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GAMETOGENIC CYCLE OF SEA SCALLOPS (*PLACOPECTEN MAGELLANICUS* (GMELIN, 1791)) IN THE MID-ATLANTIC BIGHT*

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ABSTRACT Gametogenesis of the sea scallop, *Placopecten magellanicus* (Gmelin), from three areas within the mid-Atlantic Bight was examined from January to December 1988. Histological and morphometric quantification of gonadal tissue concluded that a semiannual gametogenic cycle was characteristic of sea scallops from the mid-Atlantic Bight. The majority of spawning occurred in May and November. Gonadal development in spring comprised a longer period of time and resulted in greater fecundity than in fall. Differences were found in the timing and magnitude of the semiannual gametogenic processes between sex, area, and water depth within the study area. Varying temperature patterns between the mid-Atlantic Bight and more northerly resource areas may be partially responsible for the observed difference in gametogenic cycles. Semiannual spawning has potential implications for management strategies which are currently based on the assumption of annual spawning and recruitment events.

KEY WORDS: gametogenic cycle, sea scallop, *Placopecten magellanicus*, gonad weight

INTRODUCTION

The sea scallop, *Placopecten magellanicus* (Gmelin), supports a valuable commercial fishery throughout much of its entire distribution in the northwestern Atlantic, from the Strait of Belle Isle, Newfoundland, to Cape Hatteras, N.C. (MacKenzie et al. 1978). The United States sea scallop fishery had a catch of over 33,700,000 pounds valued in excess of $132,000,000 in 1989 (National Marine Fishery Service). Landings from Georges Bank have historically accounted for most of the United States harvests. The importance of the mid-Atlantic sea scallop fishery to the United States total commercial harvest has increased since the mid 1960s. This is primarily a result of an expanded fishery with numerous successful year classes and concommittant increases in fishing effort (New England Fishery Management Council et al. 1982).

Regulation and management of the sea scallop fishery is based, in part, on knowledge of the reproductive cycle of the species and the presumption that there is one stock distributed over several resource areas. On Georges Bank and in the Gulf of Maine, sea scallops undergo an annual gametogenic cycle with a single spawning period in the fall (MacKenzie et al. 1978, Robinson et al. 1982). Sea scallop harvesting in the United States is currently regulated by a minimum shell size restriction for scallops that are landed whole and a maximum average meat count (number of adductor muscles per pound) for scallops which are shucked at sea. In addition, there is a single temporary seasonal adjustment in the size restrictions to compensate for adductor muscle weight changes attributed to spawning in the fall. The seasonal adjustment was based on biological data from the Georges Bank area and the assumption that a similar reproductive pattern occurred in all scallop resource areas.

In the mid-Atlantic Bight, however, scallops appear to spawn twice a year (DuPaul et al. 1989). Given the relationship between adductor muscle weight and gametogenesis (Barber and Blake 1981, Robinson et al. 1981), the existence of a semiannual spawning event in the mid-Atlantic region implies that alternative regulatory strategies for each resource area may need to be considered. A detailed examination of gametogenic processes in this region is thus important for the management and regulation of the sea scallop fishery and for improving the utilization of the resource by commercial fishermen. This study examines gametogenesis of scallops within the mid-Atlantic Bight.

MATERIALS AND METHODS

Whole fresh sea scallops, *Placopecten magellanicus*, were obtained from commercial fishing vessels operating in the mid-Atlantic Bight from January through December, 1988. Sample locations ranged from south of Long Island (40°00′N 73°00′W) to north of Cape Hatteras (37°30′N 74°30′W). This includes a rectangular area of approximately 28,000 km^2 running northeast to southwest in water depths of 40 to 74 m. Three areas within this range were sampled on a monthly basis. Consistent spatial-temporal sampling was not possible because of the commercial nature of the samples. The three areas included a site off the Virginia coast (37°15′–37°45′N), a site off the Delaware-Maryland penninsula (38°00′–38°30′N) and a site off the

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New Jersey coast (39°00′–40°00′N). These three sites were believed to adequately represent distinct geographical areas and be consistent with the requirements of stratified random sampling (Zar 1984).

