SEASONAL CHANGES IN SOFT-BODY COMPONENT INDICES AND ENERGY RESERVES IN THE ATLANTIC DEEP-SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*[1]

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ABSTRACT

The relationship between the energy storage cycle and gametogenesis was investigated over a 1-year period (March 1979-March 1980) in a population of the Atlantic deep-sea scallop, *Placopecten magellanicus*, from Boothbay, Maine. Soft body component indices, dry weights, lipid, and carbohydrate levels were measured in digestive gland, adductor muscle components, and gonadal tissue. In addition, mantle, mantle edge, foot, and kidney tissues were examined histochemically for glycogen and lipid content. Gametogenesis began in early winter (December-January) during a period when energy reserves and tissue indices were falling. Gonadal growth occurred concurrently with increases in body component indices, dry weights, and replenishment of lipid and carbohydrate levels in the digestive gland and adductor muscle (January-March). The accumulated springtime energy reserves in somatic tissues were lost in the late spring-summer, as maturation of gametes was completed. Following spawning in mid-September, a slight recovery of energy reserve levels and body component index values was evident for the digestive gland and quick component of the adductor muscle. Recovery did not occur in the gonad. Energy reserves, body component indices, and dry weights all declined throughout the late fall and early winter months. A buildup of energy reserves in the early spring appears essential for the later completion of gonadal maturation. Similarly, the autumn recovery of energy reserves within the somatic tissue may be important for the subsequent initiation of gametogenesis in early winter, as well as for meeting metabolic demands during the period of low food-availability.

The Atlantic deep-sea scallop, *Placopecten magellanicus* (Gmelin), supports an extensive commercial fishery throughout most of its western Atlantic range from the Strait of Belle Isle, Newfoundland, to Cape Hatteras, N.C. (Posgay 1957; Altobello et al. 1977; Serchuk et al. 1979). In spite of its economic importance, the underlying factors which affect reproductive success are poorly understood although the basic reproductive biology is well documented. The annual cycle of gametogenesis has been described both macroscopically (Coe 1945) and microscopically (Naidu 1970). Spawning seasons have been identified throughout most of the scallop's geographical range (Dickie 1955; Posgay and Norman 1958; Naidu 1970; Merrill and Edwards 1976). Larval development has been followed in the laboratory through settlement (Baird 1953; Culliney 1974; Drew 1906) and temperature and salinity effects on development have been investigated (Culliney 1974). The lack of consistent year-class recruitment, however, probably reflects the importance of environmental influences on reproductive success (Dickie 1955; Serchuk et al. 1979).

As an initial step toward a better understanding of reproductive success in any invertebrate species, the relationship between the buildup and utilization of energy reserves and the annual cycle of gametogenesis and spawning should be investigated (Giese and Pearse 1974). Thompson (1977) undertook such an approach using Atlantic deep-sea scallops collected from three populations in southeast Newfoundland. Although his main emphasis was on the seasonal changes in blood chemistry, biochemical analyses for glycogen, lipid, and protein levels were conducted on both gonadal and somatic tissues. Other contributions to an understanding of the energy reserve-reproductive cycle relationship have been made. Naidu (1970) presented gonad wet weight data, broken

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Manuscript accepted April 1981.
FISHERY BULLETIN: VOL. 79, NO. 3, 1981.

down by scallop age, over a 2-yr period, in addition to a histological description of the gametogenic cycle. Seasonal changes in total fat, sterol, and unsaponifiable fat within the adductor muscle have been described by Idler et al. (1964), and six major phospholipids identified from whole-body extracts by Shieh (1968).

The present study was undertaken to identify and localize the major energy reserves of *P. magellanicus*, to follow the levels of these reserves within each identified storage tissue over a 1-yr period, and to monitor the gametogenic cycle histologically.

MATERIALS AND METHODS

Deep-sea scallops were collected by divers at approximately 6-8 wk intervals from natural beds at the mouth of the Damariscotta River, off Farnham Pt., Linekin Neck, Boothbay, Maine, in 10-30 m of water. Deep-sea scallops ranged from 79.8 to 163.0 mm shell height ($\bar{X}$ = 119.0, SD = 17.5 mm, N = 165), although individual size varied considerably within each sample. Animals were transported to the laboratory in chilled seawater and maintained overnight in a running seawater system. Twenty deep-sea scallops (10 of each sex whenever possible) were chosen for subsequent analyses. Shell height was measured for each deep-sea scallop prior to dissection. Wet weights were recorded for total body (exclusive of mantle cavity water), shell, both catch and quick components of the adductor muscle, digestive gland, and "gonadal mass" (defined as all gonadal tissue, overlying epidermis, inclusive connective tissue, and intestinal loop). The contents of the intestinal loop were gently squeezed out prior to weighing. Similarly, the stomach and surrounding digestive gland were split open, and all food material flushed out with seawater. Gastric shield and crystalline style were excluded from digestive gland and gonadal mass wet weights. Tissues were individually frozen and stored at −20° C for subsequent biochemical analyses.

