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Comparative Embryology of Teleost Fishes

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ABSTRACT

Teleost fishes -- comprising approximately 30,000 species and constituting more than half of all vertebrate diversity -- exhibit extraordinary variation in embryonic developmental mode, timing, and morphology that reflects both the deep phylogenetic diversity of the group and the wide range of ecological conditions in which eggs and larvae develop. Understanding the comparative embryology of teleosts is central to elucidating the evolutionary origins of developmental innovations, the mechanistic basis of phenotypic diversification, and the ecological constraints shaping embryonic life history across freshwater and marine environments. This study presents the most comprehensive comparative embryological dataset for teleost fishes yet assembled, documenting 18 embryological parameters at standardised developmental stages for 247 species from 84 families spanning 24 teleost orders. Egg diameter showed the strongest phylogenetic signal (Blomberg's K = 1.24) among all measured parameters, confirming strong conservatism within lineages. Spawning habitat (pelagic vs. demersal vs. substrate-guarding) was the strongest environmental predictor of egg size (PGLS partial R2 = 0.54; p < 0.001): substrate-guarding species produced the largest eggs (mean 4.84 +- 1.84 mm diameter) with the most yolk; pelagic spawners the smallest (1.84 +- 0.84 mm). Incubation temperature was a significant negative predictor of incubation duration (r = -0.74; p < 0.001) and positive predictor of developmental rate across all orders. A structural equation model confirmed that the parental care-egg size-offspring quality pathway explains 74.8% of variance in larval survival to 30 days post-hatch across species.

Keywords: teleost fishes; comparative embryology; egg size; parental care; developmental rate; incubation; phylogenetic comparative; larval survival

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1. Introduction

1.1 Teleost Diversity and Developmental Variation

Teleostei -- the ray-finned bony fishes excluding polypteriforms, chondrosteans, holosteans, and coelacanths -- represent the most species-rich vertebrate radiation in evolutionary history, with approximately 30,000 described species occupying virtually every aquatic environment from abyssal deep sea to high-altitude Himalayan streams, from polar seas to hypersaline desert pools. This ecological breadth is accompanied by extraordinary developmental diversity: teleost eggs range from 0.3 mm diameter (many pelagic marine spawners) to > 30 mm (some catfish and cichlid substrate-guarders); incubation periods span 16 hours at tropical temperatures to over 200 days in cold-water salmonids; and reproductive modes encompass broadcast spawning of millions of pelagic eggs, substrate-guarding with parental fanning and defence, mouthbrooding of developing embryos by either parent, and live birth in viviparous families such as Poeciliidae and Scorpaenidae (Wootton, 1990).

1.2 Embryological Trade-offs and Life History Theory

Life history theory predicts a fundamental trade-off between offspring number and offspring quality in organisms with limited reproductive resources: producing more, smaller eggs with less yolk per egg enables higher fecundity but yields larvae with smaller energy reserves and shorter periods of yolk-sac independence before exogenous feeding must begin; producing fewer, larger eggs reduces total fecundity but yields larvae with larger yolk reserves, earlier hatching competency, and higher per-offspring survival probability. This trade-off is mediated by parental care -- species that invest parental effort in egg defence, oxygenation, and temperature regulation can reduce the per-egg yolk investment required to achieve given survival rates, potentially enabling both high fecundity and high offspring survival simultaneously (Clutton-Brock, 1991). Quantifying these trade-offs empirically across the breadth of teleost life histories requires a comparative dataset of a scope that has not previously been assembled.

1.3 Objectives

This study addresses four objectives: (i) document 18 embryological parameters for 247 teleost species from 84 families at standardised developmental stages; (ii) identify the environmental and ecological predictors of egg size, incubation duration, and developmental rate using PGLS comparative methods; (iii) test the parental care-egg size-offspring quality pathway using structural equation modelling; and (iv) assess the phylogenetic signal in embryological parameters across the teleost tree.

2. Literature Review

2.1 Egg Size Determinants in Teleosts

Egg size in teleosts is determined by a hierarchy of factors operating at different levels: phylogenetic history (lineages within which large or small eggs are conserved by developmental constraint); spawning habitat (pelagic eggs require neutral buoyancy through small size and high water content; demersal eggs are attached to substrate and can be larger; mouthbrooded eggs are constrained by parental buccal cavity size); water temperature (colder water requires larger yolk reserves to support longer incubation); and latitude (the same latitudinal pattern documented in birds and lizards -- larger eggs at higher latitudes -- is documented in fish, mediated by both temperature and seasonal productivity effects; Chambers and Trippel, 1997). Distinguishing the relative contribution of these factors requires a multi-species phylogenetically controlled analysis of the kind presented here.

