

# Priming the larval pump: resurgence of bay scallop recruitment following initiation of intensive restoration efforts

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**ABSTRACT:** Bay scallop *Argopecten irradians irradians* populations and fisheries in the Peconic Bays of eastern Long Island, New York, USA, were decimated by brown tide algal blooms between 1985 and 1995. Despite the absence of brown tide since 1995, populations did not recover on their own over the next 11 yr. We hypothesized that this was due to recruitment limitation and initiated an intensive restoration program to jump-start populations by planting several million hatchery-reared scallops at high densities to ensure high fertilization success and boost larval supply. We observed 11- to 32-fold increases in larval recruitment in different embayments by 2010, compared to the period 2005 to 2006 (before intensive restoration); the most dramatic increase (3239%) occurred in Orient Harbor, the focus of restoration efforts. Recruitment was highly correlated with our index of total fertilized egg production in Orient Harbor and Hallock Bay, but not in 2 other embayments—where larval export or population overestimation probably compromised the correlation. Resurgent recruitment following restoration was not correlated to coincidental changes in adult fecundity, water temperature, salinity, rainfall, chlorophyll *a*, total particulate nitrogen, or local winds; decreased planktonic predation and allochthonous larval infusion were deemed unlikely drivers. We conclude that Peconic bay scallops were recruitment-limited following the 1995 brown tide and that resurgent recruitment was driven, initially, by our intensive restoration efforts and later by the rebuilding natural populations. Sustained restoration, conducted with high scallop numbers/densities, may help boost natural populations above threshold levels at which they become self-sustaining.

**KEY WORDS:** Annual recruitment · Bivalve larvae · Environmental effects · Larval supply · Recruitment · Recruitment limitation · Restoration · Scallop

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## INTRODUCTION

'Supply side' ecology (Doherty 1981, Connell 1985, Gaines & Roughgarden 1985) is central to understanding the population dynamics of aquatic species whose life history includes a pelagic larval stage. For such species, order of magnitude differences in larval

supply may occur on both spatial and temporal scales; these fluctuations may play a critical role in the ecology of marine communities (Gaines et al. 1985, Roughgarden et al. 1988, Menge 1991). Variations in larval supply may reflect cyclic processes (Chavez et al. 2003, Guisande et al. 2004) or episodic events (Summerson & Peterson 1990, Boero 1996). In the lat-

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ter case, catastrophic events may have long-term effects on future adult population sizes as a consequence of limited numbers of larvae available for settlement (Peterson & Summerson 1992, Caley et al. 1996).

For bivalve mollusks and other benthic marine invertebrates, limitation of recruitment ('addition of individuals to local populations following settlement from the pelagic larval phase to the benthic or demersal early juvenile phase'; Caley et al. 1996, p 478) has been attributed to (1) low larval supply due to poor fertilization success at low adult densities, e.g. when distances between spawning adults exceed some critical distance (Summerson & Peterson 1990, Peterson & Summerson 1992, Levitan & Petersen 1995, Peterson et al. 1996, Arnold et al. 1998, Marelli et al. 1999, Kraeuter et al. 2005) or when hydrographic conditions are unfavorable (Connolly et al. 2001); (2) intense predation on larvae in the water column (McNamara et al. 2010); (3) limited availability of suitable substrates for settlement (Eggleston & Armstrong 1995, Young et al. 1998); or (4) high post-settlement mortality rates (Hunt & Scheibling 1997, Gosselin & Qian 1997, Newell et al. 2000). Conversely, larval supply and recruitment rates of benthic marine invertebrates may be unusually high when (1) adult population sizes/densities are increased greatly (see Orensanz et al. 2006); (2) adult fecundity is enhanced (Caley et al. 1996, Hughes et al. 2000), e.g. by particularly favorable food quantity and/or quality (Bayne et al. 1978, MacDonald & Thompson 1985); (3) larval survival/growth increases due to higher phytoplankton concentrations (Wolff 1988, Menge et al. 2009); (4) predation pressure on larvae is relaxed (Liermann & Hilborn 2001, Strasser & Gunther 2001); (5) larval retention is enhanced by localized wind (Eggleston & Armstrong 1995, Bertness et al. 1996) or circulation patterns (Dickie 1955, Young et al. 1998); or (6) water temperatures are elevated (Wolff 1987, Shephard et al. 2010).

Recruitment limitation may be theoretically addressed within a management context by increasing population sizes and/or densities of reproductive individuals, which in turn should increase larval production and supply (Peterson et al. 1996). Deployment of 'spawner sanctuaries', which will act as 'larval pumps' (W. Arnold pers. comm.), is the most common approach followed in shellfish restoration programs (Goldberg et al. 2000). Increased larval recruitment following deployment of spawner sanctuaries is viewed by some as the best way to demonstrate their effectiveness (Leverone et al. 2010). Several marine bivalve restoration programs have been deemed successful on at least a short-term basis, e.g.

*Patinopecten caurinus yessoensis* in Japan (Uki 2006), *Crassostrea virginica* in North Carolina estuaries (Powers et al. 2009), and *Argopecten irradians* in North Carolina (Peterson et al. 1996), Florida (Arnold et al. 2005), and Massachusetts (Turner 1995, Lovewell 2010); however, increased larval supply/settlement has only been documented in some instances. Incidental recovery of local populations of *Argopecten purpuratus* in Chile and *Chlamys farreri* in China due to local aquaculture operations has also been observed (Orensanz et al. 2006). Similarly, designation of marine reserves may provide comparable benefits via increased larval production and export (Beukers-Stewart et al. 2005, Almany et al. 2007).

In the Peconic Bays of eastern Long Island, New York, populations of the bay scallop *Argopecten irradians irradians* (which is essentially semelparous; Belding 1910) were nearly extirpated by a series of brown tide *Aureococcus anophagefferens* algal blooms from 1985 to 1987 (Casper et al. 1987). Scallop populations rebounded for a few years following restoration efforts in the late 1980s to early 1990s (Tettelbach & Wenczel 1993); however, a severe brown tide in 1995 again decimated stocks (NYSDEC 2011). Despite the absence of brown tide blooms in the Peconic Bays since 1995, and seemingly favorable water quality (SCDHS 2011), bay scallop populations remained at very low levels and annual commercial fishery landings were only 1 to 2% of historical, pre-brown tide (before 1985) levels from 1996 to 2006 (Tettelbach & Smith 2009). We hypothesized, as Peterson et al. (1996) had done for a comparable scenario in North Carolina, and as Arnold et al. (1998) had suggested for the western Florida metapopulation, that the inability of bay scallop populations to recover on their own was driven by recruitment limitation. In 2006, we initiated an intensive restoration program to jump-start Peconic populations by planting several million hatchery-reared bay scallops at high densities (100 to 200 ind. m<sup>-2</sup>), in nets and directly to the bay bottom, to ensure a high probability of fertilization success (Tettelbach & Smith 2009, Tettelbach et al. 2011). As part of our restoration program we monitored larval recruitment in areas adjacent to large-scale plantings and in unplanted areas for 6 yr: 2005 to 2006 (before intensive restoration) and 2007 to 2010 (after commencement of intensive restoration).

In this paper, we document a dramatic increase in larval recruitment during the 4 yr after the start of intensive bay scallop restoration efforts, compared to 2 yr prior. We examine whether these trends are due to coincidental effects of (1) increased adult fecundity, (2) environmental factors that may have en-

hanced larval survival/growth, or (3) allochthonous supply of scallop larvae, or can be attributed to (4) restoration efforts.

## MATERIALS AND METHODS

### Monitoring of scallop larval recruitment

Larvae of bivalve mollusks are similar in appearance; thus, it is difficult to estimate abundance of a given species from plankton samples (Arnold et al. 1998). Scallops are particularly amenable to larval recruitment studies because they often byssally attach to above-bottom surfaces upon metamorphosis (Cragg 2006), and mesh 'spat' (small juvenile) collectors have been used to monitor larval recruitment of numerous pectinids, including Yezo *Patinopecten caurinus yessoensis* (Ventilla 1982), Iceland *Chlamys islandica* (Harvey et al. 1995), king *Pecten maximus* (Slater 2006) and bay *Argopecten irradians* (Eckman 1987, Ambrose et al. 1992, Peterson et al. 1996) scallops. Differential post-recruit predation inside spat collectors may potentially affect number of spats, but Ambrose et al. (1992) found no differences in post-set mortality within collectors deployed in the field or held in the laboratory for 6 wk; they concluded, as did Harvey et al. (1995), that this approach provided a valid index of larval settlement. We utilized spat abundance data to examine spatial and temporal differences in larval recruitment in the context of our restoration program.

Spat collectors used in our study, modified after Ambrose et al. (1992), were comprised of a cinder block anchor, 2 polyethylene spat bags, and a standard lobster pot buoy tied to an appropriate length of floating, 9 mm diameter, polypropylene line. Each 0.75 mm mesh spat bag (38 × 46 cm) was stuffed with a standardized piece of blue Neutron polyethylene mesh (38 × 46 cm) that was folded to keep the bag from collapsing; a small Styrofoam float (OS-4 or OS-5) was attached via plastic zip-ties to the top corner of each spat bag to keep them erect. One spat bag was attached at the top of the cinder block, ~0.5 m above the bay bottom, the second was attached to the float line ~1.0 m above the bottom. While it is known that greater numbers of *Placopecten magellanicus* larvae recruit to surfaces with a biofilm (Parsons et al. 1993), we standardized spat collectors by using new spat bags and Neutron for each deployment. Since OS-4 floats were not available for the duration of the study, we compared recruitment to spat bags deployed with the 2 different sizes of floats at the same sites.

From 2005 to 2010, spat collectors were deployed continuously during all months when bay scallop larvae might have been present in the water column (Belding 1910, Tettelbach et al. 1999); in this way we circumvented problems associated with larval sampling at discrete times (Gaines & Bertness 1993). Initial deployments (n = 3 per site) were done no later than 1 June—which was prior to or just after the earliest observed scallop spawns in Long Island waters (Bricelj et al. 1987, Tettelbach & Weinstock 2008). Since larval settlement occurs 1 to 2 wk after spawning (Belding 1910), the timing of deployment facilitated settlement of larvae resulting from the first spawns of any given year. A second set (n = 3 per site) of spat collectors was deployed 3 wk later. Every 3 wk thereafter, a new set of spat collectors replaced those that had been in the water for 6 wk; in this way, a continual record of scallop recruitment was obtained (Arnold et al. 1998, Marelli et al. 1999). In 2005 to 2007, we deployed the last set of collectors in late October and sampled them in early December. Since this deployment yielded 0 scallops, in all subsequent years our final deployment was done in early October. We deployed sets of spat collectors in early to mid-May in 2 yr, to check for early recruitment; after the usual 6 wk soak times only 1 scallop was recorded from ~250 spat bags.

Scallop larval settlement was monitored at a total of 23 sites located in 5 different embayments (Figs. 1 to 4, Supplement 1 at [www.int-res.com/articles/suppl/m478p153\\_supp.pdf](http://www.int-res.com/articles/suppl/m478p153_supp.pdf)); site depth ranged from 1.3 to 6.3 m at mean low water. Eight sampling sites were distributed within Orient Harbor (OH) at varying distances from our primary spawner sanctuary (longline site; Fig. 2); the rest were placed in embayments where we did not conduct scallop plantings (Southold Bay, SB; Hog Neck Bay, HN; Fig. 2) or where smaller plantings were done (Hallock Bay, HB; Fig. 3 and State Wildlife Grant (SWG) site in Northwest Harbor, NW; Fig. 4). A simulation model of bay scallop larval dispersal (Siddall et al. 1986, Supplement 2 at [www.int-res.com/articles/suppl/m478p153\\_supp.pdf](http://www.int-res.com/articles/suppl/m478p153_supp.pdf)) was used as a guide for choosing sites for spat collector deployment.

When collectors were retrieved from the field, spat bags were placed into individual plastic bags and brought back to the laboratory, where juvenile ( $\geq 1$  mm) scallops were washed off the outer (rarely) and inner surfaces of spat bags, and Neutron mesh contained within the bags onto a 0.8 mm mesh screen. All scallops were then counted, and shell heights were measured to the nearest millimeter.

