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A Summer Course in Invertebrate Developmental Biology at Iowa Lakeside Laboratory: A Unique Experience

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The course, "Developmental Biology of Selected Invertebrates", has been offered in alternate years at Iowa Lakeside Laboratory (ILL) on Lake West Okoboji, Dickinson County, Iowa, since the first summer session of 1983. This course has taken advantage of the great diversity of invertebrates found in the ILL area and has demonstrated to students and faculty alike the exciting phenomena and principles of developmental biology. The course is continuously evolving as new experiments and observations are discovered with each offering of the course.

INDEX DESCRIPTORS: Science teaching, laboratory experiments, Iowa Lakeside Laboratory, invertebrates, developmental biology

The invertebrates are emphasized in this course on developmental biology because of their abundance, ease of collecting, culturing and the fact that they represent about 95% of the animal kingdom. Although such courses are common at many marine biological stations, similiar offerings at freshwater biological stations are uncommon. The course was initially offered with conservative expectations, however it became apparent that this is an invaluable opportunity not normally experienced by many biology students.

Three objectives of the course are: 1) to understand the necessity for care in collecting, transporting and culturing organisms, 2) to study developmental principles commonly taught in the classroom on the main campuses with the added advantage of observing these principles at the cellular, tissue and organismal levels in the laboratory of a field station and 3) to emphasize an experimental approach.

Iowa Lakeside Laboratory's (ILL) is ideal for these goals. It has numerous microhabitats in its 140 acres and allows access to Lake West Okoboji, which in late spring and early summer has a very large faunal diversity. Also, within a few miles of ILL, are numerous other natural areas such as lakes, sloughs, fens, canals, creeks, prairies and spring ponds. Each of these habitats contain thriving invertebrate populations, some of which are unique.

Students studied many different animals early in the course and designed projects in which experiments and observations could be repeated as often as needed. Careful project selection was necessary because as the ambient water temperature increased, many species which were initially very abundant and available became difficult to locate due to algal blooms, drying of aquatic sites or possible migrations to deeper water. But these conditions also provided new species to observe and the culture clutter in the laboratory grew commensurately.

Without the burden of traditional exams and formal lectures, students and faculty worked together to examine developmental events in a wide variety of invertebrates. Grading was based on written reports which were evaluated and updated until course completion. The pace was rigorous, but the intensity could always be alleviated by a brisk game of volleyball or wildflower walk on the prairie at sunset!

MATERIALS AND SOURCES OF ANIMALS

Invertebrates were collected from numerous habitats (for example, Fig. 1) and many required special care for maintaining and culturing in the laboratory. Following are brief summaries of organisms collected including location of their habitats (Table 1) and procedures used in collecting and culturing.

In early June, adult planarians, leeches and snails were very abundant on submerged rocks or vegetation along the shore of Little Miller's Bay. Later in June their numbers decreased rapidly, possibly due to the warming of the water. These organisms were collected by carefully removing them from substrate using fingers, forceps or sharpened wooden applicators. The jelly-like egg masses of snails

Table 1. Collecting Sites of Species Used for Experiments and Observations

Species	Collection Sites
Porifera	
Spongilla sp	Jemmerson Slough
Cnidaria	
Hydra sp	Milford Water Treatment Plant
Platyhelminthes-Turbellaria	
Dugesia tigrina	Little Miller's Bay
Platyhelminthes-Trematoda	
Posthodiplostomum minimum	Lake West Okoboji, Jemmerson Slough
Bryozoa	
Plumatella sp	Hatchery Pond at Silver Lake Fen, Little Miller's Bay
Annelida-Oligochaeta	
Lumbriculus variegatus	Gull Point Slough
Annelida-Hirudinea	
Erpobdella sp	Little Miller's Bay
Helobdella sp	Little Miller's Bay
Molluska-Gastropoda	
Physa spp	Little Miller's Bay
Planorbis sp	Jemmerson Slough
Molluska-Bivalvia	
Sphaeria sp	Gull Point Slough, various ponds
Arthropoda-Insecta	
Physonota unipunctata	ILL Central Prairie
Arthropodoa-Crustacea	
Daphnia spp	West Lake Okoboji, Hatchery Pond at Silver Lake Fen
cyclopoid copepod	West Lake Okoboji
Streptocephalida seali	Green Marsh Pond
Cyzicus mexicanus	Hatchery Pond at Silver Lake Fen