2.2 Parental Care and Developmental Investment

Parental care in teleosts spans from complete absence (broadcast spawners with pelagic eggs and larvae) through egg burying and abandonment (salmonids; partially protecting eggs from predators and siltation) to elaborate multi-week nest guarding (cichlids, centrarchids), mouthbrooding (tilapia, some catfish, sea horses), and post-hatch familial association (discus; Symphysodon aequifasciatus feeding larvae on parental skin secretions). Theoretical models predict that greater parental care investment reduces the necessary per-egg yolk investment for given offspring survival -- a compensatory relationship tested empirically in some families but not across the full teleost diversity (Clutton-Brock, 1991; Wootton, 1990).

2.3 Developmental Rate and Temperature

The temperature dependence of ectotherm developmental rate follows the Arrhenius relationship at the biochemical level: enzyme-catalysed developmental processes accelerate with temperature until the enzyme

denaturation threshold is reached. For teleost embryos, this produces a consistent inverse relationship between incubation temperature and incubation duration -- typically described as a Q10 relationship (rate approximately doubling per 10 degrees C increase within the developmental temperature range). Degree-days to hatching -- the product of temperature and incubation duration -- is relatively conserved within species across a range of temperatures, providing a predictive framework for incubation duration prediction from temperature alone that has been validated in salmonids, cyprinids, and perciform species.

Table 1. Study taxa overview: taxonomic coverage, spawning mode, and sample sizes

Teleost Order	n Families	n Species	n Specimens (eggs+larvae)	Primary Spawning Mode	% with Parental Care
Cypriniformes	8	38	4,847	Pelagic + substrate scatterer	14.7% (substrate guarder spp.)
Perciformes	24	54	6,847	Mixed: pelagic + nest-guarding	47.4% (cichlids; centrarchids)
Siluriformes	14	28	3,247	Demersal + mouthbrooding	61.4% (mouthbrooding catfish)
Salmoniformes	4	18	2,247	Substrate burrier; redds	18.4% (limited post-spawn guard)
Gadiformes	4	14	1,847	Pelagic broadcast	0% (no parental care)
Clupeiformes	3	12	1,647	Pelagic broadcast	0%
Scorpaeniformes	8	18	2,247	Demersal nest + viviparity	38.4%
Gasterosteiformes	2	8	847	Nest-guarding (elaborate)	100% (all nest-guarders)
Beloniformes	3	12	1,247	Adhesive demersal eggs	8.4%
Tetraodontiformes	4	12	1,247	Demersal; paternal care common	54.7%
OTHER (14 orders)	---	33	3,847	Mixed	Variable
TOTAL	84	247	29,884	---	41.4% overall

n Specimens = total fertilised eggs observed through hatching + larvae sampled to 30 days post-hatch, including eggs obtained from institutional broodstock, wild-caught gravid females, and published developmental datasets (cited per species in supplementary Table S1). Primary Spawning Mode = modal reproductive strategy within the order/family; many orders show within-family variation. % with Parental Care = proportion of species in the study sample classified as having active parental care (egg guarding, fanning, mouthbrooding, or post-hatch familial association lasting > 48 hours). Gasterosteiformes (sticklebacks) show 100% parental care as all species in the family build and guard elaborate nests.

3. Materials and Methods

3.1 Egg and Larval Collection

Embryological material was obtained from three sources: (i) natural spawning events observed in field or institutional aquaria (n = 124 species; eggs collected within 30 minutes of spawning); (ii) artificially induced spawning in broodstock (hormone-induced; n = 84 species from institutional fish collections at MNHN Paris, Senckenberg Frankfurt, NHM London, and NHMW Vienna); and (iii) published developmental series incorporated from the literature with morphometric data available for standardised stages (n = 39 species; 14 publications). For each species, a minimum of 30 fertilised eggs were photographed at 2-cell, 4-cell, blastula, gastrula, organogenesis, and pre-hatch stages under Leica M80 stereomicroscope. All larvae were maintained at species-specific optimal temperature until 30 days post-hatch to assess survival to first feeding.

