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DENSITIES OF LARGE MARINE GASTROPODS IN SEAGRASS, OYSTER REEF, AND SANDY HABITATS IN TAMPA BAY AND ALONG THE GULF COAST OF FLORIDA

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ABSTRACT Marine gastropods in Florida are harvested by the marine-life trade, tourists (for shells), and traditional commercial fisheries, but stocks are not formally assessed for most species. The main goal of this project was to estimate biological variables that may be used to evaluate the Species of Greatest Conservation Need status of the banded tulip *Cinctura lilium* and six other large marine gastropod species that are commonly encountered in the targeted habitats. The principal target, *C. lilium*, was listed in the 2012 State Wildlife Action Plan. The densities and size structures of *C. lilium* and six co-occurring species of large marine gastropods in Tampa Bay were examined to evaluate population dynamics, seasonal variation, and habitat preferences of these species. Long-term trends in the densities of large, predatory marine gastropods in 10 regions from 2009 to 2017 were included. In Tampa Bay, strong habitat preferences were observed for all species studied: *C. lilium* and *Melongena corona* were most likely to be observed on oyster reefs, and *Fasciolaria tulipa* was found only in seagrass, whereas *Strombus alatus*, *Triplofusus gigantea*, *Sinistrofulgur sinistrum*, and *Fulguropsis spirata* were more common on soft sediments. Seasonal variations in densities were weak; seasonal differences in size structure were more pronounced. The smallest individuals of *C. lilium* appeared in spring and summer; *F. spirata*, *S. alatus*, and *S. sinistrum* reached a detectable size in fall. The smallest detectable *M. corona* appeared in winter. Regionally, there were more gastropods in southwestern bay grass beds (Tampa Bay, Sarasota Bay, and Pine Island Sound) than in coastal seagrass beds (Big Bend, Citrus, Hernando, Pasco, and coastal Pinellas) or northern bays (St. Joseph Bay and St. Andrew Bay), and each region had characteristic species. As a group, tulip snails exhibited modest local declines in densities at two sites, whereas the whelks and *T. gigantea* varied annually but did not exhibit consistent trends during 2009 to 2017. The present study establishes a baseline of abundance for seven species of common marine gastropods and recommends expanded monitoring in multiple habitats to improve future analyses of abundance trends.

KEY WORDS: Florida, Gulf of Mexico, snails, density, growth, recruitment, gastropods, *Cinctura*

INTRODUCTION

In the United States, all 50 states and five of the territories have created a State Wildlife Action Plan (SWAP) as a guidance document for conservation measures intended to protect wildlife and vital natural areas through public awareness, information management, filling data gaps, and building partnerships. The first SWAP created in Florida (Florida Fish and Wildlife Conservation Commission [FWC] 2012), which covered 5 y, included the following goals: coordinating natural resource and habitat conservation, addressing data gaps, monitoring species and habitats, creating a cooperative conservation blueprint, and creating a list of Species of Greatest Conservation Need (SGCN). To help identify those species, the FWC adopted a scoring system that was created for ranking the conservation need of vertebrate species (Millsap et al. 1990). The main ranking criteria were termed biological variables, action variables, and supplemental variables. Biological variables included population (size, trend, range, distribution, and concentration), reproductive potential, and specializations (e.g., diet, reproductive, and "other," which allowed for risks unique to any species of interest). Action variables included metrics that qualitatively estimated the knowledge base on a species and the status of its management. Supplemental variables included measures of the status within a total range of a species or range in Florida and the probability that the species might be harvested. The 2012 SGCN document is intended to identify not only species in imminent danger of extirpation but also species for which the status is largely unknown but that may face reductions in range, particularly through the loss of critical habitat. A revision in 2019 (FWC 2019) placed more emphasis on species known to be threatened or endangered and their habitats.

The number of invertebrates harvested from Florida waters each year for aquariums from 1994 to 2007 increased annually by 13.3%, or approximately 500,000 animals, and that >8.8 million animals were collected in 2007 (Rhyne et al. 2009). These numbers continue the trend seen in an earlier profile of the marine-life industry (throughout defined as animals harvested for purposes other than commercial food harvest), in which the number of marine invertebrates harvested from 1990 to 1998 increased from 849,000 to just more than 3.3 million, an increase of 290% (Larkin et al. 2001). This upward trend in marine-life collections peaked at 9.7 million invertebrates in 2008, declined, and then peaked again in 2016 at more than 16 million (http://myfwc.com/research/saltwater/fishstats/commercial-fisheries/).

The lack of species-specific harvest regulations for most invertebrates in Florida may put some species at risk of overharvest. In Florida, some large marine gastropods [here loosely defined as those that can exceed 10 cm in shell length (SL)] are easily located and targeted for collection by the aquarium industry, by shell-collecting enthusiasts, and by commercial harvesters, who sell shells to retailers and directly to the public. Many shell collectors collect only empty shells, but some collect live molluscs because they are more likely to have pristine,

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unblemished shells. Commercial marine-life dealers must adhere to harvest rules and regulations (Florida Administrative Code Chapter [FAC] 68B-42), which list all organisms protected by the specific rules. The list includes only a few gastropods including star snails *Lithopoma americanum* (Gmelin, 1791), *Lithopoma tectum* (Lightfoot, 1786), and *Lithopoma phoebium* (Röding, 1798); any species of the genus *Nassarius*, and any species of the subclass Opisthobranchia. Harvest of the queen conch *Lobatus gigas* (Linnaeus, 1758) is prohibited under separate rules. For other gastropods, the only rule is that the harvester hold a commercial products license, which does not carry any daily limit for most species. Few rules and no reporting requirements exist for recreational marine-life collectors and shell collectors. Some local ordinances and park rules do provide minimal protection. For example, in Manatee County, the limit is two live individual snails of a single species per person per day (Manatee County), and in Lee County, taking live molluscs is prohibited (FAC 68B-26.004), but in all other Florida counties, the recreational limit is 45 kg (100 pounds) of whole animals per day of each species, except for those few species on the marine-life list. For those species on the marine-life list, recreational fishers may collect five individuals of each species per day (FAC 68B-42). Many species, such as the Florida horse conch *Triplofusus gigantea* (Kiener, 1840; previously *Pleuroploca gigantea*), receive no special protection despite being highly prized by shell collectors and bearing status as the official state shell.

The banded tulip *Cinctura lilium* (Fischer, 1807) was listed in the 2012 SWAP as biologically vulnerable (FWC 2012) and was also listed as a SGCN. Commercial harvest of *C. lilium* has fallen to levels ~0.1% of 2000 levels, which may indicate that it is being overfished. According to the SWAP, the knowledge level for *C. lilium* is 0, that is, "status of the taxon is unknown beyond the observation that some commercial landings of the genus occur." The status of the genus is uncertain because taxonomic revisions are common in its family, Fasciolariidae (Snyder et al. 2012), which complicates understanding of the true distribution of species in the genus. The genus *Cinctura* is believed to be represented in most Gulf of Mexico seagrass beds, a habitat identified by the SWAP as highly threatened and in poor and declining condition (FWC 2012).

Only one study (Stephenson et al. 2013) has examined the distribution and abundance of large marine gastropods in multiple locations in Florida waters. In that study, annual baseline abundance and distribution data were established over three consecutive springs for *Fasciolaria* spp. [since revised to true tulips *Cinctura lilium* and *Fasciolaria tulipa* (Linnaeus, 1758)], the lightning whelk *Sinistrofulgur sinistrum* (Hollister, 1958), and *Triplofusus gigantea* (Kiener, 1840) (previously *Busycon sinistrum*) in seagrass beds on the Gulf Coast of Florida. Because those baseline data are limited by season and habitat, levels of sustainability are difficult to assess. And, without knowing the population dynamics of these large marine gastropods, one cannot predict what effects reductions in their density might have in their respective habitats. Many of these species play critical ecological roles. The predators consume bivalves, other gastropods, and worms. Many gastropod species scavenge and consume detritus. This biological process results in small quantities of food, often sequestered below the sediment surface, being aggregated into larger organisms that might become more accessible to higher trophic levels, much the way filter feeders accumulate the energy available as plankton. The strombids and star snails are grazers, keeping clean the surfaces on which the larvae of coral, sponges, and other encrusting organisms settle. They may improve seagrass productivity by cleaning blades of fouling organisms and bioturbating sediment, which improves oxygenation to the roots. Determining the rates and scale of such processes remains challenging without basic studies of the abundance and life histories of gastropods.

Stephenson et al. (2013) established a baseline density of three groups of gastropods: *Cinctura lilium* and *Fasciolaria tulipa* as tulips, the pear whelk *Fulguropsis spirata* (Lamarck, 1816) and *Sinistrofulgur sinistrum* as whelks, and *Triplofusus gigantea*. That survey was continued and modified slightly; gastropods were identified to species to document trends in the densities of large marine gastropods in 10 regions from 2009 through 2017. Additional species that had been identified but not analyzed in that study were added in this study, including the crown conch *Melongena corona* (Gmelin, 1791) (primarily observed on oyster reefs) and the fighting conch *Strombus alatus* (Gmelin, 1791) (primarily observed on unconsolidated soft sediments). The main objective of the present study was to evaluate the densities of those marine species across seasons and in three main habitat types in Tampa Bay (seagrass, oyster reef, and soft sediment) as the next step in a comprehensive investigation of the study of these large gastropods.

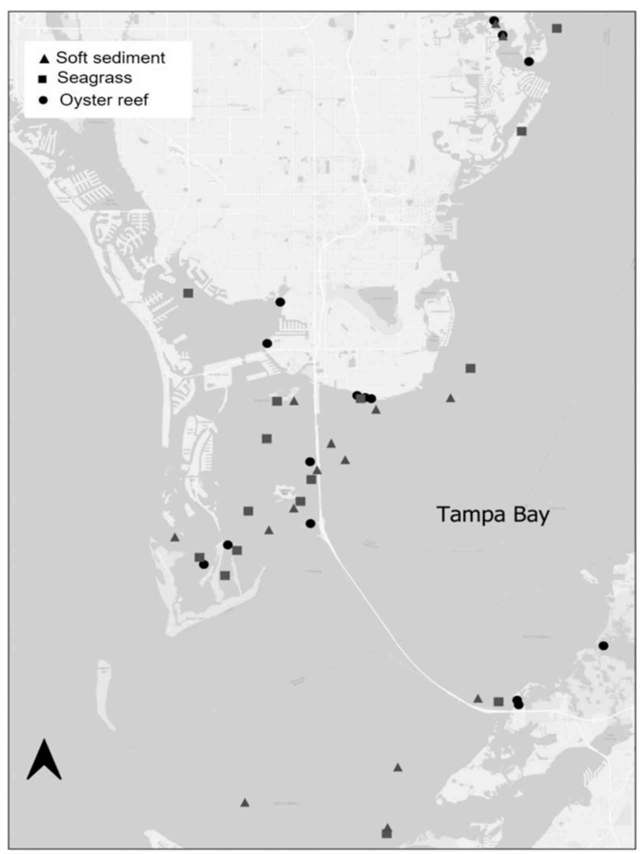

Figure 1. Seagrass (square), soft sediment (triangle), and oyster reef (circle) stations surveyed for large marine gastropods in Tampa Bay.

METHODS

Study Area

The principal study area was the estuarine portion of Tampa Bay (Fig. 1). Study sites were selected at least 5 km from the mouths of the large river systems feeding the eastern bay (Hillsborough, Alafia, Little Manatee, and Manatee rivers) to avoid the high variability in salinity resulting from their discharge. The bay has about 350 km of shoreline, as much as one-third of which has been hardened with seawall and rip-rap (FWC estimated from http://geodata.myfwc.com). Tampa Bay covers 900 km^2 (222,000 acres), of which 18% is seagrass habitat (163 km^2; 163 million m^2; 40,295 acres) (Sherwood & Kaufman 2016). Less than 1% of the total area is mapped oyster reef habitat (0.8 km^2; 793,000 m^2; 196 acres) (FWC, http://geodata.myfwc.com/pages/marine), leaving ~82% (736 km^2; 736 million m^2; 182,000 acres) as undescribed, which is mostly soft sediments of sand, mud, and shell hash. The shoreline of Tampa Bay comprises 3.8 km^2 (15,500 acres) of mangrove, 1.1 km^2 (4,600 acres) of salt marsh, small amounts of salt barren of less than 1 km^2 (~500 acres) (Cross et al. 2017), and an undocumented area of intertidal oyster reef.

