



# Seasonal abundance and diel behavior of roughneck shrimps (species of *Rimapenaeus* Pérez Farfante & Kensley, 1997) (Decapoda: Dendrobranchiata: Penaeidae) in northwestern Florida Bay, Florida, USA

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## ABSTRACT

A large number of roughneck shrimps, *Rimapenaeus* Pérez Farfante & Kensley, 1997, were collected in northwestern Florida Bay, southern Florida over four consecutive years (2000–2003) of monthly sampling during new-moon periods. Juveniles of *Rimapenaeus* spp. were more abundant than pink shrimp *Farfantepenaeus duorarum* (Burkenroad, 1939) juveniles, which are well-recognized and abundant inhabitants of Florida Bay. High *Rimapenaeus* spp. abundance was unexpected because the genus was previously reported only as occasional in Florida Bay. The populations of *Rimapenaeus* spp. were composed of late postlarvae and immature juveniles, suggesting that the northwestern border of Florida Bay serves as a nursery ground for this species. A clear seasonal recruitment pattern was observed with large peaks of postlarvae and small juveniles occurring in summer-fall and large juveniles in spring. The summer-fall peaks occurred during months with high mean water level and sea surface temperature; these two factors significantly predicted *Rimapenaeus* spp. abundance. Overnight hourly behavioral studies revealed that *Rimapenaeus* spp. juveniles were almost exclusively present in the water column during the dark hours of the ebb tide during current speed minimum. Juvenile abundance significantly differed between moon phases with shrimps being virtually absent during the illuminated full moon. These results indicate that *Rimapenaeus* spp. are phototactic negative, which may explain the low presence of this species in previous Florida Bay surveys conducted during daylight hours. This study highlights the previously unrecognized contribution of the abundance of juveniles of *Rimapenaeus* spp. to benthic-oriented crustacean communities of western Florida Bay and its border at the southwestern Florida Shelf.

**Key Words:** juveniles, postlarvae, migrations, penaeid shrimps, recruitment

## INTRODUCTION

Commercial shrimp fisheries constitute one of the largest fisheries in the US, both in terms of volume and landings value (NMFS, 2018). Landings from the Gulf of Mexico (GOM) dominate the total US shrimp catch:  $98.4 \times 10^5$  mt in 2017 accounted for 77% of the total (NMFS, 2018). Penaeid shrimp fisheries on southern Florida are dominated by the pink shrimp *Farfantepenaeus duorarum* (Burkenroad, 1939) captured on the Tortugas grounds,

an area covering approximately 10,000 km<sup>2</sup> between Key West, FL, and the Dry Tortugas in the GOM (Costello & Allen, 1966; Criales *et al.*, 2009; Hart *et al.*, 2012). Criales *et al.* (2009), however, reported that the yellow roughneck shrimp *Rimapenaeus similis* (Smith, 1885) comprised 23% of the smallest size class of the annual Tortugas shrimp landings, with a proportion within this size class as high as 59% on a quarterly (January-March) basis. Roughneck shrimps are not directly targeted for commercial exploitation because of their small size; however, they are frequently

caught in commercial shrimp fisheries targeting larger penaeid shrimps in the GOM and in the western Atlantic (e.g., Anderson, 1970; Hiroki *et al.*, 2011).

Roughneck shrimps are represented by two species in the Western Atlantic: *R. constrictus* (Stimpson, 1871) and *R. similis*, both previously included in *Trachypenaeus* Pérez Farfante, 1972 (see Pérez-Farfante & Kensley, 1997). *Rimapenaeus constrictus* is distributed from Nova Scotia, Canada to Santa Catarina, Brazil, whereas *R. similis* is restricted to the Florida Keys, Gulf of Mexico, and Caribbean Sea south to Brazil (Pérez-Farfante & Kensley, 1997).

Earlier reports concurred with later findings by Criales *et al.* (2009) that catches of both *R. constrictus* and *R. similis* from the Tortugas grounds during winter months were as high as those of the commercial pink shrimp (Eldred, 1959; Ingle *et al.*, 1959). Similarly, *R. constrictus* has also been reported as part of the commercial shrimp fishery from Campeche Bank, Mexico (Hildebrand, 1955), northeastern Florida (Joyce, 1965), and South Carolina and Georgia (Anderson, 1970). *Rimapenaeus constrictus* have been observed in commercial catches of the seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) in Brazil (Hiroki *et al.*, 2011). Despite their contributions to commercial landings, US penaeid-shrimp fisheries are managed as a single-species fishery; for the Tortugas grounds, this means consideration of only pink shrimp as the targeted species (Criales *et al.*, 2009; Hart *et al.*, 2012). Relatively little is known about the life history, ecological relationships, and commercial exploitation of the two species of roughneck shrimp.

Most studies reported that the nursery grounds of the roughneck shrimps were generally limited to the lower reaches of coastal bays (Gunter, 1950; Saloman, 1964; Subrahmanyam & Coultas, 1980). Brusher & Ogren (1976), however, concluded that roughneck shrimps utilized interior regions of the St. Andrews Bay system in Florida since the lower reaches of the system were similar to oceanic habitats. Roughneck shrimps are considered euryhaline species with an apparent preference for high salinities (Gunter, 1950; Saloman, 1964; Brusher & Ogren, 1976; Dall *et al.*, 1990). Tabb *et al.* (1962), however, commented that they are occasionally caught in water < 28 psu, whereas Gunter (1950) reported collecting one specimen at 21.9 psu and M.B. Robblee *et al.* (unpublished data) reported *R. similis* from salinities as low as ~7 psu. Roughneck shrimps occupy relatively deep waters of coastal ecosystems (Saloman, 1964; Brusher & Ogren, 1976; Hiroki *et al.*, 2011) and on a wide range of substrates, including sand, sandy shell, sandy mud, and mud (Hildebrand, 1955; Saloman, 1964; Camp *et al.*, 1977; Huff & Cobb, 1979). Their distribution is negatively correlated with both submerged aquatic vegetation (SAV) cover and canopy height as well as with seagrass cover (M.B. Robblee *et al.*, unpublished data). These generalized habitat requirements may be complicated by changes in habitat affinity associated with differing ontogenetic stages and species (i.e., *R. constrictus* and *R. similis*), as most authors did not adequately report size or species information.

Roughneck shrimps play an important ecological role in the marine food web, serving as prey of marine invertebrates and vertebrates (Sikora *et al.*, 1972; Ross *et al.*, 1989; Franks *et al.*, 1995; Costa & Fransozo, 2004a). Despite their abundances in shelf habitats and their presence in commercial shrimp fisheries, information about their life histories is limited and mainly derived from faunal and ecological surveys (e.g. Williams, 1969; Camp *et al.*, 1977; Wenner *et al.*, 1991), general penaeid shrimp studies (Brusher *et al.*, 1972; Huff & Cobb, 1979; Pérez-Farfante, 1988; Criales *et al.*, 2000), and reports on the commercial shrimp fishery (e.g. Eldred, 1959; Joyce, 1965; Brusher *et al.*, 1972; Criales *et al.*, 2009). Studies of southern Florida penaeids have focused on the commercially targeted pink shrimp. While investigating the recruitment and emigration of pink shrimp postlarvae into Florida Bay (Criales *et al.*, 2006), large numbers of roughneck shrimps were captured at its western boundary. The high roughneck shrimp catch was unexpected because *R. constrictus* has

previously been recorded only as an occasional species in Florida Bay (Tabb *et al.*, 1962), with a record of only 30 juveniles collected during an intensive biological survey conducted for three consecutive years (Tabb & Manning, 1961). *Rimapenaeus similis* has also been reported in low densities in the vicinity of Shark and Lostmans Rivers (i.e., Ponce de Leon Bay, Oyster Bay, and Lostman's River) just to the north of Florida Bay (M.B. Robblee *et al.*, unpublished data).

The aims of this research were to estimate the monthly abundances of postlarval and juvenile stages of the pink (*F. duorarum*) and roughneck shrimps (*Rimapenaeus* spp.) at two different sub-regions of Florida Bay, and investigate the environmental factors affecting the spatiotemporal abundance, seasonality and behavior of roughneck shrimps in northwestern Florida Bay.

