Oyster monitoring in the northern estuaries on the southeast coast of Florida

Final Report

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Florida Fish and Wildlife Conservation Commission

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TABLE OF CONTENTS

Executive Summary

This report summarizes oyster population monitoring at six sites within three southeast Florida estuaries from 2005 through 2014 as part of the prerestoration monitoring and assessment component of the Comprehensive Everglades Restoration Plan. Study locations included St. Lucie Estuary (3 study sites), Loxahatchee River (2 sites), and Lake Worth Lagoon. Settled oyster density was monitored twice per year at stations within each study site. Disease (*Perkinsus marinus*) prevalence and intensity, reproductive development, juvenile recruitment, and juvenile growth and survivorship were monitored on a monthly basis. Water quality monitoring, which included measurements of salinity, temperature, dissolved oxygen concentration, pH, depth and clarity, was conducted in conjunction with monthly sampling at all stations.

Salinity varied greatly among the estuaries, and each study site fell into one of three primary groups: a high salinity group, a moderate salinity group, and a low salinity group. The Lake Worth and Loxahatchee-South study sites fell into the high salinity group, with annual means that ranged from 20 to 32. The moderate salinity group included the Loxahatchee-North and St. Lucie-Central sites, where annual means ranged from 6 to 24. The St. Lucie-North and South sites comprised the low salinity group, and exhibited annual means that ranged from 4 to 19. All three estuaries were impacted, to varying degrees, by active tropical storm seasons as well as local water management practices during the study. The St. Lucie Estuary was most severely impacted by managed freshwater releases, which frequently decreased salinities below the tolerable range for oysters. As a result, live oysters were virtually absent from the St. Lucie Estuary study sites in 2005, when the freshwater introductions were most pronounced, and experienced periods of recovery and decline throughout the study. Oysters were present at all other sites, but densities were lower in 2005 than in subsequent years.

Although the impacts from low salinity events were more acute, long term exposure to high salinities also negatively impacted oysters in the estuaries. Salinities often exceeded the optimal range in Loxahatchee River and Lake Worth Lagoon, and even in the St. Lucie Estuary in 2011 and early 2012, and, during those periods, dermo prevalence in oysters was high. Increased predation and disease rates are typically associated with higher salinities and temperatures, but the extent to which a higher salinity regime can affect an oyster population is most exemplified by the dramatic increase in dermo prevalence measured

in oysters from the St. Lucie Estuary from 2011 – 2013. Prior to 2011, annual prevalence rates in the central estuary were less than 18% but by 2012, infection rates had increased to over 60%.

The timing of reproductive development in oysters varied among sites and years, but active reproductive development, including gametogenesis, spawning, and gonadal recycling, typically occurred from March to October with oysters entering the resting stage during the winter months. Analyses of gonadal tissues showed that during periods of low salinity related to storm activity and water releases, most oysters, as long as they survived, continued to develop gametes and spawn as expected; however, there were significantly fewer oysters developing gametes in those years. Recruitment patterns were also similar among estuaries, with recruits commonly present in arrays retrieved from April through December. Recruitment rates in LWL and LOX approached or exceeded 2 spat/shell/month, whereas rates in the SLE were generally less than 1 spat/shell/month. Each estuary experienced periodic decreases in oyster densities after changes in estuarine conditions, but in most cases recruits were detected shortly after conditions had returned to those tolerable to oysters. This suggests that even in sites where oysters almost disappeared completely, small relict populations, an exogenous larval source, or most likely the combination of the two, contributed recruits.

Oyster abundance, health, and population ecology within the three estuaries generally fell within expected ranges for south Florida oyster populations; however, the occurrence of heavy rainfall and subsequent freshwater releases in the summer months frequently forced estuarine salinities outside of tolerable ranges and as a result oyster populations were negatively impacted. Although oysters in the SLE exhibited the capacity to recover when salinities stabilized following low-salinity events, continued perturbations may so degrade oyster populations that appropriate substrate may no longer exist as a site of larval settlement, even if a supply of larvae persists. High salinities also negatively impacted oyster populations, although those impacts were more slowly realized. Future actions, such as consideration of minimum flows for each estuary during the dry seasons to keep salinities closer to the optimal range for oysters, may reduce predation and disease as well as allow some adaptation to the inevitable periods of low salinity.

Introduction

The eastern oyster, *Crassostrea virginica*, occupies estuarine and nearshore habitats along the Atlantic and Gulf of Mexico coasts of the United States. This species supported a subsistence fishery even before Europeans colonized what is now the United States (MacKenzie et al. 1997), and throughout recent history has provided an important economic and cultural resource to coastal residents. In addition to its direct economic benefits, the oyster provides essential habitat for many other estuarine inhabitants (Bahr and Lanier 1981). The eastern oyster is one of the most culturally, economically, and ecologically important species of U.S. coastal waters.

Oysters are frequently used as indicators of water quality in East Coast and Gulf estuaries. Oysters thrive under the variable salinity regime that is a natural component of a healthy estuary (La Peyre et al. 2009), such that too much stability can be detrimental; however, changes in freshwater inflow can have varied effects on the health and distribution of oyster populations and on economic factors such as commercial oyster landings (Turner 2006). Those impacts can be estuary specific, leading to increases or decreases in oyster productivity, depending on the magnitude and timescale of the change in freshwater supply (Wilber 1992). One of the most studied discussions of altered freshwater flow concerns the Apalachicola River in northeast Florida (Wilber 1992). In that region, reduced river flow has led to higher estuarine salinities, which in turn have allowed for increased predation on oysters and decreased primary production (Livingston et al. 1997). Water management strategies such as diversion of freshwater out of a river before it reaches the estuary, as seen in the Apalachicola River, can disrupt natural cycles for oysters and other estuarine organisms. At the opposite extreme, management strategies such as the channelization of tributaries have led to increased delivery of nutrients and organic matter to many estuaries, such as Galveston Bay in Texas, as well as increased flows of freshwater that drastically alter the ecology and health of such estuaries (Klinck et al. 2002).

In Florida, oysters occur along both the Atlantic and Gulf coasts in almost all estuarine and nearshore waters. Along the Atlantic coast, oysters are generally confined to estuaries, bays, and lagoons, such as Lake Worth Lagoon or the St. Lucie Estuary. Those waters, and other coastal waters on the southeast coast of the state, have experienced altered patterns of freshwater delivery and quantity as a result of water management practices related to the St. Johns and Kissimmee river basins, Lake Okeechobee, and the Everglades. In particular, channelization and redirection of freshwater out of inland basins and into coastal estuarine waters has altered both the frequency and the rate of salinity variations in those coastal waters. The impacts of those alterations are often most detrimental during the wet season (June to September), when rainfall can be 400% higher than during the dry season (Carriker and Borisova 2011).

The Comprehensive Everglades Restoration Plan (CERP) was implemented as a means of restoring, to the greatest degree possible, natural freshwater flow to the Everglades wetland system and reducing detrimental flow to both coasts of South Florida (U.S. Army Corps of Engineers Jacksonville District and South Florida Water Management District 1999). The monitoring and assessment component of CERP was designed to provide a diverse approach to documenting and describing the impacts of changed freshwater flow to the flora and fauna of those inland landscapes and coastal waters. Because it is so widely distributed and has such essential habitat value, the eastern oyster was chosen as a target species for inclusion in the estuarine monitoring component of CERP.

The objective of this study was to provide a baseline prerestoration description of several aspects of oyster ecology in several southeast Florida estuaries for comparison with future postrestoration conditions. Specifically, this study examined the distribution and abundance of settled oysters, prevalence and intensity of infection by the parasitic protozoan *Perkinsus marinus*, reproductive development, juvenile recruitment, and juvenile growth and survivorship in the St. Lucie Estuary, Loxahatchee River Estuary, and Lake Worth Lagoon from 2005 through 2014. All three estuaries were located in regions that have been strongly affected by freshwater management activities and stand to benefit from CERP restoration activities. Results of this study will not only provide a baseline description of oysters in each estuary, but also will serve as a guide for determining whether CERP water management strategies (Barnes et al. 2007) are appropriate for achieving restoration goals.

Methods

Study Sites

Oyster sampling was conducted from January 2005 through December 2014 on oyster reefs within three estuarine ecosystems on the southeast coast of Florida: the St. Lucie estuary (SLE), the Loxahatchee River Estuary (LOX), and Lake Worth Lagoon (LWL). Within the SLE, the north fork, the south fork, and the central estuary were considered to be separate sites each with three sampled oyster stations (i.e., oyster reefs), or three potential stations if no oysters were present (Figure 1). Similarly, in the LOX, the northwest fork and the southwest fork were considered to be separate sites each with three sampled stations. Three stations were also selected for monitoring in LWL. This strategy resulted in a total of six separate study sites (St. Lucie-North, St. Lucie-South, St. Lucie-Central, Loxahatchee-North, Loxahatchee-South, and Lake Worth) each with three stations, for a total of 18 monitored oyster reefs. Station coordinates are listed in Table 1 and locations are shown in Figure 1.

Table 1. Station coordinates for CERP oyster monitoring sites in southeast Florida.

Site	Station	Latitude °N	Longitude °W
St. Lucie North Fork	1	27 13.232	80 16.737
St. Lucie North Fork	2	27 12.686	80 15.846
St. Lucie North Fork	3	27 12.459	80 17.072
St. Lucie South Fork	1	27 11.691	80 15.636
St. Lucie South Fork	2	27 11.228	80 16.149
St. Lucie South Fork	3	27 09.949	80 15.671
St. Lucie Central Estuary	1	27 12.743	80 14.599
St. Lucie Central Estuary	2	27 12.087	80 14.493
St. Lucie Central Estuary	3	27 12.096	80 15.282
Loxahatchee NW Fork	1	26 58.164	80 07.688
Loxahatchee NW Fork	2	26 58.237	80 07.649
Loxahatchee NW Fork	3	26 58.370	80 07.686
Loxahatchee SW Fork	1	26 56.574	80 07.112
Loxahatchee SW Fork	2	26 56.630	80 07.280
Loxahatchee SW Fork	3	26 56.560	80 07.257
Lake Worth Lagoon	1	26 40.181	80 02.618
Lake Worth Lagoon	2	26 38.848	80 02.436
Lake Worth Lagoon	3	26 35.851	80 02.417

Water Quality

Monthly water quality sampling was conducted in conjunction with field sampling at all stations within each study site from 2005 through 2014. Recorded parameters included salinity, temperature, dissolved oxygen concentration, pH, depth and clarity. Depth was determined with a sounding line or incremented meter stick and clarity was obtained by using a standard Secchi disk. Water clarity is presented as a Secchi penetration value which is calculated as the percentage of the water column through which the Secchi disk could be seen. All other parameters were measured with a calibrated YSI or

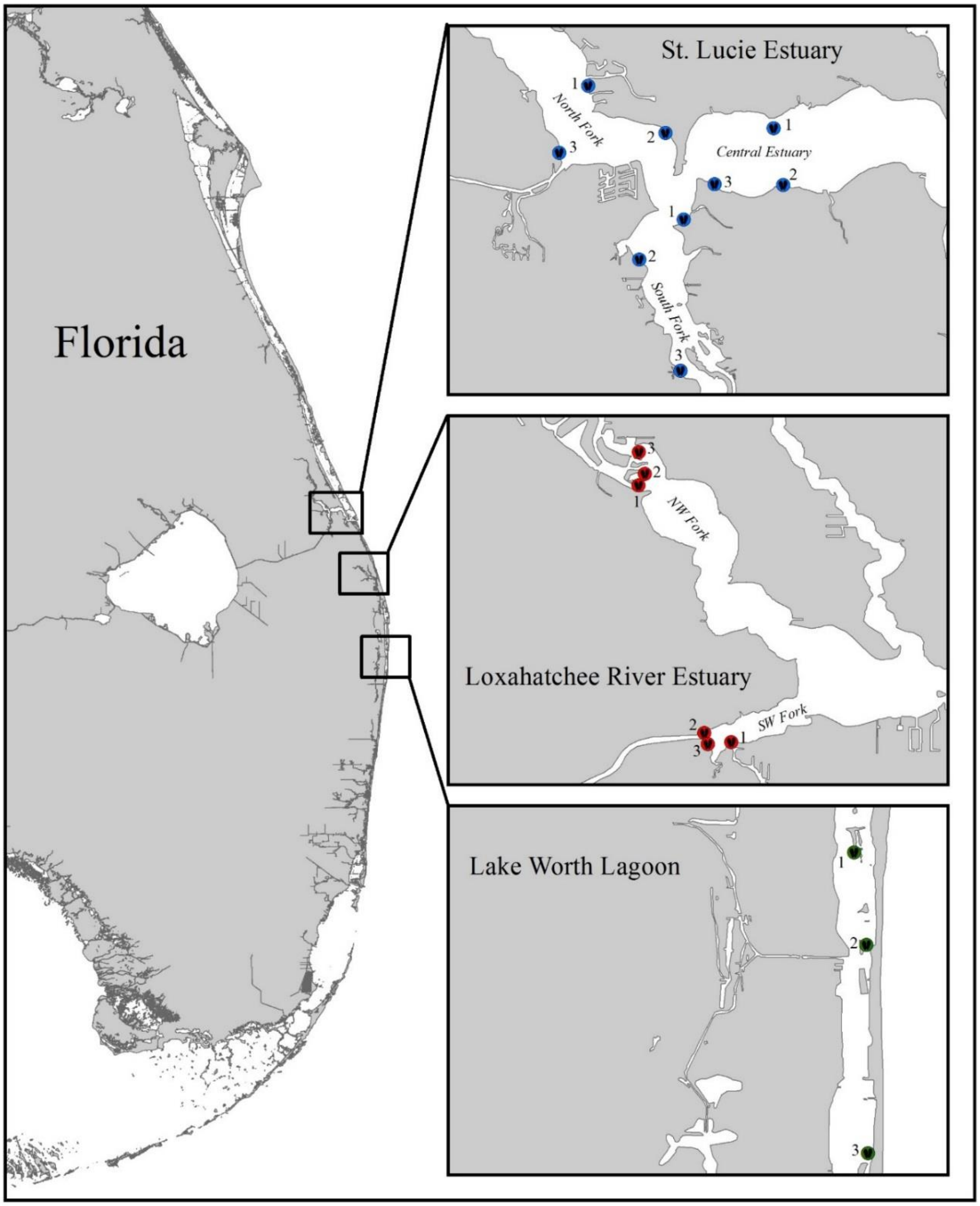

Figure 1. Oyster monitoring stations in the St. Lucie Estuary (blue), Loxahatchee River Estuary (red) and Lake Worth Lagoon (green).

EcoTestr instrument with sensors. Graphical presentations show the values measured at each station within each site. Flow rates as recorded by the South Florida Water Management District, the United States Geological Survey, and the United States Army Corps of Engineers are also included for comparisons.

Settled Oyster Density

Oyster population surveys were conducted twice per year at all stations within each study site from 2005 through 2014. In 2005, sampling occurred during the winter and summer. After 2005, it was determined that surveys in the spring and fall would be more appropriate because those would occur near the beginning and end, respectively, of the oyster spawning season. The oyster survey methodology used in the present study was based on that of Lenihan and Peterson (1998) and Grizzle et al. (2005). From 2005 – 2007, 10 replicate 1-m^2 quadrats were deployed randomly on each sampled reef. After 2007, 15 replicate ¼-m^2 quadrats were deployed randomly on each sampled reef. Throughout the present study, all oysters within each quadrat were collected for determination of the total number of live oysters and of dead oysters with articulated shells, as well as the proportion of dead oysters to the total number of live oysters and dead oysters. In addition, shell height (SH; maximum linear distance from the umbo to the ventral shell margin) was measured for a maximum of 50 live oysters from each quadrat. Mean live oyster density, ratio of dead oysters to total oysters, and mean live oyster SHs were calculated and plotted for each station within each site. The mean SH was calculated for each quadrat, resulting in 10 or 15 data points per station each survey, and used for all statistical analyses.

Disease and Reproductive Development

Live oysters were collected monthly from February 2005 through December 2014 for analysis of gonadal development stage and from March 2005 through December 2014 for the prevalence and intensity of the oyster disease *Perkinsus marinus* (dermo). Each month, a sample of five oysters from each of the three stations within a study site (total N = five oysters * three stations * six sites = maximum 90 per month) were transported, live and chilled, to the FWRI laboratory for processing. If no live oysters were available at one or two of the stations within a site, additional oysters were collected from another station within that site if possible. Each individual oyster was processed for reproductive stage and disease status according to the methods described below.

For *P. marinus* (dermo) disease analyses, prevalence and intensity were diagnosed with Ray's fluid thioglycollate media (RFTM) method (Ray 1966). Sections of mantle and gill tissue, each approximately 1 cm^2 in area, were clipped from each individual using sterile surgical scissors, placed in RFTM treated with antibiotics and antifungals, and incubated for 7 days in the dark at room temperature. After the incubation period, tissues were placed on glass slides, macerated with sterile razor blades, and stained with Lugol's solution. Mantle and gill tissues were then examined at ×40 magnification for the presence of *P. marinus* hypnospores. Parasite density (infection intensity) was ranked according to the Mackin scale (Table 2; Mackin 1962). Mean infection intensity for each oyster was calculated as the average infection intensity from mantle and gill tissues. Parasitic prevalence was calculated as the percentage of oysters infected, regardless of infection level. Mean infection intensity and the percentage of infected oysters were plotted for each station within each site.

Table 2. Mackin scale of *Perkinsus marinus* infection intensity stages (Mackin 1962)

Stage	Category	Number of cells
0	Uninfected	None detected
0.5	Very light	<10
1	Light	11–100 cells
2	Light to moderate	Local concentrations of 24–50 cells
3	Moderate	3 cells in all fields at 100×
4	Moderate heavy	High numbers in all tissues
5	Heavy	Enormous numbers

The tissues remaining after the dermo analyses were preserved for histological determination of reproductive development stage. Tissues were fixed in a modified Davidson's fixative solution (Shaw and Battle 1957), the main difference being no glycerin was included, for a minimum of 2 days. Once fixed, cross-sections were taken approximately halfway between the adductor muscle and the anterior margin, to include the gonad. Cross-sections were placed in tissue-embedding cassettes, rinsed, and then transferred to a 70% solution of ethanol. Histological preparation consisted of dehydrating each oyster in 95% ethanol then embedding the tissue in paraffin. The sections were stained with hematoxylin and eosin and mounted on glass slides for analysis. Histological cross-sections were examined at ×200-400 magnification to ascertain sex and assign a reproductive stage according to a classification scheme modified from the work of Fisher et al. (1996) which graded oysters on a scale of 0 to 10 (Table 3). Stage 0 represents a gonad with no gametes; stages 1–4 represent the progression of the gonad through developing and prespawing phases but lacking evidence of spawning; stages 5 and 6 represent stages of complete ripeness and very early gamete release; stages 7–9 represent depleting, spent, or recycling gonads, and stage 10 represents gonads devoid of gametes but exhibiting evidence of cytolysis indicative of prior spawning. Since oysters can live beyond a single spawning cycle, this scale can be interpreted as cyclical. For graphical presentation, the 11 reproductive stages were simplified by combining them into 4 different categories. The indifferent category includes those oysters that are stage 0 or 10; the developing category includes those oysters that are stages 1–4; the ripe/spawning category includes those oysters that are stages 5 or 6, and the spent/recycling category includes those oysters that are stages 7–9.

Table 3. Qualitative reproductive staging criteria for oysters collected from Florida waters (Fisher et al. 1996)

Value	Observations
0	Neuter or resting stage with no visible signs of gametes
1	Gametogenesis has begun with no mature gametes
2	First appearance of mature gametes to approximately one-third mature gametes in follicles
3	Follicles have approximately equal proportions of mature and developing gametes
4	Gametogenesis progressing, but follicles dominated by mature gametes
5	Follicles distended and filled with ripe gametes, limited gametogenesis, ova compacted into polygonal configurations, and sperm have visible tails
6	Active emission (spawning) occurring; general reduction in sperm density or morphological rounding of ova
7	Follicles one-half depleted of mature gametes
8	Gonadal area reduced, follicles two-thirds depleted of mature gametes
9	Only residual gametes remain, some cytolysis evident
10	Gonads completely devoid of gametes and cytolysis is ongoing

Juvenile Recruitment

Juvenile oyster (spat) recruitment was monitored monthly at all stations within each study site from February 2005 through December 2014. Three replicate spat monitoring arrays were deployed at each station within each site and retrieved monthly. Spat monitoring arrays were constructed and processed, as adapted from Southworth and Mann (2004). Each array consisted of 12 axenic adult oyster shells (SH, 5 -10 cm) with a hole drilled in the center. Two lengths of galvanized wire were strung with 6 shells each, which were then suspended from the arms of a T-shaped PVC frame. The shells were oriented with their inner surfaces facing downward, and the PVC frame was pushed into the sediment until the bottommost shell was approximately 5 cm above the sediment surface. Upon retrieval, the shell strings were labeled and bagged, and new shell strings were placed immediately on the PVC frame. The retrieved shell strings were returned to the laboratory, where each shell was examined for oyster spat with the aid of a magnification lamp or dissecting microscope (maximum magnification, ×65).

Because spat monitoring arrays were deployed for a period of 1 month, data were not obtained until after the initial retrieval of shell strings. As a result, recruitment data were not collected until March 2005 at any of the sites. Freshwater flushing into the SLE in summer 2005 precipitated a public health advisory resulting from a bloom of a toxic cyanobacterium (*Microcystis aeruginosa*). Consequently, no monitoring could be conducted in the SLE during August, September and October 2005, and the spat arrays deployed in July 2005 were not recovered until November 2005. Similarly, another health advisory was issued for the SLE in 2013 and, as a result, spat monitoring arrays were not retrieved from varying stations in the three study sites from August through November 2013. Last, the October 2005 monitoring in the LOX and LWL sites had to be delayed until early November because of the effects of Hurricane Wilma.

Juvenile oyster recruitment was estimated by counting settled spat on the underside of the middle 4 shells on each shell string (Southworth and Mann 2004). Recruitment rates were obtained by dividing the raw number of spat per shell by the number of days the shell had been deployed, and then standardizing to a 28-day month. Those standardized values were then used to compute the mean spat per shell per month for each successfully retrieved replicate, or spat monitoring array, resulting in a maximum of 3 data points per station each month. Mean numbers of spat per shell per month were plotted for each station within each site. Recruitment rates are reported by retrieval date throughout.

Juvenile Growth and Predation

Several methods were used to estimate juvenile oyster growth and predation during the present study. From 2005 – 2007, broodstock were collected from each estuary and delivered to Harbor Branch

Oceanographic Institution (HBOI) for conditioning and production of juvenile oysters. In 2005, after rearing cultchless juvenile oysters to a mean size of 10 and 20 mm SH, the juvenile oysters were transported from HBOI to their respective field sites for planting into wire mesh cages. Each cage included an open and closed compartment in order to estimate mortality attributable to macrofaunal predation. Monthly monitoring occurred for approximately one year and involved counting the total number of live oysters remaining in each compartment and measuring the SHs of 30 randomly selected oysters (or all remaining if < 30 live oysters) from each compartment. In 2006, the methodology was similar to that of 2005 with two major differences. First, instead of producing cultchless juvenile oysters, HBOI spawned the broodstock in tanks that contained axenic oyster shell as settlement substrate. Second, the shells with settled juvenile oysters were transported and planted into cages when the juveniles reached a mean SH of 1 to 5 mm. The 2007 methodology followed that of 2006 with one major exception. No successful spawns were completed with broodstock from SLE, so an alternative method was adapted. This method involved planting cages in the field with "blank" or clean axenic oyster shell that would serve as settlement substrate for wild juvenile oysters. Those wild juvenile oysters were then monitored monthly following standard protocols.

After 2007, hatchery production of juvenile oysters was terminated. Instead, axenic oyster shell was planted at the field sites for settlement of wild juvenile oysters, as with the SLE component of the 2007 study. From 2008 – 2010, the axenic shells were attached by fishing line to a 0.6-m L x 0.6 m W wire mesh growth array. Monitoring involved measuring the SHs of 30 randomly selected oysters (or all present if < 30 live oysters) monthly for one year. From 2011 – 2013, each study was initiated by planting large numbers of axenic shell in bags in each estuary. After enough wild juvenile oysters had settled on the shells in the bags, the shells with wild spat were sorted and counted. A shellfish tag was glued to each individual juvenile oyster and the SH of the animal was recorded. Tagged oysters were left attached to the large axenic oyster shells they initially settled on to create a more realistic, reef-like environment. After tagging, oysters were planted into one fully enclosed wire mesh cage and one open-top wire mesh cage at each station. The SH of all tagged oysters and the number of live tagged oysters was recorded during each monthly sampling trip. The 2011, 2012 and 2013 studies continued for 16, 18 and 13 months, respectively.

Statistical Analyses

Statistical analyses were performed with SAS version 9.3 (SAS Institute Inc., Cary, NC) and results were considered significant at $\alpha = 0.05$. All data were tested for normality by examining model residuals and then testing them for goodness of fit with the Shapiro-Wilk test (Shapiro and Wilk 1965). Because no data met normality assumptions, all statistical comparisons were performed using generalized linear mixed modeling with the GLIMMIX procedure (Littell et al. 2006). Statistical tests of all parameters included fixed factors of site and year.

Results

Water Quality

Salinity was highly variable in all study sites, often ranging from near 0 to more than 30 within a single year (Figures 2 and 3); however, the salinity regimes among sites varied greatly. Statistical comparison of recorded salinities revealed that each study site fell into one of three primary groups: a high salinity group, a moderate salinity group, and a low salinity group ($F_{5,2105}$=110.47, $P < 0.01$). The Lake Worth and Loxahatchee-South study sites fell into the high salinity group, with overall mean salinities for the 10-year study of 26 and 24, respectively, and annual means that ranged from 20 to 32. The moderate salinity group included the Loxahatchee-North and St. Lucie-Central sites, where overall mean salinities were 15 and 17, respectively, and annual means ranged from 6 to 24. The St. Lucie-North and South sites, with overall mean salinities of 13 and 12, respectively, comprised the low salinity group, and exhibited annual means that ranged from 4 to 19.

Salinity patterns also differed significantly among years at each of the sites ($F_{45,2105}$=2.52, $P <$ 0.01). The lowest mean annual salinities were recorded in 2005 at most sites, and were found to be significantly lower than other years in the Lake Worth site, where the 2005 annual mean was 20, and in the three SLE sites, where the 2005 annual means ranged from 4 to 6. At the opposite extreme, salinities were significantly higher at most sites in 2006, 2009, and 201l when annual means exceeded 26 in Loxahatchee-South and ranged from 15 to 24 in the SLE sites. In LWL, the highest salinities were recorded in 2006, 2007 and 2011, when mean annual salinities exceeded 28.

Flow rates from structures located upstream of the study sites illustrate the correlation between the magnitude of freshwater inputs and estuarine salinities. Figure 2 includes a plot of the sum of the daily mean flow rates measured at three canal structures (C44S80, C23S97, and C24S49; SFWMD DBHYDRO environmental database) in the SLE. Analysis of SLE flow rates revealed that rates were significantly higher in 2005, when the annual mean exceeded 2400 cfs ($F_{18,10924}$=10.67, P < 0.01). This corresponds with the significantly low salinities (annual means from 4 to 6) recorded at the three SLE sites in 2005. SLE flow rates were also significantly higher in 2013, when the annual mean was 1268 cfs. In both 2005 and 2013, salinities decreased precipitously following increased flow rates and remained low for several consecutive months. Mean annual flow rates during the other years of the study were similar and much lower (262 to 604 cfs); however, two important events are worth mentioning. The first event occurred in August 2008 when Tropical Storm Fay made landfall in Florida. Heavy rains associated with the storm impacted the SLE by increasing mean monthly flow rates from approximately 500 cfs in July to over 2600 cfs in August; flow rates remained high through October. The second event occurred in 2010 when a prolonged freshwater release increased mean monthly flow rates to approximately 1000 cfs for 5 consecutive months (March through July). During both of these events, salinities in the SLE decreased rapidly and remained below 10 at most stations for the duration.

Freshwater inflows to the LOX and LWL were less impactful than those recorded in the SLE. Figure 3 includes plots of the sum of the daily mean flow rates measured at the Lainhart Dam and S46 structures in the LOX and at three canal structures (C17S44, C51S155, and C16S41) in LWL. As with the SLE, the greatest flow rates for LWL occurred in 2005 and 2013, when mean annual rates were 1102 and 922, respectively. However, those flow rates were not significantly higher than rates recorded in LWL in most other years of the study. Perhaps what is most notable about flow into LWL, are the significantly lower flow rates recorded in 2006, 2007, and 2011, which correspond with the significantly higher mean salinities (> 28) recorded during those same years. In the LOX, mean annual flow rates were significantly lower than rates for the other estuaries ($F_{2,10924}$=623.05, P < 0.01), ranging from only 135 to 218 cfs in most years. Similar to those in LWL, flow rates in the LOX were significantly lower in 2006, 2009, and 2011 (< 100 cfs), again, corresponding with the highest salinities recorded in the estuary.

Other water quality parameters exhibited patterns and ranges that were similar among sites and years. Water temperatures reflected typical seasonal patterns with maxima in the summer months ranging from 30 to 35ºC and minima in the winter months ranging from 16 to 22ºC at most sites (Figures 4 and 5). One exception occurred in 2010, when winter temperatures were noticeably cooler and minima ranged from 11 to 13ºC. Dissolved oxygen concentrations were similar among sites with overall means ranging from 6.1 to 6.7 mg/L (Figures 6 and 7). Dissolved oxygen concentrations were significantly higher in 2009 ($F_{8,}$ 1762=10.72, $P < 0.01$), but that is likely due to errors associated with an ageing sensor and has no biological relevance. As with dissolved oxygen concentrations, pH was similar among sites with overall means ranging from 7.8 to 8.0 (Figures 8 and 9). There were differences in pH detected among years, with 2013 and 2014 exhibiting significantly higher values (8.1) than in other years ($F_{8,}$ 1773=76.6, $P < 0.01$). Dissolved oxygen concentrations and pH were not recorded in 2005. Flow rates are included on temperature, dissolved oxygen and pH plots for comparison.

Water clarity was significantly higher at the two LOX sites, where overall means were greater than 98% ($F_{5,2084}$=84.37, $P < 0.01$; Figures 10-15). The lowest water clarity occurred in the three SLE sites where the overall means ranged from 74% to 87%. Although water clarity differed significantly among years at each of the sites ($F_{45,2084}$=7.55, $P < 0.01$), those differences were most pronounced in the SLE sites where annual means were much lower in 2005 (3% to 70%) and 2013 (78% to 80%). Flow rates are included on water clarity plots for comparison.

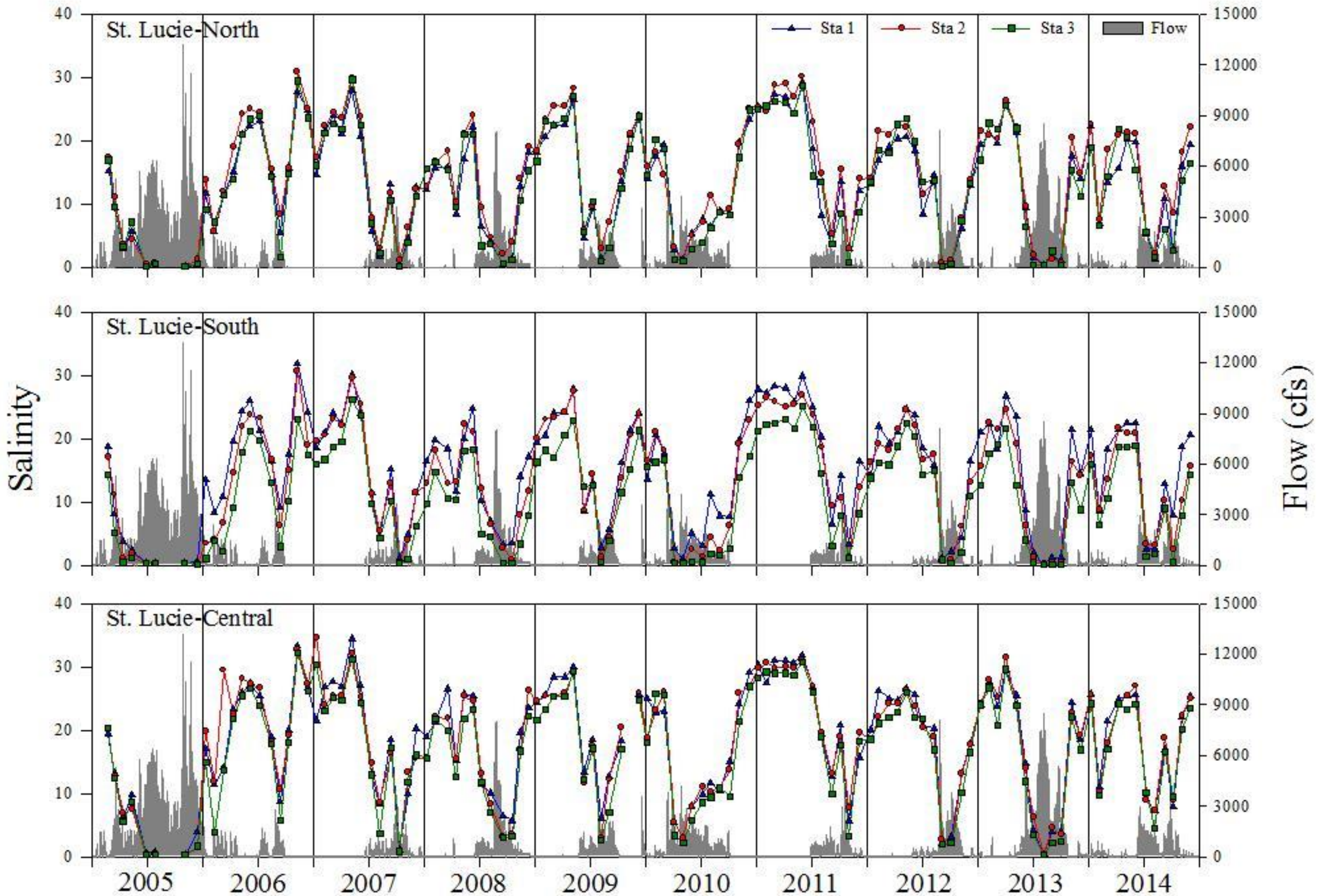

Figure 2. Monthly salinity recorded at stations from 2005 – 2014 in the St. Lucie-North (top), St. Lucie-South (middle) and St. Lucie-Central (bottom) study sites and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

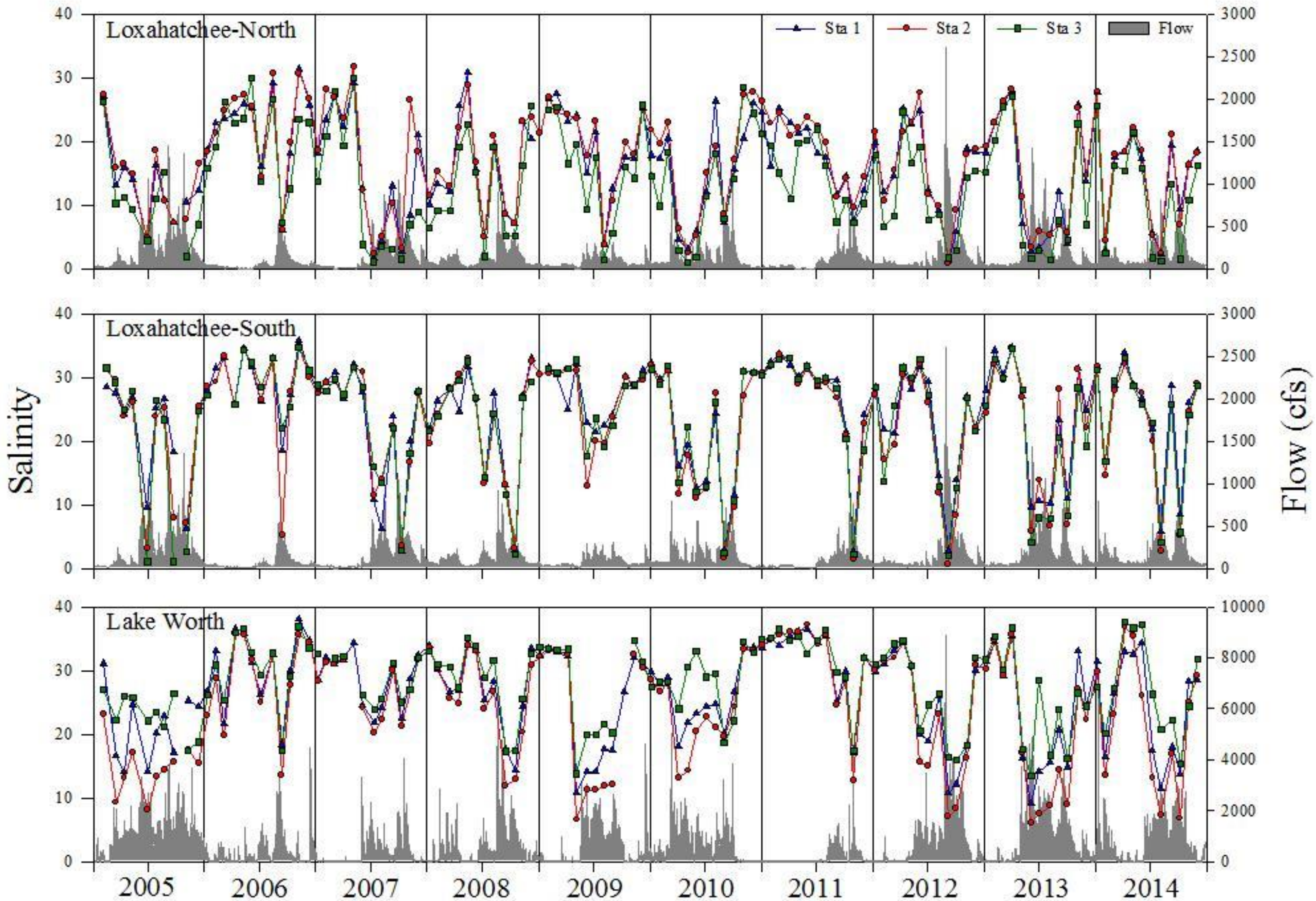

Figure 3. Monthly salinity recorded at stations from 2005 – 2014 in the Loxahatchee-North (top), Loxahatchee-South (middle) and Lake Worth (bottom) study sites and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures in the LOX and at the S44, S155, and S41 structures in LWL as recorded by the U.S. Geological Survey and the South Florida Water Management District.

