

Life history correlates and extinction risk of capital-breeding fishes

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Abstract We consider a distinction for fishes, often made for birds and reptiles, between capital-breeding and income-breeding species. Species that follow a capital-breeding strategy tend to evolve longer intervals between reproductive events and tend to have characteristics that we associate with higher extinction risk. To examine whether these ideas are relevant for fishes, we assembled life history data for fish species, including an index of extinction risk, the interval between spawning events, the degree of parental care, and whether or not the species migrates

to spawn. These data were used to evaluate two hypotheses: (1) fish species with a major accessory activity to spawning (migration or parental care) spawn less often and (2) fish species that spawn less often are at greater risk of extinction. We tested these hypotheses by applying two alternative statistical methods that account for phylogenetic correlation in cross-taxon comparisons. The two methods predicted average intervals between spawning events 0.13–0.20 years longer for fishes with a major accessory activity. Both accessories, above-average parental care and spawning migration, were individually associated with longer average spawning intervals. We conclude that the capital-breeding paradigm is relevant for fishes. We also confirmed the second hypothesis, that species in higher IUCN extinction risk categories had longer average spawning intervals. Further research is needed to understand the relationship between extinction risk and spawning interval, within the broader context of life history traits and aquatic habitats.

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Introduction

Capital-breeding species use stored energy to make a large, fecundity-independent investment at each breeding opportunity (Bull & Shine, 1979). Species

with high, fecundity-independent costs include those that make long migrations to breed and those that provide considerable parental care before birth (e.g., live-bearing) or after birth (e.g., nest-guarding). According to the capital-breeding theory, longer-than-annual intervals between breeding events evolved in association with capital breeding because more offspring were produced over a lifetime by skipping years than would be possible by spending energy to reproduce more frequently without either migrating or providing parental care. Bull & Shine (1979) give the following example,

“Suppose a fish migrates every month to lay ten eggs; the migration uses stored energy which she gathers each month and could otherwise be converted into ten more eggs. Now, if she delays reproduction 1 month and simply stores the energy, at the time of the next reproduction she will have the capacity for 20 eggs and two migrations. However, she needs to migrate only once and can thus use the energy from the “extra” migration for an additional ten eggs. Her fecundity after 2 months is 30 eggs rather than 20.”

Long spawning intervals occur both as a plastic life history response to energy stores or environmental conditions (skipped spawning) and as a “hardwired” life history feature. In this study, we focus on spawning interval at the evolutionary timescale, where the mechanism is natural selection. Jørgensen et al. (2006) used a dynamic programming model to predict that spawning should be skipped if the expected future gain in reproductive output, discounted by survival, more than balances the expected reproductive success the current year. According to their model, the incidence of skipped spawning increased linearly as the energetic or mortality costs of migration increased, thus supporting the capital-breeding hypothesis.

A distinguishing characteristic of capital breeders is that females reproduce in years when they have accumulated a threshold level of stored energy reserves; in contrast, income breeders spend energy on reproduction as it is gained (Jonsson, 1997). Murua & Saborido-Rey (2003) describe the breeding strategies of marine fishes. Among the strategies they describe for iteroparous fishes, the income-breeding strategy seems to correspond with that of fishes with

asynchronous egg development and indeterminate fecundity who develop eggs more or less continuously. The capital-breeding strategy seems to correspond with group-synchronous marine fishes that have determinate fecundity. In the marine environment, income-breeding fishes tend to be small, pelagic species in temperate waters, whereas capital-breeding fishes tend to be demersal species in cold, marine waters (Murua & Saborido-Rey, 2003).

Capital breeding may be associated not only with less-frequent breeding, but also with a suite of correlated life history traits. Storing the energetic reserves and fecundity required for less-than-annual spawning favors a large body size. Species that spend reproductive capital on long breeding migrations tend to mature late and to have a large adult body size. It is less clear that large body size is correlated with parental care, particularly for oviparous species. Large body size also reduces predation risk and increases general resistance to stressors, which in turn, makes delayed maturation a feasible strategy. Jørgensen et al. (2006) found that the optimal age and length at maturation also increased in response to increased migration costs for their simulated cod populations.