Body Component Indices

Individual soft-body component indices were calculated for catch adductor (CAI), quick adductor (QAI), digestive gland (DGI), and gonadal mass (GMI) according to Giese et al. (1967): body component index = wet weight of body component ÷ total wet body weight. Total wet body weight was determined by subtracting wet shell weight from total wet weight, and therefore includes the weight of extrapallial fluid which would have been lost if body weights were determined following separation of the animal from its valves. Linear regression analysis of body component index values (GMI, DGI, QAI, and CAI) on shell height revealed that all indices were independent of body size within the sampled range. The use of index values for comparisons between samples containing different size distributions of deep-sea scallops was therefore justified.

Histological and Histochemical Monitoring

Following wet weight determinations, a small piece of GMI tissue was fixed in Bouin's fluid for histological examination of gametogenesis. Tissues were later dehydrated, embedded in polyester wax (Steedman 1960), sectioned at 7 μm, and stained in 2% aqueous celestin blue. Gametogenic state was characterized as either early, mid, or late developing, ripe, partially spawned, or spent, based on a shortened version of the nine stages described by Naidu (1970). During early development, gonadal follicles are predominantly empty except for a few layers of spermatocytes or a single layer of oocytes closely oppressed to the follicular wall. In middeveloping follicles, the lumen is more restricted. Oocytes are enlarged in females, whereas in males, spermatids and spermatozoa become increasingly common although spermatocytes are still predominant. The follicular lumen is occluded by mature or maturing spermatozoa and oocytes in late-developing gonads, although immature stages are common toward the periphery of the follicles. In ripe gonads, follicles are tightly packed with mature gametes. Follicles show a progressive loss of ripe gametes as spawning proceeds, ultimately becoming empty when deep-sea scallops are completely spent.

Gametogenic values were assigned to each stage (early developing = 1, middeveloping = 2, late developing = 3, ripe = 4, partially spawned = 2, spent = 0). The mode, median, and range of gametogenic values were used for comparisons between sample dates.

To insure that tissues examined biochemically were sites of major energy reserves, a variety of tissues were fixed and histochemically examined from one or two animals of each sex during each sample period. In addition to the catch and quick

components of the adductor muscle, digestive gland, and gonadal mass, analyses were made on mantle, mantle edge, foot, and kidney tissue. For glycogen staining, tissues were fixed in Rossman's fluid (Humason 1972), embedded as before, and stained with Best carmine (Humason 1972). Control slides were incubated with 1% α-amylase in 0.2 *M* phosphate buffer (pH 7.0) at 40° C for 1 h. Lipid was localized in cryostat-sectioned material, postfixed in 10% calcium-Formalin[5] fixative (Humason 1972), and stained with supersaturated Oil red *O* (Lillie and Fullmer 1976). Control slides were immersed for 10 min in 95% ethanol to remove all lipid.

Biochemical Analysis of Tissues

As a result of the routine histochemical examinations, only adductor muscle, digestive gland, and gonadal mass were chosen for biochemical determinations of lipid and carbohydrate concentrations. No other tissues contained appreciable reserves of either lipid or carbohydrate at any time during the year. Tissues from the 20 deep-sea scallops chosen on each sampling date were pooled by sex into groups of 3-10 animals depending on the size of tissue sample and time of year. The pooled samples were freeze-dried to determine wet:dry weight ratios for each tissue. Subsamples of the dried tissue were used for biochemical analyses. Lipid concentrations were determined gravimetrically after extraction in acetone-isooctane (Peterson et al. 1976). Glycogen levels were determined on each of the four tissues using the glucose-oxidase method as described by Williams and Lutz (1975). All glycogen was first converted to glucose by a 2-h incubation at 55° C in 1% amyloglucosidase (Sigma A-7255). Glucose concentrations were then measured spectrophotometrically following a 30-min incubation at 37° C with a mixture of glucose-oxidase and peroxidase (Sigma Kit 510-A). The results give the combined concentrations of both glucose and glycogen for each tissue, and will hereafter be considered "carbohydrate." Since initial results indicated that wet:dry weight ratios, lipid, and carbohydrate concentrations were not significantly different in the catch and quick components of the adductor muscle (March-April samples), analyses of the smaller catch component was discontinued.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Standard Scallop

