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BENTHIC PREDATORS AND NORTHERN QUAHOG (=HARD CLAM) (*MERCENARIA MERCENARIA* LINNAEUS, 1758) POPULATIONS

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ABSTRACT Increased numbers of benthic predators, especially crabs, have been proposed as a factor contributing to the decline of hard clams (*Mercenaria mercenaria* Linnaeus, 1758) in Great South Bay, NY. The long-term trend in benthic predators in this system was examined using observations on the distribution and abundance of predators that have been collected by the Town of Islip, NY as part of an annual survey of hard clam populations. The survey began in 1978 and extends to the present and provides concurrent observations of habitat (sediment type, and presence/absence of eelgrass), and hard clam size-frequency distribution and abundance. Predator type and abundance were reported from 1978 to 1981 and 1991 to 2003, which represents one of the most comprehensive benthic predator data sets currently available for any estuarine system. The annual averages of predator abundance in the survey area primarily show interannual fluctuations in abundance. Xanthid crabs (mud crabs, primarily *Dispanopeus sayi* Smith, 1869) were the numerically dominant predator in the system; blue crabs (*Callinectes sapidus* Rathbun, 1895) appeared in the late 1990s. Hard clam abundance has declined by 44% since the early 1990s. An Empirical Orthogonal Function (EOF) Analysis of the predator and hard clam data sets showed that fluctuations in predator abundance are: 1) mostly in phase over the survey region and 2) dominated by year-to-year fluctuations in abundance. The EOF results for the hard clams show that hard clam abundance fluctuations are: 1) in phase over the survey region and 2) dominated by a decreasing trend in abundance over the time series. The primary EOF modes essentially were uncoupled, which implies no strong predator-prey interactions between the predators and hard clams. By inference, increasing predator abundance does not appear to be a primary factor producing the long-term decline in hard clam populations. Predation pressure per recruit may still have increased because of declining hard clam population abundance and the concomitant decline in recruitment.

KEY WORDS: benthic predators, crab predation, *Mercenaria mercenaria*, quahog, hard clam, empirical orthogonal function analysis

INTRODUCTION

For a long time, predation has been recognized as an important process in structuring benthic communities (Connell 1961, Connell 1975, Thorson 1966, Wilson 1991). Bivalve population abundance in soft sediment intertidal areas is influenced by epibenthic predators such as fish and crabs (MacKenzie 1977, Whetstone & Eversole 1981, Peterson 1982), infaunal predators (Ambrose 1991, Landry et al. 1993), as well as other predators such as birds (Reise 1985, Sanchez-Salizar et al. 1987, Griffiths 1990). In some soft sediment environments, such as unvegetated areas, benthic predation is a primary determinant of system structure and production (Reise 1977, Virnstein 1979, Jensen & Jensen 1985). Predation and food limitation effects on bivalve postsettlement populations can, at times, be more important in the regulation of populations than the availability of larvae (Muus 1973, Powell et al. 1984, Guillou & Tartu 1994, Olafsson et al. 1994). Few studies have explicitly examined the role of benthic predators on Northern Quahog (=hard clam) (*Mercenaria mercenaria* Linnaeus, 1758) population structure (e.g., Peterson 1982), but substantial information is available on predator/prey interactions (see review in Kraeuter 2001). The difficulty in designing experiments to eliminate potential artifacts such as migration of predators has greatly hindered establishing direct links between benthic predators and population processes. For hard clams, an added difficulty arises from the seemingly low level of juvenile abundance relative to most other bivalve species (Kraeuter et al. submitted). As a result, much of the knowledge about predation effects comes from laboratory or small-scale experimental field studies (see review in Kraeuter 2001).

Hard clams are preyed upon by a wide range of benthic predators (Gibbons & Blogoslawski 1989, Rice 1992, Kraeuter 2001). The available measurements of consumption rates suggest that crabs are a significant predator for postsettlement hard clam populations (Irlandi & Peterson 1991, Kraeuter 2001), especially for hard clams less than 20–25 mm (Kraeuter 2001). An implication of these studies is that crabs can significantly influence the distribution and abundance of postsettlement hard clams.

The hard clam has supported an economically important fishery for the state of New York. Historically the fishery in Great South Bay (Fig. 1) provided about 80% of the total annual harvest (Buckner 1984). The abundance of hard clams in Great South Bay has declined during the past 30 y, in spite of reductions in fishing pressure and sustained restoration efforts (Kraeuter et al. submitted). Changes in the benthic predator community, including increased population levels of blue crabs (*Callinectes sapidus* Rathbun, 1895), have been suggested as a factor contributing to the continuing decline in hard clam populations. Laboratory and field studies (reviewed in Kraeuter 2001) have shown that blue crabs can consume large numbers of young-of-the-year hard clams.

Since the late 1970s, the Town of Islip, NY has conducted annual surveys in the western portion of Great South Bay (Fig.

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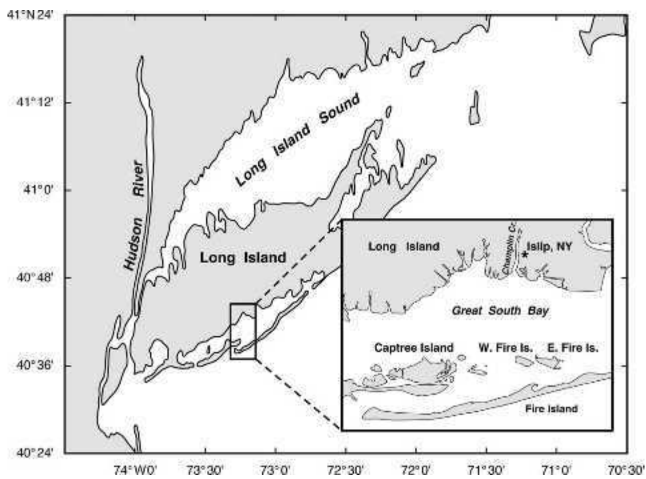

Figure 1. Map of the southeastern portion of New York showing the location of Great South Bay in relation to Long Island, New York. The box indicates the portion of Great South Bay that is sampled during the Town of Islip annual hard clam survey. The inset map shows details of the survey region. Geographic location names are abbreviated as: West Fire Island, W. Fire Is.; East Fire Island, E. Fire Is.

1) to provide quantitative information on hard clam abundance and distribution and to support effective management of this species. The survey area covers about 50 km^2 and includes most of the underwater lands that fall under the jurisdiction of the Town of Islip (Buckner 1984). As part of the hard clam surveys, concurrent data were collected on predator type, distribution, and estimated abundance. As a result, a long-term benthic macro-predator data set exists that can be used to investigate predator-hard clam interactions. Thus, the objectives of this study are to: (1) describe patterns in the macro-predator distribution, (2) relate these patterns to hard clam distribution and abundance, and (3) provide a statistical description of fluctuations in macro-predator and hard clam abundance that can be used to infer interactions between the two.

The following section provides a description of the predator and hard clam data sets and the statistical methods used to analyze these data. This is followed by descriptions of time variability in the data sets, predator and hard clam spatial distributional patterns, and the results of an Empirical Orthogonal Function (EOF) analysis, which is similar to a Principal Component Analysis, that is used to analyze patterns in the hard clam and predator distributions. The discussion and summary section puts the results of this study in a broader context, including important limitations of the data sets.

DATA SETS AND METHODS

Predator and Hard Clam Data Sets

The annual hard clam survey undertaken by the Town of Islip, NY began in 1977 and is still ongoing. The predator and hard clam data sets collected between 1977 and 2003 are the basis for this study (Table 1). The annual survey occurs primarily in July and August, but sampling occurred in spring and winter months in some years (Table 1). The survey typically consisted of more than 300 sampling sites (Table 1), distributed throughout the western part of Great South Bay (Fig. 1) on a grid with a nominal cell size of 400 m by 400 m. The sampling pattern is based on a random block sampling design (Buckner 1984). The number of sample sites occupied in a given year is variable (Table 1), but is sufficient to provide coverage of the survey area. Duplicate samples were usually taken at the sample sites and, in some years, multiple samples were taken at some sample sites (Table 1).

Details of the sampling procedures are given in Buckner (1984); a few relevant to this analysis are described here. The sampling gear is a clamshell bucket operated from a double-spool crane mounted on a 6.1 m by 12.2 m barge towed to each sample site (Buckner 1984). Each clamshell bucket sample was washed through a series of wire screens, with the final screen having a 6.4-mm mesh. The number and size of live hard clams and articulated valves of dead clams were recorded. The thickness (left-right dimension) of each hard clam was measured to the nearest millimeter. The types of predators were noted and abundance of each estimated.

Hard clam thickness has been measured at all sampling sites since the start of the annual survey (Table 1). Predator abundance and type were measured in 17 of the 26 y, with the largest gap in the data set between 1982 and 1990 (Table 1). Sample sites in the early years of the survey were located by visual piloting and dead reckoning, making accurate reconstruction of location maps difficult (Table 1). However, the data sets from these years can be used to construct averages for the survey region. Precise navigational information (e.g., LORAN C and Global Positioning System) on sample site location is available for the 1992 to 2003 surveys (Table 1). The data sets from these years provide the basis for analyses of temporal and spatial patterns in hard clam and predator distributions and predator-prey interactions. The hard clam and predator data were converted from sample log sheets to digital form and subjected to quality control procedures, such as identification of outliers in station latitude and longitude. The overall error rate in the conversion to digital data was less than 5%.

The number of predators sampled at each site was normalized to bucket volume, which varied between years (Table 1), to obtain numbers m^{-2}. Numbers of individuals from samples taken at each site (Table 1) were averaged to provide a single value.

Hard clam thickness measurements were converted to length (greatest anterior-posterior dimension) using a linear relationship given in Buckner (1984):

$$\text{Length} = a + b\ (\text{thickness}) \qquad (1)$$

where $a = 0.499$ cm and $b = 1.87$. The resulting hard clam values at each site were normalized to bucket volume and replicate samples were averaged to obtain values for total number of hard clams m^{-2} at each sample site. The hard clams at each site were binned into length categories of 2.2–4.0 cm (2-y-old hard clam seed), 4.1–5.3 cm (3-y-old seed hard clam), and 5.4–26.7 cm (4-y-old and older, neck, chowder and large clams). The number of clams <2.2 cm was calculated by difference.

Bottom Habitat Characterization

At each sampling location, bottom habitat type was assigned using a scale with 14 categories defined by the relative amounts of sand, shell, mud, and clay in the sample. The presence/absence of seagrass in the bottom samples was noted. Information

TABLE 1.