In this paper, we consider whether the capital-breeding paradigm, which was developed for birds and reptiles (Johsson, 1997), is useful for understanding fish life histories. We assembled fish species data for three life history traits (interval between spawning events, degree of parental care, and migration strategy) and an index of extinction risk. We use these data to examine whether infrequent breeding is positively related to a species’ migration strategy and degree of parental care. We also use the data to test whether extinction risk is higher for capital-breeding species.

Methods

Life history and extinction risk data

We assembled a database that included life history traits and the IUCN conservation status for a wide variety of fish species (see <http://www.esd.ornl.gov/~zjz/mypubs/>). Three primary sources of data were: (1) Winemiller & Rose (1992) for life history traits of North American fishes, (2) Vila-Gispert & Moreno-Amich (2002) for life history traits of European

freshwater fishes, and (3) FishBase (FishBase, 2004) for life history traits of additional marine and estuarine species and for the IUCN status and taxonomy (class, order, family, genus, species) for all fish species.

We conducted a literature search using terms “fishes” and {“spawning interval,” “skipped breeding,” “parental care,” and “migration”}. We also searched for publications on each taxonomic fish order represented in our database or in FishBase with the key word “reproduction”. We included those species in our analysis for which the needed life history information was available. The life history data in the Winemiller & Rose (1992) dataset were recorded by species, whereas the other two sources were organized by stock. For numeric variables, we averaged stocks in FishBase to aggregate to the species level. For IUCN status, we used the middle designation unless there were only two values, in which case the higher level of risk was assigned to the species. We excluded species known to us to be semelparous, such as Pacific salmon, lampreys, and some herrings.

We associated IUCN status, assigned by the World Conservation Union (Hilton-Taylor, 2000), to each species in the database. We converted these codes to numeric values: 4 = critically endangered, 3 = endangered, 2 = vulnerable, and 1 = lower risk. The lower risk category also included the subcategories of conservation-dependent, near-threatened, and least-concern. Species not found in IUCN Red List were assigned a code value of zero. We excluded species listed by the IUCN as data-deficient or not evaluated.

We used our data sources to quantify three life history traits: (1) the interval between spawning events (in years), (2) whether the species makes spawning migrations or not, and (3) an index that measures parental care. The interval between spawning events was reported by Winemiller & Rose (1992) and Vila-Gispert & Moreno-Amich (2002); we estimated values from the literature for species that we added from FishBase. Intervals for batch spawners were recorded as annual if oogenesis had one seasonal peak.

Migration status was indicated for a subset of fishes in all three databases. We changed the status values reported to non-migratory for some species if literature sources revealed that spawning migrations were shorter than ~50 km. Distance migrated was not known for the majority of species. We defined an indicator variable, *Imig*, and assigned it a value of 1 for species that make spawning migration and a value

of 0 for those that do not. For species listed as amphidromous in FishBase, we independently confirmed that the purpose of migration was spawning.

We adopted the index of parental care used by Winemiller & Rose (1992) and Vila-Gispert & Moreno-Amich (2002). We computed this parental care index for species that we added from FishBase for which the required information was available in the literature or the “AddInfos” field of FishBase. The parental care index (denoted as *Cindex*) was computed as a sum of three variables, $x_1 + x_2 + x_3$, that characterize effort in providing spawning habitat, effort to provide parental protection, and nutritional contribution, respectively. Index $x_1 = 0$ if there is no special placement of zygotes, 1 if zygotes are placed in a special habitat, and 2 if both zygotes and embryos are protected by a nest. Index $x_2 = 0$ if no parental protection of zygotes, embryos, or larvae; 1 = brief period of protection by one parent (<1 month); 2 = extended protection (>1 month) by one parent or brief protection by both; and 4 = extended period of protection by both parents. Index $x_3 = 0$ if parents extend no post-egg nutritional contribution to larvae, 2 = brief period of nutritional contribution to embryos or larvae, 4 = long period of nutritional contribution to embryos or larvae (1–2 months’ gestation), 6 = 2–10 months’ gestation, and 8 = >10 months’ gestation.

We derived two additional indicator values from variables *Imig* and *Cindex*. To reduce our reliance on *Cindex* as a quantitative measure of parental investment, we defined binary indicator variable, *Icare*, which we defined as zero for *Cindex* < 4 and one for *Cindex* ≥ 4. We also defined an indicator variable, *Major* = 1 for those fish species for which reproduction involves a “major accessory activity” such as a long migration (*Icare* = 1) or extensive parental care (*Imig* = 1) and assigned *Major* = 0 for all other species.

