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SETTLEMENT OF THE BAY SCALLOP (*ARGOPECTEN IRRADIANS*) ALONG THE GULF COAST OF FLORIDA

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ABSTRACT Before collapsing, bay scallops (*Argopecten irradians*) supported commercial fisheries in Florida but, following decades of restoration efforts and management actions, still support a recreational fishery. Settlement was monitored along the west coast of Florida from 1992 through 2018, using collector traps. The primary environmental variables retained in the analyses included temperature, salinity, and red tide concentration (*Karenia brevis*). The settlement rate generally increased for the first days of trap deployment, then leveled off or declined. Settlement peaked when the average water temperatures were between 21°C and 23°C at four sites: St. Andrew Bay, St. Joseph Bay, West Coast, and Pine Island Sound, indicative of a fall peak in spawning. At the Tampa Bay and Sarasota Bay sites, settlement peaked when temperatures were around 16°C, indicative of winter spawning. At most sites, the highest peak in settlement occurred in association with declines in temperature of 10°C–15°C during the fall, with a smaller, secondary peak occurring with similar increases in temperature during the spring. Warming winter temperatures may already be negatively affecting the ability of the subpopulations to synchronously spawn, with unknown impacts to population dynamics. At all sites, settlement declined rapidly when salinity fell below 30 with little settlement occurring below 27, and approached zero when salinity fell below approximately 20. The occurrence of *K. brevis* exceeding 10,000 cells/L resulted in reduced settlement. In the core populations of West Coast and Steinhatchee, *K. brevis* was uncommon, and settlement resumed rapidly when blooms abated. For sites outside the core population, settlement was reduced for 2–4 y after red tides. Recovery of populations in these noncore sites probably relies on exogenous supply of larvae from the core. If blooms of *K. brevis* that penetrate the core region, as was observed in 2021, become more severe, more frequent, or have longer durations, the entire Florida scallop population could be endangered.

KEY WORDS: environmental factors, estuary, *Karenia brevis*, long-term monitoring, *Argopecten irradians*

INTRODUCTION

Bay scallops (*Argopecten irradians*) range from Nova Scotia to northern Mexico and possibly as far south as Columbia, inclusive of the northern Gulf of Mexico (Abbott, 1974), with no recent records from South Carolina, GA or eastern Florida north of Biscayne Bay. Some authors consider there to be enough variation to consider three to five subspecies (Waller 1969, Petuch 1987), but scallops found in Florida are probably a single variant (Marelli et al. 1997). Bay scallops have been harvested from Florida waters since at least the time the Weedon Island peoples occupied Okaloosa County, FL (AD 600–900) (Mikell 1992). Commercial fisheries developed as early as the 1920s (Murdock 1955), peaked in the 1950s, and had collapsed by the 1980s (Arnold 2007). In 1992, the Fish and Wildlife Research Institute (FWRI) of the Florida Fish and Wildlife Conservation Commission (FWC) initiated a Molluscan Fishery program focused on monitoring bay scallop adult density to assess the status of the stock and juvenile settlement to identify regions where stocks were insufficient to allow either recruitment to the fishery or connectivity between subpopulations (Arnold et al. 1998). Other activities included restoration directly (Arnold et al. 2005) and with partner organizations (Leverone et al. 2010) as well as directed life history studies (Greenawalt et al. 2004, Geiger et al. 2006, Bert et al. 2014).

The state monitoring program resulted in a 30-y dataset that has been useful in the tracking of the recovery of the bay scallop in Florida and increased our understanding of the life history of the species and its population structure. In Florida, bay scallops are a metapopulation with a core consisting of two large subpopulations that encompass most of the genetic diversity of the population. The core occurs nearshore in one region consisting of four coastal counties (Pinellas, Pasco, Hernando, and Citrus Counties) and a second region that includes nearshore coastal waters of Dixie and Taylor Counties. In some years, this core exports larvae to distant subpopulations in the Panhandle and Southwest Florida (Fig. 1) (Bert et al. 2014). Following the commercial fishery closure, the northern half of the core was the remnant stable population where a small recreational fishery involving snorkelers remained open to harvest. This fishery persisted for a decade and later began to grow and spread across the core in the 2000s as the scallop population increased along the coast, densities recovered, and tourism focused on developing this fishery. Recent significant increases in harvest pressure have been observed (Granneman et al. 2021), leading to concern over the ability of the stock to sustain this pressure.

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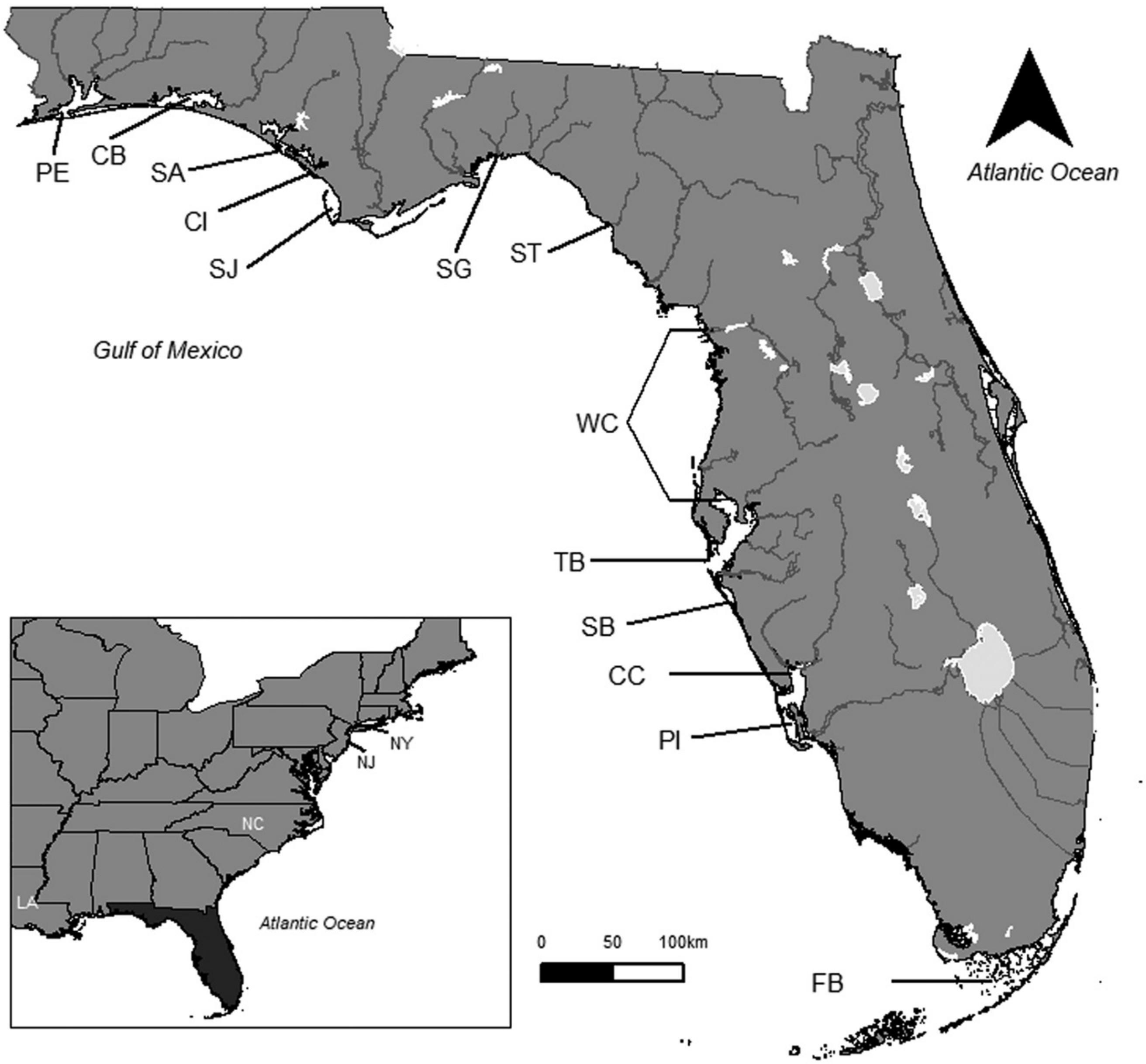

Figure 1. Study sites included Pensacola Bay (PE), Choctawhatchee Bay (CB), St. Andrew Bay (SA), Crooked Island Sound (CI), St. Joseph Bay (SJ), St. George Sound (SG), *Steinhatchee (ST), *West Coast (WC), Tampa Bay (TB, includes portions of Pinellas, Hillsborough, and Manatee Counties), Sarasota Bay (SB, includes Manatee County and Sarasota County), Charlotte County (CC), Pine Island Sound (PI), and Rabbit Key Basin in Florida Bay (FB). *ST and WC represent core populations.

One of the traditional tools of fishery management is the practice of prohibiting harvest until the stock being managed has had at least one chance to spawn. Bay scallops in Massachusetts (Belding 1910, MacFarlane 1991) and North Carolina spawn from late summer to early winter (Gutsell 1931), precluding much of the interest in recreational harvest. Reproduction in most Florida bay scallops occurs in fall when water temperatures cool (Sastry 1963, Barber & Blake 1981, 1983), but spawning was shown to also occur in winter and spring in St. Joseph Bay (SJ) (Bologna 1998). Spring settlement was later shown to occur in multiple estuaries (Geiger et al. 2006), and settlement was continuous near the Anclote River Estuary over multiple years (Geiger et al. 2010b). These observations complicate both the perception that scallops in Florida scallops function as a single synchronous annual crop (Barber & Blake 1985) and also the typical management strategy of harvesting after a species has spawned. Seasonality varies depending on locale, so monitoring settlement events and patterns may help provide management options in the future. The partially recovered stock has persisted after its collapse through a series of restoration efforts and management decisions, and the state has allowed opportunities for recreational harvest to expand. This study seeks to use the monitoring of settlement events and patterns to understand the effect of environmental conditions on recruitment, in particular where subpopulations outside the core are impacted by frequent blooms of *Karenia brevis* (Landsberg et al. 2009), a dinoflagellate known to cause mortality in scallops (Summerson & Peterson 1990, Leverone et al. 2006). The duration of this study lays the groundwork for further studies of climate change in Florida waters.

MATERIALS AND METHODS

Sample Collection and Environmental Data

Settlement of the bay scallop was monitored at 13 sites: Pensacola Bay (PE), Choctawhatchee Bay (CB), St. Andrew Bay (SA), Crooked Island Sound (CI), St. Joseph Bay (SJ), St. George Sound (SG), Steinhatchee (ST), West Coast (WC with four zones: Citrus County, CT; Hernando County, HE; Pasco County, PO; Pinellas County coastal waters, PN), Tampa Bay (TB); Sarasota Bay (SB with two zones: Manatee County, MC and Sarasota County, SC), Charlotte County (CC), Pine Island Sound (PI), and Rabbit Key Basin in Florida Bay (FB) (Fig. 1).

From August 1992 to March 2018, a total of 26,978 individual traps were deployed, of which 24,597 (91%) were retrieved (Table A1). Early sampling (1992–1996) was conducted only in the fall and winter; efforts were expanded to year-round sampling in 1997. Traps were deployed in seagrass beds at depths of 1–4 m at mean-lower-low water on a NOAA navigation chart. The sample size ranged between 3 and 34 traps deployed at a site per deployment event, dependent on specific project goals. At the beginning of the project, traps at most sites were retrieved approximately 6 wk after deployment. A second trap was deployed at the same location (i.e., station) 3 wk later. This staggered deployment approach allowed for the detection of settled scallops (i.e., spat) on the traps if the traps were retrieved within days of the spat settling onto the traps. Beginning in May 2010, the deployment period was increased from 6 to 8 wk with the second, overlapping trap deployed at each station 4 wk later. Logistics dictated that some remote sites, such as Rabbit Key in Florida Bay, were sampled less regularly. This long-term project had numerous funding sources and project goals, and the number of stations that were sampled and the number of traps that were deployed per site was changed frequently to fit project goals or to correspond with available funding.

The sampling protocol was previously described (Geiger et al. 2010a, 2010b) as adapted and modified by Brand et al. (1980) from a design described in Motada (1977). Settlement traps consisted of a 35-L (L) citrus bag containing a 47 × 31 cm sheet of Vexar with 3.2-mm mesh. Each trap was attached to a 5-m length of 7.9-mm polypropylene line that was anchored to a half cinder block (19 × 19 × 19 cm) and suspended under a 15-cm round buoy. The trap was attached to a loop in the line directly above the block using a cable tie. A small secondary donut-shaped float (approximately 5 × 10 cm) was attached to the free end of the trap, so it floated roughly 30 cm off the bottom. Upon retrieval, each trap was removed from the line, placed in a plastic bag to capture loosely attached spat, and returned to the laboratory for processing. The trap was removed from the bag and placed on a large, shallow tray. All surfaces, including the inside of the bag, the outside of the trap, the inside surfaces of the citrus bag, both surfaces of the Vexar, and the tray were examined visually for any scallops or shells. Intact scallop spat were counted and when single valves or numerous pieces of valves were encountered, an attempt was made to match valves to estimate the total number of settled spat.

Environmental data were either collected during sampling or drawn from available online resources. Beginning in 1999, water temperature and salinity were recorded using a hand-held YSI meter from a subset of the stations at each site at the time of trap retrieval. A thermometer and refractometer were used on occasions when the YSI meter was unavailable. Secchi depth was measured throughout the project unless the bottom was visible. Beginning in 1999 and ending in 2008, water samples (1 L) were collected in the field at a limited number of sites and returned to the laboratory for chlorophyll (CHL) analysis. Replicate samples of 100 mL were filtered on a 0.45 Whatman GFF microfiber filter and placed in a centrifuge tube with 10 mL methanol under refrigeration overnight. Chlorophyll concentration was determined the following day on a Turner 10-AU fluorometer calibrated against a Sigma spinach standard. For analysis, the average salinity, temperature, Secchi depth, or CHL for the site was applied to the settlement data. Additional water quality was used from multiple sources, including the Sarasota County Water Atlas and Tampa Bay Estuary (http://wateratlas.usf.edu/) and the Sanibel-Captiva Conservation Foundation River, Estuary and Coastal Observing Network (SCCF-RECON; http://recon.sccf.org/). For those datasets, data from the water quality station nearest a settlement station was downloaded and binned to the collection month.

Red tide (*Karenia brevis*) data were extracted from the long-term, in-house database at FWRI (https://myfwc.com/research/redtide/statewide/). Samples were collected and either analyzed fresh or preserved in Lugol's solution and analyzed. All counts were standardized to cells/L. For this analysis, blooms are defined as concentrations exceeding 9,999 cells/L. Within defined areas of southwest Florida, the maximum concentration of *K. brevis* observed for each sample month was recorded and plotted. The defined areas included the following sampling locations: Pine Island Sound West (west of the intercoastal waterway), Pine Island Sound East (east of the intercoastal waterway), Boca Grande Pass, Matlacha Pass, Charlotte Harbor, Lemon Bay, Little Sarasota Bay, Sarasota Bay (including Roberts Bay and Sarasota County waters), Longboat Pass, Palma Sola Bay, and four locations within Tampa Bay (divided east and west by the Sunshine Skyway and north and south by the main shipping channel). Other locations along the Gulf Coast were sampled less frequently: the coastal waters of Pinellas County (WC zone PN) were sampled more frequently than WC zones PO, HE, and CT; coastal waters of Levy to Wakulla Counties correspond to the ST site; SJ; SA; and PE. These locations were sampled occasionally, then more frequently when fish kills or red tide was detected.

Data Analysis

The sample size was unequal between sites, so settlement was assessed at each site separately. Six sites with sufficient environmental data and settlement data were analyzed using a general linear mixed model using R-studio: St. Andrew Bay (SA), St. Joseph Bay (SJ), West Coast (WC), Tampa Bay (TB), Sarasota Bay (SB), and Pine Island Sound (PI). The month, year, and station were considered random variables and were combined to create a single, unique variable. For each site, a term was included to assess variation within the site (hereafter called zone). Some sites were separated into zones as follows: St. Andrew Bay (M, Mid Bay; N, North Bay; E, East Bay); St. Joseph Bay (roughly divided equally into north of Eagle Harbor, south of Blacks Island, then west, and east quadrants between those zones; N, E, W, S); West Coast (CT, Citrus Co.; HE, Hernando Co.; PO, Pasco County; PN, coastal Pinellas Co.); Tampa Bay (IS, inside of the Sunshine Skyway south of the shipping channel; IN, inside skyway north of the shipping channel; ON, outside skyway north of the shipping channel); Sarasota Bay (LB, Lemon Bay; LSB, Little Sarasota Bay; SB, Sarasota Bay; PS, Palma Sola Bay); Pine Island (ZS, San Carlos Bay; ZN, stations north of Pineland; ZM stations along Pine Island western shore; no stations were placed west of the intercoastal waterway) (Fig. 2).

