Feeding Ecology and Predation of Marine Fish Larvae

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The objective of my three lectures in this series is to describe some of the behavioral and physiological characteristics of marine fish larvae that affect their survival and growth. The two major sources of larval mortality are probably starvation and predation. The first two lectures deal with feeding ecology of marine fish larvae; I point out differences in life history strategy and how such differences affect the ability of larvae to avoid starvation. These two lectures came from a review I had written in 1977 (Hunter, 1980), and that review is reproduced here with only minor changes. In my last lecture I discuss the problem of predation on eggs and larvae and make some general conclusions. In all lectures, I depend on my research and that of colleagues at the Southwest Fisheries Center in La Jolla, California.

Feeding Ecology

Parental Effects

Egg Size, Yolk Quantity, and Starvation

The size of a larva at the time of first feeding and the amount of time available to find food before onset of irreversible starvation are largely determined by the maternal influence of egg size and by water temperature. Shirota (1970) found that the length in millimeters of 40 species of marine and freshwater larvae at onset of feeding was related to egg diameter in millimeters by the simple relationship L = 4D. Large size at onset of feeding is an advantage because larger larvae are able to swim faster and search a greater volume of water for food.

As shown in Table 1, larvae from large eggs generally have more time to find food before the onset of irreversible starvation, because yolk persists for a longer period after feeding begins and the larvae have greater reserves in their body which can be used in metabolism (Blaxter and Hempel, 1963). Larvae from small pelagic eggs are capable of existing for about 1–2 days after yolk absorption before onset of irreversible starvation, whereas larvae from large eggs such as herring and plaice are able to exist for 6 days after yolk absorption, and in grunion larvae starvation is still reversible after 16 days (May, 1971). The ability to withstand starvation increases steadily from this point. At the beginning of metamorphosis, herring can withstand 15 days, plaice 23 days (Blaxter and Ehrlich, 1974), anchovy 14 days, and Pacific mackerel larvae 5 days (Hunter, 1976b; Hunter and Kimbrell, 1980a). These differences reflect in part differences in activity; plaice are less active than herring at this time (Blaxter and Ehrlic¹ , 1974) and anchovy less than mackerel. Differences between older fishes reared in the laboratory must be considered only in a relative sense because of the striking differences in condition between reared and wild animals (Blaxter, 1975).

The duration of egg incubation, although strongly affected by temperature, is also influenced by egg size. Ware (1975) found the relationship between the incubation time (I; days) at the water temperature for peak spawning and egg diameter (D; mm) for 14 species of Northwest Atlantic fishes was D = 0.101 I + 0.67. Similarly, the duration of the yolk sac stage is also affected by egg size (Blaxter and Hempel, 1963). Thus, larger eggs improve the survival capabilities of a larva at the onset of feeding, but at the

Table 1. Vulnerability to starvation of eight marine fish larvae at the time of first feeding.

Species	Temp. °C	Size at hatch		Yolk absorption	Days to point of no return[a] relative to:		
		Length mm	Dry weight µg	Period days	Hatch	Yolk absorption	Onset of feeding
GRUNION[c]							
Leuresthes tenuis	20	9.0	362	4	12 + [b]	8 + [b]	12 + [b]
CLYDE HERRING[d]							
Clupea harengus	7–8	8.2	189	8	25	6	22
HADDOCK[e]							
Melanogrammus aeglefinus	7	3.5	—	6–7	6	0–1	—
PACIFIC MACKEREL[f]							
Scomber japonicus	19	3.1	40	3	4.0	1.0	1.6
NORTHERN ANCHOVY[g]							
Engraulis mordax	16.5	2.9	21	4	7.7	1.5	2.5
BAY ANCHOVY[h]							
Anchoa mitchilli	24	2.5	18	1.7	3.1	1.4	1.7
SEA BREAM[h]							
Archosargus rhomboidalis	22	2.3	28	2.2	3.4	1.2	1.7
LINED SOLE[h]							
Achirus lineatus	24	1.9	22	3.3	3.8	0.5	1.3

[a] Time of irreversible starvation (Blaxter & Hempel, 1963).
[b] 50% mortality from starvation, not a point of no return, because all survivors able to survive if fed.
[c] May (1971).
[d] Blaxter & Hempel (1963); Blaxter & Ehrlich (1974).
[e] Laurence (1974); Laurence & Rogers (1976).
[f] Hunter & Kimbrell (1980).
[g] Lasker et al. (1970); Hunter (unpubl. data).
[h] Houde (1974); Houde (1978).

cost of decreasing fecundity and increasing the duration of stages most vulnerable to predation.

The optimum egg size must strike a balance between numbers and the risks of starvation and predation. At lower temperatures, where incubation periods are longer, the advantage generally falls to larger eggs, whereas the reverse appears to be true at higher temperatures (Ware, 1975). Fine adjustments in these tactics appear to exist within a species to meet seasonal and regional differences in environment. Egg size varies significantly among spawning groups of herring (Blaxter and Hempel, 1963) and is known to vary seasonally in many species, with the largest eggs produced in the spring at the coolest temperatures and egg size declining as the season progresses (Bagenal, 1971; Ware, 1975).

The estimation of days to irreversible starvation has generally been made from the time of complete yolk absorption, but the time from onset of feeding provides more insight to survival strategy, as most larvae begin to feed before the yolk is completely exhausted. Herring larvae have a prolonged period in which they are capable of feeding but still have yolk (Table 1). The thermal optimum in efficiency of yolk utilization is another possible larval

adaptation to specific environmental conditions. Sea bream larvae ret
more yolk at the onset of feeding at 26°C than at other temperatures and tl
have more yolk to sustain them if food is not present (Houde, 1974). Pla
larvae have a sharply defined thermal optimum in yolk utilization efficiei
between 6.5°C and 8°C, which if realized could produce larvae 10 perc
larger at the time of first feeding (Ryland and Nichols, 1967).

Spawning Tactics

Eggs of pelagic spawners are often distributed in extremely patchy ι
terns; 37% of Pacific sardine eggs taken in the years from 1951 to 1959
curred in only 0.6% of the samples (Smith, 1973). Helfrich and Allen (19
found the density of mullet eggs, *Crenimugil crenilabis*, to be 17 eggs/l at
surface after about one or two seconds of intensive spawning. A high den
of northern anchovy eggs taken in a neuston net was 31 eggs/l, correspond
to a density of 46,000 eggs per 10 square meters of sea surface, which is in
upper 5% of all samples of anchovy eggs collected with nylon nets (unp
lished data, NMFS, Southwest Fisheries Center, La Jolla). Other high egg d
sities include 31,000 eggs per 10 square meters for Pacific sardine (Sm
1973) and 9,000 eggs per 10 square meters for Atlantic mackerel (Se
1943).

The eggs in such patches gradually disperse; dispersion is more rapi
the perimeter of the patch, resulting in a denser centrum surrounded ł
less concentrated corona. The horizontal mean distance between neighl
ing eggs increases in a patch from one to two centimeters at spawnin,
15–20 cm in most several-day-old sardine eggs (Smith, 1973). In nortl
anchovy, dispersion of larvae as measured by the negative binomial K (Ll
1967) continues from hatching until the larvae attain a length of abou
mm, at which time they reach their most dispersed stage and contagiοι
creases thereafter (J. Zweifel, unpublished data, NMFS, Southwest Fishι
Center, La Jolla). This change from decreasing to increasing contagion ς
cides with the time anchovy begin nightly migrations to the sea surface t
their swim bladders (Hunter and Sanchez, 1976) and is close to the onsι
schooling, which begins at about 13 mm. Vertical migration may sei
stage for schooling by concentrating larvae near the surface at night and
increasing the frequency of social contacts.

Dispersion of larvae could progress to the point where it might influ
onset of schooling or delay formation of schools of viable size. *Menidia* la
reared in isolation took more time to form a school when brought togε
than socially reared larvae, and the length of the delay was proportion
the period of isolation (Shaw, 1961). Breder and Halpern (1946) showed
Brachydanio rerio larvae reared from the egg in isolation were quite hes
to join a school. Thus, onset of schooling could be retarded if larvae arε
persed to the point where social contacts are infrequent.

Intraspecific competition and cannibalism also may be affected b
tial spawn density and dispersion rates. Houde (1975) found that growtl

survival of sea bream decreased rapidly when stocking density exceeded 8 eggs/l at food levels of 1500–3000 microcopepods/l. Food concentrations of 100 microcopepods/l did not sustain sea bream larvae except at stock densities of 2 eggs/l. Bay anchovy larvae *(Anchoa mitchilli)* seem to be much less affected by stock density (Houde, 1975, 1977). Sibling cannibalism is common in rearing larvae of large piscivorous fishes such as the scombroids (Mayo, 1973), but is unreported and presumably rare in clupeoid fishes. Thus, larger and more active larvae seem to be more cannibalistic and competitive for food and possibly better able to find schooling companions because of faster swimming speeds. Formation of dense patches of eggs and slow dispersion rates may favor clupeoid larvae, but lower egg densities may be more favorable to the more active larvae.

Swimming Behavior

Swimming during the yolk-sac stage consists of bouts of continuous, very energetic swimming followed by relatively long periods of rest. This behavior appears to be common in many small marine yolk-sac larvae but has been described in detail for only the northern anchovy (Hunter, 1972; Weihs, 1980). This mode of swimming in anchovy larvae is energetically advantageous for yolk-sac anchovy larvae because water viscosity is the dominant factor when larvae are in this stage (low Reynolds number). When larvae reach 5 mm, the Reynolds number is sufficiently high that beat and glide swimming becomes the more economical mode (Weihs, 1980).

After conclusion of the yolk-sac period, the cruising speed of larvae becomes of major importance in their feeding ecology, because it affects the frequency that larvae encounter prey and also accounts for the greatest metabolic expenditure. Swimming of larvae in this period may also differ somewhat from adults, due in part to the lack of mechanical support of the caudal fin and to the low Reynolds number (Weihs, 1980). Tail-beat amplitude and tail-beat frequency are continuously modulated in northern anchovy larvae (Hunter, 1972) and Pacific mackerel larvae (Hunter and Kimbrell, 1980a), whereas in adult fishes amplitude is modulated less frequently, except during accelerations (Hunter and Zweifel, 1971). Because tail-beat frequency is inversely proportional to length in fishes (Bainbridge, 1958; Hunter and Zweifel, 1971), the frequency in early larval stages can be quite high, reaching 50 beats per second in 4–5 mm anchovy and Pacific mackerel larvae. At their cruising speed, anchovy larvae use a beat and glide mode of swimming similar to that of adults. This mode of swimming is slow and thereby reduces the volume of water that can be searched, but it has a high metabolic efficiency—25% in a 14 mm larva (Vlymen, 1974).

