INTRODUCTION

Good and poor year classes of fish may be determined during the larval stage by physical events that act upon larvae directly or indirectly by controlling their food supply (Hjort, 1914; 1926). The goal of this workshop is to evaluate our ability to identify and monitor these physical events, at appropriate scales, which might facilitate forecasting larval fish survival. Larval survival depends not only on environmental variables and prey availability at first feeding but also on a suite of species specific behavioural and physiological characteristics. Thus, minimum food concentrations needed to initiate feeding and promote larval fish survival will vary among species due to interspecific differences in egg size (hence development at hatching), resistance to starvation, feeding strategies, growth rates, growth efficiencies, and metabolic demands. Therefore, these food concentrations and other input parameters in models designed to predict survival and recruitment must incorporate species-specific functions. Presented here are pertinent life history, behavioural and physiological parameters of four important pelagic representatives of related species of the California and Peru Currents, as well as twelve predominantly demersal species of the north Atlantic Ocean (Table 1).

Table 1

EARLY LIFE HISTORY

Species	Range	Spawning season (peak)	Type	Egg diameter (mm) Range	Incubation Days	°C	Hatching Size mm	dry wt µg	Yolk absorption Days from hatching	°C	Onset of feeding Days from hatching	°C	Irreversible starvation (a) Days from hatching (b) Days from Yolk Abs.	°C	Metamorphosis Days from hatching	°C	Length (mm)
Limanda ferruginea (Yellowtail flounder) 1.	Gulf of St. Lawrence to Virginia	March–Aug.	Pelagic	0.88 0.79–1.01	5–7	10	2.0–3.5	16	4–5	10	4–5	10					14
Limanda limanda (Dab) 2.	North Sea English Channel	March–June (Feb.–April)	Pelagic	0.65–0.95			2.6				Yolk absorption						
Pleuronectes platessa (Plaice) 3.	North Sea English Channel to Norwegian Rinne Skagerrak	Dec.–April	Pelagic	2.0 1.7 – 2.2	18	7–11	5.0–6.7	151	6–10	7–11	4–6	7–10	6–8(b)	8–11	40–75	7–11	9–13
Pseudopleuronectes americanus (Winter flounder) 4.	Northern Labrador to Georgia	Dec.–May	Demersal	0.80 0.71–0.96	17–25	3	2.3–3.5	10–30	9	8	5	8	5–7(b)	8	58	8	6.5–9
Paralichthys dentatus (Summer flounder) 5.	Maine to Florida	Oct.–April	Pelagic	1.04 0.90–1.13	3	17	2.4–2.8		3–4	16	4	16	6–7	16	47–56	16	15
Solea solea (Sole) 6.	North Sea English Channel	April–June	Pelagic	1.0 – 1.5	8	10–12	3.2–3.7		7						42–56	10–12	9–10
Anchoa lyolepis (Dusky anchovy) 7.	Florida and Gulf of Mexico to Uruguay		Pelagic		1	28		21.8	3	28	2	28	3–3.5	28	16	28	4–5
Hippoglossus hippoglossus (Halibut) 8.	Nova Scotia to Eastern Florida	May–July	Pelagic	2.94 2.85–3.15	1.5	22	7.0		3	22	3						10
Archosargus probatocephalus (Sheepshead) 9.	New Jersey to Rio de Janeiro	Sept.–May	Pelagic		1	26	1.8–2.2	27.8	2	26	1.5	26	2.5	26	9–11	23–24	7–9
Gadus morhua (Cod) 10.	North Atlantic Coastal Waters	Dec.–April	Pelagic	1.52 1.30–1.72	12	5.5	3.3–5.7		6	7.2	-5	7	5(b)	7	52	7	10
Melanogrammus aeglefinus (Haddock) 11.	North Atlantic Biscay to Barents Sea Newfoundland to Cape Cod	Feb.–June	Pelagic	1.46 1.30–1.67	17	5.5	2.0–4.1		7	7	-5	7	5(b)	7	42–49	7	10
Clupea harengus (Atlantic herring) 12.	Greenland–Cape Hatteras Iceland–Gibraltar	July–Nov.; May (Sept. & May)	Demersal	1.0 – 1.4 0.36–3.0	15 (Maine, Downs)	8	4.0–10.0	90 (50–220)	6 (Firth of Clyde) 15–20(W.Baltic)	8	2–6 (Firth of Clyde) 15–20 (Baltic)	8	6(b) (Firth of Clyde) 18–22(c)	8–12 8	112–168	8–12	30–40
Sardinops caerulea (Pacific sardine) 13.	Southern Alaska to Gulf of California	Feb.–July (May–June)	Pelagic	1.7	2.8	15	3.75	36			4–5	16			45–50		31–35

Table 1 - Cont'd.

Species	Range	Spawning season (peak)	Egg Type	Egg Diameter (mm) Range	Incubation Days	Incubation °C	Hatchlings Mean mm	Hatchlings dry wt µg	Yolk absorption Days from hatch	Yolk absorption °C	Onset of feeding Days from hatch	Onset of feeding °C	Larval mortality observation (a) Days from hatch (b) Days from Yolk Abs.	Larval mortality observation °C	Metamorphosis Days from hatch	Metamorphosis °C	Length (mm)
Engraulis mordax (Northern anchovy) 14.	Northern Baja California to Arctic Alaska and Japan	Jan.–July (March–May)	Pelagic	0.66@1.35	2-3	16	2.9-3.2	21	4	16	4	15-16	2.5 (a) 4.5 (b)	16.5 15	50-60		36-48
Engraulis ringens (Anchoveta) 15.	Gulf of Peru and Chile	July-March (Sept. & Feb.)	Pelagic	0.77@1.48	2-2.25	14-16	2.19-2.72		3	18	4-5 (3.5-6.0)	18	4.5	18			30
Sardinops sagax (Pacific sardine) 16.	West coast Alaska to Southern Baja, Mexico	April-August (May-July)	Pelagic	1.06-1.14	3.4	16	3.1	40	3	19	3-3.5 4	19 16	2 (b) 3.5 (a)	19 16	25		15
Trachurus symmetricus (Jack mackerel) 17.	Magdalena Bay, Baja California to Southeast Alaska	Feb.–August (May–June)	Pelagic	1.0 0.90-1.02	2-3	15	2.13 a/ 2.6 b/	345 b/			5	15	2.5 (b)	15	40		11-16

1. Hartin and Bracey, 1938; Colton and Marak, 1969
2. Russell and Yonge, 1961
3. Blaxter and Staines, 1971; Harding, Nichols and Shumway, 1978; Hyatt, 1972, 1974
4. Hartin and Bracey, 1978; Lasrance, 1977; Laurence and Rogers, 1976
5. Hartin and Bracey, 1938
6. Blaxter and Staines, 1971; Alley, 1974
7. Houde, 1974, 1977, 1978
8. Johnson, 1978; Colton and Marak, 1969
9. Higgins, 1978; Houde, 1974
10. Hardy, 1978; Laurence, 1978
11. Hardy, 1978; Laurence, 1978
12. Jones et al., 1978; Rosenthal and Hempel, 1969; Rogers and Laurence, 1980; Blaxter and Staines, 1971; Hempel and Blaxter, 1961 (Note: Values very widely between individual stocks of Atlantic herring; stocks named where known)
13. Lasker, 1962; Lasker, 1964; Ahlstrom, 1943; Ahlstrom, 1966
14. Lasker, 1964; Lasker et al., 1970; Kramer and Demetal, 1970; Hunter, 1976; Theilacker, unpubl.; Ahlstrom, unpubl.
15. Rojas de Mendiola (this volume)
16. Kramer, 1969; Hunter and Richards, 1980
17. Kramer, 1960; Ahlstrom and Ball, 1954; Theilacker, 1980

a/ 0.90 mm egg
b/ 1.0 mm egg
c/ wt at yolk absorption, day 5

SPAWNING

With the exception of the cod, *Gadus morhua*, the Atlantic species discussed here form localized coastal populations and do not undertake extensive migrations. The stocks of these species are considered to be relatively distinct in their various localities for that reason. Each species has its own preference for bottom terrain, depth and temperature. All undertake at least a short migration before or during their spawning period, most of them toward shallower, inshore waters.

Peak spawning times vary with each species in each locality. Generally, in the northern hemisphere spawning begins in the southern part of the species' range and moves northward as the season advances following the advance of primary production cycles. This is reversed in the southern hemisphere. Spawning times of the four California Current species overlap. Northern anchovy, *Engraulis mordax*, and northeastern Pacific sardine, *Sardinops sagax*, spawn in early spring, and Pacific mackerel, *Scomber japonicus* and jack mackerel, *Trachurus symmetricus*, spawn later. Kramer and Smith (1970) summarized spawning from 1951-1960 in the California Current, 20-300 miles off the coast as follows: Pacific sardine spawning begins in small areas in January off both southern California and Baja California, the centers of the northern and southern subpopulations. Spawning areas continue to expand to the north and south and by May-June spawning is maximum, appearing as one area extending from Point Conception, California to mid-Baja California. Spawning of northern anchovy extends from Point Conception to southern Baja California from January to May; the spawning area decreases somewhat in June and July. Lasker and Smith (1977) could find no relation between amount or location of northern anchovy spawning and changes in temperature or zooplankton production over the spawning area between 1953 and 1960. Pacific mackerel spawning begins in the Spring off southern Baja California, moves north with warming water to southern California in May, June and July. Major spawning of jack mackerel first occurs in March off northern Baja California, and spawning gradually spreads northward off southern California in April and peaks in May and June as the water warms. Thus, between April and July, spawning of the four California Current species overlaps both temporally and spatially.

Frequency

Although little information is available on spawning frequency, some species are known to spawn at intervals during the spawning season. In cod and haddock, *Melanogrammus aeglefinus*, not all of the eggs within the ovary ripen at once; for cod there are at least three and possibly up to eight batches of eggs in a season (Hardy, 1978). Yellowtail flounder, *Limanda ferruginea*, also spawn more than once throughout a prolonged spawning season (Martin and Drewry, 1978). Hunter and Goldberg (1980) give evidence of batch spawning in the northern anchovy with a periodicity of about seven days and perhaps as many as 20 spawnings over the season. Thus, relationships between adult biomass and apparent egg abundance are complex.

