Fish Life History Patterns and Reproductive Strategies

Life History Theory

- The analysis of the phenotypic causes of variation in fitness and exposes the pervasive tension between adaptation and constraint
    - Stearns 1992. The evolution of life-histories
  - Since successful reproduction results in genetic contributions to future generations (evolutionary fitness), analysis of these behaviors often lead to evolutionary arguments

Life History Patterns

- A variety of traits that may differ among individuals or among species
  - Size of eggs produced
  - Age at first maturation
  - Frequency of spawning
  - Pattern of spawning
    - Iteroparity
      - Multiple spawnings
    - Semelparity
      - Single spawning

Advantages of Semelparity

- Semelparity is favored if an animal could produce at least one more viable offspring by increasing the amount of reproductive energy utilized and then dying
  - Cole (1954) The Quart. Rev. of Biol. 29:103-137
    - Evaluated tactics of Semelparity and Iteroparity
      - Age at first reproduction
      - Number of young in litter
      - Estimated gained future genetic fitness if animal survived to breed again
      - Fish have relatively large litter sizes (fecundity) and early maturation
    - Fish should be semelparous
      - however, most fish are iteroparous

Advantages of Iteroparity

- Reconciliation of Cole's predictions in that most vertebrates, especially fishes are iteroparous
    - Garth Murphy (1968) The Amer. Nat. 102:391-403
  - Asked why did natural selection favor Iteroparity based on how common it was

Advantages of Iteroparity

- Evaluated other factors that influenced iteroparity
  - Survival of young
    - Variation in successful spawning
    - Variation between reproductive success and reproductive life span
      - » The more variation in success of spawning, the longer the reproductive life span
      - » Spawning success more important than simple fecundity in determining iteroparity and semelparity

Advantages of Iteroparity

– Evaluated other factors that influenced iteroparity
  – Therefore
    » With large variations in spawning success, over time the frequency of genotypes w/ semelparous tactics would decline
    » Iteroparous tactics would then predominate
  – Putting all your eggs in a basket:
    » semelparous individuals, if reproduce in the wrong year, contribute nothing to the next generation due to poor success

Advantages of Iteroparity

- Characterized this trade off in simple terms
  - Steady reproduction
  - Variable reproduction
  - Long life
  - Short life
- Was semelparity possible?

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	Long Life	Short Life
Steady Reproduction	?	Possible
Variable Reproduction	Possible	Not Possible

Figure 17-2. *Summary of Murphy's arguments on life history strategy for marine fishes. Redrawn from Murphy (1968).*

Advantages of Iteroparity

- If reproduction relatively certain
  - Survival of young certain
  - Adaptive to allocate extra energy into breading
    - Achieve better fitness
  - Semelparity possible

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	Long Life	Short Life
Steady Reproduction	?	Possible
Variable Reproduction	Possible	Not Possible

Figure 17-2. *Summary of Murphy's arguments on life history strategy for marine fishes. Redrawn from Murphy (1968).*

Advantages of Iteroparity

- If reproduction relatively variable
  - Necessary to have long life
    - Hedge against variable years
    - Fewer young per year
    - Have a successful year and produce enough offspring
  - Iteroparity possible

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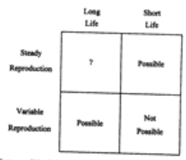

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Characterization of Trade-offs

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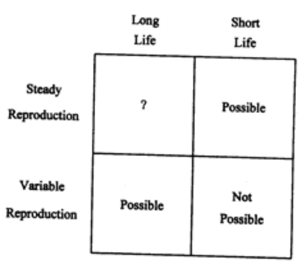


Figure 17-2. *Summary of Murphy's arguments on life history strategy for marine fishes. Redrawn from Murphy (1968).*

Life History Trade-offs

- Normal poor adult survival past spawning
  - Semelparity should be favored
  - Examples
    - Tropical fishes
      - Habitats become limiting during dry season after breeding
      - Adult survival low
      - Favors putting surplus energy into reproduction
    - Heavily preyed upon species
      - Small animals with many predators
      - Chance of living to next year low, even if it doesn't die after breeding

