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YOUNG-OF-THE-YEAR STONE CRAB (GENUS *MENIPPE*) RECRUITMENT IN THE GULF OF MEXICO OFF FLORIDA: KEY SHALLOW-WATER HOTSPOTS

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ABSTRACT Knowledge of juvenile recruitment (defined here as the quantitative addition of early benthic life stages to a local population) is important for conserving heavily harvested species and their critical habitats. Stone crabs (genus *Menippe*) are commercially and ecologically important throughout the Gulf of Mexico nearshore waters off Florida, but very little is known about their recruitment. Using standard commercial stone crab traps, megalopal and postsettlement juvenile (collectively, young-of-the-year, "YOY") stone crabs were sampled at multiple spatial scales and for multiple stone crab generations to characterize geographical, seasonal, and interannual variation in their distribution and relative abundance (numbers collected on traps) in the Gulf of Mexico off peninsular Florida and north of the Florida Keys (the "Florida Gulf"). The influences of potentially relevant oceanographic and biological variables [temperature, salinity, benthic community on the traps (trap fouling community), depth, distance from shore] on YOY stone crabs were investigated at locations distributed throughout the study area. Trap fouling communities had never been analyzed in detail prior to this study; an importance index was developed to quantify the seasonality, commonality, and density of the fouling communities and organisms composing the communities. Continuous, long-term data from the Tampa Bay location allowed investigation of the effects of biological relationships [relative abundance of female *Menippe* carrying eggs (ovigerous), occurrences of red tide (*Karenia brevis*, a toxic dinoflagellate) blooms] and meteorological events [tropical cyclones, El Niño Southern Oscillation (ENSO) occurrences] on temporal patterns of variation in recruitment. High relative abundances of YOY stone crabs were collected off peninsular Florida from dense, complex benthic biota that grew on crab traps located off large, pristine estuaries in relatively turbid water less than 5 m deep, where salinity ranged 24–36 and water temperature averaged 29°C–32°C. Two major recruitment locations, stable through decades, consistently accounted for approximately 50% of the YOY stone crabs collected; two secondary recruitment locations similarly accounted for another 25%. Relative abundance of YOY stone crabs was highest nearshore at the major recruitment locations, particularly during years of high relative abundance. Approximately 65%–75% of the recruits were collected August to October; however, the timing of both peak relative abundance and lowest relative abundance shifted to later in the year as latitude decreased. Patterns of change among months in relative abundance differed among locations within years and among years within locations. Water temperature, salinity, and trap fouling community were the important determinants of temporal and spatial variation in YOY stone crab relative abundance; depth and distance from shore were also important in areas where they varied notably among stations within locations and across broader expanses of the study area. At Tampa Bay, a sharp increase in relative abundance of ovigerous females in spring was followed by a similarly sharp increase in YOY stone crab relative abundance (principally stage 3–5 crabs) 3 mo later; whereas a sharp decrease in ovigerous female relative abundance in autumn was followed by a similarly sharp decrease in YOY stone crab relative abundance 1 mo later. Coincidence of the normal autumnal decrease in YOY stone crab relative abundance with red tides and tropical cyclones prevented assigning clear relationships between seasonal change in relative abundance and these potential external influences. Annual decreases in relative abundance were significantly related to the occurrence of tropical cyclones that came near Tampa Bay during the previous year. Twice, confluences of multiple hurricanes, timely red tides, and ENSO events were followed by nearly complete, 1- to 2-y recruitment collapses. In contrast, a single meteorologically and oceanographically highly anomalous year coincided with exceptionally high abundances of both YOY and ovigerous female stone crabs. A relationship between YOY stone crabs and subsequent fishery harvest was not evident, possibly due to a variety of fishery practices. Because stone crabs are subjected to intense fishing pressure throughout the Florida Gulf, the YOY stone crab recruitment grounds and their associated estuaries should be protected from the effects of development, agriculture, aquaculture, and commercial and recreational crabbing.

KEY WORDS: abundance, depth, distance from shore, distribution, ENSO events, fishery, Florida, geographic variation, Gulf of Mexico, juveniles, megalopae, *Menippe*, ovigerous female crab, recruitment, red tide, salinity, seasonality, stone crab, Tampa Bay, temperature, trap fouling

INTRODUCTION

Understanding the recruitment patterns of mobile marine benthic invertebrates with pelagic larval dispersal is important because the distribution and abundance of early benthic life stages can greatly influence a species' population biology, structure, dynamics, and genetics. Moreover, identifying locations where individuals in early life stages are abundant is important because the abundance of those life stages can regulate a species' population size (Moksnes et al. 1998, Méndez Casariego et al. 2004) and greatly influence its population density (Eggleston & Armstrong 1995, Caley et al. 1996, Etherington & Eggleston 2003) and demography (Palma et al. 1999). Interannual variability in settlement can extend into the age 1+ juvenile age class and generate substantial interannual variation in density among year classes (Armstrong et al. 2003); with ramifications to local ecosystems and, in harvested species, to fisheries. Thus, understanding spatial and temporal variation in recruitment (defined here as the quantitative addition of early benthic life stages to a local population; modified from Caley et al. 1996; also see Gaillard et al. 2014) is essential for designing conservation strategies; setting the limits of marine reserves;

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and for harvested species, formulating fishery management plans (Wahle & Steneck 1991, Iles & Beverton 2000, Pineda 2000, Caputi et al. 2003, Maunder & Thorson 2019).

Settlement of pelagic larvae represents the integration and product of all processes affecting pelagic dispersal (Pineda 2000, Sale & Kritzer 2003). Seasonal, interannual, and geographic variation in settlement is common in marine decapod crustaceans, and the distribution and abundance of early life stages can be strongly influenced by these variables. Recruitment in most marine decapods is seasonal (e.g., Orth & van Montfrans 1987, Eggleston et al. 1998, Robinson & Tully 2000, Negreiros-Fransozo et al. 2002, Palma et al. 2006, Vinuesa et al. 2011), in accordance with seasonal variation in water temperature (henceforth, "temperature") and salinity. For example, blue crab (*Callinectes sapidus*) megalopae orient, move, and in combination with wind and tides, settle in response to seasonal temperature and salinity conditions (Forward 1989, 1990, Tankersley et al. 1995, Hasek & Rabalais 2001, Anger 2003, Bishop et al. 2010). Recruitment location is also strongly influenced by seasonal temperature and/or salinity conditions in fiddler crabs (*Uca* species; Godley & Brodie 2007), snow crabs (*Chionoecetes opilio*; Dionne et al. 2003), and American lobsters (*Homarus americanus*; Wahle et al. 2013). Winter temperature and salinity can be important for overwintering survivorship (blue crabs, Rome et al. 2005; Caribbean spiny lobsters, *Panulirus argus*, Field & Butler 1994) or recruitment (snow crabs; Marcello et al. 2012). Temperature and salinity can also influence crustacean recruitment on shorter or longer time scales. Weekly variation in settlement of several crab species has been positively correlated with temperature and negatively correlated with salinity conditions associated with specific oceanographic states (Wing et al. 1995). Interannual variation in Dungeness crab (*Megacarcinus magister*) recruitment is driven by the timing of shifts in ocean currents during spring (Shanks & Roegner 2007).

Highly structured habitats enhance the density, growth, and survival of juvenile invertebrates (Lefcheck et al. 2019). Geographic variation in settlement can be related to spatial differences in the type and complexity of substrate. Many decapod species preferentially settle on various types of complex substrates (Minello & Zimmerman 1983, Pile et al. 1996); in specific, usually structurally complex, habitats (Fernández 1999, Loher & Armstrong 2000, Armstrong et al. 2003, Rakocinski & McCall 2005, Amaral & Paula 2007, Tapella et al. 2009, Alberts-Hubatsch et al. 2014, Tapia-Lewin & Pardo 2014); or at specific, usually protected locations (Palma et al. 2006). As structural density and complexity increase, the number of individuals that can be supported increases; the probability of survival increases (Dittel et al. 1996; Orth & van Montfrans 2002, Grabowski 2004, Stoner 2009) because predation and cannibalism decrease (Jordan et al. 1996, Moksnes et al. 1998; Luppi et al. 2001, Stoner 2009, Stoner et al. 2010, Long et al. 2012, Bromilow & Lipcius 2017) and food sources can become more plentiful (Marx & Herrnkind 1985, Knights et al. 2012).

Other environmental features and biological dynamics can affect the location and magnitude of postlarval recruitment. For example, shallow water can provide a refuge from intraspecific and interspecific predation and competition. Juvenile decapods frequently inhabit shallow waters where adults of the same species are rare (Herrnkind & Butler 1986, Comeau et al. 1998, Nielsen et al. 2007, Wahle et al. 2013). Variation in abundance of spawning females can affect juvenile crab abundance, but formal investigation of that relationship is difficult because varying abiotic and biotic factors that influence the survival of both larvae and postsettlement (PS-)juveniles can erase any relationship between the two abundances (e.g., Carloni et al. 2018), especially in brachyurans with broadcast spawning (Wahle 2003). Detecting a relationship may take an exceptional set of circumstances.

Ecological disturbances, meteorological events, and oceanographic processes can directly or indirectly affect interannual variation in the level of recruitment in marine decapods (e.g., Incze et al. 1997, Spitzer et al. 2003, Weiss & Downs 2020). In the eastern Gulf of Mexico, and particularly off peninsular Florida and north of the Florida Keys, red tides are an important, toxic, biologically sourced ecological disturbance caused by the dinoflagellate *Karenia brevis*. Red tide blooms can vary in intensity; be localized to broadly regional; and become seriously damaging or lethal to numerous fish and invertebrate species (Simon & Dauer 1972, Tiffany & Heyl 1978, Flaherty & Landsberg 2011), including stone crabs (Gravinese et al. 2018, 2019, Gravinese 2020). Extreme prolonged blooms can cause massive fish and invertebrate kills that disrupt the entire ecosystems (Gannon et al. 2009, Dupont et al. 2010). Severe storms such as tropical cyclones (i.e., tropical storms and hurricanes) can notably alter the dispersal and recruitment patterns (Etherington & Eggleston 2000, Sale & Kritzer 2003, Eggleston et al. 2010) and deplete larval pools (McConnaughey et al. 1992, 1994); but their effects can vary depending on the direction of approach and strength of the storm (Eggleston et al. 2010). Storms can distribute megalopae more broadly than they are typically distributed (Eggleston et al. 2010) but freshwater intrusion may cause mass mortality of megalopae delivered by storm-driven transport (Ariyama & Secor 2010). Early-stage juvenile abundance can also remain high immediately after a storm (Pile et al. 1996). In the longer term, variation in settlement strength can be positively correlated with interannual variation in storm-driven currents; and settlement pulses can co-occur with regional high-pressure systems or tropical cyclones (Mense et al. 1995, Morgan et al. 1996, Flores et al. 2002, Sheehy & Bannister 2002, Eggleston et al. 2010, Ogburn & Hall 2012). Broad-scale interannual variation in abundance can also depend on species-specific responses to El Niño Southern Oscillation (ENSO) events, which can alter biological productivity and larval transport (Botsford 2001).

Stone crabs inhabiting Gulf of Mexico waters (*Menippe mercenaria*, *Menippe adina*, and their hybrids) are physically strong (Melnick et al. 1996, Schenk & Wainwright 2001, Aronhime & Brown 2009), long-lived (approximately 8 y; Gerhart & Bert 2008), aggressive (Sinclair 1977), territorial, high-trophic-level, cannibalistic carnivores (Bert et al. 1978, Bert 1986) that support a substantial fishery in Gulf of Mexico waters off Florida (the "Florida Gulf") (Muller et al. 2011). The two species are morphologically and genetically distinct, and in the Gulf of Mexico, hybridize off northwestern Florida (Bert 1986, Bert & Harrison 1988). Both species typically have five planktonic zoeal stages followed by a megalopal stage that settles to the benthic environment and metamorphoses to the first crab stage (Porter 1960, Nates & McKenny 2000). Presently, information on the distribution, abundance, and seasonality of young-of-the-year (YOY) stone crabs [defined herein as megalopae and PS-juveniles with carapace widths (CWs) ≤20 mm] in the Florida Gulf is based on localized, short-term, or laboratory-based studies and on anecdotal observations (Menzel & Nichy 1958, Tabb & Manning 1961, Bender 1971, Bert et al. 1986, Wilber & Herrnkind 1986, Field 1989, Lindberg & Stanton 1989, Brown et al. 1992, Brown & Bert 1993, Munguia 2006). None of these sources provide a regional or long-term perspective on YOY stone crab recruitment patterns or dynamics; and little is known about the influence of habitat; seasonal temperature and salinity; depth; or potentially relevant biological, ecological, meteorological, or oceanographic events on recruitment. Only the recent studies of Gravinese and colleagues (cited earlier) demonstrated the effects of red tide on early-life-stage stone crabs. Moreover, the possibility of a relationship between commercial fishery landings and abundance of YOY stone crabs has not yet been investigated.

To examine the temporal and spatial variation in YOY stone crab recruitment in the Florida Gulf, the influence of some abiotic and biotic factors on that recruitment variation, and the relevance of recruitment to the Florida stone crab fishery, the data from five separate sampling programs, conducted in Everglades National Park (ENP; 1979 to 1980), Northwest Florida (1986 to 1987 and 2005 to 2009), Tampa Bay (TB; 1989 to 2010), and Southwest Florida (2006 to 2009) (Table 1) by T.M. Bert and colleagues, are integrated. Collectively, the studies span the Florida Gulf from the waters off St. Marks to near Key West (Fig. 1) and comprise a broad range of sampling locations with multiple stations within each location and multiple sites within each station. The seasonal and interannual patterns of YOY stone crab geographical distribution and relative abundance (defined as the mean number of individuals collected from standard commercial stone crab traps per defined time period) are described at multiple spatial scales ranging from 1.2 km to approximately 925 km, and across timescales of up to 31 y (i.e., 7–10 stone crab generations; Gerhart & Bert 2008). Then, abiotic and biotic variables (temperature, salinity, the benthic community colonizing traps, depth, distance from shore, variation in relative abundance of spawning females, presence and location of red tide blooms, tropical cyclones, ENSO events) are examined to ascertain their influence on the patterns of variation in YOY stone crab relative abundance.

Such hierarchical, large-scale studies of recruitment in marine species with pelagic larvae can provide a more complete understanding of recruitment patterns and dynamics than small-scale or short-term studies (Gaines & Bertness 1992, Etherington & Eggleston 2000). They can enable identification of source areas that contribute to the distribution and abundance of larger individuals and can reveal information ranging from the environmental preferences of recruits to the influences of biological, ecological, and physical events on determining the locations of recruitment grounds (Palma et al. 1999). The spatial and temporal patterns of recruitment described here also constitute important information on the life history of stone crabs in regions where they are heavily harvested. Knowledge of recruitment areas can be instrumental for conserving species and their critical habitats (Beck et al. 2001), particularly those species subject to intense fishing pressure (Sale & Kritzer 2003). Lastly, this study complements recent studies on stone crab female reproduction based on data collected from the same stations and over the same time frame in Tampa Bay (Gerhart & Bert 2008, Bert et al. 2016a, 2016b).

MATERIALS AND METHODS

Field Sampling

Figure 1 shows the positions of all study regions, subregions, locations, stations, and landmarks mentioned in the text; and Table 1 provides the geographical positions and physical characteristics of the sampling stations, the sampling periods and effort, and the annual relative abundances of YOY stone crabs. In the recent Northwest and Southwest Florida studies, sampling was initiated at some locations prior to the first sampling date reported in Table 1. The dates selected for inclusion of data in the various studies were chosen to maximize the amount of data comparable for statistical analyses. The Northwest Florida stations sampled during 2006 to 2009 were the same as those sampled during 1986 to 1987. The data from ENP were previously analyzed (Bert 1985, Bert et al. 1986), but the analyses presented here are more complex and the data are analyzed in the context of the larger framework. In all studies, the traps were deployed at least 1 mo prior to the initial sampling to allow settlement of benthic biota on the traps, which, in turn, attracts all sizes of stone crabs.

In all studies, sampling for YOY stone crabs was conducted in the same manner using the same style of commercial stone crab traps (described in Bert et al. 2016a). At each station, five traps were arrayed linearly approximately 100 m apart. Latitude and longitude coordinates where traplines were located are presented in Table 1; and how the traplines were oriented are described in Appendix 1 and shown in Figure 1. In all studies except the 1979 to 1980 ENP study, the traps were serviced approximately every 2 wk and cleaned of fouling material (sessile benthic biota and mud attached to the traps) during alternate sampling trips (i.e., approximately every 4 wk) by scraping the external surfaces, spaces between the trap slats, and trap throat (opening for entry of the crabs) using hand axes. The material scraped from each trap accumulated on the boat deck and was searched for YOY stone crabs, which hide in the crevices created by the fouling organisms and material on the trap. Dislodging the matter from the trap broke up the fouling organisms and debris, exposing the YOY stone crabs. When no additional individuals were found after approximately 1 min of searching, the search was terminated. During the ENP study, the traps were serviced every 4 weeks and YOY stone crabs were collected during each servicing. During the 1986 to 1987 Northwest Florida study, the traps were serviced every 2 weeks, but YOY stone crabs were collected only every other month.

After servicing each trap, the number of YOY stone crabs collected was recorded; then the boat deck was cleaned of all fouling matter. All individuals collected from each station were placed together in approximately 500 mL of seawater in a Nalgene bottle labeled with the station identifier and stored on ice. Missing traps were replaced, and damaged traps were repaired or replaced. In the ENP study and early years of the Tampa Bay study, traps were repositioned at the same sampling sites using triangulation; Loran or Global Positioning System units were used in later studies. The bottles containing the

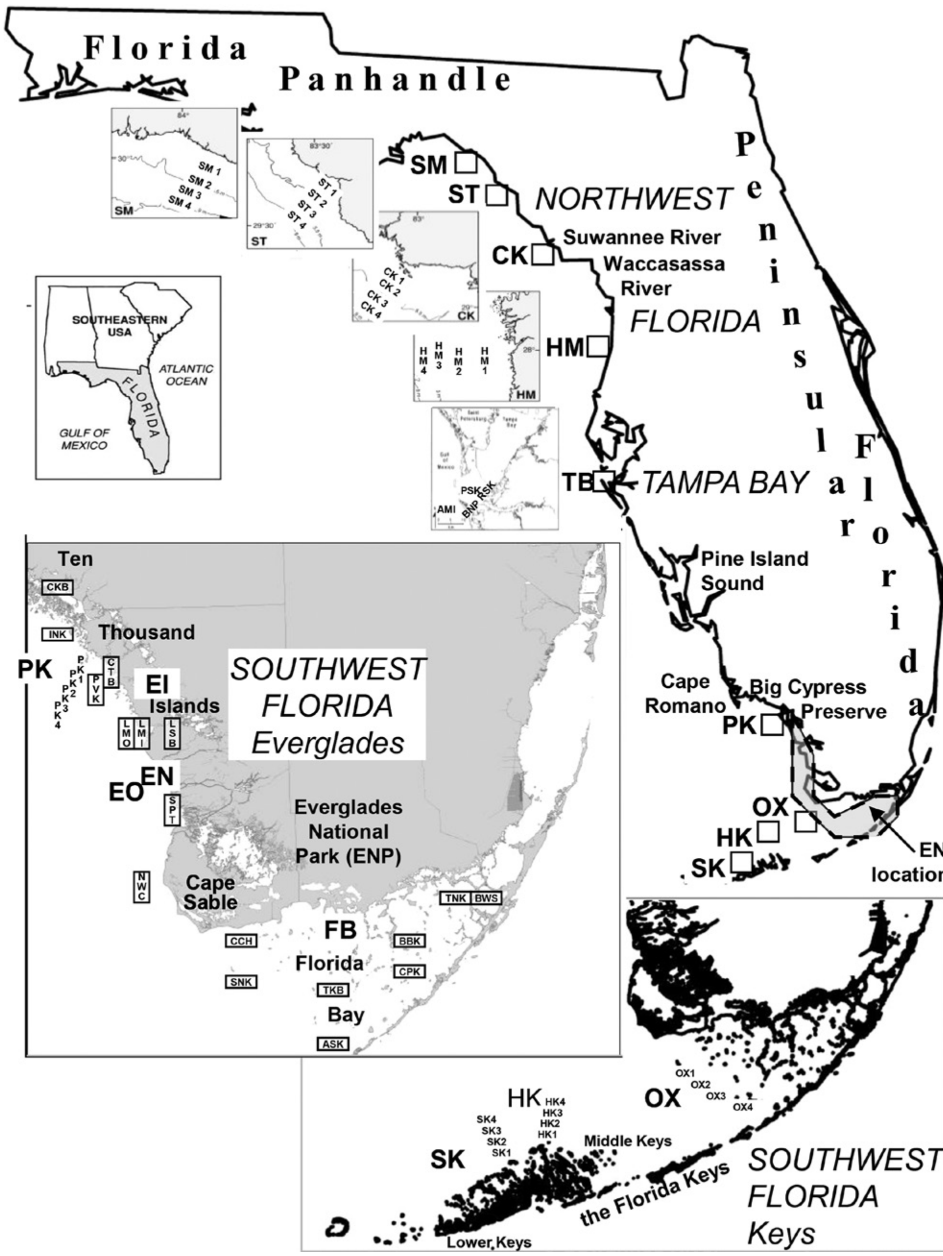

Figure 1. Sampling sites for young-of-the-year (YOY) stone crabs (genus *Menippe*). Insets: Location of Florida in the southeastern United States; positions of stations (three-character abbreviations, small print, capitalized) within locations (two-letter abbreviations, capitalized), subregions (Southwest Florida only, Everglades and Keys), and regions (large print, capitalized, italicized). All TB stations were in lower Tampa Bay. In the Everglades subdivision, stations within Everglades National Park are boxed. Other locations mentioned in the text appear in capital and lower cased letters. Abbreviations are defined in Table 1.

YOY stone crabs were kept on ice or refrigerated until measuring of the PS-juveniles (mm CW) was possible (almost always within 24 h). Megalopae were not measured and were counted separately in early studies; however, in counts performed in some recent studies, megalopae were not distinguished from PS-juveniles. Therefore, both megalopae and PS-juveniles constitute YOY stone crabs in this report.

The traps were colonized by fouling material and organisms usually within 1 mo. Because YOY stone crabs hide among benthic fouling organisms in nature and on traps, the degree of fouling (complexity, extent of coverage, and the size of benthic organisms) on the traps and the three predominating "foulers" (which included benthic organisms and mud) were recorded. The predominant foulers were qualitatively classified as "principal," "secondary," or "tertiary," according to the relative amount of trap surface area covered. At each station, bottom salinity and temperature were taken either with a Niskin bottle, refractometer, and thermometer or with a YSI instrument package. Water visibility ("visibility") was estimated monthly or seasonally by recording the depth at which a Secchi disk or Niskin bottle was visible from the boat or by visual observation from the boat when clarity was sufficient to see the sea floor. Depth was estimated by lowering a marked, weighted rope to the bottom (early studies) or by fathometer.

TABLE 1.

Physical characteristics of sampling stations and relative abundance of YOY stone crabs (genus *Menippe*) in the Gulf of Mexico offshore of peninsular Florida.

	Coordinates*			Temperature range (°C)		Salinity					Number, traps sampled		Number, YOY stone crabs per trap per year	
	Latitude	Longitude	Sampling period†	T. min. (month)	T. max. (month)	S. avg.	S. min. (month)	S. max. (month)	Mean depth (m)	Dist. off. (km)	Total	(Range, number per year)	Mean % *of total*‡	(Range)
NORTHWEST FLORIDA														
SM			11/86 – 10/87								117		0.6	
			3/06 – 2/09								676	(53–60)	0.7 *2.8%*	
SM1	20° 50.0′N	83° 53.7′W	11/86 – 10/87	10 (Jan) –	31 (Jul)	26	**19 (Feb) –**	30 (Sep)	2.3	8.3	29		1.5	
			3/06 – 2/09	8 (Jan) –	31 (Aug)	31	27 (Apr) –	**36 (Sep,** Nov)			168	(53–60)	1.6	(1.4–1.8)
SM2	29° 53.0′ N	83° 53.5′W	11/86 – 10/87	11 (Jan) –	31 (Jul)	28	24 (Feb) –	32 (Dec)	4.3	13.3	30		0.7	
			3/06 – 2/09	11 (Jan) –	30 (Aug)	34	31 (Sep) –	**38 (Jan)**			170	(55–60)	0.6	(0.3–0.9)
SM3	29° 49.9′ N	83° 55.2′ W	11/86 – 10/87	11 (Jan) –	31 (Jul)	30	26 (Feb) –	35 (Dec)	7.1	19.8	29		0.3	
			3/06 – 2/09	11 (Jan) –	31 (Jul-Aug)	35	30 (Dec) –	**38 (Aug, Nov)**			168	(54–59)	0.5	(0.3–0.9)
SM4	29° 46.9′ N	83° 56.6′ W	11/86 – 10/87	11 (Jan) –	30 (Jul- Aug)	30	27 (May) –	33 (Dec)	8.3	26.1	29		>0.0	
			3/06 – 2/09	11 (Jan) –	31 (Aug)	35	33 (Sep) –	**38 (Apr)**			170	(55–60)	0.1	(0.0–0.1)
ST			11/86 – 10/87								13.3		0.8	
			3/06 – 2/09									(52–65)	2.8 *11.1%*	
ST1	29° 35.6′ N	83° 27.0′ W	11/86 – 10/87	11 (Jan) –	30 Aug)	28	24 (Mar, May)-	**36 (Nov)**	5.1	4.1	49		1.5	
			3/06 – 2/09	10 (Jan) –	31 (Jul-Aug)	33	26 (Aug) –	**37 (Nov)**			172	(53–64)	2.6‡‡	(2.1–3.0)
ST2	29° 36.1′ N	83° 28.3′ W	11/86 – 10/87	12 (Jan) –	30 (Aug)	28	**21 (Dec) –**	32 (Nov)	5.3	5.9	48		0.8	
			3/06 – 2/09	10 (Jan) –	31 (Jul-Aug)	33	28 (Aug) –	**37 (Nov)**			171	(52–65)	3.5‡‡	(2.3–5.6)
ST3	29° 35.5′ N	83° 30.3′ W	11/86 – 10/87	12 (Jan) –	30 (Jul- Aug)	28	24 (May) –	32 (Oct)	5.3	9.3	41		0.8	
			3/06 – 2/09	11 (Jan) –	31 (Jul-Aug)	33	29 (Aug) –	**37 (Nov)**			175	(55–65)	2.9‡‡	(1.8–3.8)
ST4	29° 35.0′ N	83° 31.9′ W	11/86 – 10/87	12 (Jan) –	30 (Aug)	29	24 (May) –	32 (Nov)	5.8	12.0	48		0.3	
			3/06 – 2/09	11 (Jan) –	31 (Aug)	34	31 (Aug) –	**38 (Nov)**			172	(52–65)	2.3‡‡	(1.6–3.0)
CK§			11/86 – 10/87								122		7.0	
			3/06 – 2/09								704	(52–65)	4.2 *16.7%*	
CK1	29° 05.1′ N	83° 06.3′ W	11/86 – 10/87	12 (Dec) –	29 Jun-Sep)	27	26 (May) –	31 (Oct)	3.0	3.5	25		13.8	
			3/06 – 2/09	12 (Dec) –	31 (Aug)	29	19 (Dec) –	36 (Jul, Sep)			174	(55–62)	10.0	(5.6–13.9)
CK2	29° 03.6′ N	83° 07.8′ W	11/86 – 10/87	13 (Jan-Feb) –	30 (Jul-Aug)	28	26 (May) –	32 (Oct)	6.2	7.0	30		8.7	
			3/06 – 2/09	12 (Jan) –	31 (Aug)	34	30 (Oct) –	**38 (Sep)**			175	(53–65)	4.6‡‡	(2.7–7.1)
CK3	29° 02.6′ N	83° 09.4′ W	11/86 – 10/87	13 (Jan-Feb) –	30 (Jul-Aug)	29	27 (May-Aug) –	31 (Feb, Oct)	6.7	10.2	34		4.4	
			3/06 – 2/09	12 (Jan) –	31 (Jul-Aug)	34	30 (Mar) –	**37 (Jul)**			175	(52–65)	1.9‡‡	(1.1–3.5)
CK4	29° 01.4′ N	83° 10.5′ W	11/86 – 10/87	14 (Jan-Feb) –	30 (Jul-Sep)	30	27 (May) –	32 (Feb, Oct)	6.9	13.0	33		1.0	
			3/06 – 2/09	12 (Jan) –	31 (Jul-Aug)	34	31 (Mar) –	**38 (Jul, Sep)**			180	(55–65)	0.3‡‡	(0.0–0.7)

(*Continued*)

TABLE 1. (CONTINUED)