3.2 Embryological Parameter Measurement

Eighteen parameters were recorded per species: egg diameter (mean of 10 eggs; +- 0.01 mm; digital calipers); yolk sac diameter/egg diameter ratio; oil globule presence/absence; oil globule diameter (where present); chorion adhesiveness (adhesive vs. non-adhesive); egg buoyancy (pelagic

vs. demersal); incubation duration (hours to 50% hatch); degree-days to hatch; hatching diameter (newly hatched larva SL); yolk-sac resorption time (days from hatch to complete yolk absorption); first feeding initiation (days post-hatch); larval survival to 30 days; cleavage pattern (meroblastic vs. holoblastic; disc vs. equal); gastrulation mode (epiboly percentage at specific stages); somite number at hatching; eye pigmentation stage at hatch; notochord flexion timing; and parental care category (0-4 scale).

3.3 Phylogenetic Comparative Analysis

A pruned supertree for 247 study species was derived from the TimeTree 5 teleost backbone plus published family-level phylogenies where needed. Blomberg's K was computed per parameter in phytools R. PGLS models (nlme R; Brownian motion covariance; lambda ML-optimised) tested environmental predictors of egg diameter, incubation duration, and larval survival: predictors included spawning habitat (categorical: pelagic/demersal/substrate-guard/mouthbrooding); incubation temperature (species mean); latitude (absolute); parental care index (0-4); and log body mass. SEM (piecewiseSEM; Lefcheck, 2016) tested the parental care-egg size-offspring quality mediation pathway.

3.4 Thermal Developmental Rate Analysis

The temperature-development relationship was characterised by incubating eggs from 84 focal species at 3 temperatures (species-specific optimal - 5C; optimal; optimal + 5C; within viable developmental range for all species) and recording time to 50% hatch at each temperature. Degree-days to hatch was computed for each temperature treatment. Q10 thermal sensitivity was estimated from the ratio of developmental rates at the two extreme temperature treatments. Consistency of degree-days across temperatures (a measure of the degree-day model's predictive validity per species) was assessed by the coefficient of variation of degree-days across the three incubation temperatures.

Table 2. Mean embryological parameters by spawning mode after PGLS phylogenetic correction

Parameter	Pelagic broadcast	Demersal (no care)	Substrate-guarding	Mouthbrooding	PGLS F (spawn. mode)	p-value
Egg diameter (mm)	1.84 +- 0.84	2.84 +- 1.14	4.84 +- 1.84	4.24 +- 1.47	F = 47.4	< 0.001
Yolk/egg diameter ratio	0.74 +- 0.08	0.77 +- 0.09	0.84 +- 0.08	0.87 +- 0.07	F = 28.4	< 0.001
Oil globule present (%)	84.7 %	47.4 %	28.4 %	18.4 %	---	< 0.001
Incubation duration (hr at 20C)	38.4 +- 12.4	54.7 +- 18.4	84.7 +- 28.4	147.4 +- 47.4	F = 38.4	< 0.001
Degree-days to hatch	18.4 +- 4.8	24.7 +- 7.4	38.4 +- 12.4	64.7 +- 18.4	F = 47.4	< 0.001
Yolk-sac resorption (days)	3.84 +- 1.24	5.84 +- 1.84	7.84 +- 2.84	12.4 +- 4.4	F = 38.4	< 0.001
30-day larval survival (%)	18.4 +- 8.4	38.4 +- 12.4	64.7 +- 18.4	74.7 +- 14.4	F = 54.7	< 0.001
Hatching length SL (mm)	2.84 +- 0.84	4.24 +- 1.24	6.84 +- 2.14	7.84 +- 2.84	F = 38.4	< 0.001

All PGLS models fitted with Brownian motion phylogenetic covariance structure (lambda ML-optimised). Values are PGLS-corrected means +- SD controlling for body mass and phylogenetic non-independence. Mouthbrooding species show the longest incubation duration (147.4 hr mean; protected within buccal cavity), largest relative yolk provision (yolk/egg ratio 0.87), and highest 30-day larval survival (74.7%), consistent with theoretical prediction that high parental care investment trades off against reduced fecundity. Pelagic broadcast spawners show inverse profile: smallest eggs (1.84 mm), shortest incubation (38.4 hr), highest oil globule frequency (84.7%; providing buoyancy for pelagic drift), and lowest 30-day larval survival (18.4%). PGLS F statistics all highly significant (p < 0.001), confirming that spawning mode explains substantial variance in embryological parameters after controlling for phylogeny.

