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**Biochemical composition, gametogenesis and reproductive
ecology of the marine gastropod *Crepidula convexa* Say**

Aitken-Ander, Pamela A., Ph.D.

City University of New York, 1987

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BIOCHEMICAL COMPOSITION, GAMETOGENESIS AND
REPRODUCTIVE ECOLOGY OF THE MARINE GASTROPOD
CREPIDULA CONVEXA SAY

by

PAMELA AITKEN-ANDER

A dissertation submitted to the Graduate Faculty
in Biology in partial fulfillment of the
requirements for the degree of Doctor of
Philosophy, The City University of New York.

1987

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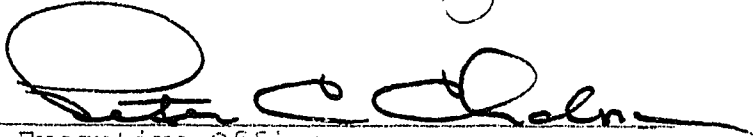
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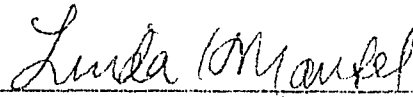

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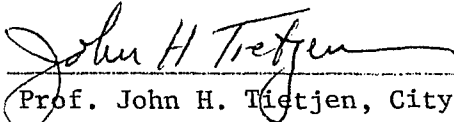
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Abstract

BIOCHEMICAL COMPOSITION, GAMETOGENESIS AND REPRODUCTIVE
ECOLOGY OF THE MARINE GASTROPOD CREPIDULA CONVEXA SAY

by

Pamela Aitken-Ander

Advisor: Dr. David R. Franz

Crepidula convexa is a filter-feeding, protandric hermaphrodite which produces large, yolky eggs. During the reproductive season (May - October) at Breezy Point, New York, females can lay 4 - 5 egg masses.

The male gonad is inactive from January - March. In April, mitotic activity increases as the spermatogonia enter the multiplication phase. Spermatogenesis does not begin until May. Although meiotic activity decreases by November, residual spermiogenesis may continue through the winter. There is no evidence of cytolysis of "old" sperm before the onset of spermatogenesis. Small oocytes are found in the gonad of functional males. Eupyrene and apyrene sperm are produced by male C. convexa.

There is very little change in the female gonad between November and February. Proliferation of oogonia and follicle cells begins in February with the onset of mitotic activity. Vitellogenesis begins between late March and early April and probably continues until November. Large, yolky oocytes, many of spawnable size, are found in the gonad all year. At the end of the

reproductive season, yolky oocytes not spawned are retained in the gonad without resorption through the winter. Females can be induced to spawn out of season by manipulating water temperature.

Seasonal and year-to-year variations occur in the protein, lipid and carbohydrate content of male and female C. convexa. These fluctuations can be correlated with the reproductive cycle of the snail. Protein, lipid and carbohydrate levels tend to increase during gonadal ripening and to decrease toward the end of the reproductive season. There is a post-reproductive feeding period in the fall during which the biochemical components tend to increase followed by a decline over the winter.

Fecundity increases with female weight, and females grow throughout the period of oviposition. Although fecundity is weight-specific, egg output per unit body weight decreases as the animals become larger. As they grow, females derive less benefit (increased fecundity) for each allocation of energy to growth (cost). Regression analysis of data for egg output and net production indicates that females of approximately 21 - 21.5 mm must allocate all net production to egg output and as a consequence cannot continue to grow. C. convexa larger than 22 mm have not been collected at this site. The maximum size attained by C. convexa at a particular geographic location may be determined by energetic constraints.

Acknowledgements

This thesis project could not have been completed without the guidance and encouragement of Dr. David Franz. I thank him for his sound advice and endless patience. I am grateful for the many years of help and support I have received from my teacher and friend, Dr. Elizabeth Worley.

Last but not least, I thank my husband who was often drafted as an assistant on collecting trips and never complained. He is a very understanding person and a great typist.

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Introduction

The remarkable sexual biology of the slipper limpets of the genus Crepidula (Mesogastropoda: Calyptraeidae) has fascinated biologists for almost one hundred years. All the members of the family Calyptraeidae are protandric hermaphrodites. Immature Crepidula become functional males for a variable period of time, and then undergo a transition during which the male reproductive system and its associated structures are transformed into the female system. Conklin (1897) studied the embryology of Crepidula, and reported that the genus was hermaphroditic. The extensive research of Coe (1936, 1938a,b, 1942a,b, 1944, 1947, 1948a,b, 1949, 1953), Gould (1947, 1948, 1952) and Moritz (1938, 1939) provided a large body of information about the embryology, anatomy, morphology, sexuality, fecundity and reproductive cycles of many species of Crepidula. More recently, knowledge of the genus has been expanded in the areas of population dynamics, ecology, reproductive strategies, evolution, systematics and taxonomy (Walne, 1956; Franz and Hendler, 1970; Hendler and Franz, 1971; Johnson, 1971; Hoagland, 1975, 1977, 1978; Gallardo, 1977; Newell and Kofoed, 1977a,b; Matusiak and Fell, 1982).

Another notable attribute of Crepidula and other calyptraeids is that they are among the few filter-feeding prosobranch gastropods. The ciliary mechanism employed

represents a functional modification of the gill and gill filaments as in the lamellibranch bivalves, and also involves changes in the rejection currents found in the mantle cavity of typical prosobranchs (Yonge, 1938). This family shows the highest degree of development of ciliary feeding among the prosobranch gastropods.

Although many species of Crepidula have been studied, the data available in the literature are often incomplete. More information about individual species is needed if we are to gain a better understanding of the form of sexuality, brooding habit (partial and complete) and differing modes of development (direct and indirect) which characterize the genus.

In 1976, I initiated research on the life cycle of the slipper limpet, Crepidula convexa, at Breezy Point, New York (Ander, 1980). This investigation raised significant questions regarding the reproductive ecology of Crepidula, and several of these form the basis of this thesis. For example:

- (1) How do female C. convexa budget available energy for growth and reproduction during the reproductive season?
- (2) Are there changes in the protein, lipid and carbohydrate content of the animals which can be correlated with the demands of reproductive activity?

- (3) What is the length of time required for C. convexa embryos to develop under temperature conditions approximating those prevailing during the period of oviposition?
- (4) How are the processes of gametogenesis and vitellogenesis related to the timing of the annual reproductive cycle at this site?

Crepidula convexa, as all calyptraeids, has a limpet-like shell, and the females are sedentary. Populations of C. convexa occur intertidally and subtidally along the eastern coast of North America from Massachusetts to Florida. The species also inhabits the west coast of Florida and the gulf coast to Texas. North of Cape Cod, C. convexa is found sporadically in warm, shallow embayments as far as Nova Scotia.

C. convexa produces large, yolky eggs which undergo direct development and are brooded beneath the female until emergence as juveniles. C. plana and C. fornicata occur sympatrically with C. convexa throughout most of its range. The eggs of C. plana and C. fornicata are smaller than those of C. convexa and development is indirect. The embryos of these species are brooded only to the veliger stage. The dispersal of C. convexa which lacks a planktonic larva is accomplished by the very motile juveniles and males.

A method was devised to mark the shell of individual

animals and maintain them in the field under natural environmental conditions (Ander, 1980). Marked females were followed through the production of successive broods. Hundreds of egg masses were examined and egg diameter (or embryo size), total number of eggs per brood, number of eggs per capsule and number of capsules per brood were recorded. The development of the embryos was described. Brooding and mating behavior were observed in the field and the laboratory. The fecundity of C. convexa is positively correlated with size, and females continue to grow throughout the reproductive season (Ander, 1980). Each female can produce 4 - 5 egg masses during the period of oviposition which begins in late May and continues until the end of September or mid-October at Breezy Point (Ander, 1980). The onset of oviposition is coincident with the seasonal increase in water temperature, and females with broods are not observed until the temperature reaches 15 - 17 °C (Ander, 1980). As water temperature declines in the fall oviposition ceases (Ander, 1980).

C. convexa is reproductively active at Breezy Point for five to five and one-half months. Females can be induced to produce broods out of season, and males contain mature, motile sperm year round. It was difficult to explain these aspects of reproductive behavior and fecundity without knowledge of the timing of gametogenesis and vitellogenesis. Although some information about the

histology of the gonad can be found in the literature, a detailed monthly study of gonadal maturation in Crepidula has not been performed (Conklin, 1897; Coe, 1936, 1938b, 1942a, 1944; Ishiki, 1939; Gould, 1952). Therefore, determination of the reproductive condition of the animals during each season of the year, and the timing of vitellogenesis was deemed to be an important next step in the study of the reproductive biology of C. convexa.

The animals cease to grow during the winter indicating a reduction in metabolic activity at low water temperatures (Ander, 1980). Feeding also is probably severely curtailed in winter. It may be assumed that serial ovipositions, brooding and growth place a great energetic demand on the resources of the female during the long reproductive season. Reproductive activity and growth also must be a drain on the reserves of the motile, promiscuous males. A number of studies have reported seasonal fluctuations in protein, lipid and carbohydrate levels associated with the reproductive cycle of other mollusks (Giese and Araki, 1962; Blackmore, 1969b; Lawrence and Giese, 1969; Williams, 1970; Vassallo, 1973; Lambert and Dehnel, 1974; Stickle, 1975; Belisle and Stickle, 1978; Taylor and Venn, 1979; Ansell et al, 1980; Barber and Blake, 1981; Devi et al, 1985). Biochemical composition also has been found to vary with feeding activity in some mollusks (Williams, 1970; Stickle, 1975; Ansell et al, 1980; Devi et al, 1985). Are there

detectable seasonal variations in the biochemical composition of C. convexa which can be correlated with reproductive condition and nutritional state? This question and others could be resolved by performing monthly biochemical analyses of whole body homogenates (both sexes) for a one year period. Assumptions about the cost of reproduction in terms of depletion of nutrient reserves cannot be confirmed without quantitative biochemical data. Also, it is not possible to determine the effect, if any, of reduced food intake and cold stress on C. convexa in winter without data for seasonal levels of protein, lipid and carbohydrate.

The time required for the embryos to complete development has been determined for several populations of C. convexa at different geographic locations (Conklin, 1897; Hendler and Franz, 1971; Ament, 1979), but no one has timed each developmental stage or monitored the effect of exposing the embryos to changes in water temperature during the brooding period. The actual physical process of oviposition has not been described or timed in C. convexa. Quantitative data for embryo development and oviposition would be a valuable addition to the ecological and behavioral observations which have already been made (Ander, 1980).

The observation that females continue to grow during the reproductive season raises the question of how C.

convexa allocate available energy between growth and reproduction. Since brood size increases with increasing body size, energy devoted to growth is an investment in future fecundity. Are available resources equally divided between growth and reproduction? If not, what factors influence the amount of energy devoted to each process at any given time? The fecundity and growth data collected using marked individuals (Ander, 1980) provided a starting point in seeking to answer these questions about energy allocation in C. convexa.

C. convexa is a successful colonizer of intertidal substrata under stressful, unstable environmental conditions. Recently, there has been a great deal of interest in the topic of comparative reproductive strategies. Theorists and researchers have sought to understand what makes a species successful and why closely related species have evolved different solutions to the same problems. The ongoing study of C. convexa at Breezy Point, N.Y. has been an attempt to make as complete an analysis as possible of the reproductive strategy of this snail. The problem has been approached from many different angles using a variety of techniques. The timing of the annual reproductive cycle has been established through field observations as well as a histological study of the gonad. Biochemical analysis has been used to link seasonal changes in protein, lipid and carbohydrate content with the reproductive cycle. Data for growth,

feeding and water temperature have been combined with the biochemical data to identify seasonal periods of energy storage and utilization. The simultaneous occurrence of growth and reproduction in C. convexa plays a critical role in its reproductive strategy. This important relationship has been examined by calculating the amount of energy allocated to these processes as females increase in body weight. The analysis of the data for energy allocation has been used to predict a possible maximum body size for C. convexa at this site and to construct a model which might explain the larger body size achieved by its sympatric congeners C. plana and C. fornicata.

Materials and Methods

The Collection Site

Crepidula convexa was collected at a site which lies between Breezy Point and the Marine Parkway Bridge in the Rockaway Inlet (New York). The area is an intertidal mud and sand flat adjacent to a sandy beach. Several small sandbars extend out from the beach and run parallel to the shore. The animals are exposed to the air for several hours at low tide. At high tide, the collecting site is covered by approximately 1 - 1.5 meters of water. There is a tendency for discarded bottles, broken crockery and glass carried by the tide, to collect behind the sandbars. The area is littered with an assortment of trash, but the concentration of bottles and broken glass at this spot is remarkable. Truck and automobile tires also are scattered over the mud flat. Many of these tires have become partially buried in the sand and mud and are semi-permanent features in the area. The glass and crockery are the primary substrate material for C. convexa at this site. However, individuals occasionally are found on empty valves of Mya arenaria and Spisula solidissima, on rocks, and on shells of living Littorina littorea and Ilyanassa obsoleta. The shells of Littorina and Ilyanassa inhabited by hermit crabs also serve as substrate.

Seasonally, the water temperature varies from 0-28^o C. In winter, thin sheets of ice often cover the substrate

and attached animals at low tide. During the summer, C. convexa is exposed to air temperatures as high as 32-38^o C when the tide is out.

Methods of Collection and Handling of Collections

Collections of C. convexa were made every 2 - 4 weeks throughout the year. Water temperature was recorded whenever animals were collected or returned to the study site. If possible, individuals were collected by removing the substrate to which they were attached and placing it into a bucket of seawater. When the substrate could not be removed easily and transported, the animals were gently dislodged and allowed to reattach to a smaller object such as a Mya shell. Brooding females reject their egg mass when they are moved. If females with egg masses had to be removed from the substrate, they were placed into separate containers immediately. The isolation of these females and their broods ensured that there would be no confusion about which female produced each egg mass. Mated pairs were not separated. The animals were maintained in the laboratory in buckets or large glass bowls of seawater which were kept in the refrigerator (4^o C) or the incubator (15-19^o C) depending on the season.

Each snail was examined in a dish of seawater and measured using a Wild stereomicroscope. Sex was determined by observing the development of the phallus and vagina. The phallus develops on the right side of the

neck behind the right tentacle. Males have a large, muscular phallus which arises from a thick base and tapers to a slender sensory tip. Transitional individuals have a reduced phallus which becomes blunt at the tip and exhibits a loss of pigmentation. Female C. convexa never lose the phallus completely, but it is reduced to a tiny remnant in the largest individuals. In young females, the vagina becomes externally visible as a small, fleshly, muscular knob above the neck on the right wall of the mantle cavity posterior to the anus. The vagina lengthens and increases in diameter as the female grows.

Egg masses were removed intact from the female by grasping the clustered stalks of the capsules with a pair of forceps and placed in the well of a depression slide. The eggs (embryos) were measured and the stage of development, number of capsules, number of eggs per capsule, and total number of eggs per mass were recorded. The eggs reserved for biochemical analysis were uncleaved or in very early cleavage stages. Capsules were teased open at one end with a dissecting needle, and the eggs were removed by carefully manipulating them through the opening. Since the egg capsules of C. convexa are transparent, it was easy to choose only capsules which were free of egg debris for use in the assays. The eggs and capsules set aside for the protein, lipid and carbohydrate assays were counted, and collected on tared, numbered

squares of aluminum foil. After washing with distilled water to remove salts, the eggs and capsules were weighed, dried in a vacuum desiccator over Drierite (CaSO_4) and CaCl_2 for at least one week (to constant weight) and re-weighed. The dried eggs and capsules were stored in vials over desiccant in the freezer until needed for the biochemical procedures.

The animals were removed from the shell by severing the shell muscle. The bodies of males and females to be used for histological study were fixed immediately in Bouin's fixative. Individuals not fixed or dissected were blotted dry, numbered, weighed, dried in a vacuum desiccator (see above) and re-weighed. This data was used to determine the relationship between shell length and dry body weight. The whole dried bodies to be used for the determination of protein, lipid and carbohydrate content were placed in vials and stored over desiccant in large jars in the freezer.

Preparation of Algal Cultures

C. convexa was maintained in the laboratory in unfiltered seawater brought from Jamaica Bay in five gallon carboys. The water was changed every 2 - 3 days. Animals retained in the laboratory for more than one or two weeks were fed Isochrysis galbana, Monochrysis lutheri, Tetraselmis maculatus and Dunaliella euchlora to supplement phytoplankton present in the unfiltered

seawater. The algae were cultured in "f/2" enriched seawater medium (Guillard, 1975) in 500 ml and one liter Erlenmeyer flasks. Algal stocks were obtained from Dr. Rhodes at the National Marine Fisheries Laboratory, Milford, Connecticut. Isochrysis galbana and Monochrysis lutheri have been found to be suitable as food for Crepidula (Ament, 1979). Guillard (1975) lists Tetraselmis and Dunaliella among algae useful for feeding marine invertebrates.

Field Studies

In order to study animals in the field under natural conditions, the shells of selected groups of males and females were marked with a file and maintained at the collecting site in chambers. The chambers were constructed from large, clear glass jars. The bottom was removed from each jar to allow water to flow freely through the chamber. Marked individuals were allowed to attach to the inside surface of the jars. Each chamber was completely covered with fine mesh aluminum screen wire to prevent the animals from escaping. The chambers were attached with heavy nylon fishing line to automobile tires partially buried in the sandy bottom. The tires chosen for this purpose were far enough from the beach so that the chambers were not easily visible at low tide. The anchoring lines were approximately 2 to 2-1/2 feet in length and permitted the chambers to float above the

bottom when the tires were covered with water. The chambers were recovered every 2-3 weeks, and the animals returned to the laboratory for examination. Each individual was identified and measured. Since the animals could not be dissected, shell length (mm) was determined rather than dry body weight. The egg masses were removed from brooding females, and the number of capsules, number of eggs per capsule and total number of eggs per brood were recorded. The eggs or embryos were measured, and their developmental stage was determined.

Laboratory Studies of Oviposition and Embryo Development

A large collection of C. convexa was obtained subtidally from Jamaica Bay using a biodredge in April, 1982. The water temperature was 10 - 11 °C, and oviposition had not begun. These animals were used to study reproductive behavior and oviposition in the laboratory. Males and females were maintained in large glass bowls in the incubator at 19 °C to induce oviposition. The unfiltered seawater in the bowls was changed every 1 - 2 days, and the bowls were cleaned. The phytoplankton in the water was supplemented with algae cultured in the laboratory (see above). Marked females were allowed to attach to glass microscope slides before being placed into the bowls. The slides could be removed easily from the bowls permitting daily observation of the female and her brood, if any, without having to move the

animal. When the slide was inverted over a small dish of seawater on the stage of a Wild stereomicroscope, the body of the animal and the eggs or developing embryos could be observed quite clearly. Using this simple laboratory setup, it was possible to observe the process of oviposition and to time the development of the embryos until emergence. Individual females were followed through the production of successive broods.

Many times during the course of this study, animals collected out of season were induced to produce broods in the laboratory. The snails were maintained in the incubator at 19 C^o in bowls of seawater or at room temperature in buckets or bowls. The unfiltered water was changed every 2-3 days. Although females would begin to produce egg masses without supplemental feeding with cultured algae, animals kept in the laboratory for more than 2-3 weeks were fed. Feeding was continued throughout the period of observation.

Histology

Reproductive condition was determined by examination of histological sections of whole animals. After fixation in Bouin's fixative (see above), the snails were embedded in Paraplast (Lancer, St. Louis, Missouri) (m.p. 56-57 C^o). Longitudinal serial sections were cut at a thickness of 9 μ m using a rotary microtome, mounted and stained with Heidenhain's iron hematoxylin and eosin. From 2-4 animals

of each sex were sectioned for each month studied. In recording oocyte diameter, only those oocytes in which the germinal vesicle was visible were measured. Very few large oocytes were perfectly round. To resolve the problem of distortion, it was decided to measure each oocyte at its widest point. Thus, the oocyte diameters determined may be slightly exaggerated, but the error is consistent throughout.

Biochemical Analyses

C. convexa is small (male, approximately 4-7 mm; female, approximately 7-22 mm), and the gonad and digestive gland cannot be dissected apart. Therefore, the whole bodies of males and females were pooled each month (1981 & 1984) to provide enough tissue for the determination of protein, lipid and carbohydrate content.

The dried bodies (see above) were ground to a fine powder with a mortar and pestle. Prior to analysis, the powder was dried overnight in the freezer over desiccant (Drierite) to remove moisture picked up during the grinding. The dried eggs and capsules were suspended in 5-10 ml of 0.1N or 10N NaOH (see Eggs and Egg Capsules), distilled water or a 2:1 (v/v) chloroform-methanol mixture depending on the assay, and ground in a Wheaton Dounce tissue grinder (25 ml). The eggs and capsules were not as difficult to grind as whole bodies so a small tissue grinder was used in an attempt to minimize the loss of

material.

The Folin phenol method of Lowry et al (1951) was used to determine protein content. The dried snail tissue powder (1.5-3.5 mg) was added to 5 ml of 0.1N NaOH in a test tube and left overnight at room temperature (after Barber and Blake, 1981). The next day, this material was ground in a Wheaton tissue grinder. After mixing with a vortex mixer, two equal aliquots (0.2 - 0.4 ml) were withdrawn with a semiautomatic Clay Adams pipette and diluted to a final volume of 1 ml for assay. The optical density of the resultant blue solution was read at 750 nm on a Gilford 240 spectrophotometer. A standard curve was constructed (Appendix A) using bovine serum albumin as the standard. The dried eggs and egg capsules were handled as above except 5.5 mg of egg powder and 0.5 mg of capsule powder were used, and 0.1 ml (diluted to 1 ml with distilled water) and 1 ml aliquots, respectively, were withdrawn for assay. One sample of egg capsules was allowed to remain in 10N NaOH for one week before the protein content was determined (see Eggs and Egg Capsules). Protein content was expressed as the percentage of protein per unit dry weight of tissue.

Carbohydrate content was determined by the phenol-sulphuric acid method of Dubois et al (1956). The dried snail tissue powder (0.5-3.5 mg) was added to 10 ml of distilled water and ground in a Wheaton tissue grinder. After mixing with a vortex mixer, two 1 ml aliquots were

withdrawn with a semiautomatic pipette for assay. The optical density of the resultant orange-yellow solution was read at 490 nm on a Gilford 240 spectrophotometer. A standard curve was constructed (Appendix B) using glucose as the standard. The same procedure was followed with the dried eggs (5.5 mg/5 ml distilled water) and egg capsules (0.5 mg/5 ml distilled water). Two 1 ml aliquots of the egg capsule homogenate and two 0.5 ml aliquots of the egg homogenate, diluted to 1 ml with distilled water, were used for the assay. Carbohydrate content was expressed as the percentage of carbohydrate per unit dry weight of tissue.

Total lipid was determined using the Barber and Blake (1981) modifications of the gravimetric method of Barnes and Blackstock (1973). Adjustments were made in the procedure based upon the amount of dried snail tissue available for analysis (3-20 mg). All glassware was rinsed with solvent immediately before use to remove dust or lint, and gloves were worn to prevent contamination of surfaces with skin oils. A portion of snail tissue powder (3-20 mg) was added to 10 ml of a 2:1 (v/v) chloroform-methanol mixture in a Wheaton tissue grinder. After grinding, the homogenate was mixed with a vortex mixer and poured into a 125 ml separatory funnel. The tissue grinder was rinsed with 10 ml of solvent which was added to the separatory funnel along with an additional 20

ml of solvent. The separatory funnel was shaken vigorously for 10-15 minutes to extract the lipid. Vapor pressure was vented every few minutes by loosening the stopper. After the extraction, the homogenate was filtered through a Whatman No. 1 filter into a second separatory funnel (125 ml). The first separatory funnel was rinsed with 10 ml of solvent which was poured onto the filter and filtered into the second separatory funnel. The filtrate was purified by shaking with 10 ml of 0.9% aqueous NaCl in the separatory funnel. The resulting biphasic mixture was allowed to separate overnight in the refrigerator (4°C). The lower lipid containing chloroform phase was drained into a clean, tared aluminum weighing pan and evaporated to dryness in a fume hood. Each weighing pan was placed on a ring stand in the fume hood, and a metal ring holding the top of a glass petri dish was positioned directly over the surface to prevent dust from falling into the weighing pan. After evaporation of the solvent, the weighing pans were put into Pyrex culture dishes and transferred to a vacuum desiccator (over Drierite) for at least one week or until a constant weight was reached before final weighing of the lipid residue. The dried eggs and egg capsules (4-25.5 mg) were handled precisely as above. Lipid content was expressed as the percentage of lipid per unit dry weight of tissue.

Results

Reproductive Condition

Male Gonad

January

There is no evidence of spermatogenesis. The gonad is relatively inactive, but it is not obviously regressed. Although extremely rare, mitotic figures can be found. Spermatogonia line the tubules, and some spermatocytes and spermatids are present. Mature sperm are scattered throughout the gonad. However, the heaviest concentration of sperm is in the area where the testicular tubules unite to form the single sperm duct and seminal vesicles. Many tubules are not completely filled and open areas of lumen are visible.

February

There is no significant change in gonadal activity in comparison with January. Some spermatids and mature sperm still can be found in the tubules.

March

In March, there is a slight increase in the number of mitotic figures. The tubules contain spermatids and mature sperm. As noted in January and February, there seems to be a tendency for mature sperm to accumulate near the sperm duct and seminal vesicles.

April

Mitotic activity increases sharply in April indicating the onset of gonial proliferation. The testis of a male fixed on April 1 showed less mitotic activity than one fixed on April 17. Therefore, the level of activity increases during the month. Many tubules are almost full of spermatogonia and spermatocytes, yet there are still open areas of lumen throughout the gonad. No spermatids are observed, and the tubules contain virtually no mature sperm except in the region of the sperm duct.

May

The gonad is very active. Mitosis continues and meiosis and spermiogenesis begin. In many areas, groups of spermatogonia are dividing. Meiotic metaphase nuclei are easily identified because the chromosomes have a very characteristic "ring" shape. All sections of the tubules are not equally active. There are regions of concentrated mitotic and meiotic activity interspersed among quiescent areas. The number of spermatogonia and spermatocytes has increased since April. Newly formed spermatids remain in tight clusters, and the new sperm cells aggregate in bundles with heads and tails aligned. These bundles tend to remain intact at sites around the periphery of the tubules where spermiogenesis is occurring. As the spermatids and mature sperm accumulate, they become packed among the spermatocytes in the lumen. The testis of a male fixed on May 14 contained fewer spermatids and sperm

than one fixed on May 30. By the end of May (5/30), there still is not a large concentration of new, mature sperm cells in the gonad.

July

Spermatogenesis continues, but the activity remains concentrated in specific areas. There are many regions where spermatocytes are not actively dividing. Mitotic figures have decreased in number indicating that gonial multiplication slows down by middle to late July. Spermatogonia, spermatocytes and many more clusters of spermatids and sperm than were observed in May fill the tubules.

September

In September, spermatogenesis is proceeding as actively as July. This activity follows the characteristic pattern described in past months. There are several active sites in each tubule, but other areas show no meiotic figures. Only a few mitotic figures are visible. It seems that the gonia essentially cease multiplying between July and September. Although the tubules contain many spermatids and mature sperm, the gonad has not become a thin-walled bag filled only with sperm. Spermatogonia and spermatocytes still form a thick layer lining each tubule, and the lumen is quite full.

November

Gonadal activity has decreased since September. There

are fewer areas with spermatocytes undergoing meiosis. The number of spermatocytes, spermatids and sperm in the lumen of the tubules is reduced. Many tubules are partially empty, and the wall of the gonad looks thinner than it did in September.

