Utility of high-density plantings in bay scallop, *Argopecten irradians irradians*, restoration

**Stephen T. Tettelbach · Debra Barnes · John Aldred · Gregg Rivara ·
Dennis Bonal · Andrew Weinstock · Chelsea Fitzsimons-Diaz ·
Josh Thiel · M. Chase Cammarota · Adam Stark · Katherine Wejnert ·
Richard Ames · John Carroll**

Abstract Two different methods of establishing high-density spawner sanctuaries for bay scallop (*Argopecten irradians irradians*) restoration were evaluated over 2 years at a site in Northwest Harbor, East Hampton, New York, USA. Hatchery-reared scallops, which had been overwintered at nearby sites, were free-planted directly to the bottom in late March/early April at an initial target density of 94–128 scallops/m^2. In addition, scallops were stocked in off-bottom culture units consisting of three vertically stacked 15-mm mesh ADPI® bags at densities of 50, 100, or 200 scallops/bag (=117, 234, or 468 scallops/m^2), respectively. Survival of scallops differed significantly by year, planting method, and scallop source. Survival of free-planted scallops was generally lower than caged scallops. Better survival of free-planted scallops in 2005 versus 2006 likely reflected the presence of luxuriant eelgrass beds in 2005, which were absent in 2006. Survival of scallops in ADPI

S. T. Tettelbach (✉) · D. Bonal · A. Weinstock
C.W. Post Campus, Long Island University, Brookville, NY 11548, USA
e-mail: Stephen.Tettelbach@liu.edu

D. Barnes · J. Thiel · M. C. Cammarota
NY State Department of Environmental Conservation, East Setauket, NY 11733, USA

J. Aldred
Town of East Hampton Shellfish Hatchery, East Hampton, NY 11937, USA

G. Rivara
Cornell Cooperative Extension of Suffolk County, Southold, NY 11901, USA

S. T. Tettelbach · D. Bonal · A. Weinstock · C. Fitzsimons-Diaz · K. Wejnert · R. Ames
Southampton College of Long Island University, Southampton, NY 11968, USA

C. Fitzsimons-Diaz
Roger Williams University, Bristol, RI 02809, USA

A. Stark
The Nature Conservancy, Shelter Island, NY 11964, USA

R. Ames · J. Carroll
Stony Brook-Southampton, Southampton, NY 11968, USA

bags was not appreciably related to stocking density. Shell growth was highest for free-planted scallops; in cages, growth was somewhat better at 50 versus 200 scallops/bag. Wet weights of epibionts were significantly higher in caged versus free-planted scallops. Reproductive condition of scallops stocked at 50/bag was usually higher than at 200/bag. Both free-planting and off-bottom systems yielded high densities of adult bay scallops at the time of spawning, which ensures a higher probability of successful fertilization of spawned eggs and thus a greater potential for success of restoration efforts.

Introduction

Scallop aquaculture in the United States has never approached the commercial success attained in China with *Argopecten irradians* (Guo and Luo 2006) or in other countries with other pectinids (e.g. Japan: Kosaka and Ito 2006), but US hatchery production has formed the basis for numerous efforts to restore bay scallops to areas where they were formerly abundant (MacKenzie 2008). The basic approach of these restoration efforts has been to plant juveniles (0+ year) into the field, where the goal is for these to survive to the age (∼1 year) at which time they will spawn and contribute to natural recruitment. US bay scallop restoration efforts have met with mixed success, but documented increases in local populations and/or fisheries have resulted from plantings in Massachusetts (Turner 1995; Karney, personal communication), New York (Krause 1992; Tettelbach and Wenczel 1993; Tettelbach and Smith 2009), North Carolina (Peterson et al. 1996) and Florida (Arnold et al. 2005).

There is no standardized methodology for bay scallop restoration over the extent of the species range in the US as local hydrographical conditions and diverse assemblages of predators dictate different approaches. Field growout of bay scallops until initiation of spawning has been done in numerous ways, including free-planting (=sowing, or seeding directly to the bottom: Morgan et al. 1980; Tettelbach and Wenczel 1993) and deployment in lantern nets (Tettelbach and Smith 2009), corrals, (Fegley et al. 2009), floating rafts, pocket nets, and bottom cages (Smith and Tettelbach 1997; Arnold et al. 2005). Free-planting is the least expensive and labor intensive of these growout methods, but typically yields the lowest rates of survival (Hatcher et al. 1996).

Traditional free-planting techniques, utilizing hatchery-reared juveniles, or wild caught spat were developed in Japan for a put-and-take fishery (Sekino 1992; Kosaka and Ito 2006); this methodology has been adapted for commercial aquaculture in numerous regions, including Canada (Parsons and Robinson 2006), Europe (Norman et al. 2006; Strand and Parsons 2006); Mexico (Félix-Pico 2006), and New Zealand (Marsden and Bull 2006) as well as for restoration in the United States. Transplantation of wild juveniles or adults has also been done for scallop aquaculture in Russia (Ivin et al. 2006) and for restoration in the US (Peterson et al. 1996). Plantings of juvenile scallops for put-and-take fisheries have often been done at relatively low densities ($\leq 10/m^2$) in order to avoid attracting high numbers of predators and/or because of concerns over growth inhibition (Kosaka and Ito 2006; Silina 2008). The utility of this approach has been confirmed by studies of scallop predation at a range of densities, where higher rates of predation typically have been observed at higher free-planting densities (Morgan et al. 1980; Tettelbach 1986; Silina 1994; Barbeau et al. 1996; Wong et al. 2005; Félix-Pico 2006); these same

studies also concluded that mortality of free-planted scallops is inversely related to scallop size.

In New York, early bay scallop restoration efforts (Tettelbach and Wenczel 1993) employed free-plantings at densities of $\sim 10/m^2$ because of concerns over high predation rates. Even though scallops were planted at sizes of >35–40 mm, when they are known to reach a partial size refuge from crab predation (Tettelbach 1986), survival from the time of free-planting in the fall until the time of spawning (~ 6–7 mo) only ranged from 0 to 12% (Tettelbach and Wenczel 1993). One major consequence of this low rate of survival is that, at the time of spawning, scallop densities may be too low to permit a high rate of successful fertilization of spawned eggs (Levitan and Petersen 1995; Marelli et al. 1999; Liermann and Hilborn 2001). This in turn may thwart attempts to restore bay scallop populations.

The purpose of this study was to evaluate the utility of establishing high-density spawner sanctuaries for use in bay scallop restoration, with the ultimate goal of ensuring that higher densities of adults would be present at the time when spawning occurred—thus providing a higher probability of successful fertilization of spawned eggs. Two different deployment methods, free-planting and placement of scallops in an off-bottom culture system utilizing ADPI® bags, were evaluated with respect to scallop survival, growth, and reproduction, and biofouling of scallop shells. Plantings were done in the spring, after hatchery-reared individuals had overwintered in mid-water nets, and monitored through the fall in two consecutive years.

Materials and methods

Scallop production and overwintering

Bay scallops were spawned and reared at two Long Island, NY facilities (the East Hampton Town Shellfish Hatchery (EHTSH) in Montauk and the Cornell Cooperative Extension (CCE) hatchery in Southold) in 2004 and 2005; East Hampton (EH) scallops were grown out and overwintered at Pond of Pines, Amagansett, while CCE scallops were grown out and overwintered by The Nature Conservancy (TNC) at Log Cabin Creek, Shelter Island (SI) (Fig. 1). Overwintering was done in 15-mm mesh ADPI bags; EH scallops were stocked at densities of 200/bag in November, while SI scallops were stocked at densities of 250/bag in September. Overwintering survival rates were calculated volumetrically as:

$$\# \text{ of scallops harvested}/\# \text{ of scallops stocked};$$

these ranged from 75 to 80% for EH scallops and 81–94% for SI scallops for the 2 years.

Spawner sanctuary site description

The study area, which formerly supported a dense bay scallop population, was located ~ 75–150 m from shore along the eastern side of Northwest Harbor, East Hampton, NY (N 41° 01.806′ W 72° 14.596′) (Fig. 1). The inshore portion of the site (~ 1.3–3 m at mean low water (MLW)), where free-plantings of scallops were conducted, was characterized in 2005 by a sandy bottom with eelgrass, *Zostera marina*, and sparse macroalgae running parallel to shore for >100 m. Median eelgrass densities, as determined on June 7, 2005 via shoot counts in 64 0.07-m^2 quadrats, ranged from 50 to 386 shoots/m^2 at the northern and southern ends of the site, respectively. Offshore (W) of the above area, where the
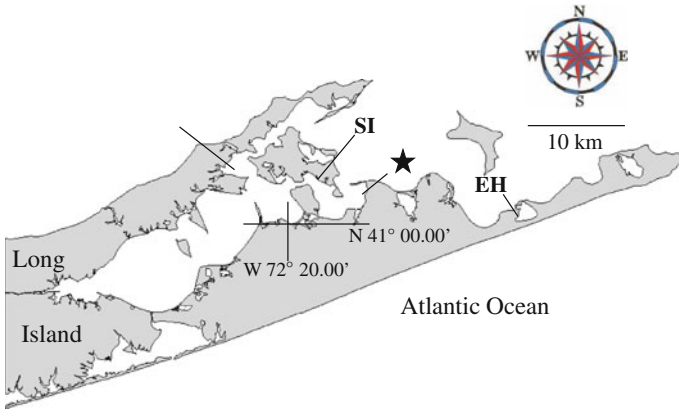
Fig. 1 Map of eastern Long Island, New York, USA, showing location of the study site (*) at 41°01.806′ N 72°14.596′ W in Northwest Harbor and the East Hampton (EH) and Shelter Island (SI) scallop overwintering sites at Pond of Pines and Log Cabin Creek, respectively

off-bottom culture systems were deployed, the bottom was cohesive muddy sand at a depth of ∼3.5–4 m at MLW. In September 2005, all *Zostera* shoots at the site died back—which is typical for some local eelgrass populations at this time of year (Pickerell and Schott 2004). However, eelgrass did not regrow in 2006.