	Coordinates*			Temperature range (°C)		Salinity					Number, traps sampled		Number, YOY stone crabs per trap per year	
	Latitude	Longitude	Sampling period†	T. min. (month)	T. max. (month)	S. avg.	S. min. (month)	S. max. (month)	Mean depth (m)	Dist. off. (km)	Total	(Range, number per year)	Mean % *of total*‡	(Range)
HM			11/86 – 10/87								148		0.6	
			3/06 – 2/09								609	(41–63)	0.1 *0.4%*	
HM1	28° 35.5′ N	82° 45.1′ W	11/86 – 10/87	13 (Jan) –	30 (Jul-Aug)	27	**21 (Apr) –**	34 (Oct)	3.0	7.8	35		0.9	
			3/06 – 2/09	14 (Jan-Feb) –	32 (Jul)	34	29 (Sep) –	**37 (Nov)**			148	(41–62)	0.1‡‡	(0.0–0.1)
HM2	28° 35.5′ N	82° 52.1′ W	11/86 – 10/87	13 (Jan) –	30 (Aug)	28	**23 (Apr) –**	34 (Oct)	3.5	17.0	33		0.6	
			3/06 – 2/09	14 (Jan-Feb) –	32 (Jul)	34	30 (May, Sep) –	**38 (May)**			150	(45–60)	0.1‡‡	(0.0–0.1)
HM3	28° 35.2′ N	82° 55.7′ W	11/86 – 10/87	14 (Jan-Feb) –	30 (Jul-Aug)	30	25 (Apr-Jun) –	34 (Jan, Oct)	3.7	23.3	40		0.6	
			3/06 – 2/09	14 (Feb) –	32 (Jul-Aug)	34	31 (May) –	**39 (May)**			156	(45–63)	0.2‡‡	(0.0–0.3)
HM4	28° 35.0′ N	82° 57.2′ W	11/86 – 10/87	13 (Jan) –	30 (Jul-Aug)	30	26 (Jun) –	34 (Oct)	7.6	25.9	40		0.4	
			3/06 – 2/09	14 (Jan-Feb) –	32 (Jul-Aug)	35	31 (May) –	**39 (May)**			155	(45–61)	0.2‡‡	(0.1–0.2)
TAMPA BAY														
TB¶			3/89 – 11/10								4,820	(51–65)	5.6 *22.2%*	
AMI	27° 30.7′ N	82° 45.7′ W	3/89 – 11/10	11 (Jan) –	**33 (Jul-Aug)**	33	27 (Dec) –	**39 (Dec)**	7.2	2.8	1,177	(45–65)	2.9	(0.1–8.5)
BNP	27° 33.0′ N	82° 42.4′ W	3/89 – 11/10	11 (Jan) –	**34 (Aug)**	33	28 (Apr, Dec)-	**38 (Jul)**	3.0	1.5	1,213	(53–65)	8.0	(0.7–16.6)
PSK)	27° 33.6′ N	82° 43.6′ W	3/89 – 11/10	11 (Jan) –	**37 (Aug)**	33	**22 (Nov) –**	**38 (Jul)**	4.6	2.0	1,191	(51–67)	6.1	(0.5–10.8)
RSK	27° 33.8′ N	82° 38.8′ W	3/89 – 11/10	13 (Jan) –	**34 (Aug)**	33	27 (Apr, Aug) –	37 (Jul)	2.3	1.9	1,239	(54–68)	5.5	(0.8–11.9)
SOUTHWEST FLORIDA, Everglades‖														
EI			7/79 – 6/80								120		0.1 *0.4%*	
CKB	25° 51.2′ N	81° 24.6′ W	7/79 – 6/80	18 (Jan) –	32 (Jun-Aug)	26	**18 (Nov) –**	34 (Jun)	0.7	0.4	57		0.1	
LSB	25° 34 1′ N	81° 09.2′ W	7/79 – 6/80	18 (Dec-Jan) –	**33 (Aug)**	**11**	**2 (Dec) –**	22 (May)	1.0	0.5	63		0.0	
EN			7/79 – 6/80								146		1.0 *4.0%*	
CTB)	25° 40.4′ N	81° 18.3′ W	11/79 – 6/80	18 (Jan) –	**34 (Jun)**	25	**19 (Nov) –**	35 (Jun)	2.0	1.9	42		1.9	
LMI	25° 32.1′ N	81° 13.5′ W	7/79 – 6/80	17 (Jan) –	**34 (Jun-Aug)**	24	**17 (Jan) –**	33 (May)	1.7	1.9	64		0.4	
SPT	25° 23.3′ N	81° 10.4′ W	11/79 – 6/80	18 (Dec) –	31 (Jun)	**20**	26 (Mar) –	**36 (May)**	1.2	2.0	40		0.6	
EO‖,**			7/79 – 6/80							987	103		6.0	
			3/05 – 2/09									7.2 *28.6%*		
INK	25° 48.1′ N	81° 27.5′ W	11/79 – 6/80	18 (Dec) –	**33 (Jun)**	29	**20 (Nov) –**	35 (Jun)	1.2	3.3	45		7.0	
PVK	25° 41.1′ N	81° 20.5′ W	7/79 – 6/80	18 (Dec-Jan) –	**34 (Jun-Aug)**	30	26 (Nov) –	34 (Jun)	3.0	3.7	58		8.6	
PK1	25° 40.9′ N	81° 21.5′ W	3/05 – 2/09	14 (Jan) –	31 (Jul-Aug)	35	26 (Aug) –	**38 (Jun)**	2.6	4.8	249	(60–65)	11.3	(4.8–19.2)
PK2	25° 39.7′ N	81° 23.1′ W	3/05 – 2/09	14 (Jan) –	31 (Jul-Aug)	35	27 (Aug) –	**39 (Apr)**	4.9	8.9	250	(60–65)	6.1	(3.7–7.9)
PK3	25° 38.3′ N	81° 25.4′ W	3/05 – 2/09	16 (Jan-Feb) –	31 (Jul-Aug)	**36**	30 (Aug) –	**39 (Apr)**	5.5	13.5	242	(55–65)	6.7	(4.7–8.3)
PK4	25° 36.9′ N	81° 28.4′ W	3/05 – 2/09	16 (Jan-Feb) –	30 (Aug)	**37**	31 (Jul, Aug) –	**39 (Mar, Apr)**	6.3	19.1	246	(56–66)	4.5	(3.0–6.8)
LMO	25° 31.3′ N	81° 15.0′ W	7/79 – 6/80	18 (Dec) –	31(May-Aug)	31	**20 (Sep) –**	34 (May-Oct)	2.0	4.6	63		7.6	
NWC	25° 13.3′ N	81° 12.3′ W	7/79 – 6/80	18 (Dec) –	31 (Aug)	33	28 (Dec) –	**38 (Sep)**	3.5	3.3	62		0.8	
FB¶¶			7/79 – 6/80								482		0.0 *0.0%*	
BWS	25° 10.3′ N	80° 26.0′ W	7/79 – 6/80	17 (Jan) –	29 (May-Oct)	33	29 (Jan) –	**38 (Aug)**	2.0	1.8	63		0.0	
BBK	25° 07.5′ N	80° 33.2′ W	7/79 – 6/80	15 (Jan) –	31 (Oct)	32	26 (Dec) –	**42 (Jun)**	1.5	1.7	65		0.0	

(*Continued*)

TABLE 1. (CONTINUED)

	Coordinates*			Temperature range (°C)	Salinity					Number, traps sampled		Number, YOY stone crabs per trap per year	
	Latitude	Longitude	Sampling period†	T. min. (month) – T. max. (month)	S. avg.	S. min. (month) – S. max. (month)	Mean depth (m)	Dist. off. (km)	Total	(Range, number per year)	Mean % of total‡	(Range)
TNK	25° 10.3′ N	80° 30.2′ W	7/79 – 6/80	17 (Jan) – **32 (May-Oct)**	**36**	30 (Jan) – **45 (Mar)**	1.2	1.7	64		0.0	
CPK)	25° 04.4′ N	80° 32.4′ W	7/79 – 6/80	16 (Jan) – 31(May-Aug)	35	26 (Nov) – **42 (Jun)**	1.2	2.0	64		0.0	
TKB	25° 00.3′ N	80° 42.2′ W	7/79 – 6/80	14 (Jan-Feb) – 31(May-Jun)	35	32 (Jan) – **39 (Jun)**	2.3	2.2	53		0.0	
CCH	25° 06.6′ N	81° 00.5′ W	7/79 – 6/80	19(Dec) – 31 (Aug)	35	31 (Dec) – **40 (Jun)**	3.0	1.7	64		0.1	
SKC	25° 01.1′ N	81° 00.4′ W	7/79 – 6/80	19 (Dec-Feb)- 32 (Aug)	35	32 (Jan) – **38 (Jun)**	3.5	0.5	64		0.0	
ASK	24° 53.4′ N	80° 49.6′ W	11/79 – 6/80	14 (Jan) – 31 (May-Oct)	34	33 (Jan) – **37 (Jun)**	2.3	2.2	45		0.0	
SOUTHWEST FLORIDA, Keys††												
OX			3/06 – 2/09						629		1.1 *4.4%*	
OX1	24° 59.1′ N	81° 00.7′ W	3/06 – 2/09	18 (Feb) – 31 (Aug)	**36**	32 (Jan) – **42 (39 + Apr-Oct)**	3.3	9.8	164	(53–56)	2.1	(1.1–3.5)
OX2	24° 57.6′ N	80° 59.2′ W	3/06 – 2/09	18 (Feb) – 31 (Jul-Aug)	**37**	33 (Jan) – **43 (39 + Mar-Aug)**	3.3	9.6	159	(50–55)	1.0	(0.5–1.6)
OX3	24° 56.3′ N	80° 57.9′ W	3/06 – 2/09	18 (Feb) – 31 (Jul-Aug)	**37**	32 (Jan) – **44 (39 + Mar-Aug)**	4.0	10.7	161	(52–55)	0.7	(0.4–0.8)
OX4	24° 54.9′ N	80° 56.6′ W	3/06 – 2/09	18 (Feb) – 31 (Jul-Aug)	**37**	32 (Jan) – **44 (39 + Mar-Aug)**	3.3	10.9	145	(47–50)	0.4	(0.2–0.7)
HK			3/05 – 2/09						948		1.0 *4.0%*	
HK1	24° 53.3′ N	81° 27.2′ W	3/05 – 2/09	18 (Feb) – 32 (Aug)	**37**	34 (Jul, Nov) – **39 (Mar)**	8.0	4.7	240	(60)	1.1	(0.8–1.5)
HK2	24° 54.8′ N	81° 26.3′ W	3/05 – 2/09	18 (Feb) – 32 (Aug)	**37**	34 (Jul, Aug) – **39 (Mar)**	7.7	4.7	237	(55–61)	0.9	(0.4–1.5)
HK3	24° 55.9′ N	81° 24.5′ W	3/05 – 2/09	18 (Feb) – 32 (Aug)	**37**	33 (Aug) – **39 (Mar, Apr)**	7.3	4.8	235	(56–60)	0.9	(0.4–1.6)
HK4	24° 56.6′ N	81° 22.4′ W	3/05 – 2/09	19 (Feb) – 32 (Aug)	**36**	32 (Aug) – **39 (Mar, Apr)**	6.7	5.2	236	(56–61)	0.9	(0.4–1.2)
SK			3/05 – 2/09						933		1.4 *5.6%*	
SK1	24° 46.2′ N	81° 36.1′ W	3/05 – 2/09	19 (Feb) – 31 (Jul-Aug)	**37**	33 (Jul) – **39 (Mar)**	7.3	1.1	239	(55–64)	1.5	(1.0–2.2)
SK2	24° 47.0′ N	81° 36.7′ W	3/05 – 2/09	18 (Feb) – 31 (Jul-Sep)	**37**	33 (Jul) – **39 (Mar)**	8.3	3.1	233	(55–60)	1.1	(0.8–1.5)
SK3	24° 47.9′ N	81° 38.3′ W	3/05 – 2/09	18 (Feb) – 31 (Jul-Sep)	**37**	33 (Jul) – **39 (Apr)**	10.3	5.6	232	(55–60)	1.6	(0.8–2.6)
SK4	24° 48.7′ N	81° 39.9′ W	3/05 – 2/09	18 (Feb) – 32 (Aug)	**37**	31 (Sep) – **39 (Apr)**	12.5	8.3	229	(55–60)	1.5	(1.0–2.3)

AMI, Anna Maria Island; ASK, Arsenicker Keys; BBK, Black Betsy Keys; BNP, Bean Point; BWS, Blackwater Sound; CCH, Conchie Channel; CK, Cedar Key; CK1, Cedar Key 1; CK2, Cedar Key 2; CK3, Cedar Key 3; CK4, Cedar Key 4; CPK, Captain Key; CKB, Chokoloskee Bay; CTB, Chatham Bend; EI, Everglades Inshore; EN, Everglades Nearshore; EO, Everglades Offshore; FB, Florida Bay; HK, Harbor Keys; HK1, Harbor Keys 1; HK2, Harbor Keys 2; HK3, Harbor Keys 3; HK4, Harbor Keys 4; HM, Homosassa; HM1, Homosassa 1; HM2, Homosassa 2; HM3, Homosassa 3; HM4, Homosassa 4; INK, Indian Key; LMI, Lostman's River, Inshore; LMO, Lostman's River, Out.; LSB, Lostman's River, Second Bay; NWC, Northwest Cape; OX, Oxfoot Bank; OX1, Oxfoot Bank 1; OX2, Oxfoot Bank 2; OX3, Oxfoot Bank 3; OX4, Oxfoot Bank 4; PSK, Passage Key; PVK, Pavilion Key; PK1, Pavilion Key 1; PK2, Pavilion Key 2; PK3, Pavilion Key 3; PK4, Pavilion Key 4; RSK, Rattlesnake Key; SK, Sawyer Keys; SK1, Sawyer Keys 1; SK2, Sawyer Keys 2; SK3, Sawyer Keys 3; SK4, Sawyer Keys 4; SKC, Sand Key Channel; SM, St. Marks; SM1, St. Marks 1; SM2, St. Marks 2; SM3, St. Marks 3; SM4, St. Marks 4; SPT, Shark Point; ST, Steinhatchee; ST1, Steinhatchee 1; ST2, Steinhatchee 2; ST3, Steinhatchee 3; ST4, Steinhatchee 4; TB, Tampa Bay; TNK, Tern Keys; TKB, Twin Key Basin; YOY, young-of-the-year. Bold print: T_{max} more than 32; S_{avg} less than 24 or more than 35; S_{min} less than 24; S_{max} more than 35. Sampling sites shown in Figure 1.

* Position of third trap.

† Month/last two digits of year.

‡ Means for continuous multiyear studies calculated by averaging annual means for locations.

§ Distance offshore was calculated from each station to Seahorse Key.

¶ Distance offshore was calculated as perpendicular from station to nearest mainland mass. Mean annual YOY stone crab relative abundance is higher here than in Figure 1A because, here, all data were used to calculate that value and, in Figure 1A, data from March 2006 through February 2009 were used.

‖ Stations sampled 1979 to 1980 were located in Everglades National Park (see Fig. 1 and Bert et al. 1986). Note that some stations were initially sampled in November.

** For some analyses, only stations PK1–PK4 were used; for those analyses, the location is designated as EO_{PK}.

†† Keys stations were north of main island chain; distance offshore was calculated from each station to the perpendicular edge of the shallow-water reef line on which the nearest islands reside.

‡‡ Mean number of YOY stone crabs differs significantly between the two sampling time periods, $P < 0.01$.

Min., minimum; Max., maximum; Dist. Off., distance offshore; Out., outside.

To determine whether the fouling organisms on traps reflected the surrounding benthic habitat, the benthic habitat was qualitatively surveyed sometime between spring and autumn by scuba diving at each station in every study. Surveys were conducted during 1990 for the Tampa Bay study and during the first year of trapping for the recent Southwest Florida, Keys subdivision (Table 1) study. At each station, approximately 3,200 m^2 was surveyed during a single dive at each of the first, third, and fifth traps in the trapline (survey procedure given in Appendix 1). At each station, a total of 9,600 m^2 was surveyed in three dives.

Statistical Methods

Various combinations of the data were used, depending on the objective of the analysis. For analyses in which YOY stone crab relative abundance was compared among locations, all full-year data in common to all recent multi-year studies was usually included. To maximize the data that could be included, a full year was defined as March (designated as month 3, in accordance with its sequence within a year) through the following February (month 2). All recent studies and the Tampa Bay long-term study were sampled March 2006 to February 2009; those data constitute the "delimited data" set. The Everglades Offshore (EO) data set contains both stations sampled in the ENP 1979 to 1980 study [Indian Key (INK), Pavilion Key (PVK), Lostman's R., Outside (LMO), Northwest Cape (NWC)] and stations sampled March 2006 to February 2009 (PK1–PK4). When only stations PK1 to PK4 were used in an analysis that included EO, the location is labeled EO_{PK}. Some comparative analyses included the delimited data set plus all data for the ENP 1979 to 1980 study and the 1986 to 1987 Northwest Florida study ("inclusive data"), to provide a historical perspective and geographically enlarge the data set. For some analyses in which locations were not directly compared, all full-year data for each location were used ("all full-year data"). When other combinations of the data were used for an analysis, they are described. Because neither quantitative coloration (Geiger & Bert 2006) nor genetic data were collected for every individual used in this study, the data were analyzed without regard to species-level taxonomic affiliation.

Most data in this study did not conform to parametric assumptions of normality of residuals or homoscedasticity, and the type of nonconformity varied greatly among and within data sets such that no single type of data transformation resulted in conformation of all data sets to parametric assumptions. In addition, both integer count data and continuous data often needed to be used in a single comprehensive analysis. Therefore, statistical analyses usually consisted of generalized linear models or nonparametric tests.

Preliminary analyses were performed to check for sampling bias due to differences in the number of days between samplings (soak times). For each location (years combined), total number of YOY stone crabs collected at a station each month was regressed on soak time for the station using the Kruskal-Wallis Test to search for significant differences followed by the Ryan-Einot-Gabriel-Welsch Multiple Range Test to locate the significant differences (collectively, the "K-W Test"). Only data from the time period during which juvenile stone crabs were generally abundant were included in those regressions.

Temporal and Spatial Variation in Recruitment

A hierarchical approach was applied to explore temporal and spatial variation in YOY stone crab relative abundance on traps, starting at the broadest level and progressing toward increasingly finer spatial and temporal scales. First, overall variation among locations and years was evaluated; second, variation among stations within locations, combining data for months and years; third, variation among months within locations, combining stations and years; and lastly, variation among months at stations, each year, within locations. The delimited data set was used for all analyses except overall variation among locations (inclusive data set). For analyses in which variation among stations, months, or years were compared within locations, all full-year data available for each location were used. For analyses involving spatial and temporal variation in size of PS-juveniles, all full-year data for each location were used. As the analyses became increasingly detailed, locations were eliminated if the relative abundances of YOY juveniles were insufficient for valid analyses.

The K-W Test was used to investigate differences among locations, years, and stations within locations in relative abundance of YOY stone crabs. The K-W Test was also used to identify significant differences in relative abundance among months (years combined) at locations with high numbers of YOY stone crabs and to search the data from those locations for significant differences in the mean size of YOY stone crabs among months. Variation among months and stations in relative abundance of YOY stone crabs was examined for each year of data (delimited data set) from the locations with high YOY stone crab numbers, using the K-W Test. Friedman's Test for Randomized Blocks was used to test for significant differences among months in the hierarchical order of mean number of YOY stone crabs per trap among stations within those locations. In the Friedman's test, significance indicates that the arrangement in hierarchical positions of the monthly mean numbers of YOY individuals at stations did not change significantly among years.

Influence of External Variables on Recruitment

Because the YOY stone crab count data exhibited overdispersion, negative binomial regression was used to comparatively evaluate the influence of the physical variables considered in this study on YOY stone crab relative abundance. Initially, 44 negative binomial regression models (Zuur et al. 2009) representing unique combinations of the variables (Appendix 2) were fitted to examine the relative importance of those variables. Recruitment of YOY juveniles is highly seasonal such that very few YOY stone crabs were collected during February, March, and April. To reduce an anticipated temperature bias, data from those months were not included in the analyses. In addition, monthly data for May, June, and July were included as covariates in every analysis and distinguished by binary indicators (1 = yes, 0 = no) because temperatures during those months increased through the same range as they decreased during August, September, and October. Further, because including field data describing degree of fouling and the three predominant foulers in the fouling community on traps as separate covariates would have resulted in a prohibitive number of covariates for the negative binomial regressions, the three levels for degree of fouling were combined with only the principal foulers as a single categorical covariate (DegPrin, Appendix 2). In addition, preliminary analyses of the principal foulers indicated a pattern of seasonally co-occurring foulers, which allowed grouping of the principal foulers into three fouling communities (Appendix 3). Thus, the three degrees of fouling and three groupings of fouling communities were combined into a single categorical variable with up to nine levels—light, moderate, or heavy fouling paired with summer, winter, or nonseasonal foulers (not all combinations were found at every location).

The other covariates included in the regression models were temperature, salinity, and depth. Temperature and salinity were considered as possible influences on recruitment linearly (T, S), nonlinearly (T^2, S^2), or interactively ($T \times S$). Another covariate, distance from shore, was not included because preliminary analysis (linear regression) indicated that it was related to depth in open waters of the Florida Gulf [locations St. Marks (SM), Steinhatchee (ST), Cedar Key (CK), Homosassa (HM), and EO, plus TB station Anna Maria Island (AMI); the "Gulf Coast" area; $r = 0.545$, $df = 23$, $P < 0.01$), where depth steadily increased with distance from shore; and of the two covariates, preliminary assessments indicated that depth accounted for a high proportion of the variation in YOY stone crab relative abundance (Table 2).

Using these predictor variables, negative binomial regressions were performed on data for locations SM, ST, CK, HM, TB, Oxfoot Bank (OX), Harbor Keys (HK), and Sawyer Keys (SK) separately; for all Everglades Gulf of Mexico locations combined [EG Gulf: Inshore (EI) + Nearshore (EN) + Offshore (EO); Table 1]; for all Everglades locations [EG All: EG Gulf + Florida Bay (FB)]; for the Gulf Coast; and for all locations combined (All Locations). For simplicity, the groupings of locations (EG Gulf, EG All, Gulf Coast, All Locations) will be referred to as "areas" when they are referred to nonspecifically.

When locations were analyzed independently, data was taken from the all full-year data set. When areas were analyzed, data was taken from the delimited data set or inclusive data set, as appropriate. Additionally, to account for potential dependence among observations collected from the same stations in each year, a Station × Year random effect (i.e., groups of observations collected from the same station in each year) associated with the model intercept was included in all candidate models (Gelman & Hill 2007). For each location or combination of locations, the 44 candidate negative binomial regression models were ranked using Akaike's Information Criterion (AIC; Akaike 1973), an entropy-based measure used to compare candidate models, with a small-sample bias adjustment (AICc; Hurvich & Tsai 1989); predictive value increases as the AIC value decreases (Burnham & Anderson 2002). The best-approximating models were identified by calculating Akaike weights (Hurvich & Tsai 1989) following Burnham and Anderson (2002). All mixed-effects negative binomial regression models were fitted in R v3.6.3 (R Core Team 2020) using the glmmTMB package (Brooks et al. 2017). We assessed goodness-of-fit for the global (all predictors) model associated with each location using a simulation-based residual assessment approach implemented in the R package DHARMa (Hartig 2019). Inferences regarding the relative importance of the covariates were made by considering the best- and second-best-approximating candidate models, based on AICc weights, for each location or area and by calculating the location- or area-specific partial weights of each covariate.

TABLE 2.

Model weights for linear regression analysis describing dependence of mean annual relative abundance of YOY stone crabs (genus *Menippe*) on water depth (m) and distance from shore (km).

Model number	Model parameters	AIC	Δ AIC	Model weight
3	Depth	124.9	0.00	0.84
2	Distance	129.4	4.52	0.09
1	Depth + Distance	130.2	5.25	0.06
4	Depth + Distance + Depth × Distance	133.0	8.13	0.01

AIC, Akaike information criteria; Δ AIC, difference between specified model number and best-approximating model (lower numbers indicate that a greater proportion of the overall variation is explained by the specified model relative to the proportions explained by other models); Model weight, proportion of the total support given by all models attributable to the specified model; YOY; young-of-the-year.

Physical Conditions. Following the battery of negative binomial regressions, the specific effects of the variables were more closely examined. For all analyses involving all locations and areas, the inclusive data set plus the Tampa Bay 1989 to 1990 data were used, to increase the temporally inclusive perspective. Several somewhat different data sets were tested in preliminary analyses, but the chosen data best represented the full spectrum of the data while preventing the extensive Tampa Bay data set from overrepresentation and dominating the analyses.

The influence of temperature and salinity on YOY stone crab relative abundance was further examined both empirically (K-W test, all full-year data, locations, stations, months, and years combined) and by negative binomial modeling. To elucidate temperature and salinity effects in the model, DegPrin (the fouler variable) was set to 3.1 (the most common fouler category) and depth was standardized at a value of 3.

To elucidate temperature and salinity effects, we used the best-approximating All Locations model (Model 1, Table 3) to predict the mean relative stone crab abundance over the full range of observed temperature and salinity conditions for traps under the most common fouler category (DegPrin 3.1) in depths of approximately 12 m (actual maximum observed sample depth). To explore location-specific temperature and salinity conditions when no YOY juveniles were captured, temperatures and salinities were grouped into "low or high," and "intermediate" categories based on the results of the empirical and modeling analyses, all traps with zero YOY stone crabs at each location (inclusive data, August–October only; months and years grouped) were placed into the appropriate temperature and salinity categories, and the frequency of traps in each category calculated. This analysis provided insights into the possible temperature- or salinity-related reasons for low to zero recruitment at locations where other variables were suitable for substantial recruitment.

TABLE 3.

Importance of covariate models tested in comprehensive negative binomial regressions to investigate the influence of physical variables on YOY stone crab (genus *Menippe*) recruitment in peninsular Florida Gulf of Mexico waters.

Model number†	Covariate†							Model weights for location or area*													
								SM	ST	CK	HM	TB	EG Gulf	EG All	Gulf Coast	OX	HK	SK	All locations	Count	Sum of AICc model weights‡
33	DegPrin	T	T^2	S	S^2	Depth	T × S	0.02	**0.02**	0.09	**0.18**	0.02	0.14	**0.25**	0.14	0.01	0.10	0.02	**0.37**	12	1.37
1	DegPrin	T	T^2	S	S^2	Depth		0.04		**0.26**	>0.00	0.07	0.02	0.01	0.12	0.02	0.01	>0.00	**0.49**	11	1.04
36	DegPrin	T	T^2	S	S^2		T × S			0.16	**0.28**	0.07	0.09	>0.00	**0.39**	0.01	**0.26**	0.01	0.06	10	1.33
35	DegPrin	T	T^2	S		Depth	T × S	0.04		0.01	0.11	0.04	>0.00	0.06	>0.00	0.02	0.11	0.04		10	0.42
4	DegPrin	T	T^2	S	S^2					**0.46**	>0.00	**0.19**	0.02		**0.33**	0.02	0.03	>0.00	0.08	9	1.13
7	DegPrin	T	T^2			Depth		0.33		>0.00	0.01			0.01	>0.00	**0.15**	0.01	0.01	>0.00	9	0.51
3	DegPrin	T	T^2	S		Depth		0.12		>0.00	>0.00	0.12		>0.00	>0.00	0.05	0.03	>0.00		9	0.30
11	DegPrin	T	T^2					>0.00		>0.00	0.02	>0.00			0.01	**0.15**	0.02	0.01		8	0.21
38	DegPrin	T	T^2	S			T × S			>0.00	0.18	0.13			>0.00	0.02	**0.30**	0.03		7	0.68
6	DegPrin	T	T^2	S						>0.00	0.01	**0.35**			0.01	0.05	0.08	>0.00		7	0.50
39		T	T^2	S	S^2	Depth	T × S	0.08	**0.98**		0.06					0.01	>0.00	0.08		6	1.21
41		T	T^2	S		Depth	T × S	0.06			0.02					0.02	>0.00	**0.22**		5	0.31
34	DegPrin	T		S	S^2	Depth	T × S						0.24	0.49		>0.00		>0.00		4	0.73
44		T	T^2	S			T × S				0.03					0.02	0.01	**0.23**		4	0.29
42		T	T^2	S	S^2		T × S				0.10					0.01	0.01	0.08		4	0.20
17		T	T^2	S	S^2	Depth		0.13								0.02	>0.00	0.03		4	0.18
37	DegPrin	T		S	S^2		T × S						0.16	>0.00		>0.00		>0.00		4	0.16
19		T	T^2	S		Depth		0.07								0.05	0.01	0.03		4	0.15
20		T	T^2	S	S^2			>0.00								0.02	0.01	0.03		4	0.06
8	DegPrin	T				Depth		>0.00						0.01		0.01		>0.00		4	0.02
23		T	T^2			Depth		0.11								0.12		0.06		3	0.29
9	DegPrin			S	S^2	Depth							0.14	0.10		>0.00				3	0.24
13	DegPrin			S	S^2								0.11	>0.00		>0.00				3	0.11
22		T	T^2	S												0.06	0.01	0.03		3	0.10
2	DegPrin	T		S	S^2	Depth							0.05	0.04		0.01				3	0.09
5	DegPrin	T		S	S^2								0.04			>0.00		>0.00		3	0.04
27		T	T^2													0.15		0.08		2	0.23

(*Continued*)

TABLE 1. (CONTINUED)

Model number†	Covariate†							Model weights for location or area*												Count	Sum of AICc model weights‡
								SM	ST	CK	HM	TB	EG Gulf	EG All	Gulf Coast	OX	HK	SK	All locations		
15	DegPrin					Depth								0.03		0.01				2	0.03
10	DegPrin			S		Depth								0.01		>0.00				2	0.01
12	DegPrin	T														>0.00		>0.00		2	0.01
16	DegPrin															0.01				1	0.01
Totals	21	26	20	23	14	16	10	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00		

Models are prioritized by (1) number of locations or areas for which the model had weights in the negative binomial model (Count) and (2) sum of model weights. Only models used at least once and having weights greater than or equal to 0.005 for at least one area or location are included. All models are listed in Appendix 2. CK, Cedar Key; EG, Everglades; HK, Harbor Keys; HM, Homosassa; OX, Oxfoot Bank; SK, Sawyer Keys; SM, St. Marks; ST, Steinhatchee; TB, Tampa Bay; YOY, young-of-the-year.

* Locations defined in Table 1, shown in Figure 1. Areas: EG Gulf, EI + EN + EO; EG all, EG Gulf + FB; Gulf Coast, SM + ST + CK + HM + TB station AMI + EO.

† Model numbers and covariate abbreviations defined in Appendix 2. The months May, June, and July were also covariates in all models. Except for July at HK, they were always significant, usually at $P < 0.001$; but for brevity, they are not listed here.

‡ AICc, Akaike information criteria with Hurvich and Tsai's (1989) correction for small sample size; model weight defined in Table 2. Bold print, most highly weighted models for each location or area based on AICc. Model weights less than 0.005 are denoted by more than 0.00; weights greater than or equal to 0.005 and less than 0.01 were rounded up to 0.01.

To further investigate the influence of trap fouling on YOY stone crab relative abundance, both degree of fouling and principal foulers were analyzed in greater detail. The number of models in which each degree of fouling/seasonal fouling community (DegPrin) was significantly associated with relative abundance was tallied and the proportions of significance levels (P range 0.05–0.01 and $P < 0.01$) calculated. Correlations between mean annual degree of fouling for each station (Gulf Coast data set, years combined; for Northwest Florida, 2006 to 2009 data only) and mean annual relative abundance of YOY stone crabs per station (Table 1) were calculated without and with adjustment of relative abundance for possible bias due to degree of fouling. For each location with adequate numbers of YOY stone crabs, correlations between degree of fouling and number of YOY stone crabs per trap were also calculated for each month (stations and years combined) to examine location-specific seasonal effects of degree of fouling on relative abundance. Lastly, correlations between fouler importance index values (defined in Appendix 4) calculated for each principal fouler at each station and mean annual number of YOY stone crabs at each station (Table 1) were calculated to examine the relationship between each principal fouler and mean annual relative abundance at each location.

To further investigate the changes in YOY stone crab relative abundance from nearshore to offshore, the effects of both depth and distance from shore were examined using correlations performed on Gulf Coast stations (for Northwest Florida, 2006 to 2009 data only). Preliminary regression analysis demonstrated that the relationships between depth or distance from shore and annual relative abundance of YOY stone crabs were similar among years at most locations (data not shown). Thus, years were combined. Distances perpendicular to the Florida shoreline were estimated using http://www.sea-seek.com/tools/tools.php. Linear and nonlinear regressions were calculated. The best-fit regression was deemed to be the simplest regression that accounted for the highest proportion of variation in the data among the set of regressions that were statistically significant. In each analysis, quadratic, cubic, and quartic regressions were tested for significant increase in proportion of variation accounted for by the next more complex model using the program in https://www.scribd.com/document/429951892/statpolyreg-Copy-xls.

Biological Relationships, Ecological Disruptions, and Meteorological Events. The lengthy sampling period at Tampa Bay allowed us to search for a relationship between the relative abundances of YOY stone crabs (this study, all full-year data from Tampa Bay) and ovigerous females [Florida Fish and Wildlife Conservation Commission (FWC), Fish and Wildlife Research Institute (FWRI) data; the same data as analyzed for Bert et al. 2016b] in two ways. (1) The monthly proportion of all YOY stone crabs collected at Tampa Bay was calculated and compared with the monthly proportion of ovigerous females directly and with the frequency of ovigerous females set back by 1, 2, and 3 mo. (2) The correlation between mean annual number of YOY stone crabs per trap and mean annual number of ovigerous females per trap was performed (stations combined for each data set).

Long-term patterns of variation in Tampa Bay YOY stone crab relative abundance also could be used to investigate the effects of red tides, tropical cyclones, and ENSO events on mean monthly (for red tides and tropical cyclones) or annual (for tropical cyclones and ENSO events) relative abundance. To explore the influence of red tides and tropical cyclones on monthly variation in YOY stone crab relative abundance, each full year of data for the 22 y of the Tampa Bay study was tested for variation among months in mean number of YOY stone crabs per trap (stations combined) using the K-W Test. Then, all red tide events in which cell counts were greater than or equal to 100,000 cells/l near the latitude/longitude coordinate range of our Tampa Bay stations and all tropical cyclones that passed through or near Tampa Bay were mapped onto the appropriate year and month in the relative abundance graphs. Their occurrences were compared with changes in YOY stone crab relative abundance for the same month and succeeding months of the same year. The dates of tropical cyclones and ENSO events were also mapped onto a graph of mean annual YOY stone crab relative abundance (all full-year data, stations combined) and their occurrences compared with changes in mean annual relative abundance. For both the monthly and annual comparisons, further analysis depended on the detection of changes in relative abundance that potentially could be attributed to red tide blooms, the passage of tropical cyclones, or ENSO events. If a relationship was suggested by the data, the comparisons were further analyzed using applicable statistics (described in Results).