Fixed factors included average temperature during the deployment period (Ta), average temperature change during the month prior to deployment (ΔST, hypothesized to be a spawning cue), average temperature change from beginning to end of the deployment (ΔT), average salinity during the deployment period (Sa), average CHL during the deployment (PreC), Secchi depth (Sec), and the number of days the traps were deployed (Days). To examine the best models for nonlinear processes, additional squared terms for ΔST^2, $PreS^2$, and $Days^2$ were added. Resulting models were examined for problems with multicollinearity among the variables, then were ranked via the Akaike Information Criterion (AIC, with the lowest AIC value considered the best) and checked for goodness of fit. Negative binomial distribution and dispersion factors were added to account for variance between zones when needed. Once the best model was selected for each site, the effects of red tide were also explored using the average cell concentration during deployment (R), log of the concentration (Log R), maximum cell concentration during deployment (Rm), days since any red tide (R0), days since cell concentration exceeding 10,000 cells/L (R10), and days since cell concentration exceeding 100,000 cells/L (R100). Pairwise multiple comparison procedures were computed using the Holm-Sidak method.

To illustrate the relationship between settlement and individual environmental variables, the large sample size was used to calculate the observed probability of settlement at two levels: >0, and >30 spat per trap. For each environmental variable, the number of spat per trap from each retrieval was paired with the observed value. The observations were sorted by the value of the environmental variable and binned into groups of $n = 50$, but following natural breaks, such that a group of traps with a similar value were retained in the same bin, led to bins with groups ranging from 20 to 80. Graphs were plotted for each site. St. Joseph Bay and St. Andrew Bay were combined to increase the power of this analysis.

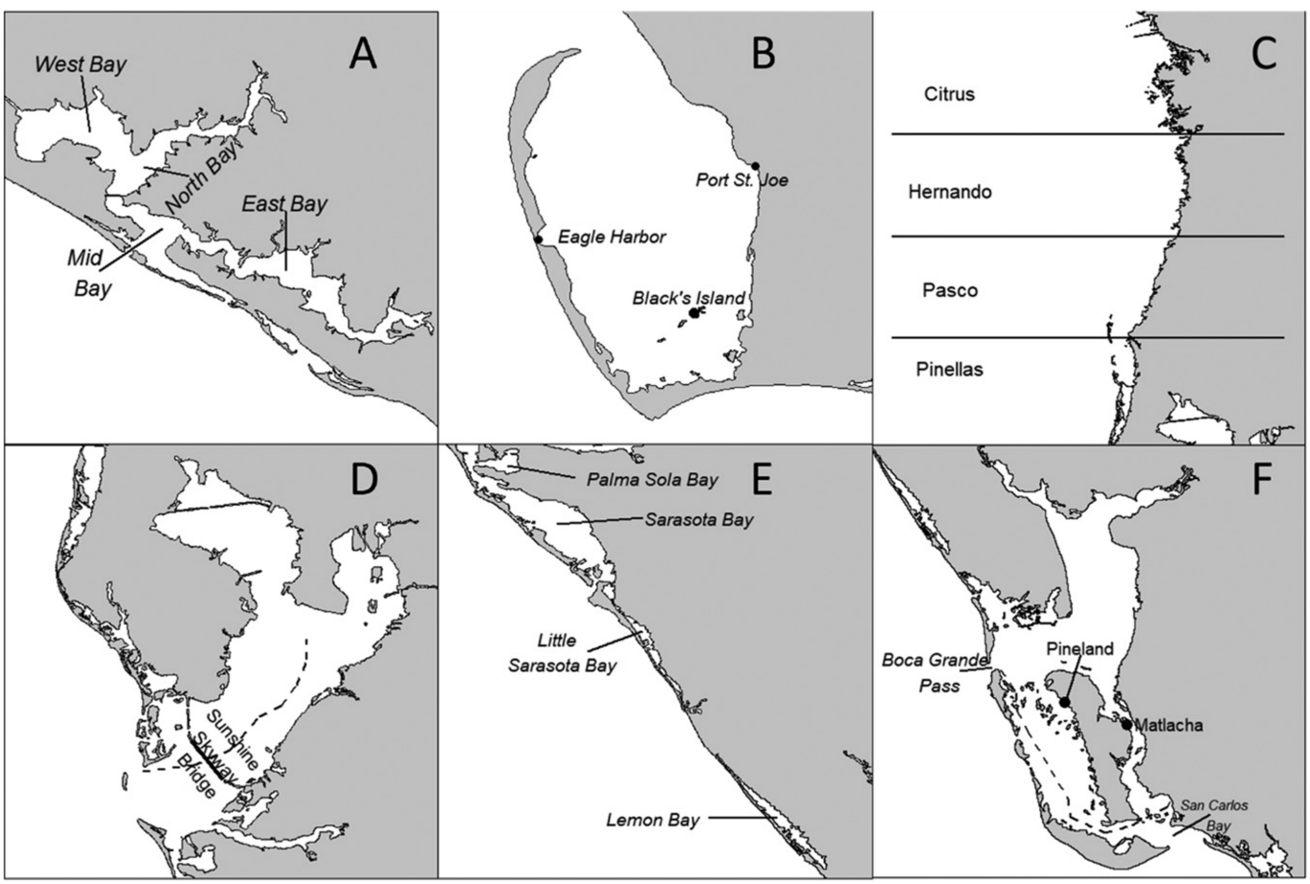

Figure 2. Map of the six sites with modeled zones: (A) St. Andrew Bay (3 modeled zones: East Bay, Mid Bay, North Bay), (B) St. Joseph Bay (4 modeled Zones: South of Black's Island, East, West, North of Eagle Harbor), (C) West Coast (4 modeled zones: Citrus County, CT; Hernando County, HE; Pasco County, PO; Pinellas County, PN), (D) Tampa Bay (3 modeled zones: inside of the Skyway and North of the shipping channel, outside North, inside South) (dashed line indicates shipping channel), (E) Sarasota Bay (3 modeled zones: Sarasota Bay, Little Sarasota Bay, Lemon Bay), and (F) Pine Island Sound (3 modeled zones: North of Pineland, Mid, South = San Carlos Bay, dashed line indicates intracoastal waterway).

RESULTS

Environmental Factors

The highest average temperatures from 2000 to 2017 occurred in Pine Island Sound (25.3 ± 0.16), Sarasota Bay (24.5 ± 0.11), and Tampa Bay (24.0 ± 0.14) sites and the highest average temperatures at all other sites ranged between 21.8°C and 23.2°C ($P < 0.001$; Fig. 3A). Data from 1993 to 1999 and 2018 were excluded because the data were only collected for a portion of those years. The five warmest years occurred between 2011 and 2017, not including 2014 ($P < 0.001$). At all sites, water temperatures rarely fell below 10°C during December and January and approached or exceeded 30°C as early as May and as late as October and showed very little latitudinal variation between study sites (Fig. 4). Temperature declines of as much as 15°C occurred within single months in the fall.

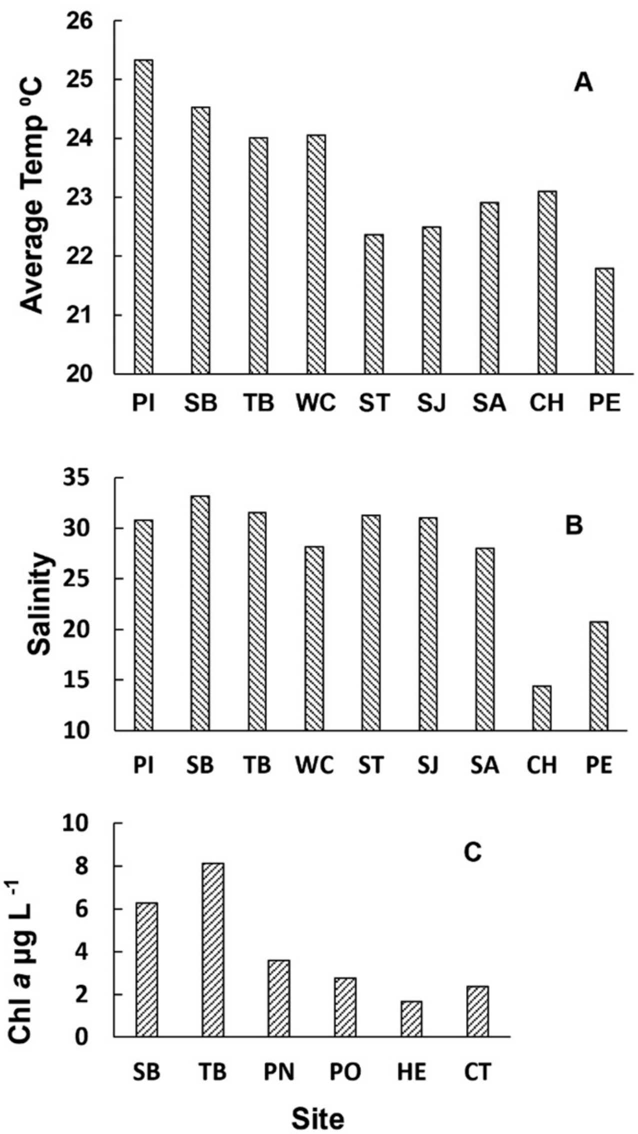

Figure 3. (A) Average temperatures at nine study sites. (B) Average salinity of nine study sites. (C) Average chlorophyll at three study sites; the data for WC is presented by zone (PN, PO, HE, and CT).

Salinity was commonly above 20 during typical sample trips to most sites. Average salinity was significantly lower at the Pensacola Bay (50% of salinities recorded were below 20) and Choctawhatchee Bay (76% < 20) sites ($P < 0.001$) (Fig. 3B). There were no years in which the statewide average salinity at the sites monitored fell below 25. Salinities below 20 occurred less frequently in Hernando County (15%), Pinellas County coastal waters (14%), St. Andrew Bay (13%), Pasco County (12%), Citrus County (9%), St. Joseph Bay (2%), Pine Island Sound (3%), Tampa Bay (<1%), and Sarasota Bay (<1%) sites. Salinity tended to be lowest from January through June in the panhandle, whereas it was lower in June through October, site dependent, at other sites (Fig. 5).

Red tide occurred frequently during the years 2001–2018 throughout the southwest region, including Pine Island Sound (Fig. A4), Sarasota Bay (Fig. A3), and Tampa Bay (Fig. A2). The toxic dinoflagellate *Karenia brevis* was essentially always present at some background level, but blooms occurred regularly in the area. The maximum time span between red tide blooms was 29 mo (average period between blooms was 7.4 mo) at the mouth of Charlotte Harbor (Boca Grande Pass) (Table 1), and 32 mo (average period between blooms was 6.2 mo) in western Pine Island Sound. In Sarasota Bay, there was one period of over 5 y without a bloom despite an average period of 8.8–10.9 mo between blooms. Some zones within Pine Island Sound and Sarasota Bay that had lower frequencies of red tide were not sampled for scallop settlement. At the mouth of Tampa Bay, conditions were similar, with an average of 10.9 mo between blooms and a maximum period of 70 mo without a bloom. In each southern site, in the areas of the bays further

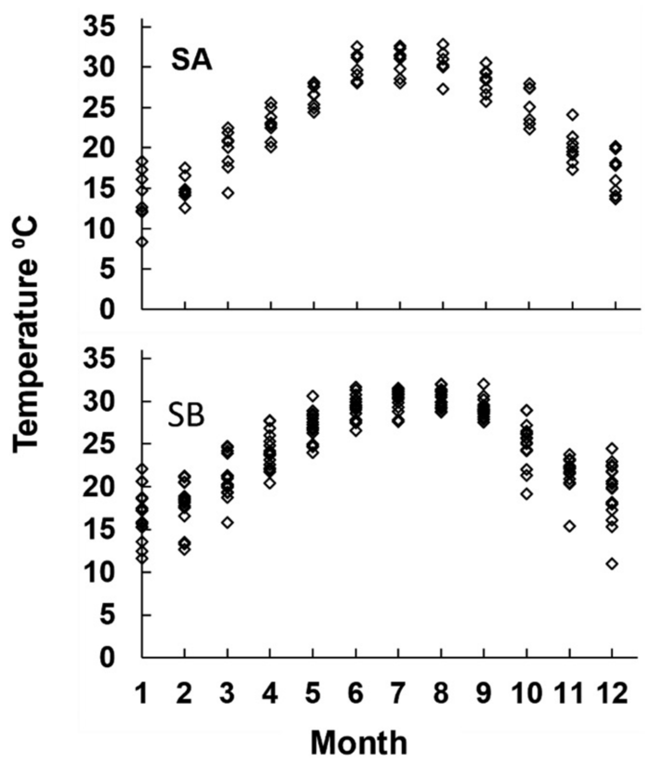

Figure 4. Seasonal temperatures at two study sites, St. Andrew Bay (top) in the Florida Panhandle and Sarasota Bay (bottom), illustrate the lack of a strong latitudinal gradient in temperature.

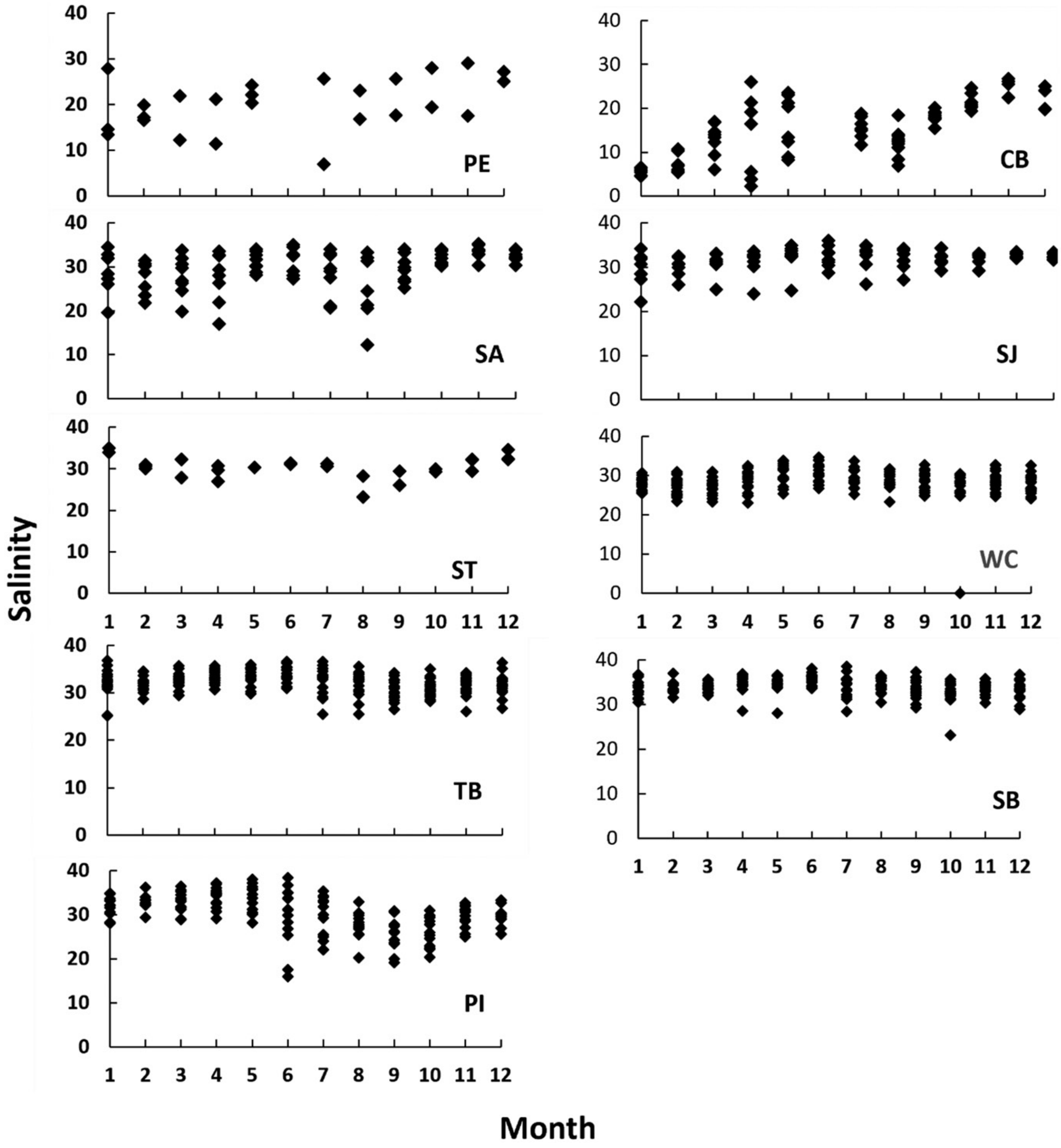

Figure 5. Seasonal salinities at nine study sites.

from the passes (Pine Island East, Palma Sola Bay, and the areas inside the Sunshine Skyway; Fig. 2), the average time between blooms was greater. In the areas immediately north of Pinellas County (Pasco–Homosassa), no red tides above background levels of 1,000 cells/L were observed between August 2005 and January 2018 (Fig. A1). The Steinhatchee site experienced four brief red tide events between 2001 and 2018, never reaching high levels (>1 million cells/L). In the Panhandle sites (St. Joseph Bay, St. Andrew Bay, and Pensacola Bay), red tide blooms were observed seven times during the 17 y, sometimes reaching 1 million cells/L.