In order to account for the influences of animal size on seasonal body changes, body component dry weights, and biochemical constituents were calculated for a "standard scallop" of 120 mm shell height. This height was close to the mean (119.0 mm) and mode (115.2 mm) for the combined yearly samples. Predictive regressions of wet tissue weight (separately for gonadal mass, digestive gland, and quick adductor) on shell height were calculated for each sex within each sample. The resulting regression equations were solved for the standard deep-sea scallop (120 mm shell height). These wet weight values were converted to estimated dry weights of each tissue using the wet:dry weight ratios. By multiplying the estimated dry weights of each tissue by the corresponding concentrations of lipid and carbohydrate, total amount of each energy reserve per tissue was calculated. These energy reserve levels were then converted to caloric equivalents using the conversion factors from Crisp (1971) (carbohydrate = 4.1 kcal/g; lipid = 9.45 kcal/g). Since the calculations for dry weight, lipid, and carbohydrate were based on mean values of pooled tissue samples and regressions of wet tissue weight on shell height, confidence limits could not be estimated for the resulting values. All results have been presented as total amount of each energy reserve per standard animal.

RESULTS

Gametogenic Cycle

During most of the year, deep-sea scallops could easily be sexed by visual examination, due to the characteristic bright pink ovaries and opaque white testes. Histological sections, however, were necessary to determine the sex of spent individuals in the September-January samples. Spent gonads were shrunken, flaccid, and lacked characteristic coloration, instead possessing semitransparent epidermal and connective tissues.

Gametogenesis, as followed histologically, conformed to the description of Naidu (1970). The seasonal gametogenic cycle, based on modal gametogenic values for each sample, is presented in Figure 1. Modal values increased throughout the winter, spring, and into the summer as gametes differentiated and ripened. Spawning was evident in 67% of the males (N = 9) and 64%

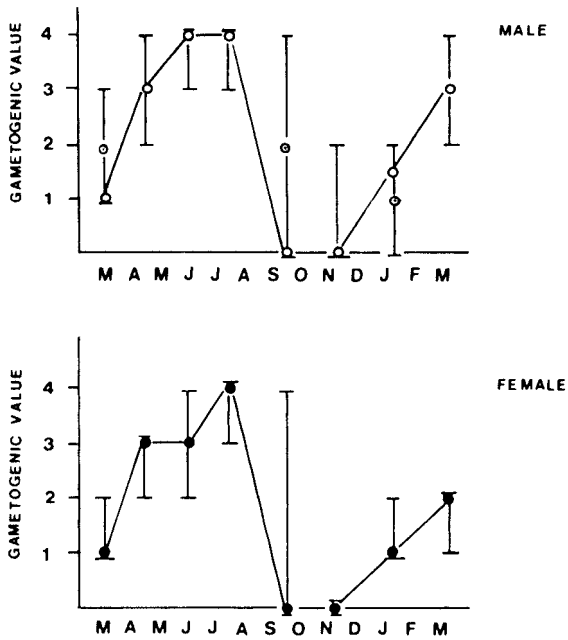

FIGURE 1.—Annual cycle of gametogenesis in *Placopecten magellanicus* based on assessment of histological sections for each sample date, March 1979-March 1980. Modal values of each sample indicated by • for females and ○ for males. Bars = ranges. Median values indicated by ⊙ in cases where median values differ from modal values.

of the females (N = 11) from the 14 September sample, resulting in a marked drop in modal rank. Variability within the population was greatest at this time since ripe, partially spawned, and spent individuals were all present in the population. By 5 November, virtually all deep-sea scallops sampled were spawned out. In January, modal values again rose. Gonial cells were distinguishable in the follicles and characteristic gonadal coloration became evident, although a few individuals showed signs of still being only partially spawned out.

Body Component Indices

Seasonal changes in mean body component indices are plotted in Figure 2. GMI, DGI, QAI, and CAI all varied significantly with time ($P < 0.01$; analysis of covariance: body component index by sample date with scallop height as a cofactor). Similar analyses using raw tissue wet weights also point out significant changes between sampling dates ($P < 0.01$). Since differences between the sexes were not significant for any of