We examined relationships between life history traits and two response variables (spawning interval and extinction risk), using a database of 353 species that represented 2 classes, 35 orders, 102 families, and 202 genera.

Phylogenetic correlation in life history traits

One complication when studying relationships among life history traits across species is the effect of phylogeny on these relationships (Pagel & Harvey,

1988; Ives & Zhu, 2006). For example, perhaps two ancestral species radiated, one with a long spawning interval and migration and the other with a short spawning interval and no migration. These two ancestral species radiated, each evolving into ten new species with the same traits. Assume also that ancestral species with the other two combinations of traits (short spawning interval, migration and long spawning interval, no migration) did not radiate and evolved only one modern species each. Together, these data, with two species-rich clusters, would produce a spurious correlation between the two traits simply due to historical accident, and not necessarily due to adaptations that arose independently as distinct evolutionary events.

Comparative methods are used to account for phylogenetic constraints (see review by Gittleman & Luh, 1992). These methods reduce the power to detect significant relationships between or among life history variables by accounting for non-independence among related species. We attempted to account for phylogenetic constraints using two comparative methods: repeated-measures' regression and phylogenetic regression using independent contrasts. Both approaches can be described by the same basic model (Eq. 1) that relates the dependent life history trait, y , to the independent life history variables, \mathbf{X} (lower case variables represent vectors and upper case, bold variables represent matrices).

$$y = \mathbf{X}\beta + \varepsilon, \quad (1)$$

where β is a vector of regression coefficients. The vector of errors, ε , follows a multivariate normal distribution with mean vector, 0 , and covariance matrix, \mathbf{R} . A regression that does not consider phylogenetic correlation would treat species (or averages of higher taxonomic nodes) as independent ($\mathbf{R} = \sigma^2 \mathbf{I}$). Instead, we estimate covariances among traits due to phylogeny and use these as off-diagonal elements in \mathbf{R} .

Repeated-measures' regression

We used repeated-measures' regression to model covariance among species sharing the same order. We implemented this approach using SASTM Proc Mixed (Littell et al., 1996; See Electronic supplementary material—Appendix I). Covariance estimates were

constrained to be positive, and species in different classes were assumed to be independent. The covariance matrix, \mathbf{R} , was constructed using compound symmetry, with variances and covariances estimated for each taxonomic order. This approach did not consider correlations between taxonomic levels lower than order (i.e., family and genus), and orders represented by fewer than three species had to be removed from the analysis to obtain estimates. Although some predictors had more missing values than others, this left about 334 species representing 19 orders. Estimates were obtained by using restricted maximum likelihood.

Phylogenetic regression

We used Grafen's (1989) method of phylogenetic regression to account for phylogeny by forming independent contrasts in which each radiation provides an independent data point. The basic idea of phylogenetic regression is not to use species as independent data points, but instead to use the higher nodes in the phylogeny (Grafen, 2006). Values at each radiation are weighted averages of species' life history traits at lower levels in its taxonomic subtree. Obtaining the weighted averages for each independent radiation involves solving a generalized least squares problem with phylogeny incorporated into the structure of the error term (Martins & Hansen, 1997). Under the model of Brownian motion evolution, the values of a species' trait follow a multivariate normal distribution with mean equal to the mean of the base of the tree and covariance matrix whose off-diagonal elements for species i and j (Eq. 2) decrease in proportion to the branch length, h_{ij} , of their shared lineage in the tree (Grafen, 1989). We assigned path lengths of 1, 2, 3, and 4 for species sharing genus, family, order, and class, respectively. Diagonal elements of \mathbf{R} are given by variance, σ^2 .

$$\mathbf{R} = E(\varepsilon_i \varepsilon_j) = \sigma^2 (1 - h_{ij}^\rho) \quad (2)$$

The idea is that if the same relationship is observed in two radiations, it cannot result from phylogenetic similarity (Grafen, 1989). Parameter ρ is the power to which heights are raised before computing path segment lengths (phylogenetic distance). The parameter ρ measures the strength of phylogenetic

correlation. Parameters β and ρ are estimated, and an F -test is provided for the overall model or for specified terms of the regression model. Phylogenetic degrees of freedom (denominator) are the number of higher phylogenetic nodes that provide useful information (e.g., nodes for which all species below a node share the same value do not provide information).

