



## Gradients of life-history variation: an intercontinental comparison of fishes

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*Key words:* fishes, geographical and taxonomic effects, life-history patterns, spatiotemporal dynamics of habitats, trilateral continuum model

### Abstract

Multivariate analysis identified a two-dimensional continuum of life-history variation among 301 fish species from Europe, North America, South America and the Atlantic and Pacific coasts of North America. The first axis was associated with larger body size, higher fecundity, delayed maturation, fewer reproductive events, and shorter breeding season on one end and small size, low fecundity, early maturity, multiple reproductive events per year, and prolonged breeding season on the other. The second axis contrasted fishes having larger eggs and more parental care against fishes with the opposite suite of traits. Phylogenetic affiliations of species were apparent in the general patterns of ordination of species within orders, indicating evolutionary divergences in life-history patterns. In fact, partitioning the variance of life-history traits showed that taxonomic order and latitude were the most important factors and geographic region and habitat the least. Despite phylogenetic constraints, basic life-history patterns showed consistency between distantly geographical regions, latitudinal ranges and basic adult habitats, indicating convergences in life-history patterns. Although the basic life-history patterns seemed repeatable among distantly related taxa, geographical and latitudinal affiliations were apparent. Species from South America are skewed toward the opportunistic endpoint, whereas North American marine species are skewed toward the periodic endpoint of the trilateral continuum model. Most of the fish species from South American data set came from fluctuating environments, so an opportunistic strategy of early maturation and continuous spawning permits efficient recolonization of habitats over small spatial scales. In contrast, most species in the North American and European data sets came from seasonal habitats that are nonetheless more hydrological stable, so a periodic strategy of delaying maturation to attain large clutches enhances adult survivorship during suboptimal environmental

conditions and recruitment when early life stages encounter suitable environmental conditions. Similarly, latitudinal affiliations were also observed: opportunistic strategists more common in tropical latitudes and periodic strategists more common in temperate and Arctic latitudes.

## Introduction

Life-history theory deals with constraints, or tradeoffs, among individual traits and demographic variables associated with reproduction, and the means by which constraints influence fitness, or demographic response, to different kinds of environments. Comparative life-history studies of fishes from a variety of habitats and regions have independently identified three similar life-history patterns as endpoints of a triangular continuum (Kawasaki, 1980, 1983; Baltz, 1984; Mahon, 1984; Wootton, 1984; Winemiller, 1989; Paine, 1990; Winemiller and Rose, 1992; Vila-Gispert and Moreno-Amich, 2002).

Following Winemiller and Rose (1992), an 'opportunistic strategy' is associated with early maturation, small eggs, small clutches, and continuous spawning. These traits enhance the intrinsic rate of population increase, and should enhance the fitness of individuals in populations that frequently colonize habitats over small spatial scales following disturbances. These small fishes frequently maintain dense populations in marginal habitats (e.g. ecotones, frequently altered or disturbed habitats) and/or experience high predation mortality in the adult stage (Winemiller and Rose, 1992). Because they tend to be small and often occur in marginal habitats, opportunistic-type fishes are not often exploited commercially, but are very important food resources for piscivores. Given their capacity to compensate heavy losses from all life-history stages, which are typically rather short, a key to the management of opportunistic strategists should be protection from large-scale or chronic perturbations that eliminate important refugia in space and time (Winemiller, 1995).

A 'periodic strategy' describes individuals that delay maturation, thereby allowing growth to a size sufficient to enhance fecundity and adult survival during periods of suboptimal environmental conditions (e.g. winter, drought, periods of reduced food availability). High fecundity is generally associated with small egg size and low parental investment per offspring. Both seasonal variation and large-scale spatial variation in environmental conditions influence the evolution of reproductive timing and effort

(Winemiller and Rose, 1992). 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 growth and survival of larvae (Cohen, 1967; Boyce, 1979; Venable and Brown, 1988; Winemiller and Rose, 1992). Strong cohorts are recruited periodically when early life stages encounter suitable environmental conditions (Murphy, 1968; Stearns, 1976; Warner and Chesson, 1985). The maintenance of some minimum density of adult stocks (so that periodic favorable conditions can be exploited), and the protection of spawning and nursery habitats during the short reproductive period, was crucial in the management of periodic strategists (Winemiller and Rose, 1992).

An 'equilibrium strategy' identifies small- or medium-sized fishes with large eggs, small clutches, well-developed parental care, delayed maturity, and protracted breeding seasons. These traits largely are associated with the *K*-strategy of adaptation to life in resource-limited or density-dependent environments (Pianka, 1970). Because equilibrium strategists produce relatively few offspring, early survivorship must be relatively high in order for these populations to persist near 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 adult habitat. Consequently, management of exploited equilibrium fishes should stress habitat quality/stability and maintenance of healthy adult stocks (Winemiller, 1995).

In order to provide a further step toward a conceptual framework of fish life-history patterns, we evaluated the trilateral continuum model of fish life-history patterns by analyzing available data for 301 freshwater and marine fish species from North America, South America and Europe. Our goal was to identify geographic and taxonomic effects on major gradients of life-history variation within the broadest possible interspecific context. Consistent intercorrelations among life-history traits across widely divergent taxa are likely to reveal both fundamental (universal) constraints and adaptive responses to environmental

conditions. Such patterns reinforced the idea that limited suites of life-history characteristics are ecologically and evolutionarily viable.

