



A case study of sequential colonization: intra- and interspecific patterns of recovery in a hydrologically pulsed ecosystem

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Abstract Community assembly is influenced by disturbance intensity, sequential colonization (arrival order) of species, and interactions between species arriving early and species arriving later. We documented both intra- and interspecific patterns of colonization following hydrological disturbance using a 20-year time series of marsh-fish density at 21 study sites located in the Everglades, Florida, USA, as a case study of sequential colonization. The critical swimming speed (U_{CRIT}) of 20 juveniles and 20 adults for six species was estimated using U_{CRIT} tests

to evaluate if U_{CRIT} predicted timing of re-colonization. We observed a consistent pattern of species colonization over 500 disturbance events. On average, juveniles of early arriving species were collected prior to adults, while adults consistently appeared prior to juveniles for late-arriving species. Density at first collection was inversely correlated with arrival order; early arriving species tended to have higher density when first collected following marsh re-flooding than later arriving ones. Females consistently arrived before males for all species where sex could be identified. Neither absolute nor size-adjusted U_{CRIT} was correlated with arrival order. Although interspecific colonization was highly repeatable, intraspecific differences among demographic groups were species-specific and possibly tied to reproductive biology and juvenile life history. Juvenile early arrival may indicate rapid colonization of pregnant females (Poeciliidae), diapausing eggs laid before marsh drying, or early development of robust swimming capacity (Cyprinodontidae and Fundulidae); in the Everglades, water currents are absent or too weak to support larval drift as an important mechanism. Stage- and sex-specific U_{CRIT} and reproductive traits such as embryo diapause in oviparous species need more attention to understand successional dynamics following disturbance in aquatic communities.

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Introduction

Community assembly is influenced by a variety of factors including disturbance intensity, sequential colonization (arrival order) of species, and tradeoffs between early successional stage species and consumers arriving later (Spiller et al. 2018). The importance of dispersal-facilitated colonization following disturbance is well known (Huston 1979; Shea et al. 2004), and large-scale processes influencing colonization dynamics may be more important than small-scale extinction dynamics for shaping communities (Baber et al. 2002). Spatial–temporal trends in species' arrival and dispersal rates are often treated as stochastic, despite the importance placed on species arrival in community assembly (Drake 1991). Although dispersal is one of the most important parameters affecting community dynamics (Leibold et al. 2004), few studies have directly quantified or even noted inter- and intraspecific variation in traits associated with dispersal (Hanly and Mittelbach 2017).

Disturbance frequency and traits of potential colonists are believed to strongly influence the historical contingency of community-assembly patterns (Chase 2003; Porensky et al. 2012). Arrival order plays a vital role in establishing both inter- and intraspecific priority effects, which provide an advantage to early-arriving individuals over later ones (Fukami 2015). For example, interspecific priority effects can prevent the establishment of late-arriving species (Eriksson and Eriksson 1998), while intraspecific priority effects can disrupt the homogenizing effects of dispersal to favor traits of early colonizing individuals (De Meester et al. 2002). These effects are driven by both arrival order and traits of early arriving individuals that alter the community assembly via niche preemption or niche modification (MacArthur and Levins 1967; Dibble and Rudolf 2016). Identifying functional traits has become a central part of describing community assembly and species interactions (Cadotte et al. 2015) and has motivated trait-based studies investigating inter- and intraspecific variation in dispersal ability to fully understand the effects of early arrival post-disturbance.

Fish swimming ability is widely used as a metric of critical ecological processes tied to their persistence and impacts in aquatic communities (Sfakiotakis et al. 1999; Plaut 2001). Of the three elements of swimming speed (burst, sustained, and prolonged),

the maximum sustained swimming speed, called critical swimming speed (U_{CRIT}), has become the most widely documented metric of fish swimming ability. This metric has been linked to foraging behavior, predator avoidance, and Darwinian fitness (Kieffer 2010; Gotanda et al. 2012). Stage-specific differences in swimming ability have also been linked to differences in dispersal potential (Stobutzki and Bellwood 1997; Fisher et al. 2000). Further, both inter- and intraspecific differences in U_{CRIT} have been used to describe self-recruitment mechanisms within lottery recruitment models (Fisher 2005). Ontogenetic shifts in swimming ability are well documented (Fuiman and Webb 1988), but information on how they influence dispersal behavior in disturbed ecosystems is lacking.

The Everglades (USA) is a large wetland experiencing seasonal drying of portions of the ecosystem, and periodic droughts drying large areas that force aquatic animals such as fishes to re-colonize flooded habitats (Loftus and Kushlan 1987; Trexler et al. 2002). The relative importance of local reproduction in recovery patterns of these populations in response to drought is poorly understood, but cannot alone explain observed increases in density following droughts (Goss et al. 2014). There appear to be too few local refuges (alligator holes) to sustain fish population sizes observed during marsh re-colonization (Loftus et al. 1992; Gaff et al. 2000; Kobza et al. 2004). Results from simulation models suggest that directed movement from large, permanent water bodies is needed to supply the biomass observed following inundation (DeAngelis et al. 2010; Jopp et al. 2010).

Previous studies observed fish assemblage composition is reset after drying events (Ruetz et al. 2005), and fish activity rates are high immediately following reflooding corresponding to recolonization (Goss et al. 2014). We hypothesize that differences in colonization potential are driven primarily by movement behavior leading to immigration and not local reproduction. U_{CRIT} has been proposed as an indicator of fish species' post-disturbance arrival order following marsh drying; however, only interspecific variation in swimming speed has been evaluated (Gatto and Trexler 2020). Stage-specific variation of swimming speed may further explain differences in species-specific and stage-specific arrival probabilities for coexisting species. In this study, we investigated inter- and

intraspecific differences in colonization potential for six co-existing fish species in a hydrologically variable environment. Our objectives were (1) to quantify both stage-specific (juvenile versus adult) and sex-specific (male versus female) arrival times post-inundation from a 20-year, multi-site dataset; (2) to evaluate both inter- and intraspecific variation in arrival order; (3) to estimate U_{CRIT} for each species throughout life history; and (4) to link differences in U_{CRIT} to field estimated colonization patterns. These objectives aim to identify whether intraspecific variation in U_{CRIT} can further explain complex colonization patterns that were not previously identified when accounting for interspecific variation alone.

Methods

Study sites and species

The freshwater marshes of the Everglades experience seasonal rainfall patterns with an annual dry (November–May) and wet (June–October) period (Duever et al. 1994). Seasonal inundation is a direct result of rainfall and sheet flow, followed by drying when less rainfall is coupled with evapotranspiration (Fennema et al. 1994). The persistence of fish communities in these landscapes is facilitated by the hydrologic connectivity between permanent and ephemeral habitats. This results in temporal shifts of fish densities, causing these organisms to immigrate with flooding or emigrate when drying or face desiccation (Loftus and Kushlan 1987; DeAngelis et al. 2010; Goss et al. 2014). Flow velocity is consistently low (<3 cm/s; Larsen et al. 2011), and colonization following inundation is driven primarily by changes in movement behaviors (Larsen et al. 2011; Hoch et al. 2015).

From 1996 to 2016, we collected fishes using a 1-m², 2-mm mesh, throw trap following a standard protocol (Jordan et al. 1997) at 21 monitoring sites in the Everglades, Florida, USA (Supplemental Appendix A). Six sites were in Shark River Slough (SRS), five in Taylor Slough (TSL), and 10 in Water Conservation Areas (WCA) 3A and 3B. Samples were collected at each site in 5 months of each year (July, October, December, February, and April) to characterize a “water year” from the wet season (begins in June) through the dry season (begins November). Each site consisted of three plots, except for

short-hydroperiod sites in TSL (MDsh and TSsh) with two plots each. Five (WCA 3A and 3B) or seven (SRS and TSL) throw-trap samples were collected within each. Plots located in WCA 3A and 3B yielded 25 samples per year (5 throws $\times$ 5 sample events), while plots in SRS and TSL yielded 35 samples per water-year (7 throws per plot $\times$ 5 sample events). Throw locations within each plot were determined using a random number table. After securing the trap, floating vegetation (non-rooted vascular plants and periphyton mat) was quantified and cleared before fishes were removed following a standardized protocol of sweeps with a bar seine and dip nets. Vertebrate organisms were euthanized using a solution of MS-222 and ambient marsh water (Jenkins et al. 2014).

Jordan et al. (1997) estimated fish-collection efficiency for throw-trap sampling in the Everglades and detected no effect of vascular-plant stem density over the range of variation represented in this data set (Jordan et al. 1997). Gatto and Trexler (2019) estimated size-based collection efficiency for these data using demographic models. Size-biased under-sampling of small fishes decreased exponentially from approximately 5 to 20 mm for all species and was estimated to be near zero at or before sexual maturity for all species (Gatto and Trexler 2019). Detection probabilities for these species using a 1-m² throw trap compared to other sample gear have also been evaluated (Parkos et al. 2019). There is no evidence of visitor impact on these long-term study sites, possibly because marsh plants re-grow quickly and periodic marsh drying overwhelms sampler effects on vegetation and soil (Wolski et al. 2004). Additional information on the study sites and sampling design is provided in Trexler et al. (2003) and Trexler et al. (2005).