The Seminal Vesicles

The seminal vesicles of a mature male are clearly visible to the right, near the shell muscle on the ventral surface of the visceral hump. This area of the sperm duct is convoluted, enlarged, and chalk white in contrast to the yellow-gold color of the gonad and greenish-brown of the digestive gland. If the wall is punctured with a needle, a milky cloud of motile sperm is released.

Although sperm were present in each of the nine months (January - May, July, September, November and December) studied, the seminal vesicles were more fully packed with sperm from January to April. During the reproductive period (May-September or October), some males show a slight reduction in the amount of sperm stored in the seminal vesicles. In November and December, the quantity of sperm observed in the seminal vesicles of different animals was quite variable.

Spermatogenesis: "Abnormal" and "Normal" Sperm

Male Crepidula produce "normal" (eupyrene) and

"abnormal" (apyrene) sperm (Gould, 1917; Coe, 1936, 1942a; present study). This phenomenon has been observed in many mesogastropods and neogastropods (Fretter and Graham, 1962, 1964; Webber, 1977; Giusti and Selmi, 1982). Both sperm types have been reported to be transferred to the female during copulation (Coe, 1942a). In Crepidula convexa, the apyrene sperm always accompany the eupyrene sperm in the gonad and seminal vesicles. If the contents of the seminal vesicles are released into a drop of seawater, the eupyrene sperm swim very actively, but the apyrene sperm show almost no movement. Apyrene sperm do not stain well with hematoxylin or eosin and can be very difficult to detect. They often take on a faint grayish or brownish tint which may be picked up as a background color among the eupyrene sperm. Several morphological types of apyrene sperm are found in C. convexa. Diagrams drawn by Coe (1936, 1942a) indicate that more than one morphological type of apyrene sperm is produced by male C. fornicata.

Oocytes in Male Gonad

All the animals sectioned were functional males with a well developed phallus. Approximately one-third of these males were part of a mated pair when collected. The shell lengths of the selected individuals ranged from 4.5 to 6.6 mm. The gonad of every male regardless of size or season of the year contained numerous oocytes scattered among

the spermatogonia lining the tubules. Some of the oocytes in the gonad of a 5.2 mm animal fixed in April had yolk granules in the cytoplasm.

Summary of Major Events Occurring in Male Gonad

1. During the period from January - March, the gonad is inactive.
2. In April, mitotic activity increases as the gonidia begin the multiplication phase. This activity declines by July, and very few mitotic figures are observed in September.
3. Between April and May, there is a great increase in the number of spermatogonia and spermatocytes filling the tubules of the gonad.
4. Spermatogenesis does not begin until May. Meiotic activity decreases by November. Residual spermiogenesis and the movement of mature sperm (apyrene and eupyrene) into the seminal vesicles may continue through the winter into early spring.
5. There is no evidence of breakdown and removal of "old" sperm from the tubules before the onset of spermatogenesis in May.

Female Gonad

January

January appears to be a resting month. The gonad of a female fixed on January 2 showed no mitotic activity. A

few mitotic figures were found in sections of animals fixed on January 28. Vitellogenesis does not begin until later in the season. Oogonia, oocytes and follicle cells line the tubules. The smaller oocytes are surrounded by follicle cells. There are very few oocytes in the 25 to 38 μm (diameter) size range. Most of the oocytes with yolk granules in the cytoplasm are 89 μm in diameter or larger. The number of 64 and 77 μm (diameter) oocytes containing yolk is negligible. Large, very yolky oocytes (>200 μm diameter) are present in the lumen (Table 1). The wall of the gonad is thin in comparison to later months, and in many areas the tubules are not full.

February

There is a significant increase in mitotic activity in February as the oogonia and follicle cells begin to divide and proliferate. Nests of newly produced oogonia and small oocytes surrounded by follicle cells are very prominent. There is a noticeable increase in the number of oocytes 12.5 - 50 μm in diameter. The accumulation of cells causes areas of the gonad wall to thicken. Oocytes smaller than 89 μm (diameter) with some yolk were not observed. Many large, yolky oocytes remain in the gonad (Table 1).

March

Mitotic activity has not diminished. Oocytes and follicle cells are building up along the wall of the gonad

TABLE 1

Oocyte
Yolk
Content

		January																				
VY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		February																				
VY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		March																				
VY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		April																				
VY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		May																				
VY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		July																				
VY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		September																				
VY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		November																				
VY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NY		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Oocyte Diameter (μm)																				
		12.5	25	38	50	64	77-80	89-102	115	128	140	150	153-165	165-167	178-179	191	204	216-217	230-250	250-300	300-330	

VY = Very Yolky
MY = Moderately Yolky
SY = Some Yolk
NY = No Yolk

+ = Present
- = Not Present

and pushing out into the lumen. There are still many clusters of oocytes 12.5 to 38 μm in diameter. More oocytes in the 64 to 77 μm (diameter) size range contain yolk granules than in January or February. This observation suggests that vitellogenesis probably begins in March. Yolk appears in the cytoplasm of previously yolkless oocytes and probably is added to the larger, partially yolky oocytes that have remained in the gonad over the winter. The animals sectioned were collected on March 20 and March 29 so it is possible that the process does not start until the middle of the month.

April

The oogonia and follicle cells continue to divide and proliferate. Mitotic figures are very common throughout the gonad. There has been a significant increase in the number of follicle cells which along with the oogonia and oocytes form a thick layer lining the tubules. By April, there are many oocytes in the 50 to 77 μm (diameter) size range as a consequence of the cytoplasmic growth of new gonia. When a comparison is made between yolk content of oocytes in the gonad in March and April (Table 1), the impact of the onset of vitellogenesis is obvious. Suddenly, oocytes as small as 38 and 50 μm in diameter contain some yolk granules. It is evident that some oocytes in each size class between 38 and 191 μm have increased in yolk content since March. There does not

seem to be any bias toward the larger, very yolky oocytes. The accumulation of yolk is a gradual process which accompanies the growth of the oocytes.

May

Although oviposition begins by middle to late May at Breezy Point, the gonad is not filled with oocytes of spawnable size ($262 \pm 1.61 \mu\text{m}$) (Ander, 1980). There are many yolky oocytes larger than $200 \mu\text{m}$ (diameter) in the lumen that will contribute to the first broods of the reproductive season. However, the gonad also contains a mixed population of oocytes which vary in size and yolk content (Table 1). Nests of oogonia are less prominent, and mitotic activity has decreased. There are still many small oocytes ($12.5 - 64 \mu\text{m}$ diameter) surrounded by follicle cells lining the tubules. Very yolky oocytes smaller than $128 \mu\text{m}$ diameter appear in May underscoring the continuing accumulation of yolk in oocytes of all sizes.

July

The gonia seem to have stopped dividing. There may be some mitotic activity associated with the follicle cells, but mitotic figures are rare. There is a noticeable increase in the number of oocytes 77 to $89 \mu\text{m}$ in diameter while those under $50 \mu\text{m}$ are much less numerous. Large, very yolky oocytes ($>250 \mu\text{m}$) dominate the gonad filling the lumen. They are packed so tightly that many are

distorted and slightly elongated, and it is difficult to distinguish one oocyte from the next. However, many smaller ($< 140 \mu\text{m}$ diameter) yolkless, partially yolky and very yolky oocytes remain around the periphery of the tubules. Oocytes between 140 and $260 \mu\text{m}$ in diameter were not observed in the gonad of the females sectioned (Table 1). The wall of the gonad looks thinner in many areas than it was in April or May. Since the tubules become greatly expanded as the oocytes increase in size, distension may be the major factor involved in this change.

September

There is no detectable mitotic activity. Oogonia lie along the wall of the gonad, but the large clusters observed in previous months have disappeared. Very few oocytes below $50 \mu\text{m}$ in diameter are found. The condition of the gonad closely resembles July. The largest size classes of oocytes are very numerous ($> 250 \mu\text{m}$ diameter) filling most of the cross-sectional area of the tubules. There are no oocytes between 140 and $255 \mu\text{m}$ in diameter. Small to medium size oocytes ($64 - 140 \mu\text{m}$ diameter) with and without yolk are scattered around the wall of the gonad (Table 1).

November

The number of large, very yolky oocytes has decreased, but many still remain in the tubules. The wide range of

oocyte sizes and yolk content observed in May is again apparent in November (Table 1). This observation strongly suggests that growth of the oocytes and vitellogenesis continue after the cessation of oviposition in early October. November probably marks the end of most of the vitellogenic activity since gonadal condition changes very little between November and February. Oocytes smaller than 50 μ m in diameter are scarce. The layer of follicle cells is reduced, and there are open areas in the lumen. The gonad seems less crowded when compared with the animals sectioned in September.

The Seminal Receptacles

The seminal receptacles are very inconspicuous and difficult to locate except in serial sections. This cluster of sacs lies at the junction of the oviduct and uterus, and there is usually a dark yellow pigmentation associated with the region. If this area is dissected and pressed under a cover glass in a drop of sea water, motile sperm are observed. The precise number of receptacles varies among different species (Giese, 1915; Ishiki, 1939; Coe, 1942a). There are at least four to five separate seminal receptacles in C. convexa. During copulation, sperm are transferred to the female and pass from the uterus into the receptacles for storage. At the time of oviposition, oocytes leave the ovary via the oviduct and enter the proximal section of the uterus where

fertilization occurs. Sperm have been observed in this area which Coe (1942a) called the fertilization chamber. Although the seminal vesicles of males contain apyrene and eupyrene sperm, only eupyrene sperm are found in the seminal receptacles. Coe (1942a) reported that both apyrene and eupyrene sperm are transferred to the uterus, but the apyrene sperm rapidly disintegrate and do not enter the seminal receptacles. Females separated from their associated males and isolated in both laboratory and field experiments deposited fertile eggs for several months (Ander, 1980). Therefore, sperm stored in the receptacles remain viable for an extended period of time. In female C. onyx sperm were found to remain functional for more than a year (Coe, 1942a). The seminal receptacles contain sperm in each of the months examined from March to December. Technical difficulties with the sectioning made it impossible to study this region in the January and February animals. Although the receptacles are almost completely full in March and April, there seems to be a reduction in the sperm present during the reproductive season (May, July, September). In November and December, the seminal receptacles still remain partially empty.

Some Comments on Oocyte Development and Vitellogenesis

Oogenesis in Crepidula proceeds only to the primary oocyte stage in the gonad. The first maturation division

occurs in the uterus immediately after sperm entry (Conklin, 1902). The large, yolky cells remaining in the gonad when oviposition ceases are retained as primary oocytes, not mature ova.

Yolk granules in the cytoplasm of the oocytes stain blue-black with Heidenhein's iron hematoxylin. The first yolk granules detected are small but larger ones appear as more yolk accumulates in the cytoplasm. It is possible that the smaller granules coalesce to form the larger ones. There is some indication that all the yolk granules found in the oocytes may not be similar biochemically. When sections stained with hematoxylin and eosin are destained, a difference is noted among the granules in their affinity for hematoxylin.

Yolk usually begins to accumulate in the cytoplasm near the region of cell membrane in contact with the gonad wall. As the yolk content increases, the granules disperse becoming more evenly distributed through the cytoplasm. Oocytes well over 100 μm in diameter remain in contact with the wall of the gonad, and it is not unusual to see quite large, yolky oocytes which have become pear-shaped or distorted while maintaining this position.

Follicle cells fully surround oocytes up to a diameter of approximately 70-80 μm . As the oocytes increase in size, they push out into the lumen of the tubules and follicle cells only remain near the area of contact with

the gonad wall.

Summary of Major Events Occurring in Female Gonad

1. Mitotic activity with proliferation of oogonia and follicle cells begins in February and continues very actively until May when a decrease in the number of mitotic figures is noted. By July, multiplication of the oogonia has ceased.
2. The onset of vitellogenesis occurs between late March and early April. Yolk is deposited simultaneously in a wide range of oocyte sizes over an eight to nine month period (March to November). Thus, oocyte development is staggered, and the gonad always contains small oocytes and those large enough to be spawned.
3. Oocytes smaller than 50 μm in diameter are less numerous by July. This decline is the result of oocyte growth, and the reduction in the rate of gonial proliferation noted in May.
4. Large, yolky oocytes, many of spawnable size, are found in the gonad throughout the year. The largest oocytes become the dominant size class by July. Yolky oocytes not spawned before the end of the reproductive period (September to mid-October) are retained in the gonad over the winter. There does not seem to be any breakdown or resorption of oocytes which remain in the gonad.

5. When animals are removed from the shell, the pale yellow gonad is quite conspicuous and any major changes in gross anatomy are easily observed. Dissections of females collected monthly reveal that the tubules of the gonad do not undergo a significant period of regression during the year. The tubules always appear full, and the pale yellow, yolky oocytes are clearly visible through the transparent gonad wall. Regardless of the season, piercing the gonad with a fine needle causes a stream of yolk granules and yolky oocytes to pour out.
6. Gonadal condition changes very little between November and February, and this is the least active period of the year.

Induction of Oviposition

Females collected before or after the reproductive period (mid-May to September or mid-October) can be induced to lay eggs in the laboratory. Animals brought to the laboratory in April, November and February, 1982 and placed in an incubator at 19 C began to produce broods within 12-21 days. These egg masses were normal, the eggs were fertile, and many broods were observed until emergence of the juveniles.

The onset of oviposition can be delayed by maintaining animals at temperatures below 15 C. Females collected in April, 1982 and kept in a tank supplied with recirculated,

chilled sea water maintained below 15 °C had not produced eggs by June 22. The water temperature in the tank rose to 15 - 16 °C after June 18, and oviposition began by June 25.

Females collected during the reproductive period and placed in the refrigerator (approximately 5 °C) do not lay eggs. Transferring these animals to an incubator at 19 °C or exposing them to room temperature will induce oviposition again.

The duration of the reproductive period at Breezy Point (Figure 1) is determined by the length of time the water temperature remains above 15 - 17 °C (Ander, 1980). Taking into consideration slight variations in water temperature from year to year, the period of oviposition is approximately 21 weeks. However, this period can be extended almost indefinitely in the laboratory. Many females brought from the field in August, 1982 and maintained in the laboratory at room temperature continued to produce normal broods and juveniles until the middle of December. Assuming that reproductive activity began in mid-May, this group of females had remained reproductively active for approximately 30 weeks.

It has been reported that the reproductive season of C. convexa at Woods Hole, Mass. extends from early or mid-June through September (Conklin, 1897; Hoagland, 1978). The delay in onset of oviposition at Woods Hole is

Figure 1

Water temperature and the percentage of females brooding
at Breezy Point, New York - 1976 and 1978.

BREEZY POINT

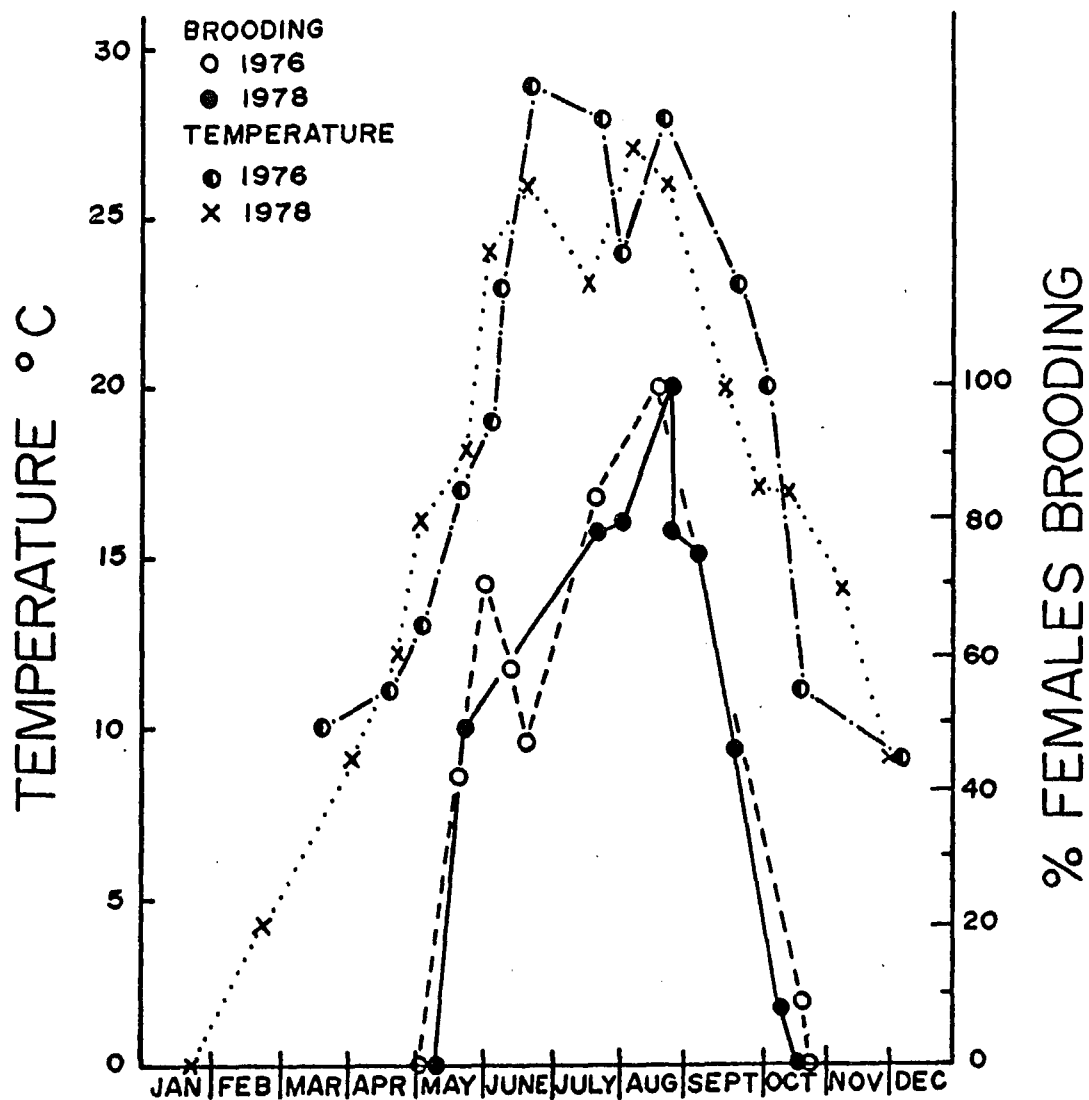
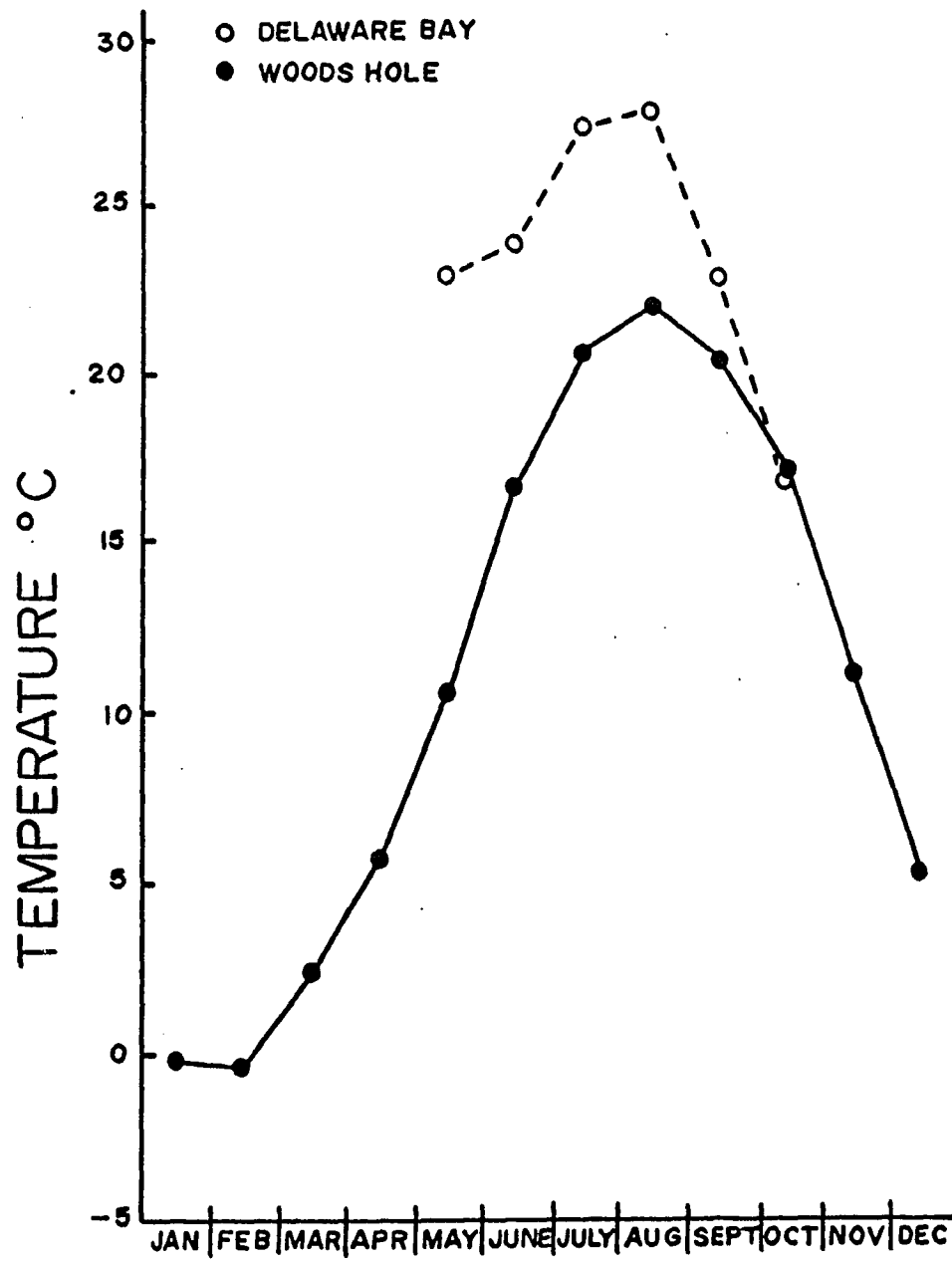


Figure 2

Water temperature at Woods Hole, Massachusetts (National Ocean Survey, 1973) and in lower Delaware Bay, New Jersey (Franz, 1966).



correlated with a slower rise in water temperature in spring (Figures 1, 2) (Ander, 1980). C. convexa collected from Quisset Harbor, Mass. on April 29, 1979 (10^o C) were placed in traps at the Breezy Point study site on May 6 (14.5^o C). Several of the transplanted females began to produce broods by the third week in May. Between May 6 and May 28, 1979, the water temperature at Breezy Point rose from 14.5 to 17^o C. Therefore, oviposition also can be induced in the field by transferring females to an area where they are exposed to the required temperature regime.

Temperature, Growth and Feeding

Crepidula convexa grow more slowly as water temperature drops in the fall, and the growth rate of both sexes is essentially zero by winter (Ander, 1980; present study). Although partially digested material and fecal pellets were found in the gut of males and females in every month studied (January-May, July, September, November, December), it has been reported that the feeding efficiency of filter-feeding mollusks is reduced when water temperature is low (Walne, 1956; Yonge, 1960; Wilbur, 1964; Owen, 1966; Johnson, 1971).

In spring, both sexes show new shell growth, and feeding efficiency increases as water temperature rises (Ander, 1980; present study).

Since the temperature of the water at Breezy Point in

summer is always well above the requirement for oviposition (15-17^o C), slight variations in summer water temperature from year to year probably are not critical. During the reproductive season, males and females continue to grow (Ander, 1980; present study).

The years (1981, 1984) in which samples were collected for the biochemical assays differed in temperature pattern (Figures 6, 7, 8). There was a difference in the severity of the winters of 1980-1981 and 1983-1984. The warmer fall and early winter of 1984 could have extended the period of oviposition and provided a more favorable post-reproductive feeding opportunity. The spring rise in water temperature each year at Breezy Point begins between March and April. By May, the temperature has reached 15-17^o C. There was no deviation from this pattern in either 1981 or 1984. However, the late winter and early spring of 1984 were noticeably warmer than 1981 and, it is possible that the animals may have begun feeding earlier in the spring of 1984.

Biochemical Composition

Biochemical Composition and the Reproductive Cycle

The results of the assays indicate that there are both seasonal and year-to-year variations in protein, lipid and carbohydrate content in the body of female and male Crepidula convexa (Table 2). There were no

TABLE 2
¹
 Biochemical Composition (% Dry Tissue Weight)
 1981

Month	% Protein		% Carbo- hydrate		% Lipid	
	F	M	F	M	F	M
Jan.	46.4	----	13.5	----	10.0	----
Feb.	60.0	57.0	13.3	8.5	10.4	----
Mar.	66.0	56.3	6.7	7.0	8.6	----
Apr.	50.0	45.0	10.0	----	----	----
May	67.4	64.5	12.0	7.9	12.3	12.5
June	66.3	88.8	17.5	12.0	10.4	----
July	85.8	87.5	14.7	9.0	12.3	7.4
Aug.	65.0	80.0	19.7	13.8	7.5	8.1
Sept.	51.4	59.2	19.4	11.1	5.0	5.5
Oct.	70.8	73.3	13.3	10.0	7.1	8.8
Nov.	61.6	65.8	12.3	6.0	9.3	11.0
Dec.	61.3	66.3	10.6	8.0	10.0	11.2

TABLE 2 (con't)

1984

Month	% Protein		% Carbo- hydrate		% Lipid	
	F	M	F	M	F	M
Jan.	56.4	61.6	13.4	10.0	8.4	11.1
Feb.	60.0	65.0	9.7	8.3	15.7	12.2
Mar.	60.7	67.5	8.6	7.7	11.1	12.2
Apr.	-----	-----	-----	-----	-----	-----
May	56.8	60.0	8.7	7.3	12.2	13.3
June	53.6	58.3	10.3	7.4	16.8	14.7
July	53.5	60.8	10.3	6.7	15.0	13.7
Aug.	62.1	61.3	9.4	6.6	14.5	9.5
Sept.	45.7	52.1	8.9	3.7	13.0	16.3
Oct.	-----	-----	-----	-----	-----	-----
Nov.	-----	-----	-----	-----	-----	-----
Dec.	56.8	56.4	12.7	9.7	12.0	19.0

1

M = Male

F = Female

statistically significant correlations between total body content of protein and carbohydrate or carbohydrate and lipid (1981 and 1984). The results for males from 1984 showed a weak correlation ($r = 0.67$, $P = 0.05$) between protein and lipid, but there was no significant correlation between protein and lipid in either females or males from 1981 or females in 1984.

Although the biochemical constituents were not directly correlated, there were similarities in annual patterns of lipid, protein and carbohydrate content in both females and males in 1981 and 1984 (Figures 3, 4, 5). However, these patterns were displaced somewhat in time in different years. A notable difference between the two years is the magnitude of the fluctuations in body components of both sexes. The observed fluctuations in biochemical composition are correlated with the reproductive cycle of C. convexa.

The data for 1981 and 1984 show that protein, lipid and carbohydrate composition increased in the spring, peaking during the summer, and declining by September to October (Figures 3, 4, 5). For both females and males, this is the time when the gonad is ripe and spawning occurs. In the male, meiotic activity increases between May and July, and the gonad becomes filled with spermatogonia, spermatocytes, spermatids and mature sperm. By July, the female gonad is dominated by large, yolky

Figure 3

Levels of protein in whole body homogenates of male and female Crepidula convexa (1981 X—X; 1984 ●—●). Each point represents the percentage of protein in a unit weight of dry tissue.

