1991

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Journal of Shellfish Research, Vol. 10, No. 2, 389–394, 1991.

TEMPORAL VARIATIONS IN SPAWNING BEHAVIOR OF SEA SCALLOPS, *PLACOPECTEN MAGELLANICUS* (GMELIN, 1791), IN THE MID-ATLANTIC RESOURCE AREA[1]

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ABSTRACT Interannual variation in spawning of *Placopecten magellanicus* (Gmelin) may be important to management agencies concerned with maximizing yield-per-recruit via restrictions on meat counts or temporal restrictions on catch and effort. In this study, temporal patterns in the spawning behavior of sea scallops in the Mid-Atlantic resource area for the period April 1987–April 1991 are analyzed using conventional time-series methods. Biannual spawning was found to be characteristic of sea scallops in the Mid-Atlantic resource area but was also found to be erratic in the timing, duration, and magnitude. The spring spawning event was the more predictable and dominant spawning event. The fall spawn was temporally-erratic; it did not occur in 1989. Longer time-series and analyses of environmental factors are recommended to more precisely determine the gametogenic and spawning cycle of sea scallops in the Mid-Atlantic resource area.

KEY WORDS: temporal spawning behavior, *Placopecten magellanicus*, gonadal weight

INTRODUCTION

The Mid-Atlantic resource area has become increasingly important to the United States sea scallop, *Placopecten magellanicus* (Gmelin), commercial fishery. The Mid-Atlantic resource area accounted for approximately 40% of the total reported U.S. landings of sea scallops between 1980 and 1990 (National Marine Fisheries Service 1989). Landings from the Mid-Atlantic area, however, have varied widely; between 1980 and 1990, landings ranged from a low of 1700 mt in 1982 to 7900 mt in 1987. In more recent years, landings have exhibited less annual variation.

Reasons for the variation in production between 1980 and 1986 and the subsequent reduced variation since 1987 probably reflect patterns in recruitment. The pre-recruitment and recruitment indices for the Mid-Atlantic resource area indicate considerable variation between 1980 and 1985 and consistently increasing levels since 1986 (National Marine Fisheries Service 1990). Consistently strong recruitment is thought to be a major reason why the Mid-Atlantic resource has not dramatically declined given the high level of landings in the past 5 years.

The occurrence of recruitment is not the only important consideration in assessing the relationship between resource levels and landings. DuPaul et al. (1989) and Schmitzer et al. (1991) demonstrated a biannual spawning pattern for sea scallops in the Mid-Atlantic resource area. Depending upon weather and other environmental factors, biannual spawning could affect recruitment patterns and the timing and magnitude of recruitment. DuPaul et al. (1989) and Schmitzer et al. (1991), however, only examined the 1988 gametogenic cycle; thus, it is unknown whether biannual spawning is a consistent characteristic of sea scallops in the Mid-Atlantic resource area. In addition, it is not known if there is a dominant spawning event.

Extensive studies on the gametogenic and spawning cycle of the giant sea scallop have been conducted by other researchers (Welch 1950, Posgay and Norman 1958, Naidu 1970, MacDonald and Thompson 1986, 1988, Barber et al. 1988). Most of the studies have limited attention to the gametogenic cycle of sea scallops in areas other than the Mid-Atlantic and over a relatively short time period—1–2 years. Conclusions derived from these studies may not apply to the Mid-Atlantic area or the long-run.

Naidu (1970) and other researchers (Sastry 1966, Newell et al. 1982, Rodhouse et al. 1984, MacDonald and Thompson 1988) have suggested the gametogenic cycle and spawning pattern may vary over time in response to environmental factors. As illustrated in Schmitzer et al. (1991), variations in the gametogenic cycle and spawning events have important ramifications for management of the fishery. Given the limited knowledge available on spawning behavior of scallops in the Mid-Atlantic area and the associated implications for management, there is a need to better understand the gametogenic cycle and spawning behavior over a longer period of time than considered in previous studies.

In this paper, temporal or short and long-run patterns in the gametogenic or gonadal cycle are examined. Analysis of variance and Scheffe tests are used to characterize major and minor spawning events. Univariate time-series models of monthly mean values of wet gonad weights between April 1987 and April 1991 are estimated and used to analyze the timing, magnitude, duration, and periodicity of spawning events.