## Material and methods

### *Life-history data set*

Estimates of fish life-history traits were obtained from our own data (Vila-Gispert, 1996; Vila-Gispert and Moreno-Amich, 1998, 2000), a study of South American fishes (Winemiller, 1989), and from data sets compiled from literature sources by Winemiller and Rose (1992) and Vila-Gispert and Moreno-Amich (2002). When no reliable data were found for a given trait, that cell in the species life-history trait matrix was left blank and any calculations calling for the trait eliminated the species from the analysis. Whenever maturation and maximum length data were reported for the sexes separately, we used the estimates for females. In some instances, standard lengths (SL) were calculated from total lengths or fork lengths using published conversion equations.

Data for the following seven life-history traits were used in the analyses: (1) age at maturation (in months); (2) maximum SL reported (in millimeters); (3) egg size as the average diameter of the largest oocyte in fully developed ovaries (to nearest 0.01 mm); (4) length of breeding season (in months); (5) spawning mode categorized as: 1 – single spawning per year, 2 – from two to four spawnings per year, 3 – more than four spawnings per year; (6) fecundity as the average number of vitellogenic oocytes of mature females in a single mature ovary or spawning event; (7) parental care following Winemiller (1989), quantified as  $\sum x_i$  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 and larvae, 1 if a brief period of protection by one sex (<1 month), 2 if a long period of protection by one sex (>1 month) or brief care by both sexes, and 4 if lengthy protection by both sexes;  $x_3 = 0$  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 month) with nutritional contribution in viviparous forms), 4 if long period of nutritional contribution to larvae or embryos (= long gestation (1–2 months) with nutritional contribution), or 8 if extremely long gestation (>2 months)).

We analyzed the effects on the variation of life-history traits of three categorical factors: geographical distribution, habitat, and latitude. Geographical distribution was coded as Europe, North America, South America, Atlantic Ocean and Pacific Ocean. Typical adult habitat was classified following Winemiller and Rose (1992) as: (1) small warmwater streams, (2) river channels, (3) river backwaters, lakes and reservoirs, (4) estuary, (5) marine benthic zone, and (6) marine pelagic zone. Species common in two categories or that occupy intermediate habitats were assigned fractional values (e.g. habitat = 2.5 for fishes which commonly occur in both rivers and lakes). Latitudinal distribution was categorized as: (1) from 8° to 29° Lat. N, (2) from 30° to 39° Lat. N, (3) from 40° to 49° Lat. N, and (4) latitude >50° Lat. N.

### *Statistical analyses*

To explore patterns of association among life-history traits and ordination of species, principal component analysis (PCA) was performed on the data set containing 48 European freshwater species (25 from Vila-Gispert and Moreno-Amich, 2002), 183 North American species (Winemiller and Rose, 1992), and 70 South American species (Winemiller, 1989). Fecundity and SL were first log-transformed to increase linearity and normality. Kaiser-Meyer-Olkin's measure of sampling adequacy was used to assess the usefulness of a PCA. KMO ranges from 0–1 and should be well above 0.5 if variables are very interdependent and a PCA is useful.

To test the relationships between life-history patterns and the three categorical factors, we performed canonical discriminant function analysis (CDF). The five life-history variables used in CDF analyses were selected based on their dominant influence in the 7-variable PCA analysis. 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 centroids of each class on the first two CDF axes. All CDF analyses reported in this paper yielded very significant functions (Wilks' lambda,  $P < 0.0005$ ).

To analyze the contribution of different sources of variation (taxonomic order, continent, habitat, and latitude) to life-history variation, we used a multivariate analysis of covariance (García-Berthou and Moreno-Amich, 1993). All factors were considered

Table 1. Correlation matrix of the seven life-history traits for all fish species. Correlations were based on all available data for European freshwater species, North American freshwater and marine species, and South American freshwater species. Above diagonal, Pearson's correlation coefficient; below diagonal,  $P$ -values ( $*** = P < 0.0005$ ). Sample sizes ranged between 259–298 (varying due to some missing values). SL and fecundity were log-transformed

|                   | SL    | Age at maturation | Fecundity | Egg size | Spawning mode | Parental care |
|-------------------|-------|-------------------|-----------|----------|---------------|---------------|
| SL                |       | 0.643             | 0.740     | 0.352    | -0.612        | -0.174        |
| Age at maturation | ***   |                   | 0.511     | 0.341    | -0.434        | -0.124        |
| Fecundity         | ***   | ***               |           | -0.067   | -0.543        | -0.384        |
| Egg size          | ***   | ***               | 0.282     |          | -0.157        | 0.143         |
| Spawning mode     | ***   | ***               | ***       | 0.011    |               | 0.106         |
| Parental care     | 0.003 | 0.034             | ***       | 0.020    | 0.068         |               |

of fixed effects and latitude was used as the covariate. We used partial eta squared ( $\eta^2$ ) as a measure of effect size. Similarly to  $r^2$ , partial eta squared is the proportion of variation explained for a certain effect (effect SS/effect SS + error SS). Partial eta squared has the advantage over eta squared (effect SS/total SS) that it does not depend on the ANOVA design used because it does not use total SS as the denominator (Tabachnick and Fidell, 2000: 191).

All statistical analyses were performed with the SPSS for Windows 11.0.