## MATERIALS AND METHODS

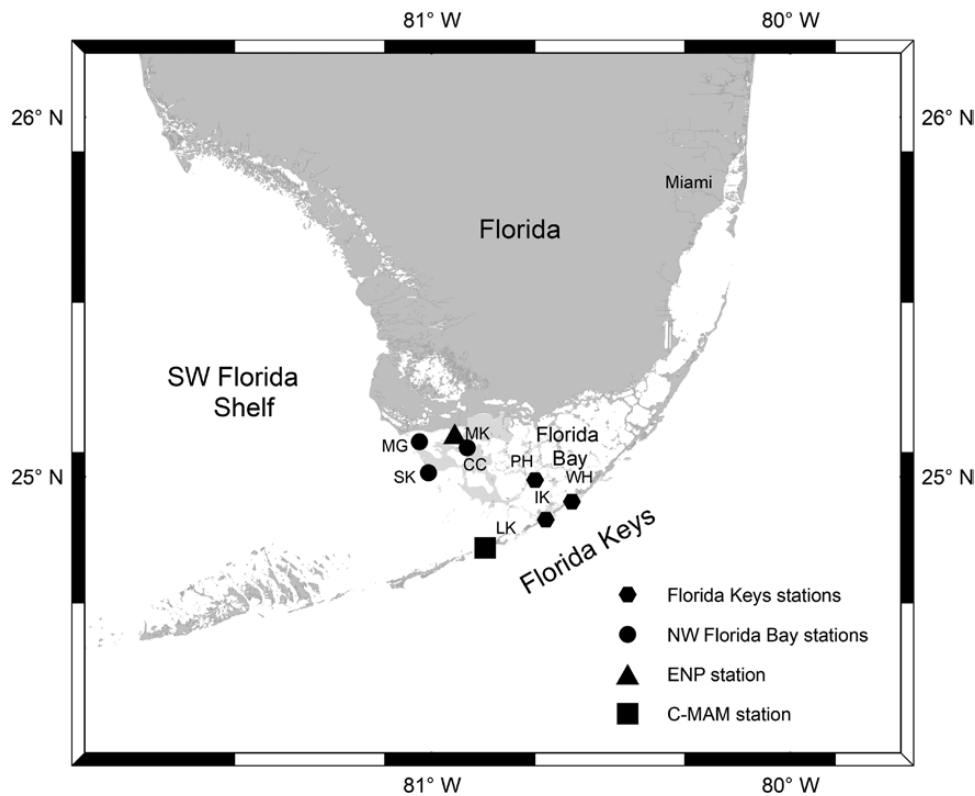
### Study location

Florida Bay is a triangular-shaped shallow estuary located at the southern tip of Florida, made up of a complex network of shallow basins separated by carbonate mud banks and mangrove islands (Fig. 1). Florida Bay is connected with the southwestern Florida Shelf of the Gulf of Mexico (GOM) through passes at its northwestern border and with the Atlantic Ocean through the channels of the Florida Keys (Lee *et al.*, 2006). Florida Bay is the primary nursery ground of several fishes and invertebrates, including the pink shrimp, which has been recognized as one of the most ecologically and economically important marine species in southern Florida.

Penaeid shrimps were sampled as part of a study evaluating the immigration and emigration pathways of pink shrimp postlarvae and juveniles in Florida Bay (Criales *et al.* 2006). Sampling occurred in two Florida Bay sub-regions: 1) passes along its northwestern border with the Florida Shelf of the GOM, and 2) channels between the Middle Florida Keys that connect southeastern Florida Bay to the Atlantic Ocean. The stations in northwestern Florida Bay were Sandy Key (SK), Middle Ground (MG), and Conchie Channel (CC). SK and MG were the most exterior stations located in passes connecting the Bay with the southwestern Florida Shelf environment. The Conchie Channel station was located along the main channel entering northwestern Florida Bay about 12 km from the two exterior stations (Fig. 1). The stations in the Middle Florida Keys were Whale Harbor (WH), Indian Key (IK), and Panhandle Key (PH). The WH and IK stations were located in channels that connect the southeastern margin of the Bay with the Atlantic Ocean, and the PH station was inside the bay about 15 km from the two exterior stations. Channel depths at the exterior stations were ~3.0 m (SK, MG, WH, IK) and ~2.0 m at the interior stations (CC, PH).

### Sampling methodology at two Florida Bay sub-regions

The penaeid shrimps collected at the two Florida Bay sub-regions were postlarval and juvenile stages of pink (*F. duorarum*) and roughneck shrimps (*Rimapenaeus* spp.). Postlarval and juvenile abundances were investigated using two different temporal sampling regimes (i.e., “monthly” and “overnight”); both employed the same methodological approach. During each sampling event, two moored channel nets (0.75 m<sup>2</sup> opening, 1 mm mesh size, and 500 µm mesh in the cod-end) were deployed from separated fixed moorings at each station for about 12 h, from dusk until shortly after sunrise. Nets swung freely, changing direction with the tidal current, and sampled below the surface at a water depth of ~0.60 m. A flowmeter (i.e., low speed rotor: General Oceanics, Miami, FL, USA) was suspended in the mouth of each net to measure the volume of water filtered through the net. Immediately after



**Figure 1.** Map of the study area depicting locations of channel net stations in northwestern Florida Bay sub-region, Florida (circles: SK, Sandy Key; MG, Middle Ground; CC, Conchie Channel) and in the Middle Florida Keys sub-region (hexagons: WH, Whale Harbor; PH, Panhandle, IK, Indian Key), the Everglades National Park (ENP) water quality station (triangle: MK, Murray Key), and the National Data Buoy Center, C-MAN (Coastal Marine Automated Network) station (square: LK, Long Key).

retrieving channel net samples, penaeid shrimps were sorted from other collected debris and preserved in 90% ethanol. Samples were transferred to the laboratory, where shrimps identified to the lowest taxonomic level possible.

The collected penaeid shrimps were grouped by ontogenetic and taxonomic classifications. This approach was both necessary due to difficulties in species identifications and convenient for investigation of penaeid immigration and emigration dynamics. Roughneck shrimps (*Rimapenaeus* spp.) and pink shrimp (*F. duorarum*) were separated into postlarval and juvenile stages using keys and taxonomic descriptions (Cook, 1966; Pérez-Farfante, 1970; Dall *et al.* 1990; Criales & Varela, 2018). Postlarvae were characterized by the presence of functional swimming pleopods and chelae on all pereopods but lacking developing thelycum (females) or petasma (males). Juveniles were identified as having a bulky body with abundant chromatophores, early development of thelycum for females, and unjointed petasmas lobes (gonadal endopods) for males. Pink-shrimp postlarvae were easily differentiated from roughneck postlarvae by their body shape and size, shape of the telson, and the number of rostral spines (Cook, 1966; Chace, 1972; Criales & Varela, 2018). The two western Atlantic species of *Rimapenaeus* (*R. constrictus* and *R. similis*) were differentiated by subtle differences in the structure and shape of the thelycum and petasma in females and males, respectively (Chace, 1972; Abele & Kim, 1986; Pérez-Farfante, 1988). The pink-shrimp postlarvae were identified using a suite of previously described characters, such as telson type, rostrum shape, spines on the six abdominal somite, and patterns of sternal thoracic spines (Dobkin, 1961; Ringo & Zamora, 1968; Ditty, 2014; Criales & Varela, 2018) and for juveniles (Pérez-Farfante, 1970; Ditty & Alvarado Bremer, 2011; Zink *et al.*, 2018; Timm *et al.*, 2019). The presence of spermatophores (sperm bearing structures) and sperm plugs (structures

inserted after the sperm is deposited) in males and females, respectively was also documented.

#### Monthly abundance sampling at northwestern Florida Bay

Monthly abundances by taxonomic and ontogenetic grouping of pink (*F. duorarum*) and roughneck (*Rimapenaeus* spp.) shrimps were used to determine the most abundant ontogenetic-taxon grouping between the two sub-regions in Florida Bay. Based on our results, analysis was focused on spatiotemporal trends in the abundances of *Rimapenaeus* spp. at the northwestern Florida Bay stations and their relationship with environmental conditions. Monthly sampling was conducted during two consecutive nights around the new moon during four years from January 2000 to December 2003 at MG and SK locations; sampling at CC occurred between July 2001 and December 2003.

To investigate monthly changes in size distribution, carapace length (CL) data were collected from *Rimapenaeus* spp. collected at MG. The CL was measured as the distance from the postorbital margin to mid-dorsal posterior margin of the carapace (Pérez-Farfante & Kensley, 1997). Where samples contained 15 or fewer individuals, all specimens were measured; samples larger than 15 specimens were subsampled selecting randomly between 15 and 45 individuals, depending on the sample size.

#### Overnight behavioral sampling

Behavioral response of *Rimapenaeus* spp. to tides, moon phases, and light were investigated during two 12 h and one 20 h experiment conducted in summer 2002 at the SK station. Channel nets, deployed as previously described, were used to collect dark-flood and dark-ebb samples. These samples were collected hourly



throughout a nocturnal tidal cycle from 1800 to 0700 h on three nights: 9–10 July (new moon), 23–24 July (full moon) and 8–9 August (new moon). The last overnight sampling event was followed by hourly daytime sampling on 9 August 2002 over 10 consecutive hours. The August 8–9 sampling event thus consisted of observations over a 20 h cycle nocturnal and diurnal sampling period (10h dark:10h light).

### Environmental data collection

A suite of climatological and oceanographic data were used to investigate relationships of monthly *Rimapenaeus* spp. abundances to environmental conditions. Hourly sea surface temperature (SST), surface salinity (psu), and mean water level (MWL in cm) for the period of January 2000 to December 2003 were obtained from the Murray Key station (MK, 25°12'N 80°93'W), which is one of many permanent, continuous water-quality monitoring stations maintained by the National Park Service South Florida Natural Resources Center (NPS SFNRC) (SFNRC, 2019). The MK station is located 12, 10, and 6 km from SK, MG, and CC stations, respectively (Fig. 1). Hourly wind speed ( $\text{m sec}^{-1}$ ) and direction data were obtained from the National Data Buoy Center (NDBC, 2019) C-MAN station at Long Key, Middle Florida Keys (24°50'N 80°51'W) for the period of January 2000 to December 2003 ([https://www.ndbc.noaa.gov/station\\_page.php?station=lonfl](https://www.ndbc.noaa.gov/station_page.php?station=lonfl)). The hourly wind speed and direction data were converted into wind components (direction to) as  $u$  = east (+) and west (–),  $v$  = north (+) and south (–). The wind data were calculated as an averaged pre-sampling period of seven days to each sampling event based on observations that wind events occur on temporal scales of approximately one week (Lee & Williams, 1999).

