Environ Biol Fish (2019) 102:595–613
https://doi.org/10.1007/s10641-019-00856-9

Seasonality of fish recruitment in a pulsed floodplain ecosystem: Estimation and hydrological controls

John V. Gatto · **Joel C. Trexler**

Received: 30 May 2018 / Accepted: 18 February 2019 / Published online: 13 March 2019

Abstract Hydrological variation is believed to be the main density-independent factor that controls fish recruitment in floodplain ecosystems. However, our ability to fully understand these controls is greatly impeded by the size-selective nature of sampling gear. To illustrate the benefits of estimating the effects of size-selective bias on population parameters, we used a cohort analysis to reconstruct a 20-year time series of larval/neonate abundance for five species in the Order Cyprinodontiformes along a hydrological gradient in the Florida Everglades. We applied generalized linear models to estimate recruit density and analyze size-selectivity for our sampling gear. The adjusted data resulted in a 7 to 40-fold increase in estimated recruit density, which varied seasonally at regional and local spatial scales and was greatest at the end of the wet season (October, December) for most species; no consistent seasonality in recruitment of any species was apparent in the raw data. Using the adjusted data, we detected a positive relationship between recruit density and recovery time following marsh drying events at short and intermediate-hydroperiod sites for all species. However, depth was the major hydrological driver of recruitment at long-hydroperiod sites. Within sites, we observed interspecific variation in species responses to changes in annual hydroperiod. We suggest that fisheries models can be applied to data from any meshed sampling gear to improve abundance estimates and reveal seasonal recruitment dynamics. Our use of such models revealed seasonal recruitment dynamics that were previously undetected, with implications for planning of restoration and management of the Everglades.

Keywords Cohort analysis · Recruitment · Floodplains · Size bias

Introduction

Fish recruitment may be tightly linked to hydrological cycles in seasonally pulsed freshwater ecosystems (Arthington and Balcombe 2011; Godfrey et al. 2017). Variations in hydrology are predicted to be the major environmental factor that influences fish recruitment in floodplain ecosystems. These are often life-history dependent with the dependence on floods highest for migratory species and lowest for sedentary species with parental care (Agostinho et al. 2004; Winemiller 2004). Furthermore, habitat loss due to hydrological regime modification is believed to be the major source of reduced recruitment in regulated rivers (Aarts et al. 2004). Fish species have adapted to hydrologically dynamic environments by evolved reproductive strategies and life histories that exploit pulses in primary production within newly inundated habitats (King et al. 2003; Zeug and Winemiller 2008; Furness 2015). These adaptations may buffer some species against anthropogenic modification of the hydrological landscape. Understanding the factors that control fish recruitment is crucial to

---

J. V. Gatto (✉) · J. C. Trexler
Department of Biological Sciences, Florida International University, Miami, Florida 33199, USA
e-mail: jgatt006@fiu.edu

determining the influence of hydrological regime on population dynamics in seasonally pulsed systems.

However, our ability to fully understand these controls is often greatly impeded by biased estimates of early life history stages associated with size-selective sampling gear. Differences among gear type have impeded quantification of age and size-structured processes in fisheries (Ghulam Kibria and Ahmed 2005). For example, several studies have shown that mesh size and shape severely impact the quantity and composition of the total catch, often selecting for larger individuals (Rudstam et al. 1984; MacLennan 1992; Millar and Fryer 1999). Organism morphology (length, width, and height) can be used to understand the magnitude of selection associated with equipment type and use (Reis and Pawson 1999; Gabr et al. 2007; Bolat et al. 2010). Other sampling methods used to study recruitment also suffer from inherent bias. Sweep net electrofishing (SNE), for example, selectively captures species based on the voltage and mesh size used (King and Crook 2002). Therefore, understanding the size-selective nature of sampling gear is crucial to assure accurate quantitative estimates of key parameters shaping recruitment and evaluate their links to environmental gradients in dynamic ecosystems.

Cohort analyses have become a popular method to reconstruct fish populations and indirectly estimate recruitment (Cadrin and Vaughan 1997; Porch et al. 2001). Two types of cohort analyses have been developed for fisheries stock assessment, the backward projection model [e.g., Virtual Population Analysis (VPA)] and forward projection model (e.g., Statistical Catch-at-Age Analysis (SCAA)). Backward projection models follow adult cohorts backward through time to estimate the abundance of younger fish and have become a useful tool in estimating the abundance of larval and juvenile recruits (Livingston and Jurado-Molina 2000; Coggins et al. 2006). Estimates of fishing and natural mortality obtained from both fisheries-dependent and -independent data are used to estimate the historical recruitment that would support the current population. Although these methods do not directly estimate recruitment, these cohort analyses are useful in estimating current and future stocks of commercially exploited species.

