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The Feeding Behavior and Ecology of Marine Fish Larvae

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HUNTER, JOHN R. 1980. The feeding behavior and ecology of marine fish larvae, p. 287-330. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

The behavioral-ecological traits of pelagic marine fish larvae diagnostic of specific ecological roles are discussed. Topics considered include: parental effects (egg size, yolk quantity, spawn distribution); swimming behavior; feeding and searching behavior; prey size relationships; and abundance and distribution of prey. Pertinent literature is reviewed and unpublished data on the larvae of northern anchovy, *Engraulis mordax,* and Pacific mackerel, *Scomber japonicus,* are presented. These two species are used as examples of two distinctly different ecological roles exhibited by marine fish larvae.

Introduction

Natural fluctuations in the size of fish populations are caused primarily by annual variability in the strength of incoming year classes. These may vary from about 0.3 to 2.0 orders of magnitude and this variability often has no obvious relation to size of parent stock (Cushing 1977).

Lack of understanding of the relation between stock and recruitment has hindered effective management of marine fish stocks. The loss in production from collapse of fisheries over the years has been huge. Murphy (1977) estimated a loss in production of clupeoid fishes of 600 million tons not including recent declines in Peruvian anchovy production. Many of these declines in production may be attributable in part to overfishing due to the failure of existing models to provide adequate management guidance owing to lack of understanding of recruitment. Many experts believe that studies of mortality in early life history stages, particularly that of eggs and larvae, hold the key to understanding the stock and recruitment relation (Hunter 1976a). Principal sources of larval mortality are generally believed to be starvation and predation. Thus, studies of behavior and ecology of larval stages in relation to these sources of mortality and stock size may provide much of the needed information. Aquaculture of marine fishes also depends upon adequate knowledge of the behavior of early life stages, for it is these stages that produce greatest technical difficulty in culture and highest labor costs. The objective of my report is to discuss behavioral-ecological traits of pelagic marine fish larvae that are diagnostic of specific ecological roles, and to consider such roles in relation to causes of mortality.

Parental Effects

EGG SIZE-YOLK QUANTITY-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 mm of 40 species of marine and freshwater larvae at onset of feeding was related to egg diameter in mm 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.

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/or 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 and in grunion larvae starvation is reversible after 16 days (May 1971; Table 1). 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 and Hunter and Kimbrell MS). These differences reflect in part differences in activity; plaice are less active than herring at this time (Blaxter and Ehrlich 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).

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

		Size at hatch		yolk absorption	Days to point of no return[a] relative to:			
Species	Temp. °C	Length mm	Dry weight mg	Period (days)	Hatch	Yolk absorp-tion	Onset of feeding	Authors
Grunion *Leuresthes tenuis*	20	9.0	362	4	12+[b]	8+[b]	12+[b]	May (1971)
Clyde herring *(Clupea harengus*	7-8	8.2	189	8	25	6	22	Blaxter and Hempel (1963); Blaxter and Ehrlich (1974)
Haddock *Melanogrammus aeglefinus*	7	3.5	—	6-7	6	0-1	—	Laurence (1974); Laurence and Rogers (1976)
Pacific mackerel *Scomber japonicus*	19	3.1	40	3	4.0	1.0	1.6	Hunter and Kimbrell (MS)
Northern anchovy *Engraulis mordax*	16.5	2.9	21	4	7.7	1.5	2.5	Lasker et al. (1970); Hunter (unpubl. data)
Bay anchovy *Anchoa mitchilli*	24	2.5	18	1.7	3.1	1:4	1.7	Houde (1974)
Sea bream *Archosargus rhomboidalis*	22	2.3	28	2.2	3.4	1.2	1.7	
Lined sole *Archirus lineatus*	24	1.9	22	3.3	3.8	0.5	1.3	

[a] Time of irreversible starvation (Blaxter and Hempel 1963).

[b] 50% mortality from starvation, not a point of no return, because all survivors able to survive if fed.

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)* at the water temperature for peak spawning, and egg diameter *(D)* 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 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 the 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). Thermal optima in efficiency of yolk utilization is another way larvae may adapt to specific environmental conditions. Sea bream larvae retain more yolk at the onset of feeding at 26°C than at other temperatures and thus have more yolk to sustain them if food is not present (Houde 1974). Plaice larvae have a sharply defined thermal optimum in yolk utilization efficiency between 6.5-8°C, which could produce 10% larger larvae at the time of first feeding (Ryland and Nichols 1967).

SPAWNING TACTICS

Eggs of pelagic spawners are often distributed in extremely patchy patterns; 37% of Pacific sardine eggs taken in the years 1951-1959 occurred in only 0.6% of the samples (Smith 1973). Helfrich and Allen (1975) found the density of mullet eggs *Crenimugil crenilabis* to be 17/L at the surface after about 1-2 sec of intensive spawning. A high density of northern anchovy eggs taken in a neuston net was 31/L, corresponding to a density of 46,000 eggs/10 m^2 of sea surface, which is in the upper 5% of all samples of anchovy eggs collected with nylon nets (unpublished data, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA). Other high egg densities include 31,000 eggs/10 m^2 for Pacific sardine (Smith 1973) and 9,000 eggs/10 m^2 for Atlantic mackerel (Sette 1943). The eggs in such patches gradually disperse; dispersion is more rapid at the perimeter of the patch resulting in a denser centrum surrounded by a less concentrated corona. The horizontal mean distance between neighboring eggs increases in a patch from 1-2 cm at spawning to 15-20 cm in most several-day-old sardine eggs (Smith 1973). In the northern anchovy, dispersion of larvae as measured by the negative binomial *K* (Lloyd 1967) continues from hatching until the larvae reach about 10 mm, at which time they reach their most dispersed state and contagion increases thereafter (J. Zweifel, unpublished data, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA). This change from decreasing to increasing contagion coincides with the time anchovies begin nightly migrations to the sea surface to fill their swim bladders (Hunter and Sanchez 1976) and is close to the onset of schooling which begins at about 12 mm by concentrating larvae near the surface at night and thus increasing the frequency of social contacts.

Dispersion of larvae could progress to the point where it might influence onset of schooling or delay formation of schools of viable size. *Menidia* larvae reared in isolation took more time to form a school when brought together than socially reared larvae and the length of the delay was proportional to the period of isolation (Shaw 1961). Breder and Halpern (1946) showed that *Brachydanio rerio* larvae reared from the egg in isolation had considerable hesitancy to join a school. Thus, onset of schooling could be retarded if larvae are dispersed to the point where social contacts are infrequent.

Intraspecific competition and cannibalism also may be affected by initial spawn density and dispersion rates. Houde (1975) found that growth and survival of sea bream larvae decreased rapidly when stocking density exceeded 8 eggs/L at food levels of 1500-3000 microcopepods per liter. Food concentrations of 100/L did not sustain sea bream larvae except at 2 eggs/L stock densities. 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 prone to cannibalism and competition 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

The cruising speed of larvae is 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 may differ somewhat from adults due, in part, to the lack of mechanical support of the caudal fin. Tail beat amplitude and tail beat frequency are continuously modulated in northern anchovy larvae (Hunter 1972) and Pacific mackerel larvae (Hunter and Kimbrell, MS), whereas in adult fishes amplitude is modulated less frequently, except during accelerations (Hunter and Zweifel 1971). Tail beat frequency is inversely proportional to length in fishes (Bainbridge 1958; Hunter and Zweifel 1971), and consequently, the frequency in early larval stages can be quite high, reaching 50 beats/sec in 4- to 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 15-mm larva; Vlymen 1974).

Temperature can have a major effect on activity or cruising speed. Two effects of temperature on activity are illustrated for the northern anchovy reared to age 12 days at various temperatures on a diet of *Gymnodinium splendens* (Fig. 1). Temperature affected the timing of the transition from the 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 and the speed-temperature relation was a function of developmental rate. At ages 8-12 days, all larvae were past this transition and 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 wk later; in pilchard *(Sardina pilchardus)* speed increased from 10 to 30 cm/min in 3 wk; in plaice from 10 to 60 cm/min over 7 wk; and in sole *(Solea solea),* from 5 to 40 cm/min over 7 wk. 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.

