Reproductive Behavior and Spawning Migrations

Introduction

- Fertilization
  - Oviparous
    - Most common type of reproduction
      - Fish lay eggs, fertilized externally
  - Ovoviviparous
    - Eggs fertilized internally
      - Held until young are born live, but no placental involvement in egg development for embryos
  - Viviparous
    - Placental development for embryos

Introduction

- Parental Care
  - Both sexes share in rearing of young
    - Mouthbrooders
    - Defense of eggs and young

Introduction

- Variation in the number of young produced
  - Highly fecund
  - Few large young

Introduction

- Prespawning behavior
  - Migration
  - Homing to spawning sites

Generalized Reproductive Behavior

1. Site Selection
2. Parental Care
3. Mate Selection

REPRODUCTIVE BEHAVIOR

- *Introduction*
  - Fish have a variety of reproductive behaviors
  - Broken down into 3 classification systems (Table 9-1):
    1. Non-guarders
    2. Guarders
    3. Bearers

TABLE 9.1 A CLASSIFICATION OF REPRODUCTIVE STRATEGIES OF FISHES BASED ON SPAWNING HABITS

I. Nonguarders
- A. Open-substrate spawners
  - 1. Pelagic spawner
  - 2. Benthic spawners
    - a. Spawners on coarse bottoms (rocks, gravel, etc.)
      - (1) Pelagic free embryo and larvae
      - (2) Benthic free embryo and larvae
    - b. Spawners on plants
      - (1) Nonobligatory
      - (2) Obligatory
    - c. Spawners on fine substrates
  - 3. Terrestrial spawners
- B. Brood hiders
  - 1. Benthic spawners
  - 2. Crevice spawners
  - 3. Spawners on invertebrates
  - 4. Brush spawners

II. Guarders
- A. Substratum choosers
  - 1. Rock tenders
  - 2. Plant tenders
  - 3. Terrestrial tenders
  - 4. Pelagic tenders
- B. Nest spawners
  - 1. Rock and gravel nesters
  - 2. Sand nesters
  - 3. Plant-material nesters
    - a. Gluemakers
    - b. Nongluemakers
  - 4. Froth nesters
  - 5. Hole nesters
  - 6. Miscellaneous-materials nesters
  - 7. Anemone nesters

III. Bearers
- A. External bearers
  - 1. Transfer brooders
  - 2. Auxiliary brooders
  - 3. Mouth brooders
  - 4. Gill-chamber brooders
  - 5. Pouch brooders
- B. Internal bearers
  - 1. Facultative internal bearers
  - 2. Obligate internal bearers
  - 3. Livebearers

After Balon (1975a, 1984).

Non-guarders

- *Introduction*
  - *Fish that do not protect their eggs and young once spawning has been completed*

Non-guarders

- *Types*
  1. Open substrate spawners
     - Simply scatter their eggs in the environment
     - Usually spawn in groups w/o elaborate courtship behavior or specialized reproductive structures
     - Males outnumber the females
     - Types
       1. *Pelagic spawners*
       2. *Benthic spawners*

Non-guarders

1. Open substrate spawners
   - Types
     1. *Pelagic spawners*
        - Function:
          - » **assure that young become widely dispersed via water currents**
        - Structure
          - » **Buoyant eggs, embryos, and larvae**
     - Examples
        - Common among marine fishes
          - » *Tuna*
        - River-dwelling
          - » *Shad (Alosa)*
        - *Surface*
          - » *Brook silversides (Labidesthes sicculus)*
          - » Alewife *(Alosa pseudoharengus)*

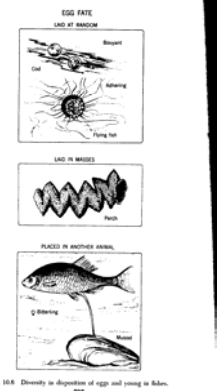

Fig. 10.8 Diversity in disposition of eggs and young in fishes.

