Comparative Growth, Mortality, and Energetics of Marine Fish Larvae: Temperature and Implied Latitudinal Effects

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ABSTRACT: Vital rates and energetics of marine fish larvae were examined in relation to temperature to determine if recruitment potential and spawning strategies might vary as a consequence of differences in these traits among species. Literature-derived values of growth rates, mortality rates, larval stage durations, gross growth efficiencies, and oxygen uptakes were considered. Results were presumed to reflect latitudinal variation among species. Instantaneous daily growth and mortality rates each increased approximately 0.01 per °C increase in temperature. But, there was no significant regression of gross growth efficiency on temperature (mean K_1 = 0.29), indicating no latitudinal relationship. The large increases in growth rate at high temperatures must be supported by increased food consumption, not increased growth efficiency. Oxygen uptakes also increased significantly in relation to temperature, but relatively slowly compared to growth rates. Larval stage duration was inversely related to growth rate. The potential variability in growth rate was observed to increase with temperature, but the opposite trend was observed for stage duration. Thus, stage durations tended to be both long and potentially variable in high latitudes. Because of these characteristics it is suggested that early life, density-dependent regulation is more probable in high than in low latitudes. The required ingestion to support average growth rate increased threefold in the 10°–30°C range, indicating that fish larvae in warm seas may be more likely to starve than larvae in cold seas. Spawning in low latitudes often is protracted with frequent batches in contrast to spawning in high latitudes, where seasons are brief, with one or a few batches. The different strategies may have been selected and maintained to counter energetic and dynamic constraints in the larval stage.

Variability in growth and mortality rates of marine fish larvae can cause fluctuations in recruitment levels. The two processes, growth and death, may interact and can be viewed as a "single process" in early life (Cushing 1975). In reviewing larval mortality rates, it is apparent that not only are rates high but they range widely (Dahlberg 1979; McGurk 1986). Growth rates also are variable, both among and within species, which could cause significant fluctuations in recruitment levels through effects on larval stage duration (Houde 1987). If variation in the magnitude of larval growth or mortality were predictable, for example, in relation to latitude, the consequences of it might be discernible in life history strategies or in physiological adaptations of fishes from different temperature zones.

Objectives of this paper are to compare vital rates and energetics parameters of marine fish larvae, and to discuss results in the context of spawning strategies and possible mechanisms in the larval stage that may regulate the recruitment process. A cursory examination of literature indicated that teleost larval growth and mortality rates increased relative to temperature and that temperature could, in a general way, be equated to latitude. A review and comparative analysis were undertaken to define the relationships between temperature and the larvae 1) growth rates, 2) stage duration, 3) mortality rates, 4) growth efficiency, and 5) oxygen uptakes. From the analysis, it was possible to estimate cohort net survivorships, to develop energy budgets, and to estimate ingestion requirements of first-feeding larvae over the range of temperatures that was surveyed. The likelihood of starvation by marine fish larvae from low and high latitudes was considered. Because spawning strategies of marine fishes may be linked to larval dynamics and energetics, results also were considered in relation to dominant spawning patterns in warm and cold seas.

METHODS

Literature was reviewed to obtain data for the analyses. Relationships and variables that were

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analyzed are defined in Table 1. Analyses were confined to feeding-stage larvae of marine fishes and to a few anadromous species. Salmonid fishes, which lack a typical larval stage, were not included.

TABLE 1.—Relationships that were analyzed and abbreviations that are used in text.

T	Temperature, °C
G	Weight-specific growth rate, d^{-1}
D	Stage duration, defined as days from hatching to metamorphosis, d
Z	Instantaneious daily mortality coefficient, d^{-1}
K_1	Gross growth efficiency, G/I
I	Weight-specific ingestion rate, d^{-1}
Q_{O_2}	Weight-specific oxygen uptake, $\mu L\ O_2/mg/h$
N_{met}	Net survivorship; fraction of a cohort expected to survive from hatching to metamorphosis

Growth

Weight-specific growth rates (G) of larvae were obtained from laboratory and field studies. Growth coefficients were taken directly from published work, when available, or calculated from the data. In a few cases, length-weight relationships were used to convert growth-in-length data to growth-in-weight. Weight-specific growth data for larvae of some commonly studied species were unavailable and those species could not be included in analyses. Weight-specific growth rates are

$$G = \frac{(\ln W_t - \ln W_0)}{t}$$

where W_0 and W_t are dry weights of larvae at hatch and at the end of a growth period of t days' duration.

A linear regression was fitted to express the relationship of weight-specific growth rates on temperature. Because both G and T for a species sometimes had a considerable range reported in the literature, the midpoints of reported G and T values were selected arbitrarily as the data for each species in the regression analysis. A Q_{10} was estimated from predicted values of G in the range 5°–30°C.

Stage Duration

Stage duration (D) was defined as days from hatching to metamorphosis. As such, it is inversely proportional to weight-specific growth

rate (G) and dependent upon species-specific weight at metamorphosis. Stage duration was calculated from the literature-derived data on G, dry weights at hatch (W_0), and dry weights at metamorphosis (W_m)

$$D = \frac{(\ln W_m - \ln W_0)}{G}.$$

A power regression was fitted, in which the geometric midpoint, i.e., antilog $[(\log_{10}$ low $D + \log_{10}$ high $D) * \frac{1}{2}]$ of the estimated range of D for each species was regressed on the estimated midpoint of temperature, to describe the relationship between stage duration and temperature.

Mortality

Instantaneous daily mortality coefficients (Z) of post-yolk-sac larvae were obtained from published field studies in which the rates had been determined or could be calculated from the authors' estimated abundances-at-age. Much of the mortality data was obtained from summaries and references in papers by Dahlberg (1979) and McGurk (1986), supplemented with Z estimates from additional and more recent sources.

A linear regression of the midpoints of the estimated range of Z on the midpoints of T for each species was fitted to describe the relationship between Z and T.

Relationship Between Mortality and Growth Rates

Solution of the equation for growth rate on temperature in terms of temperature and its substitution into the equation for mortality rates on temperature yielded an expression relating mortality rates to growth rates.

Net Survivorship

Based on the estimates of growth rates, stage duration, and mortality rates predicted from the regressions, the proportion of a cohort expected to survive to metamorphosis (N_{met}) was calculated for 10°, 20°, and 30°C. The percentage cohort survivorship at each of the temperatures was calculated from the exponential relationship

$$100\ N_{met} = e^{-ZD}.$$

Effects on survivorship of decreases in G and

increases in Z also were determined at those three temperatures.

Growth Efficiency

Gross growth efficiency (K_1) is the proportion of ingestion that goes to growth;

$$K_1 = G/I,$$

where G is the weight-specific growth rate and I is the weight-specific ingestion rate. Growth efficiencies and temperatures (T) in published reports were examined. An attempt was made to fit a linear regression to midpoints of K_1 regressed on midpoints of T for species where data were available.

Because $I = G/K_1$ and the regression relationship between G and T had been defined, weight-specific ingestion rate also could be related to temperature. That expression was applied to estimate the weight-specific ingestion rate required to attain mean, among-species growth rates in relation to temperature. It was assumed that an average food particle for a first-feeding larva weighed 0.25 μg dry weight. Then, the number of particles required to attain average growth rate and the consequences of changes in temperature on that requirement were explored. The regression relationship between I and G also was examined to determine the rate of increase in ingestion necessary to support increased growth.

Metabolism

The Q_{O_2}, i.e., weight-specific oxygen uptakes, were obtained for marine fish larvae where data were available. Values were taken directly from literature or derived if the relationship between oxygen uptake and larval dry weight was reported. Values used here were confined to those for feeding or end-of-yolk-sac stage larvae. The midpoints in the range of Q_{O_2} for a species were regressed on the midpoints of the temperature values to obtain a relationship between weight-specific oxygen uptake and temperature. A Q_{10} was derived from the predicted values of Q_{O_2} in the 5°–30°C range.

Energy Budgets

Energy budgets for average first-feeding larvae at 10°, 20°, and 30°C were developed from the information and relationships on growth

rates (G), oxygen uptake (Q_{O_2}), and ingestions (I). Budgets were expressed as

$$I = G + M + F$$

where M is metabolism and F is feces. The Q_{O_2} was converted to M using an oxycalorific equivalent of 0.00463 cal/μL O_2 (Brett and Groves 1979). The oxygen uptake estimates reported in the literature generally were made on "resting" or anesthetized larvae. These estimates were presumed to represent routine metabolism. For the energy budgets, the reported Q_{O_2} values were multiplied by 2.0 to estimate active metabolism for 12 hours of the day, the time that a larva was assumed to swim actively while feeding (i.e., daylight hours). The estimated Q_{O_2} from the regression relationship was assumed to apply during the remaining 12 hours. The 2.0 multiplier is commonly used, but may be conservative (Brett and Groves 1979). If metabolism has been underestimated, the absolute values of budget components are in error but relative effects of temperature on the larval energy budgets still will be expressed.