## Results

### Multivariate life-history patterns

Most life-history variables were significantly correlated (Table 1) and the Kaiser-Meyer-Olkin's measure of sampling adequacy was 0.66 for our data set, indicating the usefulness of a PCA. The gradients produced by PCA based on the pooled data set with seven life-history variables were essentially the same as those obtained from separate analysis of individual data sets (Winemiller, 1989; Winemiller and Rose, 1992; Vila-Gispert and Moreno-Amich, 2002). The first two PCA axes from the pooled data set explained 64% of the total variation. The first axis was strongly influenced by body size, fecundity, age at maturation, spawning mode, and length of breeding season (Table 2). The second axis was associated with egg size, and parental care (Table 2). Thus, PCA analysis (Figure 1) identified a dominant gradient of life-history characteristics that contrasts large size, high fecundity, late maturation, few reproductive events per year and short

Table 2. Factor loadings of the principal components analysis (PCA) of the seven life-history variables for all fish species ( $N = 301$ ). Eigenvalues for the first two axes (PC1 and PC2) were 3.255 and 1.195, respectively (cumulative variance = 46.5% and 63.5%). SL and fecundity were log-transformed

| Variable                  | PC1    | PC2    |
|---------------------------|--------|--------|
| SL                        | 0.903  | 0.114  |
| Fecundity                 | 0.795  | -0.361 |
| Age at maturation         | 0.745  | 0.137  |
| Egg size                  | 0.441  | 0.754  |
| Parental care             | -0.360 | 0.681  |
| Length of breeding season | -0.563 | -0.012 |
| Spawning mode             | -0.782 | 0.016  |

breeding season with small body size, low fecundity, early maturation, multiple reproductive events, and prolonged breeding season. The secondary gradient contrasted high and low parental investment in individual offspring.

Species scores on the first two PC axes were used to ordinate species along dominant life-history gradients (Figure 1). The periodic strategy (high scores on PC1), which combines large size, late maturation, and seasonal spawning of large clutches of small eggs is observed by a taxonomically diverse group of fishes. In the pooled data set, sturgeons (*Acipenser* spp.) and some pleuronectiforms (*Hippoglossus*) provide the extreme example of this strategy (Figure 1). Salmonids (*Salmo*, *Oncorhynchus*, and *Salvelinus* genera) modify this strategy by producing larger eggs (high scores on PC1 and on PC2). Some cichlids (like *Astronotus ocellatus*), cavefishes (*Amblyopsis* spp.) and some catfishes (*Noturus* spp.),