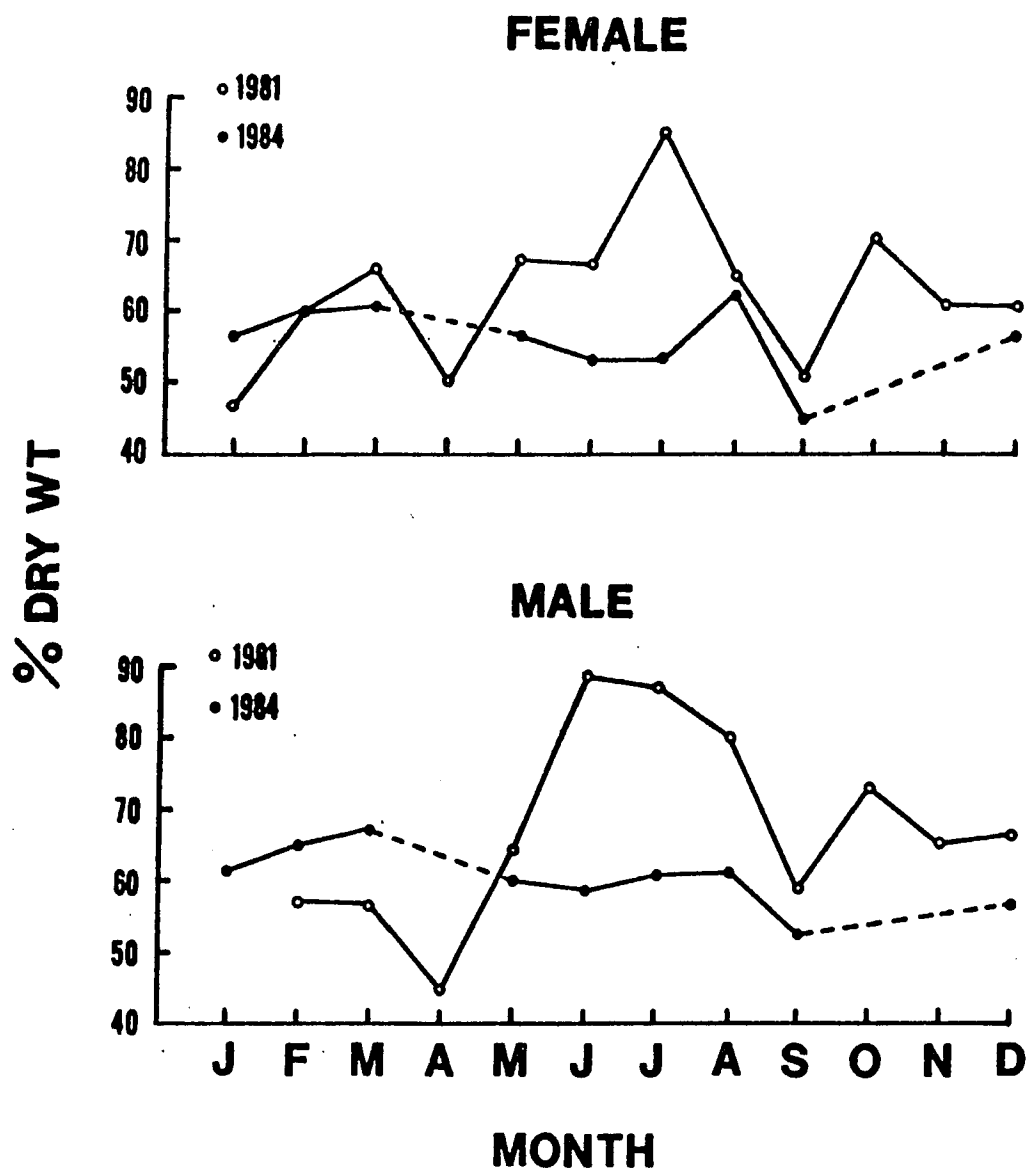


Figure 4

Levels of lipid in whole body homogenates of male and female Crepidula convexa (1981 X——X; 1984 ●——●). Each point represents the percentage of lipid in a unit weight of dry tissue.

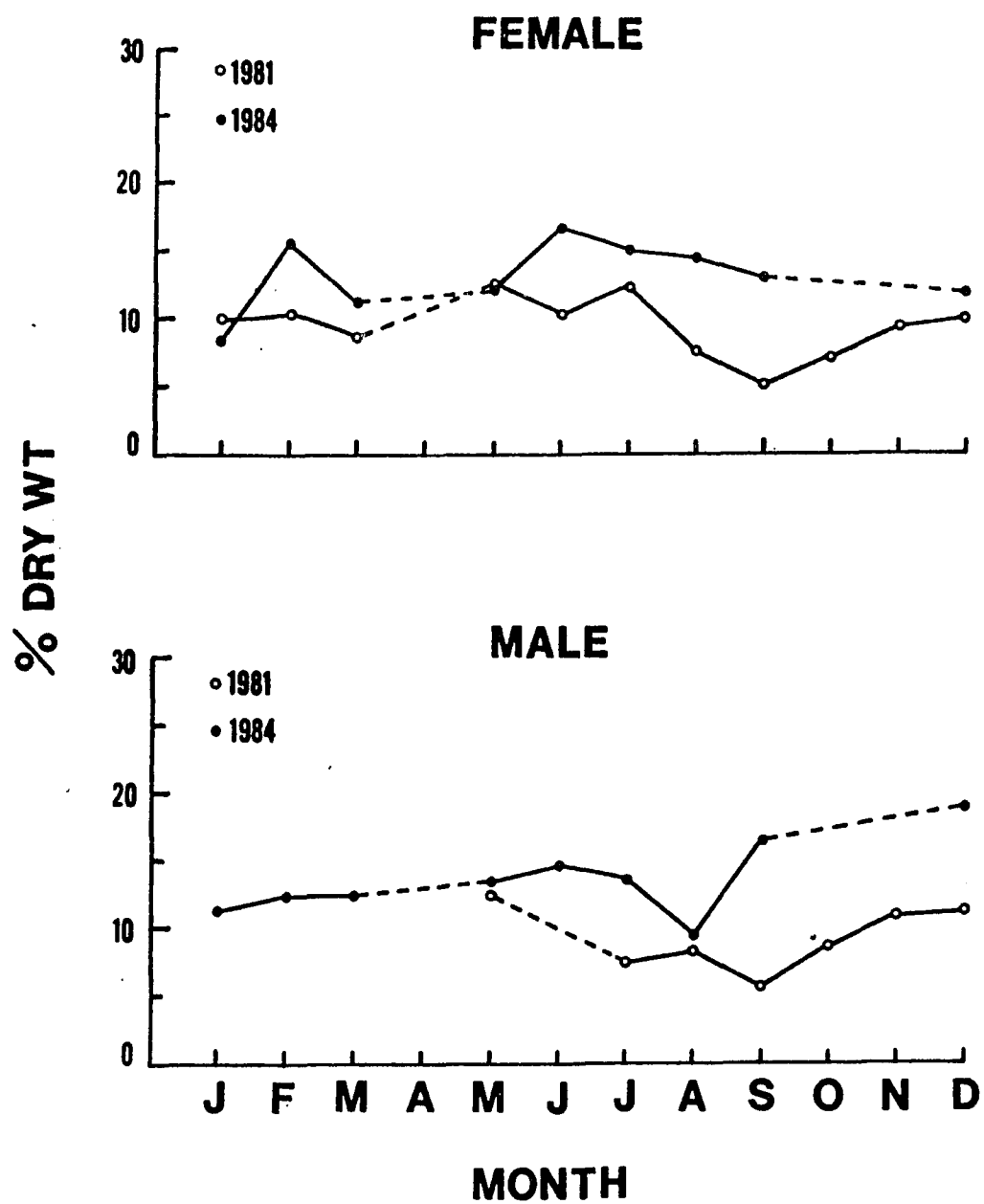


Figure 5

Levels of carbohydrate in whole body homogenates of male and female Crepidula convexa (1981 X——X; 1984 ●——●). Each point represents the percentage of carbohydrate in a unit weight of dry tissue.

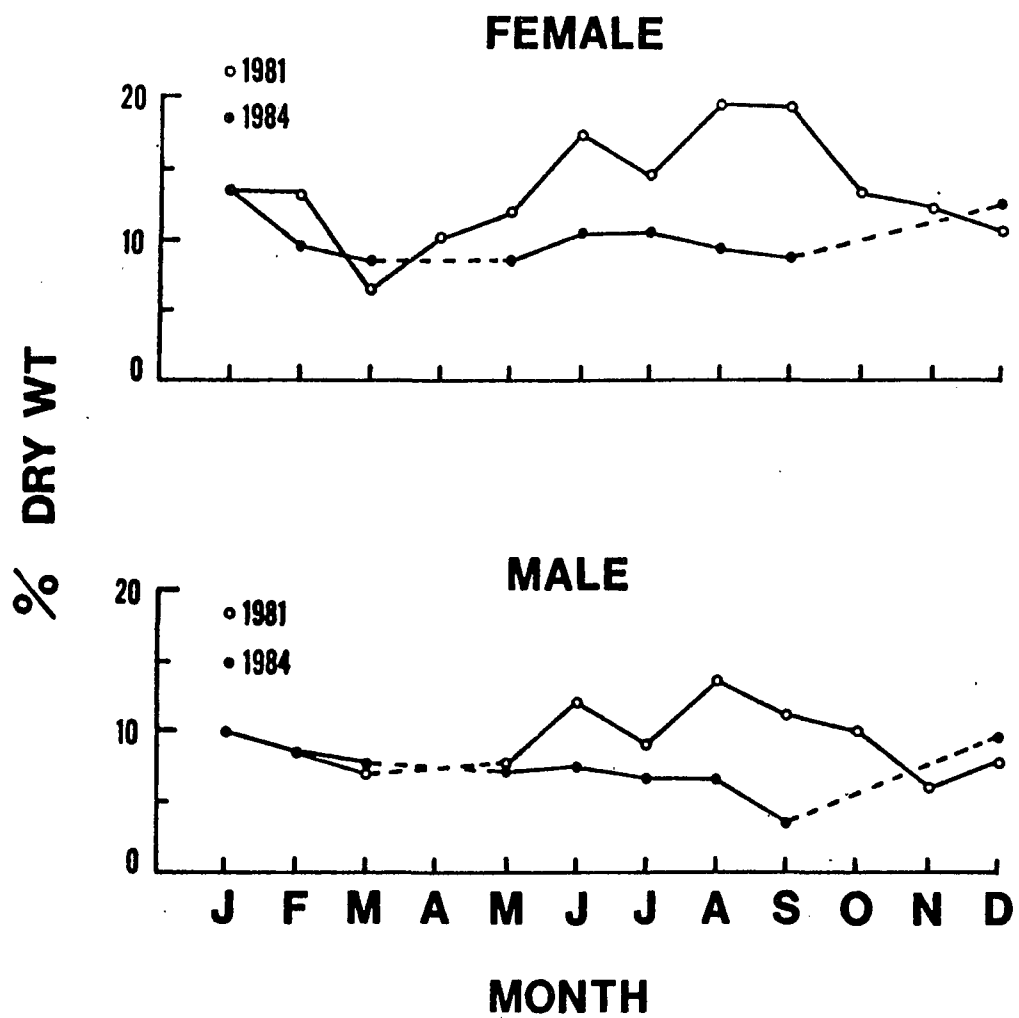


Figure 6

Water temperature at Breezy Point, New York (1981 ●——● ;
1984 X——X).

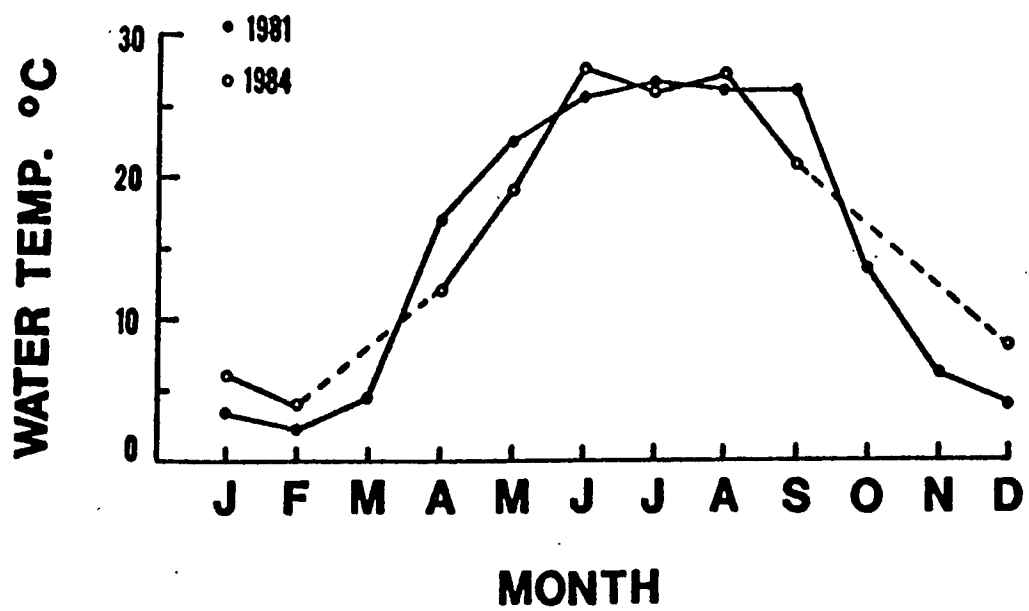
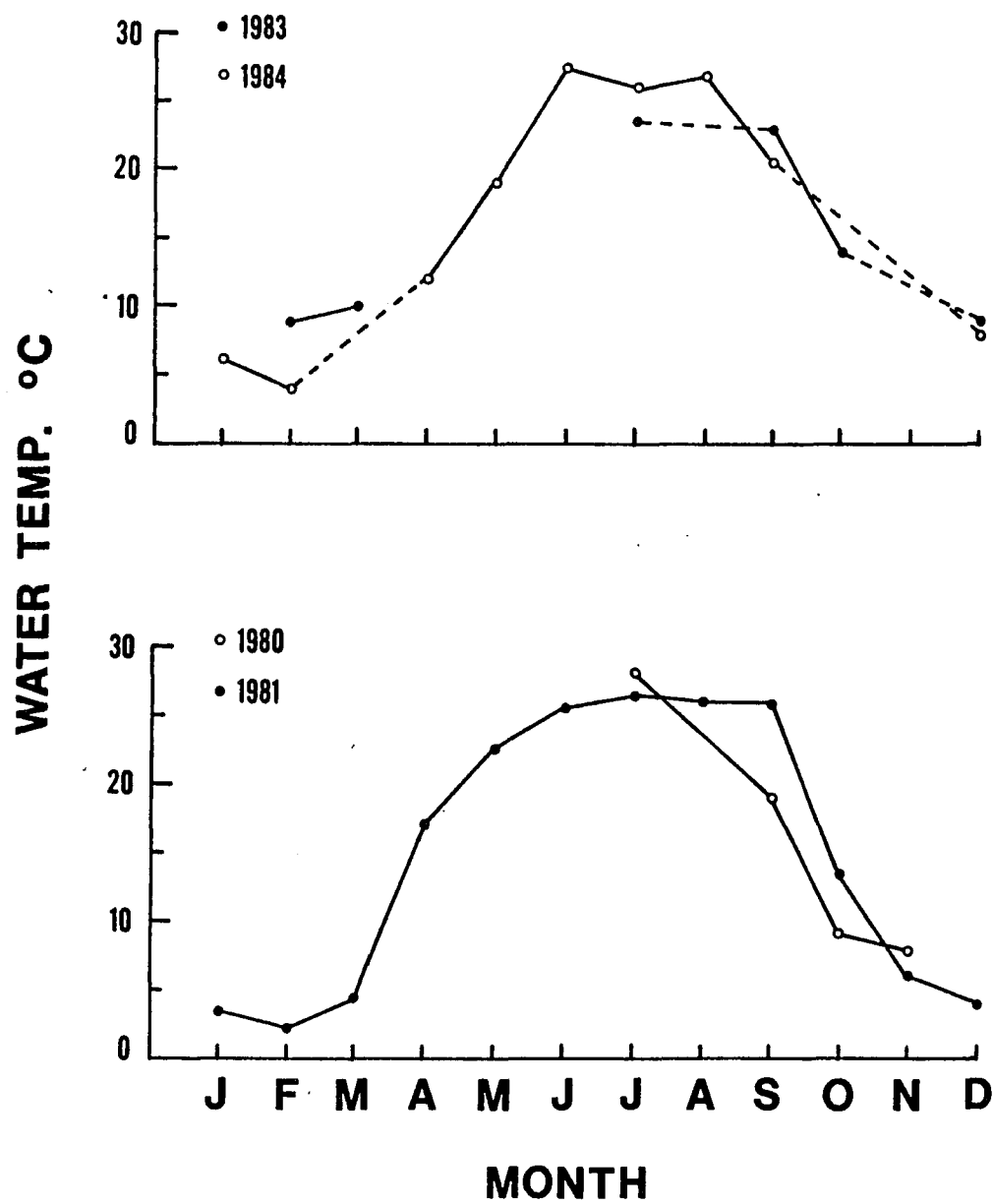


Figure 7

Water temperature at Breezy Point, New York (1983 ●——● ;
1984 X——X).

Figure 8

Water temperature at Breezy Point, New York (1980 X——X;
1981 ●——●).



oocytes. Oviposition continues for a period of approximately five months, and females can produce four to five broods. The motile males can move from female to female forming a mated pair for varying periods of time. Therefore, oviposition and copulation occur repeatedly during the reproductive season. Changes in biochemical content between May and September are gradual rather than abrupt. This is consistent with the reproductive pattern of an animal that undergoes multiple spawnings during a long reproductive period.

The protein content of females and males increased between September and December in 1981 and 1984 (Figure 3). Lipid, with the exception of 1984 females, also increased in both years. The 1984 females were found to have approximately the same lipid levels in September and December (Figure 4). In 1981, carbohydrate composition decreased between September and December, although this was not true in 1984 (Figure 5). Oviposition may continue through mid-October in some years. Gametogenesis in the male slows down by November. The female gonad contains fewer large, yolky oocytes in November as the result of serial ovipositions. However, the data indicate that vitellogenic activity and oocyte growth may continue through November (Table 1). The data for 1981 and 1984 show that there is a 2-1/2 to 3 month post-reproductive interval in the fall during which most biochemical

constituents increase.

During the winter of 1981, the protein content of female and male snails decreased, but in 1984 both sexes showed an increase in this component (Figure 3). There were not enough large males in the January and February 1981 samples for lipid assays to be performed, but the females did not show a significant change in lipid content between December and February. In 1984, the lipid composition of females increased over the winter, but a decrease was detected in the males (Figure 4). The carbohydrate content of females increased during the winter of 1981 while the level in males remained approximately unchanged. The amount of carbohydrate in both females and males decreased in the winter of 1984 (Figure 5). The male gonad is relatively inactive from January through March. The condition of the female gonad changes very little between November and February. February marks the onset of mitotic activity, and the proliferation of oogonia and follicle cells in the female gonad. Therefore, the energetic drain for reproductive processes is at its lowest during the winter. However, the animals must survive several months of very low water temperature ($1 - 2^{\circ}\text{C}$) and probably reduced feeding (Walne, 1956). The data for 1981 indicate that in most instances biochemical components decreased or remained unchanged through the winter. This trend was not as

pronounced in the winter of 1984. The data show a drop in some nutrient levels, but others definitely increased.

Between February and June 1981, the protein and carbohydrate composition of both sexes increased, but the lipid content of females remained unchanged. Lipid assays could not be performed in March, April and June, 1981 due to small sample size. In the spring of 1984, the protein content of females and males decreased while lipid showed an increase in both sexes. The amount of carbohydrate present in the bodies of females and males did not change between February and June of 1984. In April, mitotic activity in the male gonad increased, and there was a rapid rise in the number of spermatogonia and spermatocytes. Spermatogenesis begins in May. Although gonial proliferation begins by February in females, there is no evidence of the onset of vitellogenesis until late March. Thus, the gonad of C. convexa becomes active early in the spring. During this pre-reproductive period of gonadal ripening in 1981 and 1984, most nutrient levels increased or showed no change. The energy requirement for activation of the gonad may be balanced somewhat by increased feeding as water temperature rises. In April, the digestive gland of both sexes shows increased activity as evidenced by an increase in the thickness of the wall and in the amount of cellular inclusions.

Biochemical Composition and Seasonal Changes in Body Weight

When the data for total dry body weight of female and male C. convexa as a function of shell length are plotted by month, it becomes apparent that there are seasonal fluctuations in body weight (Figures 9, 10). The same pattern was observed in dry body weight data from 1981 and 1984. Regression lines were fitted to the data for each month, and the regression coefficients were significant (Table 3).

During the winter of 1981 and 1984, males and females lost weight. Therefore, a decline in dry body weight is observed at a time when biochemical constituents show a tendency to decrease or remain unchanged, feeding may be reduced, and the gonad is relatively inactive.

Between February and June 1981, males and small females gained weight while the largest females showed a slight weight loss. In the spring of 1984, both sexes gained weight. The observed weight gain coincides with gonadal ripening. As water temperature rises, conditions become more favorable for feeding, and new shell growth occurs. The observation that most biochemical components increase or remain unchanged seems consistent with a period of gonadal maturation, increased feeding and growth.

The data for 1981 indicate that males and small

Figure 9

Seasonal variation in the dry body weight of female Crepidula convexa (1984). Regression lines were fitted to the data (July, $Y = -117.5 X^{2.98}$, $P < 0.001$, $n = 53$) (September, $Y = -281.8 X^{3.21}$, $P < 0.001$, $n = 46$).

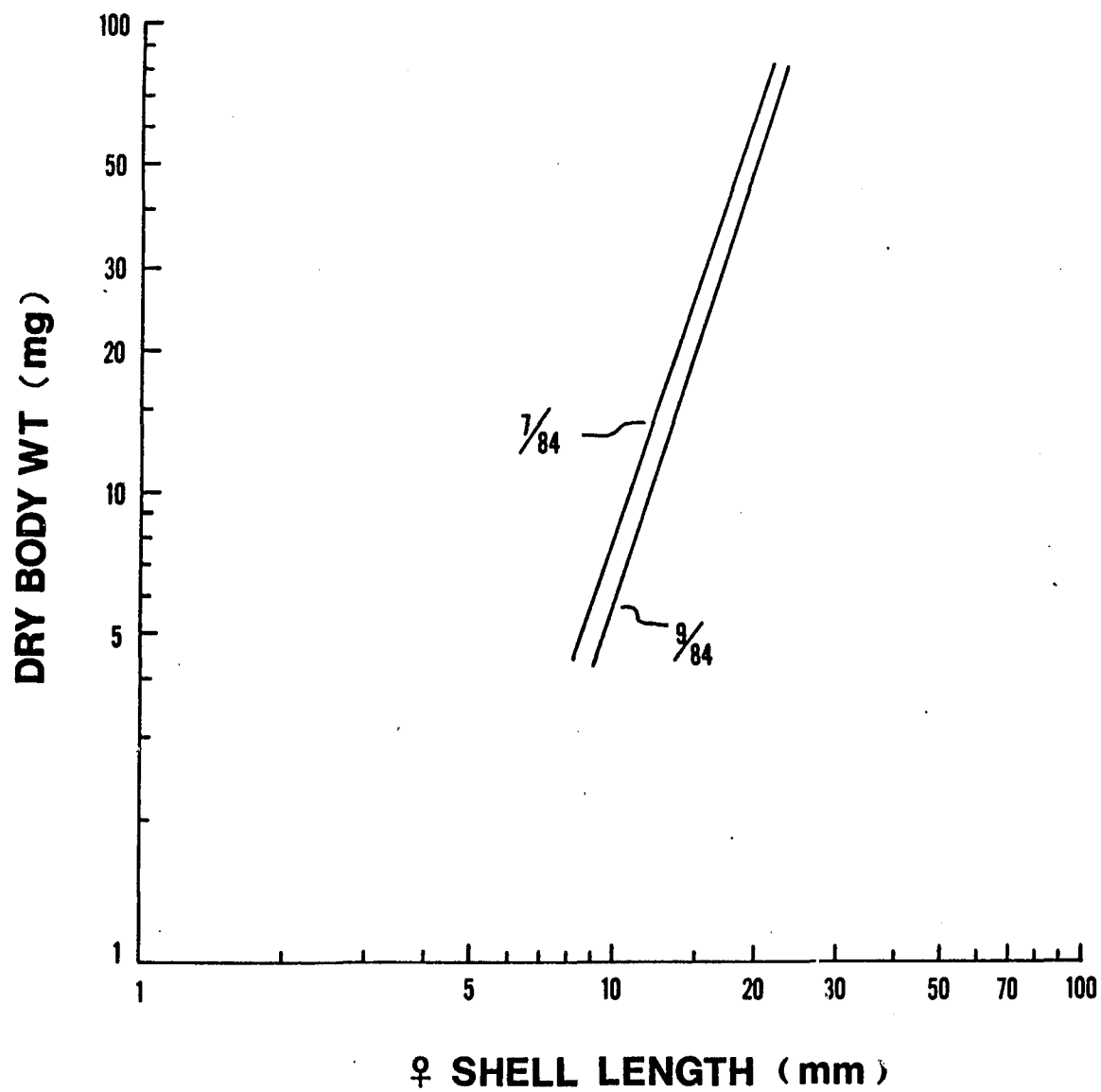
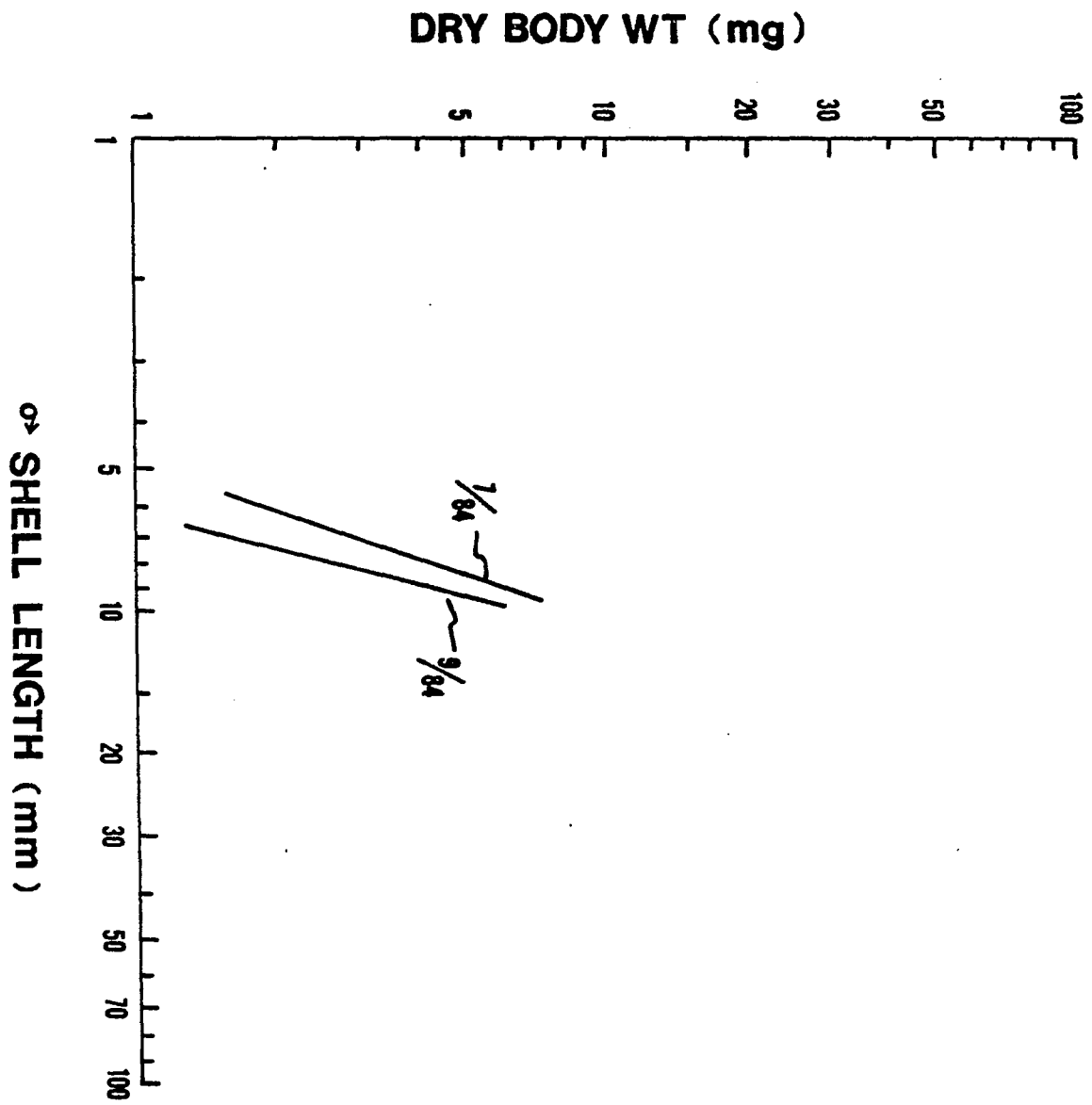


Figure 10

Seasonal variation in the dry body weight of male Crepidula convexa (1984). Regression lines were fitted to the data (July, $Y = -102.3 X^{2.93}$, $P < 0.001$, $n = 54$) (September, $Y = -1258.9 X^{3.92}$, $P < 0.001$, $n = 65$).



females lost weight between June and September. However, large females showed a weight gain. During the summer of 1984, females and males lost weight. Thus, C. convexa tend to lose weight during the reproductive period. The protein, lipid and carbohydrate levels of the body also decline by the end of the reproductive season. There is no evidence that brooding reduces feeding. Brooding females were included in the July and September samples studied for reproductive condition. The gut of these individuals was found to be full, and many fecal pellets were observed in the distal portion of the intestine. Females continue to grow while producing successive broods (Ander, 1980). Although the snails are feeding, the combined costs of growth and reproduction appear to deplete body resources (decline in body weight and biochemical components).