At the time of sample collection, the date, time, Loran C coordinates, water depth (m), and surface water temperature (C) were recorded. Four to fifteen samples were collected monthly. Each sample consisted of 100 unshucked scallops randomly selected from 1.5 to 3.0 bushels of shellstock. The adductor muscle and gonad were resected from each animal. Wet weight of the gonad, including the crystalline style and foot, was measured to the nearest 0.1 gram. The maximum distance between dorsal and ventral margins (shell height) was measured to the nearest millimeter using a standard fish measuring board. One subsample was selected each month from the Delaware-Maryland area for estimation of dry gonad weights. Ten gonads, with crystalline style and foot removed, were dried to a constant weight in a drying oven (90°C) and reweighed.

Four to six subsamples were selected each month for histological examination. Twelve gonads of each sex, when sex could be visually determined, were used from each subsample. Pieces of gonad tissue (1 to 2 cm^2) were cut from the middle anterior of the gonad. The tissue was preserved in Davidson's fixative, dehydrated, embedded in paraffin, cut 6 μm thick, mounted on slides, and stained with Harris' hematoxylin and eosin.

Volume fractions were determined for mature, developing, and resorbing gametes and nonreproductive matter following the methods of Weibel et al. (1966) and MacDonald and Thompson (1986). Five random fields of gonad tissue were examined with a compound microscope (150×) equipped with an eyepiece reticle. The reticle had a 10 mm square grid containing 61 points of intersecting lines. Volume fractions were calculated as the percentage of points occupied by each structure for each gonad section. A total of 1,326 gonads were examined histologically. Results are presented by individual areas, depths, and sex so that differences in reproductive processes can be examined and related to environmental conditions.

Mature gamete volume fractions for the three sample areas and depths were statistically examined to evaluate gametogenic processes within the mid-Atlantic Bight. The shallowest and deepest samples which were collected each month from the Virginia area were selected for water depth analysis. Volume fractions of mature gametes were selected for testing since this entity represents the potentially viable sexual products. The nonparametric Wilcoxon paired sample test was used to examine differences. Extreme heteroscadasticity precluded use of parametric tests (Steel and Torrie 1960).

Temporal changes in gonad weight were examined as an alternative monitoring method of gametogenesis. Scallops were grouped into five shell height intervals: 85–89 mm (N = 1,438), 90–94 mm (N = 1,859), 100–104 mm (N = 1,908), and 110–114 mm (N = 1,365). Mean gonad wet weight for each size interval was determined for each month with data pooled over sex and sample area. Gonad dry weight was estimated to compare the use of wet versus dry gonad weights as indicators of gametogenesis. Estimates of gonad dry weight were calculated as the product of individual gonad wet weight and the mean percentage of gonad dry weight, as determined from the representative monthly sample.

Fecundity was estimated by calculating the weight of mature gametes released upon spawning following the methods of Langton et al. (1987). Gamete weight of individual female scallops was estimated by the following regression model:

$$\ln G = \ln \beta_0 + \beta_1 \ln S + \beta_2 S + e$$

where G = gamete weight, S = height, and e = the random error term, assuming $N(0, \sigma^2)$. The equation is well suited for estimating the relationship between gonad weight and shell height. It allows for maximum weights and inflection points. The equation was estimated by ordinary least squares for the months characterized by max-