EGGS

The eggs of the subject species range in size from 0.65 to 2.2 mm in diameter (Table 1) and, with the exception of anchovy, eggs are spherical. Egg buoyancy varies; most eggs are pelagic except for those of winter flounder, *Pseudopleuronectes americanus*, and herring, *Clupea harengus*. Early-stage pelagic eggs are found in the surface waters but they may descend to mid or bottom depths as development proceeds. Cod eggs are an example of this latter process (Hardy, 1978). Variations in density within the water column may "trap" eggs in their iso-density surfaces or vertical mixing may distribute them throughout the mixed water layer, but most pelagic eggs are found at or near the surface.

Size

Within species, egg size has been shown to decline from spring to summer and vary inverseley with temperature (Ware, 1975). Decreasing egg size with season may be due to a shift in spawning from older to younger females (Ahlstrom, pers. comm.). Within species larger eggs are hypothesized to improve survival by producing larger larvae that are able to swim faster and search a greater volume of water for food (Hunter, in press). However, Hempel and Blaxter (1963) found that within a race of herring, the larvae hatching from large eggs did not survive longer than those from smaller eggs (no food was added), presumably because larger larvae have proportionately higher metabolic demands. But it has been shown that jack mackerel hatched from large eggs can grow twice as fast with the same feeding treatment as those hatched from small eggs (.09-.15 mm/day versus .05 mm/day; Theilacker, 1980a).

Incubation time is a function of egg size and temperature; larger eggs take more time to hatch at similar temperatures (Table 1). Egg size also affects duration of yolk-sac stage (Ware *et al.*, 1980), time to irreversible starvation (Blaxter and Hempel, 1963), and hatching size (Blaxter and Hempel, 1963; Theilacker, 1980a; Eldridge, pers. comm.). Temperature has a significant and reproducible effect on each of these parameters. However, at constant temperature, the influence of differing egg sizes on these parameters may vary; in particular, jack mackerel incubation time, yolk-sac stage, and time to irreversible starvation did not differ between egg sizes (0.9 versus 1.0 mm), yet size at hatching and growth rates did differ (Theilacker 1980a).

LARVAE

At hatching larvae range from 1.89 mm for lined sole, *Achirus lineatus*, to over 6.0 mm for the plaice, *Pleuronectes platessa*, and herring (Table 1). Larvae show varying degrees of development at hatching, but at yolk absorption, the described larvae have pigmented eyes, open guts, and functional mouths if development occurred within the species' optimal temperature range. Most larvae, with the exception of anchovy and sardine, are capable of feeding before their yolk is completely absorbed. There is evidence that when food is present the yolk is absorbed at a constant rate, but if food is not present the rate of utilization begins to decline (Ryland and Nichols, 1975).

At the time of complete utilization of the yolk reserves, larval survival is dependent upon the larva's ability to find and capture sufficient prey. The amount of time a larva can survive without food, before it is too weak to feed and death is inevitable, has been termed the time to "point of no return" (Blaxter and Hempel, 1963). Days to point of no return (irreversible starvation) are quite similar among described Atlantic species and among described California Current species (Table 1). In general, the Atlantic species have one week to capture a critical number of prey organisms for survival and subsequent development. The California Current and tropical Atlantic species have only 2-5 days until irreversible starvation, but they are generally exposed to higher temperatures than the subject Atlantic species. The time to irreversible starvation has been shown to decrease with increasing temperature (Lasker *et al.*, 1970; Hunter and Kimbrell, 1980).

Survival vs starvation

After the yolk has been absorbed, larvae must eat. The locomotory and perceptual capabilities of the larvae, the density of suitable prey and the behavioural patterns of larvae and prey are the important factors that influence feeding, and thus survival and growth. Delaying larval feeding for one or more days after yolk absoption decreases survival and growth rate. For example, starving northern anchovy for three days after they were capable of feeding decreased survival to age 13 days from 70% (for fed larvae) to 20% (for delayed-fed larvae) and decreased size from 7.1 mm standard length (SL) to 4.6 mm SL respectively. Four days of starvation decreased survival at age 13 days to 6% and size to 3.6 mm SL (Theilacker, unpubl.).

Starved northern anchovy larvae were active during the first day without food but activity decreased thereafter; larvae began to sink, head down, but they exhibited avoidance behaviour throughout the four-day starvation period. As anchovy larvae sink, reduction of activity may reduce risk of predation (Hunter, in press). The larvae may also enter an area of higher food concentration or enter cooler water, thus increasing available calories and/or decreasing metabolic demands, thereby increasing probability of survival for a longer time. At the time of irreversible starvation, Pacific mackerel, unlike anchovy and jack mackerel, continue to swim and eat but they cannot eat enough to survive (Hunter and Kimbrell, 1980).

The onset of starvation in anchovy and mackerel larvae is characterized by changes in the histological characteristics of the pancreas, liver and gut (O'Connell, 1976; Theilacker, 1978). The mackerels require two days of eating to repair tissue damaged by one day of starvation, and they do not grow during this period. The gut is the first tissue degenerated by starvation and apparently the last tissue to be repaired (Theilacker, 1980a).

The number of days to irreversible starvation increases with age. For northern anchovy, time to irreversible starvation from the onset of feeding (when the larvae had no body reserves) was 3-4 days (Table 1); at metamorphosis (when the fat level was 30%, dry weight) it was 15 days. Fat levels declined to about 12% in the 15-day starved metamorphosed fish and recovered to the original levels after 5-8 days of feeding (Hunter, 19760. Results were similar for herring larvae; time to irreversible starvation increased from six days at yolk absorption (6 days of age) to 15 days at 88 days of age (Blaxter and Erhlich, 1974).

Swimming modes

The food-searching ability of larvae is a function of their swimming capabilities, activity levels, perceptive distances and their ability to successfully complete the attack sequence on a prey organism.

The dominant swimming mode of larval anchovy is a beat and glide, or intermittant swimming (Hunter, 1972). In contrast, Pacific mackerel (Hunter and Kimbrell, 1980) and jack mackerel beat continuously (Theilacker, unpubl.). Vlymen (1974) has calculated that slow, intermittent swimming is efficient for larval anchovy while Weihs (1974) shows that intermittent swimming is less efficient for mackerels of all sizes. Larval Pacific mackerel swim at more than twice the speed of northern anchovy (.46 versus .2 cm/s; Table 2), owing in part to their differences in swimming mode. Swimming speeds for 6 mm jack mackerel are intermediate between Pacific mackerel and northern anchovy of the same size (Table 2). O'Connell (in press) suggests that the differences in swimming modes between northern anchovy and Pacific mackerel may be due to anatomical differences. The short post-anal tail (thus short flexure) of anchovy is due to their long digestive tract, and the long post-anal tail (thus long flexure) in mackerel is due to their short, compact digestive tract.

Swimming speed

Voluntary swimming (cruising) speeds for young larvae (Table 2) range between 0.1-0.5 cm/s; sardine, anchovy, sole and plaice are at the low end of the range with mackerel and herring at the high end. Variation in experimental methods has produced widely differing results. For example, in forced swimming experiments (Ryland, 1963) plaice swam about 2 to 7 times faster than during voluntary swimming experiments (Blaxter and Staines, 1971; Table 2). Swimming speeds of young larvae in experimental tanks may be comparable to, or typical of, speeds achieved in the field; but container size probably affects activity of older larvae. In particular, Hunter (pers.comm.) has seen 10 mm northern anchovies swim apprxomately 1 m in about two seconds (about 50 cm/s) in a large, deep tank (5 m x 10 m). This is much faster than burst speeds over short distances measured in smaller experimental tanks for northern anchovy (e.g., 15 cm/s; Hunter, 1972).

Although voluntary and sustained swimming speeds are needed to determine routine energy expenditures of larval fish, estimates of burst swimming speeds are essential to determine energy required to capture prey and avoid predators. Both burst speeds for northern anchovy larvae and distance travelled per burst (endurance) increased linearly with length (Webb and Carolla, MS; Table 2); for herring larvae the duration of single bursts decreased with length while the number of bursts per minute increased (von Westernhagen and Rosenthal, 1980). Jack mackerel burst speed and endurance is about twice that of anchovy at the same age (Table 2).

Swimming speeds appear to be inversely correlated with prey density. For example, plaice (Wyatt, 1972) and cod (Ellertsen *et al.*, 1980) increased their swimming activity in the absence of food, and northern anchovy, 4-8 days of age, swam at 0.5 cm/s outside a food patch and at 0,3 cm/s inside a patch (Hunter and Thomas, 1974). Thus, swimming speeds are apparently reduced when food organisms are encountered, and the commensurate expenditure of energy due to swimming activity could conceivably be less in high food concentrations. But it may be that within a food patch the combined energy expended in slow swimming plus attacking prey is greater than energy used outside a food patch for faster swimming (see section on Attack modes). Owing to these observed decreases in swimming speed with increasing prey density, extrapolations to calculate volume of water searched and hence prey density requirements from swimming speeds should be made with caution.

Table 2. Activity -- swimming speeds.

