

ECOSYSTEM- AND TAXON-SPECIFIC DYNAMIC AND ENERGETICS PROPERTIES OF LARVAL FISH ASSEMBLAGES

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ABSTRACT

Growth rates, mortality rates, and energetics properties of teleost larvae differ among species and among ecosystems. In this synthesis, the ingestion rates required to support mean growth of larvae were estimated and energy budgets were developed. Weight-specific growth coefficients (G), instantaneous mortality rates (Z), larval stage durations (D), gross growth efficiencies (K_1), and weight-specific oxygen uptake (QO_2) were obtained from published sources and categorized by marine and freshwater species. Rates and properties were subcategorized by marine ecosystems and by taxonomic group. The strong temperature dependencies of rates and properties for larvae were adjusted by analysis of covariance to allow mean values to be compared among ecosystems and taxa. After adjustment, relatively few significant differences were detected, indicating that, with important exceptions, teleost larvae have characteristic and predictable attributes. Marine fish larvae have higher Z , longer D and higher QO_2 than freshwater larvae, probably because marine larvae weigh less at hatch (47 μg versus 339 μg). Larvae of coral reef fishes had lower temperature-adjusted \bar{G} than larvae from other marine ecosystems. Values of K_1 (mean = 0.301) differed little among ecosystems or taxonomic groups and were not related to temperature. Energy budgets, which integrate the effects of rates and properties, differed appreciably among ecosystems and taxa. Ingestion, metabolism, and assimilation were higher for marine than for freshwater larvae. Mean temperature-adjusted ingestion rates usually were 40 to 65% of body weight, although values as high as 97% (Scombroidei) were estimated. Larvae from cool ecosystems (10°C) required two to four times less ingested energy on a daily basis than larvae from warm systems (28°C) to grow at their respective mean rates. Assimilation efficiencies declined as temperature increased. Temperature-adjusted mean assimilation efficiencies (\bar{A}) were 0.65 for marine and 0.56 for freshwater teleost larvae; \bar{A} ranged from 0.54 (shelf) to 0.75 (upwelling) for marine ecosystems, and from 0.47 (Salmoniformes) to 0.82 (Gadiformes) across taxonomic groups. Rates and relationships reported here, while not intended to predict species-specific responses, do provide information on deviations by individual species from predicted rates and can identify specific adaptations and life-history strategies. Results of the analyses will be useful to categorize, compare, and model ichthyoplankton assemblages in pelagic communities.

Most marine organisms have high fecundities and produce abundant progeny, which suffer high mortalities as they grow through early life toward recruitment. In teleost fishes, the recruitment process and its mechanisms are difficult to study because of the great potential for variability in growth and mortality rates in early life (Houde, 1987; Wootton, 1990), the problem of obtaining temporally and spatially representative samples, and the confounding effects of a dynamic, advective environment (Taggart and Leggett, 1987; McGurk, 1989; Taggart and Frank, 1990). Factors that may be categorized as either subtle or episodic affect the abundances of larval fish cohorts as they advance toward recruitment (Houde, 1989a). The causes of recruitment successes or failures often go unexplained, in part because mean rates and variability of response by larvae, as well as ecosystem and taxon-specific effects, are unknown.

The complexity of the recruitment process makes it unlikely that the process will be studied or understood in detail for many species. Thus, it is appealing to examine the problem in a general or conceptual framework. If levels of growth, mortality, and required ingestion of fish larvae are ecosystem-specific or taxon-specific, important issues could be addressed regarding life-history strategies, re-

cruitment dynamics, and early life bioenergetics. It also would be possible to consider fish larvae as components of ecosystems and to develop models that explicitly included fish early life stages.

Recently, some conceptualized approaches to understand factors that affect levels of growth and mortality in early life have been proposed. The roles of body size, of ontogenetic shifts in susceptibility to mortality, and the interdependence of growth and mortality rates, have helped to relate events in early life to overall life history strategies (Werner and Gilliam, 1984; Peterson and Wroblewski, 1984; McGurk, 1986, 1987; Miller et al., 1988; Beyer, 1989; Pepin, 1991). Growth and mortality have been found to depend upon body size, food availability, and temperature. There are strong, apparently predictable, relationships between temperature and vital rates of marine fish larvae (Houde, 1989b; Morse, 1989). Thus, the bioenergetics and ingestion requirements of larvae developing under warm or cool temperatures differ markedly, and spawning strategies of fishes may vary latitudinally as a consequence of temperature-related constraints in early life. Evolved, taxon-specific growth potential in early life also may be latitudinally regulated (Conover, 1990; Conover and Present, 1990), adding complexity to probable relationships. Taxon-specific feeding behavior and potential are morphologically determined (Hunter, 1981) and may affect growth and mortality rates, as well as energetics properties, of teleost larvae.

In this paper we examine growth and mortality rates, stage durations, metabolic rates, and growth efficiencies of fish larvae from marine and freshwater ecosystems. Within the marine category, comparisons were made among taxa from estuarine, shelf, oceanic, upwelling, and coral reef systems. Taxon-specific comparisons were made at the levels of order and suborder. Primary objectives were to determine ingestion requirements and develop energy budgets of larvae from the designated ecosystem and taxonomic categories. An overall goal was to learn whether food requirements of fish larvae are basically similar across taxa and ecosystems, regulated strongly by the physiological constraints imposed by temperature, or whether there are characteristic and adaptive differences within ecosystems or taxa that shape the recruitment process and other aspects of teleost life histories.

METHODS

Values of instantaneous mortality rates and instantaneous (weight-specific) growth rates, weight-specific oxygen uptakes, and gross growth efficiencies of teleost larvae were obtained from published literature or, if not explicitly given, were calculated when appropriate data were provided. Except for mortality rates, which came only from studies on unmanipulated wild populations, data were from both laboratory and field experiments. The data base (Appendix A) is restricted to the larval stage from hatching to metamorphosis and is expanded significantly beyond that compiled by Houde (1989b) to explore relationships between vital rates, energetics, and temperature for marine fish larvae. The analysis undertaken was not without risk because the data are of variable quality, and were collected and analyzed for different purposes. Despite these concerns, the approach is believed to be worthwhile, especially as an attempt to find generalities in teleost life histories that will be useful to understand population and community dynamics at ecosystem or broad taxonomic levels.

When weight-specific rates were not given, we converted growth rates for length to growth rates for weight using length-weight relationships. For some taxa, especially coral reef species, it was necessary to apply length-weight relationships from larvae of morphologically similar species (usually Sparidae). In cases where temperatures were not reported (e.g., coral reef species) we determined approximate temperatures from atlases of seasonal sea surface temperatures that corresponded to the areas of interest.

When rates and values were not estimated and reported explicitly in a publication, but suitable raw data were provided, we sometimes calculated rates, efficiencies, and energetics values. Except for the coral reef fishes, data points are for individual species. The coral reef larvae were treated at the genus level because, while larvae of many coral reef species have been measured and aged (e.g., Brothers et

al., 1983; Victor, 1986, 1987; Thresher and Brothers, 1989; Wellington and Victor, 1989), usually only a few individuals of any single species were analyzed.

Larvae were assigned to marine or freshwater categories. The marine larvae were subcategorized as estuarine, shelf, oceanic, upwelling, or coral reef species. Taxa were examined at the ordinal or subordinal level of classification (Appendix A). Some freshwater fishes with atypically large larvae (e.g., Salmonidae, Acipenseridae, Ictaluridae) were not included in our analyses.

The following data were used: W_0 , Dry weight at hatch (μg); W_{met} , Dry weight at metamorphosis (μg); G , Weight-specific growth coefficient ($\cdot\text{d}^{-1}$); Z , Instantaneous mortality coefficient ($\cdot\text{d}^{-1}$); D , Larval stage duration (d). Days to grow from weight at hatch (W_0) to estimated weight at metamorphosis (W_{met}); QO_2 , Weight-specific oxygen uptake ($\mu\text{l O}_2 \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$); I , Weight-specific daily food ingestion ($\cdot\text{d}^{-1}$), expressed as a fraction of body weight; and K_1 , Gross growth efficiency, defined as the ratio of G/I .

Regression relationships between these variables and temperature were derived. When more than a single value of a variable was available, the median values were regressed on median temperature. Analysis of covariance, with temperature as the covariate, was used to determine if the regression relationships or mean values differed among ecosystems or among taxa. The adjusted means (temperature effects having been removed) were tested (ANCOVA) to determine which differed significantly ($\alpha = 0.10$) and, consequently, if larvae could be categorized by ecosystem or taxon. An α level of 0.10 was selected to increase the power of tests to discern possible differences among ecosystems or taxa, admittedly at an increased risk of concluding falsely that differences existed (Type I error).

Daily ingestion requirements (I) of fish larvae seldom are reported in published literature (but, see MacKenzie et al., 1990). However, if both G and K_1 are known, I can be estimated as $I_A = G/K_1$. We examined the relationship between I and temperature. A second approach to estimate I , which accounts for temperature effects and which is based upon the relationship $I_E = G/\bar{K}_1$, also was applied, where \bar{K}_1 is mean gross growth efficiency and G is the expected growth rate derived from the relationship between growth and temperature. Because G had been derived from the equation, $G = a + bT$ (where T is temperature $^{\circ}\text{C}$), and \bar{K}_1 had been estimated, the expected relationship between daily ingestion rate and temperature was $I_E = (a + bT)/\bar{K}_1$. The I_A and I_E estimates are not completely independent, since both were derived from \hat{G} and \hat{K}_1 values that were available. The I_E estimator is a more general form because it uses the growth-temperature relationships to predict mean ingestion requirements for the ecosystem and taxon categories.

Energy budgets of teleost larvae were derived for all larvae, marine larvae, freshwater larvae, and for larvae classified by ecosystem-specific and taxon-specific categories. These budgets were developed from the mean values of ingestion, growth, and metabolism that were estimated for each of the categories. Budgets in $\text{cal} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ were expressed as: $I = G + M + U + F$ where I = ingestion, G = growth, M = metabolism, U = urine, and F = feces. The assumed conversion from dry weight to calories was $0.005 \text{ cal} \cdot \mu\text{g}^{-1}$. An oxythermal conversion coefficient of $0.00463 \text{ cal} \cdot \mu\text{l}^{-1} \text{ O}_2$ was applied (Brett and Groves, 1979) to convert oxygen uptake (QO_2) to metabolism. Reported oxygen uptake values generally were stated to be, or we presumed them to be, resting or routine rates. To determine M , we assumed that the reported QO_2 prevailed during a 12-h dark period each day when feeding and activity were minimal, and that a doubled rate ($2 \cdot QO_2$) prevailed during a lighted 12-h period when larvae were active and feeding. Urine production accounts for a small proportion of ingestion and we assumed that $U = 0.07I$, the mean value for young, carnivorous fishes (Brett and Groves, 1979). Loss as feces was obtained by difference. Assimilation efficiency was calculated as $A = (I - F)/I$. The Q_{10} values were calculated for G and M . Both temperature-specific and temperature-adjusted energy budgets were developed. The temperature-adjusted budgets, which allow direct comparisons of budget components among ecosystems and among taxonomic groups, were derived from the adjusted mean rates estimated in the analyses of covariance.

RESULTS

The regression relationships between larval G , D , Z , QO_2 , and temperature were significant but quite variable (Figs. 1–4). The addition of more marine species (primarily coral reef and oceanic) and the addition of freshwater species to the data base of Houde (1989b) did not change fundamental relationships, but the variability about the regressions increased. A total of 118 species was included in our analyses (Appendix A). A summary of the mean values for vital rate and energetics parameters is included as Table 1.

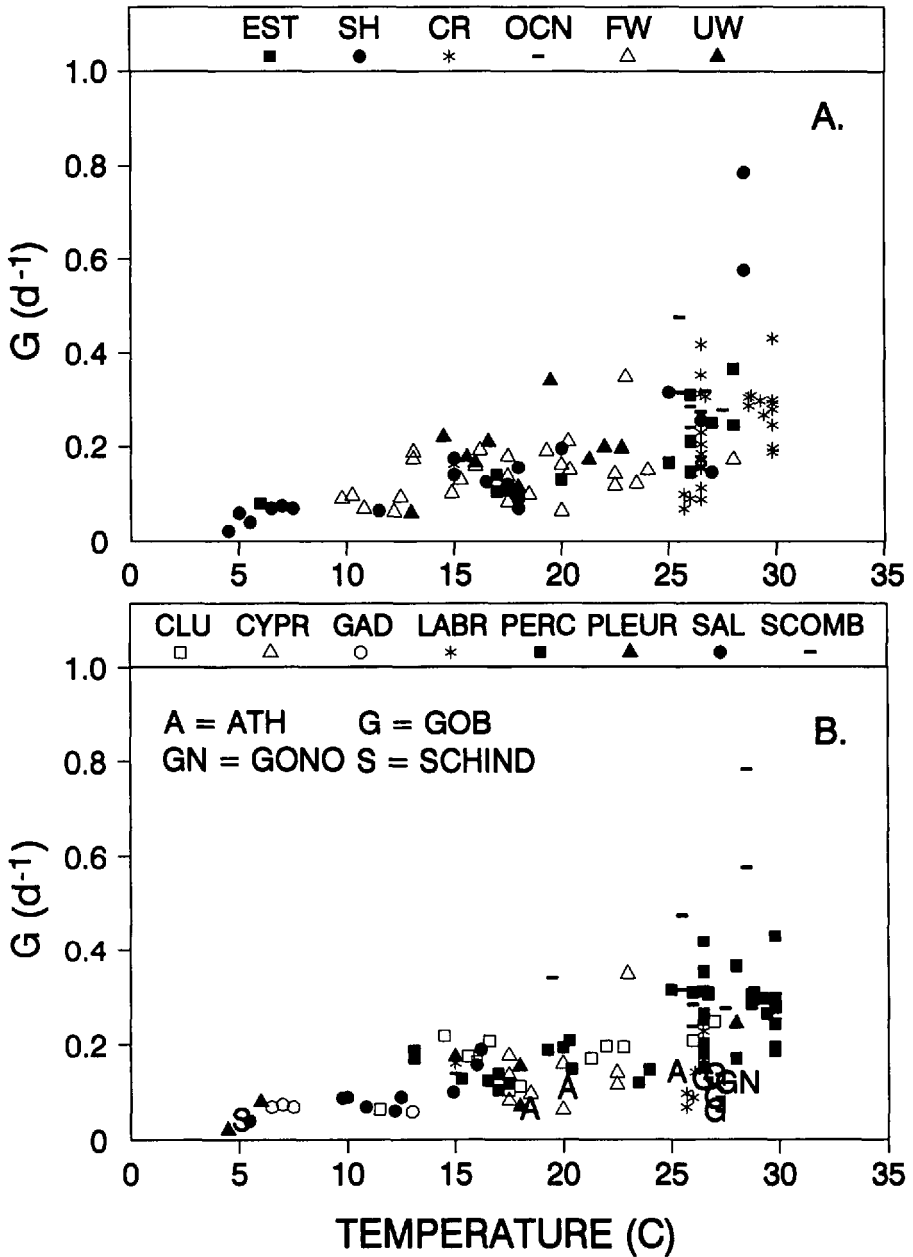


Figure 1. A. Ecosystem- and B. Taxon-specific, weight-specific growth coefficients (G, d^{-1}) of teleost larvae in relation to temperature. EST = estuarine, SH = shelf, CR = coral reef, OCN = oceanic, FW = freshwater, UW = upwelling, CLU = Clupeiformes, CYPR = Cypriniformes, GAD = Gadiformes, G = Gobioidae, LABR = Labroidae, PERC = Percoidae, PLEUR = Pleuronectiformes, SAL = Salmoniformes, SCOMB = Scombridae, A = Atheriniformes, GN = Gonorynchiformes, S = Schindlerioidei. Each data point is a reported or calculated value. In the case of species with more than one value reported for the variable of concern on temperature, the median value is plotted.