Temperature can have a major effect on activity or cruising speed. Two effects of temperature on activity are illustrated in Figure 1 for northern anchovy reared to age 12 days at various temperatures on a diet of *Gymnodinium splendens*. Temperature affected the timing of the transition from the
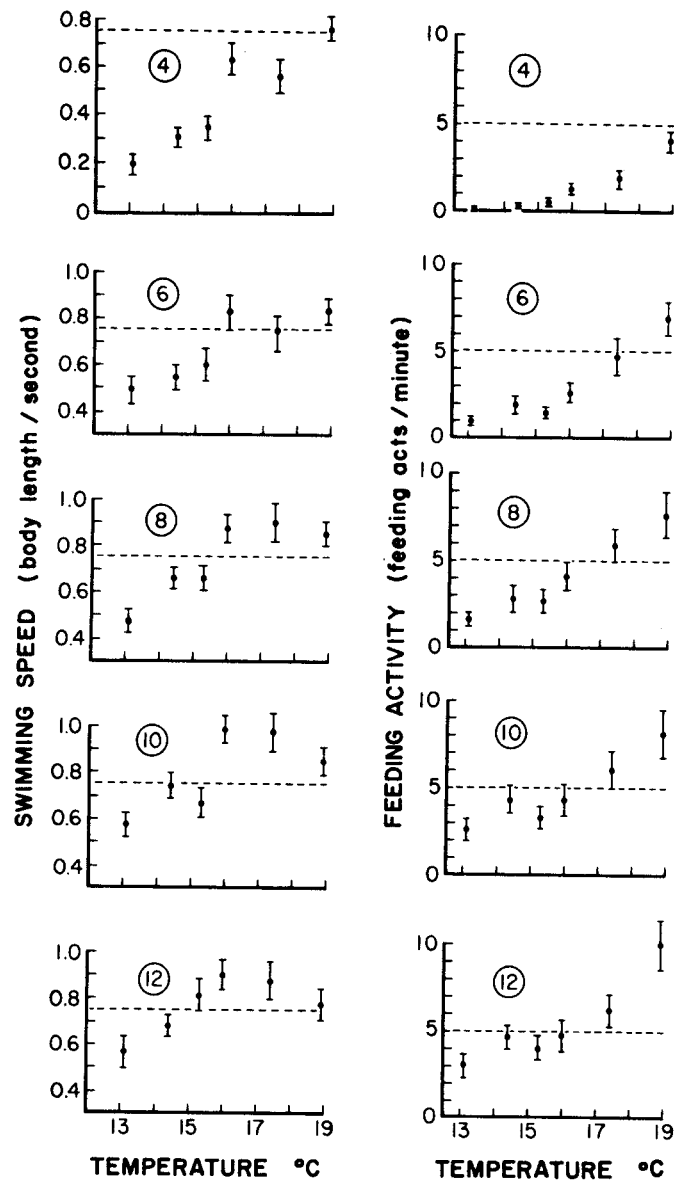
Figure 1. Effect of temperature on swimming speed and feeding rate of northern anchovy fed *Gymnodinium splendens* (mean density 400 cells/ml). Points are means, bars are 2 × standard error of mean, panel numbers are larval age in days, and dashed line is a visual reference. Data based on direct visual observation of larvae for 5 min. intervals. Each point average of value for 15 fish in two or more rearing groups.
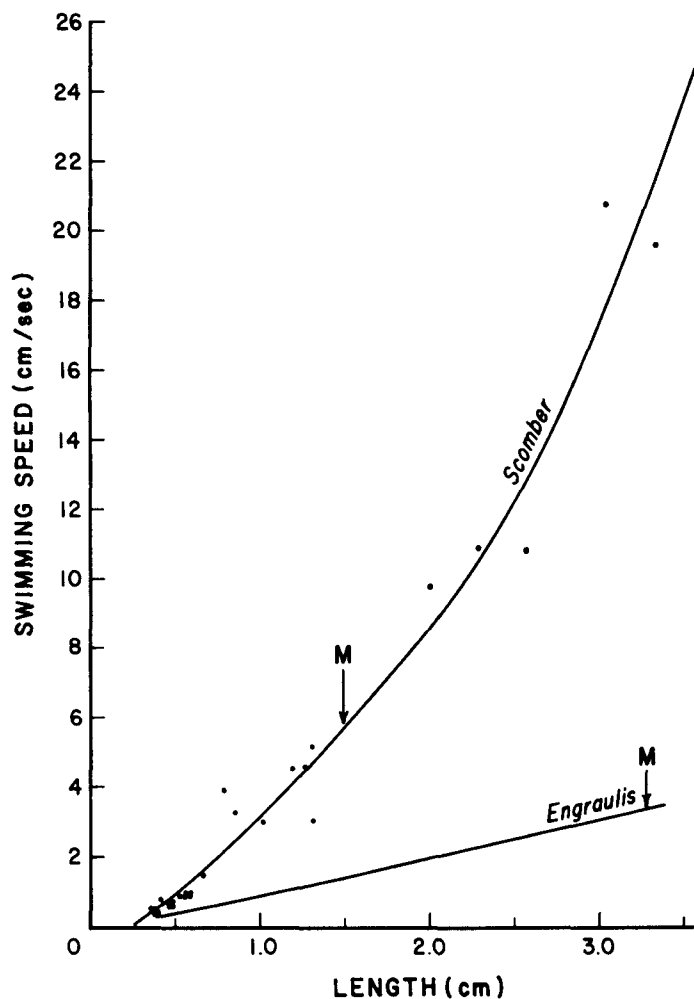
Figure 2. Swimming speed of Pacific mackerel, *Scomber japonicus*, larvae and juveniles at 19°C; points are means for five or more observations; curve fit by eye; and swimming speed of northern anchovy larvae, *Engraulis mordax*, at 17°C–18°C from Hunter (1972). Speeds are total distance covered including time spent in rest and feeding, and M indicates fish length at metamorphosis.

inactive yolk-sac stage to the active feeding stage as well as having a direct effect on activity of older larvae. At age 4 days, negligible feeding activity occurred in larvae at 15°C or lower, arid the speed-temperature relation was a function of developmental rate. At ages 8–12 days, all larvae were past this transition. A direct effect of temperature on activity is evident in the figure.

Cruising speeds increase markedly over larval life more or less in proportion to length. Blaxter and Staines (1971) observed that the cruising speed of

herring larvae increased from 20 cm/min at the end of yolk-sac stage to 80 cm/min 8 weeks later; in pilchard (*Sardina pilchardus*) speed increased from 10 to 30 cm/min in 3 weeks; in plaice from 10 to 60 cm/min over 7 weeks; and in sole (*Solea solea*) from 5 to 40 cm/min over 7 weeks. They also noted that cruising speeds of flatfish, sole, and plaice dropped by 90% at metamorphosis. Similarly, oxygen consumption of winter flounder, *Pseudopleuronectes americanus*, was shown by Laurence (1975) to decline sharply at metamorphosis.

Specific comparisons in activity or swimming speed from the literature are difficult to make because of differences in temperature, methodology, and lack of data on larval size. Data collected in my laboratory on anchovy and mackerel show that anchovy larvae swim more slowly than mackerel larvae at all stages of development (Fig. 2). Such a striking specific difference in cruising speed is diagnostic of major differences in life history tactics because it implies marked differences in searching abilities and metabolic requirements. For example, at 18°C, anchovy larvae consume 4.5 μl O_2/mg dry wt/hr, whereas mackerel consume 6.1 μl O_2/mg dry wt/hr (Hunter, 1972; Hunter and Kimbrell, 1980a). The actual difference in metabolic rate between these species is probably greater because the larvae were confined in small Warburg flasks which probably reduced the activity.

Blaxter (1969) concluded from his review that cruising speeds of larval fishes are on the order of 2–3 body lengths/sec and burst speeds (speeds that can be maintained for a few seconds) are on the order of 10 body lengths/sec. The cruising speed of anchovy is close to 1 body length/sec, and in mackerel it increases from 2 to 3 during the larval stage. Thus, these two speeds approach the upper and lower limits of the general range of cruising speeds.

Feeding Behavior

Prey Perception and Recognition

Marine fish larvae are visual feeders. All those studied so far—plaice, herring, and anchovy—lack rods and retinomotor pigment migration during the first weeks or months of life (Blaxter, 1968a, 1968b; O'Connell, 1981). That feeding is confined to daylight hours is also indicated by stomach content analysis in other species (Arthur, 1976).

To be perceived, a prey must be relatively near; first-feeding herring larvae react to prey at 0.7–1.0 body length L (Rosenthal and Hempel, 1970) or 0.4L (Blaxter and Staines, 1971), plaice at 0.5L, and pilchard at 0.2L (Blaxter and Staines, 1971). Ninety-five percent of the prey reacted to by northern anchovy were within 0.4L of the axis of progression (Hunter, 1972).

It would be unreasonable to attach much importance to differences between species among these values. The factors controlling perceptive ranges in larval fishes have not been studied, and size of prey was not isolated as a variable. In adult planktivorous fishes, perceptive distances appear to be a

linear function of prey size (Confer and Blades, 1975). If perceptive distances increase with prey size in larvae, this would certainly increase the effective searching volume of larvae specializing in such prey. In all these studies, the authors point out that perceptive ranges increase as larvae grow. Rosenthal and Hempel (1970) concluded that perceptive ranges in herring larvae also change with activity level, being greater during slow meandering swimming and shorter during faster swimming. They also state that herring larvae do not perceive prey which are beneath the plane of the horizontal axis of the body, but this does not appear to be the case for nothern anchovy larvae (Hunter, 1972).

The stimuli eliciting prey capture have not been studied in larval fishes, but in adult fishes prey size is usually the strongest factor, with movement seeming to direct attention of the fish toward the prey (Kislalioglu and Gibson, 1976a). Almost all predators which are believed to depend upon prey movement are able to detect prey even when it is motionless (Curio, 1976). The frequent occurrence of copepod eggs and other nonmotile foods in the stomachs of field-caught larvae and *Artemia* eggs and other nonmotile foods in laboratory-reared larvae (May, 1970) clearly shows that movement is not essential in many species. Prey size selection so dominates selection patterns in larval fish that it is difficult to evaluate the role of other prey characteristics such as spines and other protective structures, color, or avoidance behavior. Bowers and Williamson (1951) concluded that some copepods with spiny appendages, such as *Acartia*, occur in the stomachs of herring larvae less frequently than would be expected from their abundance in the plankton, and Arthur (1976) suggested that jack mackerel may select the more brightly colored copepods such as *Microsetella*, which occur in their stomachs in greater abundance than seen in the plankton. It would be of considerable interest to study such characteristics under controlled laboratory conditions from the standpoint of both larval feeding ecology and copepod evolution.

Motor Patterns

Upon sighting a prey, a clupeoid larva forms a sinuous posture and advances toward the prey by sculling the pectoral fins and undulating the finfold while maintaining the body in the S-posture. When the prey is a short distance from the snout, the larva opens its mouth, straightens its body to drive forward, and engulfs the prey (Breder and Krumholz, 1943; Rosenthal and Hempel, 1970; Hunter, 1972). Larvae of plaice, *Pleuronectes platessa* (Riley, 1966), and northern sennet, *Sphyraena borealis* (Houde, 1972), and other fishes are also reported to form a sinuous feeding posture, but the behavior has been studied in detail only for clupeoids and for the freshwater coregonid larvae, *Coregonus wartmanni* (Braum, 1967), and quite possibly differences exist among species.

Mackerel larvae, *Scomber japonicus*, feed in a manner more typical of the attack of many adult fishes. Upon sighting a prey, the larva advances toward the prey, stops, draws back the tail, and holds it in a slightly recurved

high amplitude position (the C-start position of Webb, 1978). The rest of the body is straight; feeding is accomplished by opening the mouth and driving the tail posteriorly. Presumably many other larvae of similar robust body form feed in this way.

Anchovy larvae often form and reform the S-posture while maintaining their orientation to a moving prey; but my observations indicate that, once the strike is made, anchovy larvae rarely strike again at the same prey. Mackerel larvae, on the other hand, frequently strike two or more times at the same prey if the preceding strike was unsuccessful. Mackerel larvae often reposition for the second strike by moving backward; anchovy and other clupeoid fishes do not appear to have this maneuverability (Blaxter and Staines, 1971). Large prey are more difficult to capture and are less abundant in the sea; consequently, persistence in a feeding attack as exhibited by mackerel may be an essential characteristic of a species whose strategy depends on larger prey.

Webb (Paul Webb, University of Michigan, Ann Arbor, unpublished data) described in detail the starting postures of feeding pike and largemouth bass. He concluded that pike, which use an S-start as do anchovy larvae, are less persistent in the attack and strike at higher speeds and at shorter range than do bass, which use a C-start. The parallels between his observations and ours on mackerel and anchovy larvae seem obvious.

The time spent poised in a striking posture in anchovy larvae is much longer at the time of first feeding than in later larval life, and gradually the strike becomes integrated with swimming movements; the duration of complete feeding acts declines from 1.5–2.0 seconds to about 0.6 seconds when larvae reach 17 mm, and relative speed of the strike also declines (Hunter, 1972). The poised stereotyped striking posture (C- or S-starting position) seems to be a common tendency in young larvae and becomes integrated into swimming movements as the larva grows, and suggests that it may be an adaptation to feeding on relatively large and fast prey. As will be shown subsequently, young anchovy larvae feed on much larger prey relative to their size than do older larvae.

