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Patterns of Life-History Diversification in North American Fishes: Implications for Population Regulation

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Interspecific patterns of fish life histories were evaluated in relation to several theoretical models of life-history evolution. Data were gathered for 216 North American fish species (57 families) to explore relationships among variables and to ordinate species. Multivariate tests, performed on freshwater, marine, and combined data matrices, repeatedly identified a gradient associating later-maturing fishes with higher fecundity, small eggs, and few bouts of reproduction during a short spawning season and the opposite suite of traits with small fishes. A second strong gradient indicated positive associations between parental care, egg size, and extended breeding seasons. Phylogeny affected each variable, and some higher taxonomic groupings were associated with particular life-history strategies. High-fecundity characteristics tended to be associated with large species ranges in the marine environment. Age at maturation, adult growth rate, life span, and egg size positively correlated with anadromy. Parental care was inversely correlated with median latitude. A trilateral continuum based on essential trade-offs among three demographic variables predicts many of the correlations among life-history traits. This framework has implications for predicting population responses to diverse natural and anthropogenic disturbances and provides a basis for comparing responses of different species to the same disturbance.

Les caractéristiques du cycle biologique communes à plusieurs espèces de poissons ont été évaluées par rapport à plusieurs modèles théoriques de l'évolution à l'intérieur du cycle biologique. On a recueilli des données sur 216 espèces nord-américaines de poissons (57 familles) afin d'explorer les rapports entre différentes variables et afin de classer les espèces. Des tests multivariés, faits sur des matrices correspondant aux eaux douces, aux eaux de mer et aux deux, ont régulièrement fait ressortir un gradient qui associe les poissons à maturation lente à une fertilité élevée, à la petitesse des oeufs et au nombre restreint de périodes d'activité sexuelle au cours d'une brève saison de fraie, et qui associe les traits opposés aux poissons de petite taille. Un deuxième gradient marqué a indiqué des associations positives entre les soins des parents, la grosseur des oeufs et l'existence de saisons de fraie prolongées. La phylogénie a des effets sur chacune des variables, et certains groupes taxonomiques supérieurs sont associés à des stratégies particulières du cycle biologique. Il tendait à exister un rapport entre la fertilité élevée et l'aire de distribution des grosses espèces en milieu marin. L'âge à maturité, la vitesse de croissance des adultes, la durée de vie et la grosseur des oeufs étaient tous en corrélation positive avec l'anadromie. Les soins des parents étaient en corrélation inverse avec la latitude médiane. Un ensemble trilatéral de données fondées sur des compromis essentiels entre trois variables démographiques, permet de prédire beaucoup de corrélations avec les caractéristiques du cycle biologique. Ce cadre d'examen est utile à la prévision des réponses de populations à différentes perturbations naturelles et d'origine anthropique, et il procure la base pour la comparaison des réponses de différentes espèces à une même perturbation.

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Balon (1975) listed the requirements for a comparative framework useful for predicting the response of fish populations to different kinds of environments and disturbances. Such a framework should contain few categories and allow researchers "to build from bits and pieces of available information about reproductive strategies" (Balon 1975). Moreover, it should group similar species irrespective of phylogenetic origin. In other words, adaptive convergences should be stressed over phylogentic affiliations. Balon's (1975; Balon et al. 1977) reproductive guild framework was based on the premise that environmental requirements and adaptations of early life stages are likely to account for a large amount of the variance in densities and geographical distributions of fish populations. Reproductive guilds permit researchers and resource managers to identify common ecological features and problems in different geographical locations involving different fish faunas.

Because it is qualitative and emphasizes the physiological ecology of early life stages, the reproductive guild concept is limited in its application to many practical problems. Much of population biology and fisheries science is founded in mathematical formulations, and a framework based on developmental physiology does not easily yield quantitative predictions. Hence, a general, yet quantitative comparative framework that could interface with both qualitative schemes, like reproductive guilds, and quantitative population models is desirable. To provide a further step toward a conceptual framework of fish ecological strategies, we examine patterns of life-history variation among North American fresh water and marine fishes and evaluate gradients of variation in relation to several earlier models of life-history evolution.

Because life-history traits are also the fundamental determinants of population performance, the investigation of life-

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strategies is central to both theoretical ecology and resource management. Life-history theory deals with constraints among demographic variables and traits associated with reproduction and the manner in which these constraints, or trade-offs, shape strategies for dealing with different kinds of environments. Life-history trade-offs may have a primarily physiological basis (e.g. clutch size and investment per offspring; Smith and Fretwell 1974), a demographic basis (e.g. intrinsic rate of increase and mean generation time; Birch 1948; Smith 1954), an ecological basis (e.g. provision of parental care and clutch size; Sargent et al. 1987; Nussbaum and Schultz 1989), or a phylogenetic basis (Gotelli and Pyron 1991). Of course, organisms consist of complex suites of life-history traits, so that genetic correlations between coevolved traits exhibiting a strong trade-off can indirectly result in correlations with other traits (Pease and Bull 1988). For example, Roff (1981) reevaluated Murphy's (1968) findings for clupeid life histories and concluded that variation in reproductive life span could be explained by its correlation with age at maturity, rather than as a direct evolutionary response to variation in reproductive success.

Insights into the evolutionary response of life-history parameters to different environmental conditions and spatiotemporal changes usually come from two approaches: theoretical models of life-history evolution (e.g. Cole 1954; Cohen 1967; Goodman 1974; Schaffer 1974; Green and Painter 1975; Boyce 1979; Roff 1984; Sibly and Calow 1985, 1986) and analyses of empirical patterns (e.g. Kawasaki 1980; Stearns 1983; Dunham and Miles 1985; Roff 1988; Winemiller 1989; Paine 1990). Both of these approaches have relied, to a large degree, on the *r–K* continuum (Pianka 1970) or similar unidimensional schemes (e.g. bet-hedging (Murphy 1968) and iteroparity–semelparity gradients (Cole 1954; Schaffer 1974)) as the basis for comparing alternative life-history strategies. Triangular continua containing three endpoint strategies (*r*-, *K*-, and stress- or adversity-resistance) have been adopted to interpret patterns and consequences of observed life-history variation in plants and insects (Grime 1977, 1979; Southwood 1977, 1988; Greenslade 1983). Studying fishes in very different environments, Kawasaki (1980, 1983), Baltz (1984), and Winemiller (1989; Winemiller and Taphorn 1989) independently identified three similar strategies as endpoints of a triangular continuum. Following Winemiller (1992), these can be classified as (1) small, rapidly maturing, short lived fishes (opportunistic strategists), (2) larger, highly fecund fishes with longer life spans (periodic strategists), and (3) fishes of intermediate size that often exhibit parental care and produce fewer but larger offspring (equilibrium strategists).

Here, we further evaluate the trilateral continuum model of fish life-history strategies by analyzing data from 216 North American freshwater and marine fish species. Even though many North American species are not included here, the breadth and evenness of phylogenetic coverage should be sufficient to identify major axes of life-history variation and to ordinate species into a framework of basic ecological and demographic strategies. We adopt broad interspecific comparisons under the assumption that consistent intercorrelations among life-history features across widely divergent taxa are likely to reveal both fundamental constraints and adaptive responses to environmental conditions. Life-history traits and strategies are then examined with respect to phylogeny, and observed patterns are evaluated in reference to several models of life-history evolution and population regulation. Finally, we argue that greater understanding of population regulation in fisheries can be achieved by contrasting alternative life-history strategies in relation to different scales of variation in resources and sources of mortality.

Materials and Methods

Life-History Data Set[2]

Estimates of fish life-history traits were obtained from literature sources that summarize large amounts of quantitative data for individual species (e.g. Carlander 1969, 1977; Hart 1973; and synopses of biological data published by Food and Agriculture Organization, Rome). In some instances, we consulted the original studies cited in the species synopses to allow better judgement of the method of estimation and reliability of data. Most fish species exhibit considerable interdemic variation in life-history traits over their geographical ranges. Therefore, we determined the average or modal value of traits by using data from populations located near the center of species' ranges. For example, if a freshwater species ranged from central Canada to the Tennesse River, we sought studies conducted near the latitudes of the Great Lakes. When limited data were available near the center of the range, we sought estimates from peripheral populations in an incremental fashion (working outward from the center of the range). When no reliable data were found for a given trait, that cell in the species by life-history trait matrix was left blank and all calculations calling for the trait eliminated the species from the analysis. Whenever maturation and growth data were reported for the sexes separately, we used the estimates for females. In some instances, total lengths were calculated from standard lengths or fork lengths using published conversion equations. Because no conversion equations were available for North American cavefishes (Amblyopsidae), we estimated conversion ratios from measurements of photographs.

Data were obtained for the following 16 life-history traits.

(1) Age at maturation — the mean age at maturation in years, or when estimates were in summarized form, the modal age of maturation.

(2) Length at maturation — the modal length at maturation in millimetres total length (TL), or if not reported, either the median or minimum length at maturation.

(3) Maximum length — the maximum length reported in millimetres TL.

(4) Longevity — maximum age in years.

(5) Maximum clutch size — the largest batch fecundity reported.

(6) Mean clutch size — the mean batch fecundity for a local population, i.e.data from a specific location or ecosystem, calculated as

$$(1)\quad E = \frac{\sum_{i=1}^{n} N_i F_i}{\sum^{n} N_i}$$

where E is the mean clutch, N_i is the number of individuals in age or size class i, F_i is the number of mature eggs per clutch, and n is the number of age or size classes in the population.

(7) Egg size — the mean diameter of mature (fully yolked) ovrian oocytes (to nearest 0.01 mm).

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[2] A database listing our principal literature sources, life history traits, and numerical estimates is available, for a nominal fee, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont. K1A 0S2, Canada.

(8) Range of egg sizes — the range of diameters for mature ovarian oocytes reported for a local population (0.01 mm).

(9) Duration of spawning season — number of days that spawning or early larvae were reported.

(10) Number of spawning bouts per year — the mean number of times an individual female was reported to spawn during a year. Because multiple spawning bouts are difficult to document in wild fishes, many of the estimates used in this analysis are probably underestimates. Several recent studies of small cyprinids and percids indicate that multiple clutches may be common in small fishes having small clutches (e.g. Heins and Rabito 1986; Heins and Baker 1988; James et al. 1991). When two fairly distinctive size classes of ova were reported in mature ovaries and other evidence was consistent with a hypothesis of repeat spawning, we recorded the species as having two bouts per year. Following Hubbs (1985), we used an average interbrood interval of 10 d for estimates of spawning bouts for several darters (*Etheostoma*, Percidae) that exhibited strong evidence of multiple clutches.

(11) Parental care — following Winemiller (1989), quantified as Σx_i for $i = 1$ to 3 ($x_1 = 0$ if no special placement of zygotes, 1 if zygotes are placed in a special habitat (e.g. scattered on vegetation, or buried in gravel), and 2 if both zygotes and larvae are maintained in a nest; $x_2 = 0$ if no parental protection of zygotes or larvae, 1 if a brief period of protection by one sex (<1 mo), 2 if a long period of protection by one sex (>1 mo) or brief care by both sexes, and 4 if lengthy protection by both sexes; and $x_3 = 0$ if no nutritional contribution to larvae (yolk sac material is not considered here), 2 if brief period of nutritional contribution to larvae (= brief gestation (<1 mo) with nutritional contribution in viviparous forms), 4 if long period of nutritional contribution to larvae or embryos (= long gestation (1–2 mo) with nutritional contribution), or 8 if extremely long gestation (>2 mo). We reason that, in terms of benefits received by offspring, gestation with nutritional contribution is approximately equivalent to biparental brood guarding during an equivalent time period. Parental care values (Σx_i) ranged between 0 (no care) and 8 (long gestation in some embiotocid fishes) in the North American fish data set.

(12) Time to hatch — the mean time to hatch within the range of values for average midseason temperatures, or when not reported, the mean, modal, or midrange time to hatch at the highest temperature reported within a reasonable range (relative to local ambient temperatures) for a given locality.

(13) Larval growth rate — mean increment in millimetres TL during the first month following hatching. We subtracted the length of larvae at hatching from the mean length attained after the first month. For the few species with larval stage duration <1 mo, we converted mean daily growth rates to mean increments for 30 d.

(14) Young of the year (YOY) growth rate — mean increment in millimetres TL during the first year following hatching or independent life for viviparous fishes. We subtracted the length of larvae at hatching from the mean or modal length attained after the first growing season.

(15) Adult growth rate — mean increment in millimetres TL per year of life over an average adult life span (in this case, data were not weighted by sample size of age cohorts).

(16) Fractional adult growth — mean fraction of millimetres TL gained per year in a normal adult life span, calculated from

$$G = \frac{\sum_{i=2}^{n} l_i/L_{i-1}}{n}$$

where l_i is the annual length gain for adults in age class i, L_i is TL for an adult entering age class i, and n is the number of adult age classes.

Within local populations and size classes, individual fish exhibit considerable variation in life-history traits. Our analysis assumes that measures of central tendency for populations near the center of their species distributions allow the investigation of relationships among life-history variables within a broad inter-specific context.

Phylogeny and Ecological Data Set

Phylogeny of North American fishes follows Lee et al. (1980) for freshwater fishes and Nelson (1984) for marine fishes. We coded family and order as categorical variables for statistical analyses of phylogenetic influences on life-history traits. Each species was classified as either freshwater or marine depending on where the greatest fraction of the life cycle occurred. Because the majority of the estuarine populations extend into other coastal marine habitats, estuarine fishes were included in the marine category. We obtained data for marine populations of *Oncorhynchus mykiss* (steelhead), *Menidia beryllina* (inland silverside), and *Gasterosteus aculeatus* (threespine stickleback) and data for a landlocked freshwater population of *Oncorhynchus nerka kennerlyi* (kokanee salmon).

For each species, the ecological data set consisted of variables characterizing its geographical range, general habitat, and general ecological niche. We recorded the midrange latitude and total range in latitude for each species based on range maps or verbal accounts of species' ranges. Each species was classified as either benthic (1), epibenthic (2), or pelagic (3) based on accounts of the normal depth distribution of adult fishes. The basic adult habitat was classified as either caves or springs (0), small cold-water streams (1), small warmwater streams (2), river channels (3), river backwaters and lakes (4), estuaries (5), marine benthic (6), or marine pelagic (7). Fishes that are common in two or more categories or occupy intermediate habitats were assigned fractional values (e.g. habitat = 2.5 for *Ictiobus bubalus* (smallmouth buffalo) which commonly occurs in both rivers and lakes). Based on summarized diet information for adults, trophic status was classified as either detritivore/herbivore (1), omnivore (2), invertebrate-feeder (3), or piscivore (4). Fishes that consume large quantities of both invertebrates and fishes formed a fifth intermediate category (e.g. trophic status = 3.5 for *Micropterus dolomieu* (smallmouth bass)). The relative migratory behavior of each species was classified under the headings anadromous (1), sedentary (0), and catadromous (−1). Fishes exhibiting spawning runs from lakes into rivers or from rivers into affluent tributaries (potamodromy) were classified as 0.5, and fishes exhibiting spawning migrations from nearshore to offshore were classified as −0.5.