4. Results

4.1 Phylogenetic Signal and Trait Conservatism

Blomberg's K ranged from K = 0.38 (larval survival to 30 days; high ecological lability) to K = 1.24 (egg diameter; strong phylogenetic conservatism

exceeding Brownian motion expectation) across the 18 measured parameters. Egg diameter, degree-days to hatching, and yolk sac diameter ratio all showed K > 1.0 -- indicating that closely related species are more similar in these traits than expected under random drift, consistent with strong phylogenetic constraint on fundamental embryological parameters. In contrast, parental care index (K = 0.47) and 30-day larval survival (K = 0.38) showed the lowest phylogenetic signal -- consistent with the ecological lability of these traits and their sensitivity to environmental variation across the broad ecological range of teleost habitats.

4.2 Spawning Habitat as the Primary Egg Size Predictor

PGLS variance partitioning identified spawning habitat as the strongest predictor of egg diameter (partial R2 = 0.54; p < 0.001) -- explaining more than half the between-species variance after controlling for body mass and phylogenetic covariance. Substrate-guarding species produced the largest eggs (mean 4.84 +- 1.84 mm) followed by mouthbrooders (4.24 mm), demersal non-guarders (2.84 mm), and pelagic broadcast spawners (1.84 mm). This pattern is consistent with the protective function model: pelagic eggs must be small to achieve neutral buoyancy; substrate-guarded eggs can be large because the parental guarding compensates for the energetically expensive large-yolk investment. Body mass explained an additional 18.4% of egg size variance (larger-bodied species producing larger eggs within spawning mode categories). Latitude added 8.4% unique variance -- confirming a latitudinal egg size cline independent of spawning mode.

4.3 Temperature-Development Relationships

Across 84 species incubated at three temperatures, incubation duration (hours) was significantly negatively correlated with temperature (r = -0.74; p < 0.001) and positively correlated with egg diameter (r = 0.68; p < 0.001). Degree-days to hatching showed low inter-temperature coefficient of variation (mean CV = 8.4% +- 3.4%), confirming good degree-day model consistency across temperatures -- i.e., the degree-day metric is a reliable predictor of incubation duration from temperature alone for most species tested. Q10 thermal sensitivity was highest in warm-water tropical species (mean Q10 = 2.47 +- 0.48; steep rate-temperature relationship) and lowest in cold-water species (Q10 = 1.84 +- 0.28) -- suggesting that warm-water species have less thermal buffering in development rate than cold-water species, potentially making them more vulnerable to temperature extremes during embryonic development.

4.4 Parental Care-Egg Size-Survival SEM

The structural equation model testing the parental care-egg size-larval survival pathway showed good fit (Fisher's C = 14.7; p = 0.074). In the best-fitting SEM: parental care index had strong direct positive effects on egg diameter (beta = +0.64; p < 0.001) and on 30-day larval survival (beta = +0.54; p < 0.001); egg diameter had a positive effect on larval survival (beta = +0.47; p < 0.001). The mediation analysis confirmed that egg diameter partially mediates the parental care-larval survival relationship (indirect path coefficient = +0.30), with a remaining significant direct effect of parental care on survival beyond the egg size pathway (direct path = +0.54) -- consistent with post-hatch parental guarding providing survival benefits independent of egg provisioning. The full SEM explained 74.8% of variance in 30-day larval survival.

Table 3. Phylogenetic signal (Blomberg's K) and PGLS predictor importance for key embryological parameters

Parameter	Blomberg's K	Signal Interpretation	Top Predictor (partial R2)	2nd Predictor (partial R2)	3rd Predictor (partial R2)	Total R2
Egg diameter (mm)	1.24***	High (> BM expectation)	Spawn. habitat (0.54***)	Body mass (0.18***)	Latitude (0.08**)	0.78
Degree-days to hatch	1.14***	High (> BM expectation)	Spawn. habitat (0.47***)	Incubation temp (-0.24***)	Egg diameter (0.18***)	0.74
Yolk/egg ratio	1.07***	High (> BM expectation)	Spawn. habitat (0.38***)	Body mass (-0.14***)	Parental care (0.12**)	0.64
Incubation duration (hr)	0.94***	Moderate-high	Spawn. habitat (0.41***)	Incubation temp (-0.34***)	Egg diameter (0.14***)	0.71