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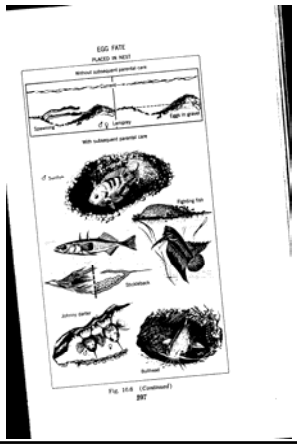
Non-guarders

1. Open substrate spawners
   - Types
     2. *Benthic spawners*
        - Eggs adhesive and stick to substrates or in long strings to attached to the surface of substrate
     - Examples
       - **Sturgeons (Acipenseridae)**
       - **Carp (*Cyprinus*), pikes (Esocidae), golden shiner (*Notemigonaus crysoleucas*)**
         - » **Vegetation**
       - **Yellow Perch (Perca flavescens)**
         - » **Rope eggs**
       - **Suckers (Catastomus) and Walleye (*Stizostedion*)**
         - » **Shoals of sand, gravel, boulders**



Non-guarders

2. Brood hiders
   - Hide the eggs as part of their spawning behavior, but do not show parental care
     - Most build nest and bury eggs
   - Types (examples)
     - *Benthic spawners*
     - *Crevice spawners*
   - Example
     - *Salmon and trout*
       - build redds by digging, protected until eggs are laid, fertilized, and buried
         - » Brook trout (Salvelinus fontinalis)
         - » Cuttthroat (Salmo clarki)
         - » Brown trout (Salmo trutta)
         - » Rainbow (Oncorynchus mykiss)
         - » Rainbow trout and Salmon (Oncorhynchus spp.)
     - *N.A. Cyprinidae*
       - build nest of piles of stones rather than depressions
       - males use tubercles on the head to move stones
         - » Creek Chubs (Semotilus atromaculatus)
         - » River Chub (Hybopsis micropogon)
         - » Horneyhead (Hybopsis biguttata)
     - Rainbow darter (Etheostoma caerulium)

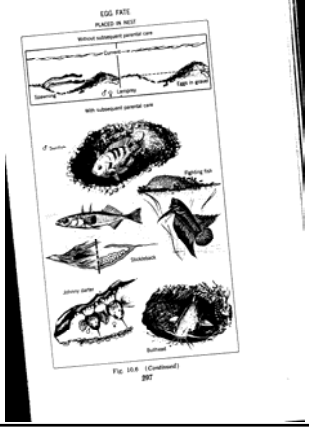
Guarders

- *Introduction*
  - *Hide their eggs and guard the fertilized eggs until they hatch*
    - *frequently care for larval stages as well*
  - *Due to care, guarders are usually*
    - territorial
    - competitive
    - undergo elaborate courtship behavior
  - *Guarded by male usually*
    - protect from predators
    - maintain high oxygen levels

Guarders

- *Types*
  1. Substratum chooser
     - do not build nest but choose a substrate
     - *Examples*
       - *Under stones or other objects*
         - » *Johnny darter (Etheostoma nigrum), fantail darter (E. flabellare), Sculpins (Cottus), bluntnose and fathead minnows (Pimephales)*

  2. Nest spawners
     - Construct some sort of structure or cavity
     - Examples
       - *Circular depression of mud, silt, sand*
         - » *Centrarchidae including: Lepomis, Pomoxis, Ambloplites, Micropterus salmoides*
         - » *Bowfin (Amia)*
         - » *Most bullheads (Ictalurus)*
       - *Circular depression of gravel bottom*
         - » *Large and Smallmouth Bass (M. salmoides and dolomiuei), an*
       - *Tunnels*
         - » *Channel catfish (Ictalurus punctatus) in bank*
         - » *Yellow bullhead (Ictalurus natalis) in bottom*



Bearers

- *Introduction*
  - *Fish that carry their embryos around with them*
  - *sometimes carry young as well*

Bearers

- *External bearers*
  - Examples
    - Seahorses and pipefish (Syngnathidae)
      - Males brood
      - After egg fertilization, female places embryos on the male
    - Sea Catfishes (Ariidae), Cichlids (Cichlidae)
      - Externally spawned young in the mouth
      - In cichlids, usually female carries the broods
    - *Other species, males or females may brood*

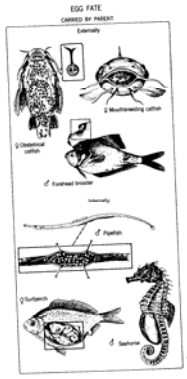


Fig. 10.6 (Continued)