Station-specific hourly salinity data were available for a subset of the entire study period. From February 2002 through December 2003, hourly salinity data were available from conductivity, temperature, and depth (CTD) recorders installed at the MG, SK, and CC stations (Hittle *et al.*, 2001). The salinity data were used to investigate differences in salinity regime among these three sampling stations.

### Data processing and statistical analysis

**Monthly spatiotemporal and environmental relationships.** The raw count of *Rimapenaeus* spp. individuals collected per sampling net were transformed to abundances ( $10^3$  shrimps  $\text{m}^{-3}$ ) by dividing counts by the volume of water filtered ( $\text{m}^3$ ) per sampling event. *Rimapenaeus* spp. abundance data were transformed [ $\ln(x + 1)$ ] to normalize the right-skewed data. This action eased nearly all distributional and variance issues. Data were tested for normality (Shapiro-Wilk tests) and equality of variance (Bartlett's test) to validate assumptions of parametric statistical analysis (Zar, 2009). Monthly time series of SST, MWL, salinity (from SFNRC MK station), and wind components (U, V, from C-MAN LK station) were used to investigate environmental factors affecting observed monthly *Rimapenaeus* spp. abundances. A generalized linear model (GLM) assuming a normal distribution and an identity-link function was developed (SPSS) (IBM SPSS statistic; IBM Corporation, New York, NY, USA). Abundance was the dependent variable and the predictors included the previously described climatological and oceanographic data as continuous variables and station and year as categorical variables. To compare and visualize differences in abundance among groups, least square (marginal) mean (LS) values were computed (Searle *et al.*, 1980). Post-hoc Tukey tests were used to analyze statistical differences for both year and station predictor treatment levels. Distributions of *Rimapenaeus* spp. size (CL) measurements were investigated among years and months using Kruskal-Wallis tests. A post-hoc Duncan test was used to compare pairwise differences between treatment levels.

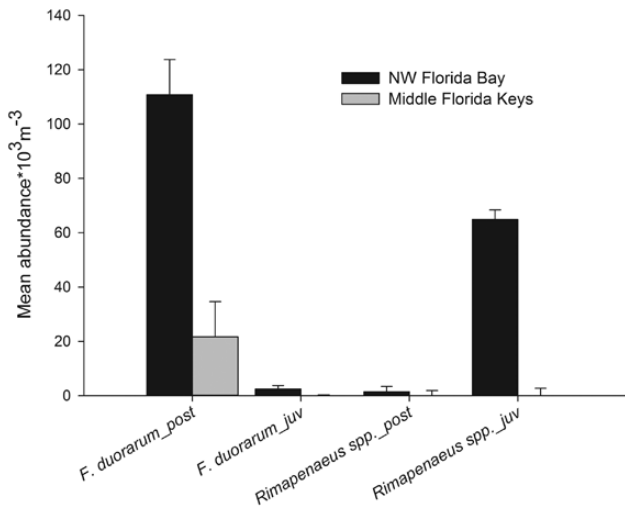
The salinity regimes at these northwestern Florida Bay stations (CC, SK, and MG) were characterized by summarizing hourly salinity data into monthly average, standard deviation, range, minimum, and maximum salinity values. The salinity regime metrics were used in a multivariate analysis to investigate differences in salinity regime among the three stations using R v.3.6.0 (R Core Team, 2016). The salinity regime metrics were arranged into a matrix with columns representing salinity metrics (mean, standard deviation, range, minimum, maximum) and rows representing sampling events (location, month, and year). A Euclidean distance matrix was computed from the monthly salinity metric matrix. The distance matrix was then investigated using PERMANOVA to test for location ( $N = 3$ ), month ( $N = 12$ ), and year ( $N = 2$ ) main effects, and their interactions, as categorical predictors (Anderson, 2001; McArdle & Anderson, 2001). The model was constructed using Type II (i.e., marginal) sum of squares formulations from the “adonis.II” and “adonis” functions of the “RVAideMemoire” version.0.9–75 (Hervé, 2019) and “vegan” version.2.5–6 (Oksanen *et al.*, 2019) packages, respectively, in the R statistical environment computed with 10,000 permutations. Because distance-based multivariate analyses can confound location and dispersion effects (Warton *et al.*, 2012), multivariate dispersion was investigated to determine whether within-group variability substantially contributed to PERMANOVA test results (Anderson, 2006). “Post-hoc” pairwise PERMANOVA testing of among-station salinity regime differences was conducted using the “pairwise.adonis2” function using Bonferroni corrections (Martinez Arbizu, 2019). A principal coordinate analysis (PCoA) assisted with visualizing differences between treatment levels (Anderson & Willis, 2003).

**Overnight behavioral sampling.** Individuals of *Rimapenaeus* spp. collected during the three experiments were referred to as juveniles since it was the dominant group. Raw counts of *Rimapenaeus* spp. juveniles were converted to abundance as previously described for the monthly sampling. The respective tidal currents were separated according to the current direction as ebb and flood. The hourly abundance values were pooled across sampling events and analyzed with Kruskal-Wallis tests in STASTICA (Statsoft, Tulsa, OK, USA). The hourly time series from the three nocturnal experiments were used to determine differences between the two moon phases (new and full) and the tide stages (ebb and flood). The complete day-night hourly time series from August 8–9 was also tested for the effect of light versus dark.

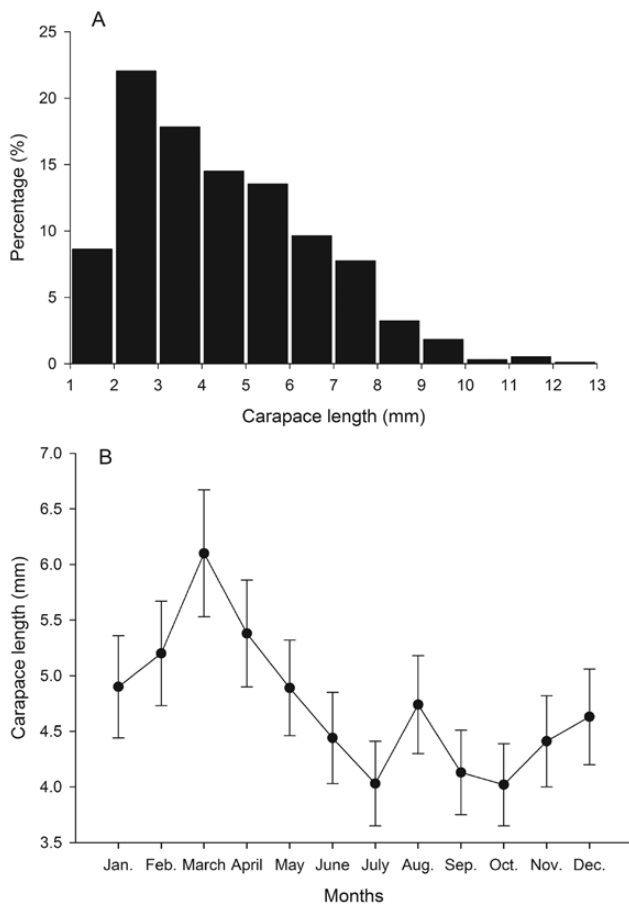
## RESULTS

### Spatiotemporal trends in abundances and sizes

Penaeid shrimps collected at the northwestern Florida Bay sub-region stations (SK, MG, and CC) and Middle Florida Keys sub-region stations (IK, PK, and WH) were postlarval and juvenile stages of *F. duorarum* and *Rimapenaeus* spp. Across the four years of sampling at both study sub-regions, comparison of mean monthly abundances by taxonomic and ontogenetic grouping revealed that *F. duorarum* postlarvae were the most abundant ontogenetic-taxon grouping (Fig. 2). Abundances of *F. duorarum* postlarvae ( $110.8 \times 10^3$  postlarvae  $\text{m}^{-3}$ ) were about five times higher in the northwestern Florida Bay sub-region than those of the Florida Keys sub-region stations ( $21.7 \times 10^3$  postlarvae  $\text{m}^{-3}$ ). Although captured in much lower numbers, *F. duorarum* juveniles indicated a similar spatial pattern with an average of  $2.5$  shrimp  $\times 10^3$   $\text{m}^{-3}$  in the northwestern Florida Bay sub-region and  $0.1 \times 10^3$  shrimp  $\text{m}^{-3}$  in the Middle Florida Keys sub-region. As with *F. duorarum*, postlarval and juvenile *Rimapenaeus* spp. were also more abundant at the northwestern Florida Bay stations (Fig. 2). Average *Rimapenaeus* spp. postlarvae and juvenile abundances in northwestern Florida Bay were  $2.5$  and  $64.9 \times 10^3$  shrimps  $\text{m}^{-3}$ ,



**Figure 2.** Mean abundances (shrimps × 10<sup>3</sup> m<sup>-3</sup> ± SE) of postlarval and juvenile stages of penaeid shrimps *Farfantepenaeus duorarum* and *Rimapenaeus* spp. collected at stations of the northwestern Florida Bay, Florida and the Middle Florida Keys sub-regions, Florida during monthly, new moon sampling from January 2000 to December 2003. This figure is available in color at *Journal of Crustacean Biology* online.