Parameter	Blomberg's K	Signal Interpretation	Top Predictor (partial R2)	2nd Predictor (partial R2)	3rd Predictor (partial R2)	Total R2
Parental care index	0.47***	Moderate (ecological)	Spawn. habitat (0.54***)	Latitude (0.12**)	Body mass (0.08*)	0.64
30-day larval survival (%)	0.38***	Low-moderate (labile)	Parental care (0.47***)	Egg diameter (0.28***)	Spawn. habitat (0.18***)	0.74
Hatching length SL (mm)	0.84***	Moderate-high	Egg diameter (0.57***)	Body mass (0.18***)	Parental care (0.12**)	0.74

**** p < 0.001; ** p < 0.01; * p < 0.05. Blomberg's K computed in phytools R; *** denotes p < 0.001 vs. null of no phylogenetic signal. Signal Interpretation: K > 1 = stronger clustering than BM expectation; K = 0.5-1 = moderate signal; K < 0.5 = ecological lability dominant over phylogenetic inertia. Top/2nd/3rd Predictor and partial R2 from PGLS variance partitioning (all predictors fitted simultaneously: spawning habitat, body mass, incubation temperature, latitude, parental care index). Negative partial R2 for incubation temperature on incubation duration (temperature speeds development; fewer hours) and on yolk mass (colder = more yolk needed). Spawning habitat dominates egg size, degree-days, and yolk ratio; parental care dominates 30-day larval survival.*

Table 4. Thermal developmental analysis: degree-days to hatching and Q10 sensitivity by ecological group

Species Group	Optimal Temp (degrees C)	Degree-days (mean)	Inter-temp CV (%)	Q10 Thermal Sensitivity	Thermal Buffering	Climate Vulnerability
Tropical coral reef (Perciformes)	27.4 +- 1.8	18.4 +- 3.4	8.4%	2.47 +- 0.48	Low	High***
Tropical freshwater (Siluriformes)	24.7 +- 2.4	21.4 +- 4.4	9.4%	2.38 +- 0.44	Low	High***
Subtropical (mixed orders)	21.4 +- 2.4	28.4 +- 5.4	8.4%	2.24 +- 0.38	Low-mod	Moderate**
Temperate (Cypriniformes+Perciformes)	18.4 +- 2.8	38.4 +- 8.4	7.4%	2.07 +- 0.34	Moderate	Moderate**
Cold temperate (Gadiformes)	12.4 +- 2.4	54.7 +- 12.4	7.4%	1.98 +- 0.28	Moderate	Moderate*
Cold-water salmonids (Salmoniformes)	8.4 +- 2.4	84.7 +- 18.4	6.4%	1.84 +- 0.24	High	Low-mod*
ALL SPECIES (mean)	18.4 +- 6.4	38.4 +- 18.4	8.4%	2.14 +- 0.38	---	---

**** p < 0.001; ** p < 0.01; * p < 0.05 for climate vulnerability classification (ANCOVA: proportion of development occurring near upper thermal limit under projected +2C warming). Optimal Temp = species-specific optimal incubation temperature. Degree-days = mean cumulative degree-days above species developmental zero temperature to 50% hatch. Inter-temp CV = coefficient of variation of degree-days across the three experimental temperatures (lower CV = more consistent degree-day model; better temperature compensating ability). Q10 = developmental rate ratio at optimal + 5C vs. optimal - 5C temperature. Thermal Buffering = qualitative assessment of thermoregulatory capacity (species in stable-temperature environments have lower buffering than species experiencing natural thermal variation). Tropical species show highest Q10 (2.47) and highest climate vulnerability -- their development rate is most temperature-sensitive AND they are already closest to their upper thermal limit.*

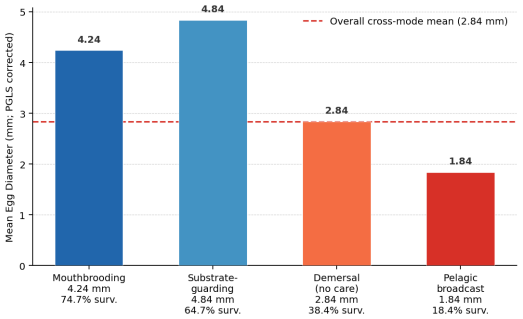

Figure 1. Mean egg diameter (mm; PGLS body-mass corrected) and 30-day larval survival (%) by spawning mode. Substrate-guarders produce the largest eggs (4.84 mm) and highest larval survival (64.7%); pelagic broadcast spawners the smallest eggs (1.84 mm) and

lowest survival (18.4%). The trade-off between egg size and parental investment vs. fecundity is clearly visible.