Factor	Semelparity	Iteroparity
Young Survival	Constant or predictable	Variable or unpredictable
Adult Survival	Low	High
Reproductive Behavior	High Energetic cost	Low energetic cost

Life History Trade-offs

- Energetically costly reproductive behaviors
  - Semelparity should be favored
  - Example
    - Large extensive Migrations
      - » Salmon
      - – Energetic cost of migration high
      - – Limits adult survival via putting energy into reproduction instead of somatic tissues
        - » Poor chance of leaving migration area
      - – Streams reach carrying capacity
        - » Can be exceeded during spawn in any given year
        - » Reach density dependence
      - – Carrying capacity allows for fairly constant
        - » Survival predictable
        - » May mean lower number of survival per adult, but constant for all adults

Factor	Semelparity	Iteroparity
Young Survival	Constant or predictable	Variable or unpredictable
Adult Survival	Low	High
Reproductive Behavior	High Energetic cost	Low energetic cost

Life History Patterns in Fishes

- Three general groups of fish life history patterns
  - (Winemiller and Rose. 1992. CJFAS 49:2196-2218)
  - Opportunistic, Equilibrium, and Periodic
    - – Some intermediate types
- – Used 216 marine and freshwater fish species
  - 16 traits each
  - Used univariate and multi-variate analysis
    - – Principle Component Analysis

Life History Patterns in Fishes

- Goal of Study
  - – Detection of invariants
    - Patterns of characteristics that are constant among animals tested

Life History Patterns in Fishes

- Examples of Invariants
  - Ratio of lifespan (E) to age-at-first reproduction (a)
    - This ratios is similar for elephant and squirrels
      - But different from fish
        - (Charnov et al. 2001. Proc. Nat. Acad. Of Sci. 98:9460-9464)
  - Jensen. 1997. CJFAS 54:987-989
    - Proposed the following invariants described the optimization of age at maturity and lifetime energetics
    1. Natural mortality (M) and age at maturation (X_m)
       1. $M^*(X_m) = 1.65$
    2. Natural mortality (M) and growth coefficient (K)
       1. $M = 1.5\ K$
    3. Length at maturity [$L(x_m)$] and maximum length (L_∞)
       1. $L(x_m) = 0.66\ L_\infty$
    4. Growth coefficient (K) and maximum length (L_∞)
       1. $L_\infty = K^{-0.33}$

Variation in Life Histories (Winemiller and Rose 1992)

- 3 Groups
  - Periodic
    - Intermediate to large body size
    - Delayed maturity
    - Long life
    - Large clutches
    - Small eggs
    - Short reproductive seasons
    - Examples
      - Salmoniformes
        - *Salvelinus (Brook)*
      - *Polyodon*
      - *Acipenser*
  - Favored in:
    - Environments with large spatial or seasonal variation

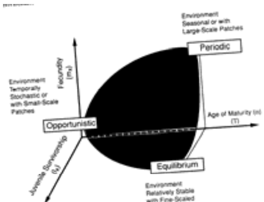
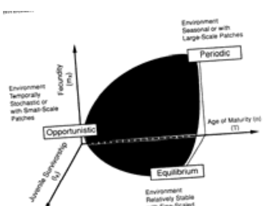


Figure 17-3. A model adaptive surface of fish life-history strategies based on demographic trade-offs selected under environmental variation. Reprinted with permission from Winemiller and Rose (1992).

Variation in Life Histories (Winemiller and Rose 1992)

- 3 Groups
  - Opportunistic
    - Small adult size
    - Early maturation
    - Small eggs
    - Long reproductive seasons
      - w/ multiple spawnings
    - Examples
      - *Perciformes*
        - *Etheostoma*
      - *Cypriniformes*
        - *Notropis*
  - Favored in:
    - Colonizing situations
      - Survival may change often or stochastically over short time scales



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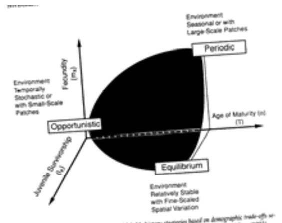
Variation in Life Histories (Winemiller and Rose 1992)

