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Size-Specific Fecundity of the Sea Scallop, Placopecten magellanicus, during One Spawning Period in the Mid-Atlantic Resource Area

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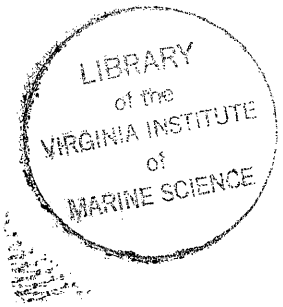
SIZE-SPECIFIC FECUNDITY OF THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*, DURING ONE SPAWNING PERIOD IN THE MID-ATLANTIC RESOURCE AREA



A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

by

Ryan Blaise Carnegie

1994

This thesis is submitted in partial fulfillment of

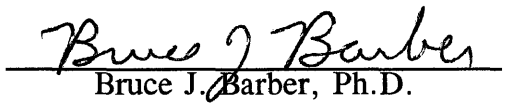
the requirements for the degree of

Master of Arts

Ryan B. Carnegie

Approved, August 1994

William D. DuPaul, Ph.D.
Committee Chairman/Advisor



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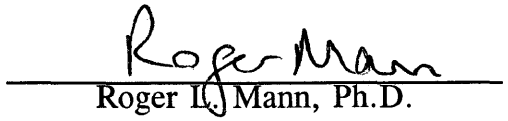

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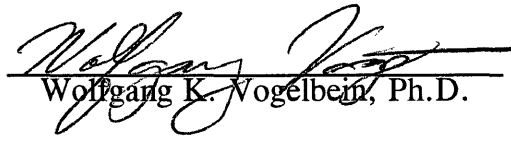

Wolfgang K. Vogelbein, Ph.D.

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Abstract

Knowledge of the size-specific fecundity of *Placopecten magellanicus* is important to managers of the commercial fishery for this species. The objective of this study was to estimate the size-specific fecundity of female sea scallops from the mid-Atlantic resource area during the spring 1993 spawning period for five shell height intervals (40-60mm, 65-75mm, 85-95mm, 105-115mm, and 120-130mm), using direct counts of oocytes suspended in seawater and using morphometric analysis of histological slides of scallop ovaries. The direct counting method involved the rinsing of oocytes from lacerated ovaries, and counting of oocytes in the resulting suspension using a compound microscope (60x mag.) and a Sedgwick-Rafter Cell (with a correction for the percentage of ovary suspended and of suspension sampled). The histologic method entailed estimating volume fractions of mature oocytes by the counting of points of a reticle superimposed over the ovary section (60x mag.). Fecundity in this case was calculated by multiplying the mature oocyte volume fraction by ovary mass and dividing by the mass of a single oocyte.

Fecundity estimates were consistently greater using the histologic method. Both methods, however, found scallops in the two largest size classes (which corresponded with the age groups five and six, respectively) to be considerably more fecund than those in the three smaller size classes (which corresponded with the age groups three, three-plus, and four, respectively). Furthermore, both methods found the commitment to germinal production to increase non-linearly with increasing scallop size (and thus age). These results suggest that scallop stocks that consist primarily of smaller, Age 3 and Age 4 scallops may not be capable of the gamete production necessary for the stocks to be self-sustained. Additionally, the non-linear increase in germinal production with age means that spawning stock biomass (SSB) may be overestimated, particularly in stocks consisting primarily of younger scallops. Since SSB is used to define appropriate levels of fishing effort, the scallop resource may be overexploited.

SIZE-SPECIFIC FECUNDITY OF THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*, DURING ONE SPAWNING PERIOD IN THE MID-ATLANTIC RESOURCE AREA

Introduction

The importance of reproductive biology as a component of management plans for marine fisheries has, in recent years, been firmly established. Annual gametogenic cycles of the commercially-important sea scallop, *Placopecten magellanicus* (Gmelin 1791), have received particular attention (Naidu 1970; Thompson 1977; MacDonald and Thompson 1986; Beninger 1987; Langton et al. 1987; Barber et al. 1988; MacDonald and Thompson 1988; DuPaul et al. 1989; Schmitzer 1990; Kirkley and DuPaul 1991; Schmitzer et al. 1991). Seasonal changes in body component indices relating to gametogenesis have been noted and used to help shape the management plan for this species.

As a case in point, the Sea Scallop Fishery Management Plan (SSFMP) originally managed this fishery in part by requiring vessels shucking scallops at sea to maintain at maximum a 30 meats per pound limit year-round (New England Fisheries Management Council 1982). Amendment 2 to the SSFMP (NEFMC 1987) adjusted this limit to 33 meats per pound during peak autumn reproductive months to compensate for a decrease in adductor muscle mass with increased gametogenic development (Kirkley and DuPaul 1989).

The question of how the local reproductive biology of *P. magellanicus* relates to its population biology over its wider geographical range is

important. Significant differences in growth and reproduction over varying latitudes and depths have been noted for *P. magellanicus* as well as for another pectinid, *Argopecten irradians* (Sastry 1970). These functions are closely related to spatially-varying environmental conditions such as temperature and food supply (Sastry 1968; MacDonald and Thompson 1986; Shumway et al. 1987). Studies using *P. magellanicus* have found not only differing growth functions over varying depths (MacDonald and Thompson 1985a; Schick et al. 1988) and latitudes (MacDonald and Thompson 1988), but spawning patterns that vary greatly in timing and magnitude (MacDonald and Thompson 1985b; Barber et al. 1988; MacDonald and Thompson 1988; DuPaul et al. 1989; Kirkley and DuPaul 1991). While the existing SSFMP governs all of the sea scallop resource areas in United States waters, the question remains whether all subpopulations of *P. magellanicus* are equally important in terms of maintenance of the population as a whole. Barber et al. (1988) noted that one deepwater sea scallop subpopulation in the Gulf of Maine exhibited such low fecundities that the likelihood of its being self-sustaining would be quite low.

This study addresses the size-specific fecundity of *P. magellanicus* in the mid-Atlantic resource area. Prior fecundity determinations for *P. magellanicus* have used the regressions of ovary mass on shell height (defined as the dorsal to ventral distance from the hinge to the outer shell

margin) at times of maximum and minimum ovary ripeness, with the loss of mass assumed to represent spawned gametes. The difference between these two functions divided by the calculated mass of a single egg would give a standardized value for fecundity for each shell height (Langton et al. 1987; Schmitzer 1990; Schmitzer et al. 1991). Cox (1988), working with *Crassostrea virginica*, made direct fecundity estimations by stripping oocytes from specimens using a blender. The suspension formed was filtered through 90 and 53 μm mesh, and oocytes in subsamples drawn from the suspension were counted in a Sedgwick-Rafter Cell using a compound microscope. Preliminary investigations have shown that such direct estimations are possible with *P. magellanicus*, though stripping in a blender resulted in very low yields of intact oocytes, as most oocytes were lysed during preparation of the suspension (Carnegie, personal observation). A better method is to lacerate the ovary and rinse the oocytes into suspension, obtaining pre- and post-laceration mass estimates of the ovary section. Additionally, the discrete nature of *P. magellanicus* ovaries and the random distribution of follicles and oocytes within the tissue (Robinson et al. 1981; MacDonald and Thompson 1985b, 1986) have made effective morphometric analysis possible. Weibel et al. (1966) noted that if structures are known to be randomly distributed in a three-dimensional space, it is permissible to extrapolate from area fractions (obtained by counting points of a grid superimposed on a thin two-dimensional

histological slide) to a three-dimensional volume fraction. Analysis of the relationships between volume fractions and ovary masses versus shell height has provided additional information on size-specific reproductive output, in this case not in terms of numbers of oocytes but rather in terms of the percentage of ovary mass occupied by material to be spawned.

Information concerning the size-specific fecundity of sea scallops is of clear importance to the management of the scallop fishery because it would affect the calculation of spawning stock biomass (SSB). SSB is defined as the total weight of all sexually mature scallops in the population, and a SSB level of <5% of maximum spawning potential (MSP, undefined in the SSFMP, but presumably the spawning potential of the scallop population if it were not commercially exploited) serves as the definition of overfishing of the scallop resource (NEFMC 1993). SSB would be overestimated if smaller scallops were not capable of producing the same number of oocytes per unit of biomass as larger scallops (i.e. sea scallop fecundity were characterized by non-linear size-specificity). Excess harvesting of the sea scallop resource would result, since SSB estimations are used to establish levels of fishing effort (NEFMC 1993).

Resource overexploitation caused by overestimations of SSB would be exacerbated if the exploited populations consisted primarily of smaller scallops. A recent survey showed that most mid-Atlantic sea scallops were 50-70mm in shell height (National Marine Fisheries Service 1993); these

primarily represented the then-Age 3 1990 year class. Recent observations questioned the importance of these Age 3 scallops to the maintenance of the natural scallop populations. McGarvey et al. (1993), in a stock-recruitment analysis, found correlation evidence that 3- and 4-yr-old scallops on Georges Bank "may not contribute measurably to recruitment," and suggested that this observation may have reflected a paucity of viable spawn produced by younger (<105mm) scallops. Amendment #4 to the SSFMP (NEFMC 1993) states that "most sea scallops become sexually mature by the spring of their third year, but these small scallops may not produce many eggs." The question of size-specific fecundity of the sea scallop is thus an important one for management, particularly considering the current predominance of 3- and 4-yr-old scallops in mid-Atlantic stocks (Northeast Fisheries Science Center 1993).

While the current SSFMP does not account for size-specific fecundity in calculating sea scallop SSB, adjustments to the SSFMP to account for size-specific fecundity would not be without precedent. Regulations governing local striped bass (*Morone saxatalis*) fisheries in the eastern U.S.A. have in the last decade typically included maximum size limits and area restrictions, measures meant to protect large, gravid females (Atlantic States Marine Fisheries Commission 1990). These large females, whose egg production vastly exceeds egg production in smaller individuals, congregate in the early spring in major eastern rivers, and are extremely

vulnerable to intense commercial fishing pressure at this time. Increases in indices of abundance of juvenile striped bass in the Chesapeake Bay appear to indicate that the above and other management regulations (notably moratoriums) have been effective in increasing the striped bass population levels (ASMFC 1993).

