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

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

1. Pelagic spawners
2. Benthic 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
  - Surface
  - Brook silversides (Labidesthes sicculus)
  - Alewife (Alosa pseudoharengus)
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 (Cyprinidae), pikes (Esocidae), golden shiner (Notemigonus crysoleucas)
              » Vegetation
            - Yellow Perch (Perca flavescens)
              » Rope eggs
            - Suckers (Catostomus) 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 nests and bury eggs
       • Types (examples)
         - Benthic spawners
         - Crevice spawners
           • Examples
             - Salmon and trout
               » build nests by digging, protected until eggs are laid, fertilized, and buried
               » Brook trout (Salvelinus fontinalis)
               » Cutthroat (Salmo clark)
               » Brown trout (Salmo trutta)
               » Rainbow (Oncorhynchus mykiss)
               » Rainbow trout and Salmon (Oncorhynchus spp.)
             - N.A. Cyprinidae
               » build nest of piles of stones rather than depressions
               » makes use tubercles on the head to move stones
               » Creek Chub (Semotilus atromaculatus)
               » River Chub (Hybopsis americanus)
               » Honeyhead (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

**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), bullhead and fathead minnows (Phoxinus)

2. **Nest spawners**
   - Construct some sort of structure or cavity
   - Examples
     - Circular depression of mud, silt, sand
       - Centrarchidae including Lepomis, Pomoxis, Ambloplites, Micropterus salmoides
       - Black crappie (Pomoxis nigromaculatus)
     - Elliptical depression (circle)
     - Circular depression of gravel bottom
       - Large and Smallmouth Bass (M. salmoides and dolomieu), 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

- **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
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)
- **Vivipary**:
  - Provision of additional nutrition while female carrying young
  - Provides added protection of young
  - Examples:
    - Sharks
    - Longspining Gambusia (Gambusia geiseri)
    - Embryos uptake nutrients from mother
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 tubercles, 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
    - Usually occurs when
      - Both sexes care for young
      - Territories for feeding and breeding are small
      - Or low encounter rates between 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 with 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 with 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 hermaphroditism
      • Possess both ovarian and testicular tissue
        – Uncommon
    – Sequential hermaphroditism
      • 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

• Protogyny
  – 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,
        - 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 with tail
      - Makes a depression that is cleaned of sediment
        - Measures depth with anal fin
        - Appropriate depth must be attained

Examples of Reproductive Behavior

- **Rainbow Trout**
  - Male Agonistic Encounters
    - Several males encounter and court her for right to breed with 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 reds
      » 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, do 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 (Anguillidae)
  – 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 larva called leptocephalus
  – 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-colonization
  – 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 (Hinkley and Hasler 1954. JRBC 11:472-478)
      – Captured upstream migrations salmon in East Fork and mainstem
      – Olfactory 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
    – Recapture 46 Control main river origin
      – 100% recognized from original capture location
      – 86% made correct choice
      – 20% correct
    – East Fork Origin
      – 71% of control fish chose the correct river
      – 86% 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 to 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
    - 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?
    - Oshima et al 1969 JFRBC 26:2123-2133
  - Recognize a series of chemicals along the way
    - 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 of 16 potential escape directions (Fig. 16-3)
  • Sunny afternoon
    – Most hiding done in north
  • Sunny morning
    – Most hiding done in north
    – 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

• 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

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<th>Direction Finding Abilities</th>
<th>School Size</th>
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<tr>
<td>2 ±48.8° ±18.3° ±8.5°</td>
<td>5</td>
</tr>
<tr>
<td>4 ±28.6° ±11.4° ±8.1°</td>
<td>30</td>
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MIGRATIONS

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