This study focused on the six most abundant marsh-fish species (Order: Cyprinodontiformes) at all study sites. These include three members of Family Poeciliidae: *Gambusia holbrooki* (Eastern Mosquitofish), *Heterandria formosa* (Least Killifish), and *Poecilia latipinna* (Sailfin Molly), two members of Family Fundulidae: *Lucania goodei* (Bluefin Killifish) and *Fundulus chrysotus* (Golden Topminnow), and one member of Family Cyprinodontidae: *Jordanella floridae* (Flagfish). We differentiated adults from juveniles based on the size of maturation (standard length, SL) (e.g., Haake and Dean 1983) and the presence of external features (e.g., gonopodium,

Loftus and Kushlan 1987): *H. formosa* (adults ≥ 10 mm), *G. holbrooki* (adults ≥ 17 mm), *P. latipinna* and *L. goodei* (adults ≥ 18 mm), *F. chrysotus* (adults ≥ 22 mm), and *J. floridae* (adults ≥ 20 mm). These species can be further classified into three life-history strategies related to recovery following drought: rapid recovery and sustained high density (*G. holbrooki*), rapid recovery followed by a decline in density (*J. floridae* and *F. chrysotus*), and slow recovery over time (*L. goodei*, *H. formosa*, and *P. latipinna*). These have been described in detail in other publications (DeAngelis et al. 2005; Trexler et al. 2005).

Drought identification

We analyzed a 20-year time-series dataset to determine the colonization patterns following re-inundation of a habitat across 21 long-term monitoring sites. Daily hydrological data were extracted from the Everglades Depth Estimation Network (EDEN) (Telis 2006; Liu et al. 2009) and adjusted for local topography by regression with depth measurements taken while sampling aquatic animals. EDEN uses an integrated network of water-level gauges and water-surface models to estimate daily water depths at 400-m by 400-m grid cells (xy locator tool, <https://sofia.usgs.gov/eden/edenapps/xylocator.php>). We used these topographically adjusted data to determine when our study plots dried and re-flooded. A plot was considered to have dried when modeled water depth dropped below 5 cm prior to a sample collection. At 5 cm, only a slurry of organic matter remains, and fishes generally suffocate in the low-oxygen conditions and organic floc blocking their gills. We used plot-level data because local topographic heterogeneity (among plots within sites) impacted frequency and return time of drying and obscured colonization patterns when data are grouped by site. All data collected prior to the first detectable drying event were not considered because colonization time could not be estimated. Plots lacking a drying event were excluded from our analyses.

Stage-specific colonization patterns

To identify when a species arrived following drought, we identified the presence or absence of each species in samples collected between drying events. Using temporal tabulations of species

presence (count > 0) or absence (count = 0), we recorded the cumulative number of sample periods that each species was absent prior to first detection following marsh re-flooding. The order fish appear in our samples collected sequentially after re-flooding following a drought (hereafter referred to drying) was treated as the order which they re-colonized each study site. However, we evaluated if the order simply reflects differences in density or size-linked detection probability. Preston (1948) described a veil-line effect for detection of rare species; species with densities below this critical density set by sampling effort may be present, but undetected (the low-density tail of the abundance distribution is hidden behind the veil). Detection probabilities unrelated to a veil-line effect for these species have been previously evaluated for a 1-mm² throw trap (Gatto and Trexler 2019; Parkos et al. 2019). It is also possible that early recolonization by juveniles could reflect local reproduction by relatively infrequent fast colonizing adults or hatching of resting eggs laid before the drought (Reutz et al. 2005). We address these possibilities in our discussion.

The arrival order of juveniles and adults of each species per plot after a reflood event was also calculated. To determine arrival order, we ranked each species/stages' (six species, two stages each = 12 species/stage combinations) arrival time (earliest = 1, latest = 12) and addressed ties by assigning the lowest rank for all species with the same arrival time. Ties occurred when species first arrived at the same sample event. Therefore, a rank of 1 was associated with all species that arrived first to ensure a range of whole numbers from 1 to 12. We used these ranks to calculate arrival probabilities or the proportion of drying events where a species arrived at each arrival order, for each species by using the following formula:

$$p_i = \frac{X_i}{n} \quad (1)$$

where p_i is the probability of arrival, X_i is the number of drying events where a species arrived in the i th order, and n is the number of drying events in the time series. We then calculated the probability mass function (PMF) and cumulative distribution function (CDF) based on binomial error distribution for the

probability of arriving first following inundation at the landscape level. This was based on the number of success (species/stages arrived among first) and failures (species/stages did not arrive among first) for all drying events observed in the time series independent of plots and hydrology.

Stage-specific colonization and density

To test whether the density of juveniles and adults was correlated with the time to re-colonize a site following drought, we calculated three metrics of density: density at first arrival post-drought, average density while inundated, and maximum density while inundated. Densities were calculated using the density of fish in each of the 5 to 7 1-m² throw-trap samples, while sites were inundated. We first determined the initial density of fish (density at first arrival) by calculating the density when fish were initially present following inundation. Mean density while inundated was calculated by averaging the densities for all samples collected between successive drying events. We determined the peak density during inundation to determine if early colonization was related to increased population size (maximum density while inundated). Spearman's *rho*, a nonparametric correlation, was used to document the relationship of recolonization patterns and density metrics. The nonparametric approach was selected because the two variables of interest were derived by ranking the magnitude of each variable. For statistical analyses, a species was assigned a colonization time equal to the maximum number of samples collected between drying events if they did not arrive post-drying. This ensured that these species received the highest rank possible, even when accounting for ties. Spearman's *rho* was calculated separately for each drying event using the rank order of arrival time and each metric of density. We then used a general linear model to test the main effects of arrival order, species, stage, and their interaction (species $\times$ stage) on mean density. Mean density was tested for normality of residuals and log-transformed prior to analysis to meet this assumption. Each plot was analyzed separately with replication within a plot as individual drying events (2 to 20 drying events per plot). Plots that lacked a drying event or experienced only one drying event were excluded from analyses because of lack of replication. This model was tested based on a priori hypotheses

that the explanatory variables best described arrival order. The full model (containing all interactions) was also estimated and compared to the a priori models using Akaike Information Criterion (AIC) for model validation. These, and all other analyses, were conducted using SAS 9.4 (Insititute 2012).

Hydrology and stage-specific arrival order

To evaluate the effects of hydrology on arrival order, we considered four hydrological variables derived from the interpolated depth data. These variables included depth at first arrival, dry-down length, day since dry (DSD), and Julian date of flooding (Year Day of Flood). Dry-down length is a count variable that records the number of days that a site was previously dry before inundation. DSD records the cumulative number of days since a site had a water depth < 5 cm. The Julian date of flooding represents the temporal aspect of flooding and records the day of the year when water levels began to exceed 5 cm (e.g., Jan 31st = 31, Feb 1st = 32). Both dry-down length and Julian date of flooding were log-transformed to meet the assumption of normality. Past work has indicated that these variables are not so highly correlated as to be redundant in ecological models similar to the ones we are fitting (e.g., Trexler et al. 2015). We then used a generalized linear model (GLM) with a Poisson error distribution to test the main effects of species, stage, their interaction (species $\times$ stage), depth at first arrival, year day of flood, dry-down length, and DSD on arrival order. A Poisson error distribution was used since arrival time is a discrete variable. AIC was used to determine whether our a priori model best explained arrival time compared to the full model with all interactions.

Sex-specific colonization patterns

We then evaluated sex-based differences in arrival order for adult individuals following re-inundation of the floodplain. Species were sexed by external features specific to sex. *Fundulus chrysotus* was excluded from these analyses because sex-specific differences in pigmentation, the only external feature to distinguish males from females, are lost during preservation. All previously described analyses used to detect stage-specific differences in colonization were repeated for this sex-based approach, which

excluded juveniles. A general linear model tested the main effects of arrival order, species, sex, and their interaction (species×sex) on density. We then used a GLM with a Poisson error distribution to test the main effects of species, sex, their interaction (species×sex), depth at re-flooding, year day of flood, DSD, and dry-down length on arrival order. Only the interactions between species and sex were considered to maintain degrees of freedom and to keep the focus of the study on sex-specific differences in arrival time. AIC was used to determine whether our a priori model best explained arrival time compared to the full model with all interactions.

Quantifying swimming speed

The critical swimming speed (U_{CRIT}), or the maximum sustained aerobic speed, was estimated as a metric of fish swimming ability (Plaut 2001). To investigate intra- and interspecific variation in U_{CRIT} , adult and juvenile fish for each species were collected from the Everglades using a dip net and transported to an indoor wet lab at Florida International University, Miami, FL. All individuals were collected from the same location which were considered long hydro-period sites between August and September. All fish were housed in 75.7-L aquaria under a 12/12 photoperiod. Individuals were fed TetraMin® once daily prior to each trial. Species were allowed 3–4 days to recover from transportation and translocation stress. No fish were placed into the swim chamber prior to the 3–4 day recovery period following collection. Individual fish were placed in a Blazka-style swim chamber (Blazka et al. 1960) and allowed to acclimate at low-flow speeds (2–6 cm/s or 1–3 BL/s) for 30 min to induce rheotaxis. Most individuals were acclimated to 1 BL/s; however, the minimum flow speed of the swim chamber was 2 cm/s. Smaller individuals were acclimated at faster velocities due to limitation of the swim chamber. Following the acclimation period, flow velocity was increased by 2 cm/s every 5 min until the individual could no longer swim against the current and was swept backward onto the meshed end of the chamber. Fatigue was assessed when an individual could no longer maintain its position against the flow and did not respond to stimulation for three consecutive attempts. Aeration was placed at the downstream end of the flume to ensure that the water was properly oxygenated and not a

limiting factor during each trial. Both the final velocity and the time until exhaustion at the final velocity were recorded. The critical swimming speed was then calculated using the formula:

$$U_{\text{CRIT}} = U + [U_i * (t/t_i)] \quad (2)$$

where U_i is the velocity increment (2 cm/s), t_i is the time increment (5 min), U is the final velocity a fish swum for the full 5 min, and t is the time swum at the final velocity (Plaut 2001).