Long-term-trend data were collected during annual bay scallop surveys (Arnold 2009) in seagrass beds in the open coastal waters of the Gulf Coast of Florida including the area around the St. Marks River (Franklin and Wakulla counties), Steinhatchee (Taylor and Dixie counties), Homosassa (Citrus County), Hernando (portions of Hernando and Pasco counties), and Anclote Key (Pasco and the Gulf of Mexico portion of Pinellas counties) (Fig. 2). These waters comprise one of the largest coastal seagrass plains in the world, with an approximate combined area of 3,440 km^2 (850,000 acres) (Yarbro & Carlson 2016). The bays surveyed included St. Andrew Bay (Bay County), St. Joseph Bay (Gulf County), Charlotte Harbor (Lee County), Sarasota Bay (Sarasota and Manatee counties), Tampa Bay (Pinellas, Hillsborough, and Manatee counties), St. Joseph Bay (Gulf County), and St. Andrew Bay (Bay County). These bays have an approximate combined seagrass area of 300 km^2 (75,000 acres; Yarbro & Carlson 2016).

Tampa Bay

The first objective of the study was to describe seasonal variation in gastropod density at selected sites in Tampa Bay,

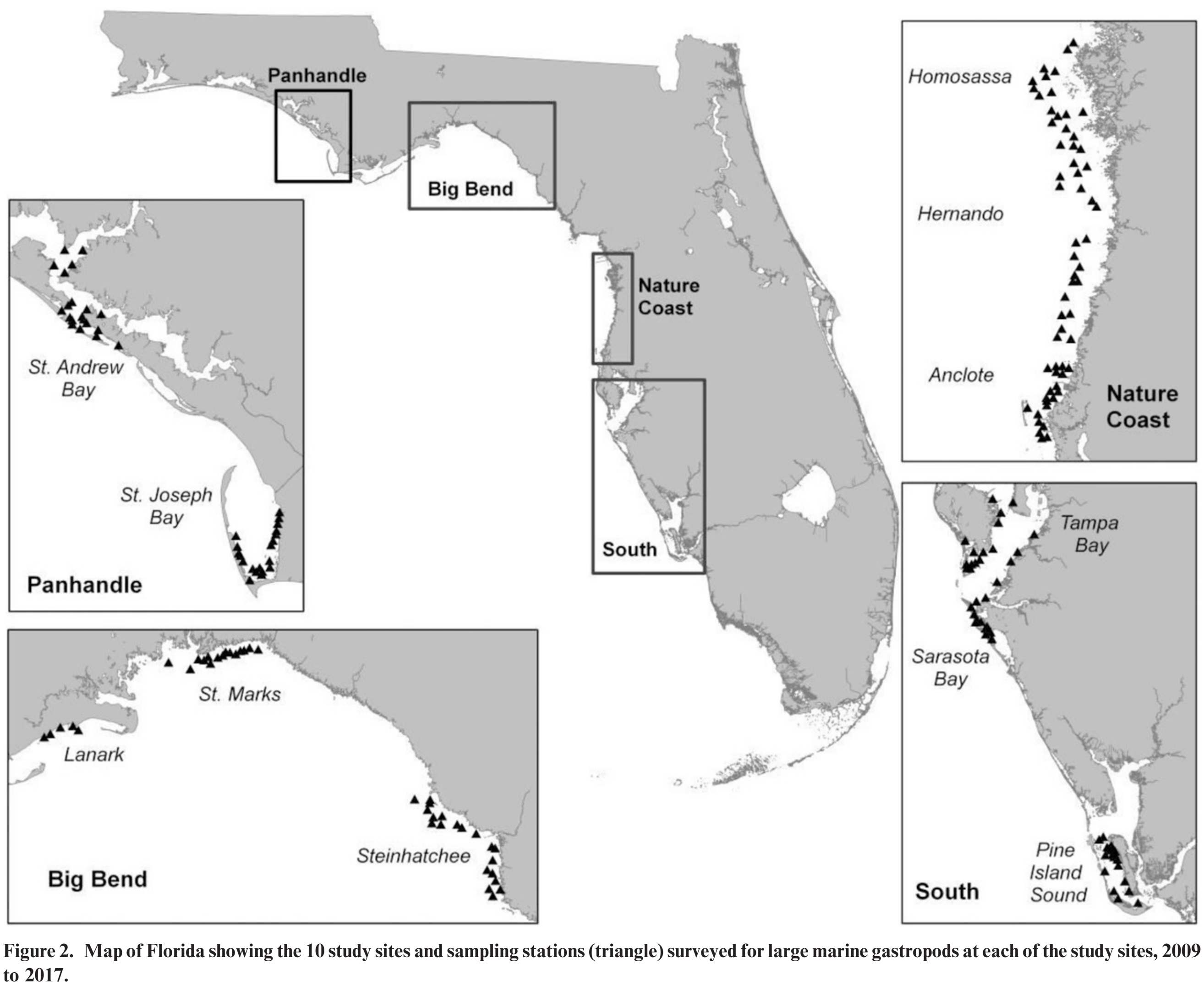

Figure 2. Map of Florida showing the 10 study sites and sampling stations (triangle) surveyed for large marine gastropods at each of the study sites, 2009 to 2017.

TABLE 1.

***P* values of three-way PERMANOVA tests of snail densities (m^{-2}), by species, among habitat (Hab), season (Seas), and year (Yr) in Tampa Bay, 2015 to 2017.**

Factor	Cl	Fs	Mc	Sa	Ss	Tg
Hab	<0.001	<0.001	<0.001	<0.001	0.005	0.016
Seas	0.130	0.283	0.435	0.990	0.061	0.564
Yr	0.523	0.105	0.475	0.546	1.000	0.109
Hab × Seas	0.233	0.525	0.530	0.999	0.687	0.798
Hab × Yr	0.847	0.147	0.741	0.654	0.408	0.335
Seas × Yr	0.265	0.728	0.623	0.381	0.688	0.214
Hab × Seas × Yr	0.516	0.692	0.711	0.230	0.591	0.807

Cl, *Cinctura lilium*; Fs, *Fulguropsis spirata*; Ft, *Fasciolaria tulipa*; Mc, *Melongena corona*; Sa, *Strombus alatus*; Ss, *Sinistrofulgur sinistrum*; Tg, *Triplofusus gigantea*.

not to create a comprehensive distribution map. To assess seasonal variation in the estuarine region of the bay (Pinellas and Hillsborough counties) (Fig. 1), underwater visual and tactile surveys were carried out. In these surveys, paired divers proceeded along a weighted transect line within 1 m on either side; they ran their hands back and forth along the substrate surface and through the seagrass canopy as they completed a visual inspection. Surveys were conducted quarterly in three habitats (seagrass, oyster reef, and unvegetated soft sediments) from August 2015 through May 2017. Fifteen stations were randomly selected from a spatial grid overlaid on known seagrass in the lower two-thirds of the bay and on soft sediment in the lower one-third. For oyster reef stations, healthy oyster reefs were chosen across approximately the lower two-thirds of the bay. In each habitat, all stations were surveyed quarterly ($n = 45$ stations; Fig. 1). At each station, the total number of *Cinctura lilium*, *Fasciolaria tulipa*, *Sinistrofulgur sinistrum*, *Fulguropsis spirata* (all pear whelk were assumed to be *F. spirata*, and no effort was made to distinguish from *Fusus pyruloides* as a separate species or subspecies), *Triplofusus gigantea*, *Strombus alatus*, and *Melongena corona* was recorded. At each station in seagrass and soft sediment habitats, a 100-m transect was surveyed by paired divers for a total searched area of 200 m^2. At each oyster reef station, a 25-m transect line was surveyed by paired divers for a total searched area of 50 m^2. For a maximum of 60 individuals of each species, SL (the distance from the tip of the spire to the end of the siphonal canal) was measured and recorded at each station, as the animals were encountered. Pertinent observations (e.g., buried snails, feeding, copulation, egg-laying, and the presence of deposited eggs) were also recorded.

West Florida Shelf

During annual surveys, snails in shallow-water seagrass beds were counted using methods described in Stephenson et al. (2013), except that they were identified to species, as follows. At most sites (Fig. 2), 20 stations were surveyed by paired divers assessing 1 m on either side of a 300-m transect line (600 m^2 search area); 10 stations were surveyed at Sarasota Bay. Twenty randomly selected target station coordinates were established at each site (Stephenson et al. 2013) for assessment of long-term trends. Each year, station location varied by as much as 500 m depending on the presence (or absence) of seagrass, visibility, weather, and the presence of other boaters. All stations were located in seagrass habitats, and surveys were conducted in water 0.6–2 m deep. Densities and SL were recorded for the same seven species assessed in the Tampa Bay seasonal study. Sampling was conducted from 2009 through 2017, beginning in May and typically ending in mid-July, although the exact dates varied each year. Gastropod survey data (2015 to 2017) were recorded by species and were also compared with 2009 to 2014 data in which Stephenson et al. (2013) grouped two species into one data type called tulips (*Cinctura lilium* and *Fasciolaria tulipa*) and another two species into one data type called whelks (*Sinistrofulgur sinistrum* and *Fulguropsis spirata*).

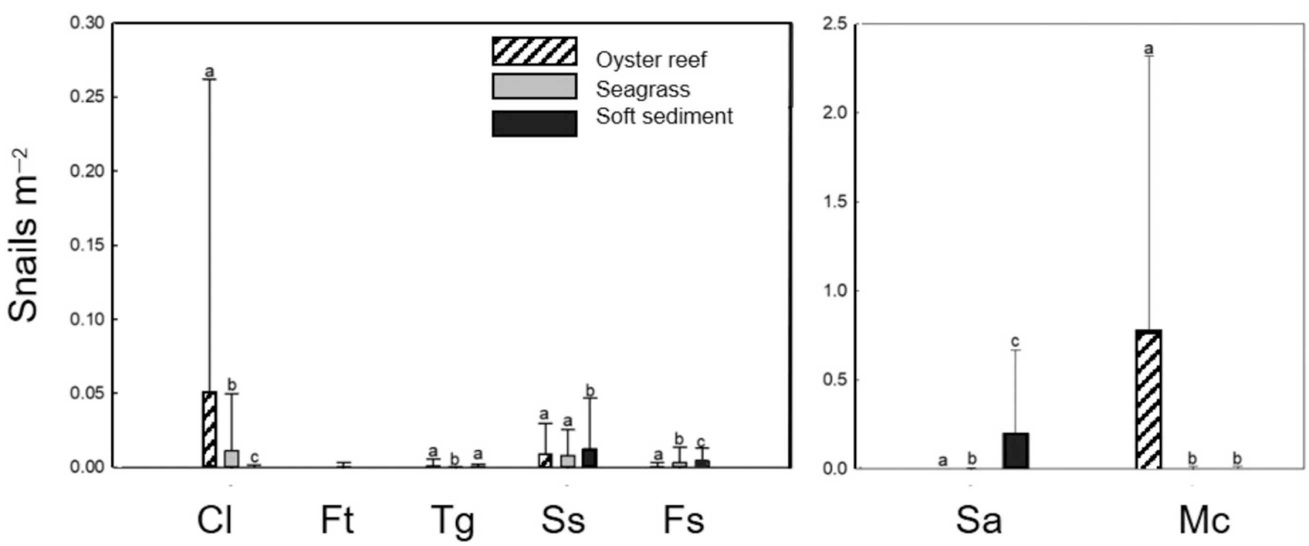

Figure 3. Densities (m^{-2}) of seven species of marine gastropods observed in oyster reef, seagrass, and soft sediment habitats in Tampa Bay, 2015 to 2017. Species codes as in Table 1.

Statistical Analyses

Statistical analyses were run using the Fathom Toolbox for Matlab (Jones 2015). Hypotheses related to variation in snail density were tested using univariate three-way permutational analyses of variance (PERMANOVA; Anderson 2001). A PERMANOVA test uses permutations to obtain P values while applying the traditional ANOVA procedure to a distance matrix. The PERMANOVA test was used because it makes no explicit assumptions about the distribution of data. The data were square-root-transformed, and PERMANOVA tests (n = 1,000 iterations) were run on Bray–Curtis dissimilarity matrices adjusted for joint absences by addition of a dummy species (Clarke et al. 2006).