Chlorophyll was higher in the enclosed bays (Sarasota Bay and Tampa Bay) than in the open coastal systems (Pasco County, Hernando County, and Citrus County); coastal Pinellas County was intermediate ($P < 0.001$) (Fig. 3C). Average CHL peaked June through October and was at a minimum in March. This effect was more pronounced in the two bays (Fig. 6). The maximum difference occurred between July and March

TABLE 1.

Red tide (*Karenia brevis*, Kb) frequencies in southwest Florida.

Site	Zone	Observed Kb = 0	Observed >10K	Presumed Kb = 0	Presumed >10K	Average M	Max M
PI	W	0.36	0.48	0.63	0.28	6.2	32
	N-S	0.48	0.25	0.72	0.13	11.8	71
	BG	0.45	0.40	0.55	0.33	7.4	29
	MTL	0.85	0.05	0.90	0.03	15.1	68
CH	–	0.53	0.18	0.79	0.08	13.4	58
SB	LB	0.85	0.10	0.92	0.06	21.3	63
	LSB	0.45	0.40	0.55	0.33	12.7	81
	SB	0.25	0.37	0.27	0.36	8.8	67
	LP	0.55	0.25	0.27	0.22	10.9	71
	PS	0.77	0.09	0.84	0.06	24	81
TB	OS	0.47	0.29	0.52	0.26	10.9	70
	IS	0.78	0.12	0.87	0.07	23.1	71
	ON	0.64	0.22	0.85	0.09	23.8	72
	IN	0.83	0.10	0.90	0.06	23.5	88
WC	PN	0.89	0.02	0.90	0.02	69	155
	PO-HE-CT	0.97	0.01	0.97	0.01	108	181
ST	–	0.95	0.01	0.96	0.01	72	128
SJ	–	0.89	0.06	0.90	0.05	34	94
SA	–	0.82	0.05	0.94	0.05	34	95
PE	–	0.94	0.01	0.94	0.00	70	97

Columns represent the percentage of months without observed red tide (Kb = 0) and the percentage of months where red tide exceeded 10,000 cells/L on at least 1 day (>10K). Observed columns represent months in which there was an observed red tide sample collected. Presumed columns presume that in months where no sample was taken, no red tide was occurring. Average M is the average number of months between months where Kb concentration exceeded 10,000 cells/L. Max M represents the longest duration observed for each location in which Kb concentration did not exceed 10,000 cells/L. Sample location as in Table 1 except where sample location included multiple zones within a site. *Pine Island Sound zones*: BG, Boca Grande Pass; MTL, Matlacha Pass; N, east of intercoastal waterway, north of Demere Key; S, east of intercoastal waterway and south of Demere Key; W, west of intercoastal waterway. *Sarasota zones*: LB, Lemon Bay; LP, Long Pass; LSB, Little Sarasota Bay; PS, Palma Sola Bay; SB, main basin. *Tampa Bay Zones*: IN, east of the Sunshine Skyway and north of the shipping channel; IS, east of the Sunshine Skyway and south of the channel; ON, west of the Sunshine Skyway and north of the shipping channel; OS, Tampa Bay west of Sunshine Skyway and south of the shipping channel. *West Coast*: CT, Citrus County; HE, Hernando County; PN, coastal waters of Pinellas County; PO, Pasco.

in Citrus County (Holm-Sidak difference of means = 2.715; $t = 7.12$), between December and March in Hernando County (1.89; 3.57), between July and March in Pasco County (4.02; 12.03), between September and March in Pinellas County (5.22; 5.24), between August and January in Tampa Bay (6.56; 13.31), and between October and March in Sarasota Bay (7.57; 25.23).

Settlement

Settlement occurred in each site except Choctawhatchee Bay. The average settlement rate at the other sites ranged from a low of 0.58 spat per trap (Pine Island Sound) to a high of 40.31 spat per trap (St. Joseph Bay) (Table A1). There were 263,425 spat collected from 24,509 retrieved traps (10.7 spat per trap). The maximum number of spat retrieved on a single trap at any site ranged from 89 (Pine Island Sound) to 5,237 (St. Joseph Bay).

Seasonal peaks in settlement were obvious wherever spat was observed on traps (Fig. 7). In Pensacola Bay, settlement largely occurred in two discrete months, October and November. In other Panhandle sites (St. Andrew Bay, Crooked Island Sound, St. Joseph Bay), and Big Bend sites (St. George Sound, Steinhatchee) as well as two zones of the West Coast site (Homosassa and Hernando), there was a settlement peak that began in traps retrieved in October and continued through December, with the Hernando peak extending into January. At sites further south, the settlement peak shifted later into winter, with a second smaller peak centered in April (Pasco, Pinellas, Tampa Bay, Sarasota Bay) or June (Charlotte County and Florida Bay). Pine Island Sound exhibited multiple peaks throughout the year, but at low levels (less than two spat per trap). Peaks that occurred in the fall were usually larger, but at many sites, low-level settlement was frequent, occurring in most months (Table 2). In 10 of the 12 sites sampled, settlement occurred in more than 50% of the months sampled, and in six of the 12 sites sampled, settlement occurred in more than 70% of the months sampled.

In all sites except Pensacola Bay and Choctawhatchee Bay, some settlement occurred every year the site was monitored, although settlement rates varied from year to year (Fig. 8). In Pensacola Bay, there was no settlement in five of the 8 y sampled. In the sites that were monitored during the period from 1993 to 2000, there were occasional years with higher-than- average recruitment, but no clear patterns were obvious. At three sites where sampling was consistent, Hernando, Homosassa, and St. Joseph Bay, the magnitude and frequency of high-settlement years were lower after 2003. From 2001 through 2003, the West Coast site (including CT, HE, PO, and PN zones) exhibited higher settlement concurrent with

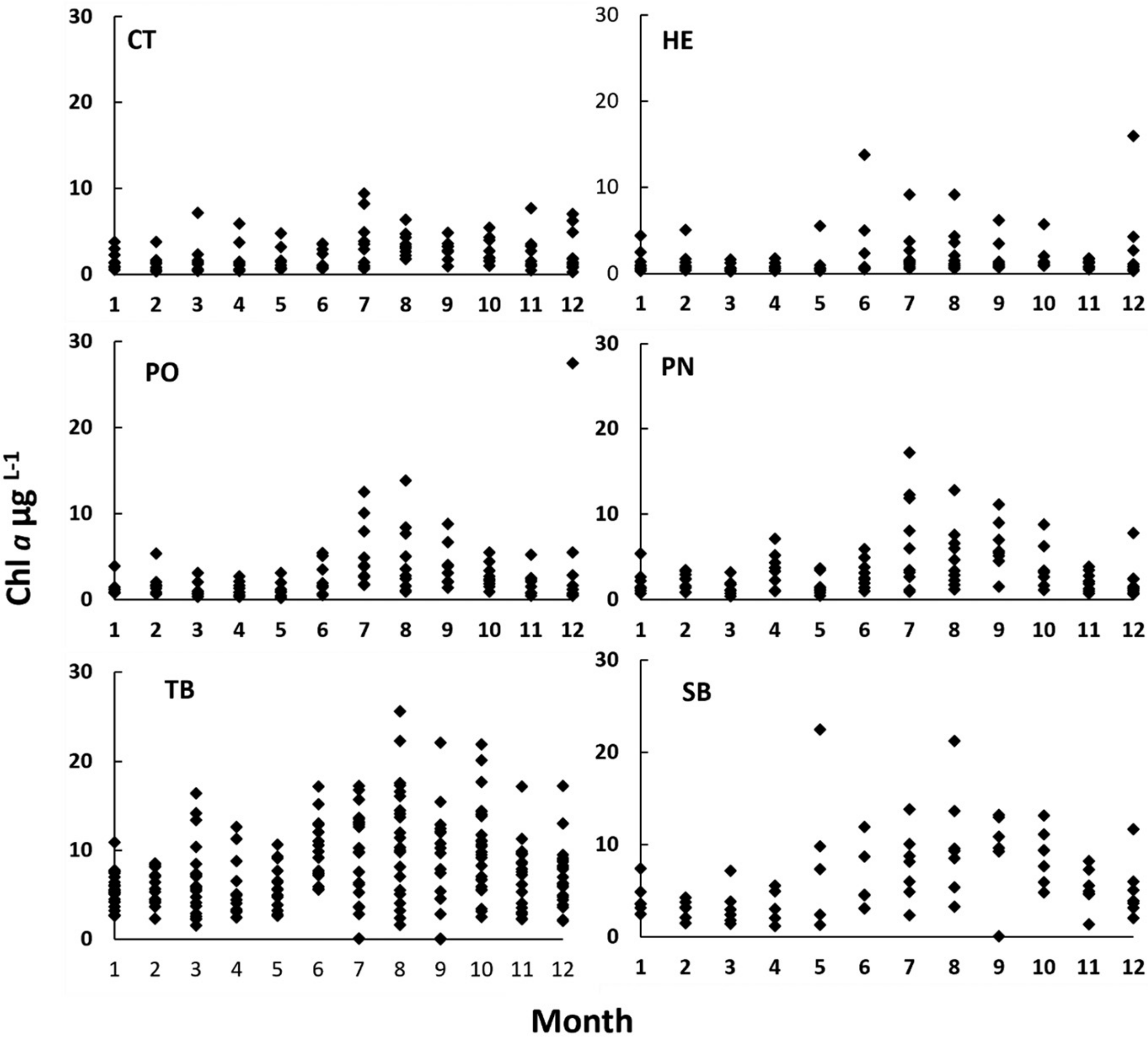

Figure 6. Seasonal chlorophyll values at three sites: WC, TB, and SB. For the WC site, data are presented for the four zones (CT, HE, PO, and PN).

restoration efforts in the area. A second period of higher settlement occurred from 2007 through 2012. This event appeared to begin in the Pasco-Hernando region, then progress to Tampa Bay, Sarasota Bay, and finally Charlotte County and Pine Island Sound. In 1993–2010, there were eight times when the average annual settlement at any individual site exceeded 50 spat per trap. No site had an average annual settlement rate above 50 spat per trap after 2010.

At least one measure of temperature, salinity, and red tide level was always a factor that influenced settlement (Table 3). Soak days (D) and a nonlinear term (D^2) were retained in all models. Although variable, the number of spat on traps climbed rapidly from around 42 days soak time to approximately 63 days, then at some sites (e.g., Sarasota; Fig. 9) fell again by day 90. This nonlinear artifact of sampling required adding the D^2 term for further analysis. Average temperature during the deployment period was always retained in the models, and all models retained during the model selection process included ΔT as well as the nonlinear squared term, except Pine Island Sound. The change in temperature during the probable spawning period, the month prior to trap deployment (ΔST), resulted in models with lower AIC in all estuaries. Salinity was retained as either S or Sa. Red tide metrics were roughly evenly split among R, Rm, R10, R100, and Log R. Secchi depth, CHL, and R0 were never retained in any model, although R0 was similar, but with a slightly lower AIC than the preferred model in both St. Joseph Bay and Pine Island. All sites had a single best fit, but in Pine Island Sound, SJ, and SB, a second or third model was described as weighting 0.001 or higher in the model selection process (Table 3). There was always differential settlement within the site, with one zone predicted to have higher settlement than the other two or three zones (Table A2).

Observed settlement peaked at most sites when the average temperatures during the deployment period were near or below

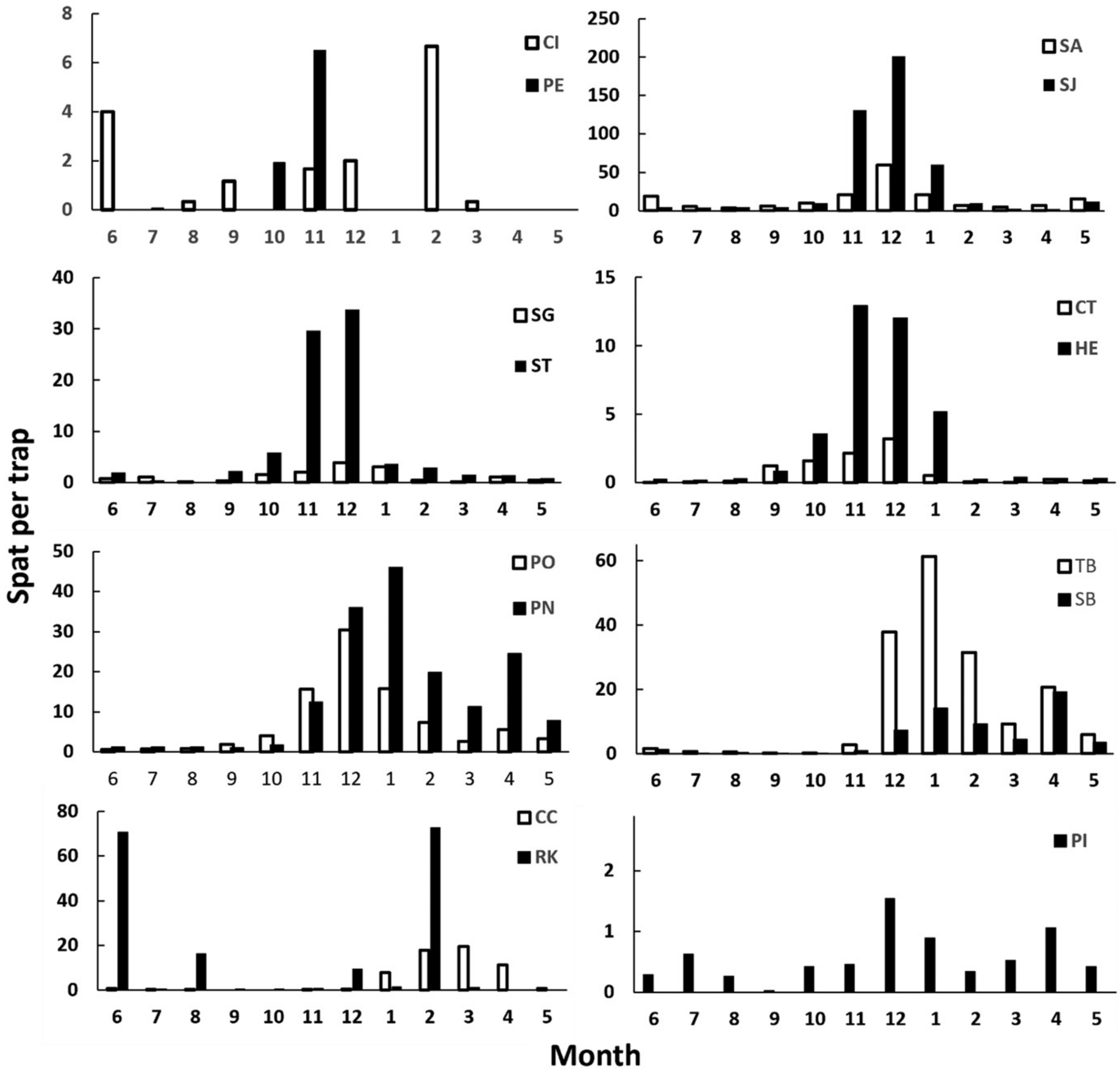

Figure 7. Average settlement per trap to traps retrieved in the calendar month indicated from each of 12 sites for the life of the project. For the WC site, settlement data are presented for the four zones (CT, HE, PO, and PN). Note the difference between scales.

22°C (black circles in Fig. 10). Large settlement events were not observed at temperatures above 25°C (open squares in Fig. 10), and the probability of large settlement events increased dramatically below 20°C. The probability of any settlement event at Pine Island Sound was always below 0.4, and there were no large settlement events observed.

The change in temperature either during the deployment period (for SA, SJ, WC, and SB) or in the month prior to the initial deployment (TB and PI) was also correlated with a higher probability of settlement (Fig. 11). Settlement peaked when there were larger changes in temperature, either positive or negative. At sites from the West Coast northward, temperature change in the month prior to deployment was not a good predictor of scallop settlement. Similarly, larger temperature changes during the 6- to 8-wk deployment period were associated with higher probabilities of any settlement from Tampa Bay southward, as well as St. Joseph Bay-St. Andrew Bay. In the southern sites, the probability of a large settlement event was higher with either increasing or decreasing temperatures, but in SJ and SA large settlement events were more common when temperatures declined. In the West Coast site, the probability of any settlement, as well as the probability of a large settlement event, increased as the temperature change went from positive to negative.