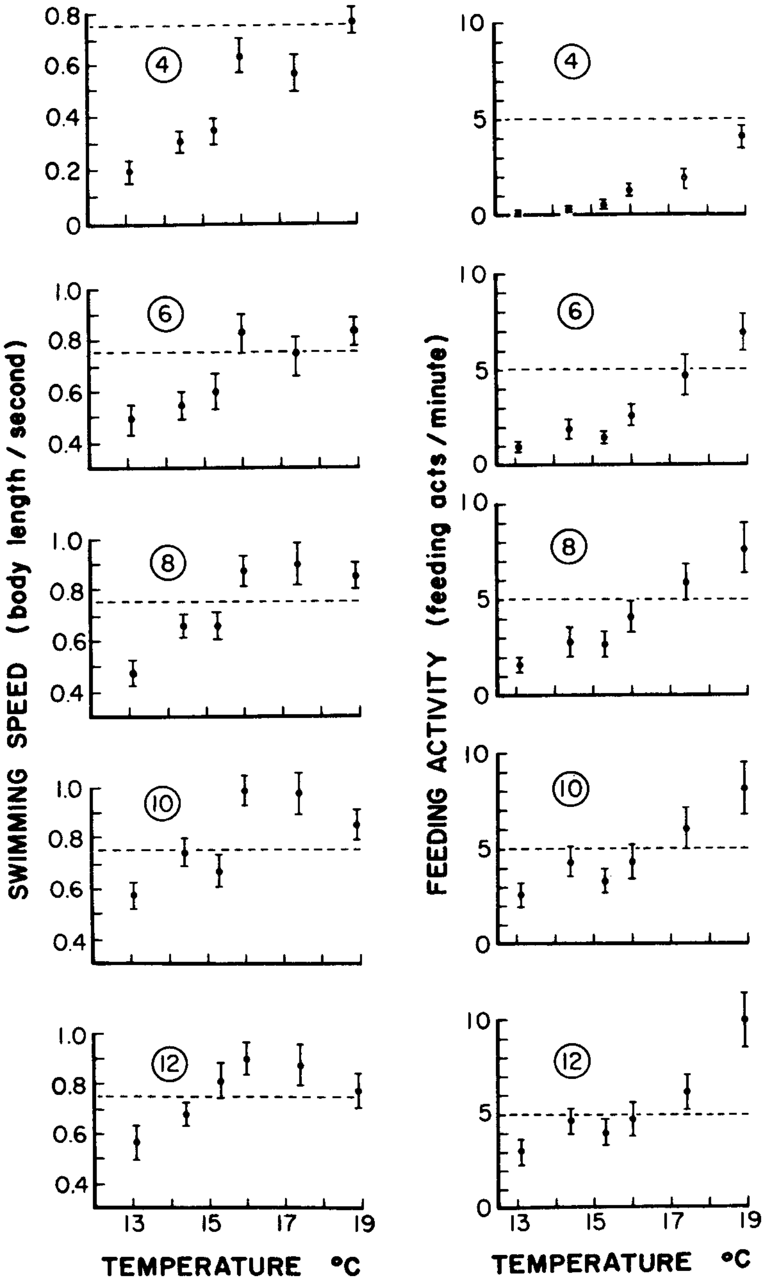

Fig. 1: Effect of temperature on swimming speed and feeding rate of northern anchovy fed *Gymnodinium splendens* (mean density 400 cells mL). Points are means, bars are 2x standard error of mean, panel numbers are larval age in days, and dashed line is a visual reference. Data based on direct visual observation of larvae for 5-mm intervals. Each point is average value for 15 fish in two or more rearing groups.

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 0_2. mg dry wt^{-1} h^{-1}whereas mackerel consume 6.1 μL 0_2 . mg dry wt^{-1} h^{-1} (Hunter 1972 and Hunter and Kimbrell MS). 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 the 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; C.O'Connell, pers. comm., National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA). 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 among these values between species. 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.

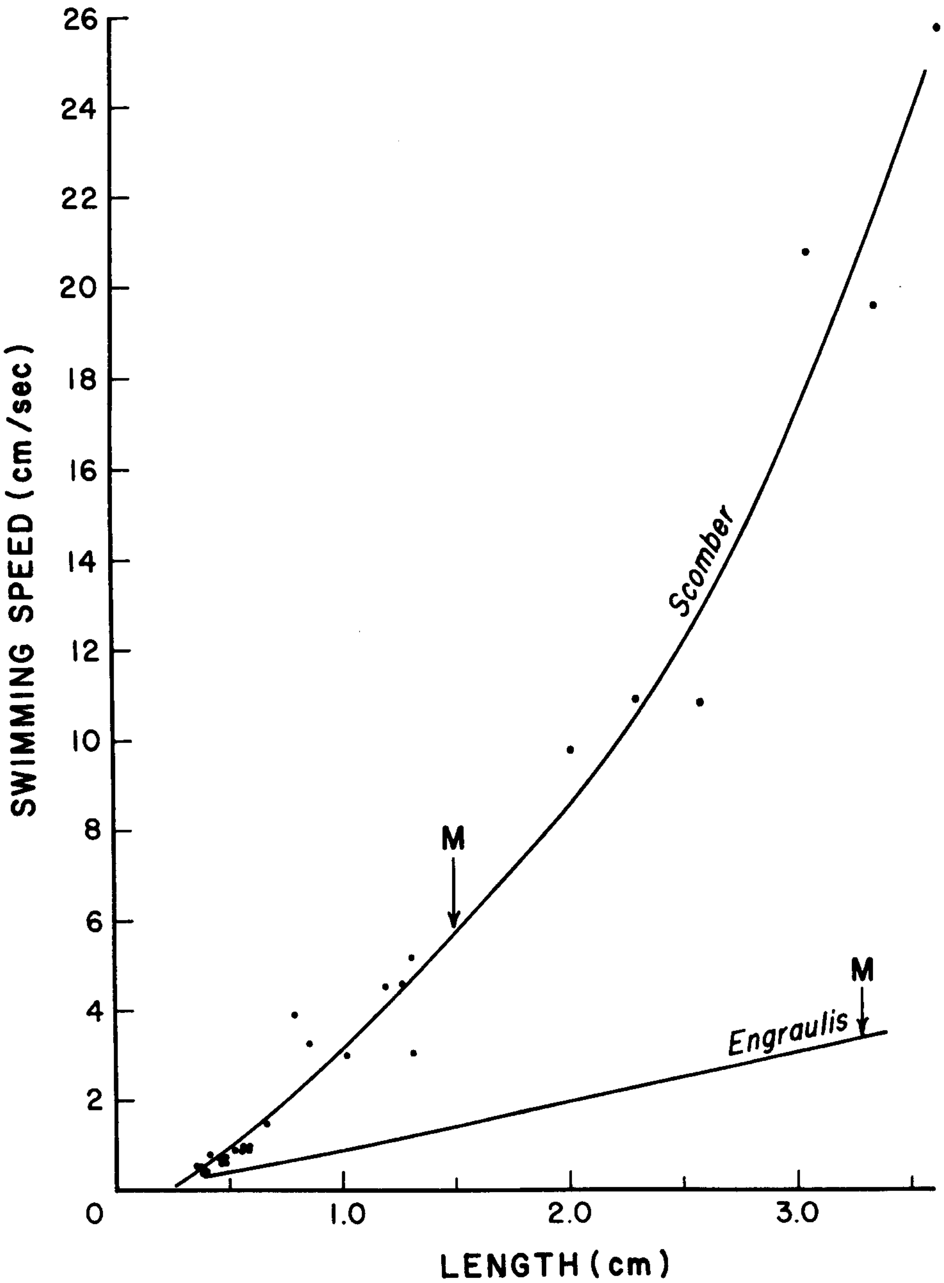

FIG. 2. Swimming speed of Pacific mackerel, *Scomber japonicus*, larvae and juveniles at 19°C; points are means for five or more observations; curve fit by eye; and swimming speed of northern anchovy larvae, *Engraulis mordax*, at 17-18°C from Hunter (1972). Speeds are total distance covered, including time spent in rest and feeding, and M indicates fish length at metamorphosis.

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 northern 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 they are 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* occurred 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 in the plankton. It would be of considerable interest to study such characteristics under controlled laboratory conditions, both from the standpoint of larval feeding ecology and copepod evolution.