The lack of information concerning the age group-specific fecundity of sea scallops in the mid-Atlantic precludes the development of an amendment to the SSFMP concerned with protecting certain age groups of the spawning stock. The objectives of this study were to expand the knowledge of the size-specific fecundity of scallops in this region by directly estimating fecundity in two ways, using direct counts of suspended oocytes, and using morphometric analysis of histological slides of scallop ovaries, and to relate the results to the age group composition of natural mid-Atlantic sea scallop populations.

Literature Review

The sea scallop, *Placopecten magellanicus* (Gmelin, 1791), is a large, epibenthic, lamellibranch bivalve mollusc of the continental shelf of the western North Atlantic Ocean. Occurring from Strait of Belle Isle, Newfoundland, Canada, to the United States' Cape Hatteras, North Carolina, *P. magellanicus* supports a lucrative commercial fishery almost everywhere it is found. Commercial landings in the United States in 1992 of 33.5 million pounds of the marketable adductor muscle, worth 162.6 million dollars, were reported (NOAA 1993a), making the commercial sea scallop fishery the United States' fifth most valuable commercial fishery and the East Coast's first, ahead of the fishery for the American lobster.

P. magellanicus has been the subject of numerous scientific investigations in recent years because of its economic importance. Early studies concerning *P. magellanicus* examined fishery-related topics such as abundance fluctuations (e.g. Dickie 1953,1955) and viability as a resource (e.g. Posgay 1950,1953,1957). Naidu (1970), however, examined the histology of the gonads over the entire gametogenic cycle. The use of histological methods and an interest in the gametogenic and reproductive cycles of *P. magellanicus* has been the focus of much of the literature regarding this species subsequent to Naidu (1970). Thompson (1977) investigated seasonal biochemical changes in Newfoundland *P.*

magellanicus specimens; Beninger (1987) qualitatively and quantitatively studied the gametogenic cycle in Bay of Fundy specimens; and Langton et al. (1987) investigated age-specific fecundity and reproductive effort in *P. magellanicus* specimens from the Gulf of Maine.

Much of the sea scallop research of the last decade has focused on local and regional life history patterns. MacDonald and Thompson (1985a) examined life history differences in sea scallops over varying latitudes and depths (presumably relating to differences in temperature and food availability (Sastry 1968)), with gametogenesis a major focus. MacDonald and Thompson (1985b) found that shallow-water *P. magellanicus* specimens in Newfoundland tended to show "greater somatic growth and reproductive output" than their deeper-water counterparts, owing perhaps to "qualitative differences in ration (e.g. fatty acids, amino acids between depths and sites)." MacDonald and Thompson (1986) found that while mean egg size was consistent between shallow- and deep-water populations, gamete output per unit ingested ration of food was higher in shallow-water populations, as was "fecundity and the rate of gamete development." Similarly, Barber et al. (1988) found that while egg size was consistent between shallow- and deep-water populations, specimens from deep-water populations exhibited lower fecundity, and noted that "when faced with the apparently less favorable conditions associated with increasing depth, the strategy of *P. magellanicus* is to produce fewer eggs

without sacrificing egg size and potential larval survival." MacDonald and Thompson (1988) found that *P. magellanicus* from lower latitudes experienced a shift in emphasis from growth to reproduction at an earlier age, were capable of greater total production, were more fecund, and experienced reduced longevity.

While *P. magellanicus* is found at shallow depths (to 2m) as well as in deeper waters in the northern part of its range, near its southern distributional limit it is always found at greater depths (to 200m) because it is intolerant of warmer inshore waters (Posgay and Norman 1958; MacKenzie 1979). Results of the many studies based on *P. magellanicus* in the Gulf of Maine and the Canadian Maritime Provinces may not necessarily be applicable to the populations near the scallop's southern distributional limit because of possible latitudinal and depth-related differences. Several studies (DuPaul et al. 1989, Kirkley and DuPaul 1991, Schmitzer et al. 1991) have investigated spawning behavior and gametogenesis in mid-Atlantic populations of *P. magellanicus* and found that behavior differed from that in northern populations. The most striking difference was the presence of a semiannual spawning period, with one spawn dominant (spring) and one erratic or sometimes absent (fall) (DuPaul et al. 1989; Kirkley and DuPaul 1991; Schmitzer et al. 1991).

Ovary Internal Structure and Oogenesis

Placopecten magellanicus, unlike most other members of the Pectinidae, is not hermaphroditic, although Naidu (1970) and Worms and Davidson (1986) report low prevalences (1.3 and 1.7 percent, respectively) of hermaphroditism. The spermatogenic cycle has been documented in the literature (summarized in Beninger and Le Pennec 1991) and will not be addressed in this study. The assumptions made in this study are that sperm are present in excess, and that males and females at a given location spawn synchronously.

The ovary of *P. magellanicus* is a crescent-shaped organ located anterior to the adductor muscle, and is composed primarily of numerous "acini" (Beninger and Le Pennec 1991) or "alveoli" (Naidu 1970). These lobules are bounded by germ cells which give rise to primary oogonia, and open into a system of ciliated tubules or gonoducts (Naidu 1970; Beninger and Le Pennec 1991) that "eventually join up and open into the kidney." "A loop of the alimentary canal passes through" the ovary, entering and leaving the ovary just posterior to the foot at the dorsal extreme of the ovary and making a long circuit within the ovary (Naidu 1970).

Oogenesis begins with a premeiotic stage in which cells produce primary oogonia that divide mitotically to form secondary oogonia. These oogonia begin the next stage, previtellogenesis, with their entry into the

first meiotic prophase. The oocytes now pass through the leptotene, zygotene-pachytene, and diplotene stages of prophase. The third, vitellogenic stage of oogenesis begins as the acinar auxiliary cells (which "probably play a trophic role for the vitellogenic oocyte" (Dorange and Le Pennec 1989)) migrate from the acinar walls, establishing "an intimate contact with the developing oocytes (Beninger and Le Pennec 1991)."

In vitellogenesis the oocytes become pedunculated as nutrients, especially lipovitellin, accumulate within the cells. As vitellogenesis nears an end, the oocytes detach from the auxiliary cells. Oocyte atresia, if it occurs, begins at this point (Beninger and Le Pennec 1991). Otherwise, the mature oocytes are evacuated from the acini in a spawning event.

While oocyte atresia is poorly documented for *P. magellanicus*, it is a common occurrence within the Mollusca. Atresia in *Pecten maximus* has been recently addressed in the literature. Lubet et al. (1987) suggest that atresia is a common component of the gametogenic cycle of *P. maximus*, with resorbed material recycled in the production of future generations of oocytes. Dorange and Le Pennec (1989) note in an ultrastructural study of the ovaries of *P. maximus* that atresia of an oocyte progresses from a degeneration of the rough endoplasmic reticulum (with a resulting vacuolation of the ooplasm), mitochondria, and nucleus, to an increase in the perivitelline space, disintegration of the cytoplasmic membrane, and glycogen accumulation at the oocyte periphery and in the vitelline coat.

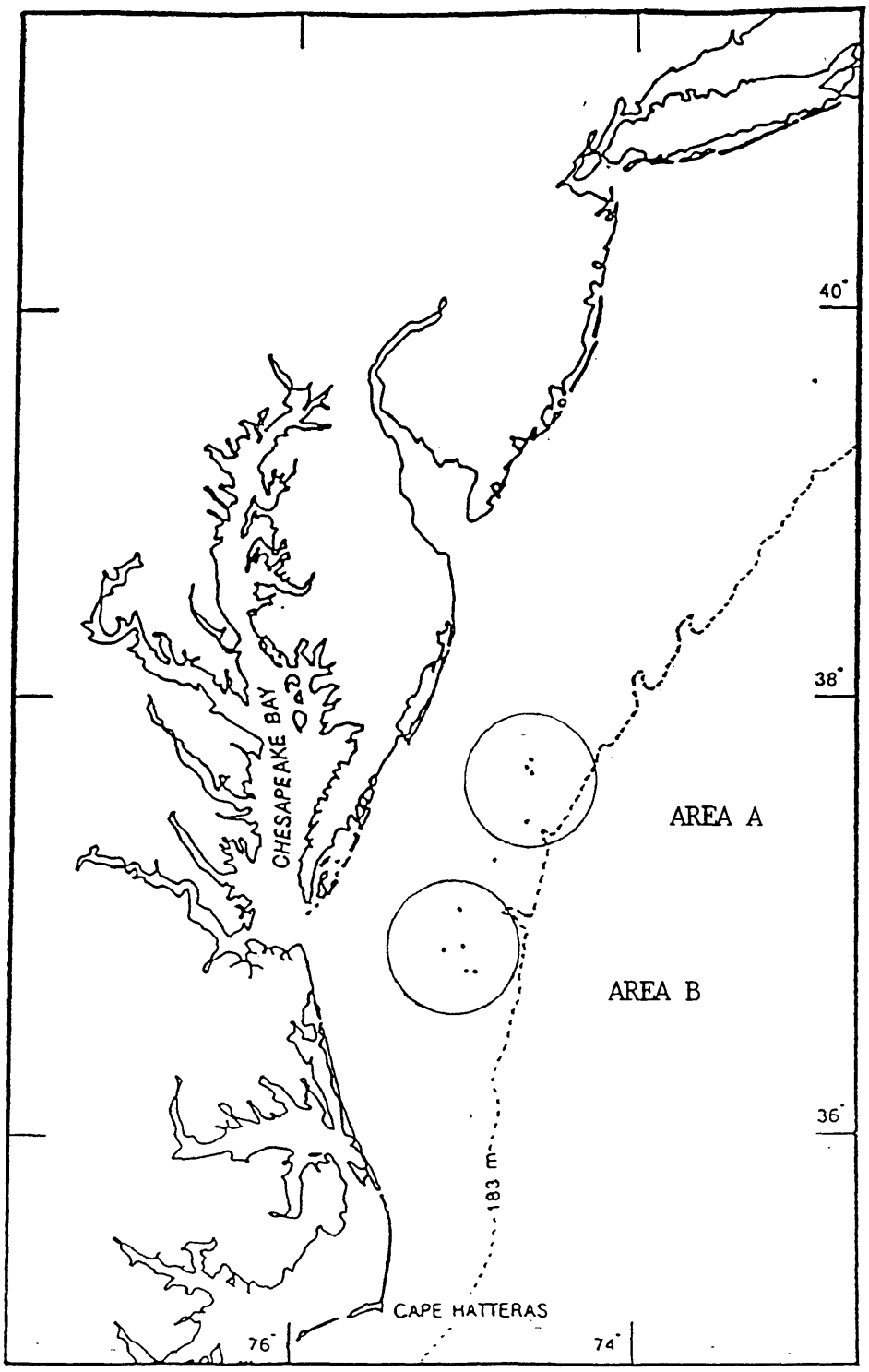
The vitelline coat ultimately breaks down, releasing the nuclei and ooplasmic contents into the acinar lumen. The authors note that "cells which have the same ultrastructural characteristics as macrophagic haemocytes are frequently observed among the remains of the lytic oocytes, in the acini, and at the junction between the gonoducts and the acini," and speculate that these probably are macrophagic haemocytes which likely play a role in resorption.