Species	°C	Age (d; mm; µg)	Cruising[1] cm/s	Cruising[1] BL/s	Burst cm/s	Burst BL/s	Duration of burst or distance traveled per burst	Reference
Sardine	15-18	yolk; 3-5 mm	0.2					Blaxter & Staines
Sardina pilchardus	"	3 wks.	0.3					1971
Herring	8-12	yolk; 6-11 mm	0.4					Blaxter & Staines[2]
Clupea harengus	"	8 wks.	1.4					1971
				2.3		8-10		Blaxter 1969
Northern anchovy	13	3 mm	0.1	.2				Hunter 1972
Engraulis mordax	19	3 mm	0.2	.6				Hunter (in press)
	13	5 mm	0.3	.5				
	19	5 mm	0.5	.9				
	17	15 mm	1.5	1.0				
" "	17	35 mm[2]	3.5	1.0				
	17	80 mm	12.0	1.5				Theilacker (unpubl.)
	17	150 mm	50.0	3.3				
	17	8 mm[3]			3		8-16 ms	Hunter 1972
	17	13 mm[3]			8		8-16 ms	
" "	17	3 mm			7.3[4]	24	1.3 cm/176 ms	Webb & Carolla (MS)
	17	8 mm			11.4[4]	14	3.1 cm/272 ms	
	17	13 mm			15.5[4]	12	5.0 cm/323 ms	
Whitefish[5]	7-15	15 mm	1.5	1.0				Hoagman 1974
Coregonus clupeaformis								
Jack mackerel	16	6.0-6.5 mm	.36 - .72	0.8 (0.6-1.2)		4-6	2-8 cm; 2 s	Devonald (pers.comm.)
Trachurus symmetricus								
Pacific mackerel	19	3.6 mm	0.46	1.3				Hunter & Kimbrell
Scomber japonicus	"	15.0 mm[2]	5.6	3.8				1980
Large mouth bass	19	2-7 d; 6-7 mm	3-4[6]	4-5				Laurence 1971
Micropterus salmoides								
Plaice[7]	10-12	yolk; 5-7 mm	0.2					Blaxter & Staines
Pleuronectes platessa	"	9-10 mm	1.0					1971
	"	5-7 mm	1.5[8]		4-9[1] ~10		9-15 cm	Ryland 1963
	"	9-10 mm	2.2[8]		9-15[1]~13		12-36 cm	
	"	25 mm	6.5[8]					
Sole[7]	10-12	yolk; 3-5 mm	0.1					Blaxter & Staines
Solea solea		9-10 mm	0.7					1971
Walleye perch[9]	13	7.5 mm	0.5	0.6				Houde 1969
Stizostedion vitreum vitreum	"	11.0 mm	3.5	3.0				
Yellow perch[9]	13	7.5 mm	1.5	1.8				Houde 1969
Perca flavescens	"	11.0 mm	3.5	3.0				

[1] voluntary swimming
[2] metamorphosis
[3] attacking prey
[4] mean burst speed = 8.18 L + 4.89; maximum distance traveled = 3.79 + 0.08
[5] no effect of temp. or age
[6] forced swimming; speed sustained for 30 m
[7] 90% decrease in activity at metamorphosis
[8] forced swimming; speed sustained 4-20 s
[9] forced swimming; speed sustained for 1 h

Attack modes

At the onset of feeding there are two basically different larval feeding behaviours, "S" and "C" postures. To illustrate, as northern anchovy sight prey their sinuous body moves into an "S" posture. Then, using their pectorals to move toward the prey, they straighten their body, driving it forward to capture the prey (Hunter, 1972). "S" posture feeding behaviour is also typical for young larvae of engraulids (bay anchovy, *Anchoa mitchelli*; Houde, 1973); clupeoids (Pacific sardine; Schumann, 1965); herring (Rosenthal and Hempel, 1970); and flatfishes (Jones, 1972). In contrast to the "S" posture behaviour, larvae of Pacific mackerel stop swimming and assume a "C" posture when sighting prey, then they open their mouths and lunge toward prey by driving the tail posteriorly (Hunter and Kimbrell, 1980). This "biting-lunge" technique is also typical for larvae of jack mackerel (Theilacker, unpubl.) and cod (Ellertsen *et al.*, 1980), but cod also appear to expand their oral cavity and suck in prey. Some fishes are more energy-efficient and opportunistic. For example, *Sebastes*, the rockfishes, use the "biting-lunge" technique but are less active and wait for prey to swim nearby (Butler, pers. comm.).

Hunter (in press) stresses two other important differences in feeding between northern anchovy and Pacific mackerel: the first, anchovy strike only once at a food particle and mackerel will move backward and persist in striking until successful. The mackerel's persistent feeding strategy is advantageous because the large prey they prefer to eat are harder to capture and less abundant than the smaller prey eaten by anchovy (Hunter, in press). Larval plaice (Blaxter and Staines, 1971), cod (Ellertsen *et al.*, 1980) and jack mackerel (Devonald, pers. comm.) also have been observed moving backward and repeatedly striking at the same particle.

The second important difference in feeding between northern anchovy and Pacific mackerel is that mackerel are cannibalistic at 10 mm (20 days) and larval anchovy are never piscivorous (Hunter, in press). Sibling cannibalism is considered to be a density-dependent disadvantage of patchy spawning (Hunter, in press; Hewitt, 1980). Neither jack mackerel nor Pacific sardine are cannibalistic in the laboratory; whether this is due to behavioural differences or an inability to physically manoeuvre this sort of prey is unknown.

The difference in manoeuvrability between species probably accounts for differences in their feeding success and habits. Initial feeding success is low for herring, 2-6% (Blaxter and Staines, 1971) and northern anchovy, 10% (Hunter, 1972). Winter flounder (Laurence, 1977), bay anchovy, *Anchoa mitchelli*, lined sole (Houde and Schekter, 1980), and big-eye anchovy, *Anchoa lamprotanea*, (Chitty, 1980) also require several days of feeding to establish and improve feeding success. On the other hand, larvae with greater manoeuvrability have relatively high initial feeding success; sea bream *Archosargus rhomboidalis*, (Houde and Schekter, 1980), plaice (Blaxter and Staines, 1971), cod (Ellertsen *et al.*, 1980), Pacific mackerel (Hunter and Kimbrell, 1980), and jack mackerel (Theilacker, 1978) are efficient feeders at the onset of feeding.

For larvae that are ineffective feeders on the first day of feeding, the energy cost of attacking prey must be relatively great. For example, the nutritional condition of first-feeding northern anchovy (determined by histological techniques) was poorer in larvae that had been feeding for one day than in larvae which were starved. Most first feeding northern anchovy larvae were not in a healthy, robust condition until they increased their capture efficiency, usually on the third day of feeding (O'Connell, 1976). On the other hand, the same experimental situation with jack mackerel larvae had opposite results (Theilacker, 1978); fed larvae were always in better histological condition than starved larvae. Thus, jack mackerel are probably more efficient than anchovy at capturing prey on the first and second day of feeding. In addition, yolk reserves in unfed jack mackerel were greater than in fed larvae, again indicating that energy expenditure for non-feeding larvae was larvae was less than for feeding larvae (Theilacker, 1978).

Visual Perception

Most larvae are believed to be purely visual feeders. Perceptive distances may depend on prey movement, orientation in relation to the eye, contrast to the background and illumination. Perceptive ranges for herring even depended on their swimming speed; ranges were greater during slow swimming than fast swimming (Rosenthal and Hempel, 1970). At first feeding, movement of prey does not appear to be a criterion for acceptance, as larvae often eat non-motile foods such as copepod eggs. Distance to the prey and prey size probably are the important factors in prey detection. In all larval fish studies, perceptive distance, usually expressed as a function of body length (BL), has been shown to increase with age/size (Hunter, in press). For example, over an eight-week period, the perceptive distance of plaice increased from 3.5 to 5.5 mm, that of pilchard, *Sardina pilchardus*, increased from 1.0 to 2.5 mm, and of herring from 3.5 to 5.0 mm (Blaxter and Staines, 1971). Average perceptive distances summarized by Hunter (in press) are:

	BL	
herring	0.7-1.0	Rosenthal and Hempel 1970
herring	0.4	Blaxter and Staines 1971
plaice	0.5	Blaxter and Staines 1971
pilchard	0.2	Blaxter and Staines 1971
anchovy	0.4	Hunter 1972
whitefish	0.4-0.7	Hoagman 1974

Most fish larvae feed only during the day, but some larvae feed in dim light, and some may feed at night. Houde and Schekter (1980) noted limited feeding of young bay anchovy, lined sole, and sea bream, at 50 mc. Freshwater larval whitefish, *Coregonus clupeaformis*, feed at one mc (Hoagman, 1974), and Smith *et al.* (1978) mentioned four species that feed at night; rockfish, *Sebastes marinus* (Marak, 1974), sole, *Solea solea* (Blaxter, 1969), plaice (Shelbourne, 1953) and yellowtail flounder. Blaxter (1969) found that feeding became reduced in herring at a light intensity range of 10^{2}-10^{-1} mc and in plaice at 10^{2}-10^{-2} mc.

Increased visual sensitivity probably occurs in northern anchovy when rod recruitment begins begins at about 10-11 mm SL or 20 days of age (O'Connell, in press). Appearance of rods occurs at about the same size in Pacific hake, *Merluccius productus*, (O'Connell, pers. comm.). Thus, older fish may feed at night or in dim light. Indeed, older larvae of plaice were capable of feeding in the dark (Blaxter, 1969). Yet, young Pacific hake (before rod recruitment) and young cod (of unknown rod appearance) feed intensively after sunset (Sumida and Moser, 1980; Ellertsen *et al.*, 1980). The role of bioluminescence should be considered.

Chemical stimuli may be a factor for location of prey by larval fish. For example, herring larvae show increased activity when extracts of *Balanus*, *Artemia* or herring are added to their tank (Dempsey, 1978) and northern anchovy appear to locate dense patches of *Gymnodinium* prior to eye pigmentation (Hunter and Thomas, 1974).

Distribution

Our knowledge of larval distribution in time and space is extremely limited. Diurnal variations in larval distribution are attributed to activity, phototaxis, temperature preference, prey distribution, and current movements. Vertical distribution studies, like most field studies, suffer from the difficulty in determining the importance of net avoidance in sampling. Net avoidance results in fewer larvae collected by day, especially larger larvae; use of high-speed nets appears to decrease avoidance.

Results of vertical distribution studies of two Atlantic species, yellowtail flounder and haddock, show that young larvae may have a different distribution than older larvae. The young larvae of both species did not migrate and remained below a thermal gradient; yellowtail flounder remained at 20-24 m, between the shallow and deep thermal gradients (Smith *et al.*, 1978), and haddock seemed to occur below the thermocline (Miller *et al.*, 1963). Older haddock (8-20 mm) did not migrate and appeared to be more abundant within the limits of the temperature discontinuity layer while older yellowtail flounder (4-10 mm) migrated as much as 15-34 m, crossing two separate 5° C thermal gradients. Ahlstrom (1959), on the other hand, found that the species he studied in the California Current did not move across the thermocline, a gradient of 4-8° C; offshore, larval Pacific mackerel and jack mackerel were observed in the upper 30 m and Pacific sardine and northern anchovy ranged deeper, to 50 m. The range in temperature where the majority of larvae were collected was restricted to 2° C for jack mackerel, 14-16° C; 3° C for northern anchovy and Pacific mackerel, 14-17° C; and 4° C for Pacific sardine, 13-17° C.

Current measurements by Smith *et al.* (1978) seemed to indicate that at night the yellowtail flounder larvae would be caught in the wind-driven surface layers, and during the day, at mid-depth, they would be transported in the opposite direction, resulting in relatively localized settling of the demersal stages.