For repeated measure and phylogenetic regression models with multiple predictors, we evaluated the importance of each predictor by testing the significance of each term, while controlling for the other predictors in the model. We report the one-sided P -value associated with the F -test because we postulate positive effects of all predictors including their interactions as the alternative hypothesis.

Power and hypothesis testing

We report the importance of each predictor by testing whether each estimated coefficient is significantly greater than zero. We report the one-sided P -value associated with the statistical tests because, in all cases, we postulate positive effects, including interactions, as the alternative hypothesis. Setting a critical Type-I error, $\alpha = 0.05$, is considered very conservative because it does not provide a good balance between avoiding wrong conclusions of significance and having the power to detect relationships (Toft & Shea, 1983; Gotelli & Ellison, 2004). We therefore specify $\alpha = 0.1$ and report the actual P -values to allow readers to make their own determinations of significance.

Accounting for phylogenetic correlation appropriately reduces the power of statistical tests, increasing P -values. Repeated-measures' regression is more powerful than phylogenetic regression because it uses more species-level data and does not consider correlations at the family or genus level. To the extent that the reduction in power is caused by properly considering correlations, the results of phylogenetic regression are more correct. To the extent that the reduction in power is caused by excluding relevant species-level information (for example, if we are interested in relationships among extant species regardless of their evolutionary histories), the results of repeated-measures' regression are more correct. Both methods could be improved on by obtaining better estimates of phylogenetic

“distances” (evolutionary branching times) separating all pairs of species.

Are spawning intervals longer for fish species that migrate to spawn or provide parental care?

Capital breeding is thought to evolve in species for which breeding involves a “major accessory activity,” such as a long migration or extensive parental care (Bull & Shine, 1979). We used repeated-measures' regression and phylogenetic regression to examine relationships between spawning interval (SI) and major accessory activity (Major). Next, we examined relationships between SI and the two constituents of Major: migration (Imig) and parental care (either Cindex, the original 9-value index, or indicator variable, Icare).

Are capital-breeding species considered at greater risk of extinction?

In our second analysis, we addressed the hypothesis that fish species that spawn less frequently tend to experience higher risk of extinction, as indicated by IUCN designation. We used box-whisker diagrams to graphically compare the probability distribution of spawning interval among IUCN risk categories. We also used phylogenetic regression to test for a positive association between our ordered index of IUCN risk status and spawning interval. This analysis included 41 independent contrasts. We are interested in a one-sided test to compare zero effect against the alternative hypothesis that SI has a positive effect on the ordered index of IUCN risk status.

Results

Species with long breeding intervals

Sixty-four species of the total 353 species in our sample had longer-than-annual breeding cycles (See Electronic supplementary material—Appendix II). The longest breeding intervals were found among the sturgeons. Like other sturgeons, female white sturgeon (*Acipenser transmontanus*) are physiologically capable of breeding at 2-year intervals, with a

1.8 year maturation cycle (Doroshov et al., 1997). In the wild, however, at least 1 year of resting has been observed for this species, and typical spawning intervals range from 3 to 9 years (Paragamian & Wakkinen, 2002). Larger shark species also exhibit longer-than-annual breeding cycles. Females of several shark species breed every other year (Frisk et al., 2001; Hueter et al., 2004), necessitated by a very long gestation period. Sturgeons and sharks accounted for a large proportion of the species in our database with longer-than-annual spawning intervals (See Electronic supplementary material—Appendix II). Other taxa included cavefishes, a sucker, several

groundfishes, the coelanth, striped bass, and several salmonids.

Are spawning intervals longer for fish species that migrate and provide parental care?