Deployment of bay scallops in spawner sanctuaries

Free-planting and deployment of scallops into the ADPI bag arrays was conducted from March 30 to April 1, 2005 and from April 3 to 7, 2006. The timing of these deployments was predicated on moving scallops out of the overwintering systems prior to late April, a period when we have observed high mortalities of hatchery-reared scallops held in nets and other containment systems in eastern Long Island (J. Aldred and S. Tettelbach, unpublished data). Free-planting was done by broadcasting scallops from a boat that transited back and forth across each of four adjacent 25 m × 25 m sectors, numbered 1–4 from north to south (Fig. 2), marked with surface floats at each corner. In both years, SI scallops were planted into Sectors 1 and 3, while EH scallops were planted into Sectors 2 and 4. The total numbers of scallops free-planted in 2005 and 2006 were approximately 290,000 and 270,000, respectively (Fig. 2); target planting densities for 2005 and 2006 were 97.6–118.4 and 94.4–128/m^2, respectively. The density of scallops in the natural population was

Estimated # of Scallops Planted Per Sector			
2005 61,000	74,000	61,000	74,000
2006 59,000	72,000	59,000	80,000

	1 SI	**2** EH	**3** SI	**4** EH
25 m				
	25 m	25 m	25 m	25 m

Fig. 2 Estimated number of scallops free-planted at the study site in Northwest Harbor, New York in late April/early May 2005 and early April 2006. Numbers planted are shown above the respective 25 m × 25 m sectors, which are labeled by number and scallop group (*SI* Shelter Island, *EH* East Hampton. Total free-plantings for 2005 and 2006 = 290,000 and 270,000, respectively

quantified prior to planting via in situ counts made by divers; mean densities on April 1, 2005 and March 17, 2006 were 0.04 and 0.15 ind/m^2, respectively.

Off-bottom culture systems (hereafter referred to as arrays) consisted of ADPI® bags that were suspended ∼2 m below the surface. Each array which we assembled had three 36″ (0.92 m) long × 18″ (0.46 m) wide × 3.5″ high (0.09 m) OBC-3 ADPI bags (ADPI Enterprises, Philadelphia, PA) made of 5/8″ (15-mm) polyethylene mesh; the three bags were stacked vertically with a pair of 9-mm polypropylene lines run through the bags near each end and through 50-mm PVC spacers between bags (Fig. 3). In 2005, a pair of arrays was hung from a 1-m-long wooden plank (2″ high (50 mm) × 4″ wide (100 mm)), with flotation provided by a standard Styrofoam lobster buoy attached to the middle of the plank. Each pair of arrays was anchored with a cinder block. In 2006, each array of three ADPI bags was deployed singly with its own cinder block, and flotation was modified to make the arrays more horizontally stable. In place of a lobster buoy, one 0.8-m-long plastic ("Taylor") float was attached to the top of each array. ADPI arrays were deployed in two rows, 2–3 m apart, running parallel to shore at a depth of ∼3.5–4 m; arrays in a given row were spaced ∼1 m apart. A total of 36 arrays were deployed each year: 18 with EH scallops and 18 with SI scallops.

Within each array, scallops were stocked into the three ADPI bags at different densities (50, 100, or 200 scallops per bag = 117, 234, or 468 scallops/m^2, respectively). Each of the six possible vertical arrangements of different stocking densities (i.e. from top to bottom: 50, 100, 200 scallops per bag; 50, 200, 100 scallops per bag, 100, 50, 200 scallops per bag, etc.) was replicated three times for each scallop group (SI and EH) in a Latin square design. Thus, the total number of scallops stocked into the ADPI bag arrays each year was 12,600 scallops (350 scallops/array × 36 arrays).

The SI and EH scallops were deployed separately in arrays and free-plant sectors because potential differences in genetic history of source broodstock populations (Cochard and Devauchelle 1993; Mackie and Ansell 1993) and/or differences in nutritional or other

Fig. 3 Photograph of ADPI bag arrays used in 2005; flotation buoys and anchors are not shown

cultural conditions might have contributed to differences in survival, growth, or reproductive condition of our scallops following planting (Sekino 1992; Davidson 2000).

Mean shell heights of scallops planted in 2005 and 2006 ranged from 35 to 40 mm. In 2005, SI scallops (mean = 40.0 mm) were larger ($P = 0.025$) than EH scallops (mean = 38.3 mm). Mean shell heights of scallops planted in 2006 (EH = 35.5 mm; SI = 35.1 mm) were statistically smaller ($P < 0.02$) than both groups of scallops planted in 2005.

Monitoring of scallops in spawner sanctuaries

Immediately after planting was completed, scallop densities as well as initial size and reproductive condition of free-planted scallops were quantified; additionally, possible mortality due to stresses of planting, including potential desiccation or temperature shock during transport from the overwintering sites, was estimated. The latter was done by comparing numbers of live scallops and cluckers (dead scallops with articulated valves) with tissues present (an indication of very recent mortality) counted in 1-m^2 quadrats during dive surveys. For each sector, we calculated maximum mortality associated with planting activities:

$$\text{maximum mortality} = \#\,\text{cluckers with tissues}/(\#\,\text{live scallops} + \#\,\text{cluckers}).$$

These estimates of mortality were compared to those for groups of 100 EH and 100 SI scallops brought back to the laboratory and monitored for 1 week.

From early May through late September (2005) or late October (2006), scallop densities were monitored monthly, while growth and reproductive condition were quantified biweekly. Monthly survival of free-planted scallops over the course of the study was estimated by monitoring changes in densities of live scallops in 12-16 1-m^2 quadrats in each of the four 25 m × 25 m planted sectors. Changes in density of free-planted bay scallops do not necessarily equate with changes in survival, due to the ability of scallops to disperse by swimming, so we conducted visual surveys of live scallops outside the sectors to estimate numbers beyond the perimeter of the planting area; these surveys were done in late September 2005, and during early May and late October 2006. Cluckers were also counted in all density surveys so that the nature of shell damage could be used to provide insight into the predators responsible for mortality (Tettelbach 1986; Prescott 1990).

Scallop survival in ADPI bags was monitored by counting numbers of live scallops, cluckers, and ½ shells in each tier of sampled arrays. On each of the 12 sampling dates per year, counts were done in six ADPI arrays; thus, each of the 36 arrays was sampled twice. The order of sampling during each year was random for the first round; arrays were then sampled in the same respective order in the second round. Survival rates were prorated for nets from which scallops were removed for reproductive sampling in the first round.

Scallop growth and reproductive condition were assessed for 20 haphazardly collected individuals, where possible, for each group sampled on each date; e.g., for free-planted scallops, 10 EH and 10 SI scallops were sampled from each of the two planting sectors (total = 40 sampled) and for scallops held in arrays, 10 EH and 10 SI scallops from bags with 50, 100, and 200/bag were sampled from each of two arrays (total = 120 sampled). Growth was monitored by measuring shell height (to the nearest mm) of each sampled group; these same scallops were used for a determination of reproductive condition using the methods of Barber and Blake (2006). Following dissection, the gonad (cut so as to include the foot) and the remaining tissue of each scallop were placed into respective Al pans and dried to a constant weight at 60–90°C. Periods of spawning were inferred by

monitoring temporal changes in gonad dry weight (GDW): a sharp decline following a peak is indicative of a spawning event (Barber and Blake 2006).

Biofouling on scallop shells from both the free-planted and ADPI groups was characterized and quantified by scraping epibionts from both shell valves of scallops sampled in mid-August of both years; total $n = 156$ and 159 in 2005 and 2006, respectively. Total wet weights of epibionts were recorded to the nearest 0.01 g with an OHaus® toploader balance; fouling organisms were identified to the lowest possible taxon.

Biofouling of the ADPI bags necessitated periodic removal of scallops and restocking into clean ADPI bags. This was first done on May 23, 2005, even though fouling was only light-moderate. Biofouling was quite heavy by late July 2005, so restocking was done again on August 8, 2005. In 2006, restocking of nets was not deemed necessary in May, but restocking was done on August 16, 2006. Epibionts were not removed from scallops during restocking.

Predator densities

Densities of potential scallop predators in the free-planted sectors were visually quantified in 1-m^2 quadrats at the same time that scallop densities were monitored. Predators were those species/sizes of crabs, gastropods, or fish that had the potential to prey on the sizes of scallops that were present in the free-planted sectors (Tettelbach 1986; Carroll et al. 2010).

Water-quality monitoring

Water temperature, salinity, and dissolved oxygen (DO) were measured at a depth of 30 cm, on each of the 12 sampling dates each year, with a YSI Model 85 m; in addition, water temperature was recorded every 6 h throughout the study periods of both years with an automated, submersible temperature logger attached to a cinder block at a depth of 1.3 m at MLW. In 2005, an Onset HOBO® Model No. 8 logger was used, while in 2006 an Onset Tidbit Stowaway® was deployed. Total chlorophyll a levels in surface water samples, analyzed via the methods of Parsons et al. (1984), were obtained for a site (#118) in central Northwest Harbor (N 41° 02.750′ W 72° 26.000′) ~1.5 km SW of our study site (SCDHS 2008).

Continuously monitored water temperatures ranged from 5.81 to 27.91°C, and 7.52–28.42°C, respectively, in 2005 and 2006 (Fig. 4a, b). Salinity levels for 2005 and 2006, respectively, ranged from 27.4 to 29.0 and 27.0–28.4 ppt. DO levels for the 2 years ranged from 5.69 to 10.3, and 5.95–10.09 mg/l, respectively. Total chlorophyll a levels at SCDHS Site #118, from late March–mid-late October, ranged from 0.2 to 3.9 mg/l (mean = 1.71 mg/l; SE = 0.38) in 2005 and from 1.0 to 4.3 mg/l (mean = 2.27 mg/l; SE = 0.39) in 2006 (SCDHS 2008).