An adaptive advantage of vertical migration for larval fish would be to accompany the diel migration of prey, and some larvae (Pacific hake, Sumida and Moser, 1980; cod, Ellertsen *et al.*, 1980) do show high post-sunset peaks in feeding incidence. But Smith *et al.* (1978) analyzed larval stomach contents and concluded that the daily movements of yellowtail flounder were not related to feeding.

Vertical migration may be an energy saving device. Northern anchovy (11 mm SL) that are below 10 m during the day migrate to the surface at night to fill their swim bladders; for larvae 13.5 mm and larger, the energy saved by using the swim bladder to maintain position in the water column at night exceeds the energy used to migrate to the surface (Hunter and Sanchez, 1976). Another advantage of these nightly migrations may be that they concentrate young larvae at the surface, thus increasing visual contacts that may facilitate schooling behaviour which begins at about 12 mm SL (Hewitt, 1980; Hunter, in press).

PREY

Size

The dimensions of prey organisms relative to larval fish mouth size are important variables which require consideration in any modelling effort. The size (usually measured at maximum width) of the prey eaten by fish larvae is a function of larval mouth width; within species mouth width is related to length, but mouth widths vary between species (Arthur, 1976; Beyer, 1980; Hunter and Kimbrell, 1980; Hunter, in press). For example, mouth width of northern anchovy and Pacific mackerel at first feeding is approximately the same size, 0.20 mm. But, between 5-15 mm SL, mouth width of Pacific mackerel rapidly increases in size; northern anchovy mouth also increases in size with age, yet at the same SL, northern anchovy mouth width averages about 30 percent smaller than Pacific mackerel width (Hunter, in press).

Although mouth width limits the maximum prey size, in nature fish larvae often do not eat maximum size prey. For example, at 14 mm Pacific mackerel have a mouth width of 1 mm; particles up to 0.8 mm are found in their guts, but the mean diameter of prey eaten by larvae in the sea was only 38 percent of their mouth width (i.e. 0.34 mm, Hunter and Kimbrell, 1980). Anchovy at the same standard length have a mouth width of 0.7 mm, and the maximum size prey observed in anchovy guts was 0.3 mm (Arthur, 1956; de Ciechomsky, 1967). Deviations are greater for hake larvae. Mouth width of 5 mm Pacific hake is 0.6 mm, and the mean width of prey eaten was about 0.08 mm, 13 percent of hake-mouth width (Sumida and Moser, 1980). Beyer's (1980) model of feeding success of clupeid fish larvae shows why optimum prey size, that allows the highest feeding success, is less than the maximum potential prey size determined from mouth measurements. However, there is a tendency for larvae in the sea to feed on progessively larger prey as they grow (Marak, 1960; Shelbourne, 1953; Rojas de Mendiola, 1974; Arthur, 1956). Furthermore, the dynamic population model of Jones and Hall (1974) postulates that cohorts of cod and haddock larvae must be spawned in the proper time to grow up with a cohort of their copepod prey (*Calanus sp.*).

In the laboratory it was found that size of prey fed to larvae must increase for larvae to grow at maximum rates. Small food particles (*Gymnodinium*; Table 3) sustained northern anchovy for more than two weeks, but growth was reduced (Lasker *et al.*, 1970). Feeding northern anchovy a larger particle (*Brachionus*) increased the growth rate (Theilacker and McMaster, 1971), however copepods were soon required for anchovy to attain maximum growth and survival through metamorphosis in the laboratory (Hunter, 1976). Hunter and Kimbrell (1980) described a similar increase in required particle size for rearing Pacific mackerel, as has Stepien (1976) for sea bream, Ware *et al.* (1980) for the anchoveta, *Engraulis ringens*, Jones *et al.* (1974) for turbot, *Scophthalmus maximus*, and Houde (1978) for three species of subtropical marine fish.

It should be stressed that both large- and small-mouth larvae eat small, more ubiquitous prey and that it is possible that fish larvae can eat enough small prey to meet metabolic demands for several days. This is the case with larval jack mackerel in the laboratory. Jack mackerel (large-mouth larvae) fed *Gymnodinium* from the onset of feeding (day 5) to age 12 days were the same size and as "healthy" (determined by histological assessment) as larvae eating *Gymnodinium*, *Brachionus* and copepods (Theilacker, unpubl.). However, northern anchovy fed on a *Gymnodinium* diet grew at maximum rate for three days only (Lasker *et al.*, 1970).

Beyer and Laurence (1980) conclude from their model of growth and mortality of larval herring that as larva reach certain sizes the energetic cost of each attack exceeds the gain from ingesting smaller food particles; this size depends upon the larva's metabolic requirements, which are both genetically and environmentally imposed.

Table 3. Prey size and caloric content.

Particle	Width (µm)	Dry wt. (µg)	Calories	Reference
Gymnodinium splendens naked dinoflagellate	50	-	0.00005	Hunter 1977
Brachionus plicatilis rotifer	133	0.16	.00085	Theilacker and McMaster 1971
Copepods[1] nauplii	200	0.80	.0042	Laurence 1977
nauplii	250	1.30	.0068	"
copepodid	600	15.40	.0809	"
nauplii		0.15		Houde and Schekter 1980
Artemia nauplii	236		.0096	Hunter 1977

[1] Copepod weight and fat varies seasonally causing caloric variations.

Selection

There is evidence for selection by food type. Gut analyses indicate that field-collected jack mackerel less than 10 days of age may select brightly coloured harpacticoid copepods (*Microsetella*, *Oncaea*, *Corycaeus*) (Arthur, 1976), and laboratory-reared jack mackerel may either be unable to catch or may reject *Labidocera* nauplii in favour of *Acartia* and *Paracalanus* (Devonald, pers. comm.). Although naupliar body size, .06-.09 mm diameter, of *Labidocera* and *Acartia* is similar, *Labidocera*'s appendages are 2-3 times longer than *Acartia*'s appendages; hence, *Labidocera* nauplii may be too large to ingest, or, owing to larger appendages, simply too fast to catch. However, most evidence points to selection related to particle size (Stepien, 1976; Uotani *et al.*, 1978; Hunter, in press). It is reasonable that larval fish exhibit little selectivity for food type; if food particles are rejected, selectivity costs energy. Something must be gained by being selective; selection of large food particles offers a gain, i.e. more calories ingested per energy expended (as particle diameter increases 2.5 times, calories increase by a factor of 10; Hunter, in press; Table 3). In the field, large-mouth larval Pacific hake, 3-8 mm contained large numbers of small organisms; however the large adult copepods that they ate accounted for 74 percent of the volume (hence, 74 percent of the calories) of food eaten (see table below, from Sumida and Moser, 1980).

	Range max.width (um)	Mean food volume (10^6 um^3)	Standard deviation (10^6 um^3)	Frequency	Frequency x volume (10^9 um^3)	% of total volume
Copepod eggs	50-100	0.364	0.083	674	0.24534	0.7
Copepod nauplii	40-300	4.013	5.148	441	1.76973	5.3
Copepodites	80-450	14.698	24.308	393	5.77631	17.4
Adult copepods	110-600	57.418	54.850	426	24.46007	73.8
Other	40-550	49.401	107.783	18	0.88922	2.7
					Σ = 33.14067	

Density

Critical prey density, the food concentration required for first-feeding larvae to initiate feeding, is a component of larval survival which has caused great controversy among scientists involved with larval fish research. Laboratory experiments to date have usually been done with somewhat uniform and high concentrations of prey and a relatively high density of larvae. Prior to 1970, threshold food-density experiments in the laboratory were considered "successful" when there was high survival and fast growth of larvae. Fishery biologists accepted that field-mortality rates in excess of 90 percent during the egg and larval stages produced healthy year-classes, but in the laboratory biologists demanded high survival rates. The critical prey densities determined by these experiments were higher than densities measured in the integrated natural larval habitats. Lowest survival rates in laboratory feeding experiments (Table 4) were usually at particle densities reported to be common in the field (Table 5); thus, these experiments may represent levels characteristic to the field. Houde's (1974; 1978) work on three species of subtropical fish reported significant survival at low prey densities; sea bream required 50 plankters/l and lined sole required 100/l (Table 4). These food levels are common in coastal and partly enclosed areas (Table 5; from Hunter, in press, and Houde, 1978).

Critical prey densities determined in the laboratory and presented in Table 4 are constant prey concentrations required for optimum survival from first feeding to 2-7 weeks of age (with the exception of the herring experiment that was conducted with older larvae). These densities vary among species and will also vary with life stages within species. For example, Laurence (1977) showed that the initial required prey density for winter flounder to meet metabolic requirements (including growth) was 800 nauplii/l; after successful feeding behaviour was established, the critical density decreased to 300 nauplii/l. Then as growth and metabolic demands increased, critical density increased to 600 nauplii/l. Laurence also showed that at the onset of feeding, winter flounder started feeding at 10 and 100 nauplii/l but did not survive longer than two weeks. Thus, threshold densities for first feeding (Table 4) are not indicative of particle concentrations required for survival during all life stages.

Laboratory experiments reveal that variations in prey density affect larval fish feeding rates, ration, activity, evacuation time, growth rates (time to metamorphosis), and gross growth efficiencies (Werner and Blaxter, 1980; Houde and Schekter, 1980; Wyatt, 1972; Laurence, 1977; Hunter and Thomas, 1974). Generally, as prey density increases, feeding rates, ration and growth rates increase (Table 6); gross growth efficiencies may increase or decrease (Table 9) and activity, evacuation time (Table 10) and time to metamorphosis decrease. Due to differences in experimental technique, comparisons of studies that depend on controlled prey levels need some qualifications. These restrictions are discussed in the final section of this review, wherein laboratory techniques and facilities for obtaining relevant physiological data are described, and comparative observations are tabled.

