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## Gonadal Cycle of Northern Quahogs, *Mercenaria mercenaria* (Linne, 1758), from Fished and Non-fished Subpopulations in Narragansett Bay

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### Keywords

Quahog; Mercenaria; fecundity; condition index; gonadal index; high density populations; NarragansettBay; hard clam

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## GONADAL CYCLE OF NORTHERN QUAHOGS, *MERCENARIA MERCENARIA* (LINNE, 1758), FROM FISHED AND NON-FISHED SUBPOPULATIONS IN NARRAGANSETT BAY

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**ABSTRACT** To determine if population density in areas closed to fishing in Narragansett Bay is causing differences in the reproductive potential of the organisms, this study used two approaches to determine the reproductive condition of the animals. The first approach consisted in employing a gravimetric condition index (CI) to evaluate the general condition of quahogs from nine different sites, 3 sites open conditionally for fishing (conditional areas) and 6 sites closed to fishing. The second approach was a determination of gonadal index (GI) of a subset of the sample sites, by histological observation of gonadal tissue sections. Initial sampling included determination of CI only, and lasted from March 25 to Sep. 22, 2005. The subset of six of the sites was sampled the next year (2006), every three weeks from April 15 until Sep. 28 to determine CI and the gonadal index (GI). Results show that there is a significant difference between the CI of northern quahogs from conditional areas and quahogs from closed areas ( $P < 0.001$ ). There is a significant difference in GI between sites at ( $P < 0.10$ ). The GI in conditional areas was consistently higher than in closed sites indicating that maturation and reproductive stages are more prevalent in conditional areas than in closed sites. When sites were separated into three categories: conditional fishing sites; coves; and Providence River sites, the GI and CI of the conditional areas were always higher than the CI and GI of all the other sites. The coves had intermediate indices, and the Providence River sites always had the lowest indices. The results indicate that the populations of quahogs in the closed sites sampled are not completing the gonadal cycle as expected and that the reproductive capability of the quahogs in conditional areas is higher than those in closed areas. Possible explanations to this condition include lower water quality in the closed areas, low dissolved oxygen concentration especially during the summer, poor bottom conditions and high population density. Although, not one single characteristic of the environment is solely responsible for the reproductive condition of the quahog population, density appears to have significant effect.

**KEY WORDS:** Quahog, *Mercenaria*, fecundity, condition index, gonadal index, high density populations, Narragansett Bay, hard clam

### INTRODUCTION

Since 1954 the State of Rhode Island has undertaken different projects to enhance the natural northern quahog population and to allow for biomass rebuilding. Those include: a set of management areas and a rotational transplant/harvest system to manage the resource; permanent and/or seasonal, conditional pollution closures; and possession limits (Rice et al. 2000, Rhode Island Fisheries Stock Status 2004). In recent years, as part of the re-evaluation of management practices, the transplant of quahogs is being questioned (Rice 2006). Because pollution closure areas are characterized by having high population density (Rice et al. 1989, Walker 1989), there has been some discussion whether pollution closure areas, which serve as a source of relay stock, do in fact serve as spawner sanctuaries so that the relocation of its shellfish stock is unnecessary (Pratt 1988).

Opponents to this view of unexploited “old growth” stocks serving as *de facto* spawner sanctuaries state hypothetically that populations of large suspension feeders may be regulated by intraspecific competition for food or space. High population densities may deplete the food resources of overlying water masses to a critical level resulting in depressed rates of growth, survivorship, and/or fecundity (Peterson & Andre 1980, Maurer 1983) or inhibiting recruitment if adults filter settling larvae from the water column, as suggested by Woodin (1976).

Opinions differ widely on whether food is limiting to suspension-feeding populations (reviewed by Buss & Jackson 1981). However, there is good evidence to support the hypothesis of intraspecific and interspecific competition in bivalves (Peterson & Andre 1980, Peterson 1983), which may result in the reduction in reproductive output relative to that attainable in less dense assemblages. In species such as *M. mercenaria* where there is little storage of food reserves, and gonadal development presumably takes place in response to food availability in the environment (Ansell 1967, Ansell & Loosmore 1963, Bricelj & Malouf 1980) intraspecific competition for food may have an even greater influence on reproductive potential. However, unequivocal evidence of competition requires the demonstration that the reproductive output of an individual is reduced as a consequence of the exploitation of (or interference with access to) a resource by the presumed competitor (Hayward & Ryland 1975, Buss & Jackson 1981).

The first stock recruitment model for *M. mercenaria* proposed by Kraeuter et al. (2005) discusses how it has been hypothesized that large densities can limit the recruitment of larvae. The authors conclude that whether negative density-dependent factors, equivalent to the compensatory effects hypothesized for fish populations exist in natural bivalve populations is unknown, but growth inhibition and implied reductions in fecundity have been found in high densities of some bivalve species (Kraeuter et al. 2005).

The best way to assess the real reproductive potential of an organism is through the direct study of the reproductive cycle and the microscopic examination of the reproductive organs and the gonads of the populations in question. By following the

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progress of gonad and gamete production, the timing and duration of spawning events can be determined (Ropes & Stickney 1965, Corni et al. 1985, Hooker & Creese 1995, Gribben et al. 2001). A knowledge of spawning periods is also needed for assessing larval abundance (Ropes & Stickney 1965), predicting periods of annual recruitment (Keck et al. 1975, Manzi et al. 1985) and for interpreting growth rates and mortality data (Keck et al. 1975). Ultimately, all these factors influence the distribution and abundance of juvenile and adult populations (Hooker & Creese 1995, Gribben et al. 2001). The documentation of gametogenesis in a fishery resource is the first logical step in estimations of population recruitment (Manzi et al. 1985).

To fully understand the reproductive potential of the quahogs in Narragansett Bay, it is therefore important to study the gonadal development of the different populations of quahogs. This study is intended to evaluate and describe the gonadal development in different areas of Narragansett Bay and to determine if there were differences in the gonadal cycles of quahogs depending on their location (i.e., from areas long-closed to fishing versus other locations). Additionally, our aim is to determine the correlation between the condition index and gonadal development and to determine if condition index can be used as an indirect, but reliable, indicator of the reproductive potential of the different subpopulations. These data may be of use by shellfishery resource managers in making decisions about programs designed to increase shellfishery production by either thinning populations of quahogs in dense assemblages in coves and/or maintaining transplant sites in open waters to act as spawner sanctuaries.

#### MATERIALS AND METHODS

All nine sites (Table 1) were sampled seven times with a commercial bullrake aboard the F/V *Thomi Boy* during the summer of 2005 for condition index (CI) determination. Six of

those sites were also sampled nine times, every 3 wk, from late spring to the end of the summer of 2006, starting on April 15, and finishing on September 30 for CI and gonadal index (GI) determinations. Twenty quahogs were collected from each site in 2005, and 35 quahogs were collected from each site on each sample date in 2006; 20 for CI determination and 15 for gonadal index (GI) determination.

A gravimetric relative condition index was used, using the procedures and formula of Crosby and Gale (1990):

$$CI = [\text{dry soft tissue wt (g)} \times 1,000] / \text{total weight (g)} \\ - \text{shell weight (g)}$$

All weights were estimated to the nearest 0.1 g. Dry soft tissue weight was estimated after 48 h of drying time at 80°C. The histological technique used in this study followed the techniques described in Howard and Smith (1983) and Eversole (1997). Each individual was classified by sex and in one of seven qualitative gonadal stages: inactive, early active, late active, ripe, partially spawned, spent, and regression (Gribben et al. 2001; adapted from Porter 1964, Keck et al. 1975, Ropes 1968, Velez & Epifanio 1981).