Estimation of gamete production and fertilization rate

As the goal of bay scallop restoration efforts is to increase the number and density of spawning adults at a selected location, we were interested in estimating total gamete production and examining how effectively our high-density plantings might be in elevating the rate of successful fertilization of spawned eggs compared to fertilization rates in natural scallop populations at recently observed, pre-restoration densities (maximum = 0.1 ind m^{-2}: Tettelbach and Smith 2009). Belding (1910) stated that bay scallops produce 2 million eggs per year, but we are not aware of any such estimates of sperm production. Using sperm dimensions given by Belding (1910), we calculated sperm volume; assuming
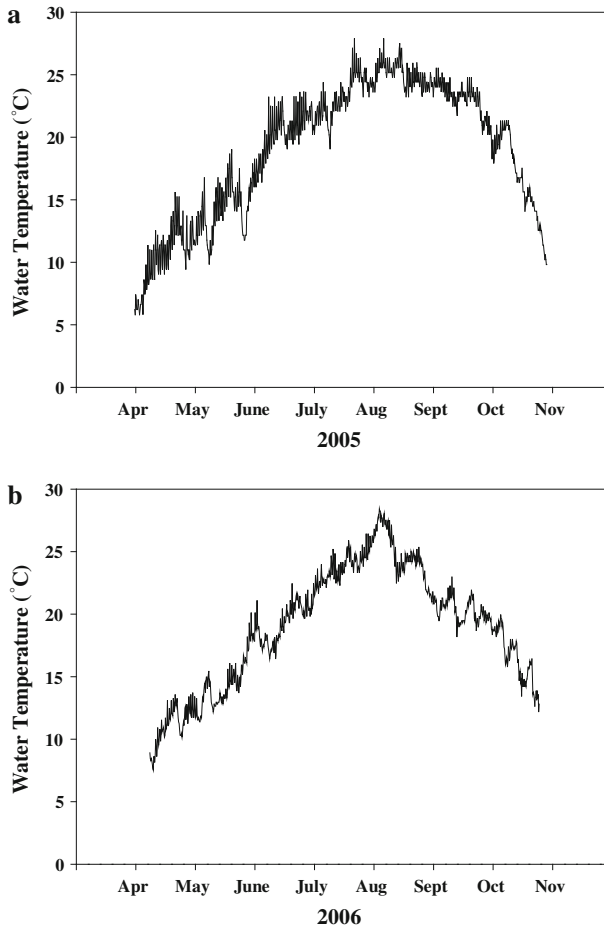
Fig. 4 Water temperature recorded every 6 h from **a** March 30–October 20, 2005 and **b** April 7–October 24, 2006 at ~1.3 m depth (at MLW) at the inshore edge of the free-planting sectors in Northwest Harbor, New York

an equal allocation of reproductive investment to ovaries and testes (*A. i. irradians* is a functional hermaphrodite), we estimated individual sperm production at 2×10^{10} ind^{-1} year^{-1}. We estimated rate of sperm release by first determining what percentage of the total sperm production for the year was shed on June 7, 2005, when we directly observed a mass spawning of our free-planted scallops (Tettelbach and Weinstock 2008). By examining seasonal changes in gonad dry weight (GDW) for 2005 (Tettelbach and Weinstock 2008), we estimated the average sum of GDW declines (=0.433 g), after reaching respective peaks, during each of three spawning periods. Based on the observed GDW decline between June 7 and 21, 2005 and a frequency of gamete release every 20 s (Tettelbach and Weinstock 2008); and assuming a total spawning time of 1 h, with individuals spawning as males and females for ½ hr each, with all sperm release occurring on 7 June during the 2-week period (=20% of the total for the year), we estimated the rate of sperm release to be 2.22×10^6 sperm sec^{-1}. This is comparable to values calculated by Styan and Butler (2003) for the scallops *Chlamys bifrons* and *C. asperrima*.

Rates of fertilization (F) were calculated for free-planted scallops on June 7, 2005 and for assumed spawnings of our caged scallops on this date as well as for the above natural populations at a density of 0.1 ind m^2, using the models of Claereboudt (1999): equations (6,7) and Metaxas et al. (2002): equations (2,3). Parameters used for the two models included field estimated values for current speed ($u = 0.05$ m s^{-1}) and the above rate of sperm release (Q). Because bay scallops are functional hermaphrodites, they switch back and forth between releasing eggs and sperm during a single spawning event; therefore, we did not simply base the mean downstream distance between individuals (x) on the observed density because nearest neighbors may be releasing the same type of gamete at a given instant. Instead, we set x as the average of the downstream distances to the nearest neighbor and the next nearest neighbor; e.g. for the observed density of 56.1 ind m^{-2}, mean distance to the nearest and next nearest neighbors in the downstream direction = 0.13 and 0.26 m; thus, x was set to 0.2 m. We set the cross-stream distance between spawning individuals (y) = 0, i.e. when nearest neighboring scallops were directly downstream from a spawning male, as this is when the model of Metaxas et al. (2002) worked best; when they used $y > 0$ the rates of fertilization estimated from their model were from 1 to 10 orders of magnitude lower than fertilization rates that they quantified in the field. We chose a value for vertical distance of gametes from the bottom (z) = 0.05, which was beneath the top of the eelgrass canopy (~ 25 cm); height of gamete release (h or s) was calculated to be 0.01 m. Diffusivity coefficients in the z and y directions (α_z and α_y, respectively) and frictional velocity (u^*) were either calculated according to Metaxas et al. (2002) or for calculations of F based on the model of Claereboudt (1999), the designated constants were employed. We used the value for cross-sectional area of a fertilizable egg (=C_{stf} of Claereboudt 1999; = Φ of Metaxas et al. 2002) given by Claereboudt (1999) as this was virtually identical to that of *A. i. irradians* (Belding 1910). Finally, because the value of sperm–egg contact time (T) is very difficult to quantify in the field (Metaxas et al. 2002), we calculated respective values of F using two values for T: an arbitrary value of 30 s, which is the estimated contact time used by Metaxas et al. (2002), and $T = 500$ s, which was calculated as:

$$T = {}^1\!/_4 L S_i / u$$

where u = estimated current velocity (=0.05 m s^{-1} beneath the eelgrass canopy); L = length of our planted bed of scallops (100 m) in the direction of prevailing current flow; and S_i = spawning synchrony, i.e. what proportion of the individuals were spawning during a given event, as observed on June 7, 2005 (=1.0; Tettelbach and Weinstock 2008). With $L = 100$ m and u estimated at 0.05 m s^{-1}, it would have taken 2,000s for gametes to travel the length of the planting area, but we set $T = 500$ s as a more conservative estimate. Bay scallop sperm remain viable for >15 min in the hatchery (S. Tettelbach, personal observation). Claereboudt (1999) modeled the effect of spatial distribution of spawning individuals on F, but for simplicity we assumed for all calculations that scallops were uniformly distributed—which is how we attempt to distribute scallops during free-planting.

Results

Scallop survival

Overall mean densities of scallops free-planted in 2005 and 2006, as determined immediately after plantings were completed, were 94.4 and 132.0/m^2, respectively (Fig. 5a, b).

In 2005, initial mean densities in the four sectors ranged from 81.1 scallops/m^2 (sector 1) to 109.8 scallops/m^2 (sector 3); in 2006, initial mean densities in the four sectors were more variable, ranging from 64.6 scallops/m^2 (sector 1) to 252.5 scallops/m^2 (sector 3) (Fig. 5a, b).

Maximum mortality associated with planting was estimated to range from 1.2 to 1.5% in 2005, and from 0 to 0.08% in 2006. In 2005, the low level of mortality associated with planting was corroborated by low mortality of scallops brought back to the laboratory: 0% after 2 d, 1% after 6 d, and 1.5% after 8 d.

There was no evidence of predation on live scallops or on cluckers with meats immediately after free-plantings of scallops in 2005 and 2006. On April 5, 2005, 4 days after free-planting had been completed, there was still no evidence of predation as cluckers with meats were present and no predators were seen.

Scallop densities declined markedly from early April to early May in both years, but the decline was much more gradual from May to early June during 2005 than in 2006; thereafter, densities continued to decline more or less gradually in both years (Fig. 5a, b). Changes in scallop density during 2005 and 2006 were clearly nonlinear, so cumulative data distributions of the respective years were compared via the Kolmogorov–Smirnov test
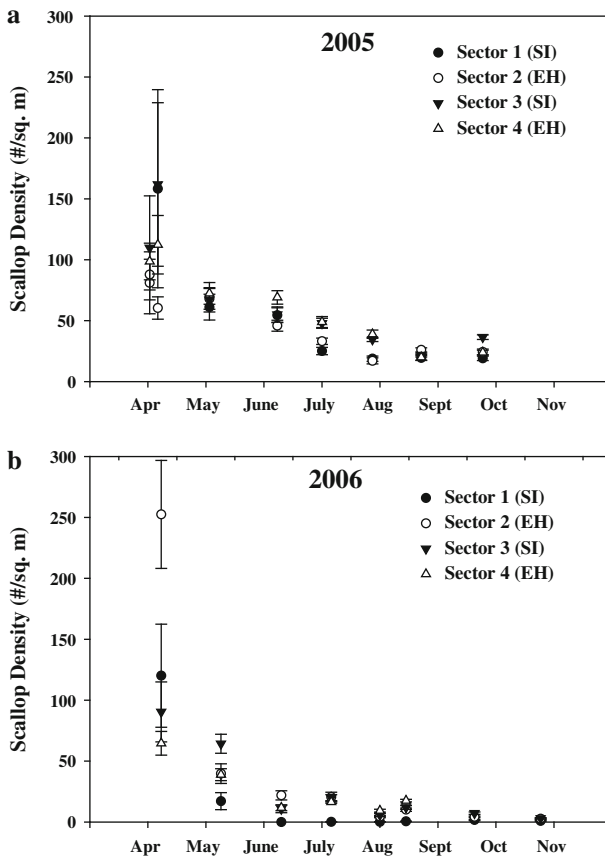

Fig. 5 Density (mean ± 1 SE) of free-planted scallops in each of the four sectors at the study site in Northwest Harbor, New York, from: **a** April–September 2005 and **b** April–October 2005

(Kirkman 1996), using the mean numbers of scallops in each of the sectors for each of the sampling dates. The maximum difference between the two cumulative distributions was significantly different ($D = 0.6354$; $P < 0.001$), indicating that the decline in scallop densities was much more rapid in 2006 than in 2005. Further comparisons specifically examined scallop densities in early June (the time of initial spawning in both years) and in mid-late August (when another spawning event occurred in both years). In early June 2005, median densities of scallops in each of the four sectors (range = 45.0–$72.0/m^2$) were significantly higher (Dunn's $Q \geq 3.29$; $P < 0.05$, after a Kruskal–Wallis one-way ANOVA on ranks: $H = 111.3$; $P < 0.001$) than median densities in sectors 1 ($0/m^2$) and 3 ($7.0/m^2$) in 2006. In mid-late August 2005, median densities of scallops in each of the four sectors (range = 19.0–$25.5/m^2$) were significantly higher (Dunn's $Q \geq 4.82$; $P < 0.05$) than median densities in sector 1 ($0/m^2$) in 2006. The two highest sector densities in August 2005 (Sector 2: median = $25.5/m^2$; Sector 3: median = $22.0/m^2$) were statistically greater than those in sector 2 (median value = $9.0/m^2$) in 2006 (Dunn's $Q > 3.32$; $P < 0.05$).