Summary of the availability of predator and hard clam data sets in each year, the number of sites sampled each year, the number of samples in each year, the availability of geographic coordinate information for samples site, the bucket volume of the dredge used to obtain the bottom samples, and sampling times. In 1981, two dredges with different bucket volumes were used and 42% of the sites sampled used the larger bucket volume. Months are abbreviated as: August, A; September, S; October, O; November, N; December, D.

Year	Predators	Clams	Number of sites yr^{-1}	Number of samples yr^{-1}	Latitude/Longitude	Bucket Size (m^2)	Survey Months
1978	yes	yes	232	464	no	1.03	June, July, A, S
1979	yes	yes	389	777	no	1.03	July, A, S, N
1980	yes	yes	306	1224	no	0.68	July, A, S, O
1981	yes	yes	326	1481	no	0.68/1.02	July, A, S, O
1982	no	yes	289	577	no	1.02	June, July, A
1983	no	yes	310	620	no	0.84	June, July, A
1984	no	yes	296	592	no	1.02	June, July, A
1985	no	yes	314	627	no	1.02	July, A, O
1986	no	yes	312	623	no	1.02	May, June, July, A
1987	no	yes	312	624	no	1.02	July, A, S, O
1988	no	yes	315	630	no	1.02	July, A
1989	no	yes	306	612	no	1.02	July, A
1990	no	yes	309	617	no	1.02	A,S
1991	yes	yes	308	612	no	1.02	S, O, N
1992	yes	yes	304	608	yes	1.02	July, A, S, D
1993	yes	yes	338	676	yes	0.94	July, A
1994	yes	yes	341	682	yes	0.94	July, A, S
1995	yes	yes	336	674	yes	0.94	July, A
1996	yes	yes	334	668	yes	0.94	July, A, S
1997	yes	yes	341	682	yes	0.94	July, A
1998	yes	yes	353	706	yes	0.94	A, S
1999	yes	yes	341	682	yes	0.94	July, A
2000	yes	yes	342	684	yes	0.94	July, A, S
2001	yes	yes	383	764	yes	0.94	July, A
2002	yes	yes	341	684	yes	1.51	July, A
2003	yes	yes	382	762	yes	1.51	July, A

on sediment grain size and seagrass density was not obtained. Also, the characterization of the seagrass beds was limited by the draft of the barge used for the hard clam survey. As a result, the majority of the bottom type samples were from the deeper waters of Great South Bay. Sampling in shallow or intertidal waters, where most seagrasses occur, was not possible.

For this study, the bottom habitat categories that included sand or mud were aggregated to give two categories that reflect the coarse division between mud and sand habitat. Subsuming the suite of sediment types into these two primary classes and excluding shell habitat removed the considerable year-to-year variability that is inherent in bottom type classifications. The bottom habitat distribution map constructed for the Town of Islip sampling region (Fig. 2A) shows the distribution of muddy and sandy bottom. Areas where seagrass was consistently found were overlaid on this bottom distribution.

Empirical Orthogonal Function Analysis

The concurrent Town of Islip predator and hard clam data sets (1992–2003, Table 1) were analyzed for spatial and temporal trends using an EOF procedure, which partitioned the variance of the data into modes that represent space patterns with distinct time history. To calculate the EOFs, the data sets were first aligned and a data matrix, $D_{s,t}$, was constructed for each station (s) and time (t). The time mean for each station ($\overline{D}_s$) is:

$$\overline{D}_s = \frac{1}{T}\sum_{t=1}^{T} D_{t,s} \tag{2}$$

where T is the total number of measurements at a given station location, which is 12 for this analysis. The mean value is removed from the measurements to construct a modified data matrix, $M_{t,s}$:

$$M_{t,s} = D_{t,s} - \overline{D}_s \tag{3}$$

The variance of the modified data matrix is calculated:

$$\sigma_s^2 = \frac{1}{T}\sum_{t=1}^{T} M_{t,s}^2 \tag{4}$$

and used to construct a scaled (zero mean and unit variance) data matrix, $S_{t,s}$

$$S_{t,s} = \frac{M_{t,s}}{\sigma_s} \tag{5}$$

Scaling the measurements by the variance removes the effects of differences in amplitude in the data sets and minimizes dominance by stations with large variability.

The scaled data were then used to calculate a cross-variance matrix, $C_{p,q}$, which provides a measure of the degree of

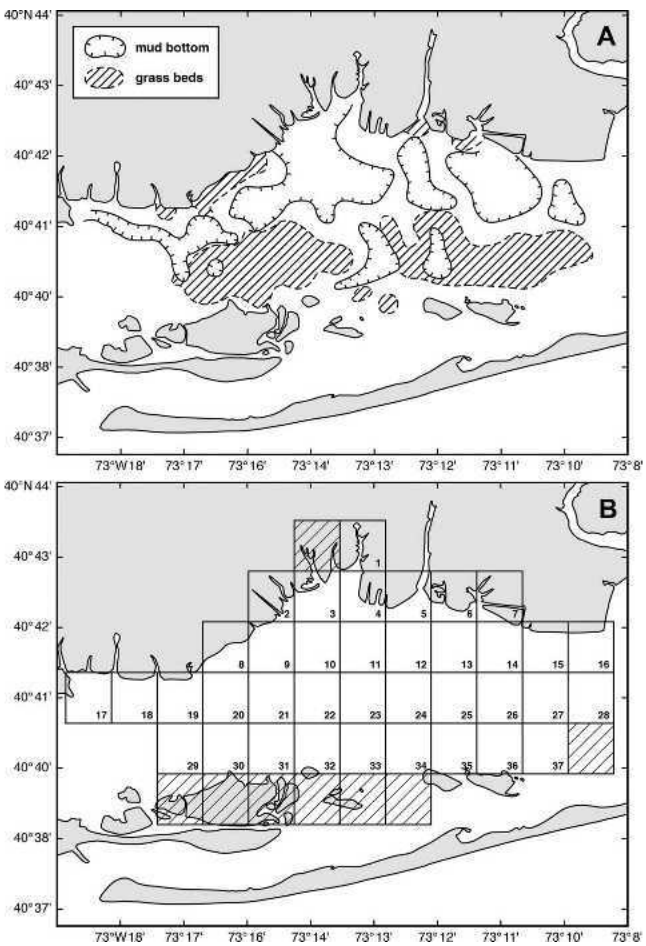

Figure 2. (A) Composite bottom habitat distribution constructed from the bottom type observations made during the Town of Islip annual surveys. Areas not designated as muddy bottom are sandy bottom. The composite distribution of seagrass beds is overlaid on the bottom habitat distribution. (B) Grid cells used for the EOF analyses (see text for details). The shaded grid cells were not used in the EOF analysis because of a scarcity of sampling within them. Numbered grid cells are areas where measurements of predators, hard clams, or both, were made each year from 1992–2003.

correlation of the variance between measurements at different stations:

$$C_{p,q} = \frac{1}{T}\sum_{t=1}^{T} S_{p,t}S_{q,t} \quad (6)$$

where p and q are individual stations and $C_{p,q}$ is an $N \times N$ matrix of values where N is the total number of stations.

The eigenvalues (λ_i) for $C_{p,q}$ provide a partitioning of the variance in the data sets with the total number of eigenvalues equal to N. The sum of the eigenvalues is the total variance in the data set. The fraction of the variance explained by each eigenvalue was obtained by dividing individual eigenvalues by the sum of the eigenvalues. The largest eigenvalues account for the highest fraction of the variance.

The spatial distribution and relative magnitude of behavior of the variance associated with individual eigenvalues is given by the eigenvectors of $C_{p,q}$. The eigenvectors, $e_{i,s}$, describe the pattern of participation of each station for each eigenvalue (i). The eigenvectors were used to extract the time behavior ($TS_{i,j}$) of the scaled data matrix that is represented by a particular pattern associated with each eigenvector:

$$TS_{i,t} = \sum_{s=1}^{N} e_{i,s}S_{t,s} \quad (7)$$

Equation (7) remaps the scaled data matrix into sets of stations with related time behavior and orders these patterns by the fraction of variance represented. A smoothed version of the zero mean, scaled data set can be constructed with $TS_{i,t}$ and $e_{i,s}$ by using a subset of the patterns ($N_{sig} < N$), which are shown to be significant:

$$R_{t,s} = \sigma_s \sum_{i=1}^{N_{sig}} TS_{i,t}e_{i,s} \quad (8)$$

Significant modes are identified by those eigenvalues that are larger than the mean of all eigenvalues. This approach includes the patterns with the largest variance, but eliminates the variance that is associated with high frequency and uncorrelated changes.

The fraction of the data variance explained by the EOF modes fit to the data, F_s, was calculated as:

$$F_s = 1 - \frac{1}{\sigma_s^2}\frac{1}{T}\sum_{t=1}^{T}(D_{t,s} - R_{t,s})^2 \quad (9)$$

A reconstruction of the original data that is based on EOF modes that perfectly represent the data would result in $F_s = 1$. Decreasing F_s values indicate that the associated individual mode represents a decreasing percentage of the data variance. Negative F_s values are associated with modes that represent the least amount of variability in the original data set.

Using the values of F_s, each grid cell in the survey region was assigned to a mode region by calculating a ranking as:

$$RankF_{s,i} = \frac{F_{s,i}}{\sum_{i=1}^{M} F_{s,i}} \quad (10)$$

where M is the total number of significant modes, which is 8 for this analysis. Equation (10) gives a measure of the percent contribution of the fit of each EOF mode to the total fit of all EOF modes to the original data set and was used to rank the EOF modes calculated for each grid cell. The EOF mode with the largest value of F_s in a given grid cell was designated as the primary mode for that location. A secondary EOF mode was designated for a grid cell if the difference between its F_s value and that calculated for the primary EOF mode was less than 10%. For some grid cells no single primary EOF mode emerged because each EOF mode contributed equally to the variability in the grid cell. These cells were designated as mixed mode.

For the EOF analysis, the predator and hard clam measurements made at the individual sampling sites were averaged onto a 1.6-km $\times$ 1.6-km grid (Fig. 2B). Grid cells were included in the EOF analysis if more than 5 y of predator and/or hard clam data were available and if the number of samples taken in a cell were at least 50% of the number of samples available for the other cells. Applying these criteria excluded eight grid cells from the EOF analysis (Fig. 2B). These grid cells were located around the edges of the sampling region and were infrequently included in the Town of Islip annual survey. The area included in the analysis (47.75 km^2) represents the certified portion of the total survey area of 60.70 km^2. The certified grounds are areas that satisfy specified bacterial water quality conditions and are open to hard clam fishing.