Table 4. Food density thresholds for 8 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	Survival at various food densities: Percent survival	Reference
PLAICE							
Pleuronectes platessa	5	14	*Artemia* nauplii	50 (larvae)	1,000	72[1]	Wyatt 1972
s					500	72	
					200	54	
					100	32	
NORTHERN ANCHOVY							
Engraulis mordax	10.8	12	Wild zooplankton (nauplii)	10 (eggs)	4,000	51	O'Connell & Raymond 1970
s					900	12	
					90	0.5	
					9	0	
BAY ANCHOVY							
Anchoa mitichilli	76	16	Wild zooplankton (nauplii-copepodites)[3]	0.5 - 2 (eggs)	5,000	64	Houde 1978
s					1,000	48	
					100	5	
					50	0-12	
SEA BREAM							
Archosargus rhomboidalis	76	16	"	0.5 - 2 (eggs)	500	72	" "
s					100	37	
					50	13	
					25	7	
					10	4	
LINED SOLE							
Achirus lineatus	38	16	"	0.5 - 2 (eggs)	1,000	54	" "
s					100	13	
					50	1	
HADDOCK							
Melanogrammus aeglefinus	37.8	42	Wild zooplankton (nauplii)	9[4] (larvae)	3,000	39	Laurence 1974
s					1,000	22	
					500	3	
					100	0	
					10	0	
HERRING							
Clupea harengus	20	21-63 58-84	*Artemia*	8	3,000	4-8	Werner & Blaxter 1980
					1,000	3-12	
					300	0-8	
					100	0-12	
					30	0-1	
WINTER FLOUNDER							
Pseudopleuronectes americanus	64	49	Wild zooplankton (nauplii)	9[4] (larvae)	3,000	34	Laurence 1977
					1,000	4	
					500	3	
					100	1	
					10	0	

[1] Survival was 100% at 50/L for first 7 days without a decrement in length; see also Riley (1966).

[2] Estimated food density for indicated survival levels.

[3] Plankton blooms of Chlorella sp. and Anacystis sp. maintained in rearing tanks.

[4] Estimated by adjusting for hatching success.

[5] Hunter, in press.

Table 5. Average[1] densities of microcopepods in the sea

	Average density of microcopepods (number per liter)				
	nauplii	copepodites	total	Location	Reference
OPEN SEA	13	2	15	Southeast Coast of Kyushu	Yokota et al. 1961
	22	36	58[2]	California Current	Beers and Stewart 1967
	40	5	45[2]	Southern California near shore	Beers and Stewart 1970
	27	7	34[3]	Eastern Tropical Pacific	Beers and Stewart 1971
	36	1	37	California Current	Arthur 1977
PARTLY CLOSED	76	19	95	Azov Sea	Duka 1969
	-	-	223[4]	Gulf of Taganrog	Mikhman 1969
	40	-	40	North Sea (0-10 m)	Ellertsen et al. 1980
	20-30	-	25	North Sea (10-20 m)	"

[1] Mean for all stations and years given in publication listed in table (Hunter, in press).

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

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

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

* *

Reported concentrations of some potential larval fish food organisms from coastal and estuarine areas. (Table 10 from Houde 1978)

Reference	Place	Organisms	Concentration
Burdick (1969, cited in May, 1974)	Kaneohe Bay, Hawaii	copepod nauplii	50-100/l common 200/l sometimes present
Duka (1969)	Sea of Azov	Acartia clausi nauplii	62-65/l
		Other copepod nauplii and copepodids	> 30/l
		Total	> 90/l
Mikhman (1969)	Gulf of Taganrog, Sea of Azov	Early stages of copepoda	39-546/l
Hargrave and Green (1970)	Two eastern Canada estuaries	Copepod nauplii and copepodids	> 60/l
Reeve and Cosper (1973)	Card Sound, South Florida	Copepod stages 20-200 µm in breadth	range 23-209/l mean for 28 collections 72/l
		Tintinnids	range 40-369/l
Heinle and Flemer (1975)	Patuxent River estuary	Eurytemora affinis nauplii & copepodids	>100/l frequently >2,000/l occasionally
Houde (unpublished data)	Biscayne Bay, South Florida	Copepod nauplii and copepodids <100 µm in breadth	usually 50-100/l
		Tintinnids	frequently >100/l

Table 6. Feeding rates at various prey concentration.

Species	°C	Age (d; mm; µg)	Container volume (liters)	Prey type	Prey concentration (#/l)	Feeding rate (#/h)	% body wt. eaten per day	Reference
YOUNG LARVAE								
Pacific sardine Sardinops sagax	16 "	first-feeding 15-17 mm	500 "	nauplii[1] Artemia	max. max.	2 60[2]		Schumann 1965
Northern anchovy[3] Engraulis mordax	17 "	4 d; 20 µg 10 d; 70 µg	500 "	Rotifer[4] "	10,000- 20,000	15.0 46.0	144 126	Hunter 1972
Bigeye anchovy[6] Anchoa lamprotaenia	26 "	2 d; 3.6 mm 8 d; 5.5 mm	9.5 "	nauplii[1-5] "	100 "	43.0 70.0	440 197	Chitty 1980
Bay anchovy[6] Anchoa mitchilli	26-28 " "	4 d; 4.8 µg 4 d; 13.4 µg 4 d; 17.4 µg	76 " "	nauplii[1-5] " "	50 100 1000	0.5 2.4 19.3	20 39 221	Houde & Schekter 1980
Sea bream[6] Archosargus rhomboidalis	26-28 " "	4 d; 13 µg 4 d; 12.7 µg 4 d; 18.2 µg	76 " "	nauplii[1-5] " "	50 100 1000	0.9 1.3 9.0	21 28 158	Houde & Schekter 1980
" "	23-26 29	2-3 d 2-3 d	75 "	nauplii[1-5] "	1000 "	8.0 18.0	199	Stephen 1976
" "	23 26-29	16 d 16 d	75 "	nauplii[1-5] "	1000 "	54.0 150.0		"
Pacific mackerel Scomber japonicus	19 " "	3 d; 38 µg 4 d; 43 µg 5 d; 85 µg	200 " "	Rotifers[4] " "	137,000 47,000 198,000	14 20 45	70 89 102	Hunter and Kimbrell 1980
Striped knifejaw[7] Oplegnathus fasciatus	22 "	7 d 3.9 mm 13 d; 5.2 mm	- -	Rotifers "	5,000 "	6 44		Fukusho 1979
Lined sole[6] Achirus lineatus	26-28 " "	4 d; 8.7 µg 4 d; 11.4 µg 4 d; 13.5 µg	76 " "	nauplii[1-5] " "	50 100 1000	0.2 1.1 12.0	6 21 80	Houde & Schekter 1980
Plaice Pleuronectes platessa	7			Rotifers		35		Howell 1973
OLDER LARVAE						Ration # food items/ fish		
Herring[6] Clupea harengus	9	4 wks.	20	Artemia	30 100 300 1000 3000	5 4.5 4 6 5		Werner and Blaxter 1980
" "	9	5 wks.	20	Artemia	30 100 300 1000 3000	6 6 8 8 7		"
						Ration (dry wt; ug)		
Winter flounder Pseudopleuronectes americanus	8	2 wks.	64	nauplii[1]	100 500 1000 3000	1 2 1 2		Laurence 1977
" "	8	5 wks.	64		100 500 1000 3000	11 19 25 23		"

[1] Wild plankton - copepod nauplii
[2] 3.5 strikes/min for 10 min until gut full; then 1/min
[3] estimated from number strikes and adjusted for percent successful capture
[4] dry wt = 0.16 µg (fresh material)
[5] dry wt = 0.15 µg (fresh material)
[6] larval dry wts determined for preserved samples
[7] hatch at 2.2 mm; gut length intermediate between Pacific mackerel and jack mackerel; growth rate begins at 0.2 mm/d and increases to 0.5 mm/d (similar to anchovy, Table 2).

Houde and Schekter (1980) compared feeding rates, ration and growth among three marine fish, bay anchovy, sea bream and lined sole, fed at several low but constant prey concentrations (Table 6). Feeding rates of the three species increased with increasing prey density; however, at the onset of feeding, the sea bream, a sparid, was more effective at capturing prey at the lowest density, 50 prey/l, than anchovy or sole. But, anchovy had the highest feeding capability at 50 and 100 prey/l after the first few feeding days when anchovy had increased their prey-capturing efficiency. Sea bream had the best potential to increase growth rates at higher food levels, 500-1 000/l, and were capable of higher survival at low prey densities, 100/l (37 percent survival) than anchovy or sole (5-13 percent survival; Table 4). Thus, although ration increased with increasing prey density, the feeding abilities of these three species, that differ in morphology and behaviour, varied at the different prey densities.

Feeding rates of older herring larvae (Werner and Blaxter, 1980) and older winter flounder (Laurence, 1977) fed at several prey levels also increased with increasing prey density until a maximum ration was achieved. This maximum ration was achieved in both cases at 1 000 prey/l. Growth rates within species were the same at prey densities from 300 to 3 000 prey/l, but were significantly less at 100/l. Laurence (1977) found that survival of winter flounder increased with increasing prey levels, but Werner and Blaxter (1980) did not find this with herring larvae. Perhaps, suitability of prey type was a factor affecting survival; winter flounder were eating copepods, a natural prey, and herring were eating *Artemia*.

In addition to depending on prey density, feeding rates also depend on life stage and temperature. A 3-6°C increase in temperature may triple feeding rates (Stepien, 1976), and a 5-6 day increase in age of young larvae raises feeding rate 2-7 times (Table 6).

At high prey densities of *Artemia* nauplii (5 000/l), herring larvae exhibited reduced ingestion of the prey; furthermore, the prey were evacuated faster from the stomach and were not complete digested or assimilated (Werner and Blaxter, 1980). Houde and Schekter (1980) also recorded a decrease in gross growth efficiency at the highest prey concentrations for the three species they tested (Table 9).

Distribution

One of the major questions arising from the evaluation of laboratory feeding experiments, such as those mentioned in the preceding sections, is where areas exist in the field with the necessary concentrations of esculent food for larval fish. The sampling gear most often employed (pumps and plankton nets) sample large volumes of water and gives results that average numbers of organisms over depths or distances. Despite these sampling difficulties, Lasker (1975) found natural occurrences of the high prey densities (20 000-40 000/ml) that are needed by northern anchovy to initiate feeding. The prey particles, a dinoflagellate, *Gymnodinium splendens*, occurred in water taken from the chlorophyll maximum layer. Similar bioassay experiments with cod larvae showed feeding at 30-40 nauplii/l. The maximum naupliar biomass was found at 0-15 m and 60-80 percent of the larvae sampled from these depths had 2-3 nauplii in their guts (Ellertson *et al.*, 1980). Owens (this volume), and Mackas (1976) have attempted to apply more sensitive and discrete sampling techniques. They have found microstratification of esculent food particles in appropriate numbers to support larval fish survival. Further use of these techniques should lead to more information on prey distribution on the scale relevant to a larval fish.