**Figure 3.** Carapace length (CL in mm) of *Rimapenaeus* spp. specimens collected at the Middle Ground (MG) station, Florida Bay, Florida from January 2000 through December 2003: Percentages of size class distributions (A) and monthly mean ± 0.95 confidence intervals (B).

respectively. In contrast, no *Rimapenaeus* spp. postlarvae were collected at the Middle Florida Keys sub-region and the average juvenile abundance was  $0.2 \times 10^3$  shrimps  $m^{-3}$ . The seasonality and transport modelling of *F. duorarum* postlarvae were already analyzed by [Criales et al. \(2006, 2015\)](#). Based on the present results, we only considered *Rimapenaeus* spp. individuals collected at the northwestern Florida Bay stations as the Florida Keys sub-region constituted less than 2% of the penaeid-shrimp catch.

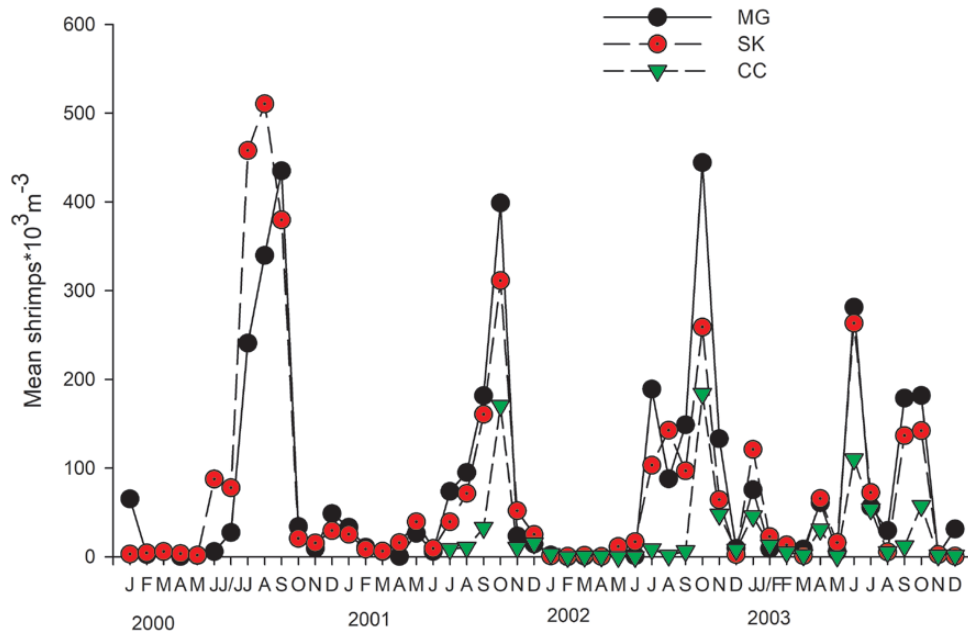
The stage of development of the thelycum and petasma in the majority of the *Rimapenaeus* spp. specimens was not sufficient to identify them to species level. Postlarval specimens ranged from 1.3 to 2.0 mm CL and constituted only 8.6 % ( $N = 160$ ) of the analyzed *Rimapenaeus* spp. shrimps (Fig. 3A). Juveniles ranged from 2.1 to 12.3 mm CL and made the remaining 91.4% ( $N = 1,695$ ) of the *Rimapenaeus* spp. specimens. The size frequency distribution of analyzed specimens indicated that the post-settlement juveniles (2.0 to 3.0 mm CL) was the most numerous size class caught (22.0%,  $N = 409$ ) with each successive 1 mm size bin representing lower percentages of the total. Juveniles 2.0 to 8.0 mm CL size class dominated the catch (94.0%,  $N = 1743$ ), and juveniles larger than 9.0 mm CL were rarely collected (6%,  $N = 112$ ; Fig. 3A). Large juveniles > 9.0 mm CL were still immature specimens with separated petasmas lobes and females with thin, transparent ovaries. Spermatophores and sperm plugs were absent in males and females, respectively.

Annual size distributions, pooled across months, indicated no significant differences ( $H = 2.1$ ;  $df = 3$ ;  $N = 1,855$ ;  $P = 0.09$ ). Significant differences, however, were detected among monthly size distributions, pooled across year ( $H = 125.1$ ;  $df = 11$ ;  $N = 1,855$ ;  $P < 0.0001$ ). Larger individuals were caught during the winter/spring months (January-April) with the largest median size observed in March (Fig. 3B). Conversely, smaller individuals were caught during the summer/fall months (July-November), with the smallest median sizes observed during July and October. Pairwise testing of monthly size distributions revealed seasonal differences in sizes (Table 1). The size distribution of the summer-fall months (June-November) differed from those of winter-spring months (January-April).

Abundance peaks of *Rimapenaeus* spp. at the northwestern Florida Bay stations occurred with a distinct seasonal pattern (Fig. 4). At SK and MG, the two exterior stations, the highest peaks in abundance were observed in late summer and fall (July-October); however, the 2003 peak was interrupted by very low catches in August at these stations (Fig. 4). The seasonal pattern was similar at the interior CC station, but abundances were lower than those of the two exterior stations (SK and MG). In contrast, abundances of *Rimapenaeus* spp. were lowest during winter

**Table 1.** Kruskal-Wallis test followed by a post-hoc Duncan test on comparisons of mean carapace length by month. Significant differences ( $\alpha = 0.05$ ) are indicated with \*.

	J	F	M	A	M	J	J	A	S	O	N	D
J			*				*		*	*	*	
F							*		*	*	*	
M					*	*	*	*	*	*	*	*
A							*	*	*	*	*	*
M								*	*			
J												
J												
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S												
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D												



**Figure 4.** Monthly mean abundances (shrimps  $\times 10^3 \text{m}^{-3}$ ) of specimens of *Rimapenaeus* spp. collected during new-moon sampling at Middle Ground (MG), Sandy Key (SK), and Conchie Channel (CC) stations, northwestern Florida Bay, Florida. MG and SK stations were sampled from January 2000 to December 2003, and CC station from July 2001 to December 2003. This figure is available in color at *Journal of Crustacean Biology* online.

and spring months, although some individuals were caught during these seasons (Fig. 4). Temporal shifts in the peak abundances suggested a phenology of recruitment and abundance of *Rimapenaeus* spp. that can be initiated earlier (e.g., June 2002 and 2003) and protracted later into the fall (e.g., November 2002; Fig. 4).

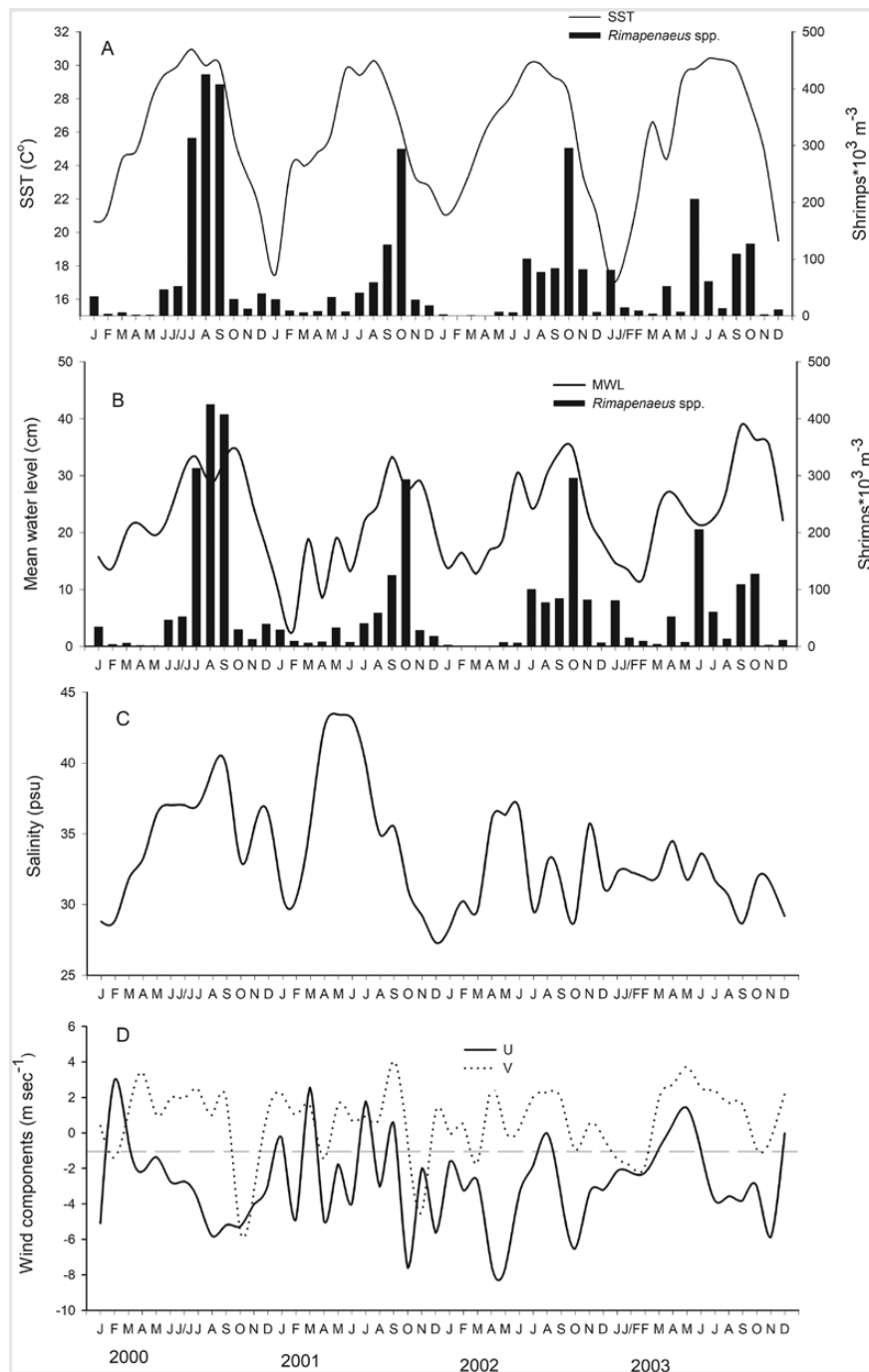
#### Monthly abundance sampling and environmental relationships