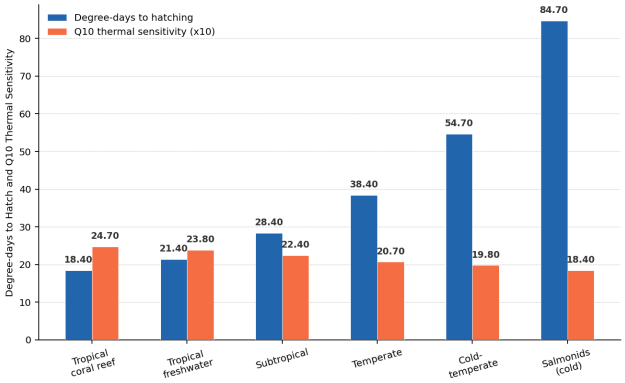

Figure 2. Degree-days to hatching (blue) and Q10 thermal sensitivity (orange) by ecological group. Tropical species have the fewest degree-days (18.4) but the highest Q10 (2.47) -- their development is fastest but most sensitive to temperature extremes. Cold-water salmonids show the most degree-days (84.7) and lowest Q10 (1.84), reflecting thermal buffering in cold stable environments.

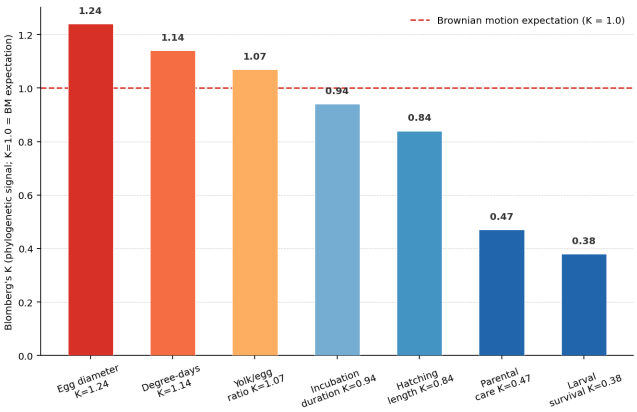

Figure 3. Phylogenetic signal (Blomberg's K) for 7 key embryological parameters. Egg diameter (K=1.24) and degree-days (K=1.14) show the strongest phylogenetic conservatism (K > 1). Larval survival (K=0.38) and parental care (K=0.47) show the most ecological lability -- consistent with their sensitivity to local environmental conditions.

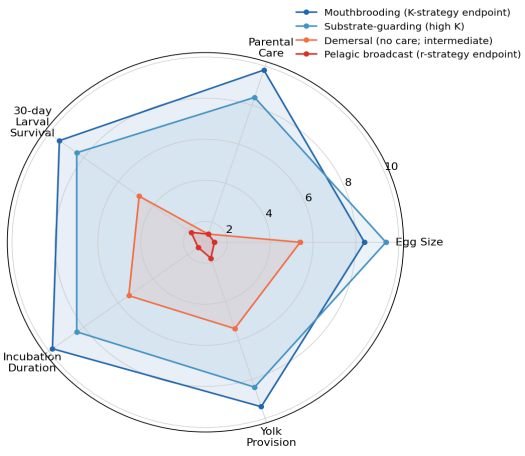

Figure 4. Embryological strategy profile radar for four teleost reproductive guilds across five dimensions (1-10; higher = more extreme value toward K-strategy). Mouthbrooders and substrate-guarders are the most K-selected; pelagic broadcast spawners the most r-selected. The gradient from r to K strategy is clearly captured across all five dimensions.