Vlymen (1977) used an empirically based mathematical model to demonstrate the importance of food microstructure (geometry) and behaviour, and how they affect growth of northern anchovy larvae. He found that the critical habitat of an anchovy larva should contain between 14 and 32 particles/ml. Within this range the numbers represent a structured environment with 14 particles/ml in the interpatch areas and 32 particles/ml in the critically dense regions of contagion.

Lasker and Zweifel (1978), using a modified version of Vlymen's model (1977) for northern anchovy larval growth, determined that "it is not the absolute concentration of the large particles that govern their capture by the larva, but rather their concentration relative to the larger number of small particles in the larval environment." In this simulation, large particles made very little contribution to survival when the immediate environment of the first-feeding larva contained 40 small particles/ml. Because it is more likely that there will be aggregations of small particles than large ones, survival of first-feeding larvae would be enhanced by a favourable number of patches of that density within their habitat.

In the laboratory, it has been shown that larval survival is increased by exposure to a food patch; however, larval behaviour to patch situations differ. Houde and Schekter (1978) found that during a 13 hour feeding day a short, 2-3 hour patch exposure increased survival of larval sea bream from 7.5 percent (on day 16) to 20 or 30 percent. On the other hand, bay anchovy larvae needed a 9 hour exposure for 10 percent survival. Thus, larval sea bream appear to be more capable of taking advantage of periodic patch conditions than bay anchovy.

LARVAL MODEL PARAMETERS AND REQUISITE LABORATORY RESEARCH

Existing larval survival models were developed from basic energetic principles based on laboratory and field studies. These models consist of conjectures concerning the manner in which excess energy (i.e. the difference between the energy expended in capturing and processing food and energy gained) results in growth and/or survival. Thus, basic physiological data are the bases for the models. In spite of the sophisticated mathematics of the models, the results can be worthless if the physiological data is gathered through inaccurate or biasing techniques. This discussion describes some parameters used in models and the techniques used to measure these parameters.

Rearing containers

Container size may be a critical variable in larval fish studies. Size of container affected results in jack mackerel rearing experiments; larvae grew faster and were in better nutritional condition in 100 l than in 10 l containers (Theilacker, 1980c). Size of container also affects swimming speed. For example, swimming speed of laboratory-held larval herring was less than *in situ* contained herring—0.9 cm as compared to 1.59 cm (von Westernhagen and Rosenthal, 1980). Likewise, northern anchovy swim 3-4 times faster in large than in small containers (Hunter, pers. comm.; see Swimming speed).

Metabolic rates

The sensitivity of the techniques used to determine oxygen consumption is limited by experimental container volume. Volumes need to be small in the case where oxygen consumption rates are low and very small total changes are expected; hence fish larvae are definitely confined and movement is probably restricted. Experimentalists that use Warburg (10 ml) or Winkler (40-60 ml) techniques (Table 7) usually assume that the respiration estimates are somewhere between "resting" and "active". Vlymen (1974), in his estimate of swimming energetics of northern anchovy, suggested that activity in the confines of a small container would be inhibited and below natural levels. However, it has been shown that average respiration rates (determined by Warburg) of groups of early stage Pacific sardine eggs were the same as rates determined for single, late stage eggs housing "active" larvae (Lasker and Theilacker, 1962). Because fish eggs probably are not affected by restrictive containers, this observations shows that shaking Warburg flasks, required to equilibrate oxygen between water and air, may induce "active" metabolism.

Variation in "resting" (standard) metabolic rates among poikilotherm species can sometimes be explained by differences in experimental temperature. The temperature coefficient of respiration (Q_{10}, a measure of the increase in rate of an activity for a 10°C temperature difference) is typically about 2-4 (Giese, 1962). The Q_{10} of respiration for Pacific mackerel (at unknown activity) between 18° and 22°C is about 5 (Table 7). But, differences in metabolic rates between anchovy and mackerel (Table 7) cannot be explained by differences in temperature and must be caused by differences in activity and metabolic demands. Hence, knowledge of activity is needed to make meaningful comparisons of metabolic rates among species. Activity has been shown to increase respiration rates up to 3.5 times for Pacific sardine larvae (Lasker and Theilacker, 1962) and 5-10 times for larval herring (Holliday *et al.*, 1964).

Because activity increases respiration rates, extrapolations of laboratory-determined respiration rates to the field conditions are difficult due to our inability to accurately measure activity in the field. Ware (1975) suggests using a value of 2.5 times "standard" ("resting") metabolic rate to estimate "active" field metabolism. However one value will not likely account for interspecific differences in metabolic demands, i.e. such as differences in activity at first feeding of "beat" and "glide" swimmers like Pacific sardine and

Table 7. Respiration rates.

Species	°C	Age (d; mm; µg)	ul/mg/hr Egg: Resting	Egg: Activity unknown	Egg: Active	Larva: Resting	Larva: Activity unknown	Larva: Active	Reference
Pacific sardine[1]	14	-	0.8		1.8				Lasker and
Sardinops sagax	14	1-2 d				1.3		2.7	Theilacker 1962
Northern anchovy[2 3]	17			1-1.5					Theilacker
Engraulis mordax	17	1-3 d					3.5		(unpubl.)
	17	4-30 d[4]					4.1(3.1-6.9)		
	17	15 mm; 30 d[5]					6.7		
Herring	8	1-10 d				2.3		10-23	Holliday et al.
Clupea harengus									1964
Pacific mackerel[3 6]	18	3.7-17.9 mm					6.1		Hunter and
Scomber japonicus		3.2-10.5 mm					11.4		Kimbrell 1980
Rockfish[6]									
Sebastes rhodochloris	11	Late		1.8					Moser 1967
Sebastes eos	11	Late		2.0					
Winter flounder[6]	5	7 d; 12 µg					5.5[7]		Laurence 1975
Pseudopleuronectes americanus	5	7 wk; 250 µg					4.8[7]		
	5	7 d; 12 µg					6.0[8](2.8-8.8)		
	5	7 wk; 250 µg					6.5[8](3.4-9.7)		
Pollack[3]	4	11-14 d; 90-120 µg				1.4-			Clarke
Theragra chalcogramma						3.0			(pers. comm.)
Striped bass[6]	18	0 d		7.5					Eldridge
Morone saxatilis		5 d					5.4[7]		(pers. comm.)
		10 d					4.6		
		15 d					4.2		

[1] determined for individual eggs and larvae
[2] Winklers; 40-60 ml
[3] weight-specific rates; slope = 1
[4] N = 43
[5] 230 ml, no agitation; n = 2
[6] Warburgs; <10 ml
[7] weight-specific rates decreased; these rates taken from weight-specific metabolism regression
[8] median rates taken from actual data points and range

northern anchovy that rest 50-60 percent of the time (Schumann, 1965; Hunter, 1972) and the continuous swimming Pacific mackerel and jack mackerel (Hunter and Kimbrell, 1980; Theilacker, unpubl.). These species-specific behaviours point to large differences in required calories at the onset of feeding.

Growth

A comparison of laboratory growth of the California Current species illustrates species-specific differences in growth rates (Figure 1; Table 8). At similar temperatures, Pacific mackerel reach metamorphosis twice as fast as Pacific sardine and northern anchovy. Sardine and anchovy reach metamorphosis at about the same size, but initially larval sardines grow faster than larval anchovies, hence sardines reach metamorphosis at an earlier age. Growth rates of larval jack mackerel are slow; although jack mackerel transform at the same size and probably similar weight as Pacific mackerel, metamorphosis occurs about two weeks later than in Pacific mackerel. Zweifel and Lasker (1976) have shown that the Laird-Gompertz growth function may be used to define the genetically determined and dynamically changing growth rates in the early life stages of many fish.

Measuring changes in length is convenient for estimating growth, but it has been shown that shrinkage in length of laboratory-preserved larvae differs from shrinkage of field-collected larvae (Theilacker, 1980b); hence, to compare animals at the same developmental stage there is a need to intercalibrate laboratory and field measurements. For northern anchovy larvae, difference in shrinkage between laboratory-preserved larvae (pipetted directly into Formalin) and netted and preserved larvae (similated field-collected) of the same initial size decreased with age. For example, 3 mm larvae that were netted and preserved in Formalin shrank 15 percent more than 3 mm larvae that were laboratory preserved, but shrinkage of 20 mm larvae was the same for both treatments (Theilacker, 1980b). Thus, for estimates of larval growth, shrinkage calibration is important for small larvae. Shrinkage appears to be species specific; shrinkage of body parts is not the same among larvae with similar body forms (e.g. compare mackerels in table below).

	Laboratory formalin			10 min. net treatment			Formalin preservation after net treatment		
	SL	HL	BD	SL	HL	BD	SL	HL	BD
Northern anchovy	.92	.91	.90	.81	.91	.70	.78	.88	.67
Jack mackerel	.92	.91	.80	.90	.91	.84	.87	.88	.81
Pacific mackerel	.92	--	--	.90	.90	.98	.86	.86	.94

Ratio = treated size/live size; 1.00 = no shrinkage

-- = no data

SL = standard length; HL = head length; BD = body depth measured at anus

A better estimate of growth than the change in larval length is the change in dry weight. Measuring changes in dry weight allows estimates of energy incorporated during growth and is more suitable for interspecific comparisons of growth. For example, at 20 days of age, northern anchovy raised at 17°C and Pacific mackerel raised at 16.8°C are about the same length, 10 mm SL, but their weights differ by a factor of 6, anchovy weigh 0.3 mg and mackerel 1.9 mg (Hunter, in press). Thus, feeding of Pacific mackerel during this 2-3 week period must be more intense and/or the size of the food eaten must be greater (hence more calories/food item) than food eaten by nortnern anchovy.

Table 8. Growth.