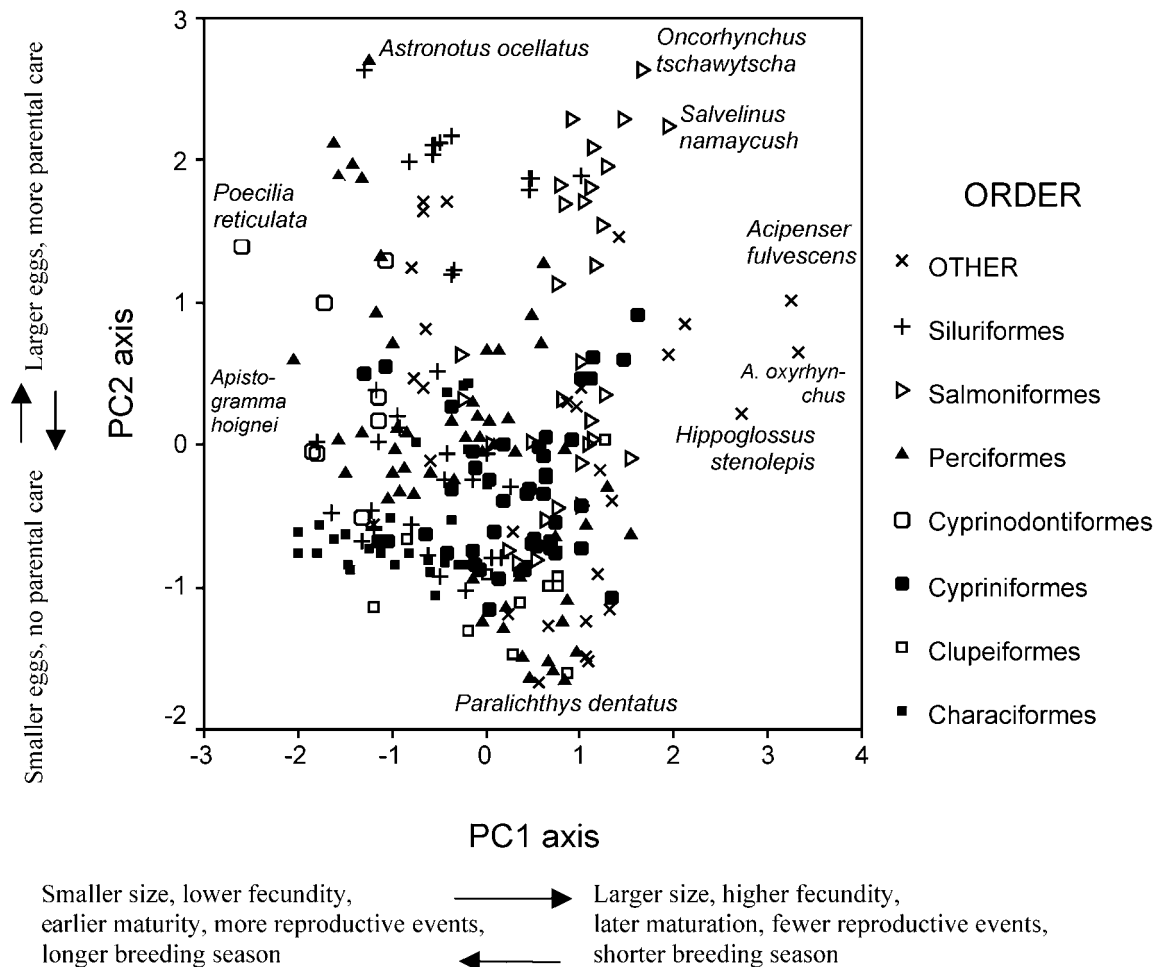


Figure 1. Scores for the data set containing all species on the first two principal component axes based on seven life-history variables. Symbols identify orders with more species in the data set. The two axes were interpreted based on the factor loadings of the life-history variables (see Table 2).

*Ancistrus* sp.) produce small clutches of large eggs and have well-developed parental care (low scores on PC1, high scores on PC2). Most cyprinodontiforms and many characiforms and perciforms (like *Apistogramma hoignei*) (Figure 1) have the opportunistic strategy of early maturation, multiple spawning of small clutches of small eggs, and little or no parental care (low scores on PC1 and PC2).

Geographical affiliations are apparent in the general pattern of ordination of species within regions in the plot of species scores on the first two PC axes (Figure 2). Species from South America tended to score low on PC1, whereas most marine species scored high on PC1. With the exception of salmonids, North American and European freshwater fishes tended to have intermediate scores on both axes.

CDF using geographical distribution as the class variable (Figure 3) showed a pattern of larger clutches, later maturity and fewer reproductive events per year in association with the Atlantic and Pacific marine fishes versus small clutches, early maturity and multiple reproductive events in association with South American fishes (Table 3). Again, North American and European freshwater fishes were intermediate between South American and Atlantic and Pacific marine fishes. CDF 2 indicated that small eggs tended to be associated with Atlantic marine fishes.

When CDF was performed using habitat as the class variable (Figure 4), marine benthic fishes tended to have the largest clutches and the latest maturity and small warmwater stream and estuarine fishes the smallest and earliest (Table 3). River channel

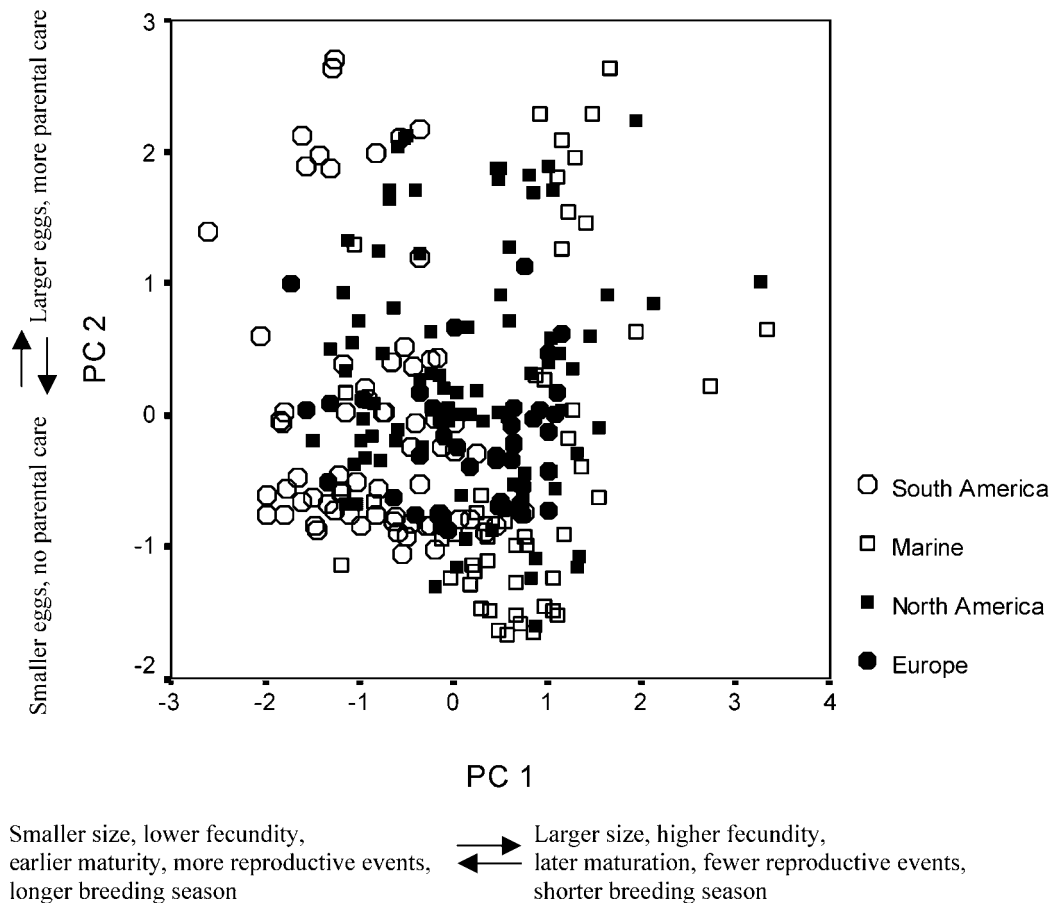


Figure 2. PCA scores for the same data set as in Figure 1, but symbols identifying geographical distribution of species. The two axes were interpreted as in Figure 1.

fishes were intermediate between lake/marine fishes and small warmwater stream/estuarine fishes. Marine pelagic fishes were associated with larger eggs.