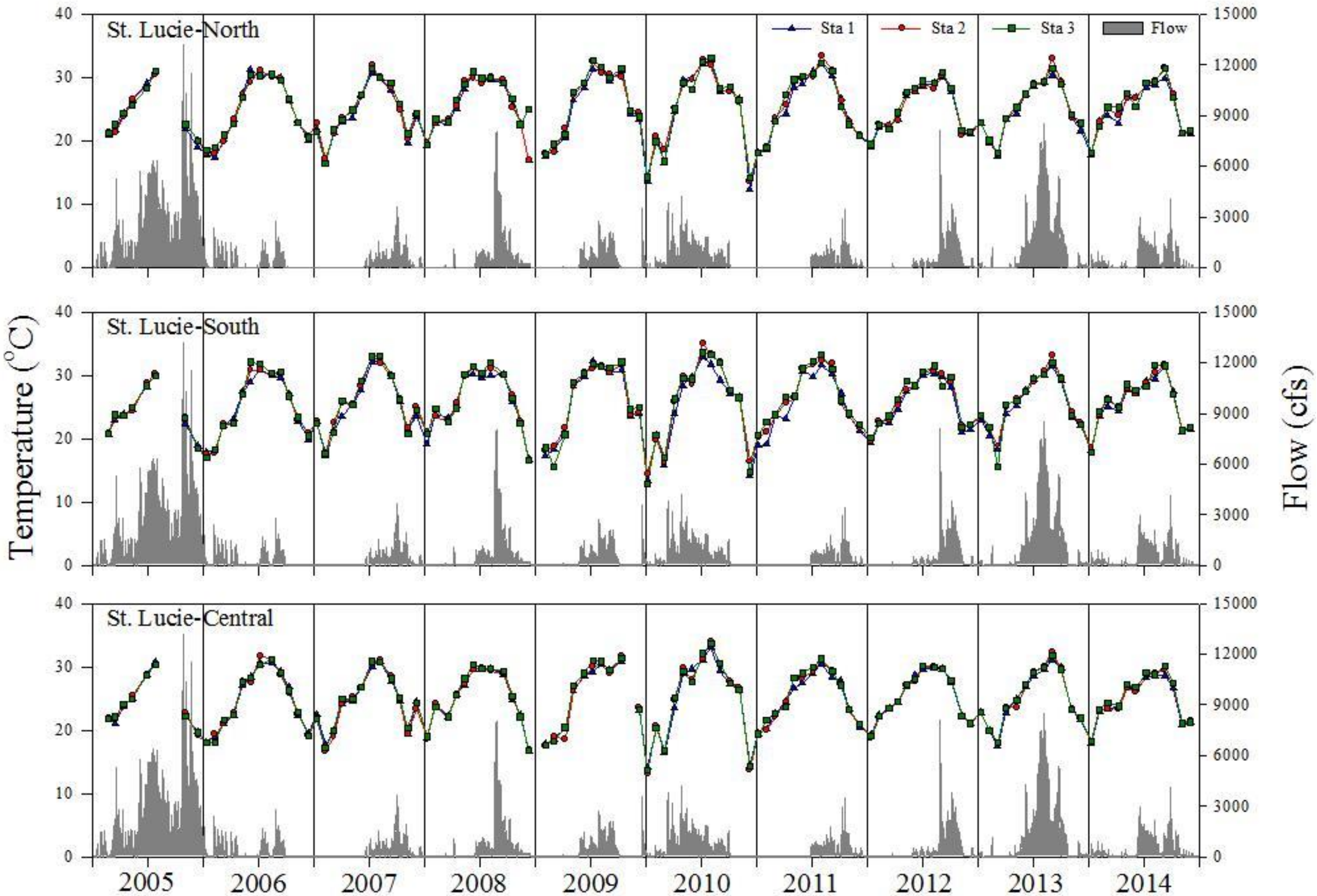

Figure 4. Monthly water temperature recorded at stations from 2005 – 2014 in the St. Lucie-North (top), St. Lucie-South (middle) and St. Lucie-Central (bottom) study sites and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

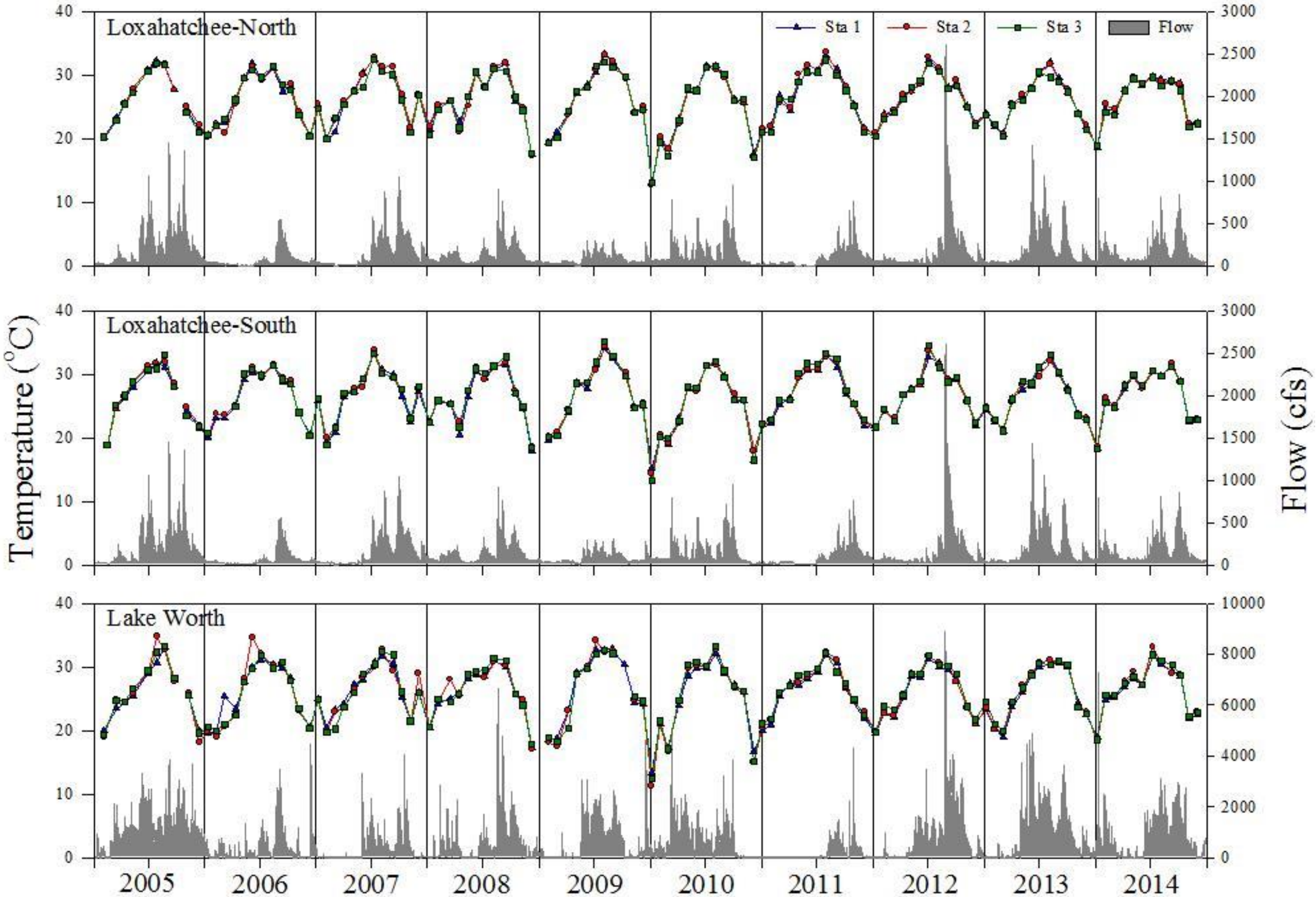

Figure 5. Monthly water temperature recorded at stations from 2005 – 2014 in the Loxahatchee-North (top), Loxahatchee-South (middle) and Lake Worth (bottom) study sites and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures in the LOX and at the S44, S155, and S41 structures in LWL as recorded by the U.S. Geological Survey and the South Florida Water Management District.

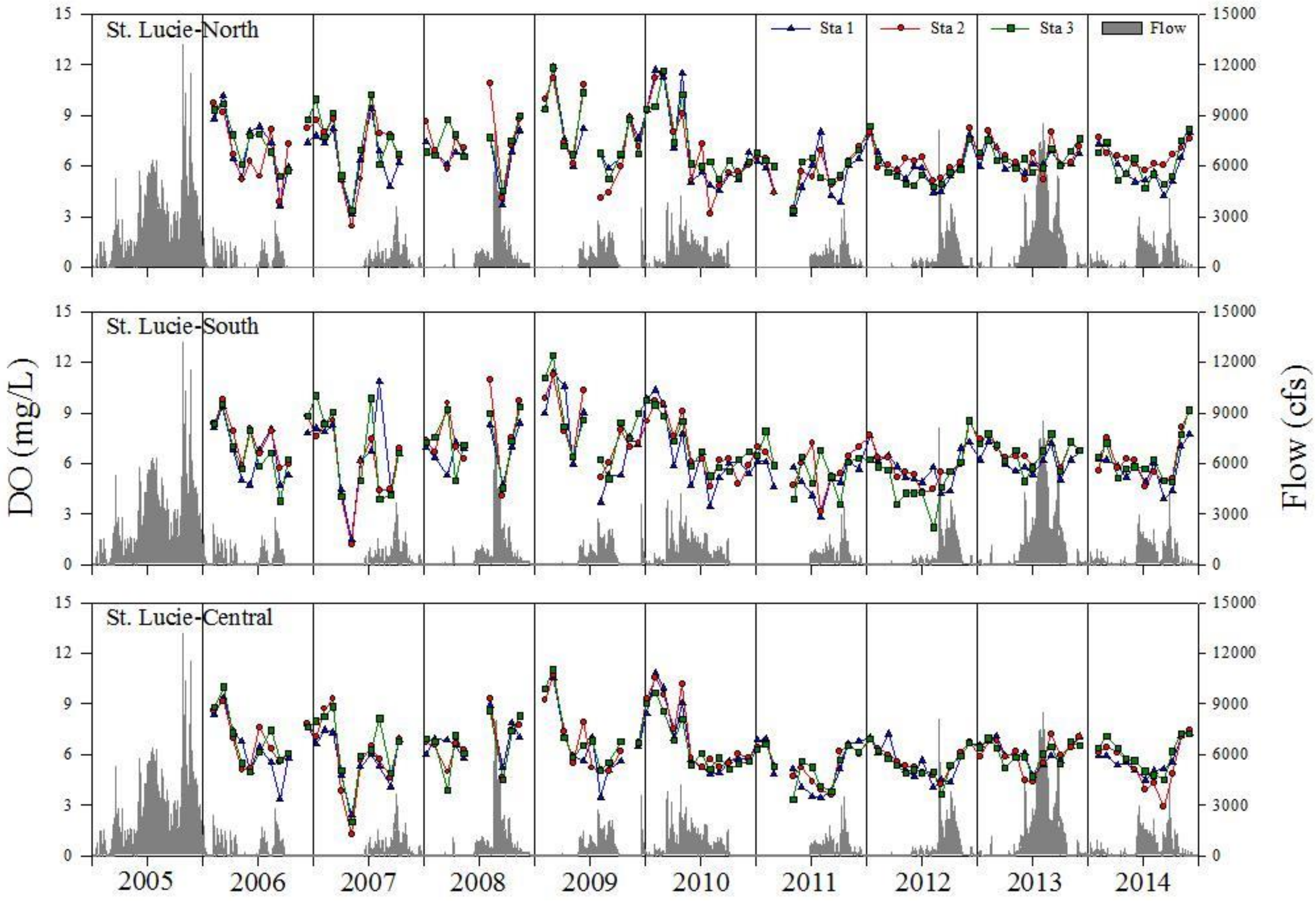

Figure 6. Monthly dissolved oxygen concentration recorded at stations from 2006 – 2014 in the St. Lucie-North (top), St. Lucie-South (middle) and St. Lucie-Central (bottom) study sites and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

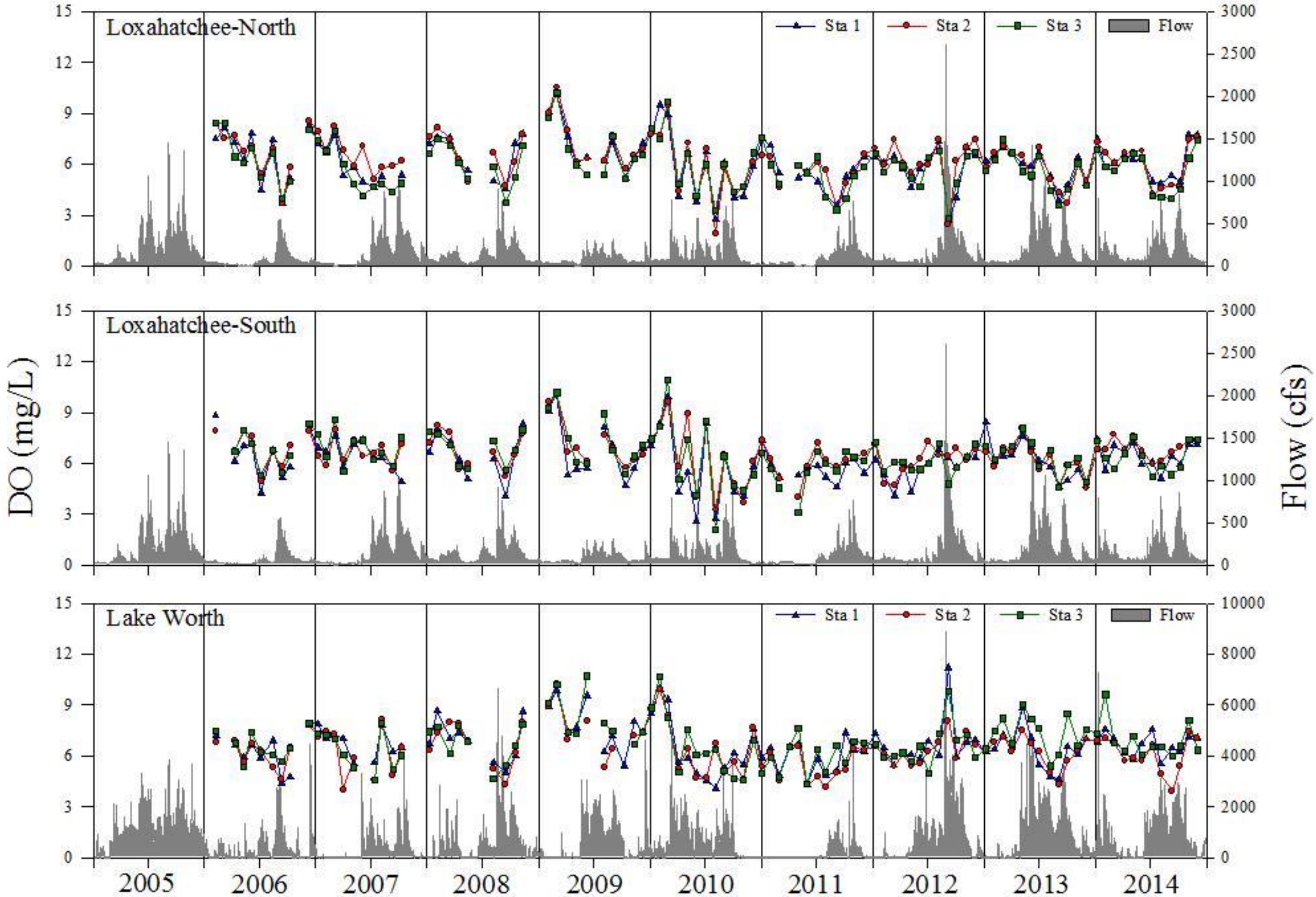

Figure 7. Monthly dissolved oxygen concentration recorded at stations from 2006 – 2014 in the Loxahatchee-North (top), Loxahatchee-South (middle) and Lake Worth (bottom) study sites and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures in the LOX and at the S44, S155, and S41 structures in LWL as recorded by the U.S. Geological Survey and the South Florida Water Management District.

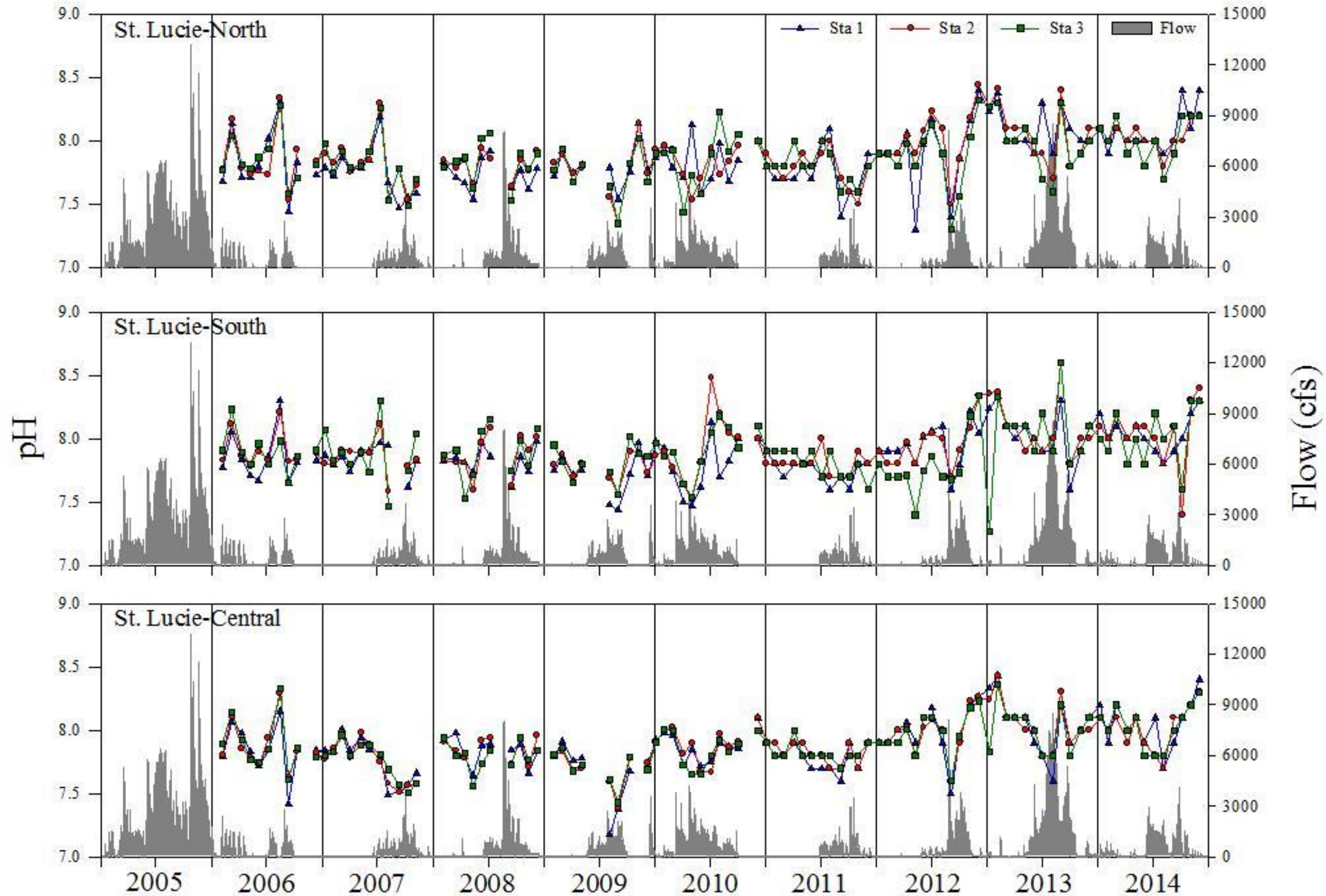

Figure 8. Monthly pH recorded at stations from 2006 – 2014 in the St. Lucie-North (top), St. Lucie-South (middle) and St. Lucie-Central (bottom) study sites and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

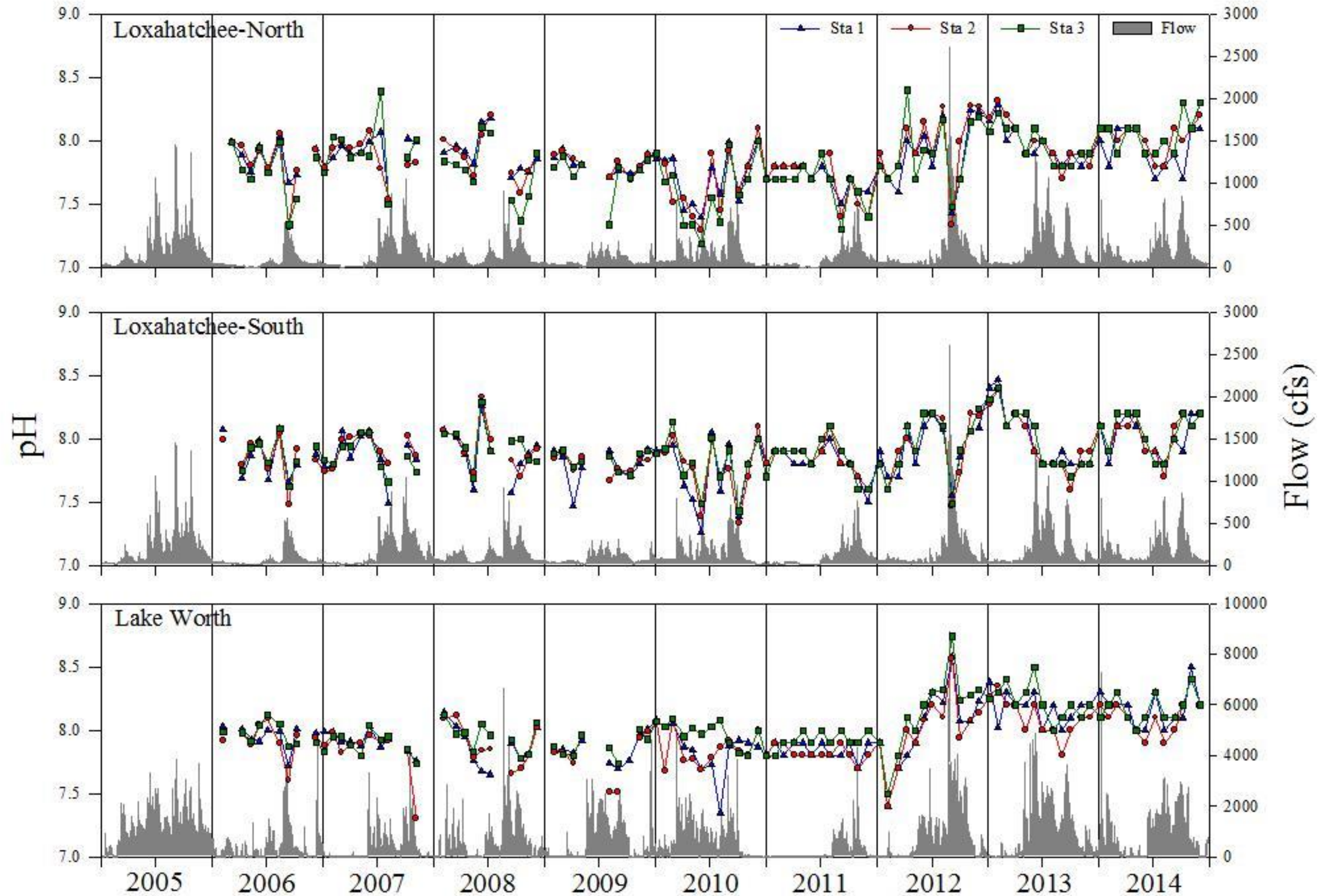

Figure 9. Monthly pH recorded at stations from 2006 – 2014 in the Loxahatchee-North (top), Loxahatchee-South (middle) and Lake Worth (bottom) study sites and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures in the LOX and at the S44, S155, and S41 structures in LWL as recorded by the U.S. Geological Survey and the South Florida Water Management District.

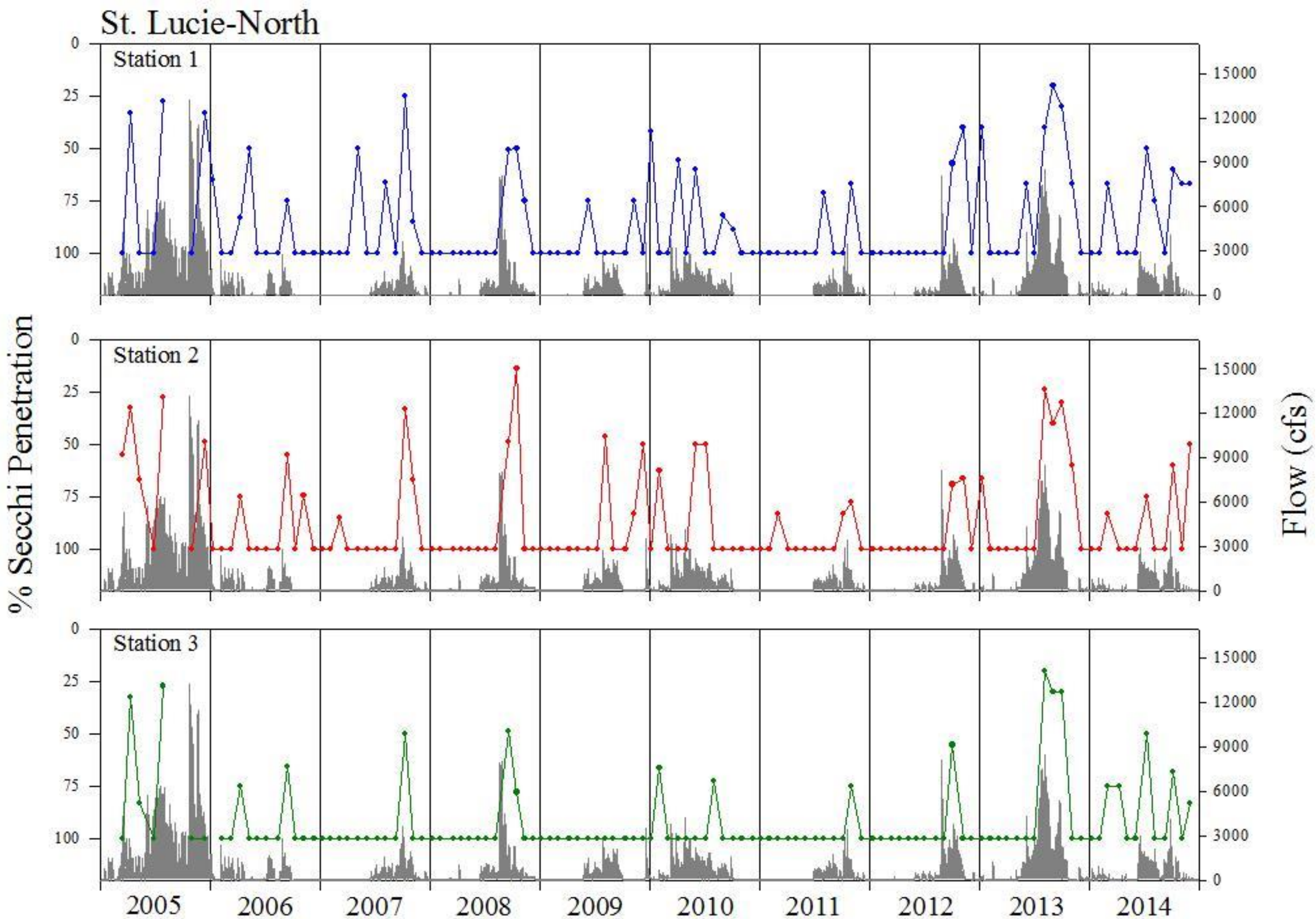

Figure 10. Monthly percent Secchi penetration recorded from 2005 – 2014 at St. Lucie-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

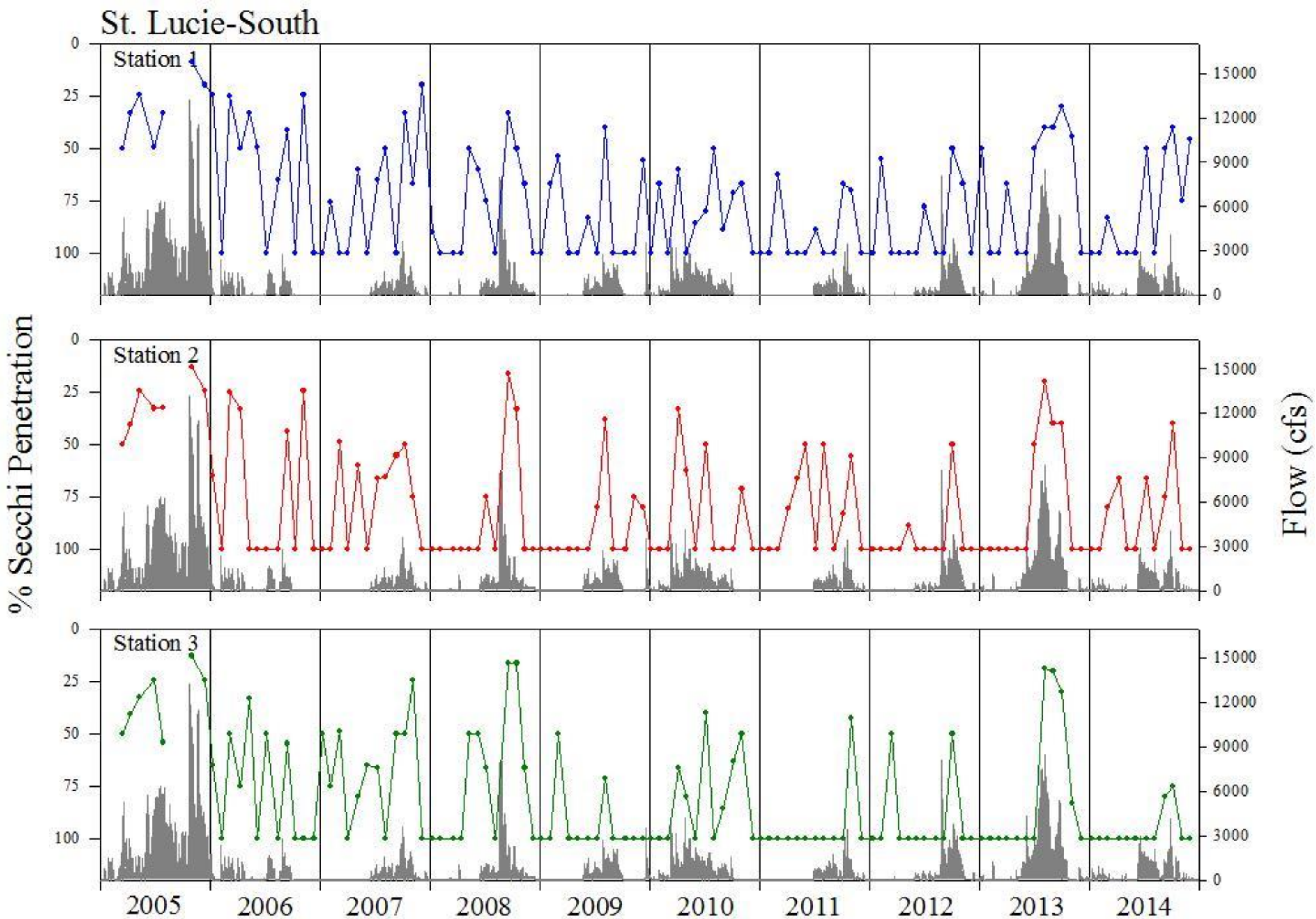

Figure 11. Monthly percent Secchi penetration recorded from 2005 – 2014 at St. Lucie-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