Both ingestion rates and growth rates were converted from dry weight to calories by assuming an equivalency of 5,000 cal/g dry weight. Values for feces in the energy budgets were obtained by difference. Energy budgets were expressed both in absolute and relative (i.e., percent) terms. After the energy budgets had been determined, assimilation efficiencies, $A = (G + M)/I$, and net growth efficiencies, $K_2 = G/(G + M)$, were derived and compared among temperatures (see Table 8).

RESULTS

Growth

Weight-specific growth coefficients ranged from <0.01 to >0.55, indicating a widely varying potential for growth among species of marine fish larvae that was strongly related to temperature and, presumably, latitude (Table 2; Fig. 1). Relative growth-in-weight ranged from <1% to >73% d^{-1}. The regression of midpoint G on midpoint T for 27 species indicated an approximate 0.01 increase in G for each degree increase in T.

$$G = -0.0036 + 0.0094\ T$$

$$r^2 = 0.57 \qquad S_b = 0.0016. \qquad (1)$$

TABLE 2.—Weight-specific growth coefficients (G) from laboratory and field-estimated growth rates of marine fish larvae. Temperatures (T), dry weight ranges, and mid-points of estimated G and T also are given. Values were taken directly from published results, calculated from the authors' data or calculated from available length-weight relationships.

Species	Temperature		Dry weight range (mg)	Growth coefficient (G)		References
	Range	Midpoint		Range	Midpoint	
Clupea harengus CH	06.0–17.0	11.5	0.06–100.00	<0.01–0.12	0.065	McGurk (1984) and numerous references therein; Gamble et al. (1985); Kiorboe and Munk (1986); Kiorboe et al. (1987)
Chanos chanos CC	25.0–29.0	27.0	0.25–60.00 (wet wts)	0.12–0.17	0.145	Liao et al. (1979); Duray and Bagarinao (1984)
Anchoa lamprotaenia ALa	26.0	26.0	0.02–0.06	0.21	0.210	Chitty (1981)
Anchoa mitchilli AM	23.0–31.0	27.0	0.01–6.00	0.15–0.35	0.250	Houde (1977d, 1978); Houde and Schekter (1981); Leak and Houde (1987); Houde (unpub. data)
Engraulis mordax EM	13.0–16.0	14.5	0.02–0.50	0.14–0.30	0.220	Hunter (1976); Methot and Kramer (1979); Smith (1985); Theilacker (1987)
Gadus morhua GM	4.0–11.0	7.5	0.05–3.00	0.02–0.12	0.070	Laurence (1978); Buckley (1979); Laurence et al. (1981); Gamble and Houde (1984); Øiestad (1985); Buckley and Lough (1987)
Melanogrammus aeglefinus MA	4.0–9.0	6.5	0.07–2.90	0.01–0.13	0.070	Laurence (1974, 1978); Laurence et al. (1981); Bergen et al. (1985); Buckley and Lough (1987); Buckley et al. (1987)
Merluccius productus MP	10.5–15.0	13.0	~0.04–~1.80	—	0.060	Bailey (1982)
Theragra chalcogramma TC	5.0–9.5	7.0	0.04–33.50	0.02–0.13	0.075	Hamai et al. (1974); Clarke (1984); Nishimura and Yamada (1984); Walline (1985); Bailey and Stehr (1986); Kendall et al. (1987)
Menidia menidia MM	19.0–21.0	20.0	~0.50–8.90 (wet wts)	~0.13	~0.130	Beck and Poston (1980)
Menidia peninsulae MP	20.0–30.0	25.0	0.03–2.24	0.08–0.25	0.165	McMullen and Middaugh (1985)
Morone americana MAm	13.0–21.0	17.0	0.02–0.09	0.03–0.18	0.105	Margulies (1986)
Morone saxatilis MS	12.0–22.5	17.0	0.15–15.00	0.09–0.19	0.140	Dey (1981); Eldridge et al. (1981); Rogers and Westin (1981); Eldridge et al. (1982); Houde and Lubbers (1986); Chesney (1986)
Dicentrarchus labrax DL	13.0–20.0	16.5	0.09–~2.80	0.07–0.18	0.125	Girin (1975); Girin et al. (1975); Barahona-Fernandes and Girin (1977); Barahona-Fernandes (1978,1979); Gatesoupe and Luquet (1981); Gatesoupe and Robin (1982)

TABLE 2.—*Continued.*

Species	Temperature		Dry weight range (mg)	Growth coefficient (G)		References
	Range	Midpoint		Range	Midpoint	
Haemulon flavolineatum HF	~25.0–~30.0	~27.5	0.02–10.00	~0.24–~0.41	~0.325	McFarland et al. (1985); Saksena and Richards (1975)–data on *H.plumieri*, used to approximate *H. flavolineatum.*
Archosargus rhomboidalis AR	23.0–29.0	26.0	0.01–4.20	0.21–0.41	0.310	Houde (1975, 1978); Stepien (1976); Houde and Schekter (1981)
Pagrus major PM	17.0–23.5	20.0	0.05–13.70 (wet wts)	0.06–0.33	0.195	Fushimi and Nakatani (1977); Kitajima et al. (1980); Fukusho et al. (1984); Kuronuma and Fukusho (1984)
Sparus aurata SA	15.0–20.0	17.5	~0.02–~10.00	0.10–0.14	0.120	Divanach (1985); Tandler and Helps (1985)
Cynoscion nebulosus CN	24.0–32.0	28.0	0.02–1.60	0.16–0.57	0.365	Taniguchi (1979, 1981)
Ammodytes americanus AA	0.0–10.0	5.0	0.04–10.00	<0.01–0.12	0.060	Buckley et al. (1984); Smigielski et al. (1984); Monteleone and Peterson (1986); Buckley et al. (1987)
Scomber japonicus SJ	17.0–22.0	19.5	0.03–34.45	0.25–0.43	0.340	Hunter and Kimbrell (1980)
Scomber scombrus SSc	15.0	15.0	0.05–2.23	0.10–0.18	0.140	Buckley et al. (1987)
Paralichthys dentatus PD	18.0	18.0	–	0.07	0.070	Buckley and Dillman (1982)
Scophthalmus maximus SM	13.0–18.0	15.5	0.04–10.00	0.10–0.25	0.175	Jones et al. (1974); Kuhlmann et al. (1981); Person LeRuyet et al. (1981); Paulsen et al. (1985); Quantz (1985)
Pseudopleuronectes americanus PA	2.0–10.0	6.0	0.01–1.45	0.02–0.14	0.080	Laurence (1975,1977); Buckley (1982); Cetta and Capuzzo (1982)
Achirus lineatus AL	28.0	28.0	0.01–0.20	0.16–0.33	0.245	Houde (1977d, 1978); Houde and Schekter (1981)
Solea solea SS	17.0–19.0	18.0	0.30–8.00 (wet wts)	0.10–0.21	0.155	Girin (1979); Fuchs (1982); Gatesoupe and Luquet (1982)

Estimated G increased from 0.04 at 5°C to 0.28 at 30°C. The Q_{10}, calculated from the predicted G, was 2.11 over the range 5°–30°C.