At all modeled sites, there was within-site variability with settlement in one zone exceeding settlement in others. The response was generally similar in shape among all zones, but usually varied in magnitude. For example, at the

TABLE 2.

Percentage of years in which the site received at least one spat in the month indicated.

Site	Zone	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	Total
PE	–	0	0	0	0	0	0	20	0	0	17	14	0	5
CB	–	0	0	0	0	0	0	0	0	0	0	0	0	0
SA	–	82	93	31	67	91	91	100	83	79	78	87	81	80
SJ	–	80	84	57	65	95	95	89	81	83	94	90	90	83
SG	–	75	67	50	40	50	100	100	33	67	100	100	75	83
ST	–	88	89	71	60	100	100	83	80	57	100	86	100	84
WC	CT	68	43	41	40	40	45	32	38	52	85	92	81	57
	HE	91	52	43	45	75	65	58	60	58	95	95	100	71
	PO	96	100	95	95	100	95	89	71	85	92	96	100	93
	PN	88	87	90	100	80	67	67	48	50	71	92	96	79
TB	–	86	80	100	89	94	89	67	72	29	33	57	81	73
SB	MC	82	59	82	88	80	50	56	25	25	29	35	59	56
	SC	43	75	89	100	90	90	70	29	20	20	22	20	56
CC	–	75	100	100	100	50	100	50	50	0	0	25	67	43
PI	–	64	64	62	71	69	62	36	27	21	33	64	53	52
FB	–	100	100	100	0	0	50	100	50	50	50	100	100	67

Total = percentage of months where at least one spat was found on a trap at a site, over the entire project.

west coast site, settlement was predicted to be highest in the Pinellas Zone, then declining in Pasco, Hernando, and Citrus (Fig. 12). All four zones were predicted to have peak settlement around 20°C with falling water temperatures. Note also that settlement increased as deployment times increased. In the four zones within the Tampa Bay site, settlement was predicted to be highest north of the shipping channel and west of the Sunshine Skyway, followed by north of the channel east of the Skyway, and south of the channel and east of the Skyway. Settlement peaked at around 14°C declining to near zero at above 28°C. In the Sarasota Bay site, under optimized conditions (no red tide, high salinity) settlement was predicted to be highest in Sarasota Bay, followed by Little Sarasota Bay and Lemon Bay. Within-site variability was minimal in Pine Island Sound, though settlement was predicted to increase from south to north.

In all sites, predicted settlement approached zero when salinity fell below approximately 20. The predicted response to higher salinities exhibited two main patterns. At some sites (Sarasota Bay, Tampa Bay, St. Joseph Bay and, St. Andrew Bay) settlement was maximal when salinity was near its maxima (35–37) (e.g., St. Joseph Bay) whereas at two sites (West Coast, Pine Island Sound) settlement was predicted to peak at around 32 **(**Fig. 13**)**.

Settlement of scallops declined when *Karenia brevis* was present. Settlement declined quickly with red tide concentrations of 10,000 cells/L or more. Modeled settlement was also observed to be suppressed following a red tide. The interval between the end of a red tide and the resumption of scallop settlement varied between estuaries (Fig. 14). In Pine Island Sound, there were never more than three spat settling in any given month for the first 48 mo after a red tide bloom. In Sarasota Bay, there was some spat settlement, but the total for any given month did not exceed 25 for 28 mo post red tide. The resumption of settlement was similar in St. Andrew Bay with small events occurring after 17 mo and larger peaks 39–64 mo post red tide. Settlement in Tampa Bay exceeded 100 total spat within 11 mo (although settlement did not exceed 300 for more than 3 y) and St. Joseph Bay exceeded 150 total spat within 14 mo after red tides with larger peaks occurring by 26–27 mo postred tide. The West Coast site (coastal waters of Pinellas through Citrus Counties) was notably different, with settlement occurring as soon as 4 mo after the end of red tides. Protracted peaks occurred by month 30.

DISCUSSION

One of the driving reasons for monitoring the settlement of pelagic larval phases into benthic juvenile forms is the identification of areas where there is limited larval supply. In this study, the core population showed no such limitation, but the subpopulations beyond the edges of the core had limited settlement. One subpopulation, FL Bay, remains poorly studied for both settlement and adult density, but did have settlement in the 1990s and adult scallops were observed there in 2020 (Geiger, personal observation).

Recorded temperatures from most sites typically remain between 13°C and 32°C, and at most sites that range is achieved in most years, so temperature alone in and of itself does not appear to be a limiting factor for Florida bay scallops. Temperature has been shown to play an important role in the reproduction of scallops, almost certainly tied to temperature change as a spawning cue (Cabiles & Soliman 2019) although many other factors probably come into play (Barber & Blake, 2016). Both temperature and one of the two metrics of temperature change were retained in settlement models for each site modeled in the current study. Some settlement occurred consistently at most sites, indicating a low level of year-round spawning, as observed in Geiger et al. (2010b), although the source for these settling larvae remains unknown. Bimodal peaks of settlement were observed at most sites. One important exception was the northern portion of the West Coast site (Hernando and Citrus Counties), and another was the Steinhatchee site. The populations in Hernando through St. Joseph Bay retained

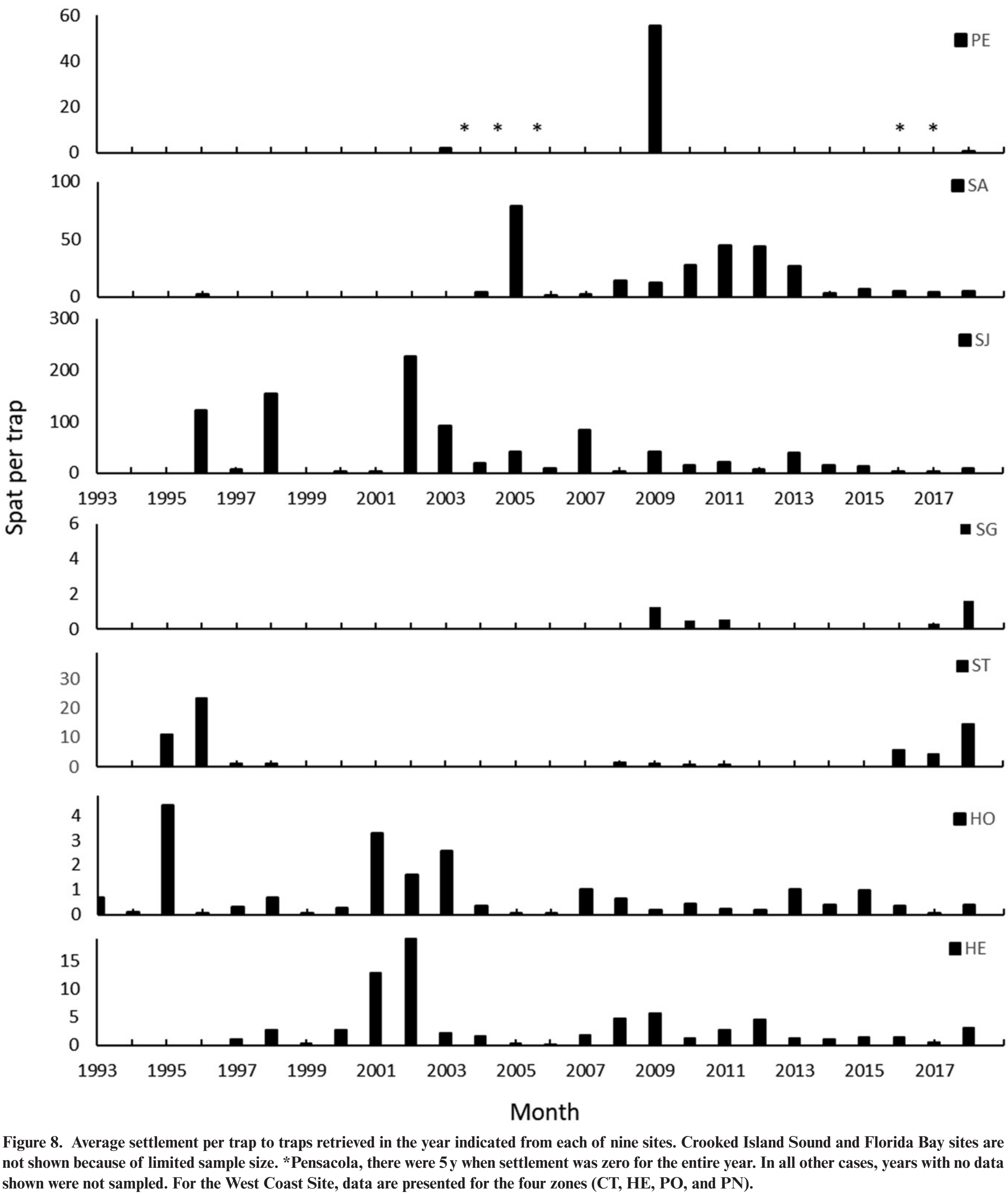

Figure 8. Average settlement per trap to traps retrieved in the year indicated from each of nine sites. Crooked Island Sound and Florida Bay sites are not shown because of limited sample size. *Pensacola, there were 5 y when settlement was zero for the entire year. In all other cases, years with no data shown were not sampled. For the West Coast Site, data are presented for the four zones (CT, HE, PO, and PN).

a strong peak of settlement in November–December, indicative of falling temperatures as a cue for spawning or during cycles of rapid cooling and gradual warming with the passage of fall cold fronts. Further south, peak settlement in Tampa Bay and Sarasota bays was generally delayed until December–January, which may just reflect the delay in cooling at more southerly sites. These two sites had predicted maximal spat settlement at temperatures below 20°C, the coldest of all the sites modeled (see Fig. 12). At the northerly and southerly limits of the study area, both St. Andrew Bay and Pine Island Sound were predicted to have peak settlement when temperature was more stable, both at relatively high temperatures of 22°C–23°C.

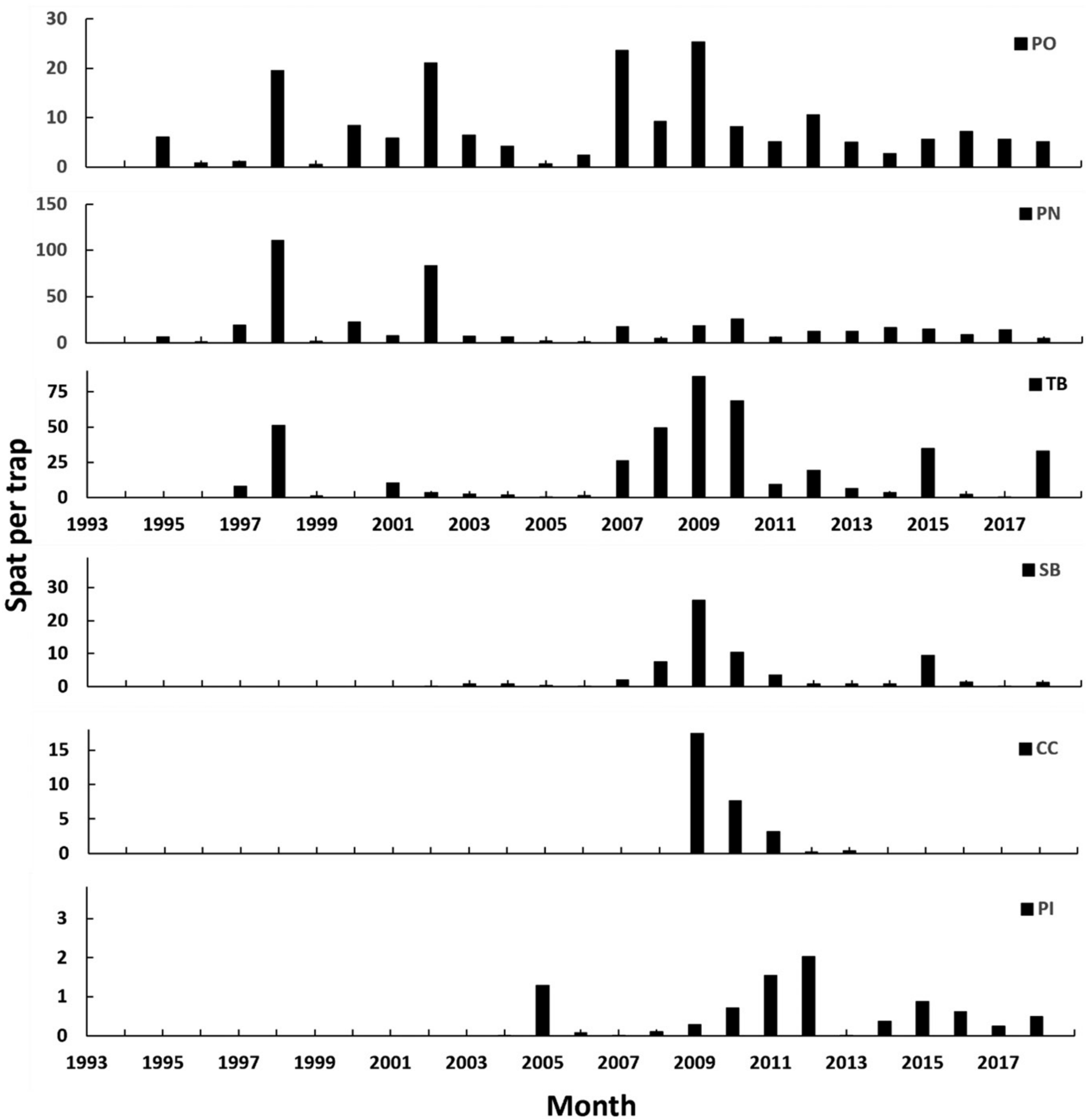

Figure 8. Continued.

Salinity can be an important limiting factor for estuarine and coastal species. Development of larval bay scallops in Connecticut began to decline below a salinity of 25 and no development occurred below salinities of 15 (Tettelbach & Rhodes 1981). Juvenile bay scallops have been observed to close and cease activity (Duggan 1975), and mortalities of juveniles have been observed as salinity falls below 15 (Mercaldo & Rhodes 1982). There is no comparable work focused on Florida scallops, although 20 is considered a lower salinity threshold (Leverone 1993). Model output with other conditions optimized suggests settlement of bay scallops will fall to low levels at salinities below 24–28. In Choctawhatchee Bay, salinity never reached a level considered suitable for scallop survival. Previous work similarly found salinities over 20 only at stations near the bay mouth and then commonly only below the halocline where hypoxia was common (Blaylock 1983), although offshore species of scallop (*Argopecten gibbus* and *Aequipecten muscosus*) have been observed to settle inside the bay (Martin & Bortone 1997) at depths of 6.5 m. In the neighboring Pensacola Bay system, suboptimal salinities were also common, but both western panhandle bays can be expected to have periods with salinities above 20 for the drier parts of the year, typically September through February (Orlando 1993). Unlike Choctawhatchee Bay, Pensacola Bay probably maintains some higher salinity water

TABLE 3.

General linear mixed model output selection for six bay scallop settlement sites with sufficient environmental data.

Site	Ra	R0	R	Rm	R10	R100	LR	LL	AICc	delta	W
SA	-	-	-	+	-	-	-	−2,728	5,484	0.00	0.99
	-	-	-	-	-	+	-	−2,734	5,496	11.13	0
	-	-	-	-	+	-	-	−2,734	5,505	11.17	0
SJ	-	-	-	-	+	-	-	−3,836	7,703	0.00	0.89
	-	-	-	-	-	+	-	−3,838	7,707	4.20	0.11
	-	+	-	-	-	-	-	−3,865	7,756	53.40	0
WC	-	-	-	-	+	-	-	−12,096	24,228	0.00	0.92
	-	-	-	-	-	+	-	−12,098	24,233	4.90	0.08
	+	-	-	-	-	-	-	−12,115	24,266	37.42	0
TB	-	-	-	-	+	-	-	−4,141	8,314	0.00	1
	-	-	-	-	-	-	+	−4,151	8,335	20.47	0
	-	-	-	+	-	-	-	−4,154	8,340	25.94	0
SB	-	-	-	-	-	-	+	−1,430	2,889	0.00	0.98
	-	-	-	+	-	-	-	−1,434	2,897	8.66	0.01
	-	-	+	-	-	-	-	−1,435	2,898	10.00	0.01
PI	-	-	-	-	+	-	-	−1,293.0	2,614	0.00	1.0
	-	-	-	-	-	+	-	−1,300.6	2,629	15.39	0
	-	+	-	-	-	-	-	−1,324.2	2,677	62.55	0

All models returned average temperature during trap deployment; the temperature change during deployment, average salinity during trap deployment, and the number of days deployed were primary environmental factors. R, Red tide (*Karenia brevis*, Kb) concentration on the day of retrieval in cells/L; Ra, average red tide concentration during deployment; Rm, maximum red tide concentration during deployment; R0, the number of days since a red tide event exceeding 0; R10, the number of days since a red tide event exceeding 9,999 Kb; R100, days since Kb exceeded 99,999; LR, log of the average red tide concentration during deployment. Factors included in the model are indicated by "+" and those not included are indicated by "-" LL is the log likelihood estimate, and delta reflects difference between optimal and lower ranked models, AICc, Akaike Information Criterion; W, model weighting.

near its mouth in most years, although at depths less ideal for seagrass and scallops (Hagy 2010). Thus, these two bays probably suffer from both low larval supply as well as conditions that are commonly not conducive to scallop population resiliency. At other sites, salinities rarely fell below 20 at the stations monitored for settlement. Upstream stations with reduced salinity may offer some refugia from red tides, but the salinity tolerance range for bay scallop settlement appears to be similar to that for *Karenia brevis* (Magaña & Villareal 2006). If any refugia exist based solely on salinity tolerance, they are likely to be a narrow region where adult scallops may persist during moderate red tides with no low-salinity event concurrently occurring in that estuary.