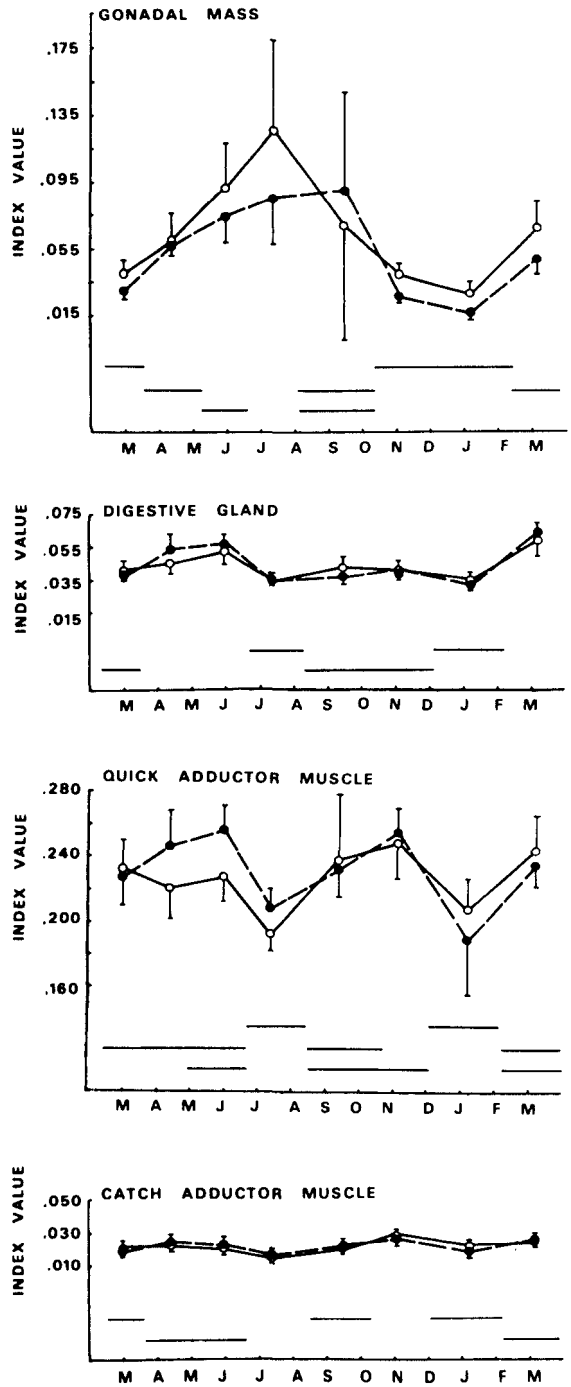

FIGURE 2.—Seasonal fluctuations in soft-body component indices for *Placopecten magellanicus*, March 1979-March 1980. Bars represent 95% confidence intervals; • = female; ○ = male; horizontal lines underscore samples which are not significantly different at the 95% confidence level (male and female data combined for each sample, least significant difference multiple range test).

the indices, data for each sex were combined. Multiple range tests (least significant difference) on the combined data indicated that GMI, DGI, and CAI values all rose in the spring. QAI, CAI, and DGI dropped in July, while GMI continued to rise until spawning in late summer. The September and November samples showed a recovery of QAI, CAI, and DGI, but a drop in GMI, representing a decline in the proportion of body mass attributable to the gonad following spawning. The late fall to early winter period showed a continued decline in all four indices except possibly GMI, with recovery evident by the subsequent March sample. Both GMI and modal gametogenic values (Figure 1) were much higher in the March 1980 sample than for the March sample of the previous year, probably reflecting the mild 1979-80 winter.

Differences in total wet animal weight and total wet body weight between samples were not significant (ANCOVA: $P > 0.05$). Variability of each of these components was too high to discern seasonal trends.

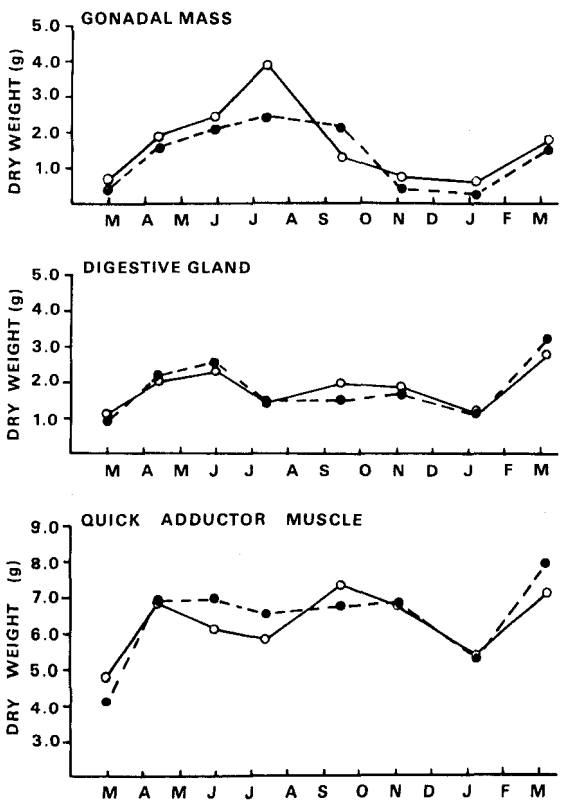

FIGURE 3.—Standard deep-sea scallop (120 mm shell height) annual tissue dry weight fluctuations. • = female; o = male.