Each gonadal stage (Table 2) was assigned a Gonadal Index (GI) value, according to (Eversole 1997), to facilitate statistical analysis.

The assigned GI values are: Inactive (0); Early active (1); Late active (2); Ripe (3); Partially Spawned (2); Spent (1); Regression (0).

These GI values were assigned such that the highest number, ripe (3), corresponds with the greatest amount of ripe gametes contained within the gonad, and therefore presumably those with the greatest spawning potential.

Thirty oocytes, from five haphazardly chosen follicles, from each one of the females in the ripe stage of development were measured using the Image Pro Plus image analysis program. Oocyte diameter was determined using a calibrated measure

TABLE 1.  
Geographical location and general characteristics of sample sites. Approximate depths are from bathymetric charts of Narragansett Bay.

Site (management strategy)	Geographic Location	Approximate Quahog Density (#/m <sup>2</sup> ) (Reference)	Approximate Depth (m)	Reference in Text & Tables
Conditional Area A (conditionally open for fishing)	41°42'29"N-71°20'18"W	5.2 (Rice 1999)	7.5	A
Conditional Area B (conditionally open for fishing)	41°40'47"N-71°20'37"W	5.2 (Rice 1999)	7.5	B
Providence River site 1 (closed to fishing)	41°45'04"N-71°22'13"W	12.5 (Rice 1999)	9.0	P
Providence River site 2 (closed to fishing)	41°44'04"N-71°21'53"W	12.5 (Rice 1999)	9.0	R
Greenwich Cove (closed to fishing)	41°40'05"N-71°26'33"W	12 (Lazar et al. 1995)	3.0	G
Warwick Cove (closed to fishing)	41°41'06"N-71°23'28"W	30 (Lazar et al. 1995)	3.0	W
Apponaug Cove (2005 only) (closed to fishing)	41°41'26"N-71°26'40"W	16 (Lazar et al. 1995)	3.0	AP
Greenwich Bay (2005 only) (managed winter fishery)	41°40'40"N-71°24'50"W	4 (Lazar et al. 1995)	4.5	GB
Allen Harbor (2005 only) (closed to fishing)	41° 37'26"N-71°24' 50"W	21.75 (Murphy et al. 2005)	3.0	AH

TABLE 2.

Description of the stages of gonadal development in northern quahogs (*Mercenaria mercenaria*). Taken from: Gribben et al. (2001), who adapted it from Porter (1964), Keck et al. (1975), Ropes (1968), and modified by addition of description of regression stage from and Velez and Epifanio (1981).

Stage	Males	Females
Early active	Follicle walls thick, lined with thick layer of spermatogonia occupying up to a third of follicle area. Spermatocytes and spermatids develop in the middle of the follicle.	Thick follicle walls, often contracted. A lot of ovogenic activity with many oogenesis and primary oocytes attached to the follicle walls. Mature oocytes and ova present. Gonad volume is small. There is often a lot of connective tissue visible within the gonad.
Late active	Follicle walls are thin. Spermatogonia restricted to lining the follicle walls. Follicle dominated by dense areas of spermatids and spermatocytes. Spermatozoa more abundant than early active.	Follicle walls are not as thick. There are a lot more ova and mature oocytes than in the early active stage, often attached to the follicle wall by a thin stalk. There are fewer primary oocytes. Mature oocytes are often rectangular or polygonal in shape.
Ripe	Spermatogonia as for late active. Follicle dominated by very dense spermatozoa with tails pointing into the lumen. Spermatids and spermatozoa occupy less follicle volume. Gametes occupy nearly all the gonad volume.	Follicle walls are thin and full of ova often lying free in the lumen. There is little ovogenic activity within the follicle except for a few mature oocytes. Ova are usually spherical in shape.
Partially spawned	Spermatozoa still occur in the follicle but with large gaps. Center of the lumen often appears empty. Spermatogonia intrude further into the follicle although no more abundant than in the previous stage. Spermatids and spermatocytes less dense but still fairly common.	Follicles are large with very thin walls often ruptured. There are usually large spaces within the lumen, although free ova are still frequent within lumen of the follicle. There are still mature oocytes present.
Spent	Follicle walls are thickened. Few spermatogonia still present, with few unspawned spermatids, spermatocytes, and spermatozoa still remaining. Gametes occupy very little of the gonad volume.	Spawned; the follicle is essentially empty with a few ova still free in the lumen. Follicle walls may be contracted and thickened with connective tissue.
Regression	Some mature spermatocytes free in lumen, thickening of follicle walls. No evidence or rupture of follicle walls to indicate gamete release.	Ripe oocytes free in lumen, but apparent deterioration and thickening of follicle walls. No evidence or rupture of follicle walls to indicate spawning.

and measuring the microscopical digital image of each oocyte. Mean oocyte diameter of the 30 oocytes was calculated for each female. Mean oocyte diameter by site was also calculated (modified from Gribben et al. 2001).

All quahogs were measured to the nearest 1 mm with vernier calipers (Table 3) according to the length, height, and width dimensions described by Belding (1931), and Ropes (1987). Internal shell surface was also visually examined to determine and record the frequency of scars, which were used as an indirect evidence of stressing conditions, particularly hypoxia, suffered by the quahogs (Kennish 1978, Alexander & Baron 2003). Scars were defined as palpable and visible abnormal

calcifications on the inner shell surface. Because of the nature of the data, only nonparametric statistics were used.

## RESULTS

Quahogs collected from the various sites ranged in mean lengths from 56 mm  $\pm$  7 SD ( $n = 35$ ) at Conditional Area A that is open to fishing and 78 mm  $\pm$  7 SD ( $n = 35$ ) at the Providence River site 1 that is closed to shellfishing. Results of condition index and gonadal index at the various sites are summarized on Tables 4, 5, and 6. For most statistical analyses and comparisons, data from sites A, B, P, R, G, and W from the 2006 data set of CI and GI values were used because the data were collected simultaneously. Because of the nature of the data, only nonparametric statistics were used in the analysis.

### Condition Index

The CI values showed great variability between sites and within sites (Tables 4 and 5). However, at the beginning, and at the end of the sampling period, CI values from all sites were much closer together than they were during the midportion of the sampling period. When grouped by type of site into three categories (Fig. 1): conditional areas, Providence River sites and coves; the conditional areas consistently had the highest CI values, ranging from 45.7–265.6 (both sites combined), with a combined mean of 91.8. Coves had intermediate CI values, ranging from 29.1–224.6, with a combined mean of 73.5. The

TABLE 3.

Mean quahog (*Mercenaria mercenaria*) measurements in mm ( $n = 35$ ) by collection site; SD = standard deviation.

Site	Length (SD)	Height (SD)	Width (SD)
A	60 (8)	50 (6)	31 (5)
B	56 (7)	47 (6)	29 (4)
P	78 (7)	66 (6)	42 (5)
R	77 (6)	65 (5)	43 (5)
G	59 (6)	50 (5)	32 (4)
W	69 (10)	57 (8)	37 (6)

TABLE 4.

Condition Index by site and by sample date for 2005. SD = standard deviation ( $n = 20$ ). A: Conditional Area A; B: Conditional Area B; P: Providence River Site 1; R: Providence River Site 2; G: Greenwich Cove; GB: Greenwich Bay; AP: Apponaug Cove; W: Warwick Cove; AH: Allen's Harbor. Sites with the same superscript (<sup>a, b</sup>) are not significantly different from one another. Different superscripts indicate significant differences among sites ( $\alpha = 0.05$ ) using the Wilcoxon rank-sum test. Data preliminarily reported by Grant and Rice (2006).