Though widely adopted in stock assessment protocols and management practices (Lassen and Medley 2001; Jurado-Molina et al. 2016), cohort analyses have not been applied to support field studies of fish recruitment using meshed sampling gear. This technique has the potential to improve biomass estimates and our understanding of recruitment dynamics in any ecosystem. Currently, little is known about the impact of size-selective bias on our understanding of seasonal recruitment dynamics for small fish species inhabiting floodplains and wetlands. In this paper, we illustrate the use of a backwards projection cohort analysis in a study of fish population dynamics from a seasonally pulsed floodplain wetland. The Florida Everglades is an excellent system to explore the effects of hydrology on fish recruitment because it supports a diverse gradient of hydrological disturbance (short to long hydroperiods). In this paper, we demonstrate how to correct density estimates derived from meshed sampling gear in a long-term dataset and improve our understanding of recruitment dynamics of fishes in hydrologically pulsed wetlands. This information can improve our understanding of links between hydrological modification of ecosystems and recruitment, and ultimately fish population dynamics, to improve restoration approaches following anthroprogenic modification of rivers and floodplains by providing more accurate information on recruit abundance and temporal patterns of recruitment along environmental gradients.

Materials and methods

Study sites and species

Between 1996 and 2016, fish were collected using a 1-m^2, 2-mm mesh, throw trap using a standard protocol (Jordan et al. 1997) at 21 monitoring sites in the Everglades, Florida, U. S. A. These sites were distributed in Shark River Slough (SRS), Taylor Slough (TSL), and Water Conservation Areas (WCA) 3A and 3B (Fig. 1). Samples were collected in five months of each year (July, October, December, February, and April), with water-year sampling starting in July (early in South Florida wet season) and ending in April of the following year (late in South Florida dry season, Fig. 2). Three or five plots were selected at each site, and five (WCA 3A and 3B) or seven (SRS, TSL) throw-trap samples were collected within a plot. Sites located in WCA 3A and 3B yielded 75 samples per year (three plots x five throws x five sample events), while sites in SRS and TSL yielded 105 samples per water-year (three plots x seven throws per plot x five sample events); in dry years requiring helicopter access, five throws were taken per plot. The location of each throw within each plot was determined using a random number table. Plot sizes varied from 10,000 m^2 (100 m × 100 m) to 2100 m^2 (70 m × 30 m), depending on surrounding vegetation and availability of sampleable habitat (Trexler et al. 2002; Trexler et al. 2003). After securing the trap, floating mat volume (submerged aquatic vascular plants, periphyton, etc.), water depth, and emergent plant stem counts (by species) were recorded before fish and macroinvertebrates were removed following a standardized protocol of sweeps with a bar seine and dip nets (Jordan et al. 1997). We used data from the Everglades Depth Estimation Network (EDEN) to provide stage data for each site that were used to estimate days since a site was last dry prior to sampling (DSD), number of days the site was inundated greater than 5 cm in the preceding 365, and depth at the time of sampling (Telis 2006; Liu et al. 2009). Long-term monitoring at these sites from July 1996, to April 2016, (20 water years) yielding over 20,000 community samples with over 400,000 fish and invertebrates. There is no evidence of visitor impact on these long-term study sites, possibly because randomization makes revisiting same sampling points unlikely, marsh plants re-grow quickly, and periodic marsh drying overwhelms sampler impacts on vegetation and soil (Wolski et al. 2004).

To assure adequate sample sizes for this study, only the six most common fish species were used. These species were Bluefin Killifish *Lucania goodei,* Least Killifish *Heterandria formosa*, Flagfish *Jordanella floridae,* Sailfin Molly *Poecilia latipinna*, Eastern Mosquitofish *Gambusia holbrooki*, and Golden Topminnow *Fundulus chrysotus*. Age estimates from otolith analyses suggest that the typical lifespan of these species is much less than one year in the Everglades (Haake and Dean 1983; Konnert 2002). The age at sexual maturity for these species is between 30 and 90 days, less than or similar to the time between sequential samples. Thus, the 100 sequential samples in this study (20 years x five samples per year) represent between 34 and 51 generations for each species.

Recruitment is the process of new individuals entering an existing population, which for fisheries is often the exploitable stock (Blackhart et al. 2006). In practice, fisheries scientists have used a variety of working definitions of recruitment and recruits to facilitate study (Miller and Kendall 2009), often focusing on the life history transition from larva to juvenile that may be accompanied by a transition of habitat-use or 'settlement' (Kaufman et al. 1992). This study includes species with (Fundulidae: Golden Topminnows, Bluefin Killifish; Cyprinodontidae: Flagfish) and without (Poeciliidae: Eastern Mosquitofish, Least Killifish, Sailfin Molly) a larval stage, complicating use of a developmentally-based recruitment criterion. Therefore, we define recruits as any individual below the size of sexual maturation (Table 1; cf. Anderson 1988). Thus, age (days since hatching or parturition) of fishes considered to be recruits in this study would be from hatch/birth up to 60–163 days depending on the species.

Population-based models

We used age-structured models to estimate population growth. Horizontal life tables for each species suggested senescing populations because of low density of early age/size classes, though long-term observation indicated that the populations were persistent over time and space (unpublished data). A graphical representation of survivorship curves produced an inverse parabola, with an inflection point near the size of maturation for each species (~15–18 mm). We assumed that individuals at lengths to the left of the inflection point were under-represented by our sampling gear. In all cases where multiple inflection points were noted, the inflection point representing the shortest length was selected as the minimum size collected efficiently. These multiple inflection points were noted at all study sites for each of the species, suggesting that movement (e.g., immigration, emigration) of early life stages, could not alone explain their absence. We hypothesized that the missing early age classes resulted from un-sampled juvenile fishes. Accordingly, we used model-based projections of survivorship curves to estimate their abundance and evaluate this hypothesis.