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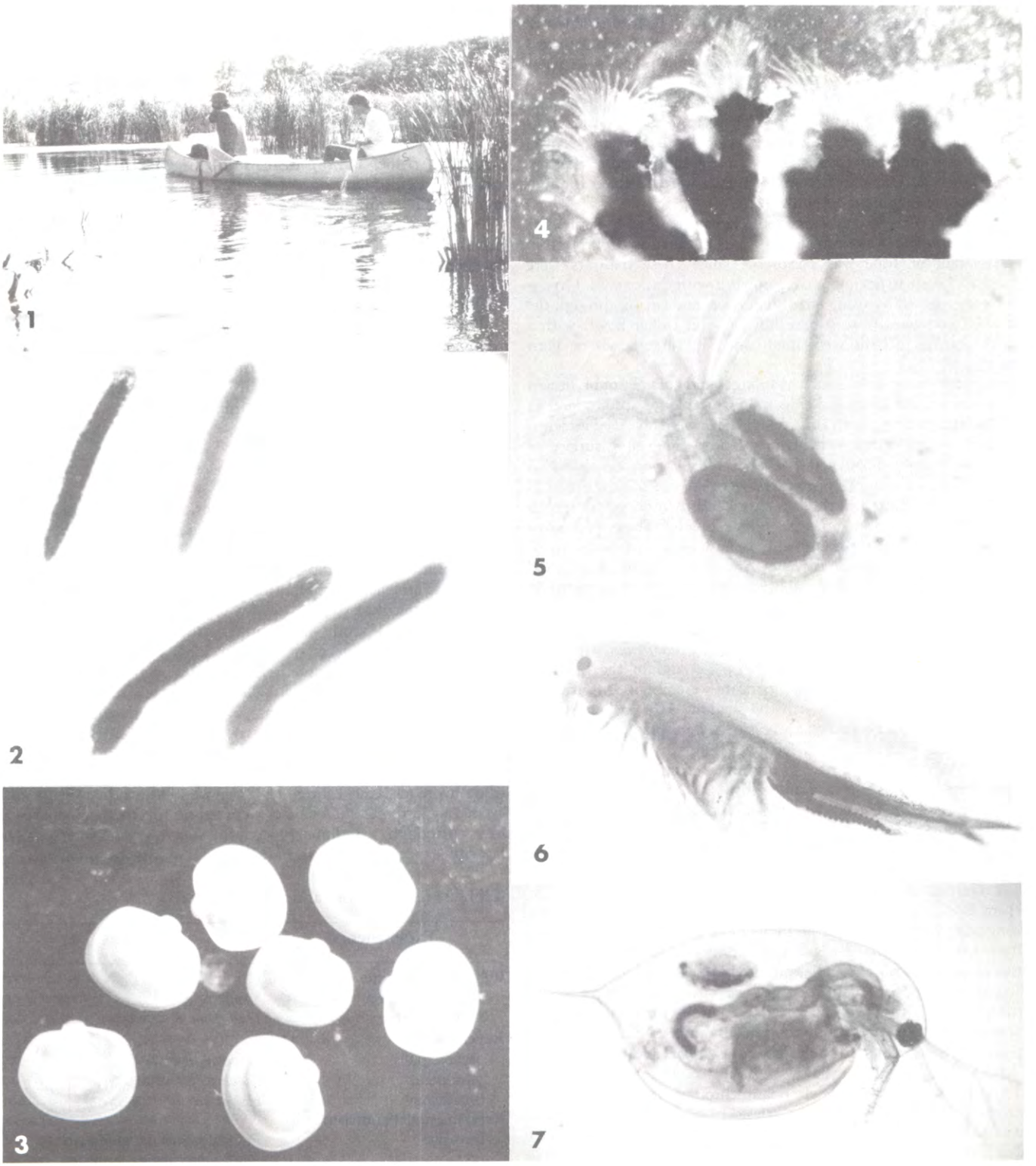
Contribution No. 444 from Iowa Lakeside Laboratory