### Monitoring of environmental parameters

Water temperature and salinity were measured approximately biweekly to monthly with a YSI Model 85 meter at selected spat collection sites; in addition, water temperatures were recorded every 6 h with Onset Tidbits® at the OH planting site, from 2007 to 2010. Supplemental long-term (1996 to 2010) data for water quality parameters that might affect larval abundance and recruitment (temperature, chlorophyll *a*, total particulate N, salinity) were obtained at sites in OH (Stn 060115) and NW (Stn 060118) (SCDHS 2011). Likewise, rainfall data were obtained for 3 representative sites around the Peconic bay system: Mattituck (WeatherUnderground 2011), Riverhead, and Sag Harbor (NYSDEC 2011). Wind data for Westhampton, New York (Fig. 1) were obtained for 2005 to 2010 via WeatherUnderground (2011).

### Estimation of dates of initial peak spawning of adult bay scallops and peak larval settlement

Temporal changes in adult scallop reproductive condition, as determined via gonad index (GI =

gonad dry weight/total tissue dry weight; Barber & Blake 2006), were monitored for broodstock held in nets at our primary spawner sanctuary in OH from 2007 to 2010; a significant decline in GI is evidence of a spawning event. GI samples were taken initially in late April to early May, and then approximately biweekly from mid- to late May/early June until late July/early August, thus covering the initial period of scallop spawning in the Peconic Bays (Bricelj et al. 1987, Tettelbach et al. 2002). To further pinpoint times of peak spawning, we inspected our continuous water temperature readings to find short-term ( $\leq 48$  h) spikes or sharp declines, which, in possible conjunction with elevated wind speeds (WeatherUnderground 2011) that might cause mechanical agitation of ripe scallops, would cue spawning (Tettelbach & Weinstock 2008). Specific periods of peak larval settlement in 2007 to 2010 were determined via: (1) forward calculation from spawning times, assuming a 2 wk larval period (Belding 1910), and (2) back-calculation, using size data for scallops in spat collectors and published shell growth rates of 8 to 12 mm mo<sup>-1</sup> for small juveniles (Tettelbach 1986, Garcia-Esquivel & Bricelj 1993).

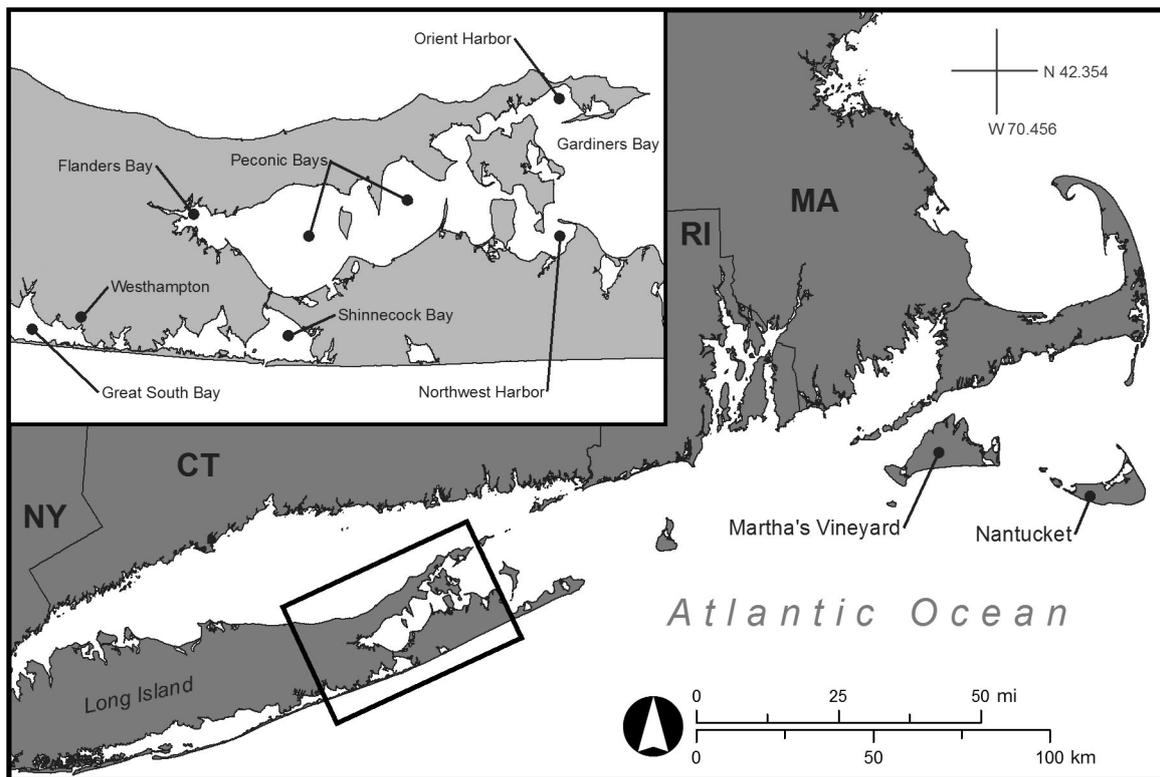


Fig. 1. Map of the northeastern USA, showing the Peconic bay system in eastern Long Island, New York, and other areas noted in the text

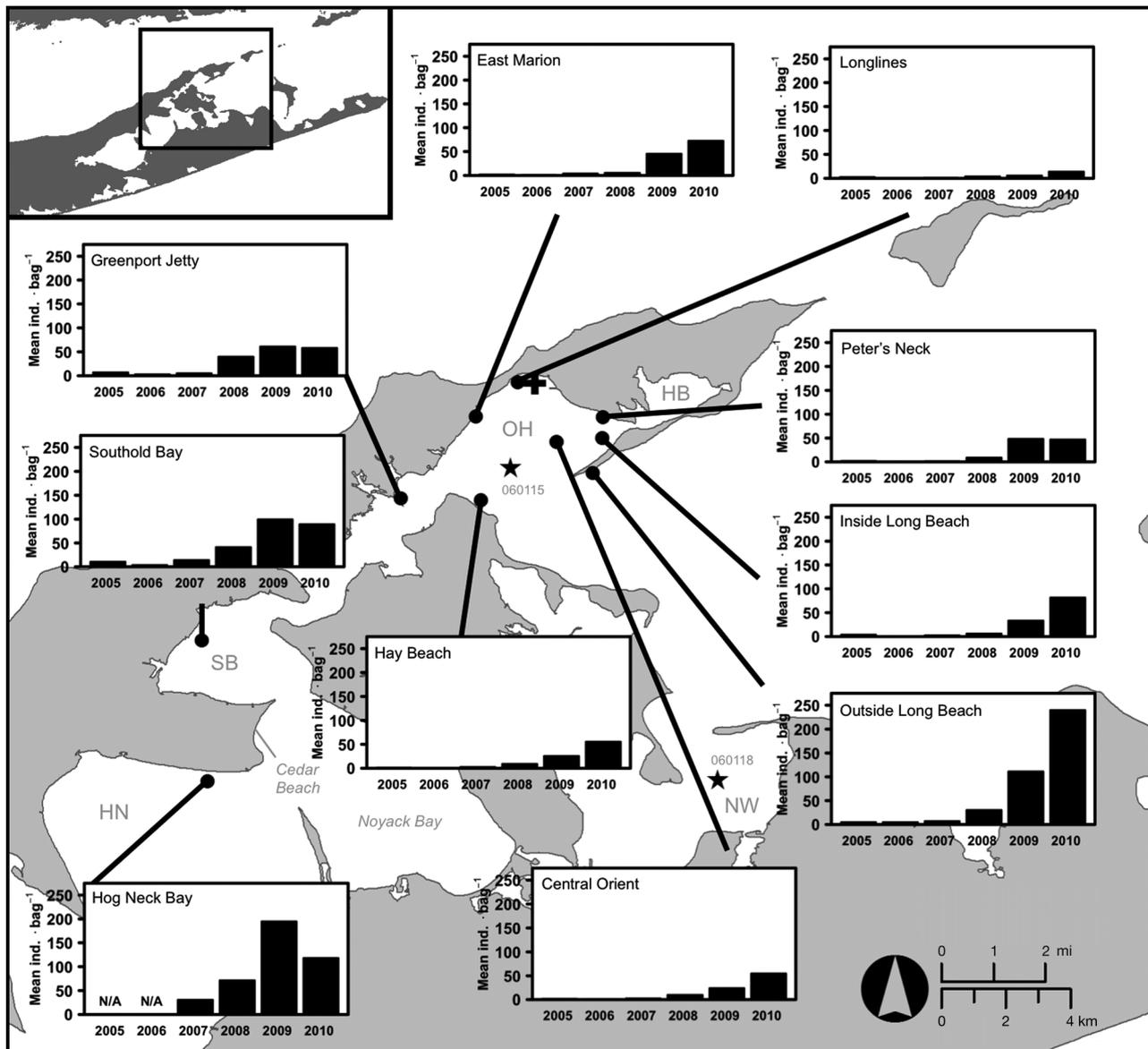


Fig. 2. *Argopecten irradians irradians*. Changes in larval recruitment (mean no. of scallop spats bag<sup>-1</sup> yr<sup>-1</sup>) at sampling sites in Orient Harbor (OH), Southold Bay (SB), and Hog Neck Bay (HN) from 2005 to 2010. +: primary OH planting site; ★: sites of water quality (water temperature, total chlorophyll *a*, total particulate nitrogen, salinity) monitoring by SCDHS (2011). Bay bottom areas ( $\times 10^6$  m<sup>2</sup>) within the 1.3 to 4.6 m (4 to 15 ft) depth stratum, where the majority of Peconic bay scallops exist, equal: 4.87 (OH), 1.71 (Hallock Bay, HB), 2.32 (SB), 7.28 (Northwest Harbor, NW) and 4.49 (HN)

### Statistical evaluation of spatial and temporal trends in scallop recruitment

We examined the effects of spat collector depth (top vs. bottom), embayment, and year on recruitment (no. of scallop spats bag<sup>-1</sup> d<sup>-1</sup>) via a 3-way ANOVA on ranks, as data were non-normal. Subsequent 2-way generalized linear model procedures and 1-way ANOVAs explored these relationships

further. For embayments with multiple sampling stations (OH, HB, NW), we pooled respective sites within embayments and did multiple comparisons of least square means via the Holm-Sidak method. We also ran a 1-way ANOVA to examine differences in mean annual recruitment levels over the 6 yr study period for SB, OH, HB, and NW combined. We examined annual differences in peak fecundity of scallop broodstock in OH from 2007 to 2010 via a Kruskal-