MATERIALS AND METHODS

Since April 1987, data relating to growth and gametogenesis of scallops in the Mid-Atlantic area have been collected on a weekly basis; data collection activities and sampling procedures are described in DuPaul et al. (1989), Kirkley and DuPaul (1989), and Schmitzer et al. (1991). For this study, whole fresh or unshucked scallops were obtained from commercial fishing vessels operating from south of Long Island (40° 00′ N 73° 00′ W) to north of Cape Hatteras (37° 30′ N 74° 30′ W) (Figure 1).

A total of 449 samples comprised of 19,351 observations on wet gonadal weight measured to the nearest 0.1 g were examined for this study. Data were pooled over sex and geographical areas and subsequently over 4 shell-height groups (85–89 mm, n = 5698; 90–94 mm, n = 6145; 100–104 mm, n = 4463; 110–114 mm, n = 3045). Pooling over sex and area was necessary because of the large number of observations and the inability to visually

[1]Contribution No. 1709 from The Virginia Institute of Marine Science, Gloucester Point, Virginia.

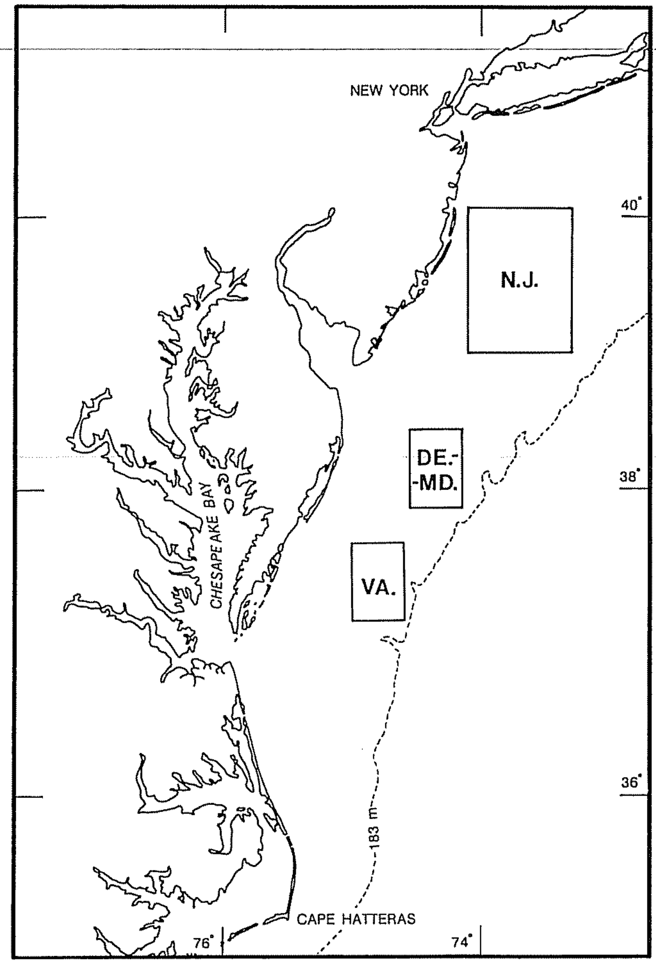

Figure 1. Virginia (VA), Delaware-Maryland (DE-MD), and New Jersey (NJ) sampling areas withing the Mid-Atlantic Bight.

determine sex during several months and to define area-specific subpopulations of *Placopecten magellanicus*. The shell-height intervals, although arbitrarily determined, were consistent with National Marine Fisheries Service shell size intervals and indicative of the commercial size distribution. Mean gonad weights for the 4 shell-height groups were subsequently calculated and analyzed to determine temporal patterns in spawning events.

Analysis of the gametogenic cycle and related spawning events was accomplished by several statistical procedures and time-series models. Initially, one-way analysis-of-variance (ANOVA) and Scheffe tests were used to determine temporal similarities and differences in spawning events. Maximum gonad weights during spring and fall months were examined for equality of means between 1987 and 1990. Minimum gonad weights during summer months were similarly examined. Analysis-of-variance, however, does not facilitate examination of periodicity, duration, and relative magnitude of spawning events.