Figs. 1-7. Fig. 1. Collecting sponges on Jemmerson Slough. Fig. 2. Planarians, *Dugesia sp,* collected from Little Miller's Bay. Fig. 3. Fingernail clams, *Sphaerium sp,* collected from Gull Point Slough. Fig. 4. *Plumatella* colony collected from hatchery pond near Silver Lake Fen. Fig. 5. Bryozoan statoblast (floatoblast) developing after freezing for two weeks. Fig. 6. Fairy shrimp, *Streptocephalida seali,* collected from Green Marsh Pond, a spring pond. Fig. 7. Cladoceran, *Daphnia sp,* collected from Lake West Okoboji. Note developing juvenile in marsupium.

(*Physa spp, Planorbis sp*) and the cocoons of leeches (*Erpobdella sp*) were also carefully removed from the substrate with forceps or sharpened wooden applicators. In the laboratory, these organisms, egg masses and cocoons were maintained in Petri dishes (Fig. 2) with frequent changes of lake water.

Fertilized eggs and early instars of the tortoise beetle, *Physonata unipunctata*, were also collected early. These were found on the big-toothed sunflower, *Helianthus grosseserratus*, located in the central pairie. Plants containing these stages were cut and placed in flasks of water inside terraria in the laboratory. Larvae were observed through all stages of development to adult form.

Aquatic oligochaetes and fingernail clams (Fig. 3) live in shallow pond or slough water among various kinds of detritus. Collection in the first half of June was preferable since these habitats were particularly prone to drying or overgrowing with duckweeds. Organisms were collected by using small hand nets and sifting through the debris. Oligochaetes were successfully kept in finger bowls with a layer of detritus. Clams were maintained in fingerbowls or Petri dishes.

Fortunately some species such as sponges and colonies of bryozoans were larger, more mature and thus more suitable for studies later in June. Sponges ranging from finger to fist size were observed attached to aquatic plants a few centimeters below the water surface of Jemmerson Slough. These could be collected by a person sitting in the bow of a canoe (Fig. 1). Specimens were covered with water in 2-gal buckets, transported to the laboratory and maintained for several days in aerated aquaria or large finger bowls. These organisms actively pumped water through oscula and, when properly maintained, continued this action for days. Around the edges of ponds and lakes not prone to drying, colonial bryozoans were found encrusted on sticks and rocks. Portions of colonies were brought to the laboratory and, like sponges, were best maintained in aerated aquaria (Fig. 4).

Another late bloomer was the trematode, *P. minimum*, which has developmental stages in the snail, *Physa spp* and in the bluegill, *Lepomis macrochirus*. Cercariae of the parasite were obtained from snail hosts collected with small nets in the shallow water at Jemmerson Slough. For this study, two or three snails were placed in Syracuse dishes, covered with water and left over night in the dark. In one experiment 24/65 dishes had swimming cercariae. Metacercariae were dissected from the liver of blue gills (100% infection) caught in Lake West Okoboji. Forceps and tungsten needles worked nicely for this procedure.

Some species including hydra and many crustaceans were available for study throughout the course. Hydra were collected from the intake tank at the Milford water treatment plant. In 1983, Dr. Richard Bovbjerg, former director of ILL, referred to this tank as a feeding and breeding paradise for hydra. The water entering this tank is from Lake West Okoboji and provides a veritable feast of small crustaceans for hydra. Literally hundreds of these organisms were collected by scraping a small aquarium net across the top of the intake stirring fan. This structure supported 1-2 cm of crustacean exoskeletons which had been egested by the liberally interspersed hydra. The organisms were transported to the laboratory in jars and were cultured in various aquaria and finger bowls. As for crustaceans, cladocerans and copepods are extremely abundant throughout June and were easily collected with plankton nets towed from piers, boats or shore. Crustaceans were maintained in the laboratory in aquaria and Petri dishes.