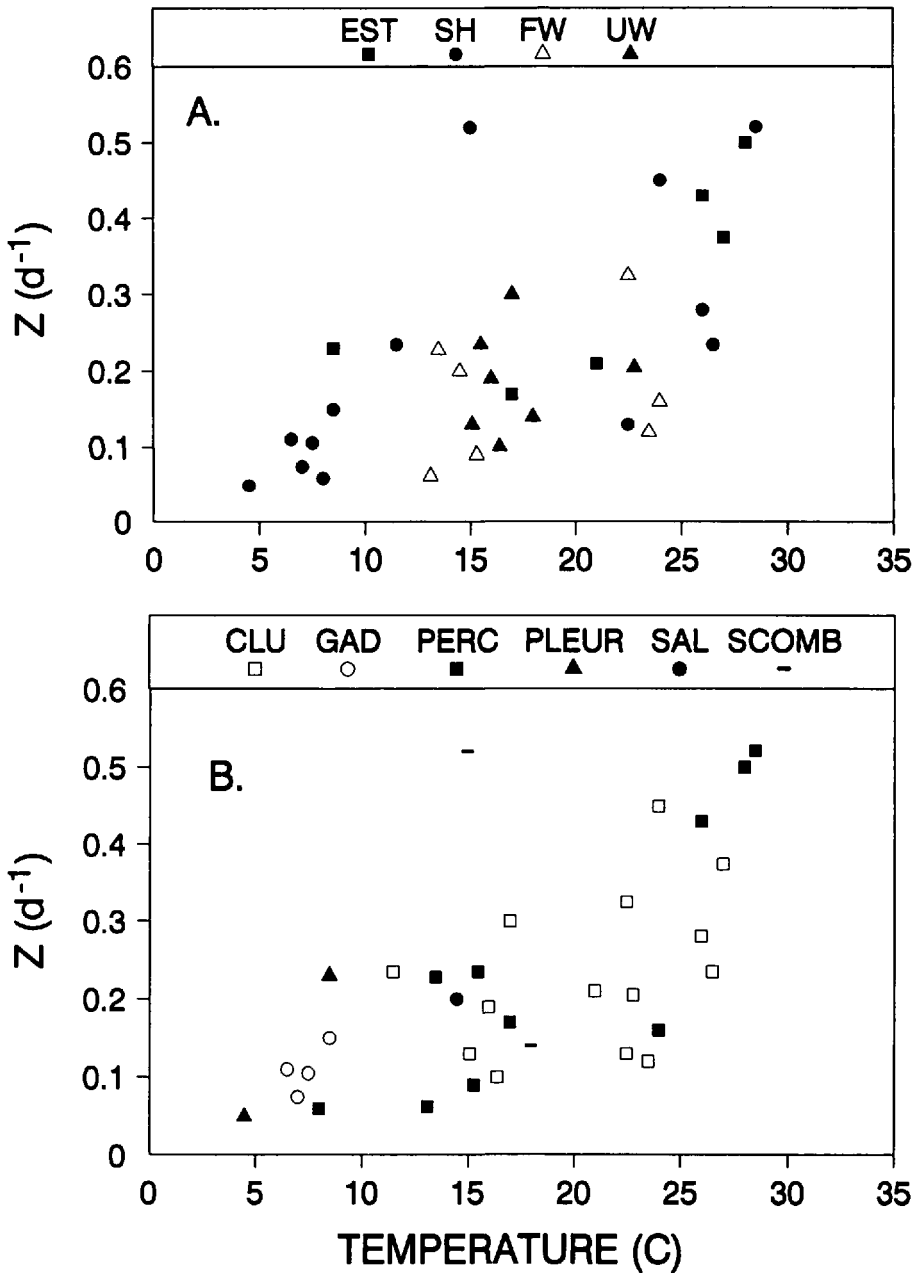


Figure 2. A. Ecosystem- and B. Taxon-specific, instantaneous mortality coefficients (Z , d^{-1}) of teleost larvae in relation to temperature. See Figure 1 for keys and explanations.

Weight at Hatch (W_0).—The mean of reported dry weights at hatch of freshwater larvae were heavier than those of marine larvae. The mean weight at hatch of 20 freshwater species was $339 \mu g$ ($SE = 74.0 \mu g$) while that of 45 marine species was $47 \mu g$ ($SE = 9.7 \mu g$). The weight differential is the probable reason for differences between marine and freshwater larvae in oxygen uptake, larval stage durations, and mortality rates that are reported in the following analyses.

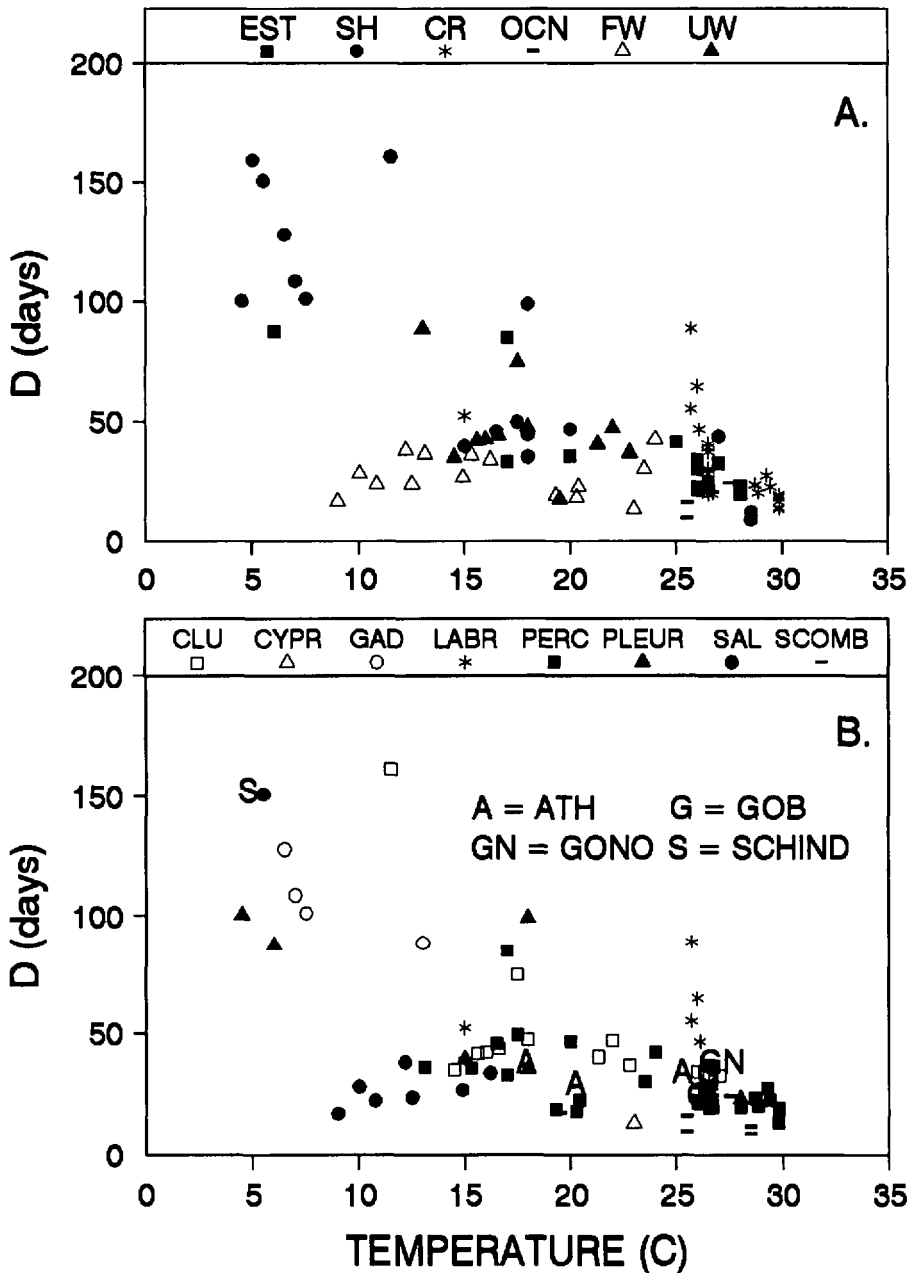


Figure 3. A. Ecosystem- and B. Taxon-specific, stage durations (D, days) of teleost larvae in relation to temperature. See Figure 1 for keys and explanations.

Growth (G).—Weight-specific growth rates, which ranged from $0.02 \cdot d^{-1}$ (*Pleuronectes platessa*) to 0.79 (*Scomberomorus maculatus*) generally increased as temperature increased. The mean weight-specific growth coefficient of 106 species was 0.194 (Table 2). On average, G of teleost larvae increases by approximately 0.01 for each $1^\circ C$ rise in temperature.

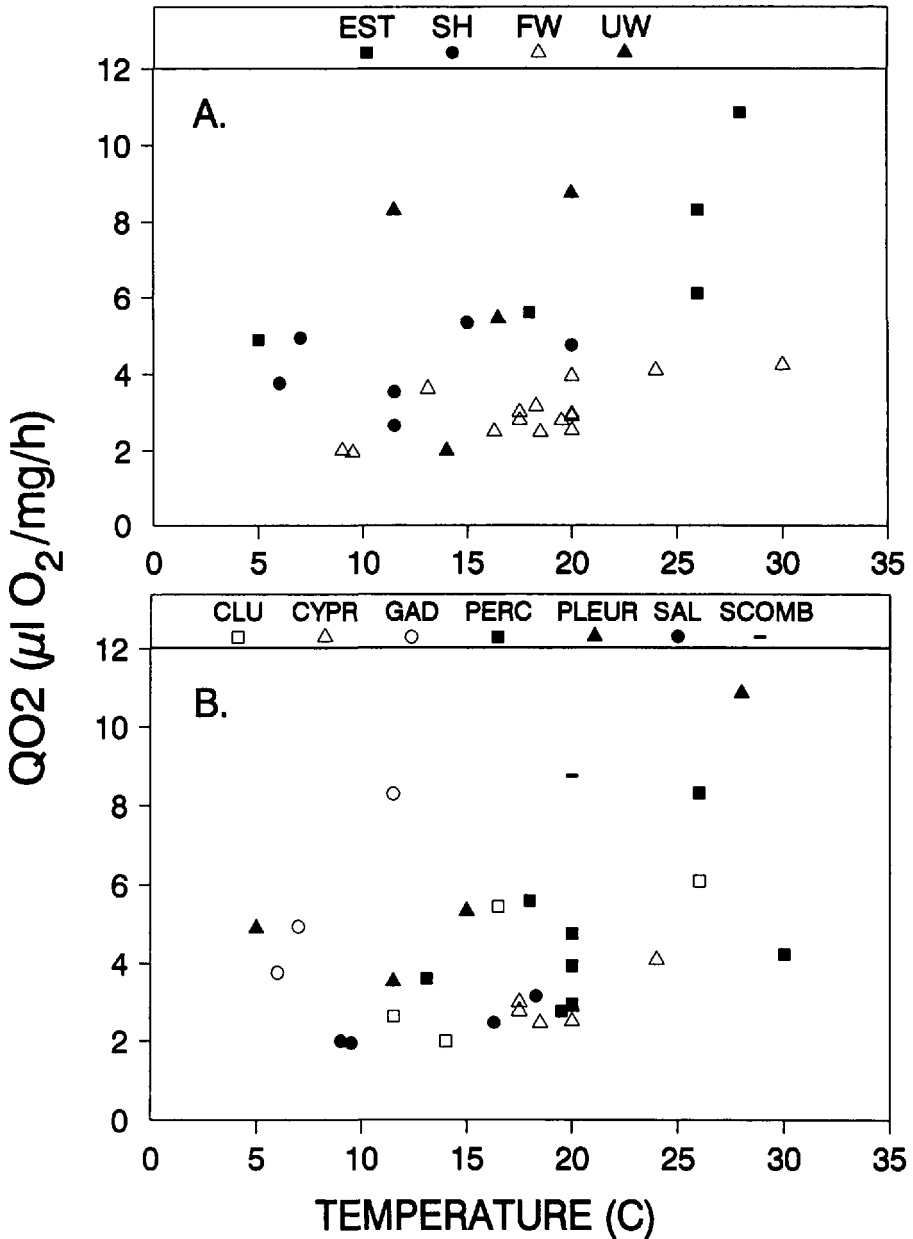


Figure 4. A. Ecosystem- and B. Taxon-specific, weight-specific oxygen uptake rate (QO₂, μl O₂ · mg⁻¹ · h⁻¹) of teleost larvae in relation to temperature. See Figure 1 for keys and explanations.

The regression coefficients for the relationships of \bar{G} on T for freshwater and marine taxa (Table 2) did not differ significantly ($P = 0.20$), although the coefficient for marine species (0.0106) appeared to be higher than that of freshwater species (0.0052). The temperature-adjusted \bar{G} values for freshwater and marine taxa, 0.177 and 0.200, respectively, do not differ significantly (ANCOVA, $P = 0.30$).

The adjusted, ecosystem-specific \bar{G} for the marine larvae were: coral reef: 0.159; estuary: 0.195; upwelling: 0.242; oceanic: 0.256; and shelf: 0.269. These means

Table 1. Teleost larvae. Ecosystem-specific and taxon-specific means of variables that were analyzed. (Except for "All Data," means for each category are the temperature-adjusted values from analyses of covariance.)

Data set	G	Z	D	K_T	QO ₂	I*	A
All data	0.194	0.222	33.06	0.301	4.35	0.530	0.65 (18°)
Freshwater	0.177	0.160	20.65	0.319	2.79	0.458	0.56
Marine	0.200	0.239	36.14	0.291	5.90	0.572	0.65
Marine ecosystems							
Estuarine	0.195	0.266	35.86	0.241	6.40	0.680	0.57
Shelf	0.269	0.250	34.14	0.296	4.78	0.477	0.54
Upwelling	0.242	0.184	36.43	0.368	6.16	0.647	0.75
Oceanic	0.256	—	25.94	—	—	—	—
Coral reef	0.159	—	35.88	—	—	—	—
Taxa							
Clupeiformes	0.196	0.179	43.85	0.308	4.04	0.620	0.59
Cypriniformes	0.162	—	14.76	0.305	2.34	0.347	0.52
Salmoniformes	0.195	0.244	19.59	0.256	3.28	0.589	0.47
Gadiformes	0.196	0.265	45.71	0.325	7.77	0.422	0.82
Percoidei	0.204	0.221	29.92	0.353	3.62	0.538	0.63
Labroidei	0.108	—	54.20	—	—	—	—
Gobioidei	0.076	—	45.08	—	—	—	—
Scombroidei	0.329	0.342	22.54	0.319	8.03	0.973	0.65
Pleuronectiformes	0.188	0.309	35.32	0.214	6.65	0.625	0.54

* Values given here are calculated from actual \bar{G} and \bar{K} values. They are the I_A values from Table 7. The alternative, and more general "expected" ingestion I_E values, were calculated from the growth-temperature relationships (Table 2) and K_T values (Table 6) (see Methods). The I_A and I_E relationships are illustrated in Figure 15.

differed significantly ($P < 0.05$). Without adjustment, G of coral reef species was high (0.228), but the adjusted \bar{G} of coral reef species was lower than that of larvae from the other marine ecosystems, except estuarine, when the temperature effect was removed (Table 2).

The linear relationships between weight-specific growth coefficient (G) and temperature (T) were significant for the shelf, estuary, and coral reef ecosystems (Table 2, Fig. 1A). In these cases, G increased by 0.01 to 0.02 per 1°C increase in T . There was no significant correlation between G and T for larvae from oceanic and upwelling systems, probably because the available temperature ranges were small for these analyses.

Most taxa had similar temperature-adjusted \bar{G} , but there were some significant differences among the nine taxonomic categories (Table 2). Goby larvae had lower \bar{G} values than other taxa except labrids, while scombrids had highest \bar{G} (Figs. 1B, 5). Most of the goby and labrid larvae were coral reef species. If these taxa were removed from the coral reef data, adjusted \bar{G} for coral reef larvae would increase from 0.159 to 0.188, but it would remain the lowest ecosystem \bar{G} , although no longer significantly lower (ANCOVA, $P > 0.20$).

Mortality (Z).—Instantaneous mortality coefficients ranged from 0.05 · d⁻¹ (*Pleuronectes platessa*) to 0.52 (*Scomber scombrus*) and generally increased as temperature increased. The unadjusted mean for 33 taxa was $\bar{Z} = 0.222$ (= 19.9% · d⁻¹). There was a significant relationship ($P = 0.0001$) between Z and temperature (T) for the 33 taxa (Table 3, Fig. 2). The mortality coefficient, like that for growth, increased by approximately 0.01 for each 1°C temperature increase.