We evaluated the U_{CRIT} of 20 juveniles and 20 adults of varying lengths (approximately one individual per mm in length) for each species ($n=40$ per species). The size range selected for each species was based on the observed size range of specimens within the 20-year time series. Time in captivity and time since last feeding were also assessed to determine any influence that these variables may have on estimated U_{CRIT} . We used fish housed for less than 12 days to prevent domestication of housing and feeding conditions. Regression analysis using ordinary least squares (OLS) was used to evaluate the relationship between individual body size and U_{CRIT} . Quantile regression (Cade and Noon 2003; Maronna et al. 2019) evaluated the relationship between body size and size-adjusted swimming speed (body lengths per second, BL/s). Quantile regression is advantageous over ordinary least squares since it is more robust to outliers in the data. It has more powerful predictive power when there is a weak relationship between the means of variables. We evaluated the possibility that the relationship between size-adjusted swimming speed and body size may be impacted by developmental stage. Our analyses evaluated the 10%, 25%, 50% 75%, and 90% quantiles to account for developmental differences among varying size class. An ANCOVA evaluated the interaction between stage-specific increases in U_{CRIT} as a function of body size (main effect). We used an ANOVA to evaluate intra- and interspecific differences in U_{CRIT} . This analysis separated juveniles and adults of each species for a 12-group comparison. Post-hoc Tukey's pairwise comparisons were used to compare the U_{CRIT} for each group based on their respective U_{CRIT} . Both absolute speed (cm/s) and size-adjusted speed (BL/s) were considered as the response variables for these analyses. Spearman's ρ was used to compare the average U_{CRIT} for each group against their average arrival order post-drying.

Results

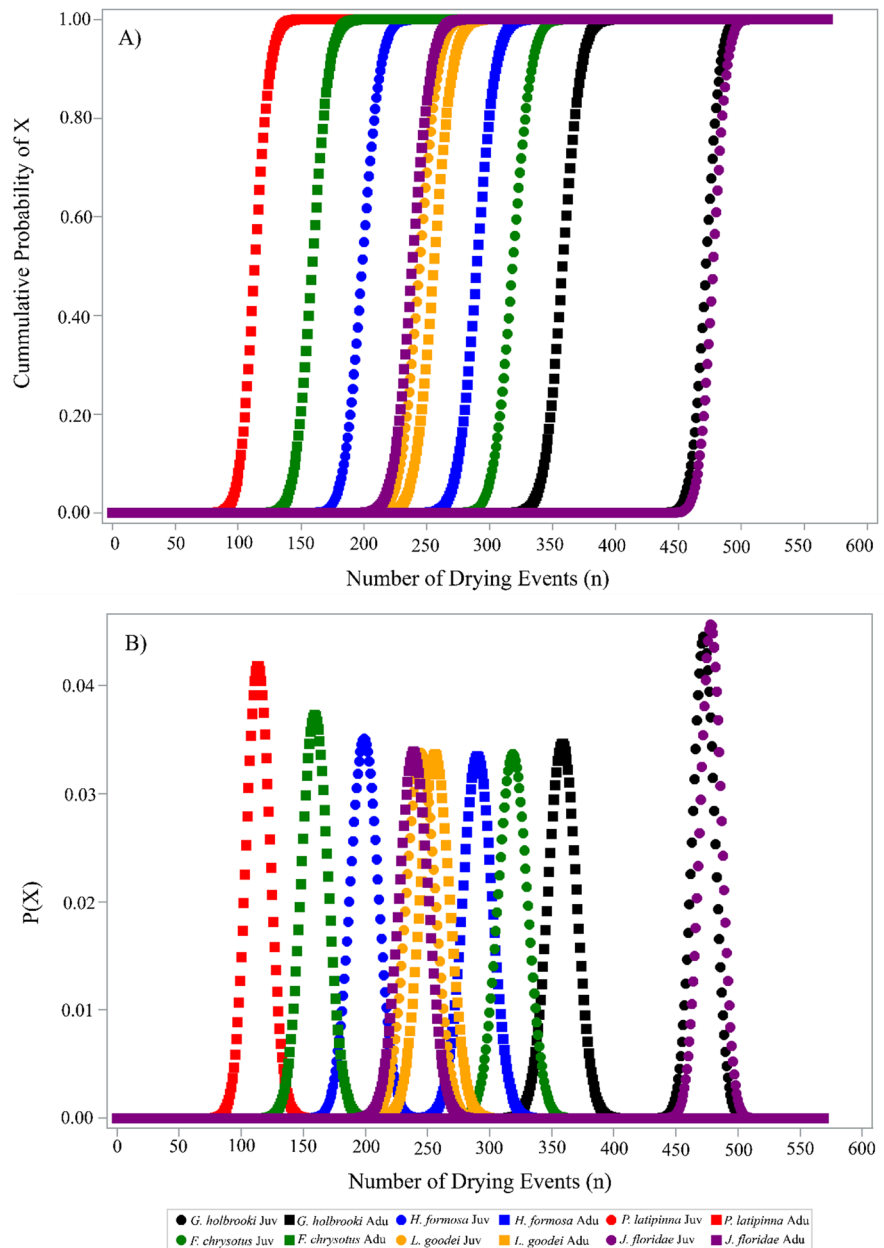
Stage-specific colonization patterns

Our analyses indicated that there were 569 drying events between 1996 and 2016 across all 21 sites. Interspecific variation in species' arrival order was similar across study sites and revealed a consistent pattern of re-colonization (*J. floridae*, *G. holbrooki*, *F. chrysotus*, *L. goodei*, *H. formosa*, followed by *P. latipinna*). Stage-specific differences in arrival patterns within species were less consistent and varied on spatial–temporal scales. Analyses determined that arrival probabilities varied substantially among species and between stages (Table 1); however, the probability of arriving first had the greatest variation among species and stages across the landscape (Fig. 1A, B). Overall, both juvenile *J. floridae* and *G. holbrooki* were among the first individuals to arrive post-drying. These species arrived concurrently with adults for 42.4% $\pm$ 3.0 (*J. floridae*) and 68.0% $\pm$ 3.2 (*G. holbrooki*) of drying events on average. Juvenile *J. floridae* also had the highest probability of arriving before adults than any other species (52.0% $\pm$ 3.0 of drying events). These were often followed by juvenile *F. chrysotus* which had a > 85% probability of being among the initial six groups to arrive. Adults of these species followed the colonization of juveniles and had a > 61% probability of being among the first groups to arrive. Early arrival of *F. chrysotus* was often by juveniles (occurring in 45.4% $\pm$ 3.2 of drying events), but these juveniles often arrived simultaneously with adults in an additional 42.0% $\pm$ 3.0 of drying events. Colonization by adult *F. chrysotus* often followed that of both juvenile and adult *L. goodei* and *H. formosa*. Adults of these late colonizers would often arrive prior to juveniles; however, simultaneous colonization of both adults and juveniles occurred in 53.9% $\pm$ 3.1 (*L. goodei*) and 50.4% $\pm$ 3.8 (*H. formosa*) of the drying events analyzed. Following adults and juveniles of all species and stages, adult and juvenile *P. latipinna* were consistently the last individuals to appear in samples post-drought. On average, juveniles and adults of this species arrived simultaneously for 57.1% $\pm$ 3.4 of arrivals and had a 0.66 (adults) and 0.59 (juveniles) probability of being among the last six groups to arrive.

Table 1 Stage-based arrival probabilities following re-inundation of the floodplain (mean $\pm$ SE) across the landscape. Probabilities were averaged across plots and are independent of hydrology