CDF using latitudinal range as the class variable (Figure 5) showed a general pattern of later maturation, fewer reproductive events, and larger eggs in association with high latitudes versus early maturation, multiple reproductive events, and small eggs in association with low latitudes (Table 3).

#### *Partitioning the variation in different sources of variation*

A multivariate analysis of covariance (MANCOVA) of the life-history variables (Table 4) showed that most sources of variation were significant but there was no three-way interaction. Taxonomic order and latitude were the most important factors (see partial eta squared) and geographic region and habitat the

least. About 22% of the variability of life-history traits was among taxonomic orders, whereas only 10% was among regions or habitats. There were several two-way interactions, so e.g. the variation among habitats in life-history traits was also dependent on taxonomic order and the variation among regions was not the same for all orders.

#### **Discussion**

Multivariate analysis identified consistent dominant gradients of life-history variation among 301 fish species from Europe, North America, South America and Atlantic and Pacific coasts of North America. In each case, the first axis was associated with larger body size, higher fecundity, delayed maturation, fewer reproductive events, and shorter breeding season on one end and small size, low fecundity, early

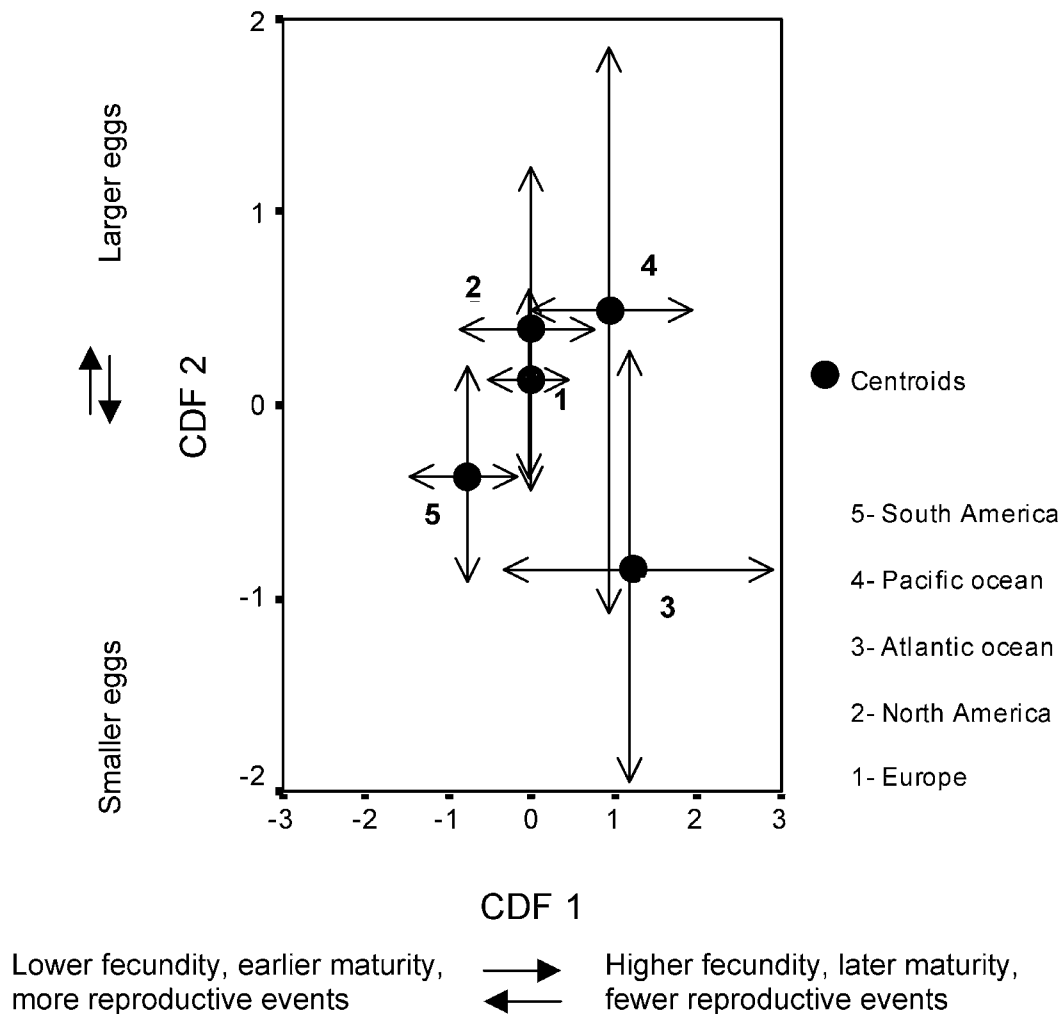


Figure 3. Centroids and standard error of species scores on the first two discriminant functions by geographical group. CDF was based on five life-history variables. Interpretations of axes were based on the matrix structure of the CDF.

maturity, multiple reproductive events per year, and prolonged breeding season on the other. The second axis contrasted fishes having larger eggs and more parental care against fishes with the opposite suite of traits. When species are ordered simultaneously on the two primary axes of PCA, three distinctive strategies are identified as the endpoints of a trilateral continuum (Winemiller, 1989, 1992) (Figure 1): (1) species with small size, low fecundity, early maturity, repeated reproductive events, small eggs, and prolonged breeding season; (2) species with intermediate to large size, high fecundity, late maturity, one or few reproductive events, small eggs relative to body size, and short breeding season; and (3) small or medium-size species with low fecundity, large eggs,

well-developed parental care, and prolonged breeding season.