Handling times are negligible when copepods and other small zooplankton are prey because the prey are engulfed by the mouth instantaneously. Piscivorous fish larvae manipulate their prey, and consequently handling times increase with prey size as is the case for adult fishes (Kislalioglu and Gibson, 1976b). The appearance of piscivorous habits requires development of a new set of motor patterns associated with grasping prey and presence of a sufficient number of teeth to accomplish this end. Larvae of the northern sennet, *Sphyraena borealis*, usually seize other larvae crosswise and, by a successive series of head shakes, move the grasp to either the head or the tail. Then without losing grip, the prey is swallowed head or tail first (Houde, 1972). Houde observed that newly hatched fish larvae were eaten by sennets at age 10 days and were the preferred food of sennets 9 mm and longer. I observed the same behavior in the Pacific barracuda, *Sphyraena argentea*,

feeding on siblings in a rearing tank. In this case, piscivorous feeding began at age 5 days when larvae were only 4.4 mm. Pacific mackerel larvae become piscivorous when they reach 10 mm. They also seize other larvae from the side, carry them crosswise in the mouth, periodically release the prey, and grasp it again until it dies. Then they release it and ingest it, usually head first.

Feeding Success

Feeding success of fish larvae is often low at the onset of feeding. Estimates for herring are 6% (Rosenthal and Hempel, 1970) and 2%–6% (Blaxter and Staines, 1971), for coregonid larvae 3%–5% (Braum, 1967), and for northern anchovy 10% (Hunter, 1972). Feeding success gradually increases, reaching 90% in about 3 weeks in anchovy (Hunter, 1972) and in about 7 weeks in herring (Blaxter and Staines, 1971). In contrast to these species, plaice larvae capture 32%–62% of prey attacked at the onset of feeding (Blaxter and Staines, 1971), and the relatively large larvae of *Belone belone* (12 mm) capture 60%–100%, depending on prey type (Rosenthal and Fonds, 1973).

Blaxter and Staines (1971) suggest that the initially high success of plaice larvae may be due to increased maneuverability of plaice relative to herring and to their ability to swim backwards. Feeding success of anchovy larvae dropped from 80% to 40% at age 17 days when the prey was changed from *Brachionus* to *Artemia* nauplii, but in 2 days their success increased to the former level (Hunter, 1972). Changes in mouth size or other developmental changes could not occur so rapidly, thus the difference appears to be attributable to experience.

Searching Behavior

Food density requirements have been estimated from behavioral search models of the basic form outlined by Ivlev (1960). These models in their simplest form require an estimate of ration, swimming speed, perceptive field, and feeding success, with many other parameters added as complexity increases. These models range in complexity from the simple models of Rosenthal and Hempel (1970), Blaxter and Staines (1971), and Hunter (1972), where only basic parameters are considered, to the increasingly complex models of Jones and Hall (1974) and—the most complex to date—Vlymen (1977). Vlymen's model is the only one that does not assume a random search pattern and that addresses the problem of a contagious food distribution. In his model the larvae have no effect on food density, and the model does not use a prey-size-dependent modulation of perceptive field and feeding success. All such models are extremely sensitive to assumptions regarding the perceptive field and swimming speed and to the accuracy of these measurements. For example, Blaxter and Staines (1971) estimated that the searching abilities of herring larvae increase from 0.1 to 2.4 l/hr over 8 weeks,

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whereas Rosenthal and Hempel (1970) estimated they increase from 1.5 l to about 10 l/hr in 10 weeks. The major difference in these results is in the differences in perceptive distances and rates of swimming (Blaxter and Staines, 1971). It would seem to be of value to use such models to set up hypotheses that could be tested in the laboratory or at sea.

Owing to these problems and to effects of temperature, specific comparisons are difficult, but these estimates do suggest that the volume searched by young larvae is often quite small: pilchard (5–7 mm) search 0.1–0.2 l/hr, plaice (6–10 mm) search 0.1–1.8 l/hr (Blaxter and Staines, 1971), and anchovy (6–10 mm) search 0.1–1.0 l/hr (Hunter, 1972). All studies show that searching abilities increase markedly with growth, since speed, capture success rates, and perceptive distances are functions of length or age.

In the two cases studied, search patterns in larval fishes were nonrandom. Larval anchovy decrease their speed and change their turning probabilities when they enter a dense patch of food. The probability of making a complete reversal in direction increased from 0.04–0.05 at low food densities to 0.23 in dense patches of *Gymnodinium* and to 0.07 in patches of *Brachionus* (Hunter and Thomas, 1974). Wyatt (1972) showed that the time plaice spent swimming increases with a decrease in food density. Similar nonrandom search patterns have been described for adult fishes (Kleerekoper et al., 1970; Beukema, 1968).

Prey

Prey Type

Naupliar through adult stages of copepods are the typical food of most marine fish larvae studied to date. Some notable exceptions to this rule exist: in the North Sea in normal years, the food of plaice larvae consists mostly of the appendicularian *Oikopleura dioica* (Shelbourne, 1962), and larval fishes may be a common item in the diet of the more piscivorous larvae. Larvae are commonly eaten by larval Pacific barracuda (Ahlstrom, personal communication, NMFS, Southwest Fisheries Center, La Jolla) and blue marlin, *Makaira nigricans* (Gorbunova and Lipskaya, 1975); and judging by high incidences of cannibalism under rearing conditions, they may be frequently eaten by many scombroid larvae (Mayo, 1973). Blue marlin larvae begin feeding on fish larvae at 6 mm, and they become the principal food by 12 mm (Gorbunova and Lipskaya, 1975). Under rearing conditions, the scombroid fishes, *Euthynnus alletteratus*, *Scomberomorus cavalla*, *Scomberomorus regalis*, and *Auxis* become cannibalistic at about 5 mm (Mayo, 1973), *Scomber japonicus* at 10 mm, and *Sphyraena argentea* at 4.4 mm (Hunter, unpublished data). Under aquarium conditions, sibling cannibalism appears to end as scombroid fishes become juveniles and begin schooling (Mayo, 1973; Clemens, 1956; Hunter and Kimbrell, 1980a).

Larvae tend to be more euryphagous during the earliest stages and often eat such organisms as tintinnids, phytoplankton, mollusk larvae, and ciliates

as well as copepods (Arthur, 1976; Bowers and Williamson, 1951; Lebour, 1921; and Rojas de Mendiola, 1974). Phytoplankton, often identified as green remains, is relatively common in the stomachs of clupeoid larvae at about the time of first feeding but is uncommon soon after. In general, the use of phytoplankton in laboratory rearing studies as a sole source of food for first-feeding larvae has been unsuccessful (May, 1970). Northern anchovy, on the other hand, are able to subsist on a diet of the dinoflagellate *Gymnodinium splendens* for up to 20 days, but at a greatly depressed growth rate (Lasker et al., 1970; Theilacker and McMaster, 1971). Anchovy will feed on a variety of dinoflagellates, *Gymnodinium*, *Gonyaulax*, *Prorocentrum*, and *Peridinium*, but not small flagellates, *Chlamydomonas*, *Dunaliella*, nor diatoms, *Ditylum*, *Chaetoceros*, *Thalassiosira*, and *Leptocylindrus* (Scura and Jerde, 1977). That larvae fed *Gonyaulax* (40 μm diameter) did not survive, whereas those fed *Gymnodinium* (50 μm diameter) did, led Scura and Jerde to conclude that it is the small size of *Gonyaulax* which makes it an inadequate food. Using the same line of reasoning, it seems doubtful that any of the other dinoflagellates they studied would support growth because they are even smaller in diameter.

The tendency for larvae to feed upon a greater variety of organisms in early larval life and subsequent specialization in stages of copepods may simply be due to the existence in the sea of a greater variety of small organisms of the proper size. The ability to subsist on the relatively small organisms such as dinoflagellates may be restricted to larvae of relatively modest energy demand, such as the northern anchovy, i.e., a larva of relatively low initial weight, low activity, existent in cool water.

Prey Size

Size dominates prey selection patterns of larval fishes and is one of the best diagnostic characteristics for evaluating specific ecological roles. The critical dimension for ingestion of copepods and other oblong prey is the maximum width including appendages (Blaxter, 1965; Arthur, 1976). Evidence for this is based on the fact that copepods frequently found in the stomachs of larval fishes are too large to be ingested if length were the critical factor (Blaxter, 1965; Hunter, 1977). Copepods are usually found in the stomachs of clupeoid larvae with antennae folded back along the body (Blaxter, 1965). Blaxter goes on to say that copepods with antennae folded in such a way are probably the only ones that are captured successfully. Inclusion of the appendages increases the maximum width of adult and copepodite stages by about 49% in *Pareuchaeta*, and 25% in *Calanus*, *Pseudocalanus*, *Acartia*, *Microcalanus*, and *Metridia*, but has a negligible effect in *Temora*, *Oithona*, *Oncaea*, and *Microsetella* (Wiborg, 1948a).

The increase in size of prey selected by marine fish larvae as they grow is well documented in the literature and occurs in every species studied. Often, prey length or life stage was used as a measure of size rather than the more informative measurement of maximum prey width. A striking feature of
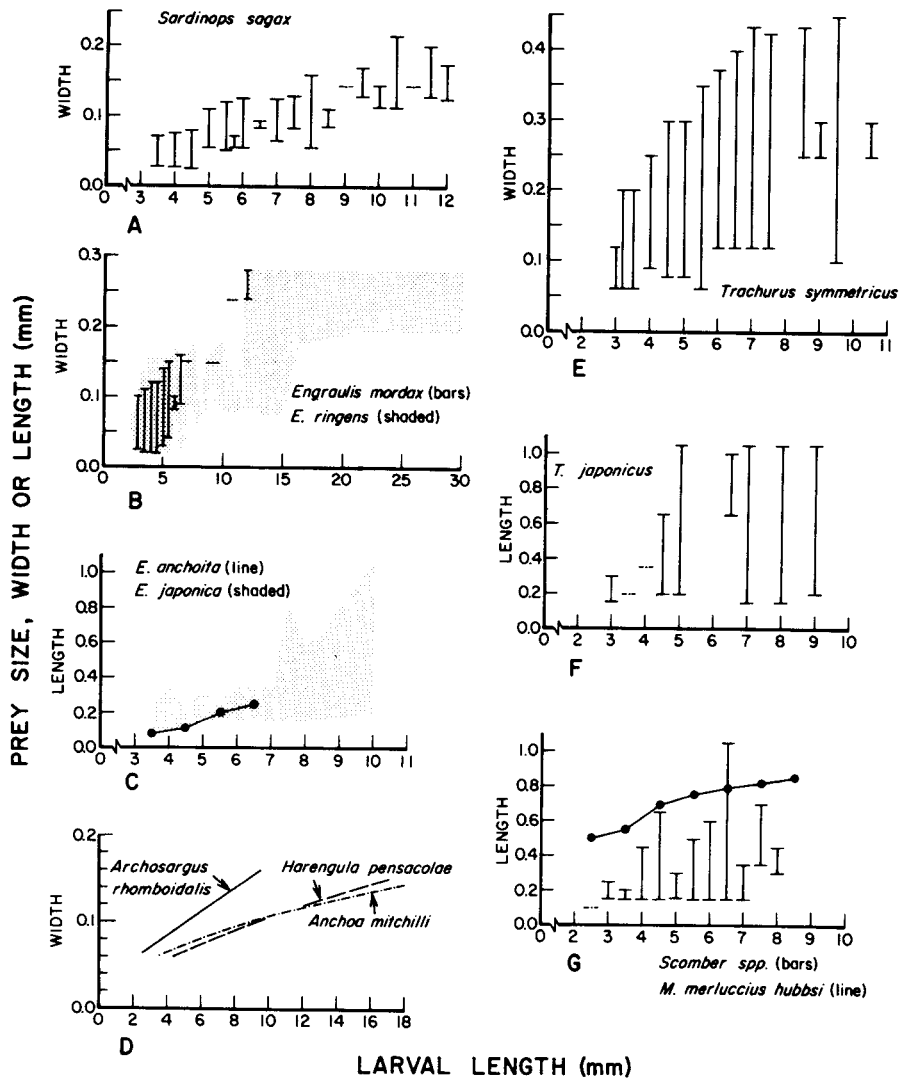
Figure 3. Relation between prey size and larval length for 12 species of marine fishes; label on ordinate indicates whether prey width or prey length were measured; vertical bars and shaded areas represent range of prey sizes; and straight lines connecting dots indicate average prey sizes. Plots were redrawn from Arthur (1976) for *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*; from Rojas de Mendiola (1974) for *Engraulis ringens*; from Detwyler and Houde (1970) for *Harengula pensacolae* and *Anchoa mitchilli*; from Stepien (1976) for *Archosargus rhomboidalis*; from Ciechomski and Weiss (1974) for *Engraulis anchoita* and *Merluccius merluccius*; and from Yokota et al. (1961) for *Engraulis japonica*, *Trachurus japonicus*, and *Scomber* spp. Data were for sea-caught larvae except panel D, which were laboratory reared.

