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ABSTRACT

Commercial catch of Caribbean spiny lobsters (*Panulirus argus*) in Florida was highly correlated with the abundance of pueruli on artificial collectors. Each lunar month from 1994–2023, we counted postlarvae on artificial collectors at two locations in the Florida Keys (USA). We compared various indices of puerulus settlement and commercial landings. Significant correlations between postlarval indices and the sum of August and September commercial landings were identified at one sampling location. Commercial landings in these first two months of the fishing season likely represent a better index because, as the fishing season progresses, fishing effort and landings are influenced more by non-recruitment factors such as tropical disturbances, catch levels, and the price of lobster. The postlarval index with the highest correlation to landings included the months with peak settlement between January and June in the year prior to the fishing season ($p < 0.001$). The timing of the postlarval index and range of months indicates that it takes between 14- and 20-months post-settlement for a lobster to enter the fishery and that these peak settlement pulses drive landings in the commercial fishery. The correlation between postlarval settlement and fishery landings suggests that the quantity of postlarvae — and not post-settlement processes — is the primary driver of the spiny lobster population in Florida. Results from this study also indicate that postlarval settlement levels have declined over the past 30 years. As a population that relies heavily on postlarval supply from outside of Florida, this highlights the need for future research into the cause of the decline and any potential link to spawning stock biomass, particularly considering declining landings Caribbean-wide.

1. Introduction

The Caribbean spiny lobster (*Panulirus argus*, Latreille, 1804) fishery is one of the largest lobster fisheries in the world with landings averaging almost 30,000 mt from 27 countries and states throughout the Caribbean, Latin and South America, and Florida (FAO, 2024; Phillips et al., 2013). Although Florida accounts for less than 7 % of *P. argus* landings Caribbean wide, this is one of the most valuable commercial fisheries in Florida, with ex-vessel values ranging from US$20 to US$50 million annually (Florida Fish and Wildlife Conservation Commission, unpubl. data; FWC, 2021; Kildow, 2008). Up to 90 % of Florida's commercial landings come from the narrow, 325 km long Florida Keys archipelago (Fig. 1a), making this relatively small geographic region one of the most productive areas for this species.

The life cycle of *P. argus* is complex and includes a lengthy planktonic larval phase, which provides considerable resilience for the pan-Caribbean population and high dispersal potential for larvae across the region (Butler et al., 2009, 2011; Kough et al., 2013). The phyllosoma larval phase persists for 5–9 months and consists of 10 or 11 stages, followed by metamorphosis into the free-swimming, non-feeding puerulus stage (Briones-Fourzán et al., 2008; Goldstein et al., 2008; Sims and Ingle, 1966). In Florida, metamorphosis to pueruli occurs offshore around the new moon each month, after which the pueruli utilize the flood tide and wind-driven currents at night for advection to nearshore settlement habitat (Acosta et al., 1997; Heatwole et al., 1991; Little, 1977). Lobsters recruit to the fishery in Florida at > 76.2 mm carapace length (CL) and are thought to be approximately 18 months old (age since settlement) (Forcucci et al., 1994; Sharp et al., 2000). Most lobsters in the Florida Keys are less than 2.5-years-old with approximately 84 % of individuals caught in the first year they recruit to the fishery (Matthews et al., 2009), and over 50 % of lobsters landed are caught during the first two months of the fishing season in August and September (FWC, 2024). Few lobsters in Florida reach their potential maximum age of 20 years (Maxwell et al., 2007). This truncation of the lobster life

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expectancy to practically a single year class by the fishery in Florida potentially allows landings to be used as an index for the year-class and stock.

Linking spawning stock to fishery recruitment for spiny lobsters such as *P. argus* — which have a long larval phase and multiple sources of larvae — is inherently difficult. However, there has been considerable success in establishing puerulus-to-fishery and juvenile-to-fishery recruitment relationships for Western Australian rock lobster (*Panulirus cygnus*) (Caputi et al., 2003). Postlarval and juvenile settlement indices for *P. cygnus* have been successful in predicting commercial catch up to four years in advance and have been used to proactively manage the *P. cygnus* fishery (Caputi and Brown, 1986; Caputi et al., 1995a, 1995b; Phillips, 1986). Puerulus and juvenile settlement indices have also been used to predict fishery recruitment for other species and populations of spiny lobster (Booth and McKenzie, 2009; Cruz and Adriano, 2001; Cruz et al., 1995; Gardner et al., 2001). Identifying the relationship between postlarval settlement and fishery landings provides resource managers with an independent method of evaluating fishery population fluctuations and can be a valuable predictive tool for management. The potential for proactive management based on predicted abundance avoids the pitfall of heavy fishing on poor recruit classes, which is a common cause of recruitment overfishing (Caputi et al., 2003; de Lestang et al., 2015).

However, development of settlement indices that consistently track their respective fisheries can be difficult and depends greatly on the extent that a population is limited either by larval settlement or post-settlement processes (Doherty and Fowler, 1994; Underwood and Fairweather, 1989; Wahle and Incze, 1997). If there is a significant relationship between larval settlement and a later life stage, such as fishery animals, this highlights the importance of the level of settlement and indicates the population is limited by the quantity of postlarvae (Doherty and Williams, 1988). Alternatively, if a population is influenced significantly by post-settlement processes such as predation or habitat availability, you would not expect settlement indices to predict fishery landings. In Florida, post-settlement processes such as post-settlement mortality, loss of juvenile lobster nursery habitats, and disease (PaV1) have long been considered the primary drivers of the lobster population and to-date no strong predictive settlement indices have been developed (Butler and Herrnkind, 1992; Butler et al., 1997; Ehrhardt and Fitchett, 2010).

This study examines the relationship between Caribbean spiny lobster postlarval settlement and commercial landings in Florida using 30 years of pueruli settlement data in the Florida Keys. The aims of this study were to: (1) examine the temporal variation in puerulus settlement, and (2) determine if puerulus settlement indices were correlated with *P. argus* landings in Florida.