Histochemical Localization of Energy Reserves

Appreciable concentrations of energy reserves were detected in only the adductor muscle, digestive gland, and gonadal mass. As indicated by routine histochemical examinations, a shift of energy reserves from these major areas to other tissues did not occur during the study period.

Glycogen was primarily concentrated in the adductor muscle, although significant levels were also seen in the digestive gland and the epithelium of both male and female reproductive ducts during most of the year. Concentrations were highest in the spring and early summer within the adductor muscle, ovary, and testes, but were only high in the spring within the digestive gland. Glycogen concentrations remained very low throughout the year in the mantle, mantle edge, foot, and kidney.

Lipid levels were highest throughout most of the year in the digestive gland, with peak levels in April-May 1979 and March 1980. High concentrations were also found in the ovary, increasing throughout the spring to a maximum in July, declining slightly in September, and dropping precipitously by November as a result of spawning. Significant lipid localization was not observed in any other tissue.

Dry Weight and Biochemical Analyses

Seasonal fluctuations in gonadal mass, digestive gland, and quick adductor muscle dry weights are presented in Figure 3 for standard deep-sea scallops of each sex. Following an initial increase in the weight of all tissues in the spring, gonadal dry weight continued to rise into July, whereas a concomitant decrease occurred in the weight of the adductor muscle and digestive gland. Gonadal dry weight fell throughout the autumn and early winter. The adductor and digestive gland on the other hand, recovered in the autumn to about their springtime levels, but then dropped during the early winter.

Calculated quantities of lipid and carbohydrate in tissues of standard scallops of each sex are shown in Figures 4 and 5. As with dry weights, both reserves showed an initial rise in the spring in all tissues although the rise in carbohydrate in the gonadal mass and digestive gland was slight. The amount of gonadal lipid and carbohydrate continued to increase into midsummer, whereas digestive gland lipid and adductor carbo-

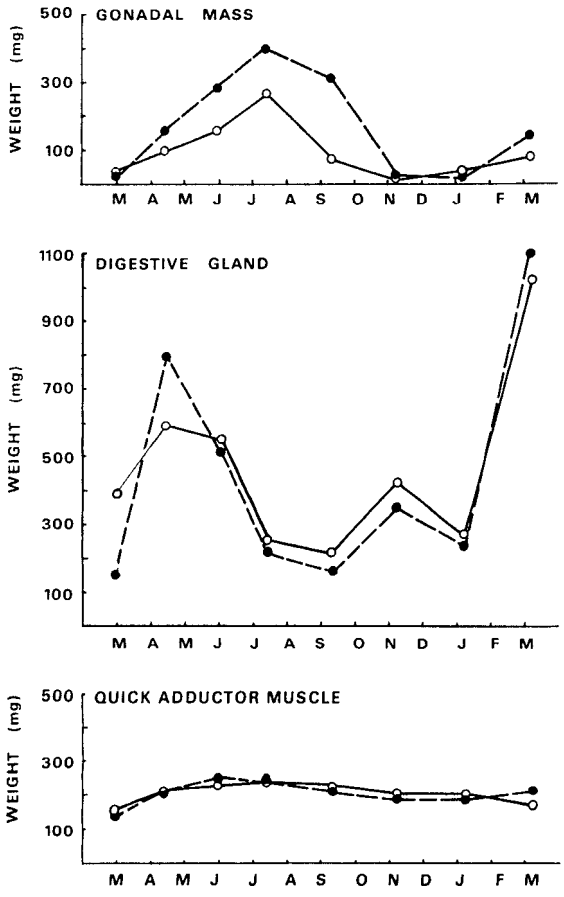

FIGURE 4.—Seasonal changes in tissue lipid content calculated for the standard deep-sea scallop (120 mm shell height). • = female; ○ = male.