Time series of the abundances of *Rimapenaeus* spp. plotted against SST indicated that higher abundance was associated with seasonal peaks in SST (Fig. 5A). SST exhibited a typical southern Florida seasonal pattern, with temperatures rising as high as  $\sim 33^\circ\text{C}$  during the summer (June to August), cooling during the fall (September), and winter lows of  $\sim 18^\circ\text{C}$  (January; Fig. 5A). Peaks in the abundance of *Rimapenaeus* spp. also seemed to coincide with seasonal peaks of MWL (Fig. 5B). MWL was lowest during winter months (January and February), progressively increased during the following months, and reached a maximum in late summer-early fall (i.e., depending on the year, July through October; Fig. 5B). Salinity at the MK station was typical of the western Florida Bay region with high inter-monthly and annual variation. Maximum salinities ( $\sim 43$  psu) occurred at the end of the dry season/early wet season in early summer (May-July) and minimum values ( $\sim 28$  psu) occurred at the end of the wet season (December-January; Fig. 5C). Hypersalinity was observed during 2000 and 2001, whereas maximal salinities in 2002 and 2003 were lower. The annual cycle of wind components indicated a prevailing northwest direction (SE winds) of light to moderate winds ( $2\text{--}4 \text{ m s}^{-1}$ ) during summer, although events of northeast direction (SW winds) were also observed (Fig. 5D). The wind changed direction in the fall and winter with moderate to strong ( $\sim 4\text{--}8 \text{ m s}^{-1}$ ) southeastward flow (NW winds). The alongshore wind was mainly northward and the cross-shelf wind was westward during most of the four-year sampling period. Besides seasonal influences, winds are also largely influenced by synoptic-scale and mesoscale motions that are highly variable.

Salinity regimes were further monitored independently at the three study locations (CC, MG, SK) during 2002 and 2003 (Fig. 6). Monthly mean salinity followed the seasonal pattern as

previously described for the MK station. Overall mean salinities at the three stations were CC  $32.96 \pm 0.58$  psu, MG  $33.37 \pm 0.62$  psu, and SK  $32.32 \pm 0.61$  psu (Fig. 6). The mean monthly salinity showed similar patterns among stations with troughs and peaks occurring almost simultaneously. Differences among the three stations, however, were apparent: the SK mean salinity trend at times deviated from that of MG and CC, which tracked each other more closely. Of the three stations, CC exhibited the highest and lowest values in the time series (Fig. 6). Multivariate analysis explained the majority ( $R^2 = 0.648$ ) of salinity regime (i.e., monthly mean, SD, minimal, maximal, and range) variability and revealed a significant station main effect and an interaction between study month and year (Table 2). Tests of multivariate dispersion did not reveal statistical differences among station, month, year, or month  $\times$  year interaction groups ( $P > 0.05$ ). The multivariate analysis revealed a bi-modal seasonal pattern in salinity regime. December, January, February, and March clustered together in one region of the PCoA map whereas May through November occurred in a separate region of the PCoA space (Fig. 7A). Statistical differences in salinity regimes between SK and CC were observed (*Pseudo*  $F_{1,19} = 3.85$ ,  $P = 0.0354$ ), but not between MG and SK (*Pseudo*  $F_{1,25} = 2.73$ ,  $P = 0.0733$ ) nor between MG and CC (*Pseudo*  $F_{1,17} = 1.46$ ,  $P = 0.2454$ ; Fig. 7B).

Outputs of the GLMs analyzing *Rimapenaeus* spp. abundances relative to environmental variables, stations, and years as predictors revealed significant differences among years and stations (Table 3, Fig. 8). The highest abundances were caught in 2000 ( $110.58 \pm 10.3 \times 10^3$  shrimp  $\text{m}^{-3}$ ) and the lowest was in 2002 ( $49.0 \pm 8.3 \times 10^3$  shrimp  $\text{m}^{-3}$ ). A post-hoc Tukey test indicated differences between 2002 and each of 2000, 2001, and 2003 ( $LS = 2.1$ ,  $df = 463$ ,  $P < 0.01$ ). Among stations, CC significantly differed from both MG and SK ( $LS = 3.1$ ,  $df = 463$ ,  $P < 0.01$ ). MG exhibited the highest abundances, but no significant differences were found with SK (Fig. 8). Outputs from the GLM identified MWL, SST, and U wind component as significant predictors of *Rimapenaeus* spp. abundance. It is noteworthy that salinity was not identified as a significant predictor. The peak of *Rimapenaeus* spp. abundance during 2000 occurred when salinity was high ( $39.5\text{--}39.6$  psu) in August-September (Fig. 5). The abundance peaks



**Figure 5.** Monthly mean time series of abundances of *Rimapenaeus* spp. (vertical bars, shrimps  $\times 10^3 \text{ m}^{-3}$ ) from northwestern Florida Bay, Florida stations together with: sea surface temperature (SST) (A), and mean water level (cm) (B) depicted as continuous lines. Monthly mean time series of salinity (psu) (C), and wind components, U and V ( $\text{m sec}^{-1}$ ) (D). Letters on the x-axis denote months of the year.

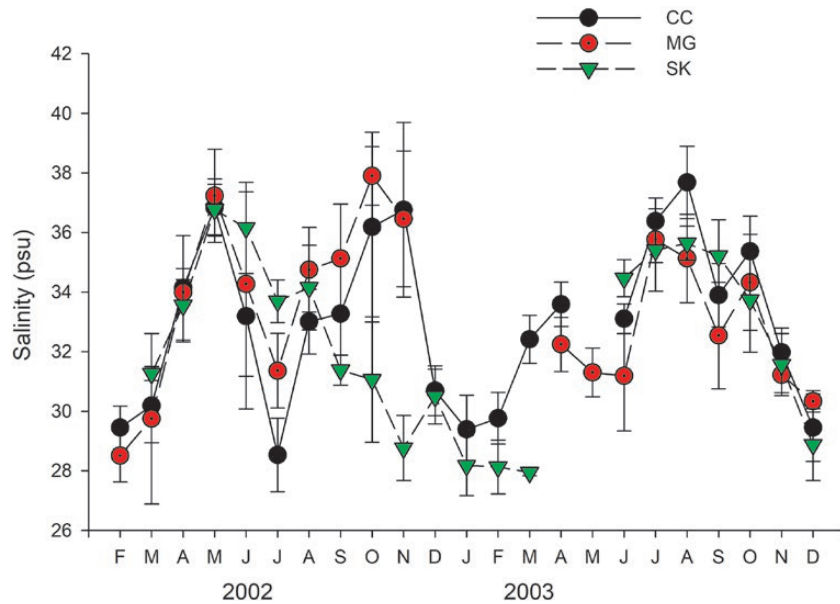
occurred at much lower salinities (range:  $\sim 28\text{--}33$  psu; Fig. 5) during the following years.