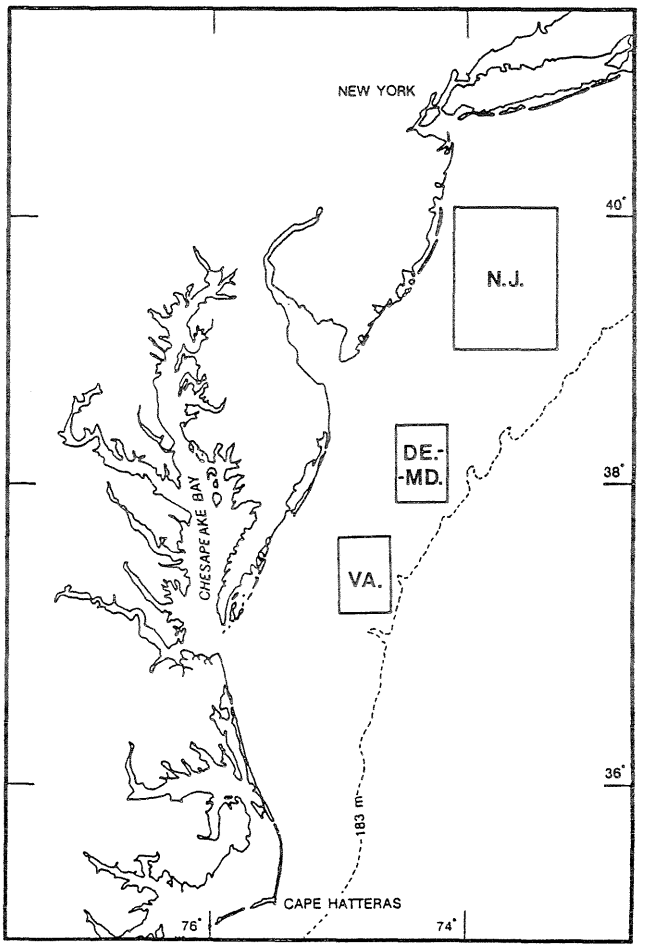

Figure 1. Location of Virginia (Va), Delaware-Maryland (De-Md), and New Jersey (NJ) sampling areas within the mid-Atlantic Bight.

imum and minimum values of the spawning cycle. Estimated weight loss was converted into ova numbers by dividing gamete wet weight loss by 1.6×10^{-7} g, the weight previously determined for wet mature ova (Langton et al. 1987).

Discrete bottom temperature data for the areas and months sampled during this study were not available. Bottom temperatures were therefore estimated with a computer program available from the Northeast Fisheries Center, National Marine Fisheries Service (NMFS) (Mountain 1989). The mean latitude and longitude coordinates from samples collected within the three areas were used to estimate temperatures. Coordinates were 37°31′N, 74°42′W (Virginia); 38°15′N, 74°11′W (Delaware-Maryland); 39°25′N, 73°08′W (New Jersey).

RESULTS

During the study period, sea scallops from the mid-Atlantic Bight exhibited semiannual gametogenic cycles (Fig. 1). Within each sampling area, the majority of spawning of male and female scallops occurred during the same months. In spring, however, female scallops from the Delaware-Maryland area initiated spawning one month earlier than scallops from the New Jersey and Virginia areas, and were more completely spent by June. Unlike females, the percentage of mature gametes for males during this period showed little variation between areas prior to spring spawning. From April to August, mature gamete volume fractions in male and female gonads from Virginia and New Jersey areas gradually declined to minimal values in August. However, both sexes of Delaware-Maryland scallops exhibited a small increase in mature gamete volume fractions during July. During the fall gametogenic cycle, development and spawning occurred in a shorter time period and in a more simultaneous manner than in the spring. It was not possible to verify spawning for New Jersey scallops in the fall due to the lack of samples from that area in November, when spawning was likely to have occurred.

While the timing of gametogenic processes within each sampling area was very similar for both sexes, significant differences in mature gamete volume fractions were detected between sex in all three areas (Wilcoxon paired sample test: Virginia, $z = -7.3338$, $p < 0.0001$; Delaware-Maryland, $z = -3.9653$, $p < 0.0001$; New Jersey, $z = -3.8760$, $p < 0.0001$). Male scallops generally had larger volume fractions of mature gametes when ripe than females. Statistically significant differences were detected between mature gamete volume fractions for female scallops from the Delaware-Maryland and Virginia areas (Wilcoxon paired sample test, $z = -4.5301$, $p < 0.0001$). Significant differences were not detected in male scallops from the two sampling areas (Wilcoxon paired sample test, $z = -1.7152$, $p < 0.0863$).