MOTOR PATTERNS

Upon sighting a prey clupeoid larvae assume a sinuous posture and advance 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 causing the body to drive forward, and the prey is engulfed (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 assume a sinuous feeding posture but the behavior has been studied in detail only for clupeoids and for freshwater coregonid larvae *Coregonus wartmanni* (Braum 1964), and quite possibly differences exist among species.

Pacific mackerel larvae *Scomber japonicus* feed in a manner more typical of the biting attack of many adult fishes. Upon sighting a prey, mackerel larvae advance toward the prey, stop, draw back the tail, and hold it in a slightly recurved, high amplitude position. 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 assume and reassume the S-posture while maintaining their orientation to a moving prey; but my observations indicate that once the strike is made, 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 previous strike was unsuccessful. Mackerel larvae often reposition for the second strike by moving backward; anchovies 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.

The time spent poised in a striking posture is much longer at the time of first feeding than in later larval life, and gradually the strike becomes integrated with swimming movements. In the anchovy, duration of complete feeding acts declined from 1.5-2.0 sec to about 0.6 sec when larvae reached 17 mm and relative speed of the strike also declined (Hunter 1972). A poised striking posture seems to be a common tendency in young larvae and declines as the larva grows and could be an adaptation to low feeding success, and perhaps to a necessity to feed by engulfing prey that are relatively large for their mouth.

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 sufficient numbers 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 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

1964), and 10% for northern anchovy (Hunter 1972). Feeding success gradually increases, reaching 90% in about 3 wk in the anchovy (Hunter 1972), and in about 7 wk 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 increased from 0.1 to 2.4 L/h over 8 wk, whereas Rosenthal and Hempel (1970) estimated they increased from 1.5 L to about 10 L/h in 10 wk. 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/h, plaice (6-10 mm) search 0.1-1.8 L/h

(Blaxter and Staines 1971) and anchovy (6-10 mm) search 0.1-1.0 L/h (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 non-random. Larval anchovies 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 increased with a decrease in food density. Similar non-random search patterns have been described for adult fishes (Kleerekoper et al. 1970; Beukema 1968).

Prey Types

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 (A. Ahlstrom, pers. comm., National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA) 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* became 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 MS).

Larvae tend to be more euryphagous during the earliest stages and organisms such as tintinnids, phytoplankton, mollusk larvae and ciliates are often eaten as well as copepods (Arthur 1976; Bowers and Williamson 1951; Lebour 1921; R. 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 anchovies, 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). Anchovies will feed on a variety of dinoflagellates, *Gymnodinium, Gonyaulax, Prorocentrum* and *Peridinium,* but not small flagellates, *Chlamydomonas, Dunaliella,* nor on 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 was the small size of *Gonyaulax* which made 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 of a greater variety of small organisms of the proper size in the sea. 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, existing in cool water.

Prey Size Relations

SPECIFIC DIFFERENCES

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 are frequently found in the stomachs of larval fishes which were too large to be ingested in any other way (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,* 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 these data is the consistency of trends among related species and groups (Fig. 3). The small clupeoid larvae, *Sardinops, Engraulis,* and *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* shows 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 begin feeding on much larger foods than the rest with only a slow increase in average prey size. De Ciemchomski 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 to 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 more marked under natural conditions because the food size preference of sea bream increased 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 50-80 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 range of first-feeding Pacific sardines, northern anchovies 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 Fig. 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*

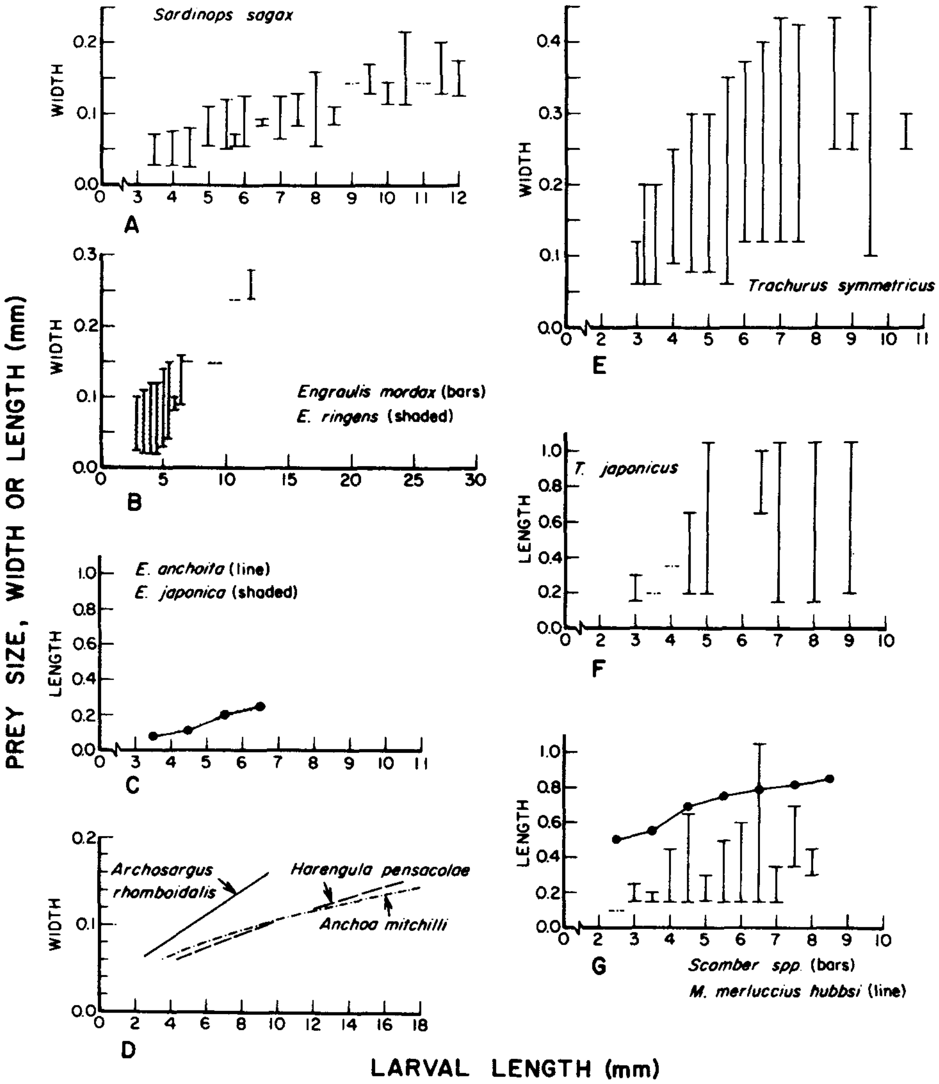

FIG. 3: Relation between prey size and larval length for 12 species of marine fishes; label on ordinate indicates if prey width or prey length were measured; vertical bars and shaded areas represent range of prey sizes; and straight lines connecting dots indicate average prey sizes. Plots were redrawn from Arthur (1976) for *Sardinops sagax, Engraulis mordax* and *Trachurus symmetricus;* from R. de Mendiola (1974) for *Engraulis ringens;* from Detwyler and Houde (1970) for *Harengula pensacolae* and *Anchoa mitchilli;* from Stepien (1976) for *Archosargus rhomboidalis;* from Cieschomski and Weiss (1974) fro *Engraulis anchoita* and *Merluccius merluccius;* and from Yokota et al. (1961) for *Engraulis japonica, Trachurus japonicus* and *Scomber* spp. Data are for sea-caught larvae, except panel D which were laboratory reared.

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 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. 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.