Arrival order	<i>J. floridae</i>		<i>G. holbrooki</i>		<i>F. chrysotus</i>		<i>L. goodei</i>		<i>H. formosa</i>		<i>P. latipinna</i>	
	Adu	Juv	Adu	Juv	Adu	Juv	Adu	Juv	Adu	Juv	Adu	Juv
1st	0.42 (0.04)	0.84 (0.03)	0.63 (0.04)	0.83 (0.03)	0.28 (0.04)	0.56 (0.04)	0.45 (0.04)	0.43 (0.04)	0.51 (0.04)	0.35 (0.04)	0.20 (0.03)	0.28 (0.04)
2nd	0.02 (0.01)	0.01 (0.01)	0.03 (0.01)	0.03 (0.01)	0.02 (0.01)	0.03 (0.01)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)
3rd	0.06 (0.02)	0.02 (0.01)	0.06 (0.02)	0.03 (0.01)	0.05 (0.02)	0.07 (0.03)	0.05 (0.02)	0.06 (0.02)	0.04 (0.02)	0.03 (0.01)	0.02 (0.01)	0.02 (0.01)
4th	0.07 (0.02)	0.02 (0.01)	0.06 (0.02)	0.03 (0.01)	0.05 (0.02)	0.06 (0.02)	0.06 (0.02)	0.05 (0.02)	0.04 (0.02)	0.03 (0.01)	0.01 (0.01)	0.02 (0.01)
5th	0.05 (0.02)	< 0.01	0.06 (0.02)	0.03 (0.01)	0.08 (0.02)	0.06 (0.02)	0.06 (0.02)	0.06 (0.02)	0.05 (0.02)	0.05 (0.02)	0.04 (0.02)	0.03 (0.01)
6th	0.07 (0.02)	0.01 (0.01)	0.05 (0.02)	0.02 (0.01)	0.12 (0.03)	0.07 (0.02)	0.07 (0.02)	0.08 (0.02)	0.08 (0.02)	0.08 (0.02)	0.05 (0.02)	0.05 (0.02)
7th	0.07 (0.02)	0.02 (0.01)	0.06 (0.02)	0.01 (0.01)	0.11 (0.03)	0.04 (0.02)	0.08 (0.02)	0.09 (0.02)	0.08 (0.02)	0.08 (0.02)	0.07 (0.02)	0.05 (0.02)
8th	0.05 (0.02)	0.01 (0.01)	0.02 (0.01)	0.01 (0.01)	0.08 (0.02)	0.03 (0.01)	0.07 (0.02)	0.06 (0.02)	0.08 (0.02)	0.07 (0.02)	0.06 (0.02)	0.06 (0.02)
9th	0.08 (0.02)	0.02 (0.01)	0.02 (0.01)	0.0	0.08 (0.02)	0.04 (0.02)	0.06 (0.02)	0.05 (0.02)	0.07 (0.02)	0.09 (0.02)	0.10 (0.02)	0.10 (0.02)
10th	0.05 (0.02)	0.01 (0.01)	0.01 (0.01)	< 0.01	0.04 (0.02)	0.02 (0.01)	0.04 (0.02)	0.05 (0.02)	0.03 (0.01)	0.11 (0.03)	0.10 (0.02)	0.09 (0.02)
11th	0.03 (0.01)	0.01 (0.01)	0.0	0.0	0.04 (0.02)	0.01 (0.01)	0.03 (0.01)	0.04 (0.02)	0.01 (0.01)	0.06 (0.02)	0.23 (0.03)	0.20 (0.03)
12th	0.02 (0.01)	0.01 (0.01)	< 0.01	0.0	0.04 (0.02)	0.01 (0.01)	0.02 (0.01)	0.01 (0.01)	0.0	0.05 (0.02)	0.11 (0.03)	0.09 (0.02)

Fig. 1 **A** Cumulative distribution function (CDF) for the probability of arriving first following disturbance. **B** Probability mass function (PMF) for the probability of arriving first following disturbance. Each function was calculated for every species and stage across the entire landscape ($n = 569$ drying events). Values for adult and juvenile *P. latipinna* overlap for both the CDF and PMF and cannot be differentiated



Results determined that early arriving species appeared with higher densities and correlation tests determined that arrival order was inversely correlated with the density at first arrival (Mean $r = -0.44 \pm 0.02$; Fig. 2). However, early arrival was not correlated with higher initial densities for 62% of drying events analyzed (Table 2). Stage-specific densities at the time of arrival decreased as arrival order increased (arrived later) but were followed by both higher maximum density (Mean $r = -0.58$

± 0.01) and average density while inundated (Mean $r = -0.60 \pm 0.01$). Both maximum density and average density were influenced by stage-specific differences in arrival order for 62% and 55% of drying events, respectively ($p < 0.05$). AIC determined that the model without all interactions best-described density for most plots (Supplemental Appendix B, Table B1.1). Partial R -squares of the full model revealed that little additional variance was explained in the few cases where the full model was preferable

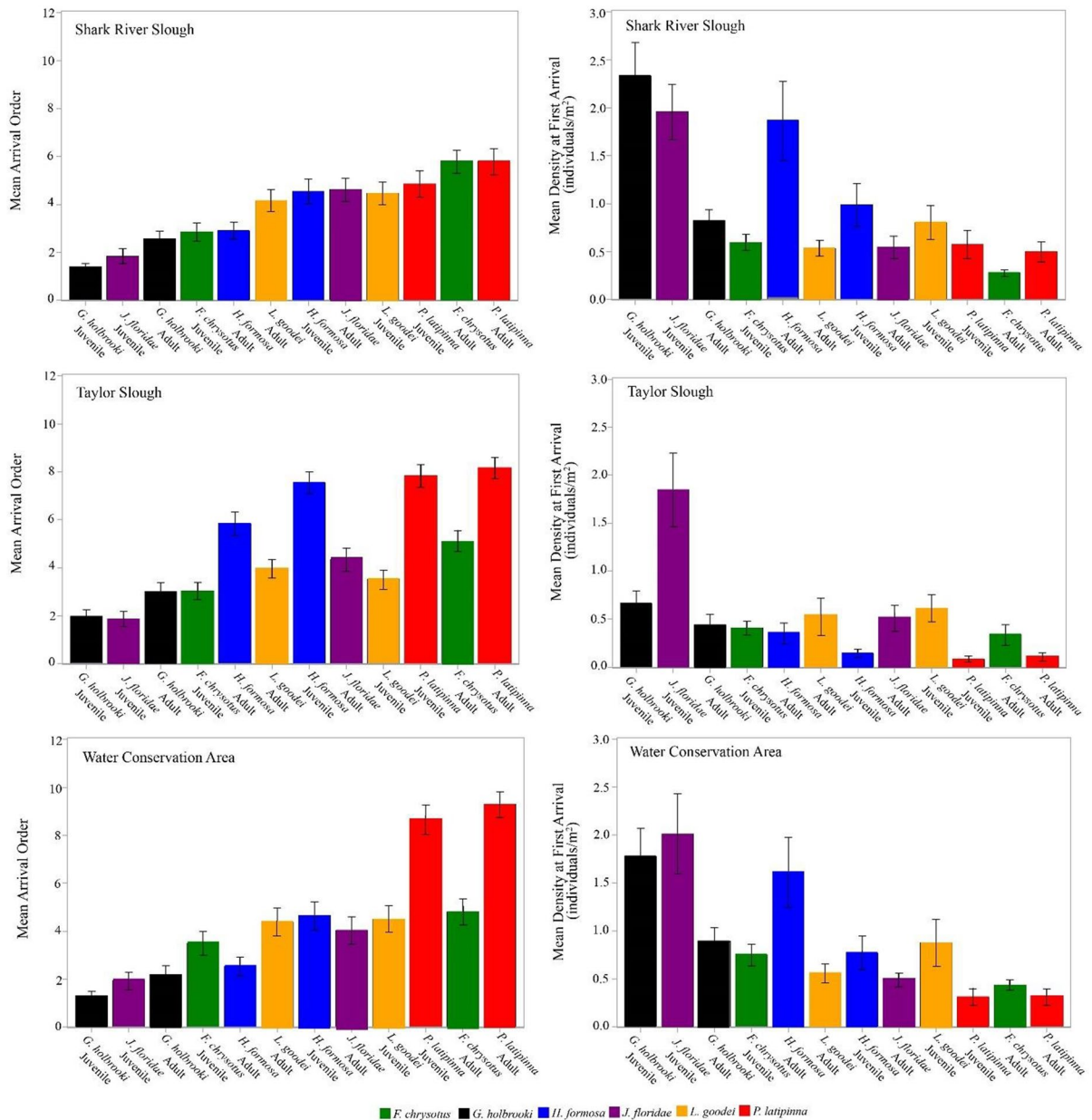


Fig. 2 The mean arrival order for each species stage (left) and density at first arrival (right) for each of the three Everglades regions. Species are arranged based on their arrival order from Shark River Slough for comparison

(Table B1.2). Our general linear models revealed that interspecific differences in density were driven by arrival order for 84% of drying events. Density-correlated colonization was weakest at long-hydroperiod sites and increased at sites that dried more frequently. Our general linear models revealed a positive correlation between arrival time and density at these sites,

indicating higher densities at later arrival. Furthermore, significant interaction between species and stage (species $\times$ stage) revealed differences in stage-specific density for 67% of drying events (Table 2, see also Fig. 2). AIC determined that the model without all interactions best-described arrival order for most plots (Supplemental Appendix B, Table B2.1). The

Table 2 Summary of general linear models used to test the main effects of arrival order, species, stage, and their interactions on density. Values indicate the number of plots where the main effect was either significant or not significant. Parentheses indicate the proportion of those plots. Plots were divided

into long- (<4 drying events in 20 years), intermediate- (4–12 drying events in 20 years), and short-hydroperiod sites (>12 drying in 20 years). Some variables were excluded from analyses due to insufficient variation in data

Main effect	Short		Intermediate		Long		Overall	
	$p < 0.05$	$p \geq 0.05$	$p < 0.05$	$p \geq 0.05$	$p < 0.05$	$p \geq 0.05$	$p < 0.05$	$p \geq 0.05$
Arrival order	10 (77)	3 (23)	21 (100)	0 (0)	0 (0)	3 (100)	31 (84)	6 (16)
Species	12 (92)	1 (8)	30 (100)	0 (0)	3 (100)	0 (0)	45 (98)	1 (2)
Age	1 (8)	12 (92)	6 (20)	24 (80)	0 (0)	3 (100)	7 (15)	39 (85)
Species*age	8 (62)	5 (38)	20 (67)	10 (33)	3 (100)	0 (0)	31 (67)	15 (33)

ratio of the generalized chi-square statistic and its degrees of freedom revealed that little additional variance was explained in the few cases where the full model was preferable (Table B2.2). We also found that DSD had the greatest effect on arrival order and influenced arrival order for 89% of all drying events (Table 3). DSD was positively correlated, when significant, with arrival order for all plots except three intermediate hydroperiod sites (species arrived later as DSD increased).