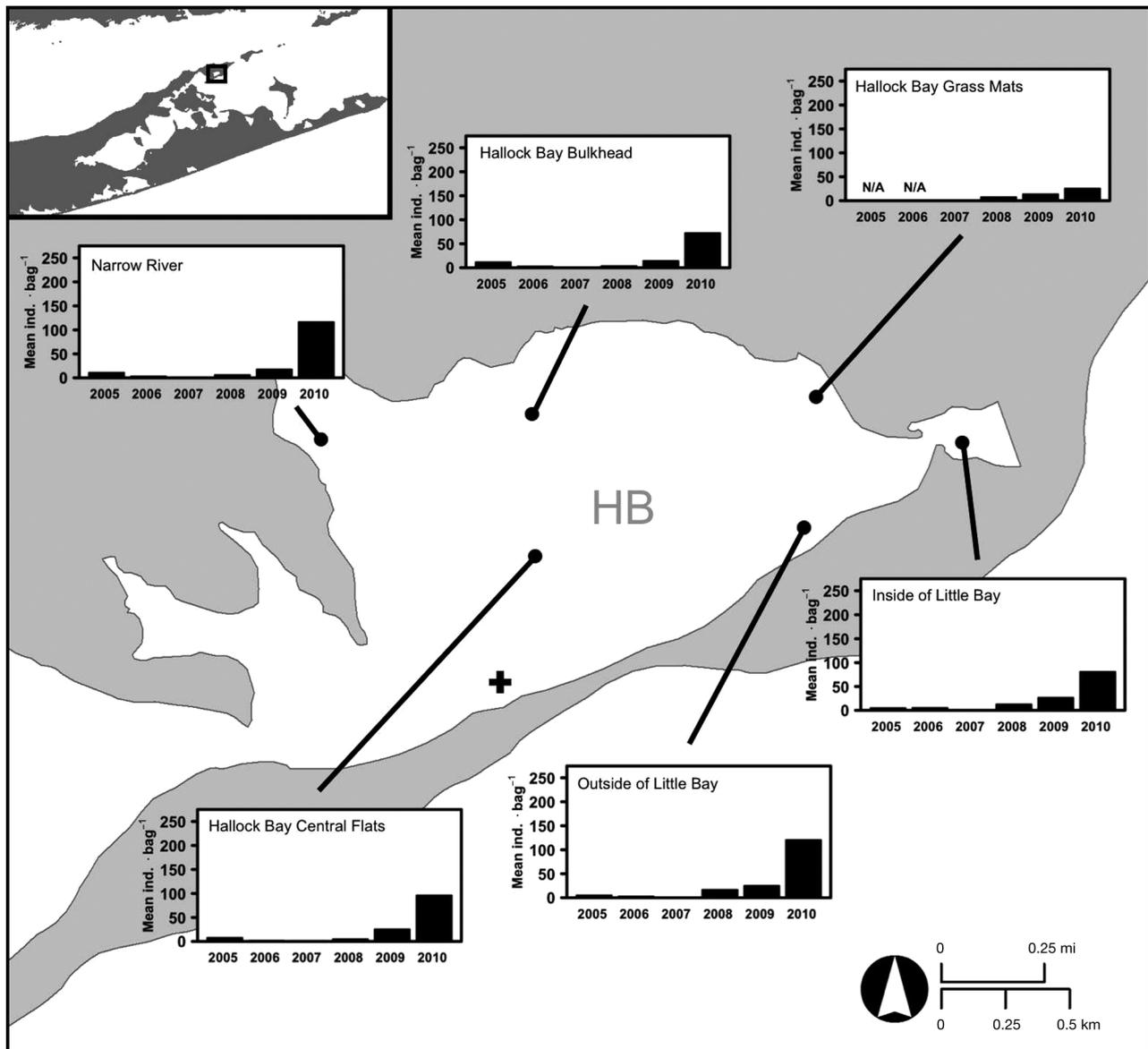


Fig. 3. *Argopecten irradians irradians*. Changes in larval recruitment (mean no. of scallop spat  $\text{bag}^{-1} \text{yr}^{-1}$ ) at sampling sites in Hallock Bay (HB) from 2005 to 2010. +: primary HB planting site

Wallis 1-way ANOVA on ranks, followed by Dunn's multiple comparisons. Since negligible numbers of scallop larvae recruited to collectors sampled in June and December, these data were excluded from statistical analyses of recruitment.

Potential effects of environmental parameters on temporal trends in larval scallop recruitment in OH were examined by determining whether seasonal (e.g. summer: June to August) magnitudes of these variables differed during the period before intensive scallop restoration was initiated in OH (1996 to 2006: during which Peconic bay scallop populations re-

mained at very low levels) (Table 1) compared to the intensive restoration period in OH (2007 to 2010). We employed unbalanced 2-way interactive ANOVAs, using a general linear test approach (R Project for Statistical Computing 2011), for each of the 5 environmental parameters, with restoration status (before/after) and season as factors. Only years for which data were available in all 4 seasons were included in analyses.

We examined whether winds may have favored larval retention within the Peconic estuarine system at respective times of initial peak settlement in 2005

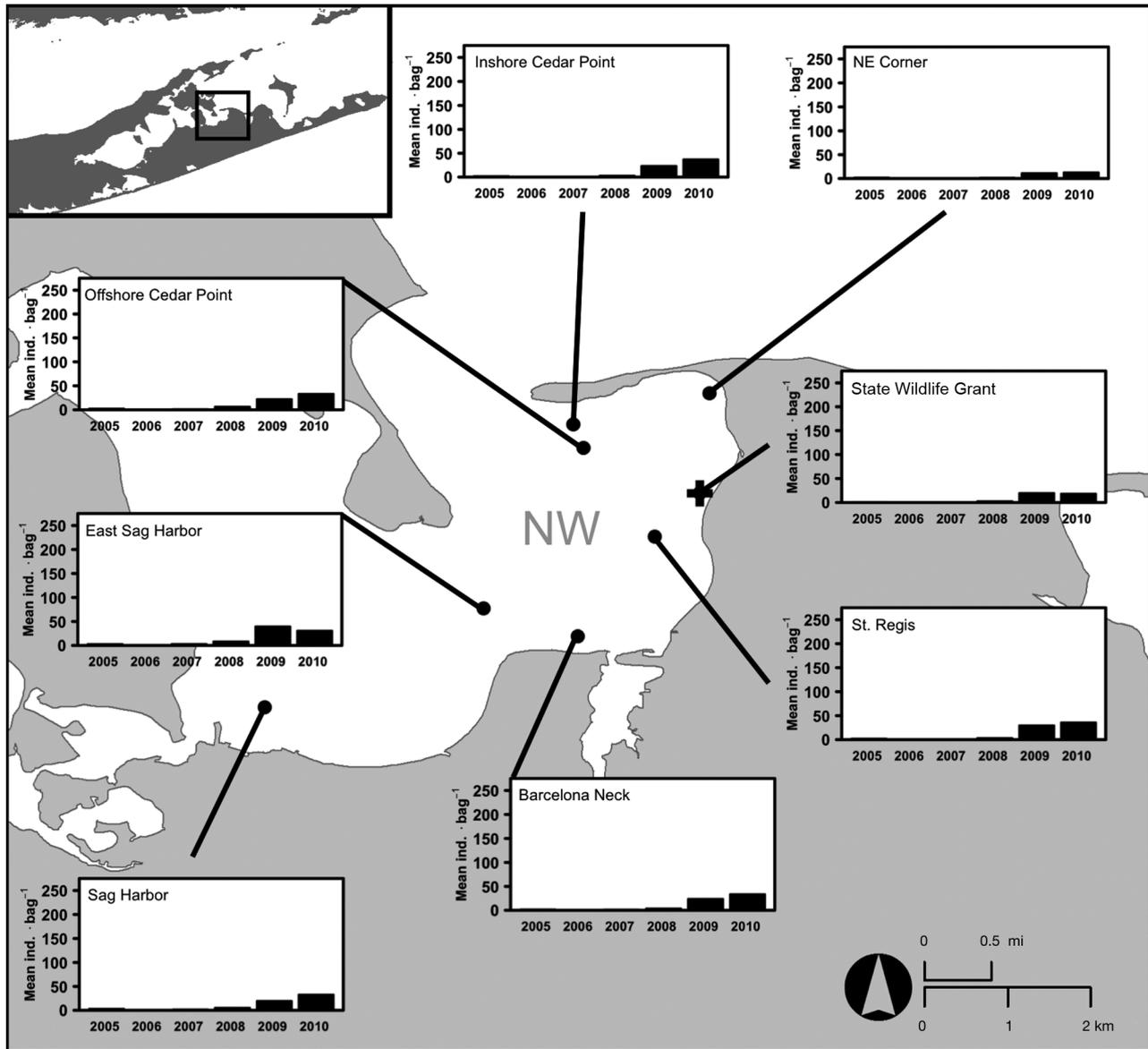


Fig. 4. *Argopecten irradians irradians*. Changes in larval recruitment (mean no. of scallop spats bag<sup>-1</sup> yr<sup>-1</sup>) at sampling sites in Northwest Harbor (NW) from 2005 to 2010. +: 2005 to 2006 planting site

to 2010; dates were back-calculated from our spat collector data (see 'Results'). For these 2 to 6 d windows, we determined the average E (easterly) wind component,  $I$  (which would tend to push water back into the Peconic Bays), using Eq. (1); the average E/W (easterly/westerly; zonal) component of the wind,  $U$ , using Eq. (2) and the average wind stress,  $\tau$ , using Eq. (3).

$$i = \Sigma E_i \div n_E \quad (1)$$

$$u = \Sigma (E_i + W_j) \div (n_E + n_W) \quad (2)$$

$$\tau = \Sigma (\rho_{\text{air}} \times C_d \times O^2) \div n_t \quad (3)$$

where  $\Sigma E_i$  and  $\Sigma W_j$  are the sums of E and W wind vector values, respectively;  $n_E$ ,  $n_W$ , and  $n_t$  are the numbers of E wind, W wind, and wind stress observations, respectively;  $\rho_{\text{air}}$  is the density of air (assumed = 1.22521 kg);  $C_d$  is the drag coefficient (assumed = 0.1); and  $O$  is the wind speed. We did 1-way ANOVAs to determine whether these wind parameters differed during respective settlement periods in years before (2005 to 2006) and after (2007 to 2010) we initiated restoration efforts in OH. We

Table 1. *Argopecten irradians irradians*. Summary of our bay scallop restoration efforts in the Peconic Bays, Long Island, New York, USA, from 2005 to 2009. Sites—NW: Northwest Harbor; HB: Hallock Bay; OH: Orient Harbor; FB: Flanders Bay. Planting methods—bags, nets: suspended bags or lantern nets; free: free-planting directly to the bay bottom. Scallops planted in fall spawned the next year; those planted in spring, in NW, first spawned ~2 mo after planting. Data for NW from Tettelbach et al. (2011). TFEP: total fertilized egg production (for a given year, in parentheses); for details see 'Materials and methods' and Supplement 3 at [www.int-res.com/articles/suppl/m478p153\\_supp.pdf](http://www.int-res.com/articles/suppl/m478p153_supp.pdf). % contribution to TFEP: percent contribution of planted scallops to TFEP for the given embayment

Planting site	Year	Date(s)	Planting method	No. of scallops planted	No. of scallops surviving to spawn	Mean scallop density (no. m <sup>-2</sup> ) at time of spawning	% contribution to TFEP
NW	2005	30 Mar–1 Apr	Free	290000	140250	56.1	30.0 (2005)
			Bags	12600	9880	214.8	
	2006	3–7 Apr	Free	270000	27750	11.1	43.3 (2006)
Bags	12600	9370	203.7				
HB	2005	14 Nov	Free	150000	6560	0.6	56.9 (2006)
	2007	14, 28 Nov	Free	73500	626	0.8	12.7 (2008)
	2008	13, 25 Nov; 2 Dec	Free	197000	26440	18.2	60.7 (2009)
	2009	9, 24 Nov; 15 Dec	Free	236000	81300	27.1	82.5 (2010)
OH	2006	Sep–Nov	Nets	250000	90000	64.3	52.6 (2007)
	2007	Sep–Dec	Nets	501500	251000	89.3	21.8 (2008)
		10 Dec	Free	30000	150	0.5	
	2008	Sep–Dec	Nets	508100	254000	89.3	24.7 (2009)
		Oct–Nov	Free	168000	1370	0.9	
2009	Sep–Dec	Nets	502000	251200	89.3	11.2 (2010)	
FB	2007	19 Dec	Free	28400	3000	7.5	–
	2008	16 Oct	Free	108000	30060	24.1	–
	2009	4 Dec	Free	117000	6060	5.1	–

also conducted linear regressions of the mean number of scallop spats per bag resulting from initial peak settlement events, in each of the 6 yr for each of 3 embayments (OH, NW, SB), versus corresponding wind parameters.

Finally, we considered the contribution of allochthonous larval supply, as well as our scallop plantings, to observed spatial and temporal patterns of larval recruitment. For the latter, we examined stock–recruitment relationships in each of 4 embayments (OH, HB, NW, SB) from 2005 to 2010 by modifying the model of Lundquist & Botsford (2004) to compute linear regressions of total fertilized egg production (TFEP) versus larval recruitment (mean number of spats bag<sup>-1</sup> yr<sup>-1</sup>). TFEP reflects higher fertilization success for more densely aggregated spawners: (see Supplement 3 at [www.int-res.com/articles/suppl/m478p153\\_supp.pdf](http://www.int-res.com/articles/suppl/m478p153_supp.pdf)).

$$\text{TFEP}_{\text{embayment}} = \Sigma[(D_{i..n} \times \text{embayment area}/n_{i..n} \times F_{i..n}) + (\text{PB}_{i..n} \times \text{planting area} \times F_{i..n}) + (\text{PN}_{i..n} \times \text{net area} \times F_{i..n})] \times \text{egg production} \quad (4)$$

where  $D_{i..n}$  is the arithmetic mean density of adult scallops (no. m<sup>-2</sup>) in natural populations at sites  $i..n$ , as observed during spring transect surveys (S. T. Tettelbach et al. unpubl. data); embayment area is the

area (m<sup>2</sup>) within the 1.3 to 4.6 m (4 to 15 ft) depth stratum (where the majority of Peconic bay scallops exist; S. T. Tettelbach pers. obs.);  $n_{i..n}$  is the number of sampling sites examined in a given embayment;  $F_{i..n}$  is the proportion of eggs fertilized at  $D_{i..n}$ ,  $\text{PB}_{i..n}$ , or  $\text{PN}_{i..n}$  (based on Lundquist & Botsford 2004, see our Supplement 3);  $\text{PB}_{i..n}$  and  $\text{PN}_{i..n}$  are the mean density of adult scallops (no. m<sup>-2</sup>), at the approximate time of spawning, which had been free-planted to the bottom or deployed in nets, respectively; planting area is the area (m<sup>2</sup>) into which scallops were free-planted; net area is the total tier area (m<sup>2</sup>) of suspended nets; and egg production equals  $2 \times 10^6$  eggs scallop<sup>-1</sup> (Belding 1910).

