

On the Determinants of Stock Abundance

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In this commentary I focus on four issues discussed in Warren Wooster's report (Determinants of Stock Abundance) which I feel warrant additional discussion or amplification. In no manner should this commentary be considered an appraisal or review of Wooster's report on Fish Ecology III (Rothschild and Rooth, 1982). I use quotations from Wooster's report to identify each of the subject areas.

"The planktonic stages of the life history are most affected by environmental conditions"

The planktonic larvae of marine fishes are more directly affected by the environment than other life stages but it may be overlooked that not all larval stages are planktonic. The larval period, after the onset of feeding, is a transitional period between the planktonic embryonic stage (egg and yolk-sac stages) and the nektonic juvenile stage. This transition may occur early in the life history, and the truly planktonic stages may be a short segment of a long larval period. In northern anchovy, this transition occurs over about a 10-day period between the 20th and 30th day (10-15 mm, 16°C) of a 70-day larval period. The following events occur during transition: the larva breaks free from the hydrodynamic realm that is transitional between the viscous realm of the yolk-sac larva and the turbulent realm of the nektonic larva (Weihs, 1980); rods appear in the retina and the lens becomes focusable (O'Connell, 1981); the swim bladder becomes functional permitting greater body mass without loss of bouyancy; diel vertical movement to the water surface each night begins (Hunter and Sanchez, 1976); the transition between integumentary and gill respiration begins (O'Connell, 1981); and schooling begins (Hunter and Coyne, 1982).

These behavioral and structural changes have very important ecological and demographic implications. The change in hydrodynamic regime, and the changes in visual, respiratory and other systems set the stage for the onset of schooling and vertical

migration. The onset of schooling reverses a trend of continuing dispersion and declining patchiness of larvae to one of increasing contagion (Hewitt, 1981; Hunter and Coyne, 1982). By the end of the planktonic phase mortality rates are much lower than during the highly vulnerable embryonic period. This fact plus the rapid increase in body weight reverses a trend of rapidly declining cohort biomass to one of increasing cohort biomass. The increase in the biomass of the cohort, and increased aggregation due to schooling imply that nektonic larvae occupy the habitat more intensively than planktonic larvae. More intensive occupation of the habitat may increase the likelihood of larval density dependent effects on growth.

Thus the planktonic larval phase is characterized by a pattern of declining contagion (increasing dispersion), high mortality rates, decreasing cohort biomass and a larval existence almost entirely dependent upon the immediate planktonic habitat. In the nektonic larval phase, the larvae become progressively more independent of the immediate planktonic habitat, are capable of extensive vertical movements in search of food, become more aggregated because of schooling, the biomass of the cohort begins to increase and the likelihood of density dependent effects on larval growth increase. Thus interpretation of the effects of the environment on larval survivorship depends upon a thorough knowledge of these developmental changes and the timing of transition from the planktonic to nektonic states. The timing of the transition depends, of course, on the availability of food, as well as temperature specific growth rates.

“The key goal of research on interannual variability of fish stocks is prediction of survivorship until the strength of the year class is identified”

It may never be practical to use the results of larval counts or extensive environmental measurements to provide timely and accurate estimates of year-class strength. In addition, methods already exist for early estimation of year class strength including commercial catches of small fish, trawl or acoustic surveys. I believe the key goal of research on year class variability is to establish how the abundance of the adult stock affects the strength of incoming year classes and to identify the conditions which cause the occasional and remarkable rises or falls in populations (Hunter et al., 1976.) Clearly, the effect of stock size on recruitment is a critical issue since the only option available to managers is regulation of catch.

“It is uncommon to encounter larvae dead of starvation”

I feel partially responsible for this quotation as it reflects perhaps an extreme position that I took in my report for Fish Ecology III. Consequently, I summarize below some of the more important evidence for the relative role played by starvation and predation of marine fish larvae.

Evidence for larval starvation

1. Most laboratory work indicates that marine larvae at the onset of feeding are highly vulnerable to starvation because they search such a small volume of water, have low feeding success, and are unable to withstand prolonged starvation (Hunter, 1981).
2. The food densities required for high survival in the laboratory are not found in the open sea, implying that larvae must depend on the patchiness of food and stable oceanographic conditions to survive (Hunter, 1981).
3. In inshore areas, the incidence of starving anchovy (4-10 mm) using histological criteria (in my mind the only reliable method) was 8% (O'Connell, 1980) and no larvae >10 mm long were starving. In offshore areas about 50% of first feeding jack mackerel larvae were starving but the fraction of starving larvae decreases rapidly with larval age, reaching zero in 2-week-old larvae (G. Theilacker, pers. comm.). These fractions were not adjusted for the duration of the larval stage and cannot be compared to daily mortality rates. On a daily basis the fraction of starving larvae may be lower as the first feeding stage of jack mackerel persists for 2-3 days.