There was no significant regression of Z on T for the freshwater fishes, for which only seven estimates of Z were available ($P > 0.50$) (Table 3, Fig. 2A). The linear

Table 2. Weight-specific growth coefficient (G , d^{-1}) and its relationship to temperature (T , $^{\circ}C$) for all data and for subsets of the data distinguished by ecosystem and taxa. When significant ($\alpha = 0.10$), linear regression equations and related parameters are provided. Adjusted means are based upon analysis of covariance with temperature as covariate. Identical superscripts on adjusted means indicate no significant difference (GLM least square means comparison). S_b = standard error of the regression coefficient

Data set	Regression equation	P	N	S_b	r^2	Mean	SE	Adjusted mean	SE
All data	$G = -0.0226 + 0.0102T$	<0.0001	106	0.0013	.36	0.194	0.009	—	—
Marine	$G = -0.230 + 0.0106T$	<0.0001	80	0.0016	.35	0.211	0.011	0.200 ^a	0.011
Freshwater	$G = 0.0511 + 0.0052T$	<0.05	26	0.0023	.17	0.142	0.011	0.177 ^a	0.019
Estuary	$G = -0.0236 + 0.0098T$	<0.01	11	0.0029	.55	0.195	0.019	0.195 ^{abc}	0.029
Shelf	$G = -0.0938 + 0.0169T$	<0.005	20	0.0037	.54	0.178	0.017	0.269 ^{cd}	0.025
Upwelling	n.s.	>0.25	11	—	—	0.178	0.022	0.242 ^{bcd}	0.031
Oceanic	n.s.	>0.30	7	—	—	0.312	0.028	0.256 ^{bcd}	0.037
Coral reef	$G = -0.1300 + 0.0132T$	<0.05	31	0.0059	.15	0.228	0.016	0.159 ^a	0.020
Clupeiformes	$G = 0.0410 + 0.0069T$	<0.05	11	0.0028	.37	0.173	0.013	0.196 ^{cd}	0.023
Cypriniformes	n.s.	>0.20	9	—	—	0.147	0.027	0.162 ^{bcd}	0.026
Salmoniformes	$G = -0.0293 + 0.0110T$	<0.05	9	0.0029	.67	0.101	0.012	0.195 ^{cd}	0.031
Gadiformes	$G = 0.0850 - 0.0019T$	<0.10	4	0.0006	.84	0.069	0.002	0.196 ^{cd}	0.045
Percoidei	$G = -0.0169 + 0.0103T$	<0.0001	38	0.0021	.40	0.237	0.011	0.204 ^{cd}	0.014
Labroidaei	n.s.	>0.85	8	—	—	0.142	0.020	0.108 ^{abc}	0.028
Gobioidaei	n.s.	>0.55	4	—	—	0.126	0.018	0.076 ^{ab}	0.040
Scombroidei	$G = -0.2252 + 0.0236T$	<0.10	11	0.0124	.29	0.366	0.049	0.329 ^f	0.024
Pleuronectiformes	$G = 0.0073 + 0.0079T$	<0.05	6	0.0026	.70	0.124	0.020	0.188 ^{cd}	0.034

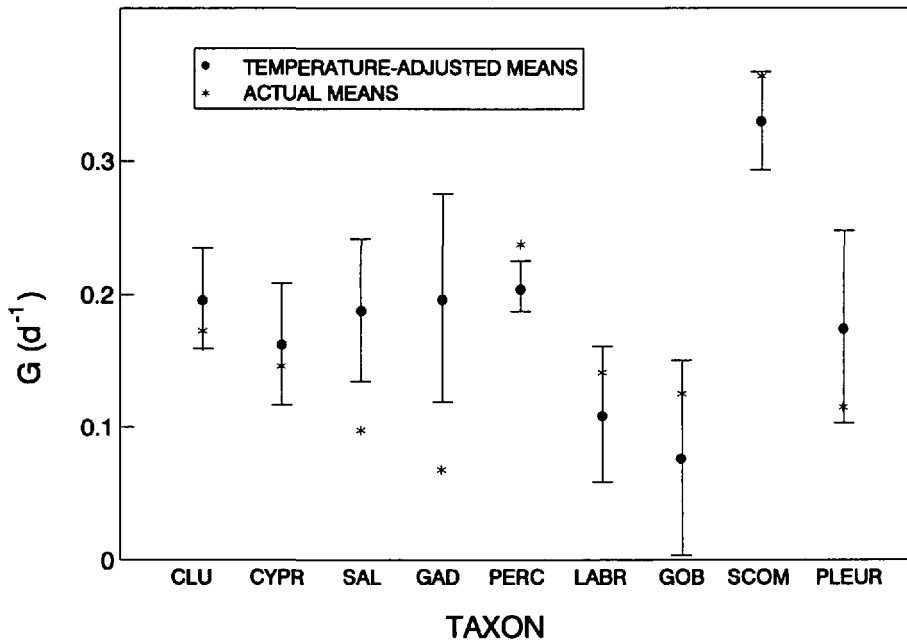


Figure 5. Taxon-specific mean weight-specific growth coefficients (G) of teleost larvae. ● Temperature-adjusted ± 2 standard errors. * Actual means. See Figure 1 for taxon keys and explanations.

regression equation for marine species ($N = 26$) was significant ($P = 0.0001$). Temperature-adjusted \bar{Z} of marine larvae ($\bar{Z} = 0.239$) was significantly higher than that of freshwater larvae ($\bar{Z} = 0.160$) (Table 3; ANCOVA, $P < 0.10$). The mean dry weight at hatch of freshwater species in this particular analysis, $247 \mu\text{g}$, was significantly ($P < 0.05$) heavier than that of the marine species, $47 \mu\text{g}$, and a probable factor affecting mortality rates.

Ecosystem-specific values of adjusted \bar{Z} for larvae in three systems (Table 3, Fig. 6) were: upwelling: 0.184; shelf: 0.250; and estuary: 0.266. These means did not differ significantly (ANCOVA, $P > 0.15$). Regressions of Z on T were significant for larvae from estuaries and shelves, but not for the upwelling system (Table 3), where data were restricted to a narrow temperature range. Regression coefficients (slopes) relating Z and T for the estuary (0.0137) and shelf (0.0130) larvae were similar (ANCOVA, $P = 0.85$).

Although adjusted \bar{Z} values for taxonomic groups ranged widely from 0.179 to 0.342 (Table 3, Fig. 7), the GLM (least square means) pairwise comparisons indicated that only the highest \bar{Z} (Scombroidei) differed significantly ($P < 0.10$) from the lowest \bar{Z} (Clupeiformes).

Stage Duration (D).—The estimated larval stage durations of 94 teleost species ranged from 9 (*Scomberomorus maculatus*) to 161 (*Clupea harengus*) days. Mean D for all taxa was 33.1 d (Table 4). Larval stage duration declines rapidly as temperature increases. The relationship between D and T (Fig. 3) for all data was described by a power function (Table 4).

Mean temperature-adjusted stage duration was 15.4 d shorter for freshwater larvae (20.7 d) than for marine larvae (36.1 d) (Table 4, Fig. 8). The temperature-adjusted \bar{D} differed significantly between the freshwater and marine larvae (ANCOVA, $P < 0.0001$).

Table 3. Instantaneous daily mortality coefficient (Z , d^{-1}) and its relationship to temperature (T , $^{\circ}C$) for all data and for subsets of the data distinguished by ecosystem and taxa. When significant ($\alpha = 0.10$), linear regression equations and related parameters are provided. Adjusted means are based upon analysis of covariance with temperature as the covariate. Identical superscripts on adjusted means indicate no significant difference (GLM least square means comparison). S_b = standard error of the regression coefficient

Data set	Regression equation	P	N	S_b	r^2	Mean	SE	Adjusted mean	SE
All data	$Z = 0.0156 + 0.0119T$	0.0001	33	0.0027	0.38	0.222	0.019	—	—
Marine	$Z = 0.0149 + 0.0129T$	0.0001	26	0.0029	0.46	0.222	0.021	0.239 ^a	0.021
Freshwater	n.s.	>0.50	7	—	—	0.169	0.036	0.160 ^b	0.040
Estuary	$Z = 0.0277 + 0.0137T$	<0.005	6	0.0057	0.59	0.319	0.039	0.266 ^a	0.044
Shelf	$Z = 0.0314 + 0.0130T$	<0.05	13	0.0042	0.46	0.225	0.037	0.250 ^a	0.029
Upwelling	n.s.	>0.70	7	—	—	0.186	0.028	0.184 ^a	0.041
Clupeiformes	n.s.	>0.10	14	—	—	0.235	0.026	0.179 ^{ab}	0.033
Salmoniformes	—	—	1	—	—	0.200	—	0.244 ^{ab}	0.111
Gadiformes	n.s.	>0.25	4	—	—	0.110	0.013	0.265 ^{ab}	0.068
Percoidi	$Z = -0.1536 + 0.0211T$	<0.005	10	0.0050	0.74	0.246	0.030	0.221 ^{ab}	0.036
Pleuronectiformes	n.s.	—	2	—	—	0.140	—	0.309 ^{ab}	0.089
Scombroidei	n.s.	—	2	—	—	0.330	—	0.342 ^b	0.078

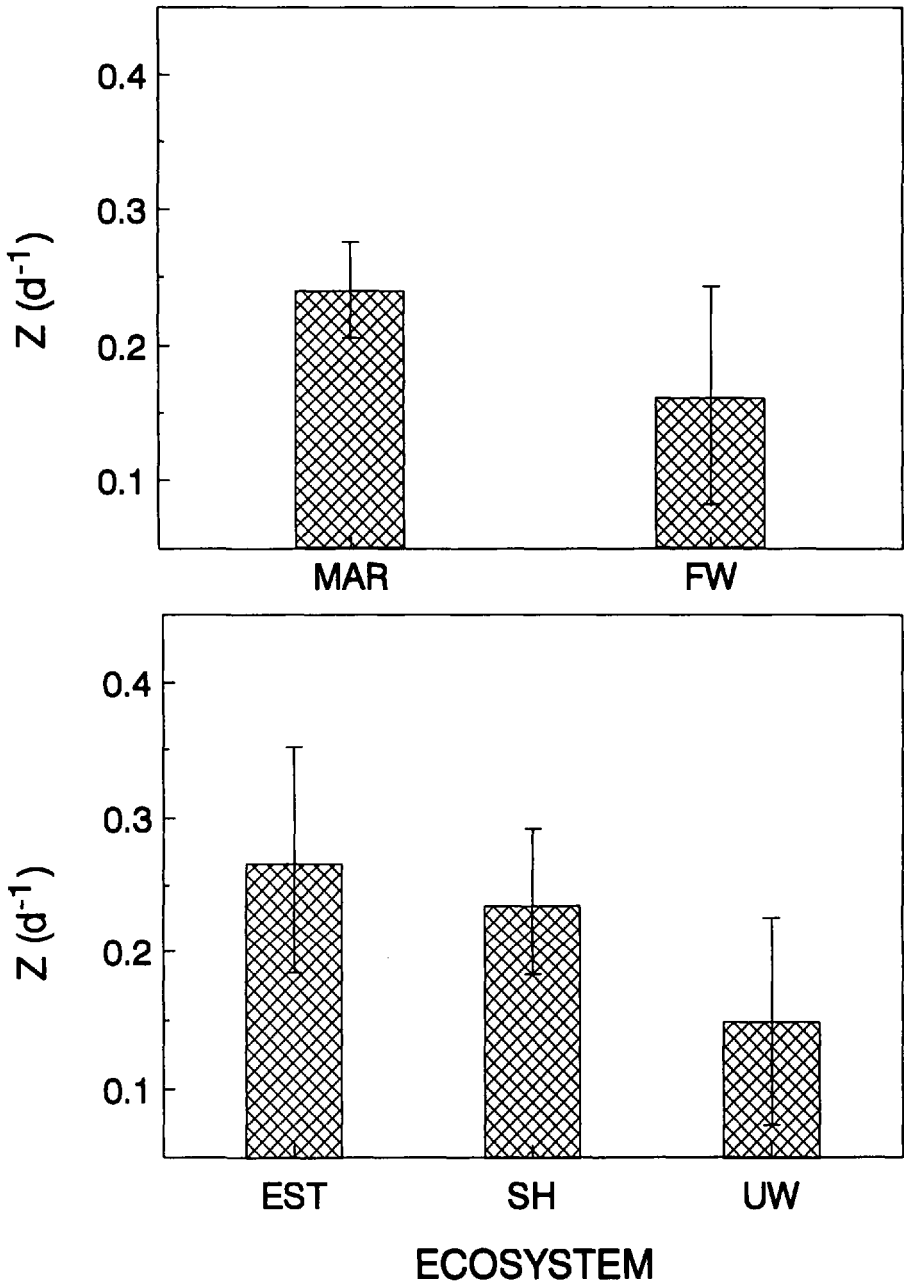


Figure 6. Temperature-adjusted, ecosystem-specific mean instantaneous mortality coefficients (Z) of teleost larvae. See Figure 1 for ecosystem keys and explanations.

The mean dry weights at hatch of freshwater and marine species in the stage-duration analysis were 384 μg and 48 μg , respectively. This seven-fold difference in weights at hatch partly accounted for the shorter \bar{D} of freshwater larvae, because there was no difference in growth rates or sizes at metamorphosis of the marine

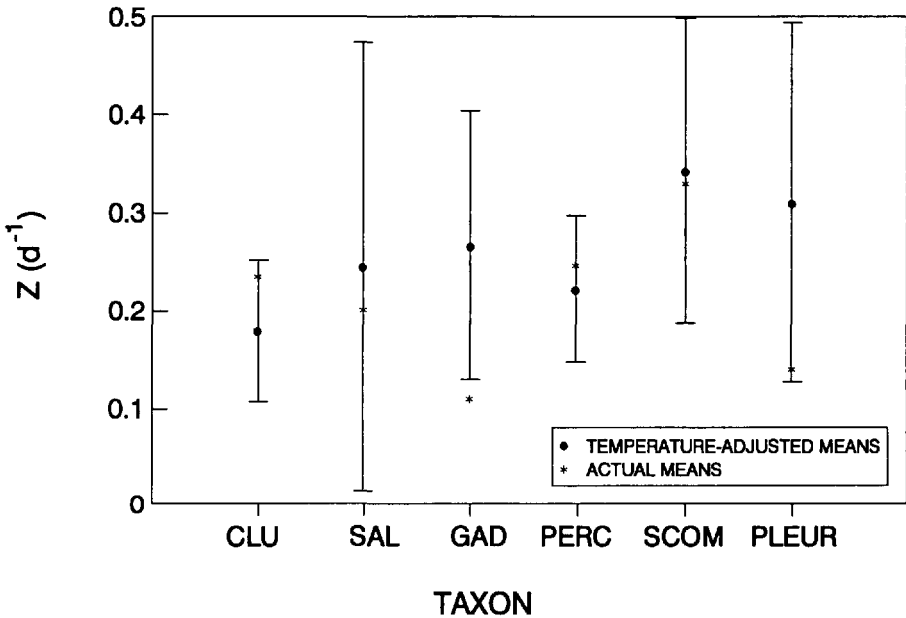


Figure 7. Taxon-specific mean instantaneous mortality coefficients (Z) of teleost larvae. ● Temperature-adjusted ± 2 standard errors. * Actual means. See Figure 1 for taxon keys and explanations.

and freshwater species. At $\bar{G} = 0.19$, the average growth rate of marine teleost larvae, it would require 11.0 d for a 48- μg (weight at hatch) larva to grow to 384 μg , the hatch weight of a freshwater larva.

The marine ecosystem \bar{D} values ranged from 20.0 d (oceanic) to 55.7 d (shelf) (Table 4). After temperature adjustment, the \bar{D} were similar (34.1 to 36.4 d) for larvae from all marine systems (Table 4, Fig. 8) except the oceanic (25.9 d), which was represented primarily by fast growing tuna larvae. There was no significant correlation between D and T for larvae from upwelling or oceanic ecosystems, probably because the temperature ranges represented were small (Fig. 3A).

Cypriniform, salmoniform, and scombroid larvae have short temperature-adjusted \bar{D} compared to other taxonomic groups (Table 4, Fig. 9). Clupeiform, gadiform, gobioid, and labroid larvae have long stage durations. The unadjusted \bar{D} ranged from 13.5 d for cypriniform larvae to 105.2 d for gadiform larvae. Temperature-adjusted \bar{D} were less variable, ranging from 14.8 d for cypriniform to 54.2 d for labroid larvae.