Materials and Methods

Samples of 100-200 *Placopecten magellanicus* specimens were obtained on a frequent (1-2 per week) basis from commercial scallop vessels. Ovary ripeness of specimens was macroscopically monitored, shell heights (mm) and gonad wet masses (g) were determined for all specimens, and latitude and longitude coordinates of the sample locations were recorded. When the samples began to contain specimens of nearly maximal ovary ripeness, females were retained. Twelve samples were collected between March 22 and April 18, 1993. The first four of these were collected on March 22 during a trip by the author aboard a commercial scallop vessel; the remainder were brought to port by commercial fishermen. Spatial and temporal proximity of the commercial samples allowed grouping into two areas. Area A was located at the latitude of Chincoteague, VA, at a depth of 55-60m, and samples from this area were collected between March 22 and March 28. Area B was located east of the mouth of the Chesapeake Bay at a depth of 37-48m; samples from this area were collected between March 29 and April 9. Additional samples were collected on March 31 (Latitude 39°40', 68m depth), April 5 (Latitude 38°30', 40m depth), and April 18 (Latitude 37°15', 46m depth) (Figure 1).

The female scallops separated from these commercial samples in the laboratory were retained on ice. Each scallop belonged to one of five size

Figure 1. Collection locations of *P. magellanicus* samples.



classes: 40-60mm, 65-75mm, 85-95mm, 105-115mm, and 120-130mm. These size classes correspond with the age groups 3, 3+, 4, 5, and 6, respectively. Processing of each specimen was completed within 100 hours from the time of harvest. The left or upper valve was removed and the dorsal to ventral distance from the hinge to the valve edge was measured on a measuring board to the nearest 1.0mm. The ovary was resected and (after removal of the foot and crystalline style, and rinsing off of debris) weighed to the nearest 0.1g. Three sections were haphazardly selected and removed from the ovary using a single-edged razor blade. The first section was weighed and placed in a plastic zip-loc bag for dry weight determination (to 0.1g after drying to constant weight at 90°C) to allow a wet:dry mass conversion. The second section was weighed and placed in modified Karnovsky's fixative (1.25% glutaraldehyde, 2.0% paraformaldehyde in 0.1M phosphate buffer at pH=7.4; Vogelbein, personal communication) and processed for high resolution light microscopy (HRLM) and quantitative analysis (Table 1). The third section was weighed and then lacerated using a razor blade. Material exuding from these lacerations was rinsed gently, using a wash bottle containing artificial sea water (salinity 34 ppt), to form a suspension of known volume. After rinsing, the ovary section was blotted dry to remove excess water and reweighed to establish the approximate mass of matter in the suspension.

Table 1: Tissue Processing Protocol

Fixation: 1.25% glutaraldehyde and 2.0% paraformaldehyde in 0.1M phosphate buffer (pH = 7.4), for 18-24 hrs, at 4°C.

Buffer Wash: 0.1M phosphate buffer, four 30 min. rinses at 4°C.

Dehydration: Ethyl alcohol (EtOH) at room temperature: two rinses of 45 min. each with 50%, 70%, and 80% EtOH; one rinse overnight with 95% EtOH and one for 30 min. the next day at 95% EtOH.

Infiltration: LKB Historesin Embedding Kit, consisting of a basic resin of glycol methacrylate, a benzoyl peroxide activator, and a barbituric acid hardener:
- 1:1 resin + activator: 95% EtOH, 3 hrs, room temperature
- 100% resin + activator, overnight, 4°C
- 100% resin + activator, 3 hrs, room temperature.

Embedding: Resin + activator + hardener; allowed to polymerize for 3 hrs at room temperature.

Sectioning: 3.0μm sections cut using Ralph glass knives on a Reichert Supercut retracting microtome.

Staining: Harris' Hematoxylin and Eosin-Phloxine, at room temperature:
- Harris' Hematoxylin, 2 hrs
- Running tap water, 5 min.
- 0.25% HCl in 70% EtOH), 2 dips
- Running tap water, 5 min.
- Saturated lithium carbonate solution (aq), 2 min.
- Running tap water, 5 min.
- Eosin-Phloxine, 20 min.
- 95% EtOH, 2 dips
- 95% EtOH, 2 dips
- 100% EtOH, 3 min.
- 100% EtOH, 3 min.
- Air dry, cover slip.

Three 1.0ml aliquots were drawn from the suspension. Oocytes in each of these were counted in a Sedgwick-Rafter Cell using a compound microscope at 60x magnification. Fecundity was calculated using the equation:

$$F = NxVxM_T/M_S,$$

where F was fecundity, N was the mean number of oocytes counted per ml in the suspension, V was the total suspension volume, M_T was the total mass of the ovary, and M_S was the mass of matter in the suspension (modified from Cox 1988).

Morphometric analysis (N = 53, all belonging to samples from Area A) was performed using histologic sections of plastic-embedded tissues that were 3.0μm in thickness and a compound microscope at 60x magnification. For each slide, each representing one specimen, volume fractions of mature and atretic oocytes (no developing oocytes were observed) and of other ovarian or alimentary structures (epithelium, connective tissue, muscle tissue, alimentary canal, gonoducts, and lumen spaces) were determined using the point-counting technique described by Weibel et al. (1966) and used previously by Schmitzer (1990). A reticle of intersecting lines forming 64 points was superimposed over the image of the tissue section, and each point was determined to overlay a certain ovary component. Volume fractions of were calculated for five haphazardly-selected fields of each tissue section, and an average volume fraction was

obtained for each component and specimen. The use of volume fractions enabled fecundity to be estimated by a second method. The size-specific fecundity trends observed using the oocyte counting method were validated using the equation:

$$F = OWMxVF_{MO}/1.6x10^{-7},$$

where F was fecundity, OWM was ovary wet mass (g), VF_{MO} was the mean mature oocyte volume fraction, and $1.6x10^{-7}$g was the wet mass of a single oocyte (Langton et al. 1987).

The relationships among fecundity, ovary mass, and shell height were explored using regression analysis. A simple $y_i = \alpha + \beta x_i + \mu$ function was used to characterize the relationships between fecundity and ovary wet mass, volume fractions and ovary wet mass, and volume fractions and shell height. The function $y_i = \alpha x_i^{\beta 1} e^{\beta 2 x i} e^{\mu}$ was used to describe the relationships between ovary wet mass and shell height and between fecundity and shell height. This function was chosen because while shell height is a linear function, ovary mass and fecundity are cubic and relate to ovary volumes. The function $\ln(y_i) = \alpha + \beta \ln(x_i)$ was selected to characterize the relationships between the combined volume fraction of mature and atretic oocytes (VF_{MO+AO}) and shell height and between VF_{MO+AO} and ovary wet mass, not because of *a priori* knowledge about these relationships, but rather because this function provided a better fit to the data than would a simple linear function.