Blooms of *Karenia brevis* routinely affect the Gulf of Mexico and the estuaries along the coast of Florida, peaking in frequency in the central panhandle and the southwest coast around Charlotte Harbor. The most visible detrimental impacts of blooms include mortalities of charismatic megafauna like turtles (Foley et al. 2019), manatees (Landsberg et al. 2009), and seabirds (Fauquier et al. 2013) and also extensive fish kills (Flaherty & Landsberg 2011). Brevotoxins from blooms of *K. brevis* are not always lethal to shellfish and can accumulate to levels which are toxic to humans who consume those shellfish (Basti et al. 2018, Abraham et al. 2021). In bay scallops, levels of *K. brevis* as low as 5,000 cells/L are inhibitory to larval feeding (Leverone et al. 2006) and 1,000 cells/L caused 79% decline in feeding in juveniles (Leverone et al. 2007). Medium to high levels of red tide are considered to be lethal to adult bay scallop populations, but there are no specific studies to provide exact concentrations or durations. Caged scallops suffered 100% mortality when exposed to average red tide concentrations of 99,000 cells/L (range = 0–665,000) during a scallop restoration project conducted in Sarasota Bay (FWC unpublished data, but for methods see Arnold et al. 2005), during the month of June 2003. Blooms of another toxic dinoflagellate *Cochlodinium polyrikoides* can cause significant mortalities of bay scallops at concentrations of 15,000 cells/L (Griffith et al. 2019) which closely aligns with the observation here that settlement declines whenever a local population is exposed to red tides exceeding 10,000 cells/L, considered to be the threshold between Very Low and Low by FWC.

The geomorphology and subsequent hydrology of an estuary controls how a bloom is expressed within an estuary. Portions of bays with open access to the Gulf of Mexico, such as upper Sarasota Bay, were subjected to 10–20 times higher *Karenia brevis* concentrations in a 2018 red tide than lower Sarasota Bay, which has no direct connection to the Gulf (Fig. A3). A 2005 spring bloom at the mouth of Charlotte Harbor near an ongoing scallop restoration project reached nearly 1 million cells/L but did not infiltrate the bay nor appear to affect scallops within the Pine Island Sound grass flats (Leverone et al. 2010). This bloom persisted through the fall, becoming more extensive but less severe (maximum of 270,000 cells/L). Adult scallop density had declined 92% by the following year (2006); no scallops were detected in 2007. Both red tide and scallop sampling frequency were insufficient to identify specific levels of red tide that coincided with the loss of scallops, but the spatial distribution and timing of the bloom suggests that in some years, a refugia may exist within certain portions of the estuary, whereas in other years blooms decimate regions where

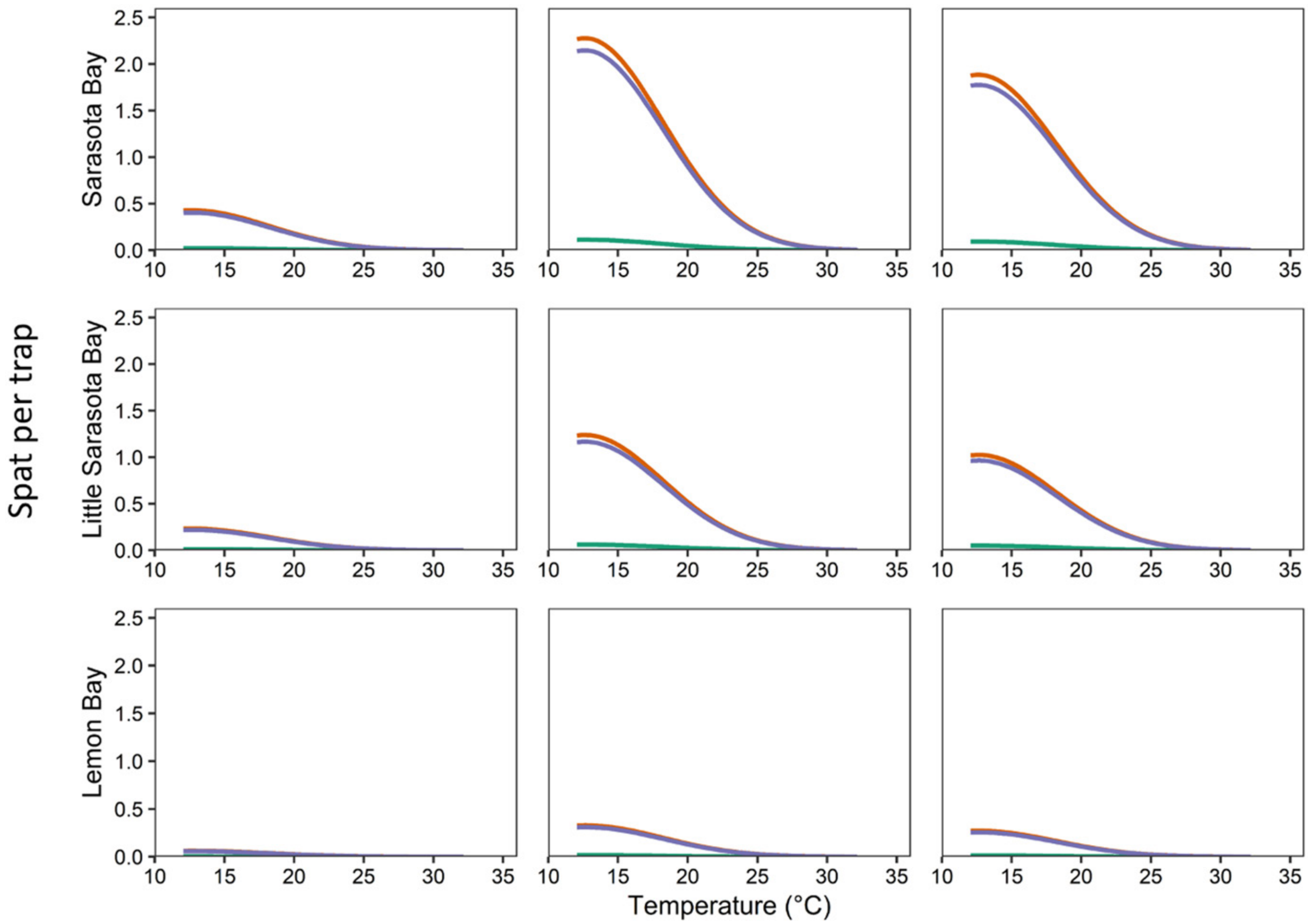

Figure 9. R model output for the Sarasota Bay site with three zones (Lemon Bay, LB: Little Sarasota Bay, LSB; and Sarasota Bay proper). In each group, the left panel represents a 42-day deployment, the center = 63 days, and the right = 80 days. Lines are as follows: green, 10°C decrease during deployment; red = median of −0.4°C temp change during deployment; blue = +10°C change during deployment. Note that in Sarasota, settlement is more common during periods of rising temperatures.

scallops are most abundant. In the Charlotte Harbor Estuary, the western half of Pine Island Sound is directly connected to the Gulf of Mexico, and blooms of *K. brevis* occur more often and for longer durations than in the eastern portion. The isolated basins of eastern Pine Island Sound and Matlacha Pass may offer some refugia from red tide. Similarly, in Tampa Bay, in small basins such as Palma Sola Bay and upper Tampa Bay there is lower red tide frequency and duration, so they may be sufficient to support remnant populations of bay scallops during some blooms of *K. brevis*. Basins in an estuary that are connected to freshwater sources would be more prone to low-salinity events and the timing of coincident freshets and blooms could create very narrow zones that were tolerable to scallops, or even eliminate them entirely.

Scallop subpopulations in Florida showed differing responses to blooms of *Karenia brevis*. The core population is only infrequently impacted by brief, patchy blooms, and the settlement of juveniles resumes almost immediately after the bloom subsides. The panhandle has been affected by multiple harmful algal blooms including both *Pseudonitzschia* spp. diatoms and *K. brevis* dinoflagellates (Heil & Muni-Morgan 2021) that are typically infrequent and brief in duration. The diatom blooms do not appear to cause mortalities in scallops, but may pose human health risks, especially if they become a recurring seasonal event that coincides with the scallop harvest season. The blooms of *K. brevis* reach levels sufficient to result in scallop mortalities. In southwest Florida, blooms of *K. brevis* are frequent, widespread, prolonged, and severe, sometimes even causing water column hypoxia (Dupont et al. 2010). The most notable difference between core populations, and those at the edges of their distribution (Pine Island Sound and St. Andrew Bay), is the protracted scallop recovery in marginal populations driven by insufficient larval supply when local populations collapse. There is an inherent risk to the stability of the entire scallop population in Florida from increases in duration and extent of blooms of *K. brevis* that impinge the shelf in the region of the core population. Risks from factors such as climate change, urbanization, increased nutrient input, and reduced freshwater inflow as those relate to potential changes in harmful algal blooms should be considered by those who manage bay scallops (Beck et al. 2022, Phlips et al. 2023).

Bay scallop populations in Florida have been observed at densities as low as 0.001 m^{-2} (approximately 4 per acre; Pine Island Sound), 0.00017 m^{-2} (approximately 0.7 per acre; St. Andrew Bay) with some years falling below detection limits of visual surveys (Arnold 2007). There may be remnant populations in

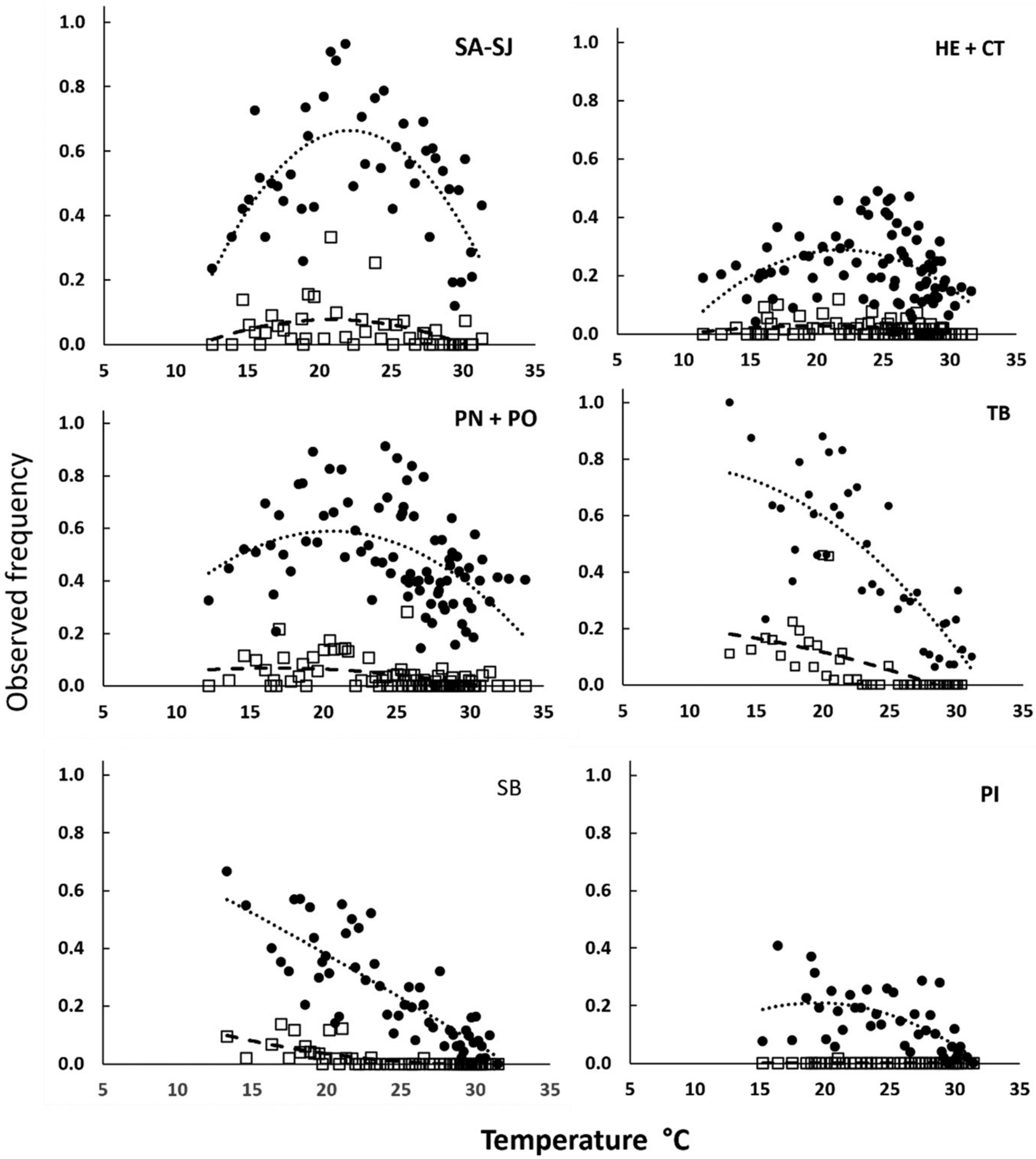

Figure 10. Observed frequencies of settlement of one or more (•, dotted line) and 30 or more (□, dashed line) spat as a function of temperature. Raw data were grouped into bins of approximately 0.5°C intervals to calculate the proportion of points which met each criterion.

isolated embayments within the estuaries or the few individuals found in low-abundance years may simply reflect a constant low-level exogenous supply of larvae from neighboring populations. There is scant evidence that significant populations of bay scallops occur offshore, so larval supply in Pine Island Sound most likely comes from neighboring or distant subpopulations. The prevalent currents on the shelf make exogenous transport from the south more likely, but current reversals do occur, and transport from Sarasota Bay, Tampa Bay, and points north may be possible (Yang & Weisberg 1999, Liu & Weisberg 2012). Based on the observation that red tide affects Pine Island Sound much more than Big Bend coastal populations, it is probable