- 3 Groups
  - Equilibrium
    - Small to medium adult size
    - Large eggs
    - Small clutches
    - Strong parental care
    - Long reproductive seasons
    - Examples
      - Some Perciforms
        - » *Aplodinotus (drum)*
      - *Dorosoma* (Shad)
      - Some Cypriniformes
        - » Carps
  - Favored in:
    - Consistent habitat quality
    - Strong biotic interactions



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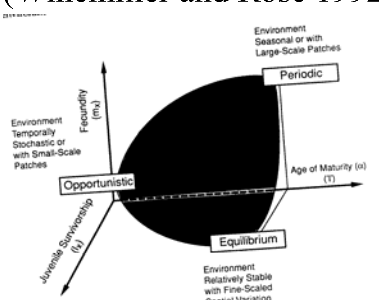

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Life History Patterns of the American Shad [*Alosa sapidissima* (Wilson)]

- Anadromous
  - Spawn in rivers
  - Young develop slowly in rivers
  - Migrate to sea by end of first year
  - Become adults in Gulf Stream
    - Water temps from 13-18 C
      - In summer far off Canada
      - In winter, Cape Hatteras
    - All life in similar environment

Life History Patterns of the American Shad [*Alosa sapidissima* (Wilson)]

- Adult shad
  - Move with Gulf Stream within the 12-18C isotherms
    - Come in contact with local rivers when marine waters come in contact with coastline
    - Adults enter stream to spawn when river temps near 18C
- Only difference in stocks (populations?) of shad
    - Spawning location
    - Early life history location
  - Different populations spawn in different rivers from Canada to Florida

Life History Patterns of the American Shad [*Alosa sapidissima* (Wilson)]

- Since most of their life is spent in common area, Gulf Stream, no differences in populations were expected
- However, large differences in life history
  - Variability in rivers across latitude

Life History Patterns of the American Shad

- Relationship between percent repeat spawners and latitude
    - Leggett and Carscadden 1978 JFRBC 35:1469-1478
  - Southern latitudes (17-04)
    - Shad semelparous
      - No individuals survived to reproduce again
  - Northern latitudes
      - North of 35°
    - Shad iteroparous
  - Distinct difference in life history

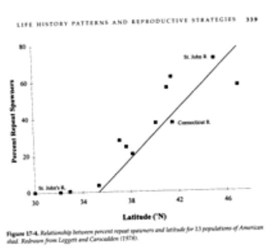


Figure 17-4. Relationship between percent repeat spawners and latitude for 13 populations of American shad. Redrawn from Leggett and Carscadden (1978).

Life History Patterns of the American Shad

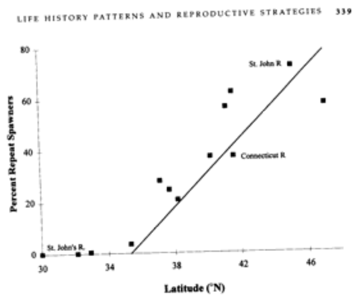
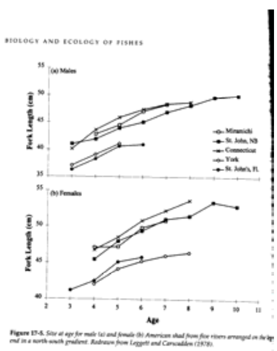


Figure 17-4. Relationship between percent repeat spawners and latitude for 13 populations of American shad. Redrawn from Leggett and Carscadden (1978).