Red tide levels, locations, and durations (dates) are monitored throughout Florida nearshore marine waters by the FWC, FWRI Harmful Algal Bloom group and were provided upon request. Tropical cyclone pathways and the dates that they passed through or near central Florida were obtained from http://www.nhc.noaa.gov/data/tcr/index.php?season=2015&basin=atl. Records of the strength and duration of ENSO events, which affect rainfall and water temperature levels in Florida (Zorn & Waylen 1997), including Tampa Bay (Schmidt et al. 2001, Schmidt & Luther 2002) were obtained from https://www.cpc.ncep.noaa.gov/products/precip/CWlink/MJO/enso.shtml, https://ggweather.com/enso/oni.htm, and http://www.stormfax.com/elnino.htm.

Fishery Applications

Correlations were used to explore the possibility of a relationship between annual stone crab fishery landings, which were recorded by National Marine Fisheries Service (NMFS 1978 to 1985) and FWC, FWRI (1986 to 2015) and mean annual relative abundance of YOY stone crabs. First, annual landings from 1978 through 2015 were averaged for all counties bordering the peninsular Florida Gulf coast and Keys. Then, the average proportions of total landings attributable to each county were calculated. The long-term averages were calculated to accommodate sometimes great interannual variation. The proportional contributions for the counties corresponding to the locations sampled for YOY stone crabs were tested for correlation with the proportions of the number of YOY stone crabs captured per trap per year (shown as percentages in Table 1) at those locations. Next, annual county landings, reported together with the total number of traps serviced to harvest the landings, were standardized by dividing the landings by the number of traps. Their proportional contributions were calculated; and values for the counties corresponding to the locations sampled for YOY stone crabs were tested for correlation with annual YOY stone crab relative abundances. Then, the same two correlations (using first total annual landings, then standardized annual landings) were performed using the fishing regions defined in Muller and Bert (1997), except for the Big Bend region, which was restricted to counties from Wakulla through Dixie (i.e., the range of counties shoreward of the Steinhatchee and St. Marks locations). Landings values for each year were calculated as the averages of the values for the counties included in each region. Correlations were also calculated between mean annual number of YOY stone crabs captured per trap and total landings for the four counties most likely to be influenced by YOY stone crab recruitment in lower Tampa Bay, for each county separately and for all counties combined (each year of data averaged for the counties). Lastly, correlations between annual mean relative abundances of YOY stone crabs from Tampa Bay and landings data for lower Tampa Bay counties, delayed by 1, 2, or 3 y, were calculated.

RESULTS

Data Considerations

Although this study is geographically extensive and spans a time frame of 31 y, two multiyear gaps in data collection exist; the various incorporated studies ranged from 1 to 22 y; a broad, potentially important geographical area in southwestern Florida between Everglades and Tampa Bay was not sampled; and the studies included here were not designed specifically to investigate geographical or temporal variation in YOY juvenile stone crab recruitment. Thus, although the data included here are comprehensive, they may not reveal the entire story of YOY stone crab recruitment in the Florida Gulf, as defined herein.

Occasionally, because of bad weather or boat failure, a location was not sampled for YOY stone crabs during a designated sampling period or sampling was delayed such that no data was collected at a location during a month. If the location was sampled twice during the previous or following month, and one of the sampling events was at the appropriate end of the month (or overlapped the month with missing data), that sample was used for the missing month. In this way, we were able to compensate for most of the few gaps in our data sets.

The regressions to check for sampling bias due to variation in soak time determined that the relative abundance of YOY stone crabs was not dependent upon soak time at any location [all $r^2 \leq 0.07$; range, number of samplings: 12–260; overall mean number of days between samplings: 30, SD = 6]. Therefore, relative abundance was defined as the mean number of YOY stone crabs per trap per sampling period.

Recruitment

Broad Spatial and Temporal Patterns

In all studies combined, a total of 27,025 traps with some degree of fouling were searched for YOY stone crabs and 50,372 individuals were collected. The highest mean relative abundance of YOY stone crabs occurred at Tampa Bay station Bean Point (BNP), October 2010 (147 individuals/trap). Annual relative abundance averaged over all locations sampled from 2006–07 through 2008–09 varied little among years (2006–07: 2.4, SD = 7.2; 2007–08: 2.5, SD = 6.3; 2008–09: 2.7, SD = 6.2), but differed significantly for each of the 3 y ($P < 0.0001$), probably because sample sizes were very large.

Broad patterns of YOY stone crab relative abundance were essentially stable throughout the Florida Gulf both when inclusive data (Fig. 2A) or delimited data (Fig. 2B–D) were analyzed. Overall, and in 2 of 3 individual years, mean annual relative abundance was significantly higher at EO_{PK} than at any other location (K-W test, overall $H = 1,100$; $P < 0.0001$; each annual $H \geq 356$; $P < 0.0001$); on average, nearly 30% of all individuals collected each year came from EO_{PK} (Table 1). Mean annual recruitment at CK was also high; nearly 20% of all individuals were collected at that location, and in 2008 to 2009, relative abundance was significantly higher at CK than at all other locations, including EO_{PK} ($H \geq 356$; $P < 0.0001$). Nevertheless, average relative abundance at CK in 2008 to 2009 was significantly lower than the averages for either of the previous 2 y at EO_{PK} (2006 to 2007: $H = 385$, 2007 to 2008: $H = 231$; $P < 0.0001$ for both). Together, the major recruitment locations EO and CK produced approximately 50% of all individuals collected 2006 to 2009 and the secondary recruitment locations ST and TB together produced approximately 25% of all individuals collected. Thus, on average, more than 75% of all YOY stone crabs collected annually came from these four principal recruitment locations. Locations SM, EN, OX, HK, and SK had similarly low mean annual relative abundances, yet accounted for nearly all of the remaining 25% of the average annual abundance. Mean annual relative abundance was very low to zero at HM, EI, and FB, which collectively produced less than 1% of the mean annual number of individuals (Table 1).

Data that had mean annual relative abundance values of at least 0.5 at locations in the delimited data set were analyzed for variation in mean annual relative abundance among stations (Fig. 3; note that data from 2005 to 2006 were included at locations where sampling was conducted during that year). At SM, CK, and EO_{PK}, where stations extend from nearshore to offshore, annual relative abundance was significantly higher at the station closest to shore (H range, 9.0–200.0; range, numbers of traps at locations, 159–250; all P values < 0.003). At the major recruitment locations, stations PK1 and CK1 respectively produced annual averages of 14% and 13% of all YOY stone crabs collected. At secondary recruitment location ST, where stations were clustered relatively closely together, recruitment was lowest at the seaward-most station; but was not highest at the shoreward-most station. At secondary recruitment location TB, recruitment was lowest at inshore-most Rattlesnake Key (RSK) and highest at BNP and Passage Key (PSK), which were located short distances behind barrier islands. Altogether, CK1, PK1, BNP, PSK, and ST2 contributed an average of 44% of all individuals collected. At OX, relative abundance was highest at the station closest to the highly productive EO stations. The

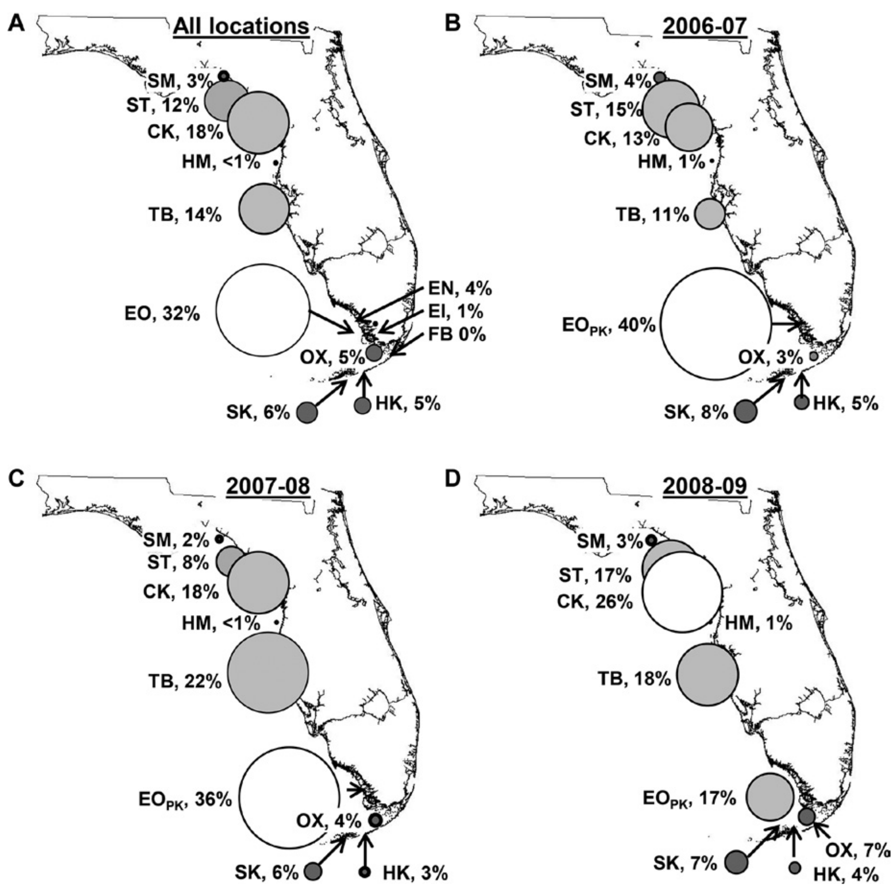

Figure 2. Spatial variation in the relative abundance (mean number per trap per sampling period) of young-of-the-year (YOY) stone crabs (genus *Menippe*) in peninsular Florida Gulf of Mexico waters. Sampling locations defined in Table 1. (A) Variation among all locations, all years combined for each location. (B-D) Annual variation among locations and years. A year extends from March through the following February. Sizes of circles represent proportions of recruits at each location. Shadings represent different statistical groupings. Ranges, numbers of traps per location: 2006–2007, 204–259; 2007–2008, 180–260; 2008–2009, 183–236.

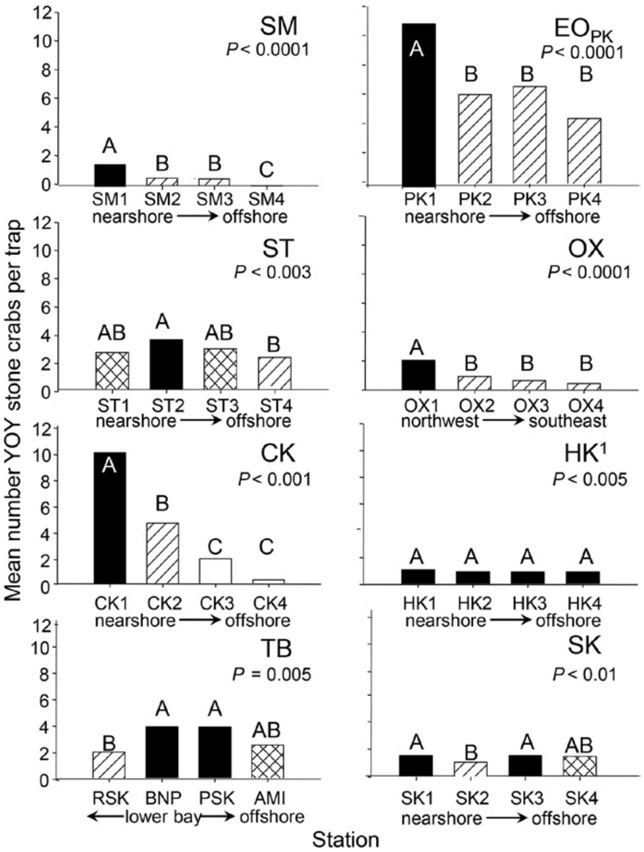

Figure 3. Mean annual relative abundance of young-of-the-year (YOY) stone crabs (genus *Menippe*) at sampling stations in peninsular Florida Gulf of Mexico waters, March–February; 2005 to 2006 (TB, EO_{PK}, HK, SK) or 2006 to 2007 (SM, ST, CK, OX) through 2008 to 2009. Locations (two-letter abbreviations) and stations (on X axes) shown in Figure 1, defined in Table 1; sample sizes given in Table 1. Letters above bars and shading on bars show statistical groupings of stations within locations. P, probability of statistical similarity among stations. *Despite the significance at HK, grouping tests failed to separate the station abundances.

nearshore–offshore decrease in YOY stone crab relative abundance common along Florida Gulf open-water locations did not occur at lower Keys locations HK and SK.

Recruitment Season

Throughout the Florida Gulf, we found YOY stone crabs during the entire year, but principally July through November (Fig. 4A), when approximately 90% of all individuals were collected. Approximately 65%–75% were collected August to October; but aspects of the seasonality shifted to later in the year with decreasing latitude. The statistically homogeneous group of months with lowest numbers of YOY juvenile stone crabs ended after June at ST, July at CK and TB, and August at EO_{PK}; the last month in the statistically homogeneous group that included the month with the highest relative abundance was September at ST and CK and October at TB and EO_{PK}. Despite these shifts, R × C G-tests for interactive effects of year and month on relative abundance were not significant (*P* range: >0.10 to <0.90). Nevertheless, seasonal patterns of variation in YOY stone crab relative abundance at other locations reinforced the trends shown here. The pattern at SM was the same as that at ST and those at OX, HK, and SK were similar to that at EO_{PK} (data not shown).

The more rapid decrease in temperatures in Northwest Florida than in Tampa Bay or Southwest Florida (Fig. 4B) may at least partially account for the decrease in recruitment earlier in the year; but temperature may not be a factor in the temporal delay in the onset of high recruitment levels with movement southward in summer. Water temperatures in Tampa Bay and South Florida are much warmer during spring (March–April) than in Northwest Florida. Other variables may influence the onset of high recruitment, or the influence of temperature may be complicated.

Using a larger data set (inclusive data; except for Northwest Florida locations, where only 2006 to 2009 data were included) and a different approach (analysis of number and size distribution of only PS-juvenile stone crabs) yielded recruitment patterns (Fig. 5) that generally supported those seen in Figure 4A. The initiation of the recruitment period, as identified by notable decreases in mean size and increases in number of PS-juveniles, was generally later at Northwest Florida locations Steinhatchee (July) and Cedar Key (August) than at more southerly Tampa Bay (June) and Everglades (July) (Fig. 5). The end of the main recruitment period, as indicated by notable increases in mean size and decreases in number of PS-juveniles, also occurred earlier at Steinhatchee and Cedar Key (November–December) than in more southerly Tampa Bay and Everglades (January–February).

Within locations, patterns of variation in relative abundance of YOY stone crabs through months were similar among stations (Fig. 6), a relationship that predominated through years (Friedman's Chi-square, adjusted for multiple tests; $P = 0.04$ for 2006 to 2007, 0.03 for 2007 to 2008, 0.01 for 2008 to 2009) despite differences in the patterns among years. Relative abundance also followed similar monthly patterns among stations at Tampa Bay in 19 of the 22 y that data were collected (figure not shown). In contrast, monthly patterns of variation in relative abundance were not similar among locations within any single year. For example, during 2006 to 2007, overall relative abundance was low at CK but high at EO_{PK}; whereas during 2008 to 2009, the reverse situation occurred (Fig. 6). During years of locally high relative abundance, individuals were usually significantly concentrated at one or two stations, principally at the station with overall highest relative abundance (see Fig. 3); but, during years of low relative abundance, monthly values were more similar among stations, except at CK. There, YOY stone crabs were concentrated at CK1 and the hierarchy of stations regarding relative abundance of YOY stone crabs remained the same regardless of its overall magnitude (Friedman's Chi-square; $P < 0.01$).

The monthly patterns of recruitment in Figure 6 support and refine the geographical differences in months of peak recruitment seen in Figure 4A. Relative abundance of YOY stone crabs was always high during September at ST and CK and during October at EO_{PK}. At centrally located Tampa Bay, relative abundance was highest during August in 2006 to 2007, September in 2007 to 2008, and October in 2008 to 2009. Recruitment season also usually initiated later in the year at EO_{PK} than at more northerly stations. Substantial recruitment occurred sometime between June and September at ST, CK, and TB, but not before September at EO_{PK}. At most locations, relative abundance precipitously declined

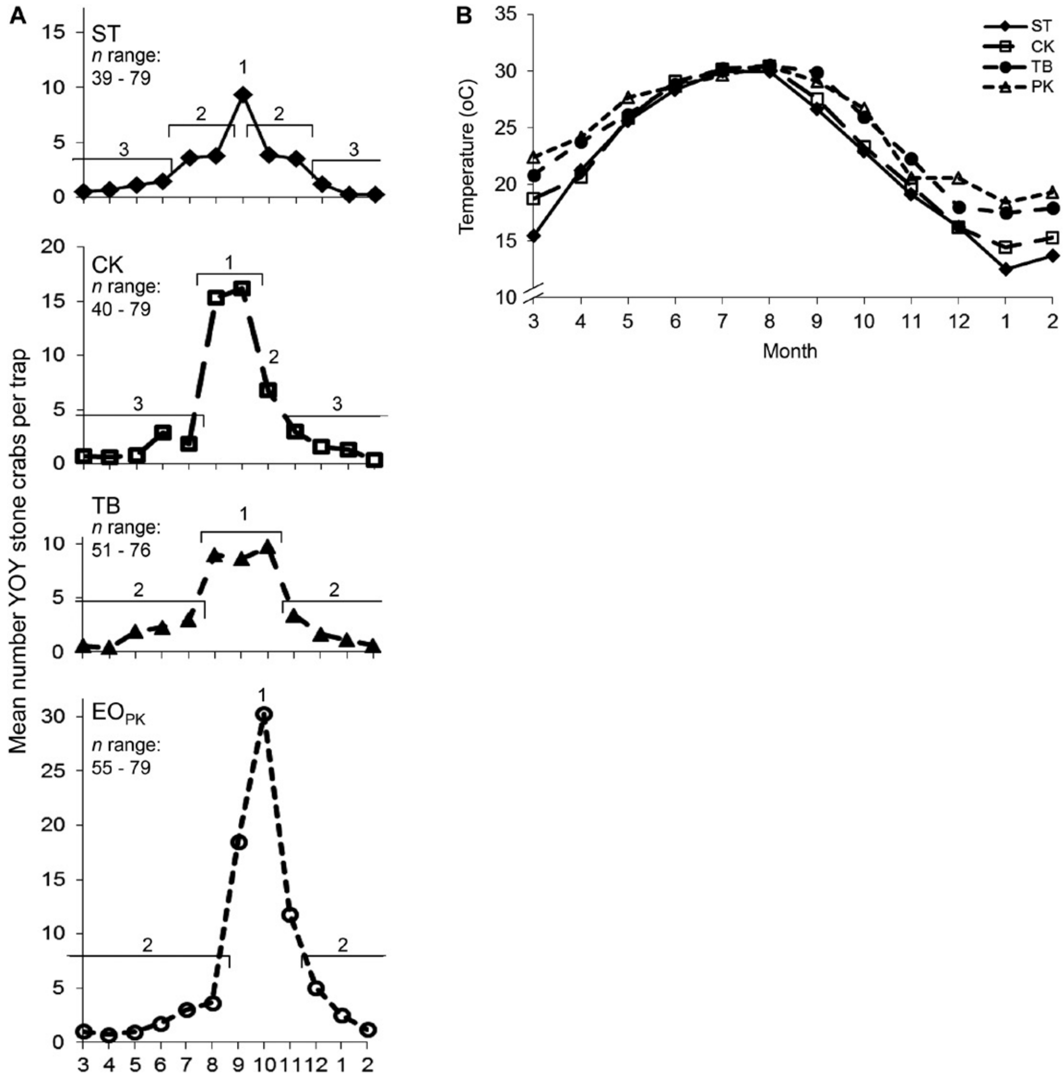

Figure 4. Temporal variation among recruitment locations (defined in Table 1, shown in Figure 1) in young-of-the-year (YOY) stone crab (genus *Menippe*) relative abundance and its relationship to seasonal temperature. (A) Major (CK, EO$_{PK}$) and secondary (ST, TB) recruitment locations. Bars connect months with statistically similar relative abundances: 1, group containing the month with highest relative abundance; 2 or 3 (highest number), group containing the month with lowest relative abundance. n, number of traps sampled per month. (B) Temperature profiles for the four locations.

during November, as seen in Figures 4 and 6 and indicated by reduced numbers of PS-juveniles at Cedar Key, Tampa Bay, and Everglades in Figure 5.

Similarity in levels of recruitment among stations also occurred on an annual basis (Fig. 7) despite general differences among stations in YOY stone crab relative abundance (Table 1). Moreover, the patterns are somewhat cyclic. At Tampa Bay, strikingly low relative abundances occurred during 1995 to 1996 and 2005 to 2006. Between those intervals, relative abundance fluctuated between two 1- to 2-y intervals of high relative abundance and similarly short intervals of lesser relative abundance.

Influence of External Variables on Recruitment

Physical Conditions

Comprehensive analysis. In all negative binomial analyses, the residual-based goodness of fit assessment indicated that the global (all predictors) negative binomial regression model provided an adequate fit to the data.

The relevance of all variables included in the negative binomial regressions to evaluate the effects of physical conditions on YOY stone crab relative abundance is evidenced by the inclusion of the model containing all covariates (model 33) in the suite of applicable models for every location and area (Table 3); but the number, composition, and weights of the models in the suites of applicable models varied greatly among locations and areas (Table 3). In the analysis for Steinhatchee, virtually all of the variation in relative abundance of YOY stone crabs was explained by model 39, which included depth and all temperature and salinity covariates but not the fouling covariate. The highest numbers of included models were in the analyses of the Keys locations. In the analysis of Oxfoot Bank, 31 models were included in the suite of applicable models, but many models had very low weights. Relatively few models explained the variation in YOY stone crab relative abundance

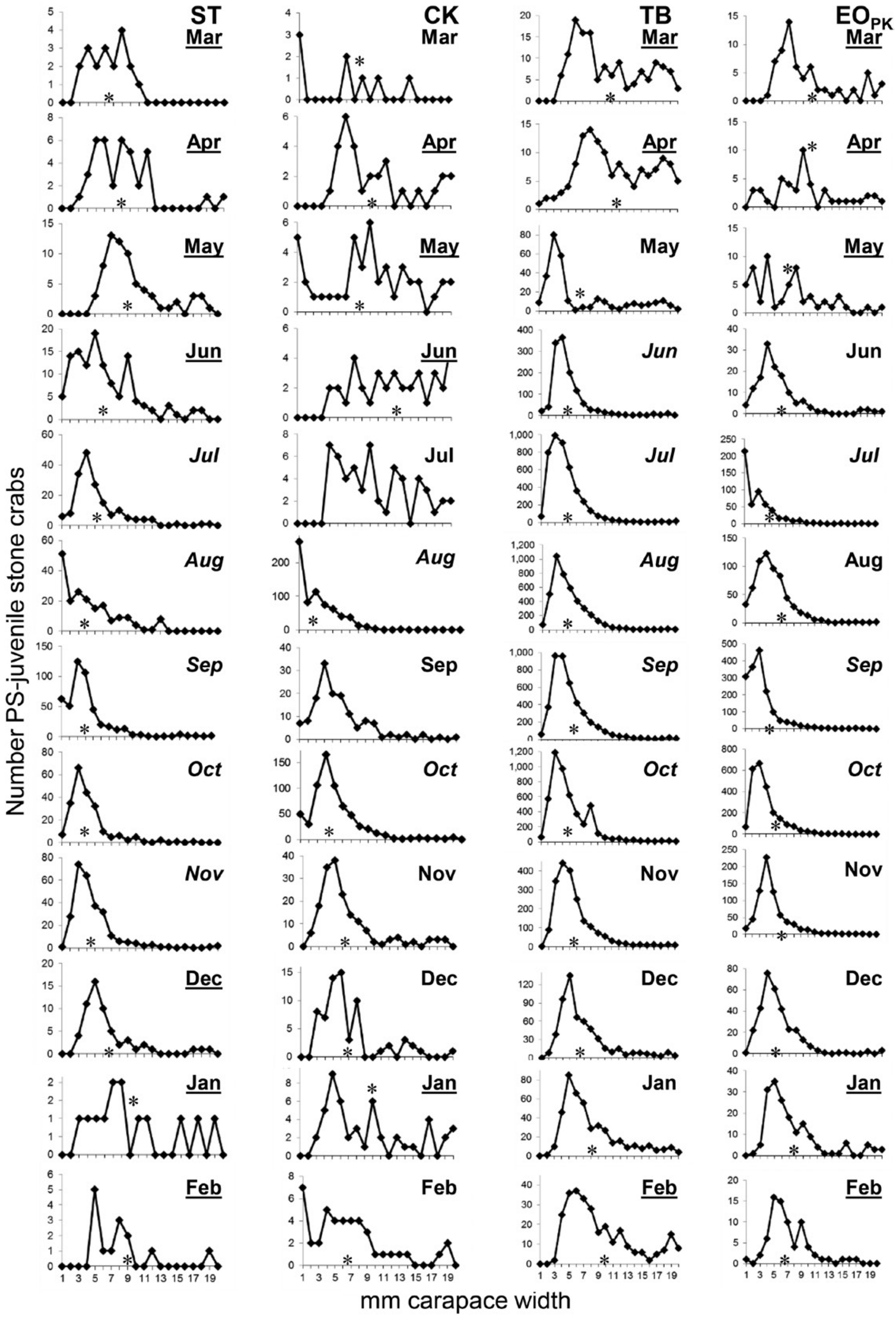

Figure 5. Monthly change in size distribution [mm carapace width (CW)] of postsettlement juvenile (PS-juvenile) stone crabs (genus *Menippe*) collected at principal recruitment locations (shown in Figure 1, defined in Table 1) in peninsular Florida Gulf of Mexico waters. SD ranged 2.1–6.3; average, 3.7. Note the differences in Y axes ranges. Underlined month abbreviations, included in the two statistical groups with highest mean sizes; italicized month abbreviations, included in statistical group with lowest mean size. Ranges, number of PS-juveniles measured each month, all years combined: ST, 13–472; CK, 9–652; TB, 141–4,606; EO_{PK}, 45–2,408. *, mean CW. Overall mean CW, all PS-juveniles: 4.8 mm, SD = 3.2. During months when recruitment was high and mean size was small, larger PS-juveniles were present in numbers similar to the numbers collected during winter and spring, but the huge numbers of new recruits collected that were less than or equal to 5 mm CW dominated the graphs.

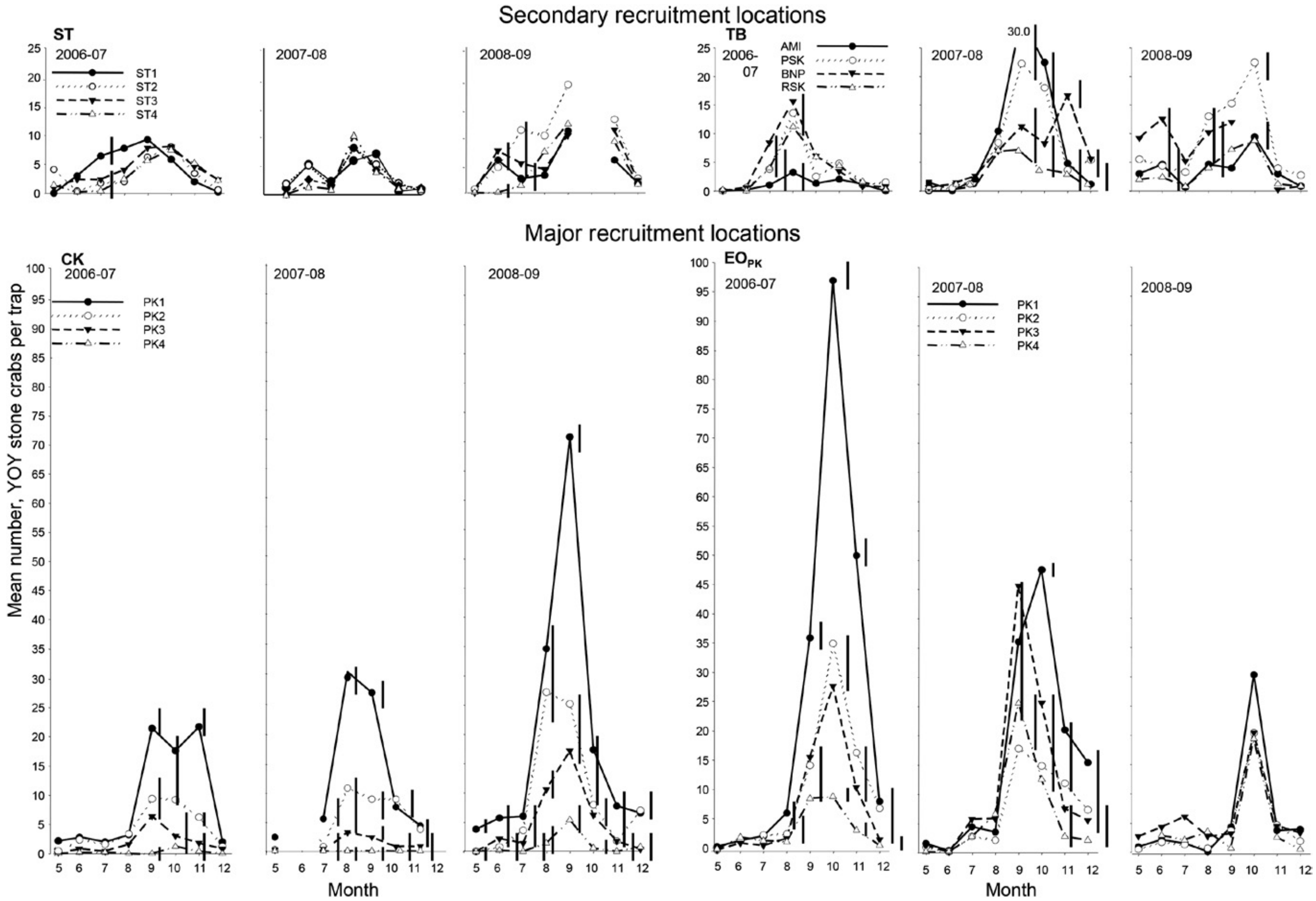

Figure 6. Variation among stations and years in the timing and magnitude of recruitment of young-of-the-year (YOY) stone crabs (genus *Menippe*) at principal recruitment locations in peninsular Florida Gulf of Mexico waters. Where relative abundance differed significantly among stations within months (*P* range: 0.05–0.001), vertical lines connect stations with statistically similar relative abundances. Months of continuously low recruitment (January to April) are not shown. Years are labeled as in other figures. Stations and locations shown in Figure 1, defined in Table 1.

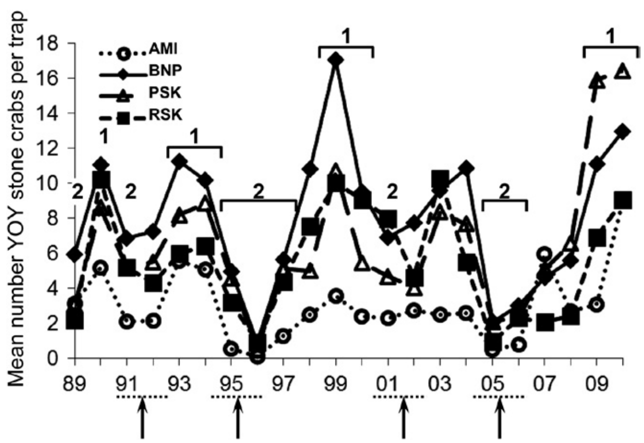

Figure 7. Long-term pattern of annual variation in mean relative abundance (mean number per trap per sampling period) of young-of-the-year (YOY) stone crabs (genus *Menippe*) in Tampa Bay, Florida. Stations defined in Table 1, shown in Figure 1. Numbers and bars above graphs connect years with statistically similar relative abundances. For at least one station, group 1 contains the year with highest relative abundance and group 2 contains the year with lowest relative abundance (*P* range, 0.05–0.005). Arrows and lines below graph show years when relative abundance was generally low throughout Tampa Bay. n range for each station given in Table 1.

in the analyses of the broadest geographical areas (Gulf Coast, all locations).