Mixed-model PERMANOVA tests of snail density and snail size in Tampa Bay from 2015 through 2017 were run for each species individually using three factors: habitat (three levels: oyster reef, seagrass, and soft sediment; fixed), year (three levels: 2015, 2016, and 2017; random), and season (four levels: spring, summer, fall, and winter; fixed). Density at stations within a habitat type did not differ significantly for any species (PERMANOVA; pseudo-F = 0.971, P = 0.45), so data were pooled across stations for each habitat type. Mixed-model PERMANOVA tests of snail densities measured on the West Florida Shelf from 2015 through 2017 were run for each species with three factors: region (10 levels: St. Andrew Bay, St. Joseph Bay, St. Marks, Steinhatchee, Homosassa, Hernando, Anclote, Tampa Bay, Sarasota Bay, and Pine Island Sound; fixed), station (20 levels: 1–20 stations; random), and year (three levels: 2015, 2016, and 2017; random). In addition, mixed-model PERMANOVA tests of snail densities measured on the West Florida Shelf from 2009 through 2017 [incorporating data published in Stephenson et al. (2013)] were conducted for three groups of species (tulips: *Cinctura lilium* and *Fasciolaria tulipa*, whelks: *Sinistrofulgur sinistrum* and *Fulguropsis spirata*, and *Triplofusus gigantea*) with three factors: region (10 levels: St. Andrew Bay, St. Joseph Bay, St. Marks, Steinhatchee, Homosassa, Hernando, Anclote, Tampa Bay, Sarasota Bay, and Pine Island Sound; fixed), station (20 levels: 1–20 stations; random), and year (three levels: 2015, 2016, and 2017; random). If a PERMANOVA test detected a significant treatment effect, then *a posteriori* permutation-based, multiple comparison (pairwise) tests were run to interpret how levels varied within a treatment. Holm-adjusted P values were used to correct for multiple comparisons (Legendre & Legendre 2012).

Multivariate statistical analyses were also performed to describe patterns of distribution of marine gastropod assemblages among habitat types and sites. Principal coordinate analyses (PCoA) of the snail density data were performed among sites to identify clusters showing similarities in molluscan communities. In addition, PCoA were used to examine how molluscan community structure varied among habitat types. Data for these analyses were averaged for each species in each region or habitat type and square-root-transformed. Principal coordinate analyses were run on Bray–Curtis dissimilarity matrices that had been adjusted for joint absences by adding a dummy species (Clarke et al. 2006).

RESULTS

Tampa Bay

The densities of all study species differed significantly among habitats from 2015 to 2017 (Table 1) but not among seasons or years, and there were no significant interaction effects (Fig. 3). Overall, *Melongena corona* exhibited the highest densities [0.26 snail m^{-2} ± 0.96 (mean ± SD)], followed by *Strombus alatus* (0.07 snail m^{-2} ± 0.29) and *Cinctura lilium* (0.02 snail m^{-2} ± 0.13) (Table 2). Two species were highly habitat specific: 96% of *M. corona* were observed on oyster reef (n = 7,165; $P < 0.001$) and 100% of *S. alatus* were found on soft sediments (n = 7,006; $P < 0.001$; Fig. 3). The other marine gastropods studied were most often observed on soft sediments (Fig. 3): *Triplofusus gigantea* (n = 26; $P \leq 0.016$), *Sinistrofulgur sinistrum* (n = 703; P = 0.005), and *Fulguropsis spirata* (n = 230; $P < 0.001$).

In three species (*Fulguropsis spirata*, $P < 0.001$; *Melongena corona*, P = 0.002; and *Sinistrofulgur sinistrum*, $P < 0.001$), the average SL differed with respect to the habitat in which snails were found (Table 3). The species *M. corona* were significantly smaller on oyster reefs than on seagrass or soft sediments (Fig. 4), whereas *S. sinistrum* and *F. spirata* were smallest on soft sediments (Fig. 4). By contrast, the average SL did not differ significantly with habitat type for *Cinctura lilium*, *Strombus alatus*, or *Triplofusus gigantea* (Fig. 4, Table 3). The largest

TABLE 2.

Abundance (Abund, in millions of snails), by species, derived by extrapolating observed densities from observed transect densities to the estimated habitat area in Tampa Bay (top).

	Soft sediment		Seagrass		Oyster reef		
	~748 km²		~160 km²		~0.8 km²		
	~7.5 × 10⁸ m²		~1.6 × 10⁸ m²		~7.9 × 10⁵ m²		
	~185,000 acres		~39,535 acres		~196 acres		
Spp	Density	Abund	Density	Abund	Density	Abund	Total
Ft	0	–	0.014	1.6	0	–	1.6
Cl	0.006	4.1	0.028	4.5	0.163	0.1	8.7
Mc	0.020	15.0	0.029	4.6	1.378	1.1	20.7
Sa	0.300	40*	0.011	1.8	0	–	41.8
Tg	0.006	4.5	0.020	3.2	0.023	0.02	7.7
Ss	0.021	15.9	0.017	2.7	0.035	0.03	18.6
Fs	0.012	8.8	0.014	2.2	0.020	0.02	11.0

No variances or error is estimated because the sample design was not a truly randomized survey design. Species codes as in Table 1.
* Estimate for lower Tampa Bay only.

TABLE 3.

***P* values of three-way PERMANOVA tests of snail SL (mm), by species, among habitat (Hab), season (Seas), and year (Yr) in Tampa Bay, 2015 to 2017.**

Factor	Cl	Fs	Mc	Sa	Ss	Tg
Hab	0.111	**<0.001**	**0.002**	0.645	**<0.001**	0.853
Seas	**0.007**	**<0.001**	**0.002**	**<0.001**	**<0.001**	0.398
Yr	0.242	**0.025**	**0.002**	**<0.001**	**<0.001**	0.459
Hab × Seas	0.757	0.080	**0.002**	0.357	1.000	0.109
Hab × Yr	**0.006**	0.868	**0.002**	0.751	1.000	0.143
Seas × Yr	**0.015**	0.106	0.238	**<0.001**	**<0.001**	0.564
Hab × Seas × Yr	0.436	0.993	0.998	0.315	1.000	0.527

Species codes as in Table 1. P values < 0.05 in bold.

species of gastropod observed in Tampa Bay was *T. gigantea*, with an average SL of 238.5 ± 102.3 mm, whereas *M. corona* was the smallest, with an average SL of 52.9 ± 17.7 mm (Fig. 5). The largest individual snail observed in Tampa Bay, however, was a *S. sinistrum*, with a SL of 420 mm. The smallest was an *M. corona*, with a SL of 13 mm. Shell length varied by season for all species, except *T. gigantea*, and by year for all species, except *T. gigantea* and *C. lilium* (Table 3). Smaller *M. corona* were found during year 2 than during year 1 or 3. The largest *S. alatus* were observed during year 2, and the smallest during year 1, whereas the largest *S. sinistrum* and *F. spirata* were observed during the first year of the study. Size differed with season in some years but not in others for three species: *S. alatus*, *C. lilium*, and *S. sinistrum*. Size differed with habitats in some years but not in othersfor two species: *C. lilium* and *M. corona*. A small number of *M. corona*, ~2.3% of that found on oyster bars (55.4 mm), with a relatively larger mean size (72.2 mm) were found in soft sediment in winter and were also larger in seagrass (0.6%, 72.0 mm) and in soft sediment (2.0%, 61.1 mm) than on oyster reef (50.0 mm) in spring. The difference between means was smallest in summer (oyster bar, 49.5 mm; seagrass 1.8%, 65.7 mm; and soft sediment 1.7%, 62.5 mm). In fall, this pattern reversed (oyster bar, 55.1 mm; seagrass 0.1%, 47.9 mm; and soft sediment 3.8%, 47.9 mm).

The smallest *Cinctura lilium* that were detectable (15–20 mm) were most abundant in fall (Fig. 6). For *Fulguropsis spirata* (10–20 mm) (Fig. 7) and *Strombus alatus* (15–20 mm) (Fig. 8), very small snails were most abundant in fall, and small numbers of very small snails were detected throughout the year. The smallest *Sinistrofulgur sinistrum* (20–40 mm) were most abundant in fall (Fig. 9), and small numbers of very small snails were detected throughout the year. Finally, the smallest *Melongena corona* (15–20 mm SL) were detected in fall and winter (Fig. 10).

Deposited eggs were observed for all species. A *Triplofusus gigantea* was observed in February 2017 depositing an egg case. Egg cases of *Cinctura lilium* and *Sinistrofulgur sinistrum* were usually observed in winter and spring, whereas *Fulguropsis spirata* egg cases were observed only in winter. Egg masses of *Strombus alatus* and *Melongena corona* egg cases were observed in spring and summer. Mating was observed in winter for *M. corona*, *T. gigantea*, and *S. sinistrum*.

West Florida Shelf

There were no significant differences in the density of any of the target species among years or among stations ($P > 0.05$; Table 4). Approximately 75% of the gastropods observed from 2015 to 2017 were located within the Southwest Florida sites (Tampa Bay, Sarasota Bay, and Pine Island Sound) (Fig. 11, Table 5). During this time, the target species *Cinctura lilium* was the most abundant gastropod ($n = 376$), followed closely by *Sinistrofulgur sinistrum* ($n = 344$). Density differed significantly among sites for five of the seven species from 2015 to 2017

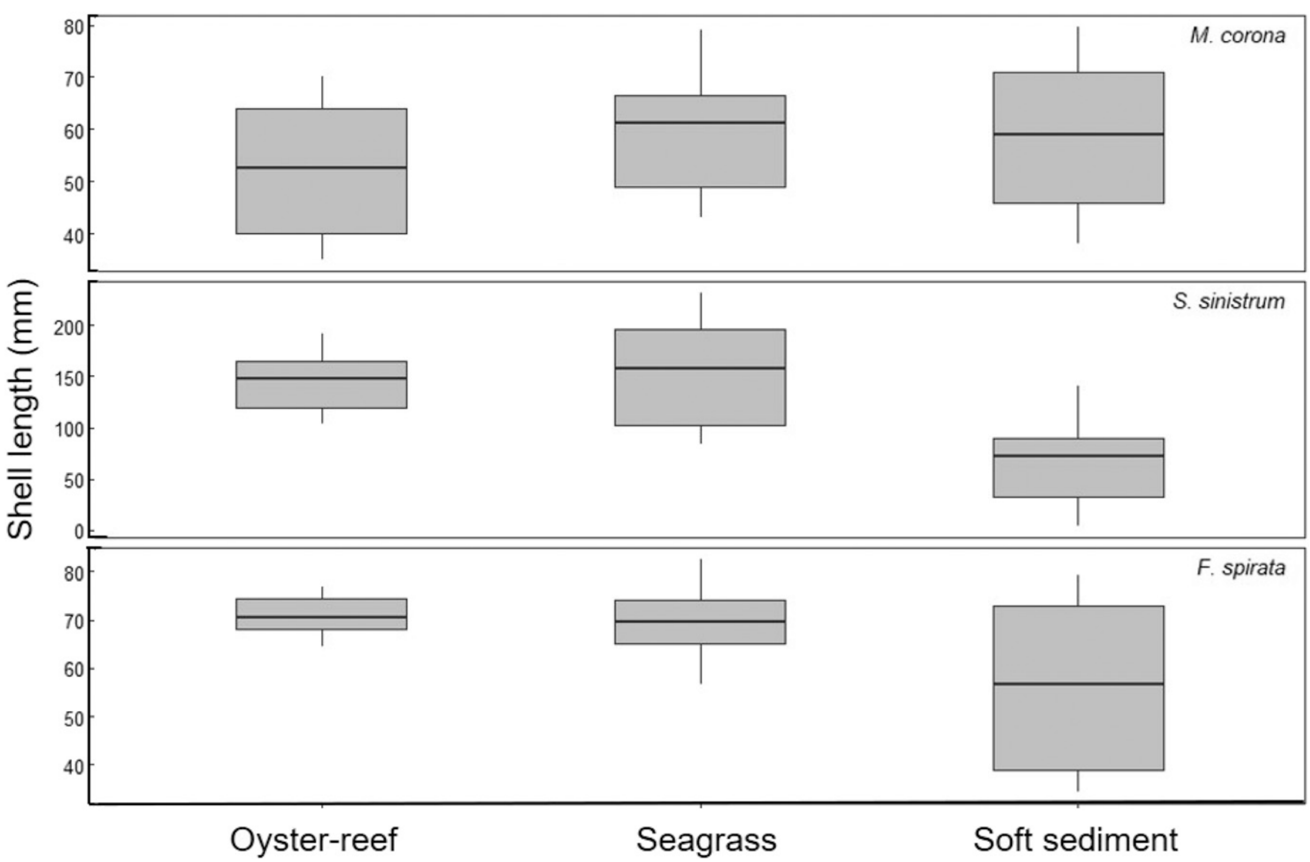

Figure 4. Range of SL (mm) for three marine gastropod species (*Melongena corona*, *Sinistrofulgur sinistrum*, and *Fulguropsis spirata*) observed in oyster reef, seagrass, and soft sediment habitats in Tampa Bay, 2015 to 2017. Box represents 25%–75%, center line represents mean, and whiskers represent SD.