Weight-Specific Oxygen Uptake (QO₂).—Values of QO₂ ranged from 2.0 (*Coregonus albula*, *C. lavaretus* and *Sardinops caerulea*) to 10.9 (*Achirus lineatus*) $\mu\text{l O}_2 \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ and increased as temperature increased for the 30 species analyzed (Table 5, Fig. 4). Mean QO₂ for all larvae was 4.35 $\mu\text{l O}_2 \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$.

Linear regressions for freshwater and marine taxa differed strongly in their QO₂ on T relationships (Table 5, Fig. 4A). The temperature-adjusted mean QO₂ (Fig. 10) for larvae from marine systems (5.90) was more than twice that of freshwater larvae (2.79), a very significant difference (ANCOVA, $P < 0.0001$).

For species in the QO₂ analysis, mean weight at hatch of freshwater larvae was 338 μg (range = 107 to 1,200 μg) and that of marine larvae was 44 μg (range = 8 to 200 μg), a 7.7-fold difference in mean weights. Because QO₂ is expected to

Table 4. Larval stage duration (D, d) and its relationship to temperature (T, °C) for all data and for subsets of the data distinguished by ecosystem and taxa. When significant ($\alpha = 0.10$), power function regression equations and related parameters are provided. Adjusted means are based upon analysis of covariance with temperature as the covariate. Identical superscripts on adjusted means indicate no significant difference (GLM least square means comparison). S_b = standard error of the regression coefficient

Data set	Regression equation	P	N	S_b	r^2	Mean	SE	Adjusted mean	SE
All data	$D = 515.94T^{-0.9213}$	<0.0001	94	0.1057	0.45	33.06	1.05	—	—
Marine	$D = 971.63T^{-1.1024}$	<0.0001	79	0.1012	0.61	34.52	1.05	36.14 ^a	1.05
Freshwater	n.s.	>0.50	15	—	—	26.36	1.09	20.65 ^b	1.12
Estuary	$D = 462.28T^{-0.8453}$	0.005	11	0.2291	0.60	35.48	1.10	35.86 ^{ab}	1.13
Shelf	$D = 997.46T^{-1.1161}$	<0.0001	19	0.1860	0.68	55.70	1.12	34.14 ^{ab}	1.12
Upwelling	n.s.	>0.20	11	—	—	43.28	1.13	36.43 ^{ab}	1.14
Oceanic	n.s.	>0.15	7	—	—	19.96	1.14	25.94 ^a	1.17
Coral reef	$D = 22,064.80T^{-2.0372}$	0.001	31	0.5711	0.30	26.72	1.07	35.88 ^b	1.09
Clupeiformes	$D = 1,393.16T^{-1.1608}$	<0.05	12	0.4166	0.46	46.99	1.11	43.85 ^{cd}	1.11
Cypriniformes	n.s.	—	1	—	—	13.50	—	14.76 ^a	1.43
Salmoniformes	$D = 722.77T^{-1.2745}$	<0.10	8	0.5784	0.45	34.36	1.20	19.59 ^a	1.16
Gadiformes	n.s.	>0.10	4	—	—	105.20	1.05	45.71 ^{cd}	1.25
Percoidae	$D = 1,061.70T^{-1.1770}$	<0.0001	35	0.2201	0.46	24.89	1.05	29.92 ^b	1.07
Labroidae	n.s.	>0.60	8	—	—	44.87	1.18	54.20 ^d	1.14
Gobioidae	n.s.	>0.45	4	—	—	34.75	1.08	45.08 ^{cd}	1.20
Scombroidei	n.s.	<0.10	11	—	—	18.49	1.14	22.54 ^a	1.12
Pleuronectiformes	$D = 286.74T^{-0.6565}$	<0.10	6	0.2972	0.55	54.83	1.24	35.32 ^{bc}	1.18

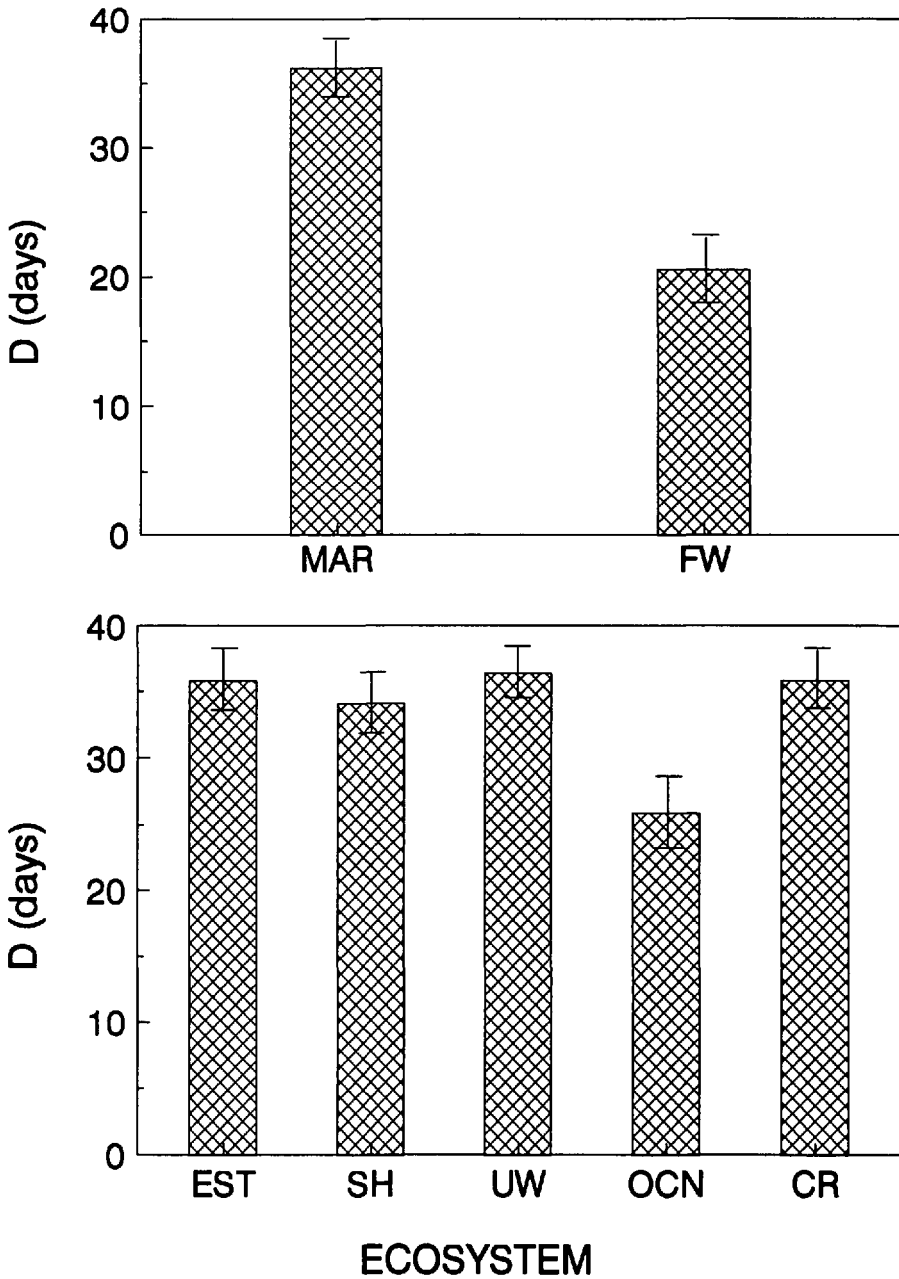


Figure 8. Temperature-adjusted, ecosystem-specific mean stage durations (D) of teleost larvae. See Figure 1 for ecosystem keys and explanations.

decline significantly as weight increases, the weight difference appears to be sufficient to account for the difference in mean QO_2 between freshwater and marine larvae (Fig. 11).

There were no demonstrable differences in larval QO_2 among marine ecosystems (Table 5, Fig. 10) for the 15 taxa that were included. Temperature-adjusted mean

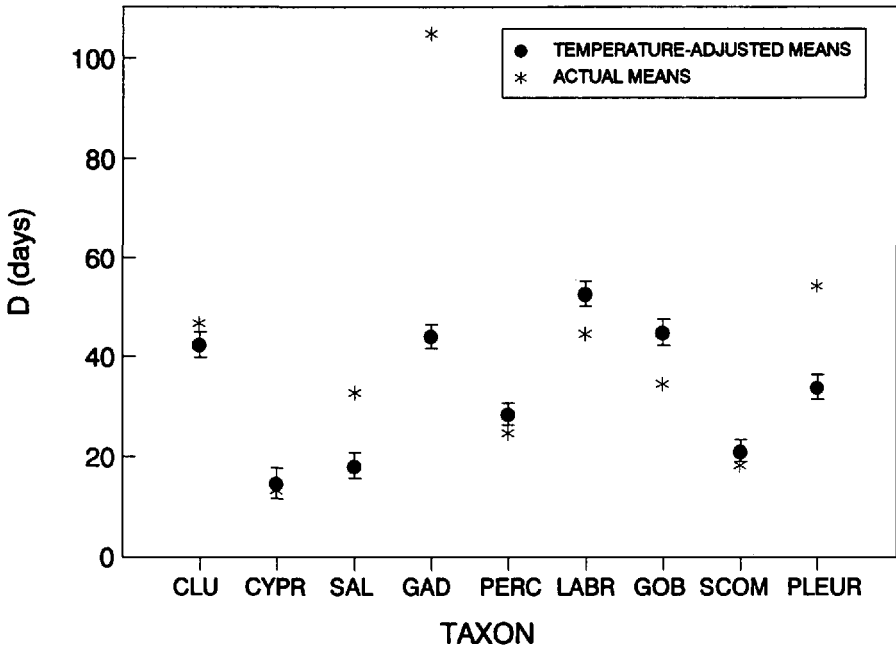


Figure 9. Taxon-specific mean stage durations (D) of teleost larvae. ● Temperature-adjusted ± 2 standard errors. * Actual means. See Figure 1 for taxon keys and explanations.

QO_2 ranged from 4.78 to 6.40 $\mu\text{l O}_2 \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ for larvae from estuary, shelf, and upwelling systems.

Taxa dominated by marine species generally had higher QO_2 than those dominated by freshwater species. The temperature-adjusted means ranged from 2.34 for cypriniform larvae to 8.03 for scombroid larvae (Table 5, Fig. 12) and differed significantly (ANCOVA, $P < 0.0001$). The scombroid, pleuronectiform, and gadiform larvae had higher adjusted mean QO_2 than other larvae (ANCOVA, $P < 0.0001$).

G/Z Ratio.—The ratio G/Z , an indicator of population biomass increase or decrease during a life stage, ranged from 0.27 to 2.43 and was not correlated with temperature ($P > 0.35$) (Fig. 13). Mean G/Z of 22 taxa for which estimates of G and Z were available (Appendix) was 0.94 (SE = 0.13). The mean G/Z for 5 freshwater species was 1.13 (SE = 0.32) and that for 17 marine species was 0.89 (SE = 0.14). These means were not significantly different ($P > 0.40$). The overall mean G/Z , and G/Z means for marine and freshwater larvae did not differ significantly from a value of 1.0 (Student's t -test, $P > 0.25$ in all cases), indicating that population biomasses are relatively constant during the teleost larval stage. The ratio of the regression coefficients from the G on T (Table 2) and Z on T (Table 3) regressions, another index of G/Z , was 0.86 for all larvae, an indication that the ratio is near or slightly less than 1.0.

Gross Growth Efficiency (K_1).—There was no significant relationship between K_1 and temperature (Fig. 14). Mean K_1 ($\pm 95\%$ confidence limits) for all data was 0.301 ± 0.042 (Table 6). The adjusted \bar{K}_1 values of larvae from marine and freshwater ecosystems were 0.291 and 0.319, respectively, values not significantly different ($P > 0.50$). Values of adjusted \bar{K}_1 for larvae from estuaries, shelf, and

Table 5. Weight-specific oxygen uptake (QO_2 , $\mu\text{O}_2 \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$) and its relationship to temperature (T , $^{\circ}\text{C}$) for all data and for subsets of the data distinguished by ecosystem and taxon. When significant ($\alpha = 0.10$), linear regression equations and related parameters are provided. Adjusted means are based upon analysis of covariance with temperature as the covariate. Identical superscripts on adjusted means indicate no significant difference (GLM least square means comparison). S_b = standard error of the regression coefficient

Data set	Regression equation	P	N	S_b	r^2	Mean	SE	Adjusted mean	SE
All data	$QO_2 = 2.2896 + 0.1209T$	<0.10	30	0.0623	0.12	4.35	0.39	—	—
Marine	$QO_2 = 2.4328 + 0.2067T$	<0.05	15	0.0727	0.38	5.69	0.51	5.90 ^a	0.38
Freshwater	$QO_2 = 1.2069 + 0.0983T$	<0.005	15	0.0259	0.53	3.00	0.13	2.79 ^b	0.38
Estuary	n.s.	>0.15	5	—	—	7.15	0.86	6.40 ^a	1.00
Shelf	n.s.	>0.50	6	—	—	4.17	0.44	4.78 ^a	0.89
Upwelling	n.s.	>0.70	4	—	—	6.13	1.84	6.16 ^a	1.01
Clupeiformes	n.s.	>0.15	4	—	—	4.05	0.71	4.04 ^{bc}	0.67
Cypriniformes	$QO_2 = -0.6995 + 0.1871T$	<0.10	6	0.0768	0.60	2.96	0.17	2.34 ^b	0.57
Salmoniformes	$QO_2 = 0.9259 + 0.1116T$	<0.10	4	0.0290	0.88	2.41	0.12	3.28 ^{bc}	0.70
Gadiformes	$QO_2 = -0.8562 + 0.7994T$	<0.10	3	0.0659	0.99	5.67	0.16	7.77 ^a	0.90
Percoidae	n.s.	>0.30	8	—	—	4.53	0.63	3.62 ^{bc}	0.52
Scombroidei	n.s.	—	1	—	—	8.75	—	8.03 ^a	1.36
Pleuronectiformes	n.s.	>0.10	4	—	—	6.16	0.92	6.65 ^a	0.68

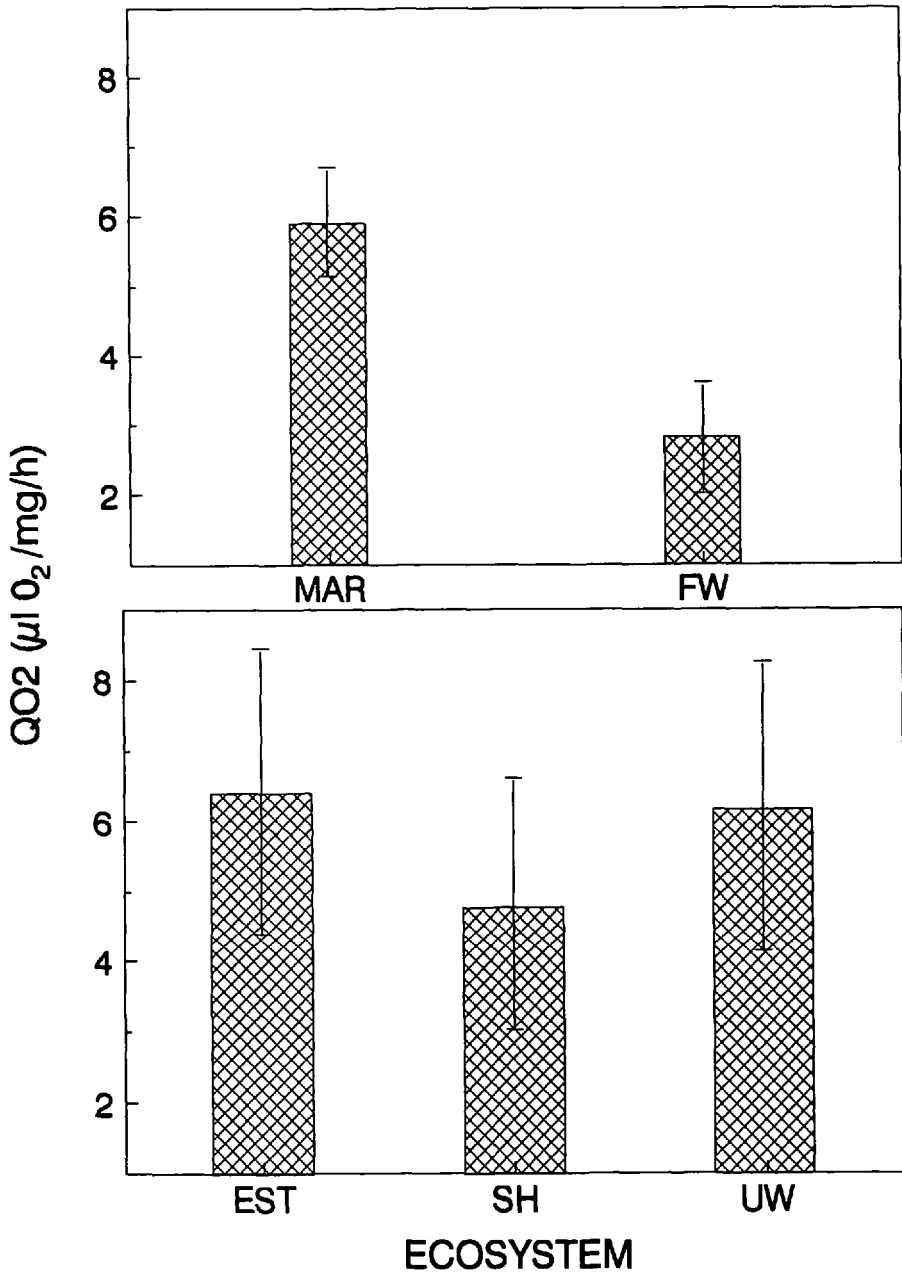


Figure 10. Temperature-adjusted, ecosystem-specific mean weight-specific oxygen uptake rates (QO₂) of teleost larvae. See Figure 1 for ecosystem keys and explanations.

upwelling ecosystems were 0.241, 0.296, and 0.368, respectively, and did not differ significantly (ANCOVA, $P > 0.20$) (Table 6).