Lagging the predator and hard clam time series relative to one another allows examination of the possibility that predator effects are most pronounced on the smaller clams, which do not appear in the hard clam data set until the clams have advanced in age. Therefore, additional EOF analyses were performed on the predator and hard clam data sets that had been lagged by one and two years. For the one-year time-lag analysis, the predators from year t were matched with the hard clams from year $t + 1$. For the two-year time-lag analysis, the predators from year t were matched with the hard clams from year $t + 2$. Application of the EOF analysis to the hard clam data time series that was truncated so that only smaller hard clam sizes (<5 cm) were included yielded unstable results because these sizes were not well represented in many of the grid cells, especially after the late 1990s (Table 3). The result was inadequate data resolution for the EOF analyses.

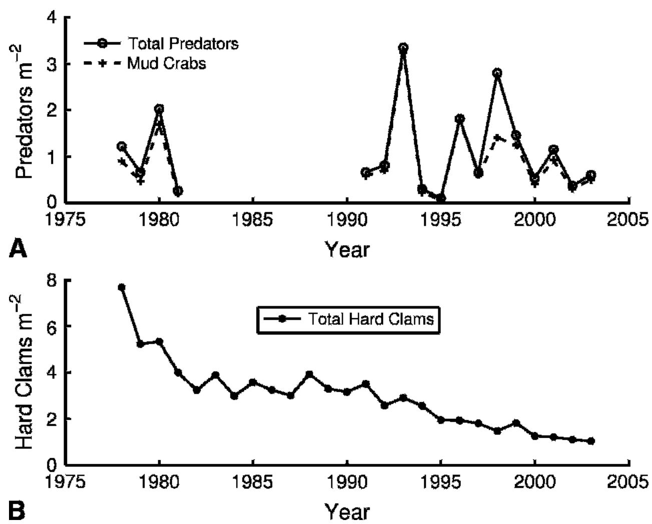

Figure 3. Time variability of area-wide averages of (A) total predators and total mud crabs (primarily *D. sayi*), and (B) total hard clams (*Mercenaria mercenaria*) obtained from the counts made during the Town of Islip annual surveys. Predator counts were not made from 1982–1990.

RESULTS

Bottom Habitat

The bottom habitat (Fig. 2A) in the northern part of the Town of Islip survey region is mostly mud because of the many creeks that empty into this part of Great South Bay (Figs. 1, 2). The bottom habitat in the remainder of the survey region is mostly sand. This general pattern agrees with an earlier assessment of bottom type in Great South Bay (USEPA Region II 1982), which showed that sediments are generally sandy throughout the area with an area of fine grain sediments around the creeks in the north part of the Bay.

The composite bottom habitat map (Fig. 2A) shows that the largest seagrass beds occur north of the islands in the southern part of the survey area. Smaller seagrass beds occur along the coast in the northern part of the survey region. The earlier assessment of seagrass distribution in Great South Bay (USEPA Region II 1982) showed that seagrasses were important to the north of Fire Island, north of Captree Island, and west of East Fire Island.

Area-wide Total Averages

Xanthid crabs (mud crabs, primarily *Dispanopeus sayi* Smith, 1869) normally accounted for more than 95% of the predators collected during the Town of Islip annual surveys (Fig. 3A). Other predators, such as other crabs, whelks (*Busycotypus*), other gastropods, starfish (*Asterias forbesi* Linnaeus, 1758), and lobsters (*Homarus americanus* H. Milne-Edwards, 1837) typically accounted for 1% to 3% of the predators captured in the bottom samples (Fig. 3A) except in 1998 when drills (*Urosalpinx*, *Eupleura*) represented about 43% of the predators captured (Table 2). Fluctuations in the relative abundance of blue crabs (*C. sapidus*) in the predator samples between 1991 and 2003 were of the same order as those associated with other predators, but numbers appeared to increase in 1998 and 2001 (Table 2).

From the late 1970s to early 1980s, total predator numbers in the Town of Islip survey area fluctuated about a total mean value of 50×10^6 (Table 3). When predator sampling resumed in 1991, the total number of predators fluctuated between a maximum of 133×10^6 in 1998 and a minimum of 5×10^6 in 1995, with a mean of about 54×10^6. Since 1999 the total predator number in the survey area fluctuated about a mean value of 39×10^6. These fluctuations did not show a strong increasing or decreasing trend over the time covered by the annual survey (Fig. 3A).

The variance associated with the predator numbers from the Town of Islip surveys was more than four times the mean (Table 3), which made discerning trends in the data difficult. Other statistical approaches can be used to discern trends in the data sets. A one-way ANOVA showed significant overall differences ($P = 0.0007$) in total predator numbers. Application of an *a posteriori* Tukey HSD test indicated that the total predator numbers could be partitioned into 6 groups of similar years (Table 4). The highest total predator numbers were recorded in 1993 and 1998 (Table 3). The largest group of years with similar characteristics indicated that predator numbers from the late 1990s and 2000s were similar to those in the later 1970s. The annual value for total crab abundance was dominated by mud crabs, which made the overall pattern of abundance significant ($P = 0.0007$, Table 4). The highest total crab number was in 1993 and the overall time series is also partitioned into six groups of similar years.

The total number of hard clams in the Town of Islip survey area has declined since the start of sampling in 1978 (Fig. 3B). An initial decline of about 54% occurred from 1978–1980, a gradual decline from 1980–1991, and then a steady decline to 2001. Total hard clam abundance ranged from a high of 378×10^6 in 1978 to a low of 76×10^6 in 2003 (Table 3). The error estimates associated with clam abundance were 1.2 times the mean, and as opposed to the predator data, allowed resolution of clear time trends in abundance (Table 3, Fig. 3B). Partitioning of total hard clam number into size categories (Table 3) showed trends similar to those determined for the total. The number of clams in the 2.2–4.0 cm and 4.1–5.3 cm categories decreased by about 94% between 1978 and 2003 (Table 3); the largest sized individuals decreased by 70%.

TABLE 2.

Total numbers for other predators calculated from the predator measurements made during the Town of Islip annual surveys. No predator data were collected from 1982–1990. The superscript indicates the species identification for each predator category.

Year	Blue Crabs[1] (No. $\times$ 10^6)	Other Crabs[2] (No. $\times$ 10^6)	Lobster[3] (No. $\times$ 10^6)	Starfish[4] (No. $\times$ 10^6)	Total Whelks[5] (No. $\times$ 10^6)	Total Drills[6] (No. $\times$ 10^6)	Moon Snails[7] (No. $\times$ 10^6)
1978	0	5	0	0.10	3.50	6.59	0.30
1979	0	1.85	0	0.06	1.49	5.84	0
1980	0.17	1.95	0	0	4.00	9.92	0
1981	0	0.99	0	0	0.44	1.80	0
1982	—	—	—	—	—	—	—
1983	—	—	—	—	—	—	—
1984	—	—	—	—	—	—	—
1985	—	—	—	—	—	—	—
1986	—	—	—	—	—	—	—
1987	—	—	—	—	—	—	—
1988	—	—	—	—	—	—	—
1989	—	—	—	—	—	—	—
1990	—	—	—	—	—	—	—
1991	0	1.29	0	0	1.14	1.14	0.15
1992	0.92	1.92	0	0	2.00	0.31	0
1993	0.30	0.83	0	0.38	2.71	1.28	0
1994	0	1.49	0	0	0.67	1.49	0
1995	0.45	0.38	0	0	0.98	0	0
1996	0.23	0.91	0	0	0.38	0.08	0
1997	0.15	0.45	0	0	1.19	0.15	0
1998	1.44	3.60	0	2.01	1.80	57.49	0
1999	1.56	2.01	0	3.95	1.34	0.97	0.30
2000	0.37	1.34	0	2.15	0.74	1.26	0
2001	2.12	4.31	0	1.86	1.72	0.80	0.20
2002	0.42	1.81	0.32	0.14	0.58	0.09	0.05
2003	0.04	3.15	0	0.66	0.62	0.08	0.12

[1] *Callinectes sapidus* (Rathbun, 1896).
[2] *Ovalipes ocellatus* (Herbst, 1799), *Carcinus maenas* (Linnaeus, 1758), *Pagurus longicarpus* (Say, 1817), *Limulus polyphemus* (Linnaeus, 1758), *Cancer irroratus* (Linnaeus, 1758), *Libinia spp*.
[3] *Homarus americanus* (H. Milne-Edwards, 1837).
[4] *Asterias forbesi* (Linnaeus, 1758).
[5] *Busycotypus canaliculatus* (Linnaeus, 1758), *Busycon carica* (Gmelin, 1791).
[6] *Urosalpinx cinerea* (Say, 1822), *Eupleura caudata* (Say, 1822).
[7] *Neverita duplicata* (Say, 1822).

An *a posteriori* one way ANOVA showed significant overall differences ($P = 0.0039$) in total clam numbers. The Tukey HDS test partitioned hard clam data into 10 groups of similar years (Table 4). The greatest abundance was in 1978 and the lowest in 2003 (Table 4). As opposed to the predator data, where time trends in abundance were not apparent, the hard clam data showed a clear long-term downward trend. The highest numbers appeared for the first three years, and the lowest were found in the last 10 y. Whereas they are not significantly different from each other, the period from 1999 to 2003 forms one low abundance period while the 1992 to 1998 was slightly higher, reflecting the continuing downward trend in abundance.

Spatial Distributions of Predators and Hard Clams

Spatial maps of predator and hard clam distributions were constructed from the measurements that were averaged onto the 1.6-km $\times$ 1.6-km grid (Fig. 2B). The aggregation to the larger scale removed some of the year-to-year variability inherent in the predator and hard clam measurements. As a check on the averaging procedure, the area-wide average of the hard clam average abundance used to construct the distributional maps was computed and compared with the area-wide hard clam average obtained directly from the Town of Islip survey (Table 5). The two values agreed to within 1%, which validated the approach used to obtain the distributional maps.

The spatial distribution of predators (Plate 1) provided general patterns and variability that characterize the 1992 to 2003 period that are not apparent from the area-averaged total predator values (Fig. 3A, Table 3). Predator distribution in the Town of Islip survey area showed considerable variability where high abundances of predators were found (Plate 1). During the 12 y, maxima in predator abundance occurred in essentially all parts of the survey area, with no one area showing consistently high or low predator abundances. The most contracted predator distribution occurred in 1994 and 1995 when predators were found only in a limited part of the eastern part of the survey region. Local patches of predators in excess of 10 m^{-2} occurred in 1992, 1993, and 1996, although the areas where the maxima occurred differed between years. In 1993,

TABLE 3.