The extent of dispersal outside the formal 25×100 m planting area increased from the beginning to the end of the study periods in both years; however, scallops were usually not found beyond 5 m from the planting area perimeter. Dispersal in 2005 was low: prior to September 2005, mean density of planted scallops beyond the perimeter was $\sim 0.5/m^2$ (=625 scallops in total: <1% of the scallops inside the planting area). Dispersal in 2006 was higher than in 2005: on May 8, 2006, mean scallop density outside the perimeter was $3.6/m^2$ and represented 18.5% of the total population on this date. The higher level of dispersal in 2006 likely resulted from surface drifting during the windy planting conditions. Scallop population size estimates at the time of the last free-plant surveys in each year (September 23, 2005, October 25, 2006), were $\sim 72,000$ inside and $\sim 7,200$ outside the 25×100 m planting site, respectively, in 2005 and $\sim 6,330$ inside and $\sim 3,530$ outside the 25×100 m planting site, respectively, in 2006. Scallops that had dispersed outside the formal planting area thus represented 9 and 36% of the respective populations on these dates in 2005 and 2006.

Mortality of scallops held in the ADPI arrays progressed steadily in both years, but generally at a slower rate in 2006 than 2005 (Fig. 6). Levels of scallop mortality at comparable sampling dates in the 2 years were examined via three-way ANOVAs (versus year, scallop source, and stocking density); for nine of these 11 dates, the year × scallop source interaction term was highly significant ($P \leq 0.004$). This necessitated separate analyses of mortality of the two source groups on given sampling dates during the 2 years. For the 2005 analyses, SI scallops had higher rates of mortality than EH scallops on 10/13 dates (Fig. 6). In 2006, there were only five sampling dates on which the mortality levels of the two groups of scallops differed significantly (Fig. 6), with no clear trend.

Significant differences in mortality rates of scallops held at the three different stocking densities were only evident on three sampling dates (from mid-late July through early August); in each case, Holm–Sidak multiple comparisons tests (Systat Software 2004) revealed that scallops stocked at 200/bag experienced significantly higher ($P < 0.05$) mortality than scallops stocked at 50/bag.

Predator densities

Densities of potential scallop predators in the free-planted sectors varied significantly between sampling dates (Fig. 7), but overall densities did not differ between the 2 years (Mann–Whitney Rank Sum Test: $T = 204,091.5$, $P = 0.656$). One-two weeks prior to when scallops were free-planted, predator densities were 0 in both 2005 (on 21 March) and
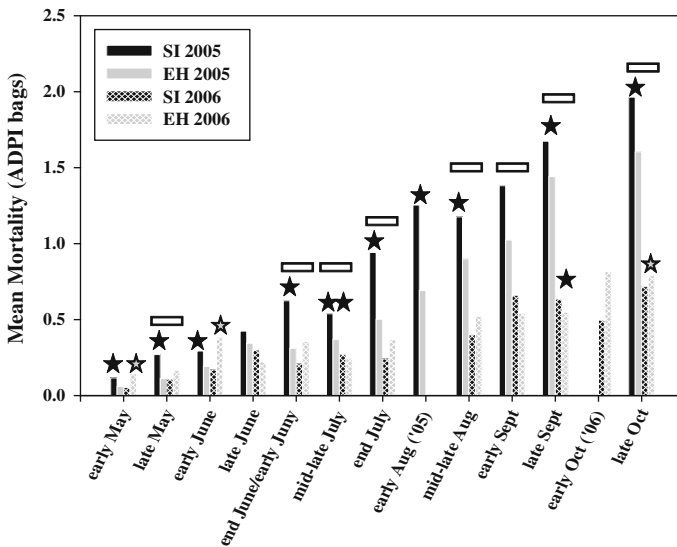
Fig. 6 Mean mortality (=−ln proportion surviving) of scallops deployed in ADPI bags at the study site in Northwest Harbor, New York, on sampling dates from early May to late October of 2005 and 2006. *EH* and *SI* scallops overwintered in East Hampton and Shelter Island, respectively. *Rectangles* above respective sampling dates signify that mortality rates differed significantly ($P < .05$) between years; in all such cases, mortality rates were higher in 2005 versus 2006. *Stars* above scallop groups for a given sampling period and year signify that mortality rates differed significantly ($P < .05$) between scallop groups; *black* and *gray* stars, respectively, signify that mortality rates were higher for SI or EH scallops

2006 (on 17 March). Immediately after free-planting of scallops in late March/early April, predator densities were also at or near 0 (Fig. 7); thus, there was no evidence of a mass influx of predators immediately after planting. By the next sampling date in early May, predator densities had increased dramatically, peaking on 8 May in 2006 and on 7 June in 2005. Thereafter, through late September of both years, seasonal trends in predator abundance were parallel—with patterns accelerated by ∼3–4 weeks in 2006. The most abundant predators were spider crabs of the genus *Libinia*, comprising 66.2% of all predators, but mud crabs *Dyspanopeus sayi* (15.6%), lady crabs *Ovalipes ocellatus* (5.9%), and channeled whelks *Busycotypus canaliculatus* (4.2%) were also common. No sea stars, *Asterias vulgaris*, were observed during the 2 years of study.

Scallop growth

There were no consistent differences in shell growth of scallops stocked in ADPI arrays at different densities for the two source groups of scallops (EH or SI) in the 2 years. The only statistical differences were seen among the EH group in 2006, where mean growth through October of scallops stocked at 100/bag (22.7 mm) was greater than that of scallops stocked at 200/bag (18.7 mm) (Holm–Sidak multiple comparisons $t = 2.88$; $P = 0.005$); mean growth of scallops stocked at 50/bag was not different (Holm–Sidak $t \leq 1.57$; $P \geq 0.121$) from growth of scallops stocked at 100 or 200/bag. Therefore, growth data for scallops stocked at the three densities in ADPI arrays were pooled within respective groups for further analyses.

Fig. 7 Temporal changes in predator density in the free-plant sectors at the study site in Northwest Harbor, New York as determined via visual counts of predators in 1-m^2 quadrats ($n = 11$–16 per sector). Data for the four sectors were pooled for each respective sampling date. Predators were those species/sizes of crabs, gastropods, or fish that had the potential to prey on the sizes of scallops that were present in the free-planted sectors. Data points = mean ± 1 SE
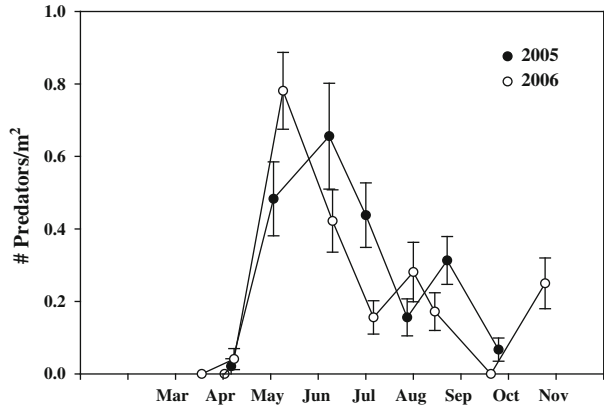
Shell growth differed significantly by year, scallop source, and planting method (Fig. 8). Scallops free-planted in 2006 grew the most (particularly the SI group: median = 32.9 mm) while growth of scallops deployed in ADPI arrays in 2005 was significantly slower (Dunn's $Q > 4.4.3$; $P < 0.05$) than that of all other groups. Median growth of the EH and SI groups held in ADPI arrays in 2005 was 13.7 and 13.0 mm, respectively. A comparison of total chlorophyll a concentrations in surface waters at Station #118 (SCDHS 2008), ~1.5 km to the SW of our study site, revealed that for the periods of late March–mid-late October, there was no statistical difference (one-way ANOVA: $F = 2.52$; $P = 0.139$) between total chl a concentrations in 2005 versus 2006.

Biofouling of scallop shells

Total wet weight of epibionts on scallop shells in mid-August (~4.5 months after planting) was significantly greater on scallops held in ADPI arrays than on free-planted scallops
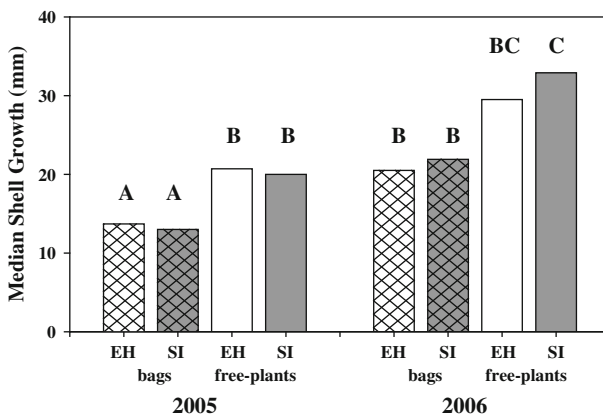

Fig. 8 Median shell growth (mm) of scallops deployed in ADPI bags or free-planted at the study site in Northwest Harbor, New York after ~6.5 mos after planting (=late October). *EH* and *SI* scallops overwintered in East Hampton and Shelter Island, respectively. Letters (*A, B, C*) above *bars* represent groups that were statistically different ($P < .05$) in Dunn's multiple comparisons tests after a significant ($P < .001$) Kruskal–Wallis one-way ANOVA of ranks

(Fig. 9). Dunn's multiple comparison tests done after a significant Kruskal–Wallis one-way nonparametric ANOVA of ranks ($H = 54.23$; df = 3; $P < 0.001$) revealed that median weights of biofouling on ADPI scallops (1.98 and 2.50 g/individual in 2005 and 2006, respectively) were not statistically different from one other ($Q = 0.31$; $P > 0.05$) but were significantly higher (Dunn's $Q \geq 4.64$; $P < 0.05$) than median weights of epibionts on free-planted scallops (0.62 and 0.91 g/individual in 2005 and 2006, respectively). The latter two groups were not statistically different ($Q = 0.69$; $P > 0.05$).