Site	Julian Date/Mean Condition Index															Overall Mean
	84		125		144		167		205		241		265			
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD		
P <sup>a</sup>	54.6	8.2	58.1	13.6	73.5	9.7	78.2	16.0	70.7	10.8	60.8	13.4	69.7	12.0	66.5	
R <sup>a</sup>	64.0	13.2	66.1	13.4	69.5	10.0	77.0	14.5	67.5	10.0	62.8	9.4	64.2	10.6	67.3	
A <sup>b</sup>	93.6	26.1	91.7	21.3	107.3	10.05	116.2	11.9	96.0	15.8	90.1	6.3	91.7	8.0	98.0	
B <sup>b</sup>	75.8	17.2	87.3	17.3	109.2	8.7	108.9	11.9	98.9	22.5	89.3	6.5	97.4	8.7	95.3	
W <sup>a</sup>	63.8	12.5	66.5	8.8	69.5	17.5	69.8	8.3	68.8	8.0	65.6	7.5	61.4	13.5	66.5	
G <sup>a</sup>	75.8	18.3	73.9	14.4	69.7	11.2	73.5	15.5	61.3	15.1	64.9	13.4	58.5	12.5	68.2	
GB <sup>b</sup>	76.3	14.8	85.0	10.8	93.5	9.5	89.7	9.6	86.7	15.5	77.2	10.3	75.1	11.6	83.4	
AP <sup>a</sup>			83.1	12.9	86.3	8.0	99.2	15.3	74.9	8.8	74.5	11.4	70.5	7.3	81.4	
AH <sup>a</sup>	78.5	9.1	85.8	13.0	91.3	21.0	82.7	6.0	77.2	8.2	76.8	10.3	79.4	19.8	81.7	

Providence River sites consistently showed the lowest mean CI values, which did not change much during the sampling period, except close to the end of the sampling period, in autumn when they increased slightly (Fig. 1). The CI of the Providence River sites in 2006 ranged from 24.3–121.5, with a combined mean of 68.2 (Table 5).

There was a significant difference in CI among sites ( $P < 0.001$ ). Wilcoxon-rank sum tests found a significant difference in CI between conditional and closed sites ( $P < 0.001$ ) in 2005 and 2006. CI among closed sites was found to be not significantly different. The comparison between the CI of from quahogs from areas conditionally open to fishing was not significantly different as well in both years. These results suggest that the significant difference among sites, found when comparing all sites, was because of differences between closed and conditional areas and not to a difference among sites under the same management category (either closed or conditionally open to fishing). Details of the contingency tables can be found in Marroquin-Mora (2007).

When comparing CI of each site between our data from 2005 and 2006 no significant difference was found for site A. However, a significant difference between years was found for

sites B, P, R, G, and W. In all cases, the CI averages at sites in 2006 were higher than those estimated in 2005 (Tables 4 and 5).

#### Gonadal Index

Great variability was found in the GI index between sites, and within sites (Table 6). There was a tendency for conditional areas to have higher GI than closed sites. When separating sites among conditional areas, Providence River sites, and coves, (Fig. 2) it was evident that the gonadal development was delayed in the two Providence River sites, and their population of quahogs never reached a mean GI as high as the GI from the conditional areas. In the case of the coves, even though the gonadal development was slightly delayed when compared with the other sites, it reached higher mean values than in the Providence River sites. However, it never reached the values of the GI in the conditional areas.

Mean GI in the Providence River sites ranged from 0.7–2.4, with a combined mean of 1.5. In the coves mean GI ranged from 0.8–2.6 with a combined mean of 1.9. Finally, the GI in the conditional areas ranged from 1.1–2.9, with a combined mean of 2.0 (Table 4). The low GI found in the Providence River sites

TABLE 5.

Condition Index by site and by sample date for 2006. First column are sample dates, expressed as Julian Dates. Data represent mean Condition Index of the sample (on each date  $n = 20$  quahogs), SD = standard deviations. A: Conditional Area A; B: Conditional Area B; P: Providence River site 1; R: Providence River site 2; G: Greenwich Cove; W: Warwick Cove. Sites with the same superscript (<sup>a, b</sup>) are not significantly different from one another. Different superscripts indicate significantly different sites ( $\alpha = 0.05$ ).

Site	Julian Date/Mean Condition Index																		Overall Mean
	105		126		147		168		186		210		231		252		273		
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
P <sup>a</sup>	64.6	11.6	62.4	21.9	60.7	14.3	68.5	15.9	72.9	15.3	68.4	12.5	64.2	9.6	82.7	10.9	75.4	14.9	68.9
R <sup>a</sup>	56.7	12.7	66.9	19.3	65.9	12.9	66.8	10.6	72.1	18.7	72.4	10.7	64.2	12.4	63.6	13.5	79.1	13.5	67.5
A <sup>b</sup>	72.9	9.2	87.4	7.5	82.1	8.1	90.2	14.6	123.5	27.4	100.7	18.5	86.7	15.9	93.3	9.1	97.0	10.8	92.7
B <sup>b</sup>	80.2	20.5	85.3	7.1	76.8	11.8	93.2	9.7	97.9	8.2	107.4	38.3	84.9	6.5	88.0	10.8	104.4	4.4	90.9
W <sup>b</sup>	58.3	13.6	82.9	16.4	72.7	11.0	76.6	12.4	79.5	14.7	77.8	7.5	77.5	11.9	85.3	10.5	75.3	13.7	76.2
G <sup>b</sup>	55.3	14.1	75.4	37.2	64.4	7.9	71.7	7.9	75.6	13.9	63.8	8.0	78.6	15.0	75.8	9.9	76.8	10.4	76.2

TABLE 6.

Summary of Gonadal Indices, by site by sample dates using the 2006 Julian calendar. Data represent mean Gonadal Index of the sample (on each date  $n = 15$  quahogs). SD = standard deviation. A: Conditional Area A; B: Conditional Area B; P: Providence River site 1; R: Providence River site 2; G: Greenwich Cove; W: Warwick Cove. Sites with the same superscript (<sup>a</sup>, <sup>b</sup>) are not significantly different from one another according to the Wilcoxon rank-sum test. Different superscripts indicate significantly different sites ( $\alpha = 0.10$ ).

Julian Day	Sample Site											
	A <sup>a</sup>	SD	B <sup>a</sup>	SD	P <sup>b</sup>	SD	R <sup>b</sup>	SD	G <sup>a</sup>	SD	W <sup>a</sup>	SD
105	1.9	0.6	1.1	0.6	0.7	0.4	1.1	0.3	0.9	0.6	0.8	0.4
126	1.3	1.0	1.6	0.7	1.1	0.5	1.1	0.4	2.0	0.5	1.2	0.7
147	2.3	0.5	1.9	0.4	1.0	0.5	1.3	0.6	2.1	0.5	1.6	0.7
168	2.9	0.3	2.7	0.5	2.1	0.6	2.3	0.6	2.6	0.5	2.7	0.6
186	2.7	0.5	2.9	0.4	2.4	0.5	2.3	0.5	2.5	0.5	2.5	0.5
210	2.4	0.5	2.3	0.6	1.2	1.0	1.1	1.1	2.5	0.5	2.3	0.5
231	1.7	1.0	1.7	0.7	1.5	1.0	1.2	1.0	2.1	1.1	2.2	1.0
252	1.7	0.8	1.7	0.8	1.9	0.8	1.3	0.8	1.9	0.8	0.9	0.7
273	1.4	0.7	1.6	0.7	1.6	0.9	1.9	0.2	1.9	1.1	1.9	0.9
<b>Overall mean</b>	<b>2.0</b>		<b>1.9</b>		<b>1.5</b>		<b>1.5</b>		<b>2.1</b>		<b>1.7</b>	