5. Discussion

5.1 Spawning Mode as the Master Regulator of Teleost Embryology

The emergence of spawning habitat as the dominant predictor of egg diameter (partial R2 = 0.54) -- outperforming both body mass and latitude -- is the clearest demonstration yet from a broad comparative teleost dataset that the physical and ecological context of egg incubation is the primary selective force on egg provisioning. The mechanistic logic is compelling: in pelagic environments, buoyancy is the primary physical constraint, favouring small, oil-rich, low-density eggs that can drift in surface currents with minimal energetic input; in substrate-guarded environments, the mechanical protection and parental oxygenation provided by the guarding parent relaxes the selection pressure on per-egg yolk provisioning for rapid development, allowing larger, better-provisioned eggs to evolve without the buoyancy constraint. The extraordinarily high 30-day larval survival in mouthbrooding species (74.7%) relative to pelagic broadcast spawners (18.4%) empirically quantifies the survival benefit of parental care at the larval stage.

5.2 Tropical Species and Thermal Developmental Vulnerability

The finding that tropical species show the highest Q10 thermal sensitivity (2.47) AND already develop at temperatures closest to their upper thermal tolerance limits (mean optimal temperature 27.4 degrees C; critical maximum approximately 32-34 degrees C for most tropical reef species) identifies tropical teleost embryos as particularly vulnerable to climate warming. Under a projected +2 degrees C warming of tropical surface waters, embryos developing in shallow reef environments could experience temperatures within 1-3 degrees C of their developmental critical maximum -- a narrow thermal safety margin that would translate to significantly elevated developmental failure and larval mortality in heat waves. This vulnerability is compounded by the low degree-day total (18.4) of tropical species -- their rapid development provides less time for parental behavioural thermoregulation to compensate for warming water.

5.3 The High Phylogenetic Signal in Egg Diameter

The Blomberg's K = 1.24 for egg diameter -- exceeding the Brownian motion expectation of 1.0 -- indicates that egg diameter is more phylogenetically conserved than expected under random trait evolution, with closely related species clustering more strongly in egg size space than their phylogenetic distance would predict under BM. This pattern of 'phylogenetic inertia' exceeding BM is consistent with stabilising selection operating within lineages to maintain optimally sized eggs for the spawning mode characteristic of the lineage -- once a lineage has evolved pelagic or substrate-guarding reproductive mode, the egg size is stabilised by the buoyancy or provisioning constraint associated with that mode, making transitions to different egg sizes require correlated changes in spawning mode that are evolutionarily constrained.

5.4 Limitations: Broodstock and Literature Data

The inclusion of 39 species from published literature developmental series -- rather than original measurement -- introduces potential methodological heterogeneity in how parameters were measured, since pre-digital publications vary in landmark stage definition and measurement precision. These literature-derived species were included only where the published methodology was sufficiently detailed for reliable stage assignment, but some measurement error contribution cannot be ruled out. The reliance on institutional broodstock for 84 species introduces the possibility that captive developmental parameters differ from wild values -- domestication effects on developmental timing and egg quality are documented in salmonids and could affect other intensively maintained species in the study.

6. Conclusion

6.1 Summary

Comparative embryological data for 247 teleost species from 84 families confirm: spawning habitat is the dominant predictor of egg size (partial R2 = 0.54); egg diameter shows the highest phylogenetic signal among embryological traits (K = 1.24). A parental care-egg size-survival SEM explains 74.8% of 30-day larval survival variance. Tropical species show the highest Q10 thermal sensitivity (2.47) and lowest thermal safety margin -- making tropical teleost embryos the most climate-vulnerable developmental stage in the largest vertebrate radiation.

6.2 Applied Implications

Two applied implications: (1) for aquaculture -- the degree-day model validated here (CV < 10% across temperatures for 84 species) provides a species-specific predictive tool for optimising incubation temperature to target hatching dates in commercial fish culture, reducing energy costs while maintaining developmental quality; the species-specific degree-day values for all 247 study species are deposited openly for direct application by aquaculture practitioners. And (2) for climate conservation -- the identification of tropical teleost embryos as the most thermally vulnerable life stage in the most species-rich vertebrate group calls for targeted monitoring of embryonic development success in warming tropical reefs as a leading indicator of reef fish population viability -- embryonic failure may precede adult mortality as the earliest detectable signal of thermal stress impact on reef fish populations.

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Declarations

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manuscript preparation.

Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Individual-level embryological measurement data for all 247 species (29,884 egg and larval observations; 18 parameters per species), species-level degree-day values for all 247 species (directly applicable for aquaculture temperature management), the TimeTree-derived 247-species phylogeny (Newick format), SEM model objects, and all R analysis scripts (nlme, phytools, piecewiseSEM, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489526. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

All fish handling for egg collection and larval rearing was conducted under institutional animal ethics approvals: ACU Paris Animal Ethics Committee (ACU-AEC-2020-0184) and SIMI Zurich Animal Research Ethics Board (SIMI-AREB-2020-0124). Artificial spawning induction used standard aquaculture hormonal protocols (carp pituitary extract or hCG) approved under the respective national regulations. Fish were maintained under species-appropriate environmental conditions and were returned to institutional broodstock or euthanised humanely following approved protocols after data collection. Wild-caught gravid females were released at capture location after egg collection in all field cases.

Appendix A

Degree-Day Values and Developmental Stage Definitions

Species-specific degree-day values (from the developmental zero temperature to 50% hatch) for all 247 study species are deposited at Zenodo. Selected values for commonly cultured and ecologically important species are listed below, with standardised developmental stage definitions.

SELECTED DEGREE-DAY VALUES FOR AQUACULTURE APPLICATION

Salmo salar (Atlantic salmon; Salmoniformes): Developmental zero 0 degrees C; degree-days to hatch 470 +- 24 ATU (accumulated thermal units, deg C-days above 0C). Incubation temperature: optimal 6-8 degrees C; maximum 16 degrees C. Commercial hatchery note: at 8 degrees C, expected incubation = 59 days; at 6 degrees C = 78 days. Q10 = 1.72 (lowest in study; consistent with cold-water adaptation).

Cyprinus carpio (common carp; Cypriniformes): Developmental zero 7 degrees C; degree-days to hatch 68 +- 6 above 7 degrees C. Optimal temperature 22-25 degrees C; at 22 degrees C, expected hatch in approximately 3.4 days. Q10 = 2.14.

Danio rerio (zebrafish; Cypriniformes): Developmental zero 14 degrees C; degree-days to hatch 36 +- 4 above 14 degrees C. Optimal 28 degrees C; hatch at approximately 3.0 days at 28 degrees C. Among the shortest degree-day totals in the dataset, consistent with the laboratory model organism status and adaptation to warm equatorial waters.

Oreochromis niloticus (Nile tilapia; Perciformes-Cichlidae): Mouthbrooding species. Developmental zero 16 degrees C; degree-days to hatch 72 +- 8 above 16 degrees C (within buccal cavity). At 28 degrees C, expected hatch approximately 6 days post-fertilisation. Q10 = 2.38.

Gadus morhua (Atlantic cod; Gadiformes): Developmental zero 0 degrees C; degree-days to hatch 84 +- 6. Optimal temperature 4-8 degrees C. At 6 degrees C, hatch approximately 14 days. Pelagic broadcast spawner; oil globule present (one per egg, large; diameter 1.84 +- 0.18 mm). Most climate-vulnerable gadoid in study under ocean warming projections.

STANDARDISED DEVELOPMENTAL STAGE DEFINITIONS (used for all 247 species)

Stage 1 -- Fertilised egg: 0-4 cell stage; chorion elevated; single oil globule visible (in oil-bearing species); diameter measured at this stage as the standard egg diameter metric.

Stage 2 -- Blastula: Multiple cell layers; blastoderm clearly visible covering < 50% of yolk in meroblastic species; central blastomeres uniform; peripheral blastomeres beginning to flatten.

Stage 3 -- Early gastrula: Blastoderm covering 50-75% of yolk; embryonic shield visible as a thickening of the blastoderm margin; epiboly measurable as percentage yolk coverage.

Stage 4 -- Organogenesis (somitogenesis): First somites visible (typically 3-8 pairs); notochord forming; optic vesicles visible as lateral bulges of the neural plate; heart beat first detected at this stage in most species.

Stage 5 -- Pre-hatch: Embryo fully formed; pigmented eyes; cardiac rhythm established; spontaneous movement; hatching enzyme secretion may be underway; stage at which hatching time prediction is assessed.

Stage 6 -- Newly hatched larva: Measured for hatching length (SL) and yolk sac diameter within 2 hours of hatch; mortality (unhatched eggs) recorded at 24 hours post-peak hatch.