Trap fouling (represented by the DegPrin covariate) and temperature (both linear, T, and quadratic, T^2 covariates) were clearly important influences for YOY stone crab relative abundance. The covariates were present in almost all used models (Appendix 2). At least one, and usually both, of the covariates DegPrin and T^2 were absent in the models that were never included in suites of applicable models for any location or area, and the T covariate was absent from approximately one-half of those models (Appendix 2). At least one temperature covariate and the fouling covariate were included the suite of models accounting for most to nearly all of the model weights for locations from Cedar Key through Everglades, for Harbor Keys, and for the Gulf Coast and All Locations areas (Table 3). Except for the two Everglades areas, temperature (T and/or T^2) were often highly significant in the best-approximating (most heavily weighted) models for locations and areas (Table 4). In Northwest Florida and the Keys, temperature may be more influential than fouling on YOY stone crab relative abundance. Models that included both temperature covariates but not the fouling covariate accounted for approximately one-half to nearly all of the total model weight for St. Marks (45%), Steinhatchee (98%), Oxfoot Bank (46%), and Sawyer Keys (87%) (Table 3).

TABLE 4.

Significance levels for the best- and second-best-approximating negative binomial regression models evaluating physical conditions potentially influential in YOY stone crab (genus *Menippe*) recruitment at locations and areas in peninsular Florida Gulf of Mexico waters.

		Covariate										
Location or area	Model number	DegPrin	T	T^2	S	S^2	Depth	T × S	K	AICc	Δ AICc	Model weight
SM	7	*	***	***			***		15	1036.5	0.00	0.33
	17		***	***	NS	***	***		11	1038.4	1.94	0.13
Total weight accounted for												0.46
ST	39		***	***	NS	***	***	***	12	2493.0	0.00	0.98
	33	NS	***	***	NS	***	***	***	20	2500.6	7.61	0.02
Total weight accounted for												1.00
CK	4	***	***	***	***	***			17	2219.5	0.00	0.46
	1	***	***	***	***	***	NS		18	2220.7	1.19	0.26
Total weight accounted for												0.72
HM	36	*	***	***	NS	NS		***	17	453.1	0.00	0.28
	33	*	***	**	NS	NS	NS	***	18	453.9	0.83	0.18
Total weight accounted for												0.46
TB	6	**	***	***	***				16	2804.6	0.00	0.35
	4	**	***	***	**	NS			17	2805.8	1.19	0.19
Total weight accounted for												0.54
EG Gulf	34	***	NS		NS	***	NS	*	19	3976.8	0.00	0.24
	37	***	NS		NS	***		*	18	3977.6	0.83	0.16
Total weight accounted for												0.40
EG All	34	***	NS		NS	*	***	**	19	4043.5	0.00	0.49
	33	***	NS	NS	NS	*	***	**	20	4044.8	1.33	0.25
Total weight accounted for												0.74
Gulf Coast	36	***	***	***	NS	***		NS	19	11068.5	0.00	0.39
	4	***	***	***	NS	**			18	11068.9	0.35	0.33
Total weight accounted for												0.72
OX	7	**	**	**			NS		16	1289.9	0.00	0.15
	27		**	***					8	1289.9	0.00	0.15

(*Continued*)

TABLE 4. (CONTINUED)

		Covariate										
Location or area	Model number	DegPrin	T	T^2	S	S^2	Depth	T × S	K	AICc	Δ AICc	Model weight
Total weight accounted for												0.30
HK	38	**	NS	***	NS			*	17	1308.7	0.00	0.30
	36	*	NS	***	*	NS		*	18	1309.0	0.26	0.26
Total weight accounted for												0.56
SK	44		NS	***	NS			*	10	1522.3	0.00	0.23
	41		NS	NS	NS		NS	NS	11	1522.4	0.10	0.22
Total weight accounted for												0.45
All locations	1	***	***	***	NS	***	*		19	17698.9	0.00	0.49
	33	***	***	***	NS	***	*	NS	20	17699.5	0.56	0.37
Total weight accounted for												0.86
Count, significance levels												
Significant		18	16	19	5	13	8	11				
NS		1	8	2	16	4	5	3				
Not included		5	0	3	3	7	11	10				

Locations (two-letter abbreviations) defined in Table 1, shown in Figure 1. Areas (grouped locations) defined in Table 3. Model numbers and covariate abbreviations defined in Appendix 2; as in Table 2, the covariates May, June, and July were included in all models and were always significant but for brevity, are not shown. K, number of parameters. AICc defined in Table 3; Δ AICc and model weight as in Table 2. ***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$; NS, covariate not significant; YOY, young-of-the-year.

TABLE 5.

Partial weight totals for covariates (abbreviations defined in Appendix 2) used in negative binomial regressions to investigate their influence in YOY stone crab (genus *Menippe*) recruitment in peninsular Florida Gulf of Mexico waters.

Location or area	Covariate						
	DegPrin	T	T^2	S	S^2	Depth	T × S
SM	0.55	1.00	0.99	0.56	*0.27*	1.00	0.56
ST	0.02	1.00	1.00	**1.00**	1.00	1.00	1.00
CK	1.00	1.00	1.00	1.00	0.97	0.35	0.27
HM	0.79	1.00	1.00	**0.97**	0.63	0.38	0.96
TB	1.00	1.00	1.00	1.00	0.35	0.26	0.24
EG Gulf	1.00	0.77	0.27	**1.00**	1.00	0.59	0.62
EG All	1.00	0.87	0.33	**0.95**	0.89	1.00	0.80
Gulf Coast	1.00	1.00	1.00	**0.99**	0.98	0.27	0.54
OX	*0.53*	0.97	0.95	0.41	0.13	0.43	0.11
HK	0.95	**1.00**	1.00	0.97	0.42	0.27	0.79
SK	0.13	**1.00**	0.99	**0.84**	0.26	0.48	0.71
All locations	1.00	1.00	1.00	**1.00**	1.00	0.86	0.43
Average	0.75*	0.97	0.88	0.89	0.66	0.57	0.59
SD	0.36	0.07	0.27	0.20	0.35	0.31	0.28

Individual weights are sums of all model weights in which the covariates appeared in each analysis and represent the relative importance of each covariate at each location or area. Locations (two-letter abbreviations) defined in Table 1, shown in Figure 1; areas defined in Table 3; covariate abbreviations defined in Appendix 2. As in Table 3 the covariates May, June, and July are not included for brevity. Bold print, covariate was not significant or was not included in the two best-approximating models (Table 4) but has a high partial weight value; italicized and underlined, covariate was significant in at least one of the two best-approximating models but had a low partial weight value. YOY, young-of-the-year.
* Average without ST: 0.81, SD 0.29.

For nearly all locations and areas, the partial-weight values for the fouling and temperature covariates (Table 5) reflected the significance levels for the two best-approximating models (Table 4). Fouling was a particularly important influence on YOY stone crab relative abundance from Cedar Key through Everglades, where seasonal foulers varied among stations (Appendix 4) and the degree of fouling was heavy throughout the year; and for the geographically and ecologically broad Gulf Coast and All Locations areas (Table 5). Because YOY stone crab recruitment is highly seasonal (Fig. 4A), temperature greatly influenced relative abundance throughout the study area; but higher significance levels from Tampa Bay northward suggest that its influence is greater where seasonal temperature variation is higher.

The influence of salinity on YOY stone crab relative abundance was enigmatic. Both S and S2 were included in many of the negative binomial regression best-approximating models (Table 4); but in many cases, only one of the two covariates was significant. At multiple locations and in both broad areas, linear S was not included or was not significant in the best-approximating models but was heavily weighted in the partial weight totals (Table 5). Geographic variation in the presence of, and significance levels for, salinity in the best-approximating models indicate that salinity influenced the relative abundance along the Gulf coast and in the Everglades subregion but had little influence in the Keys, where salinity remained very high throughout the year (Table 1). The greater influence of salinity on relative abundance compared with that of temperature, as indicated by higher significance levels in the best-approximating models (Table 4) and partial weight values (Table 5), was most pronounced in Everglades (EG Gulf, EG All), where salinity range was greatest (Table 1). Temperature and salinity were generally not interactive.

Depth and interactive temperature and salinity were less influential for YOY stone crab relative abundance than were the other variables considered (Tables 4 and 5). Depth significantly influenced YOY stone crab relative abundance at Steinhatchee, a location where all variables except fouling were highly influential for YOY stone crab relative abundance (Table 5); and at St. Marks and the Everglades All and All Locations areas (Tables 4 and 5), where depth varied considerably among stations (Table 1). Temperature–salinity interactions were significant at only a few locations and areas (Steinhatchee, Homosassa, Everglades, and lower Keys), and salinity varied widely only in the Everglades subregion.

Temperature and salinity. Throughout the study area, water temperature averaged approximately 29°C–30°C from June through August (Fig. 4B). With decreasing latitude, temperature decreased at a slower rate during autumn and minimum temperature increased. Temperature was lowest during January in Northwest Florida but during February in the Keys (Table 1). Salinity varied widely and seasonally at some nearshore stations in Northwest Florida and at many Everglades stations (Table 1). Salinity was higher than the typical peninsular Florida oceanic average for surface waters (36) during at least 1 mo and year between July and November at many stations.

In a regression of annual relative abundance of YOY stone crabs on temperature, relative abundance was not dependent on annual mean temperature ($r^2 = 0.02$). Highest relative abundance occurred when temperatures were falling from midsummer highs (Fig. 8A). Specific temperatures were associated with abrupt changes in relative abundance of YOY stone crabs. Relative abundance began to exponentially increase as temperature rose from 27°C to 31°C during early summer (best-fit, simplest regression: $y = 0.13e^{0.60x}$, $r^2 = 0.97$), remained high until temperature fell below 27°C during autumn, steadily decreased as temperature cooled ($y = -0.49x + 6.99$, $r^2 = 0.89$) to 17°C, and remained low until temperature rose to 27°C during spring. Winter temperatures below 17°C commonly occurred in Northwest Florida and Tampa Bay and occasionally occurred in Everglades. Numbers of YOY stone crabs collected per location during those months usually ranged 0–20.

Except for an abrupt, significant increase in YOY stone crab relative abundance at a salinity of 19, the shape of the plot for YOY stone crab relative abundance versus salinity (Fig. 8B) was similar to that of relative abundance versus temperature (Fig. 8A) in that recruitment exponentially increased as salinity increased from unfavorable lows to more optimal levels (salinity 21–29: $y = 0.60e^{0.35x}$, $r^2 = 0.65$) and linearly decreased as values

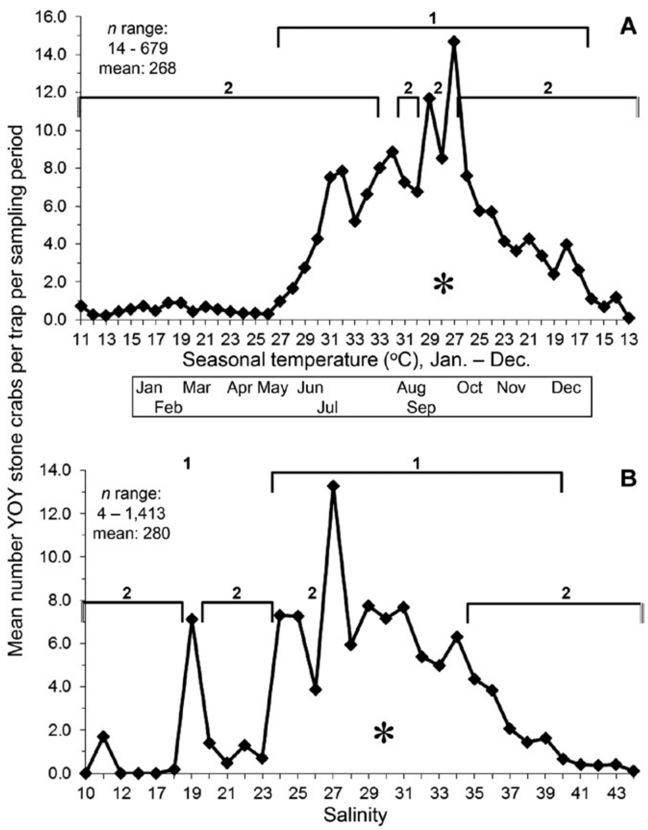

Figure 8. Relationship between (A) water temperature or (B) salinity and relative abundance (mean number per trap per sampling period) of young-of-the-year (YOY) stone crabs (genus *Menippe*) from peninsular Florida Gulf of Mexico waters. Numbers and bars above graphs connect values with statistically similar relative abundances: 1, group including value of highest abundance; 2, group including value of lowest abundance. Intermediate groupings are not shown. Asterisks show optimal values, as determined by modeling (see Figure 9). n range, minimum and maximum total number of YOY stone crabs per temperature or salinity value. Box below graph A, abbreviations of months; each is placed approximately below the average temperature for the designated month. Temperatures greater than 30°C occurred July and August; temperatures less than 17°C occurred December and January.

became unfavorably high (salinity 31–44: $y = -0.58x + 7.1511$, $r^2 = 0.90$). The abrupt increase in relative abundance of YOY stone crabs was most pronounced at a salinity of 24 and the directional linear decline started at salinity 35. At salinities of 40 and higher, relative abundance approached zero.

Parameter estimates from the best-approximating negative binomial regression model for All Locations verified that YOY stone crab abundance was lower in May, June, and July relative to the baseline August to January period (Table 6). The model estimated maximum relative abundance at 28°C during autumn (Fig. 9A, B) and at a salinity of 32 (Fig. 9C, D). Estimated relative abundance of YOY stone crabs was highest (7.0 or greater) at temperatures ranging 25°C–31°C and salinities ranging 26–36, decreased with increasingly extreme high temperature/salinity combinations, and decreased to essentially zero at temperatures of 11°C or lower and salinities of 10 or less. Temperatures higher than 31°C occurred during at least 1 mo and year between June and August at all Homosassa and Tampa Bay stations and

TABLE 6.

Parameter estimates (Mean; SE) and 95% confidence limits (Lower, Upper) from the best-approximating mixed effects negative binomial regression model (Model 1, All Locations, Table 4) relating relative abundance of YOY stone crabs (genus *Menippe*) to seasonal temperature (T) and salinity (S) across all sampling locations. Fouler denotations are explained in Appendix 3.

Parameter	Mean	SD	Lower	Upper
Fixed effects				
Intercept	0.242	0.144	−0.039	0.524
T (°C)*	0.351	0.028	0.296	0.407
S†	−0.066	0.043	−0.151	0.019
T × T	−0.296	0.026	−0.346	−0.245
S × S	−0.065	0.016	−0.097	−0.033
May	−2.213	0.084	−2.377	−2.048
June	−1.787	0.076	−1.936	−1.638
July	−0.719	0.071	−0.858	−0.580
Depth (m)‡	0.255	0.108	0.042	0.468
Fouler (2,1)	0.416	0.071	0.276	0.556
Fouler (3,1)	0.919	0.089	0.745	1.094
Fouler (1,2)	−0.005	0.069	−0.141	0.131
Fouler (2,2)	0.073	0.086	−0.095	0.242
Fouler (3,2)	0.407	0.166	0.083	0.732
Fouler (1,3)	0.088	0.130	−0.166	0.342
Fouler (2,3)	0.071	0.116	−0.156	0.299
Fouler (3,3)	0.416	0.185	0.053	0.779
Theta (dispersion)	0.068			
Random effects				
Location × Year	1.740			0.000

YOY, young-of-the-year.
* Minimum standardized, −3.24; maximum standardized, 2.45; actual mean, 25.2 (SD, 5.2; range 8–38).
† Minimum: standardized, −8.40; maximum standardized, 2.50; actual mean, 34.4 (SD, 3.9; range 2–44).
‡ Minimum: standardized, −1.98; maximum standardized, 3.1; actual mean, 5.33 (SD, 2.33; range 0.7–12.5).

many Southwest Florida stations (Table 1). Temperatures fell to 11°C or lower during at least one January at all St. Marks, Steinhatchee, and Tampa Bay stations; salinities declined to 10 or lower only at Everglades Inshore station LSB. During the full July-to-November YOY stone crab recruitment season, salinities less than 24 occurred at stations in Tampa Bay and all Everglades locations except Florida Bay; salinities higher than 35 occurred at one or more stations at every location except Everglades Inshore (Table 1).

In Northwest Florida during peak YOY stone crab recruitment season, 49%–71% of the traps sampled when temperatures were less than or equal to 26°C (almost always during October) or salinities were greater than or equal to 35 (usually during August or September) had no YOY stone crabs (Table 7). Except at Everglades Inshore and Everglades Nearshore, where

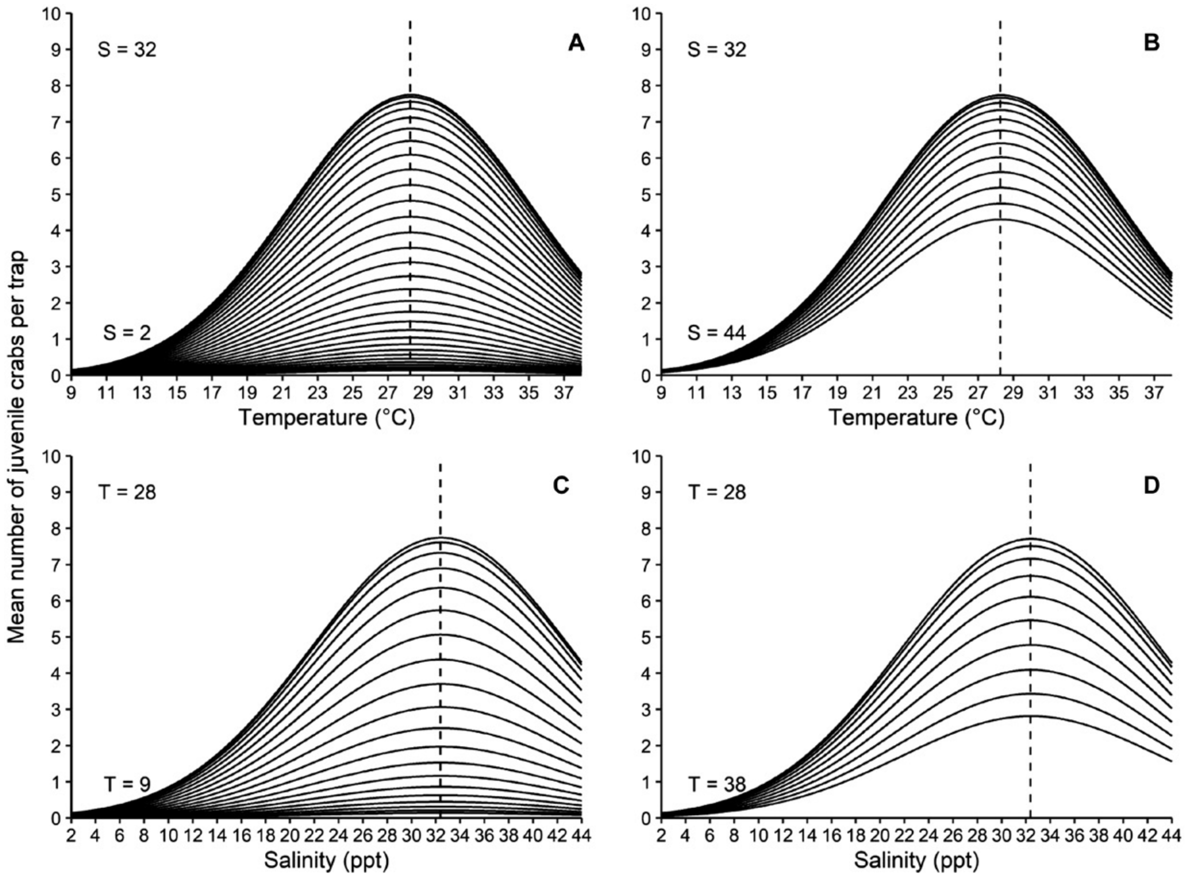

Figure 9. Modeled temperature (T) and salinity (S) profiles for relative abundance of young-of-the-year (YOY) stone crabs (genus *Menippe*) from peninsular Florida Gulf of Mexico waters. (A and B) Expected relative abundances at S intervals of 1 over a T range of 9°C–38°C from (A) an S range of 2–30 and (B) an S range of 30–44. (C and D) Expected relative abundance at T intervals of 1°C over an S range of 2–44 from (C) a T range of 9°C–28°C and (D) a T range of 28°C–38°C. Figures B and D are essentially the "back sides" of the domes of relative abundance values generated by the model. Together, each pair of graphs illustrates a three-dimensional profile.

temperatures could become very high and salinities very low during August and September, locations with zero recruitment from Homosassa southward were mainly associated with high salinities. Salinity was particularly high in Florida Bay and the Keys locations, where temperatures could also be high. The very common association of high salinity with zero recruitment throughout most of the study area supports the high partial weights calculated for salinity in Table 5.

Trap fouling. The number of entries and significance levels for the combined degree of fouling and seasonal foulers covariate (DegPrin) in the comprehensive negative binomial regression showed that heavy fouling with summer foulers was the fouling community most frequently, significantly, and positively associated with relative abundance of YOY stone crabs (Table 8), followed by moderate fouling with summer foulers. Most of the significant DegPrin categories that included winter or nonseasonal foulers were negatively associated with relative abundance.

Degree of fouling was most important as a contributing variable to YOY stone crab relative abundance at the Cedar Key and Everglades Offshore locations, where correlations between relative abundance of YOY stone crabs and degree of fouling were predominantly positive and highly significant throughout most of the year, and at Tampa Bay, where correlations were positive and highly significant during the recruitment season (Table 9). Degree of fouling was less important at St. Marks, Steinhatchee, and Sawyer Keys, where fouling was either not included or was not significant in the best-approximating models (Table 4) and correlations between YOY stone crab relative abundance and degree of fouling were rarely highly significant (Table 9). Proportions of negative correlations between YOY stone crab relative abundance and degree of fouling were high at St. Marks (six of nine correlations), Steinhatchee, and Tampa Bay (both six of 12 correlations). Most occurred October to April, but most of those were not significant. High proportions of all positive correlations (significant and not significant) occurred May to September. The correlations between mean annual degree of fouling and mean annual relative abundance of YOY stone crabs performed using direct values from Table 1 (Fig. 10A) and values standardized by dividing mean annual relative abundance by degree of fouling (Fig. 10B) were very similar and the correlation coefficients low and comparable (Fig. 10A, $r = 0.36$; Fig. 10B, $r = 0.33$; $n = 49$, $P < 0.05$ for both), indicating that, overall, relative abundance was not strongly and directly related only to degree of fouling, despite the strong positive relationships at some locations.

The monthly relative significance values and overall fouler importance indices presented in Appendix 4 are measures of the seasonal incidence and commonality of specific principal

TABLE 7.

Location-specific temperature (T) and salinity (S) conditions in peninsular Florida Gulf of Mexico waters when zero YOY stone crabs (genus *Menippe*) were captured at a station during August, September, or October (years combined).

Region location	*n*	Frequency, T ≤ 26°C or ≥ 32°C	Direction	Frequency, S ≤ 24 or ≥ 36	Direction	Frequency, T ≤ 26°C or ≥ 32°C and S ≤ 24 or ≥ 36	Direction	Frequency, 26°C < T < 32°C and 24 < S < 36	Comments
Northwest Florida									
SM	100	0.30	T low	0.28	S high	0.00		0.42	Nearly all low T were in October
ST	55	0.44	T low	0.27	S high	0.00		0.29	All low T were in October
CK	52	0.08	T low	0.46	S high	0.00		0.46	Mostly CK4; all low T were in October
HM	95	0.17	T low	0.32	S high	0.09	T and S high	0.42	All low T were in October
Tampa Bay									
TB	105	0.36	Some T low, others T high	0.05	S high	0.02	T and S high	0.57	Problem depends on year in this long-term study
Southwest Florida, Everglades subregion									
EI	30	0.17	T high	0.33	S low	0.50	T high and S low	0.00	Shallow water, seasonal rainfall decreases S (down to as low as 2); summer T up to 33°C
EN	10	0.00		0.60	LMI, S low	0.40	LMI, T high, and S low	0.00	Shallow water, seasonal rainfall decreases S; summer T up to 33°C
EO	20	0.00		0.25	S high	0.00		0.75	T and S usually within range suitable for YOY stone crab recruitment
FB	92	0.00		0.57	S high	0.11	T and S high	0.32	S high (40 or higher) at BWS, TNK, CPK, TKB, CCH; both high at BBK, SKC
Southwest Florida, Keys subregion									
OX	61	0.00		0.93	S high	0.00		0.07	Prolonged high S (40 or higher) during recruitment season
HK	53	0.04	T high	0.90	S high	0.00		0.06	Prolonged high S during recruitment season
SK	46	0.00		0.72	S high	0.04	T and S high	0.24	Prolonged high S during recruitment season

Temperatures and salinities designated as low (≤26° or S value ≤24) or high (≥32°C, S value ≥36) were determined from the analyses presented in Figures 8 and 9. Intermediate values (26°C < T < 32°C and 24 < S < 36) were deemed suitable for YOY stone crab recruitment based on statistical results conducted for this study. Locations defined in Table 1, shown in Figure 1. *n*, number of stations; YOY, young-of-the-year.

TABLE 8.

Seasonal trap fouling community incidence and significance levels in the two most heavily weighted negative binomial regressions for relationship between YOY stone crab (genus *Menippe*) relative abundance on traps and potentially influential external variables.

			Frequency of significance level	
			P range	*P*
DegPrin*	Data Code*†	Number of entries‡	≤ 0.05 – > 0.01	≤ 0.01
Heavy fouling, summer foulers	3.1	12	0.33	0.67
Moderate fouling, summer foulers	2.1	12	0.67	0.33
Heavy fouling, winter foulers	3.2	4	0.00	1.00
Heavy fouling, nonseasonal foulers	3.3	4	0.50	0.50
Light + moderate fouling, winter foulers	1.2 + 2.2	6	0.67	0.33
Light + moderate fouling, nonseasonal foulers	1.3 + 2.3	5	0.40	0.60

YOY, young-of-the-year.
* Abbreviation defined in Table 3; fouling levels, seasonal foulers, and coding described in Appendix 3.
† Light fouling, summer foulers (code 1.1), was never observed.
‡ Number of times that each degree of fouling/principal fouler combination was recorded as significant in the negative binomial models with the two highest model weights for each location. In some analyses, more than one type of DegPrin was significant.

foulers. Comparison of monthly variation in, and relative importance of, principal trap foulers revealed consistency among years within stations (data not shown), but complex associations that differed among locations and stations within locations. For example, at St. Marks, green algae were common and encrusting bryozoans were rare fouling community components only at SM1 (Table A4, Fig. 11); which differed from other SM stations in commonality or seasonality of branched hydroids and bryozoans and red or brown algae. Similarly, the fouling components at CK4 differed markedly from those at other Cedar Key stations. The greatest differences in fouling communities occurred at Everglades (Appendix 4), where seasonal and locational fouling varied greatly among and within locations.

Some foulers, such as barnacles, were generally positively related to variation among stations in YOY stone crab relative abundance, whereas others, such as branched hydroids and bryozoans and encrusting bryozoans, were generally negatively related (Fig. 11), due in part to their seasonality (Tables A4 and A5). Some foulers (e.g., worm tubes, green algae) were positively related to relative abundance at some locations but negatively related at others (Fig. 11), likely due to species changes associated with latitudinal and salinity changes. Barnacles, a common summer fouler closely associated with YOY stone crab relative abundance at Cedar Key, Tampa Bay, and Everglades Offshore, were not particularly abundant during YOY stone crab recruitment season north of Cedar Key or in Florida Bay and the Keys (Tables A4 and A5) or strongly and positively correlated with variation among stations in YOY stone crab relative abundance (Fig. 11). Notable exceptions to the close relationship between heavy fouling with barnacles and YOY stone crab relative abundance were stations NWC in Everglades Offshore, Lostman's River, Inshore (LMI) in Everglades Nearshore, and CCH in Florida Bay. Each had heavy barnacle fouling throughout the recruitment season (Table A4) but very low relative abundance of YOY stone crabs (Table 1).

Other summer biota—encrusting bryozoans and, particularly, green algae—were the common principal foulers during YOY stone crab recruitment season at locations where barnacles were not common (Table A4). Correlations between the encrusting bryozoans fouler importance index and YOY stone crab relative abundance were low or negative at all locations except Homosassa (Fig. 11). Encrusting bryozoans was never a principal fouler at station SM1 (Table A4), where YOY stone crab relative abundance was highest (Fig. 11) and the negative relationship between variation among stations in encrusting bryozoan importance index values and YOY stone crab relative abundance was significant. At St. Marks, station-specific importance index for fouler green algae was significantly and positively correlated with variation among stations in YOY stone crab relative abundance, but the green algae index was negatively correlated with relative abundance at Steinhatchee, Homosassa, Everglades Offshore, and Sawyer Keys (Fig. 11). Green algal species composition and seasonality changed markedly with latitude, salinity, and westward progression through the Keys, which probably contributed to the varying relationship with YOY stone crab relative abundance.

The seasonality of the most common cool-weather principal fouler, worm tubes, shifted with decreasing latitude; but, except for Steinhatchee and station CK4 at Cedar Key, did not coincide with YOY stone crab recruitment season (Table A4). Positive associations between the importance index for worm tubes and YOY stone crab relative abundance (e.g., SM, $EO_{PK,}$ HK; Fig. 11) were likely related to changes in species composition. Most coefficients for correlations between variation among stations in importance indices of the other cool-weather foulers—branched hydroids and bryozoans and red or brown algae—and YOY stone crab relative abundance were near zero or negative (Fig. 11).

The uncommon, nonseasonal fouler tunicates was most prevalent as a principal fouler during the mid and latter months of the YOY stone crab recruitment season at Harbor Keys and Sawyer

TABLE 9.

Correlations between mean monthly degree of fouling and mean monthly number of YOY stone crabs (genus *Menippe*) per trap in peninsular Florida Gulf of Mexico waters.

	SM			ST			CK			HM			TB			EO_{PK}			OX			HK			SK		
Month	*n*	*r*	*P*	*n*	*r*	*P*	*n*	*r*	*P*	*n*	*r*	*P*	*n*	*r*	*P*	*n*	*r*	*P*	*n*	*r*	*P*	*n*	*r*	*P*	*n*	*r*	*P*
1	40	d1		64	−0.15	ns	58	0.33	<0.010	84	<0.01	ns	421	−0.22	<0.001	111	0.46	<0.001	66	0.69	<0.001	77	0.13	ns	73	−0.12	ns
2	79	−0.08	ns	78	−0.13	ns	108	−0.04	ns	69	DI		432	−0.13	ns	116	0.37	<0.001	62	0.51	<0.001	79	0.41	<0.001	77	0.28	<0.010
3	40	0.16	ns	40	0.16	ns	45	0.34	(0.020)	77	0.41	(0.016)	370	−0.16	ns	92	0.51	<0.001	18	0.42	ns	80	−0.12	ns	74	0.22	ns
4	79	−0.14	ns	81	−0.22	ns	74	0.08	ns	59	DI		376	−0.05	ns	101	0.36	<0.001	58	0.33	<0.010	80	d1		78	d1	
5	60	d1		60	−0.08	ns	59	0.29	(0.027)	54	DI		378	0.11	(0.037)	95	0.43	<0.001	55	0.22	ns	74	0.26	(0.030)	80	0.17	ns
6	100	−0.19	ns	102	0.17	ns	58	0.52	<0.001	54	0.36	<0.010	370	0.21	<0.001	89	0.20	ns	56	0.26	ns	70	d1		100	−0.13	ns
7	59	d1		59	0.32	(0.014)	55	0.48	<0.001	58	d1		387	0.40	<0.001	84	−0.40	<0.001	78	0.13	ns	85	0.13	ns	75	0.16	ns
8	75	0.29	(0.012)	80	0.28	ns	79	0.45	<0.001	58	0.60	<0.001	376	0.22	<0.001	100	0.17	ns	52	0.23	*ns*	65	−0.10	ns	72	−0.12	ns
9	60	0.21	ns	59	0.43	<0.001	60	0.87	<0.001	58	d1		317	0.29	<0.001	109	0.49	<0.001	55	0.45	<0.001	71	0.09	ns	68	0.10	ns
10	59	−0.33	0.010	64	−0.69	<0.001	58	0.25	ns	22	d1		403	0.32	<0.001	84	0.34	<0.001	37	0.35	(0.030)	60	−0.22	ns	56	0.27	(0.046)
11	60	−0.08	ns	84	0.03	(0.022)	72	0.35	(0.029)	63	d1		359	−0.01	ns	85	0.65	<0.001	46	0.61	<0.001	75	0.32	<0.001	75	0.29	(0.014)
12	78	−0.18	ns	73	−0.09	ns	60	0.31	(0.033)	73	DI		381	−0.14	ns	79	−0.12	ns	74	0.49	(0.030)	80	−0.04	ns	77	0.06	ns

Various data limitations, defined in footnotes, prevented calculation of correlations for some station/month combinations. Adjustments to significance levels for multiple tests were not made, but levels more than 0.01 are in parentheses. Location abbreviations defined in Table 1; Month: 1 = January, 2 = February, and so on; *n*, number of traps; *r*, correlation coefficient; *P*, significance level of correlation coefficient; ns, not significant; d1, degree of fouling on all traps was 1 (light; defined in Appendix 3); DI, data insufficient, usually due to few YOY stone crabs (≤2). Other than EN in January ($n = 29$, $r = 0.69$, $P = 0.05$) and June ($n = 14$, $r = 0.35$, ns), locations EI, EN, and FB had too few YOY stone crabs to warrant testing. YOY, young-of-the-year.