at the beginning of the sampling period were caused by a large proportion of animals in the spent stage of development (Table 7). Both Providence River sites had about 40% of their population in spent stage, more than in any other site, except for the Warwick Cove. At the end of the season, the Providence River sites had the greatest numbers of quahogs in gonadal regression. The conditional areas on the other hand, had the lowest proportions of individuals in the regression stage 20% for site A, and 0% for site B. At Julian Day 168 (June 17), the time of maximum GI and known to be the around the expected time of the major spawning event for *M. mercenaria* in many areas of Narragansett Bay (Rice & Goncalo 1995, Butet 1997), the percentages of quahogs exhibiting ripe gonads in the conditional areas was 90% for Conditional Area A and 70% for Conditional Area B, whereas at the nearby Providence River sites the quahogs exhibiting gonad ripeness were 25% and 33% for Providence River Sites 1 and 2, respectively. On the same date, quahogs from Greenwich Cove were 60% ripe, and those

from Warwick Cove were 33% ripe. Data show that maximum gonad ripeness in the coves is delayed by several weeks in comparison with the conditional areas.

A Wilcoxon-rank sum test at level of significance of  $\alpha = 0.10$  (Table 5), showed that values of GI in quahogs from the conditional areas (A & B) are significantly higher than the Providence River sites (P & R), and the coves (G & W). The chi-square tests of independence showed that date of sample had a significant effect ( $\alpha = 0.05$ ) on the gonadal stage of development in all sites, except on Julian dates 168 (June 17) and 273 (September 30), which coincide with the dates with the lowest variability in gonadal index. Gonadal stage of development was also dependent on site except on sample date 168. Detailed statistical tables can be found in Marroquin-Mora (2007).

A Spearman-rank correlation analysis showed that there is a low positive correlation between CI and GI ( $\rho = 0.4134$ ). CI remains relatively constant in closed sites (Fig. 1) whereas the GI shows a strong peak for all sites between Julian days 168 and 186 (Fig. 2). However, because of the great variability in the CI

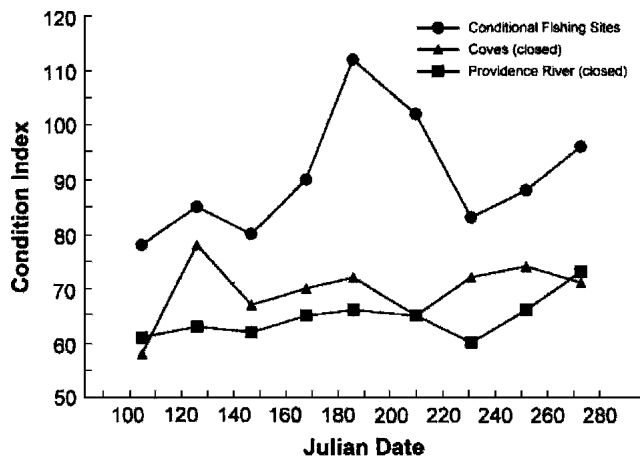


Figure 1. Condition Index by type of site in 2006. Providence River: including Providence River sites 1 and 2; Conditional Areas including: Conditional Areas A and B; Coves: including Greenwich Cove and Warwick Cove. The sites conditionally open to fishing exhibit significantly higher ( $P < 0.05$ ) CI values than either the Providence River or Cove sites that are closed to fishing.

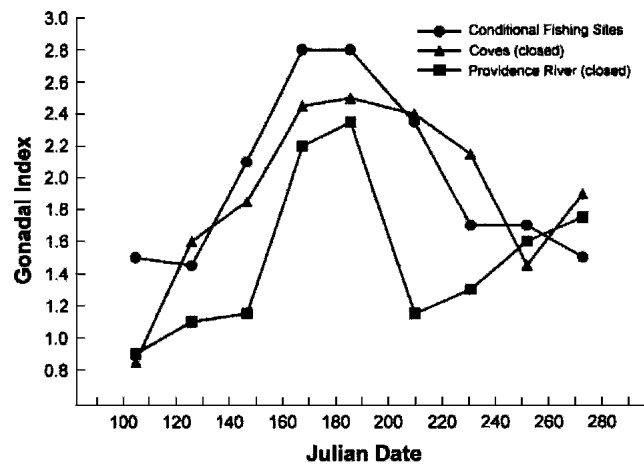


Figure 2. Gonadal Index by type of site in 2006. Providence River: including Providence River Site 1 and 2; Conditional Areas including: Conditional Areas A and B; Coves: including Greenwich Cove and Warwick Cove.



TABLE 7.

Numbers of quahogs (*Mercenaria mercenaria*) in various stages of gonadal development by 2006 Julian date in and collection site.

Julian Date	105	126	147	168	186	210	231	252	273	Total
Site A Inactive	1	4	0	0	0	0	0	0	0	5
Site A Early active	0	2	0	0	0	0	1	3	7	13
Site A Late active	12	6	10	2	2	2	2	3	1	40
Site A Ripe	1	1	4	13	11	6	2	1	1	40
Site A Spawning	0	0	1	0	2	7	7	4	3	24
Site A Spent	1	2	0	0	0	0	0	0	1	4
Site A Regression	0	0	0	0	0	0	3	1	1	5
Site A Total	15	15	15	15	15	15	15	12	14	131
Site B Inactive	2	1	0	0	0	0	0	0	0	3
Site B Early active	10	5	2	0	0	1	6	4	8	36
Site B Late active	3	8	13	4	2	3	4	3	4	44
Site B Ripe	0	1	0	10	12	6	2	2	2	35
Site B Spawning	0	0	0	0	0	5	3	5	1	14
Site B Spent	0	0	0	0	0	0	0	0	0	0
Site B Regression	0	0	0	0	0	0	0	1	0	1
Site B Total	15	15	15	14	14	15	15	15	15	133
Site P Inactive	5	1	2	0	0	0	1	0	1	10
Site P Early active	4	12	10	1	0	0	1	0	2	30
Site P Late active	0	2	2	7	8	1	1	1	2	24
Site P Ripe	0	0	0	4	5	0	1	2	2	14
Site P Spawning	0	0	0	2	1	7	7	10	5	32
Site P Spent	6	0	1	1	0	0	0	0	2	10
Site P Regression	0	0	0	0	0	5	3	2	1	11
Site P Total	15	15	15	15	14	13	14	15	15	131
Site R Inactive	0	0	0	0	0	0	1	0	0	1
Site R Early active	7	13	11	1	0	0	1	0	0	33
Site R Late active	1	2	2	8	9	0	1	3	0	26
Site R Ripe	0	0	1	5	5	1	1	1	6	20
Site R Spawning	0	0	0	1	1	7	5	2	5	21
Site R Spent	6	0	1	0	0	0	2	7	1	17
Site R Regression	0	0	0	0	0	7	4	2	3	16
Site R Total	14	15	15	15	15	15	15	15	15	134
Site G Inactive	4	0	0	0	0	0	0	0	0	4
Site G Early active	6	2	1	0	0	0	1	2	2	14
Site G Late active	2	11	9	6	5	3	1	2	0	39
Site G Ripe	0	2	3	9	8	7	7	3	5	44
Site G Spawning	0	0	2	0	2	5	4	7	5	25
Site G Spent	3	0	0	0	0	0	0	0	1	4
Site G Regression	0	0	0	0	0	0	2	1	2	5
Site G Total	15	15	15	15	15	15	15	15	15	135
Site W Inactive	4	0	0	0	0	0	0	0	0	4
Site W Early active	6	2	1	0	0	0	0	5	1	15
Site W Late active	2	11	9	7	2	1	1	1	4	38
Site W Ripe	0	2	3	8	7	9	5	0	1	35
Site W Spawning	0	0	0	0	2	7	6	3	5	23
Site W Spent	6	1	0	0	0	0	0	4	1	12
Site W Regression	0	0	0	0	0	0	1	3	2	6
Site W Total	15	15	15	15	15	15	15	15	15	135

and GI in all sites, neither the CI nor the GI, can be reliably used to predict origin of samples.