Total numbers for predators, mud crabs (primarily *D. sayi*), hard clams, year-2 hard clam seed (1.2–4.0 cm), year-3 seed hard clam (4.1–5.3 cm), and neck, chowder and large clams (5.4–26.7 cm) calculated from measurements made during the Town of Islip annual surveys. No predator data were collected from 1982 to 1990.

Year	Total Predators (No. $\times$ 10^6)	Total Mud Crabs (No. $\times$ 10^6)	Total Hard Clams (No. $\times$ 10^6)	Total Hard Clams 2.2–4.0 cm (No. $\times$ 10^6)	Total Hard Clams 4.1–5.3 cm (No. $\times$ 10^6)	Total Hard Clams 5.4–26.7 cm (No. $\times$ 10^6)
1978	58 ± 109	43 ± 98	378 ± 495	69	103	185
1979	32 ± 84	22 ± 76	258 ± 405	38	75	140
1980	97 ± 162	81 ± 146	173 ± 187	25	43	73
1981	13 ± 56	9 ± 53	173 ± 193	40	34	92
1982	—	—	158 ± 178	31	33	92
1983	—	—	157 ± 162	27	33	95
1984	—	—	145 ± 174	23	29	94
1985	—	—	175 ± 188	31	38	105
1986	—	—	158 ± 148	21	35	102
1987	—	—	146 ± 156	16	29	91
1988	—	—	191 ± 206	29	32	104
1989	—	—	161 ± 182	28	24	106
1990	—	—	155 ± 152	31	22	100
1991	31 ± 109	28 ± 106	171 ± 204	33	26	102
1992	39 ± 267	33 ± 266	126 ± 153	23	18	83
1993	160 ± 530	155 ± 526	131 ± 163	15	14	57
1994	14 ± 82	11 ± 80	116 ± 130	31	10	71
1995	5 ± 28	3 ± 25	87 ± 98	18	12	57
1996	87 ± 438	85 ± 438	87 ± 138	8	11	62
1997	31 ± 173	29 ± 173	81 ± 97	7	9	58
1998	133 ± 538	67 ± 305	67 ± 80	4	7	54
1999	70 ± 189	60 ± 188	82 ± 145	6	7	49
2000	25 ± 110	19 ± 107	57 ± 93	5	4	40
2001	55 ± 264	44 ± 238	55 ± 98	5	5	40
2002	18 ± 43	14 ± 38	80 ± 124	4	5	71
2003	29 ± 61	24 ± 55	76 ± 117	5	5	57

predators covered essentially all of the survey area with abundances above 1–2 m^{-2}. Comparison of the predator distribution with bottom habitat type (Fig. 2A) did not show any apparent correspondences.

Hard clams were found over the entire survey area in all years (Plate 2). The highest clam density was consistently found in the northern part of the survey region. The higher hard clam density in the northwestern part of the survey area and lower densities to the east produce a gradient that is present in all years. From 1993 to 1999, clam densities in excess of 5 m^{-2} were found along the northern part of the survey region. The hard clam distribution for 2001 showed the minimum values at essentially all sample sites. Again, comparison of the hard clam distribution with bottom habitat type (Fig. 2A) did not reveal any obvious correspondences. Hard clams were found in muddy and sandy bottom regions and in regions with and without seagrass.

Empirical Orthogonal Function Analysis of Predator and Hard Clam Distributions

Spatial Distributions

A qualitative comparison of the predator and hard clam distributions (Plates 1 and 2) suggested that the predator and hard clam abundances were variable, but trends and/or correlations in the fluctuations were not apparent. Therefore, the predator and hard clam distributions were examined using an EOF analysis procedure, which provides a rigorous approach for determining trends, patterns, and correspondences in the two distributions.

The distribution of the EOF modes that account for variability in the predator and hard clam data sets (Figs. 4, 5) showed that most of the variance in the data sets was accounted for by one or two primary modes for each and these differ for the two data sets. The predator distributions were dominated mostly by EOF mode 2 with a contribution by modes 3 and 4; the hard clam distribution was dominated by EOF mode 1.

The spatial distribution of the primary predator EOF modes (Fig. 5A) showed that EOF mode 2 accounted for variability in the western part of the survey region. In the eastern part of the survey region different modes accounted for the variability in the data set, but mode 3 accounted for much of the variability in this area. In two of the grid cells, no single EOF mode or combination of EOF modes was dominant. In areas where a second EOF mode made a significant contribution to the variance, mode 4 tended to be the most consistent second mode.

The distribution of the primary EOF modes calculated for the hard clams (Fig. 5B) showed that mode 1 dominated over most of the survey region. Regions not dominated by this mode were around the margins of the survey area. The contribution of a second mode to the variance in the hard clam distributions was limited to grid cells in the western part of the survey region, where

TABLE 4.

Grouping of years obtained from the Tukey HDS test for total predators, total mud crabs and total hard clams measured in the Town of Islip survey area. The letters indicate years that have similar characteristics. The ordering of the years is based upon similarity.

Year	**1993**	**1998**	**1980**	**1996**	**1999**	**1978**	**2001**	**1979**	**1992**	**1991**	**1997**	**2003**	**2000**	**2002**	**1994**	**1995**										
Total Predators m^{-2}	3.35	2.79	2.11	1.81	1.47	1.22	1.16	0.82	0.81	0.67	0.65	0.6	0.53	0.37	0.3	0.1										
	a	a																								
		b	b	b																						
			c	c	c	c	c																			
				d	d	d	d	d	d	d																
					e	e	e	e	e	e	e	e	e	e												
						f	f	f	f	f	f	f	f	f	f	f										
Year	1993	1996	1980	1998	1999	2001	1978	1992	1979	1997	1991	2003	2000	2002	1994	1995										
Total Crabs m^{-2}	3.26	1.8	1.74	1.51	1.33	1.06	1	0.76	0.64	0.62	0.62	0.57	0.44	0.34	0.25	0.08										
	a																									
		b	b	b	b	b	b																			
				c	c	c	c	c	c	c	c	c														
					d	d	d	d	d	d	d	d	d	d												
						e	e	e	e	e	e	e	e	e	e											
							f	f	f	f	f	f	f	f	f	f										
Year	1978	1979	1980	1983	1981	1985	1988	1991	1986	1989	1982	1990	1984	1987	1992	1994	1995	1993	1996	1997	1998	1999	2001	2002	2000	2003
Total Hard Clams m^{-2}	7.27	5.17	4.34	3.9	3.86	3.6	3.42	3.33	3.27	3.26	3.23	3.16	3.01	2.82	2.56	2.49	1.93	1.92	1.79	1.67	1.46	1.37	1.1	1.1	1.09	0.93
	a																									
		b	b																							
			c	c	c	c	c	c	c	c	c															
				d	d	d	d	d	d	d	d	d	d	d												
						e	e	e	e	e	e	e	e	e	e											
							f	f	f	f	f	f	f	f	f	f										
													g	g	g	g	g	g								
														h	h	h	h	h	h							
															i	i	i	i	i	i	i					
																	j	j	j	j	j	j	j	j	j	j

TABLE 5.

Comparison of the area-wide hard clam density calculated by averaging the hard clam values used to construct the hard clam spatial distribution maps with the area-wide hard clam density calculated by the Town of Islip from the annual survey.

Year	Total Density Islip Data (Hard Clams m^{-2})	Total Density This Study (Hard Clams m^{-2})	% Difference
1992	2.58	2.58	0.08
1993	2.91	2.91	0.00
1994	2.55	2.57	–0.93
1995	1.94	1.95	–0.36
1996	1.93	1.94	–0.31
1997	1.81	1.81	–0.11
1998	1.49	1.48	0.47
1999	1.82	1.83	–0.27
2000	1.26	1.26	–0.32
2001	1.21	1.22	–0.66
2002	1.13	1.11	1.53
2003	1.04	1.05	–0.67

EOF mode 2 and 3 dominated, and to three grid cells in the eastern part of the survey area where modes 6, 7, and 8 dominated. Mode 7 was the primary mode in one grid cell in the southern part of the area. Two of the cells had no primary mode.

Empirical Orthogonal Function Analysis Mode Trends

The time structure of the individual EOF patterns (the eigenvectors, $e_{i,s}$) provided insights into the trends and patterns in the predator and hard clam data sets. The time change associated with EOF mode 1 (Fig. 6A) was characterized by a long-term trend in hard clam abundance. This mode represented hard clams nearly exclusively with little influence from the predators. The direction of the trends in the time history of the EOF modes was obtained by multiplying the eigenvectors by the amplitude time series, $TS_{i,t}$, obtained for the hard clam (Fig. 7) and predator (Fig. 8) data sets. For the regions where EOF mode 1 dominates, all eigenfunctions (spatial structures) were negative (Fig. 7A). This indicates that the hard clam abundance in these regions was fluctuating in the same way (i.e., changes were occurring in phase). Subsetting the hard clam time series by mode region shows a decreasing trend through time in mode region 1 (Fig. 9). This is a hard clam response; predators do not influence mode 1. The other mode regions that contribute to the hard clam variance showed year-to-year fluctuations in abundance (Fig. 9).

In regions where EOF mode 2 dominated, the mode amplitude was negative (Fig. 8A) indicating that changes in predator abundance in these regions were in phase. The only exception to this trend was grid cell 14 in the eastern section of the survey region, which was out of phase from the rest of the mode 2 region. Subsetting the predator time series by mode region showed that mode region 2 was dominated by interannual fluctuations in predator abundance, with increased predator numbers occurring in 1993 and 1998 (Fig. 10). Mode region 3 showed a peak in predator number in 1996 (Fig. 10), but this mode accounted for only 12% of the total variance (Fig. 5A). The remaining EOF modes contributed little to the total variance of the data sets and were not significant (Fig. 5).

Mode 2 contributed to hard clam abundance only in grid cell 17, which is located in the far western part of the survey region (Figs. 2B, 5B, 7B) This grid cell lacked sufficient predator samples for inclusion in the EOF analysis, so relative fluctuations of predators and hard clams in this region could not be determined.