The epibionts that were most abundant on ADPI scallops, and which accounted for the greatest biomass, were the slippersnail *Crepidula fornicata* and the solitary tunicate *Styela clava*. Barnacles (*Balanus* sp.) were abundant on ADPI scallops in 2006, but not in 2005. Other common epibionts in both years included brown sponges (*Halichondria bower-banki*), colonial tunicates (e.g. *Botryllus*), and the recently introduced colonial tunicate *Didemnum* sp. These fouling species often overgrew scallops and contributed to formation of large aggregations of scallops in the corners of nets. *Styela* often grew through the mesh of the ADPI arrays, thereby tethering scallops to which they were attached.

The most abundant epibionts on free-planted scallops were *Crepidula fornicata* and filamentous red algae (e.g. *Spyridea*, *Gracilaria*); tunicates, sponges, and barnacles were rarely seen.

Scallop reproduction

Scallop reproduction exhibited different patterns in 2005 and 2006 (Figs. 10, 11). In 2005, there were three distinct spawning periods (late May/early June, mid-July, late August) that were revealed by sharp declines in GDW of the free-planted and ADPI scallops. Spawning patterns of free-planted SI and EH scallops were somewhat out of phase, while those of all ADPI scallops were highly synchronous (Fig. 10). On June 7, 2005, mass spawning of scallops throughout the entire free-planting area was documented and photographed (Tettelbach and Weinstock 2008); the GDW data confirmed that this was the major spawning event of the year. In 2006, there were two well-defined spawning peaks (early
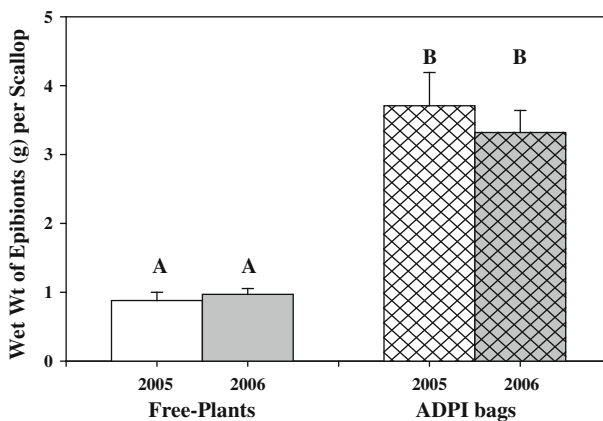

Fig. 9 Mean wet weights (+1 SE) of epibionts on shells (both valves) of scallops deployed in ADPI bags or free-planted at the study site in Northwest Harbor, New York during 2005 and 2006, ~4.5 mos after planting (=mid-August). Letters (A, B) above *bars* represent groups that were statistically different ($P < .05$) in Dunn's multiple comparisons tests after a significant ($P < .001$) Kruskal–Wallis one-way ANOVA of ranks

June, mid-July), but there was no sharp GDW decline in August that would signify a clear mass spawning event (Fig. 11). Temporal patterns of spawning of different groups in 2006 were fairly synchronous.

The magnitudes of GDWs at the time of the spawning peaks differed between scallop groups and years. At the first spawn in early June 2005, scallops in ADPI bags (EH and SI) had the highest GDWs compared to ADPI scallops from 2006 and free-planted scallops in both years (Kruskal–Wallis one-way ANOVA on ranks: $H = 68.39$, $P < 0.001$) (Figs. 10 and 11). At the time of the second spawning peak in 2005 (beginning on 13 July), EH scallops (held in ADPI bags and free-planted) had the highest GDWs. At the time of the second spawning peak in 2006 (beginning on 21 July), the free-planted EH and SI scallops had the highest GDWs. In almost all cases, the groups of scallops that had the highest GDWs at the initiation of the different spawning peaks had the largest shell heights at those times. However, GDWs of the different scallop groups at the time of the third spawning peak in 2005 (beginning on 22 August) were not statistically different (one-way ANOVA: $F = 1.23$, $P = 0.301$).
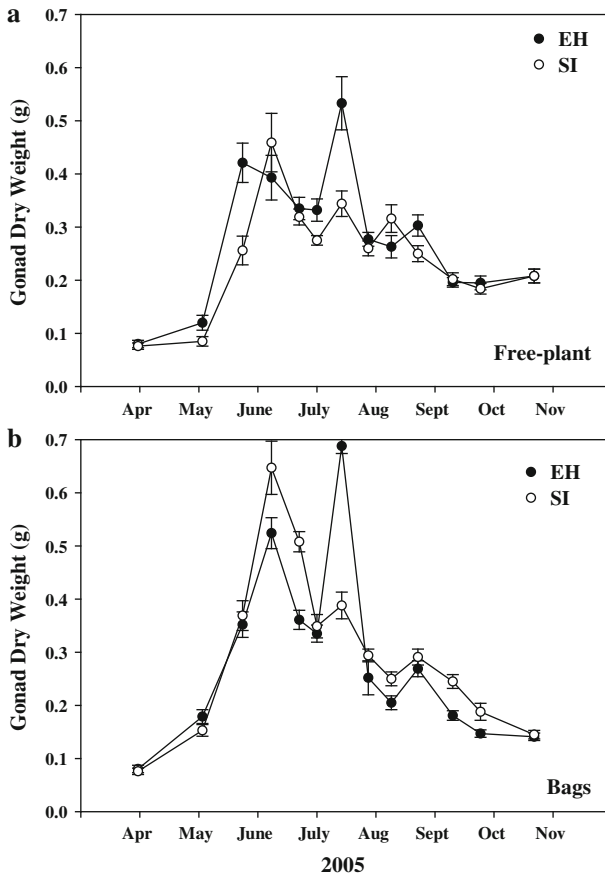

Fig. 10 Temporal changes in gonad dry weight (g) of bay scallops that were (**a**) free-planted or (**b**) deployed in ADPI bag arrays in 2005 at the study site in Northwest Harbor, New York. *EH* East Hampton; *SI* Shelter Island groups; data points = mean ± 1 SE

Fig. 11 Temporal changes in gonad dry weight (g) of bay scallops that were (**a**) free-planted or (**b**) deployed in ADPI bag arrays in 2006 at the study site in Northwest Harbor, New York. *EH* East Hampton; *SI* Shelter Island groups; data points = mean ± 1 SE
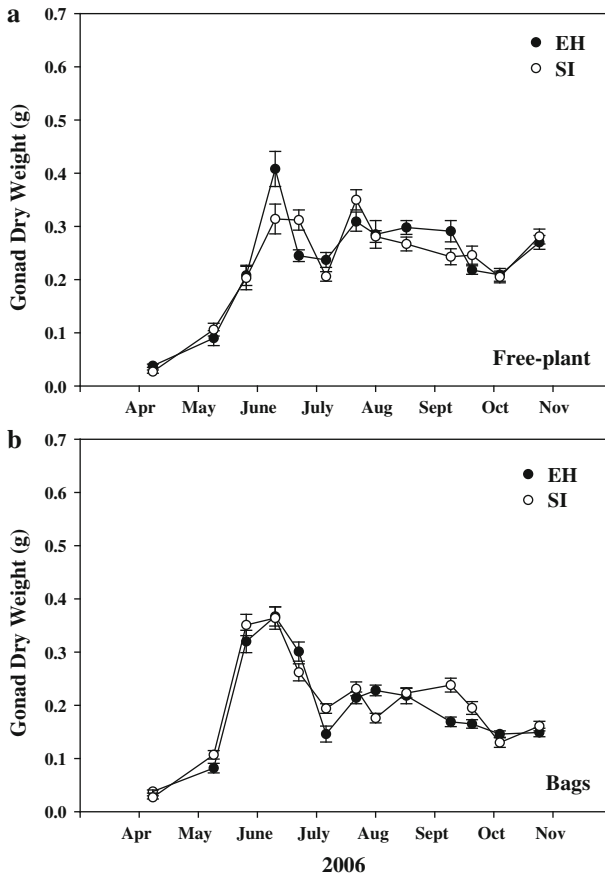
Mean values of GDW varied with stocking density in ADPI arrays, with reproductive condition often inversely related to stocking density. One-way ANOVAs of mean GDW versus stocking density, conducted separately for EH and SI scallops at each sampling date, demonstrated statistical differences ($P < 0.05$) in 6/24 (25%) and 9/24 (37.5%) analyses for the 2005 and 2006 data, respectively. Where statistical differences were noted, scallops stocked at 50/tier had significantly higher mean GDWs than scallops stocked at 200/bag in 12/15 (80%) of cases and scallops stocked at 100/bag had significantly higher mean GDW than those stocked at 200/bag in 9/15 (60%) of cases. Conversely, scallops stocked at 200/bag never had significantly higher GDW than scallops stocked at the lower densities. Scallops stocked at 50/bag had higher mean GDW than at 100/tier on only five sampling dates.

Estimation of gamete production and fertilization rate

On June 7, 2005, at the observed density of free-planted scallops (average = 56.1 m^{-2}), the overall release of gametes by the free-planted scallops, which was 20% of the total for the year, was estimated to be 5.61×10^{10} eggs (=0.4×10^6 eggs ind^{-1} × 140,250

individuals) and 5.61×10^{14} sperm ($= 4 \times 10^9$ sperm ind$^{-1} \times 140{,}250$ individuals). For scallops held in ADPI cages, total gamete release on this date (by 9,883 individuals) was estimated to be 3.95×10^9 eggs and 3.95×10^{13} sperm. In 2006, survival of free-planted scallops to the time of first reproduction in early-mid-June was about 20% of that seen in 2005; assuming equal annual rates of gamete production in the second year the overall production of gametes was considerably lower. Conversely, the survival of scallops in ADPI cages was better in 2006 than in 2005, so their overall contribution to gamete production was somewhat higher than in 2005.