Figure 1 summarizes the mean spawning intervals for classes and orders included in our analyses. Without accounting for phylogeny, average spawning interval was clearly higher for species with a major accessory activity than for those without (Fig. 2). Repeated-measures' regression found that the difference in

Fig. 1 Species counts and average spawning intervals for classes and orders of fishes in our data with more than one representative per order

	Order	No. Species	Average Spawning Interval (y)
Chondrichthyes	Acipenseriformes	18	4.21
	Carcharhiniformes	30	1.54
	Lamniformes	10	1.70
	Orectolobiformes	3	1.67
	Squaliformes	6	1.39
Osteichthyes	Atheriniformes	4	0.61
	Aulopiformes	2	1.00
	Clupeiformes	12	0.79
	Cypriniformes	48	0.89
	Cyprinodontiformes	8	0.51
	Elopiformes	2	1.00
	Esociformes	4	0.75
	Gadiformes	10	0.93
	Gasterosteiformes	3	0.83
	Perciformes	102	0.88
	Percopsiformes	5	2.00
	Pleuronectiformes	14	0.98
	Salmoniformes	22	1.25
	Scomberiformes	5	1.40
	Scorpaeniformes	21	0.91
	Siluriformes	14	0.74

Summary statistics for classes:

- Chondrichthyes:** N=71, Avg=2.22
- Osteichthyes:** N=287, Avg=0.938

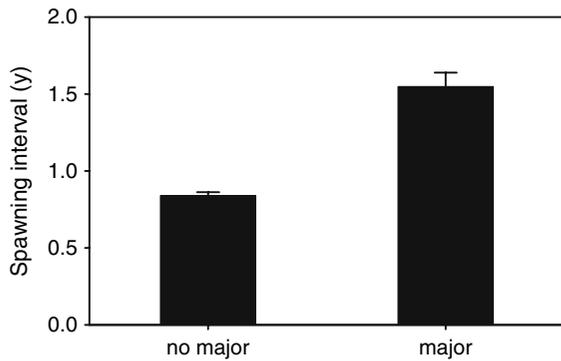


Fig. 2 Comparison of average spawning interval (± 1 SE) for fish species with no major versus a major accessory activity to spawning

average spawning interval (SI) for species with Major = 1 and species with Major = 0, after taking between-order correlation into account, was highly significant ($\chi^2 = 563$, $df = 31$, $P < 0.0001$). Estimated coefficients are shown in Eq. 3.

$$SI = 0.8335 + 0.1313 \text{ Major} \quad (3)$$

The effect of Major was significantly greater than zero (one-sided $P = 0.0007$). Phylogenetic regression produced different estimates for this relationship (Eq. 4).

$$SI = 1.280 + 0.2032 \text{ Major} \quad (4)$$

An F -test with 1,85 degrees of freedom is reported, where the numerator degrees of freedom is the number of predictor variables and the denominator is the phylogenetic degrees of freedom (higher taxonomic nodes included in the analysis). The F -test value of 1.481 had an associated probability of $P = 0.227$. This corresponds to a one-sided T -test with a P -value of 0.1135, which is not significant at $\alpha = 0.1$. The exponent used in calculating heights was estimated to be $\rho = 0.4577$, indicating a moderate influence of phylogeny.

Next, we confirmed that spawning interval increased with each of the accessory activities that comprised the Major index variable. Collinearity between the two major accessories was evident. Without adjusting for phylogenetic effects, average spawning interval varied among the nine values of Cindex with a suggestion of longer spawning intervals with higher values of parental care (Fig. 3). Repeated-measures' regression found a significant positive relationship between SI and the parental care index ($\chi^2 = 552$, $df = 28$, $P < 0.0001$), as shown in Eq. 5.

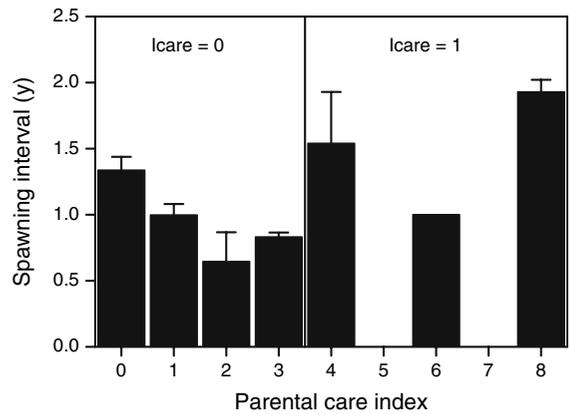


Fig. 3 Comparison of average (± 1 SE) spawning interval for fish species with different levels of parental care. The vertical line separates species with Icare = 0 and those with Icare = 1

$$SI = 0.8266 + 0.0327 \text{ Imig} + 0.0239 \text{ Cindex} + 0.0685 \text{ Cindex*Imig} \quad (5)$$