Mode regions comprised of multiple grid cells showed fluctuations that were in phase, with two exceptions. For the predators, grid cell 14 in mode region 2 was out of phase with all other grid cells in this mode region (Fig. 8A). Also, the two grid cells that comprise mode region 4 (grid cells 25 and 33) were out of phase with one another (Fig. 8B). However, hard clam fluctuations in these grid cells were in phase (Fig. 7A). These results imply that variability in predator and adult hard clam abundances did not result from predator-prey interactions; the two populations were essentially uncoupled.

Empirical Orthogonal Function Analysis Time-lag Mode Trends

The regional distribution of the EOF modes obtained for a one- and two-year time lag was similar to that obtained for the zero-lag analysis (Fig. 5). The mode region trends for the predator (Fig. 11A) and hard clam (Fig. 11B) time series for a one-year time lag show essentially the same patterns as those obtained from the zero-lag analysis. The time change of the predators within the EOF mode regions shows interannual fluctuations and no obvious trend. The hard clam time series is again dominated by mode region 1, which showed a long-term declining trend in hard clam abundance. As before, this mode represented hard clams nearly exclusively with little influence from the predators. The mode region trend for the predator (Fig. 12A) and hard clam (Fig. 12B) time series for the two-year time lag showed similar patterns. For both lagged correlations no obvious predator-prey interaction response was seen in mode regions 1–4, which together represent 71% of the variance in the data sets.

DISCUSSION AND SUMMARY

Data Set Limitations

A number of important caveats are associated with the predator data sets used in this analysis. Three major limitations are imposed by the manner in which the data were collected. First, predator abundance was measured over the summer season, and thus predators that move into the Town of Islip survey area in fall, winter, and spring were not assayed. However, predation effects are likely to be most evident in summer when temperatures are elevated and feeding rates are maximal (e.g., Powell et al. 1997). Invertebrate activity in general decreases with decreasing temperature (DeFur & Magnum 1979) and the activity of *Urosalpinx* and *Eupleura*, two of the predators in the survey area (Table 2), decreases with decreasing temperature (Carriker 1955, Manzi 1970). Also, *Busycon* (Table 2) growth and activity (Kraeuter et al. 1989) decreases with decreasing temperature.

Second, the collection method (clamshell bucket with a 6.4-mm sieve) was designed to monitor hard clam populations, and predator abundance was included as ancillary information, which does not necessarily assure consistent or most appropriate data collection for predators. Also, daytime sampling does not sample well predators with nocturnal habits.

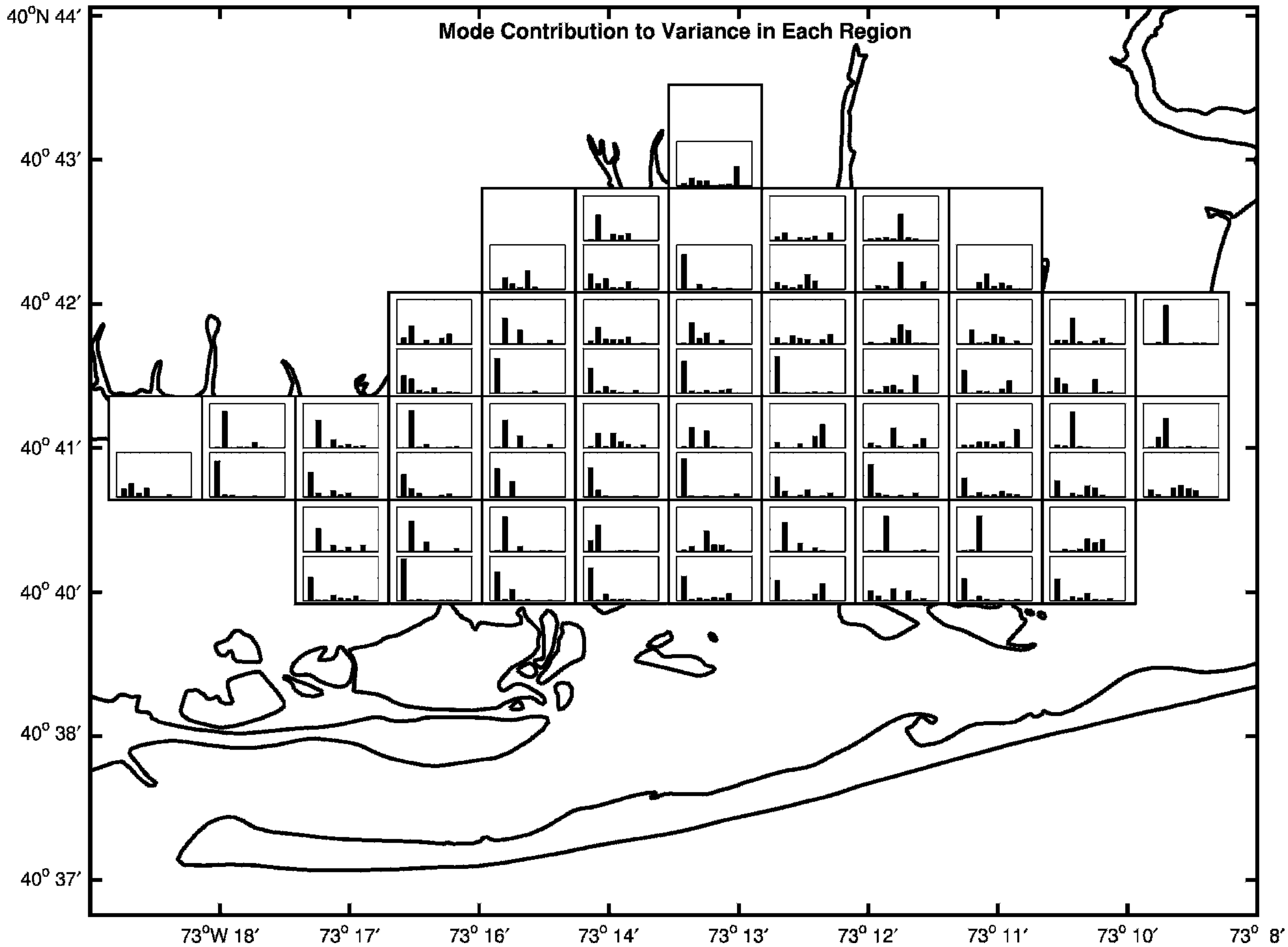

Figure 4. Distribution of fraction of the data variance explained by the EOF modes (F_s calculated by Eq. 9) in each grid cell, indicated by heavy lines, calculated from the predator (top) and hard clam (bottom) data sets. The relative height of each bar indicates the contribution of an individual mode to the total variance. Grid cells with only one F_s distribution did not contain sufficient data for calculation of the missing distribution (see Fig. 2). Negative values of F_s were set to zero to simplify the plots.

Third, the size of individual samples was large and all sorting was done on deck. Because enumeration of predators was a secondary measurement, it is likely that many of the smaller individuals (e.g., drills (*Urosalpinx cinerea* Say, 1822, *Eupleura caudate* Say, 1822), small xanthids (mostly *D. sayi*), small pagurids (*Pagurus* spp., mostly *Pagurus longicarpus* Say, 1817)) were missed or not accurately counted or not as carefully collected as was done for hard clams. Other than the seasonality, these factors are partly mitigated by the use of the 6-mm sieve, which makes it likely that larger organisms, such as whelks (*Busycotypus canaliculatus* Linnaeus, 1758, *Busycon carica* Gmelin, 1791), and starfish (*Asterias forbesi* Linnaeus, 1758) were enumerated and the large number of samples increased the likely encounter of the rarer predator contingent. The same cannot be asserted for more motile fauna such as blue crabs (*C. sapidus*) and lady crabs (*Ovalipes ocellatus* Herbst, 1799). The sampling gear would severely underestimate the abundance of such predators. An assumption in this analysis is that capture efficiency remained the same because sampling time was usually constrained to summer months and thus warmer temperatures. This implies that, whereas absolute abundance estimates are unlikely to be correct, relative abundance of these highly motile organisms should be valid.

Another limitation of the predator data set is that most of the hard clams enumerated in the Town of Islip annual survey are larger than 2.2 cm (Table 3). These clams exceed the size of clams that many of the predators can consume. Predatory losses on hard clams are believed to occur dominantly from post set to about 20-mm shell length, and the vast majority of these losses are on individuals <10 mm (Kraeuter 2001). Mortality rates decline at larger sizes until rising again at old age (Hofmann et al. 2006). Fluctuations in predator and hard clam abundance should still be indicative of trends that reflect changes in the overall populations because increased predation on recruits should propagate through the large size classes over time. This is supported by analyses of the predator and hard clam time series constructed with one-year and two-year time lags. The EOF analysis of the lagged time series gave results that were similar to those obtained with the zero-lag data sets.

Predation Effects

Mud crabs, mostly *D. sayi*, were the most abundant predator collected in the Town of Islip, which is consistent