Results

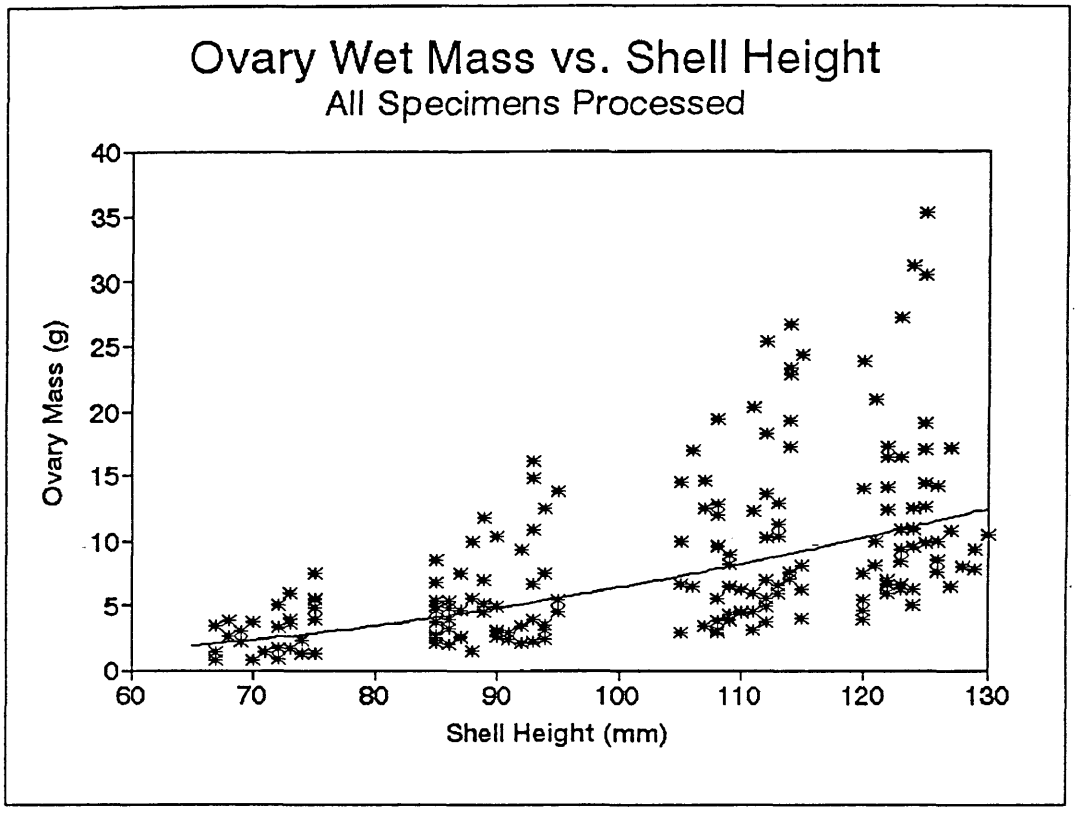
Summary statistics (sample means and standard deviations for shell height, ovary wet mass, and fecundity) for those specimens where fecundity was estimated by the counting of suspended oocytes are presented in Table 2. Data are pooled by sample and shell height interval. Ovary mass and fecundity increased with increasing shell height, a trend particularly pronounced in those samples pooled into Area B. In this area, mean values for ovary wet mass and fecundity for the 120-130mm size class were 21.6g and 7,800,000 oocytes, 5.4 and 17.8 times, respectively, the values for the 65-75mm size class. In Area A, however, ovary wet mass and fecundity for 120-130mm specimens reached mean values of 8.0g and 1,500,000 oocytes, respectively. A Chow test (Maddala 1977) was used to test the stability of the coefficients of the regression equations for fecundity on shell height for these two areas. This test proved the fecundity differences between areas to be significant at the $\alpha = 0.05$ level.

Despite the large degree of variability in ovary mass and fecundity between and within samples and shell height intervals, representations of these data graphically and using regression analysis (with compensations for heteroscadasticity, where necessary, following Wesolowsky (1976)) illustrate some trends. Ovary mass increased with increasing shell height (Figure 2). The variability in ovary mass for a given shell height, however,

Table 2. Summary statistics for all samples processed by the method of directly counting suspended oocytes. Included are, by size class (1 = 65-75mm, 2 = 85-95mm, 3 = 105-115mm, 4 = 120-130-mm), the number of specimens of *P. magellanicus* processed (N), and sample means and standard deviations for shell height (mm), ovary wet mass (g), and fecundity. Data are pooled into Areas A and B according to the geographical and temporal proximity of the commercial samples from which the scallops were obtained. The data under the category "Overall" reflect scallops included in samples A and B as well as those in the three commercial samples not pooled with the others.

Area	Size Class, N	Shell Height Mean+/-St.Dev.	Ovary Wet Mass Mean+/-St.Dev.	Fecundity Mean+/-St.Dev.
A	1, 4	72.5+/-1.0	1.8+/-1.1	9.2×10^{4}+/-1.8×10^{5}
A	2, 14	89.4+/-3.1	3.1+/-1.0	1.1×10^{5}+/-1.0×10^{5}
A	3, 21	109.9+/-2.5	5.3+/-1.9	3.0×10^{5}+/-5.3×10^{5}
A	4, 23	123.5+/-2.8	8.0+/-3.1	1.5×10^{6}+/-3.7×10^{6}
B	1, 17	72.1+/-3.0	4.0+/-1.6	4.4×10^{5}+/-5.2×10^{5}
B	2, 22	89.0+/-3.4	8.4+/-3.6	2.1×10^{6}+/-2.5×10^{6}
B	3, 26	110.3+/-3.3	15.3+/-6.0	4.6×10^{6}+/-3.6×10^{6}
B	4, 10	123.4+/-2.0	21.6+/-9.7	7.8×10^{6}+/-9.4×10^{6}
Overall	1, 27	71.8+/-2.8	3.1+/-1.8	2.9×10^{5}+/-4.6×10^{5}
Overall	2, 46	89.4+/-3.4	5.5+/-3.6	1.0×10^{6}+/-1.9×10^{6}
Overall	3, 56	110.4+/-3.0	10.1+/-6.6	2.4×10^{6}+/-3.3×10^{6}
Overall	4, 44	123.7+/-2.5	12.3+/-7.2	3.0×10^{6}+/-5.5×10^{6}

Figure 2. Regression of ovary wet mass (OWM) on shell height (SH), for all *P. magellanicus* specimens processed by the oocyte counting method (N=173). The regression equation is: ln(OWM)= -14+3.7xln(SH)-0.01xSH ($p<0.0005$; $R^2=43.9\%$; t-ratios $((m-\mu)/(s/n^{0.5}))$: $\alpha=-1.46$, $\beta_1=1.36$, $\beta_2=-0.36$ (170 degrees of freedom)).



led to even greater variability in estimates of size-specific fecundity (Figure 3), as fecundity was a function of ovary mass and each value of ovary mass was associated with its own distribution of calculated fecundity values. As would be expected, ovary mass was a better indicator of fecundity than was shell height (Figure 4).

The increase in fecundity with increasing scallop size was not explained solely by the tendency of larger scallops to have larger ovaries, but also by an increase in the concentration of oocytes within the ovary with increasing scallop size. The mean number of oocytes counted per gram of ovary mass increased with increasing shell height (Figure 5).

Histological evaluation (the summary statistics (sample means and standard deviations for shell height, mature oocyte volume fraction, atretic oocyte volume fraction, and fecundity) for which are presented in Table 3) of 53 ovaries found all to be at or approaching peak maturity. There was no evidence (such as oocytes having been evacuated from the follicles, or the presence of oocytes in gonoducts) in any section examined that a spawning event had begun. No discernible relationship was found between fecundity and the volume fractions of mature or atretic oocytes or of non-oocyte ovary components. The volume fraction of mature oocytes was similarly unrelated to shell height or ovary wet mass. The combined volume fractions of mature and atretic oocytes, however, did increase with increasing shell height (Figure 6) and ovary wet mass (Figure 7). Caution

Figure 3. Regression of fecundity (FEC) on shell height (SH), for all *P. magellanicus* specimens processed by the oocyte counting method (N=173). A semilog plot is used. The regression equation is: $\ln(FEC) = -37 + 13x\ln(SH) - 0.09xSH$ ($p < 0.0005$; $R^2 = 12.8\%$; t-ratios: $\alpha = -1.01$, $\beta_1 = 1.22$, $\beta_2 = -0.80$ (170 d.f.)).

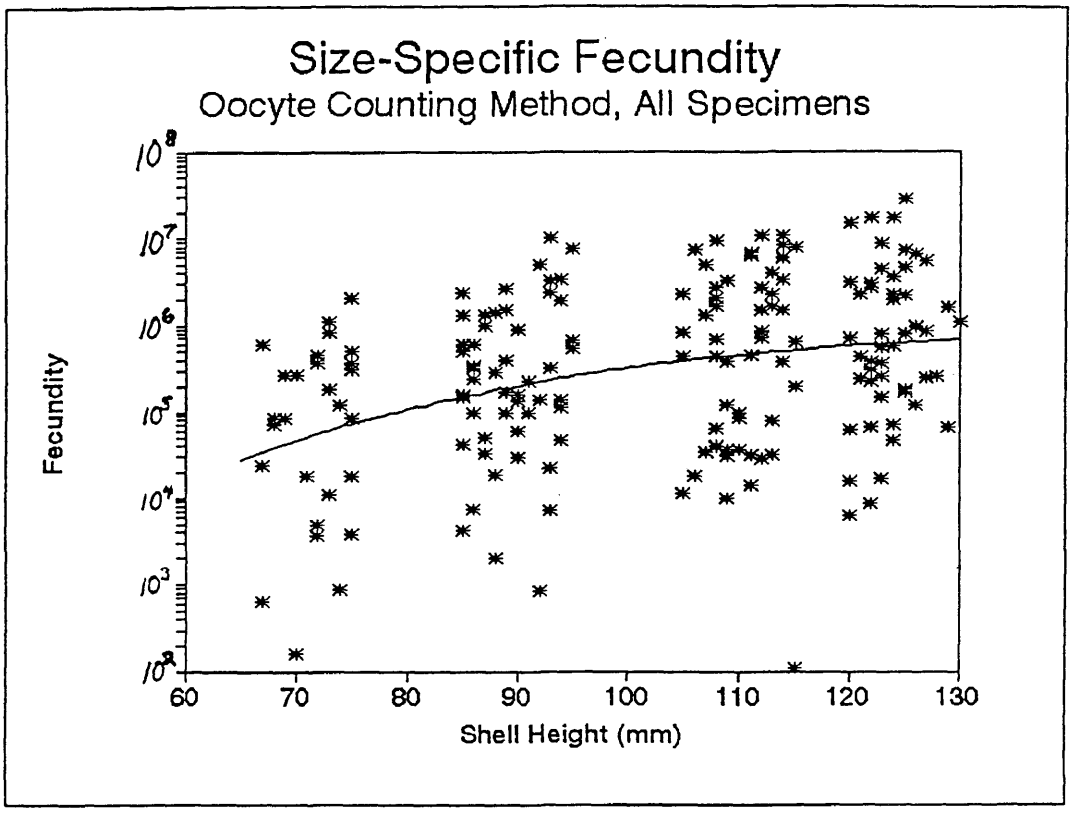


Figure 4. Regression of fecundity (FEC) on ovary wet mass (OWM), with a compensation made for heteroscadasticity, for all *P. magellanicus* specimens processed by the oocyte counting method (N = 173). The regression equation is: $FEC = 2.1 \times 10^5 (OWM) - 3.6 \times 10^5$ ($p < 0.0005$; $R^2 = 18.5\%$; t-ratios: $\alpha = 12.70$, $\beta = -6.45$ (171 d.f.)).