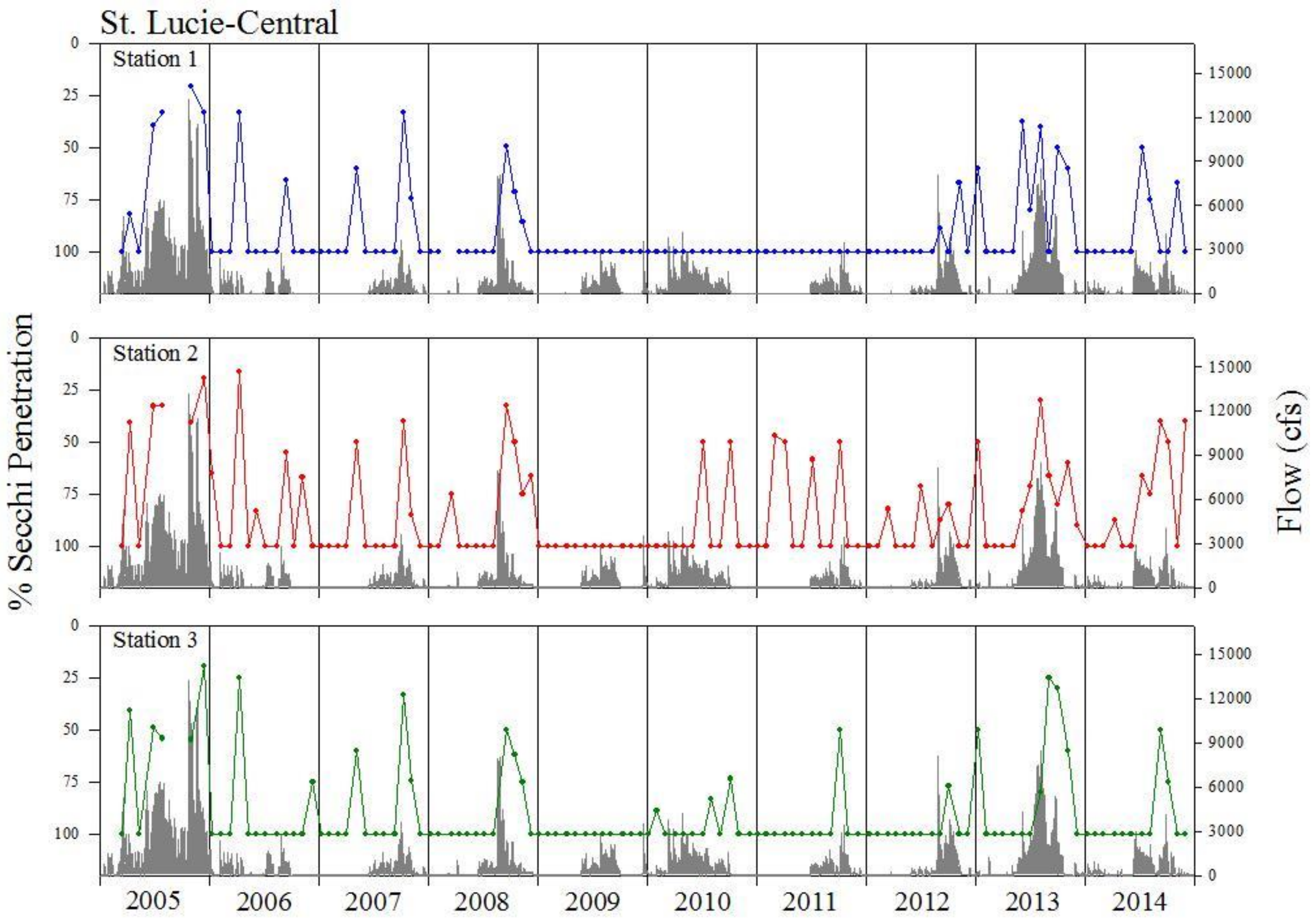

Figure 12. Monthly percent Secchi penetration recorded from 2005 – 2014 at St. Lucie-Central Station 1 (top), Station 2 (middle) and Station 3 (bottom) and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

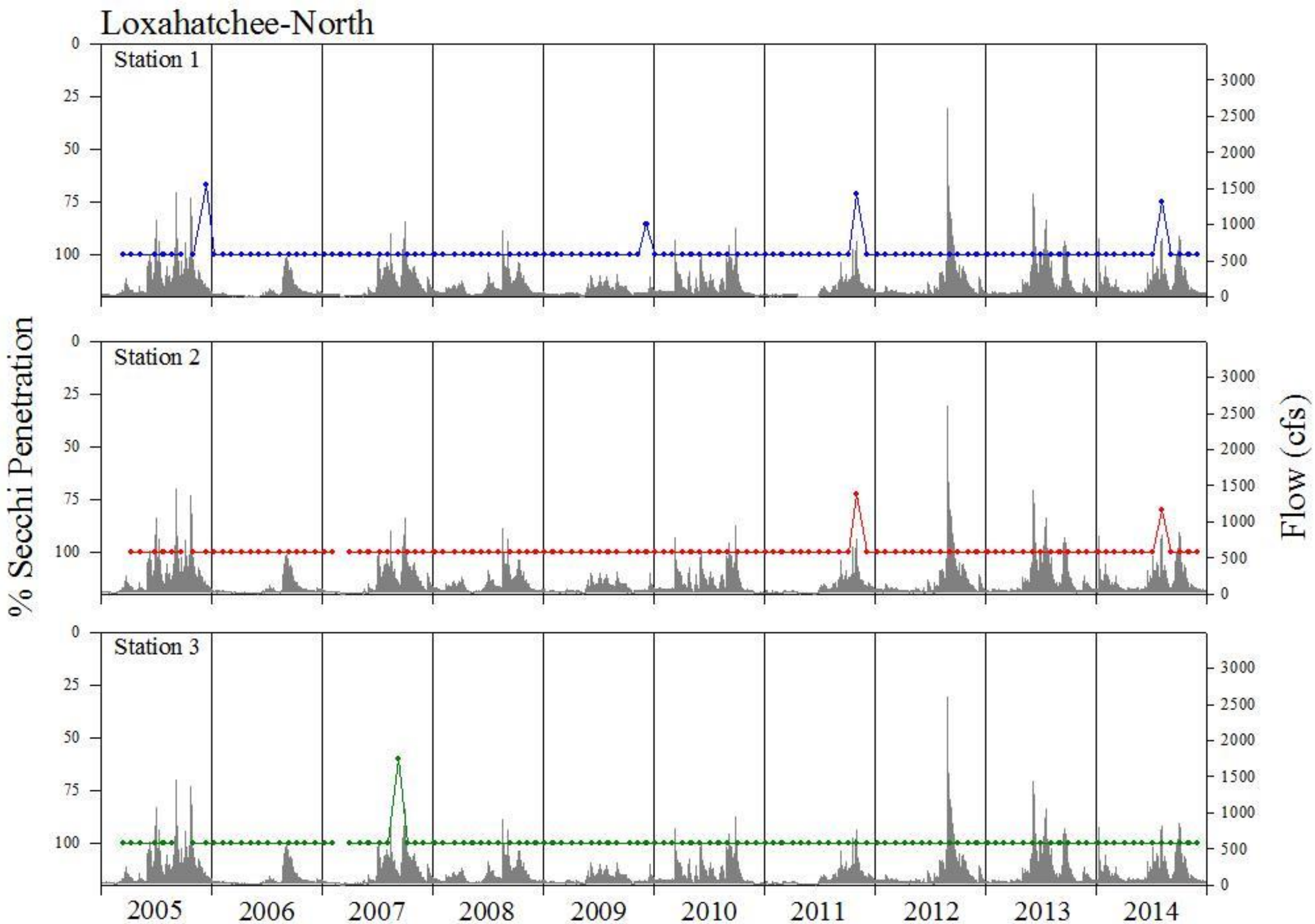

Figure 13. Monthly percent Secchi penetration recorded from 2005 – 2014 at Loxahatchee-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District.

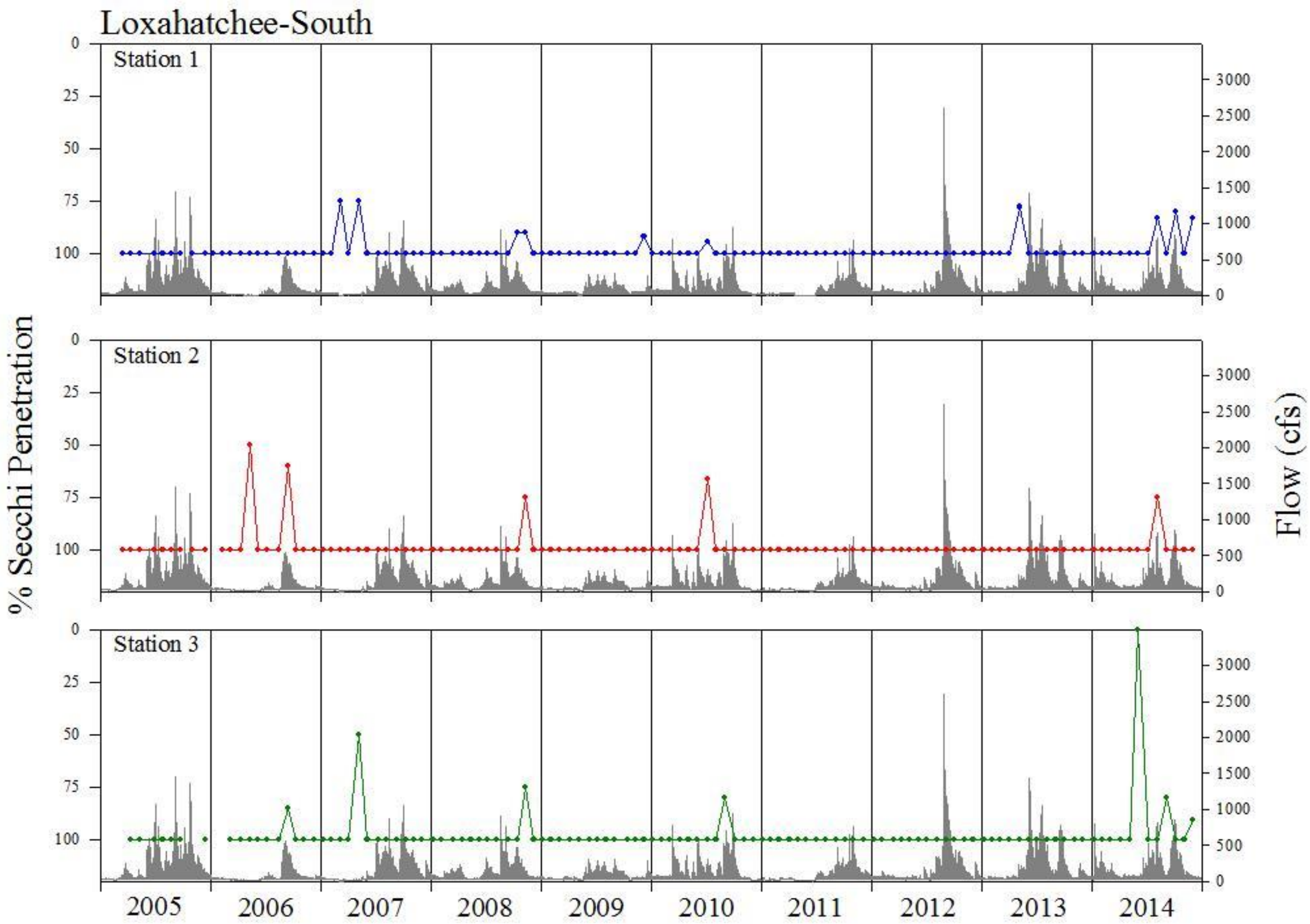

Figure 14. Monthly percent Secchi penetration recorded from 2005 – 2014 at Loxahatchee-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District.

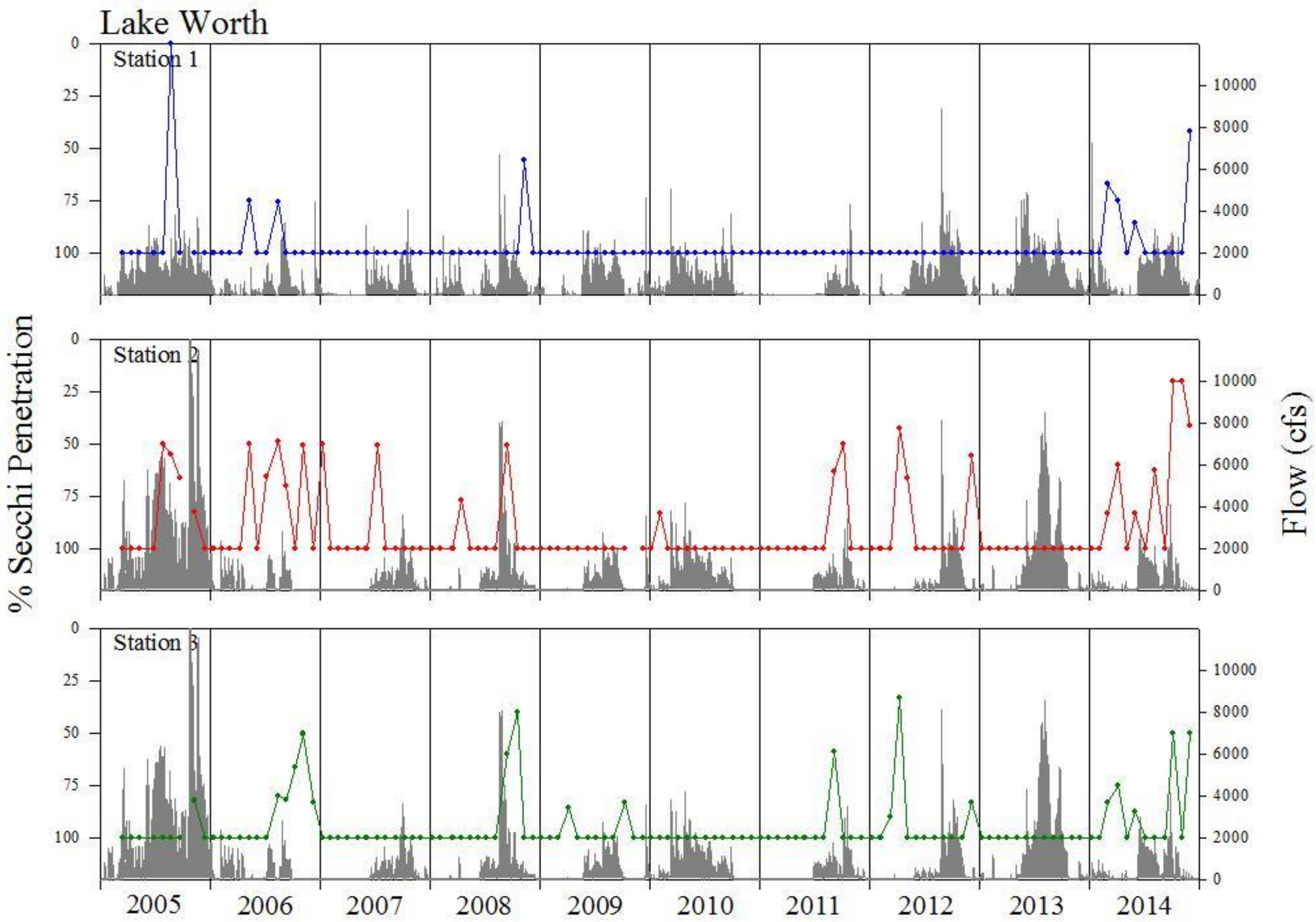

Figure 15. Monthly percent Secchi penetration recorded from 2005 – 2014 at Lake Worth Station 1 (top), Station 2 (middle) and Station 3 (bottom) and the sum of the mean daily flow rate at the S44, S155, and S41 structures as recorded by the South Florida Water Management District.

Settled Oyster Density

When sampling began in early 2005, no live oysters were observed at any of the stations in the St. Lucie-North or St. Lucie-South study sites. Settled oysters were not detected in quadrats deployed in either site until fall 2006. Although live oysters were present in the St. Lucie-Central site in 2005 and spring 2006, densities remained very low (< 2/m^2 at most stations) until fall 2006.

The highest and most stable densities of oysters were found in the Loxahatchee-North and Lake Worth sites, where annual means ranged from 122 to 697/m^2 and 121 to 613/m^2, respectively ($F_{5,4800}$=29.05, P < 0.01; Figures 16-21). Densities of live oysters were also relatively high in the Loxahatchee-South site, but fluctuated more widely, with mean annual values ranging from 30 to 533/m^2. Although oysters were almost absent from St. Lucie-Central during the surveys in 2005, spring 2006, fall 2008, and fall 2013, live densities in the remaining surveys were some of the greatest recorded among all sites, especially in 2014 when means were greater than 2000/m^2 at Station 1. The lowest densities occurred in the St. Lucie-North and South sites, where annual means ranged from 0 to 86/m^2.

Oyster density also differed significantly among years at each of the sites ($F_{45,4800}$=21.57, P < 0.01). Although there was no discernable pattern for when each site exhibited the greatest oyster densities, the lowest densities were recorded in 2005 when values ranged from approximately 120/m^2 in the Lake Worth and Loxahatchee-North sites to less than 30/m^2 in the remaining sites. This corresponds with the significantly high flow rates and low salinities recorded at most sites in 2005. Oyster densities were also significantly lower in the St. Lucie-North and South sites in 2013 (approximately 3/m^2), again, corresponding with high flow rates and low salinities in the estuary. Although mean annual densities in the three SLE sites were not significantly lower in 2008 than most years, it is noteworthy that mean overall density decreased by two orders of magnitude from 229/m^2 in March to less than 3/m^2 in September. Flow rates are included on density plots for comparison.

Comparison of the ratio of dead oysters to the total number of live oysters and dead oysters revealed differences among sites (Figures 22-27). The greatest ratios of dead oysters were found in St. Lucie-North and South where overall means were 0.58 and 0.66, respectively, ($F_{5,4556}$=134.49, P < 0.01). Ratios fluctuated most at these two sites as well, with annual values ranging from 0.02 to 1.00 during the study. Lake Worth had the lowest and most stable ratios of dead oysters, with an overall mean of 0.20 and annual means that ranged from 0.14 to 0.28. Ratios were similar at the remaining sites, where overall means ranged from 0.21 to 0.23, and annual means varied from 0.05 to 0.89.

Differences in ratios of dead oysters among years within the sites were also detected ($F_{45,4556}$=1739.33, $P < 0.01$). In all sites except Lake Worth, the highest ratios occurred in 2005, when the means were 1.00 in St. Lucie-North and South, 0.89 in St. Lucie-Central, 0.75 in Loxahatchee-South and 0.54 in Loxahatchee-North. Ratios were also high in all three SLE sites in fall 2008 and fall 2013 (> 0.75) corresponding with the large freshwater releases that occurred during the same period. In contrast, dead oyster ratios were higher at the two LOX sites in 2007 and 2012 following years with significantly greater mean salinities. No dead oysters with articulated shells were present at St. Lucie-North Station 3 in spring 2006 and spring 2007 (Figure 22), at St. Lucie-South Station 2 in fall 2005 and spring 2006, and at St. Lucie-South Station 3 in spring and fall 2006. Flow rates are included on dead ratio plots for comparison.

Oyster SHs were greatest in the St. Lucie-North and South sites where overall means reached 47 and 48 mm, respectively ($F_{5,4109}$=147.86, $P < 0.01$; Figures 28-33). Lake Worth oysters exhibited the lowest SHs with an overall mean of 32 mm. Mean overall SHs at the remaining sites ranged from 39 to 43 mm. Mean SHs at all sites differed throughout the course of the study ($F_{43,4109}$=28.09, $P < 0.01$), but were relatively stable in Loxahatchee-North, where annual means ranged from 35 to 44 mm, and in Loxahatchee-South, where annual means ranged from 38 to 48 mm. In the three SLE sites, where very few or no live oysters were present periodically, mean SHs were significantly smaller during the first season of recovery than in subsequent surveys. Flow rates are included on shell height plots for comparison.

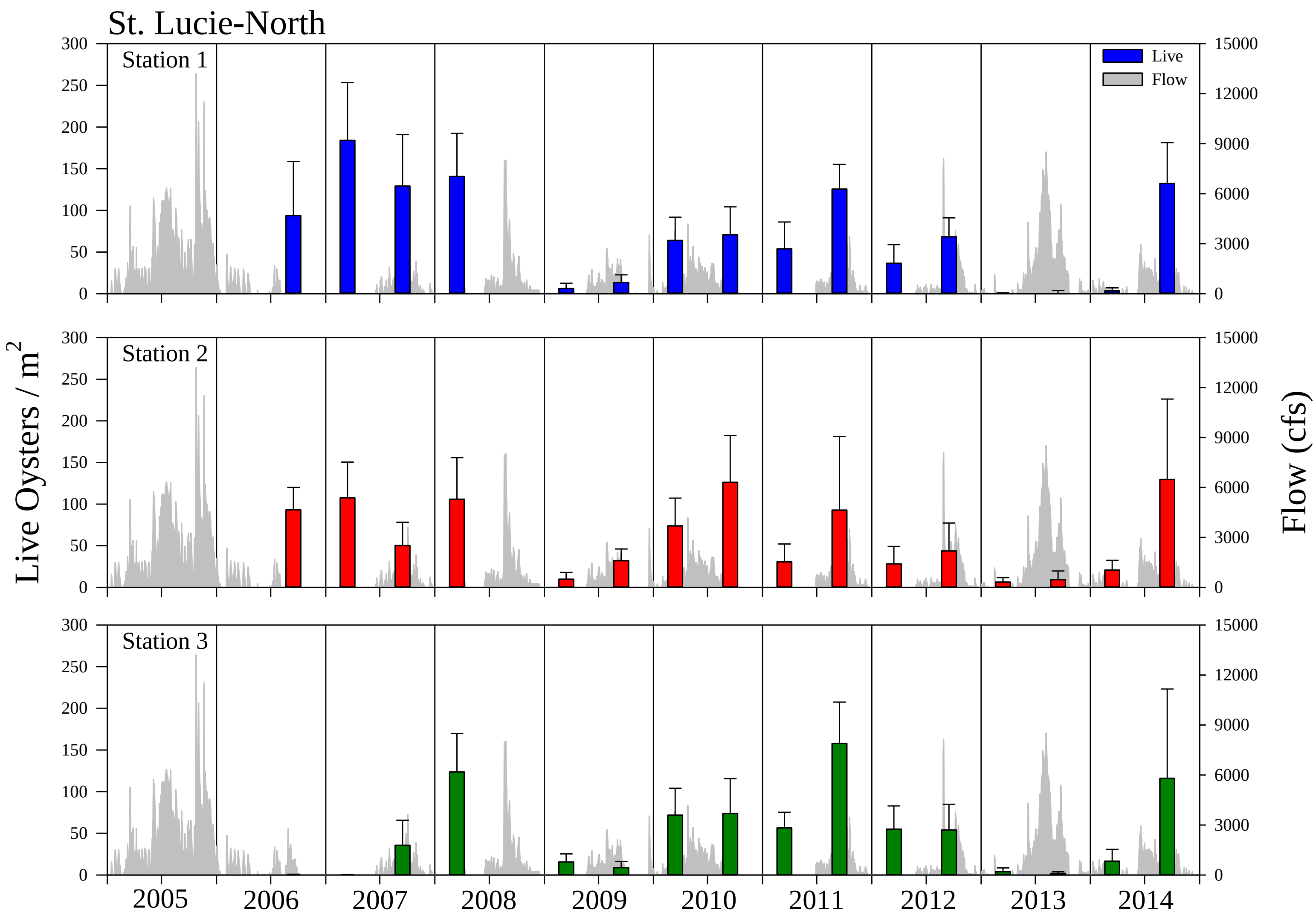

Figure 16. Mean semi-annual number (± S.D.) of live oysters present at St. Lucie-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

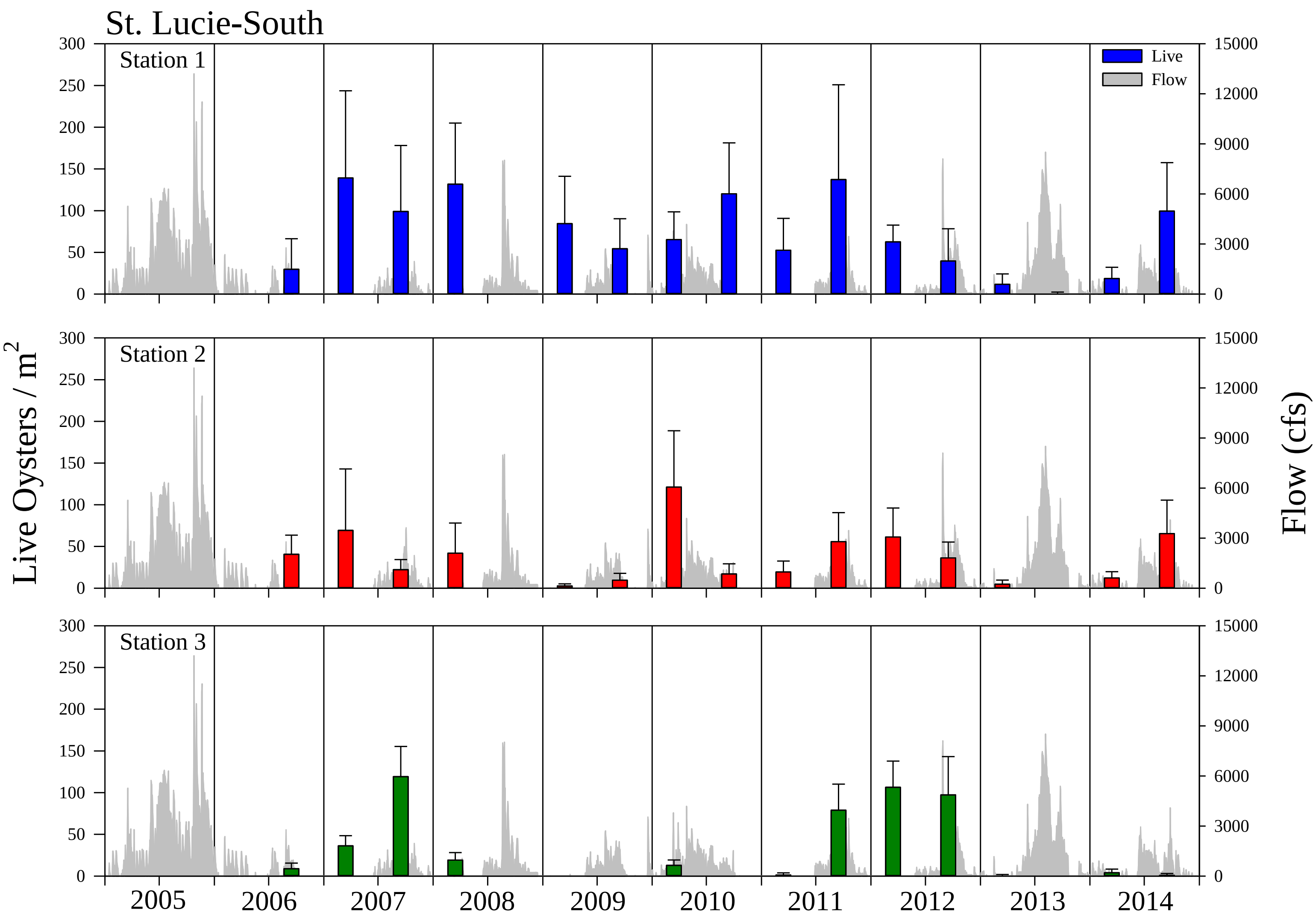

Figure17. Mean semi-annual number (± S.D.) of live oysters present at St. Lucie-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

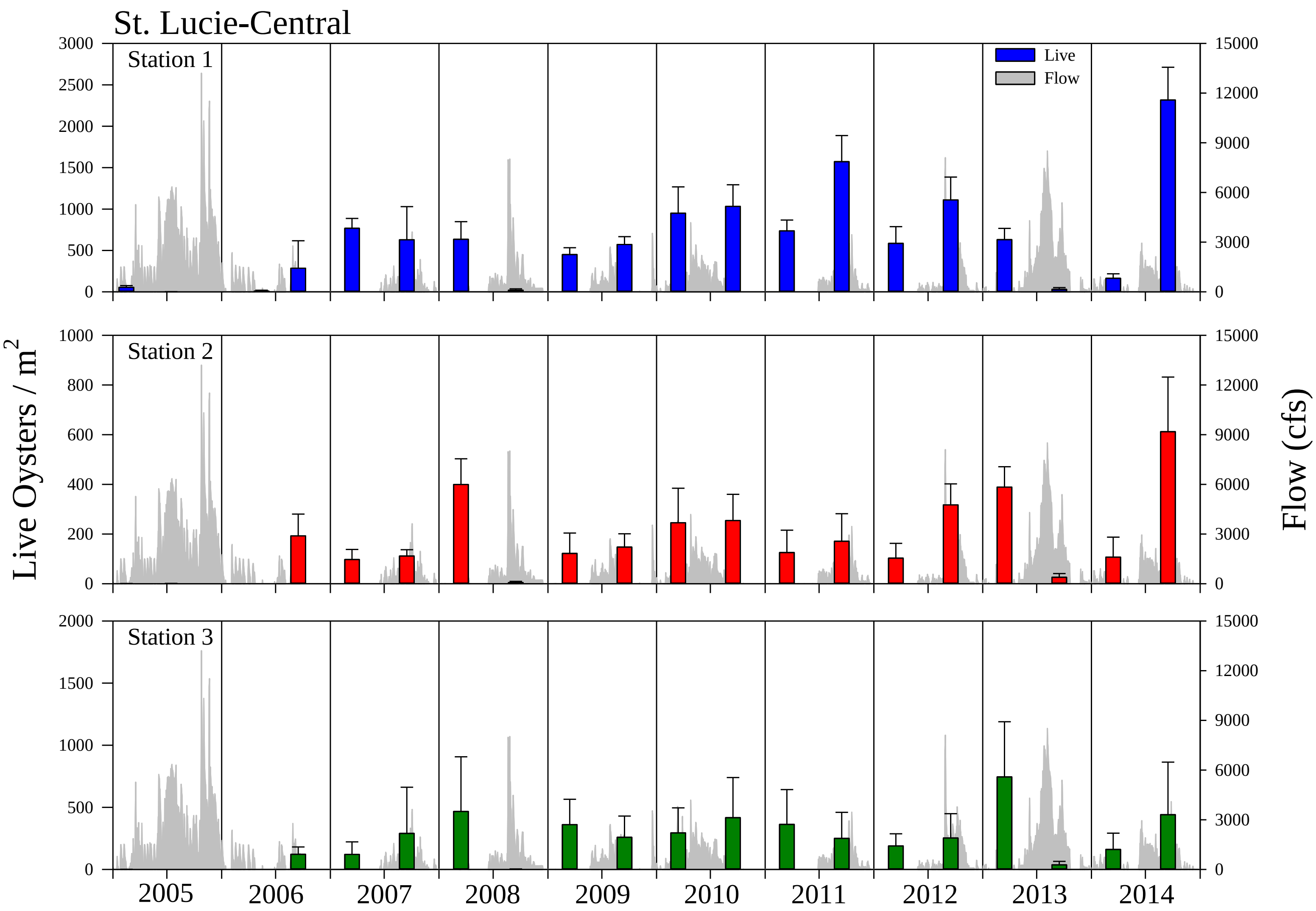

Figure 18. Mean semi-annual number (± S.D.) of live oysters present at St. Lucie-Central Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

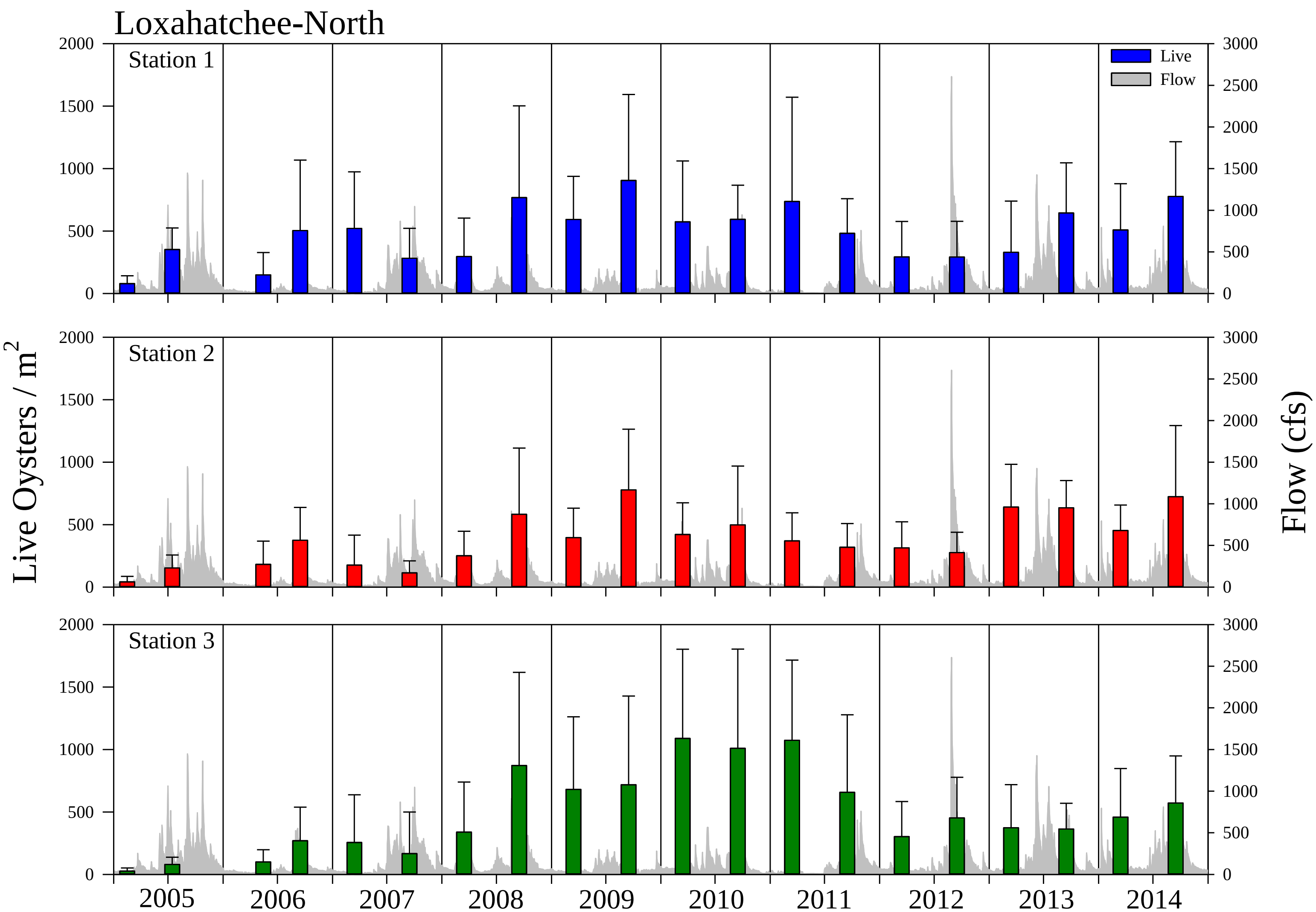

Figure 19. Mean semi-annual number (± S.D.) of live oysters present at Loxahatchee-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District.

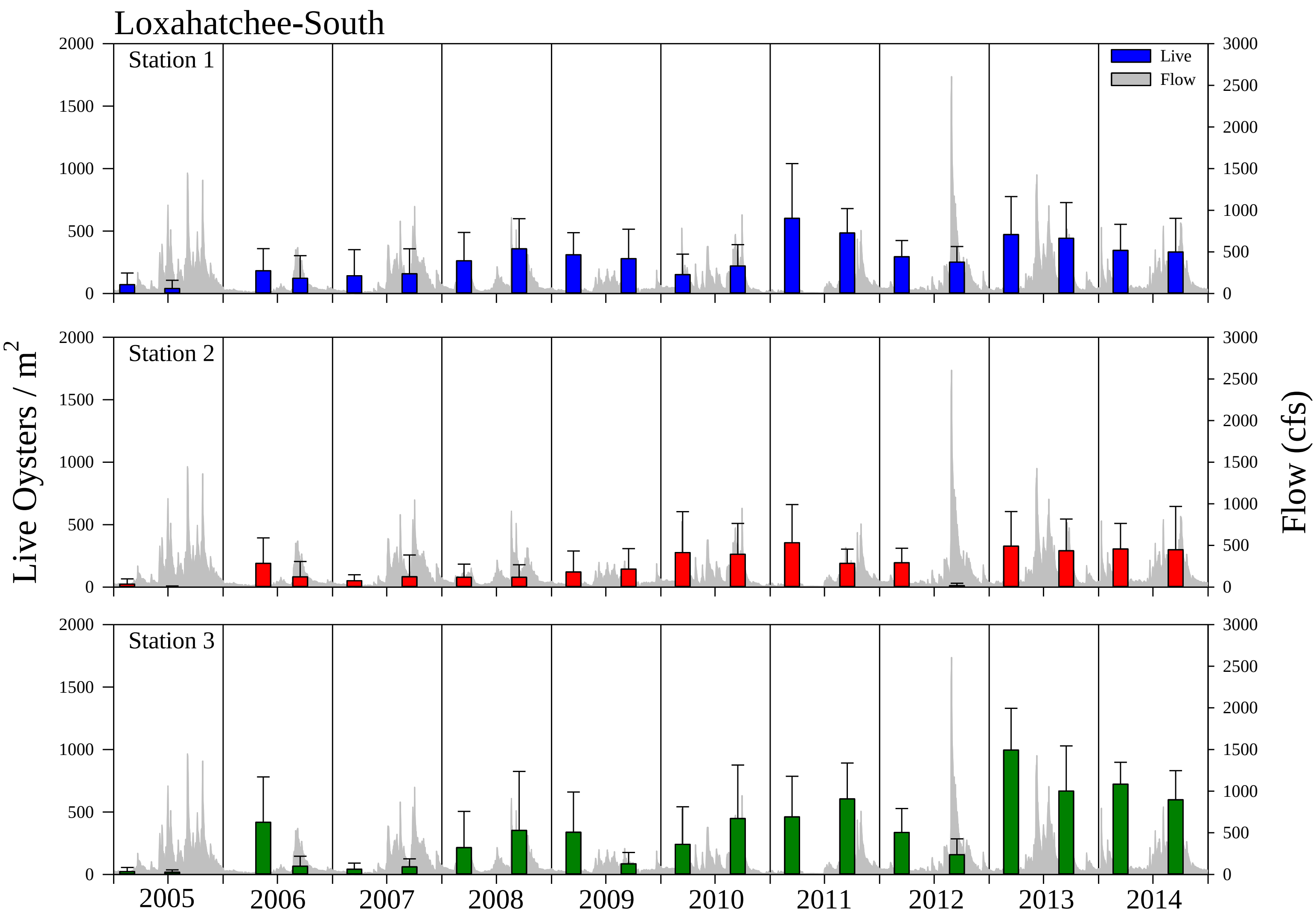

Figure 20. Mean semi-annual number (± S.D.) of live oysters present at Loxahatchee-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District.