Phylogenetic affiliations of species were apparent in the general patterns of ordination of species within orders in the plot of species scores on the first two PC axes (Figure 1). In fact, partitioning the variance of life-history traits showed that taxonomic order was the most important factor, indicating evolutionary divergences in life-history patterns. Despite phylogenetic constraints, basic life-history patterns showed consistency among distantly geographical regions (North America, South America, Europe, and Atlantic and Pacific oceans), among latitudinal ranges and among basic adult habitats, indicating convergences in life-history patterns (see also Vila-

Table 3. Means and standard errors (in parentheses) of life-history traits by geographical region, typical adult habitat, and latitudinal range. See the Methods for definition of variables with unspecified units

|                      | N  | Maximum SL (mm) | Age at maturation (months) | Length of breeding season (months) | Spawning mode | Egg size (mm) | Parental care | Fecundity        |
|----------------------|----|-----------------|----------------------------|------------------------------------|---------------|---------------|---------------|------------------|
| <b>Region</b>        |    |                 |                            |                                    |               |               |               |                  |
| Europe               | 42 | 315.7 (231.7)   | 30.5 (15.8)                | 1.9 (1.5)                          | 1.4 (0.6)     | 1.6 (0.9)     | 1.4 (0.9)     | 40719 (77822)    |
| North America        | 83 | 385.4 (406.4)   | 32.3 (28.1)                | 2.0 (1.1)                          | 1.6 (0.8)     | 2.0 (1.1)     | 1.8 (1.3)     | 38055 (102016)   |
| Atlantic ocean       | 27 | 760.7 (750.2)   | 41.7 (43.9)                | 3.7 (1.6)                          | 1.4 (0.7)     | 1.8 (2.7)     | 0.5 (0.8)     | 666105 (1208304) |
| Pacific ocean        | 23 | 663.5 (504.5)   | 45.4 (24.9)                | 2.8 (1.5)                          | 1.3 (0.7)     | 2.6 (1.8)     | 1.9 (2.4)     | 269817 (542735)  |
| South America        | 70 | 121.1 (92.5)    | 10.6 (4.1)                 | 3.8 (2.8)                          | 2.2 (0.7)     | 1.3 (0.7)     | 1.8 (1.5)     | 5411 (21043)     |
| <b>Adult habitat</b> |    |                 |                            |                                    |               |               |               |                  |
| Warmwater streams    | 31 | 189.4 (158.3)   | 22.2 (12.1)                | 2.3 (1.2)                          | 2.0 (0.8)     | 1.9 (1.1)     | 1.7 (1.0)     | 4495 (11266)     |
| River channels       | 35 | 340.1 (395.8)   | 30.8 (24.0)                | 2.1 (2.0)                          | 1.6 (0.7)     | 1.8 (1.1)     | 1.7 (1.3)     | 22317 (44048)    |
| Lakes                | 40 | 509.0 (343.6)   | 35.0 (17.9)                | 1.7 (1.0)                          | 1.2 (0.4)     | 1.9 (1.0)     | 1.3 (1.3)     | 62493 (118160)   |
| Estuaries            | 63 | 155.0 (157.3)   | 14.0 (13.0)                | 3.5 (2.0)                          | 2.1 (0.8)     | 1.3 (0.6)     | 1.8 (1.5)     | 35163 (187840)   |
| Marine benthic       | 24 | 873.7 (845.7)   | 58.0 (49.0)                | 3.0 (1.4)                          | 1.1 (0.4)     | 1.7 (1.0)     | 2.1 (2.7)     | 835334 (1342202) |
| Marine pelagic       | 14 | 657.8 (488.5)   | 36.3 (11.2)                | 2.7 (1.6)                          | 1.5 (0.9)     | 3.0 (2.2)     | 0.8 (1.0)     | 39223 (69149)    |
| <b>Latitude</b>      |    |                 |                            |                                    |               |               |               |                  |
| From 8 to 29° N      | 73 | 161.3 (249.7)   | 11.6 (7.1)                 | 3.8 (2.7)                          | 2.1 (0.8)     | 1.3 (0.7)     | 1.7 (1.5)     | 70220 (548107)   |
| From 30 to 39° N     | 65 | 406.2 (494.1)   | 27.3 (21.1)                | 2.8 (1.5)                          | 1.7 (0.8)     | 1.8 (1.9)     | 1.7 (1.4)     | 107711 (279746)  |
| From 40 to 49° N     | 64 | 462.4 (508.3)   | 39.5 (38.5)                | 2.2 (1.3)                          | 1.4 (0.7)     | 1.8 (1.0)     | 1.8 (1.7)     | 151508 (414650)  |
| >50° N               | 40 | 528.4 (372.7)   | 42.2 (18.6)                | 1.7 (1.1)                          | 1.2 (0.4)     | 2.7 (1.7)     | 0.9 (0.9)     | 177689 (711563)  |