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, correlated them with the size of natural foods and growth rates, and concluded that larvae with smaller mouths grew more slowly than those with larger ones. Blaxter (1965) showed that differences in gape of the mouth existed 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 (MS) 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 h 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, when *Artemia* or anchovy eggs were 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 indication of the size of prey a larva was capable of ingesting. Mouth gape was also measured but width was preferred because it could 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

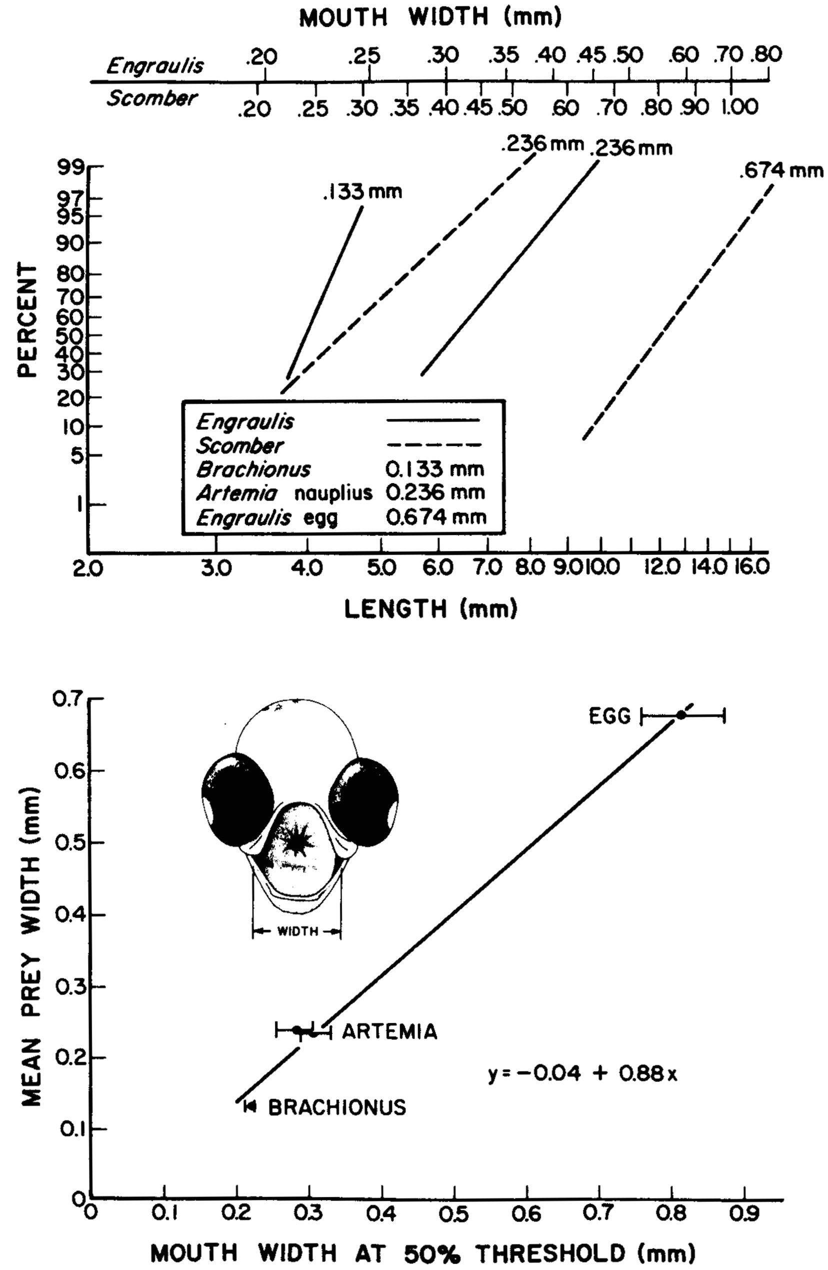

FIG. 4. Relation between width of mouth and ability of *Scomber japonicus* and *Engraulis mordax* to capture prey of various widths. Upper panel, percent of larvae that captured one or more prey shown as a function of mouth width (upper scales) and larval strength (lower scale); lines are for the regression 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.

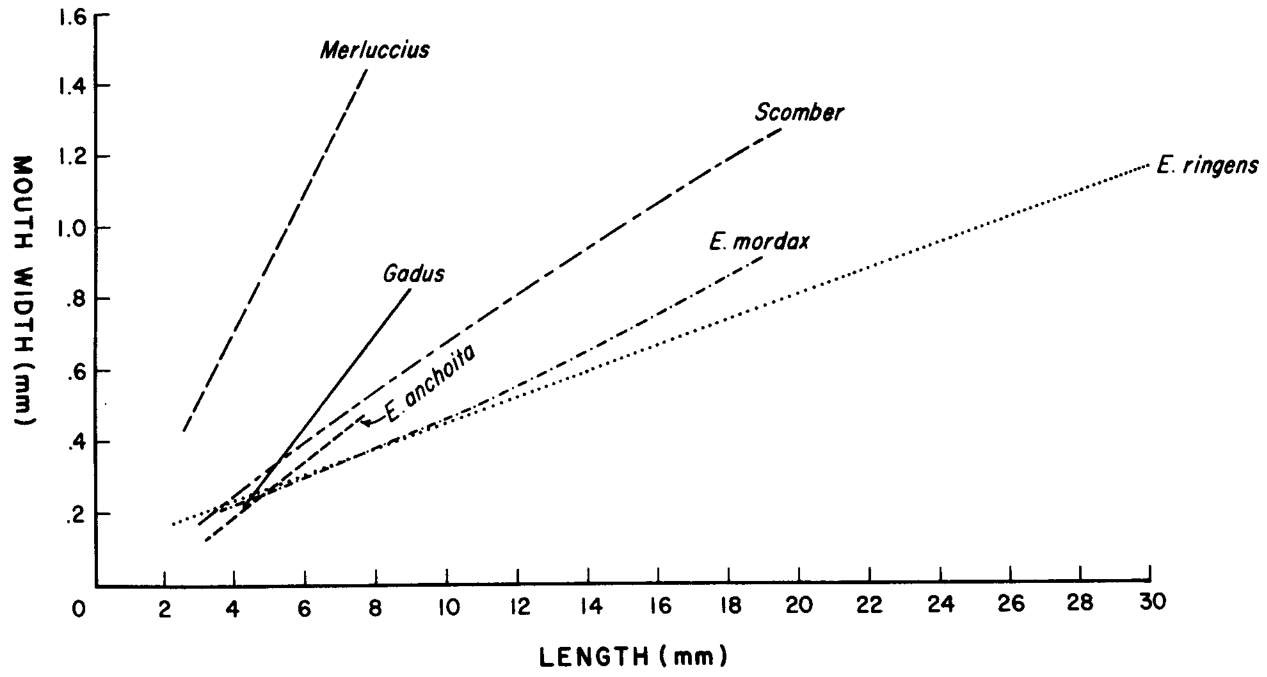

Fig. 5. The relation between mouth width and larval length of hake, *Merluccius merluccius* from de Ciechomski and Weiss (1974); cod, *Gadus morhua* from Wiborg (1948b); Pacific mackerel *(Scomber japonicus)* from Hunter and Kimbrell (MS); and three species of anchovy, *Engraulis anchoita* from de Ciechomski and Weiss (1974). *Engraulis mordax* from Hunter (1977) and *Engraulis ringens* from R. de Mendiola (1974).

gape of the mouth would be expected to be related to handling time in this case (Kislalioglu and Gibson 1976b).

These thresholds are also 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 could 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 width of all species but hake are somewhat similar in the beginning but differences increase greatly with growth. Hake stand 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 8-12 mm occurs at a time anchovies become highly proficient in capturing *Artemia* nauplii and the increase in prey size is to one of that diameter. No 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 of 2.0-2.8. 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 width produces an order of magnitude increase in dry weight. Thus, a larva feeding on copepodites 200 μm wide would have to capture 10 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 about doubles. In *Calanus helgolandicus*, the dry weight of nauplius VI is 2.0 μg and that of copepodite 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