Data Analysis and Comparisons

Analyses based on broad interspecific comparisons yield patterns that have resulted from many generations and thousands of years of evolution. As a consequence, comparisons involving many taxa and large phylogenetic breadth should contain fewer idiosyncracies due to genetic correlations carried along within a particular phylogenetic lineage (= phylogenetic constraints). If divergent lineages are not given fairly equivalent representation, taxonomic bias can enter into interspecific comparisons (Pagel and Harvey 1988). Some have even argued against the use of species in comparisons (e.g., Ridly 1989).

In essence, the comparative approach requires that a pattern be repeated consistently within a variety of taxa (i.e. conservation or convergence of pattern), or the effect of phylogeny be held constant (or adjusted for statistically), if hypotheses of adaptation are to be tested. To maximize the likelihood that emergent patterns reflect adaption, we examined life-history patterns based on a variety of different combinations of life-history traits and various ecological and phylogenetic subsets of the overall data set.

Because some distributions of raw life-history traits were lognormal, data were ln-transformed for parametric statistical tests. All statistics were calculated using SAS (SAS Institute Inc. 1987). Univariate comparisons between various subsets of the data set used either t-tests (two-sample, two-tailed) or Mann–Whitney U-tests when data were interval or did not approximate a normal distribution. Bivariate relationships among four categorical ecological variables and parental care (ordinal scale) were also analyzed using Spearman's rank correlation coefficient. Chi-square tests for goodness of fit were used to compare frequency distributions of life-history traits for marine and freshwater fishes.

Nested analysis of covariance was used to test for effects of phylogeny and body size on life-history traits. Order and family were used as independent variables in tests of phylogenetic effects (family nested within order). Mean TL at maturation (ln-transformed) was used as an index of body size. For additional insights into the effects of phylogenetic affiliation on life-history patterns, bivariate relationships among several key life-history variables were analyzed within several orders that contained many species.

To explore patterns of association among life-history traits and ordination of species, a series of principal components analyses (PCA) was performed on ln-transformed life-history data. All PCAs were calculated from the correlation matrix to standardize for the influence of unequal variances. Because data were lacking for some traits for some species, analyses that involved more life-history variables resulted in ordination of fewer species. Therefore, separate PCAs were performed on marine, freshwater, and combined fish data sets: one using 12 relatively nonredundant life-history variables (analyses omitting maximum length (redundant with size at maturity), maximum clutch (redundant with average clutch), range of egg size (redundant with egg size), and either length or age at maturation (highly correlated with each other)) and another using only five life-history variables (length at maturation, mean clutch, egg size, spawning bouts, parental care). The five life-history variables retained for the five-variable analyses were selected based on their dominant influence in the 12-variable PCA models, except that length at maturation was substituted for age at maturity in the five-variable data set in order to increase the number of species retained in the analysis.

Although values for parental care were ordinal, we included ln-transformed parental care values in multivariate analyses because they approximated a normal distribution within most groupings and were derived from an algorithm that combined several independent attributes into a single numeric value. Because some life-history researchers have identified an influence of body size on other life-history traits, some PCAs were done both with and without length partialled-out of the other variables (i.e. multivariate analyses are based on relationships among the residuals from regressions of variables with length). To test for potential biases resulting from disproportionate inclusion of some taxa in the global data set (e.g. *Lepomis* species, $N = 8$), PCA was also performed on a data set containing only one species per genus. The species used to represent genera were selected in alphabetical order to reduce experimenter bias.

To further test relationships between life-history patterns and the species' environmental biology, we performed canonical discriminant function (CDF) based on nine life-history variables and three ecological variables (habitat, trophic status, migration) and parental care recorded as classification variables. CDF derives canonical variables from the set of life-history variables in a manner that maximizes multiple correlations of the original variables within groups. To show general associations between ecological groupings and suites of life-history traits, we plotted the means and standard deviations of each class on the first two CDF axes.

Results

Univariate Comparisons

Life-history parameters showed large variation both within the entire data matrix and within orders containing the largest number of species. Standard deviations approached, and in many instances exceeded, the magnitude of the mean values for life-history traits (Table 1). The pygmy sunfish, *Elassoma zonatum* (Centrarchidae), was the smallest fish in the overall North American data set (minimum size at maturation = 25.0 mm). The largest fishes were the Atlantic sturgeon, *Acipenser oxyrhynchus* (Acipenseridae) (length at maturation = 2.5 m), Pacific halibut, *Hippoglossus stenolepis* (Pleuronectidae) (maximum length = 2.7 m), and ocean sunfish, *Mola mola* (Molidae) (maximum length = 3 m). The smallest maximum clutches (batch fecundities) were recorded for two live bearing surfperches (Embiotocidae), *Hyperprosopon argenteum* (12) and *Cymatogaster aggregata* (20). The largest clutch size estimates were for the ocean sunfish (average = 300×10^6), Atlantic cod, *Gadus morhua* (Gadidae) (maximum = 12×10^6), and tarpon, *Megalops atlanticus* (Elopidae) (maximum = 12.2×10^6). Reported estimates of average egg sizes ranged from a minimum of 0.45 mm in diameter for the bay anchovy, *Anchoa mitchilli* (Engraulidae), to a maximum of 20.5 mm for the mouthbrooding gafftopsail catfish, *Bagre marinus* (Ariidae). Average larval growth rates ranged from a minimum estimate of 1.3 mm TL/mo for lake whitefish, *Coregonus clupeaformis* (Salmonidae), to a high of 69.9 mm TL/mo for longnose gar, *Lepisosteus osseus* (Lepisosteidae).

Comparisons between marine and freshwater fishes showed differences in the distributions of life-history attributes (notable examples illustrated in Fig. 1). Statistically significant mean differences are reported with the following notation: t = value from two-sample t-test, z = value from Mann–Whitney U-test. Because both data sets were biased somewhat in favor of larger, commercial species, our interpretations of these univariate comparisons are tentative. As a group, marine fishes matured later (mean marine (m) = 3.38 yr, mean freshwater (f) = 2.74 yr, $t = 1.97$, df = 194, $P < 0.05$; Fig. 1a), matured at larger sizes (m = 320 mm, f = 186 mm, $t = 4.03$, df = 202, $P < 0.0001$), lived longer (m = 13.0 yr, f = 9.7 yr, $t = 2.19$, df = 185, $P < 0.05$), had larger mean clutches (m = 1 554 400, f = 113 376, $t = 4.34$, df = 189, $P < 0.0001$; Fig. 1b), had longer spawning seasons (m = 103 d, f = 59 d, $t = 5.55$, df = 213, $P < 0.0001$; Fig. 1c), had larger YOY growth rates (m = 131.2 mm/yr, f = 98.4 mm/yr, $z = 2.10$, $P < 0.0025$), and had larger adult growth rates (m = 50.8 mm/yr, f = 30.5 mm/yr, $z = 3.12$, $P < 0.001$) than freshwater

TABLE 1. Mean values (standard deviation in parentheses) for 16 life-history variables based on the entire data matrix (all species) and based on seven major fish orders.

Variable	All species	Clupeif.	Salmonif.	Cyprinif.	Silurif.	Percif.	Scorpaenif.	Pleuronectif.
No. of species	216	12	28	30	12	71	16	11
Maximum length	541	323	662	318	414	519	561	894
(mm TL)	(551)	(131)	(438)	(259)	(409)	(551)	(341)	(657)
Age at maturity	3.0	2.3	3.4	2.7	2.5	2.2	4.7	4.4
(yr)	(2.5)	(1.4)	(1.3)	(1.6)	(1.3)	(1.0)	(1.1)	(3.0)
Length at maturity	250	208	339	165	188	199	270	294
(mm TL)	(261)	(104)	(212)	(128)	(139)	(176)	(172)	(74)
Longevity (yr)	11.1	7.7	11.2	7.0	7.6	9.8	24.4	19.7
	(11.4)	(4.3)	(9.5)	(4.2)	(5.1)	(6.5)	(15.1)	(14.2)
Mean clutch size	234 000	129 000	13 500	38 000	2 390	356 000	229 000	818 000
(mature oocytes)	(679 000)	(160 000)	(2 600)	(86 000)	(3 330)	(941 000)	(312 000)	(711 000)
Maximum clutch	598 000	258 500	36 500	74 500	8 840	747 500	591 000	2 026 000
(mature oocytes)	(1 683 000)	(274 000)	(67 500)	(163 500)	(19 826)	(1 746 000)	(709 000)	(1 487 000)
Egg size	2.14	1.26	3.4	1.81	6.24	1.20	1.37	1.68
(mm diameter)	(2.23)	(0.66)	(1.8)	(1.06)	(6.43)	(0.42)	(0.68)	(1.08)
Range egg size	0.69	0.48	0.93	0.38	2.86	0.29	0.33	1.70
(mm diameter)	(1.53)	(0.23)	(0.54)	(0.25)	(4.35)	(0.20)	(0.22)	(3.77)
Spawn season (d)	80	108	50	50	59	91	56	118
	(49)	(49)	(17)	(31)	(25)	(52)	(19)	(63)
Spawn bouts	3.4	18.1	1.1	2.4	1.7	2.7	1.2	1.4
(no./yr)	(14.5)	(51.2)	(0.4)	(3.4)	(0.9)	(5.5)	(0.4)	(1.0)
Parental care	1.6	0.2	0.8	1.1	3.4	1.8	3.6	0
(scale 0–8)	(1.7)	(0.4)	(0.6)	(1.0)	(0.5)	(2.2)	(1.0)	(—)
Hatch time (h)	1111	88	1551	150	253	510	994	165
	(4084)	(68)	(1271)	(88)	(190)	(1522)	(637)	(120)
Larval growth	14.9	19.5	10.8	14.2	13.2	14.0	12.0	13.8
(mm TL/mo)	(10.6)	(16.9)	(8.9)	(8.2)	(3.0)	(7.6)	(—)	(—)
YOY growth	109.9	91.7	133.1	83.6	86.5	115.4	190.8	97.6
(mm TL/yr)	(76.2)	(32.7)	(65.6)	(56.9)	(36.0)	(75.5)	(61.0)	(35.7)
Adult growth	38.5	23.7	58.8	29.4	34.9	36.7	52.9	30.8
(mm TL/yr)	(29.3)	(11.6)	(44.5)	(13.2)	(185)	(24.7)	(19.1)	(10.2)
Fraction growth	0.21	0.13	0.23	0.25	0.24	0.21	0.17	(0.22
(% TL/yr)[a]	(0.12)	(0.08)	(0.12)	(0.16)	(0.16)	(0.09)	(0.07)	(0.08)

[a] Mean percentage of initial TL gained per year of adult life.

fishes. Freshwater fishes tended to have more highly developed parental care than marine fishes (f = 1.8, m = 1.4, z = 3.33, $P < 0.01$; Fig. 1d). Primarily due to skewed distributions, mean maximum clutch sizes (m = 1 102 792, f = 113,376), mean within-species range of egg diameters (m = 2.69, f = 0.49), mean hatching times (m = 786 h, f = 1381 h), and mean larval growth rates (m = 12.5 mm/mo, f = 16.3 mm/mo) did not differ statistically between groups of fishes classified as marine versus freshwater. Mean fractional adult growth rates were also nearly the same for the two groups (m = 0.20, f = 0.21). Due to a disproportionate influence of two marine catfishes (Ariidae), mean egg diameters were nearly the same for freshwater and marine fishes (f = 2.10 mm, m = 2.17 mm), yet distributions of egg size intervals differed significantly (Kolomorov–Smirnov test (K–S), $P < 0.05$; Fig. 1e), and medians differed ($f > m$) based on the nonparametric statistic (z = 3.78, $P < 0.0001$). Similarly, after the disproportionate influence of two marine anchovies was reduced through use of the nonparametric test, freshwater fishes tended to have more spawning bouts per year than marine fishes (K–S, $P < 0.05$; z = 2.15, $P < 0.05$; Fig. 1f).

Bivariate Life-History Relationships

Correlations between all pairwise combinations of life-history (ln-transformed) and ecological variables are given in Table 2. Some of the high correlations reflect measurement of similar traits or traits that would be expected to covary on a physiological basis (e.g. mean clutch and maximum clutch (0.98), maximum length and length at maturity (0.92), length at maturity and age at maturity (0.77)). Other high correlations need not follow from physiological mechanisms and reflect a diversity of life-history and ecological constraints (e.g. mean clutch and parental care (−0.54), age at maturity and spawning bouts per year (−0.61), longevity and spawning bouts per year (−0.51), length at maturity and YOY growth rate (0.77), mean clutch and YOY growth rate (0.65)).

Figure 2 compares marine and freshwater fishes while illustrating a wide range of bivariate relationships among several of the attributes frequently examined in the life-history literature. The bivariate relationship between ln length at maturity and ln clutch size was nearly the same for fishes categorized as freshwater and marine (Fig. 2a). Neither category showed a strong relationshp between egg size and ln mean clutch size or egg size and ln larval growth rate (Fig. 2b, 2d). The slope was greater for freshwater fishes in the linear relationship between ln mean clutch size and ln YOY growth rate (Fig. 2c), and this difference was due, in part, to the influence of slow YOY growth in cavefishes (*Amblyopsis rosae*, 8.8 mm/yr; *A. spelaea*, 10.6 mm/yr; Poulson 1963).