2. Methods

2.1. Study site and collector design

Spiny lobster postlarval monitoring occurred each lunar month from 1987–present at two sites in the Florida Keys (USA) (Long Key and Big Munson Island) (Fig. 1a). Consistent monitoring (i.e. similar timing, frequency, and number of collectors) began in 1994 and continued until August 2017 using modified-Witham collectors (Witham et al., 1968). The modified-Witham (herein referred to as Witham) collector consisted of a rigid PVC frame (43.2 cm×47 cm) and six pieces of hog's hair air conditioning filter material that were folded and attached to six PVC cross pieces to create 12 "pages" (Fig. 1b). This collector was originally designed in the 1960s to mimic nearshore macroalgae, the preferred settlement habitat of spiny lobster postlarvae (Witham et al., 1968). However, in the early 2010s the hog's hair material used to construct the Witham collectors degraded in quality and a replacement collector was created. A frayed rope collector was designed with similar dimensions to the Witham collector, but out of a more durable polyolefin rope. The frayed rope collector had three mesh panels, each with 22 eight-inch lengths of half-inch diameter rope attached and frayed, with each panel then secured to a PVC frame to create six "pages" (Fig. 1c). Use of the frayed rope collector began in August 2013; however, consistent monitoring using this collector began in April 2014.

Collectors were placed in shallow water (less than two meters in depth), anchored to the ocean floor, and buoyed to float at the surface. Each site contained five collectors that were aligned east to west with 50 m separating each collector. Three Witham and three frayed rope collectors were deployed from April 2014 to August 2017 when use of the two collector types overlapped.

2.2. Indices of puerulus settlement

Collectors were checked each lunar month, ideally seven days after each new moon. Actual surveys were conducted from day 5–11 after the new moon. Collectors were lifted in a mesh bag, brought onto the boat, and every puerulus and newly molted juvenile were removed from the collectors and counted. Witham and frayed rope collectors were deployed for up to 12 and 20 weeks, respectively. At the end of that deployment time collectors were removed and the Witham pages were replaced and frayed rope pages cleaned before being redeployed. To test if the age of the collector affected postlarval settlement levels we fit a generalized linear mixed effects negative binomial regression model (GLMM) separately for Witham and frayed rope collectors, with the age of the collector and lunar month as categorical fixed effects and year as a random effect (Table S1). Post-hoc pairwise comparisons of estimated marginal means indicated that puerulus catch declined on Witham

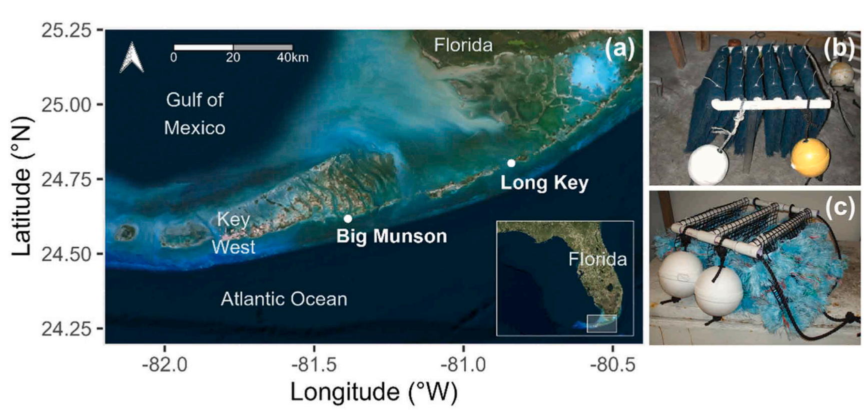

Fig. 1. (a) Map of the Florida Keys (USA) archipelago showing the two *Panulirus argus* puerulus settlement monitoring sites at Big Munson and Long Key and pictures of the (b) modified-Witham and (c) frayed rope collectors. When referring to statewide landings, this includes landings from the entire coastline of Florida.

collectors after 8 weeks, and 4-week-old frayed rope collectors caught significantly fewer pueruli than 8- to 20-week-old collectors (Table S2). Consequently, when calculating postlarval indices, settlement data were only used from 4- to 8-week-old Witham collectors and 8- to 20-week-old frayed rope collectors.

The indices of puerulus settlement were calculated as the average number of postlarvae per collector each month, averaged over specific subsets of months. Postlarval indices using both a full year of settlement data and settlement only during the winter and spring settlement peaks (December to May) were calculated. Full-year settlement indices were lagged progressively further back from the start of the fishing season and were named to indicate the number of months from the start of the settlement index to the start of the fishing season in August. For example, the 27-month lag has 27 months between the start of the postlarval index in May and the start of the fishing season in August two calendar years later (Fig. 2, Fig. S1). Postlarval indices were lagged up to 3 years prior to the fishing season, based on the estimated age of fishery animals (< 2.5 years) (Matthews et al., 2009).

2.3. Indices of recruitment to the fishery

Information related to commercial landings of *P. argus* in Florida is reported through the Florida Marine Fisheries Information System by commercial fishers as a requirement of their fishing license. Lobster landings occur statewide (i.e. along the entire coastline of the state of Florida) but predominantly come from the Florida Keys region, which accounts for approximately 98 % of state landings (Fig. 1a) (Muller et al., 1997; NOAA, 2018; SEDAR, 2010). Fishers are required to report landings by fishing area; however, there remains inaccuracies in the reporting of landings to the finer spatial scale and reporting accuracy is particularly poor prior to 2000. We did analyze the relationship between postlarval settlement and commercial landings, with landings broken down by the state defined fishing areas adjacent to each monitoring site; however, statewide landings provided the strongest correlation to settlement. Resultingly, statewide landings were used to create three indices of recruitment to the fishery for this study. These indices were the total statewide commercial landings over three distinct time frames: (1) the total fishing season (August 6th – March 31st), (2) the first month of the fishing season (August), and (3) the first two months of the fishing season (August and September). Using only the first or first two months of the season as our index of recruitment to the fishery minimized the influence of changes in fishing effort in response to the price of lobster, hurricanes, or lobster catch rates.