There also were no clear differences in larval \bar{K}_1 among the taxonomic groups. Adjusted values ranged from 0.214 (Pleuronectiformes) to 0.353 (Percoidei) (Table 6). The temperature-adjusted \bar{K}_1 values and standard errors generally over-

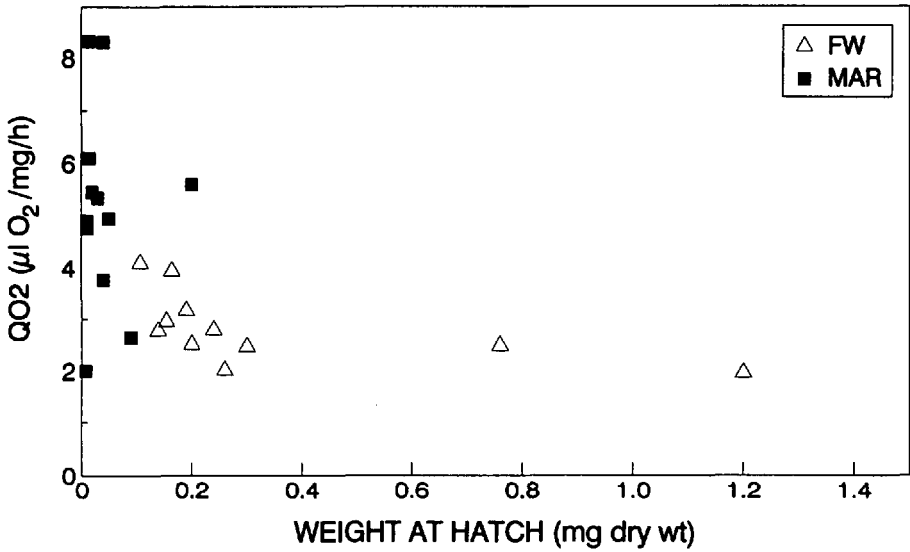


Figure 11. The relationship between weight-specific oxygen uptake rate (QO₂) and dry weight at hatch (W₀) for marine and freshwater fish larvae. Values are not adjusted for temperature effects. ■ = marine larvae. □ = freshwater larvae.

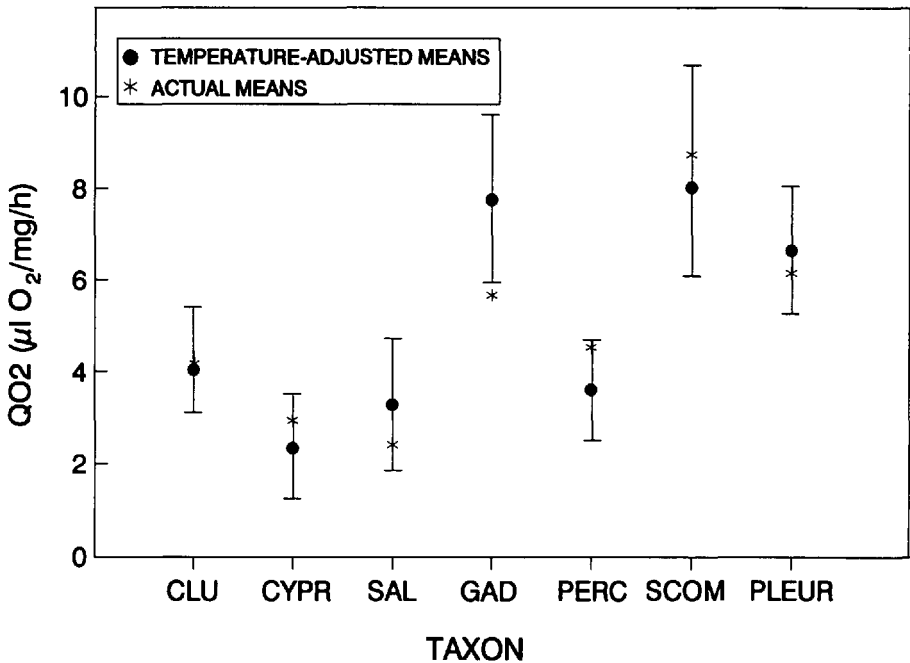


Figure 12. Taxon-specific mean weight-specific oxygen uptake rates $\mu\text{l O}_2 \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ of teleost larvae. ● Temperature-adjusted ± 2 standard errors. * Actual means. See Figure 1 for taxon keys and explanations.

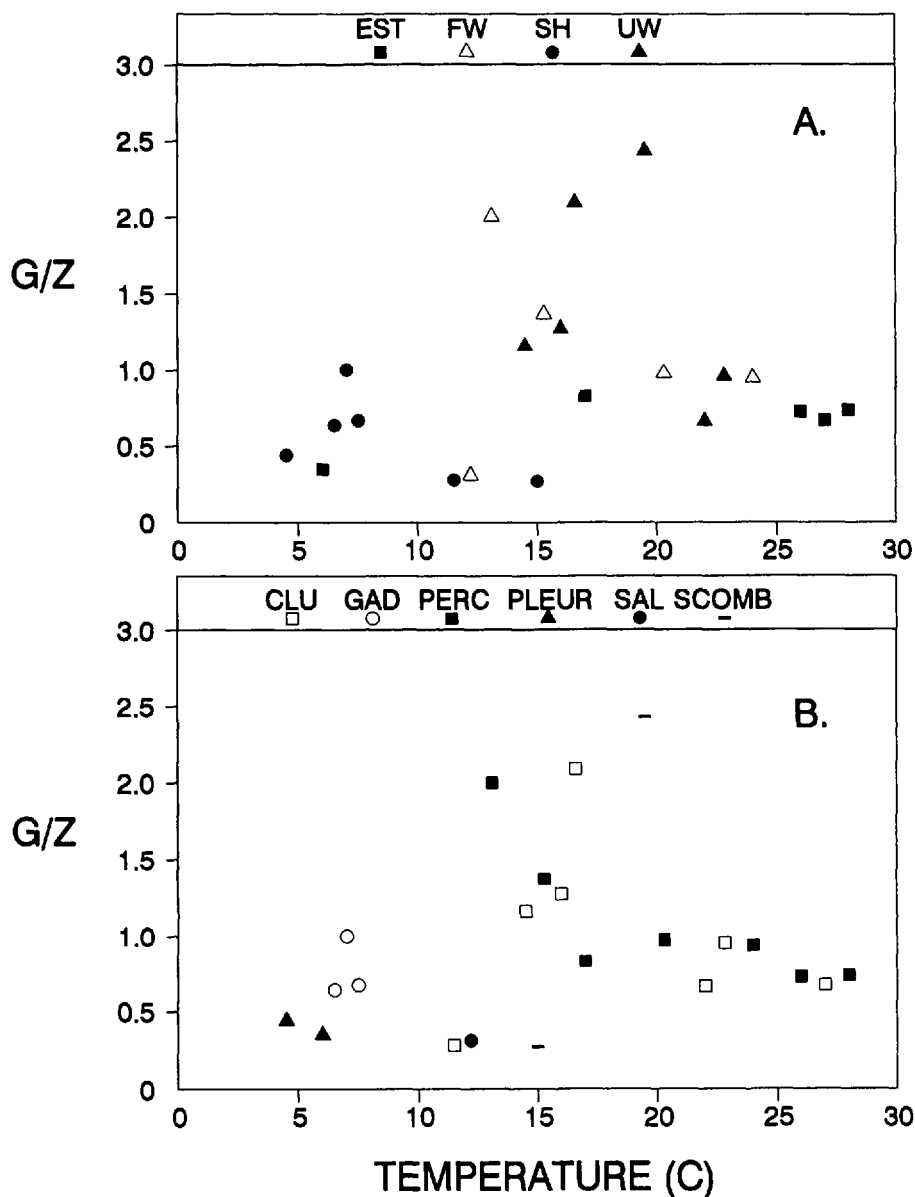


Figure 13. A. Ecosystem- and B. Taxon-specific, ratio of growth coefficient to mortality coefficient values (G/Z) of teleost larvae in relation to temperature. See Figure 1 for keys and explanations.

lapped. The ANCOVA did not detect an overall among-taxa difference in the \bar{K}_1 values ($P > 0.50$), but the paired means comparison procedure did indicate that \bar{K}_1 of percoid larvae was higher than \bar{K}_1 of pleuronectiforms ($P = 0.05$).

Ingestion (I).—The weight-specific ingestion rates required for teleost larvae to grow at their mean growth rates were calculated for the 22 taxa (Table 7, Fig. 15) for which estimates of both G and K_1 were available. Values of $I (=G/K_1)$ ranged from 0.18 (*Clupea harengus*) to $1.16 \cdot d^{-1}$ (*Anchoa mitchilli*). The mean I was

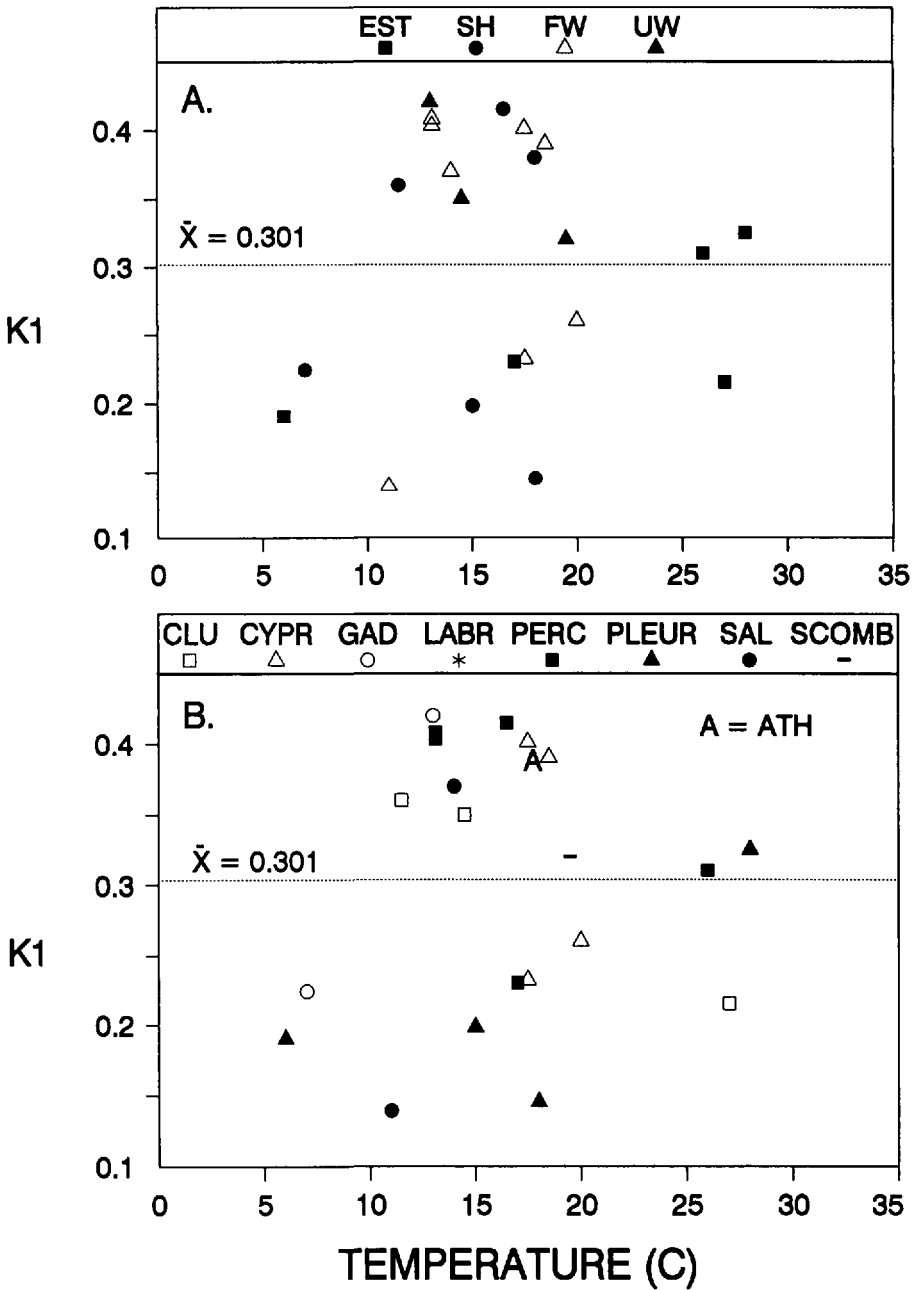


Figure 14. A. Ecosystem- and B. Taxon-specific, gross growth efficiencies (K_1) of teleost larvae in relation to temperature. See Figure 1 for keys and explanations.

$0.530 \cdot d^{-1}$, indicating that, on average, teleost larvae consume more than 50% of their body weight (dry weight basis) daily to grow at mean reported rates.

The two equations derived to describe the relationship between I and T for teleost larvae both indicated that weight-specific ingestion required to support mean growth rates increases by approximately 3% for each $1^\circ C$ rise in T . The first

Table 6. Gross growth efficiency (K_1). Mean values for all larvae data, and mean values for larvae by ecosystem and taxon. Adjusted means are based upon analysis of covariance with temperature as the covariate. Identical superscripts on means indicate no significant difference (GLM least square means comparison)

Data set	N	Mean	S_x	Adjusted mean	S_x
All data	22	0.301	0.020	—	—
Marine	14	0.292	0.025	0.291 ^a	0.025
Freshwater	8	0.318	0.037	0.319 ^a	0.035
Estuary	5	0.254	0.027	0.241 ^{ab}	0.042
Shelf	6	0.287	0.046	0.296 ^{abc}	0.037
Upwelling	3	0.363	0.030	0.368 ^{bc}	0.051
Clupeiformes	3	0.308	0.008	0.308 ^{ab}	0.056
Cypriniformes	4	0.321	0.052	0.305 ^{ab}	0.049
Salmoniformes	2	0.255	0.116	0.256 ^{ab}	0.070
Gadiformes	2	0.322	0.098	0.325 ^{ab}	0.073
Percoidei	5	0.353	0.037	0.353 ^b	0.043
Scombroidei	1	0.320	—	0.319 ^{ab}	0.097
Pleuronectiformes	4	0.215	0.034	0.214 ^a	0.048

(I_A) is the linear regression of I on T , obtained after estimating I values from reported G and K_1 estimates for the 22 taxa (Table 7, Fig. 15). The second (I_E) is the expected relationship, derived from the linear regression of G on T (Table 2) and \bar{K}_1 (see Methods) for all taxa (Fig. 15).