Two fascinating crustaceans, chonchostracans (clam shrimp) and anostracans (fairy shrimp), were a special discovery in mid-June. Clam shrimp were collected with a dip net in the hatchery pond near Silver Lake Fen. Adults (about 1 cm in length) were transported in jars to the laboratory and maintained in finger bowls for the duration of the class. A highlight of one summer (1989) was the discovery of the fairy shrimp (Fig.6), an organism which had not been collected in the area for many years. Adults (3-4 cm in length) were collected with hand nets in Green Marsh Pond, a spring pond prone to annual drying. These were tansferred in jars and were kept in finger bowls for up to three weeks.

EXPERIMENTS

A main course emphasis was to encourage students to experiment with cells, tissues and organisms so that developmental phenomena could be examined. Since experiments were performed with a minimum of equipment, the opportunity existed for students to develop their improvising ingenuity. The types of experiments are classified in the following categories: cellular and tissue interactions, regeneration, experimental parasitism and activation of arrested developmental stages (Table 2).

Cellular and Tissue Interactions

Dissociated sponge tissue was used for observations of cellular movement and aggregation (cf. Harrison, 1982). Small pieces (2-3 mm^3) of tissue were removed with scissors and pressed through a metal sieve (ICC# 400) creating a cellular suspension. Upon mixing with pond water and observing immediately with a microscope, spindle-shaped spicules, large archeocytes, choanocytes (small and difficult to observe) and other cells and materials were observed. The archeocytes exhibited amoeboid movement and within minutes joined to form small aggregates.

Several drops of the original suspension were also mixed with filtered pond water in a Petri dish. Aggregates formed on the bottom of the dish and were kept with minimal maintenance (no special saline solution or antibiotics) for the course duration. Some of these aggregates attached to the bottom and formed recognizable sponge tissue (i.e. spicules).

In a classical study on sponges, Humphreys *et al.* (1960) demonstrated the effects of calcium ions on the aggregation of dispersed cells of marine sponges. This experiment was also performed in our course with *Spongilla*. Dissociated cells mixed in calcium free artificial pond water did not aggregate while dissociated cells mixed in pond water (from habitat) or 8.8 mM $CaCl_2$ solution did aggregate.

Demonstration of tissue recognition and adherence was performed using hydra (cf. Lesh-Laurie, 1982). With a human hair, hydra with excised hypostomes and/or bases were strung together and allowed to fuse. Although a tedious procedure, success was obtained. The favorite experiment was the fusing of two hypostomes and the

Table 2. Experiments and Species Used

Experiments	species
Cellular and Tissue Interactions	
cell aggregation	*Spongilla sp*
tissue grafting	*Hydra sp*
Regeneration	
organismal	*Dugesia tigrina*
segmental	*Lumbriculus variegatus*
organismal	*Hydra sp*
Experimental Parasitism	
cercariae	*Posthodiplostomum minimum*
metacercariae	*Posthodiplostomum minimum*
Activation of Arrested Developmental Stages	
statoblasts	*Plumatella sp*
gemmules	*Spongilla sp*
crustacean embryos	*Daphnia spp*
	Streptocephalida seali
	Cyzicus mexicanus

observation of hydra behavior in the dilemma of two heads.

Regeneration

Several groups of invertebrates, particularly planarians, oligochaetes and hydra, are capable of regeneration. When damaged, these organism can either replace missing parts or reorganize remaining tissue into a functional individual. Planarians are particularly suitable for such studies since they heal rapidly and proceed through the textbook steps of regeneration: constriction of damaged area, blastema formation and differentiation (cf. Benazzi and Gremigni, 1982). Although experiments with many variations were attempted, in general, planarians were cut with razor blades into anterior and posterior halves. Each half was placed into a separate Petri dish and observations were periodically recorded. From these studies, normal regeneration time was typically 7-10 days. Anterior halves were observed to regenerate more rapidly. Since regeneration occurred without feeding the organism, new tissue had to be incorporated from the original tissue. Previous research (cf. Gremigni, 1981) has indicated that undifferentiated reserve cells (neoblasts) are present throughout the planarian body and participate in the regeneration process.