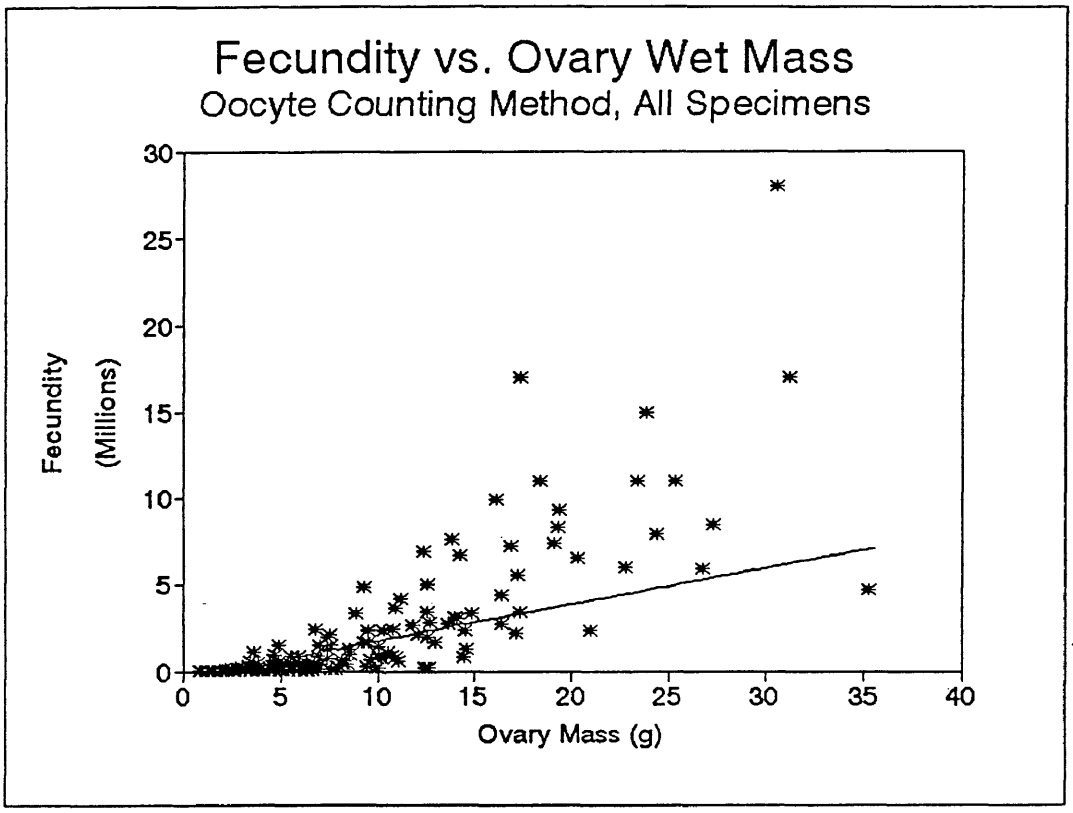


Figure 5. Regression of the mean number of oocytes counted (per g of ovary mass suspended) on shell height (SH), for all *P. magellanicus* specimens processed by the oocyte counting method (N = 173). The regression equation is: Oocytes/g = $-1.5 \times 10^5 + 2.0 \times 10^3$(SH) ($p = 0.021$; $R^2 = 6.8\%$; t-ratios: $\alpha = -1.64$, $\beta = 2.36$ (171 d.f.)).

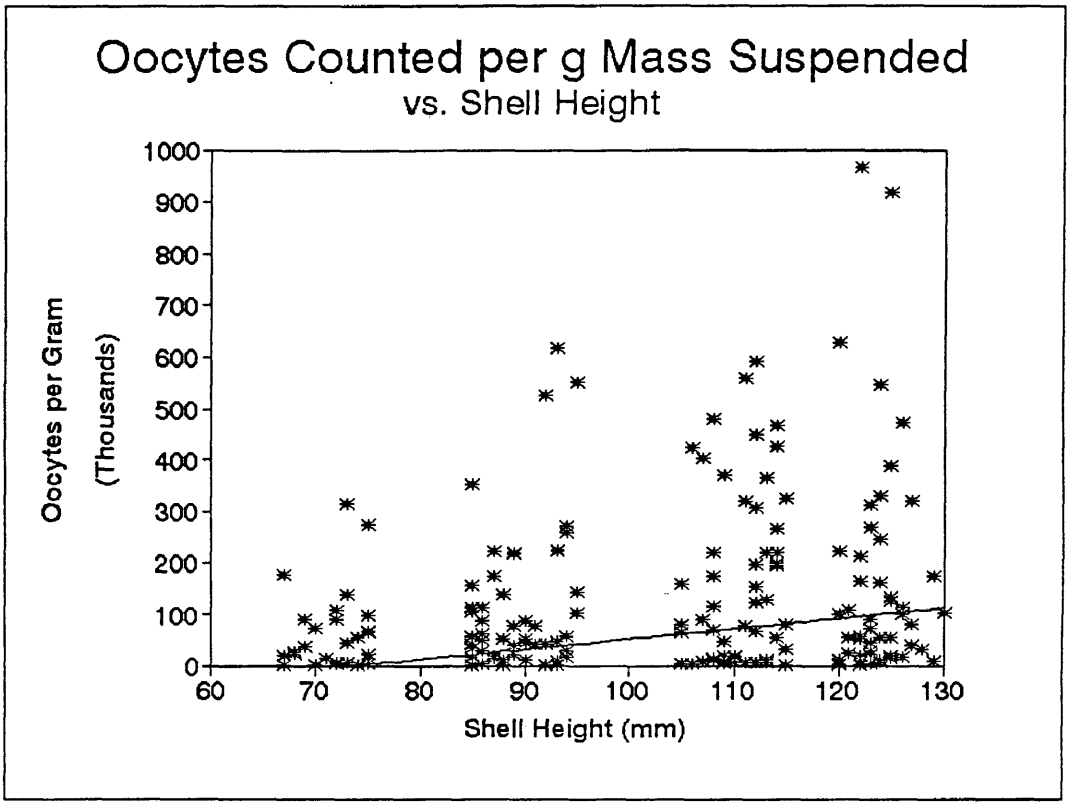


Table 3. Summary statistics for 53 *P. magellanicus* specimens processed histologically. Included by shell height interval (0 = 40-60mm, 1 = 65-75mm, 2 = 85-95mm, 3 = 105-115mm, 4 = 120-130mm) are the number processed (N) and sample means and standard deviations for mature oocyte volume fractions, atretic oocyte volume fractions, and fecundity (calculated using $F=OWMxVF_{MO}/1.6x10^{-7}g$). All histologically-processed scallops were taken from samples belonging to Area A.

Size Class, N	Mature Oocyte Volume Fraction Mean+/-St.Dev.	Atretic Oocyte Volume Fraction Mean+/-St.Dev.	Fecundity Mean+/-St.Dev.
0, 5	0.25+/-0.13	0.11+/-0.17	$4.4x10^{6}$+/-$4.1x10^{6}$
1, 1	0.31+/-N/A	0.57+/-N/A	$6.4x10^{6}$
2, 9	0.29+/-0.16	0.51+/-0.18	$6.5x10^{6}$+/-$4.2x10^{6}$
3, 19	0.34+/-0.21	0.43+/-0.22	$1.2x10^{7}$+/-$1.0x10^{7}$
4, 19	0.28+/-0.23	0.46+/-0.20	$1.7x10^{7}$+/-$1.7x10^{7}$
Overall	0.30+/-0.20	0.43+/-0.23	

Figure 6. Regression of the combined volume fraction of mature intact and atretic oocytes (VF_{MO+AO}) on shell height (SH). The regression equation is: $\ln(VF_{MO+AO}) = -5.0 + 1.0 \times \ln(SH)$ ($p < 0.0005$; $R^2 = 41.8\%$; t-ratios: $\alpha = -6.53$, $\beta = 6.05$ ($N = 53$; 51 d.f.)).