Some species deviated considerably from the average regression relationship (Fig. 1; Table 2). For example, Pacific mackerel, *Scomber japonicus*, larvae had a high growth rate; however, Atlantic mackerel, *S. scombrus*, did not deviate much from the regression line. Northern anchovy, *Engraulis mordax*, also had relatively high growth rate, while herring, *Clupea harengus*, Pacific hake, *Merluccius productus*, and milkfish, *Chanos chanos*, had lower than expected growth rates for their respective temperature. The observed variation in growth rates was greatest at high temperature (Fig. 1), indicating that fish larvae at high temperatures and, more generally, in low latitudes have potentially more variable growth rates than do larvae at low temperatures from high latitudes.
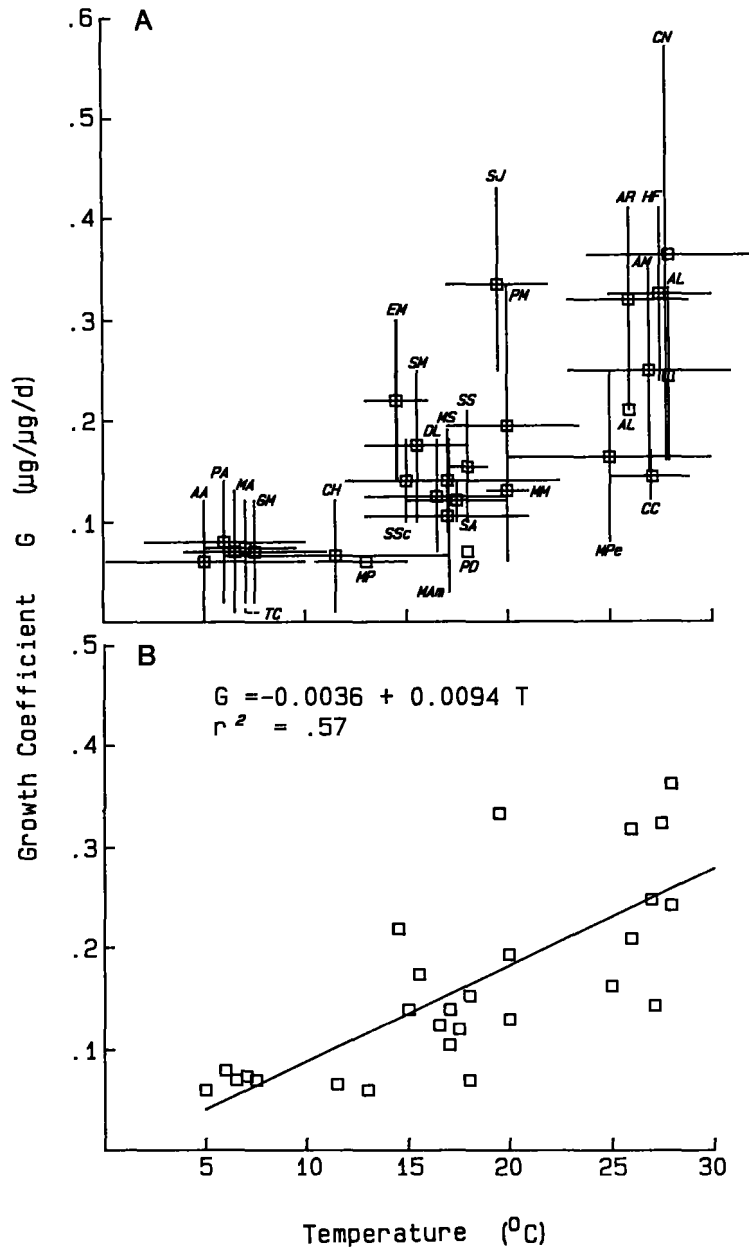
FIGURE 1.—Weight-specific growth coefficients (G) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of reported G and T values. Data, letters designating species and references are from Table 2. B. Regression relationship of midpoint G on midpoint T.

Stage Duration

Larval stage duration ranged from 10 days to >550 days, based on the reported growth rates (Table 3; Fig. 2). The regression relationship for 27 species indicated that stage duration (D) declines rapidly as temperature (T) increases.

$$D = 952.5T^{-1.0752}$$

$$r^2 = 0.70 \qquad S_b = 0.1418. \qquad (2)$$

Predicted stage duration ranged from 25 days at 30°C to >165 d at 5°C. The variability in stage duration was greatest at low tempera-

TABLE 3.—Estimated larval stage durations (*D*) from laboratory- and field-estimated growth rates, and weights at metamorphosis for marine fish larvae. Temperatures (*T*), and midpoints of *D* and *T* also are given. Values were derived from published results cited for each species in Table 1.

| Species | Temperature | | Hatch and metamorphosis dry weight (mg) | | Stage duration (*d*) | |
	Range	Midpoint	W_0	W_m	Range	Geometric midpoint
Clupea harengus CH	6.0–17.0	11.5	0.090	25.0	46.9–>550	160.6
Chanos chanos CC	25.0–29.0	27.0	0.05	25.0	36.6–51.8	43.5
Anchoa lamprotaenia ALa	26.0	26.0	0.02	25.0	34.0	34.0
Anchoa mitchilli AM	23.0–31.0	27.0	0.015	25.0	21.2–49.5	32.4
Engraulis mordax EM	13.0–16.0	14.5	0.020	25.0	23.8–50.9	34.8
Gadus morhua GM	4.0–11.0	7.5	0.050	7.0	41.2–247.1	100.9
Melanogrammus aeglefinus MA	4.0–9.0	6.5	0.070	7.0	35.4–460.5	127.7
Merluccius productus MP	10.5–15.0	13.0	0.04	7.0	88.0	88.0
Theragra chalcogramma TC	5.0–9.5	7.0	0.04	10.0	42.5–276.1	108.3
Menidia menidia MM	19.0–21.0	20.0	0.10	10.0	35.4	35.4
Menidia peninsulae MP	20.0–30.0	25.0	0.03	10.0	23.2–72.6	41.0
Morone americana MAm	13.0–21.0	17.0	0.02	10.0	34.5–207.2	84.5
Morone saxatilis MS	10.0–22.5	17.0	0.20	15.0	22.7–48.0	33.0
Dicentrarchus labrax DL	13.0–20.0	16.5	0.06	10.0	28.4–73.1	45.6
Haemulon flavolineatum HF	~25.0–~30.0	~27.5	~0.02	~7.0	14.3–24.4	18.7
Archosargus rhomboidalis AR	23.0–29.0	26.0	0.015	7.0	15.0–29.3	21.0
Pagrus major PM	17.0–23.5	20.0	0.01	7.0	19.9–109.2	46.6
Sparus aurata SA	15.0–20.0	17.5	0.02	7.0	41.8–58.6	49.5
Cynoscion nebulosus CN	24.0–32.0	28.0	0.02	7.0	10.3–36.6	19.4
Ammodytes americanus AA	0.0–10.0	5.0	0.04	10.0	46.0–>550	159.1
Scomber japonicus SJ	17.0–22.0	19.5	0.035	10.0	13.2–22.6	17.3
Scomber scombrus SSC	15.0	15.0	0.05	10.0	29.4–53.0	39.5
Paralichthys dentatus PD	18.0	18.0	~0.05	~7.0	98.8	98.8
Scophthalmus maximus SM	13.0–18.0	15.5	0.04	20.0	24.9–62.1	39.3
Pseudopleuronectes americanus PA	2.0–10.0	6.0	0.01	1.0	32.9–230.3	87.0

TABLE 3.—*Continued.*

| Species | Temperature | | Hatch and metamorphosis dry weight (mg) | | Stage duration (*d*) | |
	Range	Midpoint	W_o	W_m	Range	Geometric midpoint
Achirus lineatus AL	28.0	28.0	0.101	2.0	16.0–33.1	23.0
Solea solea SS	17.0–19.0	18.0	0.05	8.0	24.2–50.8	35.1
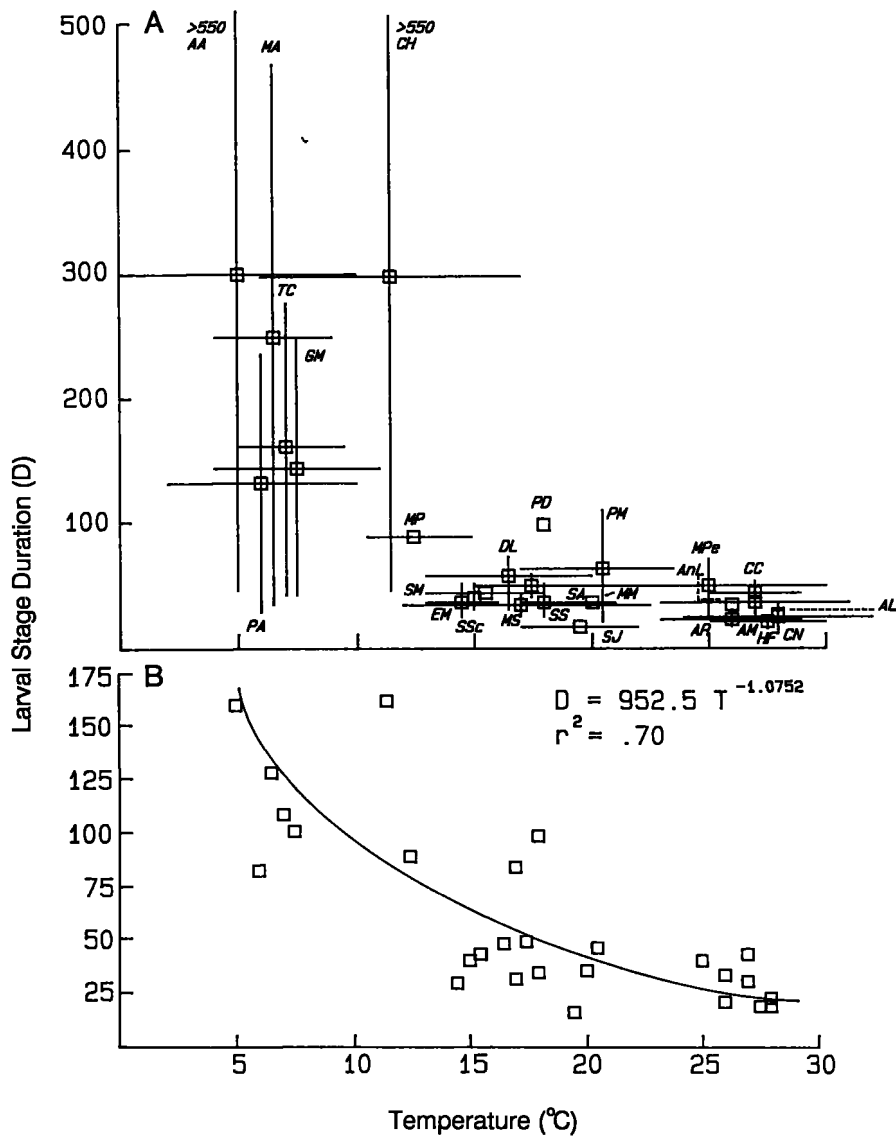
FIGURE 2.—Stage durations (D) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of D and T values. Data and letters designating species are from Table 3. References are in Table 1. B. Regression relationship of geometric midpoint D on midpoint T.

tures (Fig. 2), indicating more scope for stage duration at low temperatures and presumably in high latitudes. This result was opposite to that observed for growth rate, in which there was more variability at high temperatures (Fig. 1).