#### Overnight behavioral sampling

Nocturnal sampling conducted hourly at the SK station during a 12 h tidal cycle revealed similar patterns in abundance among the three sampling events (Fig. 9). During the first  $\sim 5$  h of sampling, the current was moving out of Florida Bay with the ebb tide. The current speed was at its minimum at 2400 h and the current reversed direction to flood tide for the remainder of the night ( $\sim 0600\text{--}0700$  h). *Rimapenaeus* spp. juveniles were essentially

absent from the water column during the early ebb tide period of each evening; however, the number of shrimps increased later in the night with most shrimps being caught during the late ebb tide (Fig. 9). Peak abundances in all three sampling events were observed at 2300 h when the current was at its minimum speed ( $< 20 \text{ cm sec}^{-1}$ ), corresponding to slack tide. The maximum abundance recorded during the dark-ebb was  $725.4 \times 10^3 \text{ shrimp m}^{-3}$  observed at 2300 on 8 August 2002 (Table 4, Fig. 9C). Abundances of *Rimapenaeus* spp. juveniles declined during the following six hours of flood tide on all three nights of sampling. The maximum flood tide density was  $173.4 \times 10^3 \text{ shrimp m}^{-3}$  at 0400 h on July 10 (Fig. 9A); this observation again coincided with a slackening tidal





**Figure 6.** Salinity (psu) monthly means  $\pm$  SD from Middle Ground (MG), Sandy Key (SK) and Conchie Channel (CC), northwestern Florida Bay, Florida from February 2002 to December 2003. Letters on the x-axis denote months of the year. This figure is available in color at *Journal of Crustacean Biology* online.

**Table 2.** Results of PERMONOVA test that included categorical location, month, year, and month  $\times$  year interaction as categorical predictors. The overall model was highly significant (Pseudo  $F_{36,60} = 2.95$ ,  $P < 0.001$ ) and explained the majority of the salinity regime variability ( $R^2 = 0.648$ ).

Predictor	DF	Pseudo F value	P	R <sup>2</sup>
Location	2	2.539	0.0468	0.048
Month	11	3.865	0.0001	0.404
Year	1	2.600	0.0727	0.025
Month $\times$ Year	10	1.907	0.0251	0.181
Residual	36	—	—	0.342

regime. Shrimp abundances between ebb and flood tides did not statistically differ ( $H = 2.955$ ;  $df = 1$ ;  $N = 36$ ;  $P = 0.0856$ ).

Abundances of juvenile *Rimapenaeus* spp. during the “new-moon” lunar phase (July 9–10 and August 8–9 2002) reached peaks of  $533.9$  and  $725.4 \times 10^3$  shrimp  $m^{-3}$ , respectively (Fig. 9A, C). In contrast, during the “full moon” lunar phase (July 23–24) the peak was two orders of magnitude lower at only  $8.9 \times 10^3$  shrimp  $m^{-3}$  (Fig. 9B). Differences in juvenile abundances between the two lunar phases were significant ( $H = 8.87$ ;  $df = 1$ ;  $N = 36$ ;  $P = 0.002$ ). Low abundances were also observed during daylight hours during the 24 h sampling event (August 8–9 2002): only  $5.1 \times 10^3$  shrimps  $m^{-3}$  were captured during the diel ebb tide (Table 4). A significant difference in juvenile abundances between light-hour and dark-hour samples was detected ( $H = 15.7$ ;  $df = 1$ ;  $N = 20$ ;  $P = 0.0001$ ). In summary, these results indicate that the abundances of *Rimapenaeus* spp. juveniles in the water column maximize during nocturnal hours, and peaks in abundance coincide with the minimum current speed of slack tide, especially during ebb tides.

## DISCUSSION

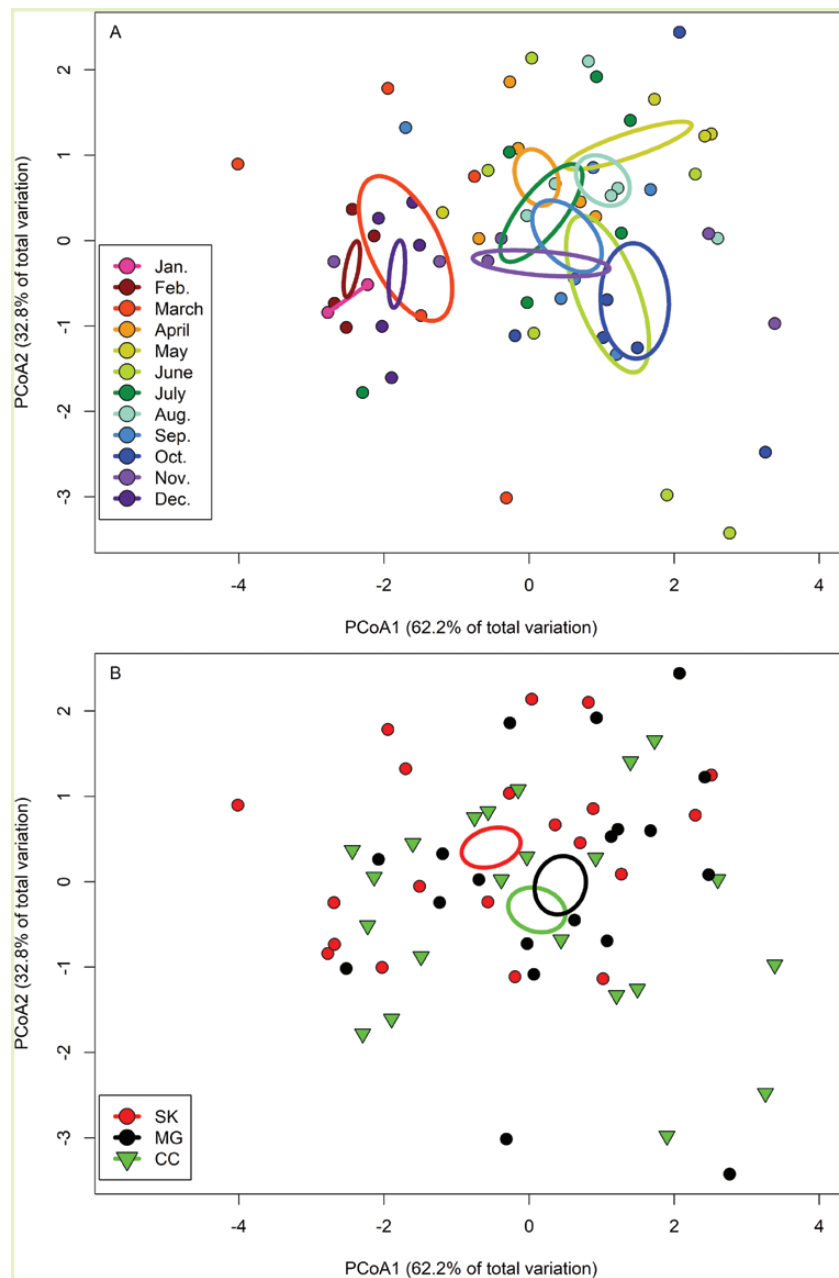
We observed relatively high abundance of *Rimapenaeus* spp. individuals in northwestern Florida Bay. This high abundance was unexpected because *R. constrictus* was previously reported only as an occasional species at the western border of the bay (Tabb & Manning, 1961; Tabb et al., 1962). M.B. Robblee et al. (unpublished

data) also reported low benthic densities of *R. similis* using throw-trap sampling gear during the day along the southwest mangrove coast in the vicinity of Shark and Lostman’s rivers just to the north of the present study sub-region in northwestern Florida Bay. A possible factor affecting the different abundances reported in previous studies could be the behavior of this species. We observed that roughneck shrimps are active exclusively during the hours of darkness, and thus they were not available for capture in previous sampling studies conducted during daylight hours.

We observed relatively sparse catches of *Rimapenaeus* spp. in the Middle Florida Keys, where they made up less than 2% of the total penaeid shrimps collected. Postlarval pink shrimp also exhibit this spatial recruitment pattern (Fig. 2; Criales et al., 2006). Larval stages of other Florida Bay crustaceans, such as the spiny lobster *Panulirus argus* (Latreille, 1804), show an opposite pattern, having higher abundance in the Florida Keys (Yeung et al., 2001) but are rare in northwestern Florida Bay (Tabb & Manning, 1961; M.M. Criales et al., unpublished data). These taxon-based differences in abundances between the two locations may be related to a number of factors including, but not limited to, differential preferences in the water chemical composition or sediment type, circulation patterns influencing larval dispersal, and spawning location.

Western Florida Bay has a relatively open connection with the southwestern Florida Shelf. Furthermore, this region exhibits strong tidal currents dominated by the semidiurnal tide with tidal amplitudes reaching almost 40 cm (Smith, 2000; Wang et al., 1998). In contrast, tidal exchange of southern Florida Bay with the coastal Atlantic Ocean is limited; there, tidal fluctuations are primarily semidiurnal constituents with a wide range of variation in the Middle Florida Keys between 7.0 and 15.5 cm (Smith, 1997, 1998). The western Florida Bay has higher concentrations of phosphorus and chlorophyll than the southeastern bay (Boyer et al., 1997). Banks of western Florida Bay are densely covered by seagrass and macrophyte communities (Zieman et al., 1989; Browder & Robblee, 2009), whereas these communities are sparser in the southeastern Bay (Fourqurean et al., 2002). The sediments on the northern banks are fine, with the silt-clay fraction comprising 53 to 71% of the total for each bank top or side, whereas the silt-clay fraction ranged from 17 to 56% at sites located on southern banks (Holmquist et al., 1989). The center of pink shrimp spawning within the region is known as the Tortugas Grounds





**Figure 7.** PCoA ordinations depicting significant differences in salinity regime among months of the time series (A) and study site locations (B). Ellipses represent standard error of the mean; SK, Sandy Key; MG, Middle Ground; CC, Conchie Channel, northwestern Florida Bay, Florida. This figure is available in color at *Journal of Crustacean Biology* online.