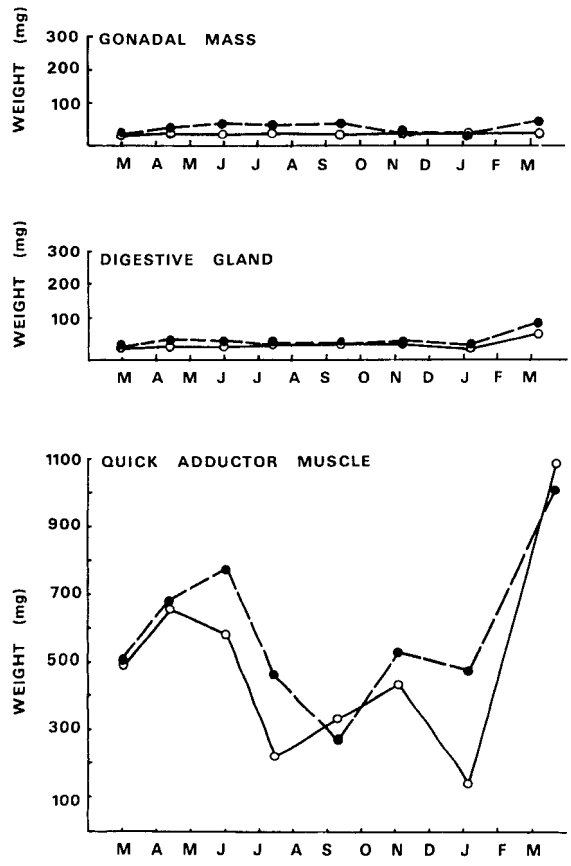

FIGURE 5.—Seasonal changes in tissue carbohydrate content calculated for the standard deep-sea scallop (120 mm shell height). • = female; ○ = male.

hydrate fell from late spring through September. Although present at lower amounts than in the gonadal mass and digestive gland, lipid in the quick component of the adductor muscle rose in the spring-summer and dropped in the autumn-winter.

Changes in caloric equivalents (kilocalories) of energy reserves from each tissue, presented in Figure 6, reflect the changes in lipid storage in both the gonadal mass and digestive gland, and fluctuations of carbohydrate in the quick component of the adductor muscle. Differences in energy reserves between the sexes are not significant, although females tend to show higher levels and greater fluctuations in energy content throughout the year. The drop in gonadal caloric equivalents in mid-September, in addition to the drop in GMI and gonadal dry weight, is indicative of spawning within the population and is corroborated by the histological appearance of the gonads.

DISCUSSION

Of the three tissues which contain appreciable reserves of either lipid or carbohydrate, only digestive gland and adductor muscle may properly be considered "storage organs" (i.e., temporary repositories of energy-rich substances which may later be utilized to meet either metabolic or reproductive demands). Energy-rich substances within the gonad, albeit temporary, are ultimately destined for gamete production and nourishment of the developing larvae. If these substances are completely lost at spawning, as is evident for *P. magellanicus*, they should not be considered as energy reserves for the adult scallop (Giese 1966), even though resorption of gametes by some

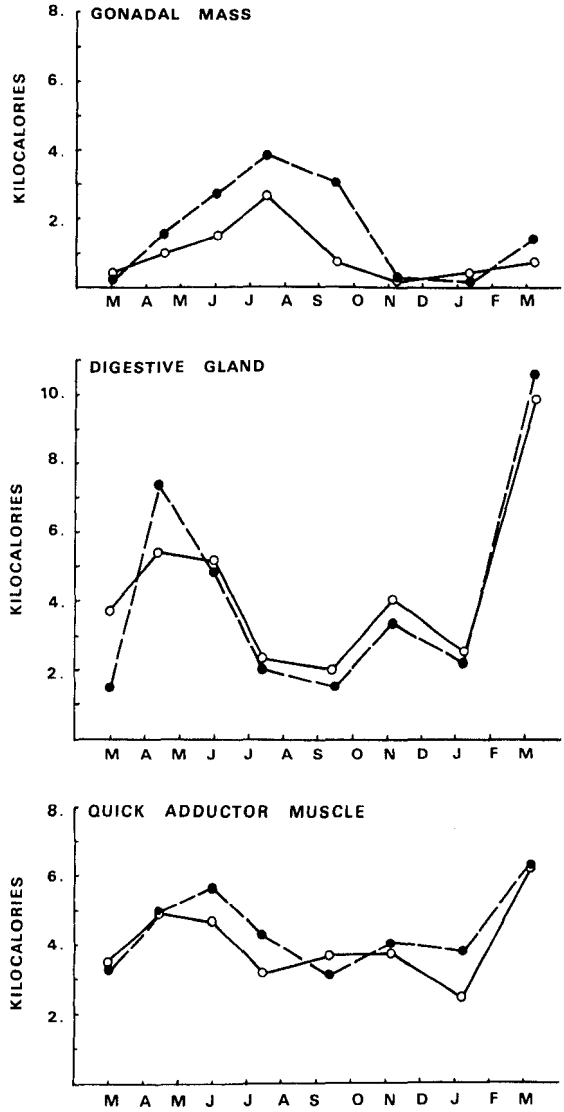

FIGURE 6.—Caloric equivalents (lipid + carbohydrate) for major energy storage tissues of the standard deep-sea scallop (120 mm shell height) over the 1-yr study period. • = female, ○ = male.