Species	°C	Growth rate (mm/d) Days 4-15[1]	16-30	31-40	41-50	Reference	Metamorphosis Size (mm SL)	Age (days)	Reference	1 year Size (mm SL)	Reference
Pacific sardine, *Sardinops sagax*	16-19	1.0	0.5	0.5	0.5	(4)	31-35	45-50	(4) (8)	120	(8)
Northern anchovy, *Engraulis mordax*	17	0.2	0.5	0.5	0.5	(5)	34-40	50-60 90	(9) (11)	95-115[2]	(11)
Jack mackerel[3] *Trachurus symmetricus*	15	0.1	0.2	0.5	1.0	(6)	11-16	40	(10)	200	(12)
Pacific mackerel, *Scomber japonicus*	16.8	0.1	1.0	-	-	(7)	15	25	(7)	272	(13)

[1] Hatching = day 0

[2] Size at 1 year = 115 mm at low anchovy biomass; high-biomass size = 95 mm

[3] Large-egg larvae

[4] Kimura 1970

[5] Kramer and Zweifel 1970

[6] Theilacker 1978

[7] Hunter and Kimbrell 1980

[8] Ahlstrom 1966

[9] Hunter 1976; lab

[10] Ahlstrom and Ball 1954; Theilacker (unpubl.)

[11] Methot (pers. comm.); field, age estimated from daily otolith increments

[12] Wine and Knaggs 1975

[13] Knaggs and Parrish 1973

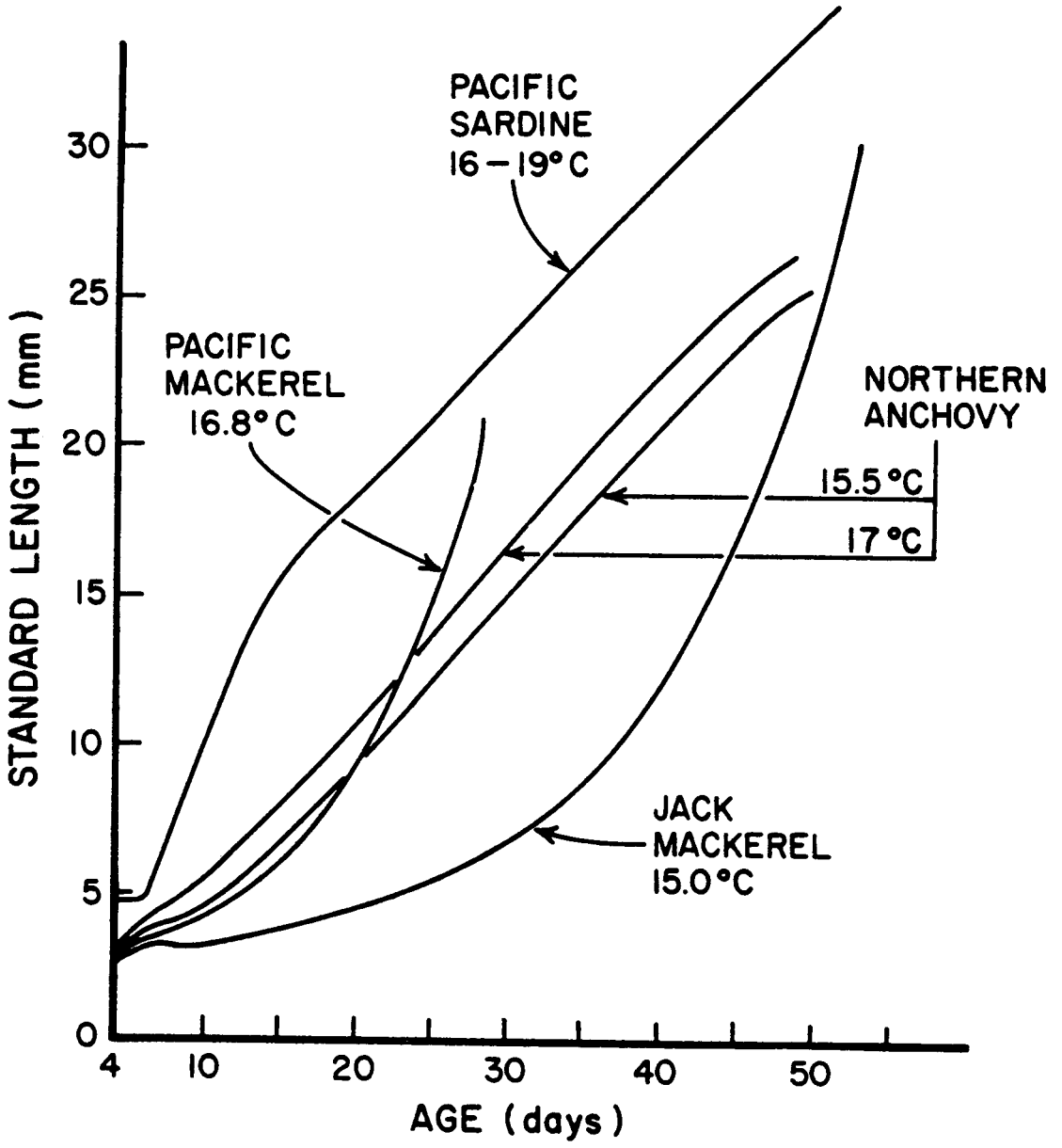

Figure 1. LABORATORY REARED FISH

It is important that dry weights be determined with fresh samples. Formalin perservation caused a 30 percent decrease in dry weight of larval sardines, and preservation in ethyl alcohol decreased dry weights of Pacific mackerel by 50 percent (30-80 percent) (Theilacker, unpubl.). These determinations were for young, 4-6 mm SL larvae. Methot (pers. comm.) weighed field-collected, alcohol-preserved anchovy to determine weight at age, estimated by increase in otolith increments. His weights for 15-30 mm SL larvae were 30-40 percent less than the fresh dry weights determined by Hunter (1977). Thus, weight loss in alcohol preservative does not appear to decrease with increasing larval size.

Laurence (1978) measured unpreserved dry weights for seven species of larval fish common to the American east coast. He presented his data as linear regressions, $\log_{10}$ weight on $\log_{10}$ length. The species were from different taxonomic families (Clupeidae, Gadidae, Sparidae, Bothidae and Pleuronectidae) but there were no obvious species-specific correlations with the length-weight regressions. The length exponents ranged between 3.78-4.77 and averaged 4.15, thus weight was proportional to length to the fourth power. Length-weight relations for northern anchovy and Pacific mackerel are curvilinear (Hunter, 1976; Hunter and Kimbrell, 1980), therefore extrapolations of linear regressions of length-weight measurements are probably inappropriate.

Prey density

Because variations in prey density affect larval fish feeding rates, ration, activity, evacuation time, growth rates, and gross growth efficiencies; accurate estimates of prey levels are needed for comparisons of experimental results. Many young larvae are delicate, and extremely susceptable to mechanical injury; thus, experimental rearing containers are not mixed to randomize prey distribution until larvae are older. As a result, in experiments that control prey levels, the effective density available to larvae must vary; at low prey levels, food patches may form and thereby elevate the actual density of food encountered by some larvae. In addition, some larval rearing techniques include use of high algal concentrations ("green" water) in rearing containers with invertebrate prey and fish larvae (Stepien, 1976; Houde and Schekter, 1980). In these experiments, it is difficult to assess whether consumed algae directly provided calories to fish in addition to the prey calories; this is particularly important at low prey levels. Inter-experimental comparisons of life functions that may be affected by prey concentration and media differences (i.e. algal content) are difficult and lead to uncertainties regarding their general comparability.

Growth efficiencies

Because it is presently impossible to accurately measure metabolic rates during various swimming and feeding behaviours and to describe behaviour and activity in the field, a comparison of interspecific growth efficiencies may elucidate those species that maximize their growth relative to others in similar environments and feeding regimes. A high growth efficiency (calories of growth/calories consumed) indicates efficient assimilation of food energy for growth, with little being lost by excretion or used in respiration, thus conservative expenditure of energy for swimming and feeding. Calories of growth can be estimated from daily increases in dry weight, and calories consumed can be estimated from the daily ration. Meaningful estimates of growth calories depend on whether energy expenditure for swimming and feeding is the same in the laboratory and the field. Laboratory and field age-length measurements are also needed.

Procedures used to estimate ration (calories consumed) for larval fish vary. Ration has been estimated by (1) feeding rate x weight of prey x hours feeding (Houde and Schekter, 1980; Stepien, 1976), (2) weight of stomach at capture x hours feeding/hours to clear gut (Laurence, 1977), or (3) weight of mean stomach contents x gastric evacuation rate x hours feeding + weight of mean stomach contents (Hunter and Kimbrell, 1980). Daily ration estimates in percent of body weight eaten per day range from 70-300 percent for larvae fed 1 000 or more prey/l (Table 9).

Table 9. Gross growth efficiencies.

	°C	Age (d; µg)	Prey density (#/L)	Container volume (liters)	Daily ration ug	Daily ration % body wt.	Gross efficiency (%)	Reference
Bay anchovy[1]	26	17 d; 200 µg	50	10	19	31	57	Houde & Schekter 1980
Anchoa mitchilli	"	15 d; 200 µg	100		37	51	32	
	"	11 d; 200 µg	1000 nauplii (wild plankton)		115	140	14	
Herring	-	12-22 d; 100-150 µg	14,000-20,000 rotifers	8			71	Eldridge et al. 1977
Clupea harengus pallasi								
Sea bream[1]	26	17 d; 200 µg	50	10	12	-	83	Houde & Schekter 1980
Archosargus rhomboidalis	"	15 d; 200 µg	100		31	42	38	
	"	10 d; 200 µg	500 nauplii (wild)		45	-	38	
" "	23-26	2-3 d	1000	75	14	68-147	33	Stepien 1976
	29	2-3 d	1000		32	199	16	
	23	10 d	1000		-	69	31	
Pacific mackerel[2]	19	3 d; 38 µg	157,000	200	27	70	20	Hunter & Kimbrell 1980
Scomber japonicus	"	4 d; 43 µg	47,000		38	89	37	
	"	5 d; 85 µg	198,000 rotifers		86	102	44	
Striped bass	18	15 d; 400 µg	10				13	Eldridge (unpubl.)
Morona saxatilis	"		100				15	
	"		500				20	
	"		1000				21	
	"		5000 Artemia				50	
	18	29 d	10				20	
	"		100				14	
	"		500				17	
	"		1000				19	
	"		5000 Artemia				32	
Lined sole	26	21 d; 200 µg	50	10	14	-	63	Houde & Schekter 1980
Achirus lineatus	"	17 d; 200 µg	100		20	29	52	
	"	12 d; 200 µg	1000 nauplii (wild)		74	~90	20	
Winter flounder[3,4]	8	2 wks.	500				10	Laurence 1977
Pseudopleuronectes americanus	8	7 wks.	nauplii-copepods				20	
	8	2 wks.				300	15	
	8	7 wks.	3000			30	33	

[1] Daily ration estimated from grazing experiments; dry weights determined with preserved larvae; wild plankton nauplii 0.15 ug, fresh dry wt.