In 1981 and 1984, female and male C. convexa gained weight between September and December. The biochemical data show that most components increase in the fall. The animals seem to make a post-reproductive recovery before winter. In early fall, the growth rate of females and males declines, and the long reproductive season ends. However, feeding probably continues until water temperature drops below 5 °C in December. Walne (1956) reported that less than 50% of C. fornicata in Essex rivers (England) were feeding when the water temperature

TABLE 3

Monthly Regression Equations of Dry Body Weight

		<u>1981</u>	
		Female	Male
Dec.	$\log Y = (-1.72) + 2.70 \log X$ ($P < 0.001$)		$\log Y = (-2.28) + 3.36 \log X$ ($P < 0.001$)
Feb.	$\log Y = (-2.36) + 3.18 \log X$ ($P < 0.02$)		$\log Y = (-3.56) + 4.71 \log X$ ($P < 0.001$)
June	$\log Y = (-1.63) + 2.51 \log X$ ($P < 0.001$)		$\log Y = (-1.49) + 2.41 \log X$ ($P < 0.001$)
Sept.	$\log Y = (-2.28) + 3.14 \log X$ ($P < 0.001$)		$\log Y = (-1.58) + 2.45 \log X$ ($P < 0.001$)
		<u>1984</u>	
		Female	Male
Dec.	$\log Y = (-2.03) + 3.00 \log X$ ($P < 0.001$)		$\log Y = (-2.07) + 3.01 \log X$ ($P < 0.001$)
Feb.	$\log Y = (-1.97) + 2.88 \log X$ ($P < 0.001$)		$\log Y = (-1.67) + 2.49 \log X$ ($P < 0.001$)
June	$\log Y = (-1.75) + 2.75 \log X$ ($P < 0.001$)		$\log Y = (-1.75) + 2.64 \log X$ ($P < 0.001$)
Sept.	$\log Y = (-2.45) + 3.21 \log X$ ($P < 0.001$)		$\log Y = (-3.10) + 3.92 \log X$ ($P < 0.001$)

1981

	Female	Male
Jan.	$\log Y = (-2.14) + 3.00 \log X$ (P<0.001)	-----
Mar.	-----	$\log Y = (-2.60) + 3.76 \log X$ (P<0.001)
Apr.	-----	$\log Y = (-1.97) + 2.91 \log X$ (P<0.01)
May	$\log Y = (-1.43) + 2.31 \log X$ (P<0.001)	$\log Y = (-1.40) + 2.25 \log X$ (P<0.001)
July	$\log Y = (-2.31) + 3.11 \log X$ (P<0.001)	$\log Y = (-2.09) + 3.10 \log X$ (P<0.001)
Aug.	$\log Y = (-1.61) + 2.55 \log X$ (P<0.001)	$\log Y = (-0.91) + 1.86 \log X$ (P<0.001)
Oct.	$\log Y = (-2.55) + 3.45 \log X$ (P<0.001)	$\log Y = (-1.62) + 2.64 \log X$ (P<0.001)
Nov..	$\log Y = (-1.59) + 2.60 \log X$ (P<0.001)	$\log Y = (-3.37) + 4.60 \log X$ (P<0.001)

1984

	Female	Male
Jan.	$\log Y = (-1.80) + 2.76 \log X$ ($P < 0.001$)	$\log Y = (-1.93) + 2.86 \log X$ ($P < 0.001$)
Mar.	$\log Y = (-2.17) + 3.10 \log X$ ($P < 0.001$)	$\log Y = (-1.98) + 2.85 \log X$ ($P < 0.001$)
Apr.	-----	-----
May	$\log Y = (-1.59) + 2.56 \log X$ ($P < 0.001$)	$\log Y = (-2.20) + 3.18 \log X$ ($P < 0.001$)
July	$\log Y = (-2.07) + 2.98 \log X$ ($P < 0.001$)	$\log Y = (-2.01) + 2.93 \log X$ ($P < 0.001$)
Aug.	$\log Y = (-2.46) + 3.25 \log X$ ($P < 0.001$)	$\log Y = (-2.38) + 3.25 \log X$ ($P < 0.001$)
Oct.	-----	-----
Nov.	-----	-----

was below 5^o C. Since energetic demands upon the animals are reduced, C. convexa have an opportunity to build up body reserves in late fall at Breezy Point.

Eggs and Egg Capsules

Crepidula convexa eggs are composed of 71.0% protein, 23.9% lipid and 9.1% carbohydrate. It was necessary to pool many eggs (600-2,800) from different broods to provide enough material for the performance of the assays. The eggs were removed from the capsules, counted, washed in distilled water to remove salts, dried and weighed. The dry weight of a single C. convexa egg in early cleavage is 0.009 mg. This weight is the mean value for 3,610 eggs collected from several egg masses.

The eggs are soft and easily dispersed in the solutions used for the different assays. However, the egg capsules are very tough and elastic. After several minutes in a tissue grinder, they are reduced to long, needle-like fibers which can only be further broken down by very vigorous grinding. Since the capsules are completely transparent, it is easy to determine that they are not contaminated with egg debris. The empty capsules were counted, washed in distilled water, dried and weighed. A C. convexa egg capsule weighs 0.012 mg. This value is the mean dry weight determined from a sample of 171 capsules. All the samples used for the assays consisted of capsules removed from more than one brood. The results of the

first assays performed on the capsules indicated that they were composed of 28.4% protein, 15.0% carbohydrate and 12.5% lipid. The sum of these values deviates significantly from 100%. The large number of capsules required made it impossible to repeat each assay. Since protein content seemed unusually low, the procedure for this assay was re-examined. Samples prepared for the protein assay were placed in 0.1N NaOH and left overnight at room temperature. This is a rather mild treatment considering the toughness of the capsule material. Therefore, capsules were placed in 10N NaOH for one week, and the assay was repeated. The change in the procedure increased the result for protein content to 35.0%.

Biochemical Composition of A Standard Animal

Figures 3, 4 and 5 show the percentage composition of protein, lipid and carbohydrate per mg (dry weight) of snail tissue. The data demonstrate that seasonal fluctuations in the levels of these biochemical constituents occur in female and male Crepidula convexa (Table 4). Since the assays were not performed on individual animals, the data represent the patterns of change for a randomly chosen group of females or males. However, it is possible to examine the impact of these changes at the level of the individual through the use of a standard animal. Using the data for seasonal changes in dry body weight (Table 3) and biochemical content (Table

TABLE 4

1

Seasonal Fluctuation in Biochemical Composition
1981

	% Protein		% Lipid		% Carbo- hydrate	
	M	F	M	F	M	F
Dec.-Feb.	-9.3 ²	-1.3	-----	+0.4	+0.5	+2.7
Feb.-June	+31.8	+6.3	-----	0	+3.5	+4.2
June-Sept.	-29.6	-14.9	-1.9	-5.4	-0.9	+1.9
Sept.-Dec.	+10.2	+7.1	+5.7	+5.0	-3.1	-8.8

1984

	% Protein		% Lipid		% Carbo- hydrate	
	M	F	M	F	M	F
Dec.-Feb.	+8.6	+3.2	-6.8	+3.7	-1.4	-3.0
Feb.-June	-6.7	-6.4	+2.5	+1.1	-0.9	+0.6
June-Sept.	-6.2	-5.9	+1.6	-3.8	-3.7	-1.4
Sept.-Dec.	+4.3	+11.1	+2.7	-1.0	+6.0	+3.8

1

M = Male
F = Female

2

Sign indicates percentage change in component during time intervals shown in column 1

TABLE 5

Estimated Body Weight And Biochemical Composition Of A
Standard (16 mm) Female, 1981

Month	Body Weight (mg)	Protein (mg)	Carbo- hydrate (mg)	Lipid (mg)
Jan.	30.50	14.15	4.12	3.05
Feb.	28.64	17.18	3.80	2.98
Mar.	-----	-----	-----	-----
Apr.	-----	-----	-----	-----
May	22.46	15.14	2.70	2.76
June	24.68	16.36	4.32	2.57
July	27.21	23.35	4.00	3.35
Aug.	28.87	18.77	5.69	2.17
Sept.	31.69	16.29	6.15	1.58
Oct.	40.20	28.46	5.35	2.85
Nov.	34.73	21.39	4.27	3.23
Dec.	33.97	20.82	3.60	3.40

TABLE 6

Estimated Body Weight And Biochemical Composition Of A
Standard (6 mm) Male, 1981

Month	Body Weight (mg)	Protein (mg)	Carbo- hydrate (mg)	Lipid (mg)
Jan.	-----	-----	-----	-----
Feb.	1.27	0.72	0.11	-----
Mar.	2.12	1.19	0.15	-----
Apr.	1.97	0.89	-----	-----
May	2.24	1.45	0.18	0.28
June	2.43	2.16	0.29	-----
July	2.10	1.84	0.19	0.16
Aug.	3.39	2.71	0.47	0.28
Sept.	2.12	1.26	0.24	0.12
Oct.	2.72	1.99	0.27	0.24
Nov.	1.62	1.07	0.10	0.18
Dec.	2.20	1.46	0.18	0.25

TABLE 7

Estimated Body Weight And Biochemical Composition Of A
Standard (16 mm) Female, 1984

Month	Body Weight (mg)	Protein (mg)	Carbo- hydrate (mg)	Lipid (mg)
Jan.	33.37	18.82	4.47	2.80
Feb.	31.47	18.88	3.05	4.94
Mar.	34.57	20.98	2.97	3.84
Apr.	-----	-----	-----	-----
May	31.08	17.65	2.70	3.79
June	36.42	19.52	3.75	6.12
July	33.00	17.66	3.40	4.95
Aug.	28.40	17.64	2.67	4.12
Sept.	26.01	11.89	2.32	3.38
Oct.	-----	-----	-----	-----
Nov.	-----	-----	-----	-----
Dec.	38.22	21.71	4.85	4.59

TABLE 8

Estimated Body Weight And Biochemical Composition Of A
Standard (6 mm) Male, 1984

Month	Body Weight (mg)	Protein (mg)	Carbo- hydrate (mg)	Lipid (mg)
Jan.	1.98	1.22	0.20	0.22
Feb.	1.85	1.20	0.15	0.23
Mar.	1.73	1.17	0.13	0.21
Apr.	-----	-----	-----	-----
May	1.88	1.13	0.14	0.25
June	2.02	1.18	0.15	0.30
July	1.86	1.13	0.12	0.26
Aug.	1.41	0.86	0.09	0.13
Sept.	0.89	0.46	0.03	0.15
Oct.	-----	-----	-----	-----
Nov.	-----	-----	-----	-----
Dec.	1.87	1.05	0.18	0.36

2), the dry weight and composition has been calculated for a standard female and male (1981 & 1984) (Tables 5, 6, 7, 8).

The shell length of males ranges from 4-7 mm and females from 7-22 mm (Breezy Point). The shell lengths chosen for the standard animals were 6 mm for the male and 16 mm for the female (approximately average sizes for this population). Shell length rather than body weight (dry) was used to define a standard animal since the size of the shell is the more stable quantity, i.e. dry body weight varies seasonally in an animal of fixed shell size. Figures 11, 12, 13, and 14 show seasonal variations in the biochemical composition of the standard animals which are similar to those already described for pooled males and females (Figures 3, 4, 5). The differences noted between graphs of standard animals and curves based on pooled data result from the use of seasonal changes in dry body weight to compute the former (Figures 11, 12, 13, 14). The estimated dry body weight and the estimated composition by weight of the three biochemical constituents are shown for each month for standard females (Tables 5, 7) and standard males (Tables 6, 8). Presented in this manner, the data reveal the combined effects of seasonal changes in biochemical content (richness) of the tissues and body weight fluctuations.

Table 9 summarizes the seasonal fluctuations in

Figure 11

Seasonal variation in the biochemical composition (estimated) of a standard animal of 16 mm shell length (female, 1981). Each point represents the level (mg) of the constituent in the body of an animal of estimated dry body weight (see Table 5).

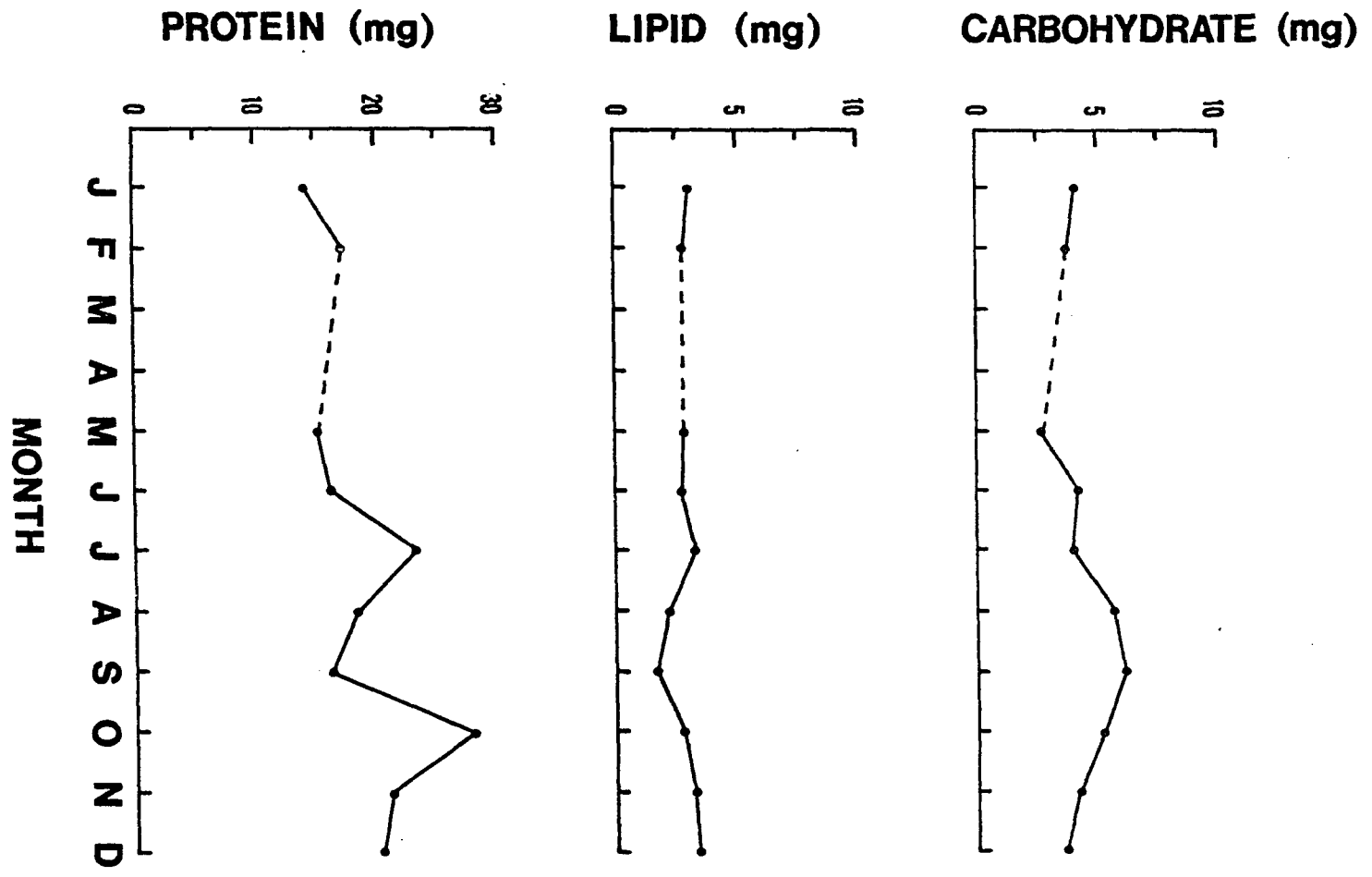


Figure 12

Seasonal variation in the biochemical composition (estimated) of a standard animal of 6 mm shell length (male, 1981). Each point represents the level (mg) of the constituent in the body of an animal of estimated dry body weight (See Table 6).

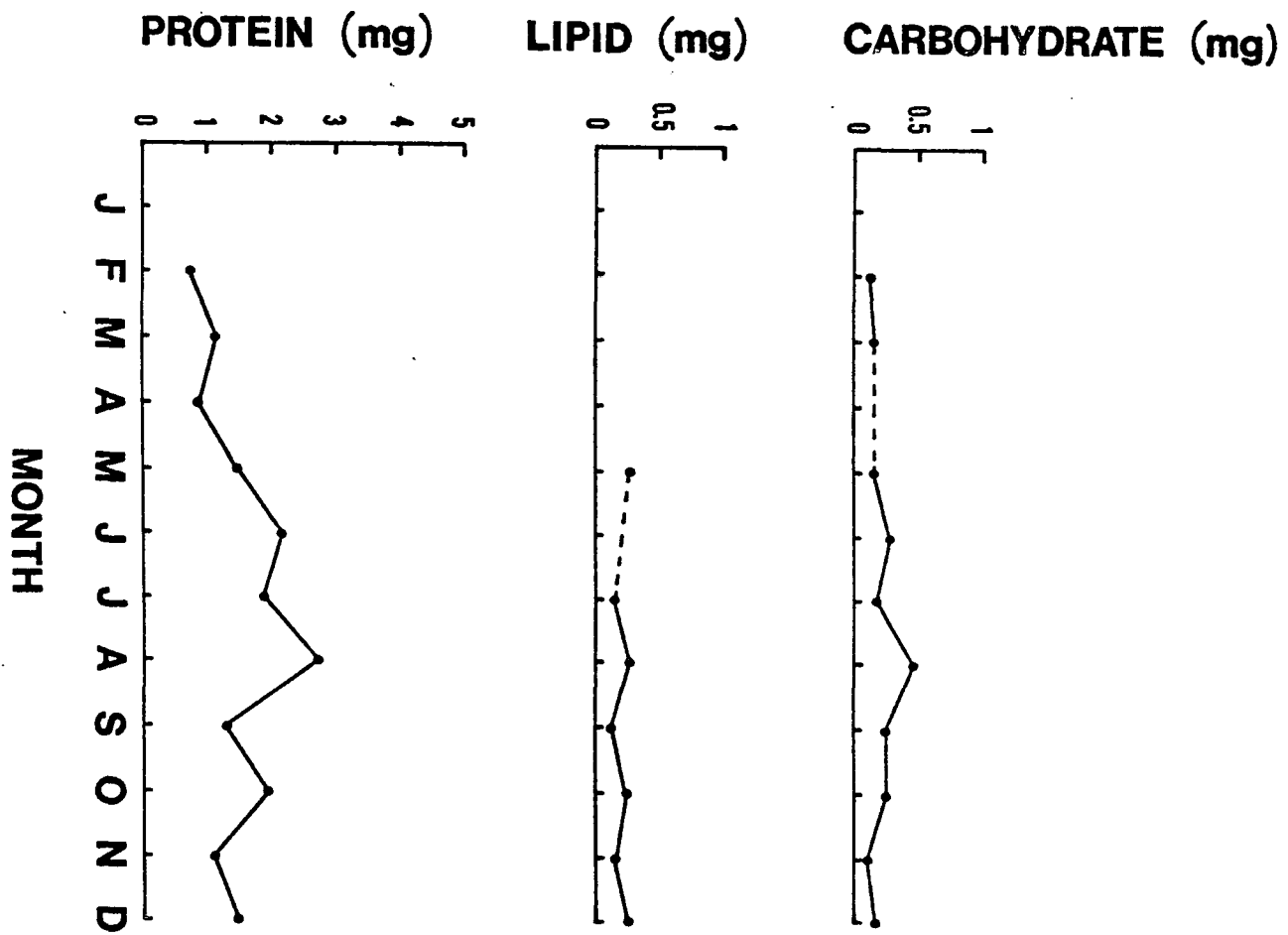


Figure 13

Seasonal variation in the biochemical composition (estimated) of a standard animal of 16 mm shell length (female, 1984). Each point represents the level (mg) of the constituent in the body of an animal of estimated dry body weight (see Table 7).

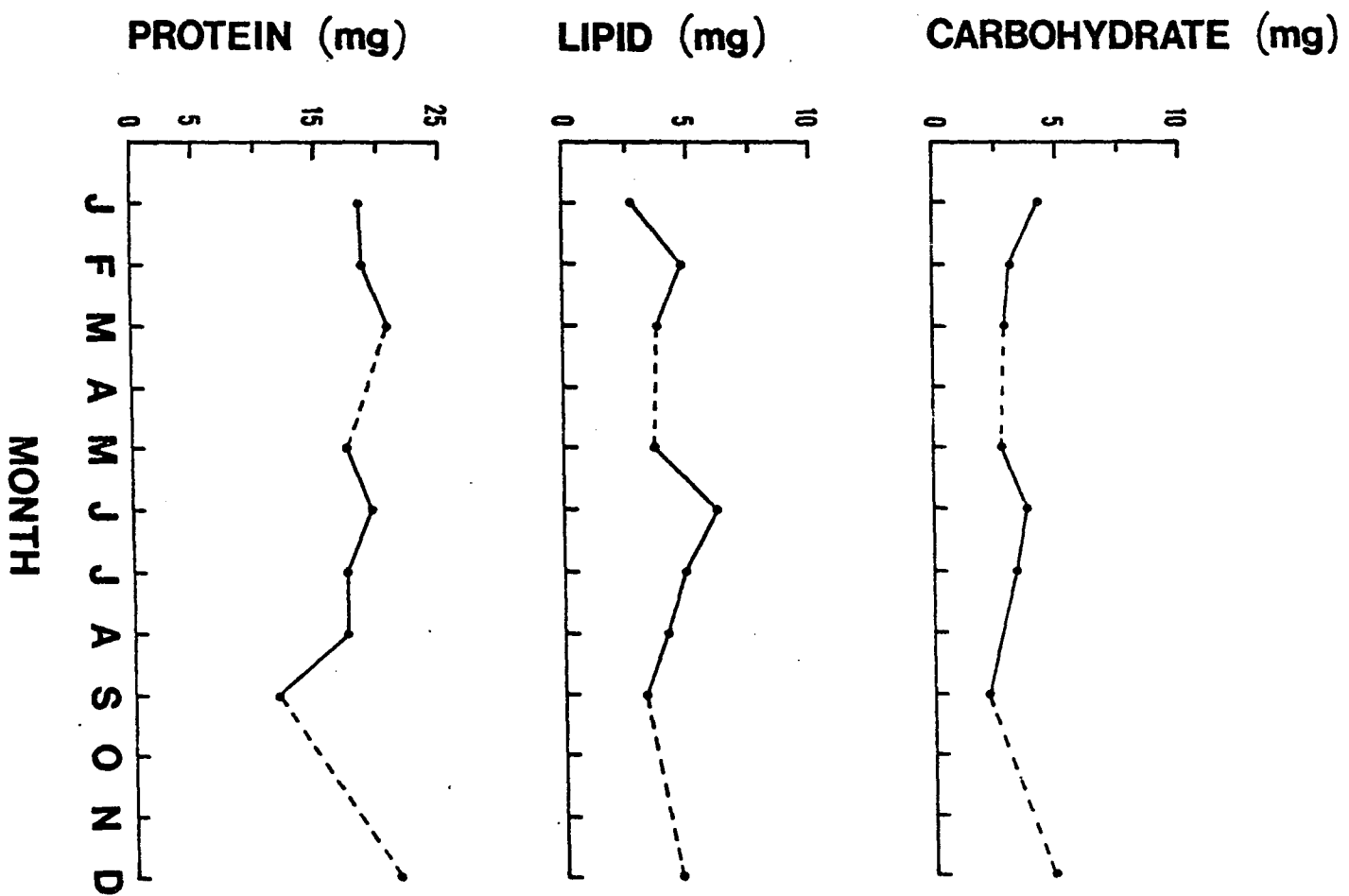


Figure 14

Seasonal variation in the biochemical composition (estimated) of a standard animal of 6 mm shell length (male, 1984). Each point represents the level (mg) of the constituent in the body of an animal of estimated dry body weight (see Table 8).