Mortality

Mortality coefficients of feeding-stage larvae reported for 22 species ranged from $Z = 0.01$ to 0.69 d^{-1}, equivalent to 1–50% d^{-1} mortality rates (Table 4; Fig. 3). Predicted mortality rate (Z) increased approximately 0.01 per degree increase in temperature (T).

$$Z = 0.0256 + 0.0123\ T$$

$$r^2 = 0.41 \qquad S_b = 0.0034. \qquad (3)$$

Estimated Z increased from 0.09 at 5°C to 0.40 at 30°C.

Although quite variable among species, the relationship between mortality rate and temperature is significant $(P < 0.01)$. Only Atlantic mackerel appeared to be an outlier from the regression line (Fig. 3); its observed mortality rate was higher than expected for species in the 15–20°C range.

Relationship Between Mortality and Growth Rates

The derived relationship between mortality rate (Z) and growth rate (G) for marine fish larvae was

$$Z = 0.0303 + 1.3085\ G. \qquad (4)$$

Also, from predicted G and Z in Equations (1) and (3), it is apparent that the ratio G/Z increases at high T.

T (°C)	$\dot{G}$	$\dot{Z}$	G/Z
5	0.043	0.087	0.494
15	0.137	0.210	0.652
30	0.278	0.395	0.704

Despite the elevated mortality rates suffered by marine fish larvae at high temperatures, their growth potential may allow such larval populations to accumulate biomass and to survive at relatively high rates when feeding conditions are favorable.

Net Survivorship

Predicted net survival at metamorphosis increased by an approximate factor of nine as temperature increased from 10° to 30°C.

	10°C	20°C	30°C
G (d^{-1})	0.0904	0.1844	0.2784
D (d)	80.11	38.02	24.58
Z (d^{-1})	0.1486	0.2716	0.3946
$100\ N_{met}$ (%)	0.0007	0.0033	0.0061

The effects on N_{met} of a 10% decline in G, a 10% increase in Z, or a combination of 10% decline in G and 10% increase in Z were large.

G declines 10%	10°C	20°C	30°C
G (d^{-1})	0.0814	0.1660	0.2506
D (d)	88.97	42.23	27.31
Z (d^{-1})	0.1486	0.2716	0.3946
$100\ N_{met}$ (%)	0.0002	0.0010	0.0021

Z Increases 10%	10°C	20°C	30°C
G (d^{-1})	0.0904	0.1844	0.2784
D (d)	80.11	38.02	24.58
Z (d^{-1})	0.1635	0.2988	0.4341
$100\ N_{met}$ (%)	0.0002	0.0012	0.0023

G declines 10% and Z increases 10%	10°C	20°C	30°C
G (d^{-1})	0.0814	0.1660	0.2506
D (d)	88.97	42.23	27.31
Z (d^{-1})	0.1635	0.2988	0.4341
$100\ N_{met}$ (%)	0.00005	0.0003	0.0007

Effects on percent larval survival at metamorphosis $(100\ N_{met})$ of declining growth rates or increasing mortality rates are greater at low than at high temperatures, a consequence of the long stage durations at low temperature and their dependency on growth rate. Calculated ratios of N_{met} from the examples given above, termed relative survival, compared to those expected from the regression relationships at average G, D and Z, are

	Relative Survival		
Example	10°C	20°C	30°C
Expected G, D, Z	1.00	1.00	1.00
G declines 10%	0.27	0.32	0.34
Z increases 10%	0.30	0.36	0.38
G declines 10% and Z increases 10%	0.07	0.10	0.12

TABLE 4.—Instantaneous daily mortality coefficients (Z) from field estimates of reported mortality rates of marine fish larvae in relation to temperatures (T). Estimates here are for feeding-stage larvae only.

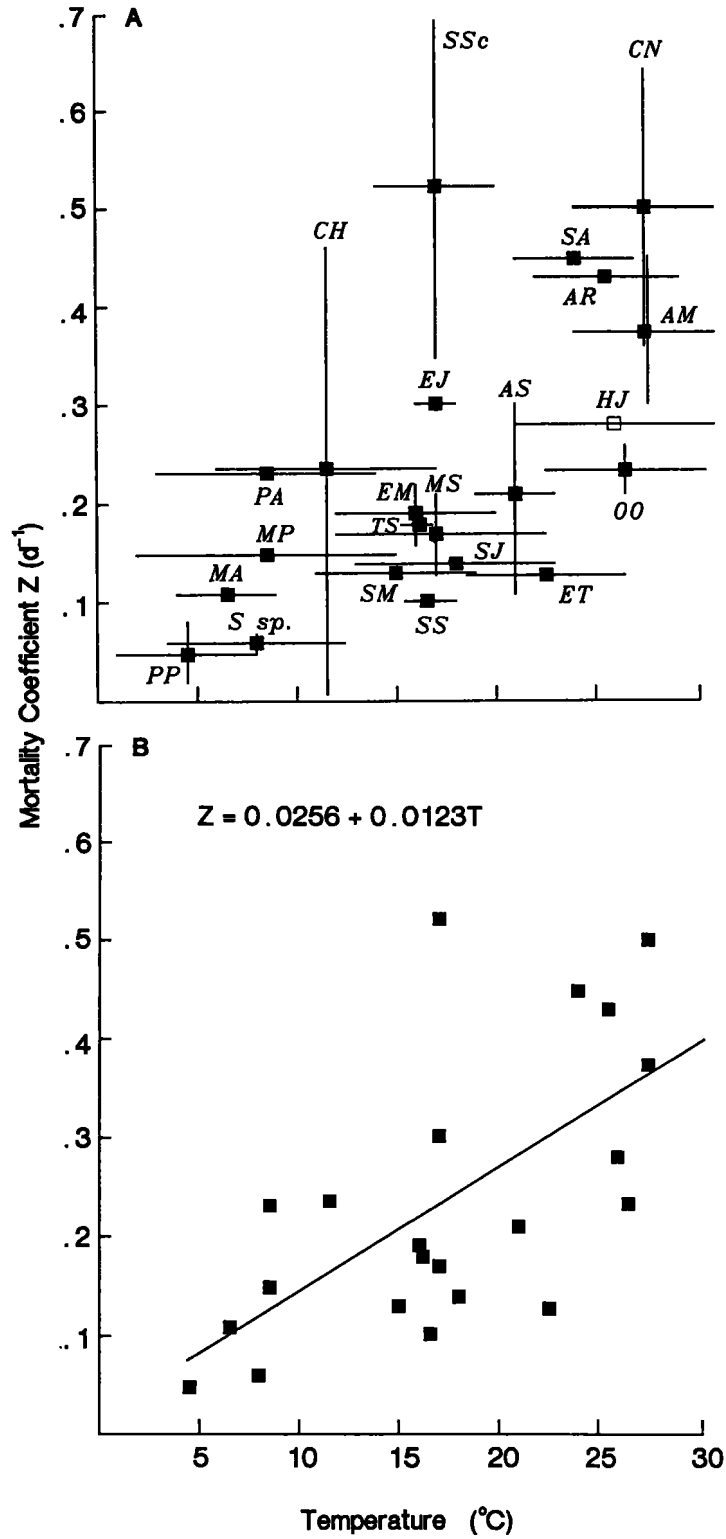| Species	Temperature (°C)		Mortality coefficient (Z)		References
	Range	Midpoint	Range	Midpoint	
Alosa sapidissima AS	19.0–23.0	21.0	0.11–0.30 (10–18 mm larvae)	0.210	Crecco et al. 1983
Clupea harengus CH	6.0–17.0	11.5	0.01–0.46	0.235	Graham and Townsend 1985; McGurk 1986; Lough et al. 1985
Etrumeus teres ET	18.0–26.5	22.5	0.13	0.130	Houde 1977a
Harengula jaguana HJ	21.0–31.0	26.0	0.28	0.280	Houde 1977c
Opisthonema oglinum OO	22.5–30.5	26.5	0.21–0.26	0.235	Houde 1977b
Sardinella aurita SA	21.0–27.0	24.0	0.45	0.450	Conand 1977
Sardinops melanosticta SM	11.1–19.1	15.1	0.13	0.130	Nakai and Hattori 1962
Sardinops sagax SS	15.5–18.0	16.4	0.10	0.100	Lenarz 1973
Anchoa mitchilli AM	24.0–31.0	27.5	0.30–0.45	0.375	Leak and Houde 1987
Engraulis japonica EJ	16.0–18.0 (from other literature)	17.0	0.30	0.300	Hiyashi 1966
Engraulis mordax EM	12.0–20.0	16.0	0.16–0.22	0.190	Hewitt and Methot 1982; Smith 1985; McGurk 1986
Melanogrammus aeglefinus MA	4.0–9.0	6.5	0.11	0.110	Jones 1973
Micromesistius poutassou MP	2.0–15.0 (from other literature)	8.5	0.15	0.150	Bailey 1974
Morone saxatilis MS	12.0–22.5	17.0	0.13–0.21	0.170	Dey 1981
Trachurus symmetricus TS	15.0–16.5	16.0	0.18 (rate estimated at 30 d posthatch)	0.180	Hewitt et al. 1985
Archosargus rhomboidalis AR	22.0–29.0	25.5	0.43	0.430	Chavance et al. 1984
Cynoscion nebulosus CN	24.0–31.0	27.5	0.36–0.64	0.500	Peebles and Tolley 1988
Scomber japonicus SJ	13.0–23.0	18.0	0.14	0.140	Watanabe 1970
Scomber scombrus SSc	14.0–20.0	17.0	0.35–0.69	0.520	Sette 1943; Kendall and Gordon 1981; Ware and Lambert 1985
Sebastes spp. Ssp	3.5–12.5	8.0	0.05–0.07	0.060	Anderson 1984
Pleuronectes platessa PP	1.0–8.0	4.5	0.02–0.08	0.050	Harding and Talbot 1973; Bannister et al. 1974; Harding et al. 1978
Pseudopleuronectes americanus PA	3.0–14.0	8.5	0.23	0.230	Pearcy 1962a, 1962b