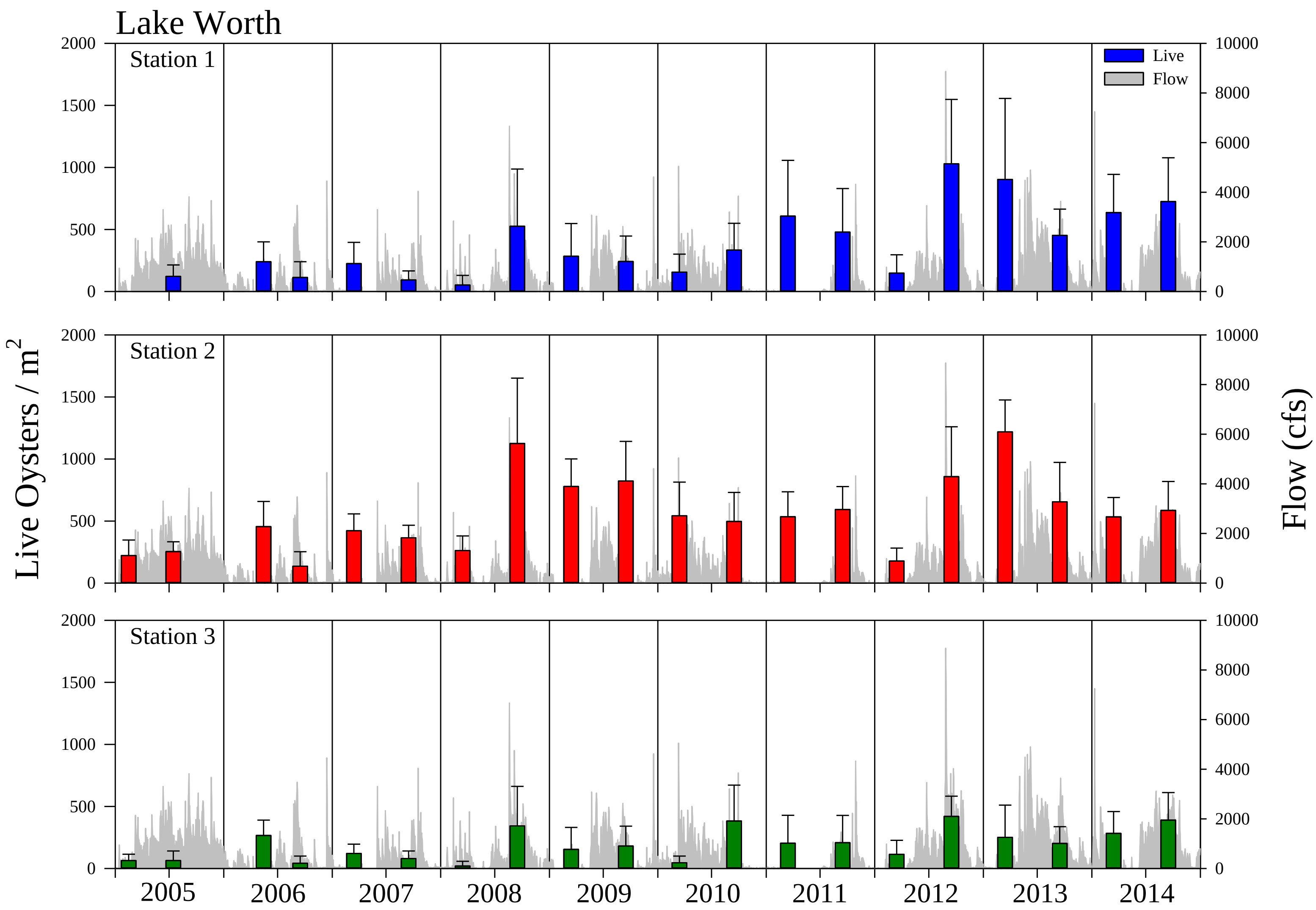

Figure 21. Mean semi-annual number (± S.D.) of live oysters present at Lake Worth Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S44, S155, and S41 structures as recorded by the South Florida Water Management District.

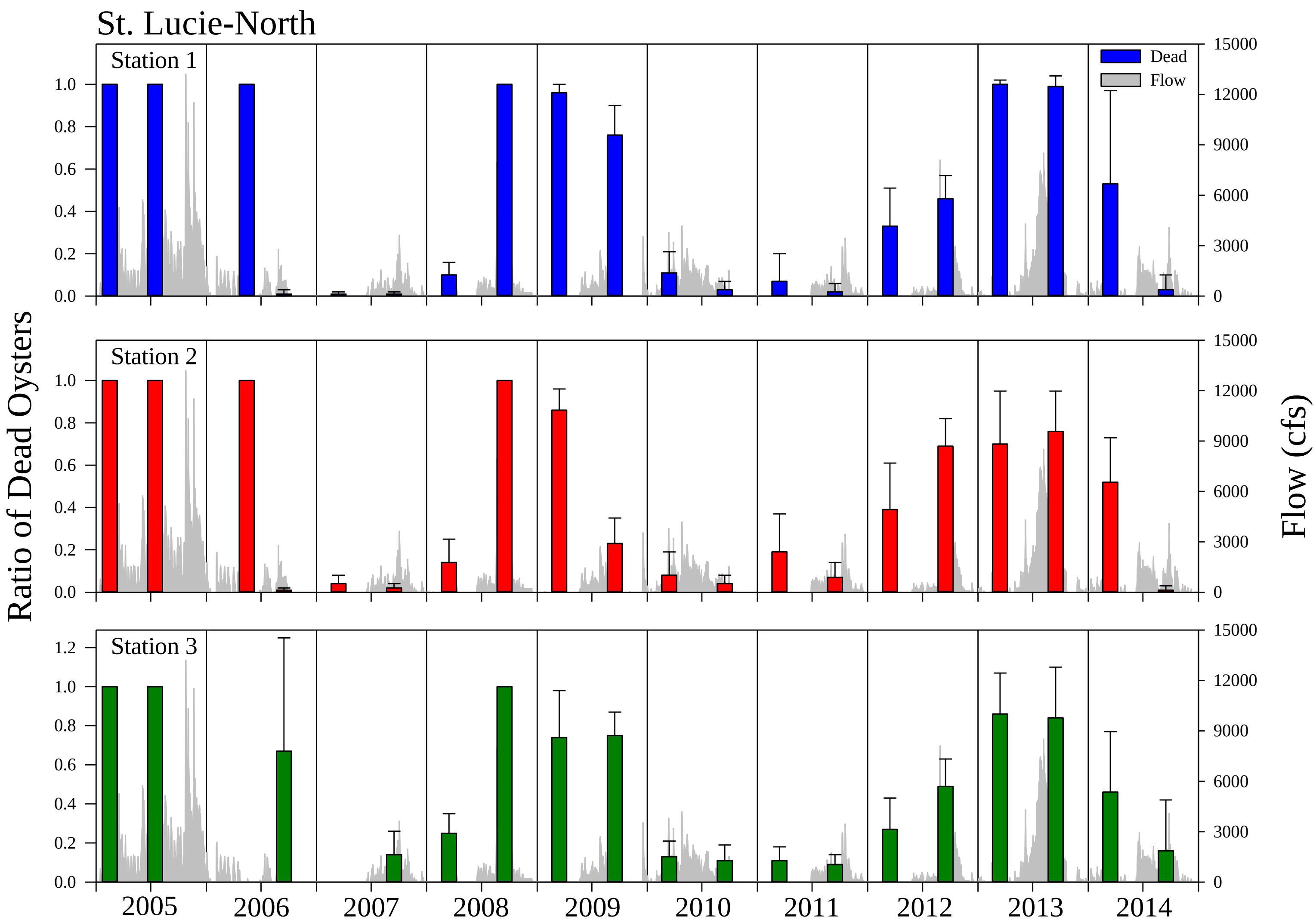

Figure 22. Mean semi-annual ratio (± S.D.) of dead oysters present at St. Lucie-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

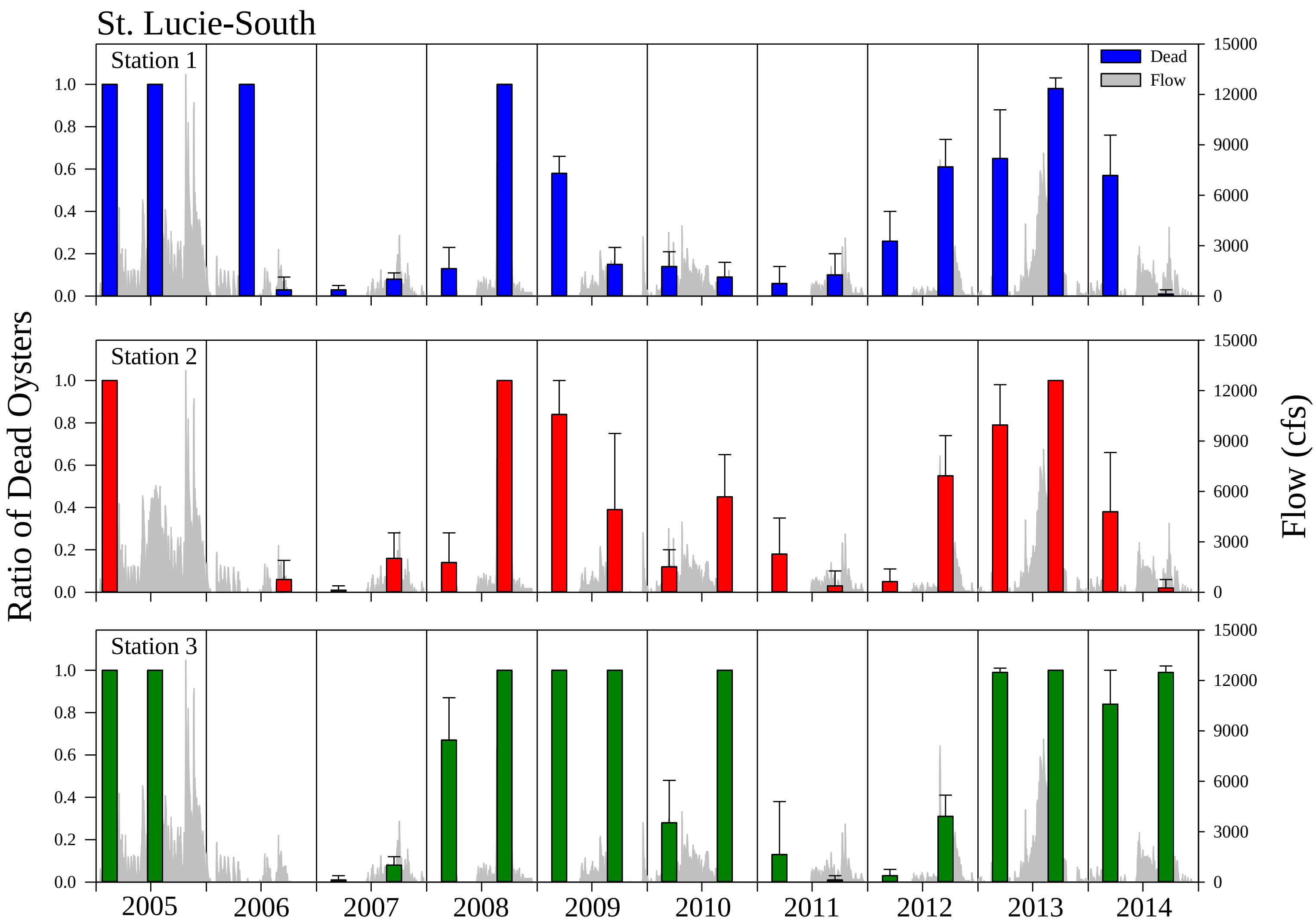

Figure 23. Mean semi-annual ratio (± S.D.) of dead oysters present at St. Lucie-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

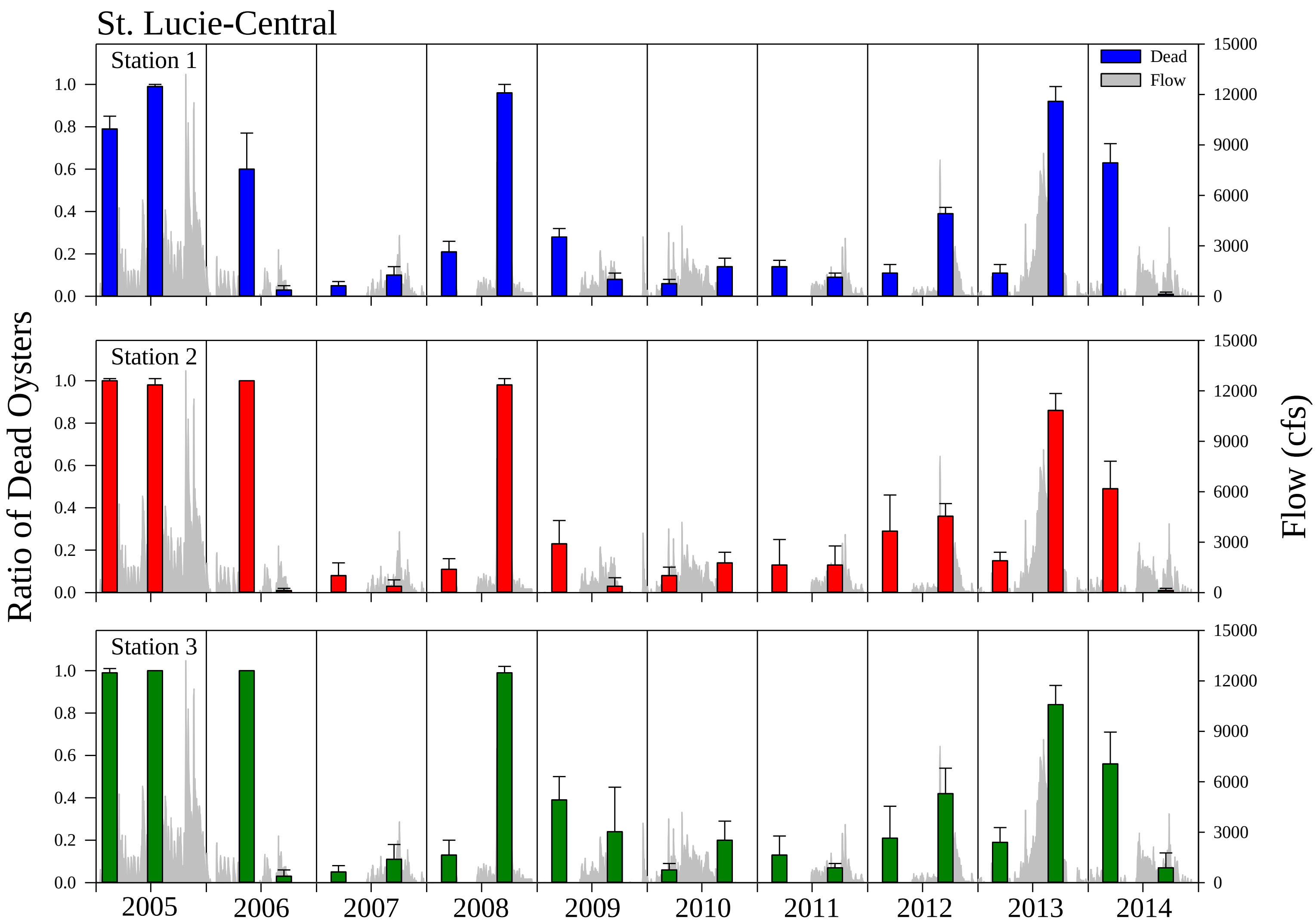

Figure 24. Mean semi-annual ratio (± S.D.) of dead oysters present at St. Lucie-Central Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

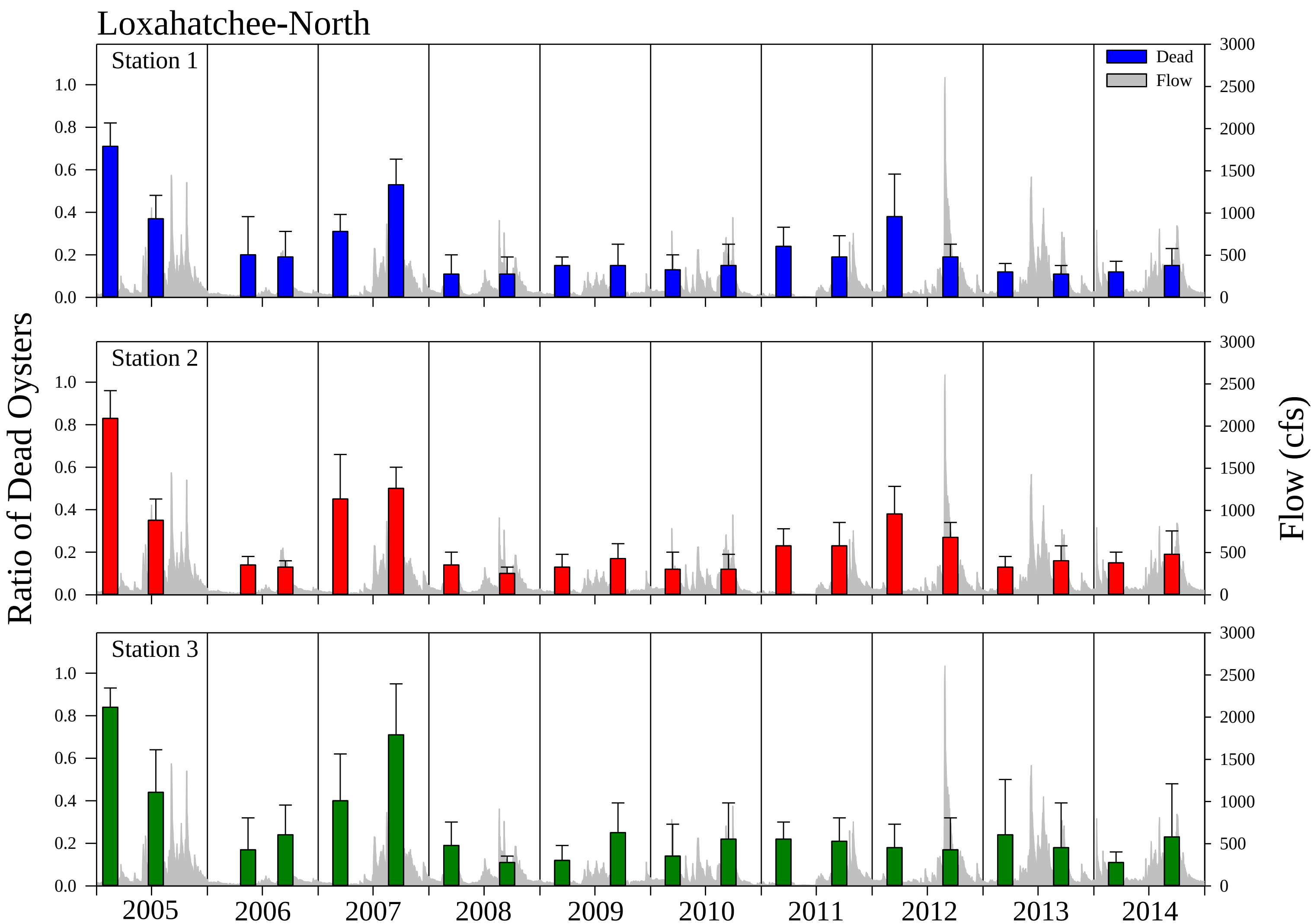

Figure 25. Mean semi-annual ratio (± S.D.) of dead oysters present at Loxahatchee-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District.

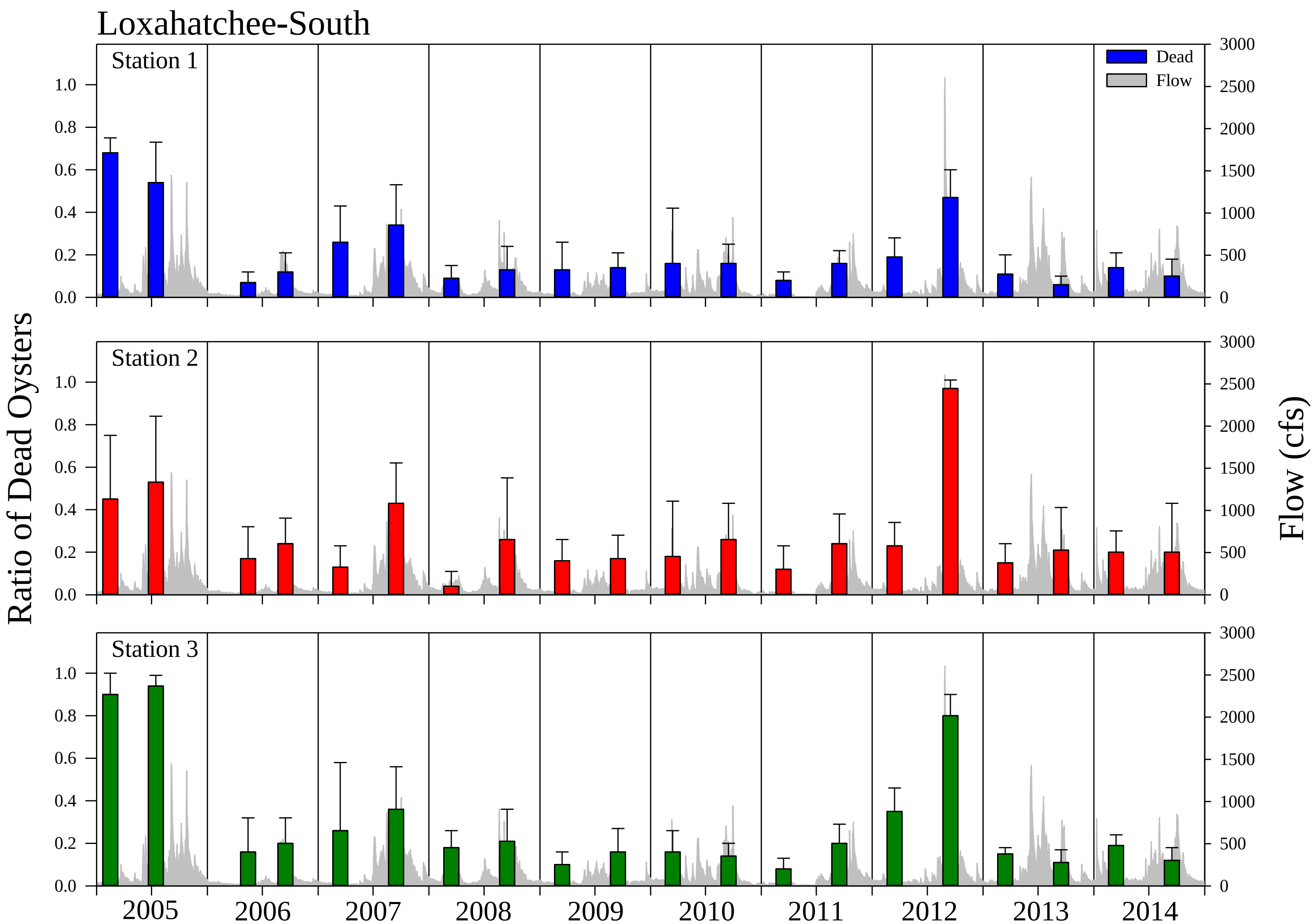

Figure 26. Mean semi-annual ratio (± S.D.) of dead oysters present at Loxahatchee-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District.

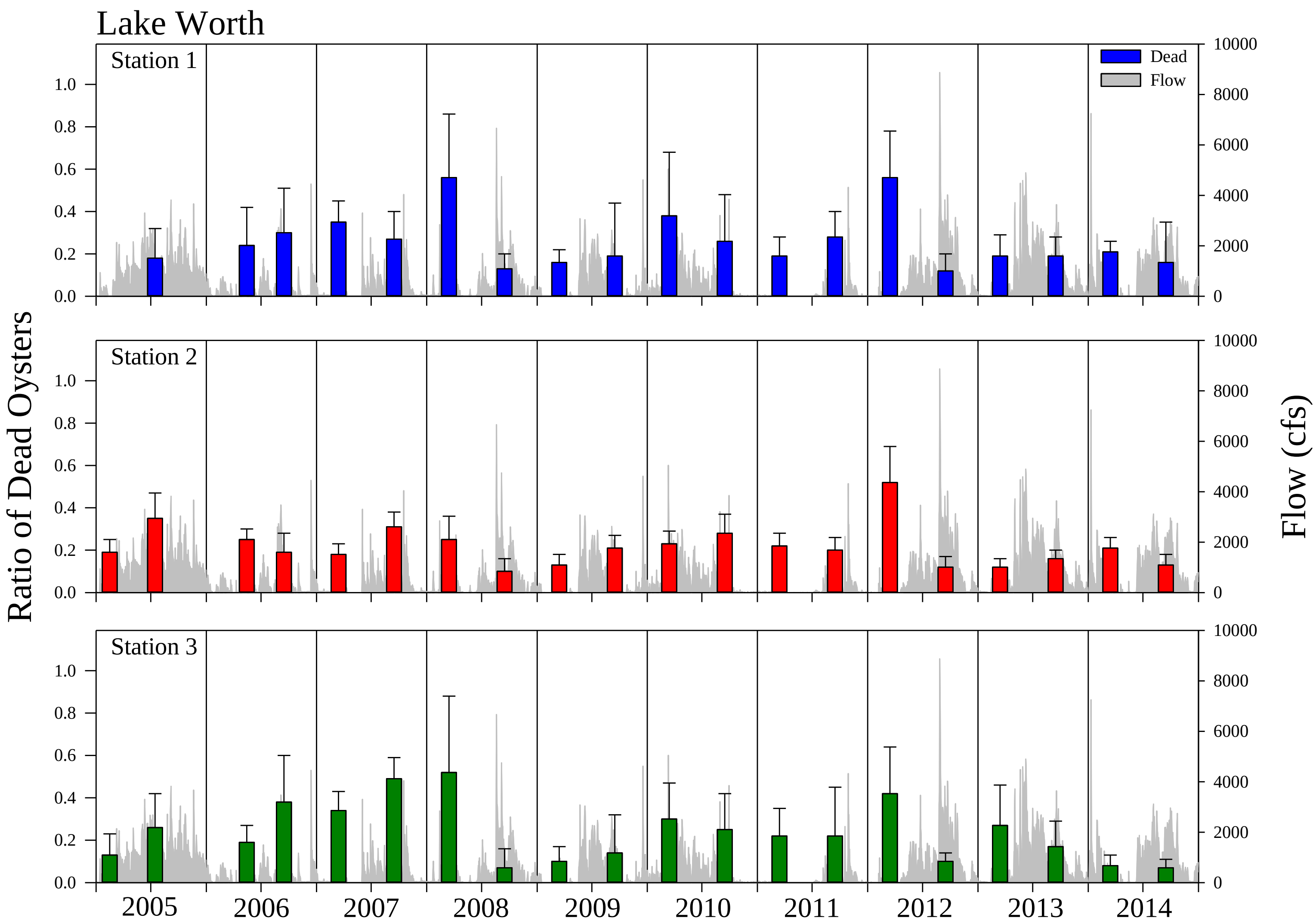

Figure 27. Mean semi-annual ratio (± S.D.) of dead oysters present at Lake Worth Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S44, S155, and S41 structures as recorded by the South Florida Water Management District.

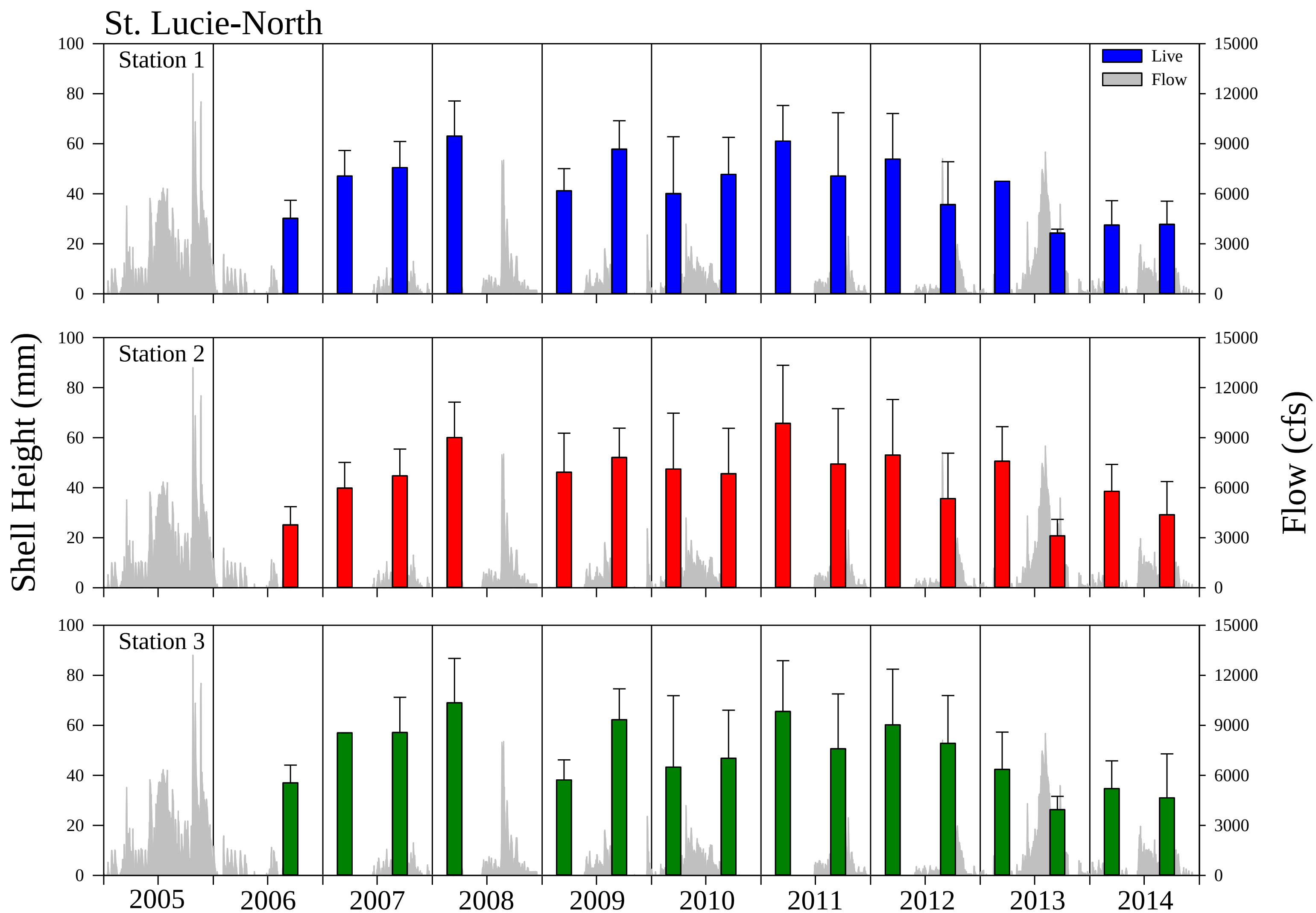

Figure 28. Mean semi-annual shell height (± S.D.) of live oysters present at St. Lucie-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

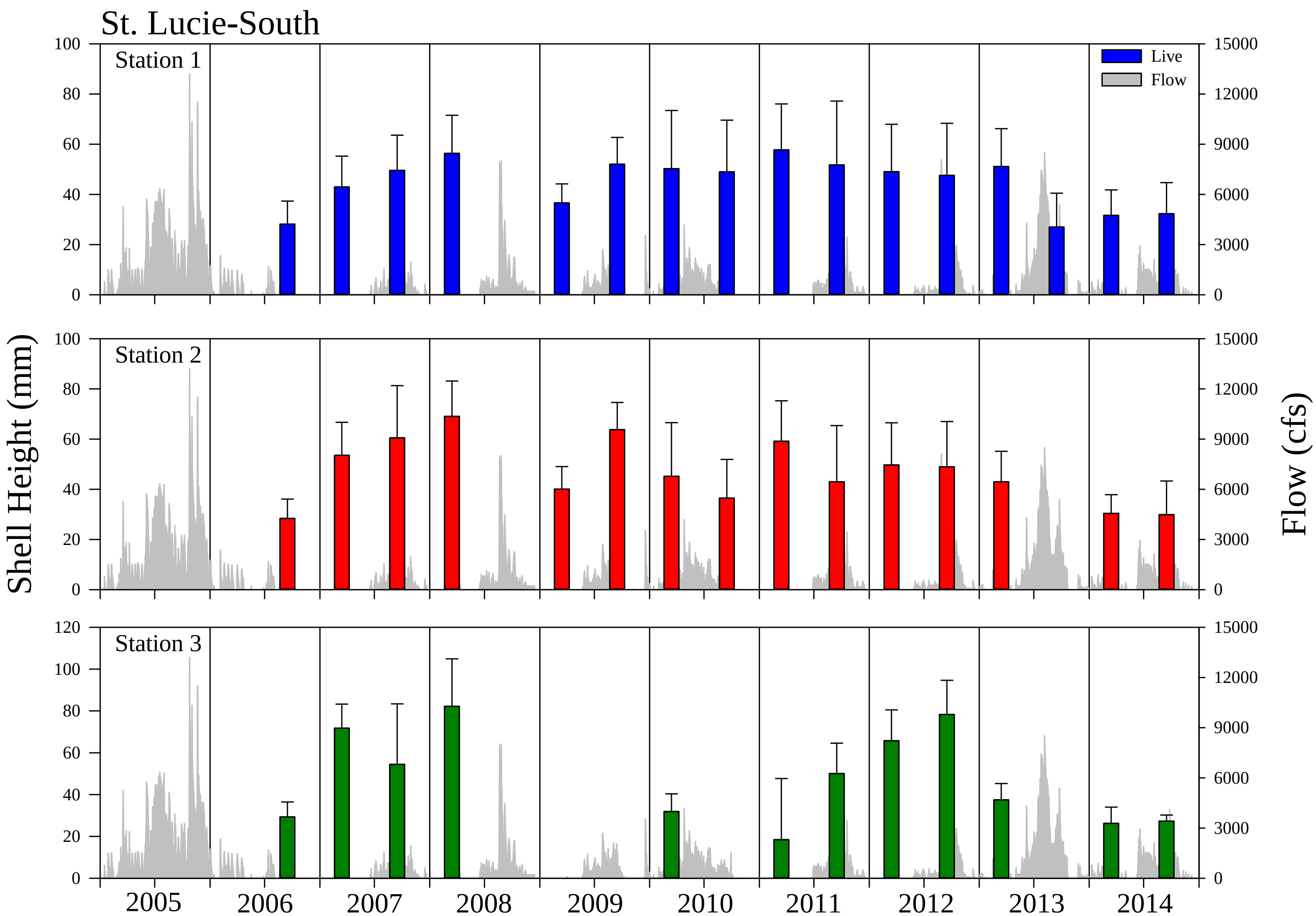

Figure 29. Mean semi-annual shell height (± S.D.) of live oysters present at St. Lucie-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