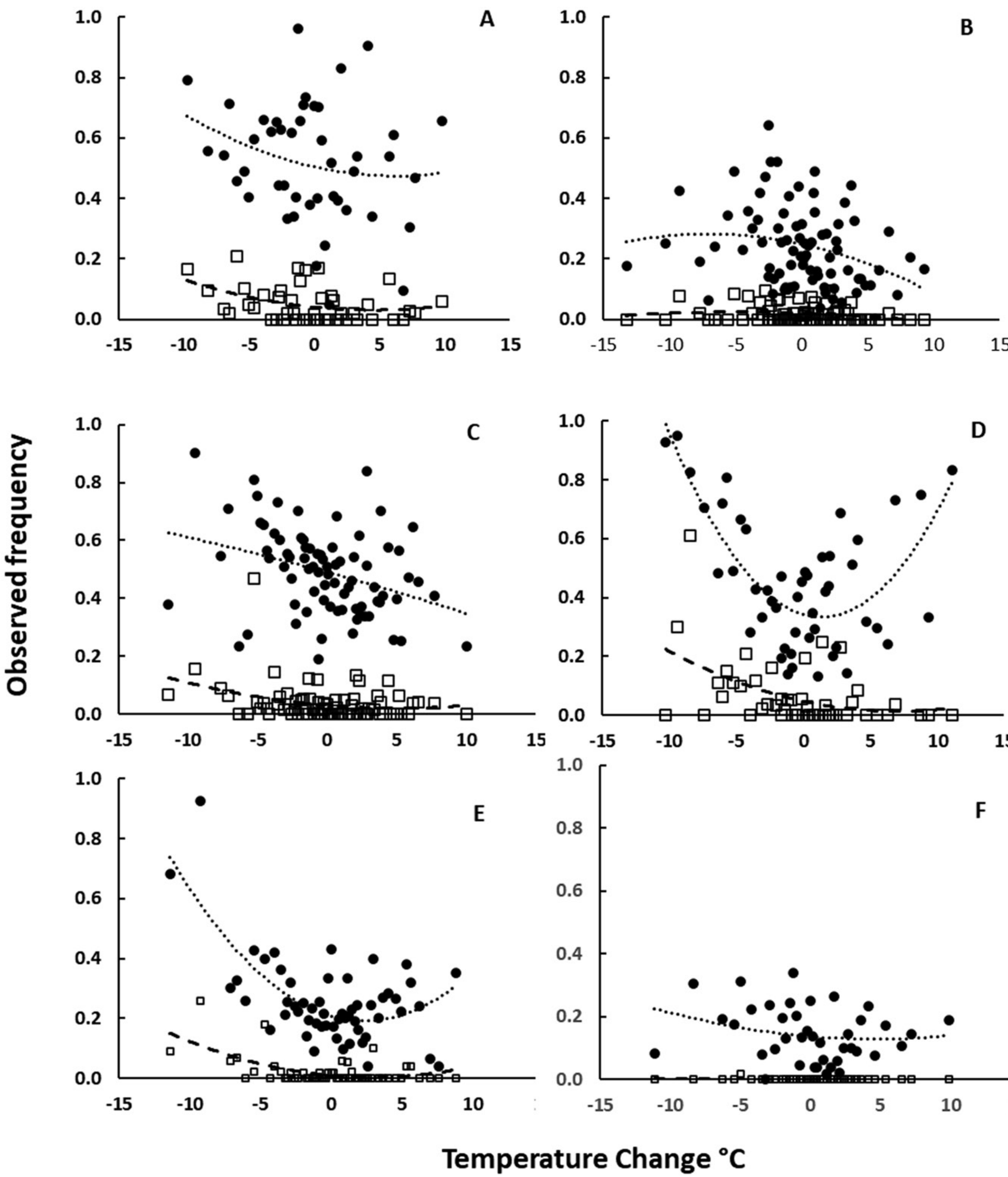

Figure 11. Observed frequencies of settlement; one or more spat (•, dotted line) and 30 or more spat (□, dashed line). (A) Panhandle sites SA and SJ are combined; (B) site WC zones HE and CT are combined; (C) site WC zones PN and PO are combined; (D) TB; (E) SB; and (F) PI. In panels A, B, C, E settlement is tabulated as a function of temperature change during deployment. For panels D and F settlement was tabulated as a function of average temperature change during the month prior to deployment (TB and PI). Raw data were grouped into bins of temperature change ≈ 0.5°C intervals to calculate the proportion of points which met each criterion.

that such introductions of larvae are rarely if ever given time to become widespread and large enough to produce sustainable, fishable populations. The West Coast and Steinhatchee sites are rarely exposed to prolonged and severe red tides, and there are essentially no coast-wide environmental deviations that are counter-indicative of scallops thriving. In St. Andrew Bay and Pensacola Bay, repopulation by exogenous larvae is almost certainly from St. Joseph Bay or the core population to the east.

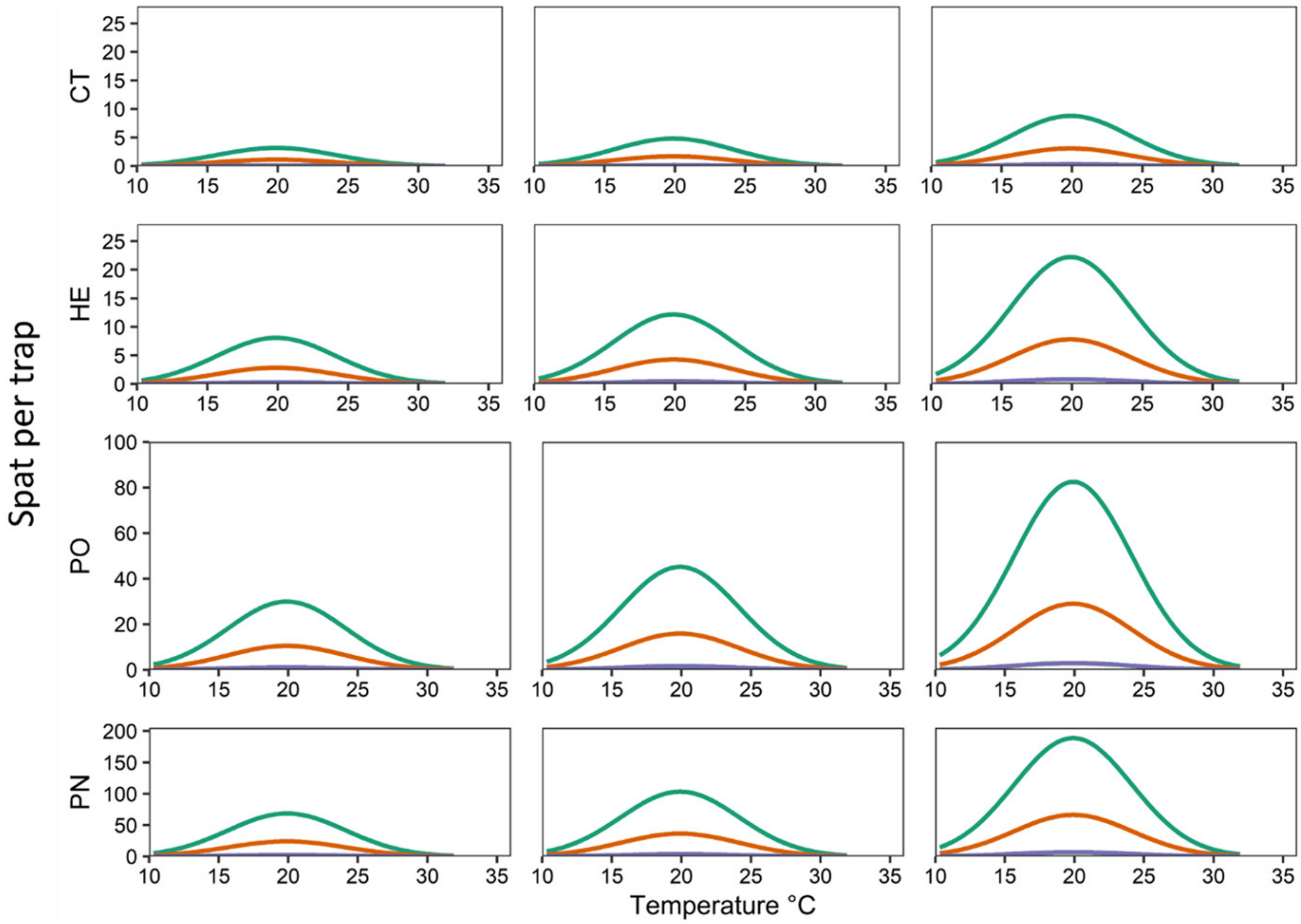

Figure 12. R model output for the four WC zones. In each group, the left panel represents a 42-day deployment, the center = 63 days, and the right = 80 days. Lines are as follows, green = a 10°C decrease during deployment; red = no temperature change during deployment, blue = +10°C change during deployment. Note the difference between scales.

Genetic evidence based on samples collected from 1995 to 1998 suggests the western Florida Panhandle subpopulations contain a subset of the diversity of the core population (Bert et al. 2014) and prior morphological work suggested there may be a remnant influence of the purported western gulf subspecies *Argopecten irradians amplicostatus* (Marelli & Arnold 2001). Many of the subpopulations have undergone periods of decline and recovery, some through restoration, so an updated genetics study that includes extensive sampling in Florida Bay might help to understand how populations outside the core persist and continue to have settlement events.

Increased settlement in areas of previously low settlement (<0.1 spat per trap; Arnold et al. 1998) occurred twice following restoration efforts. The 2001 peak in settlement in Citrus, Hernando, Pasco, and Pinellas counties occurred after extensive restoration efforts that combined both management actions (restrictions to harvest) and stock enhancement (Arnold et al. 2005). That population has persisted despite being reopened to harvest in Citrus and Hernando counties for two decades. A smaller restoration effort in Pine Island Sound (Leverone et al. 2010) correlated with a small peak in settlement (current study). The resultant settlement may reflect natural processes or the presence of a small subpopulation in this site resulting from restoration efforts, although populations that could be sustainably harvested were not established. Restoration efforts in Tampa Bay in the late 1990s may have resulted in a settlement peak, but there was no baseline for comparison prior to restoration. Similarly, it is tempting to credit a peak in St. Andrew Bay in 2005–2003 restoration efforts, but again, the data are merely suggestive and could simply be coincident.

Chlorophyll was not retained in any settlement model. Food limitation can result in variations in the spawning period over distances as small as 1.5 km (Bricelj et al. 1987). The threshold for food limitation is probably between 1 and 2 μg/L (Kirby-Smith & Barber 1974, Cahalan et al. 1989), which was observed in coastal counties of Florida at times. Conversely, high CHL levels associated with red tides suppress settlement through both negative effects upon the larvae and probably mortality of brood stock (Summerson & Peterson 1990). This mortality might drive the relationship such that the CHL model factor would be masked by whichever red tide metric was retained in the model.

The duration of the present study may be sufficient to describe early changes in spawning and subsequent settlement in terms of climate change. If the change of temperature is the driving factor that results in coordinated spawning leading to the largest settlement peaks, loss of the coldest temperatures at the southerly sites may be partially to blame for protracted

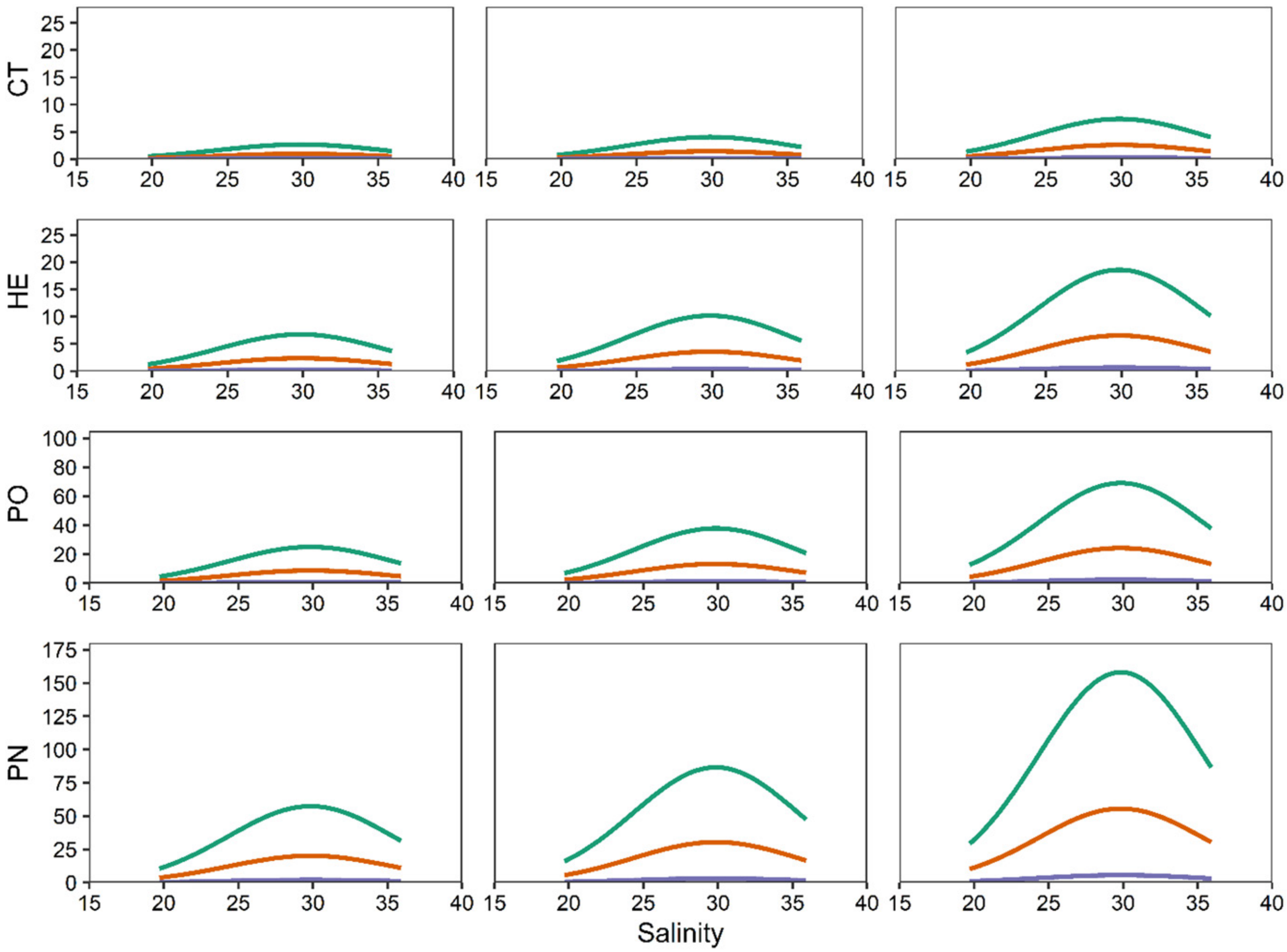

Figure 13. R model output for settlement in four WC zones (Pinellas, Pasco, Hernando, and Citrus) as a function of salinity varied in four zones. In each panel, green represents a 10°C decrease during the month before deployment, red represents no temperature change, and blue represents a 10°C increase. Deployment times were 42 days (left), 63 days (middle), and 80 days (right). Note the difference between scales.

and asynchronous settlement peaks. Evidence of climatic shifts has been observed in species such as snook (Purtlebaugh et al. 2020) and mangroves (Cavanaugh et al. 2014), so the possibility seems worth consideration. For example, in Tampa Bay declines of 10°C or more occurred in nine of 12 y from 2000 to 2011 but only twice in the following 6 y when water temperatures at the sites monitored did not drop below 12°C. Along the coast, changes exceeding 11°C occurred in eight of the first 11 y of the study (1999–2010) but only once in the subsequent 7 y. If water temperatures in colder months are warming, when peak larval abundance appears to be occurring, the larval duration and time between spawning and settlement could be declining (Cragg 2016), potentially leading to a decline in the connectivity of the subpopulations of bay scallops in Florida. Also, a shift from synchronized spawning resulting in large settlement peaks to protracted spawning distributed more broadly over many months might have important implications for juvenile survival and ultimately recruitment to the fishery.

The fate of bay scallop populations in Florida Gulf waters will depend on multiple factors. In some estuaries, such as Tampa Bay, seagrass acreage has rebounded from the 1970s (Tomasko et al. 2018). Bay scallops have been observed at low densities ($<0.01/m^2$) over a wider portion of the bay during similar surveys (Geiger et al. 2020, FWC unpublished data) than they were in the 1990s. The subpopulation cannot be considered recovered, yet the habitat recovery provides some reason for hope, especially with the possibility of more restoration efforts as the core population continues to adjust to climate change. The core populations of Citrus through Pinellas Counties and the Big Bend region still have massive seagrass habitats (Carlson et al. 2018a, 2018b, Jones et al. 2018). Scallops can inhabit most seagrass types and even open sand (Greenawalt-Boswell et al. 2007), but if loss of vegetative cover became severe, predation of spat and adults would likely increase. A loss of habitat or expansion of blooms of *Karenia brevis* that impact the core population could threaten the persistence of the species in Florida.