Model predictions for fertilization success (F) varied widely, ranging from just above 0 to 78% (Table 1). The predictions of the Metaxas et al. (2002) model were consistently higher than those of the Claereboudt (1999) model. In all cases, fertilization rate was higher at the longer sperm–egg contact time, for both models, but values of F for higher-density assemblages of scallops in ADPI cages (95.2–360.4 m^{-2}) were always lower than those for high-density free-planted scallops (56.1 m^{-2}) and often lower than those for the low-density natural population (0.1 m^{-2}).

Discussion

Scallop survival

Survival of free-planted scallops in 2005 was clearly much higher than in 2006 despite the high variability in counts of scallops made while diving in the first month after planting. This difference between the 2 years may have been due to several factors, including (1) differences in predator density or activity, (2) a greater initial planting size in 2005, and/or

Table 1 Estimated per cent fertilization rates (F) for bay scallops in: (1) high-density free-planted area; (2) ADPI cages, initially stocked at three densities; and (3) natural populations at recently observed, pre-restoration densities (0.1/m^2); with respective parameters for models developed by Claereboudt (1999) and Metaxas et al. (2002).

High-density free-plant	High-density ADPI cages (initial = 50/tier)	High-density ADPI cages (initial = 100/tier)	High-density ADPI cages (initial = 200/tier)	Low-density natural population
Claereboudt (1999) model				
Values of F (%) for $T = 30$ s:				
4.20	2.08	0.28	0.004	0.07
Values of F (%) for $T = 500$ s:				
51.5	29.53	4.64	0.074	1.11
Metaxas et al. (2002) model				
Values of F (%) for $T = 30$ s:				
8.85	6.00	2.67	0.06	5.70
Values of F (%) for $T = 500$ s:				
78.66	64.40	36.32	1.00	62.39

Estimates of F are partially based on field conditions on June 7 2005, when spawning of free-planted scallops was directly observed (Tettelbach and Weinstock 2008). On this date, the respective densities of free-planted scallops and those in ADPI cages that were initially stocked at 50/tier, 100/tier, and 200/tier were 56.1, 95.2, 186.8, and 360.4/m^2. For the model of Metaxas et al. (2002), values for α_z, α_y, and G were adjusted for different x; other parameters remained the same, except for T. See text for methods of parameter estimation and assumptions

(3) the complete absence of eelgrass in 2006. Expectedly, there were seasonal fluctuations in predator abundance but there was no difference in overall predator abundance in the 2 years. Water temperatures were very similar during the 2 years so no differences in the level of predatory activity would be expected on this basis. While shell heights of scallops at the time of planting in 2005 (38–40 mm) and 2006 (35 mm) were statistically different, these sizes are essentially equivalent in terms of their susceptibility to predation by crabs (Tettelbach 1986), including *Libinia* spp., which comprised the majority of observed predators at our study site. An extensive body of literature (e.g. Heck and Orth 2006) has shown that greater rates of predation by crabs and other invertebrates on bivalve mollusks and other prey species occur on unvegetated substrates versus seagrass beds. In light of all of the above, we conclude that the absence of eelgrass at the study site in 2006 was primarily responsible for the more rapid decline in abundance of free-planted scallops in 2006, compared to 2005. Our results reinforce the concept of the spatial refuge from predation on bay scallops which is provided by the three-dimensional structure of seagrass beds (Pohle et al. 1991; Ambrose and Irlandi 1992; Garcia-Esquivel and Bricelj 1993) and highlight the importance of selecting suitable habitat for scallop restoration efforts (Tettelbach et al. 2003) or commercial aquaculture (Parsons and Robinson 2006).

While we did not observe a massive influx of predators after scallop planting in late March/early April, as has been observed by some authors following scallop plantings (e.g. Volkov et al. 1983; Silina 2008), it is very likely that predation was the primary factor responsible for mortality of free-planted scallops throughout the study. This conclusion is supported by the fact that increases in predator densities from early April to early May of both years coincided with significant declines in scallop density over the same periods. In addition, there were generally lower rates of mortality in cages compared to free-planted bay scallops, a pattern also observed by Arnold et al. (2005). Most cluckers found during surveys of free-planted scallops showed evidence of shell damage (chips and cracks) which are consistent with predatory attacks by crabs (Tettelbach 1986; Prescott 1990). Studies with sea scallops, *Placopecten magellanicus*, free-planted at high densities demonstrated that emigration and predation were highest shortly after planting (Hatcher et al. 1996; Barbeau et al. 1996); the latter phenomenon appeared to reflect a functional response of increased rates of predation rather than an increase in predator numbers (Barbeau et al. 1996). We did not observe extensive dispersal of bay scallops following planting.

Higher rates of survival of ADPI scallops in 2006 than 2005 suggest that the modified design of the arrays in 2006 was largely responsible for this improvement in survival— most likely because the greater horizontal stability of arrays in 2006 resulted in less tipping of the structures. In 2005, many arrays were observed to be tilted steeply, so that scallops piled up in the corners of the bags. This process contributes to greater mechanical inter-actions of scallops and may result in mortality when valves of two scallops interlock. Excessive tilting of the nets may also exacerbate the restriction of water flow and over-growth by fouling organisms.

The generally higher survival of EH scallops versus SI scallops in ADPI bags in 2005 suggests that there were differences in the two source groups prior to when they were stocked into the ADPI bags under identical conditions in late March/early April. Initial differences in epibiont levels is unlikely given that there were no differences in epibiont biomass on EH and SI scallop shells in mid-August. Immediately after planting, densities of scallop cluckers with meats from the two source groups were very similar, as was survival of scallops brought back to the laboratory. This suggests that there were no overt differences in stressors associated with planting activities for the two groups of scallops. It is more likely that there was some physiological difference between the two groups which,

despite the fact that SI scallops were larger than EH scallops at the time of deployment in 2005, contributed to a higher rate of mortality of SI scallops after planting. This may have been related to the nutritional history of scallops while they were held in intermediate culture (i.e. in the fall, prior to when overwintering began), which has been shown to be highly correlated to later survival (Sekino 1992; Davidson 2000).

While we did not see significant differences in survival of caged scallops over the range of stocking densities from 117 to 469/m², Arnold et al. (2005) found that mortality rates of Florida bay scallops, *A. i. concentricus*, held in bottom cages with legs, were correlated to stocking density over a range of 139–833/m². They concluded that although survival and growth were better at lower stocking densities the numbers of scallops surviving to spawn did not necessarily result in more live scallops in a given cage at the time spawning commenced.

In this study, survival rates of scallops in ADPI bags as well as free-planted scallops both exceeded those obtained during earlier restoration efforts in New York (Tettelbach and Wenczel 1993) and raised scallops densities to over 100× those in the natural population at our study site. While densities at the time of initial spawning in ADPI bags ($\geq$75/m² for bags with the lowest initial stocking density of 117/m²) were higher than for free-planted scallops (45–69/m² in eelgrass and up to 22/m² on bare sand), the lower maintenance and costs of free-planting, and thus the potential to deploy greater numbers of scallops, suggest that this technique may be preferable for many restoration programs. Materials to construct ADPI arrays cost $\sim$US\$18 per array × 36 = US\$648. Labor for construction and deployment required $\sim$70 and 6 h, respectively, while gear change/scallop restocking required 40 h; at a wage rate of US\$12 h^{-1}, labor costs were US\$1392 year^{-1}. Thus, the additional costs for the above bottom system were $\sim$US\$2040 more than for free-planting (which do not require maintenance).

Scallop growth

The significantly greater shell growth of free-planted scallops, versus those held in ADPI arrays, likely reflected two major factors: (1) differential availability of food and/or (2) fewer disturbances that might inhibit growth. Despite the fact that there were no statistical differences in total chlorophyll a concentrations in surface waters in 2005 and 2006, higher growth rates of free-planted scallops, compared to scallops in ADPI arrays, may have reflected greater access to such food sources as benthic microalgae (Davis and Marshall 1961) or organic material at the sediment/water interface (Vélèz et al. 1995). However, significantly greater levels of biofouling of scallops in the ADPI arrays as well as heavy fouling of the bag meshes, both of which caused many scallops to be bound together and limited mobility, undoubtedly reduced water flow and seston food availability. It is likely that the same factors masked any potential differences in growth rates that might be expected at different stocking densities (Widman and Rhodes 1991; Davidson 2000). The fact that growth rates of ADPI scallops were significantly better in 2006 than 2005 probably reflects the improved design of the arrays in the second year. Increased inter-actions between scallops in the ADPI arrays, particularly when they were tilted more severely in 2005, likely led to greater disturbance of scallops and thus an increased fre-quency of growth stoppages (Palmer 1980). These factors likely contributed to slower growth of scallops in the ADPI arrays compared to free-planted scallops.

Even though mean densities of free-planted scallops in 2005 were still as high as 56.1/m² in June and 28.8/m² in September, observed growth rates and scallop sizes were comparable to those seen in natural populations in New York (Bricelj et al. 1987; Tettelbach and Bonal 2008)—suggesting that our high-density free-plantings did not result in growth inhibition.

Biofouling on scallop shells

The greater biofouling of scallops in the ADPI arrays, compared to that on free-planted scallops, can be attributed to higher levels of larval settlement by epibionts and/or reduced predation on these organisms after settlement. Heavy fouling of suspended aquaculture gear by tunicates, sponges, mollusks, barnacles, other invertebrates, and algae is well documented (see Carver et al. 2003) and is generally attributed to baffling of water currents that facilitates larval settlement (e.g. Eckman 1987). In addition, the ADPI mesh afforded greater protection for epibionts from predators. *Styela clava* and other tunicates were present on the shells of many scallops at the time of planting in both years, but the fact that virtually no tunicates were found in the months after free-planting clearly suggests that these epibionts were removed by predators. Spider crabs, *Libinia* spp., were probably major predators of fouling tunicates; we observed *Libinia* preying on tunicates and sponges attached to cinder blocks within 2–3 min after their re-deployment in another project conducted in Northwest Harbor in 2007 (Tettelbach, unpublished data).