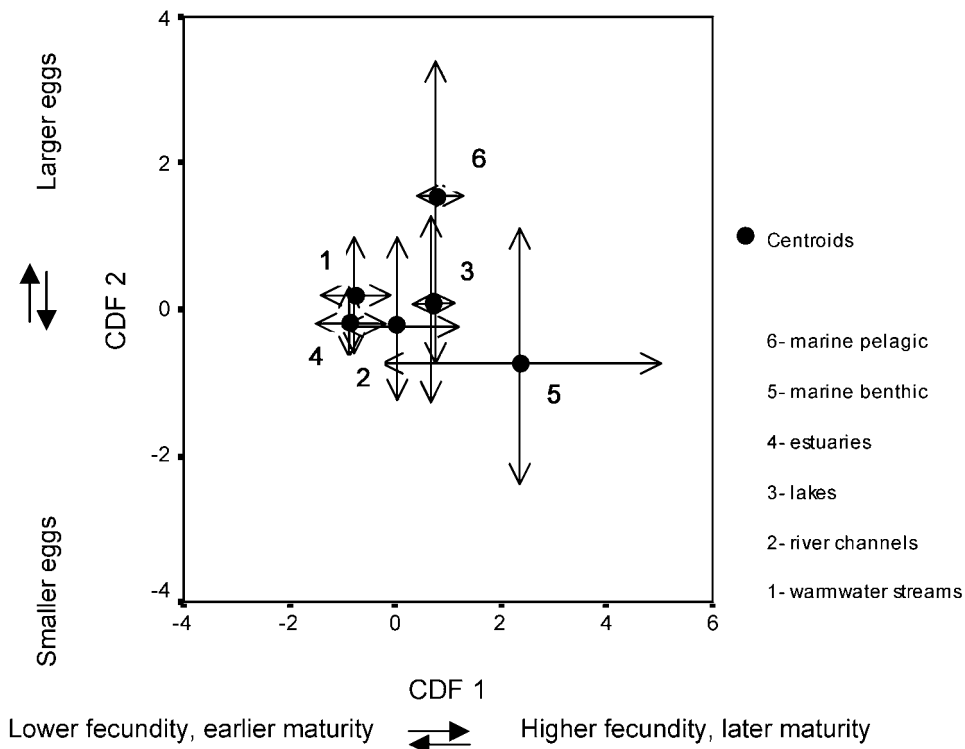


Figure 4. Centroids and standard error of species scores on the first two discriminant function axes by habitat. CDF was based on five life-history variables. Interpretations of axes were based on the matrix structure of the CDF.



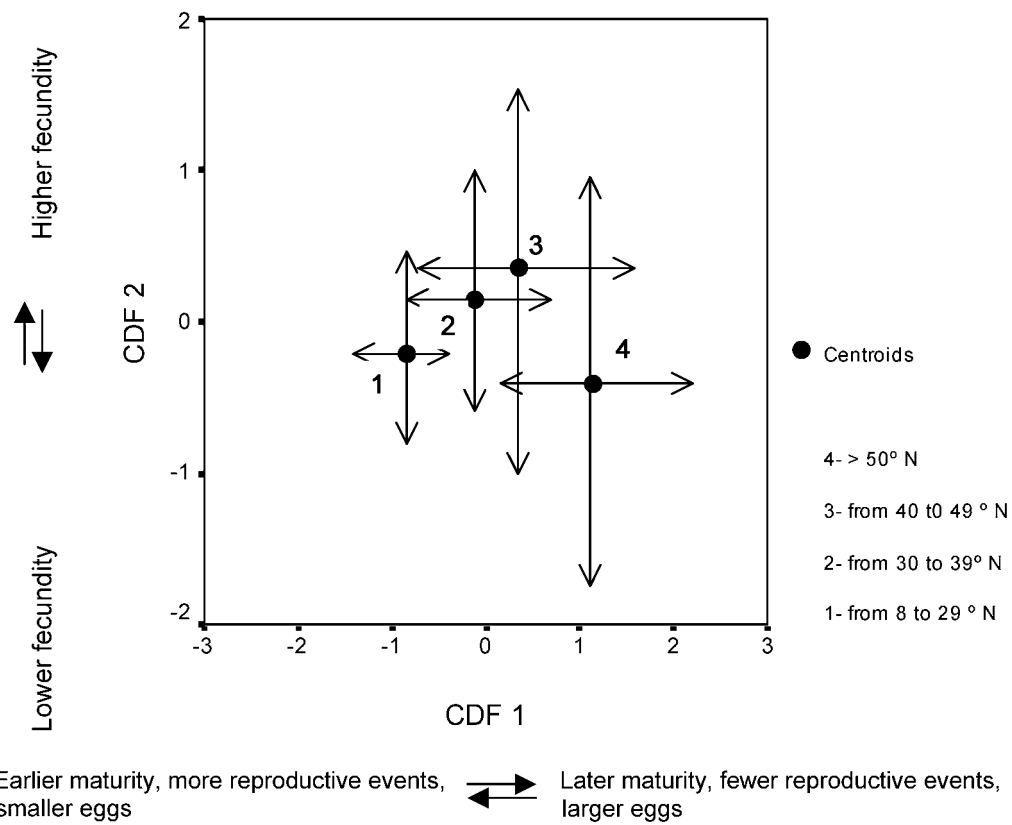


Figure 5. Centroids and standard error of species scores on the first two discriminant function axes by latitude. CDF was based on five life-history variables. Interpretations of axes were based on the matrix structure of the CDF.