Recreational harvest efforts have increased from an estimated 5,143 vessels per year in 2000–2002 (Greenawalt et al. 2004) to 21,579 vessels in 2018 in the Steinhatchee site (Granneman et al. 2021) and similar increases have probably occurred throughout the region occupied by the core. Recent actions by the FWC, the agency in charge of regulating the harvest of bay scallops, included severe restrictions (2-wk season and a reduced limit of 40 scallops per person) in St. Joseph Bay after a red tide (2015) and subsequent recruit failure (2015–2016). The season

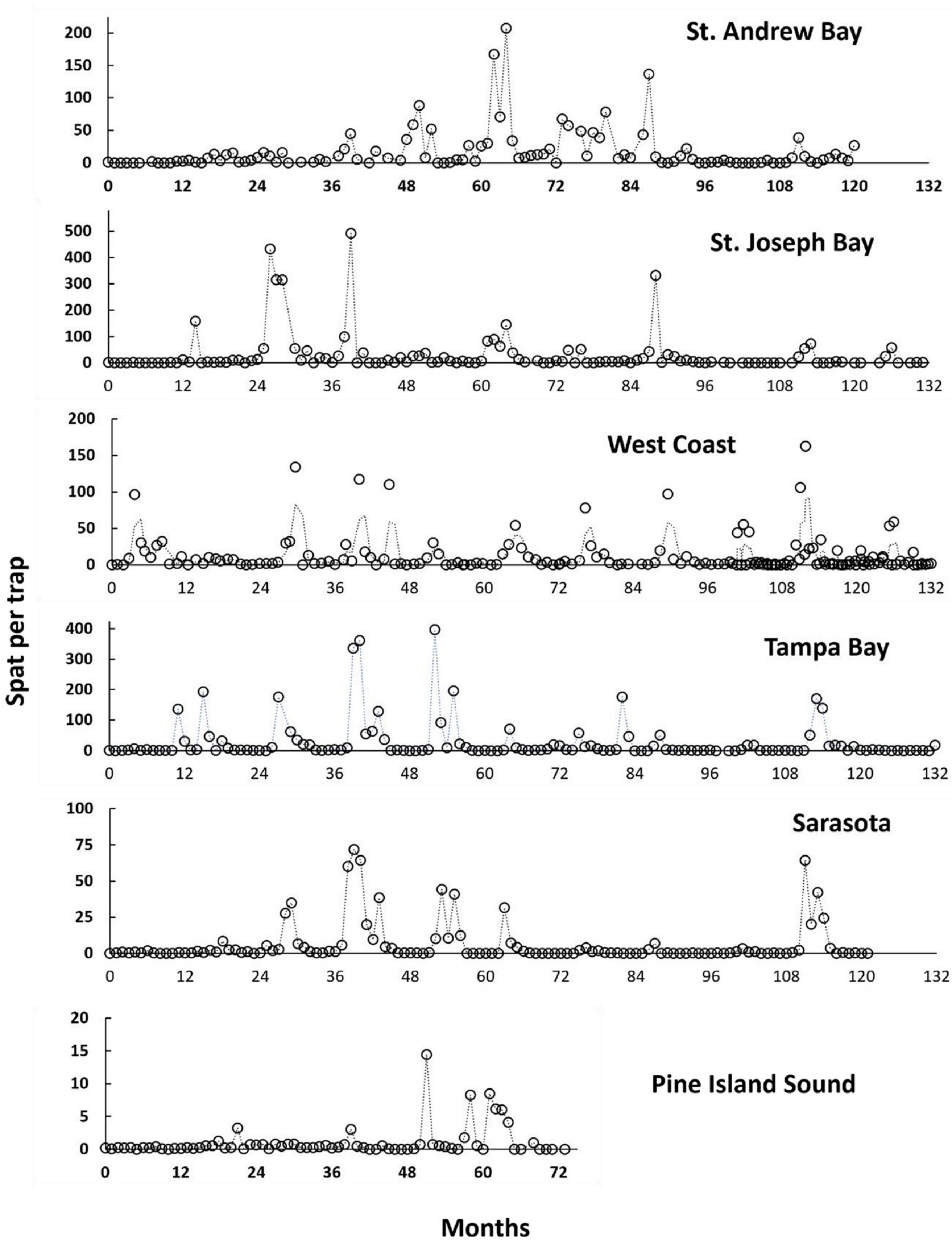

Figure 14. Spat settlement per trap (*Y* axis) in the months (*X* axis) after a red tide of 10,000 cells/L or greater. Note the difference between scales.

there remains shorter than the season in most open areas in 2022 (40 days as opposed to 86 days) with a limit of two gallons of whole scallops. Additionally, a 16-day extended early season harvest in Steinhatchee features a 1-gallon bag limit and the newly opened harvest area in Pasco County grants a 37-day season with a full 2-gallon limit (FWC rules history accessed July 2023, https://myfwc.com/fishing/saltwater/rulemaking/history/a-g/). Continued studies of the recreational fishery (Granneman et al. 2021), long-term restoration efforts, and responsive or proactive management decisions will all be required to help this restored saltwater fishery species remain a success story.

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APPENDIX

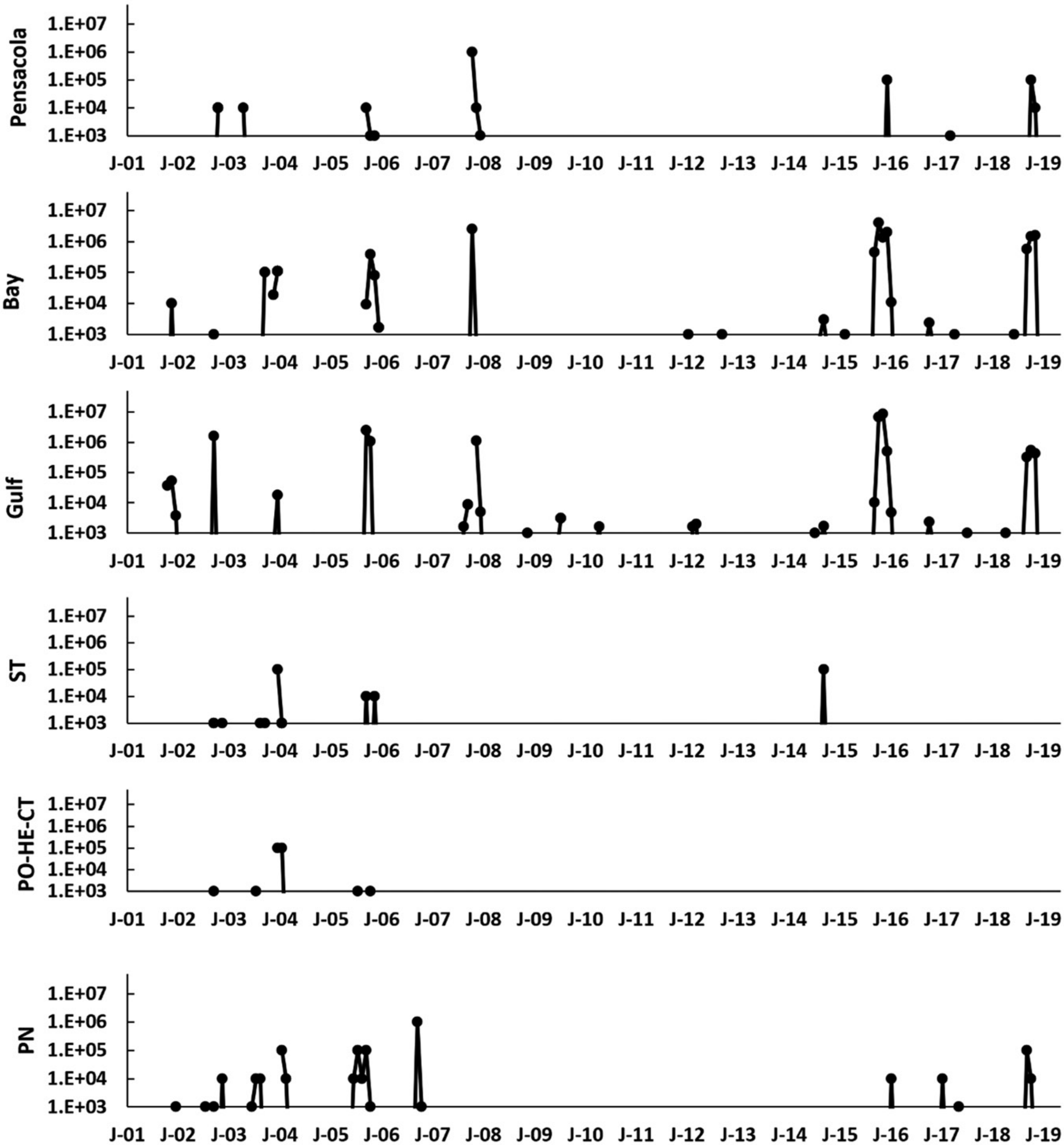

Figure A1. Monthly maximum red tide values (cells per liter) for five Gulf of Mexico sites within the central and panhandle region of Florida. Pasco, Hernando, and Citrus (PO-HE-CT) were joined for WC and presented separately from the coastal Pinellas site (PN).

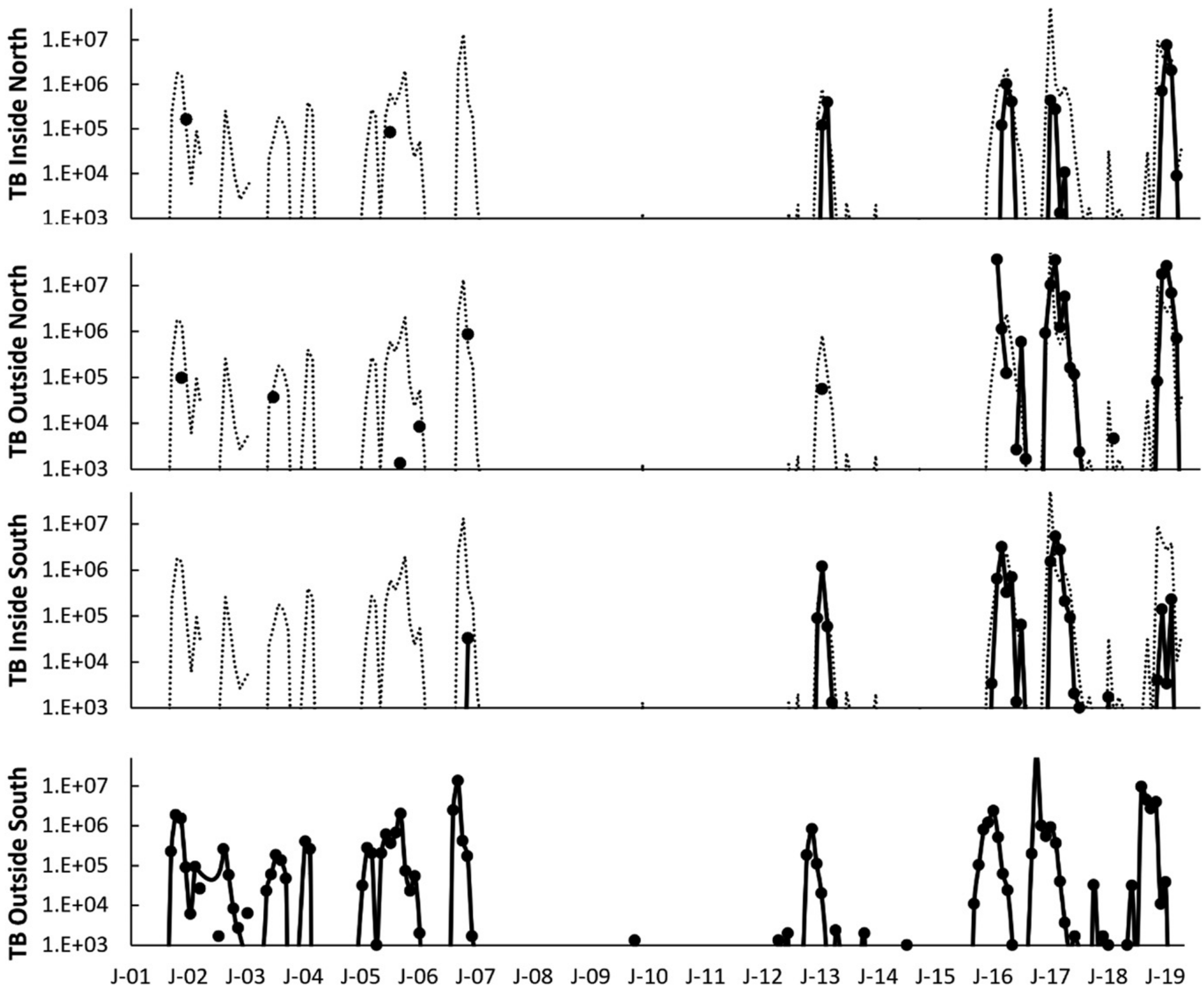

Figure A2. Monthly maximum red tide values (cells per liter) for four zones within Tampa Bay, FL. Three of the four zones of Tampa Bay may have been under sampled, so a potential red tide count based on the outer Tampa Bay South zone is shown.

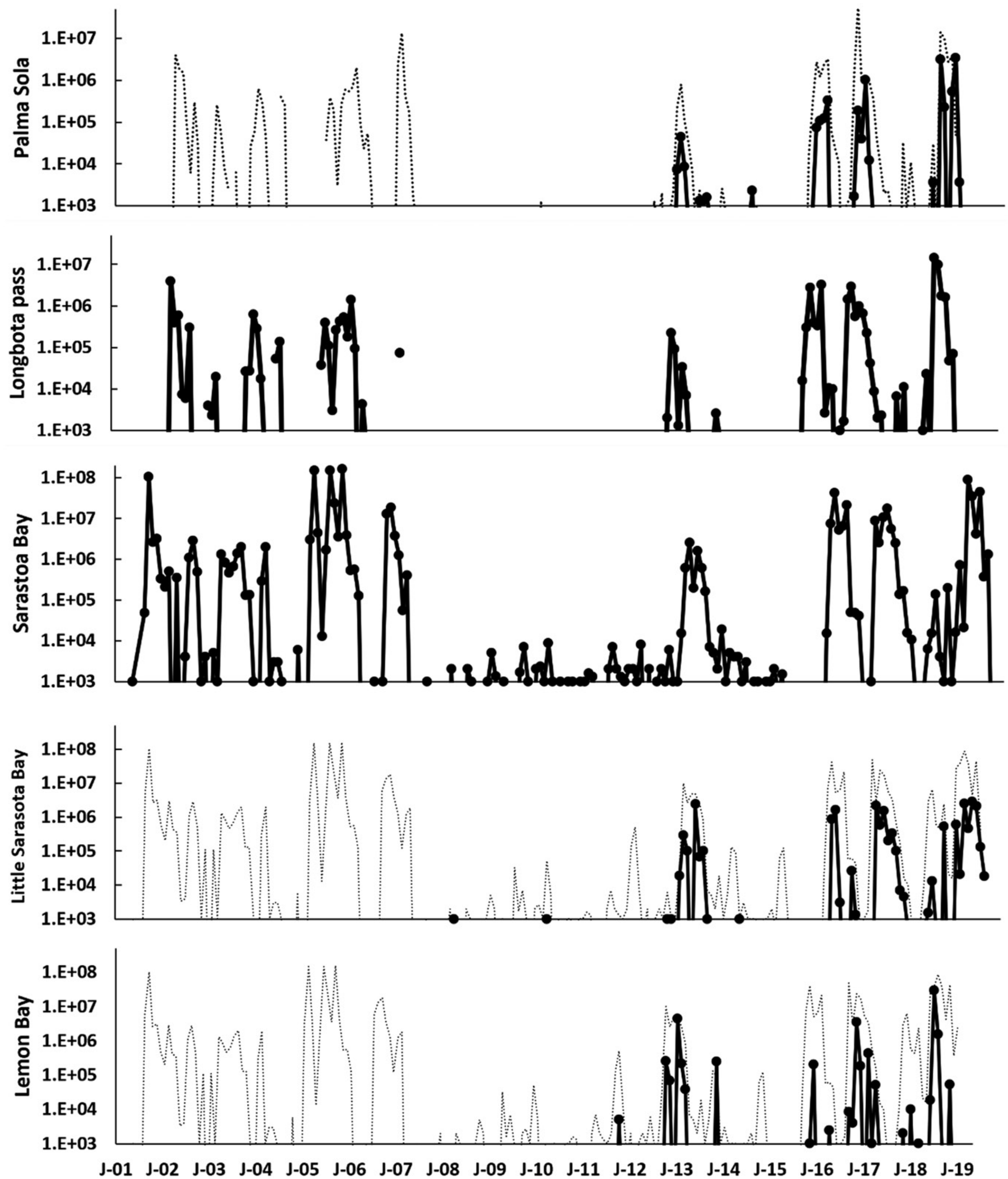

Figure A3. Monthly maximum red tide values (cells per liter) for five zones within Sarasota Bay, FL. In Palma Sola, Lemon Bay and Little Sarasota Bay, red tide may have been under sampled, therefore the nearest available red tide count is illustrated with a fine dotted line and should be considered as a potential red tide count based on the samples from Sarasota Bay and Longboat Pass.