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these data is the consistency of trends among related species and groups (Fig. 3). The small clupeoid larvae, *Sardinops, Engraulis, Harengula,* consistently feed on small prey of the order of 50–200 μm width; both species of *Trachurus* show a tendency for a marked increase in the range of food sizes eaten with length, and *Scomber* show a somewhat similar trend. In the three engraulid species, there appears to be a consistent tendency for a marked increase in the range of prey eaten between 8 and 12 mm. Hake larvae, *Merluccius,* begin feeding on much larger foods than the rest, with only a slow increase in average prey size. Ciechomski and Weiss (1974) point out that hake begin feeding on advanced copepodite and adult stages of copepods.

The consistency of these trends from different localities and species strongly suggests that these patterns are the result of positive size selection inherent in species or specific ecological groups of larvae. Stepien (1976) demonstrated that sea bream larvae select foods by size, with a slight positive electivity for prey of 100–200 μm width in larvae 4–5 mm and a stronger positive electivity for prey 200–300 μm in larvae 7–9 mm. The difference between sea bream and the two clupeoid larvae in the figure may be n┄ ╌ marked under natural conditions, because the food size preference of sea bream increases faster than the increase in size of the food in the rearing tanks.

Except for hake, specific differences are less marked at the onset of feeding, with all larvae feeding on prey of 50–100 μm width, although jack mackerel take much larger foods as well. Houde (1973) remarks that organisms 50–100 μm are eaten by a great variety of larvae at this time, including those with relatively large mouths such as the tunas and flatfishes. Arthur (1977) estimated the naupliar biomass in the California Current system and expressed it in terms of naupliar width. The naupliar biomass was at a maximum between 50 and 80 μm of naupliar width and declined sharply on either side even though there were many more nauplii of smaller sizes. He points out that the food size ranges of first-feeding Pacific sardine, northern anchovy, and jack mackerel all overlap the naupliar biomass maximum, and it appears that the feeding range of many other larvae do so as well.

Larvae in the above comparisons are relatively the same size at onset of feeding and hatch from relatively small eggs. Larvae from large eggs, for example exocetid larvae and saury (*Cololabis saira*), are 6–7 mm at first feeding and feed on a range of prey equivalent to that of older jack mackerel or *Scomber* of about the same size (Yokota et al., 1961). None of the species in Figure 3, other than hake, could eat newly hatched *Artemia* nauplii at the onset of feeding, but rearing studies reviewed by May (1970) indicate that plaice larvae, two species of *Fundulus,* a species of *Sebastes,* two cottid species, four species of atherinids, *Aulorhynchus flavidus,* and *Fugu pardalis* feed successfully on *Artemia* nauplii at the onset of feeding. Many of these species have large eggs, again emphasizing the importance of the maternal contribution in the feeding tactics of some larvae.

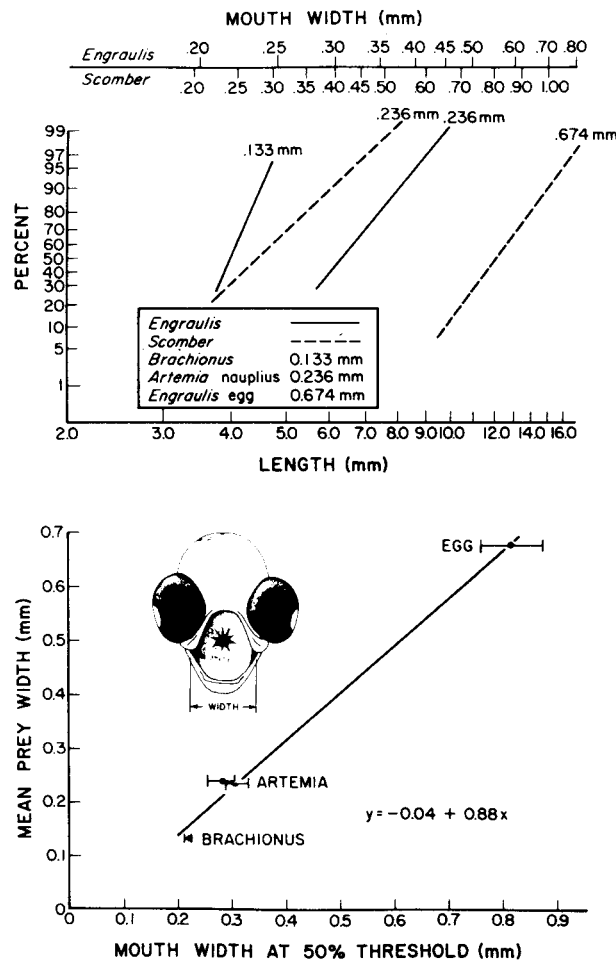An additional feature of importance in these records is the slow increase

Figure 4. Relation between width of mouth and ability of *Scomber japonicus* and *Engraulis mordax* to capture prey of various widths. Upper panel, percent of larvae that captured one or more prey, shown as a function of mouth width (upper scales) and larval length (lower scale); lines are for the regression of probit on log larval length. Lower panel, average width of prey, shown as a function of the mouth width at which 50% of the larvae ingested one or more prey; estimates taken from probit lines given in upper panel; and bars are the 95% confidence intervals for the estimate. Density of prey in the experiments were: *Brachionus* 9/ml; *Artemia* 10/ml; and *Engraulis* eggs 10/l.

in the minimum size of prey eaten in all species. The effect of this is to greatly expand the prey range in larvae that select larger prey, and this has important energetic consequences. In summary, marine larvae select foods of increasingly larger size as they grow, but the average and range of sizes selected differ greatly among species and may be diagnostic of specific ecological roles.
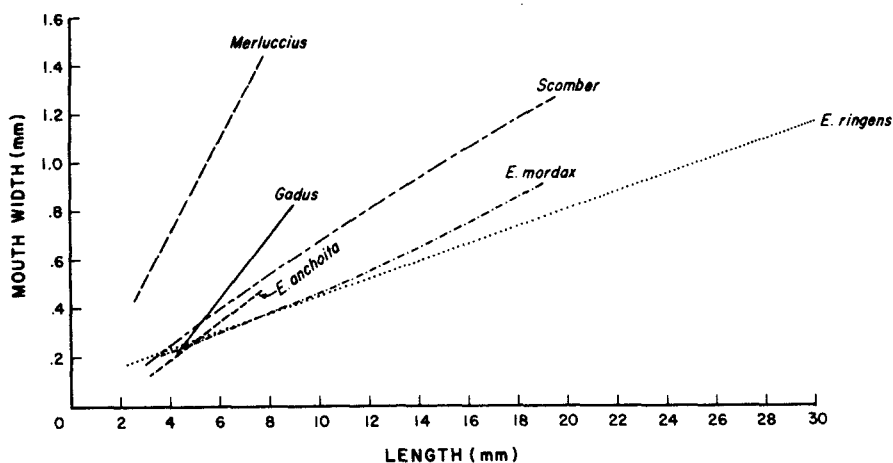
Figure 5. Relation between mouth width and larval length of hake, *Merluccius merluccius*, from Ciechomski and Weiss (1974); cod, *Gadus morhua*, from Wiborg (1948b); Pacific mackerel (*Scomber japonicus*) from Hunter and Kimbrell (1980a) and three species of anchovy, *Engraulis anchoita* from Ciechomski and Weiss (1974), *Engraulis mordax* from Hunter (1977) and *Engraulis ringens* from Rojas de Mendiola (1974).

Effect of Mouth Size

The size of the mouth and the rate it changes with length must be partially responsible for specific differences in food size selection. Shirota (1970) measured the gape of the mouth of 33 species of marine and freshwater larval fishes and correlated them with the size of natural foods and growth rates, and concluded that larvae with smaller mouths grow more slowly than those with larger ones. Blaxter (1965) showed that differences in gape of the mouth exist between different races of herring and concluded that these differences could be of great significance in early survival.

Mouth size would be expected to set the upper size limit for prey. To define this relationship, Hunter (1977) and Hunter and Kimbrell (1980a) determined for anchovy and Pacific mackerel the mouth size threshold for various prey. In these experiments, larvae were exposed to high densities of a single prey—*Brachionus*, *Artemia* nauplii, or anchovy eggs—for 2–4 hours, and the proportion of larvae that captured one or more prey was tabulated by mouth size classes. None of the larvae tested had any previous experience with the particular prey. The width of the mouth was closely correlated with the ability to capture these prey (Fig. 4). The first incidence of feeding occurred when the ratio of prey width to mouth width was close to unity with *Artemia* or anchovy eggs as the prey. In the case of *Brachionus*, it was lower (0.63), which may have been caused by the fact that first-feeding anchovy larvae were used in this experiment to avoid the effect of rapid improvement of success that occurs over the first few days.

These experiments indicated that, on the average, 50% of larval anchovy or mackerel were capable of feeding on these prey when the prey width to mouth width ratio was 0.76. The width of the mouth provided a good indica-
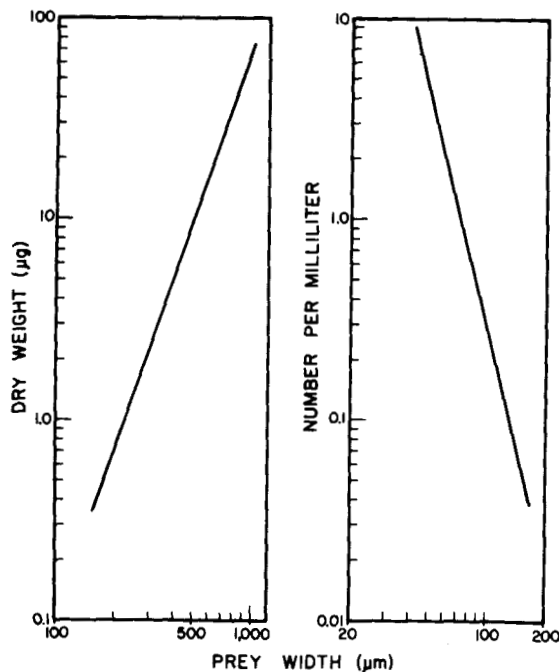
Figure 6. Left panel, relation between copepod width and dry weight (excluding nau-pliar stages) calculated from data given by Gruzov and Alekseyeva (1970). Right panel, relation between number of prey per ml in the sea and prey width, recalculated from Vlymen (1977).

tion of the size of prey a larva is capable of ingesting. Mouth gape was also measured, but width was preferred because it can be measured with greater accuracy. A different relation could be expected for piscivorous feeding or when ingestion involved manipulation of the prey because larvae are capable of greatly expanding their mouths under these circumstances. The gape of the mouth would be expected to be related to handling time in this case (Kis-lalioglu and Gibson, 1976b).

These thresholds are of interest because they indicate how feeding success is affected by prey size. They also show that prey are eaten "end first" because at the lowest success levels the prey can be ingested in no other way. Many of the trends in size selection of prey discussed in the previous section are also suggested by the relationship between mouth width and length. The mouth sizes of the three engraulid species are similar to each other and differ markedly from those of the other species (Fig. 5). The mouth widths of all species but hake are somewhat similar in the beginning, but differences increase greatly with growth. Hake stands out as being distinctly different from the rest from the onset of feeding.