Correlations between five life-history variables, each measuring an essentially different life-history trait (length at maturity, mean clutch size, egg size, spawning bouts, and parental care), were performed for the seven orders that had the most species with recorded data (Table 3). Overall, matrices of life-history intercorrelations show fairly large deviations among

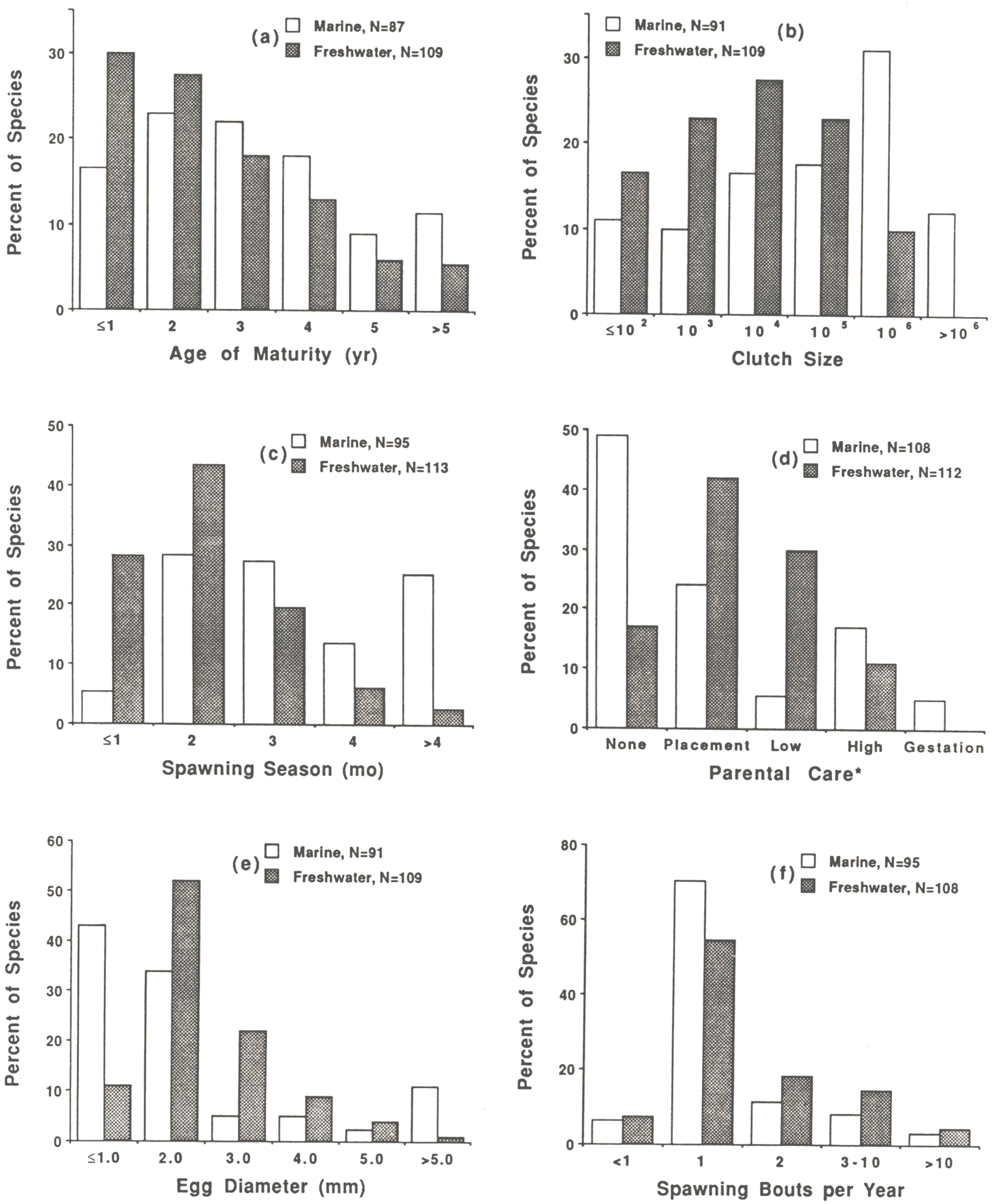

FIG. 1. Frequency distributions of (a) average age at maturation, (b) average clutch size, (c) average duration of the spawning season, (d) parental care (defined under Materials and Methods), (e) average diameter of mature eggs, and (f) average number of spawning bouts per year for fish species classified as either predominantly freshwater or marine.

TABLE 2. Correlation matrix of life-history (ln-transformed) and ecological variables (^{S}Spearman's rank correlation; otherwise, correlations are Pearson's product-moment). Correlations are based on all available data for freshwater and marine species (mean N = 171, range of N = 51–216). *$P < 0.05$; **$P < 0.0001$.

Variable	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. Maximum length	0.71**	0.92**	0.78**	0.75**	0.74**	0.19*	0.17	−0.10	−0.49**	−0.32**	−0.12	0.25*	0.77**	0.76**	−0.32*	−0.10	0.36**	0.14^S	0.40^S**	0.58^S**	0.16^S*
2. Age at maturity	—	0.77**	0.80**	0.53**	0.55**	0.37**	0.17	−0.33**	−0.61**	0.03	0.15	0.22*	0.42**	0.39**	−0.38**	0.30**	0.18*	0.01^S	0.31^S**	0.30^S**	0.25^S**
3. Length at maturity	—	—	0.75**	0.73**	0.72**	0.24*	0.23*	−0.21*	−0.51**	−0.30**	−0.04	0.26*	0.77**	0.71**	−0.39**	−0.01	−0.36**	0.18^S*	0.51^S**	0.51^S**	0.25^S**
4. Longevity	—	—	—	0.66**	0.67**	0.16	0.11	−0.17*	−0.51**	−0.17*	−0.01	0.23*	0.52**	0.44**	−0.43**	0.07	0.16*	0.02^S	0.34^S**	0.39^S**	0.06
5. Mean clutch size	—	—	—	—	0.98**	−0.29*	−0.24*	0.01	−0.37**	−0.54**	−0.45**	0.26*	0.65**	0.58**	−0.34**	−0.18*	0.40**	0.17^S*	0.44^S**	0.43^S**	0.01
6. Maximum clutch	—	—	—	—	—	−0.30*	−0.26*	0.01	−0.47**	−0.49**	−0.39**	0.27*	0.62**	0.55**	−0.36**	−0.19*	0.33**	0.17^S*	0.49^S**	0.51^S**	0.03
7. Egg size	—	—	—	—	—	—	0.76**	−0.35**	−0.19*	0.34**	0.52**	−0.13	0.09	0.19*	−0.01	0.34**	−0.13	−0.06^S	−0.21^S*	0.02^S	0.21^S*
8. Range egg size	—	—	—	—	—	—	—	−0.33*	−0.10	0.23*	0.37*	−0.04	0.13	0.13	−0.15	0.26*	−0.21*	0.06^S	−0.03^S	0.20^S*	0.24^S*
9. Spawning season	—	—	—	—	—	—	—	—	0.29**	−0.26**	−0.21*	−0.15	−0.14	−0.06	0.13	−0.41**	0.09	0.04^S	0.22^S**	−0.04^S	−0.22^S*
10. Spawning bouts	—	—	—	—	—	—	—	—	—	0.00	−0.21*	−0.15	−0.26*	−0.24*	0.22*	−0.08	−0.18	−0.01^S	−0.21^S*	−0.20^S*	−0.20^S*
11. Parental care	—	—	—	—	—	—	—	—	—	—	0.37**	−0.07	−0.27*	−0.28*	0.06	0.22*	−0.34**	−0.21^S*	−0.29^S*	−0.10^S	0.01^S
12. Hatching time	—	—	—	—	—	—	—	—	—	—	—	−0.26*	−0.27*	−0.06	−0.10	0.49**	−0.19*	−0.04^S	−0.08^S	−0.02^S	0.25^S*
13. Larval growth	—	—	—	—	—	—	—	—	—	—	—	—	0.27*	0.17	−0.21*	−0.23*	0.10	0.03^S	0.17^S	0.06^S	−0.06^S
14. YOY growth	—	—	—	—	—	—	—	—	—	—	—	—	—	0.69**	−0.42**	−0.11	0.38**	0.20^S*	0.39^S**	0.39^S**	0.14
15. Adult growth	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.16	−0.07	0.28*	0.27^S**	0.40^S**	0.47^S**	0.24^S*
16. Fractional growth	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.04	−0.15	0.05^S	−0.16^S	−0.03^S	−0.03^S
17. Median latitude	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	−0.35**	−0.27^S**	0.04^S	0.01^S	0.32^S**
18. Range latitude	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.31^S**	0.46^S**	0.25^S**	0.05
19. Water column	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.18^S*	0.36^S**	0.12^S
20. Habitat	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.30^S**	0.45^S**
21. Trophic status	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.04^S
22. Migration	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

orders, indicating evolutionary divergences in life-history strategies among higher taxa. Yet, some orders demonstrated high degrees of concordance in the signs of the 10 bivariate relationships, indicating evolutionary conservation or convergences of life-history strategies. Clupeiforms, and siluriforms showed only two of 10 differences in the sign of correlations, and salmoniforms and cypriniforms showed three sign differences, two of which involved $r^2 \leqslant 0.10$. Except for pleuronectiforms (no statistically significant relationship), length at maturity was always positively associated with mean clutch size, and length at maturity was negatively associated with spawning bouts per year. Except for scorpaeniforms (statistically nonsignificant positive relationship), clutch size was always negatively associated with spawning bouts per year (five of six cases were statistically significant; Table 3).

Large positive correlations between life-history and ecological variables (Table 2) were obtained for maximum length with trophic status (0.58), length at maturity with habitat and trophic status (both 0.51), mean clutch size with habitat (0.44), maximum clutch size with habitat (0.49) and trophic status (0.51), hatch time with median latitude (0.49), and adult growth rate with trophic status (0.47). The largest negative correlations between life-history and ecological variables were for length at maturity with range of latitude (−0.36) and parental care with range of latitude (−0.34). The largest positive intercorrelations among ecological variables (Table 2) were for habitat with range of latitude (0.46) and relative migration (0.45). Fishes at higher median latitudes tended to be associated with smaller ranges in latitude (−0.35), and this trend was heavily influenced by marine species.

Multivariate Life-History Patterns

Results of PCA were nearly the same for the data sets involving five life-history variables with all fish species (N = 147) and the data set using only one species to represent each genus (N = 83; Table 4). In each case, the first three PCs modeled 91% of the total variation in the data set and resulted in a first axis with endpoints contrasting species with large body size, large clutches, small eggs, few bouts of reproduction per year, and little parental care against those with small body size, small clutches, multiple reproductive bouts per year, and more parental care. In each case, high scores on the second axis reflect associations of large body size, large eggs, well-developed parental care, and few spawning bouts per year (Table 4). High species scores on the third axis reflect large egg size in association with multiple spawning bouts and little parental care.

When maximum length was partialled-out of the data set containing five life-history variables and 147 species, the first three PC axes modeled 85% of the total variation. The first axis reflected an association of clutches (eigenvector = −0.599), egg size (0.593), and parental care (0.509), and the second axis reflected groupings based on maturation size (0.741) in association with number of bouts of reproduction (−0.626) and clutch size (0.219). The suite of characteristics described by the first orthogonal axis from the length-adjusted analysis was similar to that described by the second axis from the unadjusted analysis. Similarly, the second PC axis from length-adjusted data approximated the primary associations predicted by the first axis from the unadjusted analysis.

With 12 life-history variables, the data set consisting of one species per genus (N = 31) yielded a PCA in which the first three axes modeled 71% of the total variation. The largest variable loadings (eigenvectors) on the first axis were longevity (0.437), age at maturity (0.375), mean clutch (0.375), YOY

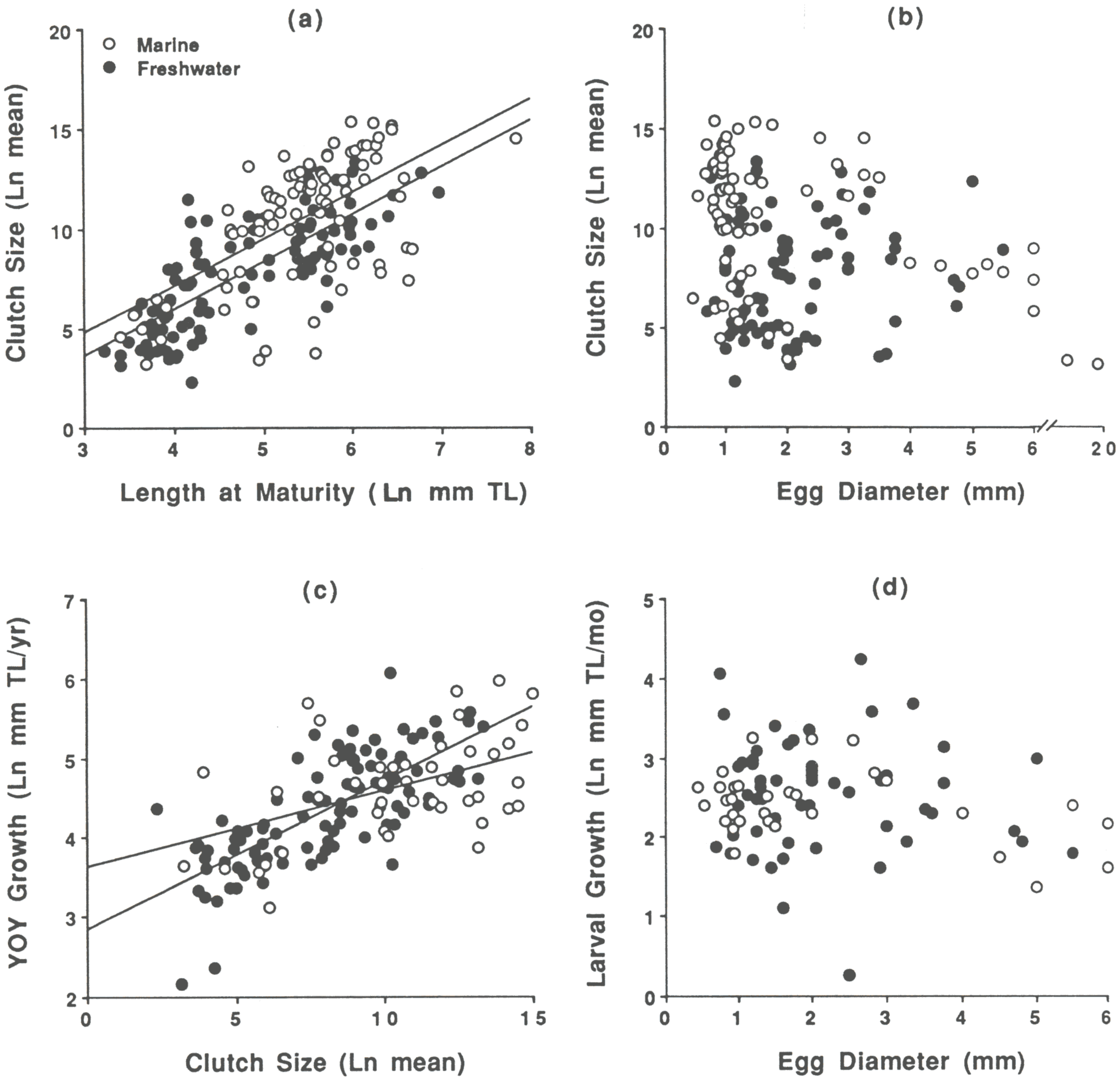

FIG. 2. Bivariate relationships among five life-history traits (open circles = freshwater fishes, closed circles = marine fishes). (a) Freshwater $r^2 = 0.62$, ln clutch = 2.36 (ln length) − 3.48; marine $r^2 = 0.35$, ln clutch = 2.34 (ln length) − 2.24. (b) Freshwater $r^2 < 0.01$; marine $r^2 = 0.17$. (c) Freshwater $r^2 = 0.55$, ln YOY growth = 0.19 (ln clutch) + 2.83; marine $r^2 = 0.35$, ln YOY growth = 0.10 (ln clutch) + 3.63. (d) Freshwater $r^2 < 0.01$; marine $r^2 = 0.20$.

growth (0.348), and spawning bouts (−0.311), and the second axis was dominated by egg size (eigenvector = 0.509), hatch time (0.474), spawning season (−0.407), and parental care (0.397). Based on 12 life-history variables, the PCA using all available fish species (N = 64) yielded a PCA that modeled 67% of the total variation. The first axis of this PCA was also dominated by longevity (0.422), age at maturity (0.417), spawning bouts (−0.368), YOY growth (0.346), and mean clutch (0.339), and the second axis was dominated by hatch time (eigenvector = 0.529), egg size (0.509), and mean clutch (−0.340). When maximum length was partialled-out of 12 life-history variables of the all-species data set, the first three PC axes modeled 59% of the total variation. The first axis was dominated by hatch time (eigenvector = 0.439), egg size (0.434), mean clutch (−0.434), and adult growth rate (0.382), and the second axis of the PCA (12 variables with length partialled-out) was dominated by age at maturity (eigenvector = −0.441), longevity (−0.389), spawning bouts (0.359), and YOY growth rate (0.340).