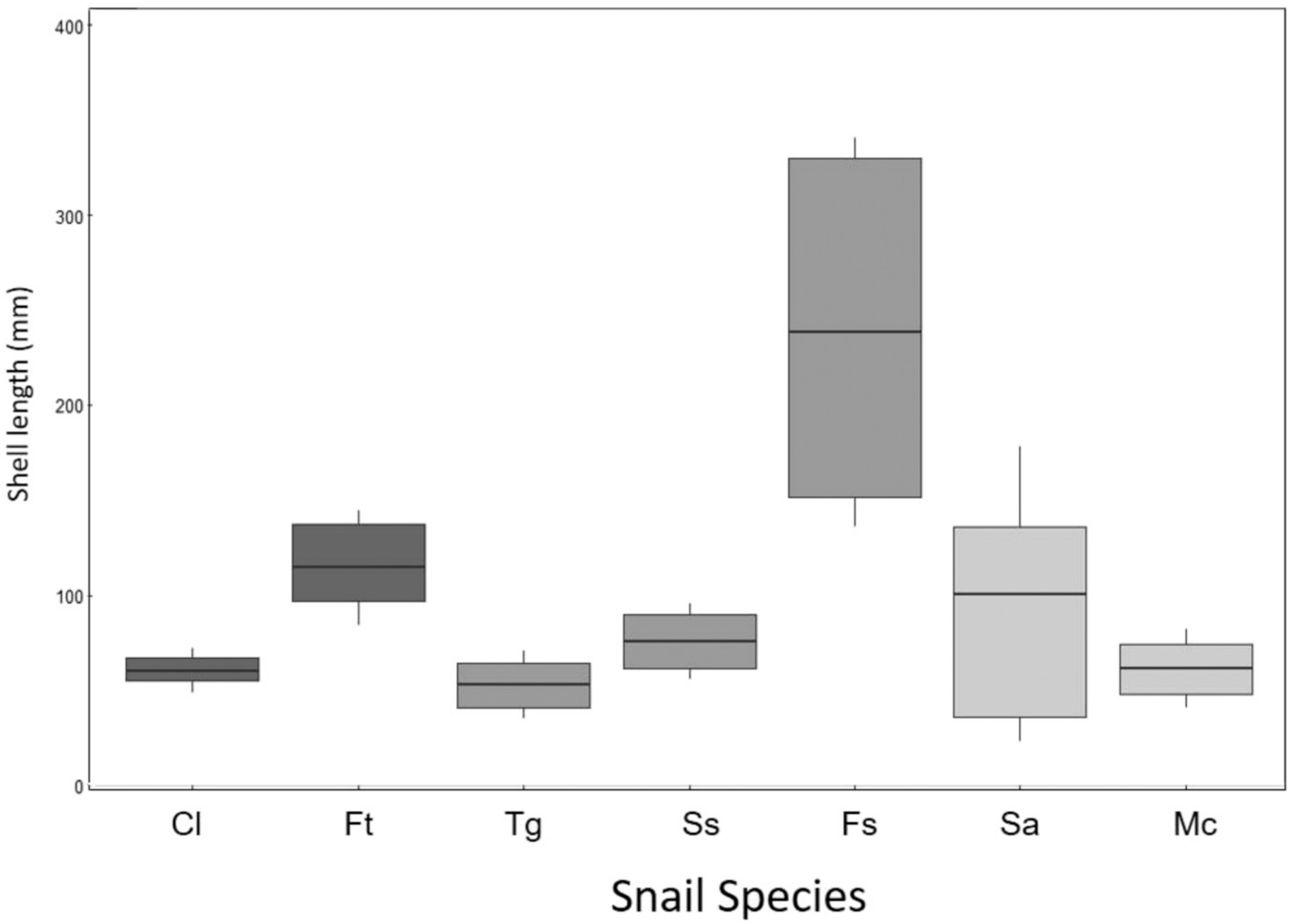

Figure 5. Range of SL (mm) for seven marine gastropod species measured during visual surveys of large marine gastropods conducted in Tampa Bay, 2015 to 2017. Box represents 25%–75%, center line represents mean, and whiskers represent SD. Cl, *Cinctura lilium*; Fs, *Fulguropsis spirata*; Ft, *Fasciolaria tulipa*; Mc, *Melongena corona*; Sa, *Strombus alatus*; Ss, *Sinistrofulgur sinustrum*; Tg, *Triplofusus gigantea*.

(Fig. 12, Table 4), the exceptions being *Melongena corona* and *Strombus alatus*. Tampa Bay and Pine Island Sound were characterized in the PCoA plot by high densities of *S. sinistrum*, *Fulguropsis spirata*, *C. lilium*, and *S. alatus*; Sarasota Bay was associated with high densities of *M. corona*; and the remaining northern sites were characterized by high densities of *Triplofusus gigantea* and *Fasciolaria tulipa* (Fig. 13A, B).

The densities of *Sinistrofulgur sinistrum* and *Fulguropsis spirata* (whelks) combined, as well as the densities of *Cinctura lilium* and *Fasciolaria tulipa* (tulips) combined, from 2009 to 2017 varied significantly by site and by year (Table 4). The densities of the tulips decreased from 2009 to 2017 ($P = 0.024$) (Fig. 14), resulting from declines in St. Marks ($P = 0.048$) and Sarasota Bay ($P = 0.010$); other sites showed no significant slope ($P > 0.05$). In the southwestern sites (Tampa Bay, Sarasota Bay, and Pine Island Sound), there were more whelks in 2011 and 2015 (Fig. 14), but the slope did not differ significantly from 0 for any site or overall ($P > 0.05$). The density of *Triplofusus gigantea* did not vary significantly by year from 2009 to 2017 ($P > 0.05$), but densities differed significantly among sites; densities of *T. gigantea* were typically the greatest in St. Joseph Bay (Fig. 14, Table 6).

DISCUSSION

Several of the species in this study were strongly associated with a certain habitat in Tampa Bay. Most species were found in association with soft sediment habitat; *Cinctura lilium* and *Melongena corona*, however, were highly associated with oyster reef habitat, whereas only *Fasciolaria tulipa* was consistently observed in seagrass habitat. The strong reliance of *C. lilium* and *M. corona* on oyster reef habitat suggests that they warrant closer monitoring in estuaries in which oyster reefs are declining or of unknown status. In estuaries where seagrass coverage is declining, the status of seagrass-dependent species, such as *F. tulipa*, would likewise warrant monitoring.

Gastropod density and size structure in Tampa Bay were relatively stable over the 3-y study. The only species for which density changed seasonally was *Cinctura lilium*, likely the result of a combination of a pattern of spring recruitment and the ability of the observer to detect the smallest individuals. The size structure of remaining target species shifted only slightly seasonally, most likely because of stochastic patterns of annual recruitment. There was no evidence of seasonal movement into or out of the bay for any of the species examined, which Paine (1963) suggested by for the horse conch and Kent (1983)

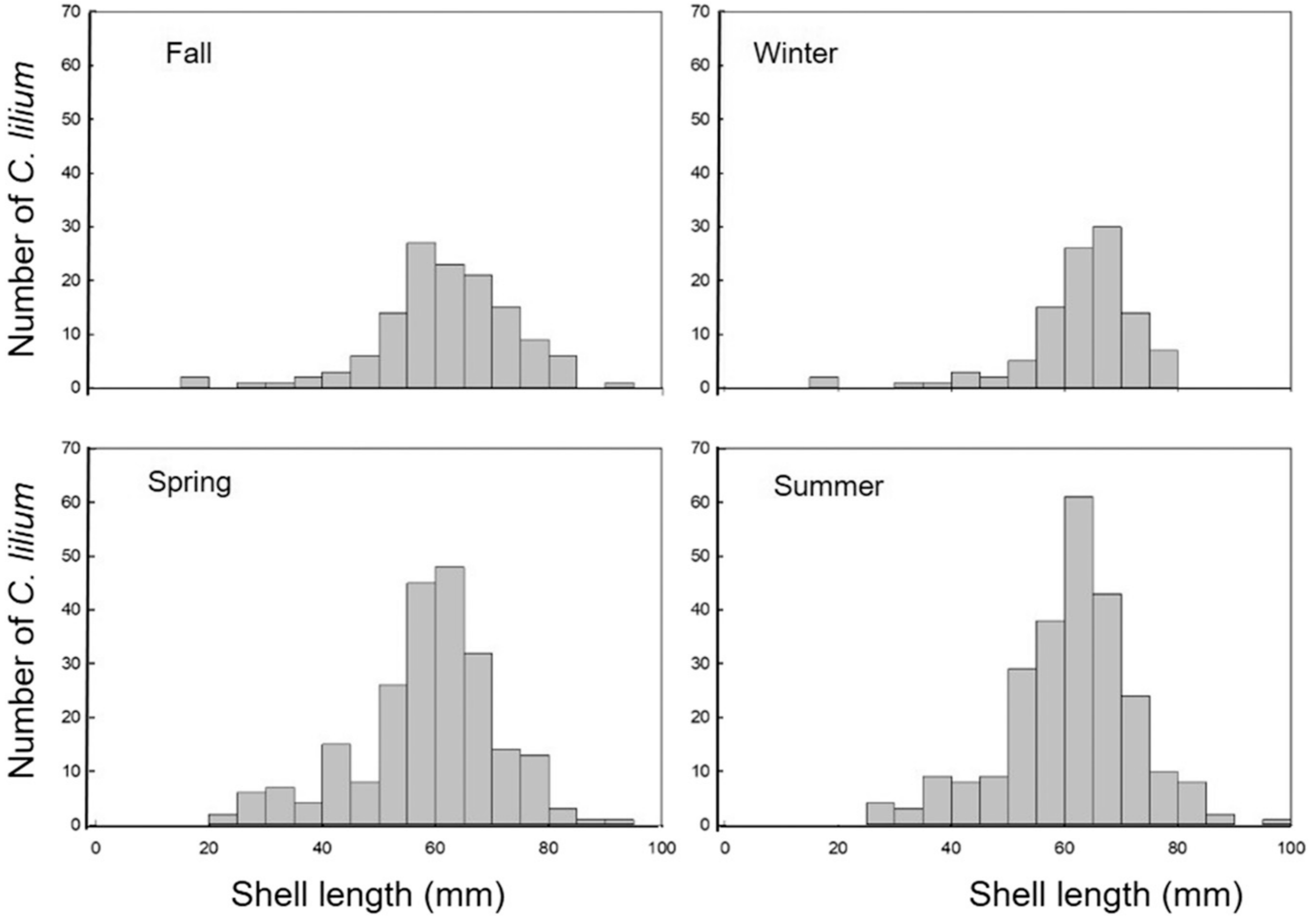

Figure 6. Seasonal size structure of *Cinctura lilium* observed in Tampa Bay, 2015 to 2017.

suggested for whelks. Without a longer time series, it is difficult to understand whether the differences reflect long-term trends or changes specific to the study sites, which differed in spatial scale. Both earlier studies focused on a single small sandbar, whereas the present study evaluated multiple sites along the gradient of an entire estuary.

In general, the southwestern sites examined in this study (Tampa Bay, Pine Island Sound, and Sarasota Bay) had the highest densities of snails on the West Florida Shelf, approximately 0.003 snail m^{-2}. In comparison, Hernando, Homosassa, and St. Marks had densities of approximately 0.0001 snail m^{-2}. Snail densities in bays were typically an order of magnitude higher than those in open, coastal seagrass areas. Few similar studies have been performed that might aid in evaluating possible causes.

Sheaves at al. (2015) suggested that differing densities of snails in their study sites had resulted from many interacting factors. Bays may provide more refugia than do areas with higher salinity (Garton & Stickle 1980), simply because lower salinity restricts the movement of some predators. If the embayments had higher coverage of seagrass beds, then they might offer more refugia from predation than do open coastal waters (Lewis & Stoner 1983, Heck & Crowder 1991), but the sites monitored in the present study specifically focused on dense seagrass beds. The bays studied are, in fact, more heterogenous than coastal waters in the present study, including oyster reefs, soft sediment unstructured areas, salt marshes, and mangroves. Bays may have greater primary productivity than coastal regions (Raymont 1980), which can affect prey availability (Herman et al. 1999). In Pine Island Sound, one of the sites with the highest densities of gastropods, collection of live snails is prohibited, so limiting harvest by humans may result in higher snail densities there.

The only sites at which all seven target species were observed were Tampa Bay and Anclote, although no site recorded all target species during all years of the study. Two species were observed in all sites studied, *Fasciolaria tulipa* and *Cinctura lilium*. The most geographically restricted species was *Strombus alatus*, which was observed mainly at the Tampa Bay site and to a much lesser extent in Anclote (where the edges of patchy seagrass often abut soft sediment habitats); this finding was undoubtedly skewed by the fact that surveys outside Tampa Bay were performed exclusively in shallow seagrass beds, which is not a preferred habitat for *S. alatus*.