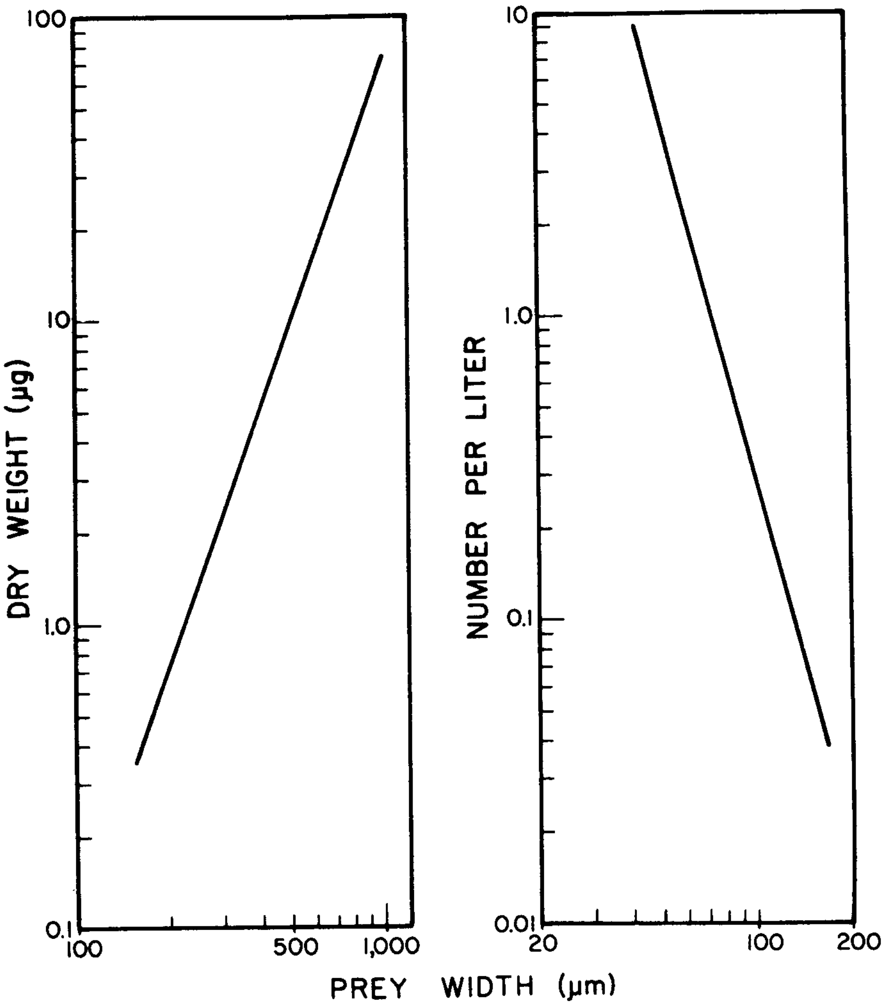

Fig. 6. Left panel, relation between copepod width and dry eight (excluding naupliar stages) calculated from data given by Gruzov and Alekseyeva (1970). Right panel, relation between number of prey per L in the sea and prey width, recalculated from Vlymen (1977).

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 anchovies (Hunter 1977) and Pacific mackerel (Hunter and Kimbrell, MS) fed different foods (Fig. 7). When anchovies 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 days 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, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA) 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-h feeding day, a temperature of 17°C, and the maximum feeding rate observed in the laboratory (about 10 attacks/min). 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 $E_1 + E_2 + E_3 + E_4 = 0.48\ R$ where:

$E_1 = (5.10 \times 10^{-2})\ L^{3.3237}$ (the basal metabolic rate in calories, where L = length (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-h day);
$E_4 = 0.29R$ (the energy cost of mechanically processing food, intestinal propulsion, etc).;
$0.48\ R$ (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 = calories per prey; and S = the 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 $S = 93.2\ \mathrm{Log}_{10}\ T^{-33.3}$ 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).

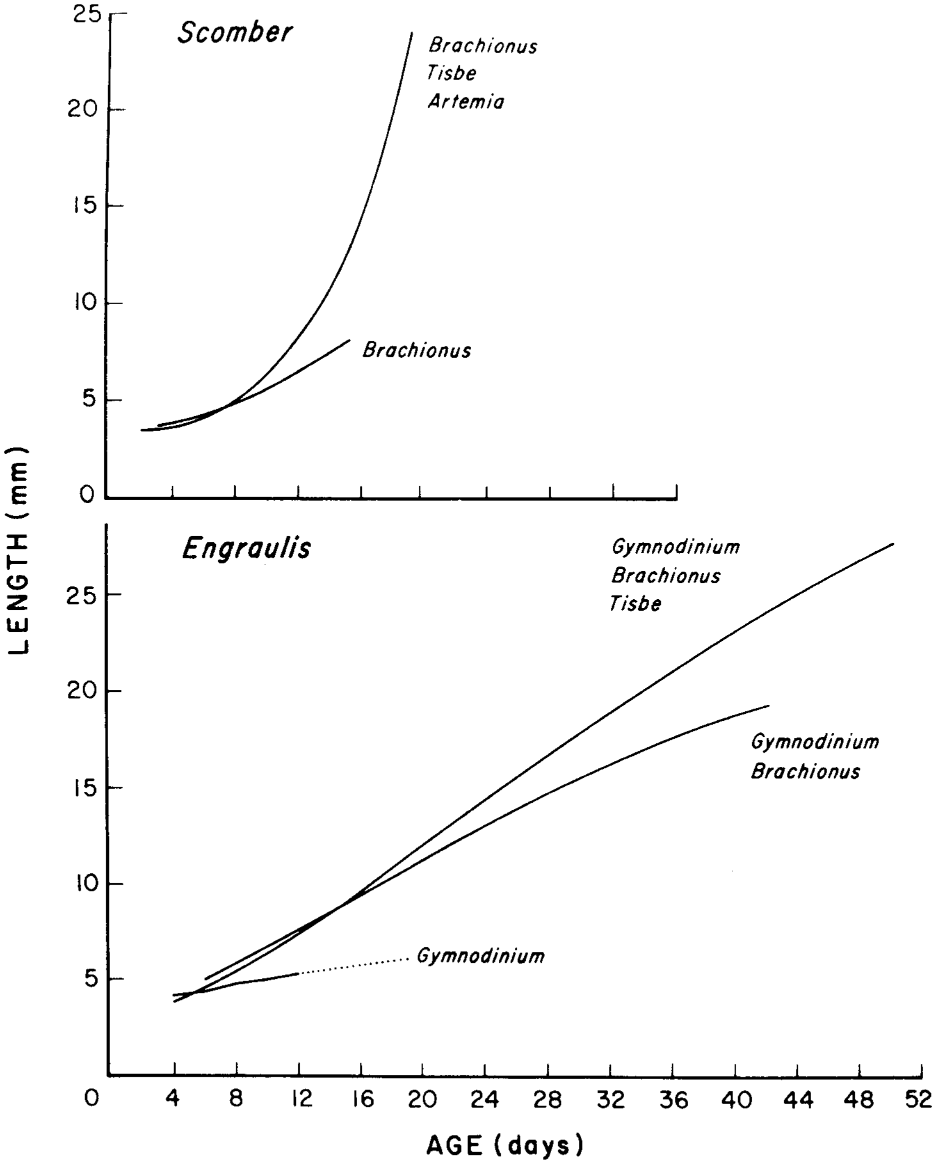

FIG. 7. Laboratory growth rates of *Scomber japonicus* at 22°C fed various foods, from Hunter and Kimbrell (MS), and of *Engraulis mordax* at 16°C, from Hunter (1977). Calorie values of prey were: *Gymnodinium* 0.00005 cal; *Branchionus* 0.0008 cal; and *Artemia* 0.0096 cal (Hunter 1977).

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* (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.

Abundance of Food and Food Density Requirements

The density of particles in the sea declines rapidly with increasing size or diameter of the particle (Sheldon, Prakash and Sutcliffe 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 (Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA) (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 larger 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 prey size changes so 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 and their results have been reviewed by Blaxter (1965), May (1974), and Arthur (1977) and are presented here in tabular form (Table 2). These studies indicate that average density in the open sea ranges between 13-40 nauplii per liter and typically between 1-7 copepodites per liter. 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 post-naupliar stages combined can exceed 200 per liter.