Table 4. Multivariate analysis of covariance of the seven life history variables with region, habitat and order as factors and latitude as a covariate.  $F$  corresponds to Wilks' lambda. Partial eta squared is a measure of effect size (see Methods). A similar design with fork length as a covariate yielded similar results

| Source of variation                    | $F$   | Hypothesis df | Error df | $P$     | Partial eta squared |
|--|-------|---------------|----------|---------|---------------------|
| Latitude                               | 3.139 | 7             | 126.0    | 0.004   | 0.148               |
| Region                                 | 1.948 | 28            | 455.7    | 0.003   | 0.097               |
| Habitat                                | 1.941 | 35            | 532.5    | 0.001   | 0.096               |
| Order                                  | 5.110 | 35            | 532.5    | <0.0005 | 0.216               |
| Region $\times$ Habitat                | 1.438 | 28            | 455.7    | 0.071   | 0.073               |
| Region $\times$ Order                  | 1.849 | 35            | 532.5    | 0.003   | 0.092               |
| Habitat $\times$ Order                 | 1.556 | 63            | 715.7    | 0.005   | 0.098               |
| Region $\times$ Habitat $\times$ Order | 0.867 | 14            | 252.0    | 0.596   | 0.046               |

Gispert and Moreno-Amich, 2002). Concordance between patterns provides evidence that essential trade-offs produce numerous convergences in life-history strategies. Such findings reinforced the idea that limited life-history patterns may be viable among fish species, independently of the origin of fish communities. As previously pointed out by Winemiller (1989, 1992), the 3-endpoint life-history model seems to be a very strong pattern in nature.

Although the basic life-history patterns seemed repeatable among distantly related taxa, geographical affiliations were apparent in the general pattern of ordination of species within regions in the plot of species scores on the first two PC axes (Figure 2). Species from South America are skewed toward the opportunistic endpoint, whereas North American marine species are skewed toward the periodic endpoint of the trilateral continuum model. Species centroids for North American and European freshwater fishes occupied intermediate positions along an axis linking the opportunistic and periodic endpoints. CDF using geographical distribution as a class variable (Figure 3) showed a general pattern of smaller clutches, earlier maturity and multiple reproductive events in association with South American fishes, versus large clutches, late maturity and few reproductive events per year in association with North American marine fishes. Thus, it seems that the opportunistic strategy of early maturity and multiple reproductive events appears to be more common in tropical freshwaters, whereas the periodic strategy of large clutch sizes is predominant among North American marine fishes. Interpretation of these faunal patterns must be made with caution, because the North American data, compiled from the literature, is dominated by species of economic importance that have been extensively studied (mostly larger species). Thus, the North American data set may be biased in terms of underrepresentation of small fishes. However, South American and European data sets included all species that co-occurred at study site containing many species, and the same trend was observed: opportunistic strategists more common in tropical freshwaters and periodic strategists in European freshwaters.

In fact, geographical affiliations in the general pattern of species ordination in the multivariable space could be related to differences in habitat characteristics. Most of the fish species from South American data set came from a swamp-creek that is converted into a marsh when the site experiences extensive sheet flooding during the wettest months (Winemiller,

1989). This aquatic habitat was reduced to a network of shallow pools during the driest months (Winemiller, 1989). Under these environmental conditions, rapid maturation rates maximize the intrinsic rate of population increase more efficiently than increasing either survivorship or fecundity (Winemiller, 1989; Winemiller and Rose, 1992); consequently opportunistic strategists dominated this South American data set. Opportunistic life-history of early maturation and continuous spawning allows species to repopulate habitats following disturbances or in the face of continuous high mortality in the adult stage (Lewontin, 1965). For example, Reznick (1982) found that Trinidadian guppies (*Poecilia reticulata*) from mountain streams exposed to predators that prey selectively on mature size classes increased their reproductive effort and decreased their age at maturity.

In contrast, most species in the North American and European data sets came from seasonal habitats that are nonetheless more hydrological stable (lakes and marine environments) compared to shallow floodplain habitats in the tropics. Consequently, most North American and European species were located near the periodic endpoint. In seasonal environments, selection favors the production of large numbers of small offspring in response to large-scale, yet predictable environmental variation in time as well as space. Among periodic strategists, large variation in the recruitment of annual cohorts is common (Rothschild and DiNardo, 1987; Armstrong and Shelton, 1990; Myers, 1995; Rose et al., 2001). Moreover, CDF using basic adult habitat as a class variable (Figure 4) showed that small warmwater stream and estuarine fishes tended to have earlier maturity and smaller clutches than lake and marine fishes. Similarly, fishes from tropical latitudes (Figure 5) tended to have earlier maturity, multiple reproductive events and smaller eggs than fishes from arctic and temperate latitudes. This trend could be related to the dominance in the data set by river and estuarine species at low latitudes, and lake and marine species at arctic and temperate latitudes. We hypothesize that observed geographical and latitudinal trends were a consequence of habitat characteristics.

To better establish the existence of geographical and latitudinal trends in life-history strategies, demographic and reproductive data are needed for more species, specially from tropical lakes and rivers.

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