Fishery landings data were compromised twice during this study. Data for the 2008/2009 fishing season were excluded due to the historic low price for lobsters and subsequent reduction in fishing effort, and for the 2017/2018 fishing season due to Irma, a category 4 hurricane, that hit the Florida Keys on September 10th, 2017. Irma disrupted fishing activity and landings reports before, during, and after the storm and an estimated 25–50 % of the 467,000 traps in use were lost (McPherson and Jepson, 2019).

2.4. Statistical analyses

An iterative approach was taken to determine the best postlarval indices. The relationships between the indices of puerulus settlement and commercial landings were evaluated with linear regression analysis and Pearson correlation coefficients. To test for differences in the average puerulus settlement per collector each month for the two different collector types, we ran a paired t-test using all months where data from both Witham and frayed rope collectors were available. Differences in slope and intercept between Witham and frayed rope collector regression models were evaluated with an analysis of covariance (ANCOVA). All analyses were conducted in R version 4.3.1 (R Development Core Team, 2023).

3. Results

3.1. Indices of puerulus settlement

Puerulus settlement was consistently higher at Long Key compared to Big Munson. Both sites exhibited seasonal variation in settlement with peaks in winter and spring (December to May), and large within-month settlement variance (Fig. 3). However, there was no correlation in settlement between the Big Munson and Long Key sites. Additionally, puerulus settlement patterns at Long Key had no strong correlations with fishery landings and averaging the settlement between the two sites provided weaker correlations than just the Big Munson site alone. Henceforth only results from Big Munson are shown.

Two postlarval indices and multiple time-lags correlated strongly with commercial landings (Fig. 4). The first index was calculated as the average postlarval settlement over the full 12-month calendar period in

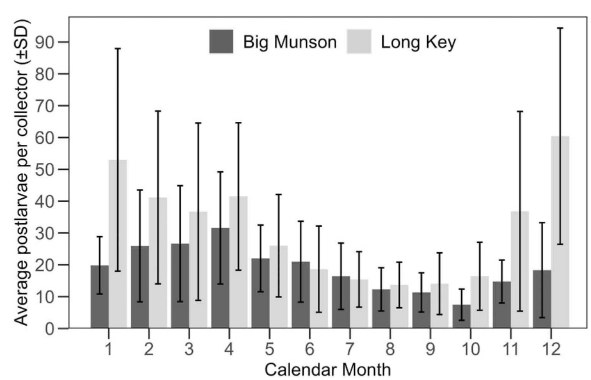

Fig. 3. Average postlarval settlement (±SD) by month on Witham collectors (1994–2017) at Big Munson and Long Key.

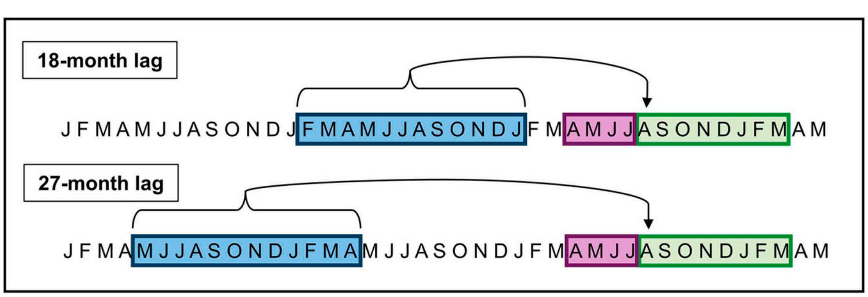

Fig. 2. Examples of the time-lags showing the 18-month and 27-month lags. Each letter represents a month in the time series. The blue box is the 12-month period used to calculate the postlarval settlement index. The purple box represents the closed fishing season from April to July and the green box represents the open fishing season from August to March. The lags are named to indicate the number of months from the start of the postlarval index (blue box) to the start of the fishing season (green box).

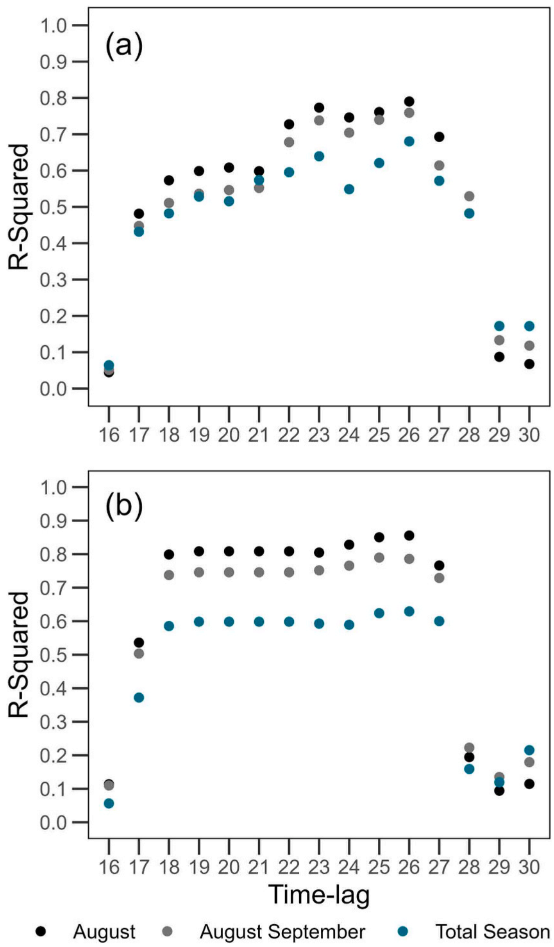

Fig. 4. R-squared values from linear regression analyses of puerulus and statewide commercial landings indices for Witham collectors at Big Munson (1994–2017, n=9). Puerulus indices were calculated as (a) the average settlement over the full 12-month calendar period in each time-lag, and (b) the average settlement for the two highest settlement months in each time-lag. See Fig. 2 for examples of time-lags and Fig. S1 for a complete list of time-lags.

each time-lag. The second index was calculated as the average postlarval settlement for only the two highest settlement months over the full 12-month calendar period in each time-lag. For the latter index, the two highest settlement months can vary year to year. For both indices, if settlement data were missing for any month between February and May, that year was excluded from the analysis in an attempt to avoid losing data from the spring settlement peaks. Across all years where there was complete settlement data between January and December, 71.4 % of the time February to May contained the highest or second highest settlement months.