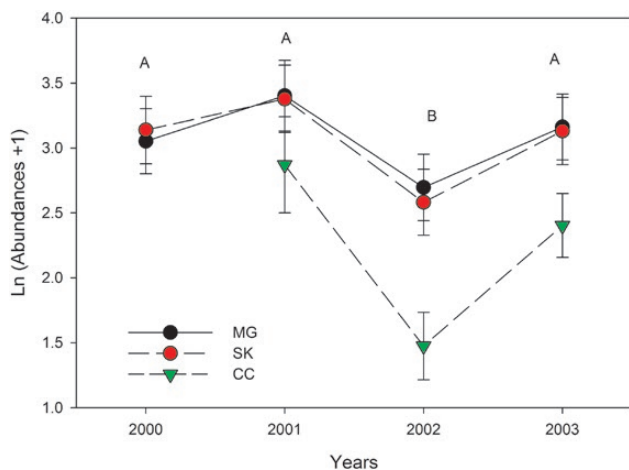
(Munro *et al.*, 1968). Larval behavior and prevailing oceanic currents during peak spawning periods facilitate pink shrimp larval recruitment directly across the Florida Shelf to western Florida Bay (Criales *et al.*, 2005, 2006, 2007, 2015). In contrast, larval dispersal of *P. argus* relies on more oceanic currents, including the Florida Current to the south and east of the Florida Keys (Kough *et al.*, 2013; Segura-García *et al.*, 2019). While the regional center for *Rimapenaeus* spp. spawning is not yet known, inseminated females have been collected near the Tortugas region of the Florida Shelf (Eldred, 1959; Ingle *et al.*, 1959; Criales *et al.*, 2009).

The *Rimapenaeus* population in northwestern Florida Bay was composed of postlarval and juvenile stages. Postlarval specimens ranged from 1.3–2.0 mm CL and constituted 8.6 % of the catch; and the remaining 91.4% were juveniles 2.1–12.3 mm CL. The 94% of juveniles ranged between 2.0 and 8.0 mm CL size

classes and only 6% were > 9.0 mm CL. These larger juveniles were still immature specimens; males with separated petasomal lobes and females with thin and transparent ovaries. Furthermore, spermatophores and sperm plugs were not observed, indicating the absence of reproductive activity in this region. The reproductive size of roughneck species reported in previous studies was 8.0 and 10 mm CL, depending on sex and species (Bauer & Lin 1994; Costa & Fransozo, 2004b; Garcia *et al.*, 2016), slightly smaller than the maximal size we observed. Although gear selectivity could have had an effect on our sampling, with large shrimps avoiding the nets, it seems unlikely to be an issue because large *F. duorarum* (10–25 mm CL) were readily captured with the same gear at these stations (Criales *et al.*, 2011). Similarly, gear selectivity cannot explain the lack of small postlarval *Rimapenaeus* spp. as numerous *F. duorarum* of a similar size were collected during these

**Table 3.** Results of a generalized linear model of the relationship between abundances of *Rimapenaeus* spp. and environmental variables, including stations and years as categorical factors. Type III test of model effects, significant fit ( $\alpha \leq 0.05$ ). Final model coefficient estimates ( $\pm$  standard error) and Wald chi-square test associated with each significant variable are shown. U and V, wind components; SST, sea surface temperature; MWL, mean water level.

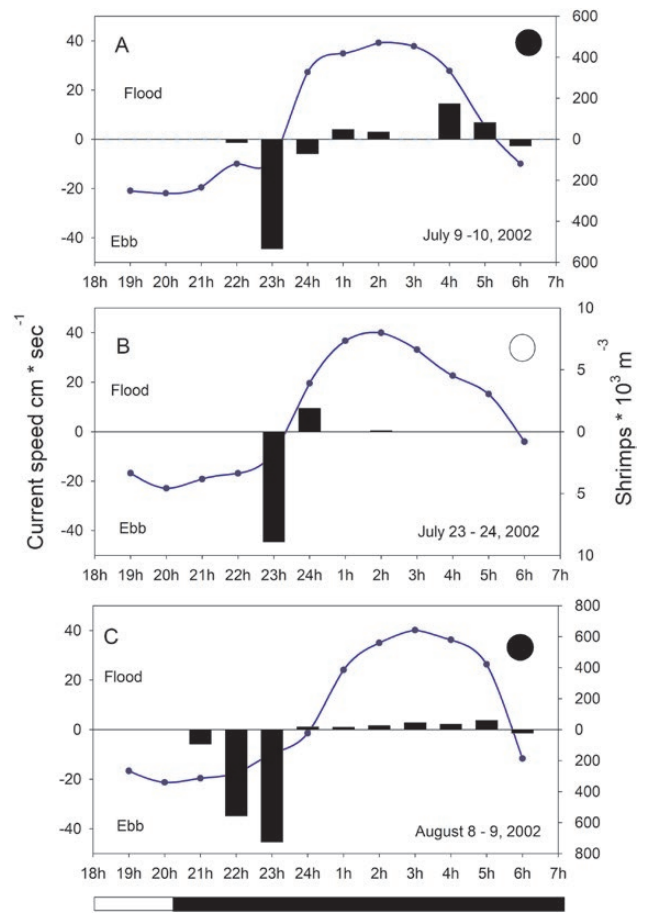
Source	Coefficient $\beta \pm$ SE	Wald chi-square test	P
Years	0.192 $\pm$ 0.526	27.89	0.0001
Stations	0.275 $\pm$ 0.403	38.69	0.0001
U wind	0.056 $\pm$ 0.027	3.96	0.0473
V wind	0.004 $\pm$ 0.039	0.011	0.9185
SST	0.152 $\pm$ 0.055	12.83	0.0001
MWL	0.227 $\pm$ 0.084	56.45	0.0001
Salinity	0.057 $\pm$ 0.067	0.077	0.7824



**Figure 8.** *Rimapenaeus* spp. means  $\ln(\text{abundance} + 1) \pm$  standard error separated by years (2000–2003) and stations (MG, Middle Ground; SK, Sandy Key; CC, Conchie Channel) in northwestern Florida Bay, Florida. Letters denote groups of statistical similarity among annual sampling. This figure is available in color at *Journal of Crustacean Biology* online.

sampling events (Fig. 2; Criales et al., 2011). The absence of reproductive activity of *Rimapenaeus* spp. population in northwestern Florida Bay may be an indication that the area does not provide the appropriate environmental conditions for reproduction and spawning. Moreover, the largest catches of *Rimapenaeus* spp. juveniles and postlarvae were observed in the two exterior stations of MG and SK, and fewer specimens were collected at the more interior station (CC). All these observations suggest that *Rimapenaeus* spp. are using the northwestern border of Florida Bay as nursery grounds and large juveniles migrate offshore to reproduce and spawn, and postlarvae attain a larger size before recruiting to the present sampling area.

Dall et al. (1990) classified *Rimapenaeus* as one of the penaeid genera having a “Type III life cycle,” in which postlarvae and juveniles occur in inshore sheltered waters while adults migrate offshore on continental shelves for spawning. Sampling in southeastern Brazil in an estuarine lagoon and adjacent oceanic waters, Garcia et al. (2016) found that juveniles of *R. constrictus* as well as mature females and males were caught at oceanic stations, but only juveniles were captured in the estuarine stations. Bauer & Lin (1994), however, reported that recruitment, mating and spawning of *R. similis* and *R. constrictus* take place in an inshore location at Horn Island, Mississippi, USA without an offshore spawning migration. Similarly, *R. constrictus* juveniles and mature



**Figure 9.** Hourly sampling conducted at the Sandy Key (SK) station, northwestern Florida Bay, Florida during a complete nightly tidal cycle during new moon, July 9–10 2002 (A), full moon, July 23–24, 2002 (B), and new moon, August 8–9 2002 (C). Right y-axis is *Rimapenaeus* spp. abundance (vertical bars, shrimps  $\times 10^3 \text{ m}^{-3}$ ; note changes in scales among panels), left y-axis is current speed (points and solid line,  $\text{cm sec}^{-1}$ ) with positive values associated with flood tidal current and negative values with ebb tidal current. Horizontal bar on the bottom denotes hours of light (white) versus darkness (black). Circles in upper right of plots depict new moon (black) and full moon (white) sampling events.

adults were found concurrently occupying inshore bays and adjacent coastal waters in Brazil (Costa & Fransozo, 2004b). Based on previous and present results, it seems that western Atlantic *Rimapenaeus* spp. may present two types of life cycles: 1) offshore migration of juveniles to oceanic waters to spawn, or 2) postlarvae, juveniles, and adults living at the same location. This second option may occur when environmental conditions and food availability are appropriate to sustain the entire life cycle in a single location. The type of migration of *Rimapenaeus* spp. juveniles from northwestern Florida Bay is unknown; it may be that juveniles migrate only a short distance from the bay’s border region to find more stable oceanic salinity and temperature conditions. Conversely, they may migrate long distances to reach the Dry Tortugas fishing grounds where a large population of *R. similis* and *R. constrictus* adults have been reported (Eldred, 1959; Criales et al., 2009). Further studies are needed to determine the extent of the migrations and the connectivity among the *Rimapenaeus* spp. subpopulations on the southwestern Florida Shelf.