Bearers

- *Internal bearers*
  - Facultative internal bearers
    - Oviparous (egg laying) killifishes (Fundulidae)
      - Eggs retained by female accidentally fertilized by normal spawning on the substrates
  - Obligate internal bearers
    - Ovoviviparity:
      - source of nutrition for embryos is the egg yolk. Similar to externally spawned eggs
    - Provides additional care for young
    - Examples
      - *Marine Rockfish (Scorpaenidae)*
      - *Lake Baikal sculpins (Comephoridae)*
  - Viviparity:
    - provision of additional nutrition while female carrying young
      - Provides added protection of young
    - Examples
      - Sharks
      - Largespring Gambusia (Gambusia geiseri)
        - » Embryos uptake nutrients from mother

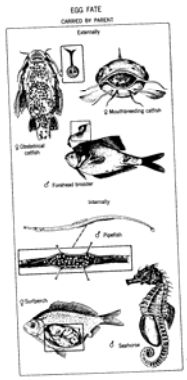


Fig. 10.6 (Continued)

Sexual Dimorphism

- *Many species, males and female are indistinguishable externally*
  - i.e. no sexual dimorphism or dichromatism
- *Dimorphism*
  - Differences in body shape
- *Dichromatism*
  - Differences in color

Sexual Dimorphism

- *Size*
  - Most widespread type of dimorphism
    - Egg laying territorial males usually larger than females
    - Example
      - **Centrarchidae**
    - Non-territorial male groups typically smaller than female
      - *Striped bass*
      - *Sturgeon*

Sexual Dimorphism

- *Breeding tubercles*
  - tiny, keratinized bumps that grow on fins, head and body scales during breeding season
    - primarily on males
  - Example:
    - fathead minnows (*Pimephales promelas*)
      - Assist in maintaining contact with counterpart during spawning, stimulating during spawning, and defense of territories

Sexual Dimorphism

- *Contact organs*
  - Similar to turbercles, but have an internal core of bone
    - Assist in maintaining contact with counterpart during spawning, stimulating during spawning, and defense of territories

Sexual Dimorphism

- *Dichromatism*
  - Bright coloration of males
    - Usually a seasonal phenomenon
  - Attract mates but also predators
  - Example:
    - Darters (Percidae)
    - Minnows (Cyprinidae)

MATING SYSTEMS

- Monogamy
- Polygyny
- Polyandry
- Promiscuity (polygynandry)

MATING SYSTEMS

- Monogamy
  - One male and one female mate exclusively
    - Uncommon in fishes
      - Often alternates with other mating systems
    - Usually occurs when
      - Both sexes care for young
      - Territories for feeding and breeding are small
        - » Or low encounter rates btw sexes
  - Examples
    - Tropical cichlids
      - Both sexes rear their young together
      - Vigorously defense against competitors and predators

MATING SYSTEMS

- Polygyny
  - One male with several females
  - Large conspicuous male
    - Defends turf
      - For which females are attracted
    - Or defends female directly from other males
  - Example
    - Cottidae (sculpins)
      - Males defend prime sites for incubation of embryos
        - » "Caves" underneath rocks
      - Females chose males
        - » Quality of breeding site
        - » And size of male
      - Males attempt to obtain exclusive mating rights w/ multiple females
        - » Use leks or other places
        - » Males gather together and display to one another
        - » and females choose highest ranking males

MATING SYSTEMS

- Polyandry
  - One females seeks to mate w/ several males
    - Relatively uncommon
      - Occurs when females are wont to change sex
      - Or males do the brooding but can take care of fewer eggs than females can produce
        - » Example of pipefish

MATING SYSTEMS

- Promiscuity (polygynandry)
  - Presumably the original fish mating system as a result of external fertilization
    - Many males and many females mate simultaneously
      - Example
        - » Herrings, where shallow waters becomes white w/ sperm and bottom covered by millions of eggs

ALTERNATIVE REPRODUCTIVE STRATEGIES

- *Hermaphroditism*
  - One individual can be both male and female
  - Synchronous hermaphroditsm
    - Possess both ovarian and testicular tissue
      - uncommon
  - Sequential hermaphroditsm
    - Individuals change sex
      - Protogyny
        - » Most common
        - » Females change into male
        - » Parrotfishes, wrasses, groupers
      - Protandry
        - » Less common
        - » Male converts into female
        - » Anemone fishes