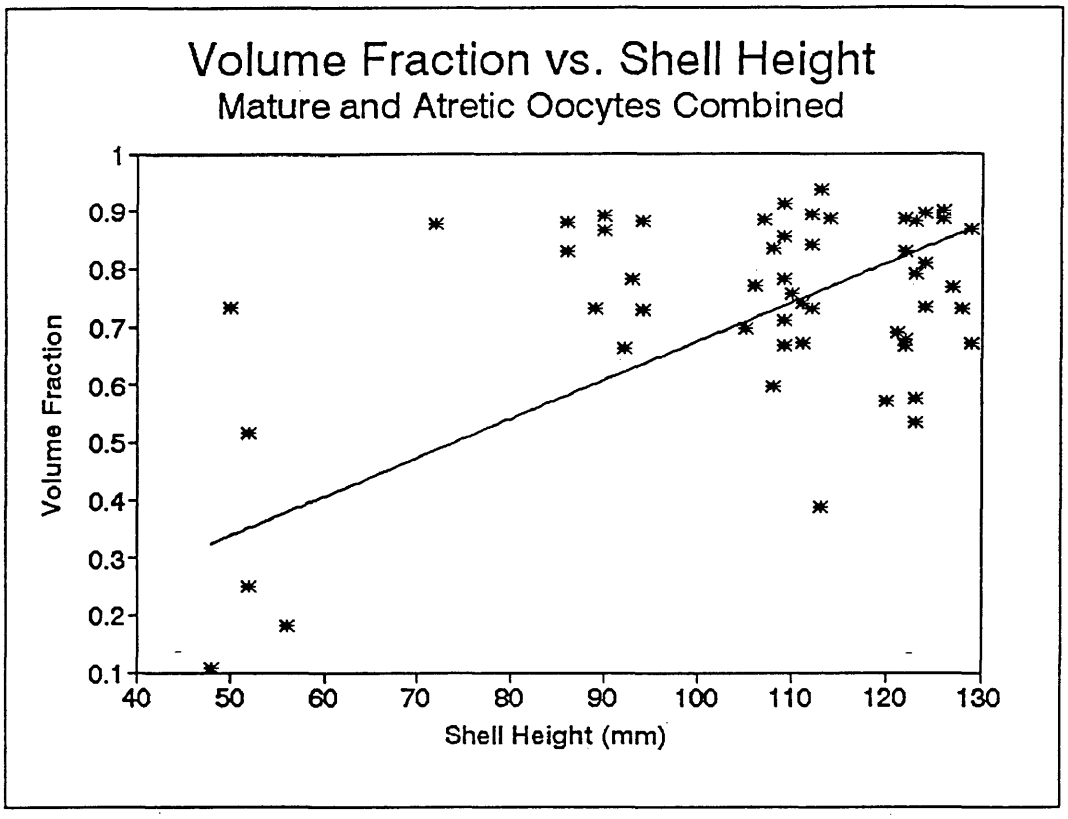
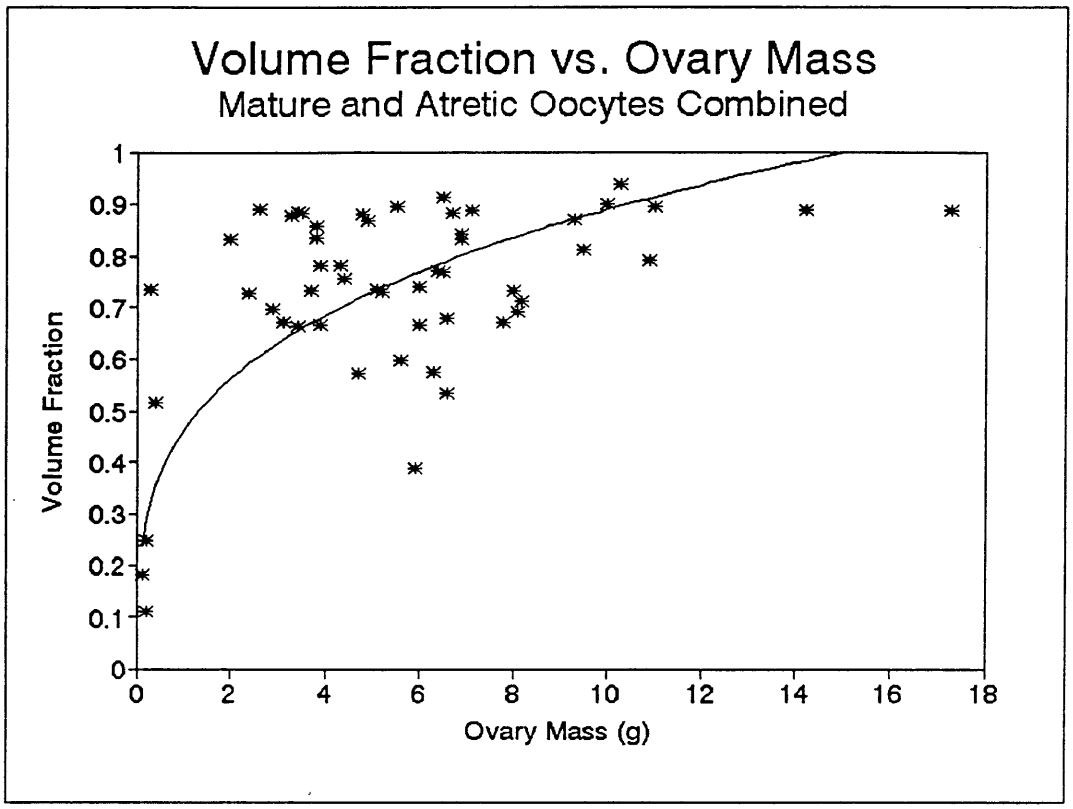


Figure 7. Regression of the combined volume fraction of mature intact and atretic oocytes (VF_{MO+AO}) on ovary wet mass (OWM). The regression equation is: $\ln(VF_{MO+AO}) = -0.78 + 0.29 \times \ln(OWM)$ ($p < 0.0005$; $R^2 = 58.8\%$; t-ratios: $\alpha = -13.12$, $\beta = 8.53$ ($N = 53$; 51 d.f.)).



should be exercised, however, in drawing inferences about relationships based on these particular regression results due to low numbers of representatives (particularly in the smaller size classes) and due to the fact that the regression functions used were technically inappropriate because the data analyzed was censored (all volume fraction values necessarily fell between zero and one). The frequencies of atretic oocytes observed in the specimens processed histologically were higher than previously documented for *P. magellanicus*. To determine whether these observations may have been a function of the time the specimens spent out of the water, the volume fraction of atretic oocytes was regressed linearly upon the number of hours elapsed between harvest and processing. This regression proved not significant ($p=0.371$).

The histologic method of estimating fecundity used the equation:

$$F = OWM \times VF_{MO} / 1.6 \times 10^{-7}.$$

Fecundity estimates obtained exceeded those produced by directly counting oocytes. The regression of histologic fecundity estimates on shell height is presented in Figure 8. The regression of fecundity on ovary wet mass for this method proved not significant after compensating for heteroscadasticity (Wesolowsky 1976). A scatterplot of fecundity versus ovary wet mass for both methods is presented in Figure 9.

The monthly mean ovary wet mass trend for sea scallop populations in the mid-Atlantic resource area during the period from October 1992 to

Figure 8. Regression of fecundity (FEC), determined by the histologic method, on shell height (SH). The regression equation is: $\ln(FEC) = -0.2 + 9.2 \times \ln(SH) - 0.07 \times SH$ ($p < 0.0005$; $R^2 = 52.5\%$; t-ratios: $\alpha = -1.60$, $\beta_1 = 2.49$, $\beta_2 = -1.51$ ($N = 53$; 50 d.f.)).