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 a prey density of 1000-4000 microcopepods/L are 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 1000/L (Houde 1973). Much higher densities are required for very small prey such as phytoplankton. Lasker (1975) found that anchovy larvae required 5000-20,000 *Gymnodinium splendens* cells per liter at 19°C and 20,000 or more at 14°C for significant feeding to occur. Standard rearing

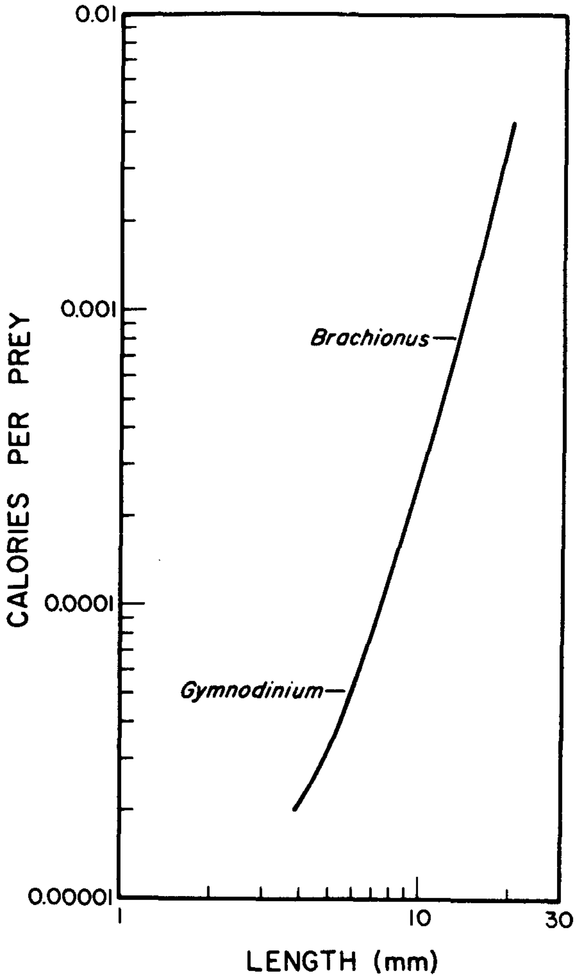

FIG. 8. Relation between minimum caloric value of prey required to meet energy needs of larval northern anchovy at 17°C and larval length. From model developed by Vlymen (1977) and Vlymen (unpublished), see text for explanation. The caloric value of *Gymnodinium* and *Brachionus* is indicated.

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

	Average density of microcopepods (number per liter)			Location	Author
	Nauplii	Copepodites	Total		
Open sea	13	2	15	Southeast Coast of Kyushu	Yokota et al. (1961)
	22	36	58[b]	California Current	Beers and Stewart (1967)
	40	5	45[b]	Southern California near shore	Beers and Stewart (1970)
	27	7	34[c]	Eastern Tropical Pacific	Beers and Stewart (1971)
	36	1	37	California Current	Arthur (1977)
Partly enclosed	76	19	95	Azov Sea	Duka (1969)
	—	—	223[d]	Gulf of Taganrog	Mikhman (1969)

[a] Mean for all stations, and years given in publication listed in table.

[b] Includes all copepods passing 202 μm mesh net.

[c] Includes all copepods passing 202 μm mesh net and caught on 35 μm mesh.

[d] Defined as food of *Clupeonella delicatula;* microcopepods account for over 90% of items eaten (Mikhman 1969).

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		Author
					Density No./L	Percent survival	
Plaice *Pleuronectes platessa*	5	14	*Artemia* nauplii	50 (larvae)	1,000 500 200 100	72[a] 72 54 32	Wyatt (1972)
Northern anchovy *Engraulis mordax*	10.8	12	Wild zooplankton (nauplii)	10 (eggs)	4,000 900 90 9	51 12 0.5 0	O'Connell and Raymond (1970)
Bay anchovy *Anchoa mitchilli*	76	16	Wild zooplankton (nauplii-copepodites)[c]	0.5-2 (eggs)	1,751[b] 75 17	50 10 1	Houde (1977 and in press)
Sea bream *Archosargus rhomboidalis*	76			0.5-2 (eggs)	199[b] 28 11	50 10 1	Houde (1975 and in press)
Lined sole *Archirus lineatus*	38			0.5-2 (eggs)	854[b] 115 44	50 10 1	Houde (1977 and in press)
Haddock *Melanogrammus aeglefinus*	37.8	42	Wild zooplankton (nauplii)	9[d] (larvae)	3,000 1,000 500 100 10	39 22 3 0 0	Laurence (1974)

[a] Survival was 100% at 50/L for first 7 days without a decrement in length; see also Riley (1966).
[b] Estimated food density for indicated survival levels.
[c] Plankton blooms of *Chlorella* sp. and *Anacystis* sp. maintained in rearing tanks.
[d] Estimated by adjusting for hatching success.

practice for northern anchovy requires 100,000 or more *Gymnodinium* cells per liter (Hunter 1976b), whereas 1,000 microcopepods per liter appear to be adequate (O'Connell and Raymond 1970).

Density thresholds determined by Houde (1975; 1977; in press) are markedly lower than those of the others listed in the table and are substantially below those used for routine rearing of larval fishes. He 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 previous 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 such areas. Many problems exist in interpreting such 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.

The disparity between most estimates of food densities required by larvae and average densities in the open sea have 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 provides 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 1-liter samples taken at the surface from an area off the southeast coast of Kyushu over 2 yr. 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 larvae have the ability of remaining 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. Thus, to meet minimum requirements, prey would have to be 1.3 times as "crowded" as they would be 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 to 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 (in press) exposed sea bream to simulated patch conditions in the laboratory by increasing the concentration of microcopepods to 500/L for periods of 2-13 h per day from a background density of 25-50/L. They found that survival at 10 days after hatching of larvae exposed to only 3 h 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.

Ecological Roles

In this section, I define two ecological roles based on the traits discussed in the preceeding sections. These roles, Engrauliform and Scombriform (Table 4), were selected because of their contrasting traits, by firsthand knowledge of the behavior of *Engraulis mordax* and *Scomber japonicus*, and because in the beginning they are of similar size and have similar yolk reserves. To fill in gaps of knowledge, I have used results for other species which I believe fall within these two ecological categories.

TABLE 4. Two contrasting ecological roles for marine fish larvae based on behavioral and physiological traits.

Trait	Relative differences	
	Engrauliform	Scombriform
Spawn		
Contagion of spawn	High	Lower (?)
Food		
Mouth size	Small	Large
Range of food size	Small	Large
Abundance of foods eaten	Higher	Lower
Calories obtained per attack	Lower Higher	Higher
Feeding behavior		
Feeding posture	Sinuous	Rigid
Persistence of attack	Infrequent	Frequent
Feeding capacity	Low	High
Ability to exploit short-term food patch	Low	High
Maneuverability	Low	High
Locomotion and metabolism		
Cruising speed	Slow	Fast
Metabolic rate	Lower	Higher
Social interactions (laboratory)		
Effect of larval density on growth	Low	High
Sibling cannibalism	Rate	Frequent
Time on onset of schooling	Late	Early
Growth	Slow	Fast
Instantaneous mortality	Lower	Higher

Food size preferences may be one of the best diagnostic traits for identifying ecological roles. To feed on large prey requires a large mouth and a greater and more efficient searching effort because of the exponential decline in density with prey size. Greater searching effort may require a faster swimming speed and this in turn implies a higher metabolic rate and energy requirements. Large prey are more efficient in satisfying energy requirements and promote faster growth (Kerr 1971a and 1971b). Faster growth reduces the duration of the larval stage and the time to the onset of schooling. A larva that is more dependent on large prey can ill afford to pass up prey if the first attack fails. Thus, persistence in attack and maneuverability would appear to be essential, and the sinuous mode of feeding seems to lack these characteristics.

The sparid *Archosargus rhomboidalis*, which seems to fit in many respects the scombriform role, 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 differences in searching power and efficiency of feeding implicit in these roles. Feeding rates and ration also could be expected to vary between these roles but few accurate measurements exist. Owing to the strong effect of food density, larval weight and temperature (Stepien 1976), specific comparisons are not possible. At least in younger larvae satiation mechanisms appear to be lacking. Death from overfeeding in the laboratory has been reported for grunion (May 1971) and the siganid, *Siganus canaliculatus* (May et al. 1974), and I have observed it in larval Pacific mackerel. Northern anchovy maintained at the same food density as mackerel did not die from overfeeding, suggesting a higher feeding capacity in the more active mackerel.

Although the evidence is weak for differences in spawn density that I have associated with these roles, it does make some evolutionary sense. At high spawn densities, suppression of intraspecific effects on growth would be adaptive as well as suppression of sibling cannibalism. Species of slow swimming abilities 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. Finally, Ware (1975) suggests that instantaneous mortality is proportional to growth rate. If Ware's argument is correct, then the slow growth of anchovies relative to mackerel (Fig. 9) is indicative of a lower mortality.