Keys, but variation among stations in its importance index was not related to YOY stone crab recruitment (Fig. 11). The importance indices for the rare fouler mud were significantly and negatively correlated with YOY stone crab relative abundance at both Homosassa and Oxfoot Bank (Fig. 11), the only locations where mud was a principal fouler during the YOY stone crab recruitment season and where assemblages of foulers were unusual compared with neighboring locations.

The consequence of this diverse variation in trap fouling was a limit on the predictability of YOY stone crab relative abundance based solely on the combined variable DegPrin. Other factors may override the influence of fouling on YOY stone crab relative abundance.

Habitat surveys. The SCUBA surveys of habitat allowed characterization of the substrate and benthic community at each location for comparison with the benthic community on traps at that location. Visibility ranged from 2 to 10 m at St Marks, Steinhatchee, Cedar Key station CK4, Homosassa, Tampa Bay, and all Keys locations and to the sea floor at all Florida Bay stations except CCH. Low to zero visibility at Cedar Key stations CK1 to CK3, Everglades Inshore and Nearshore stations, and Florida Bay station CCH prohibited SCUBA diving, but occasional observations from the boat were possible. Visibility at Everglades Offshore stations was low, but SCUBA surveys were possible.

The benthic habitats at St Marks, Steinhatchee, Cedar Key station CK4, Homosassa, and Tampa Bay stations BNP, PSK, and RSK were composed of interspersed seagrass (*Thalassia testudinum*; *Syringodium filiforme*; nearshore, also *Halodule wrightii*), low limestone outcrops (to approximately 0.5–2.0 m in height), and sandy bottom, in approximately equal proportions. The outcrops were populated by benthic macroalgae and a variety of sessile benthic invertebrates—mostly barnacles, sponges, bryozoans, tunicates, hydroids, and small soft corals—in various proportions and composed of species that were similar to or matching the types that colonized traps. One to several stone crab burrows or excavations under rock (limestone) were cited at most locations. The sea floor at Tampa Bay station AMI was composed of silicious and calcareous sand and shell fragments with occasional low limestone outcrops covered with benthic biota similar to that found at other locations. Seagrass patches were nearby, but not within the defined search area. Through the years, the benthic habitat at PSK and AMI changed to almost exclusively hard sand, most noticeably after 2003.

Everglades Inshore stations were located within lagoons in a river (LMI) or among small islands [Chokoloskee Bay (CKB)]. Observations from the boat indicated that the substrate was barren muddy sand with patches of oysters *Crassostrea virginica*) wherever roots or other firm substrates allowed their colonization, and oysters covered all mangrove roots. Everglades Nearshore stations were near the mouths of streams that opened into the Gulf of Mexico. The sea floor at CTB was soft mud and oyster shell, whereas the sea floor at LMI and Shark Point (SPT) was hard sand and shell with rock protrusions. Around and shoreward of the stations, expansive oyster reefs spread across broad areas of shallow water and oysters coated the mangrove roots. The sea floor at all Everglades Offshore stations except NWC consisted of muddy-sand hard-bottom

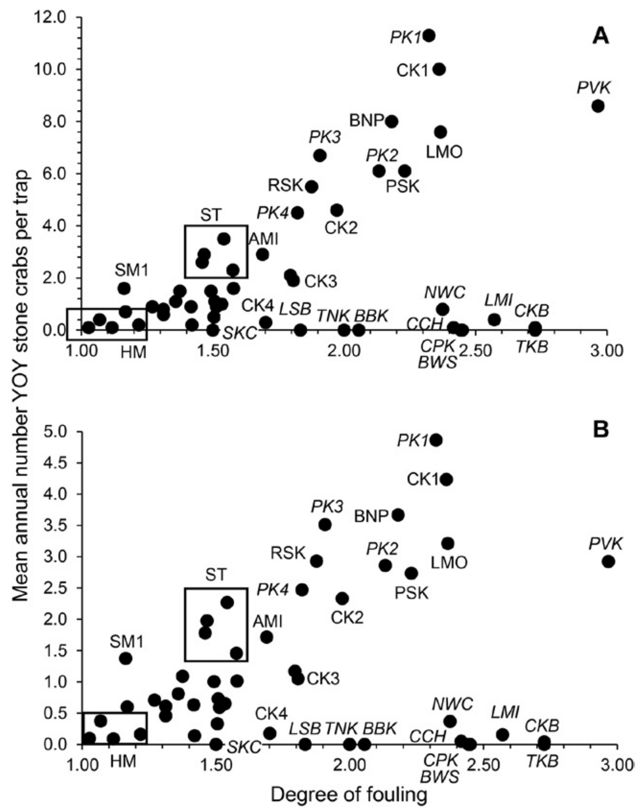

Figure 10. Relationship between mean annual degree of fouling on traps and mean annual relative abundance (number per trap) of young-of-the-year (YOY) stone crabs (from Table 1; for northwest Florida, only values for 2006 to 2009 studies were used). Identifiers are stations (three letters) and locations (two letters) defined in Table 1 and shown in Figure 1; italicized identifiers are located in the Everglades subregion. Not all stations are labeled. (A) Direct values for YOY stone crab relative abundance were used. (B) Values for relative abundance of YOY stone crabs were adjusted by dividing each value by the corresponding mean annual degree of fouling.

with emergent limestone rock and sparse seagrass (principally *Halodule wrightii*). Benthic invertebrate growth (sponges, soft corals, small hard corals, hydroids, barnacles, tunicates) and benthic macroalgae were lush on the rock. At NWC, the bottom was hard calcareous sand and shell with sparse benthic structure similarly covered with benthic organisms.

The shallow basins of Florida Bay are defined by nearly emergent to emergent banks with interspersed islands. The banks are cut by one to a few narrow channels that interconnect adjacent basins and connect outermost basins to open water. Benthic communities in some basins have changed since the time of sampling. At that time, sediments in upper Florida Bay [stations Blackwater Sound (BWS), Tern Keys (TNK), and Black Betsy Keys (BBK)] ranged from soft, calcareous, muddy sand to flocculent calcareous oolite with sparse seagrass patches (*Halodule wrightii, Syringodium filiforme*) and small, low (<1 m) limestone outcrops with benthic filamentous red and green algae. Sediments at CPK were flocculent calcareous oolite. Sparse limestone outcrops were covered with invertebrates (sponges, soft corals, and tunicates) in addition to the algae common in eastern Florida Bay. The sea floor at stations

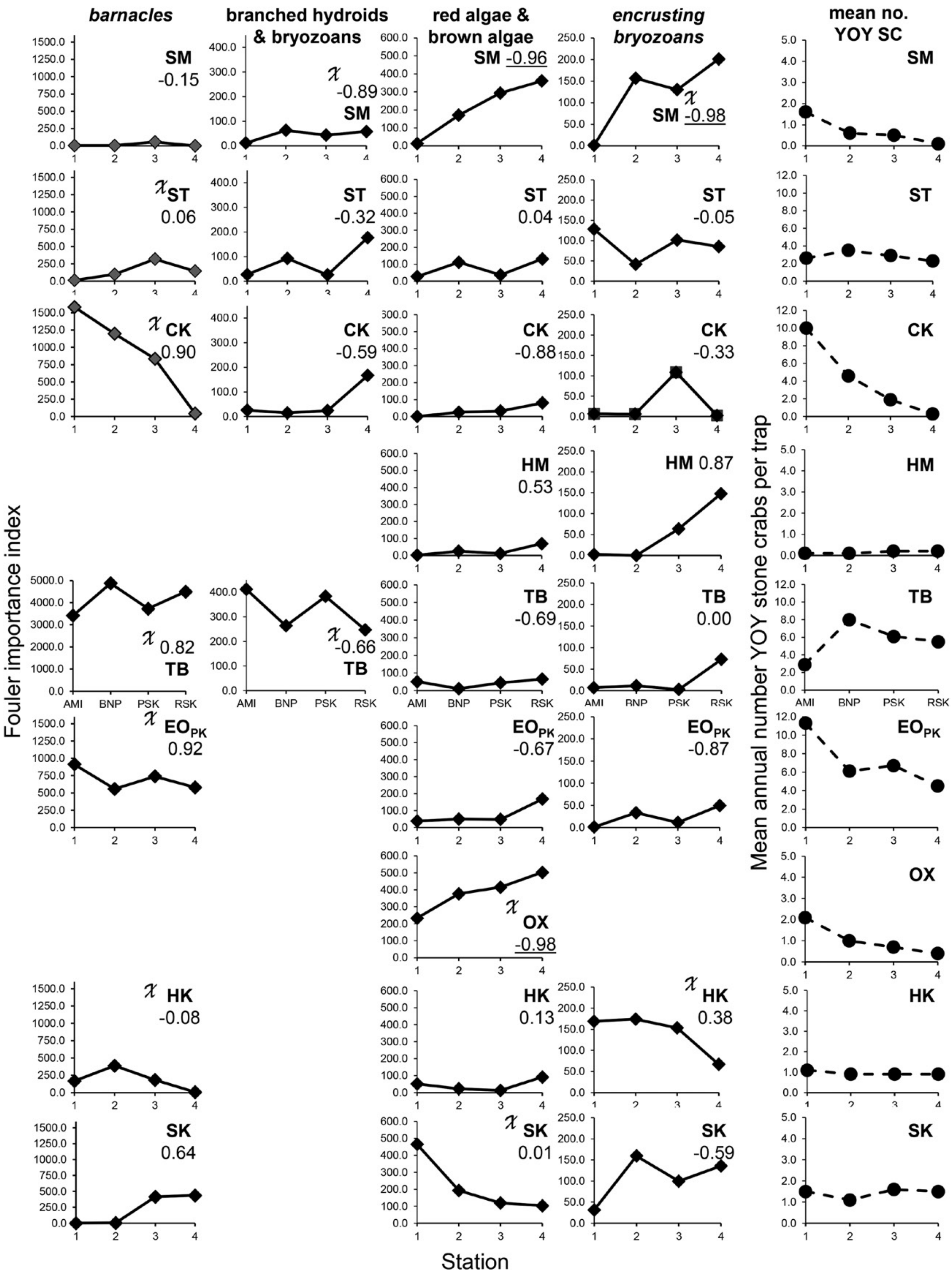

Figure 11. Comparison of variation in principal trap fouler importance indices (defined in Appendix 4) among stations and locations with mean annual relative abundance of young-of-the-year (YOY) stone crabs (mean no. YOY SC, from Table 1). Location abbreviations defined in Table 1. Italicized, predominant summer principal foulers (see Appendix 3). χ, principal fouler common during YOY stone crab recruitment season (July to November; see Appendix 4). Missing graphs signify the absence of the targeted biota (or mud) as a principal fouler at that location. Note different *Y* axis scales for barnacles and worm tubes at TB and for differences among locations in the relative abundance of YOY stone crabs. Coefficients for correlations between variation in fouler importance index among stations and mean no. YOY SC within locations are shown with location abbreviation; significant ($P < 0.05$) values are underlined.

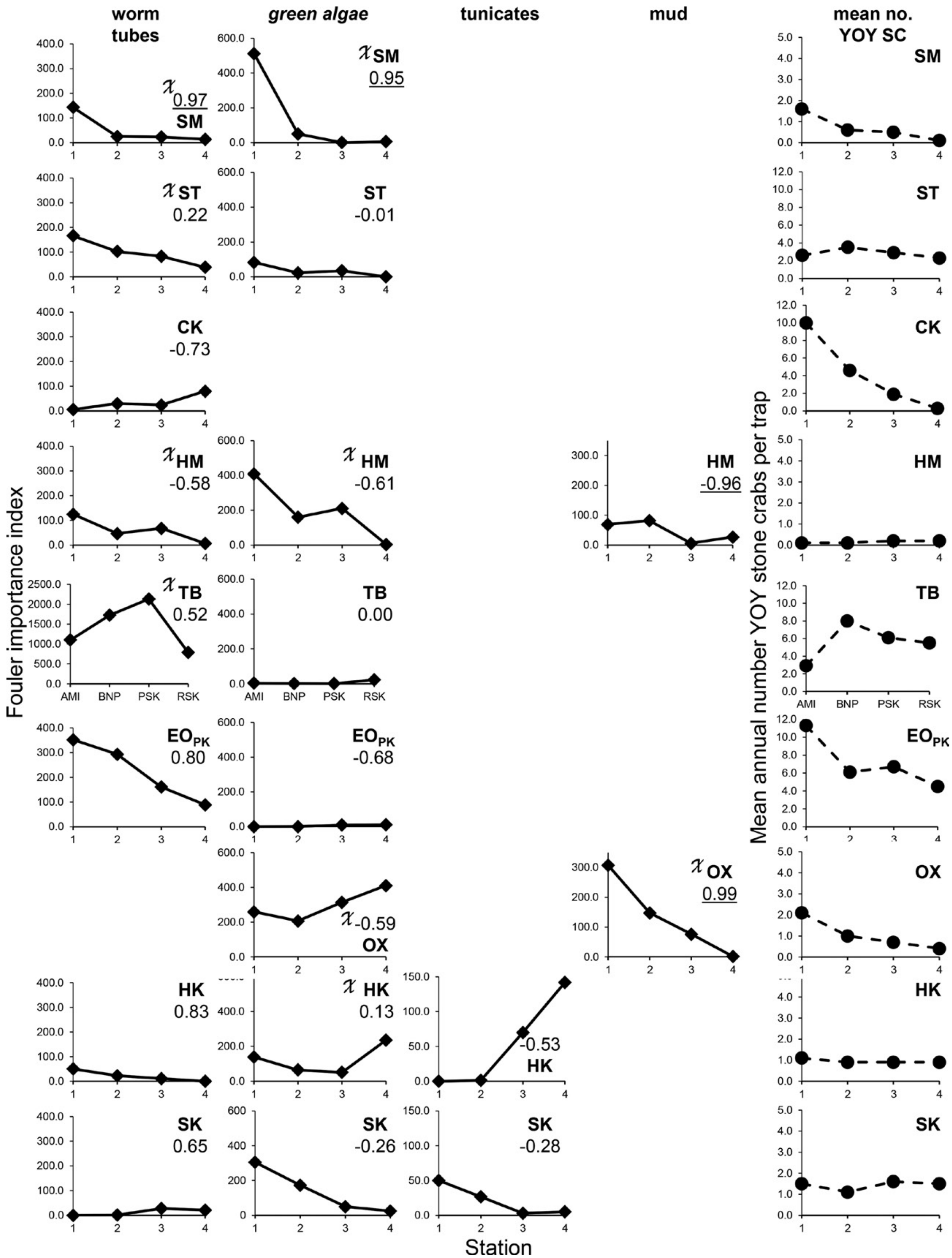

Figure 11. (Continued)

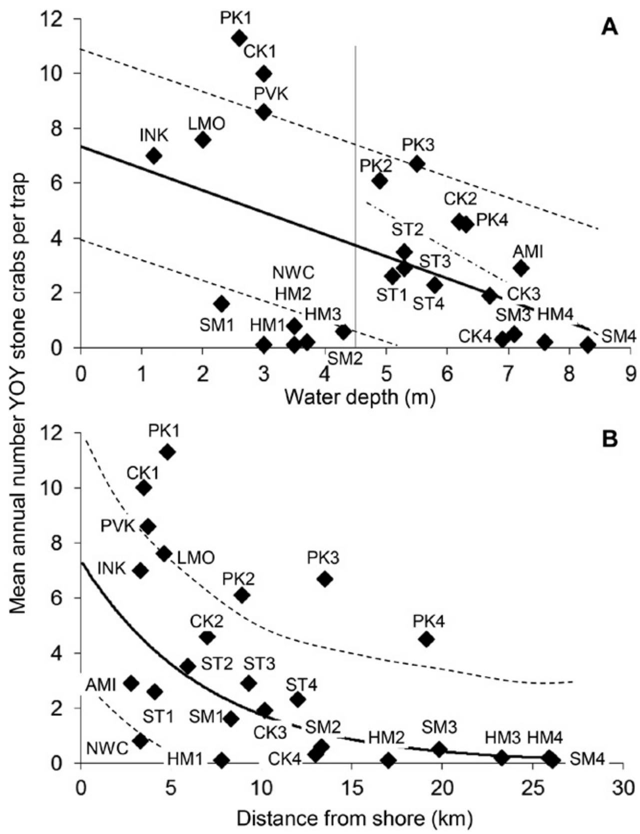

Figure 12. Dependence of relative abundance of YOY stone crab (genus *Menippe*) from peninsular Florida Gulf of Mexico waters on water depth and distance from shore. Solid lines, least-squares regression lines (highly significant; see Results); short-dashed lines, approximately ±1 SD from the mean value for the data set. Station abbreviations defined in Table 1; station locations shown in Figure 1. (A) Depth versus relative abundance. Dash-dot line, least-squares regression line for depths more than 4.5 m (demarcated by solid vertical line). (B) Distance from shore (kilometers) versus relative abundance.

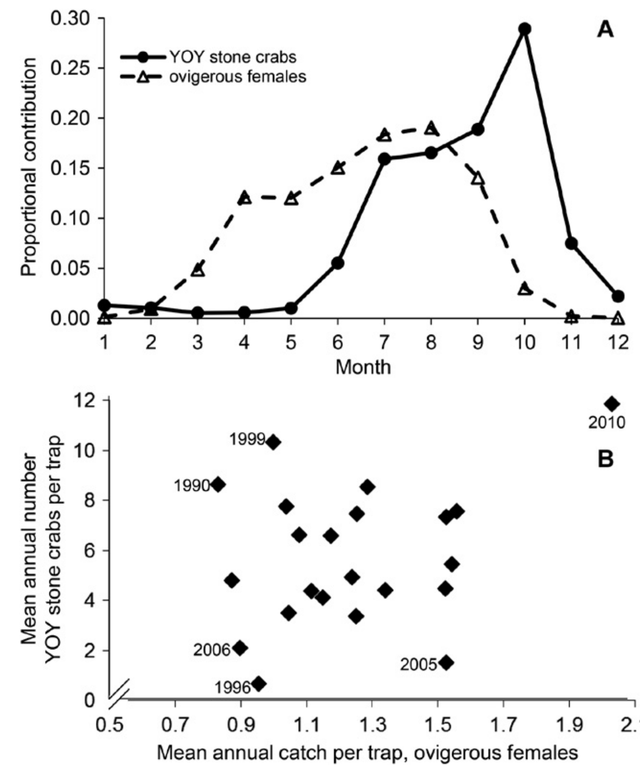

Figure 13. Associations between relative abundance of ovigerous female stone crabs (females carrying eggs) and relative abundance of young-of-the-year (YOY) stone crabs (genus *Menippe*). (A) Relationship between monthly proportional contributions of YOY stone crabs and ovigerous females. N, YOY stone crabs = 32,504; N, ovigerous females = 6,537. Month, 1 = January, 2 = February, and so on. (B) Correlation between mean annual relative abundances of YOY stone crabs and ovigerous females. Note the distinction of 2010, a year with an exceptionally cold winter followed by an exceptionally warm summer. Other outlier years of high or low YOY stone crab relative abundance are also noted (see Figure 15). n range, YOY stone crabs: 173–9,404; ovigerous females: 1,979–3,111.

TKB and ASK was of interspersed soft to firm calcareous sand and shell, robust seagrass flats (principally *Thalassia testudinum*), and emergent limestone outcrops covered with benthic organisms such as large and small sponges, soft corals, small hard corals, tunicates, hydroids, bryozoans, sea anemones, and algae. Large sponges (mostly loggerhead, *Spheciospongia vesparium*) were occasionally present. Similarly structured sea floor and benthic communities were present in the vicinity of SKC. Water flowed swiftly through CCH and SKC, which are channels leading to the open Gulf of Mexico. Channel bottoms and walls were composed of hard sand and patchy rock outcrops with barnacles, tunicates, small sponges, and algae firmly attached. Additional details of ENP-station and Florida Bay habitats are provided in Bert et al. (1986).

In the Keys, the substrate was principally patchy, emergent, porous limestone rock (less than 1.0 m height) interspersed with oolite and sand with shell fragments and occasional seagrass (*Syringodium filiforme, Thalassia testudinum*) flats. The rocks were colonized by a benthic assemblage similar to that of western Florida Bay, but with more soft and hard corals. Algal species composition differed markedly from that of Everglades stations and was more characteristic of typical coral reef flora (Mathieson & Dawes 1975). Further information on Gulf-side Florida Keys habitats is provided in Stevely et al. (2010). Altogether, the benthic communities on traps reflected the communities inhabiting hard structures in the immediate areas where the stations were located; but at some locations, (e.g., Oxfoot Bank), the diversity of benthos on the traps was limited compared with the diversity that inhabited the local limestone outcrops.

Water depth and distance from shore. Depth was a significantly important influence on mean annual YOY stone crab relative abundance at the St Marks, Steinhatchee, and Homosassa locations, Everglades subregion, and All Locations area (Table 4). Along the Gulf Coast, on average, YOY stone crab relative abundance decreased by 0.79 individuals with each meter of increasing depth ($y = -0.79x + 7.50$, $r^2 = 0.13$, $df = 23$), but the reduction was not significant due to the split between stations with very high or very low relative abundances at depths less than 4.5 m (Fig. 12A). Mean annual YOY stone crab relative abundance was greater than or equal to 7.0 at Everglades Offshore and Cedar Key stations closest to shore but less than 2.0 at shoreward St. Marks and Homosassa stations and at Everglades Offshore station NWC; and all of the low values were less than the minimal range for standard deviation. In contrast, at depths more than 4.5 m, relative abundances at nearly all stations fell within the standard deviation range and generally decreased by an average of 1.3 individuals with each increasing meter of depth ($y = -1.32x + 11.0$, $r^2 = 0.43$; $df = 12$, $P = 0.01$).

In the Gulf Coast area, relative abundance of YOY stone crabs decreased exponentially with increasing distance offshore (Fig. 12B; $y = 7.34e{-0.143x}$; $r^2 = 0.44$, $df = 23$, $P < 0.01$). Several stations with high relative abundance values were located less than or equal to 7 km from shore, whereas all stations at the two locations with lowest mean annual relative abundances (SM and HM) were more than 7 km offshore. The very low mean annual relative abundance at NWC, which was located in shallow water close to shore, and the very high relative abundances at PK2 to PK4, which were approximately 9 to 19 km offshore and in water greater than 5 m deep, indicate that other factors were also important in determining the relative abundance of YOY stone crabs at those stations.

Biological Relationships, Ecological Disruptions, and Meteorological Events

All correlations between the monthly frequencies of YOY stone crabs and ovigerous females from Tampa Bay were significant when the frequency of ovigerous females was set back, but the highest correlation was when that frequency was delayed by 2 mo (0.89, $P < 0.01$, $df = 10$) (Fig. 13A). The relative abundances of both YOY juvenile and ovigerous female stone crabs varied greatly among years, but were not correlated ($r = 0.30$, $df = 20$) at Tampa Bay. Nevertheless, the relative abundances of both ovigerous females and YOY stone crabs in 2010 were significantly higher than in all other years (t-test for comparison of a single observation with the mean of a sample, performed separately for relative abundances of ovigerous females and YOY stone crabs; t, P, respectively: 3.45, 0.01; 5.74, 0.001; $df = 20$ for both tests) (Fig. 13B).

The high level of variation in the pattern and timing of YOY stone crab recruitment at Tampa Bay (Fig. 14) made it difficult to determine whether red tides or tropical cyclones affected that recruitment. Although YOY stone crab relative abundance was high most frequently from July through October, the period of highest relative abundance could begin as early as May (e.g., 1991–92) or as late as September (1998–99) and end as early as July (2003–04) or as late as November (2009–10). The period of lowest relative abundance began most frequently during

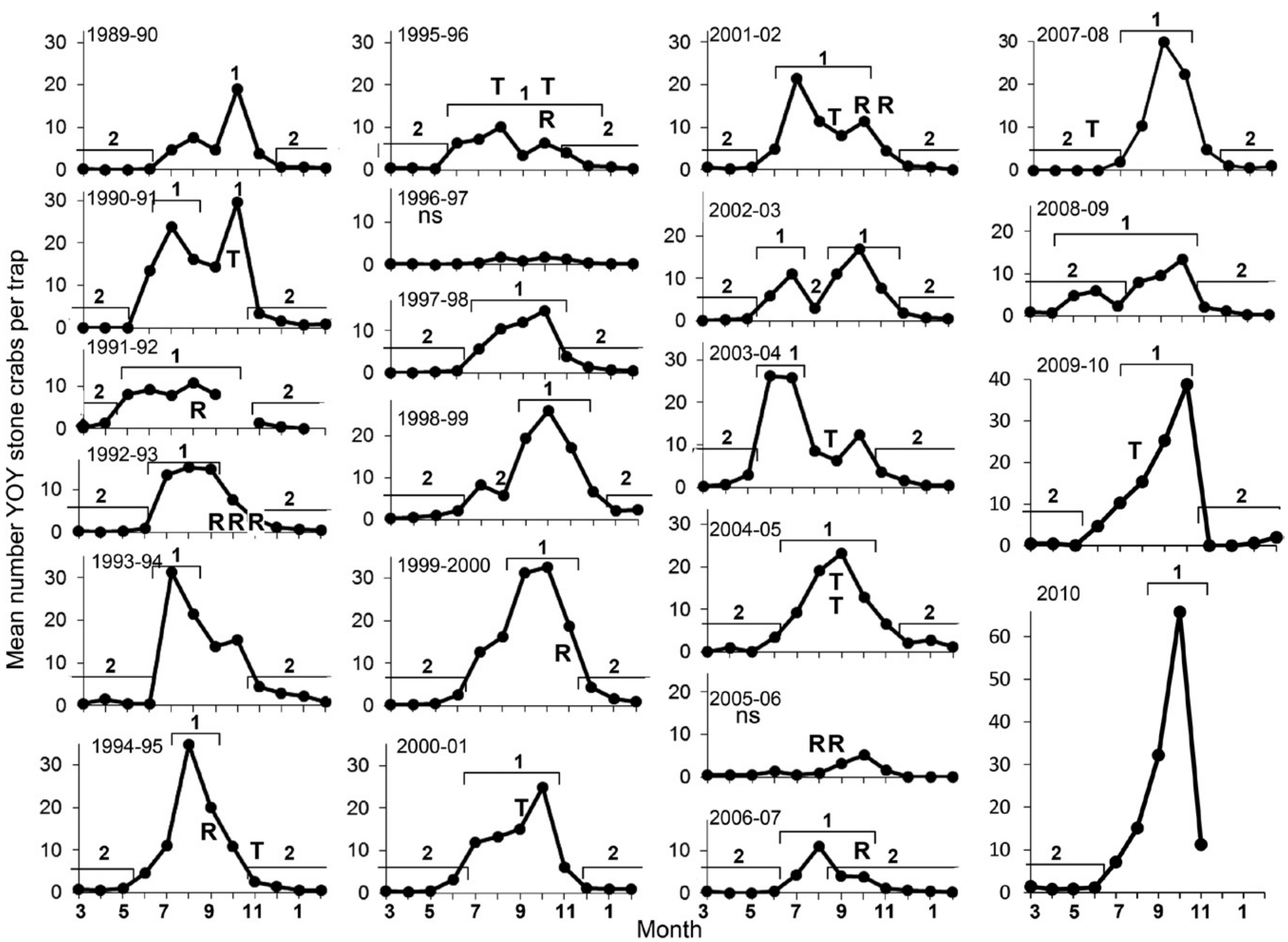

Figure 14. Relationship between variation among months in relative abundance of young-of-the-year (YOY) stone crabs (genus *Menippe*) at Tampa Bay (location shown in Figure 1) and timing of red tide (*Karenia brevis*) blooms and tropical cyclones. Months are numbered: 3, March; 5, May; 7, July, and so on. Numbers and bars above graphs connect months with statistically similar abundances: 1, group including month of highest abundance; 2, group including month of lowest abundance; ns, no significant groupings. R, months during which red tide blooms occurred in or near Tampa Bay stations; horizontally sequential letters denote single blooms that extended for more than 1 mo. T, months during which tropical cyclones passed through or near Tampa Bay; multiple letters arrayed vertically above a single month denote the number of events occurring during that month.

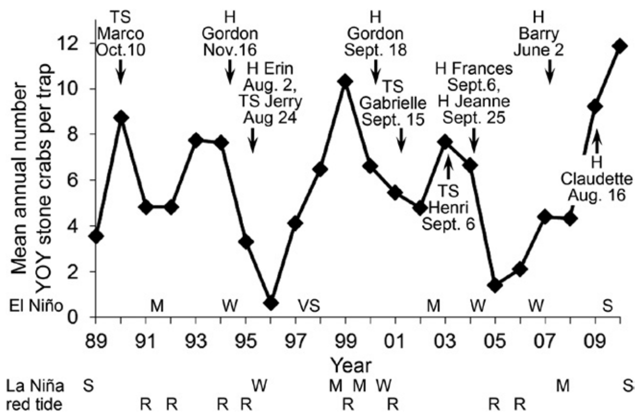

Figure 15. Relationships between mean annual relative abundance of young-of-the-year (YOY) stone crabs (genus *Menippe*) from Tampa Bay and tropical cyclones (delineated above the graph: TS, tropical storm; H, hurricane), ENSO events (El Niño, above X axis; La Niña, below X axis; W, weak; M, moderate; S, strong; VS, very strong), and red tide (*Karenia brevis*) blooms. Abbreviations for El Niño and La Niña strength appear between years because those events typically occurred during winters and crossed years. Overall annual mean relative abundance of YOY stone crabs: 5.8.

November (16 of 22 y) but could occur as late in the year as January (1998–99). The pattern of variation in the relative abundance curve also differed among years. Relative abundance could be high only early in the recruitment season (1993–94), only late in the season (1989–90), or throughout the season (2001–02). Recruitment peaks could be unimodal (many years) or bimodal (2002–03).

Red tide outbreaks occurred during 8 of the 22 y of sampling at Tampa Bay (Fig. 14); and relative abundance of YOY stone crabs decreased during the month following the red tide outbreak 7 of those 8 y; but the prevalence of red tides in September, October, and November coincided with the temporal interval when YOY stone crab relative abundance always decreased. This coincidence generated uncertainty about the influence of red tide on relative abundance. Moreover, unless an intense red tide bloom was specifically present at a station, the bloom might not affect YOY stone crab relative abundance. Nevertheless, mean annual relative abundance was low (≤5) in 6 of the 8 y that red tides were present (Fig. 15).

The influence of tropical cyclones on monthly YOY stone crab relative abundance was similarly difficult to discern. Tropical cyclones passed close to or over Tampa Bay 9 of the 22 y of sampling at that location (Fig. 14). As for the situation with red tides, tropical cyclones frequently occurred during or just prior to months when relative abundance ordinarily decreased; and tropical cyclones sometimes occurred in close temporal proximity to red tides, further complicating the interpretation of relationships between those physical variables and YOY stone crab relative abundance.