Although postlarval indices with time lags up to 3 years prior to the start of the fishing season were calculated, the linear regression analyses comparing time-lags indicated that the 18- to 27-month time lags all correlated strongly to commercial landings, with a drop in correlation before the 18-month lag and after the 27-month lag (Fig. 4). The 18- to 27-month time lags each included the months of February, March, and April, the year before the start of the fishing season, demonstrating the importance of the spring settlement peak (Fig. 2, Fig. 4, Fig. S1). Due to some years missing months within the February to May time frame (spring peak) there were only 9 years of overlapping data among the 15 respective time-lags.

To further investigate the importance of the spring peak settlement months we compared postlarval indices using combinations of the winter and spring peak settlement (December to May) and surrounding months versus postlarval indices using a full year (12-month) of settlement data. Results suggested that the best postlarval settlement index included the months January to June (Table 1). This index corresponded to the 19-month time lag in Fig. S1; however, it included a reduced set of months. The January to June postlarval index included settlement data 14 (June) to 19 (January) months before the August start of the fishing season. Herein, Puerulus Index 1 will be the average settlement over the January to June period and Puerulus Index 2 will be the average settlement for the two highest settlement months between January and June, the year prior to the start of the fishing season.

3.2. Indices of recruitment to the fishery

Overall, correlations between puerulus settlement indices and commercial landings were stronger for August and August/September landings compared to total season landings (Fig. 4, Fig. 5, Table 2). For Witham collectors (1994–2017), Puerulus Index 1 and Index 2 calculated for the January to June period, 14–19 months before the start of the fishing season, both correlated well to August and August/September landings (Fig. 5, Table 2).

Currently there are only five years of overlapping settlement and fishery landings data for the frayed rope collectors at Big Munson. The correlation between puerulus settlement and August landings was not significant for both Puerulus Index 1 and Index 2; however, this may be due to the small sample size. The strongest relationship was between Puerulus Index 2 and the combined August and September commercial landings (Table 2).

3.3. Comparison of Witham and frayed rope collectors

Witham and frayed rope collectors were monitored simultaneously from April 2014 to August 2017, with 37 months containing data from both collector types. There was a statistically significant difference in postlarval catch between the two collector types (paired t-test: t = 4.03, df = 36, p = 0.00028). The mean difference was 4.85 (95 % CI: 2.40–7.29), indicating that on average the frayed rope collectors caught approximately five more postlarvae per collector compared with Witham collectors during that time frame. However, the relationship between the settlement on Witham and frayed rope collectors was non-linear, with frayed rope collectors disproportionately having more catch at higher settlement levels (Fig. 6).

Although there were differences in catch for the two collector types during the overlapping years of use, the fitted linear regressions for Puerulus Index 2 and August/September commercial landings did not differ significantly in slope (ANCOVA, F(1,16) = 0.007, p = 0.94) or intercept (ANCOVA, F(1,17) = 0.23, p = 0.64) between the Witham and frayed rope collectors (Fig. 7). For that comparison, data for Witham

Table 1
Pearson correlation results for puerulus settlement at the Big Munson site and statewide August commercial landings indices. Only data from Witham collectors (1994–2017) were used. The puerulus indices were calculated as the average settlement for each set of months listed. The associated time-lag indicates the time lag that each set of months aligns with from Fig. S1 as determined by the starting month of the index; however, note that the number of months included in the indices vary.

Months in Puerulus Index	Associated Time-Lag	# of months in Index	N	r	p-value
Feb-Apr	18-month	3	13	0.85	0.00022
Feb-May	18-month	4	13	0.83	0.00046
Jan-Apr	19-month	4	13	0.83	0.00048
Jan-May	19-month	5	13	0.83	0.00039
Jan-Jun	19-month	6	13	0.88	8.95e−05
Jan-Dec	19-month	12	13	0.79	0.0014
Dec-Jun	20-month	7	13	0.84	0.00030
Jul-Jun	25-month	12	13	0.81	0.00078

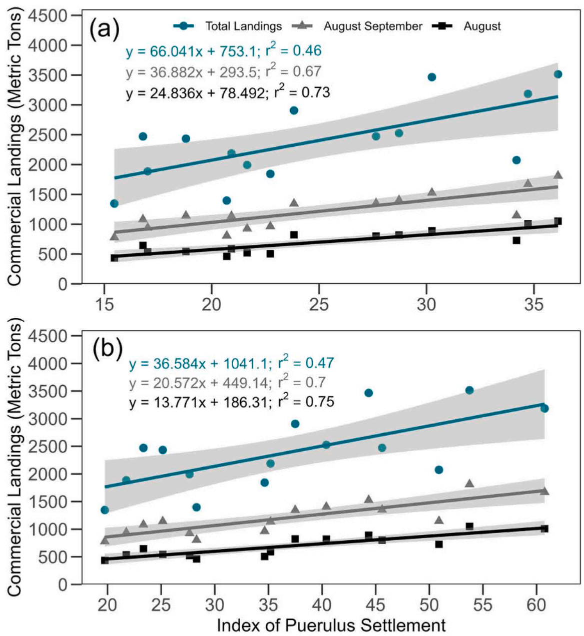

Fig. 5. Relationship between indices of puerulus settlement and statewide commercial spiny lobster landings for Witham collectors (1994–2017, n=15) at Big Munson. (a) Puerulus Index 1 and (b) Puerulus Index 2 were both calculated with settlement between January and June the year before the fishing season. Solid lines indicate fitted linear regressions with 95 % confidence limits.

collectors ranged from 1994 to 2017 and for frayed rope collectors from 2014 to 2022. The combined Witham (1994 – 2013) and frayed rope (2014 – 2023) Puerulus Index 2, correlated significantly to August/September commercial landings (Pearson r(16) = 0.87, p = 3.23e-06), and the puerulus index closely tracked fishery landings (Fig. 8, Table 2).