The positive effects of Cindex (one-sided $P = 0.0239$) and the interaction (one-sided $P = 0.0075$) were significant, but that of Imig was not (one-sided $P = 0.2644$). Phylogenetic regression estimated the relationship shown in Eq. 6 (F -test with 3,82 degrees of freedom = 2.022, two-sided $P = 0.1171$).

$$SI = 1.196 + 0.1456 \text{ Imig} + 0.0379 \text{ Cindex} + 0.0288 \text{ Cindex*Imig} \quad (6)$$

The estimated exponent used in calculating heights was $\rho = 0.6907$. Only the parental care index had a significant positive influence (one-sided $P = 0.065$). However, a model with Imig by itself showed a clearly significant positive effect (F -test with 1,80 degrees of freedom = 5.209, one-sided $P = 0.0126$), suggesting the presence of collinearity between the two predictor variables, Imig and Cindex.

An alternative way to measure the effect of parental care used the binary variable, Icare, rather than the original parental care index, Cindex. These analyses supported the idea that average spawning intervals are longer for species that provide considerable amounts of parental care and those that migrate to spawn. Without accounting for phylogenetic correlation, average spawning interval was higher for species with Icare = 1 than for species with Icare = 0 (Fig. 4). Repeated-measures regression estimated the model given by Eq. 7 ($\chi^2 = 540$, $df = 32$, two-sided $P < 0.0001$).

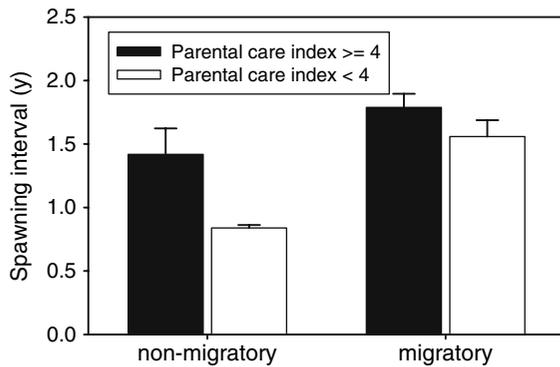


Fig. 4 Comparison of average spawning interval (± 1 SE) for fish species with all four combinations of spawning migration versus no spawning migration and higher versus lower parental care

$$SI = 0.8221 + 0.1070 \text{ Imig} + 0.2215 \text{ Icare} + 0.0326 \text{ Imig} \cdot \text{Icare} \quad (7)$$

The positive effects of *Imig* ($P = 0.0462$) and *Icare* ($P = 0.0040$) were both significant, but not that of the interaction term ($P = 0.3377$). Phylogenetic regression estimated different coefficients for the same model shown in Eq. 8 (F -test with 3,82 degrees of freedom = 1.922, two-sided $P = 0.1325$).

$$SI = 1.214 + 0.1770 \text{ Imig} + 0.2338 \text{ Icare} + 0.1837 \text{ Imig} \cdot \text{Icare} \quad (8)$$

As with repeated-measures' regression, the positive effects of *Imig* (one-sided $P = 0.0628$) and *Icare* (one-sided $P = 0.0708$) were significant. The interaction was also significantly greater than zero (one-sided $P = 0.0982$). The estimated exponent used in calculating heights was $\rho = 0.4884$. These results suggest that the effect of *Icare* on spawning interval is stronger among migratory fishes than among non-migratory fishes.

The results of using two alternative statistical methods applied to three combinations of predictor variables suggested that both parental care and migration are associated with longer spawning intervals. The statistical relationship between spawning interval and migration was weaker when *Cindex*, the original parental care index, was included in the model rather than binary variable, *Icare*. This may be because the correlation between *Icare* and *Imig* is less than the correlation between *Cindex* and *Imig*, reducing the collinearity between the two variables.