FIGURE 3.—Instantaneous mortality coefficient (Z) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of Z and T values. Data, letters designating species and references are from Table 4. B. Regression relationship of midpoint Z on midpoint T.

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It is important to note that a 10% change in either Z or G will have potentially large effects on survivorship at any temperature.

Growth Efficiency and Ingestion

There was no significant relationship between growth efficiency and temperature (Table 5; Fig. 4) for 10 species where data were adequate for analysis. Mean K_1, with 0.95 confidence limits, is 0.29 ± 0.06, a value equal to that of juvenile, carnivorous fishes (Brett and Groves 1979). One species, European seabass, *Dicentrarchus labrax*, had reported K_1 well above the mean. Two species, winter flounder, *Pseudopleuronectes americanus*, and summer flounder, *Paralichthys dentatus*, had K_1 below the mean. For some species, a large range of potential K_1 was reported (Fig. 4), indicating that estimates of growth efficiency may vary widely in relation to environment, physiology, and perhaps the method used to calculate it.

Estimated weight-specific ingestion rates were determined for the 10 species from the relationship $I = G/K_1$. For these species there is a good relationship between ingestion rate (I) and growth rate (G) (Fig. 5).

$$I = 0.1203 + 2.8691\ G$$

$$r^2 = 0.80 \qquad S_b = 0.5140. \qquad (5)$$

There was no detectable relationship between ingestion and temperature for these 10 species because of the highly variable growth rates and growth efficiencies that were reported. However, given the relationship between G and T (Equation (1)) and the mean value for K_1, an expression describing a general relationship between I and T for marine fish larvae was derived.

$$I = G/K_1 \qquad I = (-0.0036 + 0.0094\ T)/0.29,$$
yielding

$$I = -0.0125 + 0.0326\ T. \qquad (6)$$

Thus, to attain the expected growth rate, ingestion must increase with temperature. A threefold increase in weight-specific ingestion rate is required to meet the demands of expected growth at 30°C compared with that needed at 10°C. The result demonstrates that tropical fish larvae or those living at high summer temperatures must ingest relatively large amounts

TABLE 5.—Gross growth efficiencies (K_1) of marine fish larvae from laboratory experiments.

Species	Temperature (°C)		Mortality coefficient (Z)		References
	Range	Midpoint	Range	Midpoint	
Clupea harengus CH	7.0–9.0	8.0	<0.10–0.62	0.360	Checkley 1984; Kiorboe and Munk 1986; Kiorboe et al. 1987
Anchoa mitchilli AM	26.0	26.0	[1]0.11–0.32	0.215	Houde and Schekter 1981, 1983
Engraulis mordax EM	15.5	15.5	0.24–0.46	0.350	Theilacker 1987
Dicentrarchus labrax DL	18.0–19.0	18.5	0.26–0.57	0.415	Barahona-Fernandez and Girin 1977
Morone saxatilis MS	18.0–21.0	19.5	0.14–0.32	0.230	Eldridge et al. 1982; Chesney 1986; Tuncer 1988
Archosargus rhomboidalis AR	23.0–29.0	26.0	[1]0.21–0.41	0.310	Stepien 1976; Houde and Schekter 1981, 1983
Scomber japonicus SJ	17.0–22.0	19.5	0.20–0.44	0.320	Hunter and Kimbrell 1980
Paralichthys dentatus PD	18.0	18.0	0.05–0.24	0.145	Buckley and Dillman 1982
Pseudopleuronectes americanus PA	6.0–8.0	7.0	0.05–0.33	0.190	Laurence 1977; Cetta and Capuzzo 1982
Achirus lineatus AL	28.0	28.0	[1]0.13–0.52	0.325	Houde and Schekter 1981, 1983

[1]The highest values reported by Houde and Schekter (1981) were not included here, based on their note that these values were in error.

of food to grow at their observed, average rates. Because it depends on the relationship between growth rate and temperature, the Q_{10} for ingestion rate in the 5°–30°C range is 2.11, the same as that calculated for growth rate.