3.4. Decline in postlarval settlement

Overall, postlarval settlement has declined over the last 30 years in Florida. Individual monthly settlement levels have gradually declined since consistent monitoring began in 1994 (Fig. 9a). Additionally, the magnitude of monthly peaks in settlement has declined (Fig. 9a), particularly during the January to June time frame, which we identified as an important driver of fishery recruitment (Fig. 9b, Puerulus Index 2). Settlement data from the Witham collectors indicated that the average puerulus settlement per month has decreased 30 % from 1994 to 2017 (Fig. 9a; $y = -0.0008x + 29.179$). The decline in settlement has continued at a similar rate for frayed rope collectors, as indicated by the similar slope of the linear regressions between the two collector types (Fig. 9a; $y = -0.0011x + 36.933$).

4. Discussion

Using a long-term data series of puerulus settlement in the Florida

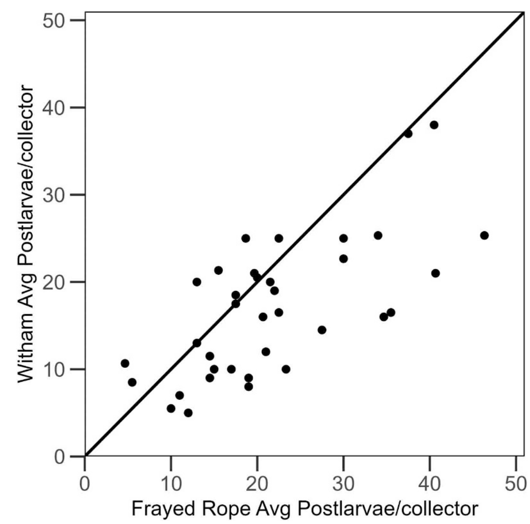

Fig. 6. Comparison of mean spiny lobster postlarvae per collector for frayed rope and Witham collectors for all sampling dates both collector types were deployed at Big Munson between April 2014 and August 2017 (n=37). The solid line represents one-to-one equivalence.

Table 2
Pearson correlation results for puerulus settlement at the Big Munson site and statewide commercial fishery landing indices. Puerulus Index 1 was the average puerulus settlement for the entire January to June period. Puerulus Index 2 was the average puerulus settlement for the two highest settlement months between January and June. For the combined Witham and Frayed rope index, data from Witham collectors were used from 1994 to 2013 and frayed rope collectors from 2014 to 2022 to remove overlapping years. The year range indicates the postlarval settlement years.

Collector Type	Puerulus Index	Commercial Landings	Year Range	N	r	p-value
Witham	Index 1	August	1994–2017	15	0.86	4.67e−05
		Aug + Sep	1994–2017	15	0.82	0.00019
		Total season	1994–2017	15	0.68	0.0054
Witham	Index 2	August	1994–2017	15	0.87	2.99e−05
		Aug + Sep	1994–2017	15	0.83	0.00011
		Total season	1994–2017	15	0.69	0.0048
Frayed Rope	Index 1	August	2014–2021	5	0.69	0.198
		Aug + Sep	2014–2021	5	0.90	0.037
		Total Season	2014–2021	5	0.88	0.049
Frayed Rope	Index 2	August	2014–2021	5	0.79	0.11
		Aug + Sep	2014–2021	5	0.98	0.0040
		Total season	2014–2021	5	0.91	0.030
Witham and Frayed Rope	Index 1	August	1994–2021	18	0.84	1.08e−05
		Aug + Sep	1994–2021	18	0.85	9.78e−06
		Total season	1994–2021	18	0.71	0.00095
Witham and Frayed Rope	Index 2	August	1994–2021	18	0.87	3.64e−06
		Aug + Sep	1994–2021	18	0.87	3.23e−06
		Total season	1994–2021	18	0.71	0.0010

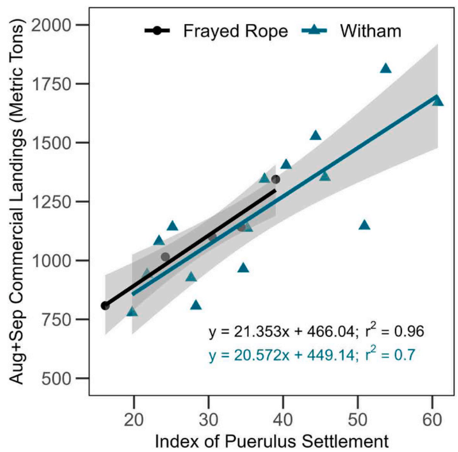

Fig. 7. Relationship between annual puerulus settlement Index 2 and statewide August/September commercial spiny lobster landings one year later for Witham collectors (1994–2017, n=15) and frayed rope collectors (2014–2022, n=5) at Big Munson. The postlarval indices were calculated with settlement data between January and June. Solid lines indicate fitted linear regressions with 95 % confidence limits.