When separate PCAs were performed on data sets that grouped species as either freshwater or marine (unadjusted for length), the variable loadings on the first three PC axes predicted suites of life-history characteristics very similar to those revealed by the combined species data sets. Each of four analyses (freshwater versus marine, 12 versus five life-history variables; based on unadjusted values) identified a continuum of

TABLE 3. Pearson product-moment correlations among five life-history variables by fish order. All variables were ln-transformed. $^{*}P < 0.05$; $^{**}P < 0.0001$; ×, no variation recorded in one variable.

Variable	Clutch size	Egg size	Spawn bouts	Parental care
Clupeiformes (N = 12)				
Length at maturity	0.87*	0.74*	−0.81*	0.54
Mean clutch size	—	0.41	−0.83*	0.50
Egg size	—	—	−0.45	0.26
Spawn bouts	—	—	—	−0.38
Cypriniformes (N = 27)				
Length at maturity	0.78**	0.71*	−0.54*	−0.35
Mean clutch size	—	0.55*	−0.65*	−0.54*
Egg size	—	—	−0.38	−0.10
Spawn bouts	—	—	—	0.36
Perciformes (N = 58)				
Length at maturity	0.88**	−0.18	−0.67**	−0.45*
Mean clutch size	—	−0.48*	−0.54**	−0.65**
Egg size	—	—	0.38*	0.59**
Spawn bouts	—	—	—	0.19
Pleuronectiformes (N = 11)				
Length at maturity	−0.08	−0.34	0.14	×
Mean clutch size	—	−0.27	−0.68*	×
Egg size	—	—	−0.24	×
Salmoniformes (N = 28)				
Length at maturity	0.28	0.71**	−0.31	−0.18
Mean clutch size	—	−0.24	−0.16	−0.44*
Egg size	—	—	−0.43*	0.07
Spawn bouts	—	—	—	−0.04
Siluriformes (N = 12)				
Length at maturity	0.78*	0.26	−0.67*	0.47
Mean clutch size	—	−0.46	−0.72*	0.19
Egg size	—	—	0.41	0.43
Spawn bouts	—	—	—	−0.28
Scorpaeniformes (n = 14)				
Length at maturity	0.57*	0.06	−0.29	0.11
Mean clutch size	—	−0.44	0.40	−0.19
Egg size	—	—	−0.01	0.05
Spawn bouts	—	—	—	−0.40

life-history strategies with large size at maturity (or late maturity), large clutches, few spawning bouts per year, and little parental care on one end and small size at maturity (or early maturity), small clutches, multiple spawning bouts, and more parental care on the other (Table 5). This continuum was associated with the first PC for the freshwater group (based on both 12 and five variables) and the marine group based on five variables, but was associated with the second PC for the marine group based on 12 life-history variables (Table 5). The separate freshwater and marine analyses each identified a second basic life-history continuum that revealed an association between smaller clutches, larger eggs, and more parental care. This axis was identified by the second PC in the freshwater group (both 12 and five variables) and the first PC (12 variables) and second PC (five variables) in the marine group (Table 5).

The ordination of species based on the first two axes of PCA (based on five life-history variables; unadjusted for length) shows a large range of life-history strategies for most orders within both the freshwater (Fig. 3) and marine (Fig. 4) groups. Relative to other freshwater fishes, lake sturgeon (*Acipenser fulvescens*) and paddlefish (*Polyodon spathula*) exhibit an extreme strategy (i.e. extreme positive values on abscissa in Fig. 3) in which age and size at maturation are large, eggs are numerous and small in relation to body size, and spawning is episodic and seasonal. Salmon and trout (*Oncorhynchus, Salmo, Salvelinus* spp.) display a variation of this strategy that involves smaller clutches and greater egg size in relation to body size. Cavefishes (Amblyopsidae) and madtom catfishes (*Noturus* spp.) exhibit a different strategy (upper left region in Fig. 3) that involves large egg size relative to body size and parental care (branchial brooding in cavefishes, nest guarding in certain madtoms). Certain species of darters (*Etheostoma, Percina* spp.) and minnows (Cyprinidae) exhibit a strategy of early maturation and multiple spawning of small clutches consisting of small eggs. A life-history strategy consisting of large maturation size and episodic or seasonal spawning of large clutches of small eggs (lower right region in Fig. 3) is displayed by a taxonomically diverse group of fishes, including the gizzard shad (*Dorosoma cepedianum*), muskellunge (*Esox masquinongy*), burbot (*Lota lota*), and suckers (*Catostomus, Moxostoma* spp.)

The pattern of ordination of marine fishes on the first two PCs (Fig. 4) followed a pattern very similar to that shown by freshwater fishes. Sturgeons again represented an extreme example of the delayed-maturation, large-clutch, periodic-spawning strategy that involves large eggs in absolute sense, but small eggs relative to body size (points on the right-hand half of Fig. 4). Again, salmon exhibited a strategy of low-frequency spawning but larger relative egg sizes and much smaller clutches. The large-clutch, episodic-spawning strategy involving small eggs can be seen in a phylogenetically diverse mixture of fishes, including the Atlantic cod, striped bass (*Morone saxatilis*), cobia (*Rachycentron canadum*), skipjack tuna (*Katsuwonus pelamis*), red snapper (*Lutjanus campechanus*), and winter founder (*Pleuronectes americanus*). Relatively few of the marine fishes fell within the region of large egg size and parental care (upper left region in Fig. 4), but an extreme form of this life-history strategy is seen in the mouthbrooding sea catfishes (*Arius felis, B. marinus*). The strategy of rapid maturation at small sizes and production of multiple small clutches of small eggs (lower left region in Fig. 4) is seen in the bay anchovy, mummichog (*Fundulus heteroclitus*), and inland silverside. Small fishes with parental care lie intermediate between the parental care strategy and early-maturation, multiple-clutch strategy and include the threespine stickleback, gulf pipefish (*Syngnathus scovelli*), and the blackbelly eelpout (*Lycodopsis pacifica*).

Phylogenetic and Ecological Correlates of Life-History Strategies

Mean values for most life-history parameters (length, longevity, clutch size, egg size, parental care, hatch time) varied considerably among fish orders (Table 1). Relative to other life-history variables, larval growth rates (12.0–19.5 mm/mo) and average fractional adult growth rate (proportion of adult TL gained per year = 0.13–0.25) showed the least variability among orders. Phylogenetic affiliations are also apparent in the general pattern of ordination of species within orders in the plots of species scores on the first two PC axes (Fig. 3, 4). Based on ANCOVA, statistically significant effects of phylogeny at the ordinal and family levels were obtained for 15 ln-

TABLE 4. PCA statistics for the North American fish data matrix based on five life-history variables and using all species ($N = 147$ species) and one representative per genus ($N = 83$ genera). Variable loadings (eigenvectors) on the first three principal axes that were between −0.250 and 0 are listed as −, and those between 0 and 0.250 are listed as +.

	All species			One species per genus		
	PC1		PC3	PC1	PC2	PC3
Eigenvalue						
% variance						
Variable						
Length at maturity	0.558	0.290	+	0.498	0.384	0.347
Mean clutch size	0.602	−	−	0.613	−	−
Egg size		0.706	0.561	−0.253	0.625	0.582
Spawning bouts	−0.372	−0.465	0.604	−	−0.601	0.652
Parental care	−0.425	0.419	−0.494	−0.507	0.318	−0.334

TABLE 5. PCA statistics for North American freshwater fish data matrices based on 12 and five ln-transformed life-history variables. Data on the left-hand side are for freshwater fishes, and data on the right-hand side are for marine fishes. Variable loadings (eigenvectors) on the first three principal axes that were between −0.250 and 0 are listed as −, and those between 0 and 0.250 are listed as +.

	PC1	PC2	PC3	PC1	PC2	PC3
		Freshwater species *N = 44*			*Marine species* *N = 20*	
Eigenvalue	4.898	2.059	1.061	3.979	3.450	1.873
% variance	40.8	17.2	8.8	33.2	28.7	15.6
Variable						
Age at maturity	0.372	+	+	−	0.504	−
Longevity	0.400	−	+	−	0.464	−
Mean clutch size	0.306	−0.397	−	−0.270	0.357	+
Egg size	+	0.531	+	0.426	+	−
Spawning season	−	−	+	−0.346	−0.274	+
Spawning bouts	−0.320	−	−	−	−0.431	−
Parental care	−	−	0.854	0.288	+	−0.402
Hatching time	+	0.580	−0.255	0.463	−	−
Larval growth	+	−0.389	−	−0.305	+	+
YOY growth	0.368	−	+	+	+	0.648
Adult growth	0.347	−	−	0.319	+	0.497
Fractional growth	−0.268	+	−	0.316	−	0.264
		Freshwater species *N = 82*			*Marine species* *N = 65*	
Eigenvalue	2.457	1.142	0.823	2.157	1.810	0.584
% variance	49.1	22.9	16.4	43.1	36.2	11.7
Variable						
Length at maturity	0.596	+	+	0.450	0.466	0.371
Mean clutch size	0.526	−0.361	−0.281	0.641	−	−
Egg size	0.267	0.696	0.551	−0.256	0.601	0.517
Spawning bouts	−0.421	−0.363	−0.511	−0.400	−0.460	0.516
Parental care	−0.345	0.502	−0.597	−0.401	0.449	−0.566

transformed life-history variables (Table 6). Except for the lack of a significant family effect on adult growth rate, significant effects for the nested ANCOVA type III sum of squares show that phylogenetic effects are present even after the influence of length (maximum TL) as a covariate and the effects of ordinal affiliations for families were removed (Table 6). Relationships between maximum length and three variables (range of egg size, hatching time, duration of spawning season) were not statistically significant within the total fish data set (Tables 2, 6).

Each of the four discriminant function analyses (CDF) resulted in a first canonical axis in which high values corresponded with larger size at maturity, larger clutches, longer life span, and faster growth (Fig. 5; Table 7). When migration was used as the class variable, the first axis was also associated with larger egg size. The second canonical axis was more discordant between tests involving different class variables (Table 7).

The CDF using habitat as the class variable (Fig. 5a) showed a general pattern of larger, longer-lived fishes with large clutches and short spawning seasons in association with the marine environment, estuaries, river backwaters, and lakes versus small fishes with small clutches, slow YOY growth, and long spawning seasons in association with headwater habitats. River fishes were intermediate between headwater and estuarine/marine fishes in the multivariate life-history space defined

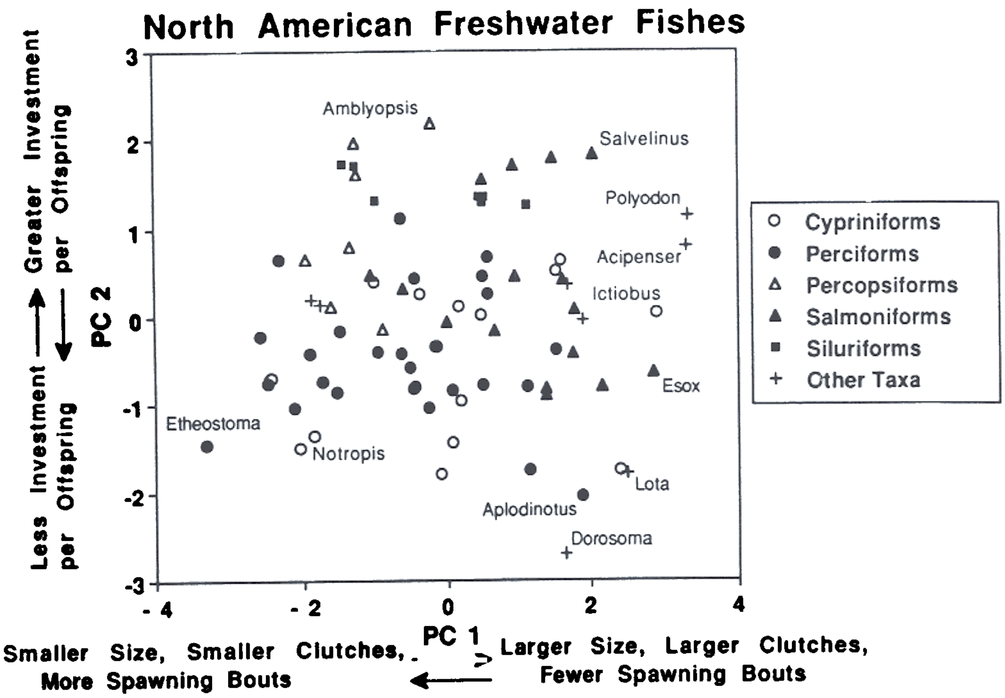

FIG. 3. Scores for freshwater fish species on the first two principle components axes based on five life-history variables (length at maturity, average clutch, egg size, bouts per year, parental care). The two axes are interpreted based on correlations of the original life-history variables (statistics associated with the PCA are given in Table 5).

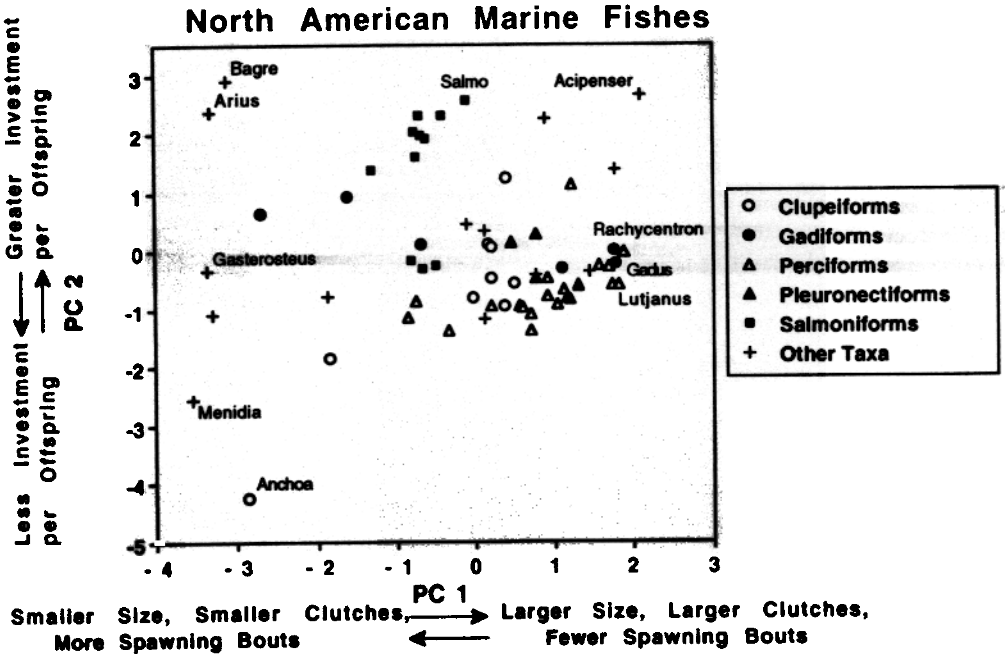

FIG. 4. Scores for marine fish species on the first two principle components axes based on five life-history variables (length at maturity, average clutch, egg size, bouts per year, parental care). The two axes are interpreted based on correlations of the original life-history variables (statistics associated with the PCA are given in Table 6).

by CDF. The CDF based on trophic status (Fig. 5b) showed a general pattern of larger, longer-lived fishes with large clutches, intermediate-sized eggs, and little parental care in association with piscivory versus small fishes with small clutches, slow YOY growth, larger eggs, and more parental care in association with feeding on invertebrates and omnivory. In addition, detritivores tended to be associated with small size, small clutches, small eggs, and little or no parental care (Fig. 5b).

