organisms. The maximum larval abundance appears to occur in a stable period between the one of turbulent mixing of winter storms and that of shoaling of the mixed layer by phenomena related to the upwelling cycle. We need efficient ways of estimating these effects over large areas.

CHEMICAL OCEANOGRAPHY

We need to know the time course of enrichment of the upper layers and the effect of insufficient or mistimed primary production on the fat cycle of the anchovy spawning biomass. We do not have an adequate description of the spatial and temporal effects of excretion by the major populations recycling some of the nutrients and incorporating others in growth.

BIOLOGICAL OCEANOGRAPHY

The major information in support of larval ecology that is required from biological oceanography is in the area of population dynamics of prey, of competition with and predators on anchovy larvae. Next in order of importance is a knowledge of the spatial structure of these populations on the 10's to 100's of metres scale. The coincidence of patches of larvae and their prey has been shown to be critical. The high mortality of embryonic stages may be due to the coincidence of predators in the patches of spawn modified by behaviour. Sampling programmes to describe the scale and intensity of patchiness of critical species are needed in the brood areas.

SUMMARY

A patch of anchovy larvae will have more survivors in the sea if it coincides with a succession of patches of food organisms and also if it does not coincide with a patch of effective predators. While adequate primary and secondary production are necessary to the reproductive processes of gonadal growth, egg and sperm maturation, embryonic survival and larval growth, they are not sufficient to insure larval survival. The pelagic environment must also foster and maintain discrete patterns in the distribution of larval food, the larvae and their predators. The interdisciplinary approach to the problem of understanding and regulation of fisheries in the context of variable and productive environments in upwelling areas remains to be effectively designed.

ACKNOWLEDGEMENTS

This work was supported in part by a grant from the Brookhaven National Laboratory of ERDA. This is MARMAP (Marine Resources Monitoring, Assessment and Prediction) Contribution No. 135.

REFERENCES

Ahlstrom, E. H. 1966. Distribution and abundance of sardine and anchovy larvae in the California Current region off California and Baja California, 1951–64: a summary. U.S. Fish. Wildl. Serv. Spec. Rep. Fish 534, 71 pp.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–1971. NOAA Tech. Rep. NMFS Spec. Sci. Rep. Fish 671, 103 pp.

Baxter, J. L. 1967. Summary of biological information on the northern anchovy *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest. Rep., 11: 110–16.

Brothers, E. B., Mathews, C. P. & Lasker, R. 1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull. U.S., 70: 1–8.

Clark, N. E., Eber, L., Laurs, R. M., Renner, J. A. & Saur, J. F. T. 1974. Heat exchange between ocean and atmosphere in the eastern North Pacific for 1961–71. NOAA Tech. Rep. NMFS Spec. Sci. Rep. Fish 682, 108 pp.

Guillen, G. O. 1974. The Peru current system: physical aspects. IDOE Workshop on the El Niño Phenomenon, Guayaquil, Ecuador, December 1974. (Mimeo).

Hunter, J. R. 1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull. U.S., 70: 821–48.

Hunter, J. R. (ed.). 1976. Report of a colloquium on larval fish mortality studies. NMFS Tech. Rep. NMFS Circ-395, 5 pp.

Hunter, J. R. Behavior and survival of northern anchovy, *Engraulis mordax* larvae. Calif. Coop. Oceanic Fish. Invest. Rep., 19. (In press).

Hunter, J. R. & Sanchez, C. K. 1977. Diel changes in swim-bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*. Fish. Bull. U.S. 74: 847–55.

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: 453–62.

Lasker, R. & Smith, P. E. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep., 19. (In press).

Lillelund, K. & Lasker, R. 1971. Laboratory studies of predation by marine copepods on fish larvae. Fish. Bull. U.S., 69: 655–67.
Messersmith, J. K. 1969. A review of the California anchovy fishery and results of the 1965–66 and 1966–67 reduction seasons. Calif. Fish Game, 147: 6–32.
Owen, R. W., Jr. 1974. Distribution of primary production, plant pigments and Secchi depth in the California Current region, 1969. Calif. Coop. Oceanic Fish. Invest. Atlas No. 20, Charts 98–117.
Owen, R. W., Jr. & Sanchez, C. K. 1974. Phytoplankton pigment and production measurements in the California Current region, 1969–72. NMFS (U.S.) Data Report No. 91, 185 pp.
Smith, P. E. 1972. The increase in spawning biomass of northern anchovy *Engraulis mordax*. Fish. Bull. U.S., 70: 849–74.
Theilacker, G. H. & Lasker, R. 1974. Laboratory studies of predation by euphausiid shrimps on fish larvae. *In* The Early Life History of Fish, pp. 287–99. Ed. by J. H. S. Blaxter, Springer-Verlag, Berlin.
Valdivia, J. 1974. Biological aspects of the 1972–73 "El Niño". Part 2. The anchovy population. IDOE Workshop on the El Niño Phenomenon, Guayaquil, Ecuador, December 1974. (Mimeo).
Vlymen, W. J. 1977. A mathematical model of the relationships between larval anchovy (*Engraulis mordax*) growth, prey micro-distribution, and larval behaviour. Env. Biol. Fish, 2: 211–33.
Vrooman, A. M. & Smith, P. E. 1971. Biomass of the subpopulation of northern anchovy *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest. Rep., 15: 49–51.
Walsh, J. J. 1976. Herbivory as a factor in patterns of nutrient utilization in the sea. Limnol. Oceanog. 21 (1): 1–13.
Zweifel, J. & Smith, P. E. 1976. Formal confidence interval estimates for survey estimates of fish egg and larva abundance. (Manuscript on file at the National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California 92038).

Printed in Denmark by Bianco Luno A/S