Several time-series methods were used to examine temporal spawning patterns as it has become increasingly apparent in recent years that time-series methods are particularly appropriate for analysis of many fishery-related phenomena (Kirkley et al. 1982, Squires 1986, Fogarty 1988). Time-series methods can be used to specifically determine periodicity, duration, and magnitude of temporally-related events. These methods appear to be particularly well-suited for determining cycles and predicting future values.

Time series data (e.g., means of monthly gonadal weights) are typically comprised of 4 components:

$$GW_t = f(S_t, T_t, C_t, E_t)$$

where GW_t is monthly mean value of gonadal weight at time t, S_t is a seasonal component, T_t is a trend component, C_t is the cyclical component, and E_t is an error or random component often referred to as "noise." Seasonality and trend indicate periodic fluctuations of constant length and the long-run behavior of a data series. The cyclical component indicates longer-term fluctuations in the data and tends to vary in length and magnitude; it is often characterized as being of an erratic or irregular nature. The 4 components may be additive, multiplicative or some combination of the two.

Normalized seasonal indices (medial average adjusted so that the sum of seasonal indices equals 1200) of monthly mean gonadal weights were calculated, and classical and Census II decomposition methods were used to examine the four components; these methods are described in Makridakis et al. (1983). Decomposition methods do not, however, facilitate modeling or predicting noise or randomness. Additional time-series methods that permit examination of noise were used to further examine the gametogenic cycle and spawning behavior of sea scallops. These other methods included exponential smoothing, Box-Jenkins (1976), and state-space (Akaike 1977, Goodrich 1989).

RESULTS

Visual examination of mean monthly gonadal weights for the 4 shell-height groups suggests biannual spawning during spring and fall and some consistency in the gametogenic cycle (Figure 2). Gonadal weights typically increased in January; they obtained maximum values between February and April; by June, gonads appeared to be nearly or completely spent. Gonadal weights were typically low between June and August which was indicative of the resting stage identified by Schmitzer et al. (1991). Gonadal weights generally increased again in September and obtained local (a peak or trough but not the most extreme peak or trough for a year) maximum values by October. Gonads were completely or almost completely spent by November.

The mean monthly gonadal weights depicted in Figure 2 indicated global (the most extreme peak or trough for a year) and local maximum values in spring and fall, respectively. Mean values also suggested similarities and differences in spawning events between 1987 and 1990. Changes in gonadal weights during spring 1988 and 1989 were quite similar; weights increased in January and obtained nearly equal maximum values between January and

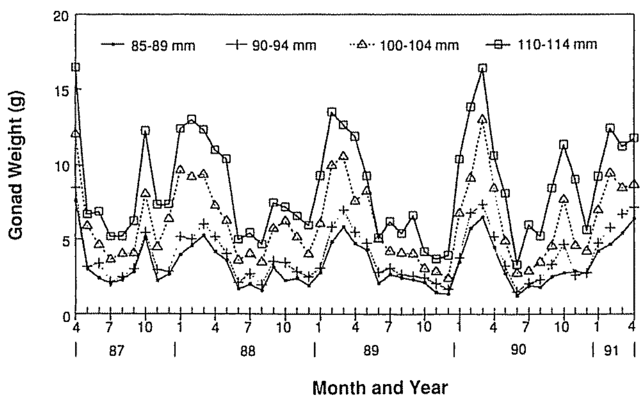

Figure 2. Mean monthly gonadal weights for 4 shell-height intervals of sea scallops in the Mid-Atlantic resource areas, 4/87–4/91.

April. Spawning, as indicated by a large decrease in gonadal weight from a peak value, occurred in June of both years. The fall spawn, however, exhibited a different temporal pattern between 1987 and 1990. In 1988, all 4 shell-height groups appeared to exhibit some level of spawning activity; in 1989, only the 110–114 mm scallops exhibited any fall spawning activity. Spring and fall gonadal patterns for 1987 closely resembled the patterns of 1990 but were quite different than the patterns of 1988 and 1989.