From the estimates of weight-specific inges-

tion (Table 6), the numbers of food organisms were calculated that would satisfy the growth requirements of first-feeding larvae of the 10 species. The number of required prey is directly proportional to growth rate and to W_0, the initial dry weight of a larva, and is inversely propor-
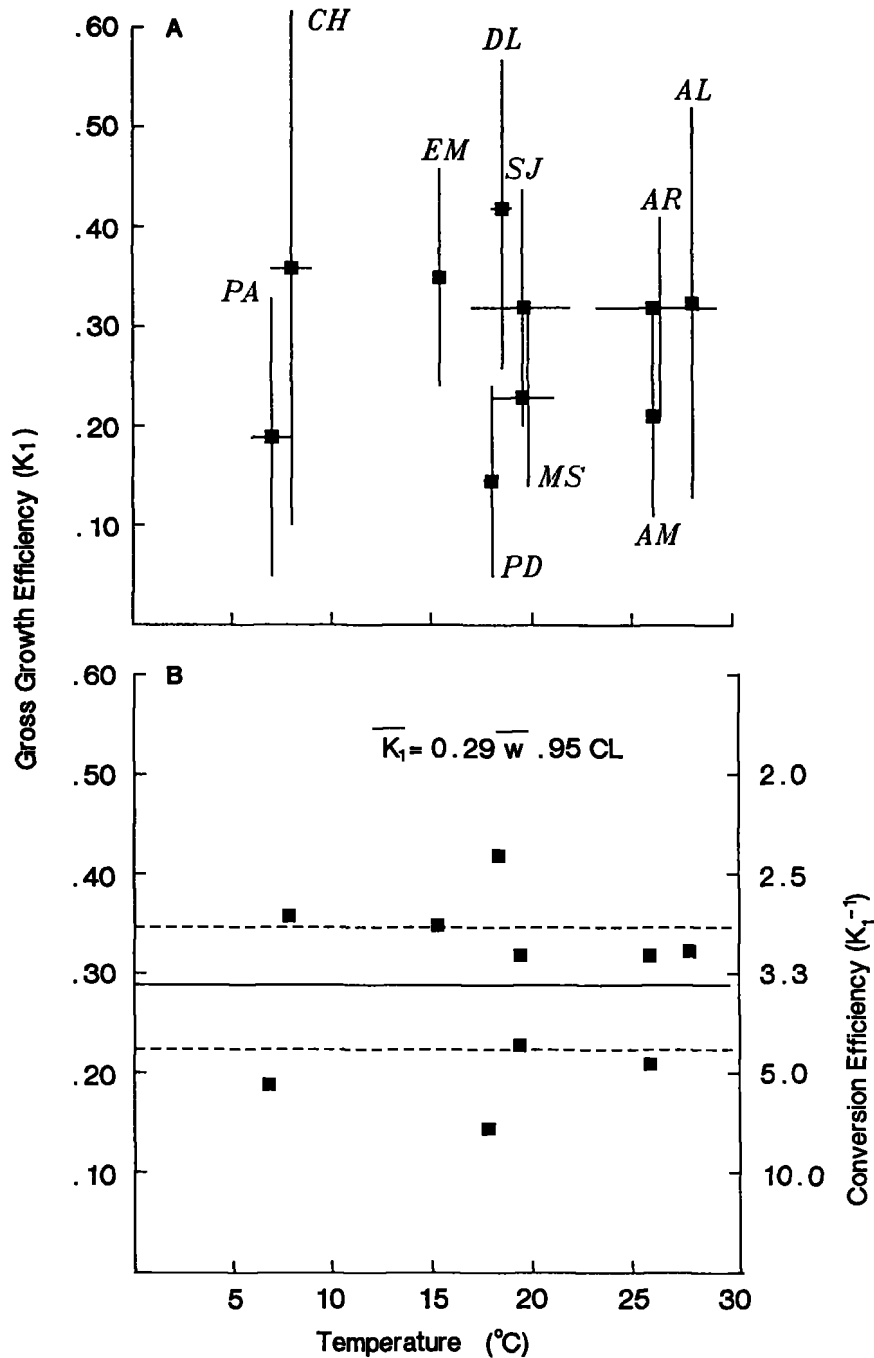
FIGURE 4.—Gross growth efficiency (K_1) and conversion efficiency (K_1^{-1}) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of K_1 and T values. Data, letters designating species and references are from Table 5. B. Mean K_1 and 0.95 confidence limits from the attempt to regress midpoint K_1 on midpoint T. There was no significant regression of K_1 on T.
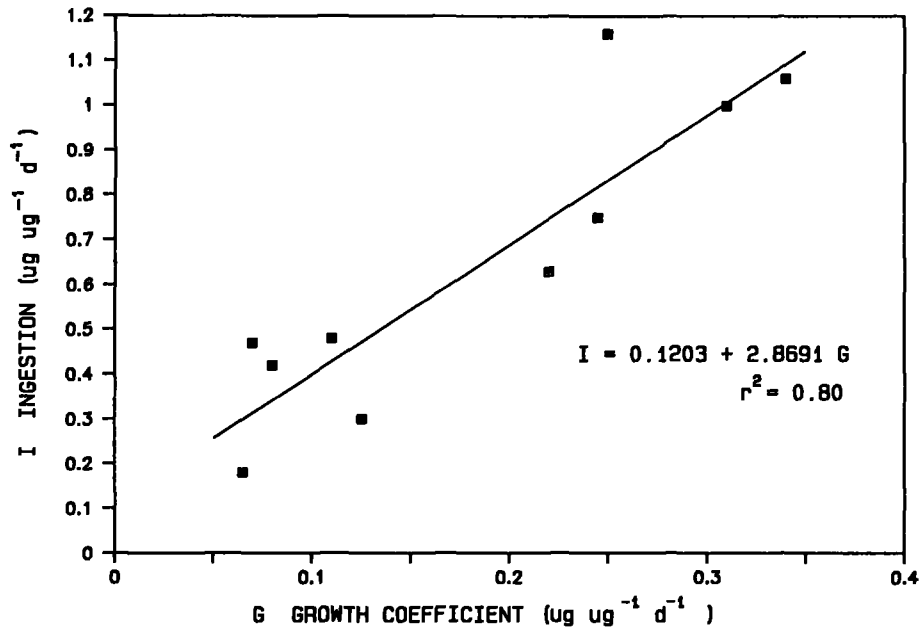
FIGURE 5.—Weight-specific ingestion rates (I) of marine fish larvae in relation to weight-specific growth coefficient (G). Data derived from Tables 2 and 5.

TABLE 6.—Estimated numbers of 0.25 µg dry weight food particles required by first-feeding marine fish larvae to meet their reported mean growth rates. Required total ingestion and weight-specific ingestion (i.e., number of particles per µg of growth) are given. Estimates were calculated from the G and K_1 values derived from published literature (see Tables 2, 4).

Species	Midpoint temperature (°C)	Midpoint G (µg µg^{-1} d^{-1})	Midpoint K_1	Initial larval weight (µg)	Daily weight increment (µg)	Number of 0.25 µg particles required (d^{-1})	Weight-specific ingestion (number µg^{-1}) d^{-1}
Clupea harengus CH	11.5	0.065	0.360	80	5.2	57.8	11.12
Anchoa mitchilli AM	27.0	0.250	0.215	10	2.5	46.5	18.60
Engraulis mordax EM	14.5	0.220	0.350	20	4.4	50.3	11.44
Dicentrarchus labrax DL	16.5	0.125	0.415	90	11.3	108.9	9.64
Morone saxatilis MS	17.0	0.110	0.230	200	22.0	382.8	17.40
Archosargus rhomboidalis AR	26.0	0.310	0.310	10	3.1	40.1	12.92
Scomber japonicus SJ	19.5	0.340	0.320	30	10.2	127.7	12.52
Paralichthys dentatus PD	18.0	0.070	0.145	~50	3.5	96.6	27.59
Pseudopleuronectes americanus PA	6.0	0.080	0.190	10	0.8	16.8	21.05
Achirus lineatus AL	28.0	0.245	0.325	10	2.5	30.2	12.32

tional to gross growth efficiency. Required prey of 0.25 µg dry weight (the approximate weight of a 100–200 µm width copepod nauplius) varied more than twentyfold, ranging from 17 to 383 d^{-1} among the 10 species (Table 6). Marine fish larvae must ingest 15.3 prey of 0.25 µg dry weight (15.3 ± 3.9 with 0.95 confidence limit) to attain a 1 µg increase in dry weight. To the extent that 0.25 µg either underestimates or overestimates the mean weight of a prey for a species of fish larva, the required numbers of prey were either overestimated or underestimated.

Metabolism

Weight-specific oxygen uptakes of feeding-stage larvae of 13 species ranged from 0.3 to 44.9 µL/mg/h and increased with temperature. All of the values, except those for haddock, *Melanogrammus aeglefinus*, which were considered outliers, were used in the regression describing the relationship between oxygen uptake (Q_{O_2}) and temperature (T) (Table 7; Fig. 6).

$$Q_{O_2} = 2.3973 + 0.2187\ T$$

$$r^2 = 0.39 \qquad S_b = 0.0870. \qquad (7)$$

The relationship was significant ($P = 0.025$), but the fit was not as good as those of the other regressions. In the 5°–30°C range, Q_{10} was 1.46, a value lower than that calculated for growth and ingestion rates.

After rearranging and substituting Equation (1) into Equation (7), an expression between oxygen uptake (Q_{O_2}) and growth rate (G) was derived.

$$Q_{O_2} = 2.2472 + 23.5000\ G \qquad (8)$$

From this relationship it can be seen that for growth rate in the sixfold range of 0.05–0.30, oxygen uptake varied only by a factor of 2.7.

Energy Budgets

There were substantial effects of temperature on the calculated energy budgets. Weight-specific ingestion rate increased threefold in the 10C°–30°C range (Table 8). Numbers of calories increased in all budget components as temperature increased. The relative contributions of each budget component show that growth remained constant, a consequence of gross growth

efficiency being constant over all temperatures, and that relative metabolism declined at higher temperatures. Assimilation efficiencies declined from 77.1% at 10°C to 59.8% at 30°C. Net growth efficiencies, K_2, increased from 37.2% at 10°C to 48.1% at 30°C. Fecal energy increased twofold, from 22.9% at 10°C to 40.2% at 30°C.

DISCUSSION

Predicted growth and mortality rates of marine fish larvae increase by approximately 0.01 per degree in temperature, implying large differences in developmental times and daily probabilities of death in larvae that are hatched in either warm or cold seas. The very high growth and mortality rates at the high temperatures in tropical latitudes indicate fast turnovers of larval populations compared with the longer turnover times expected in temperate seas. In reviewing mortality of marine organisms in relation to their size, Peterson and Wroblewski (1984) and McGurk (1986) noted the exceptionally high mortality rates of marine fish eggs and larvae and discussed some probable reasons and consequences. McGurk (1986) believed that patchiness and susceptibility to predation explained the relatively high rates of mortality. The analyses presented here demonstrate that the rates not only are high but that they vary predictably with temperature. Based on the species that are represented, the results are presumed to represent a latitudinal trend as well as to be seasonally significant. More than fourfold differences in the expected mortality rates of marine fish larvae can be attributed to environmental temperature, without considering effects of larval size, in the 5°–30°C range. Expected weight-specific growth rates of fish larvae also were demonstrated to be six times higher at temperatures in tropical seas (30°C) than at temperatures in cold seas (5°C).