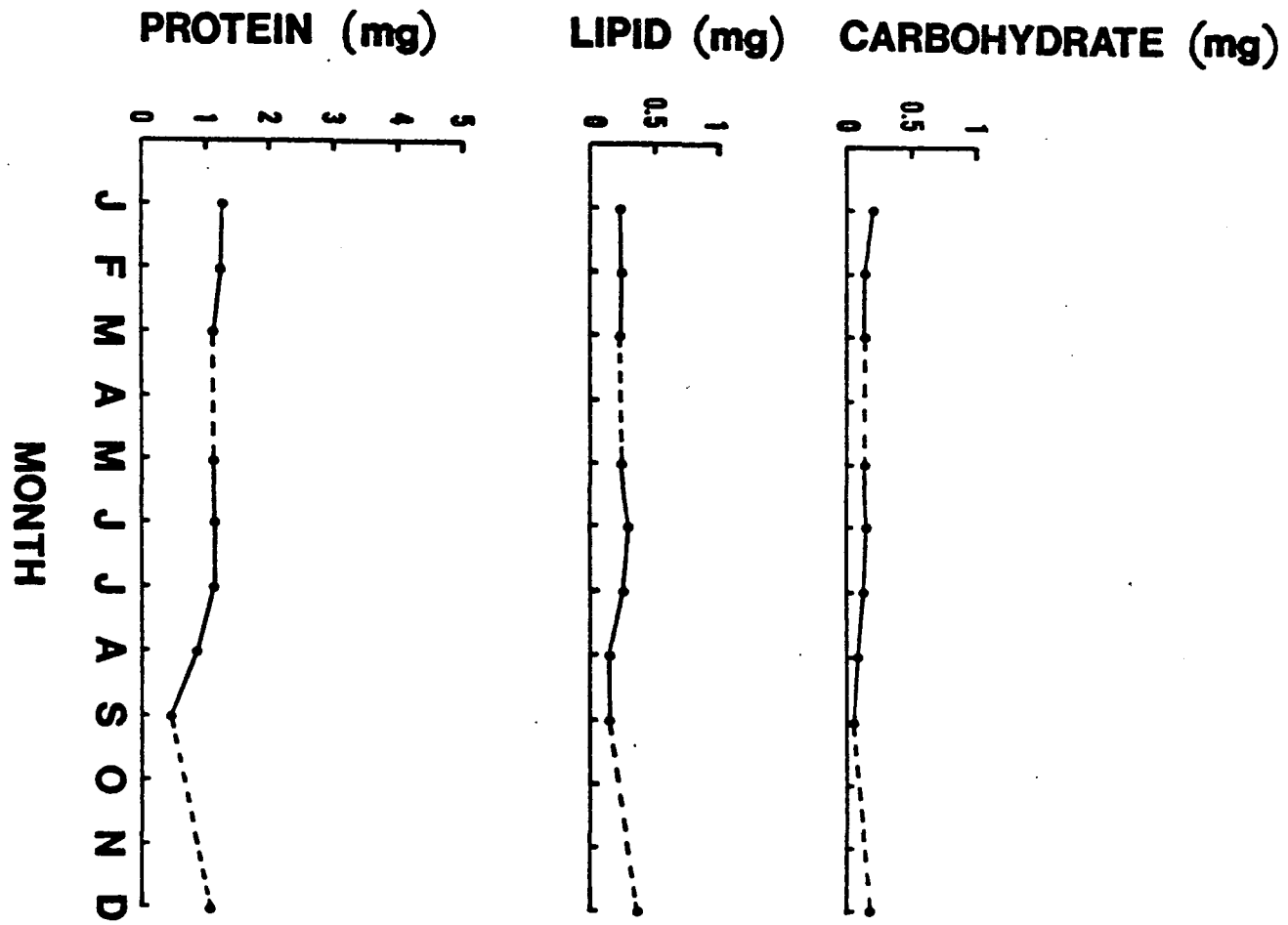


TABLE 9

1
Seasonal Fluctuation in Biochemical Composition of a
2
Standard Animal
1981

	% Protein		% Lipid		% Carbo- hydrate	
	M	F	M	F	M	F
Dec.-Feb.	-33.6	-10.5	-----	-1.2	-3.2	+0.6
Feb.-June	+113.4	-2.9	-----	-1.4	+14.2	+1.8
June-Sept.	-37.0	-0.3	-1.7	-4.1	-2.1	+7.4
Sept.-Dec.	+9.4	+14.3	+6.1	+5.7	-2.8	-7.4

1984

	% Protein		% Lipid		% Carbo- hydrate	
	M	F	M	F	M	F
Dec.-Feb.	+8.0	-7.4	-7.0	+0.9	-1.6	-4.7
Feb.-June	-1.1	+2.0	+3.8	+3.8	0	+2.2
June-Sept.	-35.6	-20.9	-7.4	-7.5	-5.9	-3.9
Sept.-Dec.	+66.3	+37.8	+23.6	+4.7	+16.9	+9.7

1
Female (F) 16 mm
Male (M) 6 mm

2

$$\frac{\triangle \text{Component (mg)}}{\text{Body Wt (mg) (initial)}} \times 100$$

biochemical composition based on standard animals of both sexes. The data for September to December (1981 and 1984) clearly show a greater increase in the body reserves of both sexes in the fall of 1984. In December of 1984, the water temperature was above 5 C, and the animals could have been feeding (see Temperature, Growth and Feeding). There was a greater reduction in body content of most biochemical constituents in the severe winter of 1981 relative to the milder winter of 1984 (Table 9). The body reserves of females increased in the spring of 1984 whereas, in 1981, there was a loss of protein and lipid by females. Between February and June 1981, the protein and carbohydrate content of males increased. In 1984, protein content decreased slightly while carbohydrate remained unchanged. The warm early spring of 1984 seems to have benefited females more than males (Table 9). Conversely, in 1981, females showed a slower recovery after the winter than males. Between June and September, at the height of the reproductive period, there was a decrease in most biochemical components in female and male animals (1981 & 1984). The data as presented in Table 9 show this decrease more clearly than Table 4 . In general, the loss of body reserves by both sexes was greater during the summer of 1984 than 1981. Since the environmental conditions seem to have been more favorable for C. convexa in 1983 and 1984, the animals probably

began the reproductive season with greater body resources than in 1981. More energy may have been available to devote to reproduction in 1984.

Seasonal Changes in Water Content

Animals were removed from the shell, numbered, blotted dry, weighed, dried (separately) in a vacuum desiccator and re-weighed. The wet and dry weight of each individual was recorded. The mean percent water content of the tissues was determined for February, June, September and December (Table 10). The water content of the body of Crepidula convexa shows seasonal fluctuations. The Mann-Whitney U-test was applied to the data, and the seasonal changes were significant, in all but one case, for males and females (Table 10). Fluctuations in water content appear to be inversely correlated with seasonal changes in dry body weight. During periods when animals show a tendency to increase dry tissue weight (February - June; September - December), the water content of the tissues seems to decrease. This trend is apparent in February to June 1981 and 1984, and September to December 1984 (Table 10). In 1981, the dry weight of males and females changed very little, and the water content of the body did not decrease in the predicted pattern. During the winter and the reproductive period (December - February; June - September), the dry weight of the snails usually decreases. There was an increase in the percentage of

TABLE 10
Seasonal Fluctuation in Body Water Content
1981

	Female (mean %)	n	Male (mean %)	n
Feb.	75.5	5	84.4	16
June	73.3	9	53.2	11
Sept.	71.2	14	67.3	29
Dec.	72.7	19	73.4	20

*
Significance of Seasonal Fluctuations (1981)

	Female	Male
Dec.-Feb.	P<0.01	P<0.001
Feb.-June	P<0.05	P<0.001
June-Sept.	P<0.05	P<0.01
Sept.-Dec.	P<0.05	P<0.01

1984

	Female (mean %)	n	Male (mean %)	n
Feb.	71.5	36	72.2	70
June	57.7	45	64.3	48
Sept.	70.6	59	76.8	59
Dec.	68.7	58	70.2	68

*
Significance of Seasonal Fluctuations (1984)

	Female	Male
Dec.-Feb.	P<0.01	NS
Feb.-June	P<0.001	P<0.001
June-Sept.	P<0.001	P<0.001
Sept.-Dec.	P<0.05	P<0.001

*

Two-tailed Mann-Whitney U-test

water in the body of both sexes during the winter and summer of 1984 (Table 10). The water content of males and females also increased during the winter of 1981 (Table 10). Large females did not lose weight during the summer of 1981, and the data show only a small fluctuation in water content (Table 10). However, the amount of water in the body of males increased between June and September of 1981. Therefore, a decrease in the dry body weight of the animals seems to be accompanied by a corresponding increase in the water content of the tissues. The data indicate that C. convexa use water to maintain body volume when there is a reduction in body weight.

Oviposition and Development of the Embryos

The ventral surface and tips of the propodium are used by Crepidula convexa to mold the egg capsules. At emergence from the vagina, the capsule is an egg-shaped bag with the eggs clustered together at its center. After manipulation by the foot, the capsule becomes approximately triangular in outline, quite flat and bears a slender stalk. During the molding process, each capsule is divided into two compartments by a compression of its walls at the midline along the axis of the stalk. Data collected on the number of eggs per capsule indicate that initially the compartments hold approximately equal numbers of eggs (Ander, 1980). The separation between the

compartments remains until the embryos reach the motile trochophore stage (Ander, 1980). The opening of the compressed area allows the capsule to expand into one large compartment which becomes inflated with the continuing growth of the embryos. An egg mass is composed of many capsules joined by the tips of the stalks. The flattened ends of the stalks form a sticky tab which anchors the egg mass directly to the substrate beneath the female, or to the ventral surface of the propodium. The latter method of attachment is the most common. Capsules measure 2.1 - 2.9 mm across at the broad end opposite the stalk (Ander, 1980; present study). All the embryos in a single capsule are usually at the same developmental stage. However, it is not unusual to find embryos in different capsules from the same brood which are not in synchrony (Ander, 1980; present study). The number of capsules per egg mass is correlated with female dry weight (Figure 16) (Ander, 1980; present study). Depending upon the weight of the female, the number of capsules produced can vary from 6 - 71 per brood. Observation of the process of oviposition reveals that the time elapsed between the appearance of each capsule at the vaginal opening can be as short as 9.4 minutes or as long as 25 minutes in different females. The timing of the process does not seem to depend on body size, since individuals of different lengths (14.0 mm, 11.5 mm) were observed to take

approximately the same time to produce a capsule (22.8 ± 3.7 min., 22.8 ± 7.3 min.) while females of the same length (10.0 mm) could differ in the time required (10.6 ± 0.8 min., 25.0 ± 5.2 min.). Therefore, capsules in a large brood may be produced hours apart resulting in differences of several cleavage divisions between embryos in different capsules. Females can produce 4 - 5 egg masses in succession during the reproductive season (Ander, 1980; present study). The production of a new egg mass by a female may occur within one day of the emergence of the juveniles from her previous brood.

The larval development of C. convexa has been divided into four stages: early gastrula, trochophore, veliger and post-veliger by Hendler and Franz (1971). The same system was employed by Ander (1980) to describe the developing embryos, but the veliger stage was further subdivided into four phases (V1 - V4). Broods of undisturbed females maintained at 19°C were observed daily to determine the developmental stage of the embryos. It takes 10.1 ± 0.9 days for them to reach the motile trochophore stage. After 4.31 ± 1.1 days, development has proceeded to the V1 (veliger stage 1) phase. The V2 phase is observed 4.0 ± 0.6 days after the onset of V1. The embryos remain in the V2 phase for 4.31 ± 1.1 days, and the duration of the V3 phase is 3.3 ± 0.9 days. The final stages of development seem to proceed more rapidly with the embryos

passing through V4 in 1.8 ± 0.6 days, and remaining post-veligers only 1.6 ± 0.9 days before emergence. Many egg masses were observed from the day of oviposition until emergence of the juveniles. Based upon these observations, the duration of the brooding period for C. convexa is 29.5 ± 1.8 days at 19°C . This determination is in good agreement with the total time required for development which can be calculated by adding up the duration of each separate stage (29.4 days). When development is complete, the capsules open along the end opposite the stalk. All the capsules in a brood do not open at the same time, and it may take several hours for all the young snails to be released and crawl free. Juvenile C. convexa are 0.92 ± 0.07 mm (shell length) at emergence.

The embryos develop more slowly at temperatures below 19°C . Broods of females maintained in a tank of chilled, recirculated sea water at $14 - 16^{\circ}\text{C}$ were found to be developing at a rate approximately 3 - 12 days behind the embryos of females incubated at 19°C . When brooding females were transferred from the incubator into the tank for varying periods of time and then returned to the incubator, the development of the embryos was retarded. The emergence of the juveniles was delayed approximately 2-6 days depending on the length of time the embryos had remained in the tank (3 - 13 days).

Reproductive Effort and Energy Allocation

Female Crepidula convexa continue to grow throughout the reproductive season during which time they can lay 4-5 egg masses (Ander, 1980). Fecundity is weight-specific (Figures 15, 16, 17) so that as they grow, individuals produce progressively larger broods at each successive oviposition (Ander, 1980; present study).

The simultaneous occurrence of growth and reproduction plays a critical role in the reproductive strategy of C. convexa. During the period of oviposition, energy is budgeted by females for respiration, growth and reproduction. Although metabolic costs were not measured, information derived from field and laboratory analyses of growth and reproduction (marked individuals) form the basis for inferences on the strategy of energy allocation by female C. convexa.

Figures 18 and 19 show the relationship between dry body weight and shell length of male and female C. convexa. Since dry body weight was found to fluctuate seasonally and from year to year, data (January - December) from several years (1980 - 1984) were pooled. Pooling the data yields a regression of dry body weight on shell length which represents no particular year or season. The regression of female weight on size (January - December) was used, when necessary, to convert shell length to dry body weight so that energy allocation and

Figure 15

The relationship between the total number of eggs or embryos per egg mass and female dry body weight (mg) in Crepidula convexa.

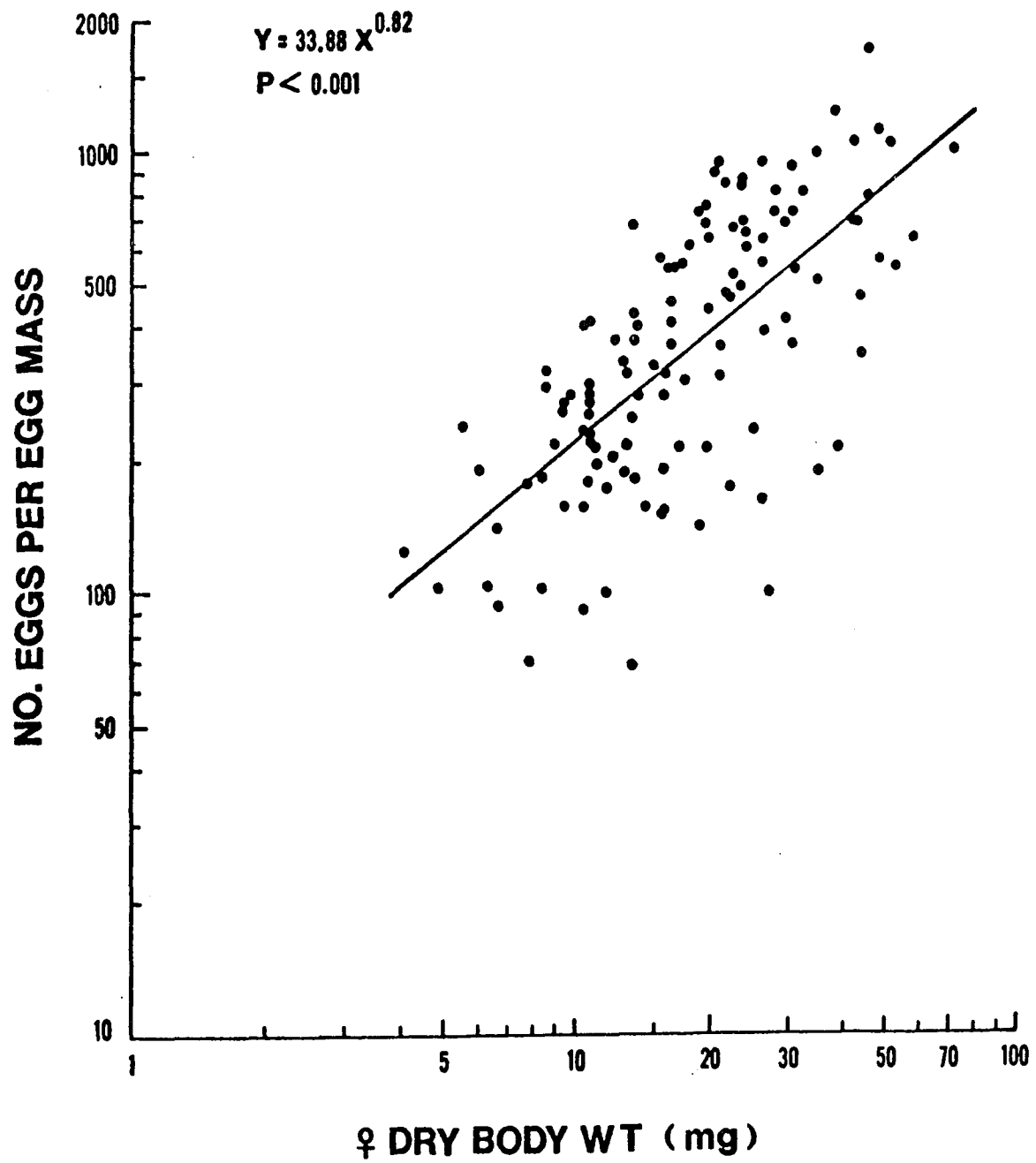


Figure 16

The relationship between the number of capsules per egg mass and female dry body weight (mg) in Crepidula convexa.

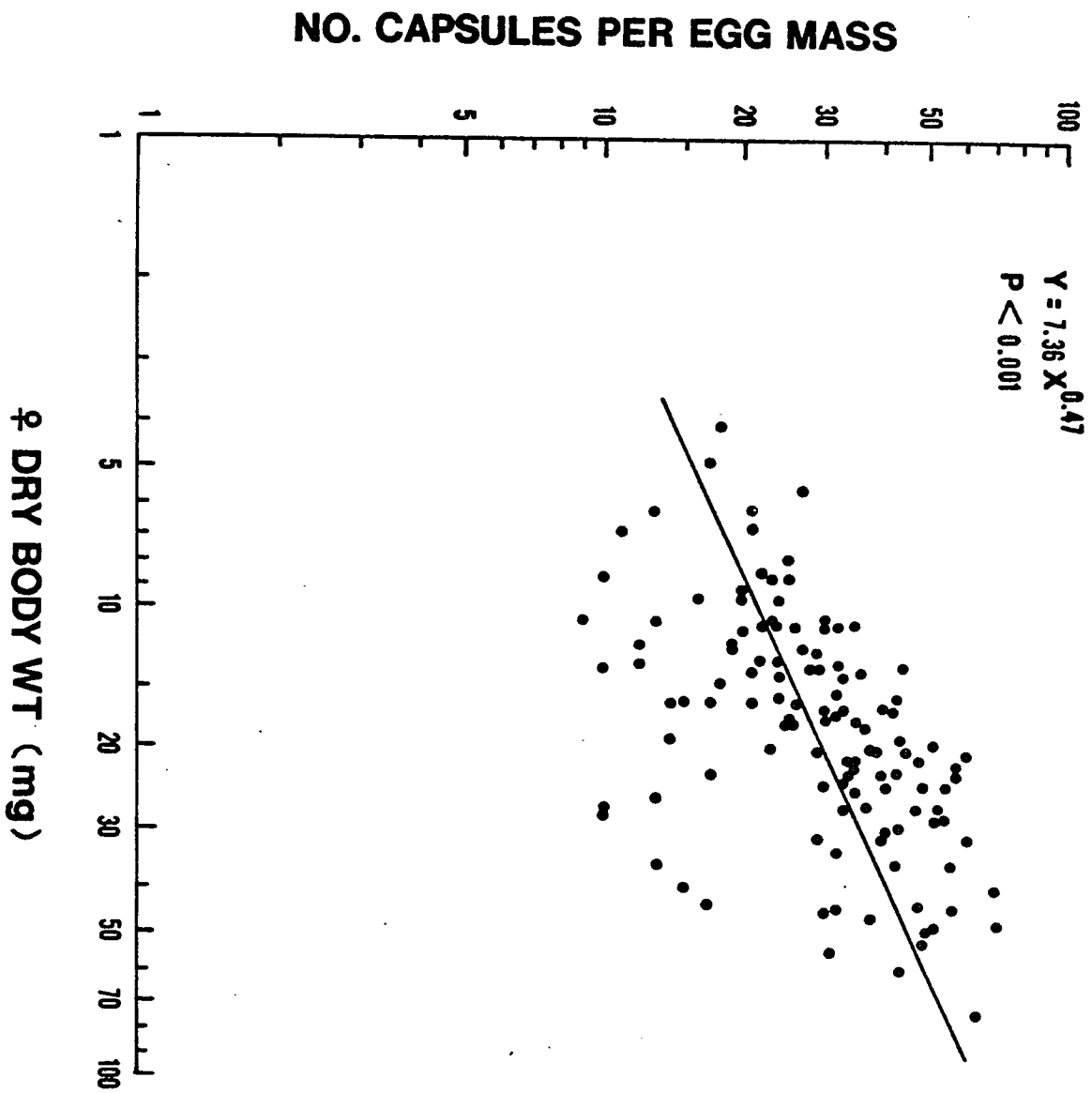
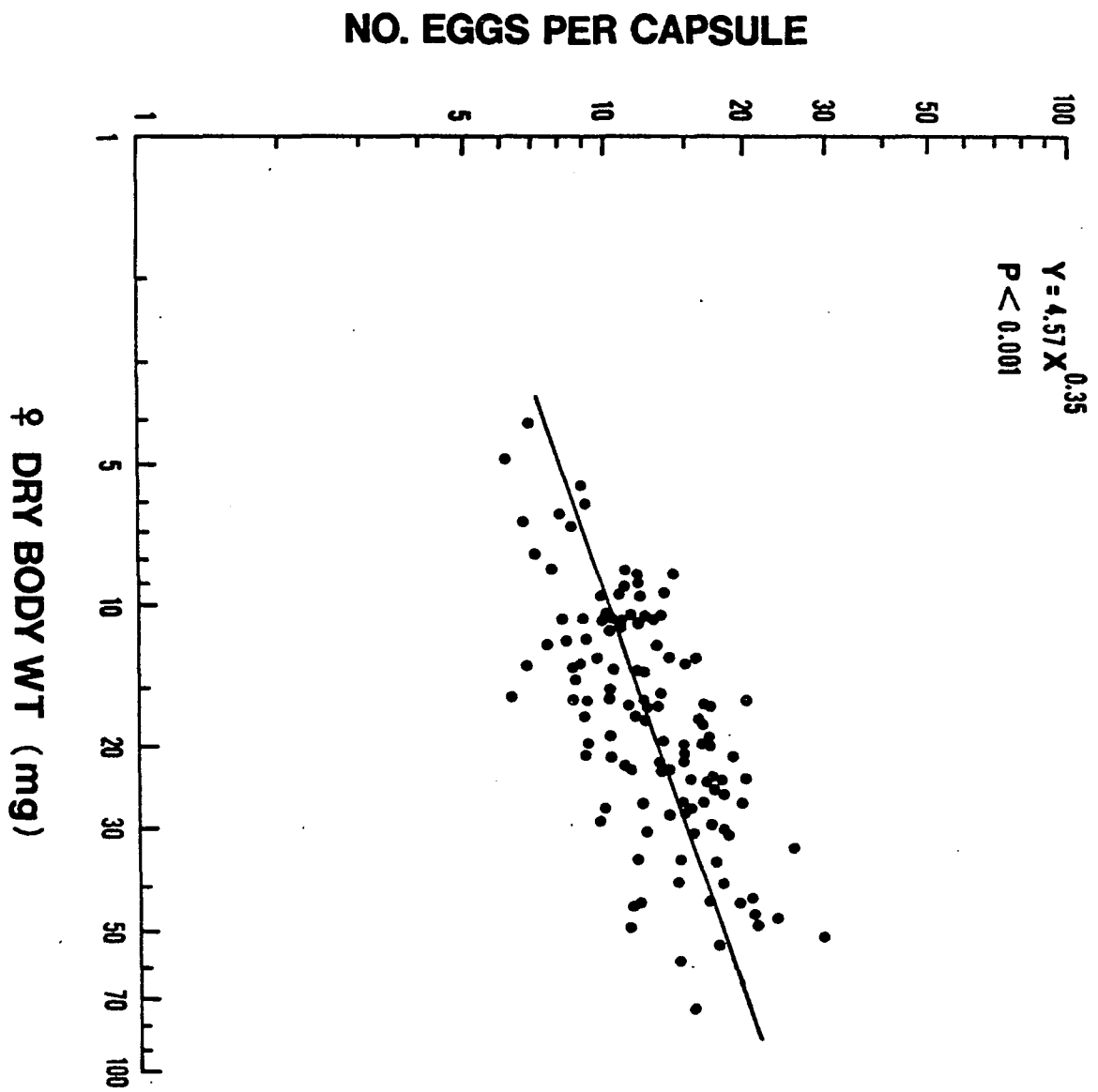


Figure 17

The relationship between the number of eggs (embryos) per capsule and female dry body weight (mg) in Crepidula convexa.



fecundity (Ander, 1980; present study) could be expressed as a function of body weight.

Egg mass weight (dry weight) was determined either by direct weighing of broods dried in a vacuum desiccator (pre-rinsed in distilled water) or indirectly by multiplying the number of eggs and capsules in the mass by their estimated mean dry weight (see Eggs and Egg Capsules).

In the following analysis of energy allocation by female C. convexa, the sum of egg output (mg) and growth (mg increase in female dry body weight) has been designated as a measure of net production (Pn), i.e. $Pn = F + G$ where:

Pn = net production of biomass (mg) at each oviposition (time period between ovipositions approximately 30-35 days)

F = estimated mass of eggs and capsular materials (mg dry weight) produced at current oviposition

G = estimated tissue biomass (mg dry weight) resulting from growth between the current and the previous ovipositions.

Figure 20 shows the relationship between female dry body weight and net production, and also between female

Figure 18

Dry body weight (mg) of female Crepidula convexa as a function of shell length (mm) (January - December, 1981 - 1984).