pectinids may occur at times of food shortage (Sastry 1966). Furthermore, neither lipid nor carbohydrate accumulates in the gonad immediately following spawning for use as an overwintering reserve (Thompson 1977; this study).

Histochemical tests do not reveal significant quantities of lipid in either the quick or catch components of the adductor muscle, whereas a substantial amount is detected biochemically. Quantities of sterols (e.g., 22-dehydrocholesterol, cholesterol, brassicasterol, and 24-methylenecholesterol) are present in adductor tissue (Idler et al. 1964) in addition to structural lipids. These high melting point lipids do not color with Oil red *O* and other Sudan dyes (Lillie and Fullmer 1976), and, therefore, cannot be localized histochemically. They are, however, readily extracted by the solvents used for gravimetric lipid analysis. When addressing the problem of distinguishing structural from reserve lipid, Giese (1966) has concluded that lipid levels >5.2% dry weight are reserve. Lipid levels in *P. magellanicus* adductor muscle are never high enough (2.3-4.1%) to meet this criterion.

Neither carbohydrate nor lipid concentrations in the quick component of the adductor muscle were significantly different from those in the catch component in the March and April 1979 samples. Analysis of the catch component was therefore discontinued. De Zwaan et al. (1980), however, found higher concentrations (2.5×) of glycogen in the phasic (= quick) than in the catch adductor of *P. magellanicus* sampled in July at a time when glycogen levels were at a peak. As with our samples, no difference in lipid concentrations was observed. Taken together, these results may indicate that both components of the adductor contain approximately the same carbohydrate levels during the winter and early spring, but that the quick component rapidly overbalances the catch adductor in importance as a site of carbohydrate reserves.

Gametogenesis is intimately related to energy-reserve fluctuations in *P. magellanicus*. In January, while gametogenesis has already reached the early-development stage (Figure 1), body component indices (Figure 2), dry weights (Figure 3), and energy reserves (Figures 4, 5) within the gonad, digestive gland and quick component of the adductor muscle have fallen to their lowest values. The initiation of gametogenesis, characterized by increased numbers of gonial cells and an apparent increase in mitotic activity, is first seen in early winter, at a time when energy reserves are declining. This initiation thus appears to be dependent on the energy reserves accumulated the previous season, although food availability data are not available to substantiate this hypothesis. Following the initiation of gametogenesis, storage products begin to accumulate in the digestive gland, adductor muscle, and gonad in the late winter to early spring (Figure 6). At the same time, gametogenesis proceeds into the middevel-

opment stage and gonad size increases. The accumulation of reserves is almost certainly due to spring phytoplankton blooms. Following this general buildup of energy reserves and continued maturation of gametes, a marked shift in the condition of the digestive gland and adductor muscle occurs. From June through July and probably into August, there is a sharp drop in DGI and QAI (Figure 2), lipid levels in the digestive gland (Figure 4), and carbohydrate in both the digestive gland and quick component of the adductor muscle (Figure 5). During this time, gametes are ripening, GMI values reach their peak and lipid generally reaches its highest level in the gonad. The completion of gametogenesis therefore seems largely dependent on energy reserves which were accumulated earlier in the spring.

Gonadal weight, glycogen, and lipid concentrations are inversely related to the weight and energy reserves of somatic tissues in a variety of other pectinids. In queen scallop, *Chlamys opercularis*, lipid content of body tissues declined as gonadal lipid increased (Taylor and Venn 1979). Similarly, inverse relationships have been shown for adductor and gonadal dry weights in *Pecten maximus* by Comely (1974) and digestive gland and gonadal indices in bay scallop, *Argopecten* (= *Aequipecten*) *irradians*, by Sastry (1966, 1970). Sastry (1966) has proposed however that the reciprocal relationship between index values may indicate that nutrients supplied by feeding might be rapidly utilized for growth and development without prior storage. Thus a decline in DGI would not represent a drop in actual digestive gland wet weight. However, direct evidence for the transfer of some quantity of materials from body tissues to the gonad has been demonstrated in *A. irradians* using ^{14}C-leucine (Sastry and Blake 1971), in *C. hericia* using lipid ^{14}C-labeled *Chlorella* extract (Vassallo 1973) and in other bivalves (vide Gabbott 1975; Sastry 1979).