[2] Ration from stomach contents and evacuation rate (discontinuous feeding).

[3] Ration from stomach contents and evacuation rate (active feeding).

[4] Net growth efficiencies.

Gut clearance times depend on feeding history; the time to a clear gut depends on the amount of food in the stomach (Werner and Blaxter, 1980) and it is more rapid at high food densities. Hence, gut clearance rates should probably be estimated from actively-feeding larvae. The technique used to avoid evacuation-time biases that may occur from discontinuous feeding (transferring larvae with full guts into tanks without food and subsequently noting the time taken to evacuate gut contents), is first to present larvae with natural prey to fill guts and then with dyed prey and note time to first dyed fecal material. Most experimentally-determined evacuation times (Table 10) are for discontinuous feeding.

From Table 10, the observed evacuation times ranged from 3-9 hours; time decreased with (1) increasing prey density (herring, Werner and Blaxter, 1980), (2) age (knifejaw, Fukusho, 1979; Pacific sardine, Arthur, 1956), and (3) temperature (herring, Blaxter, 1965; Table 9). Larvae of two *Anchoa* species (Chitty, 1980) deviate greatly from the "average", having evacuation times measured in minutes, 7-13, instead of hours. Schumann (1965) also noted a fast time, 3 minutes, for anchovy larvae fed *Artemia* nauplii to form a food plug at the anus in 15 mm northern anchovy (Table 10).

Some fish larvae are more capable of digesting certain prey types than other fish larvae. Although *Artemia* nauplii allow survival of herring and plaice, *Artemia* are an inferior food for northern anchovy; anchovy do not appear to digest *Artemia* until after gut differentiation (Hunter, 1976). Jack mackerel also may be unable to digest Artemia; mackerel defecate profusely when fed a diet of *Artemia* (Theilacker, unpubl.).

Gross growth efficiencies are not dependent on digestive efficiencies. Only Laurence's (1977) growth estimates in Table 9 are for net efficiency (assimilated calories/calories consumed); he assumed the coefficient of utilization to be 0.7.

It is well known that growth efficiencies of the young are higher than in older animals. Efficiency of yolk utilization (conversion of yolk to tissues) of fish embryos ranges between 50-79 percent (Pacific sardine 79 percent, Lasker, 1962; herring 50-74 percent, Blaxter and Hempel, 1966; herring 74 percent, Eldridge *et al.*, 1977). Growth efficiencies for exogenous feeding, on food not as well suited for assimilation as yolk, are lower (Table 9). Results from the few measurements of larval growth efficiencies in Table 9 are inconsistent. Efficiencies apparently decrease with (1) increasing prey density (Houde and Schekter, 1980), (2) age (Eldridge, unpubl.), and (3) increasing temperature (Stepien, 1976); apparent efficiencies may also increase with (1) increasing prey density (Laurence, 1977; Eldridge, unpubl.) and (2) age (Hunter and Kimbrell, 1980; Laurence, 1977). As a result, it is impractical to try to make interspecific comparisons.

The growth efficiencies for larvae fed 1 000 or more prey/l are fairly high, 14-41 percent. It seems reasonable that most of the food energy would be used in growth in larval fish. Faster growing individuals develop more quickly, hence rapidly growing larvae will become faster swimmers and more able to avoid predators at an earlier age.

Temperature

Many abiotic factors (temperature, light, salinity, currents) may influence growth of fish larvae. Because temperature is relatively easy to measure, there is more information on effects of temperature than on other factors. Temperature may affect larval fish by influencing (1) oxygen content of sea water, (2) nutrients that control algal blooms, (3) time, place and duration of spawning, (4) incubation time, (5) size at hatching, (6) efficiency of yolk utilization, (7) growth, feeding rates and time to metamorphosis, (8) behaviour and swimming speed, (9) digestion and evacuation, (10) metabolic demand, and (11) distribution (Table 11). Thus, in laboratory experiments designed to test any of the above eleven parameters, temperature must be rigidly controlled.

Table10. Evacuation; time to empty gut.

	°C	Age (d; mm; µg)	Prey density (#/L)	Time to fill gut (hr)	Time to empty gut (hr)	Reference
Pacific sardine Sardinops sagax	- - -	5.5 mm 6-9.5 mm 10-25 mm	field " "	0.15[1] - -	11 6 3	Arthur 1956
Herring[2] Clupea harengus	9	3-9 wks.	3,000-30,000 Artemia	1-3	3-4	Werner & Blaxter 1980
	"	3-9 wks.	30-300 Artemia	-	7+[3]	
" "	7 15	12d; 9 mm 12 d; 9 mm	- -	- -	8 4	Blaxter 1965
Northern anchovy Engraulis mordax	17 17	4-5 d 15 mm	20,000 rotifers; Artemia; field	0.5 -	- 5-6 <.05[4] 1-3	Hunter 1972 Moffatt, pers. comm. Schumann 1965 Arthur 1956
Big eye anchovy[2] Anchoa lamprotaenia	26	2 d 8 d	100[6] nauplii	0.1[5]	0.15[4] 0.12[4]	Chitty 1980
Bay anchovy[2] Anchoa mitchilli	26	2 d 8 d	100[6] nauplii	- -	0.22[4] 0.18[4]	Chitty 1980
Whitefish[7] Corygonus clupeaformis	14	19-20 mm	max[6]; nauplii	-	16 ½ in 6	Hoagman 1974
Striped knifejaw[7] Oplegnathus fasciatus	22 "	7-11 d; 3-4 mm 13-18 d; 5-8 mm	4,000-10,000 rotifers	0.5 -	6.5-9.4 2-2.5	Fukusho 1979
Pacific mackerel[7] Scomber japonicus	19	3-5 d	30,000 rotifers	<1.0	½ in 2	Hunter & Kimbrell 1980
Pacific hake Merluccius productus	-	3-11 mm	field	-	~11	Sumida & Moser 1980
Plaice Pleuronectes platessa	-	-	field	3	6	Ryland 1964
Winter flounder[2] Pseudopleuronectes americanus	8	-	1,000-2,000[6] nauplii	-	6.6	Laurence 1977

[1] Schumann 1965; 15 mm; Artemia
[2] evacuation determined during active feeding
[3] complete digestion; little-no evacuation
[4] incomplete digestion
[5] to 50% fullness
[6] wild plankton-copepod nauplii
[7] evacuation determined during discontinuous feeding

Table 11. Effect of temperature.

HATCHING TIME	1)	At 13° Northern anchovy hatch about 1 day earlier than Pacific sardine	Lasker 1964
	2)	Pacific sardine do not develop normally below 13°C	Lasker 1964
	3)	Pacific mackerel do not hatch below 14°C	Hunter & Kimbrell 1980
HATCHING SIZE	4)	Herring; decreases with increasing temperature	Blaxter & Hempel 1963
	5)	Pacific sardine and Northern anchovy; no temperature effect	Lasker 1964
DEVELOPMENT: YOLK-SAC STAGE	6)	Pacific sardine; Q_{10}[1] = 4 for yolk absorption, and development of pigmented eyes and functional jaw (14-21°C)	Lasker 1964
EFFICIENCY OF YOLK ABSORPTION	7)	Plaice; more efficient at 6.5° than at 8.0°C; larvae 10% larger	Ryland & Nichols 1967
TIME TO EXOGENOUS FEEDING (FROM SPAWNING AT 15°C)	8)	Pacific sardine; 8 d Northern anchovy; 6-7 d Jack mackerel; 8-9 d Pacific mackerel; 7 d	Lasker 1964 Theilacker (unpubl.)
POINT OF NO RETURN (TABLE 1)	9)	Time to starvation decreases with increasing temp.	
FEEDING RATES (TABLE 6)	10)	Northern anchovy; 6-12 d, 6°(13-16°C) increased rate 4 times (<2→8 acts/min)	Hunter (in press)
	11)	Sea bream; 16 d, 3° (26-29°C) increased rate 2 times (8→18 acts/h)	Stepein 1976
GROWTH	12)	Pacific mackerel, 17-22°C; 7-15 mm; Q_{10} = 3 no effect of temp. 12 d	Hunter & Kimbrell 1980
	13)	Northern anchovy; 17-22°; 7-15 mm; Q_{10} = 2.7	Kramer & Zweifel 1970
ACTIVITY (TABLE 2)	14)	Northern anchovy, 6-12 d, 4° increase (13-17°C) increased swimming speed 2 times (0.4→0.9 BL/s)	Hunter (in press)
RESPIRATION RATES (TABLE 7)	15)	Pacific mackerel, 18-22°C; Q_{10} = 4.8	Hunter & Kimbrell 1980
	16)	Herring; Q_{10} = 2	Holliday, et al. 1964
GROSS GROWTH EFFICIENICES (TABLE 9)	17)	Sea bream, 2-3 d, 3-6° increase (23-26 to 29°C) decreased K; 33% to 16%	Stepein 1976

[1] $\log Q_{10} = \frac{10}{t_2 - t_1} \log \frac{k_2}{k_1}$

Responses to the same temperature may differ among species (Table 11). For California Current species at 15°C, time to the onset of feeding from spawning is earliest in northern anchovy, 6-7 days, and latest in jack mackerel, 8-9 days; at 15°C, northern anchovy can withstand starvation one day longer than Pacific mackerel and two days longer than jack mackerel. Northern anchovy have a greater tolerance for cooler temperatures than Pacific mackerel or Pacific sardine; anchovy will hatch and develop at 11°C, sardine do not develop below 12°C, and Pacific mackerel will not hatch below 14°C. Miscellaneous temperature responses are outlined in Table 11.

In conclusion, it is hoped that this information on the species-specific behavioural and physiological characteristics of fish larvae may lead to the identification of critical factors needed to predict larval fish survival. This summary of physiological laboratory research and field behaviour describes differences among fish species in spawning times, resistance to starvation, feeding rates, growth rates, feeding behaviour, swimming activity, and metabolic demands. Monitoring methods and models designed to predict larval fish survival must incorporate these species-specific functions. Clearly, more comparable standardized research techniques need to be used in producing descriptions of early life histories, and far more behavioural observations are needed to fully elucidate the diverse groups of larvae.

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