Without accounting for phylogenetic correlation, we saw little visual evidence for a monotonic increase

in spawning interval with increasing values of the original parental care index (Fig. 3). At the extreme of no parental care (*Cindex* = 0), we would expect a low average spawning interval for species. However, sturgeons, which do not provide parental care, had the longest spawning intervals. As expected, species assigned a parental care code of “4” had longer mean spawning intervals than those providing less parental care. This category included nest guarders (e.g., basses, catfish, rockfishes, and sticklebacks) and cavefishes, which incubate offspring in their gills. However, these nest-guarding species had longer average spawning intervals than species assigned a parental code of “6,” which consisted of sharks with gestation periods less than 10 months. At the other extreme, species investing the most in parental care conformed to the expectations of the capital-breeding strategy, with a high average spawning interval (Fig. 3). This category included sharks with gestation periods longer than ten months and the coelacanth (See Electronic supplementary material—Appendix II).

Are capital-breeding species considered at greater risk of extinction?

The average spawning interval increased for successively higher categories of extinction risk, but there was considerable overlap of spawning intervals among the extinction risk categories (Fig. 5). Phylogenetic

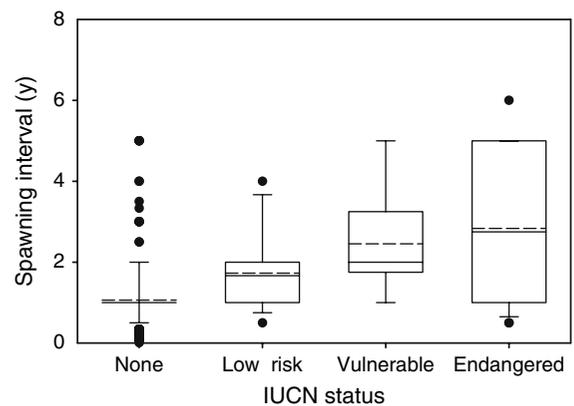


Fig. 5 Box-whisker diagrams showing the distribution of spawning intervals for species with different IUCN status. IUCN value “endangered” combines endangered and critically endangered species. The box defines 25th and 75th percentiles, the horizontal lines (usually) in each box define the mean (dashed) and median (solid). Outliers are shown as dots, and the 5th and 95th percentiles are shown by “whiskers”

regression suggested a significant positive association between extinction risk and spawning interval (F -test with 1,41 degrees of freedom = 11.745, one-sided $P = 0.0007$), as shown in Eq. 9.

$$\text{Risk} = -0.00002 + 0.3863 \text{ SI.} \quad (9)$$

The estimated exponent used in calculating heights was $\rho = 0.3133$.

Discussion

Our analysis confirmed both hypotheses concerning capital-breeding fishes in all but one statistical test, despite the fact that the power of our tests was lowered by accounting for phylogenetic correlation. We found, as Villa-Gispert et al. (2002) did, that phylogenetic effects on life history traits were important, with the majority of variation in spawning interval occurring at the level of class and order. Below, we discuss results for each of the two hypotheses tested by this study.

Are spawning intervals longer for fish species that migrate to spawn or provide parental care?

Our life history analysis demonstrated that the capital-breeding hypothesis, originally developed for birds and reptiles, shows promise for fishes. Fishes with a major accessory activity (migration or parental care) were found to have longer intervals between breeding, even when phylogenetic correlations were accounted for. Species represented in our data confirmed the expected relationships predicted by the capital-breeding paradigm. On average, fish species that migrate to spawn had longer spawning intervals than non-migratory species, and within each migratory category, fish with higher parental care had higher spawning intervals (Fig. 4). Understanding the relationships among these traits can help us to understand the evolutionary constraints that capital-breeding fishes operate under when faced with new environmental challenges.

This analysis could be refined in future by using quantitative measures of the fitness cost of each major accessory activity. For migration, a measure of migration distance or the energetic cost of making a spawning migration could be used. For parental care,

a measure of the risk of starvation incurred by the female parent due to the energy she expends on reproduction could be used. Although parental care in fish has been a popular subject for research, few studies provide quantitative information on both parental expenditure and investment (Smith & Wootton, 1995). Including this type of quantitative information would account for several things that our index did not. For example, large fishes can sustain longer periods of starvation than smaller fishes. As another example, although sturgeons do not provide parental care, their eggs can take up to 30% of female body weight (Wei et al., 1997), making it difficult for them to feed.