During the spring and summer, the loss of energy stores from the digestive gland and adductor muscle could not have been due solely to the transfer of these substances to the gonad. From 13 April to 13 July, more calories were lost from the quick adductor and digestive gland (male, −4.75 kcal; female, −6.00 kcal) than were gained by the gonadal mass (male, +1.57 kcal; female, +2.27 kcal). The real energy loss was probably greater than indicated by these calculations, since contributions from the catch component of the adductor and other somatic tissues were not included in the calculations. Metabolic demands, due to warmer water temperatures and the completion of gonadal maturation probably accounted for the remainder of the lost energy reserves. The possibility that these reserves were used entirely for metabolic needs, while gonadal maturation depended solely on food intake, seems remote.

Following spawning, the condition of the digestive gland and adductor muscle improves, as evidenced by the increase in QAI, CAI, digestive gland lipid, and quick adductor carbohydrate. Reserves do not reach or exceed their springtime levels, such as occurs in *P. maximus*, (Comely 1974), *C. opercularis* (Taylor and Venn 1979), and *C. septemradiata* (Ansell 1974) populations from the Clyde Sea area. Postspawned *Placopecten magellanicus* from Georges Bank attain total fat levels as high as those reached during the springtime (Idler et al. 1964) whereas *P. magellanicus* from a southeast Newfoundland population (Thompson 1977) do not show postspawning, autumn increases in either carbohydrate, lipid or dry weight within the gonad, or somatic tissue. The autumn recovery pattern in Boothbay scallops appears to be intermediate between the Georges Bank and Newfoundland populations.

Reproduction is dependent to varying degrees on available food levels and energy reserves in different temperate marine bivalves. In *C. opercularis* (Taylor and Venn 1979) and *Pecten maximus* (Comely 1974) for example, energy reserves are utilized for both the initiation of gametogenesis and for subsequent gonadal growth. Reserves are apparently required for both these activities in the intertidal mussel, *Mytilus edulis*, as well (Gabbott 1975). In other bivalves, however, intake of food is necessary for vitellogenesis and gonadal growth and often for the initiation of gametogenesis. Gonadal growth in *A. irradians* cannot occur without feeding, since reserve material from the digestive gland and other body tissues are not adequate to sustain maturation (Sastry 1966, 1968, 1970). However, reserves within the digestive gland may supplement nutritional intake needed for gonadal proliferation (Sastry and Blake 1971). Similarly, in *Crassostrea gigas* and *C. virginica* (Gabbott 1975), gonadal growth is accompanied both by springtime feeding and decreased glycogen content of the tissues. Gonadal growth however is supported directly by springtime feeding in *Chlamys septemradiata* (Ansell 1974), although gametogenesis begins during the

winter months when food levels are low and energy reserves in the adductor are falling. In the southeast Newfoundland population of *Placopecten magellanicus*, the initial rise in gonadal DNA content preceeds the usual springtime phytoplankton bloom, occurring instead during the period when both gonadal and somatic dry tissue weights are at an ebb (Thompson 1977). The initiation of gonadal growth in this Newfoundland population, however, appears to be dependent on available food. From measurements of seasonal rates of respiration, excretion, consumption, and filtration in *P. magellanicus* from Narragansett Bay, Ehinger[6] has concluded that intake of food is necessary to meet the energy demands of reproduction. In the present study, the initiation of gametogenesis is shown to occur at a time when reserves, dry weights, and index values of the digestive gland, adductor, and gonad are all declining. Gonadal growth however occurs concurrently with an early spring replenishment of energy reserves. Final maturation of the gametes although dependent on the transfer of energy reserves per se, ultimately relies on the springtime availability of food for the buildup of these reserves.

ACKNOWLEDGMENTS

We are indebted to D. Shick and C. Crosby, Division of Marine Resources, State of Maine, Boothbay Harbor, for both collection of deep-sea scallops and their continued interest in this project. Thanks are extended to J. Antonellis, K. Gorman, M. Misci, G. Peterson, and D. Wayne for help in sampling and histological preparations. G. Lima and G. Stacey conducted the biochemical determinations. We thank B. B. Collette, N. W. Riser, and A. N. Sastry for critically reviewing the manuscript. Special thanks are given to J. Cusack for cheerfully typing each draft of this paper. Research was supported by DOE contract EE-77-S-02-4580 to the New England Aquarium, Boston.

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