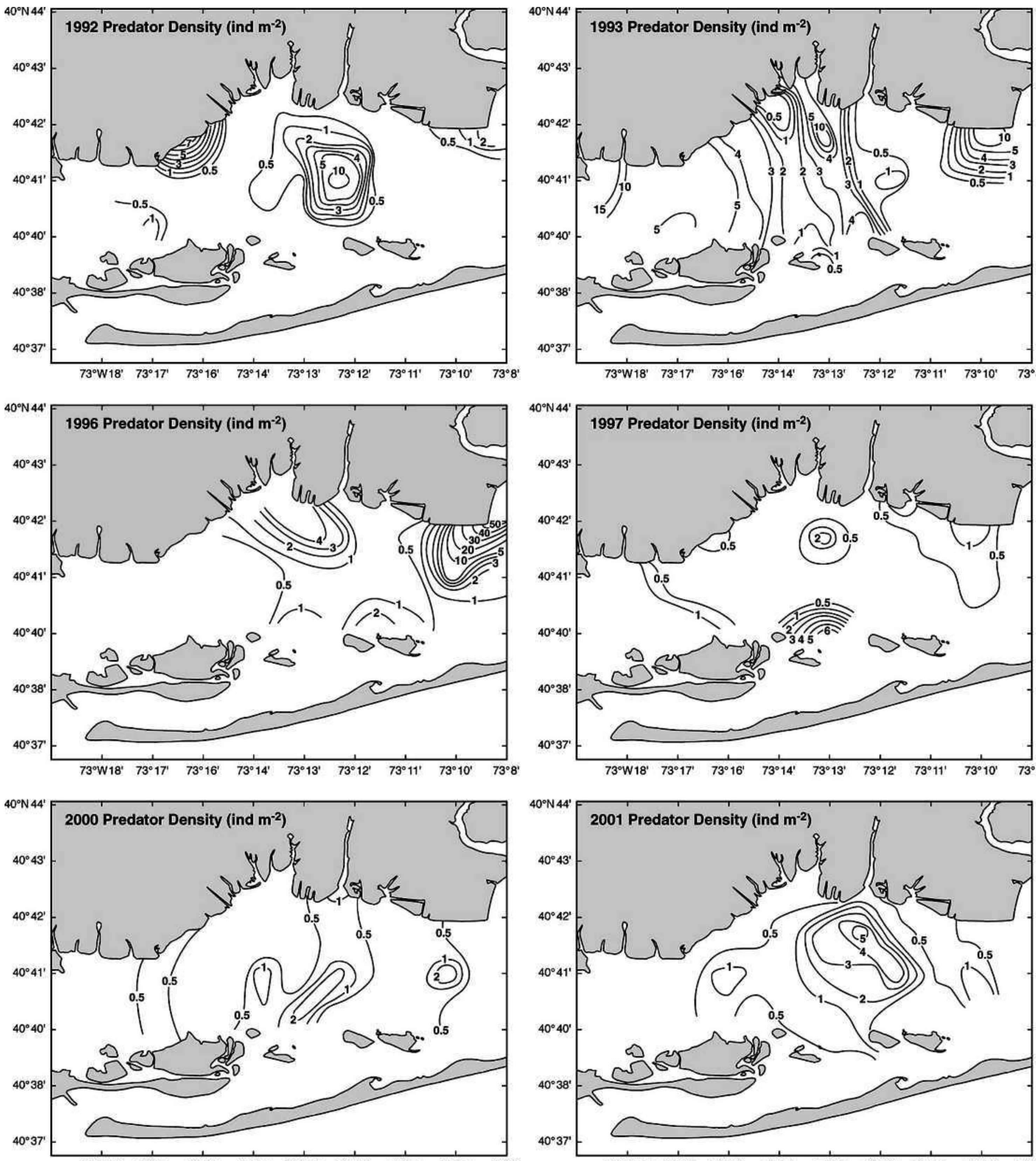

Plate 1. Spatial distributions of predators for 1992–2003 constructed from measurements made during the Town of Islip annual surveys. Contour interval is 1 ind m^{-2}. For v less than 0.5 ind m^{-2} or zero.

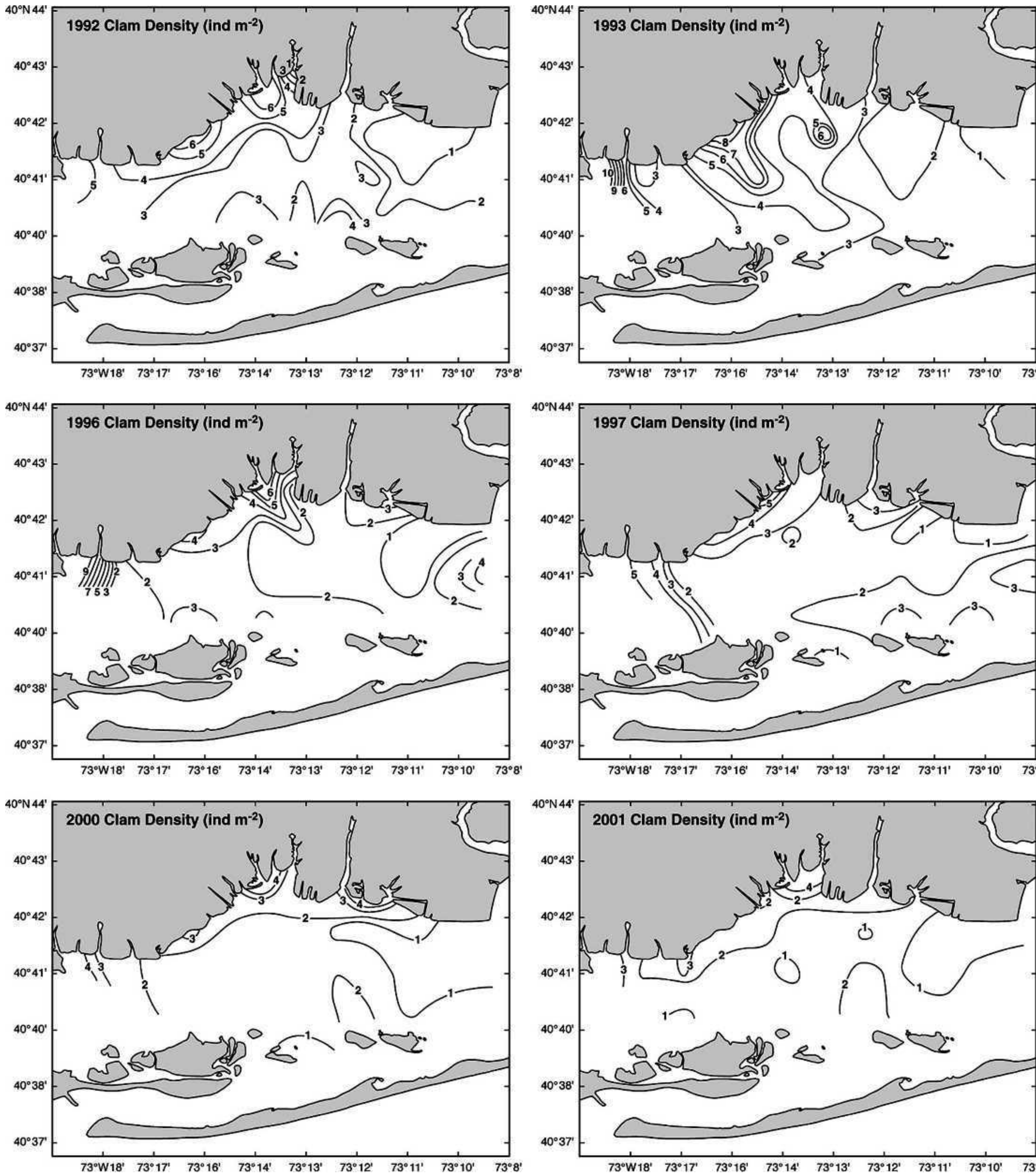

Plate 2. Spatial distributions of hard clams for 1992–2003 constructed from mea

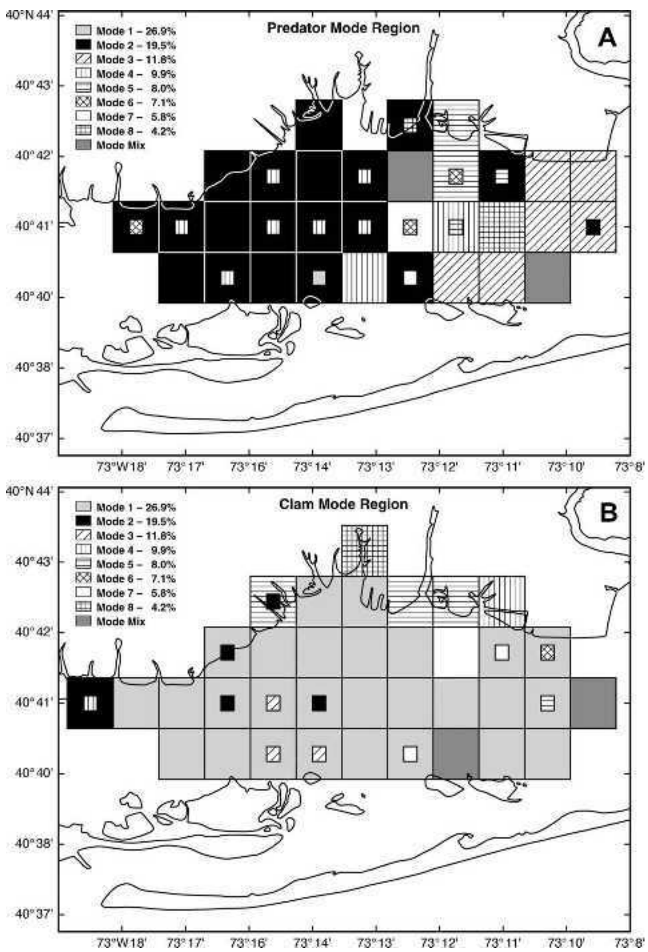

Figure 5. Spatial distribution of the primary EOF modes calculated for (A) predators and (B) hard clams. The amount of the overall variance accounted for by the individual modes is indicated by the shading. The inset in some of the grid cells indicates that a second EOF mode accounted for a significant amount of the variance in that cell (see Fig. 4). The grid cells indicated as mode mix are ones in which each EOF mode contributed almost equally to the total variance.

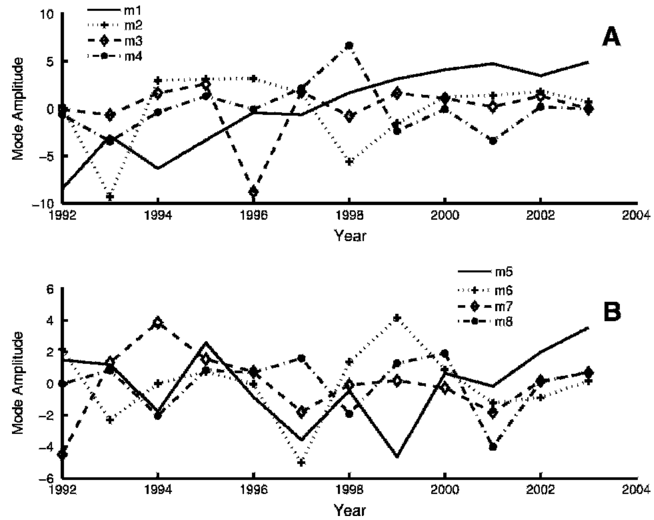

Figure 6. Time history of the EOF modes (A) 1–4 and (B) 5–8 calculated for the predator and hard clam data sets.

with previous predator studies of this region (MacKenzie 1977, WAPORA 1981). Two-year classes of mud crabs were found in Long Island bays (Strieb et al. 1995). Recruitment was in mid summer and the juvenile crab population reached 5-mm carapace width by late summer to early fall. Adults ranged in size from 7–29 mm, but various populations averaged 13–17 mm mean carapace width (Strieb et al. 1995). Mud crab densities were highest in grass beds and least in muddy areas (0.5 ind m^{-2}), but year-to-year population fluctuations in a given region could be an order of magnitude, and bay-to-bay variations were about a factor of 2.5 (Bauer 1994, Strieb et al. 1995). In Great South Bay, mud crab densities as high as 102 ind m^{-2} have been reported (WAPORA 1981), but more typical densities on a bay-wide basis are up to about 5.3 ind m^{-2} (Greene 1978). Mud crab densities in the survey region in 1993 were estimated to be 3.2 ind m^{-2} (Strieb et al. 1995). These abundances and trends are similar to those seen in the spatial distribution of predators constructed from the Town of Islip annual survey data (Plate 1). Thus, mud crab densities were likely adequately resolved by the sampling methodology or if low, underestimated because of loss of small animals passing through the 6-mm sieve.