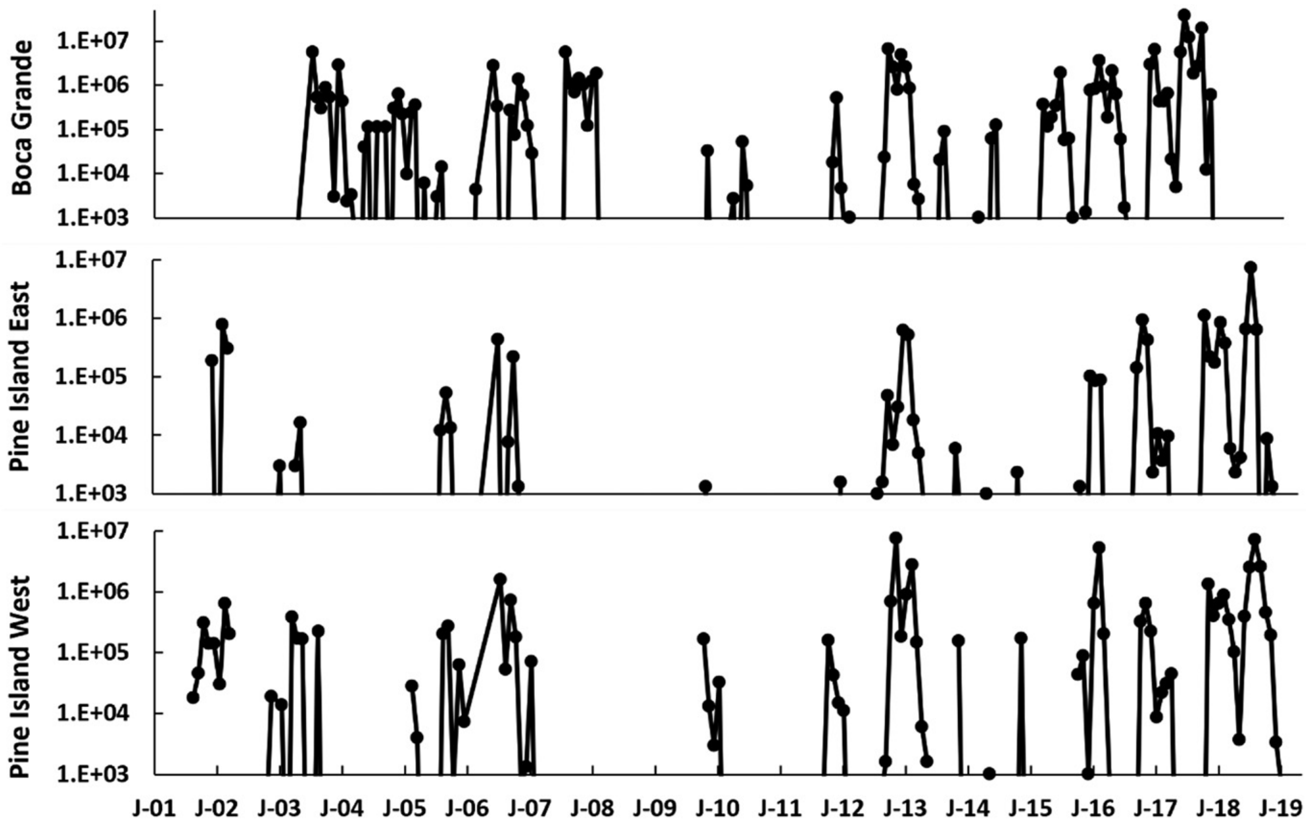

Figure A4. Monthly maximum red tide values (cells per liter) for three zones within Pine Island Sound, FL.

TABLE A1.

Summary of scallop settlement monitoring efforts.

Site	Start	End	*n*	Days	Traps	Deploy	Ret	Spat	S/T
PE	9/2/02	2/27/06	39	61.2	3	123	111	67	0.60
	10/2/08	11/20/08	1	49	4	4	4	221	55.25
	1/13/16	2/22/18	24	60.8	9	216	204	2	0.01
	–	–	–	–	–	**343**	**319**	**290**	**0.91**
CB	2/18/16	2/22/18	19	62.3	4	80	71	0	0
	–	–	–	–	–	**80**	**71**	**0**	**0**
SA	7/6/95	2/1/96	8	48.5	9	72	56	97	1.73
	9/24/03	12/9/05	18	57.0	4–9	117	116	4,732	40.79
	11/10/05	2/28/12	67	67.7	10	670	634	13,366	21.08
	1/24/12	12/15/15	46	60.5	12	552	540	7,676	14.21
	11/30/15	1/31/18	27	60.2	16	432	423	1,421	3.36
	–	–	–	–	–	**1,843**	**1,769**	**27,292**	**15.43**
CI	4/11/95	5/12/96	12	50.8	3	36	35	76	2.17
	–	–	–	–	–	**36**	**35**	**76**	**2.17**
SJ	7/23/95	6/14/96	13	46.7	15–18	213	172	19,797	115.10
	10/2/98	4/18/06	97	56.2	12	1,164	1,026	67,460	65.75
	3/20/06	12/14/15	108	64.3	12	1,296	1,160	26,401	22.76
	11/19/15	3/5/18	27	59.8	16	432	412	1,793	4.35
	–	–	–	–	–	**3,105**	**2,770**	**115,451**	**41.68**
SG	11/6/08	9/28/10	18	72.4	4	76	73	54	0.74
	1/11/16	4/2/18	26	60.0	6	155	150	215	1.43
	–	–	–	–	–	**231**	**223**	**269**	**1.21**
ST	8/11/94	2/17/95	7	44.9	27	189	177	1,923	10.86
	7/28/95	2/7/96	8	43.2	27	216	205	4,828	23.55
	12/17/96	7/31/97	7	49.1	6	42	36	38	1.06
	11/19/07	1/30/11	41	62.6	4–12	272	244	218	0.89
	11/20/15	3/15/08	27	60.7	10	270	245	2,121	8.66
	–	–	–	–	–	**989**	**907**	**9,128**	**10.06**

(*Continued*)

Site	Start	End	*n*	Days	Traps	Dep	Ret	Spat	S/T
WC (CT)	8/11/92	12/16/92	5	42.1	8–33	95	95	64	0.67
	7/13/93	3/15/94	9	46.5	27	238	173	19	0.11
	8/17/94	2/14/95	7	43.6	27	189	167	736	4.41
	7/27/95	2/8/96	8	43.8	25–29	216	175	10	0.06
	8/7/96	6/2/99	35	44.0	12	420	375	120	0.32
	4/6/99	8/6/01	37	43.0	18	666	612	903	1.48
	7/8/01	8/12/02	16	45.4	12	192	153	309	2.02
	7/16/02	6/16/06	63	46.1	11	671	613	442	0.72
	5/26/06	2/21/12	69	60.0	11	759	692	330	0.48
	1/17/12	3/16/18	73	60.8	8	584	538	277	0.51
	–	–	–	–	–	**4,030**	**3,593**	**3,210**	**0.89**
WC (HE)	8/7/96	1/29/97	7	44.9	6	42	42	48	1.14
	9/17/97	4/21/98	8	43.6	8	72	68	203	2.99
	4/2/98	8/9/02	72	43.6	6	432	417	3,351	8.04
	7/16/02	6/16/06	61	46.2	7	427	401	413	1.03
	5/26/06	6/8/10	49	59.2	7	343	327	1,072	3.28
	5/11/10	2/21/12	20	62.0	11	220	197	835	4.24
	1/17/12	316/18	73	60.8	9	657	647	904	1.40
	–	–	–	–	–	**2,193**	**2,099**	**6,826**	**3.25**
WC (PO)	8/22/94	2/1/96	17	46.1	19	323	274	1,079	3.93
	8/7/96	1/29/97	7	44.9	9	63	63	69	1.10
	9/17/97	4/21/98	8	43.6	14	126	109	2,445	22.43
	4/1/98	6/2/99	19	43.1	16	304	259	334	1.29
	5/18/99	8/6/01	37	42.9	19	703	635	4,032	6.35
	7/18/01	6/16/06	61	46.1	16	1,232	1,084	8,155	7.52
	5/26/06	6/8/10	49	59.2	16	784	628	10,560	16.82
	5/11/10	2/21/12	20	62.0	19	380	357	3,198	8.96
	1/17/12	3/16/18	73	61.0	16	1,168	1,055	5,239	4.97
	–	–	–	–	–	**5,083**	**4,464**	**35,111**	**7.87**
WC (PN)	8/22/94	2/1/96	17	46.1	8	136	97	376	3.88
	8/7/96	1/29/97	7	44.9	3	21	19	360	18.95
	9/17/97	6/16/06	142	44.7	2	284	257	6,060	23.58
	5/26/06	6/8/10	49	59.2	2	98	89	1,528	17.17
	5/11/10	2/21/12	20	62.0	4	80	71	727	10.23
	1/17/12	3/16/18	73	60.8	3	219	182	2,124	11.67
	–	–	–	–	–	**838**	**715**	**11,175**	**15.63**

Loc	Start	End	*n*	Days	Traps	Dep	Ret	Spat	S/T
TB	8/23/96	8/4/97	14	46.1	15	210	185	1,286	6.95
	8/21/97	2/10/98	7	43.9	18	126	113	7,341	64.96
	9/2/98	3/23/99	8	44.4	12	96	92	112	1.22
	8/25/00	11/25/02	36	44.6	9	324	316	1,535	4.86
	11/6/02	8/19/04	27	46.5	6	162	157	462	2.96
	7/21/04	3/22/05	8	50.1	28–34	228	216	24	0.11
	1/27/05	4/25/06	19	42.9	6	120	111	158	1.42
	3/28/06	2/15/13	83	60.0	6	498	457	17,287	37.83
	1/16/13	3/19/18	61	60.8	8	488	451	6,051	13.42
	–	–	–	–	–	**2,252**	**2,098**	**34,256**	**16.33**
SB (MC)	8/23/01	3/7/02	7	44.3	12	84	82	2	0.02
	2/13/02	8/13/03	23	45.8	8	184	167	93	0.56
	7/24/03	8/17/04	16	46.3	9	144	139	104	0.75
	7/22/04	3/12/07	40	46.9	12	480	459	77	0.17
	2/13/07	2/22/12	59	61.1	8	472	417	6,866	16.47
	1/18/12	5/8/18	73	60.5	6	450	417	1,349	3.24
	–	–	–	–	–	**1,814**	**1,681**	**8,491**	**5.05**
SB (SC)	3/17/08	1/10/12	41	63.1	15	645	621	4,488	7.23
	12/13/11	12/20/12	13	66.1	10	100	96	50	0.52
	12/20/12	12/12/17	57	63.3	6	342	336	451	1.34
	–	–	–	–	–	**1,087**	**1,053**	**4,989**	**4.74**
CC	10/13/08	2/9/12	38	62.3	12	456	397	2,694	6.79
	1/5/12	12/20/12	10	64.2	8	80	74	36	0.49
	–	–	–	–	–	**536**	**471**	**2,730**	**5.80**

(*Continued*)

Loc	Start	End	*n*	Days	Traps	Dep	Ret	Spat	S/T
PI*	5/19/03	9/6/05	38	44.2	12	417	404	200	0.50
	8/16/05	8/08/08	43	55.1	15	585	556	36	0.06
	7/11/08	1/14/12	41	63.6	18	708	640	743	1.16
	12/15/11	3/13/13	12	68.7	6	72	66	13	0.20
	1/15/13	1/24/18	9	63.2	9	513	451	228	0.51
	–	–	–	–	–	**2,295**	**2,117**	**1,220**	**0.58**
FB	1/27/95	9/4/96	8	90.3	9–16	79	69	2,772	40.17
	7/3/98	9/18/99	16	50.6	9	144	143	138	0.97
	–	–	–	–	–	**223**	**212**	**2,910**	**13.73**
Grand totals	–	–	–	–	–	**26,978**	**24,597**	**263,424**	**10.71**

Sampling sites include CB, Choctawhatchee Bay; CC, Charlotte County; CI, Crooked Island Sound; FB, Rabbit Key Basin of Florida Bay; PE, Pensacola Bay; PI, Pine Island Sound (* - in this site volunteers deployed variable numbers of traps, so the average number of traps per month is reported); SA, St. Andrew Bay; SB, Sarasota Bay (with two counties treated as Zones: MC, Manatee County; SC, Sarasota County); SJ, St. Joseph Bay; ST, Steinhatchee; TB, Tampa Bay; WC, West Coast (with four counties treated as Zones: CT Citrus County; HE, Hernando County; PO, Pasco County; PN, Pinellas County). Columns as follows: Start, start date of deployments for a given arrangement; End, end date of deployments for a given arrangement; *n*, total number of deployment events per each arrangement; Days, average number of days traps were deployed per event; Traps, the number of traps deployed during each event; Deploy, the total number of traps deployed under a given arrangement; Ret, the total number of traps retrieved under a given arrangement; Spat, the total number of spat settled to traps; S/T, average spat settlement per trap (totals for deploy, Ret, Spat, and S/T for each site in bold).

TABLE A2.

General linear mixed model output for six bay scallop settlement sites with sufficient environmental data.

SA	*n* = 1,111											
Int-ZE	Ta	Ta^2	Sa	Sa^2	ΔT	ΔT^2	Days	$Days^2$	ZM	ZN	–	Rm
0.58	−0.01	−1.18	−0.26	0.01	−0.33	0.116	0.07	0.11	−1.28	−0.45	–	−0.39
2.17	0.08	0.10	0.16	0.01	−0.12	0.04	0.08	0.04	0.23	0.27	–	0.07
−3.67	−0.15	−1.37	−0.58	0.0	−0.47	−0.258	−0.09	0.03	−1.73	−0.98	–	−0.52
4.84	0.16	−0.98	0.06	0.02	−0.18	0.01	0.23	0.19	−0.84	0.08	–	−0.26

SJ	*n* = 1,600											
Int-ZE	Ta	Ta^2	Sa	Sa^2	ΔT	ΔT^2	Days	$Days^2$	ZN	ZS	ZW	R10
0.90	−636	−0.78	0.61	0.16	−0.79	0.10	−0.05	−0.04	−0.78	−0.98	−0.16	0.66
0.20	0.08	0.10	0.11	0.05	0.10	0.07	0.105	0.03	0.32	0.17	0.22	0.07
0.51	−0.78	−0.98	0.40	0.07	−0.94	−0.05	−0.24	−0.10	−1.40	−1.31	−0.59	0.51
1.29	0.10	−0.58	0.82	0.25	−0.64	0.24	0.15	0.02	0.16	−0.64	0.27	0.81

WC	*n* = 7,712											
Int-CT	Ta	Ta^2	Sa	Sa^2	ΔT	ΔT^2	Days	$Days^2$	ZHE	ZPO	ZPN	R10
−0.51	−0.90	−0.81	0.18	−0.12	−1.02	−0.23	0.21	0.04	0.93	2.24	3.07	0.29
0.13	0.04	0.04	0.04	0.03	0.04	0.03	0.04	0.03	0.13	0.12	0.17	0.04
−0.77	−0.99	−0.89	0.10	−0.18	−1.10	−0.29	0.14	−0.01	0.67	2.00	2.74	0.21
−0.25	−0.81	−0.72	0.26	−0.06	−0.95	−0.18	0.09	0.09	1.19	2.47	3.40	0.36

TB	*n* = 2,096											
Int-IN	Ta	Ta^2	Sa	Sa^2	ΔT	ΔT^2	Days	$Days^2$	ZIS	ZON	–	R10
0.28	−1.86	−0.41	0.02	0.25	−0.43	−0.24	0.78	−0.45	−2.09	0.69	–	0.62
0.29	0.08	0.06	0.08	0.04	0.06	0.04	0.08	0.069	0.69	0.27	–	0.08
−0.28	−2.02	−0.53	0.14	0.18	0.32	−0.32	0.64	−0.57	−3.27	0.15	–	0.47
0.84	−1.70	−0.29	0.17	0.33	0.54	−0.17	0.93	−0.34	−0.92	1.22	–	0.77

(*Continued*)

SB												
	n = 1,115											
Int-ZLB	Ta	Ta^2	S	S^2	ΔT	ΔT^2	Days	Days^2	ZLSB	ZSB	–	LR
22.69	−1.84	−0.36	−1.72	0.03	0.85	−0.50	0.34	−0.32	1.33	1.94	–	−0.81
11.86	0.36	0.14	0.75	0.01	0.14	0.11	0.14	0.07	0.40	0.39	–	0.17
−0.56	−2.17	−0.63	−3.19	0.01	0.58	−0.72	−0.07	−0.46	0.550	1.17	–	−1.13
45.94	−1.51	−0.90	−0.25	0.05	1.12	−0.28	0.60	−0.18	2.10	2.70	–	−0.48
PI												
	n = 2,047											
Int-ZM	Ta	Ta^2	Sa	Sa^2	ΔT	ΔT^2	Days	Days^2	ZN	ZS	–	R10
−1.372	−0.51	−0.42	0.27	−0.61	−0.01	0.06	0.17	−0.05	−0.55	0.07	–	0.68
0.239	0.11	0.10	0.14	0.13	0.08	0.06	0.12	0.06	0.21	0.21	–	0.08
−1.84	−0.72	−0.61	−0.01	−0.85	−0.17	−0.06	−0.07	−0.15	–0.95	−0.35	–	0.52
−0.90	−0.30	−0.24	0.54	−0.36	0.16	0.17	0.41	−0.05	−0.15	0.49	–	0.84

Int, model intercept; For site abbreviations see Table 1 legend; for variable abbreviations see Table 3 legend. The top number is the model value, followed by the SE, and the upper and lower 95% confidence intervals. Zones (Z) are specific to each bay system (see the text) and the model predicts the settlement in the highest zone and the expected reduction in other zones within a site.