The oligochaete, *L. variegatus,* undergoes regeneration during normal asexual reproduction, which involves a fragmentation process followed by segmental regeneration. This phenomenon was examined by carefully cutting worms with a razor blade into anterior, middle and posterior portions, each of which was approximately 60-70 segments. In time, each portion regenerated a whole worm totalling approximately the normal 200 segments. Interestingly, experiments demonstrated that middle and posterior portions consistently regenerated an 8 segment-long head region (with mouth) at the cut anterior end. A much longer tail portion was regenerated at the cut posterior end of anterior and middle portions. Because of this relative shortness of regenerated anterior ends in the case of middle and posterior portions, the original segments attain a new and much more anterior position, a reality necessitating a morphallactic reorganization of various organ systems (Drewes and Fourtner, 1990). Newly formed segments, because they are smaller and unpigmented, can be accurately counted in 1-2 weeks after amputation. After 5-6 weeks the regenerated segments appear indistinguishable from original segments (Drewes and Fourtner, 1990).

Hydra collected from Milford water treatment plant were larger than their less common contemporaries in Little Miller's Bay. They were reasonably easy to dissect and showed rapid reorganization of tissues. New hypostomes appeared within 24 hours following excision.

Experimental Parasitism

Larval digenean parasites must be in the right place at the right time to infect an appropriate host. These organisms display adaptive behavioral traits that enhance the chances of infecting an appropriate host (Palmeiri, 1975). The cercariae of *P. minimum* were observed from the time of shedding from snails; cercariae emerged from the snail host (*Physa spp*) following exposure to light indicating they were most available in the early part of the day, just when the fish hosts are more active. The swimming behavior of the cercariae tends to be a rapid swim up in the water column, followed by a slow drift downward. This keeps the cercariae suspended in the water column, thus increasing the chances of encountering the host fish.

Parasitic platyhelminths often have stages such as metacercariae in which development is arrested until entrance into an appropriate host (Miller, 1954). Metacercariae of *P. minimum* were removed from livers of bluegills and fed to one day old chicks. At 48-72 hours, chicks were killed by cervical dislocation, the intestine was removed and the gut lumen examined for adult parasites. The metacercariae had developed sexual maturity and egg production was observed. Experiments were also performed in which metacercariae developed on the chorio-allantoic membrane of chick embryos (Fried, 1970). In this case, reproductive development occurred, but no egg production was observed.

Activation of Arrested Developmental Stages

Many species of invertebrates can, during sexual or asexual reproduction, produce buds, eggs or embryos which may arrest and survive harsh conditions that could befall the organism. Such is the case with bryozoans in which the production of statoblasts is a form of asexual reproduction. In bryozoans, statoblasts are produced in the stalk-like structure which connect the zooid (animal body) to the stolon, a structure which allows communication with other zooids (Brien, 1953). Observations of *Plumatella* zooids showed statoblasts freely floating in the body cavities and being expelled through the cuticular openings. Large quantities could be collected from the water surface. Several methods of statoblast activation (cf. Mukai, 1982) were unsuccessful in our laboratory. One method that serendipitously worked was freezing in pond water at $-18°C$ for two weeks and then warming to room temperature for 5 days. The statoblast cracked opened and the lophophore and visceral mass (polypide) was observed (Fig. 5).

In sponges, gemmules are produced by sponge archeocytes and trophocytes (cf. Harrison, 1982) which accumulate in the sponge mesohyl and are freed when the animal deteriorates in winter or under other detrimental conditions. In the sponges collected, gemmules were very abundant near the interface of the animal tissues and plant substratum. A successful gemmule activation method (20% activation) was storage at 15°C in pond water for two weeks. Some success was also obtained with freezing and thawing. At the time of activation, archeocytes, reacting to some environmental cue, exited the capsule and migrated over the gemmule surface. Presumably, these archeocytes would eventually organize and differentiate into a functional sponge (Simpson and Fell, 1974).