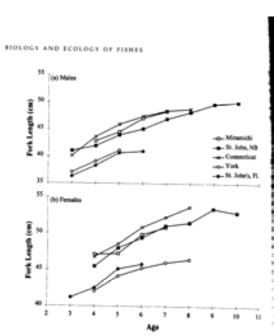
Life History Patterns of the American Shad

- Growth Rates
  - Size at Age (17-05)
    - Leggett and Carscadden 1978 JFRBC 35:1469-1478
  - Growth rates similar
    - Parallel curves, but
    - Northern river shad
      - Larger more rapid somatic growth
        - By age 3-4
    - Southern river shad
      - Smaller less rapid somatic growth
  - Also, females grow faster than males



Life History Patterns of the American Shad

- Growth Rates
  - Size at Age (17-05)
    - Leggett and Carscadden 1978 JFRBC 35:1469-1478
  - Does this pattern make sense?
    - Semelparous southern shad
      - Devote less energy into somatic, more toward reproduction
    - But contradicts idea
      - larger shad should be more fecund



Life History Patterns of the American Shad

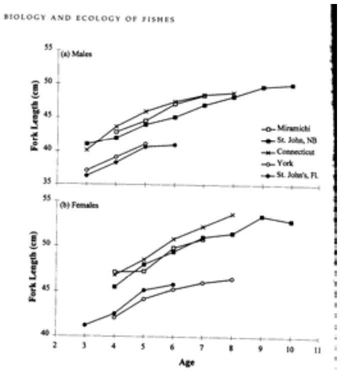


Figure 17-5. Size at age for male (a) and female (b) American shad from five rivers arranged on the le- end in a north-south gradient. Redrawn from Leggett and Carscadden (1978).

Life History Patterns of the American Shad

- Energy allocation
  - Body versus gonad growth
    - 17- 06 (Leggett and Carscadden 1978 JFRBC 35:1469-1478)
      - Number of eggs produced at a given weight
    - Southern populations
      - Higher egg production per unit body mass for
    - Northern populations
      - Lower egg production per unit body mass for

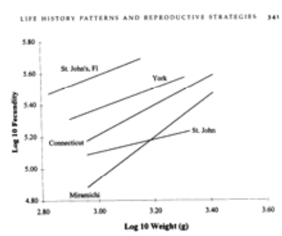
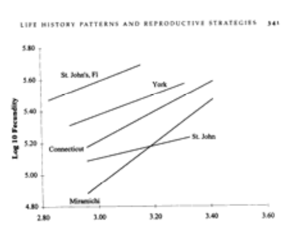


Figure 17-6. Relative fecundity at size for the same five shad populations. Redrawn from Leggett and Carscadden (1978).

Life History Patterns of the American Shad

- Energy allocation
  - Body versus gonad growth
      - 17- 06 (Leggett and Carscadden 1978 JFRBC 35:1469-1478)
    - St Johns Fl.
      - Lowest somatic growth rate,
      - with highest number of eggs produced per gram body weight
    - Meanwhile, age at maturity was not much different
      - 3.8 years – Southern
      - 4.2 years - Northern



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Life History Patterns of the American Shad

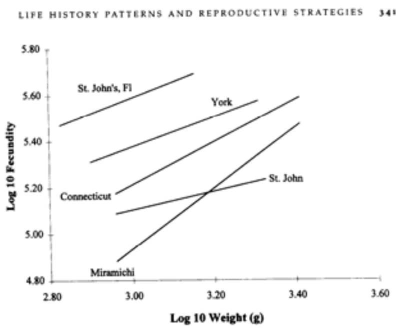

Figure 17-6. *Relative fecundity at size for the same five shad populations. Redrawn from Leggett and Carscadden (1978).*

Life History Patterns of the American Shad

- Changes in growth and fecundity
  - Should affect energy depletion during spawning
  - Northern Shad Populations
    - Shad entered fully ripe adults, eggs fully developed
    - No further gonad growth during migrations
      - 4 year old northern females → 1,400 kcal into ovaries

Life History Patterns of the American Shad

- Changes in growth and fecundity
  - Should affect energy depletion during spawning
  - Southern Shad Populations
    - Shad invest considerable energy into gonad growth after entering rivers, but prior to spawning
      - 4 year old southern females → 2600 kcal into ovaries (~2x as much)
      - Shunting of energy from body stores to gonad growth

Life History Patterns of the American Shad

- Changes in growth and fecundity
  - Patterns consistent with % body energy depleted during reproduction
    - Energy depletion calculations during migration
      - Northern populations
        - » 40% stored body energy used during migration upstream
        - » 15% stored body energy used during return migration
        - » None for gonad growth
        - » Therefore: 55% of body energy used for the reproductive migration