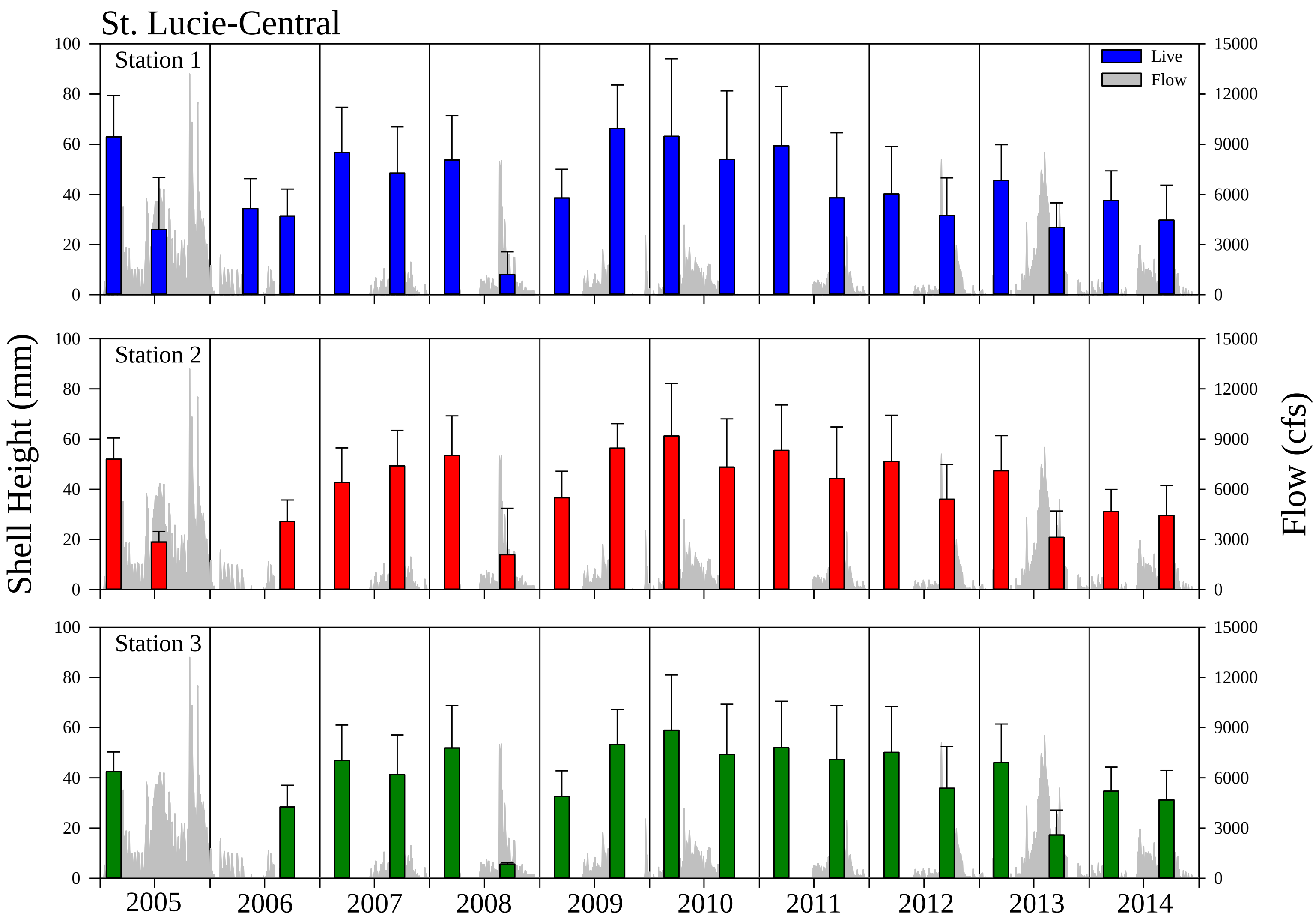

Figure 30. Mean semi-annual shell height (± S.D.) of live oysters present at St. Lucie-Central Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

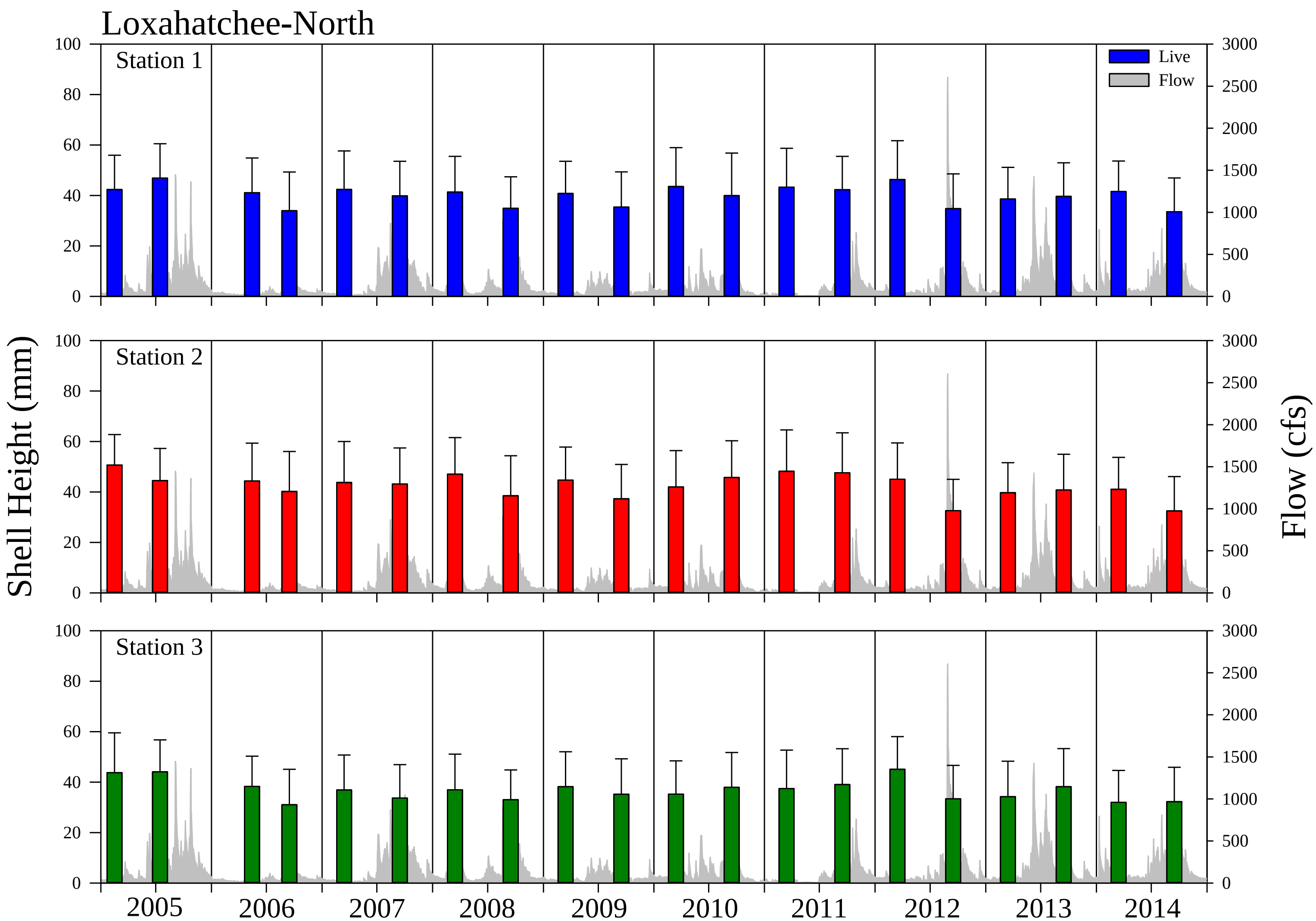

Figure 31. Mean semi-annual shell height (± S.D.) of live oysters present at Loxahatchee-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District.

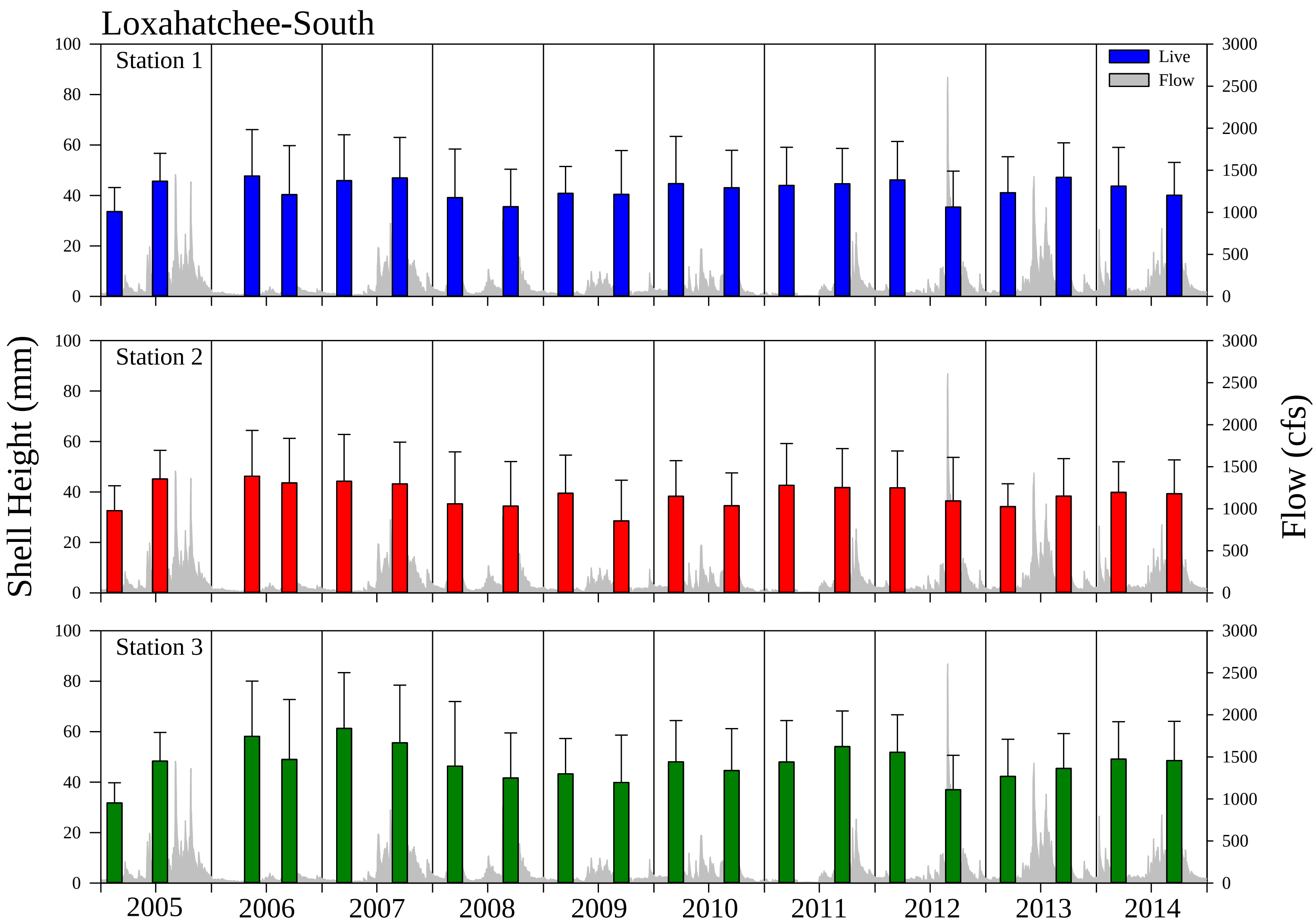

Figure 32. Mean semi-annual shell height (± S.D.) of live oysters present at Loxahatchee-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District.

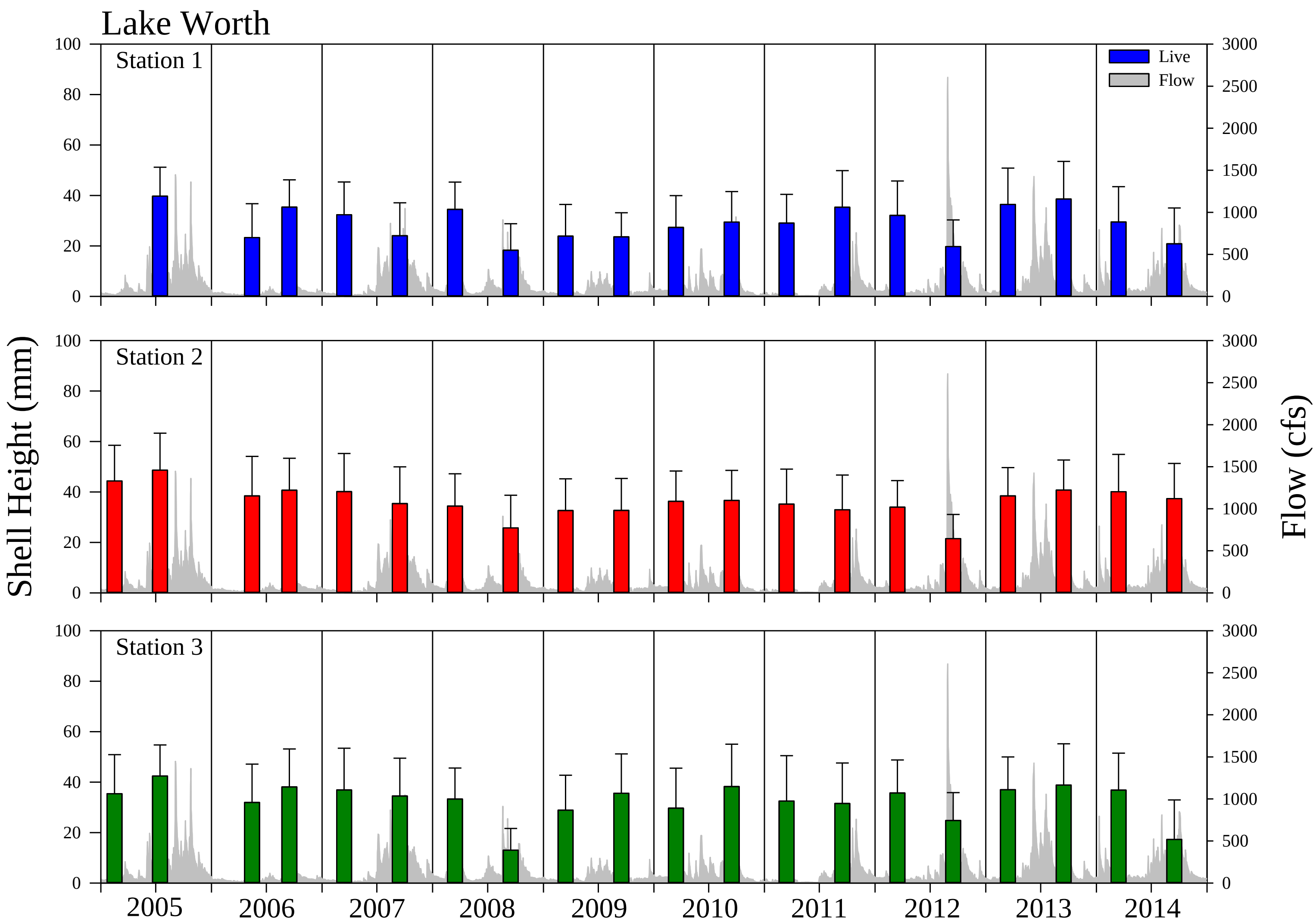

Figure 33. Mean semi-annual shell height (± S.D.) of live oysters present at Lake Worth Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S44, S155, and S41 structures as recorded by the South Florida Water Management District.

Disease

When sampling began in March 2005, no live oysters were present at any of the stations in the St. Lucie-North or South sites; oysters were either not available or too small (< 15 mm SH) to process for disease analyses in either site until December 2006 (21 months later). Similarly, oysters were not available from St. Lucie-Central from July 2005 through April 2006 (10 months). Oysters were not available from all SLE sites again in September 2008 and remained absent through January 2009 (5 months) in St. Lucie-Central and through March 2009 (7 months) in St. Lucie-North and South. Oysters disappeared from St. Lucie-North and South from August 2013 through December 2013 (5 months) and from St. Lucie-Central from September 2013 through December 2013 (4 months). Oysters were present but not collected from the Lake Worth and LOX sites in October 2005 because the sampling trip was postponed in order to avoid the effects of Hurricane Wilma.

Prevalence of infection by *P. marinus* (dermo) varied significantly among sites ($F_{5,1656}$=61.23, P < 0.01; Figures 34-39). The highest infection rates occurred in oysters from Lake Worth, Loxahatchee-North and Loxahatchee-South where overall means were 53%, 38%, and 44%, respectively. Infection rates were much lower in the SLE sites where overall means ranged from less than 1% to 11%. Dermo prevalence also differed significantly among years at each of the sites ($F_{43,1656}$=6.58, P < 0.01). This was most evident in the three SLE sites where annual mean infection rates in the latter part of the study (2011 through 2014) were much greater than previous years. In St. Lucie-North and South, annual means doubled from 11% or less to a range of 20% to 35% from 2011 to 2014. This was even more pronounced in St. Lucie-Central where means increased from less than 7% to more than 50% from 2011 through 2013. Two exceptions occurred in 2008 and 2014, when mean infection rates in St. Lucie-Central were more moderate (~17%). In the Loxahatchee-North and Lake Worth sites, infection rates were also greatest in the last four years of the study, ranging from 47% to 74% and from 63% to 79%, respectively. The pattern was similar in Loxahatchee-South, with the exception of 2013 when infection rates were substantially lower. At most sites, infection rates were lowest in 2005; infection rates were lowest in 2008 in St. Lucie-North and South. Flow rates are included on dermo prevalence plots for comparison.

Intensity of infection by *P. marinus* (dermo) followed a pattern similar to that seen with dermo infection prevalence (Figures 40-45). The highest mean overall infection intensities were found in oysters from Lake Worth (0.53), Loxahatchee-South (0.44), and Loxahatchee-North (0.31) ($F_{5,9179}=63.8$, $P <$ 0.01). Mean infection intensity was an order of magnitude lower in SLE oysters (0.07 to 0.09). Infection intensity also varied among years at each of the sites ($F_{43,9179}=7.28$, $P < 0.01$). At all sites infection intensity was highest in 2012 or 2014. In 2014, mean intensities were 0.89 in Lake Worth and 1.25 in Loxahatchee-South. In 2012, mean intensities were approximately 0.80 in Loxahatchee-North and St. Lucie-Central, 0.24 in St. Lucie-South, and 0.17 in St. Lucie-North. Infection intensities were lowest in 2005 at Lake Worth (0.21) and the two LOX sites (0.06 and 0.02), but were lowest in 2007 at St. Lucie-Central (0.01) and in 2008 at St. Lucie-North (0.00) and South (0.00). Despite these differences among sites and years, most mean infection intensity values were less than 1, indicating that sampled oysters were only lightly infected with the parasite (Table 2). Flow rates are included on dermo intensity plots for comparison.

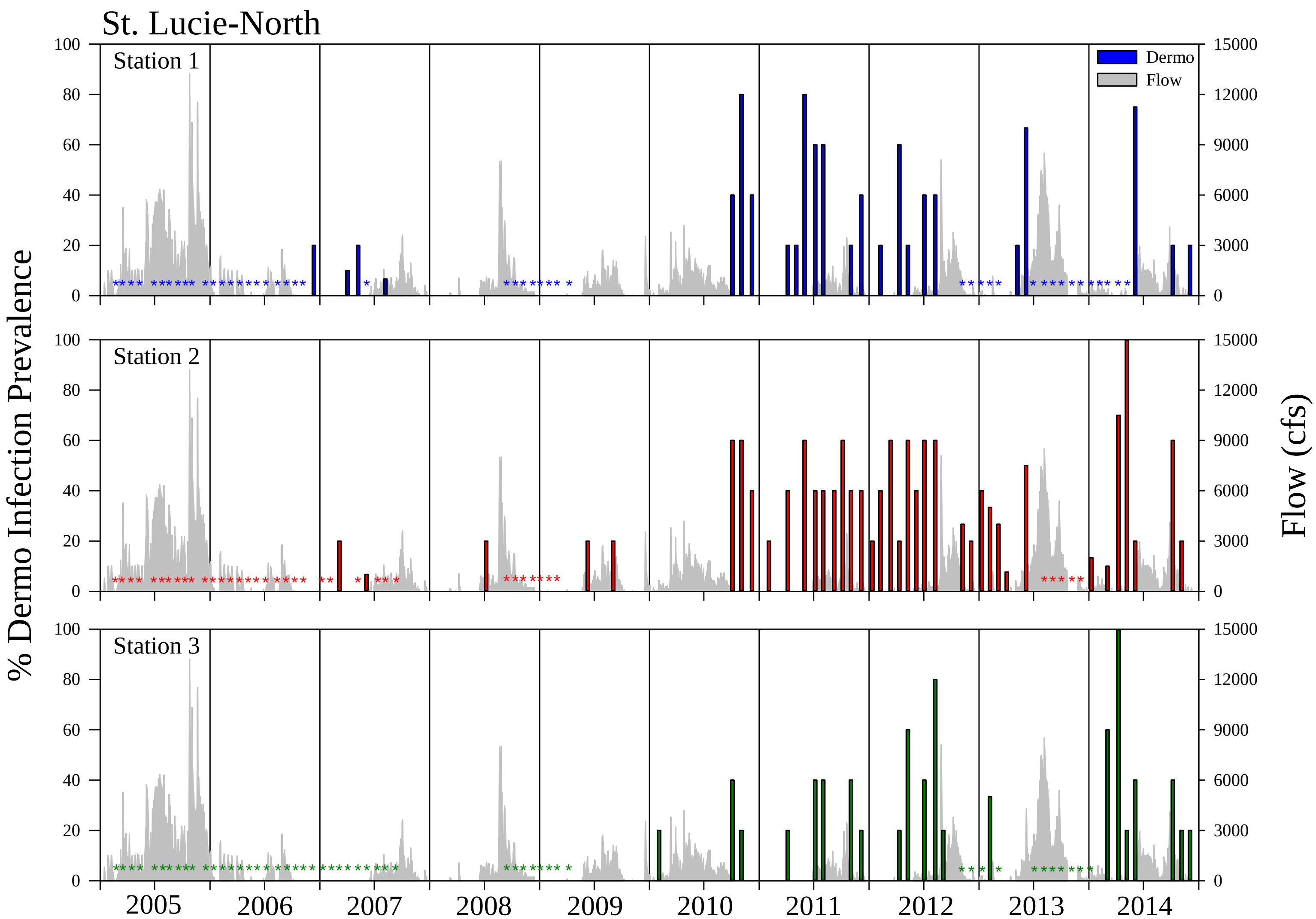

Figure 34. Monthly prevalence (%) of oysters infected with *Perkinsus marinus* at St. Lucie-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District. Asterisks denote stations where no live oysters were collected for analysis.

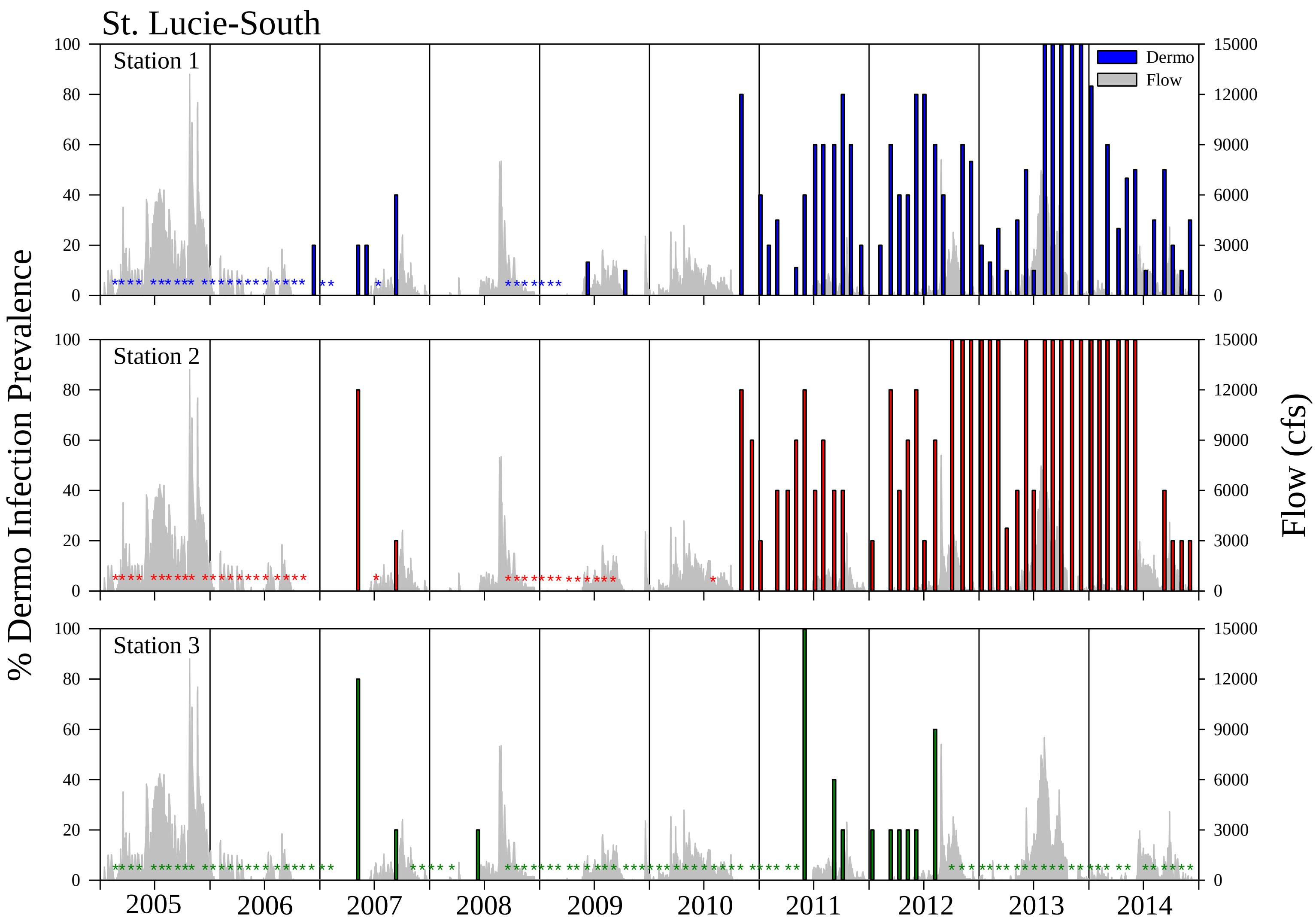

Figure 35. Monthly prevalence (%) of oysters infected with *Perkinsus marinus* at St. Lucie-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District. Asterisks denote stations where no live oysters were collected for analysis.

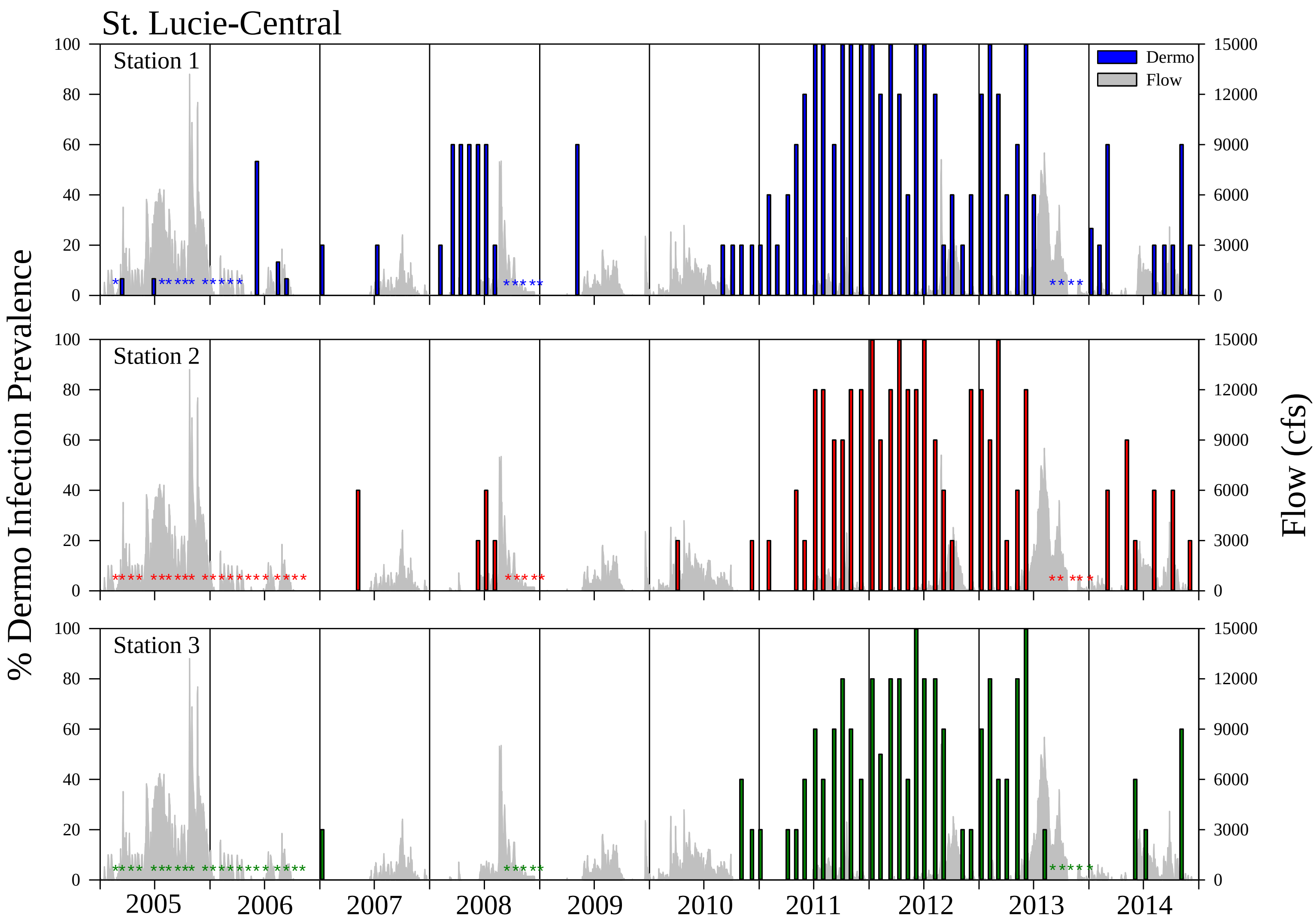

Figure 36. Monthly prevalence (%) of oysters infected with *Perkinsus marinus* at St. Lucie-Central Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District. Asterisks denote stations where no live oysters were collected for analysis.

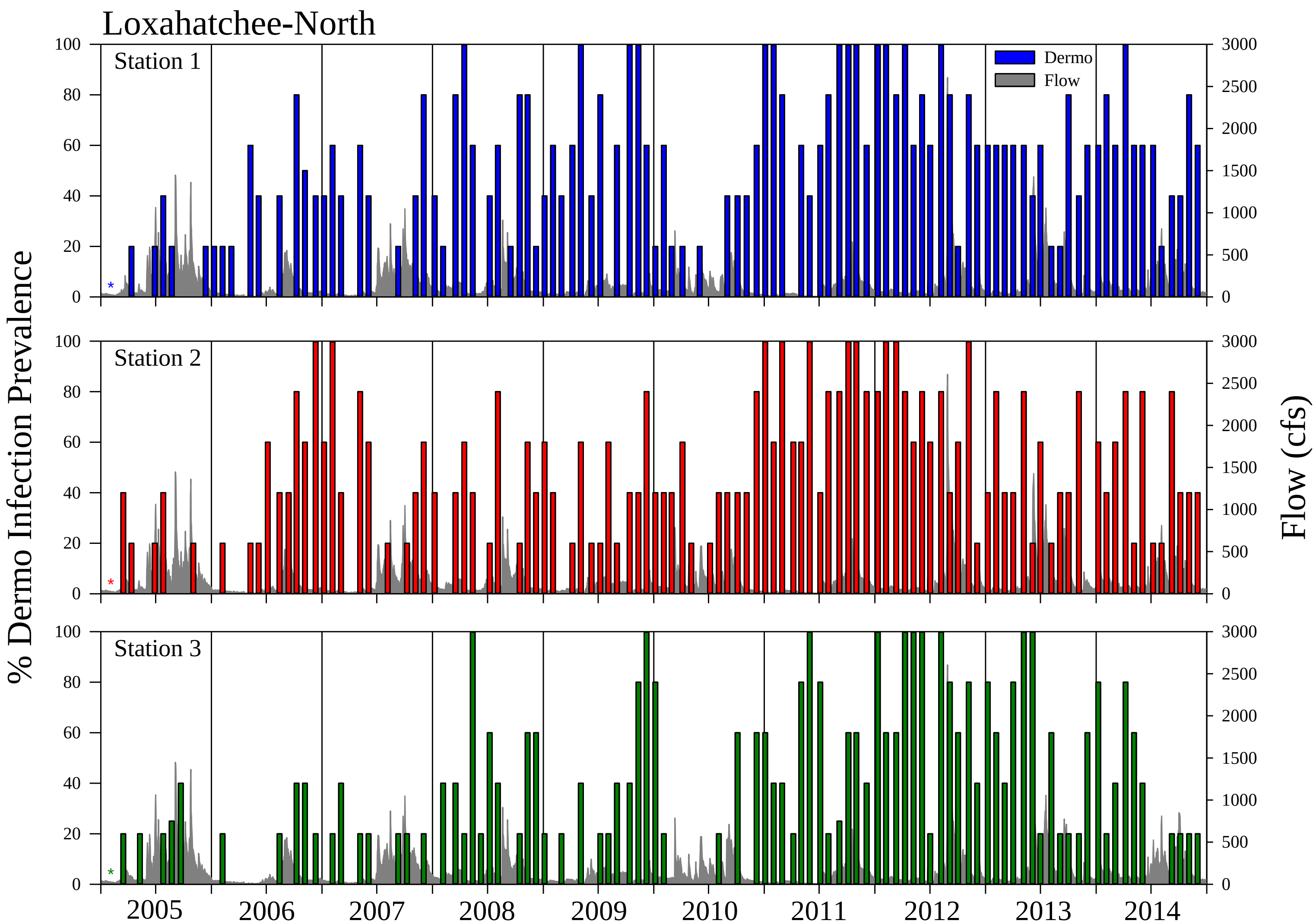

Figure 37. Monthly prevalence (%) of oysters infected with *Perkinsus marinus* at Loxahatchee-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District. Asterisks denote stations where no live oysters were collected for analysis.