The crustaceans, clam shrimp, fairy shrimp and water fleas produce eggs or embryos which can survive freezing or dehydration, and in some cases may survive several years. The fertilized eggs of the clam shrimp, *Cyzicus sp,* were collected either following natural release or by dissecting the egg batches from the dorsal region of the animal. The eggs normally have a thick shell, so it is difficult to tell if they are arrested or not (Belk, 1970). Egg batches were subdivided into sets of four and each portion was exposed to a different set of environmental conditions such as room temperature (20°C), dehydration and/or freezing and then observed for activation. Results showed these clam shrimp eggs do not have to be dried or frozen to be activiated, but will survive such treatments.

Arrested eggs or embryos were obtained from the fairy shrimp and water fleas (*Daphnia spp*) by dissection and by natural release. Although various experiments were performed to activate their arrested eggs, no success was obtained.

OBSERVATIONS

Many studies were made where experimental procedures were not used, but observations of normal events were made and recorded (Table 3). These involved direct development, indirect development and asexual reproduction.

Direct Development

In many invertebrates, larval stages are either not present or are found during development only within protective casings, cocoons or marsupia. Such development requires intracellular nutrients such as egg yolk or extracellular nutrients such as albumin. Snails, cladocerans, leeches, planarians, oligochaetes and clams exhibit these strategies.

Snail egg masses were so common that all stages of development, including cleavage, trochophore, spinning trochophore, hippo and juvenile (cf. Morrill, 1982) were repeatedly observed during the first half of June. Students witnessed hatching of embryos from the egg

Table 3. Observations and Species Used

Observations	species
Direct Development	
snails	*Physa spp*
	Planorbis sp
cladocerans	*Daphnia spp*
leeches	*Erpobdella sp*
	Helobdella sp
planarians	*Dugesia sp*
fingernail clams	*Sphaeria sp*
Indirect Development	
sponge larvae	*Spongilla sp*
bryozoan larvae	*Plumatella sp*
copepods	various species
tortoise beetle	*Physonota unipunctata*
Asexual Reproduction	
fission	*Dugesia sp*
budding	*Hydra sp*
fragmentation	*Lumbriculus variegatus*

envelope into the egg capsule and finally the rhythmic radular abrasion of the capsule to effect release for the tiny snails.

In cladocerans, "summer" eggs were routinely obtained. These are parthenogenic and undergo direct development in the marsupial pouch (Fig. 7). It was demonstrated that individual embryos could continue development to the juvenile stage even when prematurely removed from the marsupium.

One surprise was the ease with which leech development, including cleavage and later stages, could be observed in cocoons of *Erpobdella*. Juveniles hatched from egg cases and roamed the interior of the cocoon during development. Some cases held 8-10 juveniles and living quarters were close as they matured. Removal of early stages from the case reduced growth and caused death as compared to control leeches left undisturbed. Another species of leech, *Helobdella sp,* carried embryos and juveniles in a brood pouch on the ventral surface (cf. Fernandez and Olea, 1982). When removed, these juveniles would immediately return to the entanglement of the brood. This was an interesting example of parental care in an invertebrate.

In planarians and fingernail clams, development is difficult to observe. Planaria deposited dark spherical cocoons attached to substrate in culture dishes. The opaque cocoons precluded observation of internal activity and attempts to crack the surrounding envelopes were unsuccessful. However, cocoons kept and observed yielded juvenile planaria in 2-3 weeks. Fingernail clams brood juveniles in the gill tissues, a modified marsupium, and release as many as several a day (Heard, 1970). These juveniles were one fourth to one third the adult size. Embryonic clams were dissected with some difficulty from adult gill tissue. After removal from gill tissue, the smallest embryos rapidly deteriorated, but more mature ones did survive a few days.