From a broader perspective, variation in mean annual relative abundance of YOY stone crabs was related to the sporadic occurrence of large-scale meteorological phenomena operating on multiyear time scales. Tropical cyclones had a large, but delayed, effect on YOY stone crab mean annual relative abundance at Tampa Bay (Fig. 15). In seven of the nine occurrences,

TABLE 10.

Direction of YOY stone crab (genus *Menippe*) mean annual relative abundance (number per trap per sampling period) in Tampa Bay, FL, following years during which tropical cyclones did or did not pass through or very near the bay.

	Number of years	
Direction of YOY stone crab relative abundance, year following a year with or without a tropical cyclone	**With tropical cyclones**	**Without tropical cyclones**
Higher than or approximately the same as target year	2	12
Lower than target year	7	1

Mean annual YOY stone crab relative abundance decreased in the year following a year with a tropical cyclone 7 of 9 y, whereas YOY stone crab relative abundance increased in the year following a year without a tropical cyclone 12 of 13 y (see Figure. 15); a highly significant frequency difference. YOY, young-of-the-year.

TABLE 11.

Coefficients for correlations between proportional contribution of the mean annual relative abundance of YOY stone crabs (genus *Menippe*) (Table 1) and seasonal commercial fishery stone crab landings for Florida Gulf of Mexico coastal counties corresponding to sampling locations for YOY stone crabs (see Fig. 16).

	Area		
Data used	**Counties**	***n***	***r* value**
Counties corresponding to YOY sampling locations			
Total landings	Individual counties*	14	0.07
	Muller-Bert regions†	5	0.22
Standardized landings	Individual counties	14	−0.71¶
	Muller-Bert regions	5	−0.78§
Tampa Bay			
Corresponding years, landings and YOY stone crab recruitment	Individual counties	22	0.06–0.27‡
	Counties averaged	22	0.15
1-y delay in landings	Individual counties	22	0.07–0.26‡
	Counties averaged		0.17
2-y delay in landings	Individual counties	22	0.03–0.29‡
	Counties averaged		0.18
3-y delay in landings	Individual counties	22	0.03–0.20‡
	Counties averaged		0.06

The stone crab harvesting season extended from October 15 to the following May 15. YOY, young-of-the-year.
* All Gulf coastal counties.
† Regions defined in Muller and Bert (1997).
‡ Range for Pinellas, Hillsborough, Manatee, Sarasota counties.
§ $P \le 0.05$.
¶ $P \le 0.01$. Note that the only significant r values are for negative correlations, the opposite of the expected direction of the correlations.

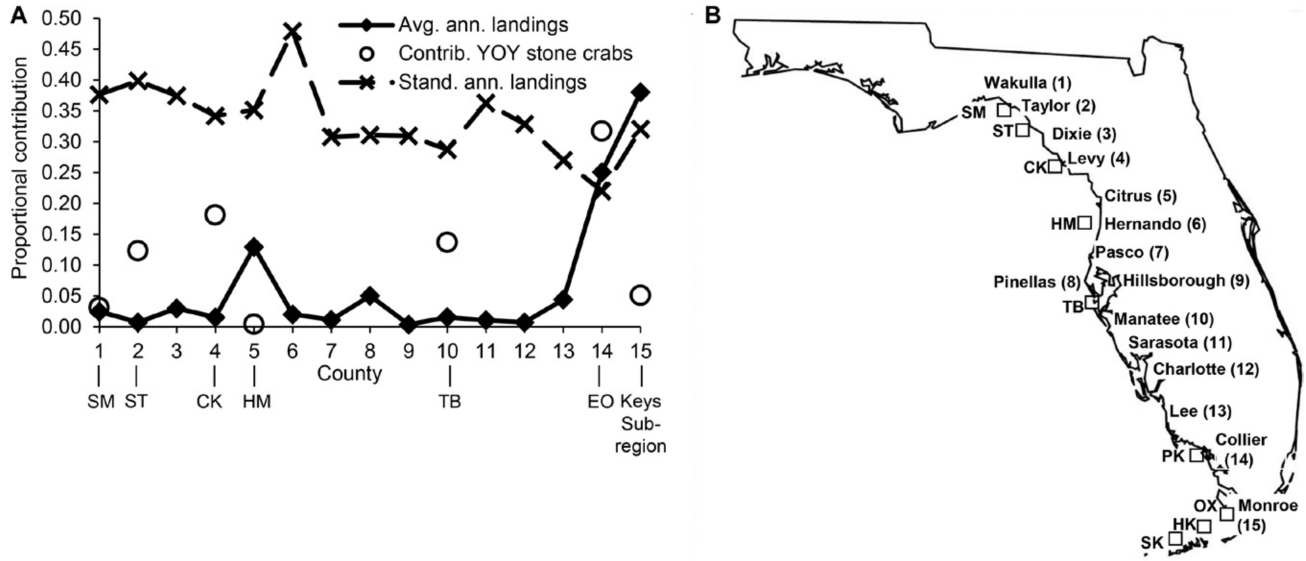

Figure 16. Relationship of direct (Avg. ann. landings) and standardized (Stand. ann. landings) proportional contribution of annual commercial stone crab fishery landings, by county (both data sets 1978 to 2015; see Statistical Methods for method of calculations) to proportional contribution of average annual number of young-of-the-year (YOY) stone crabs collected for the present study (Contrib. YOY stone crabs, from Table 1). (A) Fishery landings and relative abundances. Locations used in this study (defined in Table 1, shown in Fig. 1) are shown below county numbers. (B) County locations and numbers.

mean annual relative abundance decreased, sometimes markedly, the following year. In sharp contrast, mean annual relative abundance increased, often markedly, in 12 of the 13 y that followed years without tropical cyclones. The difference in these trends is highly significant ($P < 0.001$, 2×2 *G*-test of independence; Table 10). Additionally, the 3 y with the lowest mean annual relative abundance values (1996, 2005, and 2006) followed years when two tropical cyclones per year passed through peninsular Florida and the eastern Gulf of Mexico (1995 and 2004). Although no tropical cyclones passed very near Tampa Bay in 2005, two major hurricanes and a tropical storm traveled northward in the eastern Gulf of Mexico and major hurricanes Katrina and Wilma passed across the Southwest Florida region. Lastly, weak ENSOs occurred during the winters preceding two of the near-zero recruitment seasons (La Niña, 1995 to 1996; El Niño, 2004 to 2005); and a red tide persisted from May through December 2005 at the mouth of Tampa Bay (Flaherty & Landsberg 2011).

Fishery Applications

The proportion of the average annual relative abundance of YOY stone crabs collected at each location was not correlated with commercial stone crab fishery landings for either the corresponding counties or the groupings of counties (Table 11, Fig. 16A, B); most correlation coefficients were near zero. Correlations between standardized landings and relative abundances at individual counties and in regions defined by Muller and Bert (1997) accounted for approximately ¾ of the variation between the two measures; but the correlations were in the opposite direction from that expected. The negative correlations imply that fishery landings increased as mean annual relative abundances of YOY stone crabs decreased.

DISCUSSION

Recruitment

Broad Spatial and Temporal Patterns

YOY stone crab recruitment occurs throughout peninsular FL, but recruitment levels are not evenly distributed. Four principal recruitment grounds persist through time. The two major (Cedar Key and Everglades Offshore) and two secondary (Steinhatchee and Tampa Bay) recruitment locations persist through decades; but among years, their proportional contributions to the YOY stone crab recruitment pool vary somewhat. In contrast, none of the locations where recruitment was low exhibited temporary pulses of high, or moderately high, recruitment in any year. Recruitment was lowest—essentially zero—in Florida Bay during the year of the Everglades National Park study. The Northwest Cape Sable, Oxfoot Bank, and Keys data suggest that recruitment may be consistently low from Northwest Cape Sable southward through Florida Bay and westward along the Gulf of Mexico side of the Florida Keys. Recruitment may also be consistently low at northernmost St. Marks and at Homosassa, at least in the area encompassing the stations serviced for this report. The long-term data from Tampa Bay show that, at least at secondary recruitment locations, recruitment can vary greatly among years, ranging from very high through precipitous declines to near zero. Moreover, interannual variation in recruitment is location-specific. As demonstrated by differences in the interannual patterns of relative abundance among the four principal recruitment locations, within a specific year, recruitment may be unusually high at one location but unusually low at another location.

In the open Gulf of Mexico along the Florida peninsula, the relative abundance of YOY stone crabs is high (usually highest) nearshore, low offshore, and decreases steadily as distance from shore increases, regardless of the overall level of

YOY stone crab recruitment. At major recruitment locations, the increase in recruitment during years of high recruitment occurs principally nearshore. In contrast, recruitment offshore may not differ significantly among years, regardless of the level of recruitment at the location. Relative abundance may also be high in the mouths of large bays behind barrier islands, as exemplified by at Tampa Bay stations BNP and PSK. In contrast, relative abundance has little relationship to distance from shore along the Gulf side of the Keys.

Seasonal Patterns

Larval production, settlement, and growth through early juvenile stages of most marine crabs and lobsters occurs during the warm season of the year (e.g., Dittel & Epifanio 1982, Orth & van Montfrans 1987, Palma et al. 1999, Martínez & Navarrete 2002), and the same is true for YOY stone crabs in the Florida Gulf. But the YOY stone crab recruitment season (broadly, July–November; highest recruitment, September–October) occurs later as latitude decreases. Data from other studies also suggests that the spawning season peaks earlier at Cedar Key and later at Everglades (Fig. 17 in Bert et al. 1986). Recruitment season may be constricted at northern locations by the earlier arrival of decreasing temperatures in autumn. The earlier recruitment peak at the northerly locations may also be due in part to the presence of large fractions of *Menippe adina* and hybrid forms in the local populations. Highest densities of juvenile *M. adina* in size distributions similar to those presented herein were collected by various means July to September in Mississippi Sound (Stuck & Perry 1992, Shervette et al. 2004), suggesting that juvenile *M adina* recruitment season is shorter and initiates earlier in the year than that of *Menippe mercenaria*. The *M. mercenaria*/*M. adina* northwest Florida hybrid zone extends in the open Gulf to at least Cedar Key (Bert 1986). Hybrid forms are common in Middle Tampa Bay (T. M. Bert, personal observation), and may influence reproductive, larval, and YOY stone crab recruitment seasons. The later spawning and YOY stone crab recruitment seasons in Southwest Florida may be related to the absence of *M. adina*. Spawning and young-life-stage recruitment may occur later in the year for *M. mercenaria* compared with those seasons in *M. adina*.

Recruitment of YOY stone crabs tends to follow similar temporal patterns of variation in relative abundance throughout a location. Months of peak or low relative abundance tend to be the same from nearshore to offshore, as do unimodal and bimodal recruitment peaks and narrow or broad periods of high recruitment levels. Over long time periods, peaks in recruitment can occur during any month of the recruitment season, and the patterns of variation in recruitment among months can take a variety of forms, as exemplified by the long recruitment record in Tampa Bay.

Influence of External Variables on Recruitment

Physical Conditions

All physical variables considered were relevant for YOY stone crab recruitment, as exemplified by the most highly weighted negative binomial model, which included all covariates; but comparative importance of the variables differed greatly among locations. It is important to note that the studies included herein were not controlled experiments designed to fully describe YOY stone crab recruitment, so without sufficient range of variation compared with other variables, a specific variable might carry little weight, even if it was actually important.

Other than Steinhatchee and the comprehensive All Locations area, suites of many models accounted for variation in YOY stone crab recruitment at the locations and areas, further illustrating the relevance of all covariates considered in the analysis. Steinhatchee was unique in that the model that excluded only the fouling covariate accounted for nearly all variation in recruitment. Similarly, for All Locations, only the model that included all covariates and the model that excluded only T × S accounted for 86% of all variation.

The frequent inclusion of temperature, salinity, and fouling on traps in the two most highly weighted negative binomial models and their high partial weight totals for many locations and areas demonstrate that these were the most important physical variables related to YOY stone crab recruitment. But they were not important for every location and area, and their relationships to recruitment differed among those entities.

Temperature and salinity. The geographic expanse of this study included the eastern portion of the northwestern Florida hybrid zone between *Menippe mercenaria* and *Menippe adina* (Bert 1986, Bert & Harrison 1988). Both species (but principally *M. mercenaria*) and a broad array of hybrid types inhabit the St. Marks, Steinhatchee, and Cedar Key locations (Bert 1986). Young life stages of *M. adina* are better adapted to low temperatures and salinities than are life-stage analogs of *M. mercenaria* (Field 1989, Brown & Bert 1993). Therefore, understanding the influence of temperature and salinity on the YOY stone crabs from these locations requires considering the temperature and salinity tolerances of both species.

The strong seasonality of YOY stone crab recruitment made temperature the most influential variable for recruitment, despite the elimination of February, March, and April from the negative binomial regressions. As could be expected, temperature was most influential for recruitment where seasonal temperature changes were comparatively large—from Tampa Bay northward and for areas spanning broad latitudinal ranges. Comparatively cooler temperatures north of Tampa Bay during April and, particularly, during October may be the most important influences on the timing and duration of spawning and young-life-stage recruitment in stone crabs. Temperature was less influential on YOY stone crab recruitment in the Everglades subregion, where salinity variation among locations was greater than temperature variation.

At many locations, temperature was related to YOY stone crab recruitment both linearly and nonlinearly. Recruitment initiation during early summer is exponential, whereas recruitment cessation during autumn is linear. The abrupt increase in recruitment is likely related to the abrupt initiation of spawning (Bert et al. 1986, 2016b) coupled with reduced survival of early-season larvae and delayed metamorphosis into crab stage (Field 1989, Brown et al. 1992). Spawning in females begins to accelerate at 20°C and attains the high levels sustained through summer at 23°C (Bert et al. 2016b). Those temperatures are reached during April and early May northward of Tampa Bay and during March and April from Tampa Bay southward. Thus, the considerable spawning that occurs during April and

May (Bert et al. 1986, Wilber 1989, Bert et al. 2016b) should result in easily detectible numbers of megalopae and early-stage (1–5) juvenile stone crabs during May and June, given the length of larval duration at 25°C (Ong & Costlow 1970, Brown et al. 1992), a temperature that is attained or exceeded at every location during May. But temperatures of 20°C or lower, which occur during April everywhere except the Southwest Florida region, are far below temperatures optimal for survival of all *Menippe mercenaria* zoeal stages (27°C–29°C; Brown et al. 1992). Such low temperatures can significantly reduce larval survival and lengthen larval development time of both *M. mercenaria* and *M. adina*, even at optimal salinities (Porter 1960, Field 1989, Brown et al. 1992). Thus, relatively few stone crab larvae spawned early in the reproductive season may survive. Those that do would have, on average, a longer larval life span than would larvae spawned later in the reproductive season. Those larvae would complete development to metamorphosis during the same time frame as the more rapidly developing larvae spawned later when the water is warmer. The net result would be a sudden flush of megalopae and early-stage crabs when temperatures approached the optima for their survival. The linear decline in YOY stone crab relative abundance during autumn may be the product of the steady growth of YOY stone crabs out of the size range defined for this study, a shift in preferred habitat with increasing size, and less movement as temperatures decreases, as well as mortality through time.

The optimal temperatures for *Menippe mercenaria* and *Menippe adina* PS-juvenile survival estimated by Brown and Bert (1993; 21°C–23°C) were several degrees lower than the important temperature range determined in this study empirically (observed temperature at which relative abundance started to rapidly increase during spring) and theoretically (estimated temperature for highest relative abundance in the negative binomial model): 27°C–28°C. Timing of the initiation of spawning season and the effects of low temperature on larval survival and growth rate were not components of Brown and Bert's (1993) study, whereas in this study, they were integral background elements that could account for the temperature differences between studies. Brown and Bert's (1993) values may reflect temperature adaptation in preparation for the first winter that the YOY stone crabs must endure. The optimal temperature range estimated in this study implies that winter temperatures at Cedar Key and Steinhatchee are cold enough to kill *M. mercenaria* larvae and PS-juveniles (Brown et al. 1992, Brown & Bert 1993). The existence of those robust recruitment grounds may be because of hybridization between *M. mercenaria* and the more cold-tolerant *M. adina* (Brown & Bert 1993). In a field study, Stuck and Perry (1992) collected *M. adina* megalopae and PS-juveniles from water as cold as 7°C.

Basic salinity tolerances determine distributional proximity to the coast for YOY stone crabs. Although laboratory studies show that larval and juvenile *Menippe adina* have higher tolerances for lower salinities than do corresponding *Menippe mercenaria* life stages (Field 1989, Brown & Bert 1993), survival of early life stages of both species, particularly the megalopal and first crab stages, is low at a salinity of 20 (Field 1989). Thus, salinities were consistently or irregularly too low for substantial recruitment at the Everglades Inshore and Everglades Nearshore locations. Elsewhere, despite its lack of significance in many of the two most heavily weighted negative binomial regressions, partial weight totals established that salinity strongly influenced YOY stone crab relative abundance, at least in broad areas (Gulf Coast, All Locations) and where salinity varied greatly among stations (Everglades Gulf, Everglades All). Predicted salinity optima range 29–33 through the larval stages for *M. mercenaria* and for PS-juveniles of both species (Brown et al. 1992, Brown & Bert 1993, this study). But in field studies, *M. adina* juveniles are commonly found in lower salinity waters than are *M. mercenaria* juveniles (compare Perry et al. 1984 and Stuck & Perry 1992 with this study); and at some low-temperature low-salinity combinations, survival of PS-juvenile *M. adina* is significantly higher than that of *M. mercenaria* (Brown & Bert 1993). The unusual peak in YOY stone crab relative abundance at a salinity of 19 documented in this study may be a simple anomaly or due to a pulse of *M. adina* and *M. adina*–like hybrids in samples.

Prolonged high salinities at levels lethal to larval and YOY stone crabs were common during recruitment season in Florida Bay and every year at the three Keys locations. Other physical conditions were more favorable for YOY stone crab recruitment at those locations, implying that high salinity and temperature–salinity combinations are the most important factors limiting recruitment in Florida Bay and on the Gulf of Mexico side of the Keys. Sporadic high salinities during recruitment season also may have reduced recruitment at specific stations elsewhere, such as CK4 at Cedar Key. All traps from each location that contained no YOY stone crabs during peak recruitment season, except those at Everglades Inshore and Everglades Nearshore, were serviced when salinity was very high.

Sublethal but extreme temperatures and salinities can interact to affect larval and PS-juvenile stages of both species more than when either variable alone is extreme (Field 1989, Brown et al. 1992, Brown & Bert 1993). Although the extent of the effect depends on the temperature–salinity combination, survival is reduced when both temperature and salinity are very low or very high or when the two variables are near opposite extremes. The negative binomial regressions and their partial weights established that the temperature–salinity interaction was an important influence on mean annual YOY stone crab relative abundance at Steinhatchee, Homosassa, and throughout much of the Southwest Florida region; however, the affecting temperature/salinity combinations differed among locations. Low temperatures and high salinities were common during October and November from Homosassa northward and may have increased mortality in larvae spawned late in the reproductive season and in YOY stone crabs when their relative abundances should be high. High temperatures associated with the shallow water coinciding with low salinities as a result of summer rains throughout the larva and YOY stone crab recruitment seasons likely contributed to zero-to-low recruitment at Everglades Inshore and Everglades Nearshore. Long durations of very warm temperatures and often near-lethally high salinities during most of the recruitment season probably contributed to the near-zero recruitment throughout Florida Bay and low recruitment throughout the Keys despite the presence of numerous ovigerous females (Bert 1985, Bert et al. 1986) and suitable habitat.

Trap fouling and habitat. Comparing observations made during the scuba surveys with the observed fouling on the stone crab traps showed that the fouling communities on the traps did not precisely mimic their respective local sessile benthic communities but were representative of them. Because the traps were cleaned each month, seasonal changes in the predominant algae and invertebrates on the traps probably reflected seasonal variation in composition of the settling spores and postlarvae of those organisms. Although barnacles predominated on traps at some Cedar Key, Tampa Bay, Everglades Nearshore, and Everglades Offshore stations during YOY stone crab recruitment season, other summer foulers were also present, sometimes in substantial numbers. At other locations, the organismal composition and diversity of fouling organisms on traps resembled those on the local rocky outcrops around the trap lines. Thus, variation among stations in YOY stone crab relative abundance on the traps probably represented actual *in situ* variation rather than variation due to a lack of suitable natural settlement habitat or the presence of ample suitable habitat.

Both degree of fouling and type of fouling organisms were important factors for YOY stone crab recruitment. YOY stone crab relative abundance was highest on traps with well-developed, highly three-dimensional communities of organisms. Heavy fouling during summer with barnacles as the principal fouler is clearly related to high relative abundances at major stone crab recruitment locations Cedar Key and Everglades Offshore and at secondary recruitment location Tampa Bay. Barnacles and associated biota provide more shelter composed of small spaces than do other biota such as filamentous marine algae or encrusting bryozoans.

But a profusion of barnacles does not ensure good YOY stone crab recruitment. Other foulers and other factors are also important influences on recruitment at those locations and elsewhere. At Steinhatchee, the other secondary recruitment location, fouling had little weight in the negative binomial regressions. There, fouling was typically moderate; and although barnacles were an important feature of the recruitment-season benthos on traps, other organisms, including worm tubes, were also common. In addition, little or no recruitment occurred at multiple stations with heavy barnacle fouling on traps throughout the recruitment season (AMI at Tampa Bay; SPT, NWC, LMI, CCH, and ASK in Everglades). In Florida Bay, fouling at some stations should have been amenable to habitation by YOY stone crabs; but hostile temperature/salinity combinations apparently overwhelmed other more favorable variables. Although fouling influences YOY stone crab relative abundance, its influence at some stations is not more important than the influences of temperature and salinity.

Fouling predominated by various combinations of algae, encrusting bryozoans, and mud during recruitment season may have contributed to low YOY stone crab relative abundances at Homosassa and Oxfoot Bank. Branched hydroids and bryozoans and encrusting bryozoans were often negatively correlated with YOY stone crab relative abundance; and collectively, they were common during recruitment season at St. Marks stations 2–4, CK4 at Cedar Key, AMI at Tampa Bay, SPT at Everglades Nearshore, and all Harbor Keys stations. Hydroid nematocysts and bryozoan chemical deterrents may ward off the small YOY stone crabs typical of peak recruitment season; and flat mats of encrusting bryozoans do not offer substantial hiding places. Tunicates were common secondary or tertiary foulers in fouling communities predominated by barnacles. They were principal foulers only at lower Keys locations, but any effect they may have had on recruitment there was likely overwhelmed by the hostile temperature/salinity conditions. Sabellid worm tubes and green algae were more common as principal foulers during recruitment season north of Tampa Bay at stations where barnacles did not overwhelm other foulers. Some negative correlations between relative abundance and the winter foulers sabellid worms and red and brown algae occurred principally because the predominance of those foulers increased as the relative abundance of YOY stone crabs decreased as the recruitment season ended. From Tampa Bay southward, worm tubes are winter foulers that have little influence on relative abundance.

Taken collectively, the relationship between fouling and YOY stone crab relative abundance differs greatly among regions, locations, and even stations within locations. In the Gulf of Mexico, PS-juvenile *Menippe* of all taxonomic forms inhabit many different, complex, three-dimensional habitats that provide an abundance of small holes for shelter, and possibly food resources; but some historical confusion exists regarding the preferred habitats of stone crabs, including YOY individuals, because of the misidentification of *Menippe adina* as *Menippe mercenaria* and lack of recognition of the northwest Florida hybrid zone before the recognition of *M. adina* and description of the hybrid zone (Bert 1986, Williams & Felder 1986). The early studies in which *M. mercenaria* was reported to inhabit oyster reefs (Menzel & Hopkins 1956, Menzel & Nichy 1958, Powell & Gunter 1968) were actually conducted within the range of *M. adina* (Bert 1986, Williams & Felder 1986). Megalopal and small juvenile *M. adina* have been found in high densities from July through September in nearshore and intertidal oyster beds (Perry et al. 1984, Stuck & Perry 1992). YOY *M. adina* juveniles have also been found in mud, sand, oyster shell hash, rock rubble, and mangrove roots (Powell & Gunter 1968, Perry et al. 1984, Brown & Haight 1992, Stuck & Perry 1992, Shervette et al. 2004, Caudill 2005) and have been collected using bags filled with hard clam (*Mercenaria* sp.) shells (Stuck & Perry 1992). In the northwestern Florida hybrid zone, juvenile stone crabs have been found from May through September in or under oyster reefs, shell rubble, rock piles, sponges, seagrasses, *Sargassum* mats, and bryozoan colonies (Menzel & Nichy 1958, Bender 1971, Wilber & Herrnkind 1986, Lindberg & Stanton 1989, Herrnkind et al. 1997, Munguia 2006). In Southwest Florida, YOY *M. mercenaria* have been collected from the bottoms of tidal channels between October and April (Tabb & Manning 1961) and from the fouling biota that grew on commercial traps from September through November (Bert et al. 1986). Bert and colleagues (Bert 1985, section 2; Bert et al. 1986) searched 230 man-hours for stone crabs of any size in the expansive coastal oyster beds along the Gulf coast of Everglades National Park, where YOY stone crab relative abundance was high at Everglades Offshore. In those oyster beds, they found only a few large juvenile and adult stone crabs, most of which were riddled with chitinoclastic bacteria and missing at least one limb. They concluded that, at least in the southern Florida Gulf, *M. mercenaria* (of any life stage) rarely inhabit oyster beds and are not intertidal. The absence of stone crabs, including YOY individuals, from oyster reefs and traps with oysters as principal foulers in Everglades implies that *M. adina* and hybrids are essentially absent from the southern Florida Gulf.

Water depth and distance from shore. The relevance of the variables depth and distance from shore to YOY stone crab relative abundance also was complex and varied greatly among locations. Along the Gulf Coast, stations in water less than approximately 4.5 m deep were located either within recruitment "hotspots" (Cedar Key, Everglades Offshore) or "coldspots" (St. Marks and Homosassa) (Morgan et al. 2011, Groeneveld et al. 2012, Sigurdsson et al. 2016). At depths greater than or equal to 4.5 m, the linear decrease in relative abundance as water depth increased may have been due to decreasing YOY stone crab recruitment as distance from shallow-water recruitment hot spots increased. The particularly high relative abundances at nearshore stations in major recruitment locations were instrumental in generating the exponentially declining relationship between relative abundance and distance from shore. Notably, even at principal recruitment locations, relative abundance tended to decrease as depth and distance from shore increased, supporting the idea that relative abundances of late-stage stone crab larvae and megalopae are highest in nearshore shallow waters and decrease with increasing depth and distance from shore. Except for the seaward stations at major recruitment location Everglades Offshore (PK3 and PK4), relative abundance was near zero at all Gulf Coast stations located beyond approximately 12 km from shore. Most stations at both St. Marks and Homosassa were at least 12 km from shore. Depth and distance offshore at Keys locations Oxfoot Bank and Harbor Keys were within the ranges of more northerly Everglades Offshore and Nearshore stations with moderate to high relative abundances. The proximity of Oxfoot Bank and Harbor Keys, and of Northwest Cape in the Everglades Offshore location to the productive, more northerly Everglades Offshore and Nearshore stations indicate that the harsh temperature/salinity conditions at Oxfoot Bank, Harbor Keys, and Northwest Cape were among the principal physical features keeping recruitment levels low. Water depth, as well as harsh temperature–salinity conditions during recruitment season, may have contributed to low recruitment at Sawyer Keys.

Stone crab larvae apparently do not move offshore. Throughout the year, including recruitment season, stone crab larvae were rarely found in the Florida Current (Wisniewski 2010), a major ocean current that flows to the east south of Florida Bay and the Keys. Stone crab larvae are known to position themselves at depths that facilitate postlarval recruitment in habitats suitable for metamorphosis (Gravinese 2018), which can be induced by exudates from particular algae and by contact with natural rock, shell, and biofilms (Krimsky & Epifanio 2008). The findings presented herein demonstrate that, within suitable temperature/salinity ranges, nearshore areas with sufficient hard-bottom substrate and associated complex benthos are the preferred habitat for larval stone crab metamorphosis and early crab stages.

Recruitment hotspots. Spatially, YOY stone crab recruitment is highly heterogeneous. The Everglades Offshore and Cedar Key recruitment hotspots annually provide approximately one-half of the YOY stone crabs recruited. Moreover, within these hotspots recruitment is concentrated at surprisingly small recruitment centers—close to shore and north of Cape Sable at Everglades Offshore (vicinity of stations INK, PK1, PVK, and LMO) and the vicinity of station CK1 at Cedar Key. Particularly during years when recruitment was high at Everglades Offshore or Cedar Key, recruitment was disproportionately high at their respective recruitment centers. All recruitment-ground boundaries cannot be delineated from the studies included here, but these small areas are clearly important. The Cedar Key recruitment ground may continue northward to the Steinhatchee secondary recruitment ground but not southward to Homosassa. The northern extent of the Everglades Offshore recruitment ground is unknown; but it is clear that the southern limit is Northwest Cape Sable.

The Cedar Key and Everglades Offshore recruitment centers have a suite of environmental characteristics in common. During the recruitment season, recruitment centers typically have temperatures and salinities within the range of high larval and YOY stone crab survival, high levels of megalopal settlement, and rapid development of these life stages (25°C–32°C, salinity 24–33) (Field 1989, Brown et al. 1992, Brown & Bert 1993, Forward et al. 2001, this study). Recruitment-center salinity regimes are typical of areas immediately seaward of estuaries—slightly below that of seawater but more stable than within estuaries. Both recruitment centers are at depths less than 5 m. The importance of proximity to shore is apparent at both hotspots; mean annual YOY stone crab relative abundance decreases as distance from shore increases even when temperature, salinity, and fouling remain essentially the same. Both hotspots are within recognized pristine areas (Lacovara et al. 2003, Stern et al. 2007, Seavey et al. 2011) located just offshore from numerous, protected wetlands with comparatively pristine riverine systems (Cedar Key: Lower Suwannee River National Wildlife Refuge to the north, Waccasassa Bay Preserve State Park to the south, multiple small preserves near Cedar Key; Everglades Offshore: Big Cypress Nature Preserve, Everglades National Park, multiple other smaller preserves, all with numerous creeks and small rivers). Benthic habitats at both recruitment centers consist of patches of rock outcrops covered with robust benthic biota composed of sponges, tunicates, barnacles, hydroids, worm tubes, and branching and filamentous macro-algae. Both centers have brown murky water with visibly high densities of plankton. Neither recruitment center has well-developed seagrass beds, and *Thalassia testudinum* is rare or absent. Both have mixed sediments of sand, terrigenous soils, and detritus and are offshore of broad areas with low human population density or development.

Coastal areas and shallow waters are commonly the sites of recruitment grounds for marine crabs (Armstrong et al. 2003, Pallas et al. 2006, Rodrigues et al. 2019). The postlarvae of many decapod species select complex habitats for metamorphosis (Wolcott & DeVries 1994, Stevens & Kittaka 1998, Pardo et al. 2007, Webley et al. 2009); and high turbidity can deter aquatic predators that rely on visual prey recognition (Reustle & Smee 2020), as well as those that do not (Ortega et al. 2020). The cannibalistic nature of stone crabs of all sizes (Yang & Krantz 1976, Krimsky 2008) and susceptibility of YOY stone crabs to predation by other animals (Frick & Mason 1998, Schmid 1998, Scharf & Schlicht 2000, Shervette et al. 2004, Reeves et al. 2019) suggests that, as in other species (Kurihara & Okamoto 1987, Fernandez 1999, Luppi et al. 2001, 2002, Pirtle & Stoner 2010), refuge from predation is important in habitat selection by stone crab megalopae and PS-juveniles. Complex shelters with small openings have been shown to reduce interspecific and intraspecific competition and predation on YOY *Menippe adina* and enhance the density and survival of all sizes of juveniles (Gibbs 1994).