Resorbed gametes comprised a small portion of the volume fractions in female gonads throughout the year, ranging from 0 to 15 percent. Seasonal changes in resorbed gamete volume fractions were similar to seasonal changes in mature gamete volume fractions, with the larger values occurring in the month of or prior to maximum development. The distribution and extent of lysis activity and resorption of oocytes within individual gonads was extremely variable. Initially, lysis was detectable by the breakdown of the vitelline membrane, which caused the oocytes to lose their round or polygonal shape and take on an irregular, jigsaw appearance. As lysis progressed and egg material was resorbed, empty space and fragments of oocytes were observed in the follicles. The occurrence of resorbed gametes reduced the percentage of mature gametes present in female gonads.

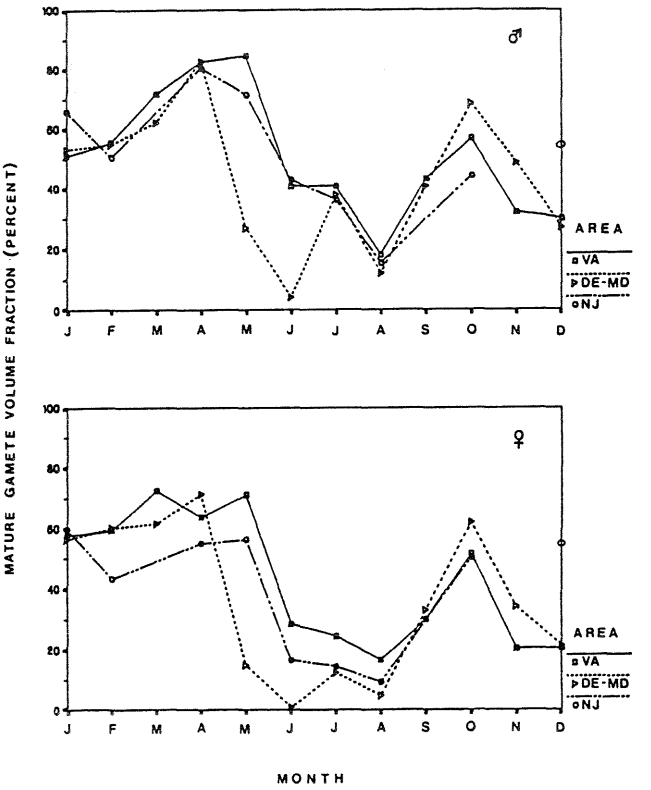

Figure 2. Monthly mean mature gamete volume fractions (percent) for male and female sea scallops from the Virginia (Va), Delaware-Maryland (De-Md), and New Jersey (NJ) sampling areas.

Results similar to those derived from histological quantification were obtained using wet and dry gonad weights as a measure of gametogenesis (Fig. 2). It was also evident that the pattern of gametogenesis did not differ significantly with shell size/age of scallops. Scallops 85–89 mm in shell height were sexually active. The percent of tissue remaining after removal of the foot and drying of the gonad varied seasonally from a maximum of 25 percent in March to a minimum of 6 percent in June. Dry gonad weights, as another measurement of gametogenic content, exhibited less monthly variation. Additionally, the semiannual cycles

TABLE 1.

Monthly mean mature gamete volume fraction ($\bar{X}$) and standard deviation (σ) for *P. magellanicus* from the Virginia (Va), Delaware-Maryland (De-Md), and New Jersey sampling areas.