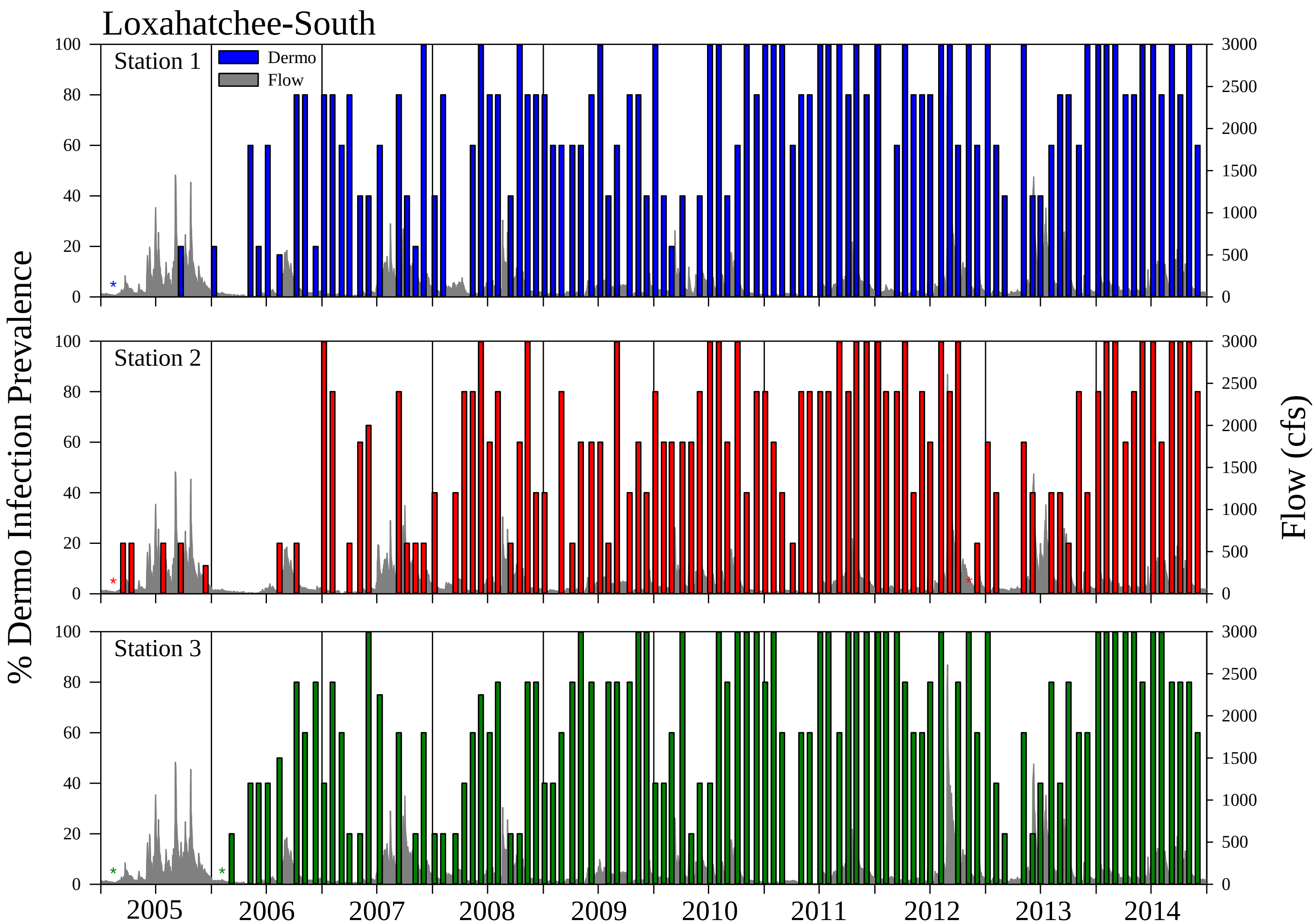

Figure 38. Monthly prevalence (%) of oysters infected with *Perkinsus marinus* at Loxahatchee-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District. Asterisks denote stations where no live oysters were collected for analysis.

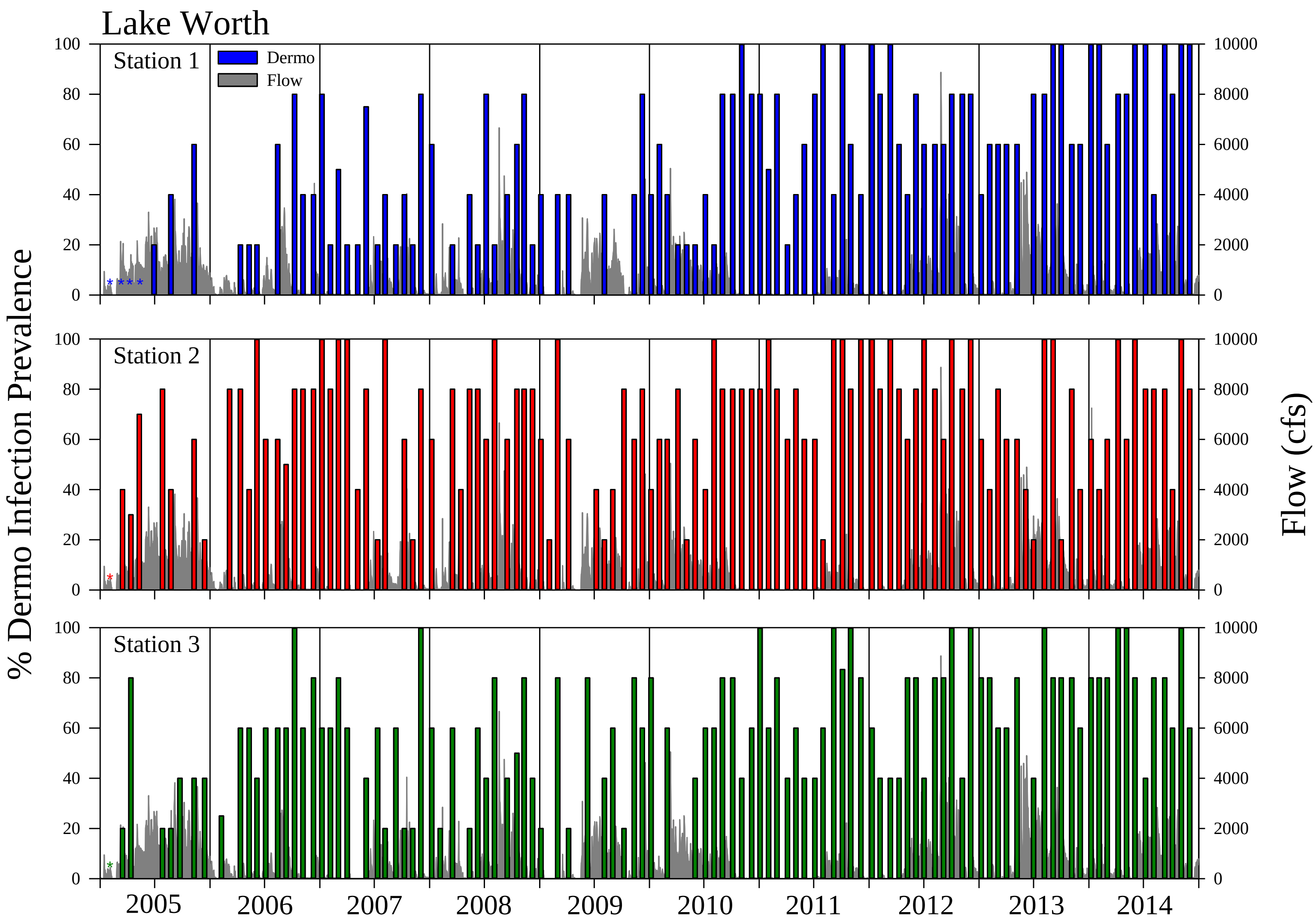

Figure 39. Monthly prevalence (%) of oysters infected with *Perkinsus marinus* at Lake Worth Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S44, S155, and S41 structures as recorded by the South Florida Water Management District. Asterisks denote stations where no live oysters were collected for analysis.

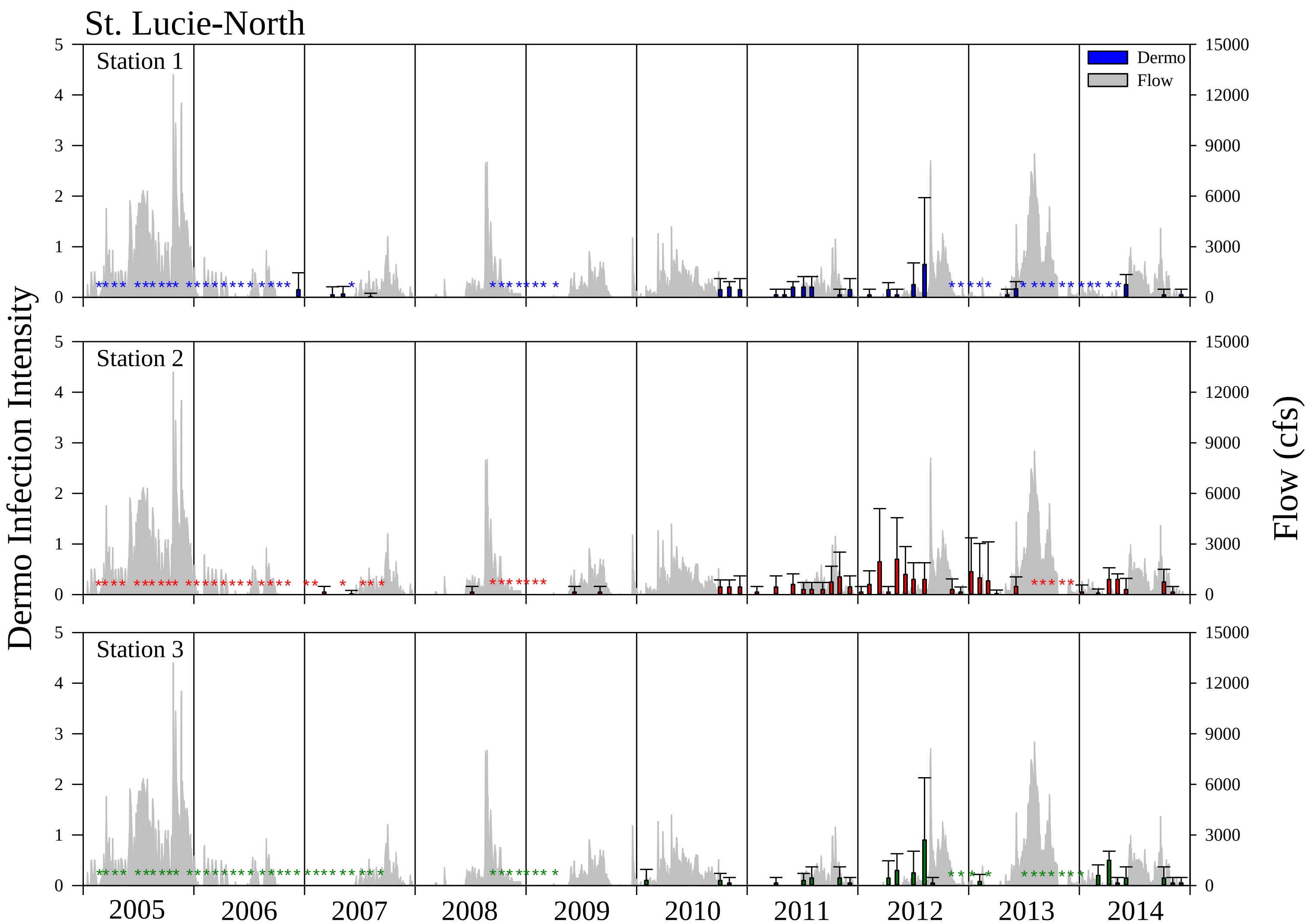

Figure 40. Mean monthly infection intensity (± S.D.) of oysters infected with *Perkinsus marinus* at St. Lucie-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District. Asterisks denote stations where no live oysters were collected for analysis.

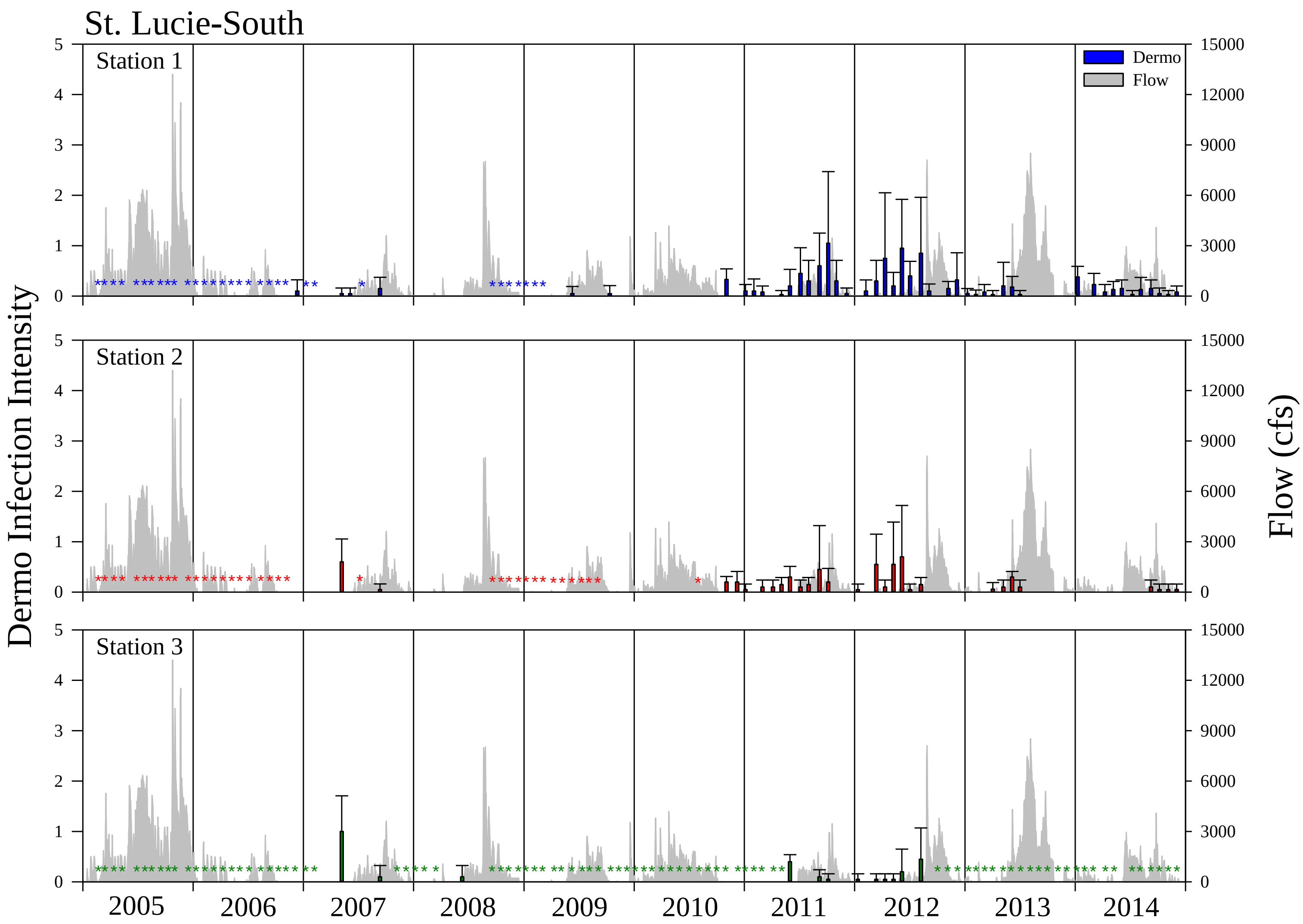

Figure 41. Mean monthly infection intensity (± S.D.) of oysters infected with *Perkinsus marinus* at St. Lucie-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District. Asterisks denote stations where no live oysters were collected for analysis.

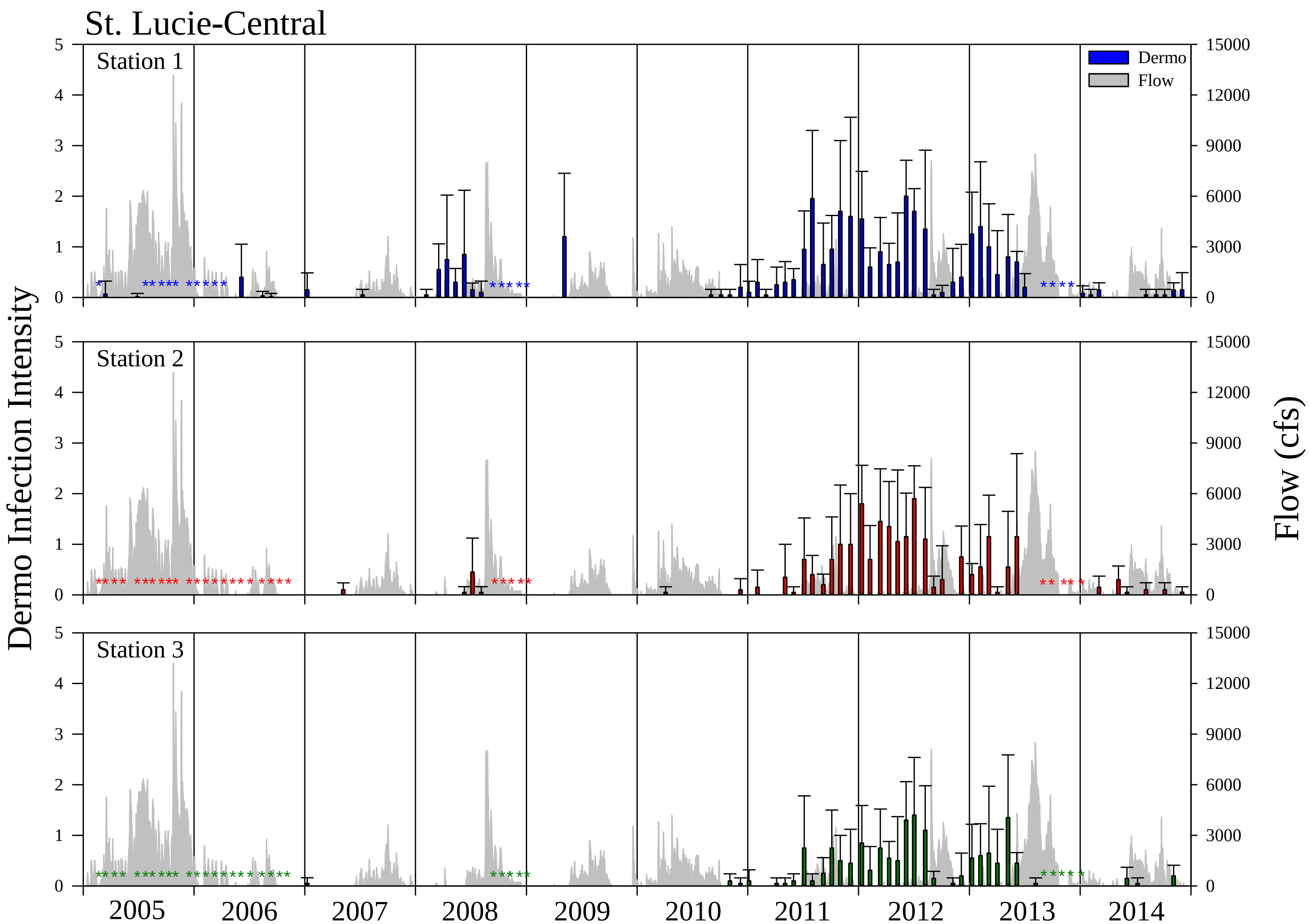

Figure 42. Mean monthly infection intensity (± S.D.) of oysters infected with *Perkinsus marinus* at St. Lucie-Central Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District. Asterisks denote stations where no live oysters were collected for analysis.

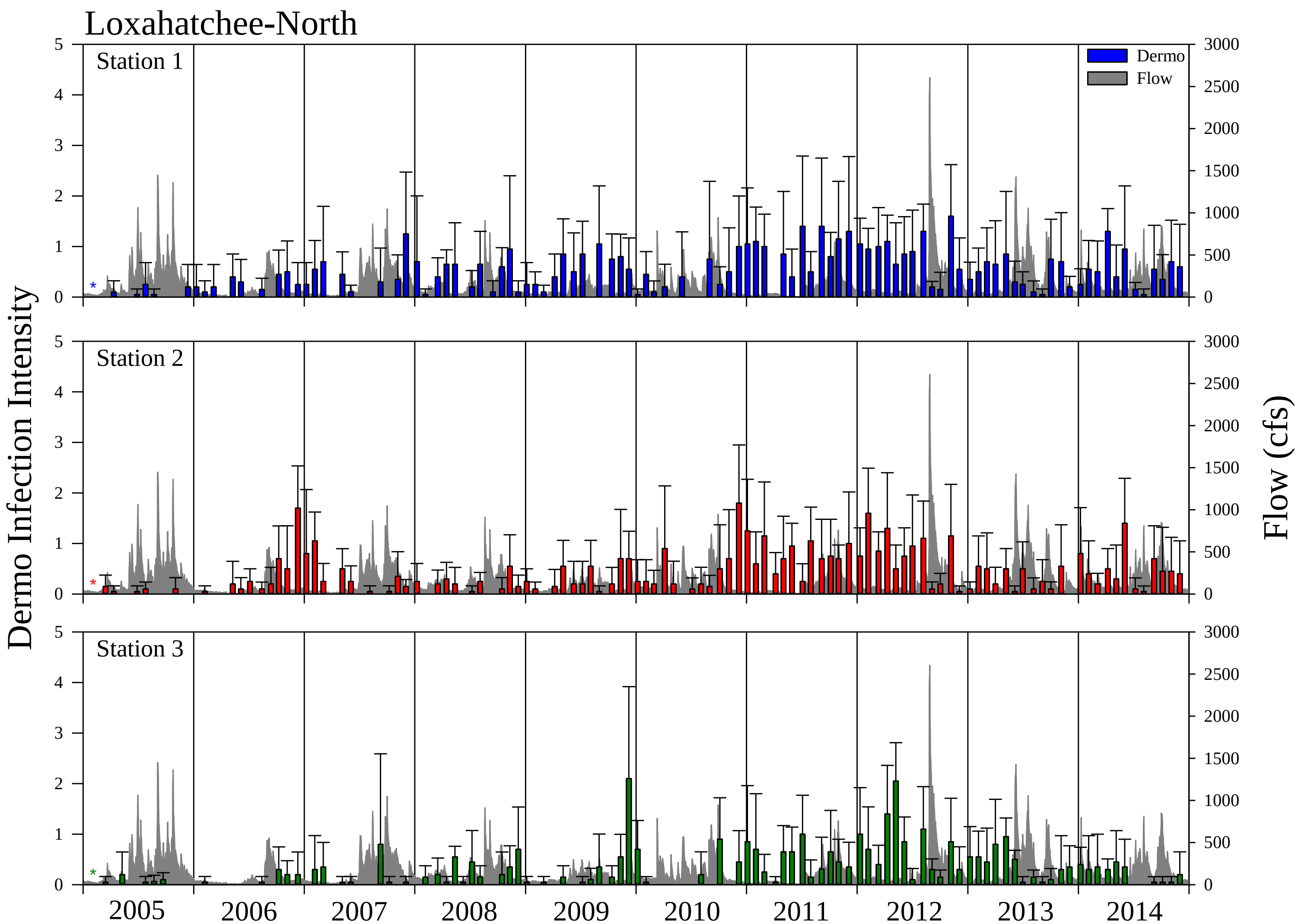

Figure 43. Mean monthly infection intensity (± S.D.) of oysters infected with *Perkinsus marinus* at Loxahatchee-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District. Asterisks denote stations where no live oysters were collected for analysis.

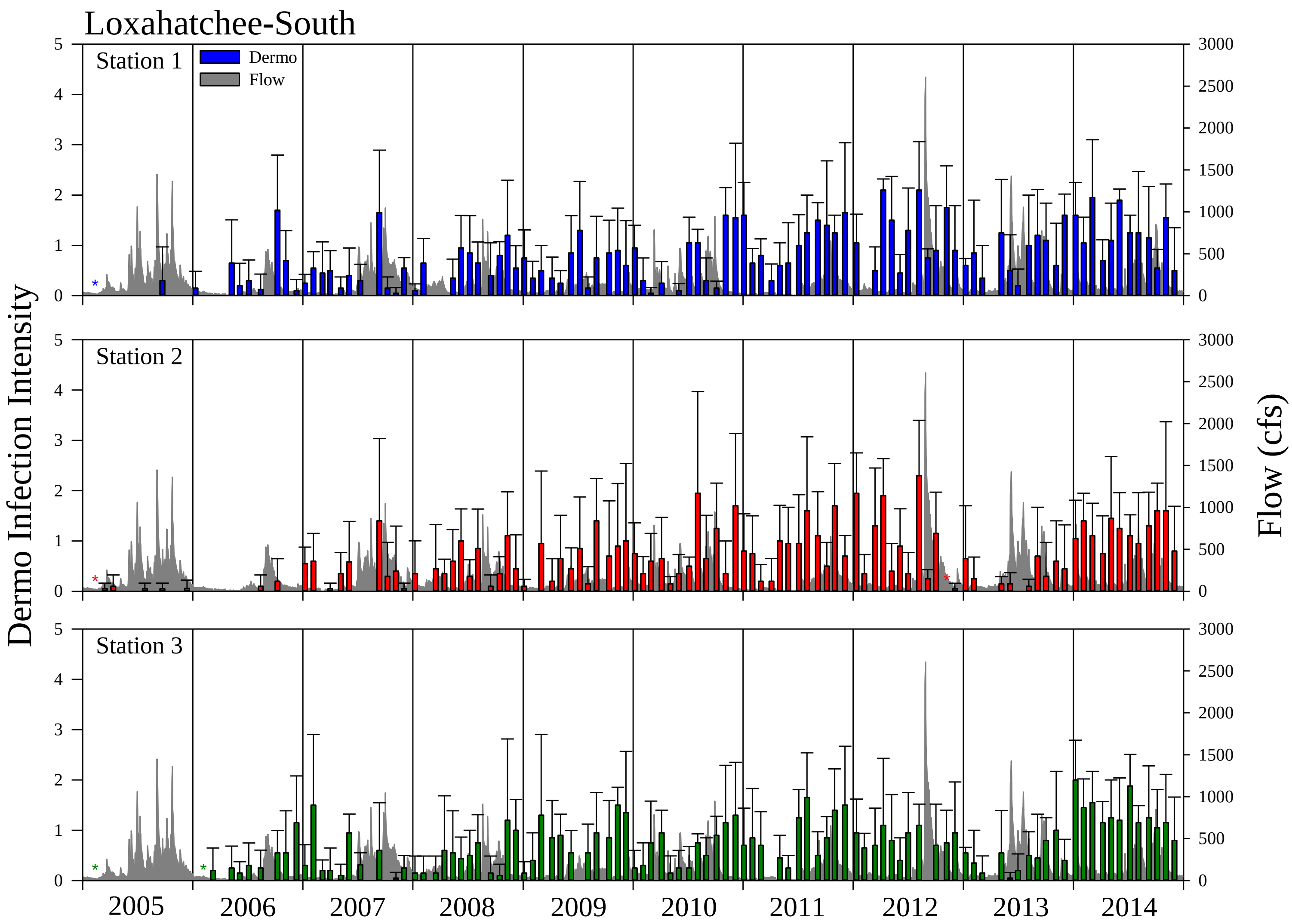

Figure 44. Mean monthly infection intensity (± S.D.) of oysters infected with *Perkinsus marinus* at Loxahatchee-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District. Asterisks denote stations where no live oysters were collected for analysis.

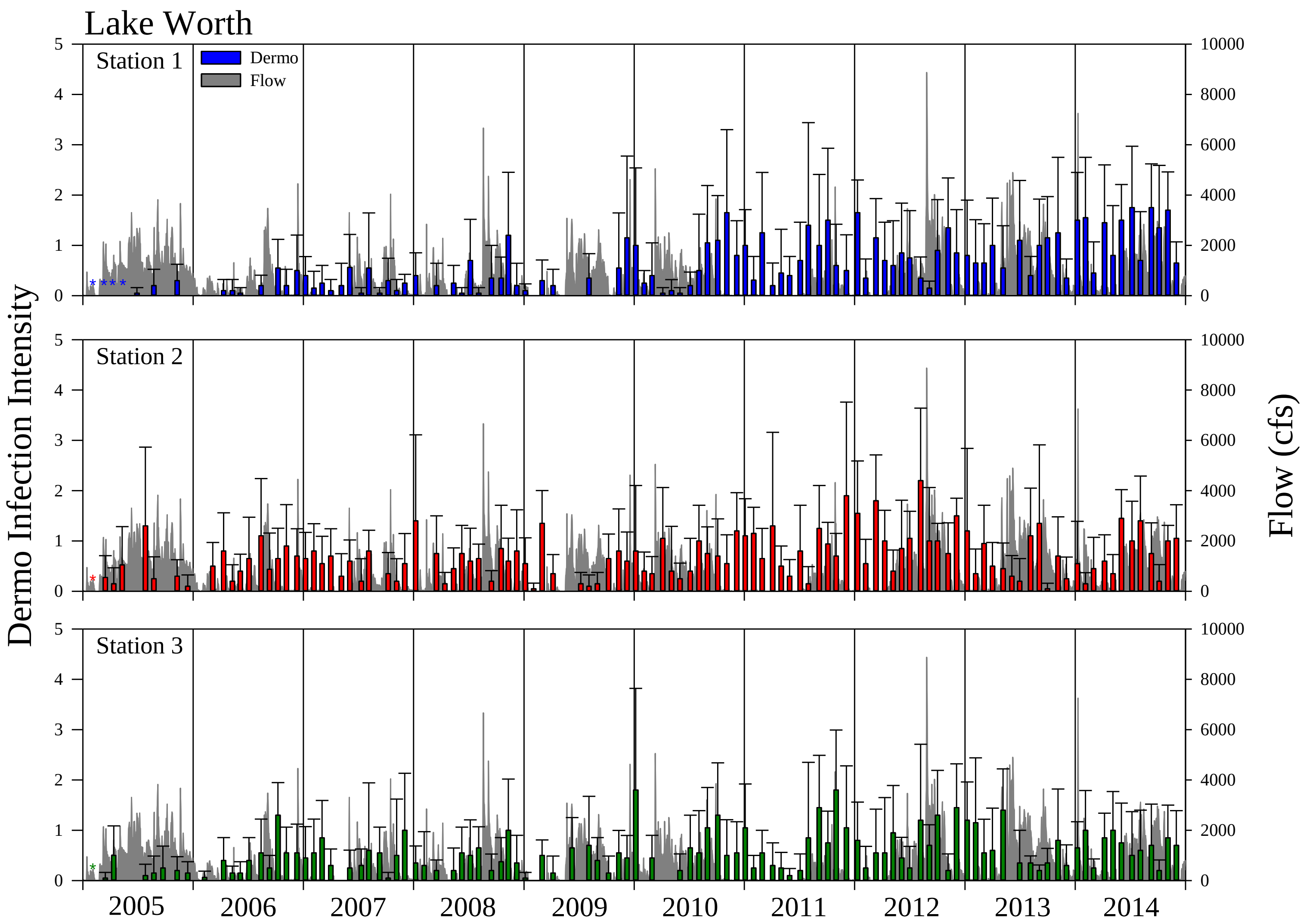

Figure 45. Mean monthly infection intensity (± S.D.) of oysters infected with *Perkinsus marinus* at Lake Worth Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S44, S155, and S41 structures as recorded by the South Florida Water Management District. Asterisks denote stations where no live oysters were collected for analysis.

Reproductive Development and Juvenile Recruitment

When reproductive sampling began in February 2005, no live oysters were present at any of the stations in the St. Lucie-North or South sites; oysters were either not available or too small to process for reproductive analyses in either site until December 2006 (22 months later). Similarly, oysters were not available from St. Lucie-Central from July 2005 through April 2006 (10 months). Oysters were not available from all SLE sites again in September 2008 and remained absent through January 2009 (5 months) in St. Lucie-Central and through March 2009 (7 months) in St. Lucie-North and South. Oysters disappeared from St. Lucie-North from August 2013 through December 2013 (5 months), from St. Lucie-South from August 2013 through February 2014 (7 months), and from St. Lucie-Central from September 2013 through December 2013 (4 months). Oysters were present but not collected from the Lake Worth and LOX sites in October 2005 because the sampling trip was postponed in order to avoid the effects of Hurricane Wilma. Oysters were collected from Loxahatchee-South and Lake Worth in September 2006 and from St. Lucie-Central in October 2006, but the samples were destroyed during histological preparation.

Although the patterns and timing of reproductive development in oysters varied slightly among sites and years, reproductive development and spawning typically occurred between March and October (Figures 46 and 47). The majority of oysters entered the resting, or indifferent, stage in November and remained resting through February. A comparison of the percentage of oysters in the gonadal development stage found that this did not vary significantly among sites ($F_{5,561}$=0.63, P = 0.68) and ranged from approximately 8% to 13%. However, significant differences were detected among years ($F_{9,561}$=3.02, P = 0.01), with lower percentages of developing oysters present in 2005, 2008, and 2013. This coincides with years that had significantly lower oyster densities and higher flow rates. An additional comparison of the percentage of oysters in any of the three active reproductive stages (developing, ripe/spawning, and spent/recycling) found no significant differences among sites ($F_{5,561}$=1.94, P = 0.09) or years ($F_{9,561}$=1.50, P = 0.14). Of all oysters collected from each site, 72% to 86% were in an active reproductive stage.

Juvenile recruitment followed seasonal patterns similar to that seen with reproductive development (Figures 48-53). Oyster spat were typically detected on arrays retrieved in the spring, summer and fall. Spring recruits were most commonly first detected on arrays retrieved in April at the LOX and

LWL sites, and in May at the SLE sites. After initiation of recruitment in the spring, juvenile recruits were often present on the arrays collected every month through December. In the three SLE sites, recruitment was often sporadic and inconsistent, and often was not detected until much later in the season, especially in years following an oyster die-off. The LOX and LWL sites often exhibited a bimodal recruitment pattern, with peaks occurring in the spring (April, May, June or July) and fall (September, October, or November). Occasionally, in each of the sites, low rates of recruitment continued through December and into January or February of the following year.

Recruitment rates were greatest in Lake Worth, where the mean for the duration of the study reached 3.32 spat/shell/month ($F_{5,6055}$=139.39, $P < 0.01$). The lowest recruitment rates, which were an order of magnitude lower than in Lake Worth, were recorded in the three SLE sites (< 0.30 spat/shell/month). Mean recruitment rates in the Loxahatchee-North and South sites were 1.75 and 0.91 spat/shell/month, respectively. The maximum rate for a single sample was 87.33 spat/shell/month, retrieved from Lake Worth Station 1 in October 2012.

Recruitment rates also differed among years at each of the sites ($F_{45,6055}$=7.32, $P < 0.01$). Although there was no consistent pattern for when each site exhibited the highest and lowest recruitment rates, four sites had the highest rates in 2012. These included an annual mean of 10.74 spat/shell/month in Lake Worth, 3.42 spat/shell/month in Loxahatchee-North, 2.46 spat/shell/month in Loxahatchee-South and 0.81 spat/shell/month in St. Lucie-Central. The highest recruitment rates occurred in St. Lucie-North in 2011 and in St. Lucie-South in 2014, when annual means were 1.50 spat/shell/month and 0.31 spat/shell/month, respectively. The lowest annual recruitment rate in Lake Worth (1.68 spat/shell/month), was recorded in 2005, when significantly higher flow rates were also recorded in that estuary. Similarly, the lowest annual recruitment rates (< 0.12 spat/shell/month) were measured in the three SLE sites in 2005, 2008, and 2010, coinciding with the substantial freshwater release events that occurred in the SLE those same years. Finally, both LOX sites exhibited the lowest recruitment rates (< 0.85 spat/shell/month) in 2007. Flow rates are included on recruitment plots for comparison.