In these comparisons, many assumptions and simplifications were made and the very significant role of temperature was not considered. In a strict sense, such roles should only be defined within specific temperature ranges. Many other possible strategies exist. Those species that hatch from large eggs in a relatively large and mature state, such as flying fish, herring larvae, saury, and many others, do not fit into these categories. The flatfishes show major deviations from either pattern because of the striking changes at metamorphosis resulting in declines in activity and metabolic rate (Blaxter and Staines 1971; Laurence 1975). Another possible role is that of a larva dependent on large prey, but using a relatively passive hunting strategy at reduced metabolic cost and experiencing a slow growth rate. This contrasts with the fast growth, high metabolism, and active hunting of scombroid larvae. This more passive large prey strategy could be relatively common in cold water where metabolic costs are less.

My emphasis has been on specific differences in feeding ecology of larvae because I feel this approach is essential for understanding the cause and effect relationships underlying mortality. The apparent similarities in feeding habits among pelagic larval fishes are striking nonetheless. The characteristics emphasized here, such as preferences for size ranges of copepods, minor differences in larval

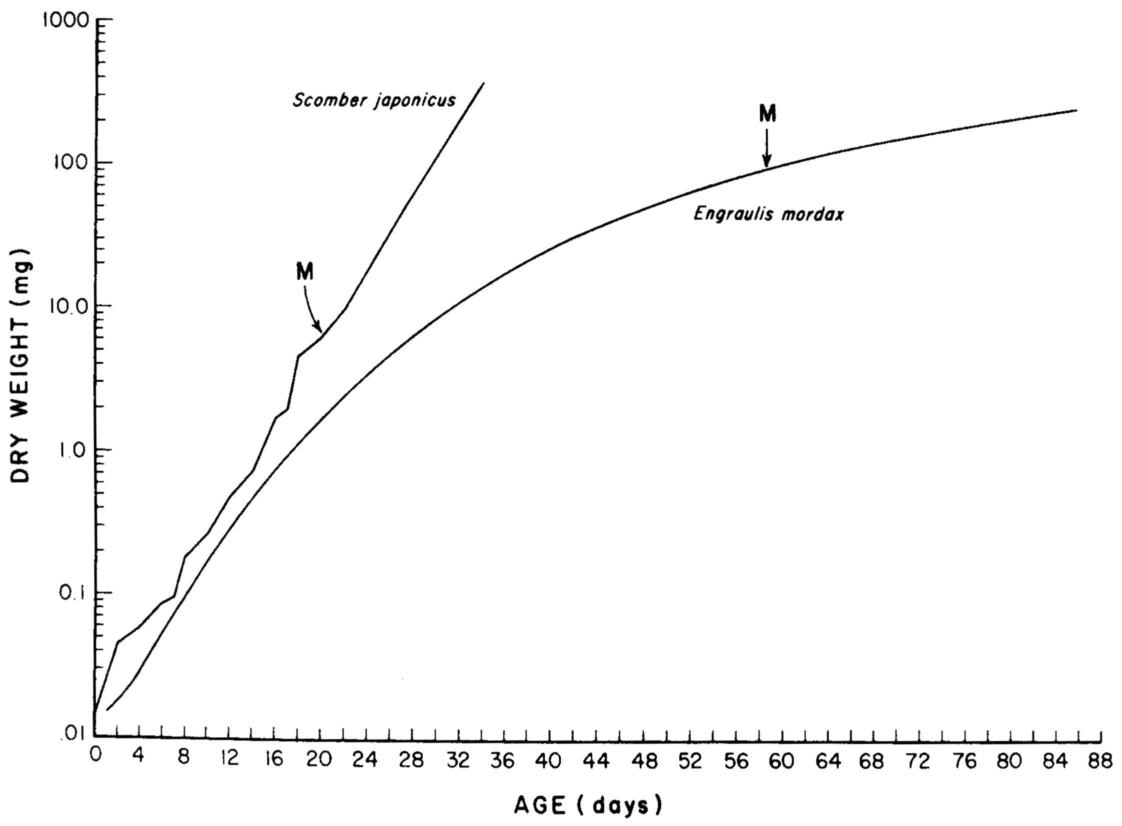

FIG. 9. Growth of larval *Scomber japonicus* and *Engraulis mordax* in the laboratory at 19°C. Data on *Scomber* is a line formed from connecting average length for three experiments and converted to weight by length-weight conversion (Hunter and Kimbrell, MS); data on *Engraulis* is a Laird-Gompertz fit (Hunter 1975) to unpublished rearing data at 19°C; and M indicates age at metamorphosis.

size and yolk reserves, and differences in swimming speed, seem subtle relative to the major differences that exist in feeding ecology of the parents. Nearly all larvae are diurnal, particulate planktivores specializing in the young stages of copepods despite the fact that the feeding habits of the parents include benthic and epipelagic piscivores, filter-feeding and particulate-feeding planktivores, and many other specializations. The feeding habits of larvae, of course, are most similar at first feeding when larvae are least specialized, and distinctions become more obvious as development proceeds and fish approach metamorphosis.

Given proper phase relationships, many species could be dependent on the same food resource. Competition between species is regulated to some extent by the timing of spawning and its relation to the production cycle. In the California Current, peak spawning by the northern anchovy occurs in early spring, whereas peak spawning by the large-mouthed larvae, jack mackerel and Pacific mackerel, occurs later, although spawning of all three species broadly overlaps (Kramer and Smith 1970a, 1971). Vertical partitioning of the water column has not been discussed but is a tactic of major importance. *Scomber* larvae seem to be more closely associated with the upper surface layers than clupeoid larvae, whereas hake are located at greater depths (Ahlstrom 1959; Nellen and Hempel 1970). It is possible that the rapid metabolism, fast growth, large prey tactics of scombroids may be designed for near-surface existence and possibly the slow growth, large prey tactics of hake are limited to cooler or deeper waters. Clearly, vertical distributions of larvae and their foods need detailed attention.

Sources of Mortality, Approaches

A critical period for survival occurring around the time of first feeding has long been hypothesized as a possible determinant of year class strength (Hjort 1914; May 1974; Vladimirov 1975). Hjort's critical period concept, as restated by May (1974), is that the strength of year classes in marine fishes is determined by availability of planktonic foods shortly after the yolk supply has been exhausted. Low feeding success, low resistance to starvation, small size, and immaturity of larvae at this time suggest that they would be more vulnerable to starvation death than at any other time, but the evidence from estimates of natural mortality is inconclusive (May 1974). Although physiological and behavioral criteria indicate the highest vulnerability at yolk absorption, it is also the time when larvae feed upon the smallest and therefore most abundant food supply. Events in later life such as the necessity to feed on larger but less abundant prey, disruption of food patches by storms, and failure to form viable schools could also be sources of mortality. In the anchovy, a major risk may be involved in the shift from very small prey such as nauplii and phytoplankton to larger copepodites. This risk would be faced by larger-mouthed larvae at a much earlier age. This risk can be hedged to some extent if larvae continue to feed on smaller prey and take larger copepods when available, which seems to be a basic strategy as evidenced by the slow increase in minimum prey size in all species. Sooner or later, these large prey must be eaten or growth will be slowed, as laboratory work has demonstrated, and retarded growth leads to greater exposure to predation (Murphy 1961).

To isolate causes of natural mortality of larval fishes, estimates must be made of incidence of starvation and predation over the spawning range and these losses compared to estimated rates of mortality. Such models must account for egg mortalities of up to 29% per day and larval mortality rates of 2-10% per day (Jones and Hall 1974). Predation is probably the most common cause of mortality during the egg and yolk-sac stage, although other causes have been suggested (Vladimirov 1975). Predation by fishes on eggs is detectable by stomach examination because the chorion is relatively resistant to digestion but may be difficult with larvae such as small 3- to 5-mm anchovy where digestion is so rapid that larvae are unidentifiable in less than 2 h (Hunter, unpublished data). The study of predation by arthropods and other predators that injure or grind prey will also be difficult. Owing to the diversity of potential invertebrate predators, bioassays of samples from predator communities might be a productive approach, perhaps using large plastic enclosures containing fish larvae. It seems unlikely much progress could ever be made using a species-by-species analysis.

Studies of starvation in the sea seem to offer a better opportunity for isolating a cause of mortality than those of predation because of the difficulty of direct observation and detection of predation. Laboratory work indicates that incidence of starvation can be identified by chemical, morphological and histological criteria (Balbontin, de Silva and Ehrlich 1973; Ehrlich 1974; O'Connell 1976; Ehrlich, Blaxter, and Pemberton 1976). If absolute criteria are to be used, histological techniques may be preferable because deterioration of cell and tissue structure appears to be less affected by laboratory rearing and is independent of size (O'Connell 1976).