Sex-specific differences in colonization patterns

Analyses indicated that adults for all species were present following re-inundation and before the next drought for 529 of 569 (92.4%) drying events. Of these drying events, Spearman's rank correlation

determined that sex-specific differences in colonization patterns were correlated with density for <1% of all drying events in the time series. AIC determined that the model without all interactions best-described density for most plots (Supplemental Appendix B, Table B3.1). Partial *R*-squares of the full model revealed that little additional variance was explained in the few cases where the full model was preferable (Table B3.2). Results from our general linear models revealed early arrival was positively associated with density at first arrival for both males and females of each species for 41% of plots (Table 4). Sex ratios were revealed to be skewed towards females for all species (Supplemental Appendix C). AIC determined that the model without all interactions best described arrival order for most plots (Supplemental Appendix B, Table B4.1).

Table 3 Summary of GLM's used to test the main effects of species, stage, species*age, and hydrological variables on arrival order. Values indicate the number of plots where the main effect was either significant or not significant. Parentheses indicate the proportion of those plots. Plots were divided into long- (<4 drying events in 20 years), intermediate- (4–12 drying events in 20 years), and short-hydroperiod sites

(>12 drying in 20 years). Some hydrological variables were excluded from analyses due to insufficient variation in data. "Dry Length" is number of days site dry before inundation, and "Dry Day" is the Julian date of flooding. "Depth" is the at the time of sampling, and "DSD" is the days since site was last dry before sample was collected

Main effect	Short		Intermediate		Long		Overall	
	$p < 0.05$	$p \geq 0.05$	$p < 0.05$	$p \geq 0.05$	$p < 0.05$	$p \geq 0.05$	$p < 0.05$	$p \geq 0.05$
Species	13 (100)	0 (0)	28 (93)	2 (7)	3 (100)	0 (0)	44 (96)	2 (4)
Age	6 (46)	7 (54)	9 (30)	21 (70)	0 (0)	3 (100)	15 (33)	31 (67)
Species*age	12 (92)	1 (8)	19 (63)	11 (37)	0 (0)	3 (100)	31 (67)	15 (33)
Log(Dry Length)	6 (46)	6 (54)	5 (17)	24 (83)	0 (0)	2 (100)	11 (26)	32 (74)
Log(Dry Day)	7 (54)	6 (46)	8 (28)	21 (72)	1 (50)	1 (50)	16 (36)	28 (64)
Depth	0 (0)	13 (100)	11 (38)	18 (62)	0 (0.0)	1 (100)	11 (26)	32 (74)
DSD	11 (85)	2 (15)	27 (90)	3 (10)	3 (100)	0 (0)	41 (89)	5 (11)

Table 4 Summary of general linear models used to test the main effects of arrival order, species, sex, and their interactions on density. Values indicate the number of plots where the main effect was either significant or not significant and the percent-

age of plots in each category are reported in parentheses. Plots were divided into long- (<4 drying events in 20 years), intermediate- (4–12 drying events in 20 years), and short-hydroperiod sites (> 12 drying in 20 years)

Main effect	Short		Intermediate		Long		Overall	
	$p < 0.05$	$p \geq 0.05$	$p < 0.05$	$p \geq 0.05$	$p < 0.05$	$p \geq 0.05$	$p < 0.05$	$p \geq 0.05$
Arrival order	6 (46)	7 (54)	13 (43)	17 (57)	0 (0)	3 (100)	19 (41)	27 (59)
Species	13 (100)	0 (0)	30 (100)	0 (0)	3 (100)	0 (0)	46 (100)	0 (0)
Sex	10 (77)	3 (23)	16 (53)	14 (47)	0 (0)	3 (100)	26 (57)	20 (43)
Species*sex	6 (46)	7 (54)	11 (37)	19 (63)	0 (0)	3 (100)	17 (37)	29 (63)

The ratio of the generalized chi-square statistic and its degrees of freedom revealed that little additional variance was explained in the few cases where the full model was preferable (Table B4.2). Hydrology did not have a large effect on sex-specific differences in arrival order and only influenced colonization for <20.9% of all drying events (Table 5, see also Fig. 3). Females consistently arrived before males and had the highest first-order arrival probabilities for all species across the landscape (Fig. 3A, B). The probability of arriving first for females was nearly twice that of males for *P. latipinna*, *J. floridae*, and *G. holbrooki* (Table 6). On average, female *G. holbrooki* and *H. formosa* were among the first adults to colonize. Male *J. floridae* and both male and female *P. latipinna* were consistently among the last three groups to colonize.

Inter- and intraspecific differences in swimming speed

U_{CRIT} tests generated swimming speed profiles for six marsh species and encompassed the entire size range of juveniles and adults for each species. This revealed that U_{CRIT} (cm/s) was highly correlated ($R^2 \geq 0.71$) with body length and increased linearly for all species (Fig. 4). Our ANCOVA revealed increases in U_{CRIT} with increased body length for all species, but we only observed stage-specific differences in slopes for *F. chrysotus* (stage: $F_{1,36} = 6.47$, $p < 0.05$, interaction: $F_{1,36} = 4.93$, $p < 0.05$). This also determined that there was an overlap in U_{CRIT} between juveniles and adult around the size of maturation for all species (Table 7). Contrary to absolute speed, we observed no relationship between body size and size-adjusted speed for five of the six species. However, quantile

Table 5 Summary of GLM's used to test the main effects of species, sex, species×sex, and hydrological variables on arrival order. Values indicate the number of plots where the main effect was either significant or not significant and the percentage of plots in each category are reported in parentheses. Plots were divided into long- (<4 drying events in 20 years), intermediate- (4–12 drying events in 20 years), and short-

hydroperiod sites (> 12 drying in 20 years). Some hydrological variables were excluded from analyses due to insufficient variation in data. “Dry Length” is number of days site dry before inundation, and “Dry Day” is the Julian date of flooding. “Depth” is the at the time of sampling, and “DSD” is the days since site was last dry before sample was collected

Main effect	Short		Intermediate		Long		Overall	
	$p < 0.05$	$p \geq 0.05$	$p < 0.05$	$p \geq 0.05$	$p < 0.05$	$p \geq 0.05$	$p < 0.05$	$p \geq 0.05$
Species	13 (100)	0 (0)	28 (93)	2 (7)	3 (100)	0 (0)	44 (96)	2 (4)
Sex	7 (54)	6 (46)	13 (43)	17 (57)	0 (0)	3 (100)	20 (44)	26 (57)
Species*sex	7 (54)	6 (46)	10 (39)	16 (62)	0 (0)	3 (100)	17 (41)	25 (59)
Log(Dry Length)	2 (15)	11 (85)	2 (7)	27 (93)	0 (0)	2 (100)	4 (9)	40 (91)
Log(Dry Day)	2 (15)	11 (85)	0 (0)	29 (100)	0 (0)	2 (100)	2 (5)	42 (95)
Depth	5 (39)	8 (62)	1 (3)	28 (97)	0 (0)	1 (100)	6 (14)	37 (86)
DSD	6 (46)	7 (54)	4 (13)	26 (87)	0 (0)	3 (100)	10 (22)	36 (78)

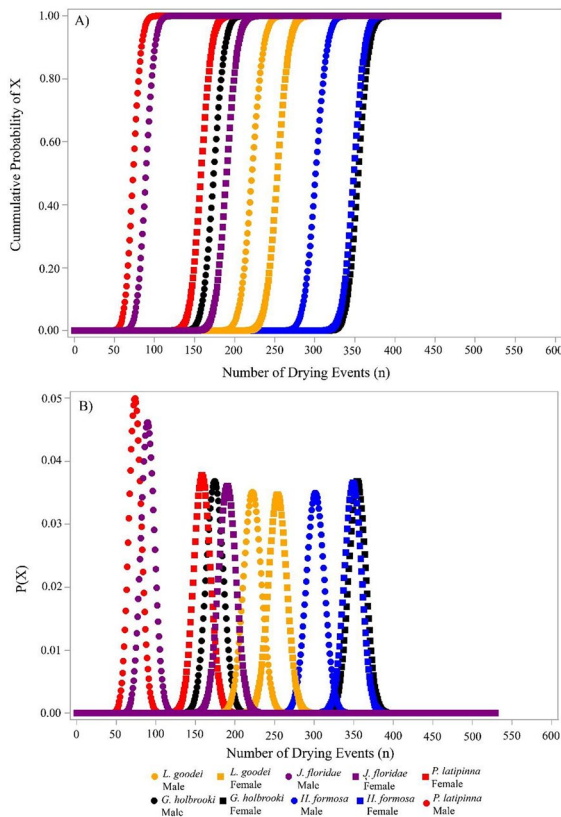


Fig. 3 **A** Cumulative distribution function (CDF) for the probability of arriving first following disturbance. **B** Probability mass function (PMF) for the probability of arriving first following disturbance. Each function was calculated for every species and sex class ($n=529$ drying events) across the landscape. *F. chrysotus* was excluded because individual sex could not be determined

regression revealed that variance in size-adjusted U_{CRIT} decreased with stage in three species (*F. chrysotus*, *J. floridae*, and *P. latipinna*), two species had relatively constant and narrow variance with size and decreasing $U_{\text{CRIT}}/\text{BLS}$ with size (*G. holbrooki* and *L. goodei*), and one species displayed no size-based pattern in variation or mean (*H. formosa*) (Fig. 5). We found no evidence to indicate that time at last feeding or time in captivity influenced our estimates of U_{CRIT} (Supplemental Appendix D).