#### Status of Gonads

We found both immature and gonads in inactive stage at all sites. The largest quahog in an inactive stage of gonadal

development was found in Warwick Cove during the second sampling date (Julian date 124; May 4). The morphometric characteristics of this organism were: length = 81 mm; height = 67 mm; and width = 43 mm. The smallest mature clam was also found during the same sampling date in Conditional Area A, with morphometric characteristics of this quahog being length = 42 mm; height = 39 mm; and width = 25 mm. Also, a few bisexual gonads, as described originally by Loosanoff (1937a), were found in the two conditional areas.

#### Oocyte Diameter

Oocyte diameters were highly variable between females but also within each female. Diameter of mature oocytes varied between 40 and 50  $\mu\text{m}$ . Mean oocyte diameters by site were: A:  $48.83 \pm 8.93 \mu\text{m}$ ; B:  $48.37 \pm 8.03 \mu\text{m}$ ; P:  $49.30 \pm 8.70 \mu\text{m}$ ; R:  $48.76 \pm 8.26 \mu\text{m}$ ; G:  $48.32 \pm 8.02 \mu\text{m}$ ; and W:  $47.10 \pm 7.58 \mu\text{m}$ . No correlation was found between oocyte diameter and any of the morphometric characteristics of females (length, height, and width). Using a Kruskal-Wallis test, no statistically significant difference in oocyte diameter was found among sites.

## DISCUSSION

#### Condition Index

Data from 2005 and 2006 showed the condition index (CI) of quahogs from areas of high population density closed to fishing, including Greenwich Cove, Warwick Cove, and the Providence River, to be substantially lower than in quahogs from the areas that are actively fished in Upper Narragansett Bay (Tables 4 and 5). Because condition index is considered to be a crude indirect measure of the reproductive potential of quahogs, this low condition index in the closed areas would imply a low reproductive capacity of those organisms.

In general terms, condition index (CI) was relatively low in mid-April, had a slow increase until approximately the second half of May and a faster increase towards the end of May and first half of June. It then declined from the end of August until the beginning of September, when a slight increase was again evident. These changes in condition index are expected and seem to point out to the fact that there was a major spawning event at the beginning of July and then probably a secondary minor spawning event, at least in some of the sites, at the beginning of September. Those observations are consistent with the gonadal index observations and previous observations of larval abundance (or lack thereof) in the respective sample areas (Butet 1997, Rice & Goncalo 1995). Peterson and Fegley (1986) found a similar pattern in adult *M. mercenaria* in North Carolina, where clams exhibited a seasonal variation in size-adjusted volumetric growth and gonadal mass growth, both exhibiting increments during the spring and decreasing in late summer, with a second increase towards the end of summer.

The Providence River sites that had the lowest condition indices overlap with the areas of the Narragansett Bay that have the highest hypoxia potential. According to Prell et al. (2006) Warwick Cove has a lower hypoxia potential than Greenwich Cove and this may explain the difference in condition index between the two coves. As described by Hammen (1980) and Fields & Storey (1987), *M. mercenaria* are able to carry anaerobic metabolism, however, growth is severely impaired at low

dissolved oxygen concentrations (Morrison 1971, Appleyard & DeAlteris 2002). If growth is impaired, reproductive capability is likely to be also impaired.

Although condition index is not a direct indication of the reproductive potential of an organism, it is a good indicator of its general condition and health. As such, our results reveal that the animals in Greenwich Cove, Warwick Cove, and the Providence River sites are subject to poorer conditions than those in the conditional areas. Additionally, the coves and Providence River sites have much higher population densities than the conditional areas (Table 1), and therefore any environmental impact on CI values may be magnified by the population density factor. The presence of a larger proportion of scars on the shells of quahogs from the Providence River (39% of the population in P and 47% in R) and coves (12% for each one of the coves) is also evidence that those animals are subject to hypoxic conditions that have caused the tissue to recede without causing the death of the animals (Kennish 1978). Only 1.3% and 1.5% of organisms have scars in Conditional Area A and Conditional Area B, respectively.

There was great variability in the condition index between sites but also within sites. This variability increased as condition index increased. Laurelle et al. (1994) also observed a direct relationship between condition index level and its coefficient of variation in *Ruditapes decussatus* and *R. phillipinarum*. They hypothesized that this phenomenon indicated that maturation is synchronized, whereas spawning is not synchronized. We observed that variability in the gonadal index increased especially during the spawning season, so our data seem to support the Laurelle et al. (1994) hypothesis.

#### Gonadal Index

The gonadal development followed, in general terms, the gonadal cycle described by previous authors (Loosanoff 1937a, Porter 1964, Ropes & Stickney 1965, Keck et al. 1975, Eversole & Michener 1980). Only one complete cycle was observed, with one spawning event that initiated in mid-July and extended until the end of the sampling season, with a peak at the end of July to the beginning of August and a minor peak in early September. The major spawning coincided with the spawning periods for quahogs reported for Rhode Island by Butet (1997), as well as Delaware and Long Island by Keck et al. (1975) and Loosanoff (1937b), respectively.

In the case of the conditional areas, quahogs were at a more advanced stage of gonadal development at the beginning of the sampling season than in the other sites. They reached maturity earlier than the other sites, by mid-June to early July, and started spawning in mid-July. On the other hand, the coves and Providence River sites were slightly delayed in their gonadal development, and reached the peak in maturation about 2 wk after the conditional areas. The Providence River sites started showing signs of gonadal regression after reaching the highest point in gonadal maturity. Conversely, quahogs in the coves maintained their gonads for longer periods of time and regression began to be evident until mid-July.

The peak in spawning coincided with a decline in the condition index in the sites where no resorption of gonads was observed, and by a relative stability in the CI in those sites where regression of the gonads was observed. In the sites where no regression was observed, gonads remained active and started

a new maturation cycle. The high variability in the gonadal index in the samples taken in June and July may be explained by the asynchronization of spawning among individuals from the same site.

The earliest spawning was seen in Greenwich Cove in late May; this coinciding with Greenwich Cove being the first of the sites to reach 20°C, the temperature at which spawning usually starts (Porter 1964). The second earliest spawning was seen in Conditional Area A, however in the following sample no spawning animals were found. It is possible that that spawning event coincided with a peak in temperature and after that temperature lowered to the normal levels for that time of year, stopping temporarily the spawning process. Later in the season spawning was resumed. Butet (1997) also found that the peak in spawning happened at different points in time in different areas of Narragansett Bay and attributed this difference to the variations in water temperature within the estuary caused by different depths in different areas, and resulting in the shallower waters reaching warmer temperatures earlier than deeper areas.