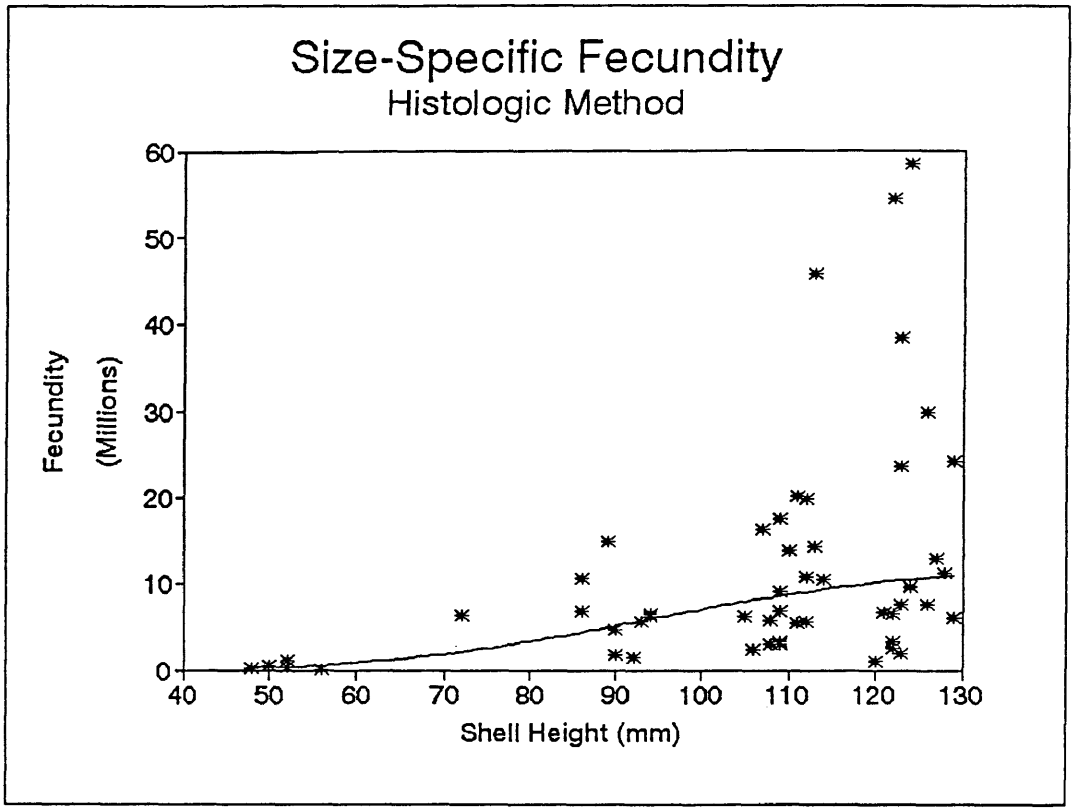
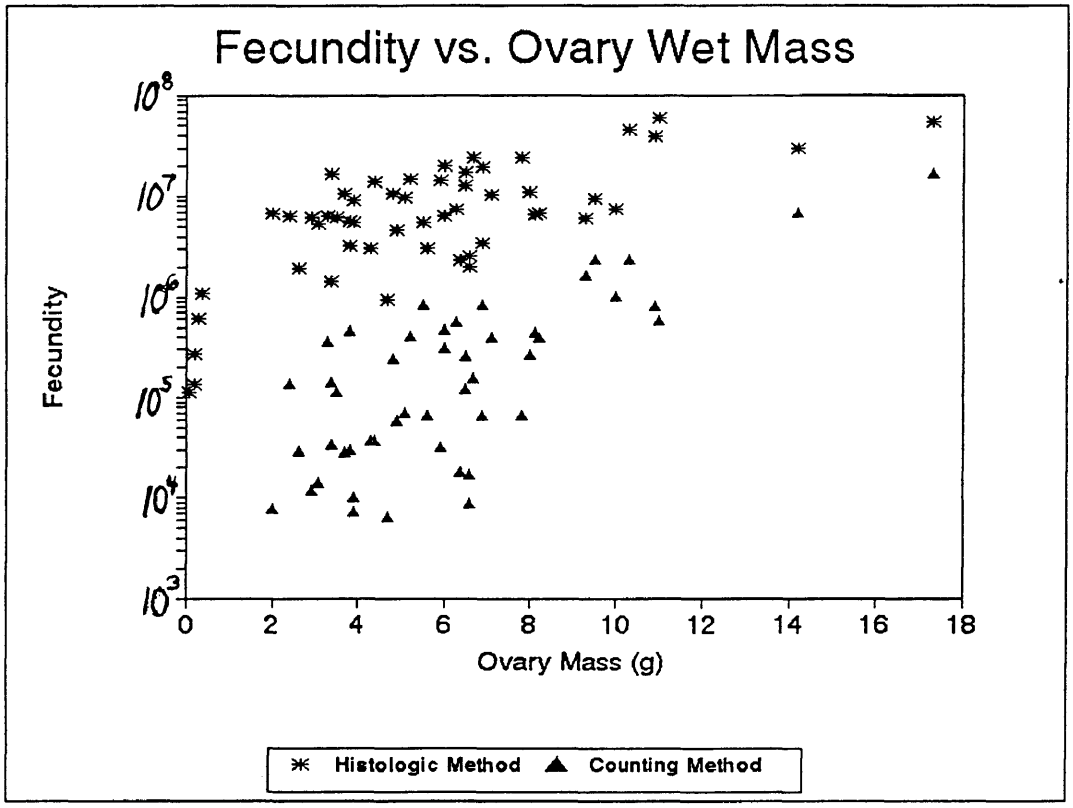
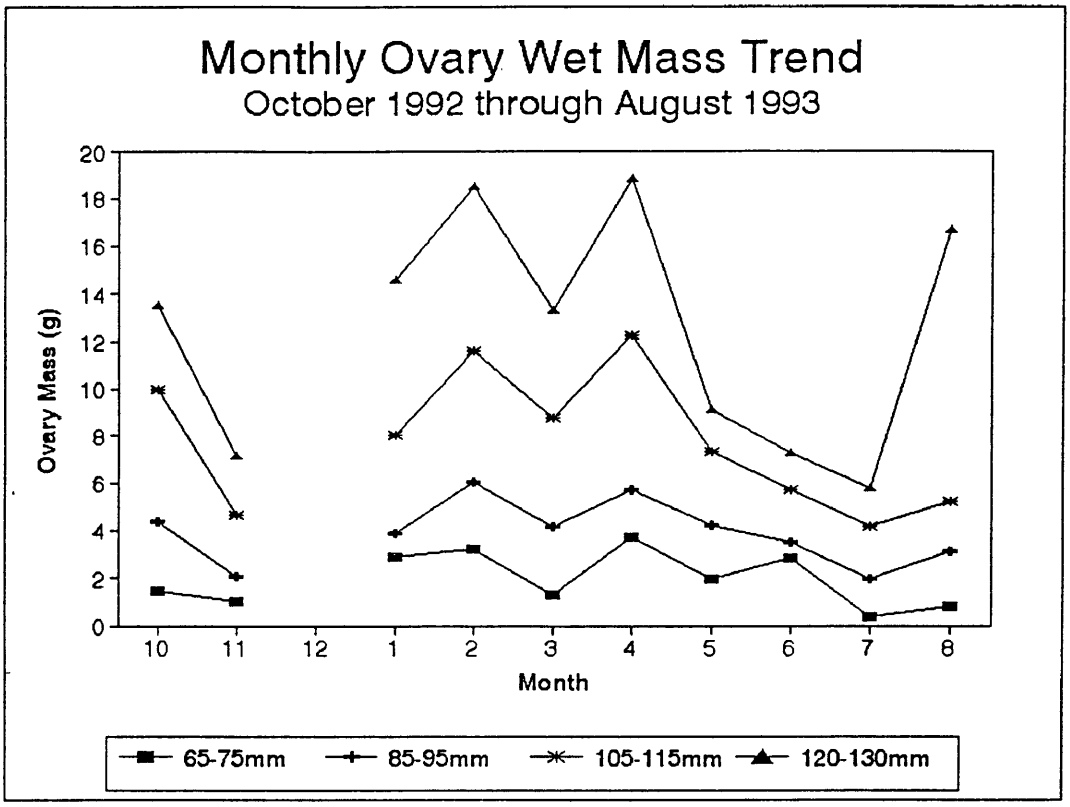


Figure 9. Scatterplot of fecundity, determined by the histologic method and the direct counting method, against ovary wet mass. A semilog plot is used.



August 1993 is illustrated in Figure 10. The trends for five shell height intervals were chosen, corresponding with those examined in this study. A departure from the typical *P. magellanicus* gametogenic cycle was observed in March 1993, as mean ovary wet mass in all five size classes decreased, then increased again in April as the normal gametogenic pattern resumed.

Figure 10. Graph of the monthly mean ovary wet mass trend for *P. magellanicus* in the mid-Atlantic resource area, for five shell height intervals, for the period from October 1992 through August 1993.



Discussion

The estimates of size-specific fecundity obtained by directly counting suspended oocytes were lower than expected based on the published data of Langton et al. (1987) and Schmitzer et al. (1991). While Langton et al. (1987) found Gulf of Maine scallops to contain 1 to 270 million oocytes per individual, and Schmitzer et al. (1991) found that a standardized scallop of 103mm from the mid-Atlantic contained an estimated 40 million oocytes, the direct counting method in this study found no scallop to contain more than 28 million oocytes.

While the absolute levels of fecundity estimated using the direct counting method were lower than those documented in the literature, the size-specific trends were similar. Langton et al. (1987) found that a 125mm scallop produced 1.6 times as many eggs as a 110mm scallop, 3.1 times as many as a 90mm scallop, and 6.5 times as many eggs as a scallop of 70mm. In this study, based on the regression equation of fecundity on shell height for the direct counting method, the corresponding factors were 1.4, 3.0, and 12.2.

The results obtained using histology validated the trend observed using the direct counting method. Using the regression equation for the relationship between fecundity (calculated using the histologic method) and shell height, a 125mm scallop in this study was found to produce 1.2

times as many oocytes as a 110mm scallop, 2.0 times as many as a 90mm scallop, and 5.5 times as many as a 70mm scallop. Estimated fecundity for all size classes was found to be higher using the histologic method than using direct counts, which suggests that oocyte recovery by the direct counting method was incomplete.

The discrepancies between fecundity estimations by the two methods in this study and between these estimations and those published may be due to the condition of the ovaries and the high level of oocyte atresia. Langton et al. (1987) and Schmitzer et al. (1991) made the assumption that the pre- versus post-spawn difference in ovary wet mass was attributed almost completely to the loss of eggs. Histological evaluation in this study, however, found an average of 43% of ovary mass to be occupied by atretic oocytes, while just 30% on average was occupied by intact, apparently viable oocytes. Fecundity estimates an average of 2.4 times greater than the histologic estimates would result if all non-structural ovarian material consisted of mature, intact oocytes.

Other factors made absolute fecundity estimations difficult to obtain. A key assumption made by Langton et al. (1987) and Schmitzer et al. (1991) was that the wet mass of a single oocyte was 1.6×10^{-7}g. To verify this figure, an independent calculation was conducted using histological sections prepared during this study. Oocyte diameters (N=520) were estimated using a compound microscope (100x) with an ocular micrometer.

In all cases, maximum distances across the sectioned oocyte were measured. The mean estimated diameter was 73μm (without taking shrinkage of sections during histological processing into account). Assuming oocytes to be spherical, oocyte volume was calculated using volume $=(4/3)\pi r^3$, and oocyte mass by multiplying the volume by density (assumed to be 1.03g/cm^3). The calculated wet mass of a single oocyte was 2.0×10^{-7}g. Lower histological fecundity estimates in this study (and lower estimates in Langton et al. (1987) and Schmitzer et al. (1991)) would have been obtained had this value for oocyte wet mass been used. Oocyte wet mass may in reality have been greater than 2.0×10^{-7}g. The true mean oocyte diameter likely was even higher than the estimated mean, because the estimated mean reflects sections of oocytes that had been grazed, rather than cut through the middle into two halves. The oocyte wet mass would thus have been calculated to be greater, and fecundity estimates to be lower.

Electron microscopy has been used to study oocyte atresia, and has produced the description of several diagnostic traits of atretic oocytes (Dorange and Le Pennec 1989). These signs are beyond the resolution of light microscopes, however. Atresia in this case becomes evident when the oocytes in section begin to assume a characteristic jigsaw puzzle-type appearance (Schmitzer 1990). Oocytes that appear mature and viable, and that are counted as such in the estimation of volume fractions, may in fact

be in the early stages of resorption. This may present a problem when making direct counts of suspended oocytes, because atretic oocytes lack the structural integrity of non-atretic oocytes (Dorange and Le Pennec 1989) and may be lysed during the preparation of a suspension. The presence of a significant though unquantifiable amount of cell membrane fragments observed in the suspensions supports this argument. It is likely that the fecundity results produced by the two methods in this study differ in magnitude because many oocytes counted as intact and mature in histological sections were in fact atretic and broke apart in suspension.

Lubet et al. (1987) found that gametogenesis in *Pecten maximus* involved the production and resorption of several generations of oocytes, with the resorbed materials being recycled within the organism during the production of future generations of oocytes. The phenomenon of oocyte atresia has not been documented as playing such a role in the gametogenesis of *P. magellanicus*. Oocyte atresia in sea scallops may occur periodically in response to adverse environmental conditions, and in particular may be indicative of an inadequate food supply (Barber, personal communication).