A consequence of declining temperature is an exponential increase in predicted larval stage duration (Fig. 2). Stage durations for larvae that develop at ≤8°C exceed 100 days, while larvae that develop at the 25°–30°C temperatures in tropical seas, metamorphose in ≤30 days. More importantly, there is a relatively large increase in its potential variability as stage duration increases. The highest variability in growth rate is observed in species that develop at high temperature (Fig. 1), but the highest variability in stage duration is observed at low temperature. Consequently, small changes in growth rate can

TABLE 7.—Weight-specific oxygen consumptions (Q_{O_2}) of marine fish larvae. Values given are for feeding-stage larvae. Some Q_{O_2} values were calculated from oxygen uptake on larval weight regressions if these were given by the authors.

Species	Temperature (°C)		Q_{O_2}(μL mg^{-1} h^{-1})		References
	Range	Midpoint	Range	Midpoint	
Clupea harengus CH	5.0–18.0	11.5	0.30–5.00	2.65	Holliday et al. 1964; DeSilva and Tytler 1973; Eldridge et al. 1977; Almatar 1984; Kiorboe et al. 1987
Sardinops sagax SS	14.0	14.0	1.30–2.70	2.00	Lasker and Theilacker 1962
Anchoa mitchilli AM	26.0	26.0	4.00–8.20	6.10	Houde and Schekter 1983
Engraulis mordax EM	16.0–17.0	16.5	3.16–7.74	5.45	Theilacker and Dorsey 1980; Theilacker 1987
Gadus morhua GM	4.0–10.0	7.0	1.00–8.87	4.95	Laurence 1978; Davenport and Lonning 1980; Solberg and Tilseth 1984
Melanogrammus aegleinus MA	4.0–9.0	6.5	4.90–44.90	[1]24.90	Laurence 1978
Merluccius productus MP	8.0–15.0	11.5	4.50–12.10	8.30	Bailey 1982
Morone saxatilis MS	18.0	18.0	3.60–7.60	5.60	Eldridge et al. 1982
Archosargue rhomboidalis AR	26.0	26.0	5.6–11.03	8.32	Houde and Schekter 1983
Scomber japonicus SJ	18.0–22.0	20.0	6.10–11.4	8.75	Hunter and Kimbrell 1980
Pleuronectes platessa PP	5.0–18.0	11.5	1.10–5.98	3.54	DeSilva and Tytler 1973; Almatar 1984
Pseudopleuronectes americanus PA	2.0–8.0	5.0	1.80–8.00	4.90	Laurence 1975; Cetta and Capuzzo 1982
Achirus lineatus AL	28.0	28.0	2.00–19.70	10.85	Houde and Schekter 1983

[1]These values were calculated from the respiration on larval weight regressions in Laurence (1978). The values seem inordinately high and were not used in deriving the Eq. 7 relationship between Q_{O_2} and temperature.

TABLE 8.—Average energy budgets of first-feeding marine fish larvae derived from the growth, metabolism and growth efficiency data in the published literature. Absolute and relative (i.e. percent) budgets are presented for 10°, 20°, and 30°C. I = ingestion and G = growth (both assumed to have equivalencies of 5,000 cal g^{-1}). M = metabolism (converted from Q_{O_2} to energy units by the oxycalorific equivalent of 0.00463 cal μL^{-1} O$_2$). F = feces (calculated by difference). Budget is $I = G + M + F$. $K_1 = G/I$ $K_2 = G/(G + M)$ $A = (G + M)/I$.

Temperature (°C)	Absolute budget (cal μg^{-1} d^{-1})	Relative budget (%)	K_1	K_2	A
10	0.00157 = 0.00045 + 0.00076 + 0.00036	100 = 28.7 + 48.4 + 22.9	0.287	0.372	0.771
20	0.00320 = 0.00092 + 0.00113 + 0.00115	100 = 28.7 + 35.3 + 36.0	0.287	0.449	0.641
30	0.00483 = 0.00139 + 0.00150 + 0.00194	100 = 28.7 + 31.1 + 40.2	0.287	0.481	0.598

induce large changes in stage duration when temperature is low, a result that may significantly affect the recruitment process.

Within a species gross growth efficiency varies inversely in relation to ingestion (Checkley 1984; Kiorboe et al. 1987), and it probably varies in relation to other environmental factors as well. But, on average, the calculated gross growth efficiency for marine fish larvae equaled 0.29 ± 0.06 and there is no apparent relationship to temperature. It is noteworthy

that the mean gross growth efficiency calculated for marine fish larvae is identical to that reported for juvenile carnivorous fishes (Brett and Groves 1979). Because growth efficiency does not increase, larvae at high temperatures must attain fast growth through increased food consumption. The derived relationship between ingestion and temperature indicates that ingestion must increase nearly threefold to support average growth at 30°C compared to 10°C.

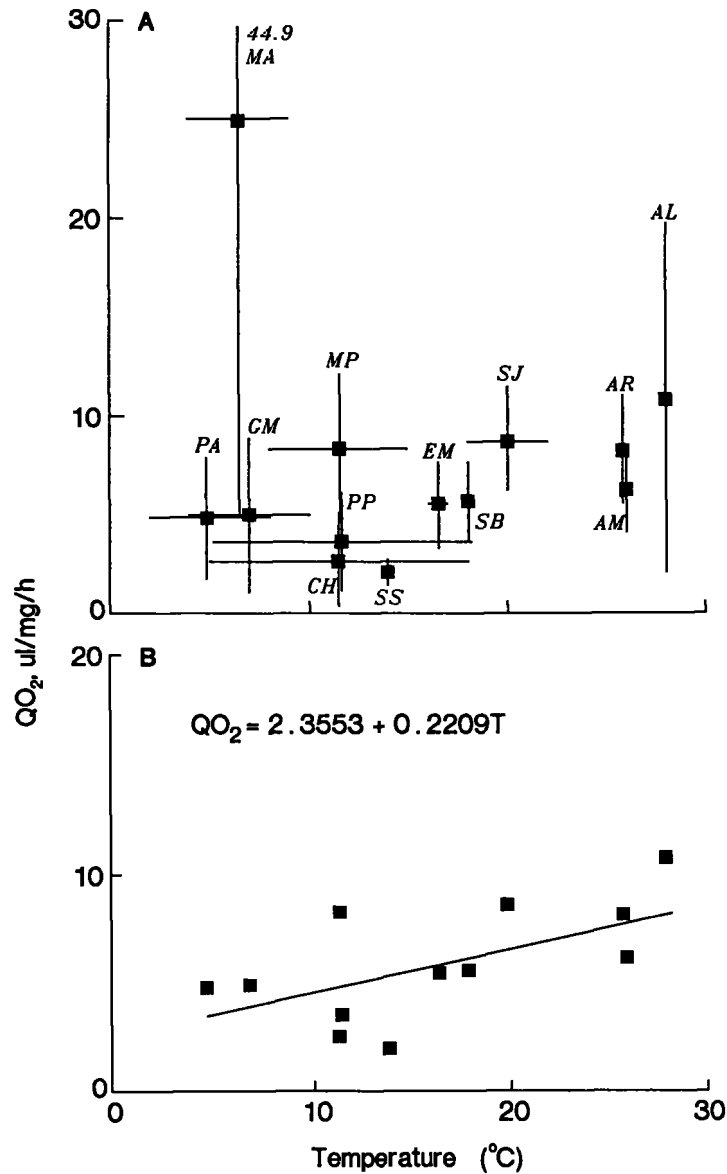Values of gross growth efficiency exceeding

FIGURE 6.—Weight-specific oxygen uptake (Q_{O_2}) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of Q_{O_2} and T values. Data, letters designating species and references are from Table 7. B. Regression relationship of midpoint Q_{O_2} on midpoint T. The data point for haddock (i.e., MA) is not included in the regression.

0.50 for marine fish larvae have been reported, e.g., in *C. harengus* (Checkley 1984; Kiorboe et al. 1987). Kiorboe et al. argued that herring, and possibly fish larvae in general, may be operating near peak growth and assimilation efficiency, but most published estimates indicate that larvae are no more efficient than juvenile fishes or other fast-growing animals. Boehlert and Yoklavich (1984) obtained assimilation efficiencies for Pacific herring, *C. harengus pallasi*, larvae in the range of 40–60%. This implies that gross growth efficiency was considerably lower, because assimilation efficiency includes energy of metabolism as well as growth.