The long-term monitoring stations that have been used to measure gastropod densities on the West Florida Shelf provide an incomplete estimate of gastropod populations. The weak association in this study between gastropods and seagrass habitat in Tampa Bay suggests that placement of these long-term monitoring stations in only seagrass habitat do not fully capture gastropod population dynamics. A reason the regional surveys indicate higher densities of gastropods in Tampa Bay,

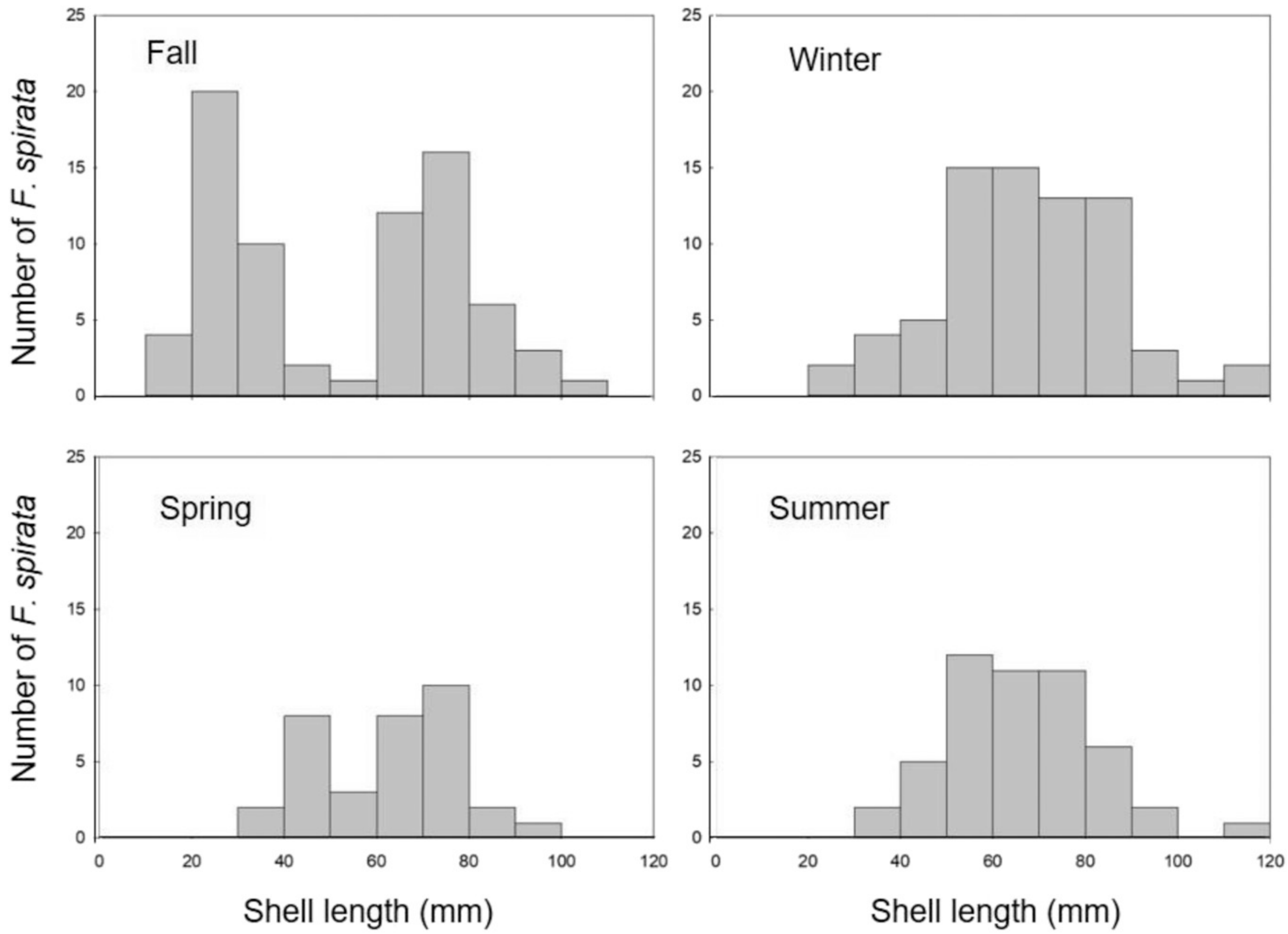

Figure 7. Seasonal size structure of *Fulguropsis spirata* observed in Tampa Bay, 2015 to 2017.

Pine Island Sound, and Sarasota Bay may be that many of the transects there were adjacent to and even included a portion of soft sediment habitat, because seagrass meadows are often more heterogenous inside the bays. Finally, there was no significant annual difference in the densities of the gastropod species measured from 2015 to 2017. The annual densities of tulips and whelks (as groups) varied significantly from 2009 to 2017. Tulips were also the only grouping for which there was a measurable trend in density, declining at two sites; even so, as a group, they remained more abundant than did other gastropods. Future studies of gastropod densities along the West Florida Shelf should include a habitat-stratified survey design targeted for the species of study (e.g., soft sediment habitat for *Strombus alatus*) and fewer replicate stations within each habitat type in each region or site. The present study establishes a baseline for species-specific relative densities.

In the marine environment, one of the chief problems in managing a species or evaluating the need to manage it is simply the lack of information for many invertebrate species that are not commercially or recreationally harvested. A few species found in Florida, like the blue crab *Callinectes sapidus* (Rathbun, 1896), are commercially harvested and so are partly monitored by fishers reporting their landings, but for most species, commercial landings are sporadic, and recreational use, including that of otherwise commercial species like the blue crab, is poorly monitored. Marine invertebrates are harvested as food items or as ornamental items, the latter either live for aquariums or for the shell (which includes both live and dead specimens) or as dried organisms, like sea stars (Larkin et al. 2001, Rhyne et al. 2009). In other regions, such as Delaware, the harvest of gastropods is thought to be occurring at unsustainable levels (Bruce 2006). The whelk fishery in the U.S. Atlantic exhibits the common trend of landings that remain below historic levels of the total weight of harvest but with increasing value, a signal that the fishery is overfished and cannot meet demand (Walker et al. 2008). Furthermore, Bruce (2006) reported that Florida was the only U.S. Atlantic state for which no whelk landings were reported. Underused marine resources usually do not remain so indefinitely, and those resources are likely to eventually be targeted for commercial harvest, especially if demand exists and other supplies remain limited. Landings of whelks in Florida from 2007 to 2018 totaled 45,678 kg (100,702 lbs) (NOAA: https://foss.nmfs.noaa.gov/apexfoss/f?p=215:200).

In Tampa Bay, *Cinctura lilium* was found to prefer oyster reef, but was also present in seagrass. Combined, these habitats total almost 162 km^2 in Tampa Bay, and both habitats are present throughout most of the nearshore waters and estuaries of the Gulf Coast of Florida. Although no live *C. lilium* or

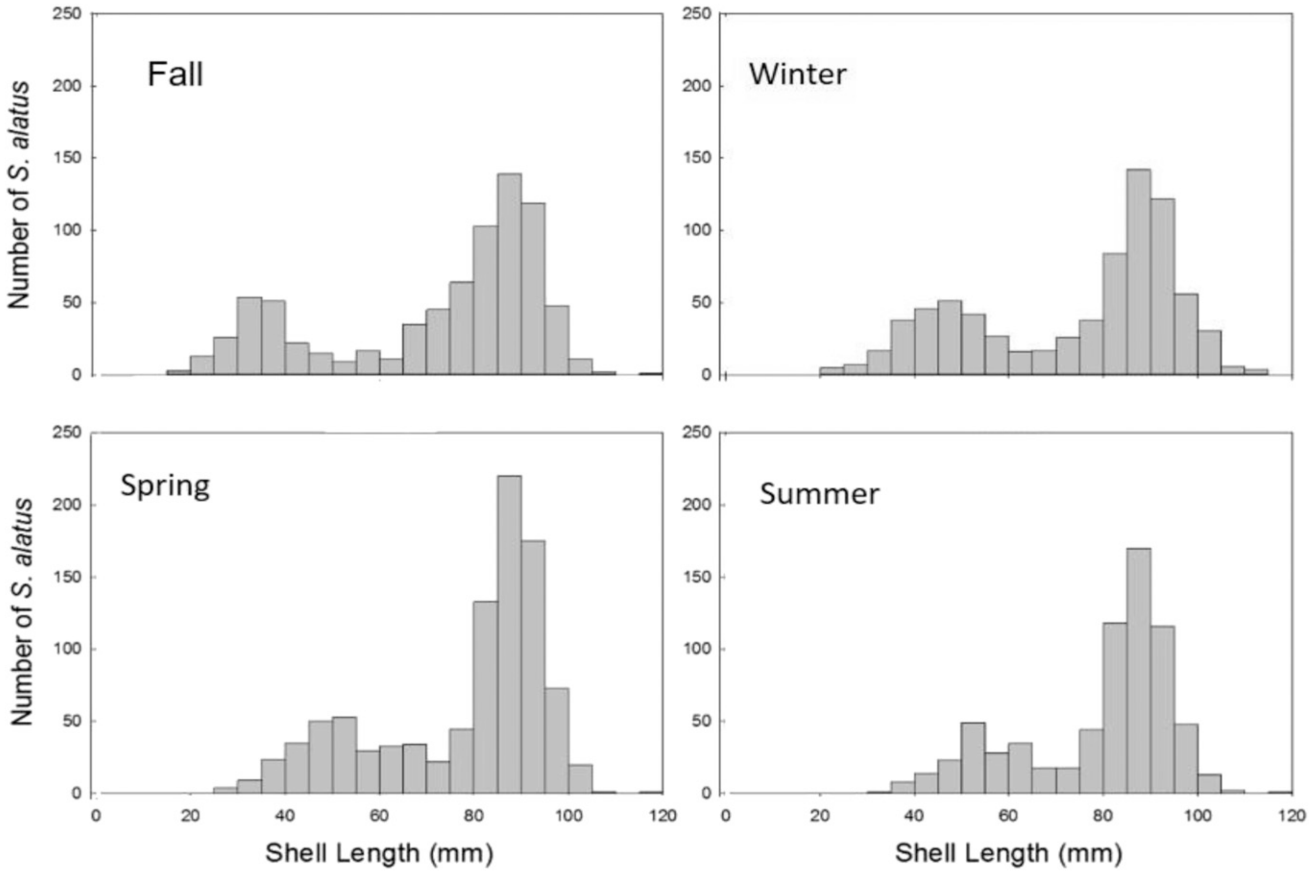

Figure 8. Seasonal size structure of *Strombus alatus* observed in Tampa Bay, 2015 to 2017.

Fasciolaria tulipa were found in a preliminary sampling of the Florida Keys (present study, data not included), both species were listed in a survey of molluscan communities there (Petuch & Myers 2014), and the Keys would provide an expanse of habitat totaling millions of acres (Carlson & Fourqurean 2016) that might sustain vast numbers of a species, even at low densities. The commercial harvestable oyster stock in Florida has declined (Camp et al. 2015), but there is insufficient evidence to suggest that either the total available oyster and seagrass habitat or the population of *C. lilium* in Florida is shrinking. In fact, seagrass has recovered since the 1980s in 12 of 23 estuaries monitored in Florida (Yarbro & Carlson 2016).

Unlike *Cinctura lilium*, *Fasciolaria tulipa* was not included in the 2012 Florida SWAP (FWC 2012), despite being in the same family. The densities of *C. lilium* were higher in bays, whereas those of *F. tulipa* were higher in open coastal seagrass meadows. An obvious possible factor is the relatively stable salinity of coastal regions, but there are likely other, unknown factors that also help determine the distribution of the two species. In both cases, their occurrence on the coastal shelf in either the Gulf of Mexico or the Atlantic Ocean increases the total amount of habitat that may be available (Lyons 1989). Because the bicoastal distribution is largely contiguous, there is reduced chance, even at low densities, that the range of *F. tulipa* might shrink. The range of *F. tulipa* extends from North Carolina to Texas and Brazil (Abbott 1974), and even if local fragmentation occurs, the metapopulations could theoretically reconnect. Although the density of *F. tulipa* is low, the distribution is wide, also including most of the Caribbean islands (Snyder et al. 2012), indicating that the total population is large and widespread.