Highly migratory fishes (Fig. 5c) were associated with large body size, long life spans, and large clutches. Catadromous fishes (represented by the American eel, *Anguilla rostrata*) exhibited a lower spawning frequency (i.e. one semelparous

Table 6. Results of nested ANCOVA for life-history variables (ln-transformed) with family nested within order and maximum total length as a covariate. Type I sum of squares (SS) are for main effects of variables without adjustment for size effects; Type III SS are for effects of family and order after adjustment for covariation due to size.

Variable		Type I SS		Type III SS		Model
		F	P	F	P	r^2
	Order	16.7	0.0001			
	Family (order)	4.0	0.0001			
	Max. length	110.0	0.0001			
Length at maturity	Order	32.7	0.0001	.5	0.082	0.91
	Family (order)	16.2	0.0001	.7	0.015	
	Max. length	317.4	0.0001			
Longevity	Order	14.3	0.0001	2.4	0.0013	0.81
	Family (order)	6.0	0.0001	2.3	0.0012	
	Max. length	91.9	0.0001			
Mean clutch size	Order	27.8	0.0001	7.8	0.0001	0.91
	Family (order)	19.6	0.0001	9.8	0.0001	
	Max. length	149.3	0.0001			
Maximum clutch	Order	26.5	0.0001	8.7	0.0001	0.92
	Family (order)	22.9	0.0001	10.7	0.0001	
	Max. length	171.3	0.0001			
Egg size	Order	14.9	0.0001	11.2	0.0001	0.80
	Family (order)	5.3	0.0001	5.1	0.0001	
	Max. length	8.5	0.0042			
Range egg size	Order	4.7	0.0001	5.4	0.0001	
	Family (order)	4.1	0.0001	4.0	0.0001	
	Max. length	3.8	0.055			
Spawning season	Order	5.5	0.0001	6.2	0.0001	
	Family (order)	2.5	0.0003	2.7	0.0001	
	Max. length	1.9	0.16			
Spawning bouts	Order	8.8	0.0001	5.9	0.0001	
	Family (order)	4.4	0.0001	2.8	0.0001	
	Max. length	36.2	0.0001			
Parental care	Order	12.2	0.001	9.5	0.0001	0.79
	Family (order)	8.7	0.0001	7.5	0.0001	
	Max. length	16.2	0.0001			
Hatching time	Order	14.6	0.0001	5.0	0.0001	
	Family (order)	9.5	0.0001	9.1	0.0001	
	Max. length	1.2	0.26			
Larval growth	Order	2.0	0.028	1.4	0.15	
	Family (order)	1.5	0.14	1.1	0.34	
	Max. length	4.3	0.042			
YOY growth	Order	10.4	0.0001	2.7	0.0006	
	Family (order)	7.2	0.0001	1.8	0.026	
	Max. length	36.7	0.0001			
Adult growth	Order	8.8	0.0001	2.7	0.0009	
	Family (order)	5.6	0.0001	1.3	0.18	
	Max. length	75.3	0.0001			
Fractional adult growth	Order	2.9	0.0005	2.1	0.013	0.46
	Family (order)	2.1	0.011	1.6	0.058	
	Max. length	6.3	0.013			

bout per 14 yr of adult life on average) and smaller egg size when compared with anadromous fishes (primarily salmon) with earlier maturation. Less-migratory fishes tended to be smaller with relatively smaller clutches and smaller eggs than migratory species; however, highly sedentary fishes tended to have longer spawning seasons and larger eggs than migratory fishes.

When CDF was performed with level of parental care as the class variable (none, placement of eggs into a special habitat, low guarding, high guarding/viviparity), fishes with highly developed parental care were associated with the small size, short life spans, small clutches, slow YOY and adult growth, and spawning seasons of intermediate length (Fig. 5d). Fishes with no parental care tended to be large with long lifespans,

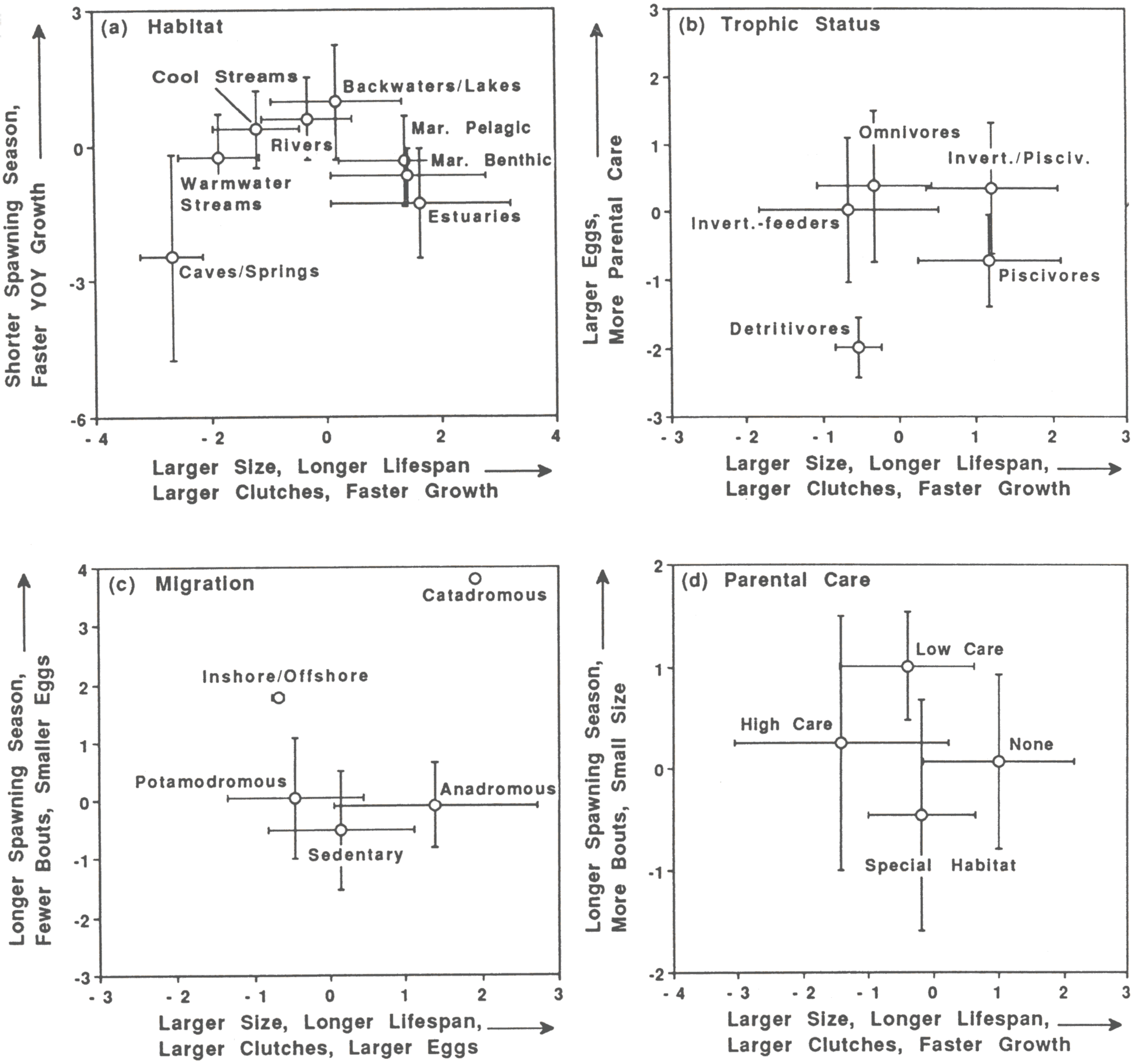

FIG. 5. Average species scores on the first two discriminant function axes by ecological and life-history groupings. Discriminant functions for a–c were based on nine life-history variables (length at maturity, average clutch, egg size, longevity, spawning season, bouts per year, YOY growth, adult growth, parental care), and plot d was based on eight variables with parental care as the grouping variable. The *x*-axis represents the first canonical axis, the *y*-axis is the second canonical axis, and verbal interpretations of axes are based on the eigenvectors of the original life-history variables. Statistics associated with each plot are summarized in Table 7.

large clutches, fast YOY and adult growth, and intermediate breeding seasons. Fishes exhibiting no parental care other than special placement of eggs (e.g. scattering over vegetation or gravel beds) tended to be smaller and less fecund with shorter spawning seasons than the group with no parental care. Fishes with low levels of parental care (e.g. brief period of nest guarding by the male) tended toward small body size, intermediate clutches, intermediate YOY growth rates, and longer spawning seasons involving multiple bouts.

Discussion

Life history trade-offs frequently are sought by means of bivariate regression analysis of attributes having a hypothesized functional relationship. For example, one way to achieve larger clutches is to partition reproductive biomass into smaller individual packages, which yields the negative correlation between clutch size and egg size frequently observed in fishes (Wootton 1984; Duarte and Alcarez 1989; Elgar 1990; Fleming and Gross 1990; Paine 1990). In the current study, egg size showed a significant, but weak, inverse relationship with clutch size when the comparison was based on the entire data set ($r = -0.29$, $P < 0.05$). This pattern is not due to a clutch size – body size interaction because many fishes (e.g. *B. marinus*) have much smaller clutches than species of much smaller body size (e.g. *Rhinichthys atratulus* (blacknose dace)). A negative relationship between clutch size and egg size was obtained for

TABLE 7. Statistics associated with canonical discriminant function analyses based on three ecological and one life-history classification variables: habitat, trophic status, migration, and parental care. P values for discriminant function axes represent the probability that canonical correlation for the axis and all that follow are zero (probability that Wilks' lambda $> F$); coefficients for variables are based on total canonical structure.

	Habitat		Trophic status		Migration		Parental care	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue								
Variance								
P								
Variable								
Length maturity	0.727	0.252	0.702	–	0.757	–	0.513	−0.743
Longevity	0.508	0.328	0.387	–	0.395	–	0.391	−0.537
Mean clutch	0.891	+	0.595	−0.347	0.447	0.265	0.770	−0.352
Egg size	–	0.285	0.232	0.655	0.419	−0.466	−0.386	−0.351
Spawn season	0.324	−0.677	–	–	−0.271	0.684	0.435	0.548
Spawn bouts	–	+	−0.260	–	−0.505	−0.464	+	0.477
Parental care	−0.692	–	+	0.525	+	+		
YOY growth	0.658	0.552	0.753	−0.335	0.326	–	0.623	−0.308
Adult growth	0.663	+	0.890	–	0.628	–	0.428	−0.551

perciforms, pleuronectiforms, salmoniforms, siluriforms, and scorpaeniforms, but the relationship was actually positive for clupeiforms and cypriniforms. Our data set, which involved a broader taxonomic and ecological survey than that used by Duarte and Alcarez (1989), indicates that larger clutches may indeed be produced by either delaying reproduction until achieving a large body size or packaging reproductive biomass into smaller eggs or both. However, not all of the narrower ecological or taxonomic groupings of fishes were consistent with these simple functional trade-offs. Simultaneous trade-offs with other life-history attributes can account for low correlations in instances in which strong functional relationships are hypothesized. Greater insights into the potential adaptive significance of individual attributes often can be gained by examining their interrelationships by multivariate methods. Much of the variance around a bivariate regression often can be explained by simultaneous trade-offs by one or both of the two life-history attributes with other attributes.

Life-History Patterns as Adaptive Strategies

Multivariate methods identified two general gradients of variation that were fairly consistent among the various subsets of life-history variables and species. In one form or another, a principal association was found between larger adult body size with delayed maturation, longer life span, larger clutches, smaller eggs, and fewer annual spawning bouts. In most data sets, a second orthogonal gradient contrasted fishes having more parental care, larger eggs, longer spawning seasons, and multiple bouts against fishes with the opposite suite of traits. When body length was partialled-out of the other life history traits, most of the strong associations were retained. When species are ordered simultaneously on the two primary gradients, three fairly distinctive life-history strategies are identified as the endpoints of a trilateral continuum (Fig. 3, 4). In most instances, the addition of a life-history gradient derived from a third or fourth axis produced little modification in the general pattern of species ordination derived from the first two principal axes.

The three primary strategies (i.e. endpoint strategies) of North American fishes have some striking similarities with earlier patterns presented in the empirical and theoretical life-history literature. We observed (1) species with delayed maturation, intermediate or large size at maturation, large clutches, small eggs, rapid larval and YOY growth rates, and short reproductive seasons, (2) species with early maturation, small size at maturation, small eggs, rapid larval growth, and long reproductive seasons with multiple spawning bouts, and (3) small- or medium-size species with large eggs, small clutches, well-developed parental care, slow YOY and adult growth, and long reproductive seasons. Freshwater fishes have a more restricted range of strategies within life-history space than marine fishes when the two groups are viewed jointly. When we plotted the first two PC coordinates of freshwater and marine fishes together (species loadings associated with Table 4), the orientation and shape of the scatterplot were very similar to Fig. 4, and each of the three endpoints was a marine representative (i.e. bay anchovy, gafftopsail catfish, Atlantic sturgeon).

We observe great consistency among the gradients of life-history variation here and among those derived from comparisons of commerical stocks of marine fishes (Kawasaki 1980, 1983), Pacific surfperches (Baltz 1984), neotropical freshwater fishes (Winemiller 1989), and North American darters (Paine 1990). Wootton (1984) clustered on Canadian freshwater fishes based on five variables reported in Scott and Crossman (1973). He discussed three prinicpal life-history groupings: (1) salmonid fishes with fall/winter spawning, large eggs, large body size, and low relative fecundity, (2) small species with low fecundities, short life spans, and spring/summer spawning, and (3) medium and large species with high fecundities, small eggs, and spring spawning. Based on fishes from a Canadian and a Polish river system, Mahon (1984) interpreted the pattern of species ordination on the first axes of PCA as a gradient of reproductive strategies correlated with a gradient of fluvial habitats (i.e. small, early-maturing, sedentary fishes with parental care and few large eggs in headwaters versus larger migratory fishes with the opposite suite of characteristics in large rivers). Mahon interpreted the second PC gradient as a trade-off between egg size and fecundity.

Given that populations exhibiting these divergent strategies are persistent, insights into population regulation can be gained by comparing suites of life-history traits in the context of adaptations for alternative environmental conditions (Southwood 1988). Next we discuss some hypothesized relationships between primary strategies, life-history trade-offs, and selection caused by different scales of environmental variation.