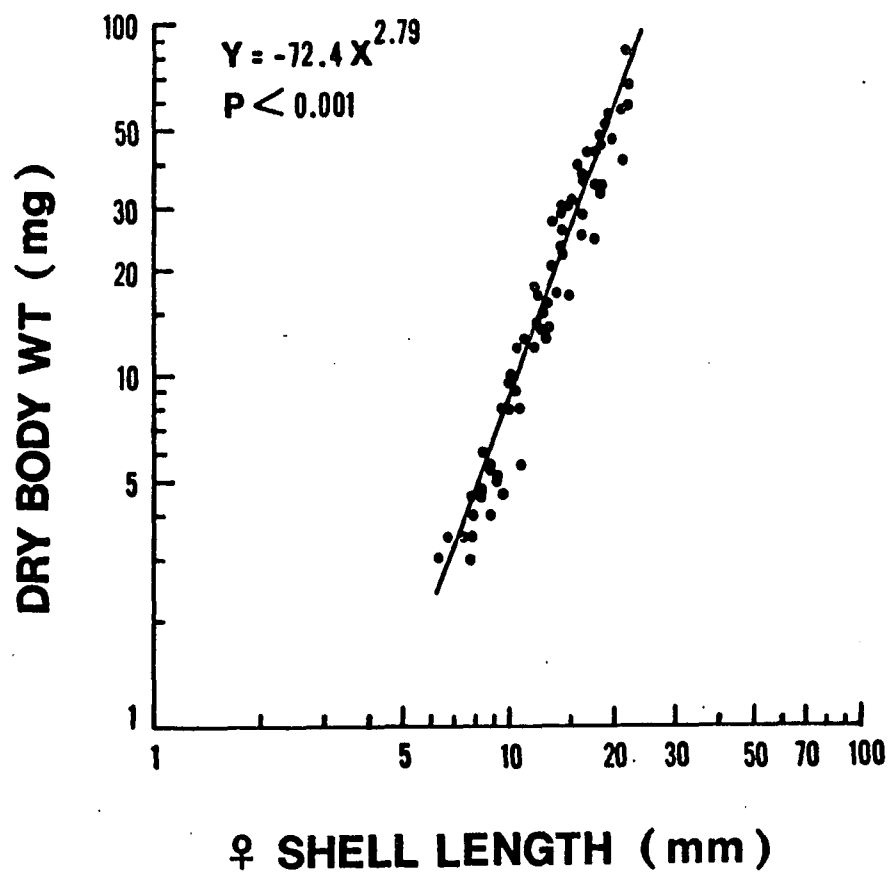
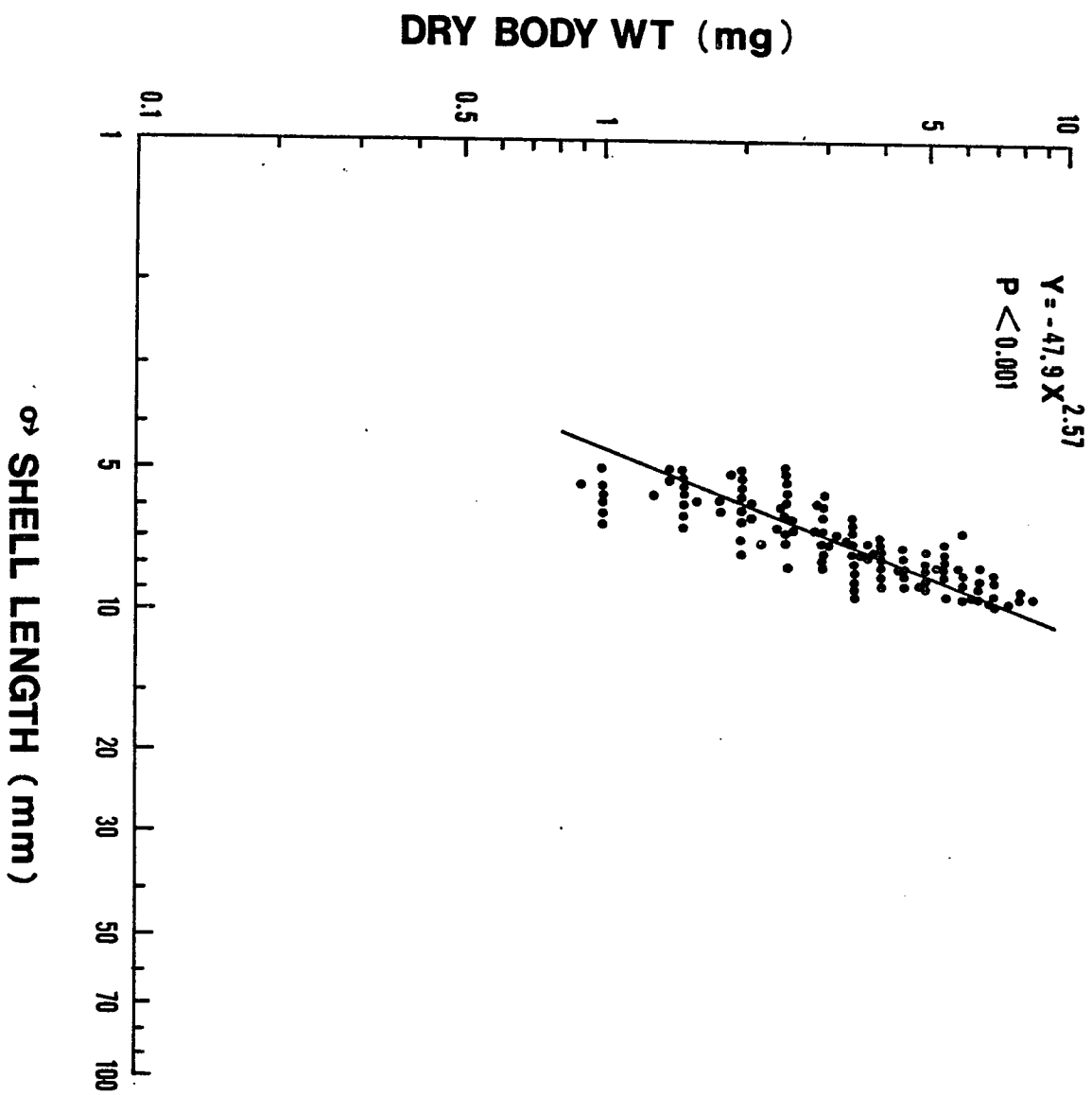


Figure 19

Dry body weight (mg) of male Crepidula convexa as a function of shell length (mm) (January - December, 1980 - 1984).



weight and net production per unit dry body weight. Weight-specific Pn decreases as the animals become larger, i.e. as females continue to grow, the proportional gain in Pn declines with increasing body weight.

The percentage of Pn allocated to egg output as a function of dry body weight is shown in Figure 21. With increasing size, females allocate a higher percentage of Pn to egg production. Since Pn has been defined as $F + G$, it follows that the percentage of Pn which can be allocated to growth (G) must decrease as individuals become larger if the percentage allocated to reproduction (F) increases with body weight. If the regression line in Figure 21 is extended to pass through 100%, it can be predicted that a female of approximately 49 mg dry weight (18-19 mm shell length) will allocate all Pn to egg output with no energy remaining for growth.

Although fecundity increases with increasing dry body weight (Figures 15, 24), weight-specific fecundity decreases as the animals continue to grow (Figure 22). Thus, the proportional increase in fecundity attained by continued growth declines as the females become larger. Figure 23 presents this important relationship in another form. Since females grow between ovipositions, the number of eggs produced in successive egg masses increases (Ander, 1980; present study). However, Figure 23 reveals that the percent gain in the number of eggs in successive

Figure 20

The relationship between female dry body weight (mg) and net production (mg)¹, and also between female dry weight (mg) and net production per unit dry body weight (mg)² in Crepidula convexa.

$$^1 \quad Y = 5.41 X^{0.28}$$

$$^2 \quad Y = 5.36 X^{-0.72}$$

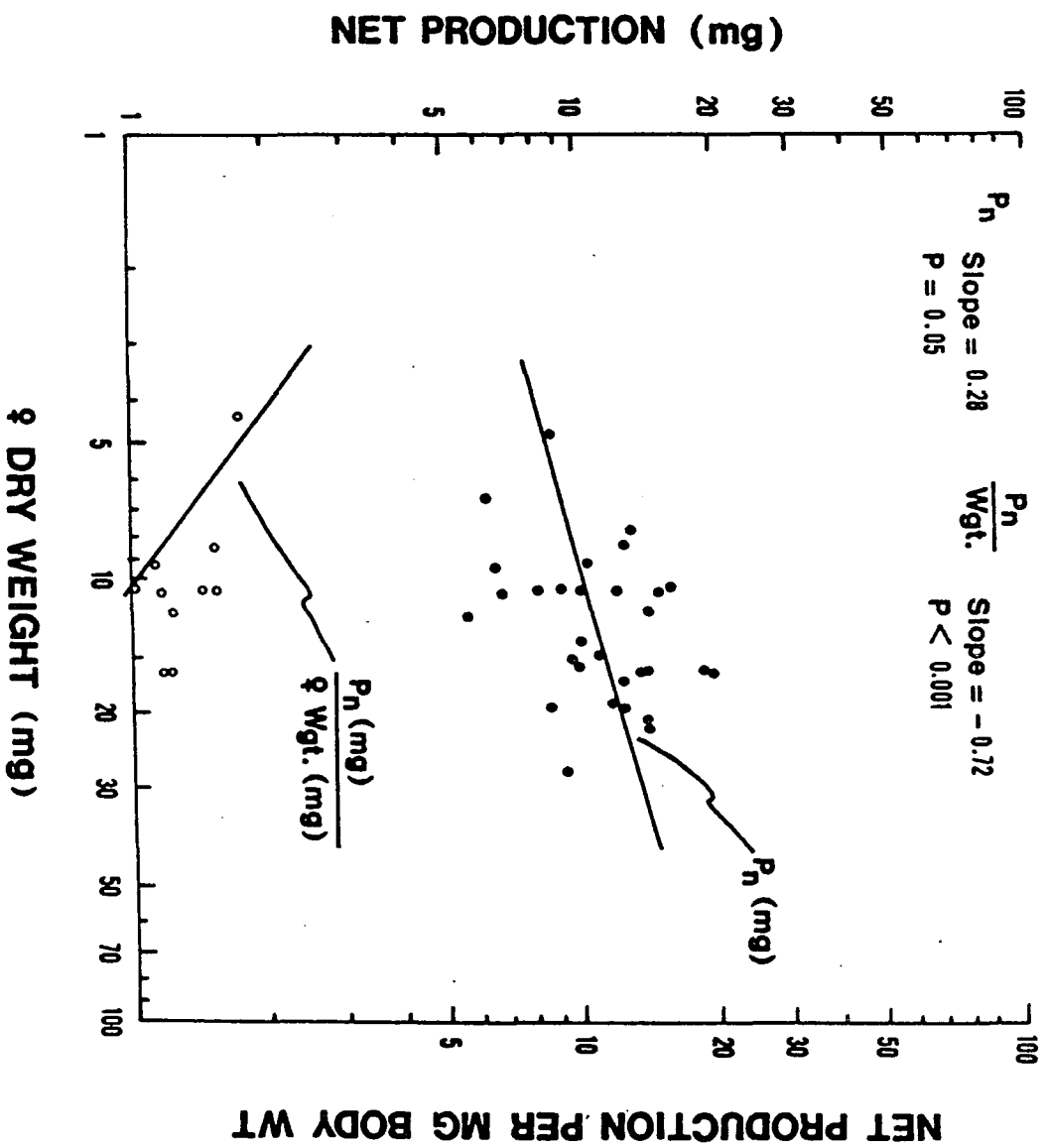
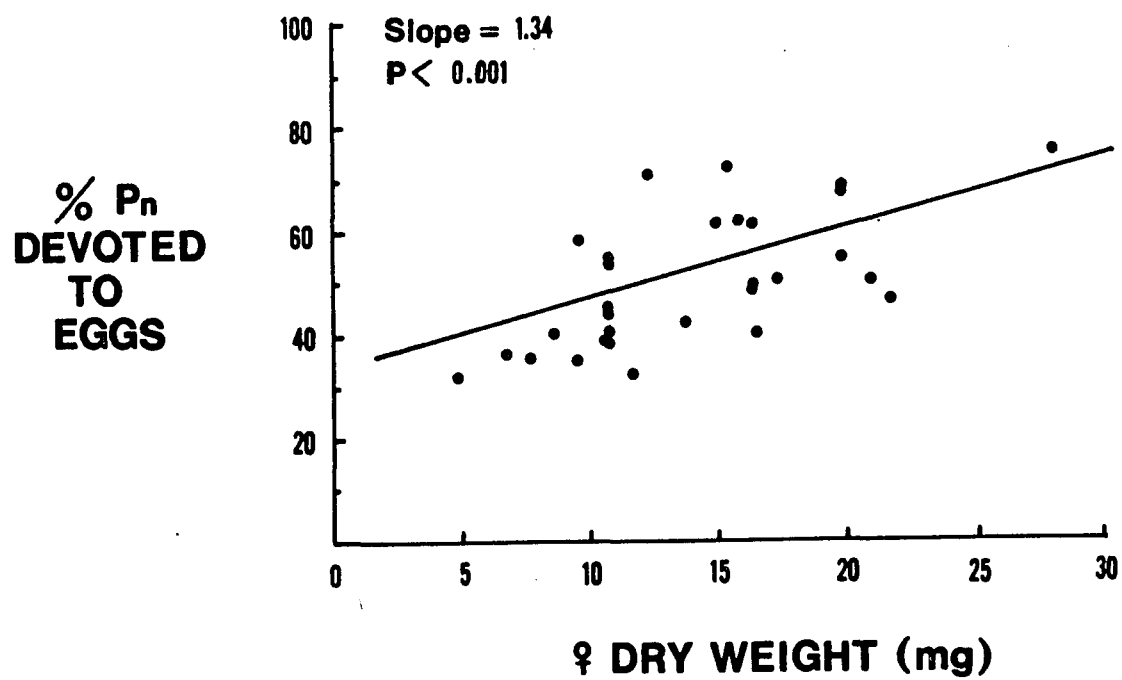


Figure 21

The percentage of Pn devoted to egg output as a function of female dry body weight (mg) in Crepidula convexa ($Y = 33.8 + 1.34 X$).



broods which accompanies each growth increment decreases with increasing dry body weight. Therefore, for each allocation of energy to growth (cost) the female derives less benefit (increase in fecundity) as she grows. As indicated by Figure 21, there is less Pn available for growth as dry body weight increases. Beyond a critical weight, why don't females reduce or stabilize brood size in order to allocate more energy to growth? Figure 23 gives some insight into why such a strategy would be inefficient. The future benefit in egg production to be gained by diverting energy from current egg production to growth becomes small for large individuals.

Figure 24 presents Pn and egg output as a function of dry body weight. When the slopes of the regression lines are compared, it is evident that egg output increases more rapidly than Pn. If the regression lines for Pn and egg output are extended until they meet, the intersection predicts the point at which Pn equals egg output, i.e. the point at which all net production is allocated to egg output. These data suggest that females of approximately 70 mg dry weight (21 - 21.5 mm shell length) allocate all Pn to egg production and as a consequence cannot continue to grow.

Specimens of C. convexa larger than 22 mm have not been found at Breezy Point, New York (Ander, 1980; present study). Figure 25 shows the relationship between weight -

Figure 22

The relationship between female dry body weight (mg) and egg output per unit dry body weight in Crepidula convexa
($Y = 1.82 X^{-0.09}$).

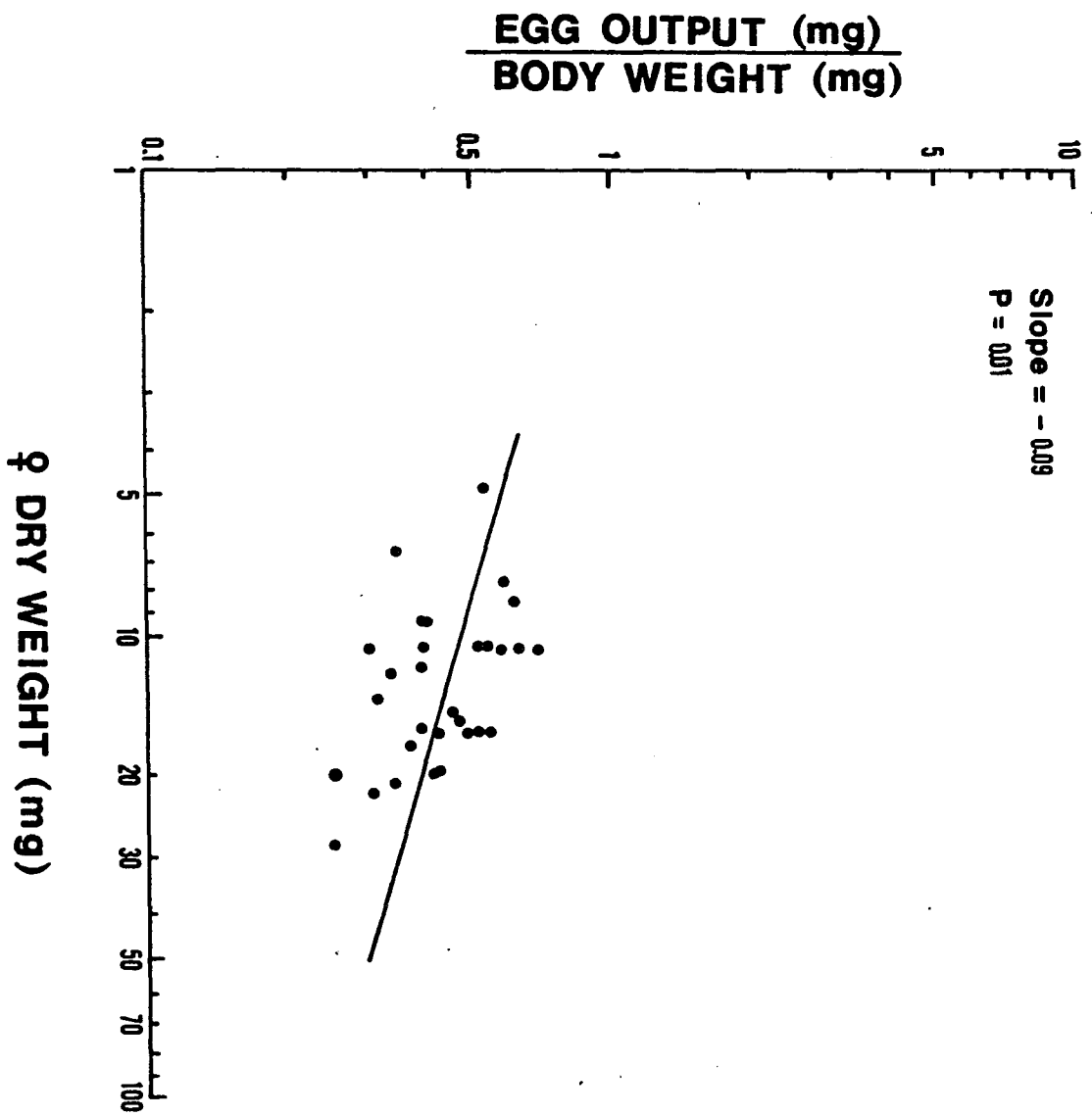


Figure 23

The percentage increase in the number of eggs in successive broods per unit dry body weight gain (mg) (growth) as a function of female dry body weight (mg) in Crepidula convexa ($Y = 28.6 - 1.1 X$).

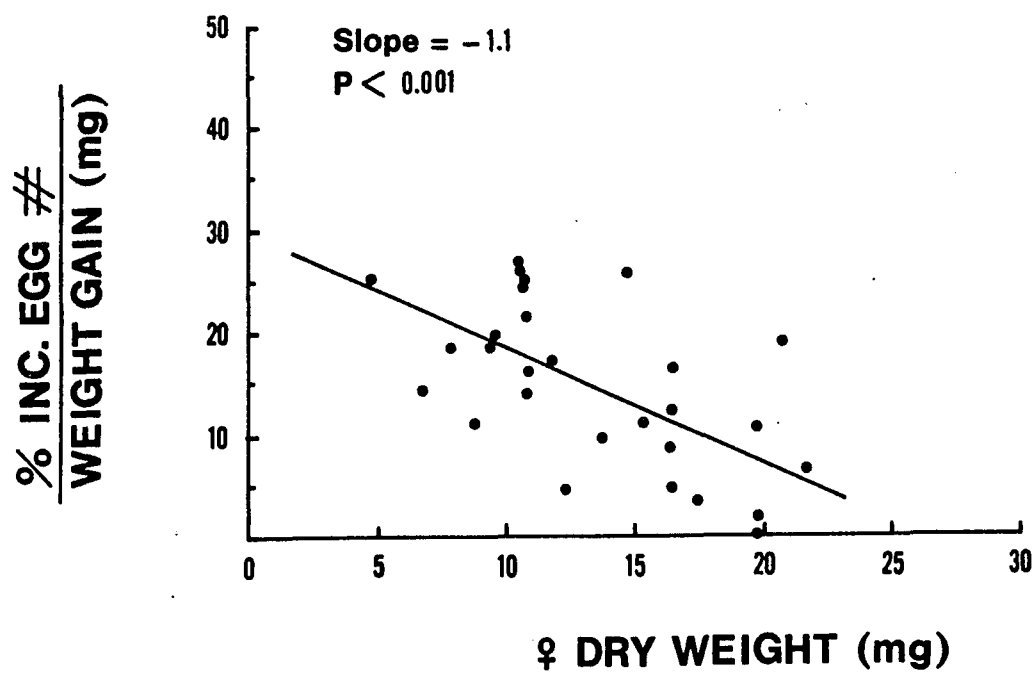


Figure 24

Net production (mg)¹ and egg output (mg)² as a function of female dry body weight (mg) in Crepidula convexa. The intersection of the regression lines predicts the point at which Pn = egg output. The data points for the Pn curve are shown in Figure 20.

$$1 \quad 0.28 \\ Y = 5.41 X$$

$$2 \quad 0.68 \\ Y = -1.44 X$$

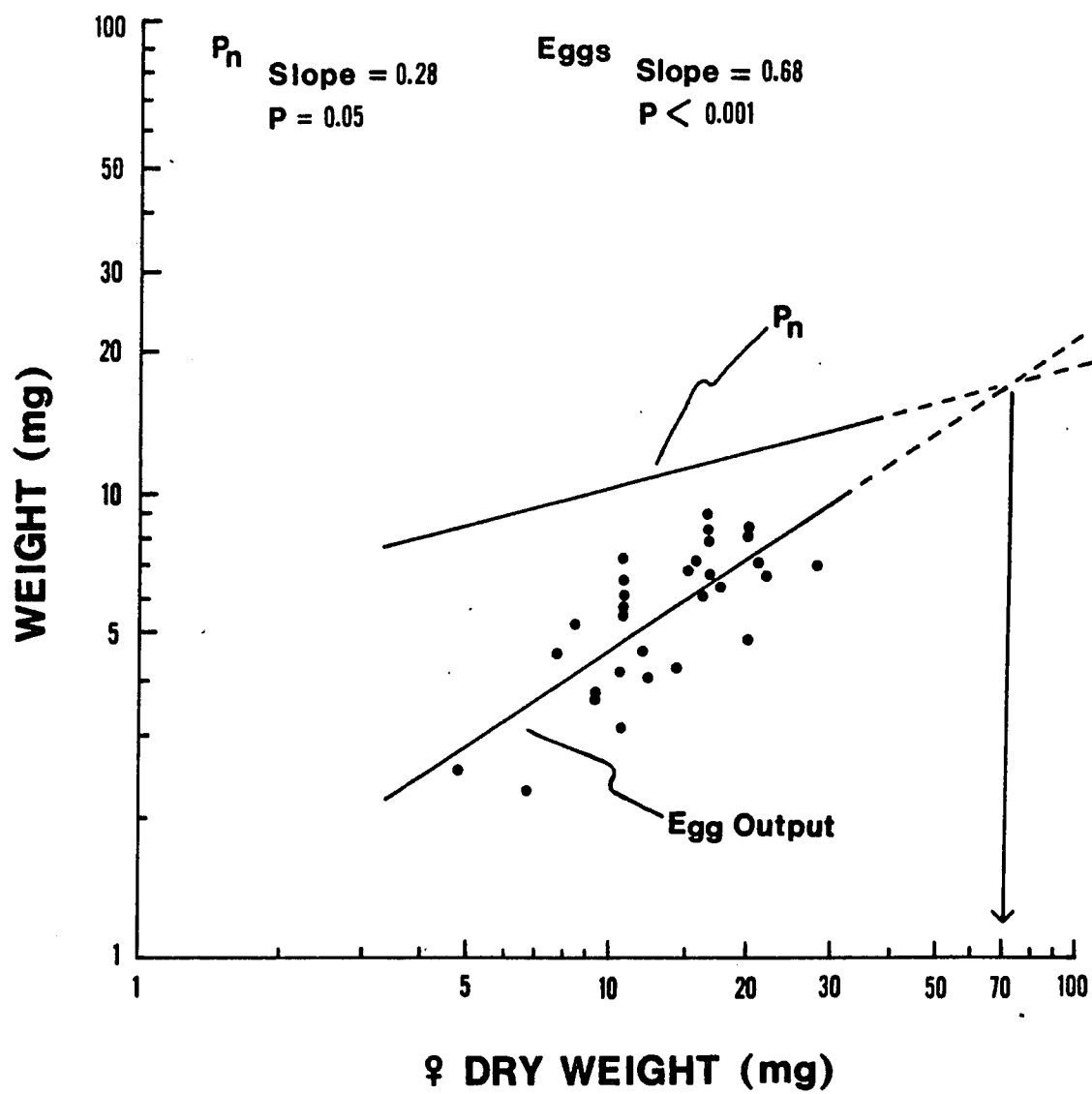
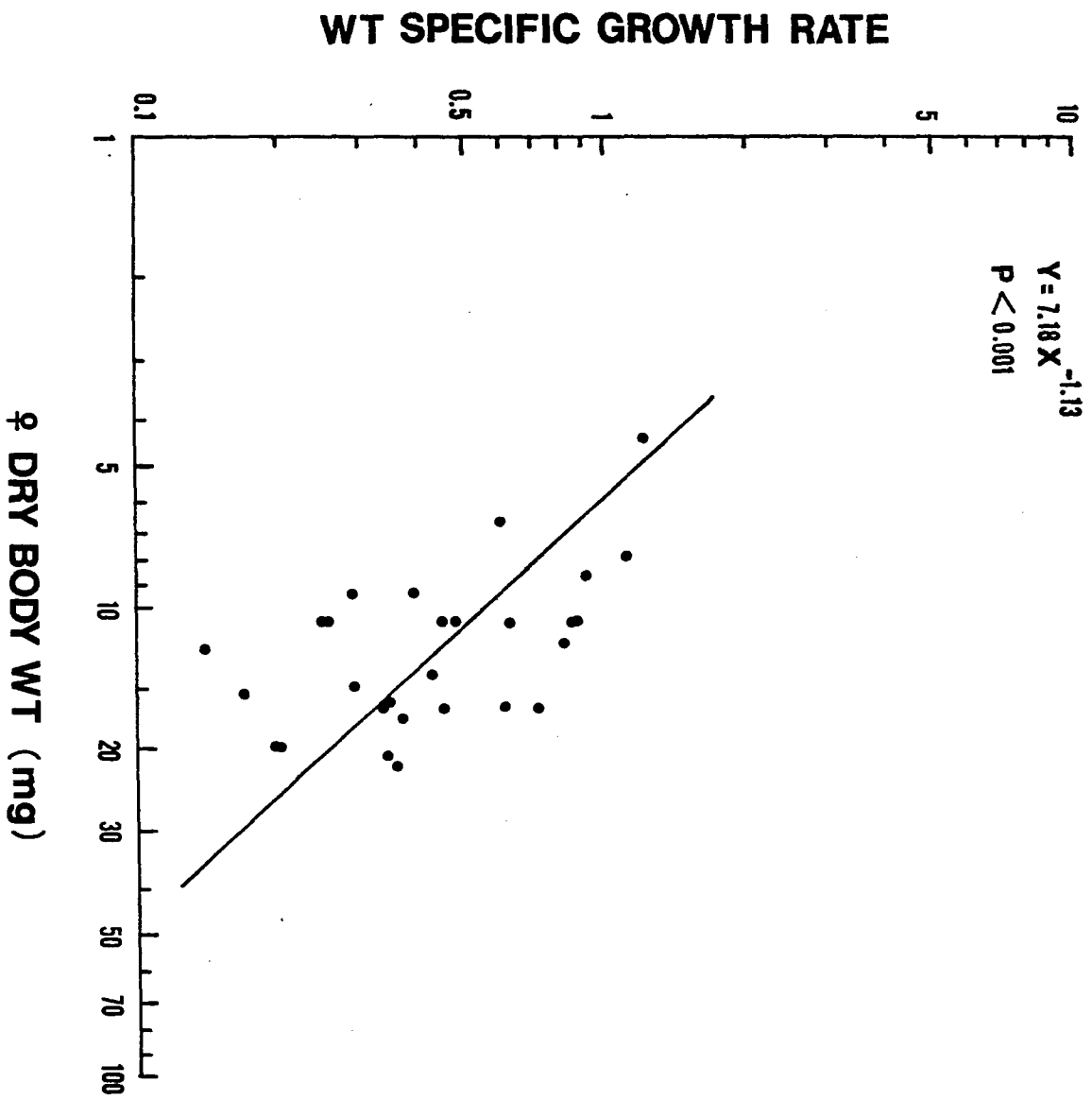


Figure 25

The ^{*}relationship between weight-specific female growth rate and dry body weight (mg) in Crepidula convexa. The specific growth rates were determined at approximately three week intervals (May-October).