We observed one major difference in the gonadal cycle of the studied populations compared with previous reports. This major difference was the presence of regressing gonads, a stage that has been reported for other venerid clams and bivalve species but is not commonly reported for *Mercenaria mercenaria*. The observed regression of the gonads may explain the delay we observed in the development of gonads in some sites, because the sites where we observed more regressing gonads at the end of the season, were the ones that had the slower start in gonadal development at the beginning of the cycle. The phenomenon of regressing gonads may also be a contributing factor in the intrasite variability in GI.

According to Keck et al. (1975) usually, the oocytes spawned in a season are first produced at the end of the previous cycle and stop maturation when organisms stop feeding because of the decrease in temperature. When temperature reaches 10°C in the next reproductive cycle, oocytes continue to mature until they are spawned (Keck et al. 1975). However, in the case in which oocytes are resorbed it is possible that the gonads are not regenerated until later in the next year. This would explain the presence of quahogs in the spent stage of development in the first samples taken in April.

Few authors have previously reported an inactive stage of gonadal development in *M. mercenaria* as we found in our study (in Heffernan et al. 1989). In the reported cases of inactive gonads, it usually occurs in small animals and only for a very short period of time (Heffernan et al. 1989, Manzi et al. 1985; Eversole et al. 1980). Most other authors have not recorded an inactive stage of gonadal development in their observations of adults (Loosanoff, 1937a, Keck et al. 1975, Dalton & Menzel 1983). Contrary to previous reports that suggest that the major redevelopment period of older clams should happen just after spawning (Porter 1964) we found more regressing and inactive gonads in the populations where there are larger animals (particularly the Providence River sites). At the beginning of the cycle we also found a large (0 to  $\approx$  25% depending on the site) portion of animals, males and females, in an inactive stage of gonadal development. According to Keck et al. (1975) this stage is practically nonexistent in the female cycle because partially spawned or totally spawned individuals start ovogenic activity immediately. In the case of males, however, it is more common (Keck et al. 1975). We not only

observed regression of gonads but also totally spawned individuals with no evidence of regeneration, a condition, which was not observed by Keck et al. (1975).

At the end of the cycle in the autumn, a minor increase in condition and gonadal index was observed, probably because the organisms were still feeding and redeveloping gonads. The increase in gonadal and condition index towards the end of the sampling season evidences the fact that the animals may improve in condition and go through the gonadal maturation cycle if they have enough time to feed and be under suitable conditions. This continuous regeneration of gonad results in "dribble spawning" evidenced by the great variability within each site observed during the spawning season (Newell et al. 1982). Rapid gonadal regeneration is common in *M. mercenaria* and was previously reported by Porter (1964) and Eversole and Michener (1980).

Previous studies have found evidence of intraspecific competition among bivalves resulting in decreased condition index and growth (review included in Rheault & Rice 1996, Peterson & Black 1987) and of effects of the food supply on the gametogenic cycle of bivalves (Newell et al. 1982, Buss & Jackson 1981, Peterson 1982, Peterson & Black 1987, Delgado & Perez Camacho 2005, Tettlebach et al. 2003). The effect of density on reproduction is also argued by some authors (Malinowski 1993, Malinowski & Whitlatch 1988); Peterson (1982) has shown that the gonadal tissue is reduced in two filter-feeding bivalves, *Protothaca staminea* and *Chione undatella*, held at high densities.

Can reduced gonadal mass or lowered GI affect shellfishery stocks? There is evidence of a stock-recruitment interaction in quahogs (Kraeuter et al. 2005), and that about 5 adult quahogs/m<sup>2</sup> is the carrying capacity of an ecosystem, with a density dependent upper level of density, at about 30 adult quahogs/m<sup>2</sup>. The relationship given by the model of Kraeuter et al. (2005) results in a linear increase in recruits with increasing broodstock biomass up to a certain biomass, after which recruits level off as biomass increases, a process known as compensation. Our data show lowered quahog CI and GI in denser assemblages, suggesting lowered fecundity as a possible explanation of the compensation mechanism.

#### GI:CI Correlation

Although we did not find a strong correlation between gonadal index and condition index, the highest gonadal indices were generally found about the same time as the highest condition indices. And as spawning took place, condition index decreased. According to Gribben et al. (2001) the lack of a strong correlation between gonadal and condition index may be related to the allocation of resources. It is possible that animals are storing energy before they are actually converting it into gametes, which should be observed as an increase in condition index before the gonadal index increases (Beninger & Lucas, 1984). However, that is not the case in our observations, because we observed a maximum in gonadal index (day 168) prior to the maximum in condition index (day 186) (Figs. 1 and 2).

Our observations of a low condition index being related to a low reproductive potential would also explain the larval distribution found by Rice and Goncalo (1995), who observed peak larval abundances in the open area of Greenwich Bay, and that the points in or near the coves were relatively free of

bivalve larvae. This also agrees with Butet's (1997) observation that the maximum bivalve larval abundance was at her northernmost sampling point just south of Conimicut Point (41°42'58" N × 71°20'44" W) slightly north of the Conditional Area A sample site of this study in which highest CI and GI values were found.

The quahogs we collected in the Providence River are larger than those we collected in either the conditional fishing areas or the coves that are closed to fishing (Table 3). An alternate explanation for reduced CI and GI in areas closed to fishing may be that these areas harbor larger quahogs and CI and/or GI may be negatively correlated with size. Although this may be a remaining concern, two previous studies (Peterson 1883, 1986) have suggested strongly that reproductive output by quahogs from relatively low density populations in comparison with our study does not appear to be affected age, indirectly suggesting that at least GI may not be affected by quahog size.

#### Oocyte Diameter

Our estimated mean oocyte diameter was slightly smaller than the one reported by Keck et al. (1975), who estimated that in the ripe stage oocyte diameter is 50–60 μm, but more consistent with Hesselman et al. (1989), who found that no monthly oocyte mean exceeded 45 μm, and that the variation in oocyte diameter was thus the result of variability between individuals and within individuals. The mature oocytes showed no significant difference in size between sites, suggesting that those organisms that are maturing may in fact reproduce effectively. However, because the closed sites do in general reach the ripe and partially spawned stages later in season than the quahogs from the conditional areas, their reproduction may result in lower recruitment of quahogs into the population if the spat encounter unsuitable conditions during their larval and juvenile development when quahogs are more subject to mortality.

Similar to our observations, Delgado and Perez Camacho (2005) did not find apparent morphological differences in oocytes of *R. decussatus* that had restricted nutritional sources available. However, they indicate that future studies of the effects of serious nutritional deficiencies on the viability of eggs, and larvae of the species would be of interest because a further consequence of nutritional limitation during gonadal development may be a lack of renovation of the germinal layers, which assure gonadal recovery after partial or total emission of gametes. The characteristics and physiology of the oocyte and, consequently, fecundity and larval viability should also be directly affected by nutritional deficiencies (Delgado & Perez Camacho 2005). This may explain why we found oocytes that looked normal, and however the gametogenic cycle was delayed in those sites where there was more resorption of gametes.

#### CONCLUSION AND RECOMMENDATIONS

Our results indicate that the reproductive ability of the animals in the closed areas in Narragansett Bay (Providence River and coves) is limited, because a smaller proportion of the animals are reaching the ripe and spawning stages of development. Whereas in the conditional areas quahogs are actively reproducing and beginning the gonadal development for next year, as evidenced by the presence of gonads in the early stage of development at the beginning and at the end of the sampling

season. Normal gonadal development appears to be correlated with low population densities, close to the density of 5 quahogs/m<sup>2</sup> estimated by Kraeuter et al. (2005) as optimal for the sustainability of the population. Coincidentally, the approximate density of quahogs in the conditional areas with greatest average CI and GI values is also about five quahogs/m<sup>2</sup> (Table 1).