ALTERNATIVE REPRODUCTIVE STRATEGIES

- *Protogymy*
  - Female changes into male
    - Most common
  - Example
    - Large dominant male gets removed by a predator and one of the females becomes a dominant male
      - parrotfishes, wrasses, groupers

ALTERNATIVE REPRODUCTIVE STRATEGIES

- *Unisexuality*
  - *Parthenogenesis*
    - Females produce only female offspring with no involvement of males
      - Asexual reproduction
    - Rare in fishes
    - Example
      - Texas silverside (*Menidia clarkhubbsi*)

ALTERNATIVE REPRODUCTIVE STRATEGIES

- *Unisexuality*
  - Gynogenesis
    - Amazon Mollies (Poeciliidae)
      - All female species
      - Sexual parasites of bisexual species of the same genus
        - » They were originally derived from these genera as hybrids
      - Sperm from host species required to activated development of Amazon Molly eggs
        - » But union of male and female chromosomes does not occur

ALTERNATIVE REPRODUCTIVE STRATEGIES

- *Unisexuality*
  - *Hybridogenesis*
    - Unisexuality of Mexican mollies
      - Mating between all female species of Mexican mollies and a host male of another species
    - Hybrid formed
      - During oogenesis in the hybrid females
        - » parental male contributed chromosomes are lost in meiosis
      - Therefore, only female genes are passed on to the next generation
        - » Self perpetuating strain of all female fish

ALTERNATIVE REPRODUCTIVE STRATEGIES

- *Unisexuality*
  - *Hybridogenesis*
    - Why are clones successful

      1. Heterosis (hybrid vigor)
         - » *Larger size, higher survival rates*
      2. Increased reproductive potential of all female population
      3. Clones genetics are advantageous in their environment

    - However
      - Need to overcome low genetic variability
        - » *Continued dependence of unisexual fish on bisexual males*
    - However
      - if sperm of bisexual male is not limiting,
        - » then competition between appropriate females and unisexual females not a problem

Examples of Reproductive Behavior

- Rainbow Trout
  - Redd building
    - Female selects site for digging redd in gravel
      - Gravel size moved directly related to female size
    - Female lies on her side
      - Swims along bottom displacing gravel w/ her tail
      - Makes a depression that is cleaned of sediment
        - » Measures depth w/ anal fin
        - » Appropriate depth must be attained

Examples of Reproductive Behavior

- Rainbow Trout
  - Male Agonistic Encounters
    - Several males encounter / court her for right to breed w/ female while she is excavating
      - Males compete for right to breed
  - Once redd dug to her satisfaction
    - Males quiver next to and over nest
      - Induces female to spawn
    - Males may also nudge her abdomen to encourage spawning

Examples of Reproductive Behavior

- Rainbow Trout
  - Female lays eggs
    - successful male fertilizes eggs
  - Female chases off her mate
    - As well as any other males
      - Other males may eat eggs
  - Female covers eggs
    - Moves gravel back over depression
      - Abandons redd
        - » Makes sense because survival after spawning is low

Atlantic Salmon Example

Film clip - Atlantic salmon creating nest and spawning - Atlantic salmon - *Salmo salar* - ARKive

Examples of Reproductive Behavior

- *Alternative male strategies*
  - Salmon and trout
    - Large aggressive males dominate spawning
    - Jack males (sneakers):
      - *small, silvery males that sneak into redds*
        - » release sperm simultaneously with a mated pair

Examples of Reproductive Behavior

- Bluegill
  - Late spring
    - Large drab-colored age 5 – 8 males build nest
      - Small circular depressions in shallow area
        - » Muddy or sandy substrate
    - Males defend nest against other males
    - Females develop bright orange coloration on ventral surface
      - A lot smaller in size than males
    - Males circle nest to attract females
      - Will attract as many females as he can to spawn in his nest
        - » Eggs therefore a composite of many females and one male
    - Once spawning complete, male drives off the females and any other fish
    - Guards the nest
    - May even fan nest