	Pooled		Virginia		Delaware-Maryland		New Jersey	
Month	$\bar{X}$	σ	$\bar{X}$	σ	$\bar{X}$	σ	$\bar{X}$	σ
MALES								
January	55.25	14.60	50.25	14.60	53.25	13.14	65.76	5.52
February	53.95	15.70	55.47	13.89	54.83	12.35	50.42	21.47
March	66.69	14.89	71.52	8.43	62.08	18.17	—	—
April	82.10	11.25	82.54	13.93	82.61	7.62	80.27	11.62
May	58.75	35.04	84.56	14.29	26.70	31.12	71.24	16.30
June	28.01	31.96	40.55	32.28	4.12	9.95	42.71	33.18
July	38.23	29.18	40.62	33.24	37.74	27.75	35.94	26.85
August	14.65	20.21	17.82	24.47	11.95	18.33	15.15	16.66
September	41.72	27.28	43.00	29.11	40.55	26.06	—	—
October	58.85	27.01	56.68	31.94	68.29	18.14	44.00	24.63
November	42.06	32.55	31.82	29.61	48.52	33.40	—	8
December	35.48	25.86	29.73	25.62	26.82	20.25	59.27	22.46
FEMALES								
January	57.92	15.48	57.79	13.88	56.34	17.00	59.75	17.92
February	55.97	19.34	59.43	18.52	60.27	15.03	43.28	21.57
March	66.73	15.51	72.42	11.48	61.69	17.02	—	—
April	65.13	17.98	63.79	20.95	71.27	10.54	55.03	20.08
May	45.30	34.14	71.13	14.73	14.84	26.02	56.39	26.58
June	15.20	26.01	28.52	31.26	0.89	1.40	16.50	26.80
July	16.91	23.35	24.49	30.29	12.33	16.78	14.33	20.41
August	10.85	17.00	16.65	20.75	4.75	10.93	9.28	13.33
September	31.38	28.62	30.11	26.79	33.02	31.48	—	—
October	55.64	27.92	51.62	27.65	62.11	26.50	50.35	30.54
November	30.22	31.57	20.50	20.21	34.25	34.72	—	—
December	27.39	27.98	20.60	24.69	21.50	20.48	57.76	31.41

were more apparent since the increased water content present in spent gonads was removed.

Variability of gametogenesis within the mid-Atlantic Bight, as determined by the standard deviation of pooled mean mature gamete volume fractions, was quite large throughout the year (Table 1). The variability of reproductive condition did not decrease when mean mature gamete volume fractions were calculated for individual areas and sex. Large standard deviations for the pooled volume fractions were therefore not due to pooling. In Virginia, estimated fecundity for a standardized scallop 103 mm in shell height was estimated at 39,688,000 eggs in spring and 9,938,000 eggs in fall (Table 2). In Delaware-Maryland, fecundity was estimated at 34,125,000 eggs in the spring,

TABLE 2.

Parameter estimates from regression of natural logarithm of gamete weight against constant, natural logarithm of shell height, and shell height.

	Parameter estimates[1]					
Month	$\ln \beta_0$	β_1	β_2	R^2	Gamete wt (g)	Egg # ($\times 1000$)
Va						
March	−28.738	7.686	−0.047	.73	7.73	
June	37.950	−9.563	0.065	.45	1.38	39,688
October	143.181	−39.158	0.383	.09	3.10	
December	39.386	−11.476	0.138	.53	1.51	9,938
De-Md						
March	−27.261	7.396	−0.050	.54	6.49	
June	6.039	−1.741	0.020	.67	1.03	33,125
October	31.373	−8.792	0.105	.16	4.21	
December	27.623	−8.340	0.112	.71	0.50	23,188

[1] Parameter estimates obtained by ordinary least squares for the model:

$$\ln G = \ln \beta_0 + \beta_1 \ln S + \beta_2 S.$$

and 23,188,000 eggs in the fall. The magnitude of fecundity for spring and fall spawning cycles was more consistent in the Delaware-Maryland area and was estimated to produce a greater number of eggs annually than in the Virginia area.