A study of laboratory predation rates, scope for growth, abundance, and other factors (Gibbons 1984) showed that of the three species of crabs (*O. ocellatus, P. longicarpus* and *D. sayi*) studied, the mud crab was the most important hard clam predator in Great South Bay. Gibbons (1984) reported highest predation rates on clams smaller than those effectively collected by the Islip sieve size. Predation rates at summer temperatures for adult crabs 19–21 mm carapace width ranged from 115 (±19) 3-mm clams d^{-1} to 22 (±7) 7-mm clams d^{-1} (Gibbons 1984). Even at 10°C, this species consumed between 45 (3-mm clams) and 11 (7-mm clams) d^{-1}. Predation by mud crabs on this size of hard clams would not be documented by the sampling gear used in the Town of Islip annual survey. There is little evidence that hard clam populations are

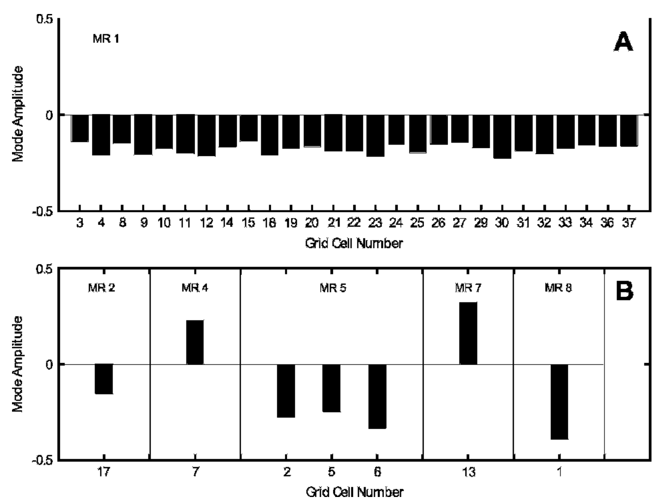

Figure 7. Amplitude of the primary hard clam eigenvalue in individual grid cells for (A) EOF mode 1 and (B) EOF modes 2, 4, 5, 7, and 8. The location of individual grid cells is given in Figure 2B. The grid cells are grouped by mode region (MR), which are areas defined by the primary mode as calculated using Eq. (10).

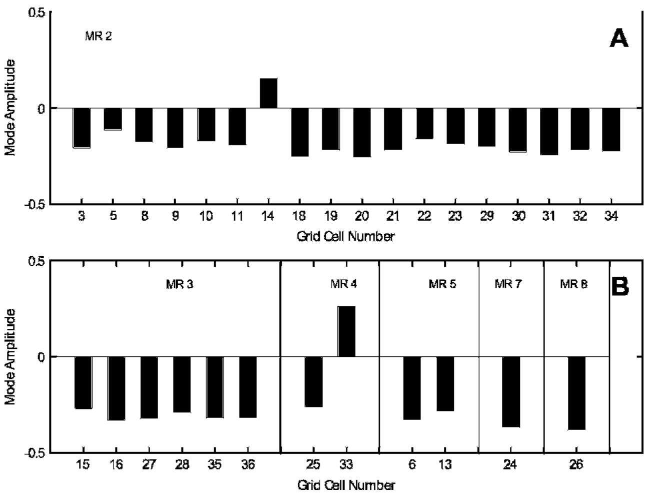

Figure 8. Amplitude of the primary predator eigenvalue in individual grid cells for areas dominated by (A) EOF mode 2 and (B) EOF modes 3, 4, 5, 7, and 8. The location of individual grid cells is given in Figure 2B. The grid cells are grouped by mode region (MR), which are areas defined by the primary mode as calculated using Eq. (10).

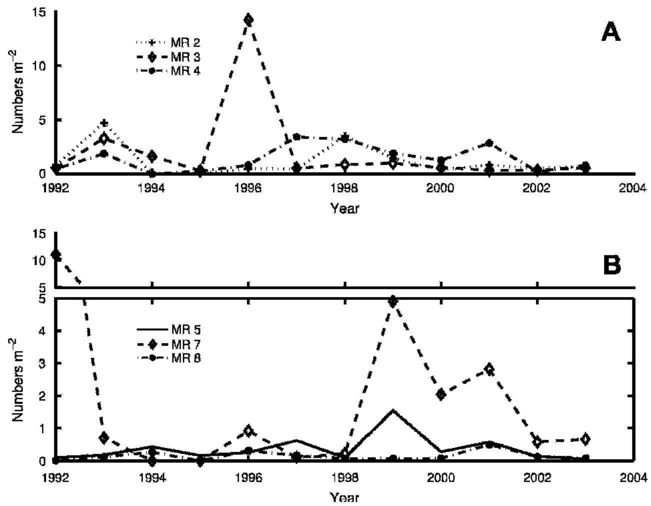

Figure 10. Averaged predator time series obtained within EOF mode regions (A) 1–4 and (B) 5–8. EOF modes 1 and mode 6 do not contribute to the predator spatial distribution (See Fig. 5A).

fluctuating in a manner that can be explained by the annual abundance of the suite of predators (Figs. 3, 9, 10, Plates 1, 2). Thus, the Town of Islip data confirm that mud crabs are the most abundant of the predators (Table 2, Fig. 3A), but the lack of correspondence between that abundance and clam populations suggests that alternate prey support the crab population.

Hard Clam Decline

The hard clam abundances measured in the Town of Islip survey area show a clear and persistent decreasing trend since the late 1970s and early 1980s (Fig. 3B). That this trend occurred over the entire area surveyed by the Town of Islip is reflected in the dominant mode extracted from the hard clam data set by the EOF analysis (Figs. 5B, 9A). The analyses of the predator data sets suggest that increased predation coincident with the decline in hard clams did not occur. Adequate alternate prey would appear to be available. Some evidence indicates an increase in blue crabs since the mid 1990s (Table 3), but this occurred well after the decline in hard clams began.

The relative effect of predation, however, may be important in limiting recovery from a severely depleted hard clam population. The long-term decline in hard clam abundance is potentially the result of changed environmental conditions that no longer favor hard clams, such as the development of blooms of the harmful alga *Aurecooccus anophagefferens* (brown tide), decreased fecundity of adult hard clams, reduced recruitment to the postsettlement population, and/or overfishing. The occurrence of brown tides in Great South Bay has potentially

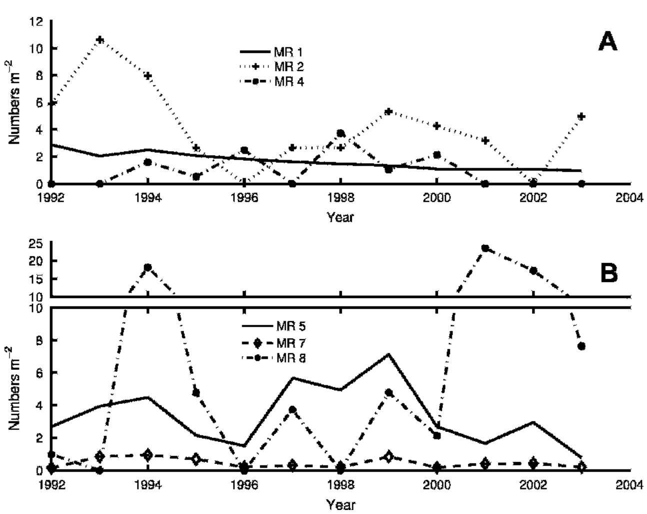

Figure 9. Averaged hard clam time series obtained within EOF mode regions (A) 1–4 and (B) 5–8. EOF modes 3 and 6 do not contribute to the hard clam spatial distribution (See Fig. 5B).

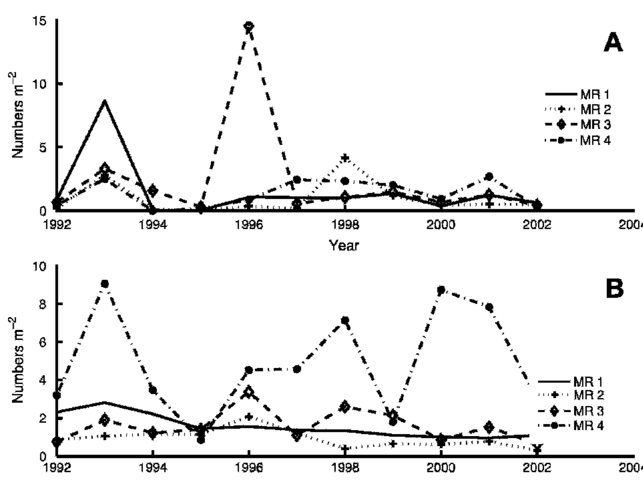

Figure 11. Averaged time series of the (A) predator and (B) hard clam data sets within EOF mode regions 1–4 when the hard clams are lagged one year relative to the predators. Only the first four mode regions are shown because these account for 71% of the total variance in the data set.

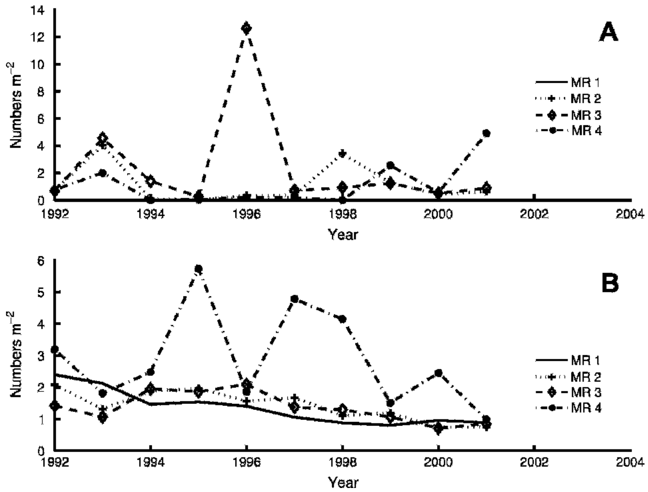

Figure 12. Averaged time series of the (A) predator and (B) hard clam data sets within EOF mode regions 1–4 when the hard clams are lagged two years relative to the predators. The fewer years included in the analysis reflect the loss of data points due to the time lag. Only the first four mode regions are shown because these account for 71% of the total variance in the data set.

limited hard clam growth (Bricelj & Lonsdale 1997, Bricelj et al. 2001) and may have a disproportionate effect on juvenile and small hard clams. Some evidence for the second and third factors is given by an analysis of broodstock-recruitment relationships for hard clams in Great South Bay (Kraeuter et al. 2005), which showed a density dependent control on recruitment for current conditions. Current hard clam densities are low enough that fecundity is reduced, or spawning and fertilization success or postfertilization survival (affected by natural and fishing mortality) are hindered (Kraeuter et al. 2005). Also, intense harvesting may have produced recruitment overfishing which contributed to the continued depletion of the Great South Bay hard clam populations, similar to what was observed for hard clam populations in North Carolina (Peterson 2002).