Periodic strategy

Following Winemiller's (1992) terminology, a "periodic" strategy identifies fishes that delay maturation in order to attain a size sufficient for production of a large clutch and adult survival during periods of suboptimal environmental conditions (e.g. winter, dry season, periods of reduced food availability). Species with large clutches frequently reproduce in synchronous episodes of spawning, and this trend yielded the negative association between clutch size and number of spawning bouts per year. This synchronous spawning often coincides either with movement into favorable habitats or with favorable periods within the temporal cycle of the environment (e.g. spring). Extreme forms of the high-fecundity strategy are often seen among marine species with pelagic eggs and larvae (e.g. cod, cobia, tuna, ocean sunfish). These marine species appear to cope with large-scale spatial heterogeneity of the marine pelagic environment by producing huge numbers of tiny offspring, at least some of which are bound to thrive once they encounter favorable areas or patches within zones and strata. Yet, on average, larval survivorship is extremely low among highly fecund fishes in the marine environment (Houde 1987). Miller et al. (1988) argued that the average larval fish dies during the first week of life, and greater understanding of recruitment may be achieved by seeking greater understanding of the unique features of survivors. Within a local population, some spawners probably contribute disproportionately large numbers of survivors to subsequent generations (relative to conspecifics with similar clutch sizes) based on purely stochastic aspects of larval movement into favorable zones. Despite the fact that egg size tends to be small in periodic fishes, both larval and YOY growth rates tended to be relatively fast. We presume that these fast growth rates for early life stages reflect assimilation from exogeneous feeding by the early survivors that encounter relatively high prey densities. This is consistent with Houde's (1989) assumption that higher growth rates for marine fish larvae at higher temperatures are supported by increased food consumption rather than increased growth efficiency.

At temperate latitudes, large-scale temporal variation in environmental conditions may be as influential as spatial variation on the timing of reproduction. Temporal variation at high latitudes is large and cyclic, hence to some extent predictable. In theory, highly fecund fishes can exploit predictable patterns in time or space by releasing massive numbers of small progeny in phase with periods in which environmental conditions are most favorable for larval growth and survival (Cohen 1967; Boyce 1979). Natural selection should strongly favor physiological mechanisms that enhance a fish's ability to detect cues that predict the moment of a periodic cycle (e.g. photoperiod, ambient temperature, solute concentrations). In the marine pelagic environemnt at low latitudes, large-scale variation in space may represent a periodic signal as strong as seasonal variation at temperate latitudes (i.e. patchily distributed physical parameters, primary production, zooplankton, etc., due to upwellings, gyres, convergence zones, and other predictable currents; Sinclair 1988; MacCall 1990).

Periodic strategists are among the most migratory of North American fishes, an association also revealed by Roff's (1988) analysis of marine fishes and observed among South American freshwater fishes (Winemiller 1989). In California, anadromous threespine stickleback were more periodic in their characteristics (e.g. large clutches, larger size at maturity) when compared with freshwater populations (Snyder 1990). Migration to favorable habitats for spawning is a means by which fishes can reduce uncertainty in their attempts to exploit large-scale temporal and spatial environmental variation. For example, American shad (*Alosa sapidissima*) are more iteroparous and devote a greater fraction of energy to migration at middle and higher latitudes where environments are less stable and less predictable (Leggett and Carscadden 1978). Rothschild and DiNardo (1987) viewed anadromy as a means by which adults seek favorable environments for larval development whereas the reproductive success of marine broadcast spawners may depend on rates of encounters by larvae with suitable zones or patches. Massive clutches of small eggs undoubtedly enhance dispersal capabilities of wide-ranging marine fishes during the early life stages. In a stable population, losses due to advection ultimately are balanced by the survival benefits derived from the passage of some fraction of larval cohorts into suitable regions or habitats (Sinclair 1988).

Opportunistic strategy

The "opportunistic" life-history strategy in fishes appears to place a premium on early maturation, frequent reproduction over an extended spawning season, rapid larval growth, and rapid population turnover rates, all leading to a large intrinsic rate of population increase (Winemiller 1989, 1992). Opportunistic fishes differ markedly from the *r*-strategists of Pianka (1970) and others in having among the smallest rather than largest clutches. The strong inverse relationship between the rate of population growth and generation time has been appreciated for a long time (Birch 1948; Smith 1954; Lewontin 1965; Pianka 1970; Michod 1979). Small fishes with early maturation, small eggs, small clutches (yet high relative reproductive effort), and continuous spawning are well equipped to repopulate habitats following disturbances or in the face of continuous high mortality in the adult stage (Lewontin 1965). This suite of life-history traits permits efficient recolonization of habitats over relatively small spatial scales. Extreme examples of the opportunistic strategy are seen in the bay anchovy, silversides, killifishes (*Fundulus* spp.), and mosquitofishes (*Gambusia* spp). These small fishes frequently maintain dense populations in marginal habitats (e.g. ecotones, constantly changing habitats) and frequently experience high predation mortality during the adult stage.

Equilibrium strategy

The "equilibrium" strategy in fishes is largely consistent with the suite of characteristics often associated with the traditional *K*-strategy of adaptation to life in resource-limited or density-dependent environments (Pianka 1970). Large eggs and parental care result in the production of relatively small clutches of larger or more advanced juveniles at the onset of independent life. Our equilibrium strategy differs from the traditional *K*-strategy model in that equilibrium strategists tended to rank among the smallest fishes rather than largest (the largest North American fishes were periodic strategists). Within the North American fish data set, marine ariid catfishes (egg diameters 16.0–20.5 mm, oral brooding of eggs and larvae) and amblyopsid cavefishes (branchial brooding of small clutches of relatively large eggs) represent extreme forms of the equilibrium life-history strategy. Cavefishes probably inhabit the most temporally stable and resource limited of the aquatic environments covered in our survey.

Intermediate strategies

Three endpoint life-history strategies are fairly distinctive, but intermediate strategies are also recognized near the center and along the boundaries of a trilateral gradient. Some of the largest periodic strategists (e.g. lake sturgeon, paddlefish) have relatively large eggs, which compromises the attainment of a theoretical maximum clutch size. Salmon and trout possess much larger eggs and smaller clutches than fishes exhibiting the extreme periodic life-history configuration. An inverse relationship between egg size and clutch size was found within the salmoniforms (Table 3). Among populations of coho salmon (*Oncorhynchus kisutch*), this inverse relationship is observed over a latitudinal gradient of declining egg size and increasing clutch size with increasing latitude (Fleming and Gross 1990). Fleming and Gross suggested that selection favors local optima in egg size with clutch size adjustments resulting from physiological constraints and ecological performance. Relative to periodic strategists with larger clutches and smaller eggs, salmon and trout appear to have adopted a more equilibrium strategy of larger investment in fewer offspring and larger offspring at the time of independent life. Migration to special spawning habitats and burial of zygotes (brood hiding) by salmon, char, and trout could be viewed as forms of parental investment that carry large energetic and survival costs in relation to future reproductive effort.

A number of medium-size fishes have seasonal spawning, moderately large clutches, and male nest guarding (e.g. *Ameiurus* spp., *Lepomis* spp.). Another intermediate group has large clutches, small eggs, and viviparity (e.g. *Sebastes* spp.). These fishes are in between the periodic and equilibrium endpoints of the gradient. Small fishes with rapid maturation, small clutches, large eggs relative to body size, and a degree of parental care (e.g. *Pimephales* spp., *Noturus* spp., *Etheostoma* spp., *G. aculeatus*, *S. scovelli*, *Cottus* spp.) lie between the opportunistic and equilibrium strategists. Similarly, small fishes with seasonal spawning, moderately large clutches, small eggs, and only one or a few bouts of reproduction per season (e.g. *Osmerus mordax* (rainbow smelt), *Notemigonus crysoleucas* (golden shiner), *Notropis* spp., *Percopsis omiscomaycus* (trout-perch) lie between the opportunistic and periodic strategists on the gradient. Determinations of multiple spawning in fishes have been difficult (Heins and Rabito 1986; Heins and Baker 1988), and we suspect that some of the small North American fishes categorized as single spawners (and some species conservatively coded as two bouts per year here) may actually spawn several times each season. With improved estimates of multiple spawning, some of the small fishes intermediate between opportunistic and periodic strategists may actually cluster nearer the opportunistic endpoint.

Life-History Strategies and Population Regulation

Life-history theory attempts to explain patterns of covariation in demographic parameters and reproductive traits in relation to alternative environmental conditions (Lack 1954; Stearns 1976; Whittaker and Goodman 1979; Southwood 1988). For example, Murphy (1968) and Kawasaki (1980, 1983) each concluded that delayed maturation, iteroparity, and high fecundity increase the probability of recruitment to the adult population in the face of variable preadult mortality in marine environments. Armstrong and Shelton (1990) used a Monte Carlo model to show that within-season serial spawning reduces variation in clupeoid brood strength when within-season variation is large. Several other studies have explored the potential influence of alternative life-history strategies on fish population responses to both natural and anthropogenic disturbances (Adams 1980; Saunders and Finn 1983; Garrod and Horwood 1984; Ware 1984; Rago and Goodyear 1987; Schaaf et al. 1987; Barnthouse et al. 1990; Beverton 1990; Leaman 1991).

Following Winemiller (1992), we propose that the essential features of the three primary life-history strategies can be captured by the interrelationships among three basic demographic parameters: survival, fecundity, and onset and duration of reproductive life. In terms of life-history strategies, fitness can be estimated by either V_x, the reproductive value of an individual or age class (Fischer 1958; Pianka 1976; Leaman 1991), or r, the intrinsic rate of natural increase of a population or genotype (Birch 1948; Cole 1954; Southwood et al. 1974; Roff 1984; Stearns and Crandall 1984), or λ, the finite rate of growth from the Euler equation (and see Ware (1982, 1984) for discussions of surplus power as a measure of fitness). Each of these fitness measures can be expressed as a function of three essential components: survivorship, fecundity, and the onset and duration of reproductive life. In the case of reproductive value:

$$(2)\quad V_x = m_x + \sum_{t=x+1}^{\omega} \frac{l_t m_t}{l_x}$$

where for a stable population, m_x is age-specific fecundity, l_x is age-specific survivorship, and ω is the last age class of active reproduction. In this form of the equation, two components of reproductive value are added together: the current investment in offspring (m_x) and the expectation of future offspring (residual reproductive value). Reproductive value is therefore equivalent to the lifetime expectation of offspring (i.e. provided that x is equal to α, the age at first reproduction) and contains survivorship, fecundity, and timing components.

The intrinsic rate of population increase can be approximated as

$$(3)\quad r \simeq \frac{\ln R_0}{T}$$

where R_0 is the net replacement rate, T is the mean generation time ($T \simeq \sum_{x=\alpha}^{\omega} x\, l_x\, m_x$), and

$$(4)\quad R_0 = \Sigma\, l_x\, m_x$$

$$(5)\quad r \simeq \frac{\ln (\Sigma\, l_x\, m_x)}{T}.$$

The finite rate of growth (λ) is computed from the intrinsic rate of increase using $\lambda = e^{r\Delta t}$, where Δt is the time interval over which population change is measured. Therefore, the relative rate of population increase (or relative reproductive success among genotypes within a population) is directly dependent on fecundity, timing of reproduction, and survivorship during both the immature and adult stages (Lewontin 1965; Southwood et al. 1974; Southwood 1988; Itô 1978; Kawasaki 1980; Roff 1984; Taylor and Williams 1984; Sutherland et al. 1986; Winemiller 1992). Over long time periods and on average, the three parameters (l_x, m_x, T) must balance or the population declines to extinction or grows to precariously high densities and crashes.

Three primary life-history strategies result from trade-offs among age at maturation (α positively correlated with T), fecundity, and survivorship and are illustrated as the endpoints of a trilateral surface in Fig. 6. Here, we choose to focus attention on juvenile survivorship, the fraction of individuals surviving from the zygote stage until first reproduction. Plotting demographic trade-offs in relation to juvenile survivorship (l_α) results in separation of the equilibrium strategy of higher juvenile survivorship from the opportunistic and periodic strategies, whereas an axis of adult survivorship (the mean expectation of future life, $\hat{E}_x$, for all adult age classes, $x = a$ to ω, where $E_x = [\Sigma l_y]/l_x$ for $y = x$ to ω) would separate the opportunistic strategy

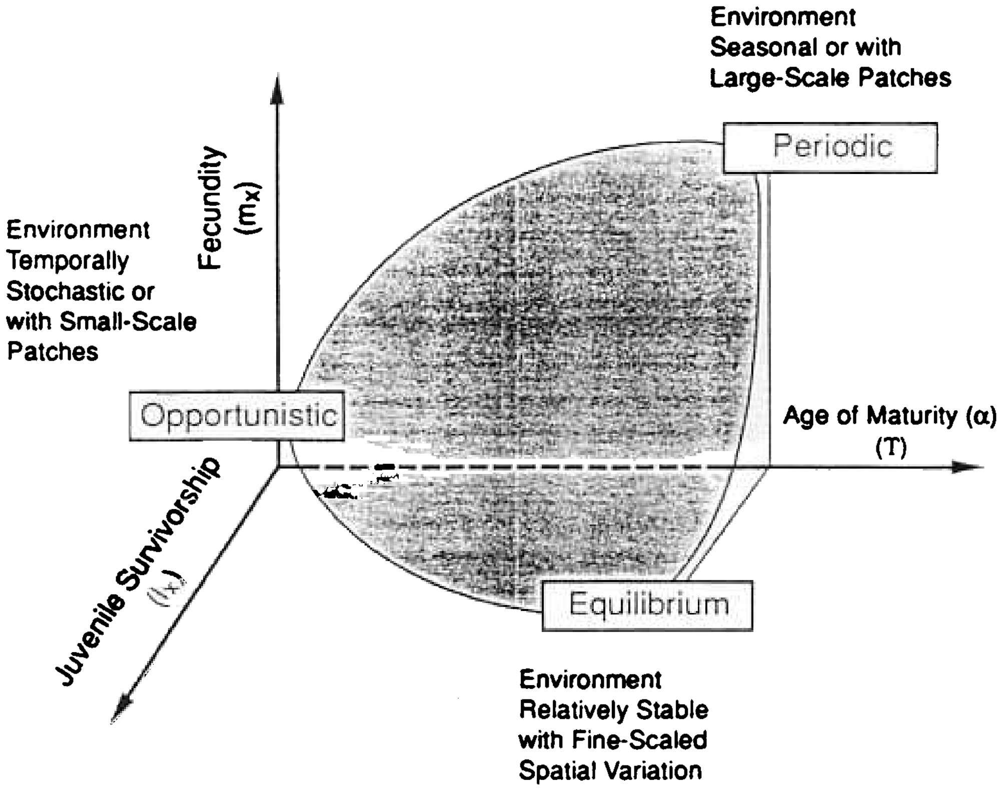

FIG. 6. Model for an adaptive surface of fish life-history strategies based on fundamental demographic trade-offs and selection in response to different kinds of environmental variation. The opportunistic strategy (small T, small m_x, small l_x) maximizes colonizing capability in environments that change frequently or stochastically on relatively small temporal and spatial scales. The periodic strategy (large m_x, large T, small l_x) is favored in environments having large-scale cyclic or spatial variation. The equilibrium strategy (large l_x, large T, small m_x) is favored in environments with low variation in habitat quality and strong direct and indirect biotic interactions. Curvilinear edges of the surface portray diminishing returns in the theoretical upper limits of bivariate relationships between adult body size and clutch size, adult body size and parental investment/offspring (a correlate of juvenile l_x), and clutch size and juvenile survivorship.

of low adult survivorship from the other two strategies. The suites of traits predicted by this adaptive surface appear similar to those described in the trichotomous comparative frameworks proposed for plants (Grime 1977, 1979) and other animal groups (Walters 1975; Allan 1976; Greenslade 1983). Our periodic strategy corresponds to high values on both the fecundity and age at maturity axes (the latter a correlate of population turnover rate) and a low value on the juvenile survivorship axis. Our opportunistic strategy (optimization of population turnover rate via a reduction in developmental time) corresponds to low values on all three axes. The equilibrium strategy is defined by low values on the fecundity axis and high values on the age at maturity and juvenile survivorship axes.