Because population densities are also higher in the closed areas than in the open areas, it is very likely that the density factor results in the significant differences in condition index observed between the conditional areas and closed sites. Decreased fecundity of quahogs in closed sites caused by water quality conditions in those areas that are prone to hypoxia may be exacerbated by quahog population density as well.

The observed gonadal cycle in Narragansett Bay follows the general pattern previously described for the species. However, a major difference with respect to previous reports was that a proportion of the population was undergoing gonadal regression and that there were quahogs in the inactive stage of development, particularly in the closed areas. Regression of the gonads possibly indicates limited energy availability to the animals. In our observations resorption coincided with the spawning process and quahogs did not appear to go into a spent phase prior to going into recession indicating that we were in fact observing resorption of gonads rather than a recycling of the left over materials.

Based on our observations of condition index and gonadal index, as well as recent models of population dynamics, we are concluding that areas long-closed to shellfishing in Narragansett Bay are not serving as spawner sanctuaries or serving as a major source of spillover larvae. Although these data are suggestive that the relocation of stock to more open areas with lesser population densities may have a positive effect on the reproductive potential of northern quahogs, more research and more baseline information is needed to confirm these preliminary observations by directly monitoring gonadal recovery of transplanted quahogs in spawner sanctuary sites.

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#### LITERATURE CITED

- Alexander, R. R. & R. M. Baron. 2003. Shell repair of mechanically induced fractures in *Mercenaria mercenaria* under experimentally suboptimum conditions. *J. Shellfish Res.* 22:689–696.
- Ansell, A. D. 1967. Egg production of *Mercenaria mercenaria*. *Limnol. Oceanogr.* 12:172–176.
- Ansell, A. D. & F. A. Loosmore. 1963. Preliminary observations of the relationship between growth, spawning and condition in experimental colonies of *Venus mercenaria* L. *Journal du Conseil Permanent Internationale pour l'Exploration de la Mer.* 28:285–294.
- Appleyard, C. C. & J. T. DeAlteris. 2002. Growth of the northern quahog *Mercenaria mercenaria*, in an experimental scale upweller. *J. Shellfish Res.* 21:3–12.
- Belding, D. L. 1931. The quahaug fishery of Massachusetts. Marine Fisheries Series No. 2. Department of Conservation, Division of Fisheries and Game, Marine Fisheries Section. 41 pp.
- Beninger, P. G. & A. Lucas. 1984. Seasonal variations in condition, reproductive activity, and gross biochemical composition of two species of adult clam reared in a common habitat: *Tapes decussatus* L. (Jeffreys) and *Tapes philippinarum* (Adams and Reeve). *J. Exp. Mar. Biol. Ecol.* 79:19–37.
- Bricelj, V. M. & R. E. Malouf. 1980. Aspects of reproduction of hard clams, *Mercenaria mercenaria*, in Great South Bay, New York. *Proc. Nat. Shellfisheries Assoc.* 70:216–229.
- Buss, L. W. & J. B. C. Jackson. 1981. Planktonic food availability and suspension-feeder abundance: evidence of *in situ* depletion. *J. Exp. Mar. Biol. Ecol.* 49:151–161.
- Butet, N. A. 1997. Distribution of quahog larvae along a north-south transect in Narragansett Bay. M.Sc. Thesis, University of Rhode Island. 85 pp.
- Corni, M. G., M. Farneti & E. Scarselli. 1985. Histomorphological aspects of the gonads of *Chamelea gallina* (Linne) (Bivalvia: Veneridae) in autumn. *J. Shellfish Res.* 5:73–80.
- Crosby, M. P. & L. D. Gale. 1990. A review and evaluation of bivalve condition index methodologies with a suggested standard method. *J. Shellfish Res.* 9:233–237.
- Dalton, R. & W. Menzel. 1983. Seasonal gonadal development of young laboratory-spawned southern (*Mercenaria campechiensis*) and northern (*Mercenaria mercenaria*) quahogs and their reciprocal hybrids in northwest Florida. *J. Shellfish Res.* 3:11–17.
- Delgado, M. & A. Perez Camacho. 2005. Histological study of the gonadal development of *Ruditapes decussatus* (L.) (Mollusca: Bivalvia) and its relationship with available food. *Sci. Mar.* 69:87–97.
- Eversole, A. G. 1997. Gametogenesis of *Mercenaria mercenaria*, *M. campechiensis* and their hybrids. *Nautilus* 110:107–110.
- Eversole, A. G. & W. K. Michener. 1980. Reproductive cycle of *Mercenaria mercenaria* in a South Carolina estuary. *Proc. Nat. Shellfisheries Assoc.* 70:22–30.
- Fields, J. H. A. & K. B. Storey. 1987. Tissue-specific alanopine dehydrogenase from the gill and strombine dehydrogenase from the foot muscle of the cherrystone clam, *Mercenaria mercenaria* (Linn.). *J. Exp. Mar. Biol. Ecol.* 105:175–185.
- Grant, J. & M. A. Rice. 2006. Condition index study of quahog populations in Narragansett Bay, Rhode Island. *J. Shellfish Res.* 25:662.
- Gribben, P. F., R. G. Creese & S. H. Hooker. 2001. The reproductive cycle of the New Zealand Venus Clam, *Ruditapes largillierti*. *J. Shellfish Res.* 20:1101–1108.
- Hayward, J. S. & J. S. Ryland. 1975. Growth, reproduction and larval dispersal of *Alcyonidium hirsutum* (Fleming) and some other Bryozoa. *Pubblicazione Stazione Zoologica di Napoli* 39(Suppl):226–241.
- Hammen, C. S. 1980. Total energy metabolism of marine bivalve mollusks in anaerobic and aerobic states. *Comp. Biochem. Physiol.* 62A:955–959.
- Heffernan, P. B., R. L. Walker & J. L. Carr. 1989. Gametogenic cycles of three bivalves in Wassaw Sound, Georgia: I. *Mercenaria mercenaria* (Linnaeus, 1758). *J. Shellfish Res.* 8:51–60.
- Hesselman, D. M., B. J. Barber & N. J. Blake. 1989. The reproductive cycle of adult hard clams, *Mercenaria* spp. in the Indian River Lagoon, Florida. *J. Shellfish Res.* 8:43–49.