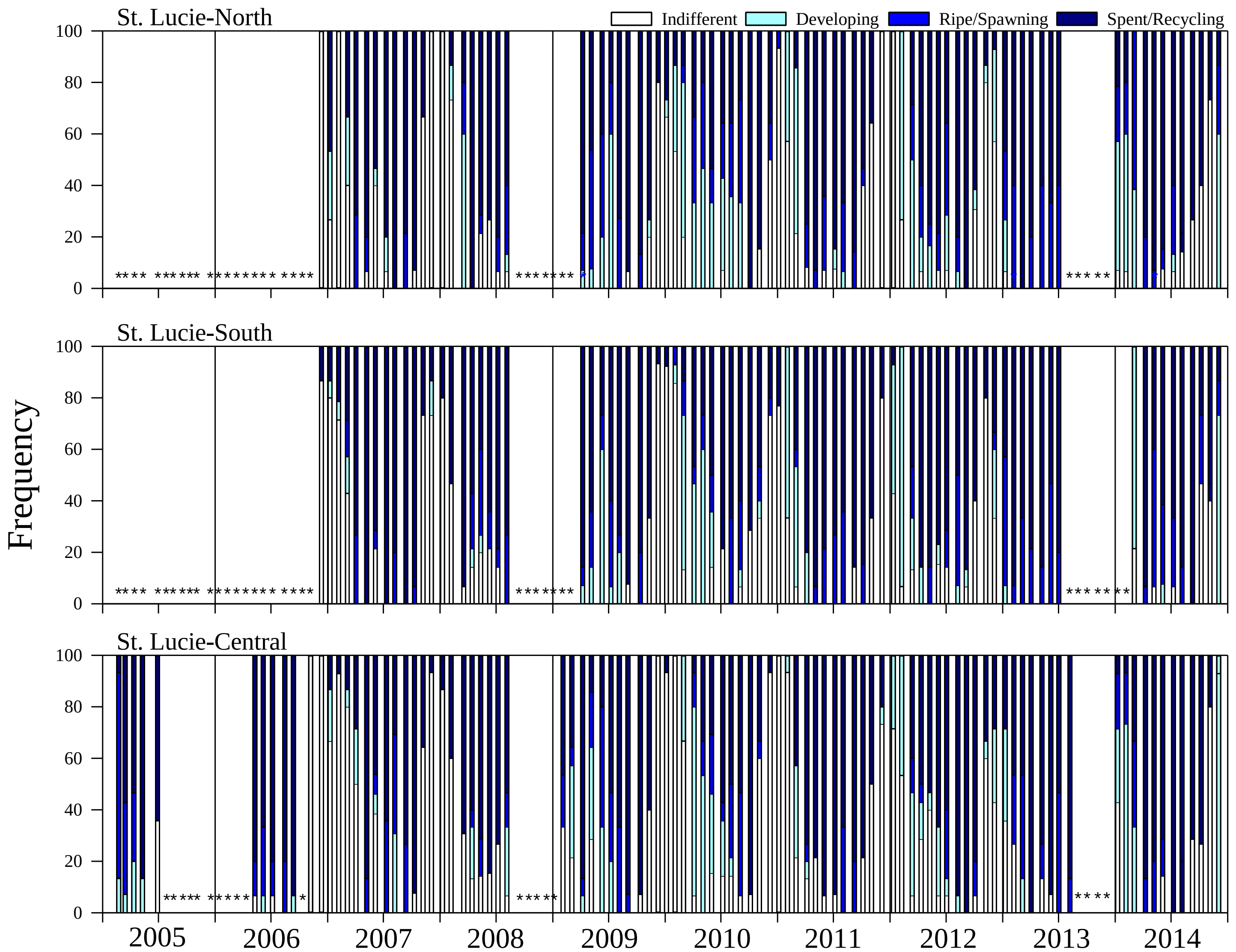

Figure 46. Monthly reproductive development of oysters from the St. Lucie-North (top), St. Lucie-South (middle) and St. Lucie-Central (bottom) study sites from 2005 – 2014. Asterisks denote sites where no live oysters were collected for analysis.

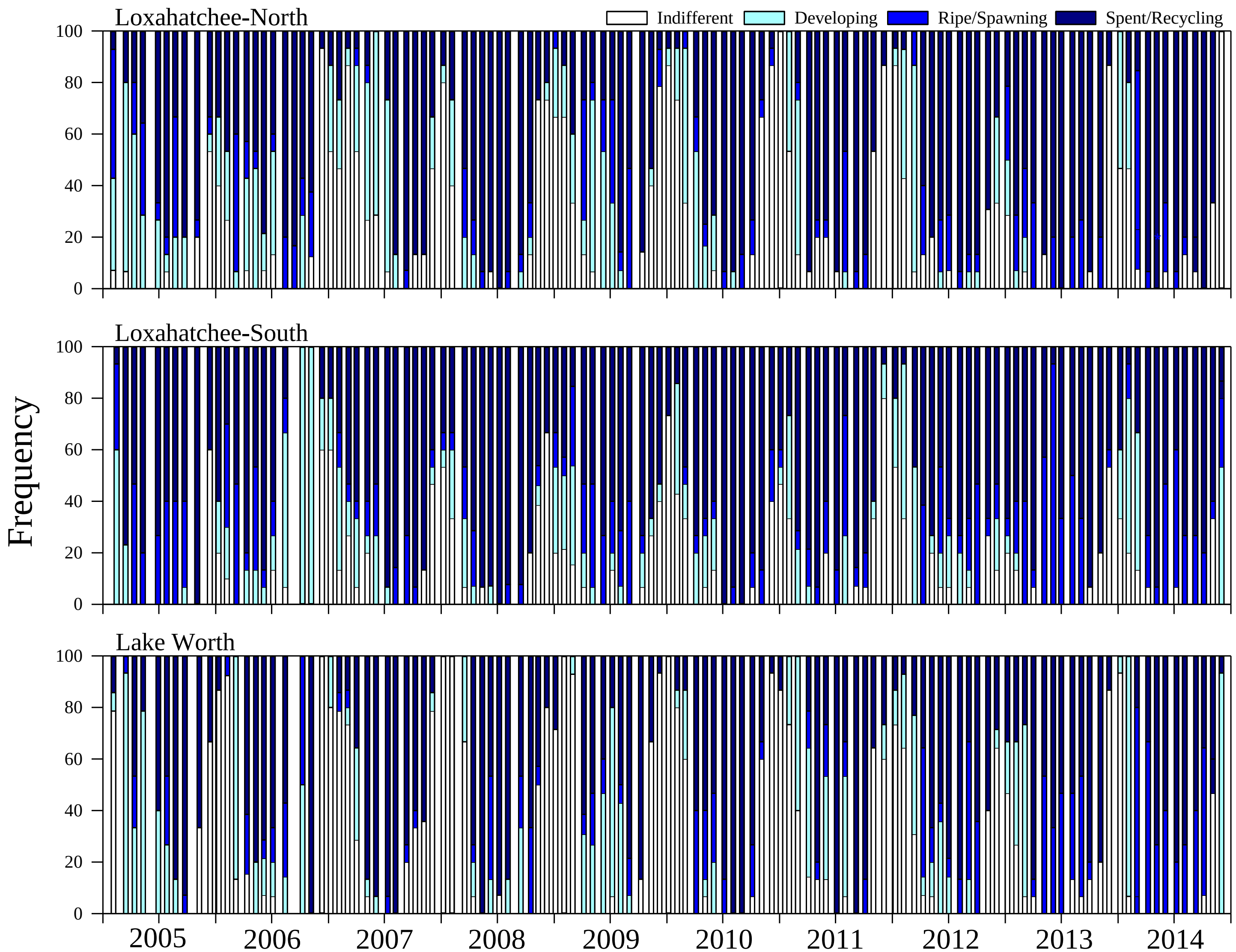

Figure 47. Monthly reproductive development of oysters from the Loxahatchee-North (top), Loxahatchee-South (middle) and Lake Worth study sites from 2005 – 2014.

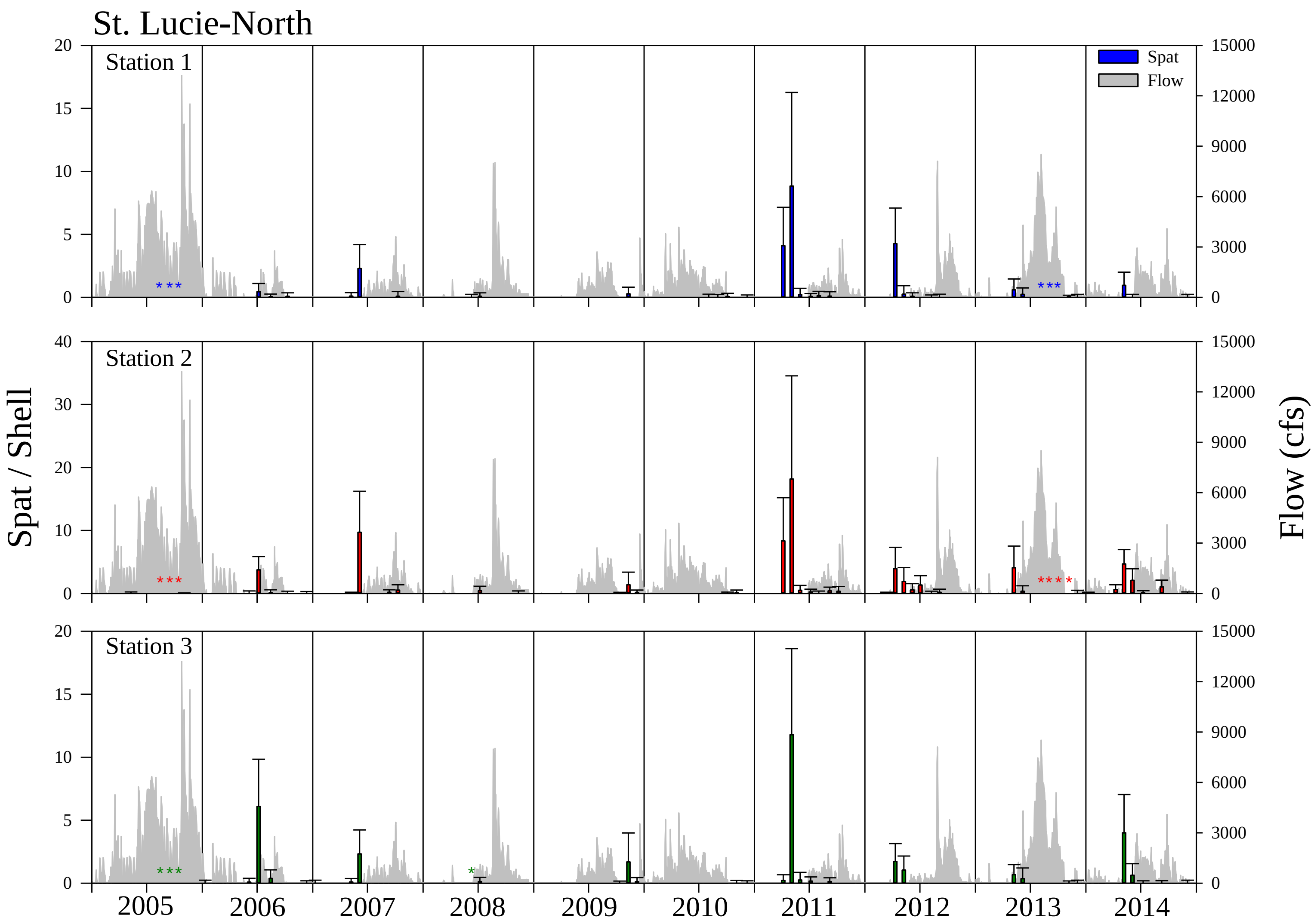

Figure 48. Mean monthly number (± S.D.) of oyster spat recruits collected per shell at St. Lucie-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District. Asterisks denote stations where no recruitment collectors were retrieved for analysis.

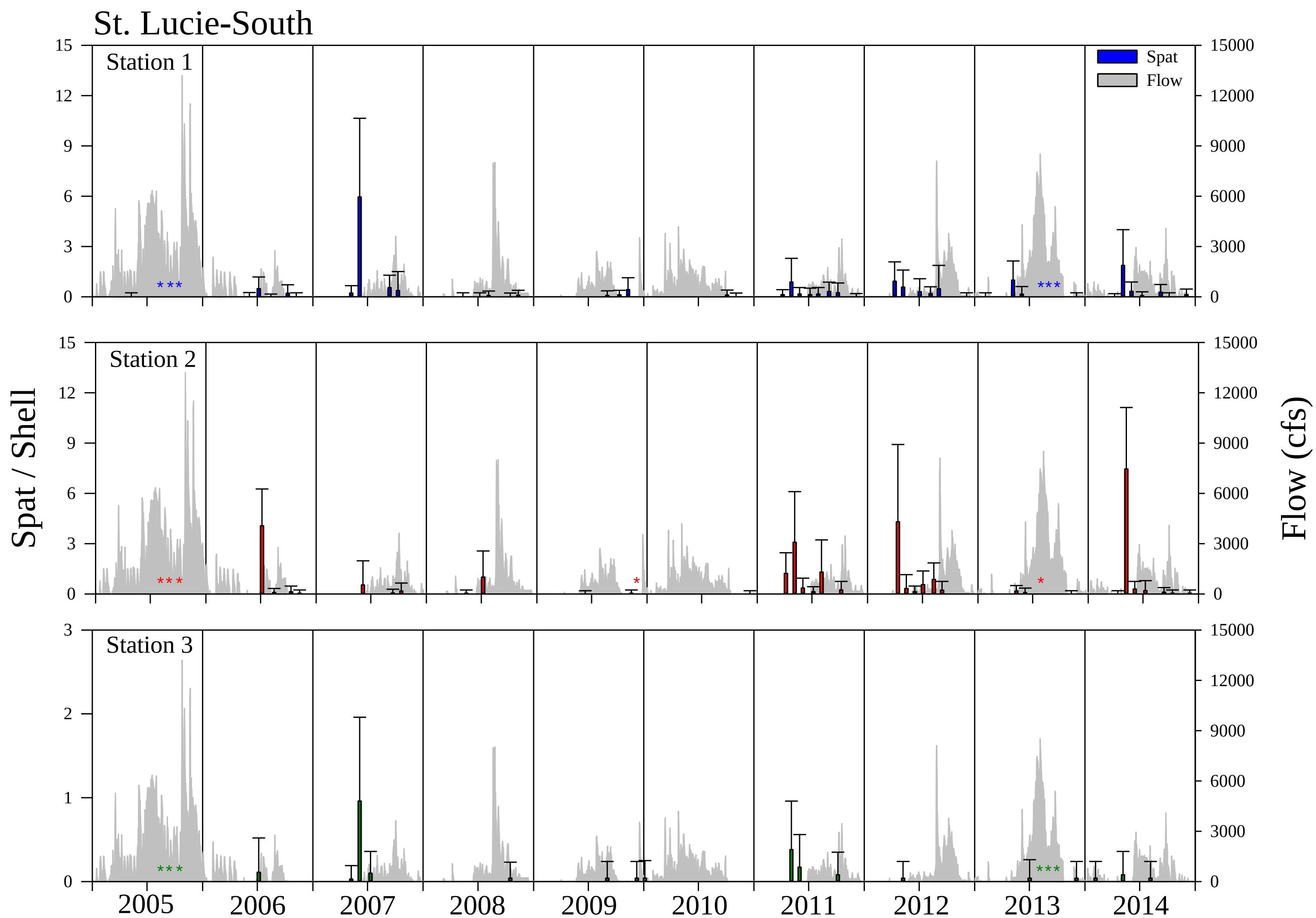

Figure 49. Mean monthly number (± S.D.) of oyster spat recruits collected per shell at St. Lucie-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District. Asterisks denote stations where no recruitment collectors were retrieved for analysis.

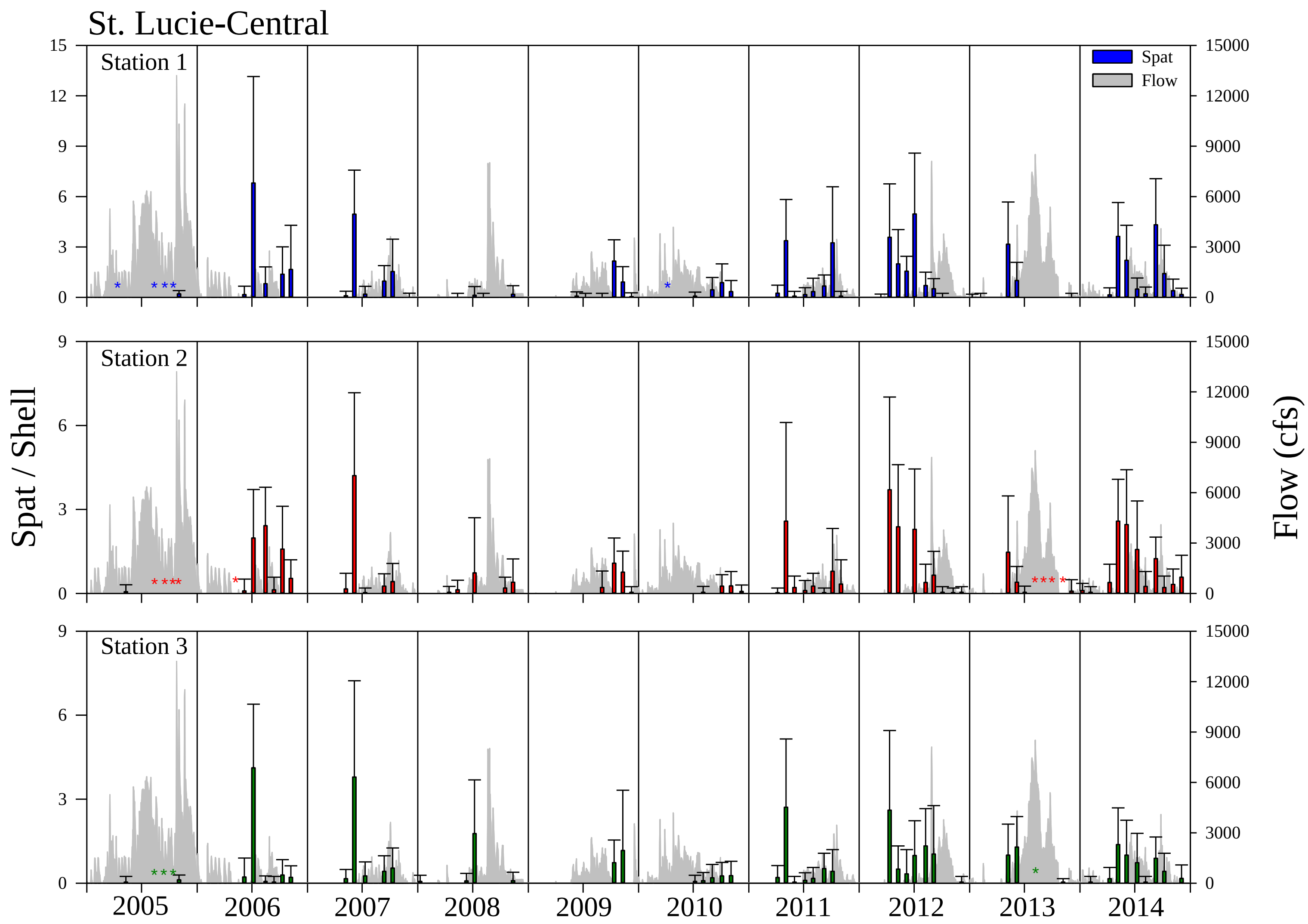

Figure 50. Mean monthly number (± S.D.) of oyster spat recruits collected per shell at St. Lucie-Central Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District. Asterisks denote stations where no recruitment collectors were retrieved for analysis.

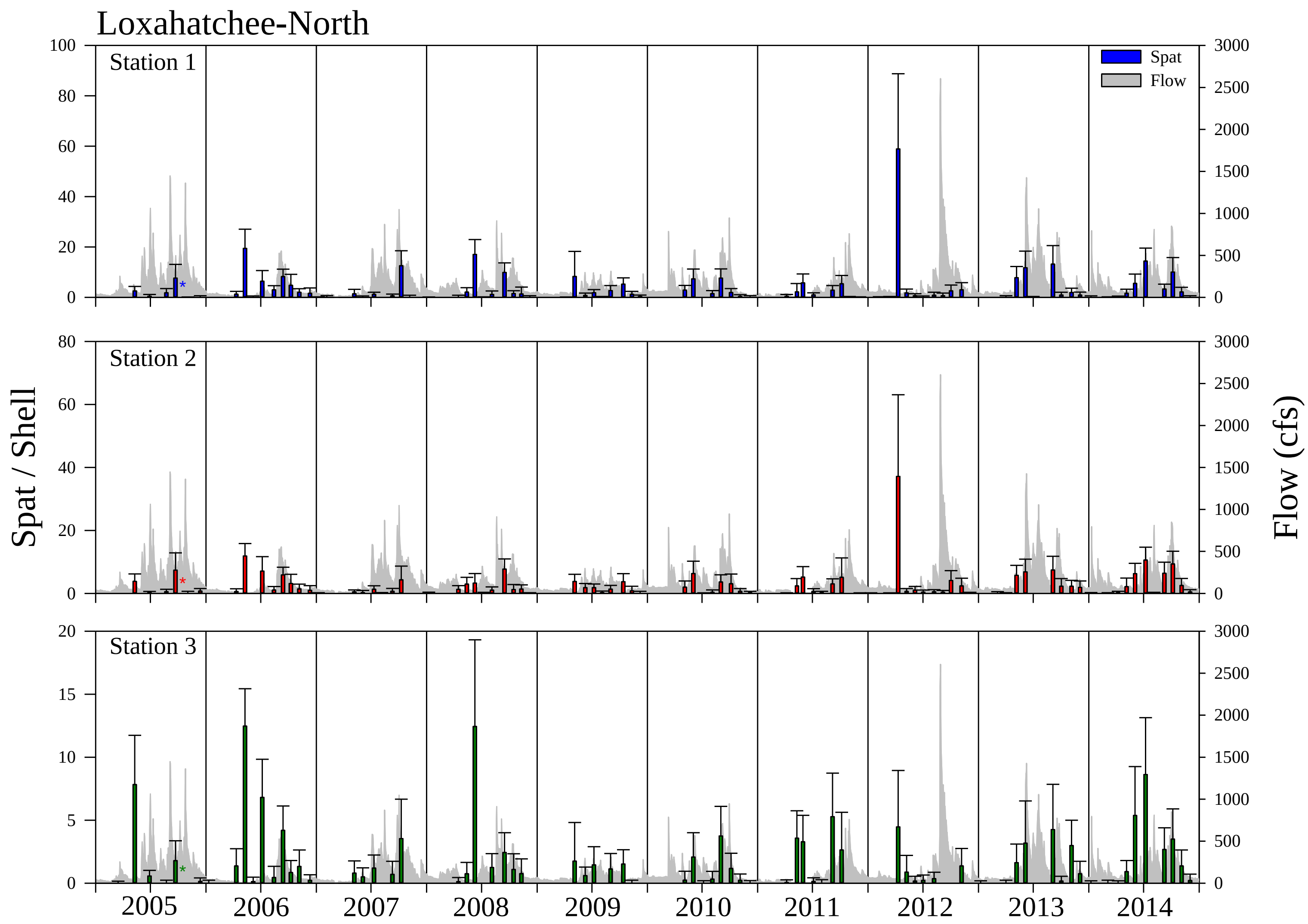

Figure 51. Mean monthly number (± S.D.) of oyster spat recruits collected per shell at Loxahatchee-North Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District. Asterisks denote stations where no recruitment collectors were retrieved for analysis.

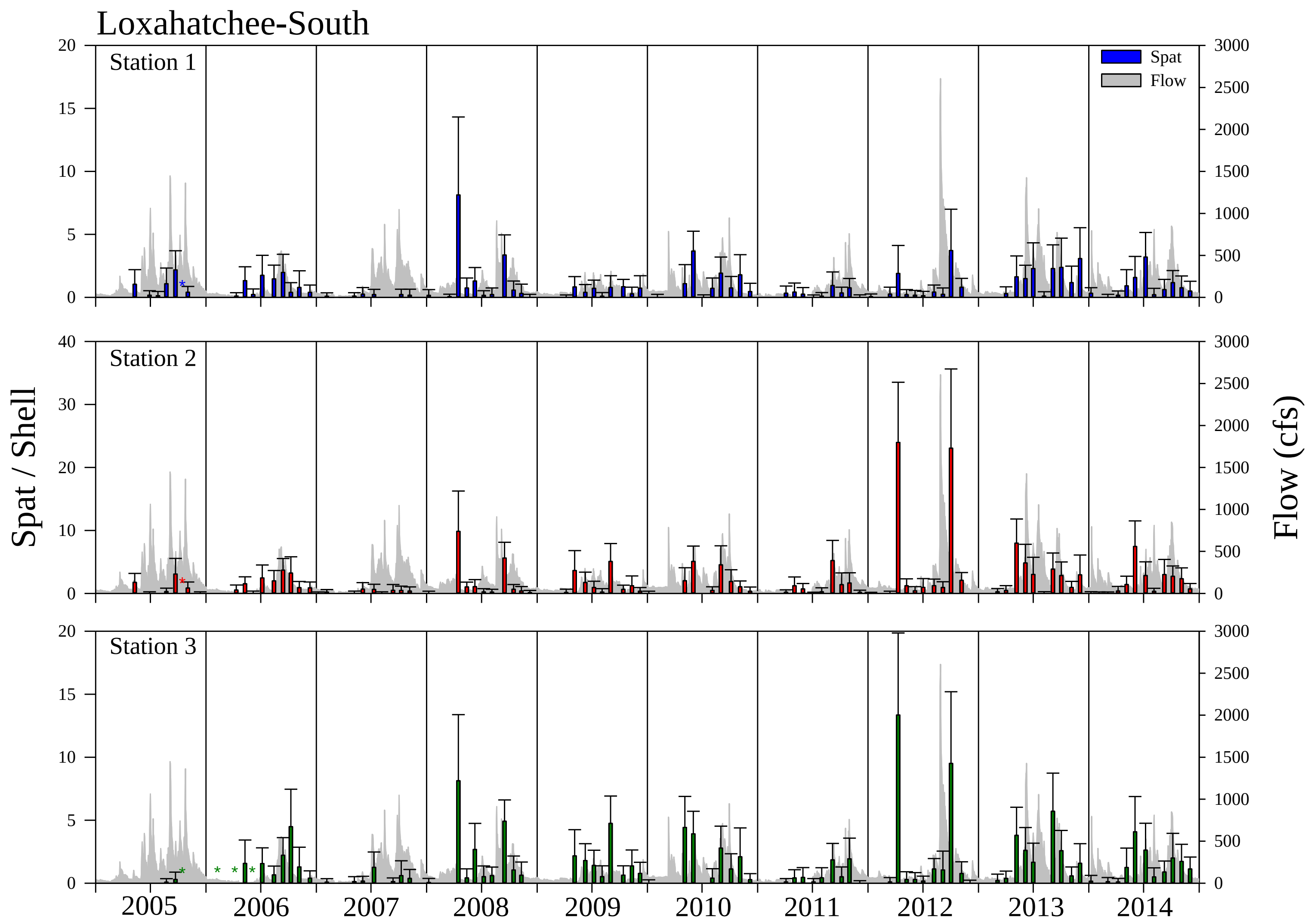

Figure 52. Mean monthly number (± S.D.) of oyster spat recruits collected per shell at Loxahatchee-South Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures as recorded by the U.S. Geological Survey and the South Florida Water Management District. Asterisks denote stations where no recruitment collectors were retrieved for analysis.

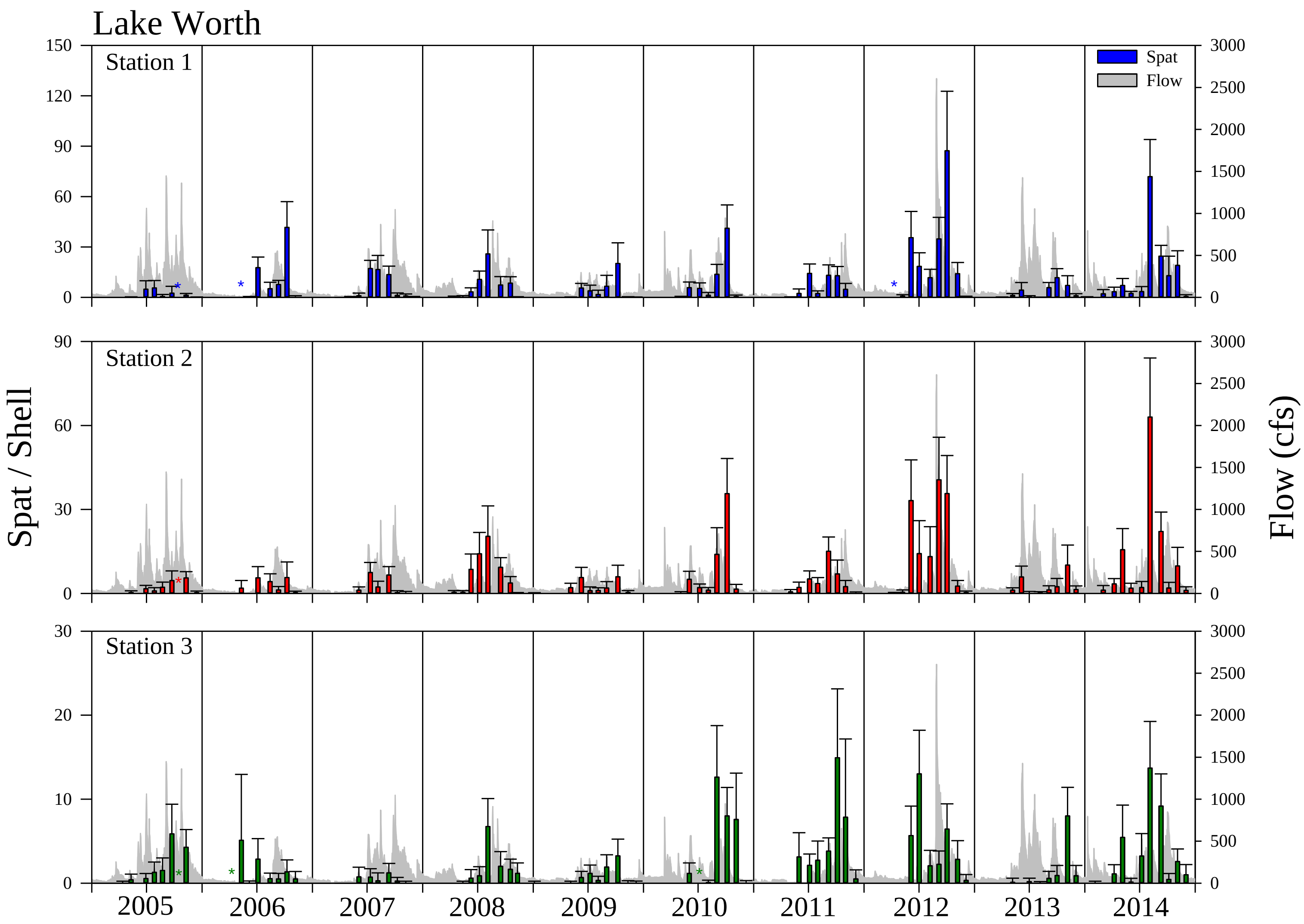

Figure 53. Mean monthly number (± S.D.) of oyster spat recruits collected per shell at Lake Worth Station 1 (top), Station 2 (middle) and Station 3 (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S44, S155, and S41 structures as recorded by the South Florida Water Management District. Asterisks denote stations where no recruitment collectors were retrieved for analysis.

Juvenile Growth and Predation

2005 – 2007

The 2005 juvenile growth study began in September 2005 when the single, cultchless oysters produced by HBOI were transported and planted into open and closed cages in the LOX and LWL sites; juveniles were planted into open and closed cages in the SLE sites in November 2005. Mean SH at planting was approximately 20 mm in all sites. Juveniles planted into cages in the SLE sites were all dead when sampled in December 2005, most likely due to persistent low salinities in the estuary. Juveniles planted into open cages in the Lake Worth and two LOX sites were all dead by December 2005, possibly due to heavy predation and/or being washed out of the cages by water currents. Juveniles in the Loxahatchee-North and South sites were monitored for 10 months and reached mean SHs of 50 and 72 mm, respectively. Juveniles in the Lake Worth site were monitored for 13 months and reached a mean SH of 48 mm. Mean overall growth rates differed among sites, with 2.18 mm/month in Lake Worth, 2.99 mm/month in Loxahatchee-North and 5.11 mm/month in Loxahatchee-South (Figures 54 and 55).

The 2006 juvenile growth study began in May 2006 when spat settled on axenic shell were transported from HBOI and planted into open and closed cages in the LOX and LWL sites; spat were planted into open and closed cages in St. Lucie-Central and into closed cages in St. Lucie-North and South in July 2006. Mean SH at planting was approximately 1 mm in Lake Worth, 3.5 mm in the LOX sites, and 2 mm in the SLE sites. Spat planted into open cages in the Lake Worth and two LOX sites were all dead by the first sampling date in July 2006. Juveniles in the LOX and LWL sites were monitored for 12 months and reached mean sizes ranging from 36 to 46 mm. Juveniles in St. Lucie-Central were monitored for 11 months with mean SHs reaching 43 mm in the closed cages and 58 mm in the open cages. Juveniles in St. Lucie-North and South were monitored for 10 and 11 months, respectively; mean SH reached 46 m in St. Lucie-North and 92 mm in St. Lucie-South. In all sites, mean SH decreased at some point during the experiment, suggesting that the mean was reflecting that either larger juveniles were dying or new, smaller recruits were settling on the shell substrate. Mean overall growth rates differed substantially among sites, ranging from 2.87 mm/month in Lake Worth to 8.17 mm/month in St. Lucie-South. Growth rates were similar between closed and open cages in St. Lucie-Central, with means of 3.71 and 5.05 mm/month, respectively.

The 2007 juvenile growth study began in May 2007 when spat settled on axenic shell were transported from HBOI and planted into open and closed cages in LWL. In July, spat were planted into open and closed cages at the LOX sites and axenic shells for wild spat settlement were planted into open and closed cages in the SLE sites. Mean SH at planting was approximately 5 mm in Lake Worth and 13.5 mm in the LOX sites. Juveniles in the LOX and LWL sites were monitored from 9 to 11 months and reached larger mean SHs in closed cages (31 to 57 mm) than in open cages (26 to 42 mm). Juvenile recruits first appeared on shell substrate planted in the SLE sites in July 2007. SLE juveniles were monitored for 5 to 7 months and reached a mean SH of approximately 40 mm in both open and closed cages in the St. Lucie-North and South sites. Juveniles in open and closed cages in St. Lucie-Central were substantially smaller, reaching just 24 mm. As with the 2006 experiment, mean SH decreased at some point in most sites as a result of larger juveniles dying or smaller recruits settling on the shell substrate. Growth rates differed among sites, with the highest occurring in Loxahatchee-South, St. Lucie-North and St. Lucie-South where the means ranged from 3.18 to 7.47 mm/month. In the remaining sites, mean rates ranged from 1.42 to 3.00 mm/month. Growth rates were similar between open and closed cages within a site.

<u>2008 – 2010</u>

The 2008 juvenile growth study began in March 2008 when axenic shells for wild spat settlement were planted onto open growth arrays in each site. Juvenile spat were first detected on shells in Loxahatchee-South in April, in Lake Worth, Loxahatchee-North and St. Lucie-Central in May, in St. Lucie-South in June, and in St. Lucie-North in July. However, survival of juveniles in the SLE sites was short-lived, as most were dead by September following Tropical Storm Fay and the resultant low estuarine salinities. However, salinities increased quickly and juvenile recruits from the last pulse of the spawning season settled onto the SLE growth arrays. Juveniles at all sites were monitored through February 2009. Final SHs in the Loxahatchee-North and South sites reached means of 31 and 42 mm, respectively. Despite 10 months of growth, the final mean SH of juveniles in Lake Worth only reached 26 mm. In comparison, final mean SHs in the SLE sites reached 28 to 32 mm in February, after only 4 or 5 months of growth.
As would be expected, the overall growth rate was low in Lake Worth where the mean was 1.91

mm/month. Growth rates were moderate in the two LOX sites (~3 mm/month) and greatest in the SLE sites (~5.5 mm/month).

The 2009 juvenile growth study began in March 2009 when axenic shells for wild spat settlement were planted onto open growth arrays in each site. Juvenile spat were first detected on shells in Loxahatchee-South in April, in Lake Worth and Loxahatchee-North in May, and in the three SLE sites in June. Mean SH increased steadily at all sites but decreased substantially in the late summer months, especially in the three SLE sites, due to a recruitment pulse that brought numerous small recruits. Juveniles at all sites were monitored through March 2010. Final SHs ranged from 24 mm in Lake Worth to 33 mm in Loxahatchee-South. Mean overall growth rates were similar among sites, ranging from 1.38 to 2.51 mm/month.