Equality of mean gonadal weights for 100–104 mm scallops over 1987–1990 was rejected by ANOVA and Scheffe tests for all three seasons at the 0.01 level of significance (Table 1). Similar results were obtained for the 3 other shell-size intervals. Maximum mean values for spring were more consistent over the 4 years than they were for fall or summer; differences were detected between 1988 and 1990 and 1989 and 1990. Fall and summer exhibited considerable differences in mean values. Fall pairwise equalities were rejected for all years except 1987 and 1990 and 1988 and 1990. Results of the Scheffe tests suggested that the gonadal cycle did not follow a consistent long-run trend (e.g., maximum mean gonad weights for spring and fall did not consistently increase or decrease from year-to-year).

Examination of the percentage distribution of gonads for 100–104 mm shell height scallops exceeding the mean values also suggested that the spring spawn dominated the fall spawn (Figure 3). Approximately 46% of the sample observations for spring exceeded the mean values, whereas, only 42% of the fall sample observations exceeded the mean values (Table 2). Moreover, maximum spring gonadal weights were consistently higher than maximum fall gonadal weights and exhibited less variation. Similar conclusions were obtained for the other three shell-height groups.

Data plotted in Figure 2 adequately depict seasonal patterns, but normalized seasonal indices provide a more discernible general pattern of seasonality for the gametogenic cycle (Table 3). Indices suggested general seasonal spawns between April and June and October and November. The indices also suggested possible differences in spawning events of different size scallops. For example, indices of gonadal weights for the 85–89 mm shell-height group suggested a temporally-irregular fall spawn.

Seasonal indices only indicate general seasonal patterns in the gametogenic cycle. They do not indicate variations in the month-

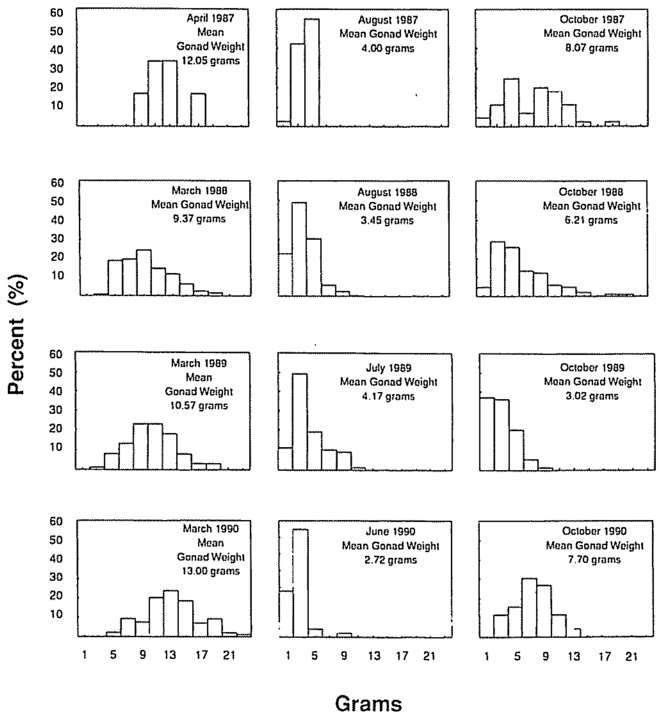

Figure 3. Percent distribution of seasonal maximum and minimum gonadal weights for 100–104 mm shell-height group during annual gametogenic cycle, 1987–1990.

TABLE 1.

Results of analysis of variance (ANOVA) and Scheffe tests of equality of means for 100–104 mm scallops.

Season	Mean Gonad Weight (g)	F-statistic	Pairwise Differences Detected by Scheffe Tests
Spring			
1987	12.05		
1988	9.37	22.32 (3,338)[1]	1988 ≠ 1990[2]
1989	10.57		1989 ≠ 1990
1990	13.00		
Fall			
1987	8.07		1987 ≠ 1988; 1987 ≠ 1989
1988	6.20	41.14 (3,291)	1988 ≠ 1989
1989	3.02		1989 ≠ 1990
1990	7.70		
Summer			
1987	4.00		1987 ≠ 1990
1988	3.45	11.70 (3,508)	1988 ≠ 1989; 1988 ≠ 1990
1989	4.17		1989 ≠ 1990
1990	2.72		

[1] Numbers in parentheses indicate numerator and denominator degrees of freedom, respectively.