We found both inter- and intra-specific differences in absolute U_{CRIT} . Our ANOVA model revealed these differences to vary among species and stage ($F_{11, 228}=93.81$, $p<0.01$). Adults for each species had estimates of U_{CRIT} that were often twice that of juveniles within the same species; however, some

Table 6 Sex-based arrival probabilities following re-inundation of the floodplain across the entire landscape (mean $\pm$ SE). Probabilities were averaged across plots and are independent of hydrology

Arrival order	<i>J. floridae</i>		<i>G. holbrooki</i>		<i>L. goodei</i>		<i>H. formosa</i>		<i>P. latipinna</i>	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1st	0.17 (0.03)	0.36 (0.04)	0.33 (0.04)	0.67 (0.04)	0.42 (0.04)	0.48 (0.04)	0.57 (0.04)	0.66 (0.04)	0.14 (0.03)	0.30 (0.04)
2nd	0.05 (0.02)	0.05 (0.02)	0.06 (0.02)	0.07 (0.02)	0.06 (0.02)	0.05 (0.02)	0.05 (0.02)	0.05 (0.02)	0.04 (0.02)	0.04 (0.02)
3rd	0.05 (0.02)	0.09 (0.02)	0.06 (0.02)	0.06 (0.02)	0.07 (0.02)	0.06 (0.02)	0.08 (0.02)	0.07 (0.02)	0.05 (0.02)	0.06 (0.02)
4th	0.06 (0.02)	0.10 (0.03)	0.10 (0.03)	0.07 (0.02)	0.08 (0.02)	0.09 (0.02)	0.09 (0.02)	0.07 (0.02)	0.05 (0.02)	0.06 (0.02)
5th	0.09 (0.02)	0.12 (0.03)	0.11 (0.03)	0.06 (0.02)	0.10 (0.03)	0.09 (0.02)	0.09 (0.02)	0.07 (0.02)	0.10 (0.03)	0.09 (0.02)
6th	0.11 (0.03)	0.10 (0.03)	0.12 (0.03)	0.04 (0.02)	0.10 (0.03)	0.09 (0.02)	0.06 (0.02)	0.05 (0.02)	0.11 (0.03)	0.10 (0.03)
7th	0.13 (0.03)	0.11 (0.03)	0.10 (0.03)	0.02 (0.01)	0.09 (0.02)	0.09 (0.02)	0.05 (0.01)	0.03 (0.01)	0.11 (0.03)	0.11 (0.03)
8th	0.16 (0.03)	0.03 (0.02)	0.06 (0.02)	0.01 (0.01)	0.05 (0.02)	0.03 (0.01)	0.01 (0.01)	<0.01	0.15 (0.03)	0.12 (0.03)
9th	0.08 (0.02)	0.03 (0.02)	0.03 (0.02)	<0.01	0.02 (0.01)	<0.01	<0.01	<0.01	0.18 (0.03)	0.10 (0.03)
10th	0.08 (0.02)	<0.01	0.01 (0.01)	<0.01	0.01 (0.01)	0.00	<0.01	0.00	0.07 (0.02)	<0.01

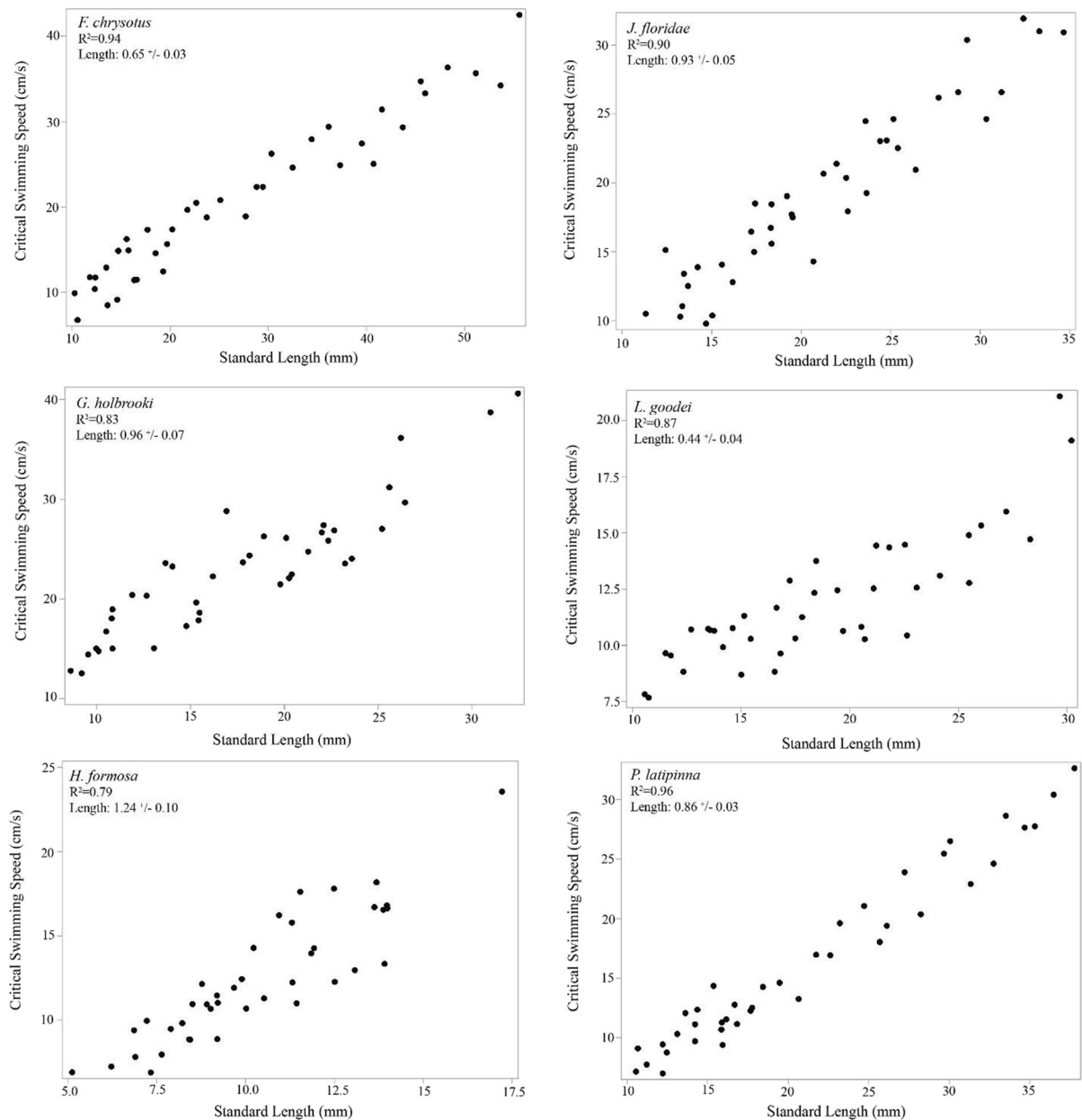


Fig. 4 Scatterplots for the relationship between standard length (SL) and absolute critical swimming speed (U_{CRIT}). Estimates for the slope ($\pm$ SE) are provided

juveniles had U_{CRIT} estimates that were higher than those of adults for other species (Fig. 6A). U_{CRIT} tests revealed that adult *F. chrysotus*, *G. holbrooki*, *J. floridae*, and *P. latipinna* were among the fastest individuals in our study. This was followed by juvenile *G. holbrooki*, juvenile *F. chrysotus*, adult *H. formosa*, adult *L. goodei*, and juveniles of the remaining

species in the study. Although we found stage-specific differences in size-adjusted U_{CRIT} among groups ($F_{11, 228}=93.81$, $p<0.01$), our analyses revealed a substantially different pattern than absolute U_{CRIT} (Fig. 6B). Estimates of size-adjusted U_{CRIT} were substantially higher for *G. holbrooki* compared to other species and stage. Relative to body size, *H.*

Table 7 Summary statistics for inter- and intraspecific differences in absolute swimming speed (cm/s)

Species	Stage	Mean ($\pm$ SE)	Minimum	Maximum
<i>F. chrysotus</i>	Juvenile	13.39 (0.83)	6.76	20.50
	Adult	28.31 (1.43)	18.78	42.49
<i>G. holbrooki</i>	Juvenile	18.28 (0.91)	12.55	28.81
	Adult	27.45 (1.20)	21.47	40.60
<i>H. formosa</i>	Juvenile	9.68 (0.39)	6.89	12.44
	Adult	15.11 (0.70)	10.69	23.55
<i>J. floridae</i>	Juvenile	14.43 (0.68)	9.77	19.02
	Adult	24.04 (1.05)	14.29	31.93
<i>L. goodei</i>	Juvenile	10.09 (0.29)	7.67	12.87
	Adult	13.80 (0.61)	10.28	21.06
<i>P. latipinna</i>	Juvenile	10.54 (0.44)	7.00	14.35
	Adult	22.25 (1.27)	13.26	32.63

formosa also had significantly higher estimates of size-adjusted U_{CRIT} (mean U_{CRIT} 12.12 $\pm$ 0.40 BLS) and were comparable to adult *G. holbrooki* (mean U_{CRIT} 11.96 $\pm$ 0.26 BLS). Juveniles swam faster relative to body size for *F. chrysotus* (mean difference +1.02 BLS), *G. holbrooki* (mean difference +2.78 BLS), and *L. goodei* (mean difference +1.23 BLS) when compared to adults. These differences were minor for *H. formosa* (mean difference -0.18 BLS), *J. floridae* (mean difference +0.01 BLS), and *P. latipinna* (mean difference -0.53 BLS). Despite inter- and intraspecific differences in U_{CRIT} , U_{CRIT} was not correlated with stage-specific arrival order ($r = -0.14$, $p = 0.66$).