The sharp increase in food size that occurs in the engraulids between 8 and 12 mm occurs at a time anchovy become highly proficient in capturing *Artemia* nauplii, and the increase in prey size is to one of that diameter. No
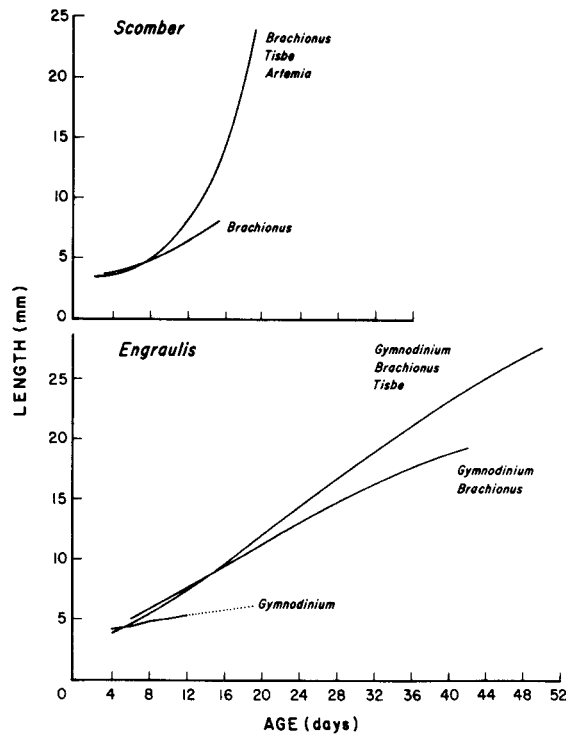
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Figure 7. Laboratory growth rates using various foods of *Scomber japonicus* at 22°C from Hunter and Kimbrell (1980a), and of *Engraulis mordax* at 16°C from Hunter (1977). Caloric values of prey were: *Gymnodinium* 0.00005 cal; *Brachionus* 0.008 cal; and Artemia 0.0096 cal.

evidence exists from mouth size information to explain the leveling of food size that occurs thereafter despite the fact that the mouth continues to grow. It seems reasonable to assume larger prey would be eaten if the opportunity existed. Thus, other limits must be imposed; one such limit may be the slow swimming speed of engraulid larvae.

Nutritive Value of Prey of Different Sizes

The nutritive value of larger prey can be illustrated by considering the relation between width of copepods and their weight. Gruzov and Alekseyeva (1970) give a wet weight to length conversion for a group of copepods including species in Calanidae, Paracalanidae, Pseudocalanidae, and other families having a cephalothorax length-to-width ratio ranging from 2.0 to 2.8. I transformed their data to show dry weight as a function of cephalothorax width by using the midpoint of their width ratio (2.4) and assuming a water content of 87% (Lovegrove, 1966). This calculation indicated that an increase of 2.5 in copepod width produces an order of magnitude increase in dry weight. Thus, a larva feeding on copepodites 200 μm wide would have to capture ten

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times the number of prey to obtain the same ration as one feeding on copepods 500 μm wide (Fig. 6). The effect of a slight increase in width of prey eaten is more marked if the change from feeding on nauplii to copepodites is considered. The change in body width of *Calanus* from nauplius VI to copepodite I is slight even when appendages are included in the measurement (Wiborg, 1948a), but the dry weight doubles. In *Calanus helgolandicus*, the dry weight of N.VI is 2.0 μg and that of C.I is 4.3 μg (Paffenhöfer, 1971). The well-known seasonal and regional variation in copepod weight (Marshall and Orr, 1955; Gruzov and Alekseyeva, 1970) should be considered in any study of food size relations in larval fishes.

The necessity for increasing prey size with growth is illustrated by comparing growth rates of larval anchovy (Hunter, 1977) and Pacific mackerel fed different foods (Fig. 7). When anchovy are fed *Gymnodinium* alone, growth becomes asymptotic at about 6 mm, whereas when *Gymnodinium* and the rotifer *Brachionus plicatilis* are used, growth becomes asymptotic at about 20 mm and few larvae survive (survival drops from 46% at age 26 to 6% at age 42 days). Similarly, Pacific mackerel growth slows on a diet of only *Brachionus*, and few survive beyond 8 mm at age 15 days. Howell (1973) was able to grow plaice larvae through metamorphosis on *Brachionus* alone, but at a much slower growth rate than when *Artemia* was used, indicating that some species are able to grow through metamorphosis on rather small prey, but at a depressed growth rate.

Vlymen (unpublished data, NMFS, Southwest Fisheries Center, La Jolla) estimated for larval anchovy the minimum caloric value of prey required to meet energetic needs for parameters in his 1977 paper. The model uses a 12-hour feeding day, a temperature of 17°C, and the maximum feeding rate observed in the laboratory (about 10 attacks per minute). Gut capacity was not included, and consequently the limit was set by the maximum feeding rate. To calculate the minimum caloric value of prey necessary to meet energy needs, Vlymen used the model

$$E_1 + E_2 + E_3 + E_4 = 0.48R$$

where:

$E_1 = (5.10 \times 10^{-2}) L^{3.3237}$ (the basic metabolic rate in calories, where L = length in cm);

$E_2 = 0.19 L^{4.48}$ (the total energy cost of swimming);

$E_3 = 0.05 L^{4.48}$ (the total energy cost of feeding attacks at maximum rate during a 12-hour day);

$E_4 = 0.29R$ (the energy cost of mechanically processing food, intestinal propulsion, etc.); and
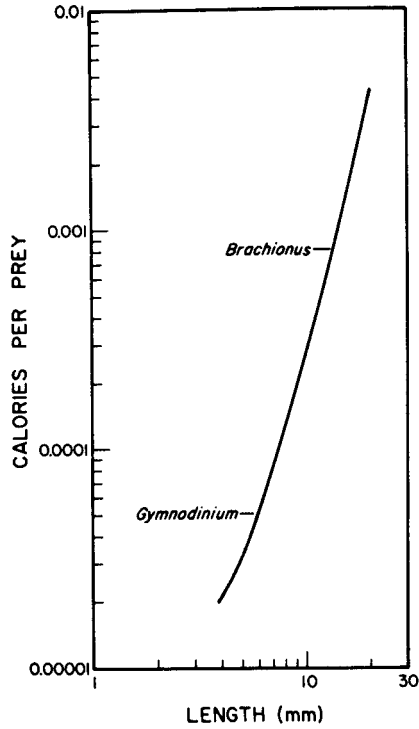
Figure 8. Relation between minimum caloric value of prey required to meet energy needs of larval northern anchovy at 17°C and larval length. From model developed by Vlymen (1977) and Vlymen (unpublished). The caloric value of *Gymnodinium* and *Brachionus* are indicated.

0.48R = the proportion of the ration R available for energetic needs.

The ration at the maximum attack rate was

$$R = (7.12 \times 10^3) C \times S$$

where 7.12×10^3 is the total number of attacks at the maximum rate in a day of feeding, C is calories per prey, and S is success of capture. By substitution he obtained

$$(3.78 \times 10^{-5}) L^{3.3237} + (1.77 \times 10^{-4}) L^{4.48} = C \times S.$$

The success of capture (S) is a function of age, not length, and is described by the function $S = 93.2 \log_{10} T - 33.3$, where T is larval age in days. To obtain the minimum caloric value of prey for larvae of various lengths, ages at specific lengths were obtained from laboratory growth rates (Hunter, 1976). The origin of the data and the derivation of the parameters used in this model are described by Vlymen (1977).

His results are reasonably close to those described above from rearing work. The model predicts no growth beyond a length of 6 mm on prey having a caloric value of *Gymnodinium* and none beyond 14 mm for *Brachionus*
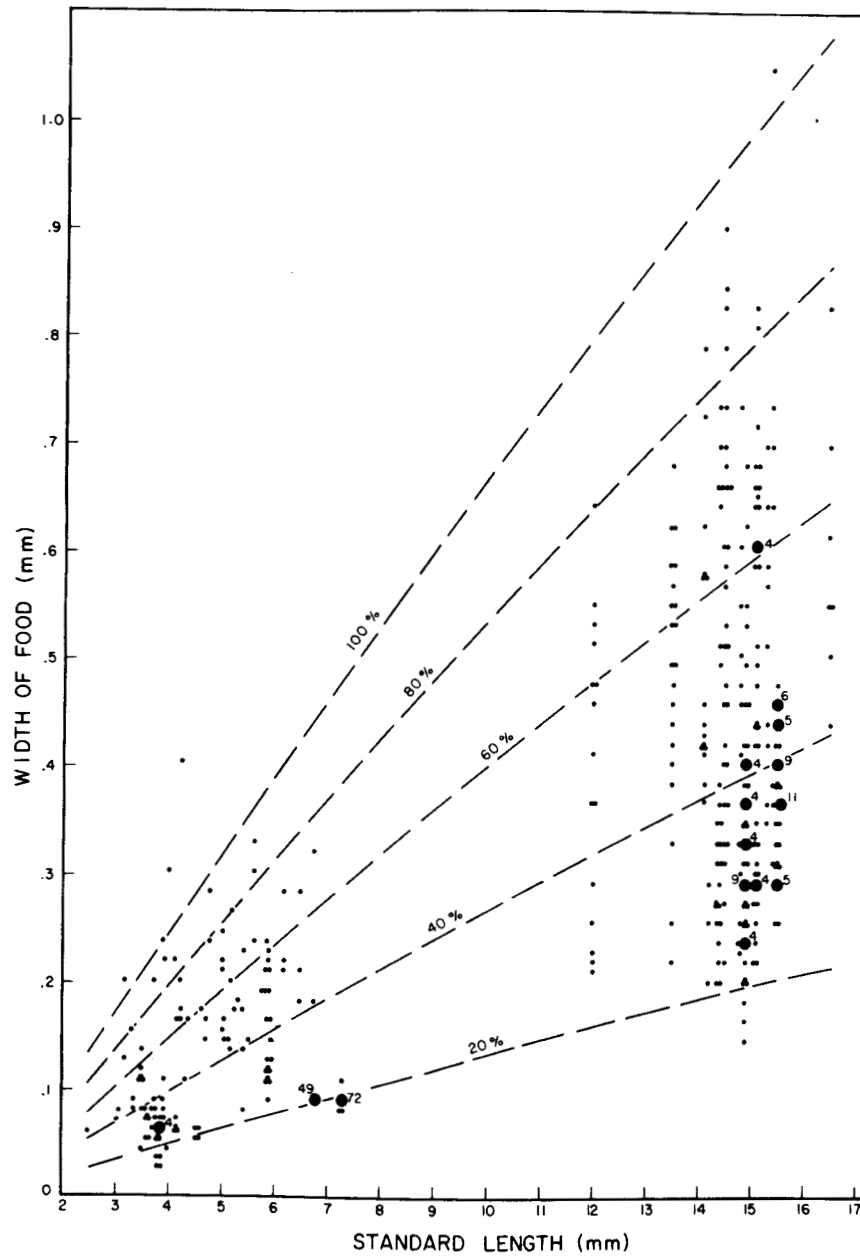
Figure 9. Width of foods eaten in the sea by Pacific mackerel larvae of various standard lengths. Each small point is the width of a single prey; larger points represent multiple points for prey of the same size and number observations. Dashed lines indicate the prey width equal to 20%–80% of the mouth width, or equal to the mouth width (100%), for mackerel larvae of 3–16 mm.

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Table 2. Average[a] densities of microcopepods in the sea.

| | Average density of microcopepods (number per liter) | | | |
	nauplii	copepodites	total	Location
OPEN	13	2	15	Southeast Coast of Kyushu[b]
SEA	22	36	58[c]	California Current[c]
	40	5	45[c]	Southern California near shore[e]
	27	7	34[f]	Eastern Tropical Pacific[g]
	36	1	37	California Current[h]
PARTLY	76	19	95	Azov Sea[i]
ENCLOSED	—	—	223[j]	Gulf of Taganrog[k]

[a] Mean for all stations and years given in publication listed in table.
[b] Yokota et al. (1961)
[c] Includes all copepods passing 202 μm mesh net.
[d] Beers & Stewart (1967)
[e] Beers & Stewart (1970)
[f] Includes all copepods passing 202 μm mesh net and caught on 35 μm mesh.
[g] Beers & Stewart (1971)
[h] Arthur (1977)
[i] Duka (1969)
[j] Defined as food of *Clupeonella delicatula*; microcopepods account for over 90% of items eaten (Mikhman, 1969).
[k] Mikhman (1969)

(Fig. 8). Thus the lower size limit of prey, at least over the first few weeks of feeding, appears to be set by metabolic relations, whereas the upper limit is controlled by mouth size.

In the sea, many more small prey are eaten than large ones, even in large prey specialists such as Pacific mackerel larvae. Stomach contents of Pacific mackerel from the sea illustrate this point. The mean diameter of prey eaten by these larvae was about 40% of their mouth width (solid line, Fig. 9), although they were able occasionally to eat prey as wide as their mouth (Hunter and Kimbrell, 1980a). If one assumes the prey in Figure 9 to be spherical, which underestimates the size of the larger prey, the small prey that contributed 50% by number contributed only 10%–15% of the total volume of prey eaten. Thus the relatively large and rare prey probably make the major contribution to growth despite the fact that many more small prey are eaten.