Keys, this study has shown that there is a strong relationship between puerulus settlement and commercial fishery landings for Caribbean spiny lobster in Florida. Similar relationships between puerulus settlement and the abundance of juvenile or fishery-sized animals have been reported for other populations and species of lobster (*Jasus edwardsii*: Breen and Booth, 1989; McGarvey et al., 2024| *Homarus americanus*: Oppenheim et al., 2019; Steneck and Wilson, 2001; Wahle et al., 2009| *Panulirus argus*: Cruz et al., (1995)| *Panulirus cygnus:* Caputi et al., 1995b, 2003; Phillips, 1986). However, it was previously thought that the population in Florida may be influenced more by post-settlement factors, such as predation, disease, habitat availability, or density-dependent survival, and thus precluded it from having a strong predictive index (Butler and Herrnkind, 1992; Butler et al., 1997; Ehrhardt and Fitchett, 2010). This study has shown that settlement does drive recruitment to the *P. argus* fishery in Florida and indicates that the population is limited by the quantity of postlarvae settling. The development of a puerulus settlement index – landings relationship also creates the capacity to predict future commercial landings in Florida.

Results from this study indicate that postlarval settlement peaks drive recruitment to the annual spiny lobster population in Florida. Although settlement occurs year-round in Florida (Acosta et al., 1997), the highest correlated postlarval indices included months which corresponded to peak settlement months at the postlarval monitoring sites. The time-lag analysis indicated that the spring peak settlement months (February to April) were particularly important; however, the postlarval index with the strongest correlation to landings included the months January to June. The inclusion of the additional winter and spring peak settlement months likely allowed for variation in timing of the settlement peaks each year. The strong correlation between just the two highest settlement months (Puerulus Index 2) and commercial landings further highlights the importance of peaks in settlement for the spiny lobster population in Florida. Puerulus Index 2 was also particularly useful for years when monthly counts of pueruli were missing due to collector loss or damage from storms and boat strikes, or collector age was outside the required deployment age. Although this introduced the possibility of missing influential peak settlement months, excluding years that were missing February to May — the months that accounted for the two highest settlement months 71.4 % of the time — minimized that possibility.

Other studies have created predictive spiny lobster settlement indices using only peak settlement months (Breen and Booth, 1989; Caputi et al., 1995b). One possible explanation for the correlation between the spring peaks in recruitment with future landings is enhanced growth and survival of lobsters at warmer temperatures. Research suggests that water temperature influences growth of *P. argus* in Florida in that cooler waters in the winter increase the intermolt period and reduce growth, whereas the warmer waters in the spring and summer reduce the intermolt period and increase growth (Forcucci et al., 1994). Thus, it is plausible to assume that the higher water temperatures that directly follow the spring settlement peak may contribute to improved postlarval survival and increased growth rates following settlement of *P. argus* in Florida. The suggestion that settlement peaks drive the correlation with landings does not exclude the potential contribution to the population of pueruli settling in non-peak months; just that those settlers represent a relatively low level and constant supply across years.

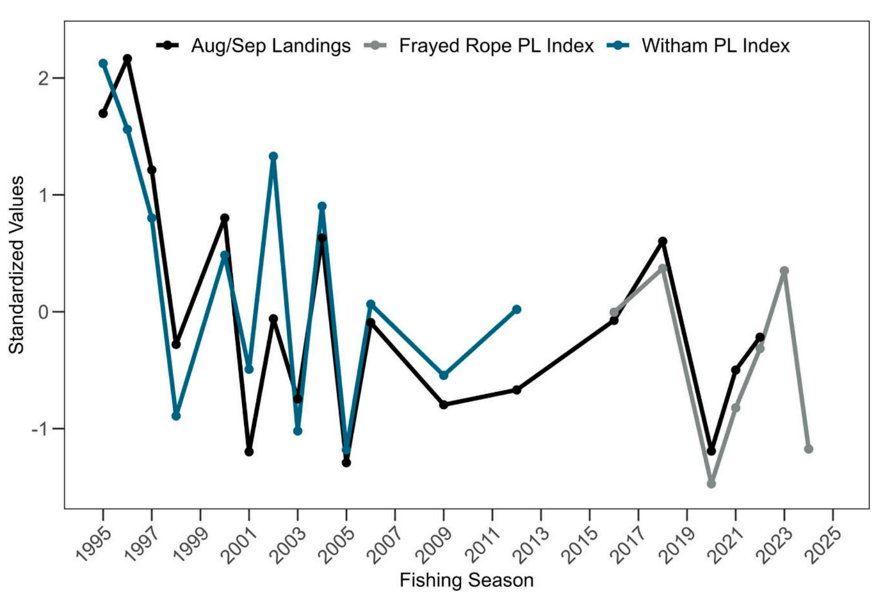

Fig. 8. Time series showing puerulus settlement Index 2 relative to the corresponding combined statewide August and September commercial fishery landings at Big Munson. Postlarval indices were calculated with settlement data between January and June. The puerulus index for 2013 and prior was calculated using data from Witham collectors (in teal) and from 2014 forward using data from frayed rope collectors (in gray). The year shown corresponds to the fishing season and is aligned with the puerulus index from the year prior. Puerulus index and commercial landings values were standardized to their means for comparison.