The two species of *Rimapenaeus* in northwestern Florida Bay exhibited a clear seasonal recruitment pattern. Large peaks in the abundance of postlarvae and small juveniles occurred in late summer-early fall (July, August, September, and/or October),

**Table 4.** Summary of hourly sampling conducted at Sandy Key, Florida Bay, Florida (SK station, see Figure 1) on August 8–9 2002 ( $N = 20$ ) collected over 20 consecutive hours, including abundances of *Rimapenaeus* spp. juveniles, current speed, tidal stage (E, ebb; F, flood) and diel period (D, daytime, N, nighttime).

Date	Time collection (hr)	Current Speed (cm sec <sup>-1</sup> )	Tidal stage	Diel period	<i>Rimapenaeus</i> spp. (10 <sup>3</sup> m <sup>-3</sup> )
8/8/2002	11:00	14.66	E	D	5.1
8/8/2002	12:00	19.83	E	D	0.0
8/8/2002	13:00	50.37	F	D	0.0
8/8/2002	14:00	46.75	F	D	0.0
8/8/2002	15:00	35.97	F	D	0.0
8/8/2002	16:00	19.67	F	D	0.0
8/8/2002	17:00	0.00	F	D	0.0
8/8/2002	18:00	0.00	E	D	0.0
8/8/2002	19:00	16.69	E	D	0.0
8/8/2002	20:00	21.32	E	D	0.0
8/8/2002	21:00	19.66	E	N	92.3
8/8/2002	22:00	17.69	E	N	557.0
8/8/2002	23:00	9.75	E	N	725.4
8/9/2002	0:00	1.447	F	N	17.5
8/9/2002	1:00	24.02	F	N	15.4
8/9/2002	2:00	34.98	F	N	25.4
8/9/2002	3:00	43.12	F	N	43.8
8/9/2002	4:00	36.21	F	N	34.8
8/9/2002	5:00	27.33	F	N	59.6
8/9/2002	6:00	11.67	E	N	22.2

whereas less abundant, large juveniles and subadults were observed in spring (March). This pattern may indicate that spawning occurs in spring-summer, which is supported by available records of *Rimapenaeus* spp. from shallow coastal waters along South Carolina, Georgia, and northeastern Florida (Anderson, 1970), as well as data on *Rimapenaeus* larvae along the Mississippi and northwest Florida Gulf coasts (Subrahmanyam, 1971; Livingston, 1976; Cooley, 1978). M.B. Robblee *et al.* (unpublished data) similarly reported highest abundance of *R. similis* in the fall. Results from Bauer & Lin (1994) differ slightly from our results in that their unidentified juveniles (CL 3–6 mm) occurred throughout most of the year with no obvious seasonal pattern.

Our results indicated that MWL and SST were the most important environmental factors significantly affecting abundances of *Rimapenaeus* spp. The peaks of abundances during the first three years of the study were observed during the months of September and October, which correspond to the months with the highest MWL. A seasonal MWL pattern similar to the one described here, with lowest values in winter and maximum water levels in fall, has been reported for Florida Bay (Holmquist *et al.*, 1989; Smith, 2000). Holmquist *et al.* (1989) attributed the seasonal MWL pattern mainly to changes in wind direction, because southeast and southwest winds that dominate during summer-fall produce an increase in the water level while northwest winds decrease the MWL. Smith (2000) observed this seasonal water-level pattern and concluded that a steric effect (i.e., changes in sea level due to thermal expansion and salinity variations) explained in large part the autumn high water and winter low water levels. Abundances of *Rimapenaeus* spp. were also significantly affected by SST, with peaks occurring during the warmer months of late summer-early fall. The SST has been considered the most influential environmental factor affecting spawning, growth, survival and distribution of estuarine penaeid shrimps (Dall *et al.* 1990; O'Brien, 1994; Castilho *et al.*, 2015). The positive correlation observed between SST and the abundances of *Rimapenaeus* spp. leads to the conclusion that this environmental factor had a significant effect on seasonal spawning, which would influence the recruitment pattern

we observed. These observations coincide with seasonal spawning and recruitment relationships reported by Garcia *et al.* (2016).

The species of *Rimapenaeus* are considered euryhaline with a preference for higher salinities (Dall *et al.*, 1990). Previous reports generally agree with this conclusion. *Rimapenaeus constrictus* has been reported to occupy salinities of >30 psu (Gunter, 1950; Brusher *et al.*, 1972), varying 28–38 psu (Costa & Fransozo, 2004a), 28–30 psu (Hiroki *et al.*, 2011), and 26.5–34 psu (DeLancey, 1989). Bauer & Lin (1994) reported *R. constrictus* and *R. similis* living in a marine environment during their entire life cycle. Conversely, M.B. Robblee *et al.* (unpublished data) reported collection of *R. similis* from ~7 psu to 48 psu, although ~19 and 37 psu represented the 25th and 75th quantiles of the salinity range from which they were collected. We collected *Rimapenaeus* spp. in salinities ranging from 27 to 38 psu. Salinity did not significantly predict the abundance of the two species, but our analysis was limited by the absence of an independent salinity record at each site during the four years of sampling. We did detect differences in salinity regime between the innermost (CC) and the outermost (SK) stations, but not between the innermost and middle station (MG) nor the outermost and middle station, suggesting a gradient in salinity regime from the inner to the outer regions of Florida Bay. Shrimps were substantially less abundant at CC than at the SK and MG stations. Perhaps the salinity minima, maxima, and/or variability at the CC station were sufficient to limit abundance there. Even so, the range of salinities and our conclusion that salinity did not predict the abundance of shrimps are similar to those reported in previous studies (Costa & Fransozo, 2004a; Hiroki *et al.*, 2011). Further studies should include observations along a salinity gradient of sufficient range to elucidate any possible relationships between salinity and the abundance of *Rimapenaeus* spp.

Another possible factor influencing differences in the abundance of *Rimapenaeus* spp. among the sampling stations could be the different types of substrate. The sediments on the northern banks are fine, with the silt-clay fraction comprising 53 to 71% of the total for each bank top or side (Holmquist *et al.*, 1989). Roughneck shrimps have been reported to utilize substrates such

as peaty marl to exposed limestone outcroppings (Brusher *et al.*, 1972; Camp *et al.*, 1977; Huff & Cobb, 1979). Other studies nevertheless have reported *R. constrictus* found living on substrate composed largely of mud, fine sand, and sand-shell (Costa & Fransozo, 2004a; Hiroki *et al.*, 2011). Furthermore, substrate type was found to have a significant effect on the distribution and abundance of *R. constrictus* in southeastern Brazil (Costa & Fransozo, 2004a). This type of sediment favors not only a higher retention of organic matter, a possible food resource, but also favors the burrowing behavior of this species. Such behavior may play a fundamental role in the defense against predators (Dall *et al.* 1990).

Abundances of *Rimapenaeus* spp. during 2002 were reduced relative to the other sampling years. During January through March 2002 and September through December 2003 a large number of ctenophores were caught in the nets due to a microalgae bloom, dubbed a “black water” event, that included the toxic dinoflagellate *Karenia brevis* Gert Hansen & Moestrup, 2000 as reported by Hu *et al.* (2003) and Pierce & Henry (2008). We noted a substantial reduction in the number of shrimps, fishes, and crabs in our nets during the black-water event. Florida Bay chlorophyll contour maps from the Southeast Environmental Research Center (Florida International University) (<http://serc.fiu.edu/wqmnetwork/CONTOUR%20MAPS/ContourMaps.htm>) depicted higher concentrations of chlorophyll in the MK area during January 2002 and July and October 2003 in comparison to previous years. Perhaps the black-water event led to an increased mortality in *Rimapenaeus* spp. by lower abundances observed in this study due to this black water event and the toxic dinoflagellate.

Results from hourly sampling conducted during three nights during complete dark tidal cycles clearly demonstrated that juveniles of *Rimapenaeus* spp. were active in the water column almost exclusively during nighttime and were highly abundant during the ebb tidal periods. Other studies have reported maximal abundance of *R. constrictus* during nocturnal sampling (Brushner & Ogren, 1976; Livingston, 1976; DeLancey, 1989). Our results also revealed that *Rimapenaeus* spp. juveniles were more active during the dark new-moon period than during the illuminated full-moon phase. These results may indicate that *Rimapenaeus* spp. show a negative phototaxis, being highly sensitive to the light of both the moon and the sun. This observation may help explain the absence or low presence of roughneck shrimps in previous Florida Bay surveys, which have been conducted mainly during daylight hours (Tabb & Manning, 1961; Tabb *et al.*, 1962; Huff & Cobb, 1979; M.B. Robblee *et al.* unpublished data). Other studies supporting our results are the large numbers of *R. constrictus* juveniles caught on surface plankton tows during nightly sampling in North Carolina estuaries (Williams, 1969) and in Tampa Bay, Florida (Sykes, 1966).

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