Scallops from shallow and deep water exhibited gametogenic development and spawning in spring and fall (Fig. 3). In spring, deep water scallops lagged one month behind shallow water scallops in the timing of gametogenic processes. In fall, the timing of gametogenic processes was very similar between water depths for both sexes. The relative fecundity of scallops, in terms of net difference in mature gamete volume fractions did not differ with depth, for either male or female scallops. A major depth related difference was that summer gametogenic activity was detected in the shallow water scallops of both sexes, but was absent from the deep water scallops (Table 3). Statistically significant differences were detected between mature gamete volume fractions of shallow and deep water samples for both sexes at the 0.05 α level, but not at the 0.01 α level (Wilcoxon paired sample test: males, $z = -2.3368$, $p < 0.0194$; females, $z = -2.4581$, $p < 0.0140$).

Estimated bottom water temperatures for the three sampling areas indicate similar annual cycles (Fig. 4). Water temperatures were generally warmest in winter months (November to January) at approximately 12–14°C and coolest in summer months (May to July) at approximately 7–8°C. Gamete development and spawning coincided with decreasing and stable temperatures in winter and spring and increasing temperatures in fall. No major deviation in mature gamete volume fractions was associated with the large decrease in temperature which occurred between January and February.

DISCUSSION

Histological examination and quantitative analysis of gonadal tissue confirmed that *P. magellanicus* from the mid-Atlantic Bight underwent a semiannual gametogenic cycle as indicated by DuPaul et al. (1989). Minor temporal differences in gametogenesis existed between the three sampling areas. During spring, initiation of spawning commenced in the Delaware-Maryland area prior to spawning in New Jersey and Virginia areas. During fall, initiation of gametogenesis and spawning occurred during identical months at all sampling areas. Significant differences were detected in the gametogenic cycle of female scallops from the three sampling areas.

Shallow water scallops generally exhibited larger values of mature gamete volume fractions and additional gametogenic activity during the summer months than deep water scallops. Relative fecundity, however, was similar between depths for both male and female scallops. This result differs from previous literature which found fecundity to decrease with depth due to decreased food availability (MacDonald and Thompson 1985, 1986, Barber et al. 1988, Schick et al. 1988). Apparently, the depth differences in this study were not large enough to demonstrate differences in relative fecundity or the relationship may not hold true for the mid-Atlantic region.

Male and female scallops within each sampling area released the majority of gametes during identical months. Such synchronous spawning is critical for reproductive success of a species which is fertilized externally (Langton et al. 1987). The statistically significant differences detected between male and female gametogenic cycles were attrib-

TABLE 3.

Samples included in the Wilcoxan paired sample test comparing gametogenic cycles of shallow and deep water scallops.

	Shallow		Deep	
Month	Date	Depth (m)	Date	Depth (m)
February	2/18	46	2/02	59
March	3/28	51	3/27	62
April	4/21	44	4/19	65
May	5/26	44	5/05	63
June	6/27	50	6/19	62
July	7/17	53	7/18	64
August	8/29	52	8/23	59
September	9/22	43	9/26	64
October	10/22	56	10/16	64
November	11/06	38	11/12	56
December	12/15	43	12/07	66