Figures 7 (freshwater) and 8 (marine) plot the positions of North American fishes in relation to three life-history variables used as surrogates (strong correlates) for the demographic axes in the trilateral gradient life-history model. Because data on size at maturation were available for more species, and size and age at maturation are highly correlated ($r = 0.77$), we used ln maturation size as a surrogate for age at maturation (x-axis). We used ln mean clutch size for fecundity (y-axis) and investment per progeny (calculated as the sum of ln parental care value and ln egg diameter) to reflect differences in the probability of juvenile survivorship (z-axis). The basic form of each empirical plot conforms well with the triangular surface predicted by the demographic model of primary life-history strategies (Fig. 6). Figures 7 and 8 strongly imply that natural selection eliminates certain combinations of life-history traits, such as late maturation/small clutches/small investment per offspring. Other combinations of life history traits, such as the "Darwinian superorganism" (early maturation/large clutches/large investment per offspring/long life span), are prohibited by direct physical and physiological constraints.

Response of the periodic strategy

The periodic strategy maximizes age-specific fecundity (clutch size) at the expense of optimizing turnover time (turnover times are lengthened by delayed maturation) and juvenile survivorship (maximum fecundities are attained by producing smaller eggs and larvae). Several theoretical models predict maximization of fecundity in response to predictable (= seasonal) environmental variation (Cohen 1967; Boyce 1979). If conditions favorable for growth and survival of immatures are periodic and occur at frequencies smaller than the normal life span (Southwood 1977), selection will favor the strategy of synchronous reproduction in phase with the periodicity of optimal conditions and production of large numbers of small offspring that require little or no parental care. In effect, the periodic strategy represents an iteroparous "bet-hedging tactic" on a scale of interannual variation.

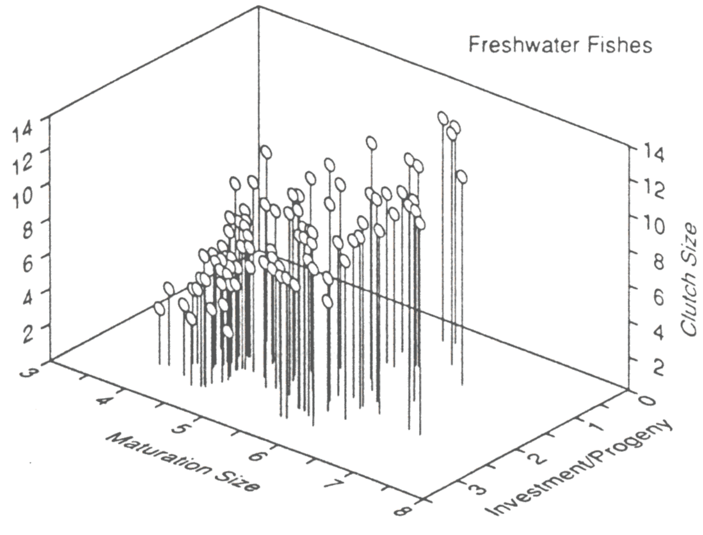

FIG. 7. Three-dimensional plot of ln maturation length (correlate of age at maturity), ln mean clutch size (fecundity), and relative investment per progeny (a surrogate for juvenile survivorship that was equal to ln ((egg diameter + 1) (parental care + 1))) for 88 freshwater fishes. The three axes permit visualization of the basic pattern of life-history variation in relation to demographic trade-offs and strategies (Fig. 6).

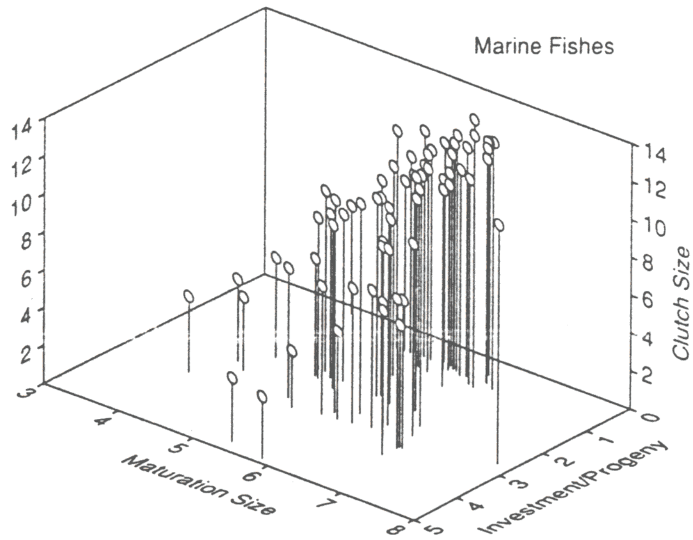

FIG. 8. Three-dimensional plot of ln maturation length, ln mean clutch, and investment per progeny for 68 marine fishes. The life-history pattern generated by marine fishes is similar to that shown by freshwater fishes (Fig. 7) and reflects essential demographic trade-offs and strategies illustrated in Figure 6.

According to this model, large body size enhances adult survivorship during suboptimal conditions and permits storage of energy and nutrients for future bouts of reproduction. The periodic production of offspring allows the organism to repeatedly sample the environment (for most perennial species, this occurs only on an annual basis) until, sooner or later, reproduction coincides with favorable conditions and the fitness payoff is collected (Murphy 1968; Armstrong and Shelton 1990). All environments exhibit either spatial or temporal variation that is to some degree predictable. This must be especially true in both freshwater and marine environments because the periodic strategy of large clutch sizes is predominant among bony fishes in both temperate and tropical settings. At arctic and temperate latitudes, the seasonal cycle appears to have selected for fish life-history cycles calibrated to annual periodicity. In marine pelagic environments, large-scale spatial patchiness of both larval food resources and predation mortality have been estimated by a variety of means (e.g. Sherman et al. 1984; McGurk 1986; Smith et al. 1989; Fortier and Gagné 1990; Brander and Hurley 1992). Large variation in the recruitment of annual cohorts appears to be the rule among periodic fishes in both marine and freshwater habitats, and the effects of climate on the distribution of larval food and predators have been implicated as principal determinants of both spatial and temporal variance in larval growth and survival (Sissenwine 1984; Fletcher and Deriso 1988; Shepherd and Cushing 1990). Variability in recruitment of several marine fishes was shown to be greater in populations closer to the latitudinal extremes of species' ranges (Myers 1992). Based on 21 marine fishes, Pepin and Myers (1991) found correlations between recruitment variability and both change in body length and duration of the larval stage. This finding is consistent with our view that the periodic strategy results in rapid growth and enhanced survival in a small fraction of initial larvae that somehow encounter zones or time periods in which food resources are abundant.

Response of the opportunistic strategy

As stated earlier, the opportunistic life-history configuration maximizes the intrinsic rate of population growth (r) through a reduction in the mean generation time (T). This reduction in T is achieved via early maturation, which in turn diminishes the capability to produce large clutches and large eggs. Owing to their small size, the relative reproductive effort of opportunistic strategists is continuously high, despite the fact that absolute clutch size and egg size are small. The production of multiple batches sometimes results in annual fecundities (mass) that greatly exceed female body mass in these small species (Wootton 1973; Hubbs 1976; Burt et al. 1988). We noted a tendency toward larger eggs and parental care in some small benthic fishes, within both freshwater and marine environments. As Mahon (1984) suggested, increasing juvenile survivorship by means of parental care may be a more viable tactic than increasing fecundity or egg size, given the material constraints imposed by small body size in these fishes. Of course, this view implies that other ecological factors (e.g. adult feeding ecology or microhabitat requirements) constrain the evolution of larger body size.

Birch (1948) was among the first to stress the strong negative correlation between population turnover time (strongly correlated with α and T) and the potential for rapid population growth in density-independent settings (high r). The advantages of early maturation for the achievement of a rapid population growth rate, and hence colonizing ability, were clearly demonstrated by Lewontin (1965), Taylor and Williams (1983), and Sibly and Calow (1986) among others. In effect, the opportunistic life history can be viewed as a sort of null life-history strategy that is favored in density-independent settings or environments that vary unpredictably on small scales of space and time. Fishes exhibiting the opportunistic strategy seem to be associated with very shallow marginal habitats: killifishes on the fringes of salt marshes and mosquitofishes in small headwater tributaries, pool edges, or swamp fringes. These shallow edge habitats (terrestrial/aquatic ecotones) are the kinds of environments that experience the largest and most unpredictable spatial and temporal changes on scales measured in days or hours. Changes in precipitation and temperature induce major alterations in water depth, substrate characteristics, and productivity in shallow aquatic habitats. The opportunistic suite of life-history charcteristics allows fishes to rebound from local disturbances in the absence of intense predation and resource limitation.

The opportunistic strategy of repeated local recolonizations through continual and rapid population turnover is well exemplified in the bay anchovy and marsh-dwelling killifishes like the mummichog. Over much of its range, the bay anchovy ranks among the most numerically dominant fishes (Morton 1989). Bay anchovies are also one of the principal food resources for a variety of fishes, birds, and invertebrates. We postulate that early maturation and frequent spawning permit the bay anchovy to sustain large numbers in regions where local subpopulations are continually cropped by predators. For bay anchovy, silversides, and other small pelagic fishes, predation pressure may partially override the signal from environmental seasonality. The opportunistic strategy appears to be more common in tropical freshwaters than in the temperate zone (Burt et al. 1988; Winemiller 1989).

Response of the equilibrium strategy

Following the basic premise of the *K*-selection theory of life histories (Pianka 1970), we postulated that the equilibrium strategy in fishes optimizes juvenile survivorship by apportioning a greater amount of material into each individual egg and/or the provision of parental care. Trade-offs between body size, egg size,and clutch size in fishes are probably inherent in the requirement for an adult body size sufficient to permit successful implementation of parental care behavior (e.g. nest defense, brooding, and gestation until larvae or embryos have attained sufficient size to escape predation or to forage efficiently). The tactic of providing parental care for a small number of offspring is of no advantage in highly seasonal habitats or environments dominated by strong density-independent selection. We believe that the equilibrium configuration of life-history traits is best understood in relation to the traditional model of density dependence and resource limitation (e.g. Pianka 1970; Roughgarden 1971; Goodman 1974). For example, some stream-dwelling darters and madtoms may experience resource limitation within shallow riffle microhabitats during periods of reduced stream flow. Microhabitats that provide refuge from predators could also be considered a resource that is either limiting or causes fishes to compete for depleted food supplies on the margins of the refuge (Fraser and Cerri 1982). In the marine environment, parental care appears to be most frequently associated with small benthic fishes (e.g. pipefishes, seahorses, some gobies, eelpouts). Among North American fishes, parental care was positively correlated with median latitude, but this trend was due to a major influence of high-fecundity marine fishes with pelagic larvae from low latitudes. Small benthic marine fishes were not well represented in the data set, and the relationship between parental care and latitude is inverse among freshwater fishes ($r = -0.36, P < 0.0001$). On a global basis, parental care appears to be most advanced and common within tropical ichthyofaunas in both freshwater (Winemiller 1989) and shallow, marine benthic environments (e.g. coral reefs; Miller 1979).

Salmon and trout life histories seem to represent variations of the equilibrium strategy that involve anadromous spawning migrations, egg hiding, and slow larval development rates rather than parental care in the traditional sense of nest guarding or brooding. The growing season at northern latitudes may be so short that large fishes are prohibited from adopting a brood guarding tactic in oligotrophic systems. Data on Arctic char (*Salvelinus alpinus*) indicated that the growing season at high latitudes probably constrains age at maturity and the frequency of spawning (Dutil 1986). Senescence associated with semelparity in Pacific salmon might have evolved as a consequence of the survival cost of returning to the sea after energetically costly upstream runs to fluvial habitats that enhance larval survivorship. By comparison, freshwater whitefishes (*Coregonus, Prosopium*) exhibit a perennial periodic strategy that involves large clutches, small eggs, and annual spawning bouts (Hutchings and Morris 1985).

Phylogenetic Trends

All life-history variables used in this study showed highly significant effects of phylogeny (Table 6). Yet, overall, the pattern of basic life-history strategies was highly repeatable within data sets containing different life-history traits and species. The high concordance between patterns revealed within this comparative study and others offers evidence that essential trade-offs produce numerous convergences in life-history strategies. For example, mouth brooding has evolved in numerous widely divergent equilibrium-type fishes worldwide (e.g. Osteoglossidae, Ariidae, Cichlidae), and miniature, multiple-clutching opportunistic-type fishes are found within many large families, especially in shallow environments in the tropics (e.g. Characidae, Cyprinidae, Cyprinodontidae, Gobiidae). Formal phylogentic studies of life-history evolution would contribute immensely to our understanding of the scenarios favoring the evolution of specific life-history strategies (Gotelli and Pyron 1991).

The restriction of some phylogenetic clades to subregions of life-history space results from historical events shaping evolution, morphological and physiological design constraints, and the interaction of these with contemporary ecology. Despite the reality of phylogentic constraints, wide divergence within several higher taxa is apparent in plots of species scores in relation to the life-history continua that were reflected in the principal axes from PCA (Fig. 3, 4). Perciforms are a widely divergent group, particularly within the freshwater data set. Cypriniforms exhibit a wide range of strategies primarily along an axis linking the periodic and opportunistic endpoints. Salmoniforms show a range of strategies along an axis between a periodic strategy and an intermediate strategy located midway between the equilibrium and periodic extremes. In the marine group, clupeiforms span an axis between opportunistic and periodic strategies, and gadiforms span an axis between the periodic and equilibrium strategy endpoints. Several other orders show much greater restrictions in their ranges of life-history strategies (e.g. percopsiforms tended to be equilibrium strategists, acipenseriforms and pleuronectiforms were relative periodic strategists).