- Hooker, S. H. & R. G. Creese. 1995. The reproductive biology of pipi, *Paphes australis* (Gmelin, 1790) (Bivalvia: Mesodesmatidae). I. Temporal patterns of the reproductive cycle. *J. Shellfish Res.* 14:7–15.
- Howard, D. W. & C. S. Smith. 1983. Histological Techniques for Marine Bivalve Mollusks. NOAA Technical Memorandum NMFS-F/NEC-25. US Department of Commerce. 97 pp.
- Keck, R. T., D. Maurer & H. Lind. 1975. A comparative study of the hard clam gonad development cycle. *Biol. Bull.* 148:243–258.
- Kennish, M. J. 1978. Effects of thermal discharges on mortality of *Mercenaria mercenaria* in Barnegat Bay, New Jersey. *Environ. Geol.* 2:223–254.
- Kraeuter, J. N., S. Buckner & E. N. Powell. 2005. A note on a spawner-recruitment relationship for a heavily exploited bivalve: the case of northern quahogs (hard clams), *Mercenaria mercenaria* in Great South Bay, New York. *J. Shellfish Res.* 24:1043–1052.
- Laurelle, F., J. Guillou & Y. M. Paulet. 1994. Reproductive pattern of the clams, *Ruditapes decussatus* and *R. phillipinarum* on intertidal flats in Brittany. *J. Mar. Biol. Ass. UK* 74:351–366.
- Lazar, N., A. Ganz & A. Valliere. 1995. Quahog stock assessment and implementation of an interim management plan in Greenwich Bay, Rhode Island. In: M. A. Rice & E. Gibbs, editors. Proceedings of the third Rhode Island shellfisheries conference. Rhode Island Sea Grant, University of Rhode Island, Narragansett. pp. 5–29.
- Loosanoff, V. L. 1937a. Development of the primary gonad and sexual phases in *Venus mercenaria* Linnaeus. *Biol. Bull.* 72:389–405.
- Loosanoff, V. L. 1937b. Seasonal gonadal changes of adult clams, *Venus mercenaria* (L.). *Biol. Bull.* 72:406–416.
- Malinowski, S. M. 1993. Effects of density on adult growth, survivorship, fecundity, and recruitment of northern quahogs. In: M. A. Rice & D. Grossman-Garber, editors. Proceedings of the Second Rhode Island Shellfish Industry Conference. Rhode Island Sea Grant. pp. 79–90.
- Malinowski, S. & R. B. Whitlatch. 1988. A theoretical evaluation of shellfish resource management. *J. Shellfish Res.* 7:95–100.
- Manzi, J. J., M. Y. Bobo & V. G. Burrell. 1985. Gametogenesis in a population of the hard clam, *Mercenaria mercenaria* (Linnaeus), in North Santee Bay, South Carolina. *Veliger* 28:186–194.
- Marroquin-Mora, D. C. 2007. Histological study of the gonadal development of northern quahogs (*Mercenaria mercenaria*) from high density populations in Narragansett Bay, RI. M. Sc. Thesis, University of Rhode Island, Kingston. 67 pp.
- Mauer, D. 1983. The effect of an infaunal suspension feeding bivalve *Mercenaria mercenaria* (L.) on benthic recruitment. *Mar. Ecol.* 4:263–274.
- Morrison, G. 1971. Dissolved oxygen requirements for embryonic and larval development of the hardshell clam, *Mercenaria mercenaria*. *J. Fish. Res. Bd. Canada* 28:379–381.
- Murphy, B. R., M. Gibson, D. Erkan & A. Ganz. 2005. Estimated abundance of shellfish resources in Allen Harbor. Rhode Island Department of Environmental Management, division of fish and wildlife, Providence, RI. 24 pp.
- Newell, R. I. E., T. J. Hilbish, R. K. Koehn & C. J. Newell. 1982. Temporal variation in the reproductive cycle of *Mytilus edulis* L. (Bivalvia, Mytilidae) from localities on the East Coast of the United States. *Biol. Bull.* 162:299–310.
- Peterson, C. H. 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. *Ecolog. Monogr.* 52:437–475.
- Peterson, C. H. 1983. A concept of quantitative reproductive senility: application to the hard clam, *Mercenaria mercenaria* (L.)? *Oecologia* 58:164–168. (Berlin).
- Peterson, C. H. 1986. Quantitative allometry of gamete production by *Mercenaria mercenaria* into old age. *Mar. Ecol. Prog. Ser.* 29:93–97.
- Peterson, C. H. & S. V. Andre. 1980. An experimental analysis of interspecific competition among filter feeders in a soft-sediment environment. *Ecology* 61:129–139.
- Peterson, C. H. & R. Black. 1987. Resource depletion by active suspension feeders on tidal flats: influence of local density and tidal elevation. *Limnol. Oceanogr.* 32:143–166.
- Peterson, C. H. & S. R. Fegley. 1986. Seasonal allocation of resources to growth of shell, soma and gonads in *Mercenaria mercenaria*. *Biol. Bull.* 171:597–610.
- Porter, H. J. 1964. Seasonal gonadal changes of adult clams, *Mercenaria mercenaria* (L.) in North Carolina. *Proc. Nat. Shellfisheries Assoc.* 55:35–52.
- Pratt, S. D. 1988. Status of the hard clam fishery in Narragansett Bay. Final report for the Narragansett Bay project. US Environmental Protection Agency Region 1: Water Management Division. Report # NBP-88-07.
- Prell, W., D. Murray & C. Deacutis. 2006. Summer-season survey of dissolved oxygen in upper Narragansett Bay beginning in 2005. Data available at: <http://www.geo.brown.edu/georesearch/insomniacs>. Accessed 7/2/2007.
- Rheault, R. B. & M. A. Rice. 1996. Food-limited growth and condition index in the eastern oyster, *Crassostrea virginica* (Gmelin, 1791), and the bay scallop, *Argopecten irradians irradians* (Lamarck, 1819). *J. Shellfish Res.* 15:271–283.
- Rhode Island Fisheries Stock Status, an Overview. 2004. Rhode Island Department of Environmental Management, division of fish and wildlife. 21 pp.
- Rice, M. A. 1999. Uptake of dissolved free amino acids by northern quahogs, *Mercenaria mercenaria*, and its relative importance to organic nitrogen deposition in Narragansett Bay, Rhode Island. *J. Shellfish Res.* 18:547–553.
- Rice, M. A. 2006. Quahog (*Mercenaria mercenaria*) spawner sanctuaries: Does size or location matter? *J. Shellfish Res.* 15:271–283.
- Rice, M. A. & J. Goncalo. 1995. Results of a study of bivalve larval abundance in Greenwich Bay, Rhode Island, 1993. In: M. A. Rice & E. Gibbs, editors. Proceedings of the third Rhode Island shellfisheries conference. Rhode Island Sea Grant, University of Rhode Island, Narragansett. pp. 31–40.
- Rice, M. A., C. Hickox & I. Zehra. 1989. Effects of intensive fishing effort on the population structure of quahogs, *Mercenaria mercenaria* (Linnaeus, 1758), in Narragansett Bay. *J. Shellfish Res.* 8:345–354.
- Rice, M. A., A. Valliere & A. Caporelli. 2000. A review of shellfish restoration and management projects in Rhode Island. *J. Shellfish Res.* 19:401–408.
- Ropes, J. W. 1968. Reproductive cycle of the surf clam, *Spisula solidissima*, in offshore New Jersey. *Biol. Bull.* 135:349–365.
- Ropes, J. W. 1987. Age and growth, reproductive cycle, and histochemical tests for heavy metals in hard clams, *Mercenaria mercenaria*, from Raritan Bay, 1974 to 1975. *Fish. Bull. (Wash. DC)* 85: 653–662.
- Ropes, J. W. & A. P. Stickney. 1965. Reproductive cycle of *Mya arenaria* in New England. *Biol. Bull.* 128:315–327.
- Tettelbach, S. T., R. I. E. Newell & C. Gobler. 2003. Linking hard clam (*Mercenaria mercenaria*) reproduction to phytoplankton community structure: I. clam growth and reproductive cycles. *J. Shellfish Res.* 22:357–358.
- Velez, A. & C. E. Epifanio. 1981. Effects of temperature and ration on gametogenesis and growth in the tropical mussel *Perna perna* (L.). *Aquaculture* 22:21–26.
- Walker, R. L. 1989. Exploited and unexploited hard clam, *Mercenaria mercenaria* (L.) populations in coastal Georgia. *Contrib. Mar. Sci.* 31:61–75.
- Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: Patterns of abundance. *J. Mar. Res.* 24:25–41.