Our analyses did not consider within-species variation or the influence of environmental factors on spawning interval. Life history traits such as spawning interval exhibit phenotypic plasticity in some taxa. Individual variation in spawning interval is found among many fishes, including some capital-breeding taxa. Rideout et al. (2005) propose that reproductive cycles can be interrupted due to poor nutrition or inadequate environmental conditions, overcrowding, and a shortage of mates. Understanding what factors influence spawning frequency and understanding the consequences of infrequent spawning can be important to the management of capital-breeding stocks with plastic reproductive timing. Uncertainties in predictions of sustainable harvest or population recovery can be reduced if efforts are made to determine and include realistic estimates of spawning interval, rather than assuming either annual spawning or adopting the minimum interval that is physiologically possible.

Are capital-breeding species considered at greater risk of extinction?

We confirmed that fishes with longer spawning intervals tended to belong to higher IUCN extinction-risk categories (Fig. 5), and that a positive association exists between our IUCN index and spawning interval. Three caveats accompany this result. First, we note that variation in IUCN status among stocks was not considered in our analysis. Second, as in any regression, the direction of causality might be reversed. IUCN status is justified, in some cases, by population modeling of species'

life history traits (Musick, 1999), as well as the actual status and trends of its stocks. However, most marine fishes listed in the IUCN Red List of Threatened Animals were placed there because of observed population declines.

Third, risks associated with spawning interval and correlated life history traits could be confounded, and parsing out the roles of individual traits on extinction risk is difficult. It is well known that migratory fishes tend to be at higher risk (e.g., Angermeier, 1995). Among migratory species large-bodied fishes tended to be at higher risk, whereas among non-migratory species small-bodied freshwater fishes with restricted geographic ranges tended to be at greater risk of extinction (Parent & Schriml, 1995; Angermeier, 1995; Reynolds et al., 2005). We recommend that further comparative studies designed to understand life history correlates of extinction risk include spawning interval with a comprehensive array of life history characteristics, and we recommend that such studies focus on including atypical species that “break” life history correlations.

When viewed in the context of existing life history classifications, capital breeding adds a new dimension that cuts across recognized strategies. Recognized life history strategies of fishes (Winemiller & Rose, 1992; Villa-Gispert et al., 2002; Villa-Gispert & Moreno-Amich, 2002; King & McFarlane, 2003) include periodic, opportunistic, equilibrium, salmonid, and intermediate strategies. We examined the list of putative capital-breeding species (See Electronic supplementary material—Appendix II) to see whether they tended to occupy similar positions within the existing life history framework. We determined that capital breeders follow every strategy except for the opportunistic strategy. Equilibrium strategists are represented by sharks (Frisk et al., 2001; King & McFarlane, 2003) and the cavefish (Winemiller, 2005). Periodic strategists are represented by long-lived and late-maturing sturgeons and paddlefishes (Jager et al., 2002). The list also includes several intermediate strategists (e.g., cod, halibut, and mackerel) and salmonid strategists (e.g., Atlantic salmon, trout, and Arctic charr).

The observation that extinction risk is higher for capital-breeding species leads to an apparent paradox. If the capital-breeding life history is an adaptive solution that results in higher fitness by minimizing the frequency of costly expenditures on reproduction, how

can it also put populations at risk? One possible answer is that the environment has changed since the capital-breeding strategy evolved (multiple times), lowering its fitness. Many capital-breeding species also migrate or have traits characteristic of a ‘slow’ life history (i.e., small litter, slow growth rate, late maturation, and long gestation period). Empirical studies have confirmed that species that migrate (this study) and those with a ‘slow’ life history (Johst & Brandl, 1997; Jennings et al., 1998; Dulvy et al., 2003) are at higher risk of extinction than their counterparts are. Changes in the environment might explain why both these groups are now less advantageous than they were in the past. In theory, the evolution of a ‘slow’ life history is favored when adult mortality is low. When human activities increase adult mortality (e.g., fishing and habitat degradation), these species cannot respond quickly by increasing their spawning frequencies. Likewise, fragmentation and degradation of aquatic habitats has increased the mortality risk associated with migration and the energetic and survival benefits of using multiple habitats. In short, it is likely that the fitness landscape has changed in such a way as to put capital-breeding fishes at a disadvantage.

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