## RESULTS

### Comparison of larval recruitment within and between spat collectors

Scallop *Argopecten irradians irradians* larval recruitment did not vary ( $p = 0.179$ ) with height above the bottom (0.5 vs. 1.0 m) at which spat bags were deployed, as revealed in a 3-way ANOVA on ranks comparing number of spats versus depth,

embayment, and year. In 23 of 25 parallel deployments of spat bags with different sized floats, over 6 different embayments, and 2 sampling periods in 2010, numbers of scallop spat were not different ( $p > 0.05$ , 2-sample  $t$ -tests). Thus, data for replicate spat collectors were pooled for subsequent analyses.

### Spatial and temporal differences in scallop larval recruitment

A dramatic increase in larval recruitment (no. of scallop spats  $\text{bag}^{-1} \text{d}^{-1}$ ) occurred in OH after initiation of intensive restoration in that embayment, compared to mean values before restoration (2005 to 2006) (Table 2, Figs. 2 to 4). Mean larval recruitment was 40% higher in OH in 2007, and by 2010 increased to >3200%, compared to the mean for 2005 to 2006. In HB and NW, respective recruitment in 2007 decreased by 88 and 4%, but then increased markedly from 2008 to 2010. In SB and HN, recruitment levels also increased dramatically—but peak numbers were seen in 2009, not 2010 (Fig. 4). In the 3-way ANOVA mentioned above, scallop recruitment varied significantly with the single factor effects of embayment and year (for each,  $p < 2 \times 10^{-16}$ ). A subsequent 2-way ANOVA of larval recruitment (log transformed) for OH, HB, and NW combined revealed significant effects of year ( $F = 140.8$ ,  $p < 0.001$ ), embayment ( $F = 20.1$ ,  $p < 0.001$ ), and embayment  $\times$  year ( $F = 5.4$ ,  $p < 0.001$ ). A 1-way ANOVA comparing annual recruit-

ment for OH, HB, NW, and SB combined (Table 2a) was highly significant ( $F = 80.89$ ,  $p < 0.001$ ). Overall larval recruitment was 11- to 32-fold higher by 2010, compared to 2005–2006, for embayments sampled for 6 yr (Table 2b).

Within embayments, there was more variability in annual recruitment among sites in OH than in HB or NW (Figs. 2 to 4). Larval recruitment increased at sites exhibiting the entire spectrum of benthic habitats encountered within the Peconic Bays—including mud (OH: central Orient; HB: Narrow River), muddy sand with *Crepidula fornicata* barrens (OH: outside Long Beach; NW: inshore Cedar Point), sand (multiple sites in all 3 embayments), and eelgrass (OH: Hay Beach) (see Supplement 1).

Temporal peaks in proportions of spat collected within respective years were fairly similar for OH, NW, SB, and HN (Figs. 5 & 6) even while patterns differed between years. For these 4 sites, 1 major recruitment peak, and 1 or more minor ones, were seen in all years but 2005. The highest annual proportions of spat were collected during October in 2005 (OH, NW, SB), 2007 (SB, HN), and 2008 (OH, SB, HN) and during mid-July to early August in 2006 (OH, NW, SB), 2009, and 2010 (all 4 sites above). Patterns of recruitment in HB paralleled those of adjacent OH in 2007, 2009, and 2010, but in other years differed with respect to timing of peak settlement (2005), number of recruitment peaks (only 1 in 2008), or relative proportions of spat recorded during settlement peaks (2006, 2008).

Table 2. *Argopecten irradians irradians*. Annual larval recruitment of bay scallops in different embayments within the Peconic bay system, Long Island, New York, from 2005 to 2010. (a) Holm-Sidak multiple comparisons of annual recruitment ( $\log_{10}$  transformed) for Orient Harbor (OH), Hallock Bay (HB), Northwest Harbor (NW), and Southold Bay (SB) sites combined, following a 1-way ANOVA ( $F = 80.89$ ;  $p < 0.001$ ). Years with different letters in (a) are significantly different ( $p < 0.05$ ). (b) Mean annual larval recruitment and percent change from the 2 yr prior to initiation of intensive restoration in OH (2005 to 2006) compared to each of the 4 yr of restoration (2007 to 2010). Holm-Sidak multiple comparisons of mean annual larval recruitment ( $\log_{10}$  transformed) within embayments, for those that had multiple sampling sites, following a 2-way ANOVA ( $F = 20.08$  for embayments;  $F = 140.77$  for years;  $p < 0.001$ ). Years with different letters in (a,b) are significantly different ( $p < 0.05$ )

<b>(a) Multiple comparisons of mean annual larval recruitment (no. of spats <math>\text{bag}^{-1} \text{d}^{-1}</math>)</b>										
Embayment	2005	2006	2007	2008	2009	2010				
OH, HB, NW, SB	B	A	A	C	D	E				
<b>(b) Mean annual larval recruitment (no. of spats <math>\text{bag}^{-1} \text{d}^{-1}</math>) and comparisons</b>										
Embayment	2005	2006	2007	2008	2009	2010	<b>% change in mean larval recruitment from 2005–2006 to:</b>			
							2007	2008	2009	2010
Orient Harbor	3.10, B	1.56, A	3.27, B	14.06, C	44.24, D	77.78, D	40	504	1799	3239
Hallock Bay	7.70, C	2.79, B	0.64, A	8.14, C	20.01, D	84.90, E	–88	55	282	1519
NW Harbor	2.08, BC	0.50, A	1.24, B	4.19, C	23.52, D	29.29, D	–4	225	1724	2172
Southold Bay	10.36	3.41	14.19	41.25	99.39	89.36	106	499	1344	1198
Hog Neck Bay	–	–	30.55	71.27	194.68	117.95				

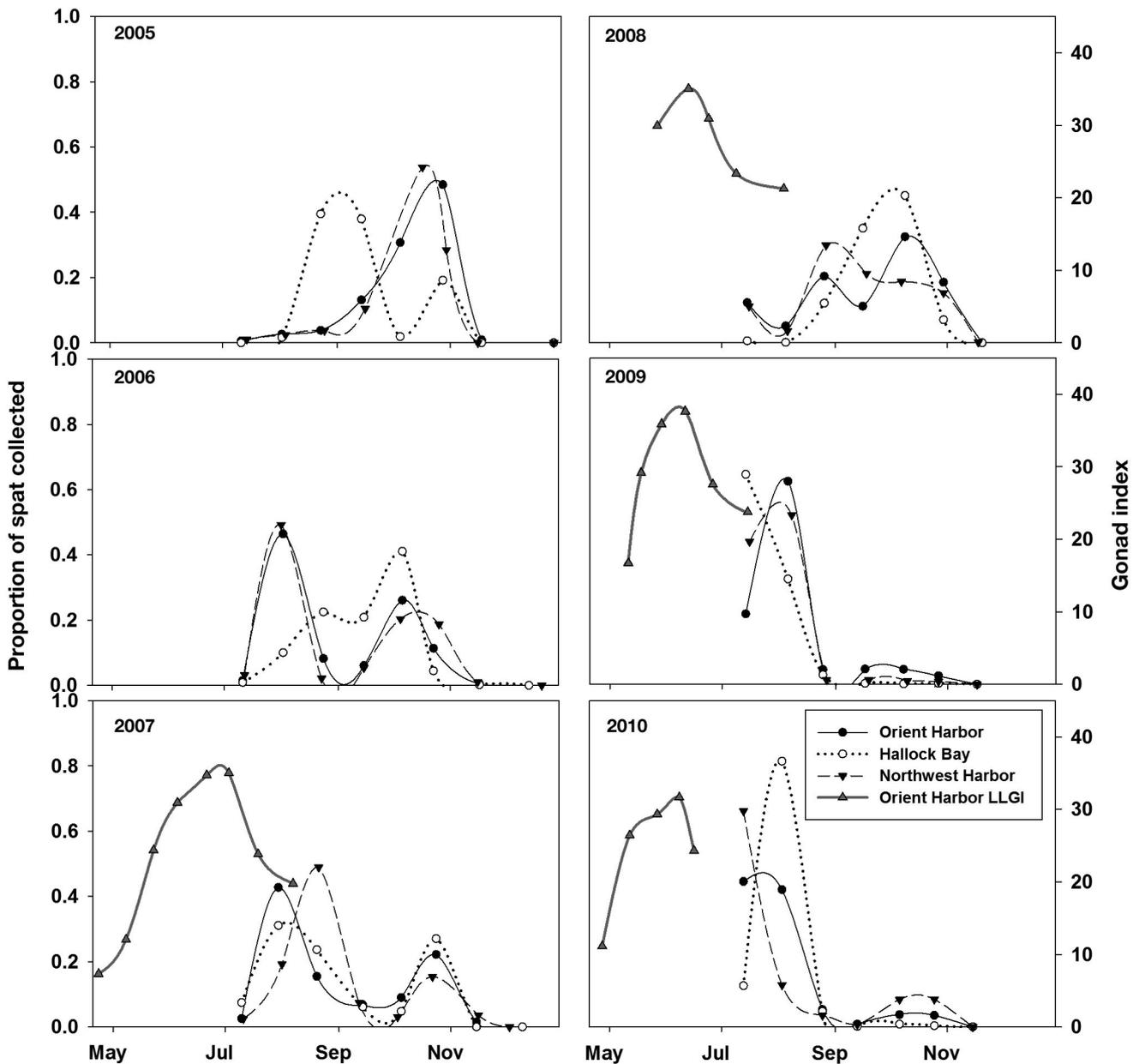


Fig. 5. *Argopecten irradians irradians*. Temporal peaks in proportions of bay scallop spat collected within respective years (2005 to 2010) in Orient Harbor, Hallock Bay, and Northwest Harbor, and mean values for gonad index of scallops held in nets (LLGI) at the Orient Harbor spawner sanctuary

**Temporal differences in adult scallop reproductive condition**

Maximum median gonadal index (MMGI) of OH scallops varied significantly (Kruskal-Wallis  $H = 26.91$ ,  $p < 0.001$ ) during the 4 yr period from 2007 to 2010 (Table 3). MMGI in 2009 (41.26) was significantly higher ( $p < 0.05$ ) in Dunn's multiple comparisons tests than MMGI in 2010 (32.73) and 2007 (36.30). MMGI in 2008 (37.71) was significantly

higher than that in 2010, but not different from those in other years.