Examples of Reproductive Behavior

- Alternative Male Strategies
  - Bluegill (Gross and Charnov 1980; Gross 1982)
    - Large male (nest defender)
    - Alternatives
      - Sneaking
        - » *Small male hides near active nest and dashes in to release sperm while resident male spawns with female*
      - Satellite male
        - » *Mimics females in coloration and behavior*
        - » *Hovers over a nest of a breeding male, reaching mating pair in time for spawning*
        - » *These males spawn at earlier age than nest defender male, d*o to not have to defend nests

SEX CHANGE IN FISH

- *Environmentally determined sex*
  - Atlantic silversides (*Menidia menidia*)
    - low temperatures:
      - *larvae more likely to develop into females*
  - Southern brook lamprey (*Ichthyomyzon gagei*)
    - larval densities high and temperatures are low
      - *more males*

SPAWNING MIGRATIONS

- Spawning Migrations
  - Allow fish to use resources that are geographically isolated and maximize benefits of both
    - Shallow areas
      - Early survival and growth are best
    - Deeper waters
      - Allow for optimal adult growth
  - Feeding and survival migrations
    - Arctic species
      - Migrate to main rivers or estuarine environment before winter
      - small tributaries may freeze solid

SPAWNING MIGRATIONS

- Catadromous Eels (Angullidae)
  - Spawning as adults in the open ocean
    - Occurs in tropical to subtropical seas
      - Usually at great depth
  - Adults are semelparous
    - Die after spawn
  - Eggs develop into segment larvae call leptocephalous
    - Larvae are so different from adults, originally thought of as different species
  - Rearing of larvae for some time at sea
    - 1 to several years
    - Propelled back to streams by oceanic currents
  - Return to streams for adult life
    - Unlikely that larvae home to same stream system as their parents
      - North American and European eels
        - » Appears to spawn in different locations and larvae show fidelity to continent
    - Also unlikely adults home to same ocean location to spawn

SPAWNING MIGRATIONS

- Anadromous Salmon
  - Swim upstream to spawning in as adults
  - Larval and juvenile stage in stream for some time
  - Migrate to oceans for adult life

SPAWNING MIGRATIONS

- The Stream phase of Salmon Migrations
  - Why should fish develop elaborate migration and homing? (Hasler et al 1978)
    - Consistency in numbers and early survival
      - Animals that breed in certain kinds of special habitats
        - » Produce similar number of young per year
    - If adults disperse widely, finding appropriate site for spawning and survival is not easy
    - Homing then becomes important, even more important the further it disperses from spawning area
      - Especially if spawning is brief during fall
        - » Difficult to judge flow conditions, predator density, and other characteristics
      - Homing provides predictability

SPAWNING MIGRATIONS

- The stream phase of Salmon Migrations
  - Advantages of homing
    - Homing also allows for adaptation to local conditions
      - » Example of the American shad
      - Adaptations are related to characteristics of spawning sites
        - » Allow for adaptation to occur and stocks differentiate
        - » Via limited gene flow
  - Problems of homing
    - If spawning of habitat vulnerable
      - Perfect homing could cause a gene pool to become extinct under habitat damage
      - Examples
        - » Impassible log jams
        - » Deforestation
    - Therefore
      - Some degree of straying may allow for limited genetic mixing and re coloniation
  - Fortunately
    - There is some intermixing during spawning
      - But is variable among salmon stocks

SPAWNING MIGRATIONS : The stream phase of Salmon Migrations

- Use of Olfactory Cues
  - Hasler et al. Hypothesized
    - Salmon could smell the odor of their home stream for homing
    - Issaquah River Washington (Wisby and Hasler 1954. JFRBC 11:472-478)
      - Captured upstream migrations salmon in East Fork and mainstem
        - » Distinctively marked them
      - Plugged (Occulated) nasal passages of half the fish
        - » Other half used as controls
      - Transported both groups back downstream and released them
    - Expectations
      - East fork 1/5 size of main stem
        - » Therefore based on random movements, 80% should go up mainstem, 20% up East fork
    - Recaptures 46 Control main river origin
      - » 100% recaptured from original capture location
      - Plugged mainstream origin fish
        - » 80% made correct choice
        - » 20% did not
      - East Fork Origin
        - » 71% of control fish chose the correct river
        - » 84% occulated fish returned to wrong river