Both *Cinctura lilium* and *Fasciolaria tulipa* egg cases were found in late winter and spring, and seasonal variations in density of these species were modest. This suggests that there is little reproductive specialization, such as a limited number of spawning aggregations. Recruitment of *C. lilium* to the size at which individuals could be detected in visual surveys occurred in spring, and the most straightforward interpretation of this observation is that they took about 1 y to reach ~20 mm since hatching the prior spring. For both species, the number of egg cases per clutch, the number of hatchlings per egg case, and hatchling survival show that they can produce at least hundreds of offspring per breeding event (Winner 1985). The number of clutches per year remains unknown, as does the size or age at maturity. Improved estimates of growth rate, maximum age, potential sexual dimorphism, and total reproductive potential remain unavailable and are being studied.

Both species of tulip have a broad diet, can consume diverse gastropods and bivalves as prey, and can exist in multiple habitats (although they do appear to have preferences), and neither is restricted to Florida. They make excellent candidates for indicator species in their preferred habitats. Because of decreases in landings of *Cinctura lilium* and in the densities of tulips recorded in this study during annual surveys from 2009 to 2017 (Fig. 14), monitoring their distribution and abundance, as well as continued studies of their biology, is warranted.

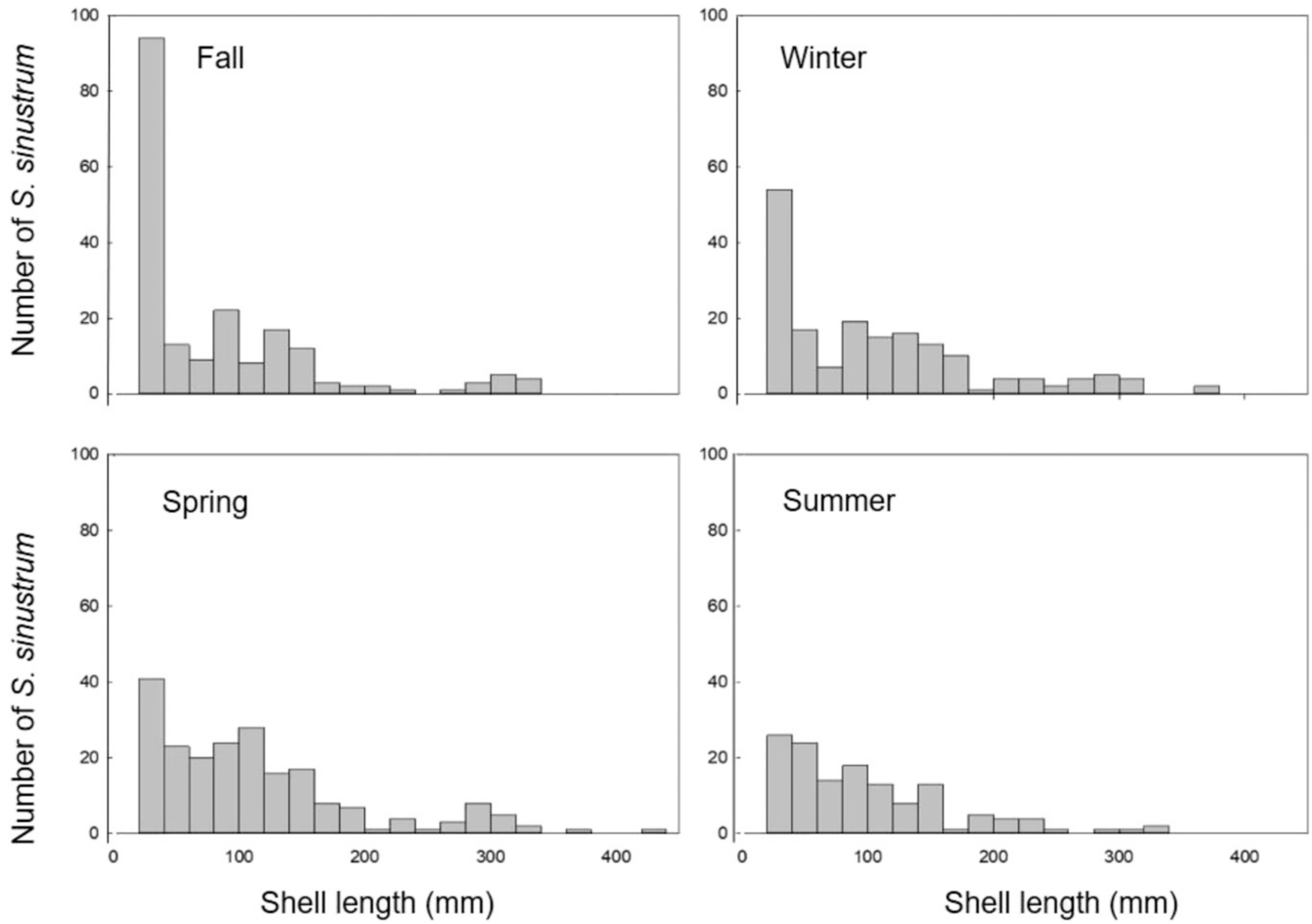

Figure 9. Seasonal size structure of *Sinistrofulgur sinistrum* observed in Tampa Bay, 2015 to 2017.

Conch meat is highly prized throughout the Caribbean and Florida to the point at which at least one strombid species, the queen conch *Lobatus gigas*, is widely overharvested (Brownell & Stevely 1981). By contrast, *Strombus alatus*, also a strombid, is not commonly exploited in the United States. A search of the National Marine Fisheries Service landings database reveals that not even 1,000 kg of *S. alatus* meat was harvested from 2006 through 2016 (https://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/; accessed May 2018). The distribution of *S. alatus* was almost exclusively on soft sediment. Godcharles and Jaap (1973) found that *S. alatus* was widespread on the Florida shelf, and, because soft sediment is its preferred habitat, it may remain common and widespread in Florida. Unfortunately, the species is not commonly found at the long-term monitoring stations used in this study because those stations are located mostly in seagrass, so trends in distribution and abundance cannot be defined. To better understand the status of this species, future surveys should include sample stations in unconsolidated soft sediments.

Egg cases of *Strombus alatus* were observed from late spring into summer, and each egg mass can consist of thousands of tiny eggs that yield pelagic larvae (Shawl et al. 2003). Although mortality of pelagic larvae can be expected to be high, a pelagic larval phase can allow for greater dispersal than the crawl-away juveniles that occur in the other species in the present study (Hedgecock 1986, Shanks 2009). In small captive juveniles, observed growth rates of approximately 1 mm SL per week (Shawl et al. 2005) indicate that it would take 16–20 mo for *S. alatus* individuals to reach the smallest size that was detectable in the present study (~20–40 mm), which occurred in fall. If the growth rates observed are comparable to those in a natural environment and remain steady throughout life, the largest individual observed in Tampa Bay, at 115 mm SL, was approximately 500 days old. It is more likely that growth slows once *S. alatus* is mature, probably at around 90 mm SL based on observations that the shell margin begins to thicken and flare outward at that size, as occurring in *Lobatus gigas* (Aldana Aranda & Frenkiel 2007), but published rates or observations of growth in mature *S. alatus* are not available. They are one of the more common shells on coastal beaches in Florida (Geiger, personal observation) and have been observed in nearshore aggregations (Hewitt 2013). Although these aggregations in soft and unstructured sediments might put *S. alatus* at risk for commercial exploitation, the high fecundity resulting from multiple batches per year per female and thousands of eggs per batch (Shawl & Davis 2004) would provide some resilience to harvest pressure unless densities fell to a level at which fertilization success dropped.

The species *Triplofusus gigantea* was widespread in this study, but it was observed at low densities and frequencies. Although it appeared that *T. gigantea* slightly preferred soft sediment and oyster reef to seagrass habitat, the relatively low observed densities may not offer an accurate portrayal of its

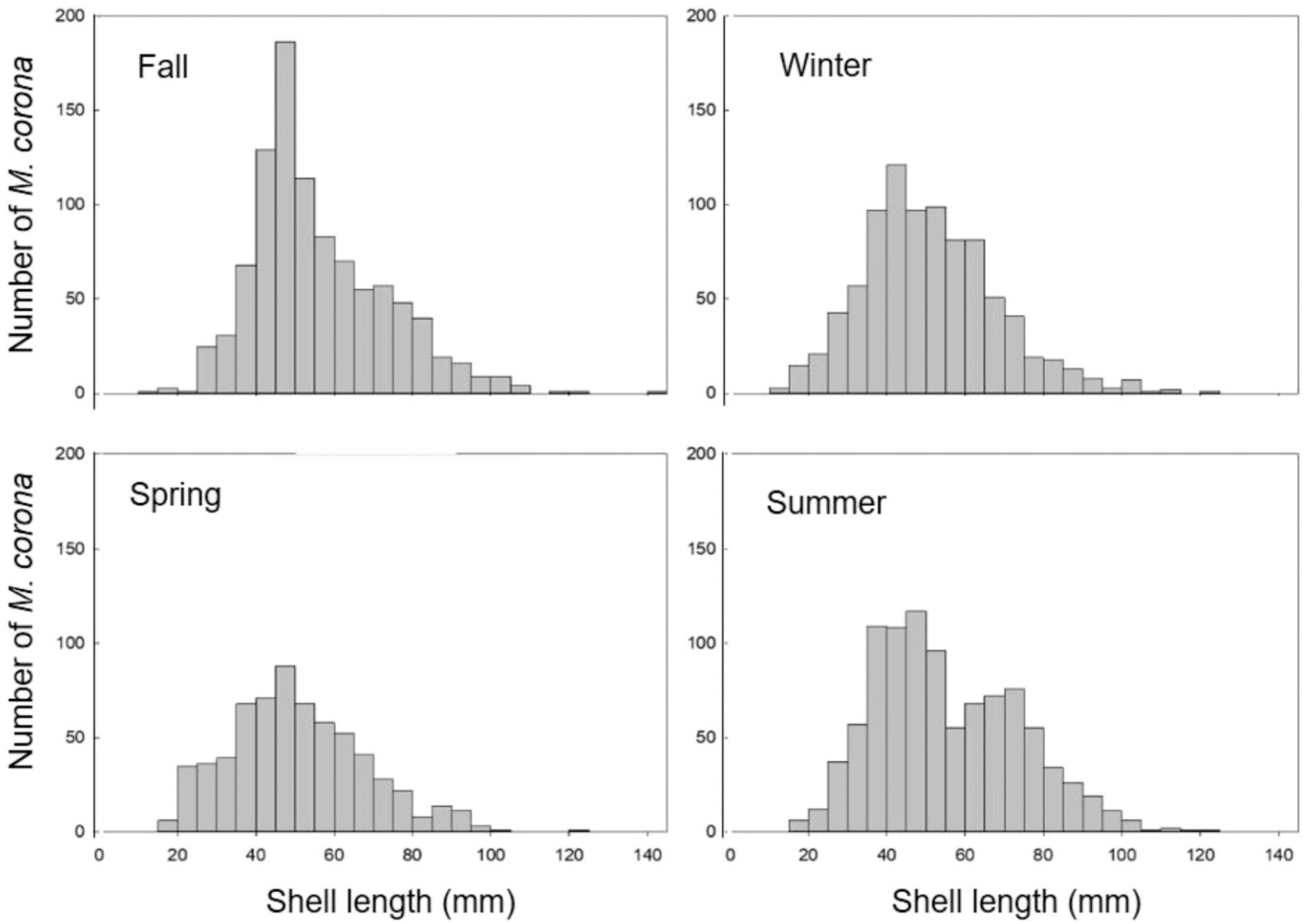

Figure 10. Seasonal size structure of *Melongena corona* observed in Tampa Bay, 2015 to 2017.

distribution. Similarly, *T. gigantea* was recorded in low densities at long-term monitoring stations on the West Florida Shelf, although those may be underestimates because the surveys did not sample the preferred habitat of the species. At one site, St. Joseph Bay, densities were modest. Unfortunately, this site is one of the only places for which significant recent harvests of this species have been reported, at approximately 4,000 pounds per year (2015 to 2017) (https://public.myfwc.com/FWRI/). The largest individual ever recorded, at 606 mm (http://catalog.shellmuseum.org/shells/southwest-florida-shells/triplofusus-giganteus), would have been many years old, and assuming that growth rate slows with maturity, possibly decades old. The relatively long life span offers multiple chances for successful offspring survival, and the fact that females produce many offspring from each egg mass (Winner 1985) suggests that this species has relatively high lifetime fecundity. The combination of a long life span,

TABLE 4.

***P* values of three-way PERMANOVA tests of snail density (m^{-2}), by species, among sites (Site), stations (Sta), and years (Yr) on the West Florida Shelf, 2015 to 2017.**

Factor	Cl	Fs	Ft	Mc	Sa	Ss	Tg
Site	**<0.001**	**<0.001**	0.079	0.054	0.449	**<0.001**	**<0.001**
Yr	0.057	0.104	0.484	0.140	0.763	0.071	0.787
Sta	0.714	0.694	0.511	0.114	0.755	0.201	0.856
Site × Yr	0.296	**<0.001**	**<0.001**	0.112	0.118	**0.002**	**0.015**
Site × Sta	**<0.001**	**<0.001**	**<0.001**	0.068	0.338	**0.003**	0.212
Yr × Sta	0.430	0.068	0.692	0.915	0.661	0.880	**0.044**

Species codes as in Table 1. *P* values < 0.05 in bold.