Recruitment at secondary recruitment locations Tampa Bay and Steinhatchee follows different patterns. The high relative abundances at BNP and PSK in Tampa Bay demonstrate that substantial YOY stone crab recruitment can occur at the mouths of large bays just shoreward of barrier islands and suggest that similar areas, such as those in Pine Island Sound and Cape Romano, may also be good recruitment grounds. At Steinhatchee, recruitment was not highest at the most nearshore station, but was more evenly spread among stations. All Steinhatchee stations were in water of similar depths more than 5 m deep, which may partially explain the similarity in mean annual relative abundance at those stations. At stations in relatively deep water, most recruitment may result from larvae drifting seaward from close to shore and dispersing from recruitment centers.

The numbers of stone crabs, including the numbers of juveniles of all size classes (Gerhart & Bert 2008) captured in traps at CK1 and at Everglades Offshore stations LMO, PVK, and PK1 were often the highest captured anywhere; and the proportions of females carrying eggs were often higher than the proportions elsewhere (Bert et al. 1986; FWC, FWRI unpublished data). Thus, Cedar Key and Everglades nearshore waters function not only as YOY stone crab recruitment grounds but also as stone crab nurseries (Beck et al. 2001). Continued protection of both areas from extensive development and maintenance of unpolluted water conditions is vital for these recruitment/nursery areas. Climate change and Everglades restoration efforts [Comprehensive Everglades Restoration Plan (CERP); U.S. Army Corps of Engineers (USACE) 1999, 2014, Ogden et al. 2005, Wingard & Lorenz 2014] are likely to result in shifts in precipitation and freshwater discharge, both of which may change salinity regimes along south Florida coasts (Mitsch 2016). Salinities in the Everglades Offshore location will depend on the balance between two driving forces—sea level rise as a result of climate change and freshwater input as a result of Everglades restoration—in waters along the ENP coast (Dessu et al. 2018, Zhao et al. 2020). Sufficient salinity reduction in Everglades Offshore waters within ENP will push that recruitment center out of the park and into commercially fished waters. Certainly, the two recruitment hotspots should be continuously monitored for changes in YOY stone crab recruitment, in relative abundance of juvenile stone crabs of all sizes, and in the physical factors influencing those abundances.

Recruitment coldspots. Relative abundance of YOY stone crabs was consistently very low at St. Marks and Homosassa, and from Northwest Cape Sable southeastward through Florida Bay and westward through the Gulf side of the Florida Keys. Some stations with near-zero mean annual recruitment at these locations were in same depth/distance range as other stations with high relative abundance, and some traps at those coldspots had fouling levels and communities similar or identical to those that harbored robust YOY stone crab relative abundances elsewhere (e.g., compare, during recruitment season, SM1, HM1, NWC, and CCH with CK1, PVK, and LMO). Prolonged sublethally to lethally high temperature/salinity combinations during recruitment season likely eliminate or drastically reduce larval and YOY stone crab numbers throughout Florida Bay and along much of the shallow-water habitat extending from Northwest Cape Sable through the Gulf side of the Keys, regardless of degree of fouling or type of fouling community. Females carrying eggs are common throughout these areas (Bert et al. 1986; FWC, FWRI unpublished data). Thus, the effects of these variables must reduce the survival of the young life stages. Water depth and distance from major recruitment grounds also were additional contributing variables at Harbor Keys and Sawyer Keys and may have been the most important variables at St. Marks and Homosassa. The coasts at St. Marks and Homosassa are broad areas of pristine, highly dissected marshes and swamps with multiple freshwater inputs into Gulf waters, and are protected by multiple wildlife preserves, refuges, and management areas. Where salinity regimes permit, higher recruitment may occur closer to shore.

High salinities have prevailed in Florida Bay since the early 1900s (Swart et al. 1999, Swart & Price 2002). Anthropogenic changes that diverted freshwater flow from the bay have changed the timing and spatial distribution of the flow, increasing salinity in some areas by a value of up to 20 (McIvor et al. 1994, Marshall et al. 2009) in all years but those of highest rainfall (Fourqurean et al. 1993). Western basins bordering the Gulf of Mexico maintain high-salinity regimes throughout the year (Herbert et al. 2011). Additionally, dramatic changes in habitat after the 1979 to 1980 ENP study may have exacerbated the unsuitability of Florida Bay for stone crab recruitment. Repeated losses of large areas of seagrasses (Robblee et al. 1991, Durako 1994, Hall et al. 1999, 2016) and resultant increases in turbidity (Boyer et al. 1999, Stumpf et al. 1999), as well as toxic phytoplankton blooms (Accoroni et al. 2020), have dramatically changed some basins in Florida Bay. Stone crab PS-juveniles have been collected from spiny lobster (*Panulirus argus*) habitats in the southernmost margin of Florida Bay (D. Eggleston, NC State University, personal communication); but as with spiny lobsters (Field & Butler 1994), YOY stone crab recruitment may be restricted from all but that margin of the bay. Substantial water flow changes underway through projects associated with the Comprehensive Everglades Restoration Plan (Perry 2004, Sklar et al. 2005) will restore freshwater flow into Florida Bay in an attempt to mimic prealteration, historical seasonal flow patterns. Beneficial changes in habitats and reductions in the occurrences of detrimental plankton blooms are expected to accompany the changes in salinity regimes. Areas of Florida Bay may become YOY stone crab recruitment grounds; Everglades National Park waters should be monitored for this potential.

Biological Relationships, Ecological Disruptions, and Meteorological Events

The highest correlation between the proportional distributions of YOY stone crabs and ovigerous female stone crabs, which occurred when the frequency of ovigerous females was set back by 2 mo, was an average through time of actual occurrences. The March to April sharp increase in frequency of ovigerous females was followed 3 mo later by a June to July sharp increase in frequency of YOY stone crabs, but the sharp September to October decrease in the frequency of ovigerous females was followed only 1 mo later (October–November) by a similarly large decrease in YOY stone crabs. Several influences likely contributed to the difference in timing between the two events. When mortality is high and growth to metamorphosis is slow for larvae and megalopae at early spring temperatures (see details abovementioned), growth of YOY individuals to the sizes most commonly found on traps may take 3 mo. When warm water during summer increases survival and accelerates growth of all young life stages, the average developmental time from zoea 1 to crab stage 2 or 3 may be only 1 mo.

Mean annual relative abundance of YOY stone crabs was not correlated with mean annual relative abundance of ovigerous females; but during 2010, both values were distinctively high. By all accounts, 2010 was a most unusual year due to a confluence of meteorological and climatic events. A strong El Nino event during the winter of 2009 to 2010 followed by a strong La Niña event in 2010–2011 affected the weather throughout Florida (Sun & Furbish 1997, Schmidt et al. 2001). The most severe and prolonged cold weather in 122 y enveloped Florida from December 28, 2009 through January 13, 2010 (Wang et al. 2010, Lirman et al. 2011, Colella et al. 2012, Kemp et al. 2016, Stevens et al. 2016). February and March were among coldest months on record for central and southern Florida; and June, July, and August were among the hottest months (https://www.ncdc.noaa.gov/cag/time-series/us). In Tampa Bay, unusually cold water persisted through April (Barlas et al. 2011); but the second highest water temperature recorded in this study occurred during June. During October, when YOY stone crab relative abundance was particularly high, the average precipitation was the lowest of all years of the Tampa Bay study (2 mm; https://www.ncdc.noaa.gov/cag/divisional/time-series/0804/pcp/1/10/1986-2010?base_prd=true&firstbaseyear=1901&lastbaseyear=2000). The 4-mo period September to December was the driest ever recorded for the Tampa area; September and October were, respectively, the second driest and driest ever recorded for those months (https://www.ncdc.noaa.gov/cag/city/rankings/USW00012842/pcp/201012); and the period of the entire stone crab reproductive season (April–December) was the third driest in Florida since records have been kept (1895; https://www.ncdc.noaa.gov/cag/statewide/rankings/8/pcp/201012). In addition to unusual water temperatures, anomalous, prolonged, substantial deep-ocean upwelling inhibited red tide outbreaks throughout Florida Gulf waters (Weisberg et al. 2014). Lastly, that year was also among the most active hurricane seasons ever recorded, but only one tropical storm entered the eastern Gulf of Mexico (http://www.srh.noaa.gov/images/mfl/news/2010WxSummary.pdf). Collectively, these events could have affected female stone crab survival and reproduction, larval survival, and YOY stone crab recruitment. In contrast, during 1999—the only other year in which mean YOY stone crab annual recruitment was very high—the frequency of ovigerous females was not unusual compared with other years, mean monthly water temperatures exhibited no remarkable values or patterns, and rainfall during the YOY stone crab recruitment season was within the normal range; however, a prolonged La Niña persisted through the year in the eastern Pacific and two tropical cyclones passed through southernmost Florida (https://www.nhc.noaa.gov/data/tcr/index.php?season=1999&basin=atl).

Although monthly decreases in YOY stone crab relative abundance in Tampa Bay could not be clearly attributed to red tide outbreaks or tropical cyclones, these ecological and meteorological phenomena, and perhaps also ENSO events, which are associated with tropical cyclones (Pielke & Landsea 1999, Goldenberg et al. 2001, Donnelly & Woodruff 2007), were related to mean annual relative abundance of YOY stone crabs. Relative abundance almost always decreased in the year following a year when one or two tropical cyclones passed near the bay. Moreover, during the 2 y prior to each of the years of lowest mean annual relative abundance (1996 and 2005), three hurricanes passed near Tampa Bay (one 2 y prior, two the previous year); a red tide occurred either late the previous year (1994) or early during the year (2005); and July to September rainfall was the lowest (1996) or second lowest (2005) recorded for the entire 1989 to 2010 Tampa Bay study period (https://www.ncdc.noaa.gov/cag/divisional/time-series/0804/pcp/3/9/1989-2010?base_prd=true&begbaseyear=1901&endbaseyear=2000). Recruitment may have remained very low in 2006, in part, because the 2004 hurricane season was the worst on record for Florida (Smith & McCarty 2009) and the 2005 hurricane season, the most active on record (Beven et al. 2008). The paths of six tropical cyclones, including four major hurricanes, moved through the eastern Gulf of Mexico, and two crossed the Southwest Florida region.

The combination of two consecutive years of hurricanes, timely red tides, and absence of precipitation when larvae and megalopae are in the water column may be the principal forces that nearly extinguish a year's YOY stone crab recruitment. High red tide concentrations and associated hypoxia can result in high mortality of larval and small juvenile stone crabs (Gravinese et al. 2019; Gravinese 2020). Close passages of hurricanes can have dramatic effects on water currents in Tampa Bay and throughout the Florida west coast (e.g., Chen et al. 2018, So et al. 2019, Liu et al. 2020) and can generate subterranean freshwater outflows that may contribute to persistent red tides (Hu et al. 2006).

The complex cyclic pattern of change in mean annual relative abundance of YOY stone crabs continued from 2011 through 2015 (FWRI, unpublished data), but without an extreme low or high in YOY stone crab relative abundance (range: 2.9–7.9). An early-season tropical storm crossed Florida from St. Marks to the east coast during June in both 2012 and 2013, but the eastern Gulf of Mexico was free of tropical storms of any level during 2011, 2014, and 2015; red tide incidence was negligible in and offshore from Tampa Bay (FWC, FWRI Harmful Algal Bloom Laboratory, St. Petersburg, FL); and no ENSO events occurred from late 2012 through mid-2014. If extreme levels of YOY stone crab recruitment are related to a "perfect storm" of red tides, tropical cyclones, and perhaps ENSO-related precipitation extremes, then no recruitment extremes would be expected between 2011 and 2015.

High variation in relative abundance of other juvenile crustaceans occurs among years as a result of the environmental effects of meteorological events in the Gulf of Mexico (Piazza et al. 2010, Sanchez-Rubio et al. 2011). Recruitment cycles can also arise endogenously in populations if recruitment and/or abundance of one age group declines in response to increasing abundance of older age groups, if older cohorts cannibalize younger ones (Wahle 2003), or if recruitment is density-dependent for other reasons (Botsford & Wickham 1978, McKelvey et al. 1980, Botsford 1995). Certainly, the relationships between tropical cyclones, red tides, precipitation, other potentially related biological, ecological, and oceanographic elements, and YOY stone crab recruitment should be further monitored and studied in detail. Extremes in YOY stone crab recruitment may be related to the effects of these physical phenomena on some aspect of female reproduction or on mortality or dispersal of some important life stage of the parental or offspring generation. Collectively, tropical cyclones, red tides, and rainfall can cause changes in water salinity, quality, and current patterns; habitat quantity or quality; and predator–prey dynamics that can influence YOY stone crab relative abundance. Clearly, this is an open field that is important to investigate in this commercially important crustacean.

Fishery Applications

The principal YOY stone crab recruitment grounds and hotspots described herein are very small and geographically isolated compared with the extent of the widespread juvenile and adult stone crab population. The expanses of the Southwest Florida fishery and Northwest Florida fishery, the two historically most important fisheries in the Florida Gulf (Bert et al. 1978), can be respectively estimated at 8,575 km^2 (2,500 nm^2) and 3,430 km^2 (1,000 nm^2); the known recruitment grounds can be estimated as 257 km^2 (75 nm^2) and 137 km^2 (40 nm^2), or 3% and 4% of the estimated fishing areas. The importance of the recruitment grounds to stone crab fisheries is thus greatly elevated. Understanding the dynamics of, and causes of variation in, juvenile recruitment in those grounds may lead to some ability to better regulate the fishery if recruitment can be related to subsequent abundance of legal-sized crabs. Linkages between settling juveniles and subsequent levels of recruitment to fisheries are possible (Wahle 2003).

Particularly in the Tampa Bay and Southwest Florida regions, the autumn peak in YOY stone crab recruitment coincides with the initiation of the commercial and recreational stone crab fishing season (October 15–May 1), when fishers tend to deploy the maximum number of traps, and to which YOY stone crabs readily recruit. The effects of commercial fishing on YOY stone crab recruitment are unknown, but may be substantial as a result of loss, dehydration, and crushing of YOY individuals on vessel decks during trap handling. A common and frequently successful fisheries management strategy to protect important recruitment grounds is to close the area to harvest (Palma et al. 2006). Although some lands and waters within or near to each major recruitment ground are protected state or federal areas, considerable expanses of the watersheds are occupied by towns and farms. Additional protected areas in the watershed may be needed for these recruitment grounds to persist.

Preserving the YOY stone crab recruitment grounds themselves is as important as preserving the wild areas inshore of the recruitment grounds. Eliminating harvesting of stone crabs from the two small major recruitment grounds would protect an average of 50% of the annual YOY stone crab recruits from any effects of harvest, with minimal impact on the fishery. Protecting an additional 48.5 km^2 (14 nm^2) in the vicinity of stations PSK, BNP, and RSK in lower Tampa Bay would protect an average of an additional 14% of these individuals. Fully protected marine reserves can produce huge increases in numbers and biomass of harvested species (Palumbi 2004). If the Cedar Key and Everglades Offshore recruitment grounds were fully protected, stone crab abundance might significantly increase in the Northwest and Southwest Florida regions because those recruitment grounds also serve as nursery grounds. Geographically restricted recruitment grounds and nursery grounds can be the source of older individuals that range over large regions (Armstrong et al. 2003). Thus, protecting the YOY stone crab recruitment grounds would impart an additional degree of resilience to the population (Apostolaki et al. 2002, Webley et al. 2009).

Annual harvesting quotas can be set if recruitment success is known and a stock-recruitment relationship can be established (Caddy 1986, but see Méndez Casariego et al. 2004). Our analyses did not reveal a spatial relationship between relative abundance of YOY stone crabs and commercial landings of stone crab claws for any grouping of counties, regardless of lag time between YOY stone crab relative abundance and average annual landings and the time frame considered. The relationship may be obfuscated because the geographic expanses of the recruitment grounds are very small compared with the geographic extents of the regional fisheries; and some of the most intense fisheries are not in counties that include recruitment grounds. For example, fishery landings in Citrus County (location of Homosassa) and Monroe County (Oxfoot Bank, Harbor Keys, and Sawyer Keys) are high, but YOY stone crab recruitment is low, whereas landings are low in Levy County (Cedar Key), but recruitment is high (see Fig. 16). In addition, more effort (trap pulls) is required to harvest a unit of claws in some counties than in others, so high average annual landings do not translate to high standardized annual landings. Links between local recruitment and commercial harvest have also become obscured because, in the past, commercial crabbers went on single-day trips, and harvested and landed stone crab claws locally (Bert et al. 1978); but in recent years, crabbers have traveled to other areas where stone crabs were more plentiful than they were locally; and some crabbers go on multiday trips. Variation among counties and regions in fishing intensity and differences among counties in effort between local and nonlocal crabbers make determining catch–recruitment relationships for this fishery complex.

Nevertheless, when recruitment follows cyclic patterns or is affected by defined external influences, as YOY stone crab recruitment seems to be, years of low recruitment can be predicted or at least estimated. This is important if the fishery is recruitment fishing, as has been the situation for the stone crab fishery in recent decades (Muller et al. 2006, 2011). Overexploitation can destabilize the recruitment cycles and lead to greater variability in recruitment if the overharvesting modifies the abundance of the life stages promoting the population cycling (Berryman 1991, Botsford 1995, Sainte-Marie et al. 1996). Protection of the YOY stone crab recruitment grounds, combined with development of a stock-recruitment model that includes (if appropriate) a predictable pattern for YOY stone crab recruitment, could greatly benefit this maximally exploited fishery.

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APPENDIX 1: FIELD METHOD DETAILS

Trap Location and Orientation

At locations SM, ST, CK, HM, and EO_{PK}, the four stations were arrayed east to west and the traplines were oriented north to south, approximately parallel to shore (Fig. 1, main text). Three of the four Tampa Bay stations were in the seaward part of the bay and one station was offshore of Anna Maria Island (AMI). The traplines at AMI were oriented generally east to west. The ENP stations were distributed throughout the basins and nearshore waters of ENP (detailed map in Bert et al. 1986, Fig. 1A). The traplines for ENP stations CTB, SPT, INK, PVK, LMO, and NWC were oriented parallel to the coastline. Traplines for CKB and LSB were oriented east to west and placed near the centers of the respective basins; LMI traps were placed along the south side of the open-water section of the Lostman's River boat channel. The traplines for Everglades stations PK1–PK4 were oriented north to south, outside of ENP waters. In Florida Bay, traplines in the basins were oriented in various directions and, when possible, in habitats that stone crabs were likely to occupy. Traplines in channels were placed along the south sides of the channels, which ran generally east to west. The OX stations were west of, and parallel to, the ENP boundary; the traplines were oriented generally perpendicular to the boundary. The HK and SK stations respectively extended northeastward and northwestward from the Gulf of Mexico side of the island groups that the traplines were named for. At both locations, individual traplines were oriented east to west.

Scuba Surveys

In each survey, two divers swam a series of 100-m × 2-m transect lines arrayed in a modified Maltese cross configuration (see Fig. 14 in Bert 1985) at the locations of traps 1, 3, and 5 of a given station. At each trap, the research boat was anchored in close proximity to the trap and a 100-m measuring tape was fixed to the boat anchor. A random initial direction was chosen for the first 100-m swim. One diver was stationed on each side of the tape and each diver inspected a 2-m width on his or her side while swimming the length of the unreeling tape. At the end of 100 m, the tape was dragged to the left by the divers until it was approximately 45 degrees from the previous transect. On the return swim to the boat anchor, the tape was reeled in for 50 m and a 4-m width was again inspected by the divers. At the 50-m mark, the tape was again dragged approximately 45 degrees to the left to minimize overlap in the area surveyed. (The area of overlap near the anchor was approximately 1.8% of the total area covered and was considered negligible.) At the end of each 100-m swim, estimates of the proportions of bare sea floor, emergent rock/coral/algae/benthos, and seagrass were recorded by each diver, and the common benthic biota noted.

APPENDIX 2: MODELS FOR NEGATIVE BINOMIAL ANALYSIS

Forty-four unique models were constructed for the negative binomial analysis designed to elucidate the location-specific variables important for influencing the relative abundance of YOY stone crabs (Table A1). May, June, and July were included as covariates in all models to distinguish rising water temperatures during those months from identical falling temperatures during August, September, and October because relative abundance of YOY stone crabs in August to October was much higher than in May to July.

TABLE A1.

Covariate combinations tested in comprehensive negative binomial analyses for influence of external variables on YOY stone crab recruitment.

Model number	Covariate								
1	May	June	July	DegPrin	T	T^2	S	S^2	Depth
2	May	June	July	DegPrin	T		S	S^2	Depth
3	May	June	July	DegPrin	T	T^2	S		Depth
4	May	June	July	DegPrin	T	T^2	S	S^2	
5	May	June	July	DegPrin	T		S	S^2	
6	May	June	July	DegPrin	T	T^2	S		
7	May	June	July	DegPrin	T	T^2			Depth
8	May	June	July	DegPrin	T				Depth
9	May	June	July	DegPrin			S	S^2	Depth
10	May	June	July	DegPrin			S		Depth
11	May	June	July	DegPrin	T	T^2			
12	May	June	July	DegPrin	T				
13	May	June	July	DegPrin			S	S^2	

(*Continued*)

TABLE A1. (CONTINUED)

Model number	Covariate									
14*	May	June	July	DegPrin			S			
15	May	June	July	DegPrin					Depth	
16	May	June	July	DegPrin						
17	May	June	July		T	T^2	S	S^2	Depth	
18*	May	June	July		T		S	S^2	Depth	
19	May	June	July		T	T^2	S		Depth	
20	May	June	July		T	T^2	S	S^2		
21*	May	June	July		T		S	S^2		
22	May	June	July		T	T^2	S			
23	May	June	July		T	T^2			Depth	
24*	May	June	July		T				Depth	
25*	May	June	July				S	S^2	Depth	
26*	May	June	July				S		Depth	
27	May	June	July		T	T^2				
28*	May	June	July		T					
29*	May	June	July				S	S^2		
30*	May	June	July				S			
31*	May	June	July						Depth	
32*	May	June	July							
33	May	June	July	DegPrin	T	T^2	S	S^2	Depth	T × S
34	May	June	July	DegPrin	T		S	S^2	Depth	T × S
35	May	June	July	DegPrin	T	T^2	S		Depth	T × S
36	May	June	July	DegPrin	T	T^2	S	S^2		T × S
37	May	June	July	DegPrin	T		S	S^2		T × S
38	May	June	July	DegPrin	T	T^2	S			T × S
39	May	June	July		T	T^2	S	S^2	Depth	T × S
40*	May	June	July		T		S	S^2	Depth	T × S
41	May	June	July		T	T^2	S		Depth	T × S
42	May	June	July		T	T^2	S	S^2		T × S
43*	May	June	July		T		S	S^2		T × S
44	May	June	July		T	T^2	S			T × S

DegPrin: Degree of trap fouling and Principal foulers (see Appendix 3 for explanation and categorization). T, temperature; S, salinity; T^2 and S^2, quadratic terms to account for possible nonlinearity of temperature and salinity effects; T × S, temperature-salinity interaction. YOY, young-of-the-year.
* Model was never included in sets of applicable models in any analysis.

APPENDIX 3: CHARACTERIZATION OF FOULING ON TRAPS

Degree of Fouling

Originally, in the 1979 to 1980 ENP study, seven fouling categories were defined, ranging from no fouling (which occurred on new traps at few stations, for about 1 mo) to extreme fouling. Through the years, these categories were combined into light, moderate, and heavy fouling, as follows:

1. Light fouling—traps had thin coatings of mostly small benthic organisms; patches of trap were visible on the external surfaces of slats and throat; spaces between trap slats were open.
2. Moderate fouling—traps had single-layer coatings of small- to mature-sized benthic organisms completely covering trap slat and throat external surfaces; growth of organisms narrowed the spaces between trap slats but did not obstruct them.

TABLE A2.

Seasonal variation in number of traps with common fouling organisms as principal foulers.

	Principal fouler number and description							
	1	2	3	4	5	6	7	8
Month*	Barnacles	Branched hydroids & bryozoans	Red algae and brown algae	Encrusting bryozoans	Worm tubes	Green algae	Tunicates	Mud
1	<u>*137*</u>	**158**	**215**	<u>*45*</u>	**286**	84	**45**	65
2	<u>*166*</u>	**169**	**235**	115	**293**	100	20	**76**
3	<u>*105*</u>	96	176	**133**	237	69	25	44
4	249	**168**	110	109	176	**173**	24	15
5	243	95	125	**142**	161	**161**	27	20
6	357	70	129	**126**	161	76	14	64
7	**485**	<u>*20*</u>	134	79	<u>*70*</u>	87	<u>*10*</u>	45
8	**506**	93	<u>*54*</u>	41	*71*	**143**	<u>*10*</u>	50
9	**491**	58	117	66	113	109	25	<u>*20*</u>
10	427	<u>*35*</u>	91	73	109	<u>*44*</u>	34	46
11	367	132	111	<u>*24*</u>	169	88	**46**	35
12	209	110	130	87	**286**	88	26	64
Total	3742	1204	1627	1040	2132	1222	**306**	544
mean	312	100	136	87	178	102	26	45
SD	145	50	51	39	81	39	12	20
SD lower limit	167	51	85	48	96	63	14	25
SD upper limit	457	150	186	125	259	140	37	65
% of total number of traps examined†	31.7	10.2	13.8	8.8	18.0	10.3	2.6	4.6

Bold numbers, value greater than or equal to SD upper limit; numbers italicized and underlined, value less than or equal to SD lower limit.
* 1, January; 2, February, and so on.
† n = 11,817.

3. Heavy fouling—traps had crowded, often multilayered coatings of benthic organisms in all stages of maturation completely covering external surfaces of traps and throat and nearly closing most spaces between trap slats.

Predominant Foulers

The predominant foulers on traps included barnacles, algae, tunicates, sponges, hydroids, bryozoans, and sabellid worms that made small, flexible tubes; other types of organisms were rare. Calcareous or terrigenous fine-grained mud or sand, all of which were classified as "mud," also occasionally predominated on traps at some stations. Large benthic organisms (e.g., sponges, tunicates) sometimes also grew on exterior trap surfaces. The sizes of some organisms (e.g., barnacles, tunicates) were characteristic of maturity.

To facilitate the negative binomial and other analyses, preliminary analyses were conducted to search for ways to group the predominant foulers. The principal foulers (those covering the most trap surface) were numerically coded and their seasonality determined. For each month, the total number of traps with each fouler listed as principal fouler (using the inclusive data set; see ***Statistical Methods***) was tallied (Table A2). Graphing those data revealed, for most foulers, temporal changes in numbers of traps fouled that appeared to be seasonal and similar among some foulers (Fig. A1). Pearson's correlation analysis (Table A3) established that the occurrences of worm tubes, red algae and brown algae (considered together), and branched hydroids and bryozoans (considered together) were correlated and that the occurrences of those organisms were significantly negatively correlated with the occurrences of barnacles as the principal fouler. Therefore, worm tubes, red and brown algae, and branched hydroids and bryozoans could be grouped as co-occurring on traps; and their high co-occurrence during winter (Fig. A1A) opposed the summer seasonal prevalence of barnacles on traps (Fig. A1B). The simultaneous test procedure (STP) for frequencies, performed on monthly frequencies of worm tubes combined with correlated foulers versus all other foulers combined established that fouling with worm tubes and correlated organisms was significantly high from December to February and significantly low from July to October (Fig. A1A). The STP performed on monthly frequencies of barnacles versus all other foulers combined established that barnacle fouling was significantly high in July to October and significantly low in January to March (Fig. A1B). To examine the occurrences of the encrusting bryozoans, tunicates, and mud relative to those of barnacles and worm tubes + correlated organisms, the monthly numbers of traps fouled by encrusting bryozoans, tunicates,

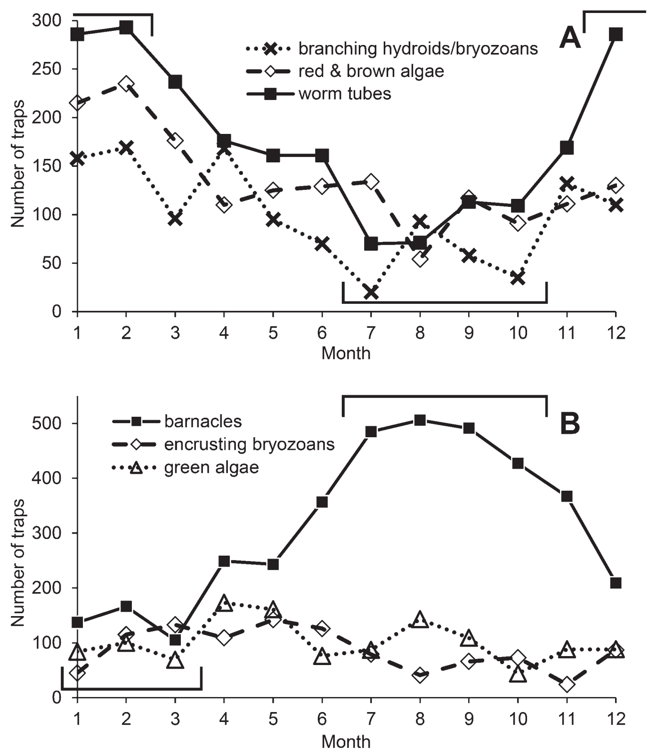

Figure A1. Seasonal predominance of organisms in the benthic community fouling external surfaces of stone crab traps in the Gulf of Mexico off Florida. Note different Y axis scales. (A) Seasonally co-occurring biota predominant during winter. Bars above and below graph respectively show significantly high and low seasonal frequencies of traps fouled by the listed biota. (B) Seasonally co-occurring biota predominant during spring to summer. Bars are as in Figure A1, but show significant seasonal frequencies of only barnacles. *n* range: 869–1,176.

and mud were compared with the mean number of traps ± one SD for each of those foulers (Table A2). Encrusting bryozoans and green algae tended to be principal foulers on traps more frequently than their respective means ± SDs during warming months (March–May; Figs. A1B and 4B, main text), before barnacles completely covered traps at some stations during the warmest months of the year. Tunicates and mud were, overall, rare as principal foulers on traps, respectively, constituting only 2.6% and 4.6% of all traps examined (Table A2). They, together with other rare principal foulers (oysters, sponges) were considered to be nonseasonal. Their overall more common occurrence as principal foulers during winter was related more to the extensive coverage of barnacles on traps during summer at some stations, which physically excluded other foulers.

Together, these analyses allowed grouping the fouling organisms into three categories: "summer" (barnacles, encrusting bryozoans, green algae); "winter" (worm tubes, red and brown algae, branched hydroids, and bryozoans); and "nonseasonal" (tunicates, mud, other foulers) for the comprehensive negative-binomial analyses. These categories were combined with the three degree-of-fouling categories to generate a single covariate that expressed both degree and seasonality of fouling,

TABLE A3.

Pearson's correlation coefficients for seasonal variation in number of traps fouled by common principal fouling organisms.

Foulers	Barnacles	Branched hydroids and bryozoans	Red algae and brown algae	Encrusting bryozoans	Worm tubes	Green algae	Tunicates
Branched hydroids and bryozoans	**−0.681**						
Red algae and brown algae	**−0.742**	0.481					
Encrusting bryozoans	−0.466	0.005	0.289				
Worm tubes	**−0.908**	**0.714**	**0.784**	0.244			
Green algae	0.019	0.382	−0.264	0.168	−0.158		
Tunicates	−0.360	0.383	0.228	−0.391	0.405	−0.248	
Mud	−0.291	0.150	0.513	−0.047	0.505	−0.550	−0.094

Bold, $P \leq 0.05$; bold and underlined, $P \leq 0.01$.

as follows: 1.1, light fouling, summer foulers; 1.2, light fouling, winter foulers; 1.3, light fouling, nonseasonal foulers; 2.1, moderate fouling, summer foulers; 2.2, moderate fouling, winter foulers; 2.3, moderate fouling, nonseasonal foulers; 3.1, heavy fouling, summer foulers; 3.2, heavy fouling, winter foulers; 3.3, heavy fouling, nonseasonal foulers.