There were no significant differences in \bar{I} among ecosystems. The temperature-adjusted \bar{I} for marine fish larvae was 0.572 (SE = 0.065), while that for freshwater larvae was 0.458 (SE = 0.087) (Table 7). These means did not differ significantly (ANCOVA, $P > 0.30$). Temperature-adjusted \bar{I} of larvae from estuarine, shelf, and upwelling marine systems also did not differ (Table 7; ANCOVA, $P > 0.50$).

Temperature-adjusted \bar{I} did differ significantly among taxonomic groups, ranging from 0.347 (Cypriniformes) to 0.973 (Scombroidei) (Table 7, Fig. 16). Scombroid larvae have generally higher required \bar{I} than the other taxa and significantly higher \bar{I} than the cypriniform and gadiform larvae ($P < 0.08$).

Estimates of I were strongly affected by temperature. Values of I , calculated for 8, 18, and 28°C (Table 8) indicated that ecosystem- and taxon-specific ingestion rates required to support average growth generally are less than 35% of body weight at 8°C, increase to more than 50% at 18°C, and are near 100% at 28°C. Taxon-specific I at 28°C ranged from 77% (Percoidei) to 137% (Scombroidei) (Table 8).

Energy Budgets.—Temperature-specific energy budgets were calculated for 10, 18, and 28°C for all larvae, marine larvae and freshwater larvae (Table 9). Required ingestion increased by more than a factor of three for all larvae and marine larvae, and by a factor of two for freshwater larvae as temperature rose from 10 to 28°C. Caloric allocations to growth increased at higher temperatures but relative allocations (i.e., as a percentage) remained constant because K_1 did not change significantly with temperature. The Q_{10} for growth of all larvae and marine larvae in the 10 to 28°C range was 1.95, but for freshwater larvae it was only 1.43. An obvious difference in energy budgets of marine and freshwater larvae was the relatively high allocation to metabolism by the marine larvae (Table 9). The Q_{10} for metabolism was 1.40 for the marine and freshwater larvae. Predicted assim-

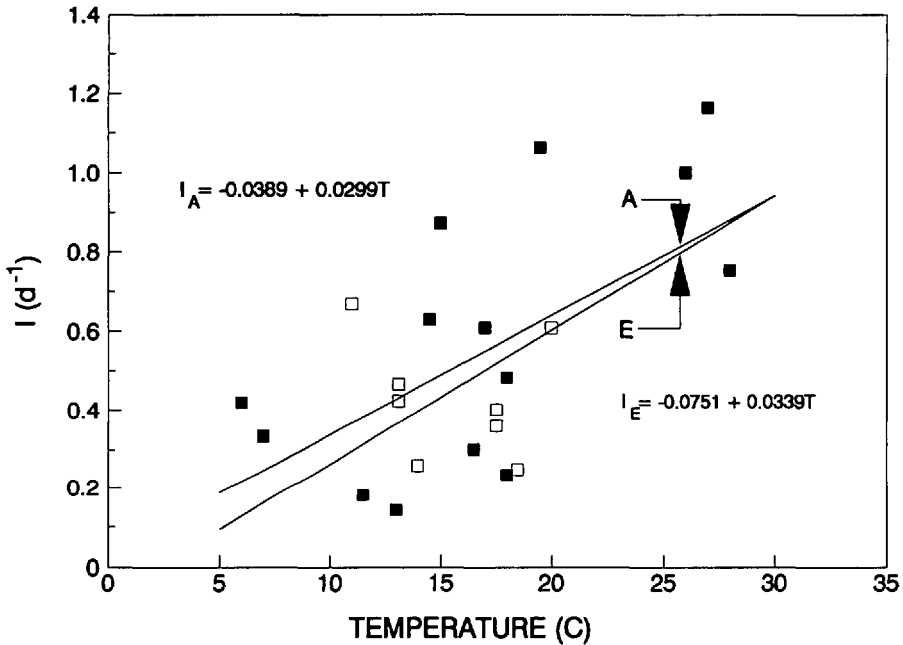


Figure 15. The relationships between estimated weight-specific ingestion (I , d^{-1}) and temperature of teleost larvae. I_A regression based upon $\hat{I} = \hat{G}/\hat{K}_1$ for species where both \hat{G} and \hat{K}_1 were estimated. I_E is the equation based upon $\hat{I} = \hat{G}/\bar{K}_1$, where $\hat{G} = a + bT$, from the regression for all larvae and $\bar{K}_1 = 0.301$ (Table 1), the mean gross growth efficiency of teleost larvae. ■ = marine larvae. □ = freshwater larvae.

ilation efficiencies of all larvae declined from 81 to 59% in the range of 10 to 28°C. The predicted declines in assimilation efficiency for marine and freshwater larvae in that temperature range were 89 to 65% and 61 to 60%, respectively, suggesting that assimilation rates of freshwater larvae are less sensitive to changes in temperature.

Temperature-adjusted budgets for larvae in the marine and freshwater categories, which allow direct comparison of components because temperature effects have been removed, were derived from the adjusted mean values of G , QO_2 , and K_1 (Tables 2, 5 and 6). The marine larvae had a higher weight-specific ingestion (24% higher) than the freshwater larvae and a much higher allocation to the metabolism category (Table 10). The relative allocation to metabolism by marine larvae was 11.7% higher and, consequently, they had a higher assimilation efficiency (65 vs. 56%).

The estimated weight-specific caloric investment in metabolism is >2 times higher for marine than for freshwater larvae (Table 10). The relationship between QO_2 and dry weight at hatch for 12 marine and 11 freshwater species (Fig. 11) indicates that QO_2 is affected by weight and that freshwater larvae, being heavier, will have lower metabolic rates.

Within the marine category, temperature-adjusted energy budgets of upwelling species may be different than budgets of estuarine and shelf species (Table 10). The upwelling larvae have relatively high allocations to growth and metabolism, and their assimilation efficiency was estimated to be approximately 20% higher.

The temperature-adjusted energy budgets for seven taxonomic groups indicate

Table 7. Daily food ingestion requirement (I , d^{-1}) and its relationship to temperature (T , $^{\circ}C$) for all data and for subsets of data distinguished by ecosystem and taxon. When significant ($\alpha = 0.10$), linear regression equations and related parameters are provided. Adjusted means are based upon analysis of covariance with temperature as covariate. Identical superscripts on adjusted means indicate no significant difference (GLM least square means comparison). S_b = standard error of the regression coefficient

Data set	Regression equation	P	N	S_b	r^2	Mean	SE	Adjusted mean	SE
All data	$I_A = 0.0389 + 0.0299T$	0.005	22	0.0095	0.33	0.530	0.052	—	—
Marine	$I_A = 0.0144 + 0.0338T$	<0.01	14	0.0110	0.44	0.586	0.071	0.572 ^a	0.065
Freshwater	n.s.	>0.50	8	—	—	0.433	0.056	0.458 ^a	0.087
Estuary	$I_A = 0.2383 + 0.0265T$	<0.10	5	0.0101	0.70	0.789	0.084	0.680 ^a	0.131
Shelf	n.s.	>0.70	6	—	—	0.404	0.116	0.477 ^a	0.116
Upwelling	n.s.	>0.20	3	—	—	0.612	0.123	0.647 ^a	0.157
Clupeiformes	n.s.	>0.10	3	—	—	0.658	0.115	0.620 ^{abc}	0.131
Cypriniformes	n.s.	>0.30	4	—	—	0.405	0.068	0.347 ^{ab}	0.115
Salmoniformes	n.s.	—	2	—	—	0.478	—	0.589 ^{abc}	0.164
Gadiformes	n.s.	—	2	—	—	0.238	—	0.422 ^{ab}	0.164
Percoidaei	$I_A = -0.2060 + 0.0447T$	0.05	5	0.0142	0.77	0.560	0.067	0.538 ^{abc}	0.101
Scombroidei	n.s.	—	1	—	—	1.063	—	0.973 ^{bc}	0.131
Pleuronectiformes	n.s.	—	4	—	—	0.636	0.116	0.625 ^{abc}	0.113

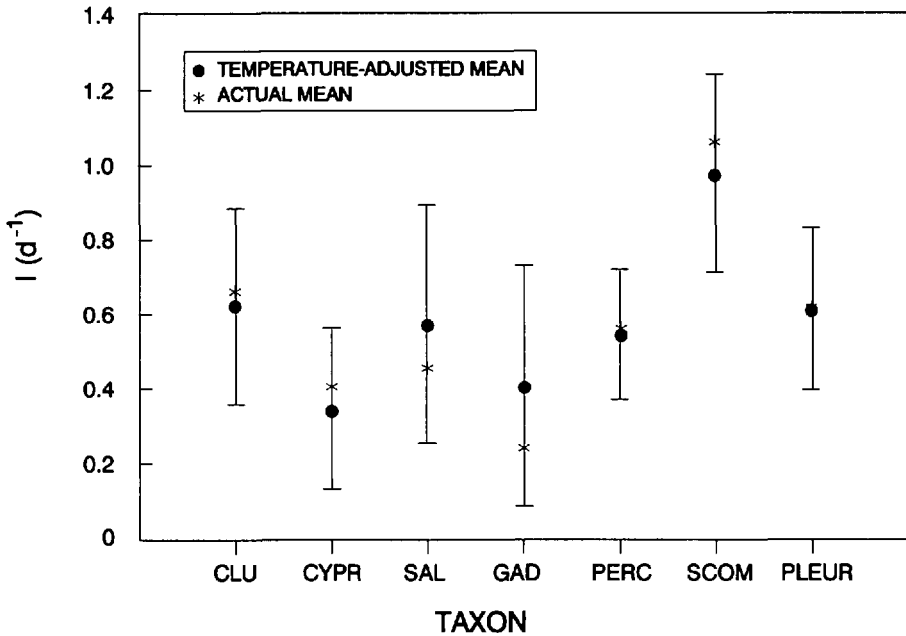


Figure 16. Taxon-specific, mean required ingestion rates (proportion of body weight) of teleost larvae. ● Temperature-adjusted ± 2 standard errors. * Actual means. See Figure 1 for taxon keys and explanations.

probable differences among taxa (Table 11). Required weight-specific caloric ingestion to meet mean growth rate varied two-fold from 2.7 (Cypriniformes) to 5.2 $\text{cal} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ (Scombroidei). The percentage of ingested energy allocated to growth varied from 21 (Pleuronectiformes) to 35% (Percoidei). Relative metabolic

Table 8. Predicted daily food consumption (i.e., required ingestion, I , d^{-1}) required to meet the mean weight-specific growth rates and the relationship of I to temperature (T , $^{\circ}\text{C}$). The equations are derived from the relationship $I_E = G/\bar{K}_1$, where $G = a + bT$ (Table 2), and temperature-adjusted \bar{K}_1 (Table 6) values appropriate for each data set

Data set	Expected relationship	Predicted ingestion (/d)		
		8°C	18°C	28°C
All data	$I_E = -0.0751 + 0.0339T$	0.20	0.54	0.87
Marine	$I_E = -0.0790 + 0.0364T$	0.21	0.58	0.94
Freshwater	$I_E = 0.1607 + 0.0164T$	0.29	0.46	0.62
Estuary	$I_E = -0.0979 + 0.0407T$	0.23	0.63	1.04
Shelf	$I_E = -0.3169 + 0.0571T$	0.14	0.71	1.28
Upwelling*	$\bar{I} = 0.66$	—	0.66	—
Clupeiformes	$I_E = 0.1331 + 0.0244T$	0.33	0.57	0.82
Cypriniformes*	$\bar{I} = 0.51$	—	0.53	—
Salmoniformes	$I_E = -0.1154 + 0.0433T$	0.23	0.66	1.10
Gadiformes	$I_E = 0.2625 - 0.0059T$	0.31	0.37	—
Percoidei	$I_E = -0.0479 + 0.0292T$	0.19	0.48	0.77
Scombroidei	$I_E = -0.7060 + 0.0740T$	—	0.63	1.37
Pleuronectiformes	$I_E = 0.0341 + 0.0369T$	0.33	0.70	1.07

* Upwelling larvae and cypriniform larvae only occurred in the 15 to 20°C range. In these cases, I was calculated as the ratio of temperature-adjusted mean G (Table 2) and mean K_1 (Table 6) for each category.

Table 9. Temperature-specific energy budgets of all teleost larvae, marine larvae, and freshwater larvae at 10, 18, and 28°C. Actual budget components are given in $\text{cal} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ and relative budget components, in parentheses, are percentages. I = ingestion, G = growth, M = metabolism, U = urine, F = feces, A = assimilation efficiency. Budgets were calculated using \bar{G} (Table 2), \bar{QO}_2 (Table 5), unadjusted \bar{K}_1 (Table 6) and assumed $U = 0.07$ I. F was obtained by difference

Category	Temperature	I	=	G	+	M	+	U	+	F	A
All	10	1.32	=	0.40	+	0.58	+	0.09	+	0.25	0.81
		(100.0)	=	(30.1)	+	(44.2)	+	(7.0)	+	(18.7)	
	18	2.67	=	0.80	+	0.74	+	0.19	+	0.94	0.65
		(100.0)	=	(30.1)	+	(27.7)	+	(7.0)	+	(35.1)	
	28	4.37	=	1.32	+	0.95	+	0.31	+	1.80	0.59
		(100.0)	=	(30.1)	+	(21.7)	+	(7.0)	+	(41.2)	
Marine	10	1.42	=	0.42	+	0.75	+	0.10	+	0.16	0.89
		(100.0)	=	(29.2)	+	(52.7)	+	(7.0)	+	(11.1)	
	18	2.87	=	0.84	+	1.03	+	0.20	+	0.81	0.72
		(100.0)	=	(29.2)	+	(35.7)	+	(7.0)	+	(28.1)	
	28	4.70	=	1.37	+	1.37	+	0.33	+	1.63	0.65
		(100.0)	=	(29.2)	+	(29.2)	+	(7.0)	+	(34.6)	
Freshwater	10	1.62	=	0.52	+	0.37	+	0.11	+	0.63	0.61
		(100.0)	=	(31.8)	+	(22.5)	+	(7.0)	+	(38.7)	
	18	2.28	=	0.72	+	0.50	+	0.16	+	0.90	0.61
		(100.0)	=	(31.8)	+	(21.8)	+	(7.0)	+	(39.4)	
	28	3.09	=	0.98	+	0.66	+	0.22	+	1.23	0.60
		(100.0)	=	(31.8)	+	(21.3)	+	(7.0)	+	(39.8)	

requirements ranged from 14 (Salmoniformes) to 43% (Gadiformes) of the ingested ration. Taxa that are principally or entirely marine (e.g., Gadiformes, Scombroidei, Pleuronectiformes) had the highest metabolic allocations. Estimated assimilation efficiencies ranged from 47 (Salmoniformes) to 82% (Gadiformes).

DISCUSSION

After temperature effects were removed by analysis of covariance, relatively few differences in rates or properties emerged that were specific to larvae from particular ecosystems or taxonomic groups. But, some significant differences in rates and energetics properties were found that are indicative of taxa- and ecosystem-specific differences in teleost early life histories. Marine and freshwater teleost larvae had similar weight-specific growth and ingestion rates, and similar gross growth efficiencies. Temperature-adjusted mean mortality rate of marine larvae was $6.5\% \cdot \text{d}^{-1}$ higher than the mean rate of freshwater larvae. Marine larvae had significantly higher oxygen uptake rates and longer stage durations. The temperature-adjusted mean oxygen uptake rate of freshwater larvae was only one half that of marine larvae and mean stage duration of freshwater larvae was 15.5 d shorter.