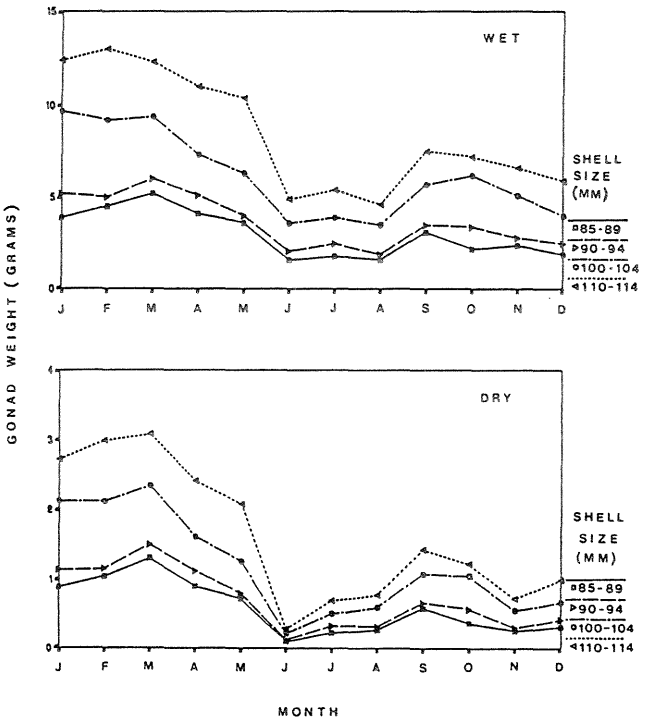

Figure 3. Pooled monthly mean wet and dry gonad weight (grams) for sea scallops of four shell height intervals (85–89 mm, 90–94 mm, 100–104 mm, and 110–114 mm).

uted to morphometric differences between sex rather than temporal differences in gametogenesis.

Spring and fall gametogenic cycles differed in magnitude and duration, with the spring cycle encompassing a greater amount of time and exhibited in greater estimated fecundity. Such inequality is typical of semiannual reproductive cycles (Comely 1974). Temperature has often been implicated as a primary environmental factor controlling the duration and timing of gametogenic events (Sastry 1966, Giese and Pearse 1974). The low uniform temperatures in spring relative to fall could therefore be responsible for the differing durations of the gametogenic cycle. Greater and more consistent fecundity in spring relative to fall may be an indication that environmental conditions in the mid-Atlantic Bight are more favorable for reproduction at that time (Newell et al. 1982, Rodhouse et al. 1984).

There was no quiescent period between the two gametogenic cycles, unlike sea scallops examined from Newfoundland (MacDonald and Thompson 1986). In addition to the two major spawnings, a small amount of gamete development and spawning in July and August as detected in Delaware-Maryland scallops. A small percentage of mature gametes were also released from New Jersey scallops in February prior to the major spawning period. The small release of spermatozoa has been referred to as dribble spawning by Newell et al. (1982) and MacDonald and Thompson (1988). The premature release of gametes may be a necessary sloughing mechanism for an animal that is reproductively mature for a prolonged period.

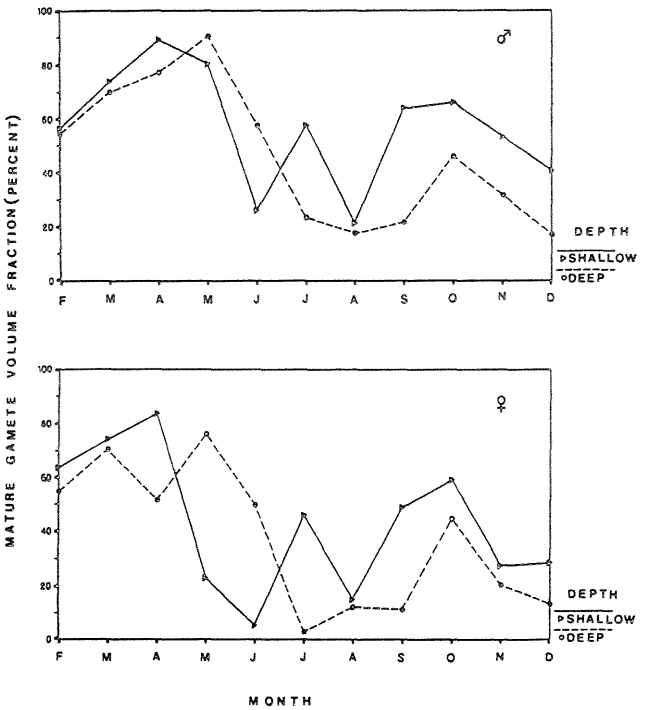

Figure 4. Monthly mean mature gamete volume fractions (percent) for male and female sea scallops from shallow and deep sampling areas.