Prey Abundance and Density Requirements

The density of particles in the sea declines rapidly with increasing size or diameter of the particle (Sheldon et al., 1972; Sheldon and Parsons, 1967). Such a relationship was presented by Vlymen (1977) for particle size distribution from Niskin casts measured with a Coulter Counter by Richard Eppley

Table 3. Food density thresholds for six species of marine fish larvae.

Species and common name	Container volume (liters)	Duration (days)	Food type	Stock density (No./L)	Survival at various food densities	
					Density (No./L)	Percent survival
PLAICE[a]						
Pleuronectes platessa	5	14	*Artemia* nauplii	50 (larvae)	1,000	72[b]
					500	72
					200	54
					100	32
NORTHERN ANCHOVY[c]						
Engraulis mordax	10.8	12	Wild zoo-plankton (nauplii)	10 (eggs)	4,000	51
					900	12
					90	0.5
					9	0
BAY ANCHOVY[d]						
Anchoa mitichilli	76	16	Wild zoo-plankton (nauplii-copepodites)[f]	0.5-2 (eggs)	4,700[e]	65
					1,800	50
					110	10
					60	5
					30	1
SEA BREAM						
Archosargus rhomboidalis	76			0.5-2 (eggs)	2,600[e]	75
					890	50
					130	10
					90	5
					50	1
LINED SOLE						
Achirus lineatus	38			0.5-2 (eggs)	610[e]	75
					220	50
					30	10
					20	5
					9	1
HADDOCK[g]						
Melanogrammus aeglefinus	37.8	42	Wild zoo-plankton (nauplii)	9[h] (larvae)	3,000	39
					1,000	22
					500	3
					100	0
					10	0

[a] Wyatt (1972).
[b] Survival was 100% at 50/L for first 7 days without a decrement in length; see also Riley (1966).
[c] O'Connell and Raymond (1970).
[d] Houde (1978).
[e] Estimated food density for indicated survival levels.
[f] Plankton blooms of *Chlorella* sp. and *Anacystis* sp. maintained in rearing tanks.
[g] Laurence (1974).
[h] Estimated by adjusting for hatching success.

(Scripps Institution of Oceanography, University of California San Diego, La Jolla) (Fig. 6). Sheldon et al. (1972) pointed out that roughly similar amounts of organic material exist in logarithmically equal size intervals in any water mass; hence, in any sample, many more small particles exist than large ones. This implies that to feed on larger prey, a larva must search a much greater volume of water, and it also may explain why the minimum and average prey sizes change slowly in larvae that select larger prey.

The density of particles in the size range relevant to larval marine fishes has been studied by a number of workers. Their results have been reviewed by Blaxter (1965), May (1974), and Arthur (1977) and are presented here in Table 2. These studies indicate that average density in the open sea is 13–40 nauplii/l and typically 1–7 copepodites/l. On the other hand, in enclosed areas such as lagoons, bays, and estuaries, much higher densities are found. Average densities in these areas of naupliar and postnaupliar stages combined can exceed 200/l.

Larval fishes have been maintained in the laboratory at various food densities to determine the density of prey required for survival. Some of these density experiments are summarized in Table 3. Most indicate that a prey density of 1,000–4,000 microcopepods/l is required for high survival rates in the laboratory. These results agree in general with what has become standard rearing practice in recent years; in such techniques, the highest densities are used initially and are subsequently reduced to about 1,000/l (Houde, 1973). Much higher densities are required for very small prey such as phytoplankton. Lasker (1975) found that anchovy larvae required 5,000–20,000 *Gymnodinium splendens* cells/l at 19°C and 20,000 or more at 14°C for significant feeding to occur. Standard rearing practice for northern anchovy requires 100,000 or more *Gymnodinium* cells/l (Hunter, 1976b), whereas 1,000 microcopepods/l appear to be adequate (O'Connell and Raymond, 1970).

Density thresholds determined by Houde (1975, 1977, 1978) are markedly lower than those of the others listed in the table and are substantially below those used for routine rearing of larval fishes. Houde attributes his lower thresholds to use of lower stocking densities, general improvement in culture techniques, and frequent daily monitoring and adjustment of food density. He also maintains a dense phytoplankton bloom in his containers, which may also contribute in some way to higher survival. Of particular interest is the very low threshold determined for sea bream, emphasizing the importance of specific feeding tactics. This species selects larger prey (Stepien, 1976) than the other species studied by Houde and, judging by the density threshold, is much more efficient in finding and catching prey.

In general the density thresholds determined for larvae in the laboratory are much higher than average microcopepod densities in the open sea, described in the preceding section. On the other hand, the high microcopepod densities in enclosed areas are within the range that Houde (1975, 1977) found to support survival and growth. Thus food may not be as critical for species such as those he studied, which exist in enclosed areas. Many prob-

lems exist in interpreting laboratory findings and extending them to field conditions. The interactions of stock density, food density, and mortality are problems which may be overcome to some extent by use of low stocking densities and frequent monitoring of food density. Changes in ration with development and prey size distributions in the tank are also critical. The few larvae that survive at very low prey densities may be those that captured, either by good fortune or because of a larger mouth, the few larger prey in the container. Selection of the appropriate criteria also poses problems. Growth as well as survival declines with food availability; this is evident in all the food density studies cited but perhaps best illustrated by Riley (1966), Wyatt (1972), and Houde (1975, 1977). Reduction of growth may be nearly as lethal as starvation because of the increased exposure to predation.

Patchiness

The disparity between most estimates of food densities required by larvae and average densities in the open sea has led to the hypothesis that larvae may be dependent on small-scale patchiness of food. In the sea, large-scale sampling will always tend toward the mean concentration between such patches. Data collected by Yokota et al. (1961) on naupliar abundance provide one of the better examples of patchiness of larval forage because the samples were taken on a scale relevant to larval searching behavior. They counted all the nauplii occurring in one-liter samples taken at the surface from an area off the southeast coast of Kyushu over two years. The average naupliar density for their 4,730 samples was 13/l. The greatest number in a single sample was 524, and only 2% of the samples accounted for over 20% of the nauplii.

Laboratory experiments on searching behavior discussed previously indicate that larva have the ability to remain in patches of food if they find them. The search model of Vlymen (1977) indicated that the average anchovy larva could not exist in the sea if food were distributed randomly. He concluded that first-feeding anchovy larvae require a food contagion of K = 0.17, where K is the negative binomial, just to meet minimum energy requirements. To meet minimum requirements, therefore, prey would have to be 1.3 times as "crowded" as they are on the average, if the population had a random distribution (Lloyd, 1967).

Lasker (1975) tested the patchiness hypothesis by exposing anchovy larvae to samples of water taken from the surface and from the chlorophyll maximum layers usually 15–30 m below the surface. Feeding by larvae was minimal in samples taken from the surface, but extensive feeding occurred in water from the chlorophyll maximum layer when these samples contained prey of about 40 μm at densities of 20,000–400,000 prey/l. The prey were primarily the phytoplankter *Gymnodinium splendens*; microcopepods were never at high enough densities to be eaten by the larvae. Houde and Schekter (1978) exposed sea bream to simulated patch conditions in the laboratory by increasing the concentration of microcopepods to 500/l for periods of 2–13

hours per day from a background density of 25–50/l. They found that survival at 10 days after hatching of larvae exposed to only three hours of food at 500/l was similar to that of larvae fed at a constant 500/l. Thus, even very short-term patchiness could enhance survival in this species. Lasker (1975) has considered a much broader time scale; the bloom of *Gymnodinium* had persisted for at least 18 days until a storm obliterated the chlorophyll maximum layer. His measurements after the storm indicated that the density of food was insufficient for feeding.

If patchiness of food is a key to larval survival in the open sea, one could expect survival and growth of larvae to show considerable small-scale patchiness within the species spawning region. Present evidence for northern anchovy larvae supports this view. O'Connell (1981) measured the incidence of starvation of larval anchovy in the sea using histological techniques that had been calibrated by starving larvae in the laboratory (O'Connell, 1976). He found that 8% of larval anchovy in the Los Angeles Bight in March were in poor histological condition, indicating that death from starvation was imminent. For larvae of the size he studied (about 8 mm SL) this could represent about 40% of the daily rate of mortality. Of great importance to this discussion is the high variability that existed in the condition of larvae occurring in different tows. In some tows, 60% of the larvae were starving, yet all larvae in tows taken a few nautical miles away were in excellent condition. Thus as much variability in starvation existed within a few nautical miles as existed over the entire Los Angeles Bight. Similarly, Methot and Kramer (1979) found as great a difference in growth of anchovy larvae (estimated from daily increments of otoliths) in samples taken a few nautical miles apart as among all samples taken in the Bight area. Thus larval foods, larval growth, and starvation all appear to exhibit small-scale patchiness. It may be the summation of such small-scale events over time and space that ultimately determines the success of a year class.

Predation

Little literature exists that is concerned specifically with predation on pelagic egg and larval stages of marine fishes. Many species within the major groups of pelagic invertebrates, including Medusae, Siphomedusae, Ctenophora, Chaetognatha, Cephalapoda, hyperiid amphipods, euphausiids, and carnivorous calanoid copepods, as well as pelagic fishes, have been reported to feed on the eggs and larvae of marine fishes. That predation exists is amply documented by food habit studies of organisms in these groups as well as by some aquarium observations, but most studies give no indication that the predation by a species is a significant part of natural larval mortality. The records of egg and larval predation are drawn primarily from general descriptions of food habits of the predators, and incidence of predation is often summarized without regard to the seasonal changes in larval and egg abundance. On the other hand, these studies indicate that larval fishes and eggs typically constitute a small and highly variable proportion of the foods usually eaten.

Estimates of mortality of egg and yolk-sac stages indicate that predation must be very high. Starvation can be eliminated as a source of mortality in these stages because larvae subsist on their yolk. Losses range from 10% to 95% per day and typically are 30%–40% (Jones and Hall, 1974; Vladimirov, 1975; Riley, 1974). Although predation is possibly the largest source of mortality in larval fishes, it remains at present largely undocumented.

In this lecture I will first discuss characteristics of the behavior of the parents and the larvae that affect vulnerability to predation and then consider the evidence for effects of specific marine predators. I restrict my presentation to predation in the pelagic realm, recognizing that predation on demersal eggs of marine fishes is often a major source of mortality. The larvae of many demersal spawners are pelagic, however, and may encounter the same groups of predators as those of pelagic spawners.

Factors Affecting Vulnerability

Parental Behavior

The spawning behavior of the parents affects the vulnerability of pelagic eggs and larvae to predation. These influences include the time and location of spawning and the density of eggs. Nocturnal spawning occurs in many

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clupeoids (Blaxter, 1970); in the northern anchovy, for example, spawning begins at sunset, reaches a maximum about midnight, and declines thereafter (Hunter and Goldberg, 1980; Hunter and Macewicz, 1980). Johannes (1978) concludes that the majority of tropical marine fishes with pelagic eggs spawn at twilight or night and suggests that this may reduce the intense predation by diurnal planktivores in tropical reef communities, because eggs are transported by currents into the open sea away from inshore planktivores. Hobsen and Chess (1978) reported that pelagic fish eggs are an important component of the diet of diurnal planktivores at Enewetak but were insignificant in diets of nocturnal planktivores. In the open sea, nocturnal spawning may also reduce vulnerability to predation because it permits some dispersion of egg patches before they become vulnerable to diurnal planktivores. The dense egg patches produced by clupeoid fishes may increase vulnerability because predators could converge on such patches and feed selectively on eggs and larvae.

Vulnerability to predators may also be reduced by the location of spawning. Johannes (1978) points out that many tropical reef fishes spawn in localities (on the outer reef slope, near channel mouths, in open water, and at other sites) where eggs are transported by currents away from the intense predation of the reef. Northern anchovy may spawn in areas in the open sea that have fewer large planktonic predators (Alvariño, 1980), a topic discussed in greater detail further on.