Differences in O_2 uptake rates, stage durations, and mortality rates between marine and freshwater larvae probably are attributable to differences in weight at hatch. Freshwater larvae in our analyses averaged nearly seven times heavier than marine larvae. Weight-specific O_2 uptake in fishes is negatively related to body weight (Rombough, 1988) and this relationship may be particularly strong during early life (Wieser and Forstner, 1986). The larval stage is relatively brief in freshwater because, while freshwater larvae are large at hatch, their growth rates and sizes at metamorphosis are similar to those of marine larvae. Our comparative

Table 10. Temperature-adjusted energy budgets of marine and freshwater teleost larvae. Actual budgets in $\text{cal} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ and relative budgets, in parentheses, in percentages. Symbols as in Table 9. Budgets were calculated from adjusted mean G (Table 2), QO_2 (Table 5), and K_1 (Table 6). U was assumed to equal $0.07 I$. F was obtained by difference

Category	I	=	G	+	M	+	U	+	F	A
Marine	3.44 (100.0)	=	1.00 (29.1)	+	0.98 (28.6)	+	0.24 (7.0)	+	1.21 (35.3)	0.65
Estuary	4.06 (100.0)	=	0.98 (24.1)	+	1.07 (26.3)	+	0.28 (7.0)	+	1.73 (42.6)	0.57
Shelf	4.54 (100.0)	=	1.34 (29.6)	+	0.80 (17.5)	+	0.32 (7.0)	+	2.08 (45.9)	0.54
Upwelling	3.29 (100.0)	=	1.21 (36.8)	+	1.03 (31.2)	+	0.23 (7.0)	+	0.82 (25.0)	0.75
Freshwater	2.78 (100.0)	=	0.89 (31.9)	+	0.47 (16.9)	+	0.19 (7.0)	+	1.23 (44.2)	0.56

analysis of marine and freshwater larvae supports the proposed inverse relationship between larval mortality and size (McGurk, 1986, 1987; Miller et al., 1988). Pepin (1991) found an ontogenetic effect of declining mortality as length increased in marine fish larvae, although neither he nor Houde (1990, in press) could demonstrate an effect of size at hatch on larval mortality rate.

Temperature-adjusted \bar{G} values were similar among larvae from shelf, upwelling, and oceanic ecosystems, ranging from 0.24 to 0.27. After temperature adjustment, larval stage durations were similar (34 to 36 d) in all of the marine ecosystems except the oceanic (26 d). Data from the oceanic system were predominantly for fast-growing tuna larvae. Adjusted mean mortality rates may have been lower for upwelling-system larvae ($\bar{Z} = 0.18$) than for larvae from estuaries or shelves ($\bar{Z} = 0.27$ and 0.25). Neither the adjusted mean oxygen uptake rates nor ingestion rates were significantly different among marine ecosystems but, in each case, shelf species had slightly lower values.

Temperature clearly is not the only important factor that affects rates and energetics properties of fish larvae. Body size is important and has been proposed as a primary factor controlling rates (Peterson and Wroblewski, 1984; McGurk,

Table 11. Taxon-specific, temperature-adjusted energy budgets of teleost larvae. Actual budgets in $\text{cal} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ and relative budgets, in parentheses, in percentages. Symbols as in Table 9. Budgets were calculated from adjusted mean G (Table 2), QO_2 (Table 5), and K_1 (Table 6). U was assumed to equal $0.07 I$. F was obtained by difference

Taxonomic group	I	=	G	+	M	+	U	+	F	A
Clupeiformes	3.18 (100.0)	=	0.98 (30.8)	+	0.67 (21.2)	+	0.22 (7.0)	+	1.31 (41.0)	0.59
Gadiformes	3.02 (100.0)	=	0.98 (32.5)	+	1.30 (42.9)	+	0.21 (7.0)	+	0.53 (17.6)	0.82
Salmoniformes	3.82 (100.0)	=	0.98 (25.6)	+	0.55 (14.3)	+	0.27 (7.0)	+	2.03 (53.1)	0.47
Cypriniformes	2.66 (100.0)	=	0.81 (30.5)	+	0.39 (14.7)	+	0.19 (7.0)	+	1.27 (47.8)	0.52
Percoidei	2.89 (100.0)	=	1.02 (35.3)	+	0.60 (20.9)	+	0.20 (7.0)	+	1.07 (36.8)	0.63
Scombroidei	5.16 (100.0)	=	1.65 (31.9)	+	1.34 (26.0)	+	0.36 (7.0)	+	1.81 (35.1)	0.65
Pleuronectiformes	4.38 (100.0)	=	0.94 (21.4)	+	1.11 (25.3)	+	0.31 (7.0)	+	2.02 (46.3)	0.54

1986, 1987; Miller et al., 1988; Beyer, 1989; Pepin, 1991). MacKenzie et al. (1990) reported that temperature, body size, and prey abundance explained 85% of the variance in laboratory-estimated ingestion rates of marine fish larvae. Werner and Gilliam (1984) argued that ontogenetic shifts occur, causing rates to change as growth proceeds. Our analyses did not consider probable ontogenetic changes, but have estimated averaged values of G , Z , K_1 , and QO_2 during the larval stage. Pepin (1991) indicated that temperature, but not initial size, affected mortality rates of eggs and yolk-sac larvae of marine teleosts, but that body size also affected mortality rates of postlarval fish. Houde (1990, in press) partitioned marine fish larvae data into species with hatch weights $< 50 \mu\text{g}$ dry wt and those $> 50 \mu\text{g}$ dry wt. At that level he was unable to show a weight-specific effect on growth or mortality rates and concluded that temperature probably was a more important factor during early life.

Energy budgets integrate the effects of different rates and properties that were estimated. Temperature-adjusted energy budgets (Table 10) of freshwater larvae differ in some respects from those of marine larvae. On a weight-specific basis, freshwater larvae apparently require only 81% as much ingested energy and only 48% as much energy for metabolism as marine larvae to meet estimated mean growth rates. Despite the lower metabolic requirement, freshwater larvae do not have significantly higher gross growth efficiency. Consequently, the estimated assimilation efficiency of marine larvae is 9% higher than that of freshwater larvae, mostly attributable to higher metabolic requirements.

The mean assimilation efficiencies (A) of both the marine and freshwater larvae are lower than expected for juvenile carnivorous fishes, which have a reported mean A of 80% (Brett and Groves 1979). Only the gadiform larvae have a mean A at that level (Table 11). Our estimated A values are dependent upon the highly variable estimates of growth, metabolism, and ingestion. The A values have been calculated and are presented as the probable efficiencies, recognizing that their accuracies are uncertain.

Ingestion rate required to support average growth rates increased by a factor of two to four as temperature increased from 10 to 28°C. MacKenzie et al. (1990) estimated that maximum ingestion by an average marine fish larva at 18.7°C was 57% of the body weight, based upon a model that included temperature, body weight, and prey density as independent variables. Our ingestion estimates for an average teleost larva at 18.7°C from the I_A and I_E relationships (Table 7, Fig. 15), in which temperature is the only independent variable, are 60 and 56%, respectively, results essentially the same as obtained by MacKenzie et al. (1990).

MacKenzie et al. (1990), based upon laboratory-derived functional response relationships, calculated that consumption rates of marine fish larvae in the sea should be resource constrained and thus less than maximum. But, their estimated in situ ingestion rates of eight species of fish larvae indicated that these larvae had consumed food at maximum rates, leading the authors to hypothesize that variable encounter rates and temporal-spatial variability in distributions of larvae and prey had enhanced feeding success. In our analysis, the Q_{10} value for growth and ingestion for all and for marine teleost larvae was 1.95, indicating that mean ingestion and growth rates of larvae that survived are approximately those expected, based solely upon enzyme kinetics and without considering prey densities or complex predator-prey behaviors. In reality, it is certain that prey density, its distribution, and the probability of encounter between larvae and prey all affect individual growth rates and variability in growth, but at the aggregated taxa or ecosystem levels, survivors were growing, on average, at mean rates that were governed primarily by temperatures that they experienced.

The taxon-specific ingestion estimates in the energy budgets do not necessarily indicate different sensitivities to food limitation among first feeding stages. The numbers of prey required depends not only upon the caloric weight-specific demand (Table 11), but also upon larva size and size of prey that can be consumed. If teleost larvae ate primarily copepod nauplii of mean dry weight $0.25 \mu\text{g}$ and the mean body weights of newly hatched larvae were $47 \mu\text{g}$ (marine) and $339 \mu\text{g}$ (freshwater), then numbers of prey required for larvae to grow at mean expected rates would differ more between these ecosystems than would weight-specific caloric intakes. For example, marine larvae have a higher weight-specific ration (Table 7), but they require relatively few prey when they first feed (108 nauplii/d) because the larvae are small at hatch. In contrast, if the freshwater taxa ate $0.25 \mu\text{g}$ nauplii at first feeding, they would require, on average, $621 \text{ nauplii} \cdot \text{d}^{-1}$. For taxa that eat prey larger than $0.25 \mu\text{g}$ mean weight (e.g., *Coregonus* spp., Salmoniformes), the actual required prey numbers would be considerably lower than these calculated values.

Growth rates and mortality rates of marine fish larvae were demonstrated to be highly correlated (Houde, 1990; Pepin, 1991). In previous analyses that were restricted to marine fish larvae, Houde (1989b, 1990) found that the ratio G/Z was < 1.0 , implying a loss of biomass during the larval stage. Morse (1989) reported $G/Z > 1.0$ for several northwest Atlantic fish larvae and suggested that if ratios are < 1.0 , sampling bias associated with gear avoidance by larger larvae is the probable cause. Our present analysis, on an expanded data base, indicated mean G/Z of 0.94 for all larvae, a value near 1.0. Results for all larvae, marine larvae ($G/Z = 0.89$), and freshwater larvae (1.13) did not differ significantly from 1.0, suggesting that biomasses during the teleost larval stage are relatively stable.

If G/Z is near 1.0 and gross growth efficiency is constant during the larval stage, then the daily ingestion of a cohort required to support mean growth rate would remain approximately constant throughout larval life. A cohort's biomass normally will increase at some stage of development and the G/Z eventually will exceed 1.0, a consequence of relatively fast decline in Z as larvae grow (Ware, 1975; Beyer, 1989). The cohort's daily ingestion of its prey resources then will increase. It is easy to demonstrate from our compiled and analyzed data that small changes in either G or Z can cause two-fold or greater changes in a cohort's daily ingestion requirement, an ecosystem-level effect that potentially is important in the recruitment process.

We found that larvae of coral reef fishes grow slower than expected under the temperature conditions prevalent in their environment. A major factor contributing to their low adjusted \bar{G} was the surprisingly slow growth of reef labrid and goby larvae. Stage durations of these larvae, based upon otolith increment counts, have repeatedly been found to be long and variable compared to other taxa (Brothers et al., 1983; Victor, 1986, 1987; Thresher and Brothers, 1989). The temperature-adjusted \bar{G} for labrids and gobies are those expected for teleost larvae at only 10 to 13°C, based upon our regression of G on T for all fish larvae (Table 2), despite the fact that coral reef labrids and gobies develop at temperatures $> 26^\circ\text{C}$. Removing labrid and goby larvae from our analysis did not change the rank of \bar{G} for coral reef larvae. It still was the lowest of the ecosystem-specific adjusted \bar{G} , indicating that even the pomacentrids, which dominate the data base (Brothers et al., 1983; Thresher and Brothers, 1989; Wellington and Victor, 1989; Thorrold and Milicich, 1990), grow relatively slowly for temperatures that they inhabit.

Temperature also may explain some of the geographic variability in stage durations that has been observed in coral reef fish larvae. There is a complex literature

discussing the biogeography of coral reef teleosts, which relates larval stage durations to observed distribution patterns and ranges of adults. Larval stage duration is presumed to be evolved and adaptive, and closely linked to dispersal possibilities and island geography. Although interpretations vary, it appears that stage durations are longer in the western Atlantic and in Hawaii than in the West-Indo Pacific (Thresher and Brothers, 1989; Wellington and Victor, 1989). Our growth and stage duration analyses (Tables 2, 4), suggest that a large fraction of the geographic variability in G and D might be explained by temperature. Published reports on coral reef larvae seldom provide temperatures, but atlases of sea surface temperature (Robinson, 1973; Bramwell, 1977) indicate that annual means are 24.3°C (Hawaii), 26.8°C (Caribbean), and 28.1°C (West-Indo Pacific). Expected stage durations at those temperatures, calculated from our relationship between D and T for coral reef larvae (Table 4), range from 24.2 d (West-Indo Pacific), to 27.2 d (Caribbean), to 33.2 d (Hawaii). There appears to be a strong physiological influence of temperature, in addition to adaptive components, in life histories of reef fish larvae that contributes to stage duration variability.

While results of our analyses and of other recent conceptual analyses (Miller et al., 1988; Houde, 1989; Morse, 1989; Pepin, 1991) should not be used to predict responses of individual species, determining species-specific deviations from expected dynamics or energetics values may serve to identify particular life-history strategies and specific adaptations. Ecosystem- and taxon-specific ingestion estimates and derived energy budgets of fish larvae can be compared with those of other zooplankton. Given seasonal surveys of ichthyoplankton abundance, diversity, temperature, and larva weight-frequency distributions, the weight-specific growth and ingestion estimates of larval teleost assemblages could be obtained. Temporal and spatial variability in ingestion, growth, and production could be estimated and incorporated into ecosystem and recruitment models.

In future research, more effort should be made to obtain weights as well as lengths of ichthyoplankton to allow dynamics of larvae to be linked in a meaningful way to population- and community-level energetics processes. Good temperature data are essential to estimate the production potential of ichthyoplankton in any ecosystem, including tropical systems, where seasonal temperature differences, though small, can still have important consequences for fish early life histories. We did not examine effects of ontogeny and body size on vital rates or energetics, but there is a need to do it, as Miller et al. (1988) and Beyer (1989) proposed and Pepin (1991) has done. A further consideration is the possibility that dynamics of teleost larvae and energetics properties are related in a predictable way to overall ecosystem productivity. That hypothesis and others related to community-level dynamics of fish larvae can be tested as better data on bioenergetics and vital rates become available for ichthyoplankton assemblages.

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Appendix A. Ecosystem-specific and taxon-specific vital rates and energetics data for teleost larvae. Values in the Table are those reported by the authors or calculated by us from data and information that the authors provided. Length-weight relationships, particularly for coral reef (CR) species, frequently were used to convert reported lengths to weights when weight data were not provided in the published papers. ECOS = ecosystem: FW = freshwater, CR = coral reef, EST = estuarine, OCN = oceanic, SH = shelf, UW = upwelling, SP = species. Taxa: CYPR = Cypriniformes, CLU = Clupeiformes, PERC = Percoidae, SAL = Salmoniformes, GOB = Gobioidae, LABR = Labroidae, PLEUR = Pleuronectiformes, ATH = Atheriniformes, SCOM = Scombroidei, SCHIND = Schindlerioidei, GONO = Gonorhynchiformes, GAD = Gadiformes, G = weight-specific growth coefficient (d^{-1}). D = stage duration (d). Z = instantaneous daily mortality coefficient (d^{-1}). QO_2 = weight-specific oxygen uptake rate ($\mu l O_2 \cdot mg^{-1} \cdot h^{-1}$). K_1 = gross growth efficiency. I = weight-specific ingestion rate ($\mu g \cdot \mu g^{-1} \cdot d^{-1}$). W_0 = dry weight at hatch (μg). W_{met} = dry weight at metamorphosis (μg). Ref. = references, coded by number. Code numbers and citations at foot of Appendix table are listed in Literature Cited

ECOS	SP	Taxa	T (°C)	G	D	Z	QO_2	G/Z	K_1	I	W_0	W_{met}	Ref.
FW	<i>Abramis brama</i>	CYPR	17.5	0.178	—	—	2.52 (20°)	—	—	—	200	—	1, 2, 3
FW	<i>Alburnus alburnus</i>	CYPR	22.5	0.142	—	—	—	—	—	—	—	—	4
FW	<i>Alosa pseudoharengus</i>	CLU	23.5	—	—	0.12	—	—	—	—	—	—	5
FW	<i>Aplodinotus grunniens</i>	PERC	24.0	0.157	42.0	0.16	—	0.98	—	—	455	33,200	6, 7
FW	<i>Catostomus commersoni</i>	CYPR	20.0	0.160	—	—	—	—	0.260	0.608	—	—	8
FW	<i>Chalcalburnus chalcoides</i>	CYPR	20.0	0.064	—	—	2.90	—	—	—	—	—	4
FW	<i>Coregonus albula</i>	SAL	10.0	0.090	28.0	—	2.01	—	—	—	260	3,200	3, 9
FW	<i>Coregonus artedii</i>	SAL	10.5	0.075	25.8	—	(9°)	—	—	—	890	6,180	214, 215
FW	<i>Coregonus clupeaformis</i>	SAL	12.2	0.062	40.4	0.20 (14.5)	—	0.31	—	—	800	9,820	10, 11, 12, 13
FW	<i>Coregonus hoyi</i>	SAL	12.5	0.100	23.6	—	1.96	—	0.139	0.683	700	7,440	14, 15
FW	<i>Coregonus lavaretus</i>	SAL	9.5	0.095	19.2	—	(9.5°)	—	(11°)	(11°)	1,200	7,440	3, 16, 17, 18, 39
FW	<i>Coregonus schinzi</i>	SAL	14.9	0.101	29.0	—	2.49	—	0.370	0.273	760	14,190	19, 20, 21
FW	<i>Cyprinus carpio</i>	CYPR	23.0	0.348	12.9	—	(16.3°)	—	(14°)	(14°)	107	9,900	22, 23, 24, 25, 26, 27, 28, 29
FW	<i>Dorosoma cepedianum</i>	CLU	22.5	—	—	0.325	(24°)	—	—	—	—	—	5
FW	<i>Esox lucius</i>	SAL	16.2	0.191	33.6	—	3.17	—	—	—	190	10,830	2, 3, 30, 32, 33
FW	<i>Esox masquinomy</i>	SAL	16.0	0.158	—	—	(18.3°)	—	—	—	—	—	34
FW	<i>Hypophthalmichthys molitrix</i>	CYPR	18.5	0.098	—	—	2.47	—	0.390	0.251	300	—	35
FW	<i>Lepomis gibbosus</i>	PERC	20.4	0.150	22.4	—	—	—	—	—	130	3,750	36
FW	<i>Lepomis macrochirus</i>	PERC	23.5	0.121	30.1	—	—	—	—	—	150	4,970	37