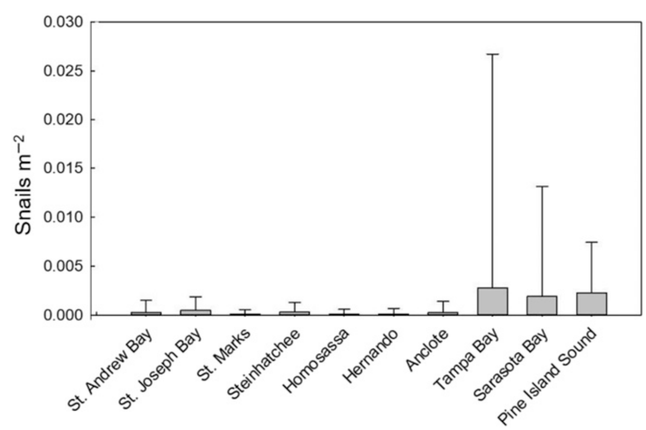

Figure 11. Total combined density (m^{-2}) of marine gastropods observed in seagrass beds during 2015 to 2017 within multiple sites on the West Florida Shelf.

TABLE 5.

Average snail density (m^{-2}), by species, in seagrass habitat at 10 sampling sites along the West Florida Shelf from 2015 to 2017.

Species	St. Andrew Bay	St. Joseph Bay	St. Marks	Steinhatchee	Homosassa
Cl	0.00131	0.00093	0.00006	0.00013	0.00002
Mc	0.00033	0.00002	0.00000	0.00008	0.00000
Sa	0.00003	0.00000	0.00000	0.00015	0.00000
Tg	0.00006	0.00086	0.00011	0.00023	0.00025
Ss	0.00000	0.00046	0.00017	0.00033	0.00000
Fs	0.00000	0.00015	0.00022	0.00000	0.00002
Ft	0.00028	0.00118	0.00028	0.00102	0.00048
Species	**Hernando**	**Anclote**	**Tampa Bay**	**Sarasota Bay**	**Pine Island Sound**
Cl	0.00008	0.00013	0.00370	0.00160	0.00494
Mc	0.00003	0.00007	0.00037	0.00813	0.00003
Sa	0.00017	0.00031	0.01060	0.00000	0.00003
Tg	0.00000	0.00004	0.00014	0.00000	0.00014
Ss	0.00006	0.00015	0.00282	0.00292	0.00569
Fs	0.00000	0.00002	0.00162	0.00056	0.00472
Ft	0.00031	0.00092	0.00028	0.00028	0.00042

Species codes as in Table 1.

broad geographic distribution, including coastal shelf habitats (Abbott 1974), and relatively high-batch fecundity may offer some resilience to harvest, and the life span may offer some resilience in the face of depletion and short-term environmental variation (King & McFarlane 2003).

The crown conch *Melongena corona* has often been maligned as a principal consumer of oysters but is most likely opportunistic (Hathaway & Woodburn 1961). When present, *M. corona* was more abundant than any of the other gastropod species considered in this study, approaching mean densities on some transects of 1 m^{-2} on oyster reef. Although within-transect patchiness was not recorded, patches in some transects sometimes greatly exceeded this value. This species was virtually absent on any seagrass survey, except those in Tampa Bay, where some transects were near oyster reefs and so may account for its presence on this habitat type. Long-term monitoring stations on the West Florida Shelf, located in seagrass habitat, most likely did not adequately measure *M. corona* densities. In the present study, multiple strings of egg cases of *M. corona* were observed in spring and summer, any of which might have contained hundreds of eggs (Hathaway & Woodburn 1961). Based on SL measurements, observations of mating, and observations of deposited egg cases, *M. corona* likely spawns in late winter and spring, possibly into summer, and individuals reach a size at which they can be detected in visual surveys the following winter. Although some morphological differentiation at the subspecies level may be evident in limited ranges in northeast (*M. corona sprucecreekensis*) and south Florida (*M. corona bicolor*) (Abbott 1974, Karl & Hayes 2012), only one species of *Melongena* (*M. corona*) likely exists in Florida (Hayes & Karl 2009). The variation from one estuary to another, in combination with its early life history, which includes eggs hatching as crawl-away juveniles rather than as pelagic larvae, does raise a concern for this species. This species complex is largely restricted to Florida, and the metapopulation is vulnerable to further fragmentation because its primary habitat, oyster reef, is vulnerable.

Several species of the family Buccinidae are found in the Atlantic Ocean and Gulf of Mexico coasts of the United States. The species *Sinistrofulgur pulleyi* (Hollister, 1958), a congener found in Texas waters (Tunnell et al. 2010), is not found in Florida. The species *Busycon carica* (Gmelin, 1791), along the U.S. Atlantic coast, is probably limited to northeastern estuaries and in Florida to coastal waters. The channeled whelk *Busycotypus canaliculatus* (Linnaeus, 1758) and *B. carica* are considered overfished in neighboring Georgia (Shalack et al. 2011). The most widely distributed snail within the Buccinidae in Florida is perhaps *Sinistrofulgur sinistrum*. The modest densities of *S. sinistrum* observed in the present study, combined with the occurrence of the species in all three habitats studied, suggest that in Florida waters, this species may not be threatened by habitat fragmentation or diminishing range. The main concern for this species would be that a commercial fishery based on it could develop, although it is already taken for ornamental purposes and in a recreational harvest. In the Gulf, the species is largely restricted to Florida waters; on the Atlantic coast, its range extends north to New Jersey (Abbott 1974). The extremely high fecundity of large females (hundreds of egg cases per string and sometimes hundreds of eggs per case; Winner 1985), combined with plentiful appropriate habitat and a geographic range that extends beyond Florida, would provide a buffer for overexploitation.

Lightning whelk juveniles, *Sinistrofulgur sinistrum*, were detectable at approximately 20 mm SL, which was reached in fall and winter at the age of 9 mo. This estimate of recruitment aligns with observations of mating, which was observed in winter, followed by observations of deposited egg cases in winter and spring. Age and growth models have not been developed for this species, and this remains an information need for proper management. Age at maturity for *S. sinistrum* is likely similar to that for the related confamilial knobbed whelk *Busycon carica*, in which most males mature by the age of 9 mo (Walker et al. 2008) and females probably later because no females had matured by the age of 10 mo in captive-reared populations (Castagna & Kraeuter 1994).

Another snail in the Buccinidae, *Fulguropsis spirata*, was more abundant in southern Florida estuaries than in coastal meadows or northern bays, and in the present study was more

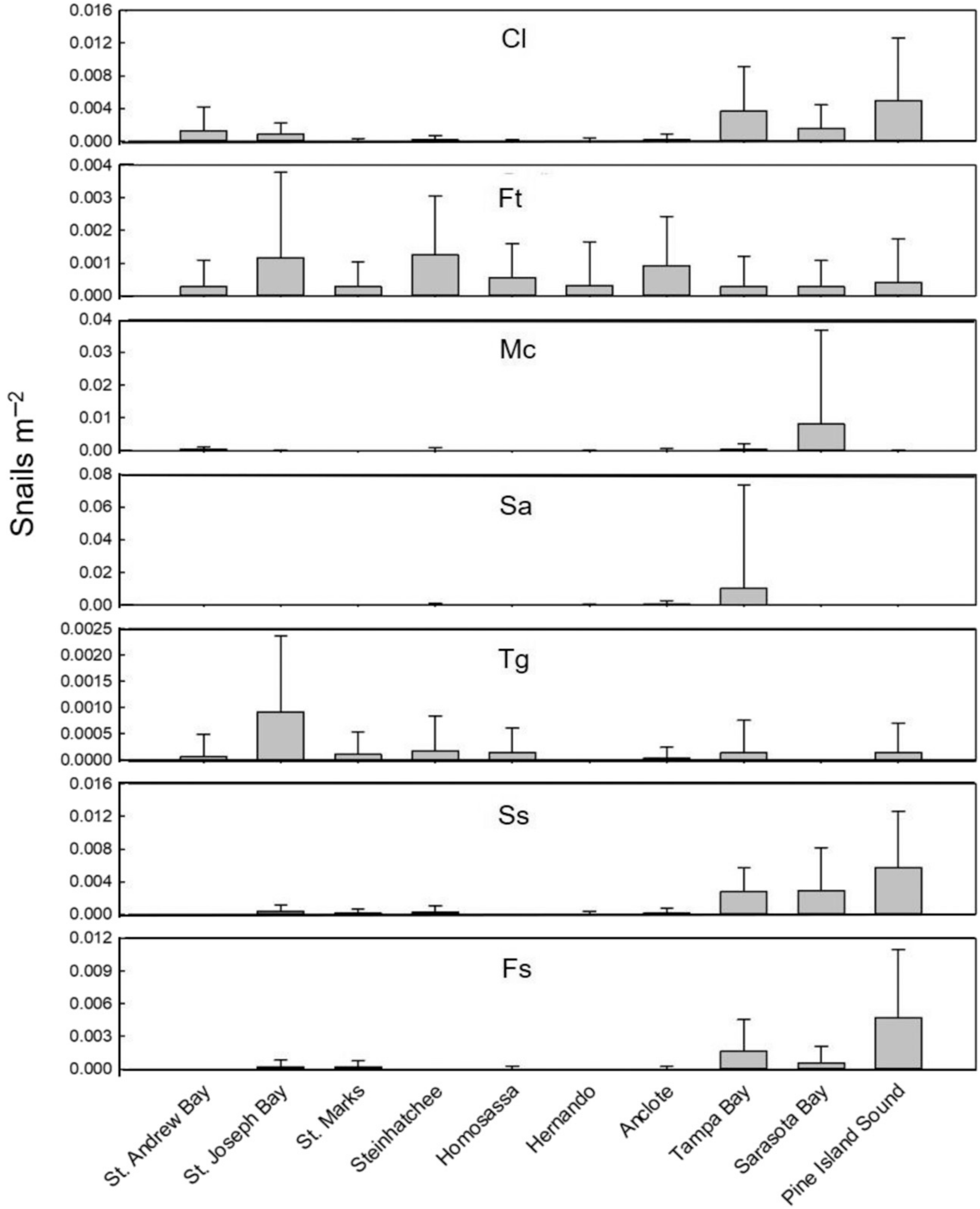

Figure 12. Individual densities (m^{-2}) of marine gastropod species observed in seagrass beds during 2015 to 2017 within multiple regions on the West Florida Shelf. Note that the *Y* axis differs with site. Species codes as in Table 1.

common on soft sediment or seagrass habitat than on oyster reefs. Individuals were typically observed with only the anterior tip exposed above the sediment, so the density has probably been underestimated. Mating individuals and deposited egg cases were observed in winter, and size at first detection was around 10 mm, which occurred in fall, approximately 7 mo later. The maximum size of *F. spirata* recorded in Tampa Bay was 118 mm SL, and if the monthly