Weight-specific oxygen consumption increases slowly in relation to temperature compared to the observed increase in growth rate. Rombough (1988) noted that the Q_{10} for oxygen uptake by individual species of fish eggs and larvae ranges from 1.5 to 4.9, averaging 3.0. These values are considerably higher than the Q_{10} of 1.46 estimated here as the among species temperature (presumed latitudinal) effect on marine fish larvae. Still, fish larvae in warm seas have a

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higher oxygen demand than larvae in colder seas. If gross growth efficiency is constant in relation to temperature, then assimilation efficiency should decline as temperature increases, while net growth efficiency should increase. Based on the calculated energy budgets at 10°C, 20°, and 30°C (Table 8), predicted assimilation efficiency declined from 77.1% at 10°C to 59.8% at 30°C. Average assimilation efficiencies of larval fish generally are thought to be similar to or less than the 80% mean assimilation efficiency of juveniles (Brett and Groves 1979; Govoni et al. 1986). Net growth efficiency increased from 37.2% at 10°C to 48.1% at 30°C. The range of predicted values of larval net gross efficiency lies just above the 36% mean value reported for juvenile fishes (Brett and Groves 1979). Recently, Wieser et al. (1988) estimated the net growth efficiency for larvae of the freshwater *Rutilus rutilus* and indicated that it was high and independent of temperature in the 15°–20°C range. Inspection of their table 4 data indicates that the net growth efficiency did in fact increase by approximately 4% in the 5°C range of their experiments, a percentage similar to that predicted from the energy budget analysis for marine fish larvae.

The mean assimilation efficiency for marine fish larvae declined as temperature increased. There also is good evidence that both assimilation and gross growth efficiency of an individual species decline at high ingestion rates (Houde and Schekter 1981; Checkley 1984; Boehlert and Yoklavich 1984; Kiorboe et al. 1987; Theilacker 1987). The ability of larvae to capture prey, the feeding conditions, and environmental factors all affect assimilation and growth, as well as their variability. Nevertheless, the efficiencies predicted here and their relationships to temperature still are believed to describe important latitudinal effects.

Despite expected high mortality rates, average survivorship of larval cohorts at tropical temperatures was predicted to exceed that of cohorts at high latitude temperatures. This result is a consequence of the high growth rates and the relatively short stage durations that tropical larvae experience. While net survivorship to metamorphosis in tropical systems may be relatively high, the daily probability of death also is high. Unless larval food abundance is higher or tropical larvae are better able than high latitude larvae to feed on scarce prey, neither of which has been demonstrated, starvation or other "critical period" mortalities (sensu

Hjort 1914) may be more probable in the tropics. Cohort survivorship is sensitive to small changes in mortality and growth rates in either tropical or high latitude systems. But, larval cohorts developing in high latitudes are likely to suffer proportionally greater declines from small decreases in growth rates or increases in mortality rates, a consequence of their extended larval stage duration. If even weak or sporadic density-dependent growth or mortality operates in the larval stage (Rothschild 1986), its effect could be substantial in high latitudes where the larval stage is long.

Based on this analysis, starvation of first-feeding larvae is hypothesized to be more likely in warm seas because of their relatively great ingestion requirement combined with low assimilation efficiency. If it were possible for fish larvae to live on a maintenance diet, they would face less risk of food-limitation. But, in laboratory experiments it has been observed that slow-growing larvae are less likely to survive (Laurence 1977; Houde and Schekter 1980, 1981). Estimates here indicate that approximately 15 food particles of 0.25 µg dry weight are required to produce 1 µg dry weight of larval growth. Tropical fish larvae that are growing 2–3 times as fast as larvae from cold seas, and which also have an elevated metabolism, must consume nearly three times as much prey to achieve average growth at ambient temperatures.

Average relationships reported here indicate that larval mortality rates exceed weight-specific growth rates. Morse (1989) also has examined the relationship among growth, mortality, and temperature for 26 species of North Atlantic fish larvae. He found that both growth rates and mortality rates increased with temperature. He concluded that the ratio of mortality rates to growth rates is less than 1.0 for most of those species, and suggested that, when ratios exceeded 1.0, gear avoidance is the possible cause. In my analysis I have accepted the possibility that mortality rates may exceed growth rates for teleost larvae, implying that there is a loss of biomass between the egg stage and metamorphosis in most species. The ratio of mortality rates to growth rates, based on the regression coefficients in the mortality rates on temperature and growth rates on temperature regressions is 1.31. Morse (1989) concluded that if larval growth rate is known, then mortality rates can be predicted because the two rates are correlated. This conclusion supports the obser-

vation that mortality rates potentially can be derived from relatively easy to obtain information on larval growth rate and its variability (Houde 1987). Before such estimates are possible, it will be necessary to explicitly determine the growth rates and mortality rates of many species to establish how reliable this approach might be.

Differences in spawning strategies of marine fishes may have evolved as a consequence of the different constraints on growth and survival of larvae from high and low latitudes. The constraints for low-latitude larvae, i.e., high mortality rates, high growth rates with attendant short stage duration, and required high ingestion, suggest that few larval cohorts will find the necessary local conditions conducive for growth and survival. In most cases cohorts will starve or be eaten. It is hypothesized that protracted spawning, serial spawning and frequent batch production of eggs, a common strategy in the tropics, will insure that some larval cohorts hatch during those brief periods when conditions favor the high growth rates that promote survival. In high latitudes, where spawning often is temporally and spatially confined, larvae have different constraints. There, both mortality and growth rates tend to be low, ingestion is relatively low, but stage duration is long and potentially very variable. Under such circumstances small changes in either mortality rates or growth rates can have major impacts on recruitment potential (Shepherd and Cushing 1980; Houde 1987). And, long larval stage durations also provide ample time for density-dependent mechanisms to develop which may regulate abundance and dampen fluctuations in stocks that originated from one or a few batch spawnings that occurred during a brief time. Under these conditions the timing of spawning (Cushing 1975) and the selection of favorable spawning sites (Iles and Sinclair 1982) by adults are critical to the recruitment success of a cohort.

Although density-dependent regulation in early life often is assumed, there is relatively little evidence that it does in fact play a major role in the egg and larval stage. Jones (1973), Cushing and Harris (1973), Ware (1975), and Shepherd and Cushing (1980) have modeled the recruitment process, demonstrating how density-dependent mortality and/or growth can regulate abundance. They have argued that regulation may be most effective in the larval stage. In support of those arguments, Savoy and Crecco (1988) have demonstrated that density-depen-

dent mortality during the egg and larval stage may play a significant role in the regulation of anadromous American shad, *Alosa sapidissima*, populations. Based on analyses of larval life history characteristics reported here, if density-dependent regulation is significant, it seems more likely to be effective in high latitudes than in tropical seas. The long stage duration and its potential variability, caused by varying temperature or food availability, may promote competition or allow predators to aggregate, favoring density-dependent control. In contrast, because larval stage durations in tropical seas are short and less variable, the probabilities of competitive or predator-mediated, density-dependent effects seem less likely.

The production of multiple cohorts during protracted spawning by tropical fishes and by many summer spawners in higher latitudes is a bet-hedging strategy that will allow some daily-produced cohorts to experience conditions favorable for survival. Lambert (1984) and Lambert and Ware (1984) have proposed that single batch, demersal spawners in high latitudes (e.g., herring and capelin, *Mallotus villosus*) are more likely to produce easily discernible cohorts of larvae than are summer-spawning pelagic species (e.g., Atlantic mackerel, *Scomber scombrus*, and white hake, *Urophycis tenuis*) in the same region because the demersal spawners are characterized by waves of females that deposit eggs at discrete time intervals. They argued that, in the cases of herring and capelin, widely spaced cohort production represented bet-hedging by reducing potential intraspecific competition among larvae and by assuring that cohorts of prey would develop with cohorts of fish larvae (Jones 1973; Jones and Hall 1974). Lambert and Ware (1984) believed that Atlantic mackerel and white hake females spawned every 2-3 days and that spawning in such species would appear to be continuous during their summer spawning season. In agreement with that argument, it is hypothesized here that teleost stocks spawning at high temperatures are more likely to produce daily cohorts of eggs than are those stocks spawning at low temperatures because the larvae of warm-water stocks have short stage durations and are constrained by the necessity for high growth and by their high mortality rates. This point is supported by Lambert and Ware's (1984) figure 4, in which they show that when larval growth rates are high, as they are in the tropics and in many high-latitude summer spawners, the predicted time period between

cohorts is reduced to only a few days. Under such conditions tropical species may spawn frequently for long periods (Clarke 1987) as a mechanism to promote recruitment success.

Several attempts have been made to develop unifying theories that explain recruitment fluctuations and regulation, including the match-mismatch hypothesis (Cushing 1975), the stable ocean hypothesis (Lasker 1978; 1981), and the larval retention hypothesis (Iles and Sinclair 1982). None of these is entirely satisfying, given the diverse nature of teleost fishes and the environments in which they live. Miller et al. (1988) have demonstrated that interspecific variation in larval size is a strong determinant of growth rate and a predictor of starvation-induced mortality. Hunter (1981) also recognized that larvae could be classified by their relative first-feeding abilities as judged by mouth size and general morphology. Miller et al. (1988) and Hunter (1981) have demonstrated that larvae can be categorized by their morphology as starvation-prone or not. Here, it is demonstrated that temperature, and by implication latitude, exercises a strong influence on the energetics, growth, and mortality rates of marine fish larvae. Furthermore, it is proposed that these traits have favored selection of spawning strategies that have evolved in warm and cold seas.

ACKNOWLEDGMENTS

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