Fishing mortality is likely the dominant cause of the hard clam population decline through the 1980s (Buckner 1984, Kraeuter et al. submitted). Analyses of the Town of Islip data set do not support a role for small predators in this decline. The broodstock-recruitment relationship given by Kraeuter et al. (2005), however, suggests an important Allee effect that would limit recovery after population collapse. Adding to this limitation might be a still large predator contingent adept at consuming hard clam recruits adventitiously. Peterson et al. (1995) showed that these predators select hard clams as prey down to abundances as low as the threshold for depensatory recruitment (0.75 ind m^{-2}) suggested by Kraeuter et al. (2005). Thus, the large mismatch in predator and hard clam abundance that presently exists in Great South Bay might provide a severe limitation on population recruitment that would not be easily resolved in survey abundances of larger juvenile and adult hard clams.

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LITERATURE CITED

Ambrose, W. G., Jr. 1991. Are infaunal predators important in structuring marine soft-bottom communities? *Am. Zool.* 31:849–860.

Bauer, S. I. 1994. The dynamics of mud crab, *Dyspanopeus sayi*, predation on juvenile bay scallops, *Argopecten irradians irradians*, in eelgrass. MS Thesis, Graduate School-Marine Environmental Sciences, State University of New York, Stony Brook. 109 pp.

Bricelj, V. M. & D. J. Lonsdale. 1997. *Aureococcus anophagefferens*: causes and ecological consequences of brown tides in US mid-Atlantic coastal waters. *Limnol. Oceanogr.* 42:1023–1038.

Bricelj, V. M., S. P. MacQuarrie & R. A. Schaffner. 2001. Differential effects of *Aureococcus anophagefferens* isolates ('brown tide') in unialgal and mixed suspension on bivalve feeding. *Mar. Biol.* 139:605–615.

Buckner, S. C. 1984. Aspects of the population dynamics of the hard clam, *Mercenaria mercenaria* L., in Great South Bay, New York, Ph.D. Dissertation, State University of New York at Stony Brook. 217 pp.

Carriker, M. R. 1955. Critical review of biology and control of oyster drills *Urosalpinx* and *Eupleura*. *U.S. Fish. Wildl. Serv. Spec. Sci. Rpt. Fish* 148:1–150.

Connell, J. H. 1961. Effects of competition, predation by *Thais lapillis*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* 31:61–104.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: M. L. Cody & J. M. Diamond, editors. Ecology and evolution of communities. Cambridge, MA: Harvard University Press. pp. 460–490.

DeFur, P. L. & C. P. Magnum. 1979. The effects of environmental variables on the heart rate of invertebrates. *Comp. Biochem. Physiol.* 62A:283–294.

Gibbons, M. C. 1984. Aspects of predation by the crabs *Neopanope sayi*, *Ovalipes ocellatus*, and *Pagurus longicarpus* on juvenile hard clams *Mercenaria mercenaria*. Ph.D. Dissertation, Graduate School-Coastal Oceanography, State University of New York, Stony Brook, NY. 96 pp.

Gibbons, M. C. & W. J. Blogoslawski. 1989. Predators, pests, parasites, and diseases. In: J. J. Manzi & M. Castagna, editors. Clam mariculture in North America, Developments in aquaculture and fisheries science, Vol. 19. Amsterdam: Elsevier. pp. 167–200.

Greene, G. T. 1978. Population structure, growth and mortality of hard clams at selected locations in Great South Bay. MS Thesis, Marine Environmental Sciences. State University of New York, Stony Brook. 199 pp.

Griffiths, C. L. 1990. Spatial gradients in predation pressure and their influence on the dynamics of tow littoral bivalve populations. In: B. Morton, editor. The Bivalvia- Proceedings Memorial Symposium in Honor of Sir Charles Maurice Yonge, Edinburgh, 1986, Hong Kong University Press. Hong Kong. pp. 321–332.

Guillou, J. & C. Tartu. 1994. Post-larval and juvenile mortality in a population of the edible cockle *Cerastoderma edule* (L.) from northern Brittany. *Neth. J. Sea Res.* 33:103–111.

Hofmann, E. E., J. M. Klinck, J. N. Kraeuter, E. N. Powell, R. E. Grizzle, S. C. Buckner & V. M. Bricelj. 2006. A population dynamics model of the hard clam, *Mercenaria mercenaria*: Development of the age- and length-frequency structure of the population. *J. Shellfish Res*. 25:417–444.

Irlandi, E. A. & C. H. Peterson. 1991. Modification of animal habitat by large plants: mechanisms by which seagrasses influence clam growth. *Oecologia* 87:307–318.

Jensen, K. T. & J. N. Jensen. 1985. The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *J. Exp. Mar. Biol. Ecol*. 89:157–174.

Kraeuter, J. N. 2001. Predators and predation. In: J. N. Kraeuter & M. Castagna, editors. Biology of the hard clam. Developments in aquaculture and fisheries science, Vol. 31. Amsterdam: Elsevier. pp. 441–589.

Kraeuter, J. N., S. Buckner & E. N. Powell. 2005. A note on a spawner-recruit 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.

Kraeuter, J. N., M. Castagna & R. Bisker. 1989. Growth rate estimates for *Busycon carica* (Gmelin, 1791) in Virginia. *J. Shellfish Res*. 8:219–225.

Kraeuter, J. N., J. Klinck, E. N. Powell, E. Hofmann, S. Buckner, R. E. Grizzle & V. M. Bricelj. Effects of the fishery on the hard clam (*Mercenaria mercenaria*) population in Great South Bay, New York. A modeling study. *J. Shellfish Res*. (Submitted).

Landry, T., T. W. Sephton & D. A. Jones. 1993. Growth and mortality of the northern quahog, (Linnaeus, 1758) *Mercenaria mercenaria* in Prince Edward Island. *J. Shellfish Res*. 12:321–327.

MacKenzie, C. L., Jr. 1977. Predation on hard clam (*Mercenaria mercenaria*) populations. *Trans. Am. Fish. Soc*. 106:530–537.

Manzi, J. J. 1970. The effect of temperature on the feeding rate of the rough oyster drill, *Eupleura caudata* (Say). *Proc. Natl. Shellfish Assoc*. 60:54–58.

Muus, K. 1973. Setting, growth and mortality of young bivalves in the Oresund. *Ophelia* 12:79–116.

Olafsson, E. B., C. H. Peterson & W. G. Ambrose, Jr. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: The relative significance of pre-and post-settlement processes. *Oceanogr. Mar. Biol. Ann. Rev*. 32:65–109.

Peterson, C. H. 1982. Clam predation by welks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. *Mar. Biol*. 66:159–170.

Peterson, C. H. 2002. Recruitment overfishing in a bivalve mollusk fishery: hard clam (*Mercenaria mercenaria*) in North Carolina. *Can. J. Fish. Aquat. Sci*. 59:96–104.

Peterson, C. H., H. C. Summerson & J. Huber. 1995. Replenishment of hard clam stocks using hatchery seed: Combined importance of bottom type, seed size, planting season, and density. *J. Shellfish Res*. 14:293–300.

Powell, E. N., H. Cummins, R. J. Stanton, Jr. & G. Staff. 1984. Estimation of the size of molluscan larval settlement using the death assemblage. *Est. Coast. Shelf Sci*. 18:367–384.

Powell, E. N., J. M. Klinck, E. E. Hofmann & S. Ford. 1997. Varying the timing of oyster transplant: implications for management from simulation studies. *Fish. Oceanogr*. 6:213–237.

Reise, K. 1977. Predator exclusion experiments in an intertidal mud flat. *Helgolander wiss. Meeresunters* 30:263–271.

Reise, K. 1985. Tidal flat ecology: an experimental approach to species interactions. *Ecolog. Studies* 54:1–191.

Rice, M. A. 1992. The northern quahog: the biology of *Mercenaria mercenaria.* Rhode Island Sea Grant Publication No. RIU-B-92-001. University of Rhode Island, Narragansett, RI. 60 pp.

Sanchez-Salizar, M. E., C. L. Griffiths & R. Seed. 1987. The interactive roles of predation and tidal elevation in structuring populations of the edible cockle, *Cerastoderma edule*. *Est. Mar. Coast. Shelf Sci* 25:245–260.

Strieb, M. D., V. M. Bricelj & S. L. Bauer. 1995. Population biology of the mud crab, *Dyspanopeus sayi*, an important predator of juvenile bay scallops in Long Island (USA) eelgrass beds. *J. Shellfish Res*. 14:347–357.

Thorson, G. 1966. Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Komm. Danm. Fiskeri-og havunders Ser. Plankton* 4:1–523.

U.S.E.P.A., Region, II. 1982. Impact assessment on shellfish resources of Great South Bay, South Oyster Bay, and Hempstead Bay, New York. Draft Report, November 1982. 115 pp.

Virnstein, R. W. 1979. Predation on estuarine infauna: response patterns of component species. *Estuaries* 2:69–86.

WAPORA. 1981. Estuarine impact assessment (shellfish resource) for the Nassau-Suffolk streamflow augmentation alternatives, draft report. US Environmental Protection Agency, New York. 114 pp.

Whetstone, J. M. & A. G. Eversole. 1981. Effects of size and temperature on mud crab, *Panopeus herbstii*, predation on hard clams, *Mercenaria mercenaria. Estuaries* 4:153–156.

Wilson, H. H., Jr. 1991. The foraging ecology of migratory shorebirds in marine soft-sediment communities: the effects of episodic predation on prey populations. *Syst. Zool*. 31:840–848.