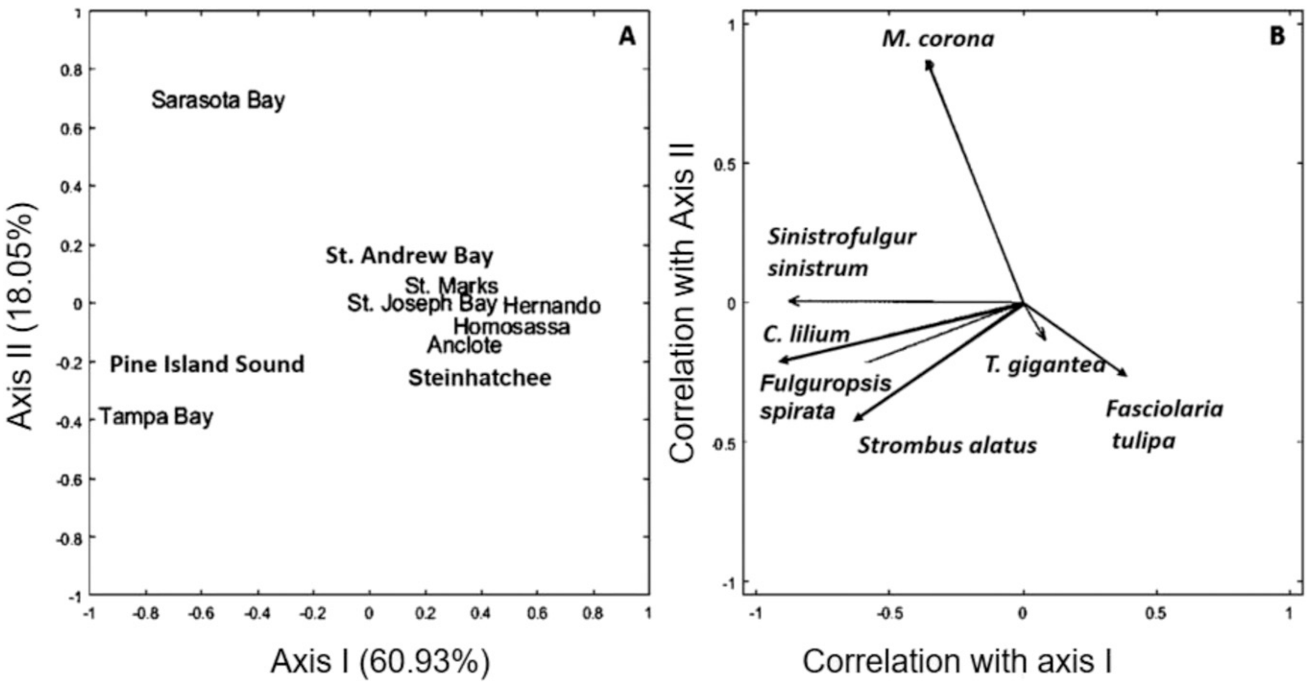

Figure 13. Principal coordinate plot (A) and species bi-plot vectors (B) representing the marine gastropod community structure within multiple sites on the West Florida Shelf, 2015 to 2017.

growth rates seen in juveniles remain consistent throughout life, then that individual was likely 9- to 10-y old. Additional studies could verify or refine this estimate. The combination of high fecundity (hundreds of offspring per mating), small maximum size, and a cryptic nature should make this species unlikely to suffer from high commercial or recreational fishery pressure. The range of *F. spirata* extends from North Carolina to the Yucatan Peninsula (Abbott 1974); therefore, there seems to be little risk of habitat decline.

Improved understanding of the distribution and life history of gastropods in Florida waters, as well as the commercial and, especially, the recreational and ornamental harvests, appears to be needed, because densities of most species at most Florida study sites are at least comparable to if not below densities considered to be overfished elsewhere. An early study in Florida waters found whelks in the family Buccinidae present at 0.04 m^{-2} (Menzel & Nichy 1958). Few gastropod studies have revisited sample sites decades later, but in 1977 to 1979, the 1958 study was replicated, and, based on declining mean size, absence of larger size classes, and densities of around 0.0016 m^{-2}, whelks were considered to be overharvested in Florida (Kent 1983). The density of whelks in Florida seagrass beds measured in the present study ranged from 0 to 0.0175 m^{-2} but was almost always less than 0.008 m^{-2}. The density of *Triplofusus gigantea* did not exceed 0.002 m^{-2}. An assemblage of large gastropods similar to those found in Florida (horse conch, lightning whelk, conch, and others) in a fishery considered to be overexploited off the Yucatan was present at about 0.001 m^{-2} (Pérez & Aranda 2000). In Georgia, the density of whelks native to that region was 0.02 m^{-2} in 1988, when the harvest exceeded 450,000 pounds of meat, but harvests there had collapsed by 2006 to less than 1% of that amount (Walker et al. 2008). This is not necessarily only a modern process, as gastropods are common items in Native American shell middens from 1,000 y ago or more (Marquardt & Kozuch 2016), so a true understanding of the virgin stock density is not possible.

A factor that should be considered by management when large gastropods are being removed from a local system is age at maturity. Reproductive traits vary among species, including the number and frequency of reproductive periods annually and the number and size of gametes produced (Aranda et al. 2003). Castagna and Kraeuter (1994) found that *Busycon carica* takes at least 9 y to reach sexual maturity and that the larger individuals were usually females. Schlerochronological studies have been widely applied to bivalve molluscs to determine the age, age at maturity, and growth rate (Hickson et al. 1999, Goodwin et al. 2001, Carré et al. 2005) but have not been widely applied to the aging of gastropods. If harvesters are removing larger animals, whether they are more desirable or are easier to find, and if the gastropods reproduce at levels that do not allow new recruits to the fishery to replace brood stock, then their removal will result in reduced stock levels (Wells 1989).

MANAGEMENT IMPLICATIONS

In the present study, the banded tulip *Cinctura lilium* was fairly common in Tampa Bay, suggesting that it should no longer be listed as an SGCN, but its somewhat limited geographic distribution and preference for habitats that are susceptible to fluctuations suggest that continued monitoring is warranted. The true tulip *Fasciolaria tulipa* was found at all sites but was most abundant in coastal seagrass meadows and uncommon in other habitats, especially in the upper estuary.

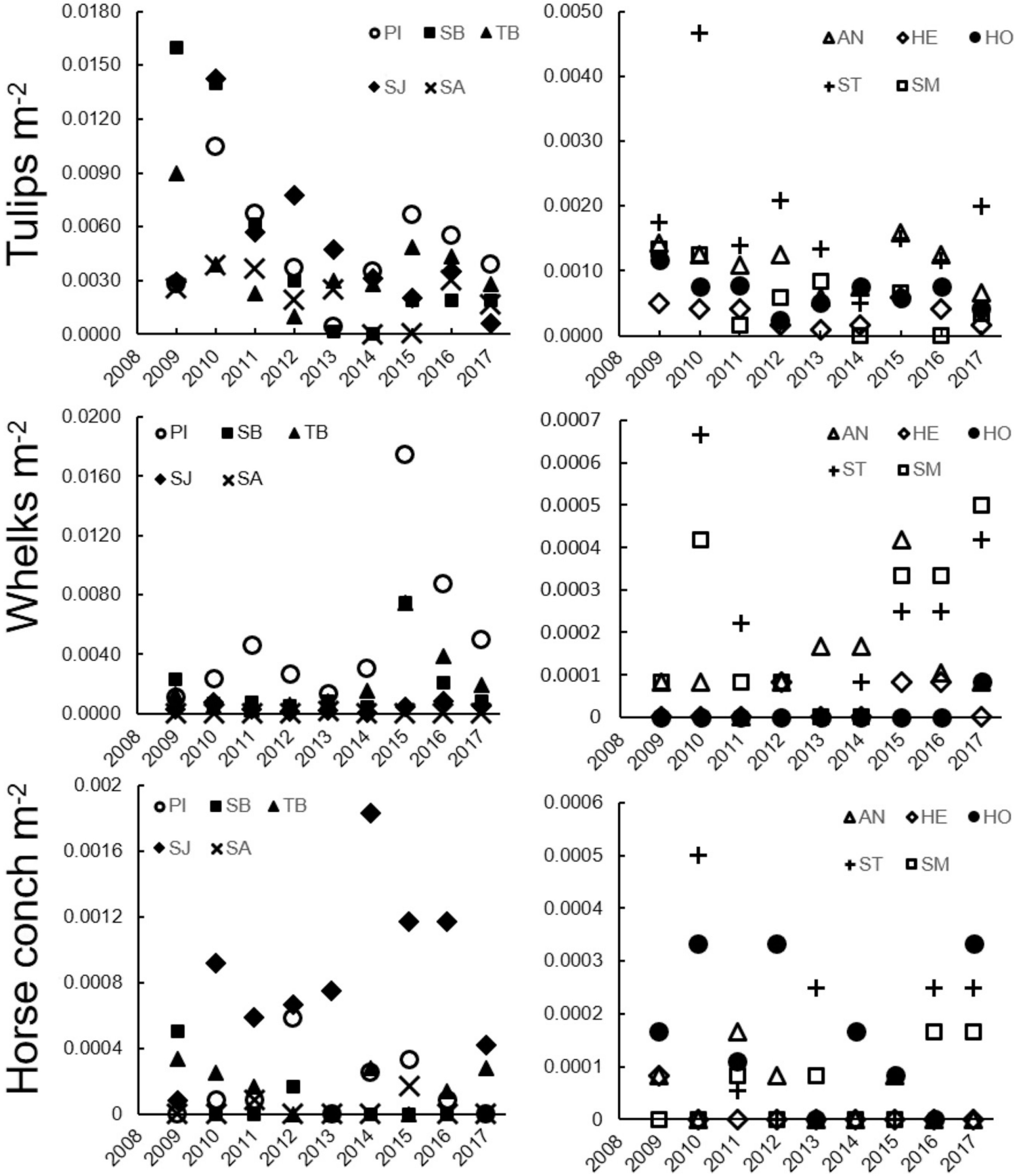

Figure 14. Densities (m^{-2}) of tulips (*Cinctura lilium* and *Fasciolaria tulipa*) (top), whelks (*Sinistrofulgur sinistrum* and *Fulguropsis spirata*) (middle), and *Triplofusus gigantea* (bottom) observed in seagrass beds during 2009 to 2017 within multiple regions on the West Florida Shelf at 10 sites: AN, Anclote; HE, Hernando; HO, Homosassa; PI, Pine Island Sound; SA, St. Andrew Bay; SB, Sarasota Bay; SJ, St. Joseph Bay; SM, St. Marks; ST, Steinhatchee; TB, Tampa Bay. Tulips and whelks were not identified to species in 2009 to 2014.

This greater geographic distribution suggests this species should not be an SGCN and that its removal from the 2019 SWAP (FWC 2019) was justified. Evaluation of the Fasciolariidae remains challenging because of fluid taxonomic classification, but continued studies would aid in future management options.

Three species have high fecundity and generalist habitat requirements that suggest little need for the SGCN listing.

TABLE 6.

***P* values of three-way PERMANOVA tests of densities of tulips (*Cinctura lilium* and *Fasciolaria tulipa*), whelks (*Sinistrofulgur sinistrum* and *Fulguropsis spirata*), and *Triplofusus gigantea* among sites (Site), stations (Sta), and years (Yr) on the West Florida Shelf, 2009 to 2017.**

Factor	Whelks	Tulips	*T. gigantea*
Site	**<0.001**	**<0.001**	**<0.001**
Yr	**<0.001**	**<0.001**	0.607
Sta	0.485	0.461	0.684
Site × Yr	**<0.001**	**<0.001**	**<0.001**
Site × Sta	**<0.001**	**<0.001**	**<0.001**
Yr × Sta	0.530	**<0.001**	0.615
Site × Sta × Yr	0.850	0.407	0.547

The fighting conch *Strombus alatus* was abundant in soft sediment in Tampa Bay and uncommon in other habitats. Its presence in coastal waters, geographic distribution from the Carolinas to Texas, growth to maturity within 2–3 y, high fecundity with the ability to disperse as pelagic larvae, and habitat preference (unstructured soft sediment is unlikely ever to be a limiting habitat) suggest that this species would be reasonably resilient to harvest. The lightning whelk *Sinistrofulgur sinistrum* was present at modest densities but in all habitats surveyed. It reaches an especially large size, suggestive of a life span that likely exceeds a decade. Its ability to spawn in multiple years and high fecundity would increase its resilience in local populations. The pear whelk *Fulguropsis spirata* was limited to southern bays. Although possibly slow growing, probable high fecundity and cryptic habitat suggest limited probability of overexploitation.

The density of the horse conch *Triplofusus gigantea* was low at all sites, but the species was present in almost all habitats, over a wide geographic distribution. It is estimated to be capable of living for a decade or more because of its large maximum size, with a high probability of multiple spawning events in its life and exceptionally high fecundity, both of which would add to its resiliency to overharvest. Its size and attractive shell, however, make it a visible target for commercial harvest and recreational take. This species should be given consideration as an SGCN and its commercial and recreational harvest be considered candidates for management.

The crown conch *Melongena corona* was strongly associated with oyster reefs. Although fairly abundant, its apparent reliance on this restricted habitat type—the oyster itself listed as an SGCN—places them at some risk. It warrants consideration for listing as an SGCN and for management.

For all species studied, accurate estimates of age at maturity and fecundity do not exist, and improved measures of growth would be important. Additional information on gastropod distribution in oyster reef and soft sediment habitat outside of Tampa Bay is needed before stock sizes can be estimated accurately. For most species, commercial harvest data are limited to marine-life landings, and essentially no data are available on the recreational harvest.

Densities of the two species capable of reaching the largest sizes (*Sinistrofulgur sinistrum* and *Triplofusus gigantea*) in Florida Gulf waters are comparable to those in other regions considered overfished and appear to have remained comparable to levels considered overfished in Florida waters almost four decades ago (Kent 1983). Additional studies are needed to monitor density and distribution, especially if commercial food, recreational, or other harvest is shown to increase for any of these species.

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