The monthly mean ovary wet mass trend for October 1992 through August 1993 (Figure 10) shows that the mean ovary wet mass decreased from a peak value in March 1993, only to increase to another peak in April. It is unlikely that this represented a spawning event, because no

evidence of spawning was found macroscopically or histologically. This decrease in mean ovary mass more likely was the result of atresia and resorption, perhaps because of adverse environmental conditions caused by the strong late-winter storms that occurred in early 1993 in the study areas (NOAA 1993b). Caution must be exercised in drawing this conclusion, however. The samples in March may have been collected from areas in which maximal ovary mass was not attained, perhaps because of adverse environmental conditions. The apparent loss of ovary mass in March may therefore be an illusory product of the inconsistency in sample collection locations.

The differences in fecundity between and within Areas A and B in this study confirm previously published observations of variability in *P. magellanicus'* spawning patterns (MacDonald and Thompson 1985b; Barber et al. 1988; MacDonald and Thompson 1988; DuPaul et al. 1989; Kirkley and DuPaul 1991) over small geographic scales. This temporal and geographical variability in fecundity may limit the value of absolute fecundity estimations, particularly with respect to management of the commercial fishery. Size-specific fecundity trends, however, are important for the management of the commercial sea scallop fishery. MacDonald and Thompson (1985b, 1988) found that larger sea scallops allocate more energy to germinal production relative to somatic production than do smaller scallops. This study supports the view that sea scallops commit

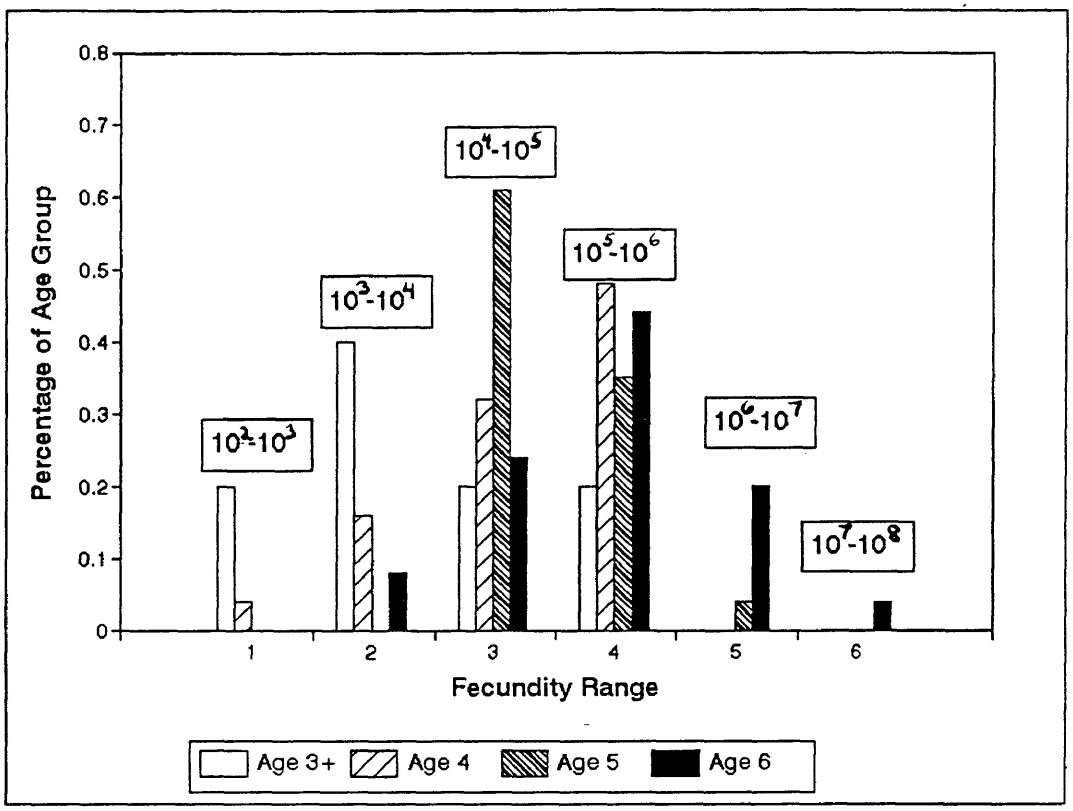
more energy to reproduction with age. This is reflected in the significant increases with age in the number of oocytes counted per g ovary mass and in the volume fraction occupied by the combination of mature and atretic oocytes. The failure of the SSFMP to account for these trends may lead to overestimation of SSB and MSP, resulting in overexploitation of the sea scallop resource, due to the establishment of excessive levels of fishing effort.

Relevance to the Management of the Sea Scallop Fishery

The objective of Amendment 4 to the SSFMP is to maintain a fishing mortality (defined as the part of the total mortality rate applying to a scallop population that is caused by fishing) of 0.71 through restrictions on the number of vessels entering the fishery, the annual number of days at sea, the crew size, and the harvesting gear (30ft. overall dredge width equipped with rings of 3.25" interior diameter until March of 1996, 3.5" thereafter). This fishing mortality theoretically corresponds to a SSB maintained at 5% of maximum spawning potential (NEFMC 1993). The concepts of SSB and MSP are problematic, however, because they assume that a given level of SSB has a given spawning potential, regardless of the size or age composition of the scallops that comprise the stock. This study has shown this assumption to be invalid.

The paucity of scallops 4-yrs-old and older in the mid-Atlantic makes the results of this study particularly relevant to managers of the fishery. Five- and 6-yr-old scallops recently were found to comprise <1.3% of existing scallop stocks (National Marine Fisheries Service 1993). Yet it is these 5- and 6-yr-olds that in this study consistently produced the largest numbers of oocytes (Figure 11). That the most fecund scallops should comprise such a small percentage of the stock is troublesome; the question of whether mid-Atlantic scallop stocks are self-sustaining is

Figure 11. The frequency distribution of estimated fecundity values, by age group, for Area A.



raised. The tendency of commercial fishermen to target larger scallops for harvest compounds the problem of the age composition of the stocks. DuPaul and Kirkley (1994) found that commercial tows in the mid-Atlantic near the time of the NMFS abundance survey (NEFMC 1993) contained higher percentages of Age 4 and Age 5 scallops than were found by NMFS. This is a function of sampling or collection strategy: NMFS randomly selects sample locations, while commercial fishermen, upon finding a population of large scallops, will fish in that location until it is no longer productive.

Preliminary observations on the impact of the gear change from 3" rings to 3.25" rings showed that while Age 3 and, to a lesser degree, Age 4 scallops experienced a reduced fishing mortality, Age 5 and Age 6 scallops continued to be heavily exploited by the new harvesting gear (DuPaul and Kirkley 1994). The reduced fishing mortality of Age 3 scallops may do little, though, to improve scallop stocks, since these young scallops contribute relatively little to reproduction. Additional intervention by management may be necessary if the resource condition is not found to improve soon.

The analogy to the striped bass fishery may be relevant. Like the current sea scallop stocks, striped bass stocks a decade ago were found to be dependant on a relatively small number of highly fecund females. A Striped Bass Fishery Management Plan (SBFMP) was enacted to protect

these females through size and area restrictions (summarized in ASMFC 1990), and striped bass stock conditions have begun to improve (ASMFC 1993). The effects that changes to harvesting gear and reductions in fishing effort will have on sea scallop stocks remains to be seen. Should stock conditions not improve, however, measures to protect the highly fecund Age 5 and Age 6 scallops may prove desirable to managers of the sea scallop fishery in the future.

Conclusions

This study has shown that direct fecundity estimations are possible for *P. magellanicus*. That fecundity levels differed greatly between the direct counting method and the histologic method, however, underscores the need for caution in interpreting any of these estimates as absolute. Each method for estimating fecundity has its limitations. The direct counting method may overestimate fecundity, as oocytes in suspension that may never have been spawned in a natural setting are counted. Conversely, fecundity may be underestimated if the recovery of oocytes is incomplete. The use of volume fractions in the histologic method has the potential of introducing bias as well. The method used by Langton et al. (1987) and Schmitzer et al. (1991) may be flawed in assuming that the pre- versus post-spawn difference in mass represents nothing but spawned gametes. To have used this method for the spawning period examined in this study would have produced overestimates of fecundity because the frequency of oocyte atresia would not have been accounted for.

The high level of variability in size-specific fecundity in this study indicates that fecundity is not simply a function of ovary mass and shell height. Spatial and temporal variability in physical variables and in food supply contributed greatly to the variability in size-specific fecundity. This study would have been more effective had the variability caused by

environmental variables been minimized. Future studies should focus on extensively sampling one particular location at one point in time, rather than on collecting a number of smaller samples from several locations at different times.

Oocyte atresia in *P. magellanicus* is poorly documented, but the high rates of atresia observed in this study suggest that it is a phenomenon that deserves more attention. The presence of a semiannual spawning period in the mid-Atlantic resource area (DuPaul et al. 1989) suggests that the gametogenic cycle of the sea scallop near the southern limit of its range is peculiar. Oocyte atresia may be found to play a similar role in *P. magellanicus* in the south as in *Pecten maximus*, though on a more sporadic basis. More research is needed on the frequency and extent of oocyte atresia in *P. magellanicus*, particularly in relation to the time series of environmental variables, as well as on the fate of the products of lysis in this organism.

Current sea scallop stocks remain at historically low levels (NEFMC 1993). High fishing pressure has resulted in a dearth of larger scallops. Surveys in 1993 found that 98.7% of all scallops caught were below 100mm in size (NMFS 1993). McGarvey et al. (1993) found that these 3- and 4-yr-old scallops were of questionable importance to recruitment in one location, on Georges Bank. As alternative management plans for sea scallops come under consideration (Moore 1994), it is imperative that

these plans account for size-specific trends in reproductive capacity, particularly as sea scallop stocks necessarily have become increasingly dependent on younger year classes for maintenance of the populations.

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