[2] Significant differences detected at the 5% level of significance.

TABLE 2.

Maximum spring and fall and minimum summer mean values of gonadal weights (g) and coefficient of variation for 100–104 mm shell height scallops 1987–1990.

Season and Year	Number of Observations (N)	Mean Gonad Weight (g)	Coefficient of Variation (%)	Number and Percent Exceeding Mean Value	
				$N > \bar{g}$	%
Spring:					
1987	6	12.05	23.85	3	50.00
1988	128	9.37	35.99	63	49.22
1989	100	10.57	31.64	51	51.00
1990	108	13.00	28.06	51	47.22
87–90	342	10.92	34.42	158	46.20
Summer:					
1987	40	4.00	24.71	23	57.50
1988	290	3.45	50.15	116	40.00
1989	99	4.17	54.30	38	38.38
1990	83	2.72	44.45	33	39.76
87–90	512	3.51	50.85	191	37.30
Fall:					
1987	45	8.07	47.89	24	53.33
1988	104	6.21	60.88	40	38.46
1989	94	3.02	55.88	33	35.11
1990	52	7.70	33.69	26	50.00
87–90	295	5.74	63.43	123	41.69

TABLE 3.

Seasonal indices of mean values of gonadal weights for 85–89, 90–94, 100–104, and 110–114 mm scallops.

	Shell-height Interval (mm)			
Month	**85–89**	**90–94**	**100–104**	**110–114**
January	114.4	108.0	119.0	125.2
February	147.5	145.9	157.0	155.9
March	175.4	173.8	163.4	146.7
April	146.5	144.1	124.0	128.8
May	108.6	101.0	101.1	106.7
June	61.8	67.3	69.3	62.2
July	68.0	67.0	65.0	67.0
August	66.3	62.0	62.9	59.3
September	86.2	83.3	76.5	88.0
October	81.9	109.0	117.3	110.0
November	73.1	72.1	76.7	82.0
December	70.5	66.3	67.8	67.5

to-month changes in gonadal weight. Based on decomposition analyses, seasonality explained only 34–37% of the average monthly change in gonadal weight of the 4 shell-height groups (Table 4). Noise or randomness accounted for 57–59% of the average per period change. The trend-cycle was relatively unimportant and responsible for no more than 7% of the average monthly change in weight. Analysis of cyclical factors for June-December 1989 indicated a major change in the gametogenic cycle. Values of cyclical factors for this period were very low which suggested a downward shift in the 1989 fall spawning pattern. Interestingly, the months for cyclical dominance (MCD) factor or time it takes the trend-cycle to dominate the noise was approximately 5 months; an MCD of 5 suggested a need for more extensive analysis of the noise.

Exponential smoothing, Box-Jenkins (1976), and state-space models were thus used to further analyze the possible randomness and underlying dynamics. Standard statistical criteria (Akaike and Schwarz criteria and Ljung-Box) suggested the exponential smoothing models did not adequately model the gonadal cycle. The Box-Jenkins models were determined by statistical criteria to better describe the data patterns of gonadal weight for the 4 shell-height groups, but they also failed to adequately model the randomness or noise of the series (Table 5). The models could only explain 70–74% of the monthly variation in mean gonadal weights. Moreover, predictions of 1991 fall gonadal weights were likely incorrect and had large 95% confidence intervals; forecast intervals suggested no spawn and a major spawn.

The Box-Jenkins models for the 100–104 and 110–114 mm shell-height groups both included short-run moving averages of 5. A moving average of order 5 indicated that current values of gonadal weights were explainable by 5 previous forecast errors. The models for the 85–89 and 90–94 mm groups were also similar in structure. Both models had a 1st-order non-seasonal (short-run) and seasonal (long-run) autoregressive component; a moving average component was not supported by analyses of the data.