Starvation

It is generally believed that a prudent predator would select prey that are about to die anyway, that is, the youngest ones and those weakened by starvation or other causes. No information exists on the effect of starvation on vulnerability to predation of marine fish larvae, but one might expect it to vary with effect of starvation on sustained high-speed swimming. Laurence (1972) observed that the maximum speed that starved largemouth bass larvae, *Micropterus salmoides*, could sustain for 30 minutes declined with starvation, from about 3 to less than 2 body lengths per second, whereas the sustained speed of fed larvae was about 4–5 lengths per second. Ivlev (1961) in his classic work on the feeding ecology of fishes provides an example for freshwater juveniles and fry. Ivlev found that the effect of starvation on the vulnerability of roach fry to pike was strongly size dependent. Starvation of 10 cm roach fry had little effect on the vulnerability to predation by 12–15 cm pike, whereas predation doubled when 29 cm roach fry were starved. Ivlev goes on to say that the relation between starvation and vulnerability was similar in form to the swimming fatigue curve for roach fry (flow rate fish could sustain for 5 minutes), implying that a decrement of swimming ability caused by starvation was equivalent to a decrement in avoidance. An important conclusion that can be drawn from Ivlev's work is that the decrement in avoidance behavior caused by starvation is probably important only when the difference in size between predator and prey is not great.

Larval Size and Time of Day

Catch data from plankton nets illustrate that avoidance capabilities appear to increase exponentially with larval length. Murphy and Clutter (1972) compared the daytime catch of tropical anchovy, *Stolephorus*, taken in one-meter plankton nets with that taken at about the same time in a plankton purse seine. The ratio, purse seine catch to one-meter net catch, increased markedly with larval length after anchovy attained a length of about 5 mm (Fig. 10). The ratio of night catches in plankton nets to day catches follows a similar exponential trend with length in several other clupeoid fishes. That Murphy and Clutter's data for daytime avoidance are about the same as the day/night ratios for plankton net catches of clupeoids indicates that the apparent exponential form of the relation is not entirely the result of improvement in nocturnal vision. Recent work by Paul Webb (unpublished data, University of Michigan, Ann Arbor, Michigan) indicates that maximum speed of burst-swimming in anchovy larvae increases at a rate proportional to larval length times 20 and the duration of such bursts by length times 4. An explanation for the exponential increase in avoidance capabilities with length in clupeoid larvae is that avoidance is a function of both absolute speed and the duration that larvae are able to sustain that speed, as both factors increase with length; when combined they might yield an exponential relation.

In the more robust, fast-swimming larvae, such as jack mackerel and Pacific mackerel, day/night differences in catch are barely detectable. These larvae are able to escape almost as well by night as by day. The rapid decline of the catch curve of jack mackerel larval length in comparison with clupeoid larvae suggests that these more robust and fast-swimming larvae have a much greater avoidance ability (Lenarz, 1973). Few jack mackerel or Pacific mackerel larger than 7–8 mm are taken in routine oblique plankton tows (P. Smith, unpublished data, NMFS, Southwest Fisheries Center, La Jolla, Ca.).

Clupeoid larvae, as well as other species, do not develop a functional scotopic visual system until late in larval life (Blaxter, 1968a, 1968b; O'Connell, 1981); hence they would be more vulnerable to predators at night than in the day, as the day/night ratio of catch indicates. Murphy and Clutter (1972) also show that anchovy larvae avoid nets at night; however, detection of the net and perhaps predators at night, may be dependent on lateral line sense, because the lateral line is functional at hatching in anchovy (O'Connell, 1981). Vulnerability at night may also increase if larvae enter a less responsive state. Adult fishes have been shown to be less responsive to olfactory alarm stimuli at night than in the day (Thines and Vandenbussche, 1966). Anchovy fill their swimbladder at the water surface at night and remain relatively inactive, supported by the distended swimbladder until dawn (Hunter and Sanchez, 1976). Larval *Blennius pholis* survival was lower when maintained under continuous light than when given a daily light cycle (Qasim, 1959). These studies indicate existence of a diel rhythm in activity, and thus larvae might be less reactive to stimuli at night because of a different reactive state, but definitive evidence does not exist.
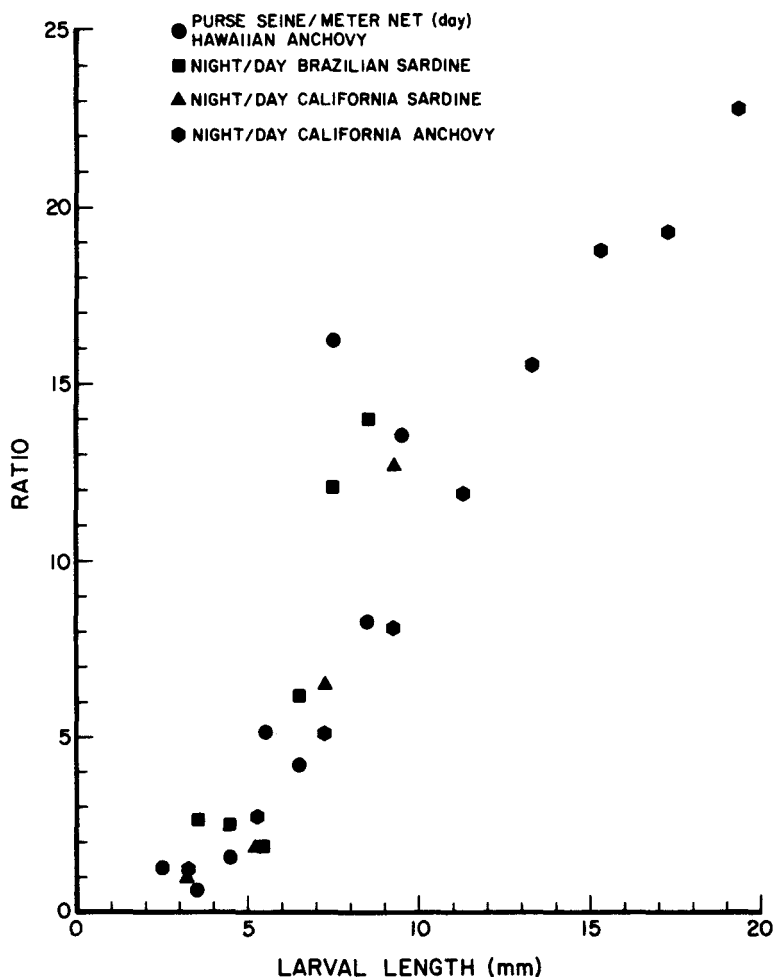
Figure 10. Change in avoidance ability of four species of clupeoid larvae with length. Avoidance ability indicated by the ratio of purse seine to 1-m net catches of the Hawaiian anchovy, *Stolephorus purpureus* (Murphy and Clutter, 1972); and by the ratio of night to day plankton net catches of the Brazilian sardine, *Sardinella brasiliensis* (Matsuura, 1977), California sardine, *Sardinops sagax*; and California anchovy, *Engraulis mordax* (Paul Smith, unpublished data, NMFS, Southwest Fisheries Center, La Jolla.)

State of Maturity

Maturation of sensory and locomotor systems must affect the ability of larvae to avoid predation. Although maturation continues throughout the larval phase, the greatest changes occur during the yolk-sac period. In northern anchovy larvae at hatching, innervation of the Mauthner cells is incomplete, the eye is nonfunctional (O'Connell, 1981), and activity consists of relatively long periods of rest, interrupted by brief periods of vigorous swimming (Hunter, 1972). By the end of the yolk-sac stage, innervation of the

Mauthner cells is complete, and the larva becomes capable of the rapid star-
tle response of most teleosts (Eaton et al., 1977); the eye becomes functional
for daytime vision, and the larva is almost continually active in the day. One
would expect vulnerability to predators to decrease as these developmental
events occur; this seems to be supported by laboratory evidence. The ability
of copepods (Lillelund and Lasker, 1971) and euphausiid shrimp (Theilacker
and Lasker, 1974) to capture yolk-sac larvae in the dark declined markedly
over the yolk-sac period. For example, the feeding success of *Euphausia paci-
fica* declined from 60% for 1–2-day-old yolk-sac larvae to 17% for 3-day-old
larvae and 11% for 4-day-old larvae. Theilacker and Lasker (1974) suggest
that this decline is related to the increase in larval activity, because small
predators such as copepods and euphausiids may be unable to capture mov-
ing prey and it is the long periods of rest that make larvae vulnerable to these
predators.

Types of Predators

Planktonic Invertebrates

Consumption of marine fish larvae by marine copepods, euphausiid
shrimps, hyperiid amphipods, and chaetognaths has been studied in small
containers in the laboratory. Lillelund and Lasker (1971) showed that 11 spe-
cies of calanoid copepods were capable of capturing or fatally injuring yolk-
sac anchovy larvae. The number of yolk-sac anchovy killed by a *Labidocera
jollae* female declined with larval age from 16 newly hatched larvae per day
to about 7 for 168-hour-old larvae, and from about 5 larvae to 1 for *L. trispi-
nosa* females. The median number of yolk-sac anchovy larvae eaten by the
euphausiid shrimp, *Euphausia pacifica*, was 2 per day when the density of
larvae exceeded 1 per 3,500 ml (Theilacker and Lasker, 1974); and at a den-
sity of 50 yolk-sac herring larvae/50 ml, the hyperiid amphipod, *Hyperoche
medusarum*, attacked larvae at a rate of 0.45/hour (Westernhagen and Rosen-
thal, 1976). Two species of chaetognaths, *Sagitta elegans* and *S. setosa*, con-
sumed on the average 1.5 fish larvae after a 48-hour starvation period, but
larvae were not taken in significant numbers if the chaetognaths were not
starved at least 24 hours (Kuhlman, 1977).

In *Sagitta* (Kuhlman, 1977) and *Labidocera* (Lillelund and Lasker,
1971), the number of larvae eaten or attacked was found to be independent
of larval density as long as the density exceeded a certain minimum; on the
other hand, in *Hyperoche* (Westernhagen and Rosenthal, 1976) and *Euphau-
sia* (Theilacker and Lasker, 1974), the number of larvae attacked increased
initially with larval density, then became asymptotic with density, the type
two predator response of Holling (1966).

Probably only yolk-sac larvae are vulnerable to attacks of *Labidocera*,
Euphausia, and *Hyperoche*, because older larvae easily avoided attack even in
the small containers used in these studies. The two species of *Sagitta* are re-

stricted to an even smaller size range because yolk-sac larvae were not attractive, presumably because of their lack of movement (Feigenbaum and Reeve, 1977), and larvae older than 4 days easily escaped. These small predacious invertebrates feed, of course, on foods other than fish larvae; the number of anchovy eaten by *Labidocera* declined in proportion to the density of the alternate food (*Artemia* nauplii), and *Sagitta* showed a strong preference for copepods when both copepods and larvae were offered (Kuhlman, 1977). *Hyperoche*, however, showed a strong preference for herring yolk-sac larvae over flatfish larvae.

It seems unlikely that *Sagitta setosa* and *S. elegans* have a significant impact on larval fish populations. In addition, Cushing and Harris (1973) conclude that chaetognaths are present in sufficient numbers to account for a larval mortality of only 1% per day. On the other hand, hyperiid amphipods, *Labidocera*, and *Euphausia* may be significant predators on yolk-sac stages of fish larvae. The first of the year populations of *Hyperoche* co-occur for 40 days with yolk-sac herring larvae, and fish larvae remains are the most abundant item in their gut (Westernhagen, 1976). In addition, Sheader and Evans (1975) report that fish larvae, especially *Clupea* and *Ammodytes*, make up 23.4% of the food of the hyperiid amphipod, *Parathemisto gaudichaudi*, during April and June. Both *Euphausia* and *Labidocera* co-occur with anchovy larvae along the California coast, but no food habit studies exist. Theilacker and Lasker (1974) estimated from the abundance of *Euphausia* and their median feeding rate in the laboratory that *Euphausia* could consume 2,800 anchovy larvae per day per square meter of sea surface, which is more than 40 times the average number of yolk-sac anchovy existent per square meter.

Certainly the potential predation by these small planktonic predators could have a significant effect on survival of early yolk-sac stages, but larger and more agile predators are required for older larval stages. Larger planktonic predators could include some of the larger Chaetognatha, Siphonophorae, Chrondrophorae, Medusae, and Ctenophora. No detailed studies on the impact of these larger invertebrate predators exist, although incidental observations of feeding behavior and food habit studies are available (Lebour, 1922, 1923, 1925; Frazer, 1969; and others).