Discussion

We found that interspecific variation in order of post-drought recolonization was highly repeatable and that intraspecific order varied among species. Juveniles tended to appear in our samples before adults in three species, while adults appeared before juveniles in two, and one species displayed no pattern. These patterns were influenced by the number of days since a site became inundated and not by the severity of the drying event (measured by the length of time marsh was dried) or by the timing of reflooding (Julian date of reflood). Rapidly recovering species were also species with juveniles appearing first and at relatively

high density, while late recovering species had adults appearing first and initially at relatively low density. In several species, adult females appeared prior to adult males following inundation. Although we found repeatable patterns of colonization, U_{CRIT} was a poor metric for predicting the patterns. This trait-based approach did reveal both inter- and intraspecific differences in U_{CRIT} across all six species of the study. U_{CRIT} increased monotonically in all species (never asymptotically), but adults were not always the first to appear, and species with large adult size were not necessarily earlier to re-colonize than smaller species. The smallest species in the study (*H. formosa*) revealed the highest size-adjusted U_{CRIT} but was not a rapid colonizing species. Size-adjusted U_{CRIT} decreased with size in three species, including two with early juvenile recolonization, suggesting greater swimming effort in juveniles than in adults.

Recovery of species following large-scale disturbances has been linked to reproductive strategies (Ensign et al. 1997). These include reproductive phenology, size at reproduction, and specialization of spawning habitats (Detenbeck et al. 1992). This study revealed interspecific variation in stage-specific patterns that were indicative of early versus later arriving species and may contribute to the successful recovery of these species. Juveniles of early-arriving species (*J. floridae*, *G. holbrooki*, and *F. chrysotus*) were dependably among the first to arrive, and adults of later-arriving species tended to arrive prior to or together with juveniles. Intraspecific differences in arrival order have been shown to influence levels of both intra- and interspecific competition for late colonizing individuals (Dibble and Rudolf 2016) and top-down effects more generally (Spiller et al. 2018). Early colonization of juveniles may allow them to take advantage of early feeding opportunities, possibly reducing competition, and a refuge from predation by adults of the same or other species. Mesocosm experiments have demonstrated that *G. holbrooki* aggressively feed on juveniles of their own and other species (Taylor et al. 2001), suggesting that rapid juvenile recolonization could create trade-offs between adult and juvenile recruitment.

We originally hypothesized that local reproduction could not adequately explain colonization dynamics, but stage-specific and sex-specific differences in arrival order may have been influenced by differences in reproductive strategies. Using an earlier

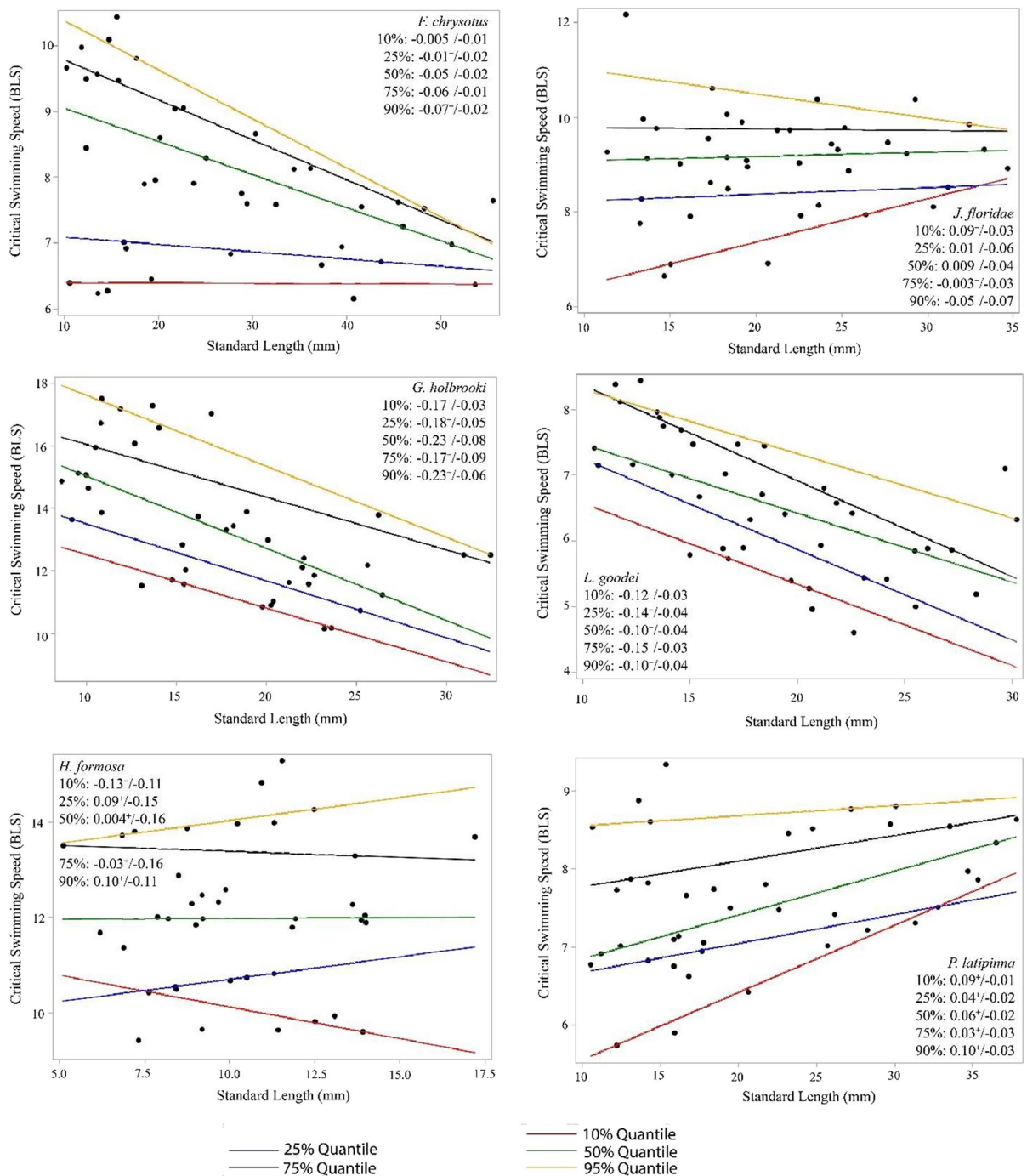


Fig. 5 Scatterplots for the relationship between standard length (SL) and size-adjusted critical swimming speed (U_{CRIT}). Lines indicate 10%, 25%, 50%, 75%, and 90% quantile regressions. Estimates for the slope at each quantile (+/- SE) are provided

version of our dataset, Ruetz et al. (2005) observed that *G. holbrooki* appeared to re-populate sites after a drying event faster than the time between sampling

events (2–3 months) and identified evidence for local reproduction (Ruetz et al. 2005). Based on size and known age-size relationships (Haake and Dean 1983;

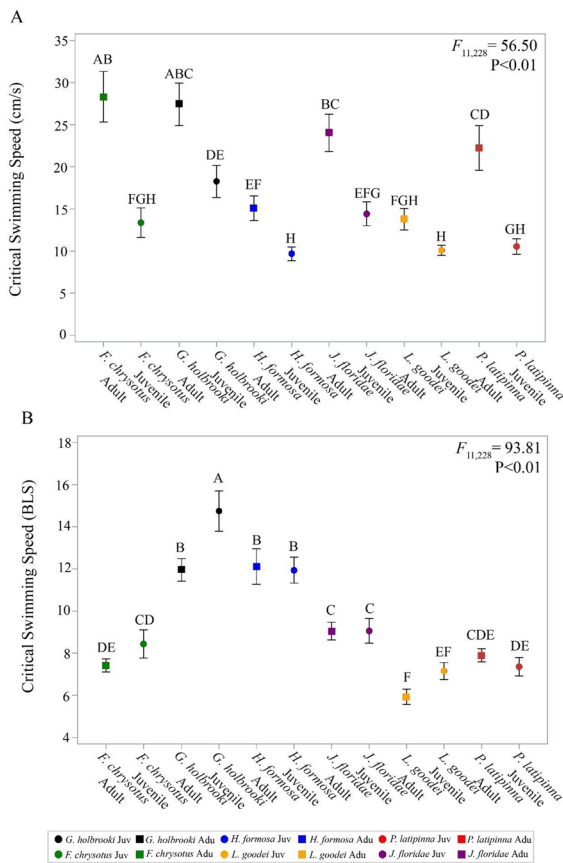


Fig. 6 Results from our ANOVA's using Tukey's pairwise comparisons for **A** absolute speed (cm/s) and **B** size-adjusted speed (BLS). Matching letters indicate groups are not significantly different

Gatto et al. 2021), the early arriving juveniles in our study were almost always born after the date of marsh reflooding at the site where they were collected. In addition, the DSD following reflood for the first arrival of an individual averaged 174 ± 9.41 days (but was as early as 10 days at shorter hydroperiods) leaving ample time for pregnant females of *G. holbrooki*, a viviparous species, to colonize the marsh and release young. Eggs of *J. floridae* are known to hatch within 4–6 days after spawning (St. Mary et al. 2004), which could also allow time for low-density adults to colonize a site, spawn, and produce the juveniles at high enough densities to be consistently caught in the first samples following reflooding of our study sites. Oviparous *J. floridae* and *F. chrysotus* are in families (Cyprinodontidae and Fundulidae) that include species known to produce eggs capable of

surviving terrestrial incubation and delaying hatching for weeks to months (Harrington 1959; Loftus and Kushlan 1987). More work is needed to determine if these species lay eggs before the drought capable of hatching upon re-flooding (Furness 2015). Although we were unable to rule out local reproduction driving early arrival of juveniles of some species, factors that influence rapid colonization likely contribute to the relative success of early arriving species.