The estimated state-space models provided more accurate fitted values but likely incorrect predicted values. These models predicted either a minimal fall spawn or no discernible fall spawn for 1991. There are no apparent reasons why there should be no 1991 fall spawn. The approach, therefore, was not further considered in the examination of the gametogenic cycle.

TABLE 4.

Percent variation of month-to-month change in mean values of gonadal weights of 85–89, 90–94, 100–104, and 110–114 mm scallops attributed to trend-cycle, seasonality, and random noise.

Shell Height Interval (mm)	Temporal Factor	Percent Explained by Temporal Factor and Noise (%)
85–89	Trend-cycle	7
	Seasonality	34
	Noise	59
90–94	Trend-cycle	6
	Seasonality	35
	Noise	59
100–104	Trend-cycle	7
	Seasonality	36
	Noise	57
110–114	Trend-cycle	6
	Seasonality	37
	Noise	57

DISCUSSION

Analyses of mean monthly gonadal weights indicated temporal similarities and differences in the gametogenic cycle of *Placopecten magellanicus* in the Mid-Atlantic region. Over a 4 year period, mean values of gonadal weights suggested biannual spawning but erratic temporal patterns. The temporal patterns for

TABLE 5.

Autoregressive-integrated-moving-average (ARIMA) models used to examine the gonadal cycle of 4 shell-height groupings of Mid-Atlantic sea scallops and summary statistics.

Shell height interval	Transformations To Achieve Stationarity	ARIMA Structure or Form of Model and Summary Statistics[1]
85–89	Logarithmic and 1 seasonal difference	ARIMA (1,0,0) $(1,1,0)^{12}$ Ljung-Box: chi-squared (18) = 23.90 R^2 = .72
90–94	Logarithmic and 1 seasonal difference	ARIMA (1,0,0) $(1,1,0)^{12}$ Ljung-Box: chi-squared (18) = 17.66 R^2 = .70
100–104	Logarithmic and 1 seasonal difference	ARIMA (1,0,5) $(1,1,0)^{12}$ Ljung-Box: chi-squared (18) = 17.64 R^2 = .74
110–114	Logarithmic and 1 seasonal difference	ARIMA (1,0,5) $(1,1,0)^{12}$ Ljung-Box: chi-squared (18) = 14.78 R^2 = .70

[1] ARIMA (p,d,q) $(P,D,Q)^s$ is the shorthand notation for autoregressive-integrated-moving-average models. Lower case letters d and D indicate the short-run or nonseasonal differencing and long-run or seasonal differencing required for stationarity; p and P indicate the nonseasonal and seasonal autoregressive nature of the model; q and Q indicate the nonseasonal and seasonal moving average nature of the model; s indicates the length of seasonality.

fall indicated major fall spawns in 1987 and 1990 and minimal or negligible spawns in 1988 and 1989. In contrast, the temporal patterns for spring were less erratic which is likely indicative of a dominant or major spawning event. Seasonal indices suggested more regularity in spawning events and greater fecundity per individual scallop in the spring; Schmitzer et al. (1991) obtained the latter conclusion via histological analysis.

Although statistical results obtained in this study appear reasonable, they may be biased because of pooling data over sex and area. Pooling may obfuscate patterns of the timing of spawning events by different sexes and in different areas. A small change in the mean value of gonadal weight may erroneously suggest minor spawning events or changes in the reproductive cycle. Alternatively, periods and magnitudes or duration of spawning events determined from analyses of pooled gonadal weights may be imprecise.

Unfortunately, analysis of the gonadal cycle of *Placopecten magellanicus* by sex and area would be costly and difficult. The laboratory work necessary to accurately determine sex would be expensive and time consuming, and area-specific or spatial subpopulations of scallops in the Mid-Atlantic resource area are not defined. Moreover, Schmitzer et al. (1991) found that although a detailed analysis provided a more accurate determination of the reproductive cycle, analysis of gonadal weights pooled over sex and areas was sufficient to determine the general gonadal cycle of sea scallops in the Mid-Atlantic region.