**Estimated dates of peak spawning versus dates of peak recruitment**

Initial peak spawning events in OH from 2007 to 2010 (Table 4, Figs. 5 & 6) occurred as early as 8 to 16 June (2010) until as late as 15 to 17 July

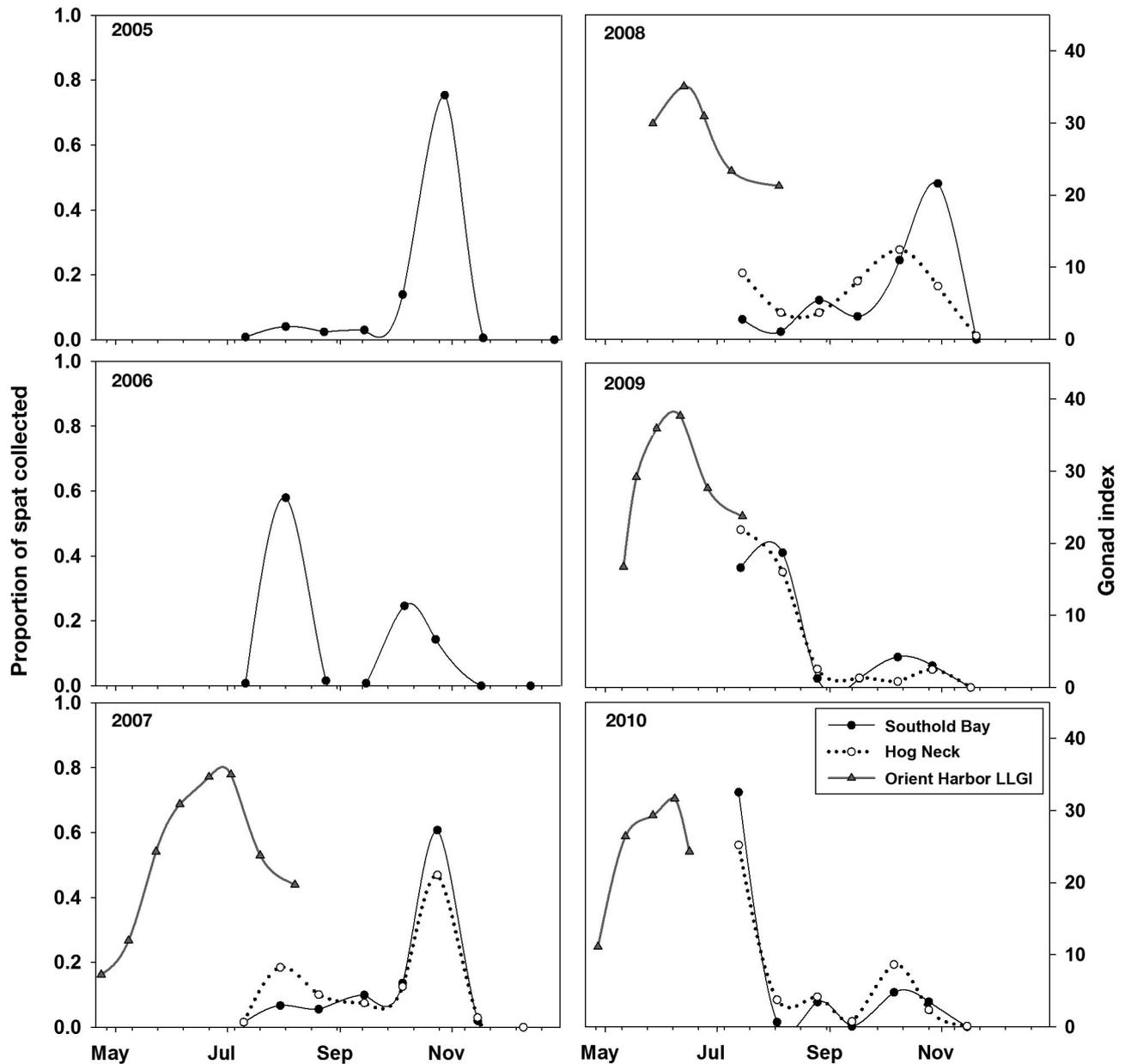


Fig. 6. *Argopecten irradians irradians*. Temporal peaks in proportions of bay scallop spat collected within respective years (2005 to 2010) in Southold Bay and Hog Neck Bay, and mean values for gonad index of scallops held in nets (LLGI) at the Orient Harbor spawner sanctuary

(2008); respective water temperatures were 18.7 to 21.3°C and 23.3 to 26.1°C. Initial peaks of larval settlement in OH, as estimated by forward calculation of 2 wk, thus ranged from 22–30 June 2010 to 29–31 July 2008. Peak settlement periods in 2007, 2008, and 2010 were congruent with dates estimated via back-calculation from OH spat collector size–frequency data (Table 4, Fig. 5); in 2009, the

2 estimation methods yielded dates that were roughly 2 wk apart. The initial peak of larval settlement in NW and SB was very close to that in OH in 2008 to 2010. Initial peak recruitment dates for HB and OH only closely corresponded in 2007 (Table 4, Fig. 5). In 3 of the 4 yr of sampling, larval recruitment in HN occurred earlier than at the other 4 sites (Table 4).

**Relationship of environmental parameters to temporal trends in larval recruitment**

None of the seasonal means of key environmental factors (Fig. 7A to E) differed between the pre-restoration (1996 to 2006) and intensive OH restoration

(2007 to 2010) periods: water temperature ( $p = 0.679$ ), total chlorophyll *a* ( $p = 0.822$ ), total particulate nitrogen ( $p = 0.897$ ), rainfall ( $p = 0.986$ ), and salinity ( $p = 0.671$ ). None of the interaction terms in the model were significant ( $p > 0.05$ ).

Table 3. *Argopecten irradians irradians*. Dunn's multiple comparisons tests for annual maximum median gonadal index (MMGI) of scallops held in lantern nets at the Orient Harbor spawner sanctuary, from 2007 to 2010, following a Kruskal-Wallis 1-way ANOVA on ranks ( $H = 26.91$ ,  $p < 0.001$ ). Years underscored with different lines are significantly different ( $p < 0.05$ )

Year	2009	2008	2007	2010
MMGI	41.26	37.71	36.30	32.73

One-way ANOVAs of wind data at respective times of initial peak larval settlement showed that the easterly wind component ( $p = 0.434$ ) and average wind stress ( $p = 0.672$ ) did not differ during pre-restoration (2005 to 2006) and OH restoration (2007 to 2010) years; the average **u** vector (E + W) component was different ( $p = 0.018$ ), with a greater westerly wind component in 2005 to 2006 versus 2007 to 2010. Linear regressions of the mean number of spats per bag that resulted from these peak settlement events in OH, NW, and SB during the 2 time periods, versus corresponding wind data, were all non-significant: easterly wind component ( $R^2 = 0.009$ ,  $p = 0.708$ ), **u** vector ( $R^2 = 0.073$ ,  $p = 0.277$ ), and wind stress ( $R^2 = 0.105$ ,  $p = 0.191$ ).

Table 4. *Argopecten irradians irradians*. Estimated dates of initial peak spawning of adult bay scallops in Orient Harbor (OH) and first peak of larval settlement in OH, Hallock Bay (HB), Northwest Harbor (NW), Southold Bay (SB), and Hog Neck Bay (HN), New York, from 2007 to 2010. Spawning periods were determined via analysis of temporal trends in gonadal index, and pinpointed through inspection of continually recorded water temperature and published wind speed data (see 'Material and methods'). Times of first (or only) peak larval settlement were determined via: (a) forward calculation from initial peak spawning dates, assuming a 2 wk larval period and (b) back-calculation using size data for juvenile scallops in spat collectors and a published shell growth rate of 8 to 12 mm mo<sup>-1</sup> for small juveniles

Year	Estimated peak of initial spawning	(a) Estimated 1st peak of larval settlement	(b) Estimated 1st peak of larval settlement
2007	OH: 26–27 Jun	OH: 10–11 Jul	OH: 9–12 Jul HB: 12–15 Jul NW: 27–31 Jul SB: 7–13 Aug HN: 28 Jun–9 Jul
2008	OH: 15–17 Jul	OH: 29–31 Jul	OH: 28 Jul–2 Aug HB: 29 Sep–1 Oct NW: 28 Jul–2 Aug SB: 26–31 Jul HN: 26–30 Jun
2009	OH: 15–17 Jun	OH: 29 Jun–1 Jul	OH: 16–17 Jul HB: 6–7 Jul NW: 16–17 Jul SB: 12–15 Jul HN: 6–8 Jul
2010	OH: 8–16 Jun	OH: 22–30 Jun	OH: 1–3 Jul HB: 20–22 Jul NW: 28 Jun–1 Jul SB: 28–30 Jun HN: 21–25 Jun

**Relationship of larval recruitment to stock size of spawning adult scallops**

Linear regressions of larval recruitment (mean number of spats bag<sup>-1</sup> yr<sup>-1</sup>) versus TFEP (Fig. 8) were highly significant for OH ( $F = 26.34$ ,  $R^2 = 0.868$ ,  $p = 0.007$ ) and HB ( $F = 66.54$ ,  $R^2 = 0.943$ ,  $p = 0.001$ ), but not for NW ( $F = 4.83$ ,  $R^2 = 0.547$ ,  $p = 0.093$ ) or SB ( $F = 0.02$ ,  $R^2 = 0.008$ ,  $p = 0.886$ ). Slopes of regression lines for the different embayments varied widely. For the SB data, polynomial regression [larval recruitment =  $-39.875 + (0.176 \times \text{TFEP}) - (0.0000411 \times \text{TFEP}^2)$ ] improved the fit of the overall model ( $F = 4.22$ ,  $R^2 = 0.809$ ,  $p = 0.176$ ), but this was not the case for the other 3 embayments. Percent contributions of planted scallops to TFEP (Table 1) highlight the importance of our restoration efforts: in OH these were 52.6, 21.8, and 24.7% in 2007, 2008, and 2009, respectively; in HB, 56.9, 60.7, and 82.5% in 2006, 2009, and 2010, respectively; and in NW, 30.0 and 43.3% in 2005 and 2006, respectively.

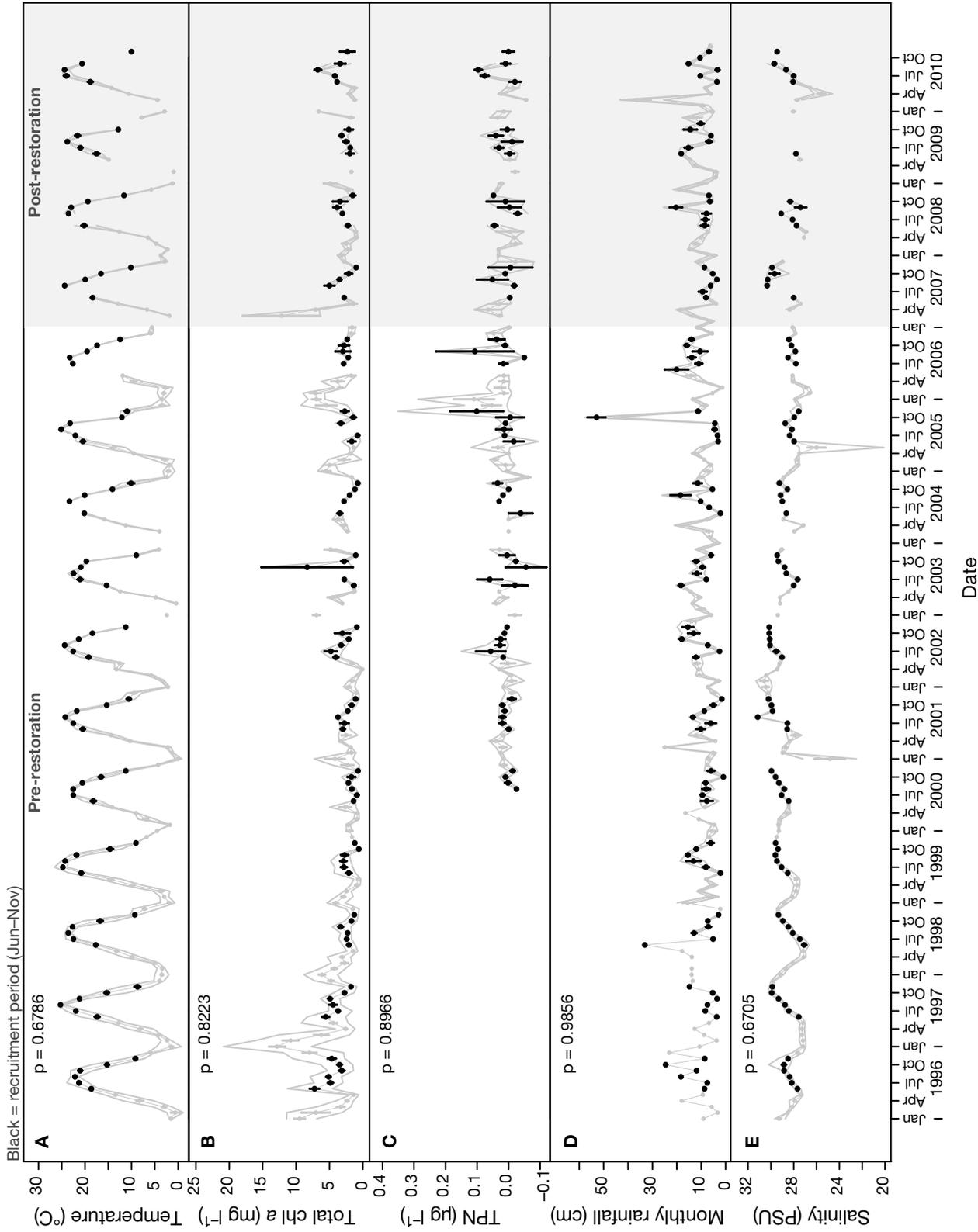


Fig. 7. *Argopecten irradians irradians*. Time-series plots of environmental factors (A: water temperature, B: total chlorophyll *a*, C: total particulate nitrogen [TPN], D: monthly rainfall, E: salinity) that may have affected bay scallop larval survival/growth, and hence larval recruitment, from 1996 to 2006 (before intensive restoration in Orient Harbor; unshaded) and 2007 to 2010 (restoration period; shaded). For individual plots, upper and lower solid lines (when  $n > 3$ ) indicate minimum and maximum values; data points are shown for the recruitment period (June to November); points with error bars = means  $\pm$  1 SE; p-values indicate whether seasonal means (e.g. summer: June to August) of respective parameters differed between the pre-restoration and restoration periods