*

$$\frac{\triangle \text{ Body Wt (mg)}}{\text{Initial Body Wt (mg)}}$$



specific female growth and dry body weight. The data indicate that growth per unit dry body weight decreases as the animals become larger. Therefore, females grow more slowly as their dry body weight increases. Based on the regression line fitted to the data ($P < 0.001$), growth increase per unit dry body weight approaches zero at approximately 47 mg dry body weight (18 - 19 mm shell length). It costs more to grow as individuals become larger because each increment in shell length corresponds to a greater increase in tissue volume. The amount of Pn allocated to growth is decreasing with increasing dry body weight (Figures 21, 24), and this decreasing amount of energy will subsidize less and less growth with increasing female size (weight).

Discussion

Reproductive Condition

Male

Although mitosis and meiosis are suspended in the male between January and March, the gonad does not show significant regression and the sex of the individual is easily determined from histological sections. Spermatogonia, spermatocytes and mature sperm are present in the tubules in almost every month of the year. In April, the onset of mitotic activity results in a rapid proliferation of spermatogonia and primary spermatocytes preparatory to the start of spermatogenesis in May. The onset of mitotic activity in the male lags behind the female by approximately 2 months. Proliferation of the gonia may begin earlier in the female (February) to allow a significant number of new oogonia and oocytes to accumulate before vitellogenesis begins (late-March - April). Also, the observed increase in the number of spermatocytes in the gonad in May indicates that spermatogonia can complete the cytoplasmic growth phase (spermatogonium to ^o 1 spermatocyte) within a month. Therefore, mitotic activity need not begin as early in the season as it does in the female. At the end of the reproductive season (October - November), the supply of spermatocytes and spermatids in the tubules seems to decline. This may be related to the decline in

mitotic activity after July which brings a halt to the production of new gonidia.

Spermatogenesis begins in May, but even late in the month the tubules of the gonad do not contain large concentrations of mature sperm. Since oviposition also begins in May, there is some question as to the ability of males to provide the sperm needed early in the reproductive season. However, the seminal vesicles of mature males contain sperm throughout the year, and this stored sperm can be transferred during copulation even if the tubules of the gonad do not contain sperm. Also, individuals that were female during the previous reproductive period can use sperm stored in the seminal receptacles to fertilize their first egg mass in the spring making them independent of males at the start of the season.

Oviposition in Crepidula convexa continues for a 5 - 6 month period during which the mobile males have the opportunity for repeated copulations with one or more females. Therefore, sperm must be continuously available during this period. The histological sections of the gonad are consistent with this reproductive pattern. Activation of different regions of the gonad is staggered, and the production of spermatogonia and sperm is not synchronous in all areas. Newly formed sperm move from the lumina of the tubules into the seminal vesicles from which they are

transferred to the female at copulation. As sperm are withdrawn from the seminal vesicles, they can be replaced by sperm which continue to be formed in the gonad throughout the reproductive season. The lack of synchrony in the production of sperm explains why, in May, the gonad does not ripen into a thin-walled bag completely filled with mature sperm.

Meiotic activity declines by November, and sections of a December animal show none. However, residual spermiogenesis may continue until the following spring (March). This conclusion is based upon two observations: (1) spermatids are found in the tubules from November to March but are absent in April and (2) spermatids and mature sperm remaining in the gonad at the end of the reproductive cycle are not cytolysed. Therefore, spermatids, once formed, probably complete the process of differentiation into mature sperm and collect in the tubules even though meiotic activity has ceased. The "old" sperm are not cytolysed, yet have virtually disappeared from the tubules by April. From January to March, sperm appear to be moving toward, and becoming concentrated near, the area where the tubules unite to form the sperm duct and seminal vesicles. Therefore, sperm remaining in the gonad at the end of the reproductive season are probably conserved and stored in the seminal vesicles.

Mated pairs are found in every month of the year.

Since the seminal vesicles also contain stored sperm in all months studied, copulation and insemination might be possible at any time of the year. Therefore, the reproductive season may not be the only opportunity for females to receive and store sperm in their seminal receptacles. For an animal with a patchy distribution and limited ability to disperse (especially females), it seems efficient for males to be able to transfer sperm whenever a female is encountered regardless of the season. The slight reduction in the amount of sperm stored in the seminal vesicles from May - October is correlated with the period of oviposition when males may be more reproductively active.

"Abnormal" sperm can be distinguished from "normal" (eupyrene) sperm by morphological differences (e.g. larger size, an excess of cytoplasm, many tails) and are characterized by reduced (oligopyrene, dyspyrene) or absent (apyrene) chromatin (Fretter and Graham, 1964; Webber, 1977; Giusti and Selmi, 1982). The lack of chromatin in apyrene sperm may explain why these cells do not stain well with hematoxylin. Only the normal sperm are capable of accomplishing fertilization (Fretter and Graham, 1964; Webber, 1977). The modes of development and function of "abnormal" sperm in prosobranchs remain unclear (Giusti and Selmi, 1982). Some workers have suggested that atypical sperm may provide nourishment for

eupyrene sperm in the female genital tract (Fretter and Graham, 1964; Webber, 1977; Giusti and Selmi, 1982). However, "abnormal" sperm have not been found in the seminal receptacle(s) where they would be expected to make such a nutritive contribution (Coe, 1942a; Giusti and Selmi, 1982). A number of species of mesogastropods and neogastropods produce nurse eggs, and it has been hypothesized that "abnormal" sperm play a role in the formation of these specialized eggs (Fretter and Graham, 1962; Webber, 1977; Giusti and Selmi, 1982). This theory does not adequately explain the phenomenon since all prosobranchs found to have normal and "abnormal" sperm do not produce nurse eggs, and some species which produce nurse eggs only have eupyrene sperm (Fretter and Graham, 1962, 1964). Specialized motile structures (spermatozeugmata) are believed to act as a transport mechanism to carry eupyrene sperm in some species. It has been suggested that these structures develop from "abnormal" sperm in aphyllid species as a method to effect internal fertilization (Fretter and Graham, 1964; Webber, 1977; Giusti and Selmi, 1982). Yet, there are aphyllid species with internal fertilization which do not produce spermatozeugmata (Webber, 1977). Some or all of the functions suggested so far for atypical sperm may be correct in specific cases. However, it seems that researchers have been seeking an explanation for this phenomenon that would apply in all species. Giusti and

Selmi (1982) pointed out that atypical sperm are found only in prosobranchs with internal fertilization, and they suggested that the function of these cells was originally linked to this process. Regardless of their original function, "abnormal" sperm may have become adapted to carry out different roles in different species (Giusti and Selmi, 1982). More research is needed before this controversy can be resolved.

The presence of oogonia and oocytes in the gonad of functional males has been described in many species of Crepidula including C. convexa by Gould (1917), Coe (1936, 1938b, 1942a, 1944) and Ishiki (1939). Coe (1936) reported that oocytes in the gonad of male C. convexa often grow while spermatogenesis is occurring. Histological sections made for this study confirm Coe's observation, and indicate that some vitellogenic activity occurs before transition to the female phase (see Male Gonad, April). During the transition, residual spermatogenic cells in the gonad as well as sperm in the seminal vesicles are cytolysed (Gould, 1917; Coe, 1936, 1938b, 1942a, 1944, 1947; Ishiki, 1939). The oogonia and most of the oocytes around the wall of the male gonad at the time of transition are retained into the female phase (Coe, 1936, 1938b, 1942a, 1944; Ishiki, 1939). Therefore, transitional individuals have a head start on the female phase. Coe (1938b, 1944) has described the resumption of

activity and rapid increase in size of oocytes present in the gonad at the end of the transitional period.

The animals sectioned were chosen from 5 years of collections, and individuals from more than one year were included in most monthly samples. Sections of males from the same month and year showed similar gonadal development. There was essentially no difference in the reproductive condition of males collected in the same month but different years. Slight variations were noted in the degree of development of the gonad in animals fixed at different times of the month (see Male Gonad, April, May).

Female

There is no evidence for self-fertilization in Crepidula (Coe, 1936, 1942a, 1947; Wyatt, 1960). Although oocytes are present in the male gonad, the male and female phases do not overlap functionally. Mature ova and sperm are never found in the gonad simultaneously. Residual sperm in the tubules of the gonad and seminal vesicles are cytolysed at the time the structures of the male system are dedifferentiated and reconstructed into the organs of the female genital tract (Gould, 1917; Coe, 1936, 1938b, 1942a, 1944, 1947; Ishiki, 1939). Therefore, sperm from the male phase could not be retained by shunting into the newly formed seminal receptacles for use in the female phase.

As in the male, the female gonad undergoes a period of reduced activity (November - February). However, the gonad does not show regression and remains obviously female in character.

Mitosis begins early in February and seems to be timed to prepare the gonad for the onset of vitellogenesis in late March - April. The proliferation of oogonia between February and March increases the number of cells available to receive yolk when vitellogenesis begins. New gonia are not produced continuously throughout the reproductive season. Mitotic activity begins to decline in May with a corresponding reduction in the rate that growing oocytes are replaced. By July, mitotic activity is no longer detectable, and the impact of cessation of gonial proliferation can be seen in the decreased number of oocytes smaller than 50 μm (diameter) in the gonad.

There is essentially no change in gonadal activity between November and February (Table 1). In February, oocytes of 12.5 μm diameter reappear, and there is an increase in the number of oocytes smaller than 50 μm (diameter). Mitotic figures are prominent (February), and the sudden increase in smaller oocytes at this time of year indicates that active proliferation of the gonia has begun.

Based upon observed changes in the yolk content of the oocytes, vitellogenesis probably begins between late March and early April (Table 1). In March, more oocytes in the

64-77 μm (diameter) size range contain yolk than in January or February. By April, oocytes as small as 38-50 μm in diameter are found to contain some yolk (Table 1). A comparison of the yolk content of oocytes in the gonad in March and April shows the increased yoliness of some oocytes in each size class between 38-191 μm (diameter) (Table 1). Thus, completion of the growth of the largest oocytes need not occur before yolk is deposited in the smaller size classes. When vitellogenesis begins, it appears that yolk deposition takes place simultaneously in all but the very smallest oocytes (12.5-25 μm diameter).

When oviposition begins in middle to late May, the gonad is not completely filled with large, yolky oocytes of spawnable size (Table 1). The tubules also contain many small and medium size oocytes of varying yolk content. The appearance of very yolky oocytes smaller than 128 μm (diameter) in May indicates that vitellogenesis does not cease with onset of reproductive activity. Therefore, at the start of the reproductive season, the female gonad contains mature oocytes immediately available for spawning, and a pool of developing oocytes which can be drawn upon for future ovipositions.

The condition of the gonad is very similar in July and September (Table 1). The largest oocytes are most numerous and dominate the cross-sectional area of the

lumina. In July, there is a definite increase in the number of oocytes 77-89 μm in diameter. Thus, as oocyte growth and vitellogenesis continue, there is a gradual shift in the size distribution of the oocytes in the gonad toward the larger end of the range. This trend is reflected in the decline in the number of oocytes smaller than 50 μm (diameter) after the cessation of mitotic activity, and may help to explain the sudden disappearance of oocytes between 140 and 250 μm (diameter) from the gonad in July and September (Table 1). By May, all the oocytes larger than 140 μm in diameter have accumulated enough yolk to be categorized as very yolky. Since these oocytes already contain a considerable amount of yolk, their final growth to spawnable size probably occurs rapidly. Therefore, very yolky oocytes in the 140 - 250 μm (diameter) size range may reach spawnable size more rapidly at this time of year than they can be replaced by the growth of smaller (< 140 μm diameter) oocytes containing less yolk. This explanation is consistent with the observation that oocytes of spawnable size (> 250 μm diameter) suddenly dominate the gonad in July and continue to do so through September. This dominance could not be maintained through September unless the removal of the largest oocytes by successive ovipositions was balanced by continuous replacement.

Between September and November (Table 1), very yolky oocytes 140 - 250 μm in diameter reappear as a gonadal

component while the number of oocytes of spawnable size is reduced. The range of oocyte sizes containing some yolk and a moderate amount of yolk has expanded (64 - 179 μm diameter) (Table 1). The observed changes in the size distribution and yolk content of the oocytes indicate that oocyte growth and vitellogenesis continue after the cessation of oviposition in early October. The gonad may appear less crowded in November as a result of the decline in the number of oocytes larger than 250 μm in diameter. Although vitellogenic activity does not cease in October, it may slow down in the fall, reducing the rate at which the largest oocytes are replaced after the last brood(s) of the season are produced. Vitellogenesis probably ends in November since no significant changes in gonadal condition are noted between November and February.

Proliferation of the follicle cells accompanies gonial multiplication in C. convexa. This type of egg formation has been called follicular by Raven (1972). The association of follicle cells with developing oocytes has been noted in several species of Crepidula (Coe, 1936, 1942a; Ishiki, 1939). In C. convexa, follicle cells surround the smaller oocytes (<80 μm diameter). As the oocytes grow and push out into the lumen of the tubules, follicle cells are observed only in the area of contact with the gonad wall. The histological sections show that some follicle cells lying near oocytes in which

vitellogenic activity is evident have granular inclusions in their cytoplasm. Yolk usually begins to accumulate in the oocytes near the region of the cell membrane proximal to the gonad wall. Therefore, the follicle cells may be involved in the transfer of materials to the oocytes for cytoplasmic growth and yolk formation. Although the participation of follicle cells in the nutrition and growth of oocytes has not been demonstrated in C. convexa, there are studies indicating that follicle cells perform these functions in other mollusks (Balinsky, 1970; Raven, 1972; Webber, 1977).

Study of the histological sections of the gonad provides insight into the ability of C. convexa to produce 4-5 successively larger broods over a 5-6 month period. Table 1 shows that the gonad contains oocytes of varying sizes and yolk content throughout the year. Growth of the oocytes and vitellogenesis continue for 8-9 months and these processes do not cease at the start of the reproductive season. Therefore, oocyte development is staggered and mature oocytes are continuously produced to replace those withdrawn from the gonad at each oviposition. Individuals grow between ovipositions, and the gonad expands as the volume of the visceral hump increases. With the expansion of the gonad, there is space for increasing numbers of large, very yolky oocytes in the tubules. The observed size-specific increase in fecundity is possible because ongoing vitellogenic

activity and oocyte growth generate mature oocytes to fill the enlarging gonad.

After transition to the female phase, the mobility of C. convexa declines, and the larger animals are almost totally sessile. Mated pairs are formed for varying periods of time, but the males are very motile and move readily from female to female. The patchy distribution of the animals, and the requirement of a firm substrate for movement can lead to the isolation of individuals. Since the ability of the female to seek a mate is limited, her fertility depends on chance encounters with more mobile males. Female C. convexa can take full advantage of each opportunity for copulation by storing sperm in their seminal receptacles. Isolated animals that were previously mated can lay fertile eggs for long periods. It might be possible for an individual to produce fertile broods for an entire reproductive season using stored sperm. The seminal receptacles contained sperm in each of the months studied from March to December. Therefore, previously mated females can begin oviposition without delay in the spring even if they are unmated. The observed reduction in the amount of sperm in the seminal receptacles during the period of oviposition (May, July, September) probably reflects withdrawal of sperm to fertilize successive broods.

A period of regression in which oocytes remaining in

the gonad are cytolysed does not follow the reproductive season in C. convexa. The immature and mature oocytes (many of spawnable size) in the tubules when oviposition ceases are retained over the winter. The digestive gland, gonad and foot have been identified as sites of nutrient storage in gastropods (Wilbur and Yonge, 1966; Lambert and Dehnel, 1974). The yolky oocytes in the gonad of C. convexa may be maintained as a form of energy storage (see Biochemical Composition and the Reproductive Cycle). Support for this hypothesis can be found in the fact that yolk continues to be deposited in the oocytes after the reproductive season has ended (October - November).

As the oocytes increase in size, crowding pushes them away from the wall and out into the lumen of the tubules. Large oocytes become quite deformed by continuing to maintain a point of contact with the gonad wall. Therefore, it must be important for the oocytes to retain their connection with the germinal epithelium for as long as possible. Ishiki (1939) observed that yolk begins to accumulate in the oocytes of C. aculeata in the region touching the germinal epithelium. This phenomenon also has been observed in the histological sections of C. convexa (present study). Follicle cells are found in the area where the oocytes contact the gonad wall. As discussed above, these cells may play an important role in oocyte development. Therefore, one of the reasons for the prolonged attachment of growing oocytes to the gonad wall

may be the need to preserve direct contact with the follicle cells.

The histological sections show that large, yolky oocytes, many of spawnable size, are present in the gonad throughout the year (Table 1). Yet, the reproductive season of C. convexa in Jamaica Bay is confined to a 5 to 6 month period. The major factor determining the onset and duration of reproductive activity seems to be water temperature (Ander, 1980). Brooding females are not observed until water temperature reaches 15-17 °C in the spring, and cessation of oviposition is coincident with the decline of water temperature in the fall (Figure 1). Water temperature has been identified as a significant factor in gonad maturation and spawning in mollusks (Fretter and Graham, 1964; Wilbur and Yonge, 1964; Webber, 1977). The importance of water temperature as the trigger for spawning in C. convexa has been confirmed by laboratory experiments and field transfers in which temperature was manipulated. Females collected before and after the reproductive season can be induced to produce normal broods when they are maintained at 19 °C. Oviposition can be delayed or halted by exposing the animals to water temperatures below 15-17 °C. While cessation of oviposition occurs in the field in early October, individuals maintained in the laboratory at 19 °C seem capable of extending their reproductive period almost

indefinitely. The transfer of animals from Quisset Harbor to Breezy Point demonstrated not only that spawning can be induced in the field if temperature conditions are met, but also that populations of C. convexa which are widely separated geographically have the same temperature requirement for oviposition. This explains why spawning does not begin at Woods Hole in mid-May. Water temperature at Woods Hole remains below 15-17 °C until June (Figure 2), which is when oviposition begins.

The study of reproductive condition makes it possible to explain the ability of C. convexa to spawn out of season. The gonad does not undergo regression, and it contains immature and mature oocytes in every month examined. Therefore, the animals are in a state approaching reproductive readiness throughout the year. When the appropriate water temperature cue is supplied, individuals can be induced to produce broods, regardless of the season, because spawnable size oocytes are always present in the gonad. However, a lag period of 12-21 days has been observed between the time the animals are exposed to water temperatures above 15-17 °C, and the appearance of the first egg masses. Onset of oviposition may require exposure of females to the critical water temperature for a minimum period of time. This strategy would protect the snails from premature spawning induced by temporary fluctuations in water temperature. Maintaining C. convexa in the laboratory at 19 °C can extend their natural

reproductive season by many weeks. Why don't these females exhaust the reserve of spawnable size oocytes in the gonad? Cessation of vitellogenic activity seems to be correlated with declining water temperature (see Biochemical Composition and the Reproductive Cycle). At a constant temperature of 19 C, oocyte growth and vitellogenesis probably do not cease. If these processes continue, small and medium size oocytes in the gonad could be brought to maturity for use in successive ovipositions.

The potential for extension of the reproductive season which is observed in the laboratory also seems to exist in the field. In lower Delaware Bay, water temperature rises more rapidly in the spring than it does at Woods Hole or Breezy Point, and C. convexa begin to produce broods in April (Figures 1 & 2) (Hendler and Franz, 1971). The length of the period of oviposition is not known for populations of C. convexa inhabiting the southern section of the species range along the southeastern coast of North America. However, Coe (1942b) reported that C. onyx and C. nummaria continued to reproduce throughout the year off the coast of southern California. C. adunca also breeds year round along the California coast (Moritz, 1939). Gallardo (1977) found brooding female C. dilatata every month except February in Chile.

C. fornicata and C. plana can spawn at a lower water temperature than C. convexa. All three species were

collected in Jamaica Bay in April when the water temperature was approximately 10^o C, but only C. plana and C. fornicata were brooding. Walne (1956) reported C. fornicata with egg masses in the rivers of Essex, England at a water temperature of 10^o C. Both C. fornicata and C. plana can be induced to produce broods in the laboratory, regardless of the season, when maintained at 19^o C. A female C. plana brought into the laboratory in January (water temperature 3.5^o C) and placed in an incubator at approximately 10^o C produced an egg mass within three weeks. This observation is consistent with the lower water temperature requirement for oviposition observed for C. plana in the field. Since oviposition can be induced in several species of Crepidula out of season, it is possible that all species in the genus maintain oocytes of spawnable size in the gonad year round. Also, C. plana and C. fornicata lay several egg masses in succession during the reproductive season indicating that they may have the same pattern of staggered oocyte development observed in C. convexa.

The females sectioned were chosen from collections made in six different years. Animals from a single year were used only for the February sample, and gonadal development was essentially the same in these individuals. The reproductive condition of females from the same month but different years was very similar. However, a slight difference was observed in the degree of development of

the gonad in animals fixed for the January sample. No mitotic activity was evident in the gonad of a female collected on January 2, but a few mitotic figures were observed in sections of an animal collected on January 28. Although a significant increase in mitotic activity accompanied by gonial proliferation was not noted until February, it seems that preparation for this phase of the reproductive cycle may begin at the end of January.

Temperature, Growth and Feeding

Crepidula convexa grow most rapidly in the spring and summer at Breezy Point (Ander, 1980; present study). Measurements of animals maintained in the field indicate that the growth rate declines in the fall, and it is essentially zero in winter. Animals collected during the winter and maintained in the laboratory at 19 °C began to show white rings of new shell growth within a few weeks. A similar relationship between growth rate and water temperature was observed in studies of C. plana and C. fornicata along the southern coast of New England (Coe, 1942b; 1949). Walne (1956) reported that the growth of C. fornicata at Essex, England increased in spring with rising water temperature and declined in the fall. According to Walne's observations, C. fornicata experience a period of arrested growth during the winter (October - February) comparable to the one observed in C. convexa. The studies discussed above concern populations of

Crepidula inhabiting temperate waters with large seasonal fluctuations in water temperature. However, Coe (1942b) found that C. onyx and C. nummaria continue to grow year round along the coast of southern California.

Wilbur (1964) stated that studies of the effect of temperature on the growth rate of mollusks can be complicated by the influence of other factors such as food intake. Rising water temperature has a direct effect on metabolic activities involved in shell and tissue growth. However, increased feeding at higher water temperatures may affect growth rate indirectly. The feeding efficiency of filter-feeding mollusks is related to the filtration rate of the gill(s) (activity of gill cilia), and this rate declines at low water temperature (Walne, 1956; Yonge, 1960; Wilbur, 1964; Owen, 1966; Johnson, 1971). Working with C. fornicata in England, Walne (1956) found that feeding rate was directly related to water temperature. He observed that less than 50% of the animals were feeding when the water temperature dropped below 5^o C. Although partially digested material was present in the gut of C. convexa throughout the year, the digestive gland appeared to be less active during the late fall and winter. The available information suggests that C. convexa probably feed more efficiently in the spring, summer and early fall when water temperature at Breezy Point is above 5^o C. The length of time feeding activity

is curtailed as the result of low water temperature is probably reduced in warm years such as 1984 (Figure 6).

The role of water temperature in determining the onset and duration of the reproductive season of Crepidula species at different geographic locations has been discussed above. However, it should be noted that the length of the breeding season can vary slightly at the same location as the result of yearly temperature fluctuations. If water temperature drops rapidly at the end of the summer, cessation of oviposition at Breezy Point usually occurs by the last week in September, but brooding females can be found in mid-October in years with a warm fall (Figures 1, 6). Walne (1956) observed a delay of several weeks in the onset of spawning by C. fornicata in a year with a very cool spring.

Water temperature may affect biochemical composition (storage and utilization) indirectly by influencing growth, feeding and the timing of the reproductive cycle (see Biochemical Composition).

Oviposition and Development of the Embryos

Mesogastropods and neogastropods are capable of internal fertilization as the result of structural changes in the excretory and reproductive systems not present in the archaeogastropods (Fretter and Graham, 1962). The female genital duct of the mesogastropods and neogastropods has been lengthened and enlarged by the

addition of a section derived from the mantle. Areas of the pallial portion of the female genital tract have become specialized for sperm reception and storage and capsule formation. The cells lining the oviduct, uterus and vagina of Crepidula convexa are ciliated. The walls of the uterus are thick and muscular, and it is lined with columnar epithelial cells whose cytoplasm contains many granular cellular inclusions. The cells of the oviduct are notably free of such inclusions. The vagina has thinner walls than the uterus, but the area is also muscular and often appears to be thrown into folds along its length. The folded appearance of the vagina may be a reflection of its extreme elasticity as observed during the processes of copulation and oviposition. The cells lining the vagina are flatter than those of the uterus and contain very few cellular inclusions. Since fertilization occurs in the uterus (Coe, 1942a), capsule material cannot be added around the eggs in the oviduct. The glandular nature of the cells of the uterus suggests that these cells produce the secretions that form the egg capsules. Ishiki (1939) described the walls of the uterus in C. walshi and C. aculeata as glandular. Coe (1942a) found that the uterus of C. onyx had muscular walls lined with columnar ciliated and glandular epithelial cells. He concluded that these glandular epithelial cells were the source of the capsule material.

Most mesogastropods use the foot to manipulate and

attach the egg capsules (Fretter and Graham, 1962). The capsules also may be given a final molding after leaving the genital duct in some species. Female neogastropods typically possess a ventral pedal gland which is used to mold and attach their egg capsules (Fretter and Graham, 1962). There are some neogastropods which appear to lack the ventral pedal gland, and a very specialized group of mesogastropods with a comparable structure (female only) used to embed their capsules in the tissues of compound ascidians (Fretter and Graham, 1962). The final shape of the egg capsules of C. convexa is entirely the result of the molding activity of the foot. The foot catches the capsules after they leave the vagina, shapes them, forms the stalk and then affixes them to its ventral surface or to the substrate.

The timing of the appearance of each egg capsule at the vaginal opening during oviposition does not seem to be directly correlated with female body size. Although the absolute age of an animal cannot be determined by its shell length or body size, larger females, in general, are older than smaller ones. Since larger females do not consistently shape and deposit their egg capsules more rapidly than smaller animals, experience does not seem to be important in determining the timing of the process. It is possible that individual differences occur naturally between females, and each animal may deposit the capsules

of all her broods at approximately the same rate. However, the time between the emergence of the capsules may vary randomly from one brood to the next. Since no female was observed during the production of two or more successive egg masses, it is difficult to draw more definite conclusions about the factors influencing the timing of capsule formation.

Females can lay a new egg mass within one day of the emergence of the previous brood. This is possible for three reasons: (1) vitellogenesis and oocyte growth continue throughout the reproductive season (2) the gonad always contains moderately yolky and very yolky oocytes, and (3) the brooding period of 29.5 days seems sufficient to ready enough oocytes for the next oviposition (lost or removed broods are replaced within 1 - 3 weeks) (Ander, 1980; present study).

Development of the embryos from females collected at Breezy Point required approximately 29.5 days at a constant temperature of 19 C. Ament (1979) found that broods of animals collected from Cape Cod Bay and Delaware Bay emerged after 30.3 ± 0.63 days when maintained at 18.5 C. Therefore, the length of the incubation period for northern and southern populations seems to be similar when brooding females are exposed to the same temperature regime. However, the embryos of Breezy Point females took longer than 29.5 days to complete development at 14-16 C. The effect of exposure to lower water temperature appears

to be irreversible. Broods maintained at $14 - 16^{\circ}\text{C}$ and then warmed to 19°C did not emerge at the predicted time, and the delay seemed to be correlated with the time the embryos remained at the colder water temperature. Conklin (1897) indicated that the incubation period of C. convexa at Woods Hole (Figure 2) was longer than four weeks. In 1971, Hendler and Franz found that C. convexa brooded for approximately two weeks in Delaware Bay (Figure 2). Therefore, the incubation time of the embryos of C. convexa may vary at geographic locations with significantly different water temperature profiles.