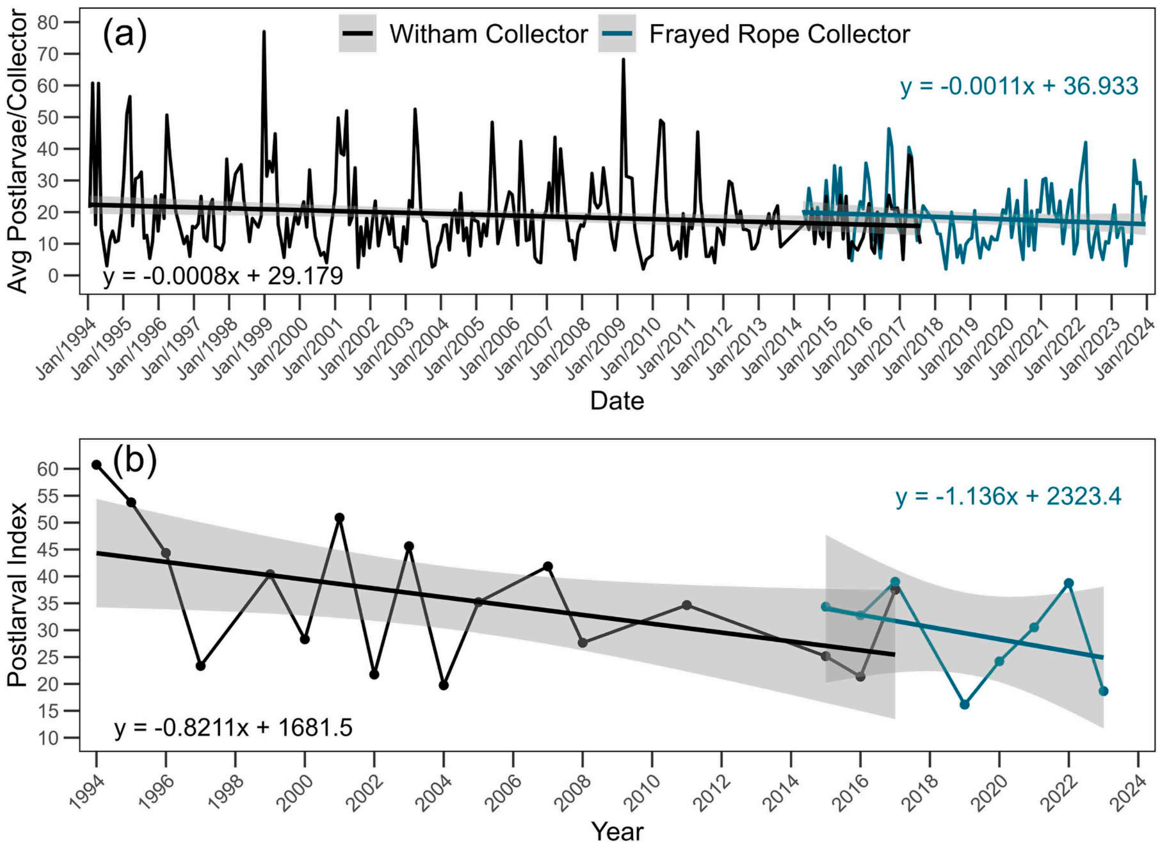

Fig. 9. (a) Average postlarvae per collector as measured each lunar month and (b) average postlarval settlement of the two highest settlement months between January and June (Puerulus Index 2) at Big Munson from 1994 to 2023. Solid lines indicate fitted linear regressions with 95 % confidence limits for Witham collector data from 1994 to 2017 and frayed rope collector data from 2014 to 2023. For analysis purposes "Date" was transformed to the number of days since January 1, 1970.

The timing of the puerulus index, with settlement between January and June, and the relationship to August/September commercial landings indicates an interval of 14–20 months between settlement and recruitment to the fishery. Previous mark-recapture studies in Florida have estimated that it takes between 9 and 14 months for *P. argus* to grow to 45 mm CL from settlement, while growth from ~45 mm CL to legal fishery-size (> 76.2 mm CL) takes an additional 9–12 months (Davis and Dodrill, 1980; Forcucci et al., 1994; Hunt and Lyons, 1986; Sharp et al., 2000). However, tag recapture studies from the 1980s and 1990s may have included tagging artifacts from tagging mortality and tag loss that caused underestimation of growth (Davis and Dodrill, 1989; Lyons et al., 1981). Growth rates of spiny lobsters can vary widely, but *P. argus* has a rapid growth rate, reaching fishery-size more quickly than other warm water spiny lobsters (Phillips, 2006). The 14- to 20-month interval determined from our postlarval index suggests fast growth and time to recruitment to the fishery but is consistent with growth estimates using the ageing pigment lipofuscin (Matthews et al., 2009) and direct ageing using the gastric mill ossicles (Hutchinson et al., 2024). The rapid growth rate supported by the more recent research appears more consistent with the apparent independence of each fishing season to natural perturbations and the extreme fishing mortality rate in Florida (Muller et al., 1997).

Puerulus settlement in the Florida Keys correlated strongly with both August and August/September statewide commercial fishery landings. Approximately 30 % of total season landings are caught in August, and 50 % by the end of September (FWC, 2024). Settlement may not have correlated as well with total season landings because as the season progresses fishing effort adjusts with hurricane occurrence, winter storms, the market price of lobster, and competition with co-occurring fisheries such as the stone crab fishery that overlaps the lobster fishery from October 15th – March 31st. For example, if it was a low-landings year or if the price of lobster was low, fishermen may switch effort away from the spiny lobster fishery and towards the stone crab fishery, lowering even further the potential lobster landings for that year. Alternatively, higher prices or high catch rates of lobsters appear to increase fishing effort. Using August or August/September fishery landings minimized the influence of non-recruitment factors. In Florida it is thought that the majority of legal-sized lobsters are caught each year, effectively reducing the population to a single year class due to the consistent and intense fishing pressure (Matthews et al., 2009). Consequently, August and September landings may function as an index for the Florida lobster population.

We found a strong relationship between puerulus settlement and commercial landings at one of the two long-term research sites. Spatial variation observed in puerulus settlement in the Florida Keys and individual-based modelling of recruitment suggest that it is unlikely that all sites monitoring puerulus recruitment would be correlated with landings or the population (Butler, 2003; Butler et al., 2001). This was also the case for P. *cygnus* in Western Australia in that a single site successfully predicted recruitment to the fishery (Phillips, 1986). Both fishing areas adjacent to the postlarval monitoring sites contributed a similar percentage of the total landings each year, that varied between 20 % and 40 % depending on the year; however, only settlement at the Big Munson site correlated with fishery landings. Additionally, we found no correlation between settlement levels at the two sites, indicating that what the two sites were measuring was fundamentally different.