SPAWNING MIGRATIONS : The stream phase of Salmon Migrations

- Use of Olfactory Cues
  - Hypothesize that young salmon could identify water at rearing site and use that as adult so find home
    - Donaldson et al
    - Pheromones
      - Hormones used to communicate with others
    - Emit chemicals with excretory products
  - Donaldson and Allen 1957 TAFS 87:13-22
    - Marked and released fingerling salmon from a distant hatchery into ponds at UW or a nearby river
      - Naturally smolted there
        - » Smolt = saltwater capable form
        - » Parr = freshwater form
    - Several years later
      - Collected returning adults in traps in rivers or fish ladders of UW ponds
    - Salmon learn chemical cues from their home waters at smolting, not something that was genetic

SPAWNING MIGRATIONS : The stream phase of Salmon Migrations

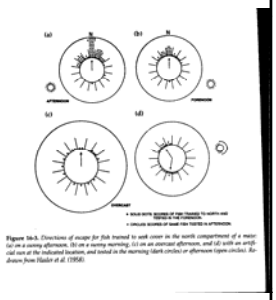
- Use of Olfactory Cues
  - How can a fish that breeds in a small mountain stream, but migrates thousands of miles to the Pacific find that small home stream?
    - Recognize a series of chemicals along the way
      - » Oshima et al 1969 JFRBC 26:2123-2133
    - Allows simpler solving of straying
      - » Reach mouth of first river, many stock have same chemical cues
      - » Move upstream, next cue differentiate stocks

SPAWNING MIGRATIONS :

- Open Ocean Phase of Migration
  - Chemical cues unlikely cues to migrate open ocean to the coast of their natal stream
  - Sun Compass
    - Suns position and time of day must be known
      - Rises in east
        - » Early morning
      - South
        - » At noon in northern hemisphere
      - Sets in west
        - » Afternoon
    - Some scientist think
      - Fish use polarized light
        - » Once light hits water it becomes polarized in direction of sun
      - May aid fish in their ability to detect the direction of the sun

SPAWNING MIGRATIONS :
Open Ocean Phase of Migration

- Sun Compass
  - Bluegill trained to escape to north when frightened
    - Area w/ 16 potential escape directions (Fig. 16-3)
    - Sunny afternoon
      - Most hiding done in north
    - Sunny morning
      - Most hiding done in north
    - Completely overcast
      - Moved in any direction
    - Artificial light
      - Orientated to light as if were the sun
        - » Located north in morning
        - » But south in afternoon because lights position was changed



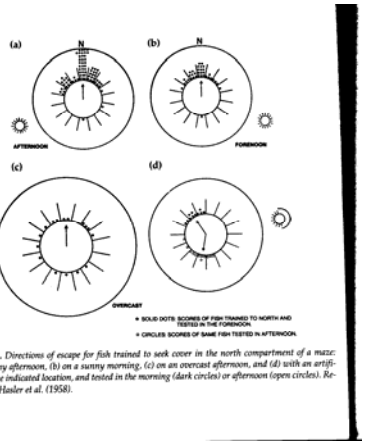


Figure 16-3. *Directions of escape for fish trained to seek cover in the north compartment of a maze: (a) on a sunny afternoon, (b) on a sunny morning, (c) on an overcast afternoon, and (d) with an artificial sun at the indicated location, and tested in the morning (dark circles) or afternoon (open circles). Redrawn from Hasler et al. (1958).*

SPAWNING MIGRATIONS :
Open Ocean Phase of Migration

- Other cues shown to be used
  - Magnetic
  - Celestial objects at night
  - Oceanic currents
- Probably a combination to all cues

SPAWNING MIGRATIONS :

Open Ocean Phase of Migration

- Schools and Oceanic Migrations
  - Schools of fish w/ no obvious leader and continual swimming readjustment
    - May navigate more precisely than isolated individuals
      - Statistical theory of central limits theorem supports this
      - Larger schools of fish should be more accurate in homing than smaller schools
        - » Larkin and Walton 1969. JFRBC 26:1372-1374

Direction Finding Abilities	School Size		
	5	30	100
2	±48.6°	±18.3°	±9.5°
4	±28.6°	±11.4°	±6.1°

MIGRATIONS

- Ictaluridae
  - Longer range migrations
    - Move along stream corridors
- Centrarchidae
  - Small range of migrations
- Percidae
  - Smaller range of migrations
    - Localized riffles