Life-History Strategies and Fisheries Management

Life-history theory can provide some general insights into where attention might be most profitably focused in monitoring and research (Adams 1980; Garrod and Horwood 1984; Ware 1984; Schaaf et al. 1987; Barnthouse et al. 1990; Leaman 1991). For example, the periodic strategy is designed to exploit differences in environmental quality on temporal and spatial scales that are relatively large and to some degree regular or predictable. We have noted that the periodic strategy is predominant among commercial fish stocks worldwide. At arctic and temperate latitudes where spawning is largely annual and synchronous, generations are often recognizable as fairly discrete age cohorts. Correlations between parental stock densities and densities of YOY recruits are frequently weak or negligible in periodic strategists (Garrod 1983; Fletcher and Deriso 1988; Shepherd and Cushing 1990). Consequently, fisheries projections rely on juvenile cohort estimates as short-term forecasters of catchable stocks.

We view the periodic strategy as the perennial tactic of spreading reproductive effort over many years (or over a large area), so that high larval/juvenile survivorship during one year (or in one spatial zone) compensates for the many bad years (or zones). For example, anadromous female striped bass live up to 17 yr on average and produce an average clutch of 4 × 10^6 eggs every year or two, which translates to an egg to maturation survivorship of roughly 3 × 10^{-8} to maintain an equilibrium population. We speculate that most years probably result in a larval survivorship approaching zero for most females. From the standpoint of an individual female, it is likely that the fitness payoff only comes during one or two spawning acts over the course of a normal life span. These extremely low expectations for larval survivorship are far smaller than measurement errors involved with field estimates of mortality. In species like striped bass, the variance in larval survivorship that serves as input for population projections lies well beyond our ability to measure differences in the field (Koslow 1992). The maintenance of some critical density of adult stocks and the protection of spawners and spawning habitats during the short reproductive period should be crucial in the management of long-lived periodic fishes. If most larvae never recruit into the adult population even under pristine conditions, it follows that spawning must proceed unimpeded each year in fairly undegraded habitats if a fitness payoff is to be collected during the exceptional year.

Because they tend to be small and occur in shallow shoreline habitats, opportunistic strategists are not usually exploited commercially. Some species intermediate between opportunistic and periodic are very important commercial stocks (e.g. gulf menhaden (*Brevoortia patronus*)). Yet, opportunistic species are often the most important food resources for larger piscivorous species. By virtue of their small size and rapid turnover rates, these species should be efficient colonizers of frequently disturbed habitats like intermittent streams and salt marshes. Some opportunistic strategists, like the bay anchovy and silversides, inhabit more stable habitats and sustain dense populations in the face of intense predation. Given the innate ability of opportunistic strategists to sustain losses during all stages of life spans that are typically rather short, one of the keys to their management might be protection from large-scale or chronic perturbations that eliminate key refugia in space or time. Obviously, what may be perceived by humans to be a minor disturbance (e.g. a few degrees centigrade, or a few parts per thousand salinity) might pose a major impact from the perspective of a small fish that must maintain high reproductive output over a short life span.

Because equilibrium strategists produce small numbers of offspring, larval and juvenile survivorship must be comparatively high if these populations are to maintain themselves around some average density. Parental care is often well developed in equilibrium strategists, so that survivorship of eggs and larvae is dependent on the condition of adults and the integrity of the adult habitat (e.g. threatened cavefishes and some species of darters and madtoms). These fishes ought to conform to stock–recruit fishery models to a greater extent than periodic and opportunistic strategists (and see Koslow (1992) for a discussion of the effect of fecundity on the stock–recruit relationship). Yet, relatively few equilibrium strategists are commercially exploited in North American marine and freshwaters. Several species exploited by sport fisheries exhibit brood guarding and appear to be intermediate between equilibrium and periodic strategies, including lingcod (*Ophiodon elongatus*) and the black basses (*Micropterus* spp.). In general terms, management of these larger equilibrium-type species should be aimed at maintenance of a productive environment that promotes surplus yields (which can be harvested and replaced via compensation) and the maintenance of healthy adult stocks. We suggested that anadromous salmonids could represent a variation on the equilibrium strategy, in which parental investment in the form of costly migrations to oligotrophic habitats take the place of guarding, brooding, or bearing. Following this view, degradation of spawning habitats or impedement of access to spawning sites would have the same net impact as removing nest-guarding or brooding adults during the spawning season.

Finally, we point out that a variety of fishes with divergent life-history strategies frequently coexist in the same habitats. The feeding niche probably determines a large proportion of the total environmental variance experienced by an organism. Inherited design constraints, including the morphological features required for trophic function in particular microhabitats, place restrictions on the evolution of life-history features. A diversity of life-history strategies are consequently observed among species that perceive the same environment very differently from another. As a consequence, management efforts designed to abate a problem for a given species may sometimes have unanticipated effects on sympatric species that exhibit alternative strategies.

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Appendix: List of Fishes Used in Statistical Analyses

Freshwater

Lake sturgeon, *Acipenser fulvescens*; paddlefish, *Polyodon spathula*; longnose gar, *Lepisosteus osseus*; bowfin, *Amia calva*; goldeye, *Hiodon alosoides*; gizzard shad, *Dorosoma cepedianum*; threadfin shad, *Dorosoma petenense*; cisco/lake herring, *Coregonus artedi*; lake whitefish, *Coregonus clupeaformis*; bloater, *Coregonus hoyi*; sockeye salmon, *Oncorhynchus nerka kennerlyi*; round whitefish, *Prosopium cylindraceum*; mountain whitefish, *Prosopium willamsoni*; brook trout,[3] *Salvelinus fontinalis*; lake trout,[3] *Salvelinus namaycush*; Arctic grayling, *Thymallus arcticus*; Alaska blackfish, *Dallia pectoralis*; central mudminnow, *Umbra limi*; redfin pickerel, *Esox americanus americanus*; northern pike, *Esox lucius*; muskellunge, *Esox masquinongy*; chain pickerel, *Esox niger*; central stoneroller, *Campostoma anomalum*; redside dace, *Clinostomus elongatus; spotfin shiner*, *Cyprinella spiloptera*; Utah chub, *Gila atraria*; Mississippi silvery minnow, *Hybognathus nuchalis*; hornyhead chub, *Nocomis biguttataus*; golden shiner, *Notemigonus crysoleucas*; emerald shiner, *Notropis atherinoides*; spottail shiner, *Notropis hudsonius*; rosyface shiner, *Notropis rubellus*; sand shiner, *Notropis stramineus*; redfin shiner, *Lythrurus umbratilis*; bluntnose minnow, *Pimephales notatus*; fathead minnow, *Pimephales promelas*; northern squawfish, *Ptychocheilus oregonensis*; blacknose dace, *Rhinichthys atratulus*; longnose dace, *Rhinichthys cataractae*; redside shiner, *Richardsonius balteatus*; creek chub, *Semotilus atromaculatus*; river carpsucker, *Carpoides carpio*; longnose sucker, *Catotstomus catostomus*; white sucker, *Catostomus commersoni*; mountain sucker, *Catostomus platyrhynchus*; lake chubsucker, *Erimyzon sucetta*; smallmouth buffalo, *Ictiobus bubalus*; bigmouth buffalo, *Ictiobus cyprinellus*; silver redhorse, *Moxostoma anisurum*; black redhorse, *Moxostoma duquesnei*; golden redhorse, *Moxostoma erythrurum*; shorthead redhorse, *Moxostoma macrolepidotum*; black bullhead, *Ameiurus melas*; yellow bullhead, *Ameiurus natalis*; brown bullhead, *Ameiurus nebulosus*; channel catfish, *Ictalurus punctatus*; Ozark madtom, *Noturus albater*; stonecat, *Noturus flavus*; tadpole madtom, *Noturus gyrinus*; brindled madtom, *Noturus miurus*; freckled madtom, *Noturus nocturnus*; flathead catfish, *Pylodictis olivaris*; Ozark cavefish, *Amblyopsis rosae*; northern cavefish, *Amblyopsis spelaea*; spring cavefish, *Chologaster agassizi*;

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[3] The authors prefer the term "char

swampfish, *Chologaster cornuta*; southern cavefish, *Typhlichthys subterraneus*; pirate perch, *Aphredoderus sayanus*; trout-perch, *Percopsis omiscomaycus*; burbot, *Lota lota*; banded killifish, *Fundulus diaphanus*; plains killifish, *Fundulus zebrinus*; western mosquitofish, *Gambusia affinis*; freshwater drum, *Aplodinotus grunniens*; white bass, *Morone chrysops*; rock bass, *Ambloplites rupestris*; flier, *Centrarchus macropterus*; banded pygmy sunfish, *Elassoma zonatum*; redbreast sunfish, *Lepomis auritus*; green sunfish, *Lepomis cyanellus*; pumpkinseed, *Lepomis gibbosus*; warmouth, *Lepomis gulosus*; orangespotted sunfish, *Lepomis humilis*; bluegill, *Lepomis macrochirus*; longear sunfish, *Lepomis megalotis*; redear sunfish, *Lepomis microlophus*; smallmouth bass, *Micropterus dolomieu*; spotted bass, *Micropterus punctulatus*; largemouth bass, *Micropterus salmoides*; white crappie, *Pomoxis annularis*; black crappie, *Pomoxis nigromaculatus*; naked sand darter, *Ammocrypta beani*; greenside darter, *Etheostoma blennioides*; rainbow darter, *Etheostoma caeruleum*; Iowa darter, *Etheostoma exile*; fantail darter, *Etheostoma flabellare*; yoke darter, *Etheostoma juliae*; greenthroat darter, *Etheostoma lepidum*; johnny darter, *Etheostoma nigrum*; tessellated darter, *Etheostoma olmstedi*; orangethroat darter, *Etheostoma spectabile*; variegate darter, *Etheostoma variatum*; banded darter, *Etheostoma zonale*; yellowperch, *Perca flavescens*; logperch, *Percina caprodes*; blackside darter, *Percina maculata*; slenderhead darter, *Percina phoxocephala*; dusky darter, *Percina sciera*; sauger, *Stizostedion canadense*; walleye, *Stizostedion vitreum*; slimy sculpin, *Cottus cognatus*.

Marine

Shortnose sturgeon, *Acipenser brevirostrum*; Atlantic sturgeon, *Acipenser oxyrhynchus*; ladyfish, *Elops saurus*; tarpon, *Megalops atlanticus*; American eel, *Anguilla rostrata*; blueback herring, *Alosa aestivalis*; alewife, *Alosa pseudoharengus*; American shad, *Alosa sapidissima*; gulf menhaden, *Brevoortia patronus*; Atlantic menhaden, *Brevoortia tyrannus*; Atlantic herring, *Clupea harengus*; Pacific sardine, *Sardinops sagax*; bay anchovy, *Anchoa mitchilli*; anchoveta, *Cetengraulis mysticetus*; northern anchovy, *Engraulis mordax*; cutthroat trout, *Oncorhynchus clarki*; pink salmon, *Oncorhynchus gorbuscha*; chum salmon, *Oncorhynchus keta*; coho salmon, *Oncorhynchus kisutch*; rainbow trout/steelhead, *Oncorhynchus mykiss*; chinook salmon, *Oncorhynchus tshawytscha*; Atlantic salmon, *Salmo salar*; Arctic char, *Salvelinus alpinus*; Dolly Varden, *Salvelinus malma*; capelin, *Mallotus villosus*; rainbow smelt, *Osmerus mordax*; longfin smelt, *Spirinchus thaleichthys*; eulachon, *Thaleichthys pacificus*; hardhead catfish, *Arius felis*; gafftopsail catfish, *Bagre marinus*; plainfin midshipman, *Porichthys notatus*; oyster toadfish, *Opsanus tau*; Pacific cod, *Gadus macrocephalus*; Atlantic cod, *Gadus morhua*; Pacific hake, *Merluccius productus*; Atlantic tomcod, *Microgadus tomcod*; red brotula, *Brosmophycis marginata*; blackbelly eelpout, *Lycodopsis pacifica*; California grunion, *Leuresthes tenuis*; inland silverside, *Menidia beryllina*; Atlantic silverside, *Menidia menidia*; mummichog, *Fundulus heteroclitus*; tubesnout, *Aulorhynchus flavidus*; threespine stickleback, *Gasterosteus aculeatus*; ninespine stickleback, *Pungitius pungitius*; gulf pipefish, *Syngnathus scovelli*; skipjack tuna, *Katsuwonus pelamis*; chub mackerel, *Scomber japonicus*; Atlantic mackerel, *Scomber scombrus*; Atlantic threadfin, *Polydactylus octonemus*; Pacific barracuda, *Sphyraena argentea*; cobia, *Rachycentron canadum*; American sand lance, *Ammodytes americanus*; northern sand lance, *Ammodytes dubius*; jack mackerel, *Trachurus symmetricus*; bluefish, *Pomatomus saltatrix*; tomtate, *Haemulon aurolineatum*; white grunt, *Haemulon plumieri*; pigfish, *Orthopristis chrysoptera*; spotted seatrout, *Cynoscion nebulosus*; weakfish, *Cynoscion regalis*; spot, *Leiostomus xanthurus*; Atlantic croaker, *Micropogonias undulatus*; red drum, *Sciaenops ocellatus*; pinfish, *Lagodon rhomboides*; scup, *Stenotomus chrysops*; black grouper, *Mycteroperca bonaci*; red grouper, *Epinephelus morio*; Nassau grouper, *Epinephelus striatus*; black sea bass, *Centropristis striata*; red snapper, *Lutjanus campechanus*; tautog, *Tautoga onitis*; common snook, *Centropomus undecimalis*; white perch, *Morone americana*; striped bass, *Morone saxatilis*; shiner perch, *Cymatogaster aggregata*; striped seaperch, *Embiotoca lateralis*; walleye surfperch, *Hyperprosopon argenteum*; rubberlip seaperch, *Rhacochilus toxotes*; pile perch, *Rhacochilus vacca*; high cockscomb, *Anoplarchus purpurescens*; arrow goby, *Clevelandia ios*; clown goby, *Microgobius gulosus*; coastrange sculpin, *Cottus aleuticus*; showy snailfish, *Liparis pulchellus*; Pacific ocean perch, *Sebastes alutus*; brown rockfish, *Sebastes auriculatus*; copper rockfish, *Sebastes caurinus*; splitnose rockfish, *Sebastes diploproa*; yellowtail rockfish, *Sebastes flavidus*; chilipepper, *Sebastes goodei*; shortbelly rockfish, *Sebastes jordani*; black rockfish, *Sebastes melanops*; bocaccio, *Sebastes paucispinis*; canary rockfish, *Sebastes pinniger*; stripetail rockfish, *Sebastes saxicola*; shortspine thornyhead, *Sebastolobus alascanus*; lingcod, *Ophiodon elongatus*; gulf flounder, *Paralichthys albigutta*; California halibut, *Paralichthys californicus*; summer flounder, *Paralichthys dentatus*; southern flounder, *Paralichthys lethostigma*; flathead sole, *Hippoglossoides elassodon*; Pacific halibut, *Hippoglossus stenolepis*; rock sole, *Pleuronectes bilineatus*; Dover sole, *Microstomus pacificus*; English sole, *Pleuronectes* starry flounder, *Platichthys stellatus*; winter flounder, *Pleuronectes americanus*; ocean sunfish, *Mola mola*.