Spiny lobsters are highly reliant on offshore ocean currents and gyres for larval transport over the long 6- to 9-month larval phase, and as *P. argus* metamorphose into postlarvae and migrate from deep offshore to shallow nearshore waters, they are influenced by the Florida current, local winds, and coastal eddies (Chiswell and Booth, 1999; Cobb, 1997; Lee et al., 1992; Yeung, 1996; Yeung et al., 2001). A lack of a correlation with landings at Long Key could be due to differences in these oceanic processes and consequently how the larvae and postlarvae are transported and retained in the region. Unpublished research we conducted in 2017 at the Long Key site, measuring the efficiency of a collector compared to a plankton net, indicated that there was a higher volume of water flowing past the collectors than would be expected given the current and semidiurnal tides for the area (Yeung and Lee, 2002). This could possibly be caused by an eddy existing at the study site, resulting in the collectors oversampling and explaining the disproportionately higher catch of pueruli during the winter and spring peaks compared to Big Munson. However, further research is needed to understand the oceanic processes in that region and determine the functionality and future of Long Key as a puerulus monitoring site.

Critical to a long-running postlarval monitoring program is the consistent performance of the sampling device. Witham collectors were used for monitoring postlarval settlement in the Florida Keys until 2017; however, in the early 2010s the hog's hair material used to construct the collectors was inconsistent, often degraded more quickly, and affected collector performance. Collectors would fall apart shortly after being deployed in the water, reducing the settlement of lobster on the collectors, and often resulting in no settlement data being available for multiple months. The new frayed rope collectors were designed and tested to replicate the catch rates of the Witham collectors. Ultimately, this experimentation resulted in a collector of the same size, adjusted to match the dimensions of the Witham collector, that required one month of soaking before replication of pueruli counts was consistent and was able to be deployed for a longer time before pueruli counts declined.

The head-to-head comparison of Witham and frayed rope collectors over the time frame they were monitored simultaneously showed that, on average, frayed rope collectors caught approximately five more postlarvae per collector. Particularly, frayed rope collectors caught more postlarvae at higher settlement levels. The comparison of the collector types was only conducted after the Witham collectors began to degrade and was only conducted for 4 years. We are no longer able to obtain the Witham material, so no further testing can be conducted. It is impossible to know if the Witham collectors caught fewer pueruli at higher settlement levels compared to the frayed rope collectors because of their degraded quality or a true result of a "saturation" effect. However, in previous years where settlement levels were higher, the Witham collectors caught up to 100 pueruli per collector, making it unlikely they were "saturating" at around 20 pueruli per collector (Fig. 6). Additionally, the regression analysis from this study showed that the puerulus indices calculated from each collector type had the same slope and intercept, as shown by the fitted regressions between the settlement indices and commercial landings. This indicates that it may be possible to combine the puerulus index data series from the two collector types. However, with only five years of data from frayed rope collectors, additional years of monitoring with the new collector design are needed to evaluate the continued functionality of the puerulus monitoring program and the ability to combine postlarval indices.

While postlarval settlement levels have often fluctuated between years in Florida, we observed an overall decline in settlement levels over the past 30 years. A possible cause of the reduced recruitment of pueruli to Florida is potentially a decline in the lobster population Caribbean-wide, as indicated by a general 20 % regional decline in landings (CLME+, 2019; FAO, 2024). Although landings data are not necessarily an indicator of the lobster population, the general high level of exploitation of this species throughout its range supports that possibility. The decline in landings Caribbean-wide matches the scale of the decline in pueruli recruitment to Florida.

The geographical boundaries and potential stocks of the Caribbean spiny lobster populations and connectivity through larval transport are not well defined (Cochrane and Chakalall, 2001; Winterbottom et al., 2012). Hydrographic models suggest larval supply between locations in the Caribbean basin is sporadic and the magnitude is highly variable, producing source and sink dynamics relevant to different stocks' population structure (Kough et al., 2013). Genetically, it appears likely spiny lobster stocks comprise a single pan-Caribbean population (Naro-Maciel et al., 2011), but dispersal occurs over a continuum where variation in basin-wide larval retention likely creates genetic structure (Cruz et al., 2021; Diniz et al., 2010; Truelove et al., 2017) that may be the result of larval settlement events at a monthly scale (Segura-García et al., 2019; Truelove et al., 2015). Recent interdisciplinary research combining genetics with hydrographic modelling suggest the potential for local larval retention and self-recruitment of lobsters to Florida (Segura-García et al., 2019; Yao and Zhang, 2018), but studies that include sampling for phyllosome larvae have not demonstrated larval retention (Yeung et al., 2000; Yeung and Lee, 2002). The retention of phyllosome larvae and self-recruitment in the Florida Keys remains unclear. Research investigating the decline in Caribbean spiny lobster postlarval settlement in Florida and its connection to Caribbean wide population and landings trends is needed to understand the ongoing repercussions for the lobster population and the commercial fishery that is dependent upon successful recruitment of postlarvae to the fishery.

5. Conclusions

Spiny lobster postlarval settlement has been monitored for over 30 years in the Florida Keys, and the reexamination of this long-term data series has shown that the level of puerulus settlement is highly correlated with commercial fishery landings in Florida. The development of a reliable puerulus settlement index provides the opportunity to predict fishery landings one year in advance. While it appears that the level of settlement, and not post-settlement factors, is the significant driver in fishery recruitment, future research is needed to examine the puerulus settlement-fishery landings relationship to try and understand environmental, economic, or social factors that may decouple the relationship in certain years. Additionally, the decline in postlarval settlement levels over the past 30 years raises concerns for the future of the Caribbean spiny lobster population in Florida and highlights the need for future research into the cause of the decline.

CRediT authorship contribution statement

Gabrielle F. Renchen: Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **Emily Hutchinson:** Writing – original draft, Supervision, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Thomas R. Matthews:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107137.

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