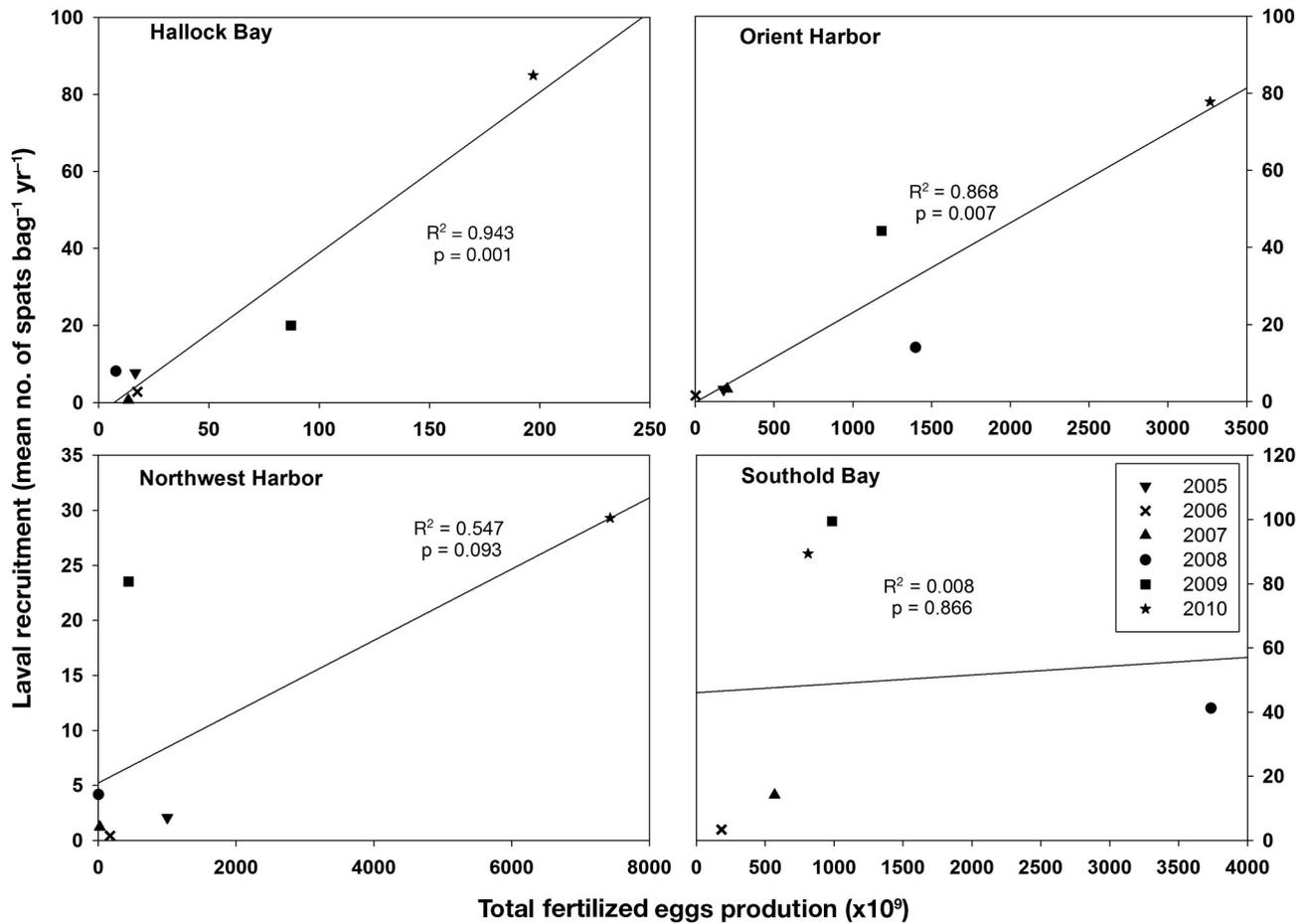


Fig. 8. *Argopecten irradians irradians*. Linear regressions of scallop larval recruitment versus total fertilized egg production (TFEP), for the 2005 to 2010 sampling period, for 4 embayments in eastern Long Island, New York. Hallock Bay:  $y = -2.91 + 0.417x$ ; Orient Harbor:  $y = -0.199 + 0.0233x$ ; Northwest Harbor:  $y = 5.245 + 0.00324x$ ; Southold Bay:  $y = 46.077 + 0.00274x$

## DISCUSSION

### Spatial and temporal differences in scallop larval recruitment

The dramatic increases (11- to 32-fold) in Peconic bay scallop *Argopecten irradians irradians* larval recruitment in the 4 yr following initiation of our intensive OH restoration efforts represent one of the highest documented examples of molluscan restoration (Arnold et al. 1998) and confirmed that New York bay scallop populations were recruitment limited. The possibility exists that recruitment to our 0.75 mm mesh spat collectors included post-set transported by byssal drifting (Sigurdsson et al. 1976, Newell et al. 2010) or bedload transport (Hunt et al. 2009), but these processes probably did not contribute signifi-

cantly to numbers of spat collected because (1) byssal drifting by bivalves primarily occurs at 0.9 to 2 mm (Newell et al. 2010) and (2) if bedload transport had been important, spat bags deployed at 0.5 m above the bottom might be expected to show higher recruitment than those at 1.0 m above the bottom (numbers were equal). Larval recruitment may vary dramatically in natural populations of bivalve mollusks (e.g. Loosanoff & Nomejko 1956, Young et al. 1998), and, in our study, patterns of recruitment differed in various embayments with different planting histories, population densities at the start of restoration efforts, and connectivity. A fair question to ask is to what extent was the dramatic resurgence in larval recruitment throughout the Peconic Bays due to natural repopulation, coincidental changes in environmental conditions, allochthonous larval supply, or our intensive restoration efforts?

In Orient Harbor (OH), where we have our most complete data set, increases in larval recruitment likely were driven by a largely self-seeding population (Arnold et al. 1998) that was significantly augmented by scallops first planted here in fall 2006—as reflected in a marked increase in larval recruitment in 2007, relative to 2005–2006. Annual larval recruitment correlated very well with TFEP, and seasonal peaks in recruitment aligned in 3 of 4 yr with pinpointed spawning dates in OH. These results reinforce the conclusions of Siddall et al. (1986) that a high proportion of spawned bay scallop larvae are likely to settle in OH (see Supplement 2).

In Hallock Bay (HB), larval recruitment correlated very well with TFEP. This trend was largely driven by dramatic increases in TFEP in 2009 and 2010 that resulted from more successful plantings in 2008 and 2009; these yielded higher numbers and densities of spawning adults than in 2005 and 2007. Warren (2007) released LaGrangian drifters from within HB, on an ebbing tide, and found a small eddy just outside the mouth that may promote retention of larvae produced within HB. These results suggest that HB also may be a self-seeding system.

In Northwest Harbor (NW), recruitment from 2005 to 2010 did not correlate significantly with TFEP, despite high contributions from spawns of scallops planted in 2005 and 2006. We concluded that most larvae were exported from the embayment in these 2 yr (Tettelbach et al. 2011)—probably to Gardiners Bay (but not to as far away as OH). Some larvae may have been exported to SB (Siddall et al. 1986) and enhanced the relatively higher recruitment levels there in 2005 and 2006. TFEP in NW was low in 2009, suggesting that high recruitment was driven by larvae imported from elsewhere—perhaps Gardiners Bay or OH. Higher natural population densities/numbers in 2010 contributed to the dramatic increase in TFEP and larval recruitment.

Higher recruitment levels in Southold Bay (SB), at least in 2005 to 2006, were likely driven by higher natural population densities/sizes and higher resultant fertilization success (Tettelbach & Smith 2009), but SB also may have received larvae resulting from spawns of scallops planted in OH and NW (Siddall et al. 1986)—whose densities were 2 orders of magnitude higher than those of the natural SB population. SB does not appear to export a high proportion of larvae to OH, HB, or NW (Siddall et al. 1986); thus, SB populations do not appear to have driven increases in recruitment in these other embayments between 2007 and 2010. The poor correlation of larval recruitment versus TFEP in SB is mostly due to 1 yr (2008)—

when recorded density at our single sampling site probably overestimated actual levels. If this year is omitted, the regression ( $y = -32.226 + 0.132x$ ) yields a better fit ( $R^2 = 0.844$ ,  $p = 0.081$ ).

Hog Neck Bay (HN) exhibited the highest observed levels of mean larval recruitment and probably represents a scenario similar to that of SB, but because we did not sample here until 2007 we cannot know how much recruitment increased relative to 2005–2006. Siddall et al. (1986) modeled a site close to our HN site, and found high larval retention. So, the HN site is not likely to have driven increases in the recruitment observed in OH, HB, or NW. Furthermore, differences in the timing of initial peak larval settlement in HN compared to other embayments, which probably reflect differences in spawning times of nearby populations (Bricelj et al. 1987), suggest that larval sources were different.

Flanders Bay (FB), where we did scallop plantings from 2007 to 2009 but did not deploy spat collectors, is a highly entrained system (Hardy 1976) which would be very unlikely to contribute directly to larval recruitment at our monitoring sites in the eastern Peconic Bays. However, export of larvae from FB is possible (Siddall et al. 1986). Such incidences of export may have led to population increases in the western Peconic Bays that subsequently could have augmented spat numbers at HN.

To summarize, based on available data, it appears that scallop populations in OH, HB, and HN may largely be self-seeding. OH also may export larvae to both SB and NW, but larval import to OH from these other embayments (including HN) seems less likely—even while the timing of spawning in relation to tidal stage (Siddall et al. 1986, Young et al. 1998) and short-term wind patterns (discussed below) may affect larval advection processes. It is safe to assume that Peconic bay scallops comprise a metapopulation, but our conclusions about larval dispersal are tentative given limited knowledge of local hydrodynamics (Gilg & Hilbish 2003), and definitions of larval 'sources' and 'sinks' should be done on the basis of habitat rather than larval origin or destination (Lipcius et al. 2008). While many studies have examined effects of pelagic larval duration (PLD) on genetic connectivity between marine populations, most show a poor correlation (Weersing & Toonen 2009). We did not directly examine genetic connectivity, but we began rearing and planting an uncommon color morph in 2007 to track the contribution of our planted stock to benthic recruitment; by 2010, prevalence of this color morph in wild Peconic bay scallop populations was substantially higher than

prior to plantings (Tettelbach et al. 2012). This suggests that, in addition to self-seeding in OH, larvae from our primary spawner sanctuary are also being exported considerable distances (>10 km) and contributing to population increases in other areas within the Peconic ecosystem.