The 2010 juvenile growth study began in March 2010 when axenic shells for wild spat settlement were planted onto open growth arrays in each site. Juvenile spat were first detected on shells in the two LOX sites in May, in Lake Worth in June, in St. Lucie-North and Central in July, and in St. Lucie-South in August. Juveniles at all sites were monitored through March 2011. Final SHs in the Lake Worth, Loxahatchee-North and St. Lucie-Central sites were smaller (28 to 32 mm) than those in the other sites, where means ranged from 42 to 49 mm. Despite the differences in final SH, overall growth rates were similar among sites, ranging from 0.35 to 1.88 mm/month.

<u>2011 – 2013</u>

The 2011 juvenile growth study began in February 2011 when wild oyster spat were tagged, measured and planted into open and closed cages in each site. Mean SH at planting was approximately 27 mm in Lake Worth, 29 mm in the LOX sites, and 34 mm in the SLE sites. Tagged juveniles planted into open cages in Lake Worth were all dead by May 2011. Tagged juveniles were monitored at remaining sites through May or June 2012. Final mean SHs were smallest in the Lake Worth closed cages (39 mm) and St. Lucie-Central open cages (41 mm). The largest final mean SHs were measured in St. Lucie-North (63 to 65 mm), St. Lucie-South (61 to 66 mm), and Loxahatchee-South (56 to 66 mm). Mean overall growth rates were relatively low among sites and cages, ranging from < 1 mm/month in Lake Worth and St. Lucie-Central to approximately 2 mm/month in in the remaining sites. Rates of survivorship differed among sites

(Figures 56 and 57). As previously mentioned, all juveniles planted in open cages in Lake Worth were dead within 3 months; all but six oysters planted in closed cages in Lake Worth were dead by December 2011. At the remaining sites, survivorship was greatest in the closed cages where 10% to 18% remained alive in June 2012. Less than 5% of tagged oysters remained alive in June 2012 in the open cages, with the only exception occurring in St. Lucie-North where 14% remained alive.

The 2012 juvenile growth study began in July 2012 when wild oyster spat were tagged, measured and planted into open and closed cages in each site. Mean SH at planting was approximately 18 mm in Lake Worth and the two LOX sites, and 15 mm in the SLE sites. Most of the tagged oysters were dead by July 2013, but a few persisted in the Loxahatchee-North and Lake Worth cages through December 2013. Final mean SHs were similar among most sites and cages, ranging from 46 to 61 mm. Exceptions occurred in the Loxahatchee-North open cage, where one oyster reached 70 mm, and in the Loxahatchee-South closed cages, where two oysters reached a mean SH of 101 mm. Mean overall growth rates were similar among open cages (~3 mm/month), except in the Loxahatchee-South cages where the mean rate was 7 mm/month. Mean overall growth rates were also near 3 mm/month in the open cages, except in St. Lucie-North and South where the mean rates were near 5 mm/month. Survivorship decreased rapidly in the Loxahatchee-South, St. Lucie-North and St. Lucie-South cages, falling to less than 8% by October 2012. Survivorship was greater in the St. Lucie-Central closed and open cages where 13% and 2%, respectively, remained alive before the cages were lost in August 2013. All of the oysters in the Lake Worth closed cage were dead by June 2013, but one oyster in the open cage survived until December 2013. A few oysters also remained alive in the Loxahatchee-North cages through December 2013.

The 2013 juvenile growth study began in December 2013 when wild oyster spat were tagged, measured and planted into open and closed cages in each site. Mean SH at planting was approximately 17 mm in Lake Worth, 18 mm in the LOX sites, and 22 mm in the SLE sites. The tagged oysters planted three cages were lost within the first several months of the study; two of those cages (St. Lucie-Central Station 1and Loxahatchee-South Station 2 open cages) were flipped upside down between sampling trips thus spilling all tagged oysters and one cage (St. Lucie-Central Station 1 closed cage) was completely missing upon arrival in February 2014. Final mean SHs were smallest in the Loxahatchee-North (33 mm) and St. Lucie-South (46 mm) open cages. At the remaining sites, the final mean SHs ranged from 52 to 70 mm.

Mean overall growth rates were similar among the Lake Worth and LOX sites and cages, ranging from 2.21 to 4.03 mm/month. In the St. Lucie-North and South sites, growth rates were lower in the closed cages (~3.75 mm/month) than in the open cages (~5.75 mm/month). Survivorship in the Loxahatchee-North, St. Lucie-North, and St. Lucie-South open cages was lowest, with all tagged oysters at those sites dead by July 2014. By the end of the study in December 2014, survivorship at the remaining stations ranged from < 1% to 10%.

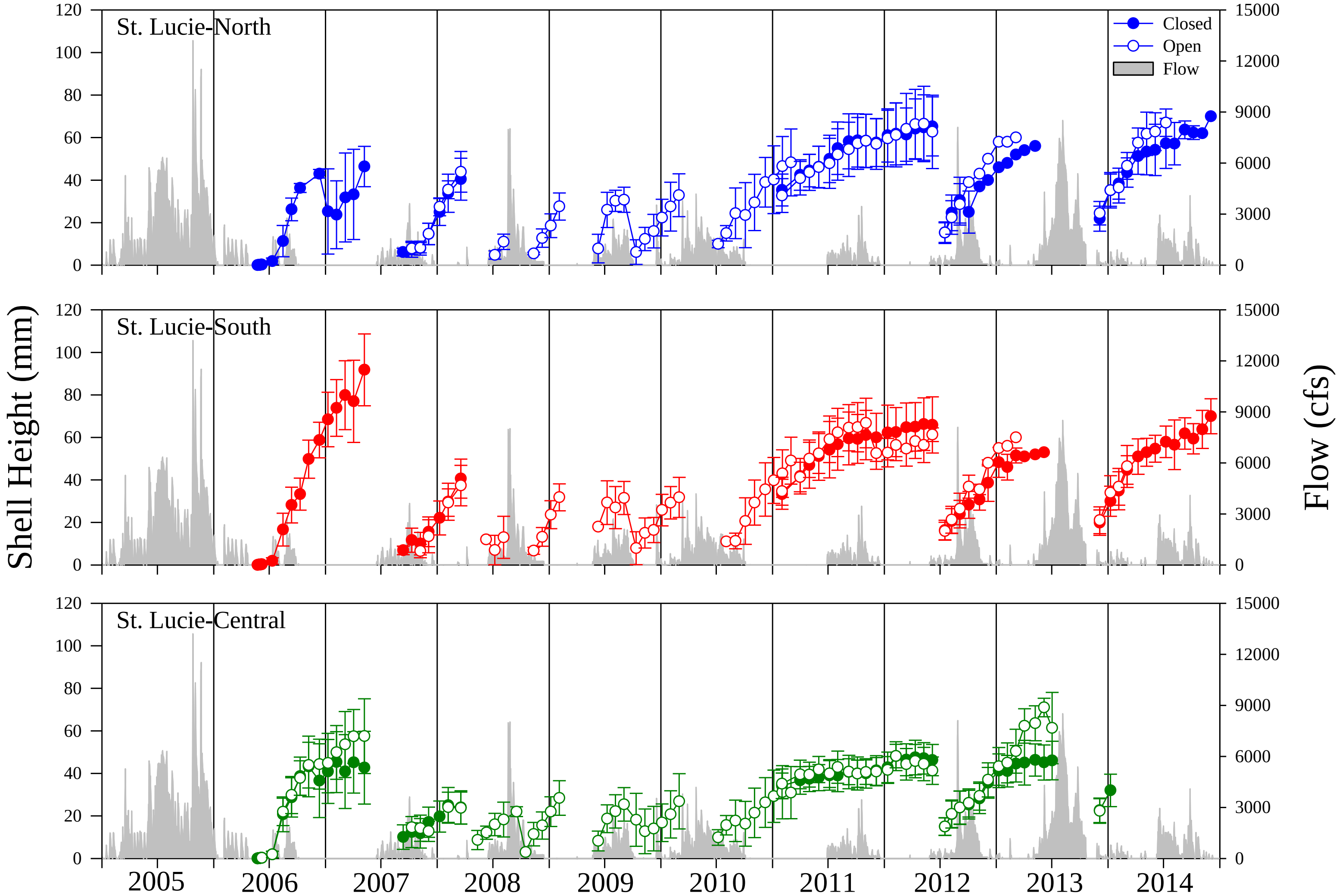

Figure 54. Mean monthly shell height (± S.D.) of juvenile oysters in closed and open cages planted at stations in St. Lucie-North (top), St. Lucie-South (middle) and St. Lucie-Central (bottom) from 2005 – 2014 and the sum of the mean daily flow rate at the S80, S97 and S49 structures as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District.

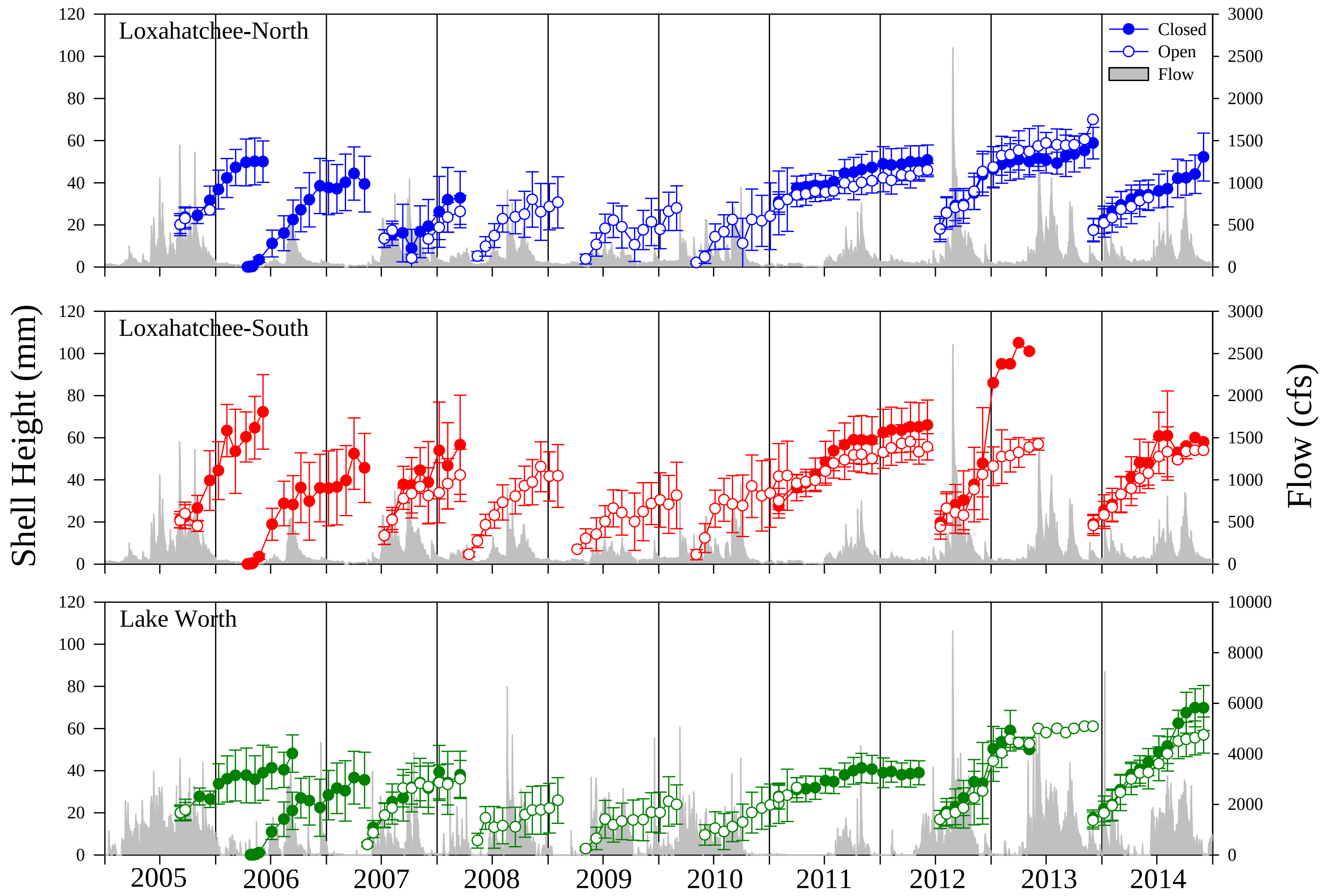

Figure 55. Mean monthly shell height (± S.D.) of juvenile oysters in closed and open cages planted at stations in the Loxahatchee-North (top), Loxahatchee-South (middle) and Lake Worth (bottom) study sites and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures in the LOX and at the S44, S155, and S41 structures in LWL as recorded by the U.S. Geological Survey and the South Florida Water Management District.

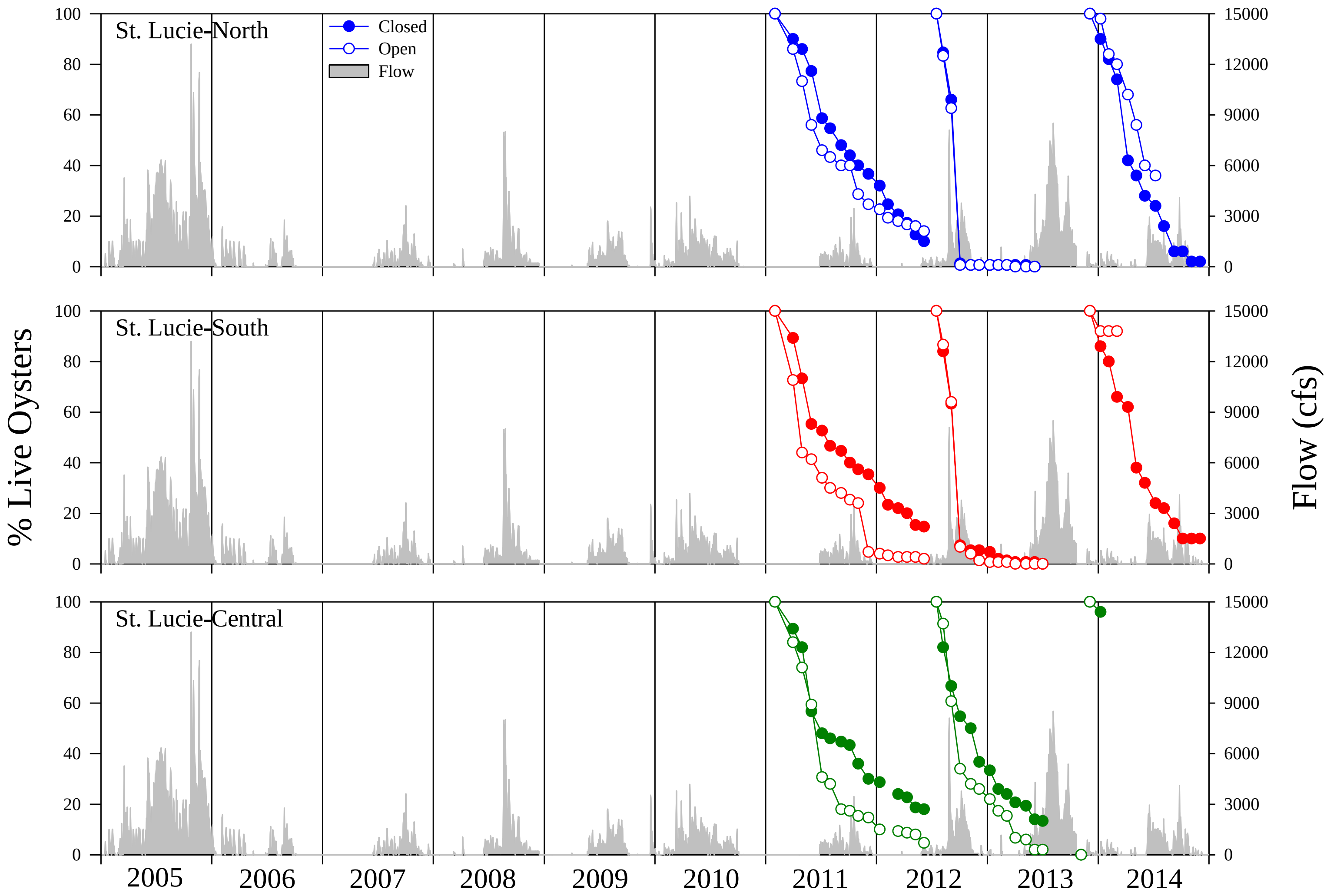

Figure 56. Monthly percentage of live tagged oysters remaining in closed and open cages planted at stations in St. Lucie-North (top), St. Lucie-South (middle) and St. Lucie-Central (bottom) from 2011 – 2014 and the sum of the mean daily flow rate at S80, S97 and S49 as recorded by the U.S. Army Corps of Engineers and the South Florida Water Management District. No oysters were tagged prior to 2011, therefore no mortality data is available from 2005 – 2010.

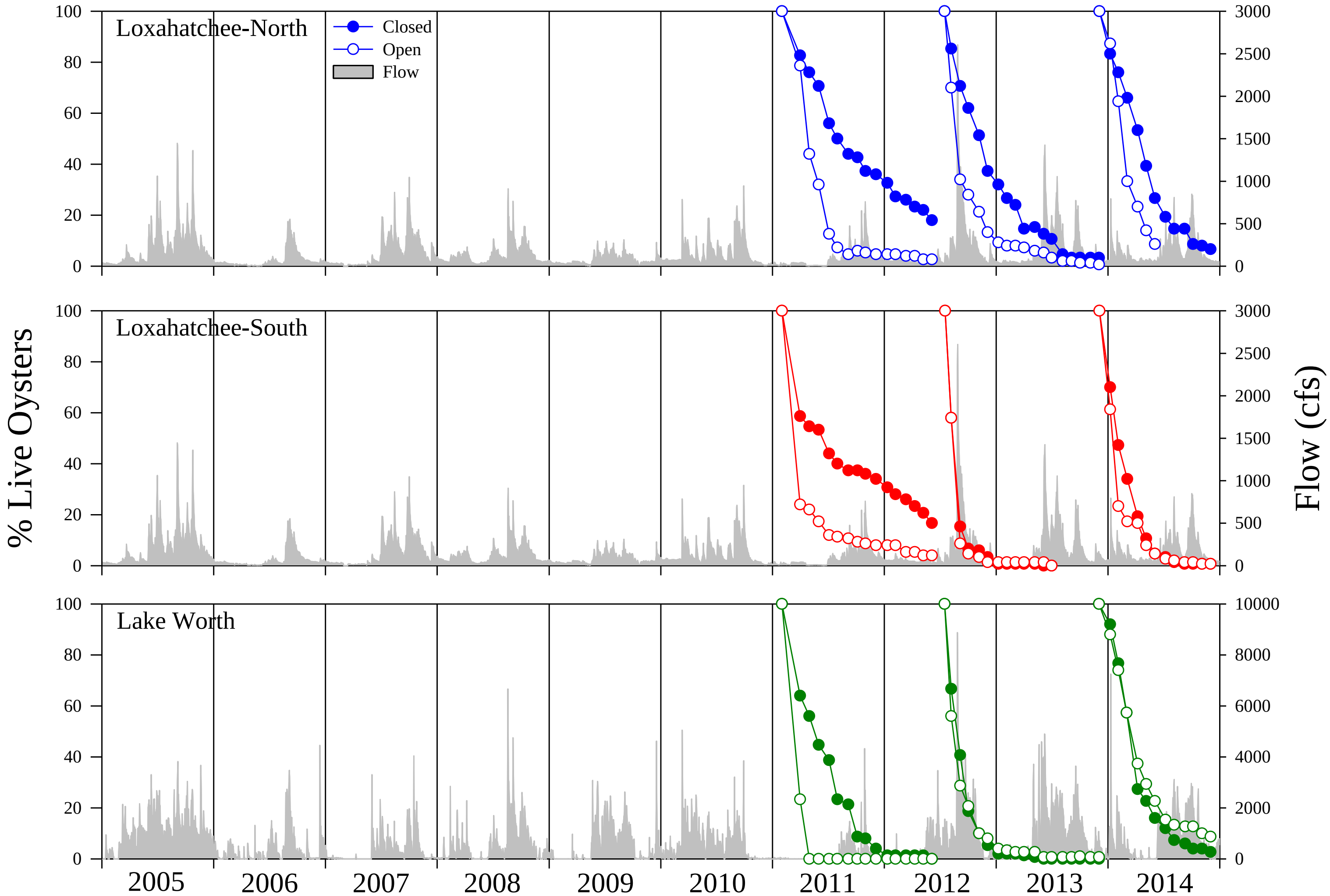

Figure 57. Monthly percentage of live tagged oysters remaining in closed and open cages planted at stations in the Loxahatchee-North (top), Loxahatchee-South (middle) and Lake Worth (bottom) study sites and the sum of the mean daily flow rate at the Lainhart Dam and S46 structures in the LOX and at the S44, S155, and S41 structures in LWL as recorded by the U.S. Geological Survey and the South Florida Water Management District. No oysters were tagged prior to 2011, therefore no mortality data is available from 2005 – 2010.

Discussion

Oyster monitoring in the St. Lucie Estuary, Loxahatchee River Estuary and Lake Worth Lagoon was initiated in 2005 after an extremely active 2004 hurricane season. The sequence of storms that occurred in 2004 resulted in considerable rainfall in Central and South Florida, substantially reducing salinity in many coastal waters via natural and anthropogenic (primarily flood control releases) contributions (Paperno et al. 2006, Steward et al. 2006). Those reductions in salinity were exacerbated by another active hurricane season in 2005. The effects of the 2004/2005 storms on salinity are best demonstrated in the SLE, where mean monthly salinity measurements were less than 20 during 2005 and, in fact, were near 0 most of the year. Those extremely low salinity values are not solely attributable to direct inputs of freshwater via rainfall and runoff, but also include inflow of freshwater from flood control releases implemented by local water management practices. The SLE watershed tripled in size during the 20th century as a result not only of urban and agricultural development (Haunert et al. 1994), but also of the addition early in the century of three flood control canals that flow into the estuary, the largest of which links it directly to Lake Okeechobee (Sime 2005).

Water quality has a large influence on oyster health and survivorship; rapid changes in salinity, high temperatures, low dissolved oxygen concentrations, and siltation can all be stressors to oyster populations. Temperature and salinity are two of the most important physical parameters that impact oyster populations (Shumway 1996), but during this study the magnitude and frequency of salinity fluctuations were a major driving force behind changes in oyster ecology. Eastern oysters survive exposure to a wide range of salinities, 1.2 to 36.6 in Apalachicola Bay, FL (Menzel et al. 1966), but the optimal salinity range may be much less and may also differ slightly among populations in different locations. Survivorship of oysters is also affected by the interaction of salinity and temperature (Shumway 1996). Florida oysters are commonly exposed to temperatures likely near their upper physiological tolerance limits; some years, water temperatures can remain warmer than 32^{o}C for four months or more, and oysters can experience even higher temperatures if they are exposed during afternoon low tides. When animals are subjected to environmental conditions that meet or exceed tolerance limits, their energetic capacity to deal with additional stresses, such as low salinity and disease, are diminished or lost.

Settled oyster density measurements from the SLE reflect earlier conditions in which salinities fell below tolerance limits; the most marked instance was seen during the winter and summer 2005 surveys, in which few or no live oysters were observed at those sites. Although in early 2005 salinities remained within the range of tolerance for *Crassostrea virginica*, the 2004 storms probably lowered salinities to intolerable levels that year, resulting in an oyster die-off in the north and south forks of the SLE. This conclusion is based on the proportion of dead oysters present at the SLE stations, suggesting recent mortality of those oysters. Empty oyster shells remain intact 1 to 2 years before disarticulating, depending on size and environmental conditions (Christmas et al. 1997, Ford et al. 2006), so those oysters may have died as a result of unrecorded events that preceded the 2004 hurricane season. Although the validity of dead oyster counts in estimating mortality has been disputed, they are helpful when used to show recent extreme mortality events or when used as an indicator of relative changes in the proportion of dead oysters within a population (Mackin 1959). Regardless of the cause, few live oysters were observed at any of the sampled stations in the SLE during the 2005 surveys. Because live oysters were relatively common in the nearby LOX and LWL estuaries during the 2005 surveys, the factors that contributed to the dearth of live oysters in SLE in 2005 appear to have been specific to that estuary.

In the SLE, salinities remained near 0 throughout 2005 but began increasing in early 2006 and generally remained within tolerance limits until August 2008 when Tropical Storm Fay impacted the estuary. Although this resulted in near complete mortality of settled oysters in the SLE, this event was less severe than that observed in 2005. In 2005, the low salinity event continued throughout the fall recruitment season, such that most reefs in the SLE were devoid of oysters until fall 2006. The result was that an entire year of oyster growth was lost, potentially having serious implications for siltation and loss of shell substrate on the reefs. After the die-off in fall 2008, salinities increased sufficiently to allow for settlement and growth of new recruits before the end of the 2008 spawning season. Those recruits successfully overwintered, allowing for a more rapid recovery of oysters in 2009. This is reflected in the 2009 survey results, when mean densities increased from near $0/m^2$ in fall 2008 to over $100/m^2$ and mean SH of oysters increased from less than 15 mm to over 50 mm in the central estuary by fall 2009.

The reprieve was short-lived as salinities decreased again in 2010 during a prolonged freshwater release event that lasted from March through October. Although there was not a major die-off of settled oysters related to the release event, oysters were disappearing and exhibiting poor health at stations in the north and south forks during the warm, summer months. In addition, the timing of the event perfectly coincided with the months of peak reproductive development and spawning. Analyses of oyster gonadal tissues showed that oysters were developing and spawning as expected in 2010; however, recruitment rates were significantly lower in the SLE in 2010. This suggests that the vast majority of newly spawned larvae were either physically flushed out of the estuary or killed by the low salinities.

Salinities in the SLE were relatively high in 2011 and 2012, with the only major exception occurring in fall 2012, when rainfall and subsequent freshwater releases associated with Hurricane Isaac (August) negatively impacted oysters in the most upstream SLE stations. Salinities recovered quickly in late 2012 and for the first several months of 2013, drought-like conditions kept salinities so high they often exceeded the optimal range. Salinities then decreased rapidly to sub-optimal levels in June after heavy rainfall and high magnitude freshwater releases began impacting the estuary. This time the inundation of freshwater caused another massive oyster die-off in all three study sites in the SLE, and also led to high levels of enteric bacteria and a cyanobacterial bloom, both of which prompted the Martin County Department of Health to issue a health advisory that recommended avoiding contact with SLE waters. When water quality finally improved in December, the fall 2013 survey was conducted and of the sparse numbers of live oysters present, all were juvenile spat that just settled in the past few weeks. This is reflected in the significantly smaller SHs measured during the fall 2013 survey. To reiterate, no live, adult oysters were found at any sampled station, suggesting that there was a complete loss of all settled oysters.

Although the impacts from low salinity events are often more acute, long term exposure to high salinities can also have negative impacts. Salinities often exceeded the optimal range in the LOX and LWL estuaries, and even in the SLE in 2011 and early 2012, and, during those periods, dermo prevalence in oysters was high. Increased predation and disease rates are typically associated with higher salinities and temperatures, but the extent to which a higher salinity regime can affect an oyster population is most exemplified by the dramatic increase in dermo prevalence measured in oysters from SLE in 2011, 2012 and 2013. Prior to 2011, mean annual dermo prevalence rates ranged from only 1 to 17% of sampled oysters infected. By 2012, infection rates had increased to approximately 30% in the two fork sites and to over 60% in the central estuary. In June 2013, at those SLE stations where live oysters were present, 50 to

100% of sampled oysters were infected; however, infection intensity remained low at in all three sites with sampled oysters commonly exhibiting only light to moderate infections. At present, there are no metrics in place to study short term acclimation to changes in salinity, but it is important to note that oysters that are physiologically acclimated to high salinities may have reduced ability to cope with sudden decreases in salinity. In other words, the tolerance limits of a high-salinity oyster are unlikely to be as low as those adapted to optimal or low salinity. It follows that a high-salinity oyster that is weakened by a parasitic infection, i.e., dermo, would be even less able to withstand extreme changes, and more rapidly succumb to death when salinities decrease abruptly.

Both the LOX and LWL estuaries were also affected by salinity fluctuations as a result of the active storm season and water management practices, but neither estuary experienced an extensive oyster die-off. Except during periodic storm-related inundations of freshwater, the LOX received minimal freshwater inflows and commonly experiences tidal encroachment of oceanic waters. This is a result of physical alterations that include a rerouting of upland waters from the northwest fork to the southwest fork via a flood control canal, and the stabilization of the natural opening of the Jupiter inlet (VanArman et al. 2005). Lake Worth Lagoon, which was a freshwater lake prior to the permanent opening of the Palm Beach and Boynton Beach inlets, received most of its freshwater inflows as a result of periodic releases from three flood control canals (Crigger et al. 2005), but those effects are minimal, as evidenced by the relatively high and stable salinities recorded over the course of the study. Live oyster densities in both estuaries were lower in 2005 than in subsequent years, indicating that the 2004/2005 storms did have some impact, but a rapid and substantial recovery was realized under the higher salinity regime of 2006.

Despite the fact that the LOX and LWL were rarely impacted by low salinity events, local salinity regimes did influence live oyster density patterns both directly and indirectly. Oftentimes, densities increased between seasons in the LOX northwest fork but remained the same or decreased slightly in the LOX southwest fork and LWL. A possible explanation for those differences may be the relatively lower salinity regime in the LOX northwest fork. While salinities in all three sites vary considerably, the LOX northwest fork typically experiences salinities that fall well within the optimal salinity range. In contrast, salinities in the LOX southwest fork and LWL were much higher, often reaching or exceeding the upper boundary of the tolerance range. As a consequence, oyster densities in those two sites were likely kept in check by a resultant increase in disease and predation rates.

Both prevalence and intensity of dermo infections were markedly higher in the LOX and LWL than in the SLE prior to 2011. The most straightforward explanation for the differences in parasite incidence is that the salinities experienced in much of the SLE were too low for completion of the life history cycle of the *Perkinsus marinus* (dermo) parasite. It is well established that low temperature and low salinity are correlated with reduced levels of infection (Craig et al. 1989), thus oysters in the SLE suffered reduced prevalence and intensity of the disease relative to oysters in the LOX and LWL. It appears that, because salinity fluctuated so consistently in the SLE prior to 2011, dermo never gained a foothold and although the parasite was present, the intensity of the infection remained low. The frequent low salinity events that the SLE experienced may have further reduced the success of the parasite by killing off its host organism. Infection intensity levels in the LOX and LWL were similar, but because those estuaries experience longer periods of higher salinity the oysters that occupy those estuaries experience a relatively elevated infection rate. Nonetheless, infection intensity remained low in all three estuaries with levels rarely exceeding a 1 (light infection) on the Mackin scale.

Although the timing of reproductive development in oysters varied among sites and years, active reproduction (gametogenesis, spawning, and gonadal recycling) typically occurred from March to October in most years; the majority of oysters entered the resting or indifferent stage in November and remained resting through the winter months. Analyses of gonadal tissues showed that during periods of low salinity related to storm activity and water releases, most oysters, as long as they survived, continued to develop gametes and spawn as expected; however, there were significantly fewer oysters developing gametes in those years. Oftentimes in those circumstances, spawned larvae did not successfully recruit. Whether the larvae were killed outright by low salinities or were simply flushed downstream and out of the estuary is unknown.

General recruitment patterns were also similar among estuaries, with recruits commonly present in arrays retrieved from April through December; recruitment, however, was sporadic and inconsistent in the SLE. Not surprisingly, recruitment rates differed among estuaries. Mean recruitment rates in LWL and LOX approached or exceeded 2 spat/shell/month, whereas rates in the SLE were generally less than 1 spat/shell/month. Each estuary experienced periodic decreases in oyster densities after changes in estuarine conditions, but in most cases recruits were detected shortly after conditions had returned to those tolerable to oysters. This suggests that even in sites where oysters almost disappeared completely, small relict populations, an exogenous larval source, or most likely the combination of the two, contributed recruits.

Juvenile oyster growth was studied with a variety of methods, but each methodology yielded similar results. Growth rates differed among estuaries and were generally higher in the LOX southwest fork, SLE north fork and SLE south fork, where overall means often reached or exceeded 5 mm SH/month. Those higher growth rates are typical of oysters in the southeastern United States and particularly in the Gulf of Mexico, but are more rapid than those reported for more northern populations (Shumway 1996). Consistent with other bivalves, the more rapid growth of oysters in southern latitudes may be attributed to the longer growing season rather than to an inherently more rapid growth rate (Jones et al. 1990). This distinction is important, because factors other than temperature also influence growth rate. In particular, oysters do not grow well at salinities less than 10 (Loosanoff 1953). Ramifications of growth variation can be significant, as faster growing oysters will more quickly escape the ravages of size-limited predators and also would be expected to reallocate energy from growth to reproduction at an earlier age. Growth rates were lower in the LWL, LOX northwest fork, and SLE central estuary, where means were typically between 2 and 3 mm SH/month. Growth rates also differed among years. Growth was slower in 2009 and 2011, but the lowest growth rates were measured in 2010 when means were less than 1 mm SH/month in most sites. This was likely due to low estuarine salinities, especially in the SLE, caused by the prolonged freshwater release event that occurred that year.

Survivorship of tagged juvenile oysters was measured in conjunction with the 2011, 2012 and 2013 growth studies in order to estimate the impacts of macrofaunal predators. The 2011 study (February 2011 – June 2012) was relatively successful as oysters in both the closed and open cages survived for the duration of the experiment at most sites. Predation rates were high in LWL, where all oysters planted in the open cages were dead within three months while 56% of those in the closed cages remained alive. At the other sites, predation rates were lower with approximately 20% more oysters remaining in the closed cages than in the open cages. In the 2012 study (July 2012 – December 2013), efforts to quantify predator impacts on oysters planted in the SLE were complicated by the freshwater induced die-offs that occurred in late 2012 and again in 2013, i.e., the majority of oysters planted in the SLE north and south forks died in September following the sharp salinity decline associated with Hurricane Isaac. At the remaining sites, overall survivorship was low but 10% to 15% higher in closed vs. open cages. Similar rates (5% to 15% higher in closed vs. open cages) were measured at most sites in the 2013 study (December 2013 – December 2014); however, survivorship in LWL was actually 5% higher in the open cages than in the closed cages. The same thing occurred in the SLE north fork until the open cage was lost in August 2014. In summary, the extensive mortalities documented in LWL and the differential survivorship recorded in closed and open cages during these three studies suggests that in addition to death by natural causes, macrofaunal predators were present and actively killing oysters planted in open cages within each estuary.

Conclusion

This report summarizes oyster population monitoring at six sites within three estuaries in southeast Florida from 2005 through 2014. Oyster abundance, health, and population ecology within the three estuaries generally fell within expected ranges for south Florida oyster populations; however, the occurrence of heavy rainfall and subsequent freshwater releases in the summer months frequently forced estuarine salinities outside of tolerable ranges and as a result oyster populations were negatively impacted. Although oysters in the SLE exhibited the capacity to recover when salinities stabilized following low-salinity events, continued perturbations may so degrade oyster populations that appropriate substrate may no longer exist as a site of larval settlement, even if a supply of larvae persists. Evidence from oyster reef mapping efforts in the SLE suggests that natural oyster reef coverage has declined relative to historic extent (URS Greiner Woodward Clyde 1999), likely as a result of shell disarticulation or burial by sedimentation. The loss of essential larval settlement substrate provided by an extant reef may require decades to rebuild without intervention (Mann and Powell 2007). Because oysters function as ecosystem engineers, providing habitat for a variety of organisms, impacts to oyster populations have unique, broad-ranging consequences for a host of ancillary organisms and for the oysters themselves, whose recovery from such events may be degraded serially to the point of no return. High salinities also negatively impacted oyster populations, although those impacts were more slowly realized. Future actions, such as consideration of minimum flows for each estuary during the dry seasons to keep salinities closer to the optimal range for oysters, may reduce predation and disease as well as allow some adaptation to the inevitable periods of low salinity.

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