Alvariño (1980) tabulated the abundance and co-occurrence with northern anchovy larvae of five major groups of large invertebrate predators—Chaetognatha (22 species), Siphnophora (48 species), Medusae (20 species), Ctenophora (4 species), and Chondrophorae (1 species)—taken in over 2,000 routine ichthyoplankton tows off the California coast in 1954, 1956, and 1958. In general, the abundance of all species combined showed an inverse relation to the abundance of anchovy larvae; that is, these potential predators were the most abundant in tows when anchovy larvae were not taken or were less abundant than average. To pursue this analysis further, she selected among the species those she felt to have the highest potential as larval predators because of their size, abundance, and feeding habits. These planktonic

Table 4. Most abundant large planktonic invertebrate predators taken in standard oblique plankton hauls along the California coast in 1954, 1956, and 1958 and their occurrence with larval anchovy (from Alvariño, 1980).

Abundance of anchovy larvae:	1954 High[a]		1954 Zero		1956 High[a]		1956 Zero		1958 High[a]		1958 Zero	
Species abundance:	Frequency (%)[b]	Mean number[c]	Frequency (%)[b]	Mean number[c]	Frequency (%)[b]	Mean number[c]	Frequency (%)[b]	Mean number[c]	Frequency (%)[b]	Mean number[c]	Frequency (%)[b]	Mean number[c]
Chaetognatha												
Sagitta enflata	56	491.3	73	1093.7	43	191.8	47	121.6	74	271.6	82	308.4
S. hexaptera	22	5.5	55	16.1	27	1.8	53	62.0	26	15.5	52	42.2
S. scrippsae	33	48.1	52	19.2	20	3.2	33	17.4	16	6.5	27	9.9
Siphonophorae												
Stephanomia bijuga	7	0.2	27	0.8	13	1.2	22	2.0	11	0.2	27	1.8
Chelophyes appendiculata	33	10.0	76	89.3	17	5.0	47	7.6	32	2.6	67	46.2
Diphyes dispar	22	14.7	48	44.1	0	0	0	0	0	0	3	0.4
Medusae												
Liriope tetraphylla	22	20.9	64	253.6	37	96.5	42	41.8	21	6.8	58	89.4
Rhopalonema velatum	7	0.6	46	30.3	7	0.3	28	4.1	5	0.3	33	18.2
Aglaura hemistoma	0	0	12	40.2	0	0	3	1.1	5	0.2	18	51.7

[a] Greater than the average number of anchovy per positive haul (241 anchovy larvae per 10 square meters of sea surface).
[b] Percent of stations in which species occurred.
[c] Average number of individuals taken in positive stations.

predators occurred much less frequently and at lower abundances where anchovy were abundant and usually occurred most commonly where no anchovy larvae were taken (Table 4). The dominant constituents in collections where anchovy were abundant were copepods and euphausiids, whereas collections without anchovy were dominated by jelly-like plankters, salps, doliolids, and pyrosomes. Thus, anchovy spawn most intensely in areas where large planktonic predators capable of feeding on post yolk-sac larvae were rare and where foods for the adults and larvae were abundant (copepods and euphausiids).

In sum, planktonic invertebrate predators do not appear to be an important source of mortality for anchovy larvae other than during the yolk-sac stage. These predators may have an important effect on other fish larvae, however, but no adequate documentation exists. Squid, *Loligo opalescens*, might be an important predator of anchovy larvae; they co-occur with anchovy (Cailliet et al., 1979) and feed upon them, but *Euphausia* is their principal food (Karpov and Cailliet, 1978).

Fishes

Perhaps the most important group of predators of marine fish eggs and larvae are schooling pelagic juvenile and adult fishes. Analysis of stomach contents of such fishes usually indicates they do indeed eat larval fishes and eggs. It would be a formidable task to review this large literature, but I will cite a few examples for clupeoid fishes, the most important group of larval and egg predators because of their abundance, schooling behavior, and planktonic feeding habits.

Larval sand eel, *Ammodytes* (ca. 33 mm), comprise about 10% of the total food items eaten by North Sea herring in the Shields area from 1930 to 1934 (Savage, 1937) and about 42% of the food organisms eaten by herring from the southern North Sea and Tyne area (Hardy, 1924). Both authors cited found a variety of other fish eggs and larvae in herring stomachs as well, but at lower abundances. More recently, Pommeranz (in press) observed that at one station 54% of the wet weight of the stomach contents of herring and 45% of that of spratt (*Sprattus sprattus* L.) were composed of fish eggs and larvae. Average values for eggs in herring stomachs ranged from 0.03% to 51.1% (on the average, about 4 eggs per stomach) and the proportion of fish larvae from 0% to 3%. Harding et al. (1978) found that stomachs of herring taken in egg patches in the North Sea contained about 3% fish eggs and 62% fish larvae.

Feeding of the scombrid (*Rastrelliger kanagurta*) on the eggs of the labrid (*Thallusoma*) has been actively observed by Colin (1976). *Thallosoma* engaged in mass spawning which involved an upward rush and visible release of eggs and sperm; about five *Rastrelliger* converged on the site and began filter feeding on the eggs while swimming in tight circles.

My observations of the feeding behavior of northern anchovy are nearly identical to those of Colin (1976); when anchovy eggs were added to a tank,

the school swam over the area and began filtering intensively while swimming in an elliptical orbit through the egg patch. Many reports exist for anchovy feeding on eggs and larvae of marine fishes including their own. In southern California, the most abundant pelagic planktivorous fish is the anchovy, hence they may be one of the major predators of fish eggs and larvae in the open sea. In a recent study (Hunter and Kimbrell, 1980b), stomach contents of anchovy taken during a peak spawning month contained on the average 5.1 anchovy eggs per fish. They used these data to calculate a daily ration of eggs of 86 eggs per fish and estimated that this represented about 17% of the eggs spawned per night, or about 32% of the daily mortality of eggs. They point out that the number of anchovy eggs in stomachs increased exponentially with the density of eggs in the sea, indicating that patchiness of eggs and selectivity of filtering by the schools probably play a major role in egg consumption. Very few larvae of any species occurred in the stomachs, but Hunter and Kimbrell's laboratory observations indicate that the smallest and most abundant anchovy larvae (3–5 mm SL) are digested beyond recognition in less than half an hour, whereas eggs are more resistant to digestion. Although no evidence exists, I believe that the younger larval stages are as vulnerable as eggs. Larvae probably remain highly vulnerable to schooling planktivorous fishes until avoidance abilities develop sufficiently. Yolk-sac larvae are readily eaten in the laboratory by anchovy, and their low incidence in field-caught specimens is probably the result of the rapid digestion rate and the decline in patchiness and abundance.

Conclusions

An understanding of the causes of larval mortality demands a thorough understanding of early life history traits. Traits discussed in these lectures include parental factors of time and place of spawning, pattern of spawn distribution, egg size and yolk reserves and such larval characters as feeding behavior, prey selection patterns, swimming and searching behavior, metabolism, growth rate, and time to the onset of schooling. These traits are interrelated and consequently form distinct life history strategies.

Food size preferences may be one of the better traits for identifying life history strategies. For example, to feed on a large prey requires a large mouth and a greater and more efficient effort because of the exponential decline in food density with food size. Persistence in attack and maneuverability would appear to be essential for a large prey strategy. Greater searching effort may require a faster swimming speed, and this in turn implies less vulnerability to predation and higher metabolic rate and energy requirements. The latter promotes faster growth (Kerr, 1971a, 1971b), and faster growth reduces the duration of the larval stage, the period of greatest vulnerability to predation, and the time to the onset of schooling. Mackerel and tunas appear to have adopted this large prey-fast growth strategy, whereas anchovy follow a small

prey strategy. The sparid *Archosargus rhomboidalis*, which seems to fit in many respects the large prey feeding strategy, is affected much more by laboratory stocking density and is better able to take advantage of short-term patchiness of food than is the engraulid fish *Anchoa mitchilli* (Houde and Schekter, 1978). These tendencies are in keeping with the difference in searching power and efficiency of feeding implicit in large and small prey feeding strategies.

At high spawn densities, suppression of intraspecific effects on growth would be adaptive as well as suppression of sibling cannibalism. Species with slow cruising speeds, such as anchovy, might require higher initial larval densities to assure the socialization necessary for the onset of schooling or to form schools of viable size. Mackerel and tunas, on the other hand, are prone to sibling cannibalism and may not be affected by low spawning densities because the time to school formation is less, because growth is rapid and cruising speeds are higher, thus permitting more rapid formation of schools. Many other possible strategies exist other than those discussed for anchovy and scombroids. Species that hatch from large eggs in a relatively large and mature stage—flying fish, herring larvae, and saury, for example—have distinctly different life strategies.

My emphasis in these lectures on feeding ecology was on specific differences and how they form distinct life history strategies in the larval phase. The apparent similarities in feeding habits among pelagic larvae are striking nonetheless. Nearly all pelagic larvae are diurnal particulate planktivores, specializing in the young stages of copepods, whereas the feeding habits of the adults are much more diverse. Pelagic fish larvae are the most similar in the early stages of development, and distinctions become marked as development proceeds and larvae approach metamorphosis.

The literature I have reviewed on feeding ecology and on predation in larval fishes indicates that the smallest life stages are without doubt the most vulnerable to starvation and predation. Low feeding success, low resistance to starvation, and slow absolute swimming speeds all indicate that larvae are more vulnerable to starvation at the time of first feeding than at any other time. Similarly, the ability to avoid predation is dependent on burst speeds, the ability to sustain that speed, and the developmental state of sensory and locomotor systems. All of these improve rapidly with larval size or age. In addition, the number of potential predators may decrease with an increase in larval size; the highest number may occur during the yolk-sac period when larvae may be eaten by small planktonic invertebrates as well as by larger invertebrates and fishes.

Although the high early mortality of marine larvae is documented (May, 1974; Jones and Hall, 1974; Vladimirov, 1975), no conclusive evidence exists that variation in the rates of early mortality determines the strength of incoming year classes. This idea, Hjort's critical period concept (Hjort, 1914; May, 1974; Vladimirov, 1975), has long been postulated as a mechanism for variation in year class strength. It now appears, at least for the northern an-

chovy, that except for a few extreme cases it is not possible to detect changes in recruitment potential from the abundances of embryonic or postembryonic larvae up to 15 mm in length (Zweifel and Smith, in press). Thus identification of mechanisms regulating recruitment will probably require study of the entire larval and juvenile stages.

A recurrent theme in these lectures has been the role of patchiness in the early life history of fishes. Patchiness affects food availability which in turn may produce patchiness in larval survival and growth. Although direct links between food patches and survival have not been documented, the circumstantial evidence is strong. Larval food exists in patches (Lasker, 1975), and small-scale patchiness in growth and starvation exists (Methot and Kramer, 1979; O'Connell, 1981). Patchiness may also affect vulnerability to planktivorous predators, the onset of schooling behavior, and sibling cannibalism.

If patchiness controls larval survival, variation in recruitment ultimately may be the result of the summation of events occurring in a multitude of egg and larval patches. Although this increases the complexity of the problem, techniques now exist to study it. It is now possible to make reliable instantaneous estimates of the incidence of starvation (O'Connell, 1976, 1981; Theilacker, 1978) and of larval growth (Buckley, 1980; Methot, in press). Such estimates need to be related to the condition of the plankton community from which they were taken. Measures of community condition, such as standing crop of microcopepods, indices of naupliar production rate, primary production, oxygen, and nutrients, and other biotic and abiotic characteristics need to be related to instantaneous growth rates and starvation from the same patch. Such a dynamic description of the local community or patch condition could then be used to calibrate oceanic events in terms of larval growth and survival. In addition, these sets of dynamic descriptions and their larval correlates would provide the necessary data for a dynamic model of larval mortality.

Most of the work on the ecology of marine fish larvae has been laboratory studies on behavior and feeding ecology of the larvae produced by major offshore fish stocks. Little work has been done on the early life history of tropical reef fishes and many other inshore forms. Predation has received little attention in all species. Field studies on natural causes of mortality and variation of growth are just beginning, but the tools now exist for such work. If we are to identify the causes of natural mortality in the sea, the incidence of starvation and predation must be estimated over the spawning range of the species and at all life stages, and these losses compared with estimated rates of mortality. The vertical position of larvae in the sea in relation to their foods, predators, and time of day also needs to be considered in such an analysis.

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