Life History Patterns of the American Shad

- Changes in growth and fecundity
  - Patterns consistent with % body energy depleted during reproduction
    - Energy depletion calculations during migration
      - Southern populations
        - » 50% stored body energy used during migration upstream, (higher temperatures = higher metabolic demand and higher cost of migration)
        - » 0% stored body energy used during return migration because they died after spawning
        - » 30% body energy allocated to gonad growth during upstream migration
        - » Therefore, 80% body stores at river entry used for spawning
        - » No energy left for return migration

Life History Patterns of the American Shad

- What differences between northern and southern rivers causes this large variation in life history?
  - Thermal regime of rivers?
    - FL rivers
      - Min of 15 C
      - Max of 30 C
    - CT
      - Min of 4 C
      - Max of 24 C

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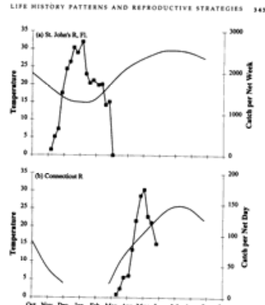
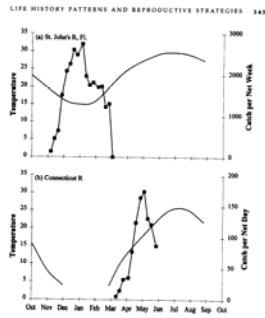


Figure 17-7. Shad catches (squares) and water temperature (line) for (a) St. John's River, Florida and (b) Connecticut River. Redrawn from Leggett and Whitney (1972).

Life History Patterns of the American Shad

- Shad enter rivers at 13-18 C water of Gulf Stream near cost
  - FL (17-07a)
    - In streams
      - December to February
    - Spawn
      - Temps then climb, so spawn when near 18 C
      - Feb or March
    - Hatching
      - Optimal is 13 – 15 C, but these rivers are typically 15-18 C
        - » So a bit higher than optimal
    - Young develop
      - Temps increase from 20 – 30 C
      - Same time as spring primary production pulse
        - » Lots of food
  - Overall, temperatures are predictable,
    - Warm consistently over spring to summer
  - but not optimal for
    - spawning, hatching, and developing



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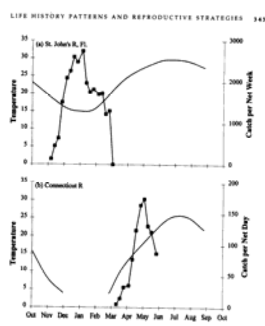
Life History Patterns of the American Shad

- Shad enter rivers at 13-18 C water of Gulf Stream near cost
  - CT
    - In streams
      - April to May
    - Spawn
      - April or May
    - Hatching
      - May or June
        - » Good temps possibly
      - Depending on the summer, temperatures may continue to climb or stabilize
    - Young develop
      - Max temp at 25 in July
      - primary production pulse already gone by
        - » Not much food and time for shad to accumulate energy to survive winter
  - Overall, temperatures are less predictable, food less predictable
  - At times, temperature may be better in CT than FL, but less predictable



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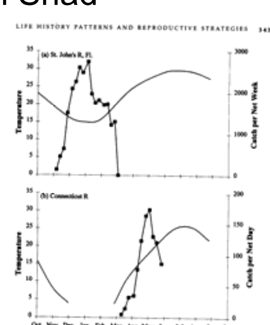
Life History Patterns of the American Shad

- Differences btw populations
  - Temperatures and food resources,
  - rather than absolute abundances
- This predictability has a hypothesized significance on survival of the young



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Life History Patterns of the American Shad

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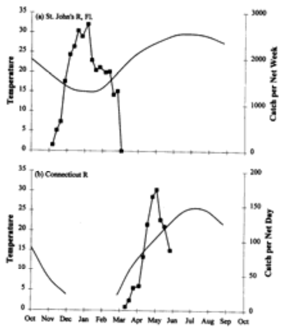

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