Indirect Development

In the life cycle of many invertebrates, free-living larval stages represent means by which organisms take advantage of different habitats during development or allow means of species survival in various environmental conditions. Larvae of several representatives of invertebrates, including insects, copepods, sponges and bryozoans were observed.

Sponge larvae, stereoblastulae, are difficult to collect and observe (cf. Harrison, 1982) therefore little is known about their behavior. Sponge size and water temperature seemed to be critical. A large (6-9 cm diameter, 10-15 cm along stick substrate) sponge placed in a five gallon aquarium and left undisturbed for one or more hours yielded numerous ciliated larvae. The larvae were observed swimming about in an erratic manner and could be collected with pipettes. These events occurred during late June and early July near the end of the course, thus critical observations on selection of habitat and metamorphosis were not possible.

Bryozoan larvae were collected by placing a rock covered with a colony into a large finger bowl and patiently waiting for larvae to be released. Release occurs at different times of the day depending on the species (Oda, 1960). The characteristic rotating swimming pattern could be observed with the naked eye and the larvae were collected with pipettes. Larvae are small colonies each with two polypides enclosed (cf. Mukai, 1982). These larvae did not attach to the glass surface or undergo metamorphosis. Plans for future study will involve studying optimal environmental conditions for release and metamorphosis of the larvae.

Adult cyclopoid and harpacticoid copepods are commonly found in Lake West Okoboji and area ponds. Some carried fertilized eggs which hatched and developed through several nauplius instars. Since the copepod nauplius is a typical crustacean larva, the observation of these forms was particularly meaningful.

An interesting observation was the actual development of the clam shrimp. As development progressed, a thin embryonic envelope appeared inside the tough outer dark egg envelope. The outer envelope was observed to split allowing the thin inner envelope to enlarge providing the embryo with more space. This process is similiar to development in the horseshoe crab, *Limulus polyphemus,* embryos (Bannon and Brown, 1980). Eventually the typical nauplius hatched out and became planktonic.

Insect larvae of many species are easily collected and are particularly fascinating to observe. Although the life cycles of most species are lengthy, tortoise beetle development from fertilized eggs through five instars, pupation and emergence of adult was observed within the 5 week course. Tiny (1.2 mm) larvae are gregarious during early instars, and become even more so as they mature. The larvae possess a particularly offensive method of detering predators. A slimy fecal sack held on the posterior abdominal segment can be swiftly swung forward depositing mucus and excrement on an attacker.

Asexual Reproduction

Fission, budding, and fragmentation represent rapid methods to increase the size of a population without sexual reproduction. These are methods commonly found in invertebrates that have limited growing seasons, such as the planarians, hydra and oligochaetes examined in this course.

Horizontal fission was very common in freshly obtained planarians maintained at temperatures of 18-20°C. This presented a problem when parts of animals isolated for regeneration studies also underwent fission. This dilemma was greatly reduced when planarians were starved for two or more days before cutting.

Budding is a common occurrence in well fed hydra and was observed repeatedly in the hydra collected from the intake tank. The budding region was mapped (Campbell, 1973), and the time period for a new individual to form and separate from its parent was noted. Behavioral observations of attached and detached juveniles were made.

Fragmentation does not seem to be a common form of asexual reproduction in freshwater or terrestrial invertebrates, but was observed in the oligochaete, *L. varieqatus.* Isolated tail portions (in experiments) were especially likely to fragment. This probably reflects natural habitat conditions (Drewes and Fourtner, 1989). The oligochaetes have highly vascularized posterior ends which actually break the surface tension and provide highly efficient respiration strategy (Drewes, 1990). Presumably surface predators (birds) could seize the posterior end which then fragments, saving the worm.

CONCLUSION

The excitement generated by the "birth" of a snail, the pupation of a beetle larva or the emergence of a single statoblast, is a class phenomenon that can not be described, only felt. The positive experience of this type of learning is part of what makes Iowa Lakeside Laboratory a unique and treasured memory for so many people.

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