Many of the observed differences between the gametogenic cycle of *P. magellanicus* in the mid-Atlantic and those from more northerly regions support established zoogeographic principles. As latitude decreases, there may be a shift from annual to semiannual spawning cycles, initiation of gametogenesis and spawning later in the year, less synchronous spawning, or a difference in relative fecundity (Pfitzenmeyer 1965, Barber and Blake 1983, Newell et al. 1982). Sea scallops located off the coast of Newfoundland spawn annually from late August to early September (MacDonald and Thompson 1986). Sea scallops from Georges Bank also spawn annually from late September to early October (MacKenzie et al. 1978). Results from this study indicate that at the southern extent of the species range, *P. magellanicus* shifts to semiannual spawning and initiates fall gametogenesis and spawning later in the year.

In this study, the estimated fecundity of each seasonal cycle, with the exception of the Virginia fall spawn, was similar to values reported by Langton et al. (1987) and MacDonald and Thompson (1986) for sea scallops from the Gulf of Maine and Newfoundland, respectively. Since there were two spawning events per year in the mid-Atlantic Bight, however, estimated fecundity was actually much greater on an annual basis at the more southerly location. MacDonald and Thompson (1988), when comparing sea scallops from Newfoundland and New Jersey waters, also concluded that relative fecundity was greater in the southern location.

Lack of a distinct quiescent period between cycles, dribble spawning in males, and resorption of oocytes in female scallops contributed to increased variability of mature gamete volume fractions. The standard deviation of female mature gamete volume fractions in this study were larger than in the Newfoundland study (MacDonald and Thompson 1986). Thus, there appears to be less synchrony of gametogenic processes at the southern extreme of *P. magellanicus'* range. Estimated water temperatures in the mid-Atlantic Bight differ from other scallop resource areas and may be responsible for the observed deviations in the gametogenic cycle between geographic locations. High water

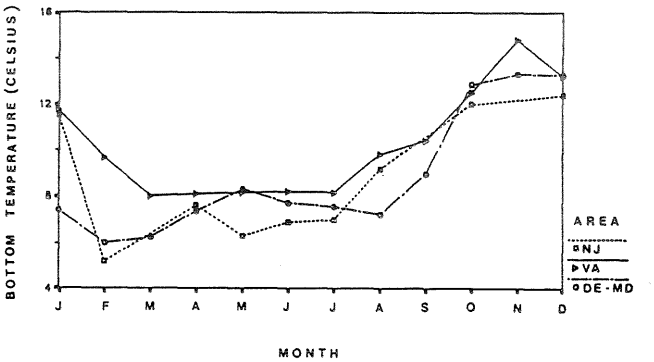

Figure 5. Monthly estimated bottom water temperature (Celsius) at the Virginia (Va), Delaware-Maryland (De-Md), and New Jersey (NJ) sampling areas.

temperatures in fall and winter in the mid-Atlantic Bight are caused by slope water intrusion (O'Reilley et al. 1987, Mountain, personal communication). At the southern region of the shelf, slope water extends onto the shelf to at least the 60 m line in fall and winter, causing an increase in bottom water temperature at that time despite the cooling and mixing of surface waters. Presence of the warm nitrate-rich slope water subsequently elevates primary production. The elevated productivity could provide the energy necessary to sustain gonadal development from December through April. Scallops on Georges Bank, without access to this energy source and subjected to cooler water temperatures, may not be energetically capable of undergoing gonadal development in the winter.

Although histological quantification of gonad tissue provides very accurate information on reproduction, it is costly and labor intensive, and thus, may be prohibitive to fishery management agencies desiring a long-term monitoring program. Morphometric changes in reproductive organs offer an accurate alternative approach. The similarity of results from morphometric measurements and histological quantification of gonadal material verified that future monitoring of gonadal development could be accurately conducted through measurement of wet or dry gonad weights.

Sea scallop management strategies that consider recruitment models or seasonal meat count adjustments related to annual spawning event may not be consistent when a significant part of the commercially harvestable resource exhibit biannual spawning. Meat count adjustments to compensate for spawning induced changes in meat yield should follow documented seasonal reproductive patterns to be effective. However, the critical issue for management will center around whether or not both spawning events contribute to the recruitment of commercially harvestable scallops.

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