Scallop reproduction

The timing and number of observed spawning peaks were consistent with observations reported for bay scallops in New York during other years (Bricelj et al. 1987; Tettelbach et al. 2002). Our direct observations of scallop spawning on June 7, 2005 suggested that this event was triggered by a sharp spike in water temperature coupled with sustained high winds that caused an increase in wave action and, in turn, mechanical disturbance of the scallops (Tettelbach and Weinstock 2008). Similar spikes in water temperature, with or without comparable wind events, may also have triggered spawning later in the summer of 2005 (Tettelbach and Weinstock 2008).

Although significant differences in mortality and growth rates were not consistently seen among scallops stocked at the three different densities in the ADPI arrays, consistently lower GDW levels were seen at the highest stocking density (200/bag). This same pattern was seen by Davidson (2000), who concluded that once spawning was initiated bay scallops held in lantern nets at lower stocking densities ($312/m^2$) maintained a higher level of reproductive condition than did scallops held at the highest stocking density ($1,250/m^2$). Larger gonad mass in the scallops *Chlamys bifrons* and *C. asperrima* is not thought to result in sperm being released in higher quantities or at a faster rate, but may lead to more frequent spawning (Styan and Butler 2003). In restoration efforts, a greater frequency of spawning and/or spawning over a longer period of time may translate to a higher probability of successful recruitment to the bay bottom (Kelley and Sisson 1981; Tettelbach et al. 2001; Bishop et al. 2005). In light of this possibility, we suggest that stocking of bay scallops in ADPI bags or other off-bottom enclosures for restoration purposes be done at the lower densities of 50–100/bag (=$117–234/m^2$), rather than at a density of 200/tier (=$468/m^2$).

Estimation of gamete production, fertilization rate, and contribution to larval recruitment

Gamete production by bay scallops that were free-planted or held in cages was considerable and illustrates the potential contribution of restoration efforts to increased zygote production and larval recruitment. Clearly, higher survival of planted scallops is paramount to maximizing production of gametes; the choice of suitable bottom types (i.e. vegetated versus bare sand) for free-planting is thus critically important.

Our estimates of fertilization success (F) are based on model predictions at selected parameter values, some of which were not measured directly; thus, their validity is subject to debate. Computations of F were very sensitive to differences in flow rate, frictional velocity and coefficients of diffusivity. One would expect that at higher densities, and thus closer proximity of spawning individuals, that F should be higher (Claereboudt 1999; Metaxas et al. 2002); however, F values for the higher densities (95.2–360.4 ind m^{-2}) of scallops in ADPI cages were consistently lower than those for free-planted scallops (56.1 m^{-2}). This trend does not seem to necessarily reflect biological processes in the field (such as the potentially higher probability of polyspermy at higher densities (Styan 1998) but may be due to selection of parameters that were less than optimal for the model. Metaxas et al. (2002) concluded that their model did not work well for seagrass habitats.

The fact that the calculated values for F based on the two models are inconsistent does not mean that we can not draw inferences about the utility of high-density plantings for scallop restoration. On the contrary, if we base our conclusions on trends generated from empirical studies of fertilization success in the field (see reviews by Levitan 1991; Liermann and Hilborn 2001; and Metaxas et al. 2002), it is clear that plantings conducted at high densities (whether as free-plants or in cages) and over large areas should provide a much greater probability that spawned eggs will be successfully fertilized because individuals are in close proximity—which serves to reduce losses of sperm due to dilution effects and increase egg–sperm contact times. Furthermore, it has been shown that actual fertilization rates in the field may be considerably higher than those predicted by the models (Metaxas et al. 2002; Yund et al. 2007). Flow rates within eelgrass beds may be 1 order of magnitude lower than outside (Eckman 1987) and therefore reduced mixing rates in eelgrass likely prolong the contact time between eggs and sperm (Metaxas et al. 2002). Additionally, synchronous spawning may override sperm dilution effects (Metaxas et al. 2002). This may well have been true during the observed bay scallop spawning on June 7, 2005 (Tettelbach and Weinstock 2008) when we estimated that an average of 7.5% of the population was releasing gametes at a given instant but 100% of the population was spawning during this event; the water turned noticeably cloudy at this time and lateral visibility was reduced from ∼3 to ≤2 m due to the very high numbers of gametes that were released. Conducting plantings where the long axis of the area is parallel to the predominant flow also should serve to increase sperm–egg contact times during spawning.

In conjunction with the study described here, we monitored larval recruitment to spat collectors placed at varying distances from our planted scallops in Northwest Harbor; however, we saw only low levels of recruitment—probably because most larvae were exported outside of this embayment in 2005 and 2006 (Tettelbach 2008). Nevertheless, we have seen increases of greater than 1 order of magnitude in larval recruitment, and juvenile and adult scallop densities, in another local embayment that were attributed to our high-density (75–200 m^{-2}) plantings of large numbers (∼500,000 year^{-1}) of scallops over several years (Tettelbach and Smith 2009). Similar population increases have resulted in two other embayments where we have been conducting scallop restoration and overall fishery landings in the Peconic Bays have increased by an order of magnitude in the last 3 years (Tettelbach, unpublished data).

Conclusions

This study demonstrated the utility of high-density plantings in the creation of bay scallop spawner sanctuaries for restoration efforts. Although we did not observe increased larval

recruitment in the vicinity of our planted scallops, we have seen clear evidence of this phenomenon in subsequent restoration efforts (Tettelbach and Smith 2009). Observed differences in survival rates of scallops in 2005 and 2006 illustrate the importance of selecting appropriate habitat for free-planting and the necessity of utilizing systems for suspending scallops that minimize horizontal instability and tilting of nets. While the two methods offer their respective advantages and disadvantages, the overall goal of our bay scallop restoration efforts—to achieve high densities and numbers of spawning adults—was attained with both methods. Such high densities and numbers of adult bay scallops at the time of spawning should serve to improve the probability of successful fertilization and subsequent larval recruitment (Levitan and Petersen 1995; Liermann and Hilborn 2001) and, in turn, the likelihood that restoration efforts may be successful. Our current resto-ration efforts (Tettelbach and Smith 2009), which employ high-density free-plantings and deployments in off-bottom lantern nets, have indeed contributed to a marked increase in New York bay scallop populations and fisheries in the last 3 years.

References

Ambrose WG Jr, Irlandi EA (1992) Height of attachment on seagrass leads to trade-off between growth and survival in the bay scallop *Argopecten irradians*. Mar Ecol Prog Ser 90:45–51

Arnold WS, Blake NJ, Harrison MM, Marelli DC, Parker ML, Peters SC, Sweat DE (2005) Restoration of bay scallop (*Argopecten irradians* (Lamarck)) populations in Florida coastal waters: planting tech-niques and the growth, mortality and reproductive development of planted scallops. J Shellfish Res 24(4):883–904

Barbeau MA, Hatcher BG, Scheibling RE, Hennigar AW, Taylor LH, Risk AC (1996) Dynamics of juvenile sea scallop (*Placopecten magellanicus*) and their predators in bottom seeding trials in Lunenburg Bay, Nova Scotia. Can J Fish Aquat Sci 53:2494–2512

Barber BJ, Blake NJ (2006) Reproductive physiology. In: Shumway S, Parsons J (eds) Scallops: biology, ecology and aquaculture, 2nd edn. Developments in aquaculture and fisheries science, vol 35. Elsevier, Amsterdam, Boston, Heidelberg, pp 357–416

Belding DL (1910) The scallop fishery of Massachusetts. Marine Fisheries Series—No. 3, Division of Fisheries and Game, Department of Conservation, Commonwealth of Massachusetts, Boston, 51 pp

Bishop MJ, Rivera JA, Irlandi EA, Ambrose WG Jr, Peterson CH (2005) Spatio-temporal patterns in the mortality of bay scallop recruits in North Carolina: investigation of a life history anomaly. J Exp Mar Biol Ecol 315:127–146

Bricelj VM, Epp J, Malouf RE (1987) Intraspecific variation in reproductive and somatic growth cycles of bay scallops *Argopecten irradians*. Mar Ecol Prog Ser 36:123–137

Carroll JM, Peterson BJ, Bonal D, Weinstock A, Smith CF, Tettelbach ST (2010) Comparative survival of bay scallops in eelgrass and the introduced alga, *Codium fragile*, in a New York estuary. Mar Biol 157:249–259

Carver CE, Chisholm A, Mallet AL (2003) Strategies to mitigate the impact of *Ciona intestinalis* (L.) biofouling on shellfish production. J Shellfish Res 22(3):621–631

Claereboudt M (1999) Fertilization success in spatially distributed populations of benthic free- spawners: a simulation model. Ecol Modelling 121:221–233

Cochard JC, Devauchelle N (1993) Spawning, fecundity and larval survival and growth in relation to controlled conditioning in native and transplanted populations of *Pecten maximus* (L.): evidence for the existence of separate stocks. J Exp Mar Biol Ecol 169:41–56

Davidson MC (2000) The effects of stocking density in pearl nets on survival, growth, and reproductive potential of the bay scallop, *Argopecten irradians irradians*. Thesis, State University of New York at Stony Brook

Davis RL, Marshall N (1961) The feeding of the bay scallop, *Aequipecten irradians*. Proc Nat Shellfish Assoc 52:25–29

Eckman JE (1987) The role of hydrodynamics in recruitment, growth, and survival of *Argopecten irradians* (L.) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. J Exp Mar Biol Ecol 106:165–191

Fegley SR, Peterson CH, Geraldi NR, Gaskill DW (2009) Enhancing the potential for population recovery: restoration options for bay scallop populations, *Argopecten irradians concentricus*, in North Carolina. J Shellfish Res 28(3):477–489

Félix-Pico EF (2006) Mexico. In: Shumway S, Parsons J (eds) Scallops: biology, ecology and aquaculture, 2nd edn. Developments in aquaculture and fisheries science, vol 35. Elsevier, Amsterdam, Boston, Heidelberg, pp 1337–1390