Evidence for predation

1. The highest losses occur during the embryonic period (egg and yolk-sac stages) where starvation can be eliminated as a source of mortality.
2. A great variety of invertebrates and fishes are known to consume eggs and larvae (Hunter, 1981; Bailey and Yen, 1983) and high consumption rates of eggs or larvae have been documented in a few cases (Hunter and Kimbrell, 1981; Möller, 1980).
3. Our most accurate mortality estimates for post-embryonic anchovy (1980-1983) larvae give no sign of an increase in mortality at the onset of feeding. Inaccurate aging might mask the critical period; the first feeding period is the most difficult life stage to assign an age or duration because otoliths cannot be used to age larvae.
4. Growth rates of clupeoid larvae in the sea based on daily increments in otoliths seem to indicate that they grow at the same rates as they do at the laboratory when given abundant food (Blaxter and Hunter, 1982).
5. In large enclosures cod larvae have extremely high survival when predators are excluded and food densities are equivalent to those in the sea (Ellertsen et al., 1981).

These assertions are based on very few field studies and clearly the dominant mechanism may vary among species, habitats and years. What is certain is that the incidence of starvation or slow growth

can be documented with greater ease and accuracy than rates of predation because of the existence of starvation-histology and otolith-ageing methodologies. No similar advances have been made that facilitate studies of predation.

“One must conclude that in recent years meso-scale ichthyoplankton surveys have not greatly improved understanding and Rothschild et al. propose as an alternative, a more holistic approach on trophodynamics of micro- and fine-scale ecosystem”

This point of view reflects an interesting hypothesis which links survival of planktonic larvae to the environment in a novel and functional way (the stability hypothesis, Lasker, 1981). On the other hand, I believe that this is misleading advice for an overall program on recruitment mechanisms when the species spawn over a large geographic area and the localities from which the survivors originate vary unpredictably in space and time. Under these circumstances surveys which delimit the spawning habitat (meso-scale surveys) are essential for the following reasons:

1. Testing of the stability hypothesis or any other larval survival mechanism must be set in the context of the spawning distribution of the population and this information can only be provided by meso-scale surveys. Knowledge of events in a small segment of the population is not sufficient for estimating effects on the population as a whole.
2. Rates of mortality are powerful research tools but they require meso-scale surveys. Mortality rates cannot be measured over a segment of the population because of dispersion and advection of larvae.
3. The annual production of eggs and larvae over the season must be known in order to determine whether changes in year class size are a result of differences in larval mortality or due to differences in the annual or seasonal production of eggs. If the annual egg production is unknown one is unable to use a powerful tool, the birthdate distribution of the juveniles, for assaying the quality of the environment (Methot, 1981).
4. Many of the hypotheses of survivorship of larvae can only be studied on a meso-scale, for example, the larval drift hypothesis and the expansion of spawning range hypothesis of MacCall (1980) and Lasker and MacCall (1983).
5. Most of the significant advances that have been made in recent years on the ecology of northern anchovy were made chiefly as a result of meso-scale surveys.

These comments apply to most of the commercially important marine fish stocks that spawn over a broad geographic area. On the other hand, micro-scale, site intensive studies alone would be preferable under several special circumstances: when the young destined to perpetuate the population originate from a small area

that is constant in location and time; or when they originate from an oceanographic feature which is predictable in space and time; or when they suffer the same fate over the entire spawning habitat. Most importantly, the answer to the question of whether or not these special circumstances apply to a given species probably requires spawning-habitat-scale (meso-scale) surveys. Perhaps the failure of many meso-scale surveys has been that they were not sufficiently extensive to delimit the spawning habitat in space and time nor sufficiently intensive to reveal biological processes.

In summary, to limit work on recruitment mechanisms to site intensive microscale studies is not advisable unless documentation exists that the site is truly representative or that it contains most of the potential survivors. If these conditions are not met then use of only site intensive work is to focus on only a few of the possible mortality processes without adequate geographic and temporal context, and to ignore some of the most powerful tools for understanding (birthdate distributions, juvenile abundance, life stage specific mortality rates and variation in spawn distribution). It is certainly important to do such work, not as an alternative to meso-scale research, but in conjunction with it.

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