#### Possible drivers of increased recruitment following restoration

Increased larval recruitment following initiation of restoration efforts in OH was not driven by a concomitant increase in fecundity of adult scallops in our spawner sanctuary. While MMGI increased from 2007 to 2009, the lowest MMGI value was seen in 2010—when the highest larval recruitment occurred. There is no evidence for increasing fecundity in Peconic bay scallops: MMGI in 2007 to 2010 was approximately equal to that in 1994 (MMGI = 35.2 to 44.5; Tettelbach et al. 2002) and in 1984 (MMGI = 37; Bricelj et al. 1987). While *Macoma balthica* in the Dutch Wadden Sea produced more eggs following winters with lower temperatures (Honkoop & Van der Meer 1997) and scallops often show increased reproductive output in years when temperatures are elevated during the ripening period (MacDonald & Thompson 1985, Wolff 1988, Shephard et al. 2010), we saw no differences in respective seasonal temperatures in the years before and after initiation of intensive restoration efforts. Similarly, coincidental environmental factors (temperature, total chlorophyll *a*, total particulate N, rainfall, salinity) that might affect egg or larval survival/growth (Wolff 1987, Morita et al. 2006, Shephard et al. 2010) were not different in the 2 periods.

Short-term variations in wind intensity and direction just prior to larval settlement are known to significantly affect recruitment patterns (Eggleston & Armstrong 1995, Bertness et al. 1996). We recognize the limitations of wind data available to us, i.e. they were not taken at the exact locations of our spat collectors and specific effects of wind intensity and direction on dynamics of larval settlement in the Peconic Bays are unknown; nevertheless, 5 of 6 analyses suggested that trends in wind direction/magnitude at times of estimated peak settlement did not contribute to the dramatic differences in scallop recruitment during pre-restoration and intensive OH restoration periods.

Reduced abundance of planktonic predators from 2007 to 2010 might have permitted higher rates of larval scallop survival, compared to earlier years;

however, McNamara et al. (2010) reported that abundance of the ctenophore *Mnemiopsis leidyi* (an important predator of bivalve larvae) was 2- to 3-fold higher in the Peconic Bays in 2006 compared to 1978–1979. These authors also observed that peak abundance of *M. leidyi* in the Peconic Bays occurred in late June/early July 2006, compared to previously reported peak abundance in mid-October 1978. These trends are consistent with those reported elsewhere in the northeastern United States (Sullivan et al. 2001). Thus, there is no evidence for a temporal match–mismatch with planktonic predators (Strasser & Gunther 2001) that might have prompted higher larval scallop survival following the start of restoration efforts. While benthic meiofauna and macrofaunal predators may contribute to substantial mortality of post-set bivalves (Hunt & Scheibling 1997, Goselin & Qian 1997, Newell et al. 2000) these should not have affected survival of scallop recruits in our above-bottom 0.75 mm mesh spat collectors (Arnold et al. 1998).

Another potential explanation for increased scallop recruitment between 2007 and 2010 is the contribution of allochthonous larvae. With a larval period of up to 2 wk (Belding 1910), bay scallops may be advected considerable distances (Menge et al. 2009). Arnold et al. (1998) concluded that bay scallop larvae may be periodically transported >30 km within the west Florida metapopulation. Campanella et al. (2007) concluded that scallop recruitment in New Jersey in 2004 to 2005 resulted from import of larvae from Long Island, New York (>100 km to the NE); although, this was viewed as a rare event. Currents offshore (~11 km) of Long Island, New York, predominantly run NE to SW (Townsend et al. 2006), at velocities of ~20 cm s<sup>-1</sup> (Scott & Csanady 1976), so it is highly unlikely for larvae to be advected eastward from populations in south shore bays of Long Island (Shinnecock, Moriches, Great South) into the Peconic Bays. The Shinnecock Canal connects Shinnecock Bay to the Peconic Bays, but locks only permit flow to the south. More plausible sources of allochthonous larval transport to the Peconic Bays are from states to the NE. Populations in Connecticut and Rhode Island have been very low for decades, as evidenced by the lack of commercial landings since 1993 and 1996, respectively (NOAA Fisheries 2011), and thus are unlikely candidates. Recent restoration efforts in Rhode Island coastal ponds have contributed to increases in local larval recruitment; however, spawning peaks were different from those in our study (B. Hancock & B. DeAngelis unpubl. data). Bay scallop populations in Massachusetts, particularly on

Martha's Vineyard and Nantucket (which are ~120 and 175 km, respectively, from OH) are robust and support significant commercial harvests (NOAA Fisheries 2011); however, very low scallop landings in the Peconic Bays from 1996 to 2007 (NYSDEC 2011) suggest there was no significant allochthonous infusion of larvae from Massachusetts during this period.

Calculated values of TFEP for OH and HB confirm the important contribution of our restoration efforts to overall larval supply, with the latter increasing markedly by 2009 and 2010; significant linear regressions of recruitment versus TFEP for OH and HB illustrate the contribution of increasing spawner densities and population sizes to recruitment in the years following commencement of intensive restoration efforts. The latter is also apparent for NW and SB, even though correlation of recruitment and TFEP was not as high. Differences in regression line slopes for the different embayments may reflect differential larval retention (as discussed above); there is no basis for speculating that differential survival of zygotes occurred.

Orensanz et al. (2006) concluded that species exhibiting high annual and spatial variability in recruitment, like most scallops, are likely to exhibit recruitment limitation; however, that variability may constrain our ability to statistically demonstrate the phenomenon. The dramatic increase in recruitment following initiation of our restoration efforts suggests that recruitment limitation, due to low population sizes/densities (Peterson & Summerson 1992, Liermann & Hilborn 2001), was the underlying reason for the inability of scallop populations to rebuild on their own after the 1995 brown tide. This parallels the scenario described by Peterson et al. (1996) in which bay scallop populations did not recover during the 4 yr following severe impacts of red tide *Ptychodiscus* (= *Karenia*) *brevis*, but increased benthic recruitment (up to 735%) occurred following restoration efforts to increase adult population sizes/densities. Caley et al. (1996) noted that measures of average densities may underestimate those experienced by spawning adults, because of possible aggregative behavior, but it is clear from our population surveys that adult densities were extremely low ( $<0.1 \text{ m}^{-2}$ ) throughout most of the Peconic Bays in 2005 to 2006 (Tettelbach & Smith 2009), in NW from 2000 to 2004 (S. Tettelbach unpubl. data), and presumably in most of the Peconic system from 1996 to 2004 (based on commercial landings data; NYSDEC 2011).

By planting several million scallops, at high densities, we jump-started the process of larval recruit-

ment by increasing fertilization success and larval supply. Significant increases in natural population sizes and recruitment were not immediately apparent, but the size of the larval pool increased further as we continued and expanded our restoration efforts; then, natural populations began to rebuild throughout the Peconic Bays within a few years (Tettelbach & Smith 2009, present study). Arnold et al. (1998) similarly observed increases in peak recruitment, of 1 to 2 orders of magnitude, at sites with higher adult bay scallop densities in Florida. They concluded, as did Peterson & Summerson (1992) and Orensanz et al. (2006), and as we have shown, that the magnitude of scallop recruitment usually reflects patterns of adult abundance. Our NW plantings in 2005 and 2006 did not contribute directly to higher recruitment there but probably augmented populations elsewhere in the Peconic system—illustrating that benefits of restoration may not be obvious if larvae are exported beyond the monitoring area.

Evidence is mounting (see also Orensanz et al. 2006, Juinio-Meñez et al. 2008, Powers et al. 2009) that recruitment limitation may be addressed within a management context by restoration programs, provided that the scale, methods of broodstock deployment, and location are appropriate (Lenihan & Peterson 1998, Caddy & DeFeo 2003). Furthermore, restoration over multiple years may be necessary to rebuild natural populations to levels well above those being planted; this may be true, in general, for restoration programs. High adult densities at the time of spawning are a key to restoration efforts for bay scallops (Peterson et al. 1996, Tettelbach et al. 2011) and other bivalve mollusks. The Lundquist & Botsford (2004) model suggests that, under appropriate hydrographic conditions, elevation of densities of spawning adults to  $\geq 2 \text{ ind. m}^{-2}$  can ensure almost complete fertilization success. Thus, spawner sanctuaries, whether stocked with transplanted natural or hatchery-reared animals, can serve as 'larval pumps' that increase the supply of larvae—much as marine reserves may do (Stoner & Ray 1996, Beukers-Stewart et al. 2005, Almany et al. 2007). As bay scallop populations have experienced significant declines in much of their historical range (MacKenzie 2008), and self-seeding may be necessary for year-to-year maintenance of discrete populations (Arnold et al. 1998), it is likely that sustained restoration efforts (Uki 2006) will be an important tool for buffering this semelparous species from the catastrophic impacts of episodic events and for increasing natural population densities/sizes to threshold levels above which they may become self-sustaining.

**Acknowledgements.** We gratefully acknowledge funding from the Suffolk County (New York) Water Quality Protection and Restoration Program and the Coastal Management Program of the New York State Dept. of State. Our bay scallop restoration project has benefitted from the dedication of dozens of individuals from Long Island University, Cornell Cooperative Extension of Suffolk County, Stony Brook-Southampton, the Southold Project for Aquaculture Training, and numerous interns and volunteers. In particular, we thank M. Patricio, K. Cahill, J. Chagnon, J. Clauss, K. Tetrault, G. Rivara, and N. Stark. We also appreciate the assistance of R. Langan, University of New Hampshire, and R. Taylor, Taylor Seafood of Fairhaven (Massachusetts), as well as the insightful comments of the reviewers.

#### LITERATURE CITED

- Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science* 316:742–744
- Ambrose WG Jr, Peterson CH, Summerson HC, Lin J (1992) Experimental tests of factors affecting recruitment of bay scallops (*Argopecten irradians*) to spat collectors. *Aquaculture* 108:67–86
- Arnold WS, Marelli DC, Bray CP, Harrison MH (1998) Recruitment of bay scallops *Argopecten irradians* in Floridian Gulf of Mexico waters: scales of coherence. *Mar Ecol Prog Ser* 170:143–157
- 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 techniques and the growth, mortality and reproductive development of planted scallops. *J Shellfish Res* 24:883–904
- Barber BJ, Blake NJ (2006) Reproductive physiology. In: Shumway SE, Parsons GJ (eds) *Scallops: biology, ecology and aquaculture*, 2nd edn. Elsevier, New York, NY, p 357–416
- Bayne BL, Holland DL, Moore MN, Lowe DM, Widdows J (1978) Further studies on the effects of stress in the adult on the eggs of *Mytilus edulis*. *J Mar Biol Assoc UK* 58: 825–841
- Belding DL (1910) The scallop fishery of Massachusetts, including an account of the natural history of the common scallop. Marine Fisheries Series No. 3, Division of Fisheries and Game, Department of Conservation, Commonwealth of Massachusetts, Boston, MA
- Bertness MD, Gaines SD, Wahle RA (1996) Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Mar Ecol Prog Ser* 137:103–110
- Beukers-Stewart BD, Vause BJ, Mosley MWJ, Rossetti HL, Brand AR (2005) Benefits of closed area protection for a population of scallops. *Mar Ecol Prog Ser* 298:189–204
- Boero F (1996) Episodic events: their relevance to ecology and evolution. *PSZN I: Mar Ecol* 17:237–250
- 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
- Caddy JF, DeFeo O (2003) Enhancing or restoring the productivity of natural populations of shellfish and other marine invertebrate resources. *FAO Fisheries Technical Paper* 448, FAO, Rome
- Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. *Annu Rev Ecol Syst* 27: 477–500
- Campanella JJ, Bologna PAX, Kim LEJ, Smalley JV (2007) Molecular genetic evidence suggests Long Island as the geographic origin for the present population of bay scallops in Barnegat Bay, New Jersey. *J Shellfish Res* 26: 303–306
- Chavez FP, Ryan J, Lluch-Cota SE, Niquen M (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299:217–221
- Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J Exp Mar Biol Ecol* 93:11–43
- Connolly SR, Menge BA, Roughgarden J (2001) A latitudinal gradient in recruitment of intertidal invertebrates in the Northeast Pacific Ocean. *Ecology* 82:1799–1813
- Cosper EM, Dennison WC, Carpenter EJ, Bricelj VM and others (1987) Recurrent and persistent brown tide blooms perturb coastal marine ecosystem. *Estuaries* 10: 284–290
- Cragg SM (2006) Development, physiology, behaviour and ecology of scallop larvae. In: Shumway SE, Parsons GJ (eds) *Scallops: biology, ecology and aquaculture*, 2nd edn. Elsevier, New York, NY, p 45–122
- Dickie LM (1955) Fluctuations in abundance of the giant scallop, *Placopecten magellanicus* (Gmelin), in the Digby area of the Bay of Fundy. *J Fish Res Board Can* 12: 797–856
- Doherty PJ (1981) Coral reef fishes: recruitment-limited assemblages? *Proc 4th Int Coral Reef Symp* 2:465–470
- 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
- Eggleston DB, Armstrong DA (1995) Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. *Ecol Monogr* 65:193–216
- Gaines SD, Bertness M (1993) The dynamics of juvenile dispersal: why field ecologists must integrate. *Ecology* 74: 2430–2435
- Gaines S, Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc Natl Acad Sci USA* 82:3707–3711
- Gaines S, Brown S, Roughgarden J (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67:267–272
- 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
- Gilg MR, Hilbish TJ (2003) The geography of marine larval dispersal: coupling genetics with fine-scale physical oceanography. *Ecology* 84:2989–2998
- Goldberg R, Pereira J, Clark P (2000) Strategies for enhancement of natural bay scallop, *Argopecten irradians irradians*, populations: a case study in the Niantic River estuary, Connecticut, USA. *Aquac Int* 8:139–158
- Gosselin LA, Qian PY (1997) Juvenile mortality in benthic marine invertebrates. *Mar Ecol Prog Ser* 146:265–282
- Guisande C, Ulla A, Thejll P (2004) Solar activity governs abundance of Atlantic Iberian sardine *Sardina pilchardus*. *Mar Ecol Prog Ser* 269:297–301