Conclusions about the regularity and dominance of the spring spawn in the Mid-Atlantic resource area differ from previously accepted conclusions about the spawning pattern of Mid-Atlantic and Georges Bank scallops (MacDonald and Thompson 1988, Posgay and Norman 1958, MacKenzie et al. 1978, Robinson et al. 1981). Interestingly, temporal regularity in the fall spawn in the Mid-Atlantic was rejected by analyses of data; the fall spawn appeared to be erratic from year-to-year and nonexistent in 1989.

The absence of an observed 1989 fall spawn may be the result of meterological events. Hurricane Hugo and several tropical storms occurred in the Mid-Atlantic during October 1989; these storms may have affected normal temporal-related spawning events. Alternatively, the conclusion of no 1989 fall spawn may be associated with possible biases of the data which may have occurred because of the storms. Samples for all weeks of October, however, were obtained, and geographical coverage of the samples remained unchanged relative to samples obtained in other months. Interestingly, analysis of cyclical factors suggested a major downward shift in 1989 fall spawning events (i.e., a temporal intervention).

Unfortunately, extensive time-series analyses of the data failed to adequately characterize short and long-run patterns of the gonadal cycle. General or average seasonal patterns were detected but lacked precision. There was no evidence of a consistent trend in gonadal weight between 1987 and 1991. Cyclical influences, although contributing to variations in weight over the 4 years, were not predictable. At best, the time-series analyses permitted determination of basic patterns of the gonadal cycle; the analyses and models, however, were inadequate for predicting future spawning events.

Failure of the time series approaches to adequately predict future spawning events does not imply, however, that these approaches lack merit. For one thing, the time-series approaches facilitated determination of general seasonal and cyclical patterns and demonstrated an absence of a long-run trend. More important, associated analyses suggested that shocks or stochastic signals of lag 5 substantially affected spawning events. It is not known why stochastic shocks to the system 5 periods ago would affect the current values. This result may be an anomaly caused by the magnitude and duration of the spring cycle (January–May). The time-series analyses also indicated that numerous interventions or innovations affected the spawning pattern of *Placopecten magellanicus* between 1987 and 1991; these interventions may be associated with meterological events. Last, the time-series approaches indicated a need for longer time series and continued routine monitoring of the gonadal cycle in order to accurately determine the occurrence and temporal pattern of spawning.

Based on the statistical and time-series analyses, the gonadal cycle of sea scallops in the Mid-Atlantic resource area appears to be best characterized as a series of interventions or shocks. There are similarities over time, but for the most part, the timing, duration, and magnitude of spawning events appear to vary widely. These conclusions are not particularly startling given that Naidu (1970) and Rodhouse et al. (1984) demonstrated that environmental factors play a large role in spawning behavior.

Although environmental factors were not considered in this study, results of the time-series analyses indicated that influences other than temporal factors affected spawning. After extracting all temporal related patterns from the gonadal weight data, 25–30% of the variation could not be explained. Considerable attention, thus, needs to be given to examining other factors that may influence the gametogenic cycle and spawning behavior.

The inability to determine the gametogenic cycle and spawning behavior with a high degree of precision may be one reason why it has been difficult to determine an adequate stock-recruitment relationship for *Placopecten magellanicus*. Alternatively, the spring spawn, although consistently occurring, varies widely in magnitude, and the fall spawn varies in timing, magnitude, and duration. Biannual spawning and irregular periodicity of spawning events suggest recruitment may be erratic and occur more than once a year. Empirically determined stock-recruitment relationships that assume single-period, knife-edge recruitment, thus, may be inadequate characterizations of the stock-recruitment relationship of sea scallops in the Mid-Atlantic.

ACKNOWLEDGMENTS

We thank the owners, captains, and crew of Seaford Scallop Company who donated the sea scallops for this project. We are particularly appreciative of the data collection support provided by W. Wells, D. O'Neal, B. Brauer, B. Rose, R. Stotz, E. Berg, and the East Coast Fisheries Association. We remain indebted to the Virginia Sea Grant College Program which provided partial funding for the research. We thank Roger Mann, Maurice Lynch, George Grant, Sandra Shumway, and two anonymous reviewers for constructive advice and comments on an earlier draft of this paper.

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