Garcia-Esquivel Z, Bricelj VM (1993) Ontogenetic changes in microhabitat distribution of juvenile bay scallops, *Argopecten irradians irradians* (L.), in eelgrass beds, and their potential significance to early recruitment. Biol Bull 185:42–55

Guo X, Luo Y (2006) Scallop culture in China. In: Shumway S, Parsons J (eds) Scallops: biology, ecology and aquaculture, 2nd edn. Developments in aquaculture and fisheries science, vol 35. Elsevier, Amsterdam, Boston, Heidelberg, pp 1143–1161

Hatcher BG, Scheibling RE, Barbeau MA, Hennigar AW, Taylor LH, Windust AJ (1996) Dispersion and mortality of a population of sea scallop (*Placopecten magellanicus*) seeded in a tidal channel. Can J Fish Aquat Sci 53:38–54

Heck KL, Orth RJ (2006) Predation in seagrass beds. In: Larkum AWD et al (eds) Seagrasses: biology, ecology and conservation. Springer, Dordrecht, The Netherlands

Ivin VV, Kalashnikov VZ, Maslennikov SI, Tarasov VG (2006) Scallops fisheries and aquaculture of Northwestern Pacific, Russian Federation. In: Shumway S, Parsons J (eds) Scallops: biology, ecology and aquaculture, 2nd edn. Developments in aquaculture and fisheries science, vol 35. Elsevier, Amsterdam, Boston, Heidelberg, pp 1163–1224

Kelley KM, Sisson JD (1981) Seed sizes and their use in determining spawning and setting times of bay scallops on Nantucket. In: Kelley KM (ed) The Nantucket bay scallop fishery: the resource and its management. Shellfish and Marine Department, Nantucket, MA

Kirkman TW (1996) Statistics to use. http://www.physics.csbsju.edu/stats/KS-test.html. Cited 6 Mar 2008, University site

Kosaka Y, Ito H (2006) Japan. In: Shumway S, Parsons J (eds) Scallops: biology, ecology and aquaculture, 2nd edn. Developments in aquaculture and fisheries science, vol 35. Elsevier, Amsterdam, Boston, Heidelberg, pp 1093–1141

Krause MK (1992) Use of genetic markers to evaluate the success of transplanted bay scallops. J Shellfish Res 11:199

Levitan DR (1991) Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. Biol Bull 181:261–268

Levitan DR, Petersen C (1995) Sperm limitation in the sea. Trends Ecol Evol 10:228–231

Liermann M, Hilborn R (2001) Depensation: evidence, models and implications. Fish Fisher 2:33–58

MacKenzie CJ (2008) The bay scallop, *Argopecten irradians*, Massachusetts through North Carolina: its biology and the history of its habitats and fisheries. Mar Fish Rev 70:6–79

Mackie LA, Ansell AD (1993) Differences in reproductive ecology in natural and transplanted populations of *Pecten maximus*: evidence for the existence of separate stocks. J Exp Mar Biol Ecol 169:57–75

Marelli DC, Arnold WS, Bray C (1999) Levels of recruitment and adult abundance in a collapsed population of bay scallops (*Argopecten irradians*) in Florida. J Shellfish Res 18:393–399

Marsden ID, Bull MF (2006) New Zealand. In: Shumway SE, Parsons GJ (eds) Scallops: biology, ecology and aquaculture, 2nd edn. Developments in aquaculture and fisheries science, vol 35. Elsevier, Amsterdam, Boston, Heidelberg, pp 1413–1426

Metaxas A, Scheibling RE, Young CM (2002) Estimating fertilization success in marine benthic invertebrates: a case study with the tropical sea star *Oreaster reticulatus*. Mar Ecol Prog Ser 226:87–101

Morgan DE, Goodsell J, Matthiessen GC, Garey J, Jacobson P (1980) Release of hatchery-reared bay scallops (*Argopecten irradians*) onto a shallow coastal bottom in Waterford, Connecticut. Proc World Maricul Soc 11:247–261

Norman M, Roman G, Strand Ø (2006) European aquaculture. In: Shumway SE, Parsons GJ (eds) Scallops: biology, ecology and aquaculture, 2nd edn. Developments in aquaculture and fisheries science, vol 35. Elsevier, Amsterdam, Boston, Heidelberg, pp 1058–1066

Palmer RE (1980) Behavioral and rhythmic aspects of filtration in the bay scallop, *Argopecten irradians concentricus* (Say), and the oyster, *Crassostrea virginica* (Gmelin). J Exp Mar Biol Ecol 45:273–295

Parsons GJ, Robinson SMC (2006) Sea scallop aquaculture in the Northwest Atlantic. In: Shumway SE, Parsons GJ (eds) Scallops: biology, ecology and aquaculture, 2nd edn. Developments in aquaculture and fisheries science, vol 35. Elsevier, Amsterdam, Boston, Heidelberg, pp 907–944

Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford, UK

Peterson CH, Summerson HC, Luettich RA Jr (1996) Response of bay scallops to spawner transplants: a test of recruitment limitation. Mar Ecol Prog Ser 102:93–107

Pickerell C, Schott S (2004) Eelgrass trend analysis report: 1997–2002. Report to the Peconic estuary program, Yaphank, NY, 100 p

Pohle DG, Bricelj VM, Garcia-Esquivel Z (1991) The eelgrass canopy: an above-bottom refuge from benthic predators for juvenile bay scallops *Argopecten irradians*. Mar Ecol Prog Ser 74:47–59

Prescott RC (1990) Sources of predatory mortality in the bay scallop *Argopecten irradians* (Lamarck): interactions with seagrass and epibiotic coverage. J Exp Mar Biol Ecol 144:63–83

SCDHS (2008) Surface water quality monitoring data, 1976–2007. Suffolk County Department of Health Services Office of Ecology, Yaphank, NY

Sekino T (1992) Scallop (*Patinopecten yessoensis*). In: Ikenoue T, Kafuku T (eds) Modern methods of aquaculture in Japan, 2nd edn. Elsevier, Tokyo

Silina AV (1994) Survival of different size-groups of the scallop, *Mizuhopecten yessoensis* (Jay), after transfer from collectors to the bottom. Aquaculture 126(1–2):51–59

Silina AV (2008) Long-term changes in intra- and inter-specific relationships in a community of scallops and sea stars under bottom scallop mariculture. J Shellfish Res 27(5):1189–1194

Smith CF, Tettelbach ST (1997) Restocking bay scallops. Final Report to the National Marine Fisheries Service

Strand Ø, Parsons GJ (2006) Scandinavia. In: Shumway SE, Parsons GJ (eds) Scallops: biology, ecology and aquaculture, 2nd edn. Developments in aquaculture and fisheries science, vol 35. Elsevier, Amsterdam, Boston, Heidelberg, pp 1067–1091

Styan CA (1998) Polyspermy, egg size, and the fertilization kinetics of free-spawning marine invertebrates. Am Nat 152(2):290–297

Styan CA, Butler AJ (2003) Scallop size does not predict amount or rate of induced sperm release. Mar Fresh Behav Physiol 36(2):59–65

Systat Software Inc (2004) SigmaStat 3.1 for windows, Point Richmond, CA

Tettelbach ST (1986) Dynamics of crustacean predation on the northern bay scallop, *Argopecten irradians irradians*. Dissertation, University of Connecticut

Tettelbach ST (2008) Bay scallop spawner sanctuary evaluation study, New York State Wildlife Grant Program. Final Report submitted to NY State Department of Environmental Conservation, East Setauket, NY

Tettelbach ST, Bonal D (2008) The importance of fall recruitment in New York bay scallop populations: variability in size of annual growth rings and total shell size. J Shellfish Res 27(4):1056

Tettelbach ST, Smith CF (2009) Bay scallop restoration in New York. Ecol Restor 27(1):20–22

Tettelbach ST, Weinstock A (2008) Direct observation of bay scallop spawning in New York waters. Bull Mar Sci 82(2):213–219

Tettelbach ST, Wenczel P (1993) Reseeding efforts and the status of bay scallop *Argopecten irradians* (Lamarck, 1819) populations in New York following the occurrence of "brown tide" algal blooms. J Shellfish Res 12(2):423–431

Tettelbach ST, Wenczel P, Hughes SWT (2001) Size variability of juvenile (0 + yr) bay scallops *Argopecten irradians irradians* (Lamarck, 1819) at eight sites in eastern Long Island, New York. Veliger 44(4):389–397

Tettelbach ST, Smith CF, Wenczel P, Decort E (2002) Reproduction of hatchery-reared and transplanted wild bay scallops, *Argopecten irradians irradians*, relative to natural populations. Aquacult Internat 10:279–296

Tettelbach ST, Smith CF, Wenczel P (2003) Selection of appropriate habitats/sites for bay scallop restoration. J Shellfish Res 22(1):357

Turner WH (1995) "Bags to drags", the bay scallop restoration project in the Westport River, a two-year update. J Shellfish Res 14(1):249

Vélèz A, Freites L, Himmelman JH, Senior W, Marin N (1995) Growth of the tropical scallop, *Euvola* (*Pecten*) *ziczac*, in bottom and suspended culture in the Golfo de Cariaco, Venezuela. Aquaculture 136:257–276

Volkov YP, Dadaev AA, Levin VS, Murakhveri AM (1983) Changes in the distribution of Yezo scallop and starfishes after mass planting of scallops at the bottom of Vityaz Bay (Sea of Japan). Sov J Mar Biol (Engl Transl Biol Morya) 8:271–285

Widman JC, Rhodes EW (1991) Nursery culture of the bay scallop, *Argopecten irradians irradians*, in suspended mesh nets. Aquaculture 99:257–267

Wong MC, Barbeau MA, Hennigar AW, Robinson SMC (2005) Protective refuges for seeded juvenile scallops (*Placopecten magellanicus*) from sea star (*Asterias* spp.) and crab (*Cancer irroratus* and *Carcinus maenas*) predation. Can J Fish Aquat Sci 62:1766–1781

Yund PO, Murdock K, Johnson SL (2007) Spatial distribution of ascidian sperm: two-dimensional patterns and short vs. time-integrated assays. Mar Ecol Prog Ser 341:103–109