- Hardy CD (1976) A preliminary description of the Peconic Bay estuary. Special Report 3, Reference 76-4, Marine Science Research Center, State University New York, New York, NY
- Harvey M, Bourget E, Legault C, Ingram RG (1995) Short-term variations in settlement and early spat mortality of Iceland scallop, *Chlamys islandica* (O.F. Müller). *J Exp Mar Biol Ecol* 194:167–187
- Honkoop PJC, van der Meer J (1997) Reproductive output of *Macoma balthica* populations in relation to winter-temperature and intertidal-height mediated changes of body mass. *Mar Ecol Prog Ser* 149:155–162
- Hughes TP, Baird AH, Dinsdale EA, Moltschanivskyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology* 81: 2241–2249
- Hunt HL, Scheibling RE (1997) Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Mar Ecol Prog Ser* 155:269–301
- Hunt HL, Fugate DC, Chant RJ (2009) Modeling bedload transport of juvenile bivalves: predicted changes in distribution and scale of postlarval dispersal. *Estuar Coasts* 32:1090–1102
- Juinio-Meñez MA, Bango HG, Malay MC, Pastor D (2008) Enhancing the recovery of depleted *Tripneustes gratilla* stocks through grow-out culture and restocking. *Rev Fish Sci* 16:35–43
- Kraeuter JN, Buckner S, Powell EN (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
- Lenihan HS, Peterson CH (1998) How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecol Appl* 8:128–140
- Leverone JR, Geiger SP, Stephenson SP, Arnold WS (2010) Increase in bay scallop (*Argopecten irradians*) populations following releases of competent larvae in two West Florida estuaries. *J Shellfish Res* 29:395–406
- 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 Fish* 2:33–58
- Lipcius RN, Eggleston DB, Schreiber SJ, Seitz RD and others (2008) Importance of metapopulation connectivity to restocking and restoration of marine species. *Rev Fish Sci* 16:101–110
- Loosanoff VL, Nomejko CA (1956) Relative intensity of oyster setting in different years in the same areas of Long Island Sound. *Biol Bull* 111:387–392
- Lovewell MA (2010) Tribe bay scallop study shows sanctuaries can revive fishery. *Vineyard Gazette*, 2 April 2010
- Lundquist CJ, Botsford LW (2004) Model projections of the fishery implications of the Allee effect in broadcast spawners. *Ecol Appl* 14:929–941
- MacDonald BA, Thompson RJ (1985) Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. II. Reproductive output and total production. *Mar Ecol Prog Ser* 25:295–303
- 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
- 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
- McNamara ME, Lonsdale DJ, Cerrato RM (2010) Shifting abundance of the ctenophore *Mnemiopsis leidyi* and the implications for larval bivalve mortality. *Mar Biol* 157: 401–412
- Menge BA (1991) Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *J Exp Mar Biol Ecol* 148:89–100
- Menge B, Chan F, Nielsen KJ, Di Lorenzo E, Lubchenco J (2009) Climatic variation alters supply-side ecology: impact of climate patterns on phytoplankton and mussel recruitment. *Ecol Monogr* 79:379–395
- Morita K, Morita SH, Fukuwaka M (2006) Population dynamics of Japanese pink salmon (*Oncorhynchus gorbuscha*): Are recent increases explained by hatchery programs or climatic variations? *Can J Fish Aquat Sci* 63: 55–62
- Newell RE, Alspach GS Jr, Kennedy VS, Jacobs D (2000) Mortality of newly metamorphosed eastern oysters (*Crassostrea virginica*) in mesohaline Chesapeake Bay. *Mar Biol* 136:665–676
- Newell CR, Short F, Hoven H, Healey L, Panchang V, Cheng G (2010) The dispersal dynamics of juvenile plantigrade mussels (*Mytilus edulis* L.) from eelgrass (*Zostera marina*) meadows in Maine, USA. *J Exp Mar Biol Ecol* 394:45–52
- NOAA Fisheries (2011) Annual commercial landing statistics. Office of Science and Technology, NMFS Commercial Fishery Landings Data. Available at [www.st.nmfs.noaa.gov/st1/commercial/landings/annual\\_landings.html](http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html) (accessed August 2012)
- NYSDEC (New York State Department of Environmental Conservation) (2011) Annual commercial shellfish landings for New York state, 1946–2010, and rainfall records for eastern Long Island locations, 1996–2010. NYSDEC, East Setauket, NY
- Orensanz JM, Parma AM, Turk T, Valero J (2006) Dynamics, assessment and management of exploited natural populations. In: Shumway SE, Parsons GJ (eds) *Scallops: biology, ecology and aquaculture*, 2nd edn. Elsevier, New York, NY, p 765–868
- Parsons GJ, Dadswell MJ, Roff JC (1993) Influence of biofilm on settlement of sea scallop, *Placopecten magellanicus* (Gmelin, 1791), in Passamaquoddy Bay, New Brunswick, Canada. *J Shellfish Res* 12:279–283
- Peterson CH, Summerson HC (1992) Basin-scale coherence of population dynamics of an exploited marine invertebrate, the bay scallop: implications of recruitment limitation. *Mar Ecol Prog Ser* 90:257–272
- Peterson CH, Summerson HC, Luettich RA Jr (1996) Response of bay scallops to spawner transplants: a test of recruitment limitation. *Mar Ecol Prog Ser* 132:93–107
- Powers SP, Peterson CH, Grabowski JH, Lenihan HS (2009) Success of constructed oyster reefs in no-harvest sanctuaries: implications for restoration. *Mar Ecol Prog Ser* 389: 159–170
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. [www.r-project.org](http://www.r-project.org)
- Roughgarden J, Gaines SD, Possingham H (1988) Recruitment dynamics in complex life cycles. *Science* 241: 1460–1466

- SCDHS (Suffolk County Department of Health Services) (2011) Surface water quality monitoring data, 1976–2010. SCDHS, Office of Ecology, Yaphank, NY
- Scott JT, Csanady GT (1976) Nearshore currents off Long Island. *J Geophys Res* 81:5401–5409
- Shephard S, Beukers-Stewart B, Hiddink JG, Brand AR, Kaiser MJ (2010) Strengthening recruitment of exploited scallops *Pecten maximus* with ocean warming. *Mar Biol* 157:91–97
- Siddall SE, Vieira ME, Gomez-Reyes E, Pritchard DW (1986) Numerical model of larval dispersion. Special Report No. 71, Marine Science Research Center, Stony Brook, NY
- Sigurdsson JB, Titman CW, Davies PA (1976) The dispersal of young post-larval bivalve molluscs by byssus threads. *Nature* 262:386–387
- Slater J (2006) Development and application of techniques for prediction of the scallop *Pecten maximus* (L.) spatfall. *J Shellfish Res* 25:795–806
- Stoner AW, Ray M (1996) Queen conch, *Strombus gigas*, in fished and unfished locations of the Bahamas: effects of a marine fishery reserve on adults, juveniles, and larval production. *Fish Bull* 94:551–565
- Strasser M, Gunther C (2001) Larval supply of predator and prey: temporal mismatch between crabs and bivalves after a severe winter in the Wadden Sea. *J Sea Res* 46: 57–67
- Sullivan BD, Van Keuren D, Clancy M (2001) Timing and size of blooms of ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, RI. *Hydrobiologia* 451:113–120
- Summerson HC, Peterson CH (1990) Recruitment failure of the bay scallop, *Argopecten irradians concentricus*, during the first red tide, *Ptychodiscus brevis*, outbreak recorded in North Carolina. *Estuaries* 13:322–331
- Tettelbach ST (1986) Dynamics of crustacean predation on the northern bay scallop, *Argopecten irradians irradians*. PhD dissertation, University of Connecticut, Storrs, CT
- Tettelbach ST, Smith CF (2009) Bay scallop restoration in New York. *Ecol Rest* 27:20–22
- Tettelbach ST, Weinstock A (2008) Direct observation of bay scallop spawning in New York waters. *Bull Mar Sci* 28: 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 appearance of 'brown tide' algal blooms. *J Shellfish Res* 12:423–431
- Tettelbach ST, Smith CF, Smolowitz R, Tetrault K, Dumais S (1999) Evidence for fall spawning of northern bay scallops, *Argopecten irradians irradians* (Lamarck, 1819), in New York. *J Shellfish Res* 18:47–58
- 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. *Aquac Int* 10:279–296
- Tettelbach ST, Barnes D, Aldred J, Rivara G and others (2011) Utility of high density plantings in bay scallop, *Argopecten irradians irradians*, restoration. *Aquac Int* 19:715–739
- Tettelbach ST, Smith CF, Europe JR, Cahill K and others (2012) Bringing 'em back: bay scallop restoration in the Peconic Bays, Long Island, New York. *J Shellfish Res* 31: 228
- Townsend DW, Thomas AC, Mayer LM, Thomas MA, Quinlan JA (2006) Oceanography of the Northwest Atlantic continental shelf (1,W). In: Robinson AR, Brink KH (eds) *The sea*, Vol. 14. The global coastal ocean: interdisciplinary regional studies and syntheses. Harvard University Press, Cambridge, MA, p 119–168
- Turner WH (1995) 'Bags to drags', the bay scallop restoration project in the Westport River, a two-year update. *J Shellfish Res* 14:249
- Uki N (2006) Stock enhancement of the Japanese scallop *Patinopecten yessoensis* in Hokkaido. *Fish Res* 80:62–66
- Ventilla RF (1982) The scallop industry in Japan. *Adv Mar Biol* 20:309–382
- Warren J (2007) A study of the circulation of Orient Harbor and Hallock Bay, Long Island, New York. Report prepared for Cornell Cooperative Extension, Riverhead, NY
- WeatherUnderground (2011) East Hampton, New York (11937) conditions and forecast: weather [Internet]. The Weather Underground, Inc., Ann Arbor, MI. Available at [www.wunderground.com/history/airport/21N/2005/1/21/MonthlyHistory.html#calendar](http://www.wunderground.com/history/airport/21N/2005/1/21/MonthlyHistory.html#calendar) (accessed February 2012)
- Weersing K, Toonen RJ (2009) Population genetics, larval dispersal, and connectivity in marine systems. *Mar Ecol Prog Ser* 393:1–12
- Wolff M (1987) Population dynamics of the Peruvian scallop *Argopecten purpuratus* during the El Niño phenomenon of 1983. *Can J Fish Aquat Sci* 44:1684–1691
- Wolff M (1988) Spawning and recruitment in the Peruvian scallop *Argopecten purpuratus*. *Mar Ecol Prog Ser* 42: 213–217
- Young EE, Bigg GR, Grant A, Walker P, Brown J (1998) A modelling study of environmental influences on bivalve settlement in The Wash, England. *Mar Ecol Prog Ser* 172: 197–214

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Submitted: March 5, 2012; Accepted: October 11, 2012  
Proofs received from author(s): February 28, 2013