Morphometric techniques are desirable because they can be applied routinely over the spawning range of a species and can be easily incorporated into standard ichthyoplankton analysis. They have been used by Shelbourne (1957) and Blaxter (1971) to assess condition of sea-caught larvae, but Blaxter's work indicates that their application should be confined to a relative assessment. He found in herring that body depth and condition factor changed with starvation in the laboratory, but larvae captured in the sea had a lower condition factor than those dying of starvation in the laboratory. I obtained nearly identical results with northern anchovies using body depth (Hunter, unpublished data). Thus, the most practical approach for assessment of starvation on a population basis may be morphometric analysis calibrated in terms of starvation using histological analysis of sea-caught specimens. Finally, intensive studies in the laboratory and at sea are essential for defining ecological roles and causes of mortality, but in the long term these studies must lead to identification of parameters that can be measured routinely over the spawning range of the species.

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Discussion

FISHELSON

What do you think science may contribute after 5 yr or more to stock maintenance from the point of view of larvae?

HUNTER

I think we'll know the probable effect of the environment on year-class strength or at least know whether or not it is even practical to approach the problem from the standpoint of larval mortality. We have many field studies going on. We'll be able to assess the proportion of starving larvae in the sea in the next few years and perhaps separate starvation from predation as a cause of mortality.

BARDACH

When you talk about recruitment, do you talk about recruitment to the fishery?

HUNTER

Yes.

BARDACH

When is the onset of fishing?

HUNTER

When the fish are about 1 yr old and about 10 cm in length.

MURPHY

I don't think they're fully recruited until they're 2 yr old.

BARDACH

How does this compare with the Peruvian stocks?

MURPHY

Full recruitment occurs at 1 yr, but heavy fishing mortality starts at about 6 mo.

FUJIYA

You said something about cannibalism. Is that real cannibalism or just biting?

HUNTER

It's real cannibalism. Mackerel larvae eat fish about half their size.

BLAXTER

There must be a size hierarchy before that occurs.

HUNTER

It depends on the species: barracuda, for example, become cannibalistic at about 4 mm long when the larvae are all nearly the same size, and they prefer fish by the time they're 10 mm.

MURPHY

What is the thinking now with respect to the size of the larvae when the relative survival for a year-class is more or less stabilized? From what you told me, it's not just when they're starting to feed.

HUNTER

Correct. Paul Smith of our laboratory has preliminary estimates of mortality now of fish up to 20 mm for 25 yr. You can see a higher mortality at the onset of feeding and a great deal of differential mortality in different years, but the year-class strength is not established even at 20 mm.

MURPHY

You're talking about numbers of fish, and those have a tremendous variance. The estimate for a given year is pretty wide.

BLAXTER

How does growth in your tanks compare with that in the sea?

HUNTER

We're beginning to get data on growth of anchovies in the sea by counting daily rings on the otoliths. Differences between laboratory and sea growth can be as great as the difference caused by a 2-3°C difference in rearing temperatures. In general, larvae in the sea grow slower than larvae reared in the laboratory at the same temperature, but occasionally we find some samples in which sea-caught larvae appeared to be growing faster than laboratory-reared larvae.

BLAXTER

You might think there'd be stronger selection for size in the sea than in a tank where there are no predators.

HUNTER

Yes. Growth may appear to be faster in the sea because of predation.

LILEY

When you do have more information about the larval ecology and feeding behavior, how do you see its being applied? Are you not looking at the possibility of culturing these pelagic fish?

HUNTER

No.

LILEY

What do you think could be the long-term application of this? This helps you to make predictions, but I'm wondering if there are things that you can go into and do.

HUNTER

Our objectives are to learn what is causing the large fluctuations in the annual number of recruits in fish populations. We feel that if we had a better idea of the mechanisms, we could better manage fish stocks. Nobody as far as I know has yet been able to solve these problems.

HASLER

Is the Peruvian anchovy coming back?

MURPHY

They started to recover and then apparently faltered and are falling off. The data from Peru aren't as available as they used to be, but I understand they closed anchovy fishing and turned everybody on to sardines and mackerel.

HASLER

That fishery makes such a huge contribution to the world's protein supplies that it would seem important to focus on that.

HUNTER

Yes. The world's largest fisheries are based on these clupeoids, which is why we're working on them.

MYRBERG

How does your knowledge of these species provide information relative to those species that are cultured? Can we learn something from this that can be applied to those species that are well known in culture?

HUNTER

Many of us have reared fish larvae for a number of years, and I think collectively the techniqes from our own and others' research are beginning to follow certain patterns. A reservoir of information exists, and many of the techniques that are almost intuitive now were developed by hard work in many laboratories over the last 10 yr. For example, the rule of one nauplius per mL didn't always exist.

MAY

It seems to me that fish species that are now commercially cultured are primarily the species that are easy to rear through the larval stages. The kinds of fishes that John is talking about are not commercially cultured anywhere, but I think the information he and other people are gathering will provide the basic knowledge which will enable these species to be cultured in the future. I don't know if it will ever happen on a commercial scale, but it may, and if it does, it will depend fairly heavily on the kind of basic knowledge that's being accumulated now.

HUNTER

There are many incidental findings that may be useful for rearing other species. For example, we found the best way to reduce cannibalism was to rear mackerel at the highest temperature possible. Cannibalism stops at metamorphosis when they start schooling, and you can double the survival by reducing the time to metamorphosis.

FISHELSON

Is it possible then that we can use heated waters of reactors and power plants to farm in the sea, using large ponds in which we can grow the small larvae till they pass the cannibalistic stage and then let them out?

HUNTER

People working on tropical fishes have greater problems with water chemistry than those working on temperate, coldwater species. When I speak of warm water I mean about 22-23°C, which is warm for Pacific mackerel but is not warm by tropical standards.

BLAXTER

Surely cannibalism is partly an artifact of the crowding in the tank, isn't it?

HUNTER

Yes, although cannibalism is common even in adult scombroids. I don't think there's much doubt that if a scombroid encounters another it would eat it if it were the correct size. But I think spawn is much less dense than that of clupeoids and encounters may be infrequent.

MAGNUSON

I think that about 10% of the stomach contents of adult skipjack captured on the high seas consist of their own juveniles. You gave two strategies for pelagic larvae. Are these essentially the only two strategies? Or is there some continuum?

HUNTER

I think many larvae may fall into these classes, but hake would be a good example of one that does not, and there are many others. A continuum may exist, but other variables, especially temperature, would have to be considered before all differences could be accounted for in a continuous pattern. Some larvae that feed on large prey grow slowly and may have a more passive feeding strategy than scombroids, but these seem to be adapted to cooler temperatures. A continuum seems likely because the range of feeding strategies is more limited in larvae than adults. Nearly all larvae are diurnal, particulate planktivores specializing in the young stages of copepods.

BLAXTER

In the past the work on rearing larvae, at least Shelbourne's work, has led to a technology for rearing flatfish for farming; turbot are now at the point of being farmed commercially. The technology all comes from the general work that was done in the sixties, and so there's been a fairly rapid practical spinoff from that work. Of course it's for valuable fish; it's a luxury market.

MURPHY

If we succeed in artificially spawning milkfish, there's some guidance about how to go about rearing the larvae.

BLAXTER

I think with *Brachionus* as a food almost any species could be reared.

HUNTER

I think the critical element is a 240-μm-diameter particle. In other words, a food is needed as a substitute for *Artemia* nauplii, because many larvae do not grow well when fed *Artemia* nauplii, although plaice and others do. I think many major improvements can be made in the *Brachionus* system, and I think it's a waste of time to worry about artificial foods of the size of *Brachionus*.

ATEMA

I recall the famous story on the East Coast where they used to raise lobsters in hatcheries up to the fourth stage and then release them. Nobody has ever shown that the operation was successful. I suspect they released them in the wrong place, but another possibility is that if they raised them to the sixth stage, would they have been successful? I wonder about that in your fish stituation. How large is the dangerous window?

BLAXTER

All the early work on releasing plaice and cod never improved the fishery. In fact the only case where there apparently was some improvement was when Dannevig released cod into the Skagarak.