APPENDIX 4: RELATIVE IMPORTANCE, GEOGRAPHIC PATTERNS, AND DETAILED SEASONALITY OF TRAP FOULERS

"Importance indices" were calculated for each fouler at each station where both trap fouling and number of YOY stone crabs were recorded monthly for more than one continuous year. For these calculations, the data were drawn from the all full-year data set. The predominance and seasonality of foulers did not change markedly among years at any station. Thus, years were combined. First, for each station each month, a "relative significance value" was calculated as the number of traps fouled by each principal fouler multiplied by the frequency of occurrence for the fouler (Table A4). For example, of the 94 traps surveyed during January at station AMI (in the Tampa Bay location), the relative significance of the principal foulers recorded were as follows: barnacles, 20 traps total × 0.21 (21% of all Tampa Bay traps surveyed that month, years combined) = 4.3; branched hydroids and bryozoans, 19 traps × 0.20 = 3.8; red algae and brown algae, 15 traps × 0.16 = 2.4; worm tubes, 31 traps × 0.33 = 10.2; green algae, 4 traps × 0.04 = 0.16; mud, 5 traps × 0.05 = 0.25. Then, the relative significance values of each fouler were summed across all months for each station; and that sum was multiplied by incidence of that fouler through the year at that station, providing the importance index for each fouler at each station (Table A4). For example, the total of the relative significance values for the fouler "barnacles" at station AMI was 284.6 and barnacles were recorded as the principal fouler for all 12 mo. Thus, the barnacle importance index for AMI was 3,415.1 (284.6 × 12).

Fouling was recorded intermittently during the earlier, single-year studies included in this report (Northwest Florida, 1986 to 1987; Everglades National Park, ENP, 1979 to 1980). Essentially, predominant foulers and seasonality of foulers on traplines at all Northwest Florida locations were the same as reported here for the multiyear studies, indicating that fouling at those stations did not change considerably for prolonged time periods. Trap fouling differed markedly among stations in ENP. A seasonal summary (Table A5) shows that fouling at Everglades Offshore stations (INK, PVK, and LMO) was essentially the same as that at proximal EO_{PK} stations, particularly PK1 and PK2; and fouling at ENP Florida Bay stations SKC and ASK was similar to that at geographically proximal OX1–OX4 (Fig. 1, main text). These results, and the long-term continuous data from Tampa Bay stations indicate that seasonal variation in benthic settlement did not markedly change across decades throughout the study area.

Geographical variation in temperature, salinity, depth, distance from shore, (Table 1, main text), local habitat, water clarity, and environmental factors that were not measured likely contributed to the differences among stations and locations in seasonality and commonality of the principal foulers listed in Table A4. Nevertheless, some trends and associations among stations within and among locations could be identified (Tables A4 and A5; see Table 1 and Fig. 1, main text, for location and station information) and are summarized below.

Barnacles

Several barnacle species inhabit the coastal areas of western Florida nearshore waters. Differences in seasonality and personal observation (T. M. Bert) ascertained that the species composition of the barnacles occurring on traps shifted with decreasing latitude. Clearly, the fouler "barnacles" predominated on traps during summer at Cedar Key, Tampa Bay, Everglades Offshore, and station CCH in Florida Bay. Barnacles were also among the principal warm-weather foulers at Steinhatchee, Harbor Keys, and Everglades Nearshore; but that fouler was most commonly a winter principal fouler at Sawyer Keys. In contrast, although barnacles were often present, particularly during summer, they were rarely a principal fouler at St Marks and never a principal fouler at Homosassa (both the 1986 to 1987 and 2006 to 2009 Northwest Florida studies), Oxfoot Bank, Everglades Inshore, or—other than CCH—Florida Bay. In addition, the presence of barnacles could vary among stations within locations. Compared with other stations at their respective locations, barnacles were rarely a principal fouler at ST1, CK4, HK4, SK 1, and SK2. At Cedar Key, barnacles steadily declined in occurrence as a principal fouler from CK1 to CK4.

Branched Hydroids and Bryozoans

Except at Homosassa, these organisms were a common principal fouler on traps from Tampa Bay northward; and they were a occasional principal fouler at Everglades Nearshore and Offshore, and at CCH in Florida Bay. As a principal fouler, branched hydroids and bryozoans showed little seasonality in Northwest Florida and variable seasonality farther south. This fouler was more common during the fall and spring transitions and through winter at Tampa Bay and Everglades Offshore stations and at CCH; but was more common from spring through fall at SPT, an Everglades Nearshore station. Branched hydroids and bryozoans were often present at many stations, but were not a principal fouler. In Northwest Florida and at Tampa Bay, they were a principal fouler more frequently at the offshore-most stations.

Red Algae and Brown Algae

As a principal fouler, algae in these color groups were more common during cooler months of the year (fall through spring) from St. Marks through ENP Gulf of Mexico locations (Everglades Inshore, Nearshore, and Offshore); but were common throughout the year in Florida Bay, particularly at western stations, and at Oxfoot Bank. In the lower Keys (Harbor Keys, Sawyer Keys), red and brown algae was a more common principal fouler during summer and fall (June–November). Species composition of the algae in these color groups changed markedly with decreasing latitude. The seasonal differences described here are associated with changes in algal species composition. Spatial differences within locations were most noticeable at St Marks and Oxfoot Bank, where the incidence of those algae as a principal fouler steadily increased with distance from

TABLE A4.

Monthly relative significance values and overall importance indices for common principal trap foulers at stations where fouling was reported monthly for more than 1 y.

Fouler	Location Station	Month 1	2	3	4	5	6	7	8	9	10	11	12	Sum	Incidence	Importance index
Barnacles	SM															
	SM1											1.7	1.3	2.9	2	5.8
	SM2								1.3			1.7		2.9	2	5.8
	SM3	2.5	1.3						1.3	1.7		1.7	1.3	9.6	6	57.5
	SM4								1.3					1.3	1	1.3
	ST															
	ST1										1.7	**5.0**		6.7	2	13.3
	ST2	1.6	1.7					1.7	1.4	1.7	1.7	4.8		14.4	7	100.7
	ST3	1.7	1.2	2.5	1.2		1.0	1.7	1.2	**15.0**		4.8	1.7	31.8	10	318.3
	ST4	1.6	1.2		0.5			1.7	1.2	**6.7**		1.2	1.6	15.5	8	124.2
	CK															
	CK1	**5.8**	**8.2**	2.5	**5.0**	**6.7**	**14.0**	**15.0**	**20.0**	**15.0**	**6.7**	**18.0**	**15.0**	131.8	12	1581.4
	CK2	1.7	**9.0**	**6.7**	**18.0**	**5.8**	**6.7**	1.7	**11.3**	**6.7**	**6.7**	**19.0**	**6.7**	99.7	12	1196.4
	CK3		**7.5**	2.5	**9.4**	1.7	**19.0**		4.3	**6.7**	**5.8**	**20.0**	**6.7**	83.4	10	834.4
	CK4		2.8		4.3						1.7	1.7		10.4	4	41.6
	TB															
	AMI	4.3	**10.2**	**8.0**	**25.5**	**15.0**	**24.5**	**45.9**	**51.6**	**33.7**	**38.7**	**18.2**	**8.9**	284.6	12	3415.1
	BNP	0.9	3.3	**6.2**	**7.5**	**12.3**	**57.3**	**95.2**	**81.3**	**68.8**	**63.0**	**9.7**	0.9	406.3	12	4876.0
	PSK	0.2	4.9	0.3	1.8	**11.6**	**26.8**	**86.8**	**69.1**	**53.8**	**40.6**	**13.5**	1.1	310.4	12	3725.3
	RSK	0.2	0.9	2.3	0.9	**12.3**	**36.0**	**69.8**	**95.0**	**75.6**	**70.7**	**6.9**	4.0	374.7	12	4496.1
	EO_{PK}															
	PK1					1.3	1.3	**19.0**	**25.0**	**25.0**	**20.0**	**11.3**	**11.3**	114.0	8	912.0
	PK2			1.3	1.3			**11.3**	4.0	**25.0**	**11.3**	**11.3**	4.3	69.5	8	556.1
	PK3	1.3	1.0				**11.3**	**11.3**	**16.0**	**24.0**	**9.4**	**6.7**	1.3	82.1	9	738.5
	PK4	1.3			1.3		1.3	**11.3**	**16.0**	**25.0**	**11.3**	**5.0**		72.3	8	578.0
	HK															
	HK1	**5.0**	**5.0**		**5.0**	1.3			1.3			**5.0**	1.3	23.8	7	166.3
	HK2	**5.0**			**5.0**	1.3	1.3	**9.0**	1.7	**7.6**	1.7	**5.0**	1.3	38.6	10	386.5

(*Continued*)

TABLE A4. (CONTINUED)

Fouler	Location Station	Month 1	2	3	4	5	6	7	8	9	10	11	12	Sum	Incidence	Importance index
	HK3	1.3			1.3	1.7		4.0	1.7		**6.7**	**5.0**	1.3	22.8	8	182.0
	HK4				1.3								1.3	2.5	2	5.0
	SK															
	SK1											1.3		1.3	1	1.3
	SK2					1.3						1.3		2.5	2	5.0
	SK3	1.7	1.3		**5.0**	**5.0**	**16.0**	**11.3**				1.5	**10.3**	52.0	8	415.6
	SK4	4.5	1.3		**5.0**	11.3	**16.0**	1.7				4.5	**10.3**	54.5	8	436.4
Branched	SM															
hydroids and	SM1		1.3		1.7		1.0							3.9	3	11.8
bryozoans	SM2		1.3		1.7				**11.3**	1.7				15.8	4	63.3
	SM3				1.7				**11.3**	1.7				14.6	3	43.8
	SM4		1.3		1.7				**5.0**	**6.7**				14.6	4	58.3
	ST															
	ST1	1.7			1.3			1.7					2.2	6.8	4	27.2
	ST2				**12.2**	1.2	1.4		2.0			1.7		18.5	5	92.4
	ST3		**5.8**						1.7			1.2		8.7	3	26.0
	ST4	2.3	**5.8**	2.5	**5.6**				**5.8**			1.2	2.3	25.3	7	176.9
	CK															
	CK1		1.0	2.5	1.3						1.7			6.5	4	25.8
	CK2	1.7					1.7				1.7			5.0	3	15.0
	CK3	1.7			1.4	1.7			1.3					6.0	4	24.2
	CK4	1.7	0.9		1.3		**6.7**		**5.0**			1.7	**6.7**	23.8	7	166.9
	TB															
	AMI	3.8	3.6	0.8	0.7	1.0	2.1	1.1	**1.1**	4.6	1.1	**10.2**	4.3	34.3	12	411.5
	BNP	**10.6**	3.6	3.5	**5.5**	0.3				0.2	0.3	**9.0**		32.9	8	263.6
	PSK	**9.3**	3.4	**6.6**	3.8	2.4	1.2			2.0	0.2	3.2	**6.2**	38.3	10	383.3
	RSK	**7.8**	**8.3**	4.4	3.4	4.3	0.3					**6.9**		35.3	7	246.9
Red algae	SM															
and brown	SM1						1.0			1.7	1.7			4.3	3	13.0

(*Continued*)

TABLE A4. (CONTINUED)

Fouler	Location Station	Month 1	2	3	4	5	6	7	8	9	10	11	12	Sum	Incidence	Importance index
algae	SM2	2.5	**11.3**	**10.0**	1.7		1.7						1.3	28.3	6	170.0
	SM3	2.5	1.3	**10.0**	1.7	1.7	1.0	**6.7**			1.7	1.7	1.3	29.3	10	293.3
	SM4		1.3	**10.0**	1.7	1.7	4.0	**6.7**	1.3		1.7	**6.7**	1.3	36.1	10	360.8
	ST															
	ST1			2.5		1.7	1.0			1.7				6.8	4	27.3
	ST2	2.3	1.7	2.5			3.8			1.7			**6.7**	18.6	6	111.6
	ST3			2.5	1.2		4.0				1.6			9.3	4	37.0
	ST4		1.2	2.5			**9.0**	1.7			1.6	1.2	1.6	18.7	7	130.7
	CK															
	CK1													0.0	0	0.0
	CK2			1.7		1.8		1.7	1.3					6.4	4	25.5
	CK3		3.3	2.5				**5.0**						10.8	3	32.5
	CK4	1.7	3.4	2.5		**6.7**		1.7						15.9	5	79.7
	HM															
	HM1						1.7							1.7	1	1.7
	HM2		**5.0**						1.7				1.7	8.3	3	25.0
	HM3	1.0	1.3	1.7										3.9	3	11.8
	HM4	1.8	1.3	1.7							3.6	1.7	1.7	11.6	6	69.6
	TB															
	AMI	2.4		0.3		0.8	0.3		1.1	0.1	0.3	0.2	0.3	5.7	9	51.4
	BNP		0.9	0.2	0.8	0.9								2.8	4	11.1
	PSK		0.9	1.1	1.1	0.7	0.2			0.2	0.2	0.3	0.3	4.9	9	44.4
	RSK	1.8	0.9	0.3	3.4	1.1	0.3			0.2		0.3		8.2	8	65.4
	EO_{PK}															
	PK1	**10.3**	1.0			1.3								12.6	3	37.7
	PK2	**11.3**	4.0					1.3						16.5	3	49.5
	PK3	**5.0**	4.0		1.3							1.7		11.9	4	47.7
	PK4	**5.0**	4.0	1.3	1.3	1.7	1.3				1.3	1.3	1.7	18.6	9	167.3
	OX															
	OX1	**12.0**	**5.0**		1.7			**5.0**		1.7		**6.7**	1.3	33.3	7	232.8
	OX2	2.5	**8.3**	**5.0**	1.7			**6.7**		**10.0**		1.7	**11.3**	47.1	8	376.7
	OX3	4.9	**14.0**	4.0		1.7	1.9	**5.0**	1.7	1.7		1.7	**5.0**	41.5	10	415.1

(*Continued*)

TABLE A4. (CONTINUED)

Fouler	Location Station	Month 1	2	3	4	5	6	7	8	9	10	11	12	Sum	Incidence	Importance index
	OX4	4.2	**6.7**	**5.0**	1.7	1.7	2.5	**5.0**	1.7	1.7	3.6	1.7	**6.7**	41.9	12	502.9
	HK															
	HK1	1.3						1.0		5.0	1.7	1.3		10.2	5	50.8
	HK2							1.0		1.6	1.7	1.3		5.5	4	21.9
	HK3	1.3	1.3				1.7							4.2	3	12.5
	HK4	0.2	1.3	1.3			1.7	2.5		1.0			5.0	13.0	7	91.1
	SK															
	SK1	**5.0**	**5.0**	**5.0**	1.3	1.3	1.0	1.3		**5.0**	**<u>11.3</u>**	**5.0**	1.3	42.3	11	465.2
	SK2	1.3		1.3		1.3	1.0	**5.0**		**6.7**	2.5	1.3	1.3	21.4	9	192.8
	SK3			1.3			1.0	1.3	**5.0**	**5.0**	2.1	1.5		17.1	7	119.4
	SK4	0.9		1.3				1.7	**5.0**	2.9	1.7	1.4		14.7	7	103.2
Encrusting	SM															
bryozoans	SM1												1.3	1.3	1	1.3
	SM2	2.5				1.7	**6.7**	2.5		1.7	1.7	1.7	1.3	19.6	8	156.7
	SM3		1.3			1.7	**9.0**	1.7		1.7	1.7	1.7		18.6	7	130.1
	SM4	2.5	1.3			1.7	**9.0**	1.7		1.7	1.7	1.7	1.3	22.3	9	201.0
	ST															
	ST1		**5.0**		1.3	1.7	1.0		**5.8**		**6.7**			21.3	6	128.1
	ST2					**5.8**			1.4		**6.7**			13.8	3	41.5
	ST3				1.7	**<u>21.0</u>**	1.0	1.7						25.4	4	101.5
	ST4					**<u>16.0</u>**	1.4	1.7			2.3			21.4	4	85.4
	CK															
	CK1							1.7					1.7	3.3	2	6.7
	CK2					1.7			1.3					3.0	2	6.0
	CK3	1.7	0.9		1.3	1.7	1.7	**6.7**		1.7				15.5	7	108.6
	CK4		2.5											2.5	1	2.5
	HM															
	HM1		2.5											2.5	1	2.5
	HM2													0.0	0	0.0
	HM3	1.0			1.0			1.7	1.7		4.0		1.3	10.6	6	63.5
	HM4		**<u>11.3</u>**	1.7	1.7		**6.7**			1.7			1.7	24.6	6	147.5

(*Continued*)

TABLE A4. (CONTINUED)

Fouler	Location Station	Month 1	2	3	4	5	6	7	8	9	10	11	12	Sum	Incidence	Importance index
	TB															
	AMI						0.2	0.3		0.2			1.1	1.7	4	6.9
	BNP	0.2		0.9	0.7								1.1	2.9	4	11.5
	PSK			0.3	0.4								0.2	0.8	3	2.5
	RSK	0.2	2.1	2.0	3.7	0.3	0.3					0.3	0.3	9.0	8	72.3
	EO_{PK}															
	PK1		1.0											1.0	1	1.0
	PK2			1.3	1.3	1.7	1.3				1.3			6.7	5	33.3
	PK3			1.3	1.3	1.3								3.8	3	11.3
	PK4		1.0	**5.0**	1.3	1.7			1.0					9.9	5	49.6
	HK															
	HK1			**5.0**	1.3	**5.0**	**5.0**			1.3	1.7		**5.0**	24.2	7	169.2
	HK2		1.3	**5.0**	1.3	1.3	**5.0**	1.0	1.7		1.7		1.3	19.3	9	174.0
	HK3			**5.0**	1.3	1.7	1.7	4.0		**6.7**	1.7			21.9	7	153.4
	HK4			**5.0**			1.7		1.7	3.4		1.7		13.4	5	66.9
	SK															
	SK1	1.3	1.3	1.3	1.3								1.3	6.3	5	31.3
	SK2	**5.0**	1.3	**5.0**	1.3	1.3	4.0						**5.0**	22.8	7	159.3
	SK3		1.3	**<u>11.3</u>**	1.3	1.3				1.3	0.3			16.6	6	99.5
	SK4		1.3	**<u>11.3</u>**	1.3	1.3	1.0	1.7			1.7			19.4	7	135.8
Worm tubes	SM															
	SM1	2.5	1.3					1.7	**6.7**		1.7	1.7	**5.0**	20.4	7	142.9
	SM2										1.7	1.7	**5.0**	8.3	3	25.0
	SM3					1.7	1.0						**5.0**	7.7	3	23.0
	SM4										1.7		**5.0**	6.7	2	13.3
	ST															
	ST1	1.7		2.5	1.3			**6.7**	1.2	1.7		1.3	4.5	20.7	8	165.9
	ST2	1.6	1.7					**6.7**	0.2	1.7		1.2	1.7	14.6	7	102.5
	ST3	**6.7**					1.0		1.2		1.6	1.7	1.7	13.8	6	82.8
	ST4	1.6							1.2	1.7	1.6	1.7		7.7	5	38.5

(*Continued*)

TABLE A4. (CONTINUED)

Fouler	Location Station	Month 1	2	3	4	5	6	7	8	9	10	11	12	Sum	Incidence	Importance index
	CK															
	CK1	1.8	1.0											2.8	2	5.7
	CK2		**6.7**							1.7			1.7	10.0	3	30.0
	CK3	1.7	0.8								1.8		1.7	6.0	4	23.8
	CK4								**5.0**	**6.7**	**6.7**	1.7		20.0	4	80.0
	HM															
	HM1	1.7				1.7	1.7			**5.8**	**5.0**	**5.0**		20.8	6	124.7
	HM2	1.7				1.7				**6.7**		1.7		11.7	4	46.7
	HM3	1.0					1.7			1.7		**6.7**	2.5	13.5	5	67.5
	HM4									1.7		1.7		3.3	2	6.7
	TB															
	AMI	**10.2**	**19.4**	**19.0**	**16.3**	**8.8**	**5.6**	2.1	0.3	2.0	1.1	0.9	**6.1**	91.8	12	1101.2
	BNP	**22.9**	**25.3**	**15.5**	**9.3**	**16.2**	4.3	0.2	0.3	2.1	1.0	**9.0**	**37.4**	143.5	12	1722.4
	PSK	**35.0**	**25.3**	**25.5**	**22.5**	**15.4**	**6.7**	0.8	0.9	2.0	**8.1**	**12.7**	**22.8**	177.6	12	2130.7
	RSK	**18.8**	**11.2**	**9.0**	3.7	2.4	4.0	0.8		0.2	0.9	1.1	**19.6**	71.7	11	788.7
	EO_{PK}															
	PK1	1.3	4.0	**20.0**	**11.3**		**11.3**					1.3	1.3	50.3	7	352.2
	PK2	1.3	**9.0**	**5.0**	1.3	**6.7**	**11.3**		1.0			1.3		36.7	8	293.3
	PK3	1.3	4.0	**5.0**	1.3	1.3	1.3	1.3			1.4		1.3	17.9	9	161.0
	PK4	1.3	1.0	1.3	1.3	1.7	**5.0**	1.3						12.7	7	88.7
	HK															
	HK1	1.3	5.0	1.3								1.3	1.3	10.0	5	50.0
	HK2		5.0	1.3									1.3	7.5	3	22.5
	HK3	1.5	0.8	1.3										3.6	3	10.7
	HK4													0.0	0	0.0
	SK															
	SK1													0.0	0	0.0
	SK2						1.0							1.0	1	1.0
	SK3	**6.7**	1.3										1.3	9.2	3	27.7
	SK4	1.4	1.3						1.3				1.3	5.3	4	21.1

(*Continued*)

TABLE A4. (CONTINUED)

Fouler	Location Station	Month 1	2	3	4	5	6	7	8	9	10	11	12	Sum	Incidence	Importance index
Green algae	SM															
	SM1	2.5	**5.0**	**10.0**	**6.7**	**5.0**	4.0	1.7	1.7	**6.7**	1.7	1.7		46.5	11	511.5
	SM2				1.7	**6.7**		2.5		1.7				12.5	4	50.0
	SM3		1.25											1.3	1	1.3
	SM4		1.25			1.7								2.9	2	5.8
	ST															
	ST1		1.3		1.3	1.7	4.0		1.2			1.3	1.1	11.7	7	82.2
	ST2			2.5	1.2		3.8							7.5	3	22.6
	ST3		1.2		1.2			1.7	1.2				1.7	6.9	5	34.5
	ST4													0.0	0	0.0
	HM															
	HM1	**6.7**		**7.1**	1.7	**6.7**		**6.7**	1.7	1.7		**6.7**	**6.7**	45.5	9	409.3
	HM2	1.0			**9.0**			1.7	1.7	**6.7**		1.7	1.3	22.9	7	160.4
	HM3	**5.8**		1.7	**6.7**			1.7	**6.7**	1.7	0.6	1.7		26.4	8	210.9
	HM4	0.2				0.3				0.2	0.3			0.9	4	3.7
	EO_{PK}															
	PK1													0.0	0	0.0
	PK2								1.0					1.0	1	1.0
	PK3			1.3		1.3			1.0					3.5	3	10.5
	PK4		1.0									1.3	1.7	3.9	3	11.8
	OX															
	OX1		1.3		**6.7**	**12.0**	1.7	1.3	**6.7**	1.7			1.3	32.4	8	259.3
	OX2		0.3		**6.7**	**15.0**	1.7	1.7	2.5			1.7		29.5	7	206.5
	OX3	1.9			**15.0**	**1.7**	0.7		**6.7**	1.7	**10.0**	1.7		39.3	8	314.3
	OX4		4.2		**6.7**	**6.7**	2.5	**5.0**	**6.7**	**6.7**	0.6	**6.7**		45.6	9	410.1
	HK															
	HK1	1.3	1.3	1.3	1.3				**5.0**	1.3	1.7	1.3	1.3	15.4	9	138.8
	HK2		1.3	1.3	1.3	1.3	1.3		1.7				1.3	9.2	7	64.2
	HK3				1.3	1.7	1.7	1.0	1.7				1.3	8.5	6	51.0
	HK4	1.5			1.3	**15.0**	1.7	2.5		4.2	1.7	1.7		29.4	8	235.1
	SK															
	SK1	1.3			1.3	**11.3**	**15.0**	**5.0**	**8.5**				1.3	43.5	7	304.6

(*Continued*)

TABLE A4. (CONTINUED)

Fouler	Location Station	Month 1	2	3	4	5	6	7	8	9	10	11	12	Sum	Incidence	Importance index
	SK2	1.3	**11.3**		**11.3**			1.3	2.5			1.3		28.8	6	172.5
	SK3		1.3		1.3	1.3			**5.0**	1.3				10.0	5	50.0
	SK4		1.0		1.3				2.5	1.3				6.0	4	24.0
Tunicates	HK															
	HK1													0.0	0	0.0
	HK2	1.3												1.3	1	1.3
	HK3	**5.0**	1.3	1.3						1.7		1.3	1.3	11.7	6	70.0
	HK4	1.5	1.3		1.3				**6.7**		**6.7**	1.7	1.3	20.3	7	142.0
	SK															
	SK1		1.3	1.3						**5.0**	1.3	1.3		10.0	5	50.0
	SK2									1.7	2.5	1.3	1.3	6.7	4	26.7
	SK3											2.9		2.9	1	2.9
	SK4										1.7	0.9		2.6	2	5.1
Mud	HM															
	HM1			1.7	7.1		1.7	1.7	1.7					13.8	5	69.0
	HM2			1.1	1.7		2.5	1.7	1.7		**5.0**			13.6	6	81.9
	HM3		1.3				1.7							2.9	2	5.8
	HM4					1.7	1.7	1.7					1.7	6.7	4	26.7
	OX															
	OX1		1.3	**5.0**			**6.7**	1.3	1.7	1.7	**10.0**	1.7	**5.0**	34.2	9	307.5
	OX2	2.5					**6.7**		2.5		**10.0**	1.7	1.3	24.6	6	147.5
	OX3						1.9	**5.0**		1.7		1.7	**5.0**	15.3	5	76.3
	OX4												1.7	1.7	1	1.7

Methods of calculation described above. YOY, young-of-the-year. Vertical lines demarcate principal YOY stone crab July to November recruitment season.
* 1, January; 2, February, and so on. Bold print, monthly values greater than or equal to 5.0; bold and underlined, monthly values greater than or equal to 10.0.

TABLE A5.

Seasonal variation in principle foulers and degree of fouling at stations sampled in Everglades National Park, July 1979 to June 1980.

Location	Season*				
Station	Winter	Spring	Summer	Fall	Degree†
Everglades Inshore					
CKB	Oysters, mud, red and brown algae	Oysters	Oysters	Oysters	3
LSB	Oysters, green algae, red/brown algae	Tunicates	Green algae	Oysters	3
Everglades Nearshore					
CTB‡	Green algae, red/brown algae, mud	Barnacles, tunicates	Barnacles, tunicates	Barnacles, tunicates	3
LMI	Red/brown algae, mud	Red/brown algae, mud	Barnacles	Barnacles	3
SPT‡	Barnacles	Branched hydroids and bryozoans	Barnacles, branched hydroids and bryozoans	Green algae, branched hydroids and bryozoans, barnacles	3
Everglades Offshore					
INK‡	Barnacles, tunicates, worm tubes	Barnacles	Barnacles	Barnacles	3
PVK	Worm tubes, encrusting bryozoans, red and brown algae	Worm tubes, branched hydroids, and bryozoans	Barnacles	Barnacles	3
LMO	Branched hydroids and bryozoans, mud	Worm tubes, red and brown algae	Barnacles	Barnacles	3
NWC	Branched hydroids and bryozoans, red and brown algae	Branched hydroids and bryozoans	Barnacles	Barnacles	2
Florida Bay					
BWS	Green algae	Green algae	Green algae	Green algae	3
BBK	Green algae, mud	Red and brown algae, mud	Green algae	Mud	2
TNK	Red and brown algae, mud	Green algae	Green algae	Green algae	2
CPK	Red and brown algae	Red and brown algae	Green algae	Green algae	1
TKB	Red and brown algae	Red and brown algae	Red and brown algae	Red and brown algae	3
CCH	Branched hydroids and bryozoans, red and brown algae	Barnacles, red and brown algae	Barnacles	Barnacles	3
SKC	Red and brown algae	Red and brown algae	Red and brown algae, green algae	Red and brown algae	2
ASK‡	Red and brown algae	Red and brown algae, green algae	Barnacles	Red and brown algae	2

Locations and stations shown in Figure 1.
* Winter, December to February; spring, March to April; summer, May to September; fall, October to November. The spring and fall seasons are short, transitional periods between very warm to hot summer conditions and cool to occasionally cold winter conditions.
† Defined in Appendix 3. Degree of fouling at each station was similar throughout the year.
‡ Station sampled only October to June.

shore and at Sawyer Keys, where the opposite trend occurred. In general, however, a trend toward increasing occurrence of these algae with increasing distance from shore was present at many Florida Gulf locations.

Encrusting Bryozoans

Encrusting bryozoans were the most common principal fouler during spring and early summer at locations where barnacles were less important as a principal fouler (St Marks, Steinhatchee, Homosassa, lower Keys). They were also very rarely a principal fouler in Florida Bay and at Oxfoot Bank. At stations where barnacles were overwhelmingly the most common principal fouler during summer, other encrusting or spreading benthos, including encrusting bryozoans, diminished as barnacles colonized trap surfaces. At most locations, the incidence of encrusting bryozoans as a principal fouler increased with distance from shore.

Worm Tubes

Sabellid worms that form small flexible tubes was a common cool-weather principal fouler at many Gulf Coast stations, particularly those close to shore. Exceptions occurred at Cedar

Key, where fouling at CK4 differed markedly from fouling at other Cedar Key stations, and at EO_{PK} stations where, with movement shoreward, barnacles increasingly predominated as the principal fouler much of the year. In contrast, at Keys locations, worm tubes were rarely (lower Keys) or never (Oxfoot Bank) a principal fouler. Worm tubes was the principal fouler only during winter at Everglades Offshore stations INK, PVK, and LMO but predominated from summer through fall and into winter in Northwest Florida. This shift in seasonality, as well as the increased commonality of worm tubes as a principal fouler at Tampa Bay and Everglades Offshore stations, suggests that species composition changes between Homosassa and Tampa Bay.

Green Algae

Green algae was an important warm-weather fouler at locations where barnacles did not predominate. Green algae was never a principal fouler at Cedar Key or Tampa Bay and was rarely a principal fouler at EO_{PK}, locations where barnacles overwhelmed other fouling organisms during warm weather. At St Marks, Steinhatchee, and Homosassa, green algae was more common as a principal fouler at stations closer to shore. In ENP, green algae was a principal fouler at inshore and nearshore stations LSB, CTB, and SPT and was common as a principal fouler at eastern Florida Bay stations (BWS, BBK, TNK, and CPK). Green algae was also a principal fouler at all Keys locations, but its commonality varied among stations. The seasonality of green algae as a principal fouler was variable in Northwest Florida, temporally sporadic at inshore and nearshore ENP stations, extended throughout the year in eastern Florida Bay, and tended to be common from the spring through summer in the Keys. Regional differences in seasonality and personal observation (T.M. Bert) verify that species composition differed among regions and locations (e.g., filamentous green algae in Northwest Florida, *Acetabularia* in the lower Keys).

Tunicates

These organisms appeared on traps at most locations but were rarely common, becoming a principal fouler only at lower Keys locations. At Harbor Keys, tunicates increased in occurrence as a principal fouler with increasing latitude; but the opposite trend occurred at Sawyer Keys. At both locations, tunicates were a principal fouler most frequently from late summer through winter. In ENP, tunicates were a principal fouler mainly at a single Everglades Nearshore station (CTB) from spring to fall but were rarely a principal fouler at other stations (LSB, spring; INK, winter).

Mud

Mud was common on traps at locations where, occasionally, few living organisms colonized traps. Calcareous mud became the principal fouler on traps at Homosassa most frequently during spring and early to midsummer (March–August) and on traps at Oxfoot Bank from summer to early winter (June–December). At both locations, mud was a principal fouler more frequently at nearshore stations. In ENP, mud was a principal fouler during winter and, occasionally, spring or fall at Everglades Inshore (CKB) and Nearshore (CTB, LMI) stations and in eastern Florida Bay (BBK, TNK).