Appendix A. Continued

ECOS	SP	Taxa	T (°C)	G	D	Z	QO ₂	G/Z	K ₁	I	W ₀	W _{max}	Ref.
FW	<i>Leuciscus cephalus</i>	CYPR	22.5	0.117	—	—	—	—	—	—	—	—	4
FW	<i>Lucioperca lucioperca</i>	PERC	13.1	0.188	—	—	3.62 (20°C)	—	0.403 (19.3)	0.466	—	—	1, 3, 38
FW	<i>Micropterus dolomieu</i>	PERC	20.0	—	—	—	2.96	—	—	—	154	4,970	40
FW	<i>Micropterus salmoides</i>	PERC	19.3	0.190	18.8	—	2.78 (19.5°)	—	—	—	139	4,660	41, 42
FW	<i>Oreochromis mossambicus</i>	PERC	28.0	0.172	—	—	—	—	—	—	130	—	43
FW	<i>Oreochromis niloticus</i>	PERC	30.0	—	—	—	4.24	—	—	—	—	—	44
FW	<i>Perca flavescens</i>	PERC	15.3	0.129	35.7	0.090 (11.8°C)	—	1.36	—	—	114	11,500	45, 46, 47
FW	<i>Perca fluviatilis</i>	PERC	13.1	0.173	36.1	0.063 (20°)	3.94	2.00	0.408	0.424	164	11,600	1, 3, 38, 48
FW	<i>Pseudorasbora parva</i>	CYPR	17.5	0.083	—	—	3.01	—	0.232	0.358	—	—	49
FW	<i>Rutilus rutilus</i>	CYPR	17.5	0.136	—	—	2.79	—	0.339	0.401	240	—	2, 3, 4, 49, 50
FW	<i>Stizostedion vitreum</i>	PERC	20.3	0.210	18.0	0.228 (13.5°)	—	0.97	—	—	110	4,820	51, 52
CR	<i>Abudefduf</i> spp.	PERC	28.7	0.286	23.1	—	—	—	—	—	16	11,671	53, 54
CR	<i>Amblyglyphidodon curacao</i>	PERC	29.8	0.431	13.1	—	—	—	—	—	5	1,350	54
CR	<i>Amblygobius rainfordi</i>	GOB	26.5	0.158	40.3	—	—	—	—	—	14	8,390	55
CR	<i>Amphiprion</i> sp.	PERC	29.8	0.196	13.7	—	—	—	—	—	116	1,694	53, 54
CR	<i>Apogon</i> sp.	PERC	26.5	0.312	20.4	—	—	—	—	—	11	6,419	55
CR	<i>Chaetodon</i> spp.	PERC	26.5	0.204	37.0	—	—	—	—	—	4	7,209	55
CR	<i>Cheilodipterus quinqueineata</i>	PERC	26.5	0.265	23.1	—	—	—	—	—	11	5,017	55
CR	<i>Chelmon rostratus</i>	PERC	26.5	0.353	25.5	—	—	—	—	—	4	30,448	55
CR	<i>Chromis</i> spp.	PERC	29.2	0.297	27.3	—	—	—	—	—	4	13,246	53, 54, 56
CR	<i>Chrysiptera</i> spp.	PERC	29.8	0.291	18.9	—	—	—	—	—	3	740	53, 54
CR	<i>Cirrhitabrus temmincki</i>	LABR	26.5	0.175	28.0	—	—	—	—	—	3	465	55
CR	<i>Coris variegata</i>	LABR	26.5	0.170	29.7	—	—	—	—	—	3	532	55
CR	<i>Dascyllus</i> spp.	PERC	29.4	0.266	22.5	—	—	—	—	—	6	2,372	54, 55
CR	<i>Dischistodus</i> spp.	PERC	29.8	0.299	16.1	—	—	—	—	—	44	5,158	54
CR	<i>Glyphidodontops rollandi</i>	PERC	26.5	0.184	23.1	—	—	—	—	—	116	8,134	55
CR	<i>Gobiodon</i> spp.	GOB	26.5	0.112	30.2	—	—	—	—	—	6	169	55
CR	<i>Haemulon</i> spp.	PERC	26.7	0.306	19.6	—	—	—	—	—	20	8,000	57, 58
CR	<i>Halichoeres hoeveni</i>	LABR	26.1	0.143	46.5	—	—	—	—	—	5	3,862	55, 59

Appendix A. Continued

ECOS	SP	Taxa	T (°C)	G	D	Z	QO ₂	G/Z	K ₁	I	W ₀	W _{max}	Ref.
CR	<i>Hemiglyphidodon plagiotometopon</i>	PERC	29.8	0.245	18.0	—	—	—	—	—	65	5,366	54
CR	<i>Labroides dimidiatus</i>	LABR	26.5	0.229	26.0	—	—	—	—	—	3	1,101	55
CR	<i>Neopomacentrus nemurus</i>	PERC	29.8	0.279	19.2	—	—	—	—	—	34	7,209	54
CR	<i>Paraglyphidodon</i> spp.	PERC	29.8	0.188	19.0	—	—	—	—	—	111	3,913	54
CR	<i>Paragobiodon</i> spp.	GOB	26.5	0.088	38.8	—	—	—	—	—	6	177	55
CR	<i>Petrosicirtes</i> spp.	PERC	26.5	0.153	24.5	—	—	—	—	—	12	504	55
CR	<i>Pomacentrus</i> spp.	PERC	28.8	0.308	19.8	—	—	—	—	—	4	1,786	53, 54, 55, 56
CR	<i>Pseudojulis</i> sp.	LABR	25.7	0.099	55.0	—	—	—	—	—	6	1,364	59
CR	<i>Scoplopsis dubiosus</i>	PERC	26.5	0.418	19.0	—	—	—	—	—	11	30,449	55
CR	<i>Semicossyphus pulcher</i>	LABR	15	0.162	52.2	—	—	—	—	—	6	27,876	60
CR	<i>Stegastes</i> spp.	PERC	28.7	0.304	23.3	—	—	—	—	—	8	9,534	53, 54
CR	<i>Thalassoma</i> spp.	LABR	26	0.090	64.4	—	—	—	—	—	5	1,645	55, 59
CR	<i>Xyrichtys</i> sp.	LABR	25.7	0.069	88.5	—	—	—	—	—	6	2,587	59
EST	<i>Achirus lineatus</i>	PLEUR	28	0.245	23.0	—	10.80	—	0.325	0.754	11	3,100	61, 62, 63, 64
EST	<i>Alosa sapidissima</i>	CLU	21	—	—	0.21	—	—	—	—	—	—	65
EST	<i>Archosargus rhomboidalis</i>	PERC	26	0.310	21.0	0.43	8.32	0.72	0.31	1.000	15	7,000	62, 63, 64, 66, 67, 68
EST	<i>Anchoa lamprotaenia</i>	CLU	26	0.210	34.0	—	—	—	—	—	20	25,000	69
EST	<i>Anchoa mitchilli</i>	CLU	27	0.250	32.4	0.375	6.1	0.66	0.215	1.163	15	25,000	61, 62, 63, 64, 70, 71
EST	<i>Cynoscion nebulosus</i>	PERC	28	0.365	19.4	0.500	—	0.73	—	—	20	7,000	72, 73, 74
EST	<i>Gobiosoma boscii</i>	GOB	17	0.146	30.9	—	—	—	—	—	20	1,821	75
EST	<i>Morone americana</i>	PERC	17	0.105	84.5	—	—	—	—	—	20	10,000	76
EST	<i>Morone saxatilis</i>	PERC	17	0.140	33.0	0.170	5.6	0.82	0.230	0.609	200	15,000	77, 78, 79, 80, 81, 82, 83
EST	<i>Menidia menidia</i>	ATH	20	0.130	35.4	—	—	—	—	—	100	10,000	84
EST	<i>Menidia peninsulae</i>	ATH	25	0.165	41.0	—	—	—	—	—	30	10,000	85
EST	<i>Pseudopleuronectes (=Pleuronectes) americanus</i>	PLEUR	6	0.080	87.0	0.230	4.9	0.34	0.190	0.421	10	1,000	86, 87, 88, 89, 90
OCN	<i>Auxis rochei</i>	SCOM	25.5	0.315	16.0	—	—	—	—	—	140	21,630	91, 92
OCN	<i>Auxis thazard</i>	SCOM	25.5	0.476	9.5	—	—	—	—	—	197	18,130	92
OCN	<i>Euihynnus alletteratus</i>	SCOM	26	0.285	24.4	—	—	—	—	—	19	19,800	93
OCN	<i>Katsuwonus pelamis</i>	SCOM	26.7	0.318	20.2	—	—	—	—	—	32	19,900	91, 94
OCN	<i>Thunnus albacares</i>	SCOM	26.5	0.274	25.1	—	—	—	—	—	21	20,200	91, 95
OCN	<i>Thunnus maccoyii</i>	SCOM	27.5	0.277	24.1	—	—	—	—	—	25	19,580	96, 97

Appendix A. Continued

ECOS	SP	Taxa	T (°C)	G	D	Z	QO ₂	G/Z	K _i	I	W ₀	W _{max}	Ref.
OCN	<i>Thunnus thynnus</i>	SCOM	26	0.240	27.9	—	—	—	—	—	25	20,000	98
SH	<i>Acanthopagrus cuvieri</i>	PERC	25	0.315	—	—	—	—	—	—	5	7,000	99
SH	<i>Ammodytes americanus</i>	SCHIND	5	0.060	159.1	—	—	—	—	—	40	10,000	100, 101, 102, 103
SH	<i>Chanos chanos</i>	GONO	27	0.145	43.5	—	—	—	—	—	50	25,000	104, 105
SH	<i>Clupea harengus</i>	CLU	11.5	0.065	160.6	0.235	2.65	0.27	0.360	0.181	90	25,000	106, 107, 108, 109, 110, 111, 112, 113, 114, 115, 116, 177
SH	<i>Dicentrarchus labrax</i>	PERC	16.5	0.125	45.6	—	—	—	0.415	0.301	60	10,000	118, 119, 120, 121, 122, 209
SH	<i>Etrumeus teres</i>	CLU	22.5	—	—	0.130	—	—	—	—	—	—	123
SH	<i>Gadus morhua</i>	GAD	7.5	0.070	100.9	0.105	4.95	0.66	—	—	50	7,000	124, 125, 126, 127, 128, 129, 130, 138, 207
SH	<i>Harengula jaguana</i>	CLU	26.0	—	—	0.280	—	—	—	—	—	—	131
SH	<i>Leuresthes tenuis</i>	ATH	18.0	0.090	44.2	—	—	—	0.380	0.237	362	19,350	132
SH	<i>Mallotus villosus</i>	SAL	5.5	0.041	150.4	—	—	—	—	—	15	7,160	133
SH	<i>Melanogrammus aeglefinus</i>	GAD	6.5	0.070	127.7	0.110	—	0.63	—	—	70	7,000	103, 124, 126, 134, 135, 137, 138
SH	<i>Micromesistius poutassou</i>	GAD	8.5	—	—	0.150	—	—	—	—	—	—	140
SH	<i>Opisthonema oglinum</i>	CLU	26.5	—	—	0.235	—	—	—	—	—	—	141
SH	<i>Pagrus major</i>	PERC	20.0	0.195	46.6	—	4.76	—	—	—	10	7,000	142, 143, 144, 145, 161
SH	<i>Paralichthys dentatus</i>	PLEUR	18.0	0.070	98.8	—	—	—	0.145	0.483	50	7,000	146
SH	<i>Pleuronectes platessa platessa</i>	PLEUR	4.5	0.022	100.0	0.050	3.54	0.44	—	—	101	904	31, 107, 111, 147, 148, 149, 210, 213
SH	<i>Sardinella aurita</i>	CLU	24.0	—	—	0.450	—	—	—	—	—	—	150
SH	<i>Sciaenops ocellatus</i>	PERC	26.5	0.255	22.4	0.521	—	—	—	—	—	—	151, 211, 212
SH	<i>Scomber scombrus</i>	SCOM	15.0	0.140	39.5	0.520	—	0.26	—	—	50	10,000	139, 152, 153, 208
SH	<i>Scomberomorus cavalla</i>	SCOM	28.5	0.576	11.7	—	—	—	—	—	23	19,770	154
SH	<i>Scomberomorus maculatus</i>	SCOM	28.5	0.785	8.6	—	—	—	—	—	19	19,770	154
SH	<i>Scophthalmus maximus</i>	PLEUR	15.0	0.175	39.3	—	5.34	—	0.198	0.884	30	20,000	155, 156, 157, 158, 159, 160
SH	<i>Sebastes</i> spp.	PERC	8.0	—	—	0.060	—	—	—	—	—	—	162

Appendix A. Continued

ECOS	SP	Taxa	T (°C)	G	D	Z	QO ₂	G/Z	K _i	I	W ₀	W _{int}	Ref.
SH	<i>Solea solea</i>	PLEUR	18	0.155	35.1	—	—	—	—	—	—	—	163, 164, 165, 166
SH	<i>Sparus aurata</i>	PERC	17.5	0.120	49.5	—	—	—	—	—	20	7,000	167
SH	<i>Theragra chalcogramma</i>	GAD	7.0	0.075	108.3	0.075	3.77	1.00 (6°)	0.224	0.335	40	10,000	138, 139, 168, 169, 170, 171, 172, 173, 174
UW	<i>Engraulis capensis</i>	CLU	18.0	0.150	47.4	—	—	—	—	—	15	18,665	175
UW	<i>Engraulis encrasicolus</i>	CLU	22.8	0.196	36.7	0.205	—	0.95	—	—	17	22,830	176, 177, 178
UW	<i>Engraulis japonica</i>	CLU	22.0	0.198	47.1	0.300 (17°)	—	0.66	—	—	81	18,000	179, 180, 181, 182
UW	<i>Engraulis mordax</i>	CLU	14.5	0.220	34.8	0.190 (16°)	5.45 (16.5°)	1.15	0.350	0.629	20	25,000	116, 180, 181, 182, 183, 184, 185, 186, 187, 188
UW	<i>Engraulis ringens</i>	CLU	17.5	0.105	74.3	—	8.30	—	—	—	6	12,270	189, 190, 191, 196
UW	<i>Merluccius productus</i>	GAD	13.0	0.060	88.0	—	—	—	0.420	0.143	40	7,000	192
UW	<i>Sardina pilchardus</i>	CLU	21.3	0.172	40.3	—	—	—	—	—	12	12,500	176, 193
UW	<i>Sardinops sagax</i>	CLU	16.6	0.209	43.8	0.10 (16.4°)	—	2.09	—	—	13	12,920	194, 195, 196, 197
UW	<i>Scomber japonicus</i>	SCOM	19.5	0.340	17.3	0.140 (18°)	8.75 (20°)	2.42	0.32	1.063	—	—	198, 199
UW	<i>Sardinops caeruleus</i>	CLU	15.6	0.177	41.8	—	2.00 (14°)	—	—	—	8	12,150	200, 201
UW	<i>Sardinops melanostictus</i>	CLU	16.0	0.165	42.0	0.130 (15.1°)	—	1.26	—	—	12	12,270	202, 203, 204
UW	<i>Trachurus symmetricus</i>	PERC	16.0	—	—	0.235 (15.5°)	—	—	—	—	—	—	205, 206

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