The observed arrival order was inversely correlated with density at the time of arrival, which could arise by density-related detection probability if a low density of females colonize to rapidly produce a pulse of young. The relatively high density of early arriving juveniles could result from high reproductive success of relatively rare early-arriving females or by directed movement into newly flooded habitats by young swimming-competent (post-larval) fish. Parkos et al. (2019) reported that the probability of detecting some of these species dropped rapidly when using throw traps, and their density was below 0.4 individuals/m², a density similar to most of the adults caught at first arrival in this study. Thus, juveniles may have been produced by early-arriving adults too rare to be detected in our samples. This is a likely scenario because Goss et al. (2014) and Loftus (unpublished data) caught adults of all of our study species within several days of reflooding using passive sampling gear in shorter hydroperiod Everglades wetlands than those of this study. The earliest colonizers in this study, *G. holbrooki* and *J. floridae*, were also the first species to recolonize and most active species following reflooding (Goss et al. 2014).

Several studies have suggested that larger species move faster than smaller ones, but smaller species tend to move faster relative to their body size (Clark et al. 2005; Faria et al. 2009). These studies also suggest that earlier life stages swim faster relative to their body size, which decreases with ontogeny (Bellwood and Fisher 2001). Interspecific variation in U_{CRIT} unadjusted for size revealed that species with larger terminal size swim faster than smaller ones. Both *H. formosa* and *L. goodei* were among the slowest and smallest species in the study. Our results also indicated that adults of each species achieve higher absolute speeds, which increased with body size. This study indicated that juvenile *G. holbrooki*, *L. goodei*, and *F. chrysotus* had higher estimates of U_{CRIT} relative to their body size compared to adults. Also, the

inter-individual variance in $U_{\text{CRIT}}/\text{BLS}$ was greater for small specimens than larger ones in three species. The latter could be from handling effects of small fish in the experimental setting, but we took care in handling all fish and the species showing this pattern are generally robust in the laboratory. Our results may be limited by exclusion of larval and neonate size classes, whose swimming behavior may not be predictable from the data we gathered on life stages after development of fins and swimming-related physiology (Blaxter 1986; Kunz-Ramsay 2013). Only individuals > 10 mm (except *H. formosa*) were included in this study because of limitations from the swim tunnel, which could only generate a minimum flow speed of 2 cm/s. There is conflicting evidence that swimming performance is influenced by both the increments of flow velocity and timing (Jones 1971; Farlinger and Beamish 1977). The swimming performance of smaller individuals may have been underestimated because some individuals were acclimated to flow velocities > 2 BLS. However, only a few individuals experienced these increased acclimation speeds ($< 10\%$ of individuals for the species where this was a concern), and those individuals were not outliers in our analyses. Therefore, we do not believe that this impacted our results linking swimming performance to colonization. Since swimming ability develops with ontogeny, we believed that larvae/neonates of all species would have low colonization potential until the juvenile life stage. Furthermore, flow velocity is generally low (< 3 cm/s) in the Everglades (Larsen et al. 2011), and dispersal potential for larvae/neonates by passive transport may be limited. Wet-season flow pulses prior to anthropogenic modification were greater than experienced today, possibly permitting a role for flow-driven dispersal in the historical ecosystem.

Environmental conditions (temperature and salinity), food availability, and hydrological stress have been shown to influence individual body condition and impact U_{CRIT} (Brett and Glass 1973; Abujanra et al. 2009; Casini et al. 2016). Individuals in our study were collected at long hydroperiod sites during the wet season and may explain why arrival time was not correlated with U_{CRIT} . Since individual growth and body condition have been linked to hydrological stress, it is possible that our estimates of U_{CRIT} are skewed to individuals living in less stressful environments (longer hydroperiods). Juveniles that were

born/hatched at shorter hydroperiods experience reduced growth, poorer body condition, and lower U_{CRIT} when compared to juveniles born/hatched in less stressful environments. However, Gatto et al. (2021) collected individuals from short, intermediate, and long hydroperiod within the same study sites and determined that length-mass relationships and species growth curves were not influenced by hydrological stress. Individuals in that study were collected in October (peak of wet season) under stable water conditions. Colonization of habitats post-inundation would generally occur at the beginning of the wet season (April–July), with individuals experiencing different growth conditions compared to those later in the wet season. Droughts have also been shown to increase the extremes in water quality (Magoulick and Kobza 2003). Spatial–temporal differences in water quality in refuge habitats may contribute to differences in body condition across the landscape. Further information is needed on how hydrological stress impacts body condition, growth, and U_{CRIT} for pre- and post-colonization juveniles and adults.

Theory describes tradeoffs between life-history traits, such as reproduction, size at maturity, and traits related to dispersal, when describing coexistence of species in non-equilibrium communities (Chesson 2000). Tradeoffs of swimming performance, reproductive allocation, and predation risk are known for Trinidadian guppies (*Poecilia reticulata*) (Banet et al. 2016). We observed tradeoffs between adult size, absolute U_{CRIT} , and size-adjusted swimming speed. *F. chrysotus* had high estimates of U_{CRIT} when considering absolute U_{CRIT} , and their adults were among the fastest swimmers in this study. However, size-adjusted U_{CRIT} revealed that this species as among the slowest assayed, possibly reflecting a relatively low energetic investment in locomotion, though analysis of swimming efficiency would be needed to confirm this (Svendsen et al. 2013). Absolute speed determined that *H. formosa* was among the slowest species and had weak colonization potential, but its size-adjusted speed determined it to be among the fastest (comparable to *G. holbrooki*). *F. chrysotus* consistently arrived early and had high U_{CRIT} , reached sexual maturity late (20 mm, ~60–70 days), and had a relatively large body size (≤ 70 mm), but persists at relatively low densities compared to other study species. In contrast, *H. formosa* was late to colonize and displayed relatively low estimates of U_{CRIT} . It achieves

some of the highest densities in this assemblage and has a small body size (≤ 25 mm) and fast maturation (10 mm, ~40–50 days). Although *H. formosa* can swim fast relative to its body size, the smaller terminal size greatly reduces its overall absolute speed. Poor colonization potential, low U_{CRIT} , and faster maturation are also indicative to *L. goodei*. A species may tradeoff absolute U_{CRIT} (rapid colonization) for the advantages of earlier maturation. Smaller species must also exert more energy to cover more distance than larger species. For poorly dispersing species (*H. formosa*, *L. goodei*, and *P. latipinna*), colonization of juveniles was later than that of adults. This may be a result of generally low estimates of U_{CRIT} for these species and the restrictive nature of body size in absolute U_{CRIT} . However, our results indicate that U_{CRIT} alone was insufficient in understanding colonization patterns.

We observed inter- and intraspecific differences in colonization potential at all study sites throughout the 20-year time series. Stage-specific patterns were observed, indicating intraspecific variation in colonization potential; juveniles often arrived prior to adults for three of the six species. Size-biased collection efficiency constrains our ability to document early recruitment of juveniles relative to adults, making these results striking (Gatto and Trexler 2019). Sex-specific arrival probabilities also contributed to intraspecific variation in arrival post-inundation, with females preceding males in all species when adults were present. Absolute U_{CRIT} increased with increasing body size; however, variation in U_{CRIT} failed to explain species-specific or stage-specific arrival orders. This may have been caused by a few factors that were not evaluated in the present study. Colonization is dependent on the regional source pool of species (Butaye et al. 2002; Stoll et al. 2014). These species coexist in the regional pool of species, but their regional abundance and age frequency may vary in drought refuges over time. Also, environmental conditions at refuge habitats may vary both spatially and temporally. Individuals born in, or exposed to, stressful environmental conditions (drying) may exhibit lower body condition, which can impact U_{CRIT} . Finally, interspecific variation in arrival order has been linked to two traits, speed and directedness, and directedness had a much greater impact on determining arrival order than speed (Gatto and Trexler 2020). Both inter- and intraspecific variation in latency time (boldness) have also been shown

to influence dispersal behavior of these species (Hoch et al. 2019). The scope of this study was limited to evaluating one trait (speed) because we do not know if directedness varies with stage or sex in any of the study species. Further studies are needed to determine if stage-specific and sex-specific variation in movement strategies (directed vs non-directed) will improve our interpretation of observed colonization patterns. Trait-based approaches have proven successful in describing ecological phenomena. Movement traits related to stage and sex-specific differences in swimming performance and reproductive traits related to diapause in oviparous species need more attention to understand successional dynamics following disturbance.

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Data availability The datasets generated during and/or analyzed during the current study are available in the Florida Coastal Everglades Long-Term Ecological Research (FCE LTER) repository, <https://fcelter.fiu.edu/data/>.

Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval Vertebrate organisms were euthanized using a solution of MS-222 and ambient marsh water as approved by the FIU Animal Use and Care permits. This work was conducted under multiple FIU Institutional Animal Use and Care permits, including IACUC-16–034 and IACUC-17–035.

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