The size of C. convexa at emergence from the capsules probably does not vary significantly between populations. Juveniles from broods of animals collected at Breezy Point are 0.92 ± 0.07 mm (shell length) at emergence. Ament (1979) reported that newly emerged juveniles from Cape Cod Bay females were 0.97 ± 0.03 mm and those from broods of Delaware Bay animals were 0.94 ± 0.03 mm. The work of Ament (1979) is consistent with the shell length of 0.95 ± 0.09 mm reported by Hendler and Franz (1971) for emergent juvenile C. convexa in Delaware Bay.

Biochemical Composition

Biochemical Composition and the Reproductive Cycle

Seasonal fluctuations occur in the biochemical composition of Crepidula convexa. A comparison of the

protein, lipid and carbohydrate content of both sexes from 1981 and 1984 revealed that biochemical levels vary from year to year. However, similarities were noted in the overall seasonal pattern of fluctuations in biochemical content for male and female animals in 1981 and 1984. These fluctuations are correlated with seasonal changes in the reproductive condition of the snails. Biochemical constituents have been reported to vary seasonally with the reproductive cycle in a number of gastropods, bivalves and amphineurans (Giese and Araki, 1962; Blackmore, 1969b; Williams, 1970; Stickle, 1975; Taylor and Venn, 1979; Ansell et al, 1980; Barber and Blake, 1981; Devi et al, 1985).

Gonadal maturation begins in late winter to early spring with the onset of gonial proliferation in both sexes. Vitellogenesis and oocyte growth become apparent by late March to April, and spermatogenesis begins in May. The events of gonadal ripening are accompanied by increases in the protein, lipid and carbohydrate levels in both sexes. In the spring as water temperature rises, the gonad becomes active, growth resumes and feeding increases. Since most nutrient levels and dry body weight tend to decrease over the winter, the pre-reproductive feeding period in the spring is probably very important to C. convexa in balancing the combined energy costs of new growth and gonadal development. Feeding does not cease with the onset of reproductive activity in May.

Therefore, the animals do not have to rely solely on stored nutrients to carry them through the reproductive season.

The protein, lipid and carbohydrate composition of both sexes declines by September or October coincident with the end of the reproductive season. C. convexa undergoes multiple spawnings between May and October. The effect of the long spawning season is noted in the histological sections which show a reduction in the number of very large, yolky oocytes in the female gonad, and in the amount of sperm in the tubules of the male by October to November. Since the activity level of the gonad is declining from September to November, a partial emptying of the tubules occurs by the end of the season.

The increase in protein, lipid and carbohydrate composition observed in C. convexa during gonadal ripening, and the decline in these constituents at the end of the spawning period have been observed in other gastropods (Blackmore, 1969b; Stickle, 1973, 1975; Belisle and Stickle, 1978; Devi et al, 1985).

During the post-reproductive period in the fall (September - December), most biochemical components in both males and females tend to increase. At this time, the animals are released from the energetic drain of reproduction, and the growth rate is declining. There is a 2-1/2 to 3 month interval of reduced energy demand

during which C. convexa can feed and build up nutrient reserves before winter. The vitellogenic activity and oocyte growth observed in November indicates that some of the energy taken in by the females after spawning may be shunted directly to the gonad. The levels of at least two biochemical constituents also were found to rise in conjunction with feeding activity after spawning in Littorina littorea, Thais lamellosa, Donax truncatus and Morula granulata (Williams, 1970; Stickle, 1973, 1975; Ansell et al, 1980; Devi et al, 1985).

The gonad is relatively inactive, and growth essentially ceases during the winter. Although the energetic cost for growth and reproduction is at a yearly minimum, most biochemical components decrease or remain unchanged in both sexes. C. convexa at Breezy Point must survive the stress of several months of very low water temperature. Feeding may be interrupted completely or occur only sporadically during intermittent periods of elevated water temperature. The reserves built up in the fall may contribute significantly to winter survival.

In the same year (1981 or 1984), the range of fluctuation in each biochemical component was comparable in both sexes (Table 2). In 1981, for example, protein content varied from 46 to 86% in females and 45 to 89% in males. Lipid levels in both sexes fluctuated about 7% (male 5 - 12%, female 6 - 13%) during the year while carbohydrate content varied about 13% in females (7-20%)

and 8% in males (6-14%). The data indicate that there is no difference in energy storage and utilization by male and female C. convexa. Many of the studies concerning seasonal changes in biochemical composition in mollusks do not deal specifically with sexual differences, but a few have reported similar patterns for both sexes (Giese and Araki, 1962; Blackmore, 1969b; Stickle, 1975; Belisle and Stickle, 1978).

Although the pattern of seasonal variation in the biochemical composition of male and female animals was similar in 1981 and 1984, differences in the magnitude of the fluctuations were noted between the two years. The year-to-year differences are difficult to explain, but a partial explanation may lie in the different temperature regimes of 1980-1981 and 1983-1984. Biochemical composition tended to fluctuate more in the colder year (1981). The multiple effects of water temperature have been discussed above (see Temperature, Growth and Feeding), and the observed year-to-year differences may reflect the impact of these factors upon C. convexa.

C. convexa probably do not depend on stored nutrient reserves except for a brief period during the winter. At Breezy Point, the timing of the reproductive cycle is such that the animals can feed during the critical periods before, during, and just after spawning. The post-reproductive feeding period in the fall when energy

demands are reduced gives C. convexa the opportunity to recover from spawning and to accumulate some reserves before winter.

Seasonal Changes in Body Weight and Water Content

The data indicate that seasonal fluctuations in the biochemical composition of Crepidula convexa are accompanied by changes in dry body weight and water content.

Changes in dry body weight during the year showed a similar pattern in both sexes (1981 and 1984). The animals tended to lose weight during the winter and the reproductive season. A decline in most biochemical components was correlated with decreasing dry body weight. Although C. convexa are feeding, they lose weight during the spawning period indicating that there is a net loss of energy. This observation suggests three things: (1) The amount of energy that can be stored during the spring feeding period is not sufficient to carry the animals through the reproductive season (2) C. convexa probably could not meet the energetic demands of a 5 to 6 month spawning period without feeding, and (3) energy is not stored during the reproductive period. Since feeding activity probably is interrupted in winter, the animals must depend on reserves built up in the fall after spawning. Fall appears to be the most favorable time for C. convexa to accumulate nutrient reserves, yet the amount

stored is not enough to prevent loss of weight over the winter.

In the spring and fall, the animals showed a tendency to gain weight, and the levels of most biochemical constituents increased. Most of the increase in dry body weight in spring can probably be attributed to gonadal maturation while storage, as mentioned above, may be minimal. The increase in dry body weight in the fall is correlated with the 2-1/2 to 3 month post-reproductive feeding period.

The relationship between dry body weight and the reproductive cycle observed in C. convexa has been reported in other mollusks. Several studies have shown that seasonal fluctuations in total dry body weight and/or the dry weight of body components (i.e. foot, gonad, digestive gland, adductor muscle) of a number of gastropods and bivalves were related to the reproductive cycle and often to feeding as well (Blackmore, 1969b; Williams, 1970; Stickle, 1973, 1975; Belisle and Stickle, 1978; Griffiths and King, 1979; Taylor and Venn, 1979; Ansell et al, 1980; Barber and Blake, 1981).

The water content of the body of male and female C. convexa varied seasonally (1981 and 1984). During the spring and fall when the dry body weight of the snails tended to increase, the percentage of water in the body decreased. The dry body weight of the animals usually decreased during the reproductive season and in winter,

and the loss of weight was correlated with an increase in the water content of the tissues. Thus, there seems to be an inverse relationship between dry weight and the water content of the body in C. convexa. Although studies of biochemical composition usually include seasonal data for dry body weight, very few discuss the topic of water content. However, the occurrence of seasonal fluctuations in water content which were inversely correlated with dry weight have been reported in Chlamys opercularis, Donax truncatus and Morula granulata (Taylor and Venn, 1979; Ansell et al, 1980; Devi et al, 1985). C. convexa may maintain body volume when there is a reduction in body weight by increasing the water content of the tissues. Taylor and Venn (1979) found that there was an uptake of water into the gonad of Chlamys opercularis after spawning when body weight was low. In 1980, Ansell et al reported that decreased body weight in Donax truncatus was accompanied by the uptake of water into the tissues.

Eggs and Egg Capsules

It was interesting to find that the egg capsules of Crepidula convexa contain lipid (12.5%). Lipid does not seem to be a common constituent of gastropod egg capsules (Hunt, 1966; Bayne, 1968). Stickle (1975) reported that the egg capsules of Thais lamellosa contained 12.9% lipid, and Belisle and Stickle (1978) found 7% lipid in the capsules of Thais haemastoma. Carbohydrate has been found

in association with protein in the capsules of a number of gastropods (Fretter and Graham, 1962; Hunt, 1966; Bayne, 1968; Stickle, 1975; Belisle and Stickle, 1978). The carbohydrate content of the egg capsules of Buccinum undatum (5-6%), Thais lamellosa (2.3%) and Thais haemastoma (2%) is much lower than the value determined for C. convexa in this study (15.0%) (Hunt, 1966; Stickle, 1975; Belisle and Stickle, 1978). Protein appears to be the major component of the egg capsules of many gastropods (Fretter and Graham, 1962; Hunt, 1966; Bayne, 1968; Flower et al, 1969; Stickle, 1975; Belisle and Stickle, 1978). The protein content of C. convexa capsules (35.0%) is significantly less than the amount reported for Thais lamellosa (50.8%), Thais haemastoma (53%) and Buccinum undatum (77.5%) (Hunt, 1966; Stickle, 1975; Belisle and Stickle, 1978). The strength and durability of the capsules might be related to their protein content. Although the egg capsules of C. convexa are remarkably strong and elastic, their walls are thin. The capsules of Thais and Buccinum which have a higher protein content are tougher and thicker walled than those of C. convexa. It is possible that the capsules of C. convexa contain more than 35% protein. Since the value for protein content increased when the capsules were treated with stronger alkali, incomplete breakdown of protein fibers may affect the accuracy of the assay. Also, the color obtained with

the Lowry et al (1951) method of protein determination is related to the tyrosine and tryptophan content of the material used. Therefore, proteins with few tyrosine and tryptophan residues will not produce an intensely blue color with this assay, and protein content may be underestimated. The protein in the egg capsules of C. convexa may contain very little tyrosine and tryptophan. Hunt (1966) determined the amino acid composition of the capsule material of Buccinum undatum; tyrosine and tryptophan were not among the fifteen amino acids identified.

Raven (1972) stated that the reserve substance in the egg cells of mollusks can be divided into two types, fatty yolk and protein yolk. Carbohydrate also has been found associated with the protein yolk in a number of mollusks (Raven, 1972). In 1917, Conklin reported that more than 75% of the volume of Crepidula eggs was occupied by protein yolk. The results of the present study indicate that protein (71.0% by weight) is the major constituent of C. convexa eggs. The eggs also contain a significant amount of lipid (23.9%). Although carbohydrate (9.1%) is present in the eggs of C. convexa, it is a minor component.

Biochemical Composition of A Standard Animal

It is a common practice for whole animals or their component parts to be pooled for use in assays to

determine biochemical composition. As in the case of Crepidula convexa, this procedure often is necessary because individual animals are too small to provide enough material to assay or the various organs cannot be dissected apart. The levels of protein, lipid and carbohydrate usually are expressed as the percentage content per unit dry weight of tissue. However, data for dry body or organ weight and biochemical composition can be combined to determine seasonal changes in the composition of a standard animal. Some studies of mollusks have used the standard animal as a tool to show the effect of seasonal fluctuations in percentage composition at the level of the individual animal (Blackmore, 1969b; Lawrence and Giese, 1969; Ansell et al, 1980).

The calculated values for a standard male and female C. convexa (1981 and 1984) show that protein, lipid and carbohydrate content tends to gradually rise during the reproductive season and then decline. In 1984, the biochemical constituents reached their maximum values earlier in the reproductive season than in 1981 for both sexes. This difference may be related to the favorable effect of higher water temperatures on feeding behavior in the spring of 1984. The decline in almost all component levels at the end of the reproductive period demonstrates the drain of reproduction on the body reserves of the animals. The effect of the post-spawning recovery period

in the fall is shown very clearly by the standard animal data. The increase in protein, lipid and carbohydrate content was particularly noticeable in 1984 when water temperature remained above 5 °C in December and January, and feeding may have continued into early winter. The stress of winter on C. convexa is reflected in a net loss of biochemical constituents (1981 and 1984). However, most components declined less during the relatively mild winter of 1984. The fluctuations in biochemical composition in the spring are difficult to characterize. There is a tendency for constituent levels to increase, especially in 1984 (see above), but considerable variation is apparent at this time of year. Some of the shifts in content may result from a complex interaction between the energetic demands of gonadal maturation and new growth, and the energy input from increased feeding.

Reproductive Effort and Energy Allocation

Most theories and models that seek to explain the evolution of life history strategies make the basic assumption that a trade-off exists between growth and reproduction (Williams, 1966; Stearns, 1976; Snell and King, 1977; Calow, 1979; Griffiths and King, 1979; Sebens, 1982). Resources are assumed to be limited either by environmental or physiological constraints upon the individual. Therefore, energy allocated for reproduction reduces the amount available for growth and maintenance.

Since Crepidula convexa grow throughout the reproductive season, the study of this snail offers an opportunity to test the assumption that future growth will be sacrificed if increasing amounts of energy are shunted to reproduction.

Net Production in Relation to Growth

P_n increases with female dry body weight (Figure 20). However, P_n per unit body weight decreases as the animals become larger. In a filter-feeding gastropod such as C. convexa, energy intake is dependent upon the filtering efficiency of the gill. The functioning of the gill is related to its surface area. The decrease of weight-specific production with growth may result because the surface area of the gill does not increase in proportion to the increase in body volume it must support (Von Bertalanffy, 1957; Sebens, 1982). It has been shown that feeding efficiency in bivalves decreases as the individual becomes larger resulting in a reduced intake of food per unit tissue (Wilbur, 1964). Shumway and Newell (1984) found that the filtration rate of the bivalve Mulinia lateralis didn't increase as rapidly during the reproductive season as the metabolic demands of growth, reproduction and respiration. These data indicate that C. convexa are subject to resource limitation as they grow, and one of the contributing factors may be the allometric relationship between gill size and body volume.

Reproductive Allocation of Production

C. convexa allocate a progressively larger proportion of Pn to reproduction with increasing dry body weight (Figure 21). As a consequence, less energy is available for growth as the animals become larger, and the growth rate declines (Figures 20, 25). The data show that growth increase per unit dry body weight approaches zero at approximately 47 mg dry body weight (18-19 mm shell length), and this is consistent with the prediction that a female of approximately 49 mg allocates all available Pn to egg output (Figures 21, 25). These observations demonstrate the existence of a trade-off between growth and reproduction in C. convexa. Walne (1956) noted that the growth rate of C. fornicata declined in individuals over 35 mm (shell length) even when the snails were not subject to substrate restriction. A decrease in growth rate with age/size has been observed in other mollusks (Wilbur, 1964; Griffiths and King, 1979). Figure 21 also indicates that reproductive effort in C. convexa increases with age. Although body size and age are not directly correlated in Crepidula, larger individuals are older. For an iteroparous species like C. convexa which lives in an unstable environment, residual reproductive value should begin to decrease with age (Williams, 1966; Pianka, 1976; Stearns, 1976; Calow, 1979). Williams (1966) and Pianka (1976) predicted that reproductive effort should

vary inversely with residual reproductive value (expectation of future offspring). Therefore, the relationship between egg output and body weight in C. convexa is consistent with theoretical expectations. At any given age (size) females are making a trade-off between current reproduction and the expectation of future offspring (Williams, 1966; Pianka, 1976; Stearns, 1976). Increasing current reproductive effort carries with it a cost to future reproduction (Williams, 1966; Calow, 1979). Since fecundity is positively correlated with dry body weight (Figure 15), the reduction in the amount of energy available for growth which accompanies increased reproductive effort acts to restrict future reproductive potential (increase in brood size).

Females produce larger broods as their dry body weight increases (Figure 15). However, as discussed above (Figure 20), weight-specific production decreases with increasing dry body weight. Figure 22 shows the impact on weight-specific fecundity of resource limitation as the animals grow. The proportional increase in egg output attained by continued growth declines in larger females (Figures 22, 24). The percent increase in the number of eggs in successive broods per unit dry body weight is high for smaller individuals, and each growth increment results in a significant increase in fecundity (brood size) (Figure 23). As they grow, females derive less benefit (increase in fecundity) for each allocation of energy to growth

(cost). Williams (1966) suggested that organisms will distribute available resources so that the rate of reproductive profit on the investment is maximized. Large C. convexa probably do not reduce or stabilize egg output in order to divert energy from reproduction to growth because such a strategy would not be profitable. The increase in brood size (future benefit) that can be gained by further growth (current investment) becomes small for large individuals (Figure 23).

Egg output increases more rapidly than P_n with increasing dry body weight (Figure 24). The response of P_n probably is more sluggish as the animals grow because it is related to the surface area of the gill rather than body volume (see above). As dry body weight increases, more gonadal tissue can be packed into the expanding visceral hump. Therefore, increases in body volume are accompanied by proportional increases in gonad volume and egg production. By extending the regression lines fitted to the data in Figure 24 until they intersect, the point at which P_n equals egg output can be predicted. It appears that individuals of approximately 70 mg dry weight (21 - 21.5 mm shell length) must allocate all P_n to egg output and as a consequence have no energy available for further growth. Based upon the data in Figure 21, 24 and 25, C. convexa reach the critical point in the trade-off between growth and reproduction at a shell length of

approximately 18-21 mm (47 - 70 mg). C. convexa as large as, but not exceeding, 22 mm have been found at Breezy Point. Hoagland (1977) reported a maximum shell length for C. convexa of 18.5 mm (recent) and 24.0 mm (fossil). Coe (1942b) found that C. convexa were seldom larger than 10-16 mm along the southern coast of New England. It is possible that the species reaches a maximum size at a particular geographic location. The maximum size attainable may be determined by energetic constraints upon the individual associated with filter-feeding, brooding and the direct mode of development as well as the physical characteristics of the habitat. Walne (1956) observed that the percentage of C. fornicata which exceeded a given size in his samples varied with the location of the study site. He suggested that these size differences were the result of better growing conditions in certain habitats.

Does Crepidula convexa Optimize Body Size?

Why do C. convexa continue to grow when Pn and egg output per unit dry body weight (Figures 20, 22) are higher for smaller individuals? It would be profitable to stop growing at a smaller size if the energy that would have gone to growth could be utilized to increase fecundity at that size. However, the volume of the gonad may restrict the number of eggs that can be produced per oviposition at a given size, regardless of the amount of energy available for reproduction. Also, C. convexa brood

the egg mass beneath the anterior portion of the shell. Females cannot successfully brood more egg capsules than can be contained in this space. Therefore, the number of eggs produced at any size cannot exceed brooding capacity. Since brood space is a function of shell volume, it can be increased only if individuals continue to grow. Matusiak and Fell (1982) studied the reproductive cycle of C. convexa living in an eelgrass community. Since the animals used the blades of eelgrass as a substrate, their growth was restricted, and the maximum shell length attained was 9 mm. A comparison of the fecundity of this population with the Breezy Point population shows that animals of equal shell length produce approximately the same number of eggs. Reducing the energy allocated for growth does not appear to produce an increase in the fecundity of the individual. Therefore, this study indicates that energy not used for growth is not readily shunted to reproduction.

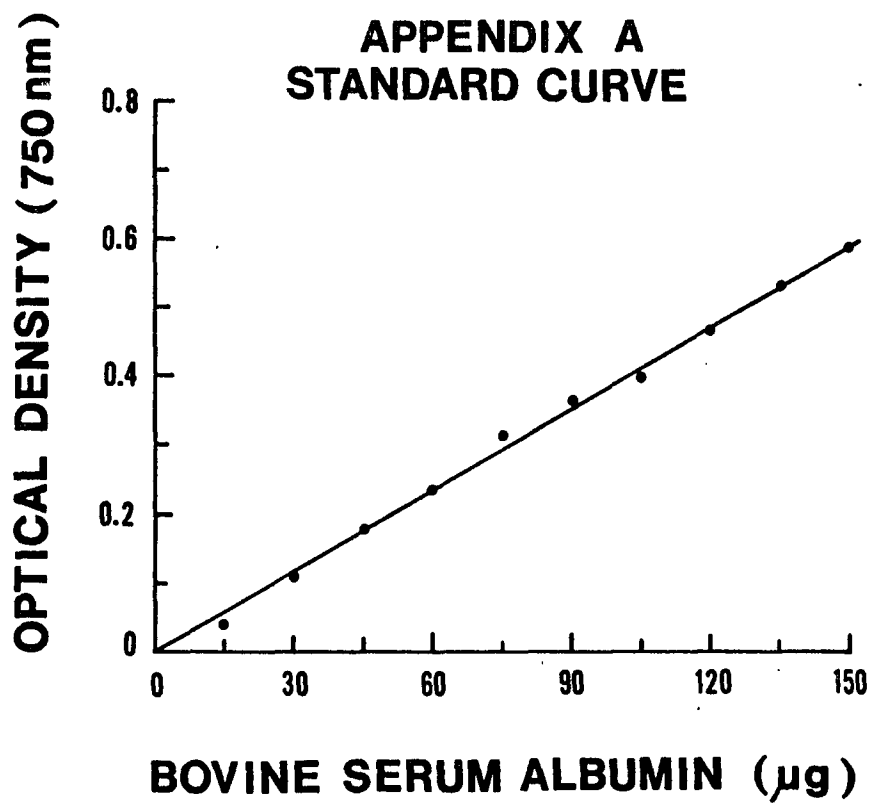
Allocating energy for continued growth allows C. convexa to optimize brood size at each successive oviposition (Figures 15, 24) and to maximize lifetime fecundity. This is important in an unstable environment where there is a high probability that individuals may not survive the winter to reproduce again (Williams, 1966; Pianka, 1976; Stearns, 1976).

How Do Other Crepidula Species Attain Larger Size?

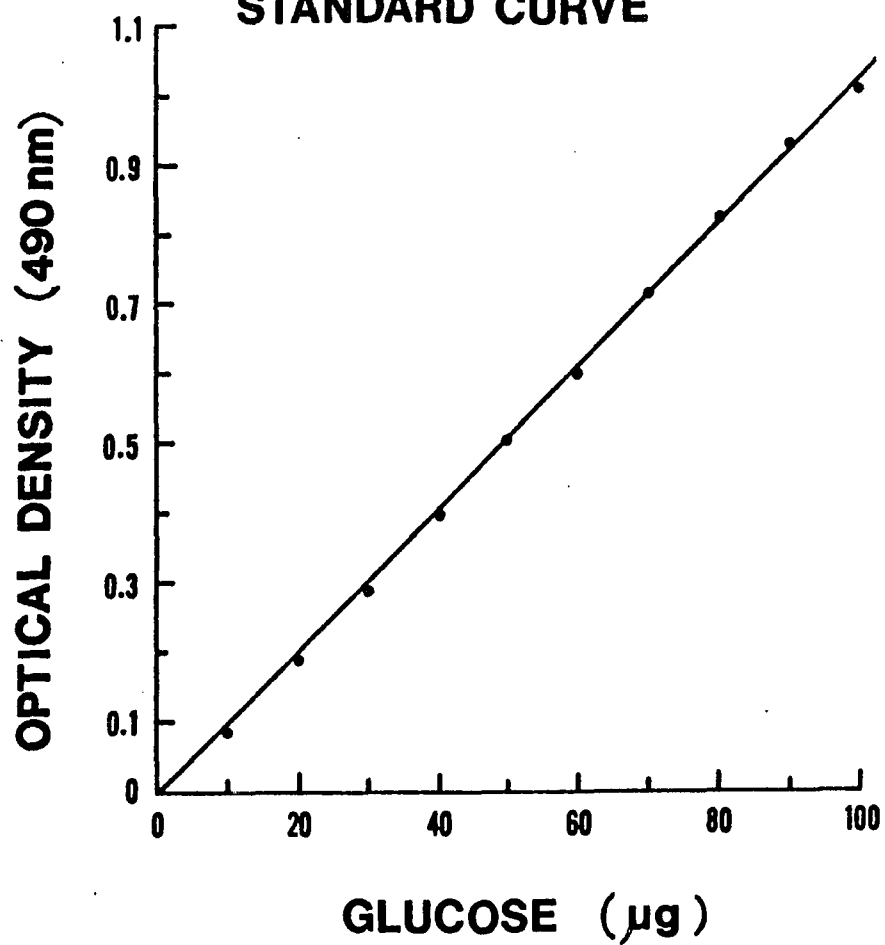
With the insight gained from the analysis of energy allocation in C. convexa (Figures 20-25), it is possible to speculate about how C. plana and C. fornicata occurring in the same habitat attain larger body size (shell length). Although these species produce many small eggs rather than a few large ones and have a different mode of development (indirect) than C. convexa, their method of energy acquisition is the same, and the embryos must be brooded to the veliger stage. The energy allocated to reproduction by C. plana, C. fornicata and C. convexa can be compared if egg output is expressed as the dry weight of the egg mass (mg) rather than the number of eggs produced per oviposition. The maximum shell length reported for C. plana is 47 mm (Hoagland, 1977), and the species name describes the extremely flat shell. A C. plana equal in shell length to the more convex C. convexa has a lower body weight (unpublished data) due to the flatness of the shell. As C. plana grow, the increase in body volume is less disproportionate in relation to the surface area of the gill than it is in C. convexa. Therefore, weight-specific P_n may not decrease as rapidly with increasing body weight in this species (Figure 20). The relationship between egg output (mg) and body weight in C. plana (unpublished data) and C. convexa seems to be similar. Assuming a more favorable relationship between P_n and increasing body weight, C. plana could allocate

approximately the same amount of energy to reproduction as C. convexa and still have energy available for growth. Figure 24 can serve to visualize the impact of the difference in shell shape between the species. If the slope of Pn was greater, the point at which Pn equals egg output would be shifted to the right predicting a larger maximum shell length for C. plana than C. convexa. The shell of C. fornicata is convex. The maximum shell length reported for the species by Hoagland (1977) is 59 mm, but Walne (1956) found some specimens as large as 66 mm. The relationship between shell length and body weight appears to be similar in C. fornicata (unpublished data) and C. convexa. Therefore, C. fornicata probably face the same energetic constraints associated with the relationship between gill surface area and body volume as C. convexa (see above). The egg output (mg) of C. fornicata (unpublished data) seems to be lower than C. convexa of the same body weight. This indicates a species difference in the partitioning of available energy between growth and reproduction. C. fornicata may not increase the percentage of Pn devoted to egg output with increasing body weight as rapidly as C. convexa (Figure 21). Therefore, the point at which Pn equals egg output and growth stops would be shifted to the right in Figure 24, and C. fornicata could grow beyond a shell length of 22 mm. The data for C. plana and C. fornicata are too

sketchy at present to reach definite conclusions about the dynamics of energy allocation in these species. However, resource allocation of this form may account for the shift from complete to partial brooding in larger slipper limpets, such as C. fornicata and C. plana (e.g. see Strathmann and Strathmann, 1982).



APPENDIX B STANDARD CURVE



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