We applied a generalized linear model to the adult cohorts within the abundance-at-age data for each species. This equation linearized the discrete-time model:

$$N_t = N_0^{-Mt} \tag{1}$$

where N_t is the population size at time *t*, N_0 is the initial population size, and *M* is the instantaneous mortality rate [proportion of individuals which recruit to next size class (individuals mm^{-1})]. Several assumptions about the population structure for each species were necessary

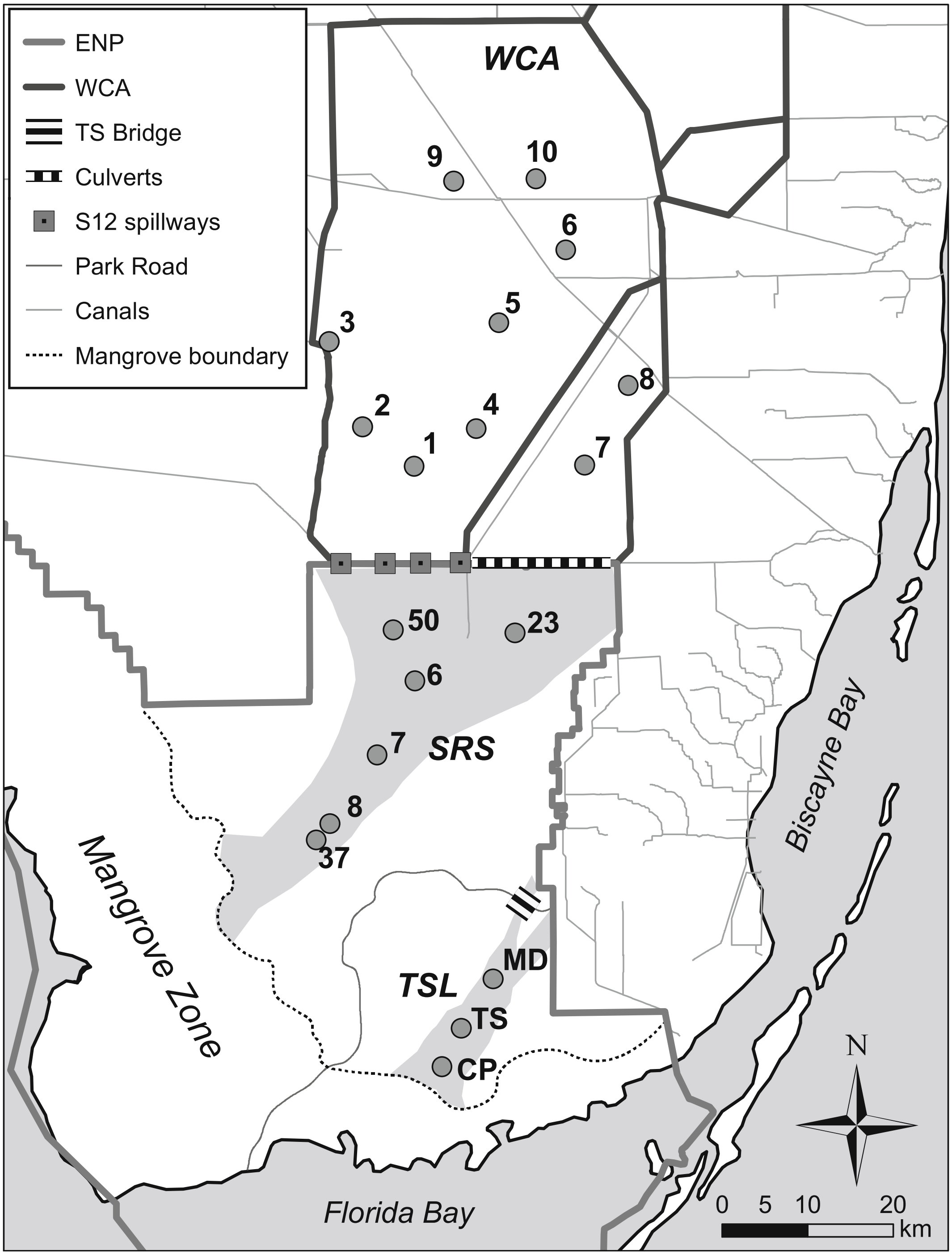

Fig. 1 Map of the sites in this study

to apply this model (Table 1). We fit a negative binomial error distribution because the response variable (cohort density) was estimated as integers (counts). To account for the annual lifespan of these species (<300 days), every water-year was treated separately by producing a single model for each site by water-year (July–April), creating a maximum of 420 (21 sites × 20 water-years) cohort models for each species. Following model approximation, we tested their fit by comparing the observed abundance and the model-predicted values using

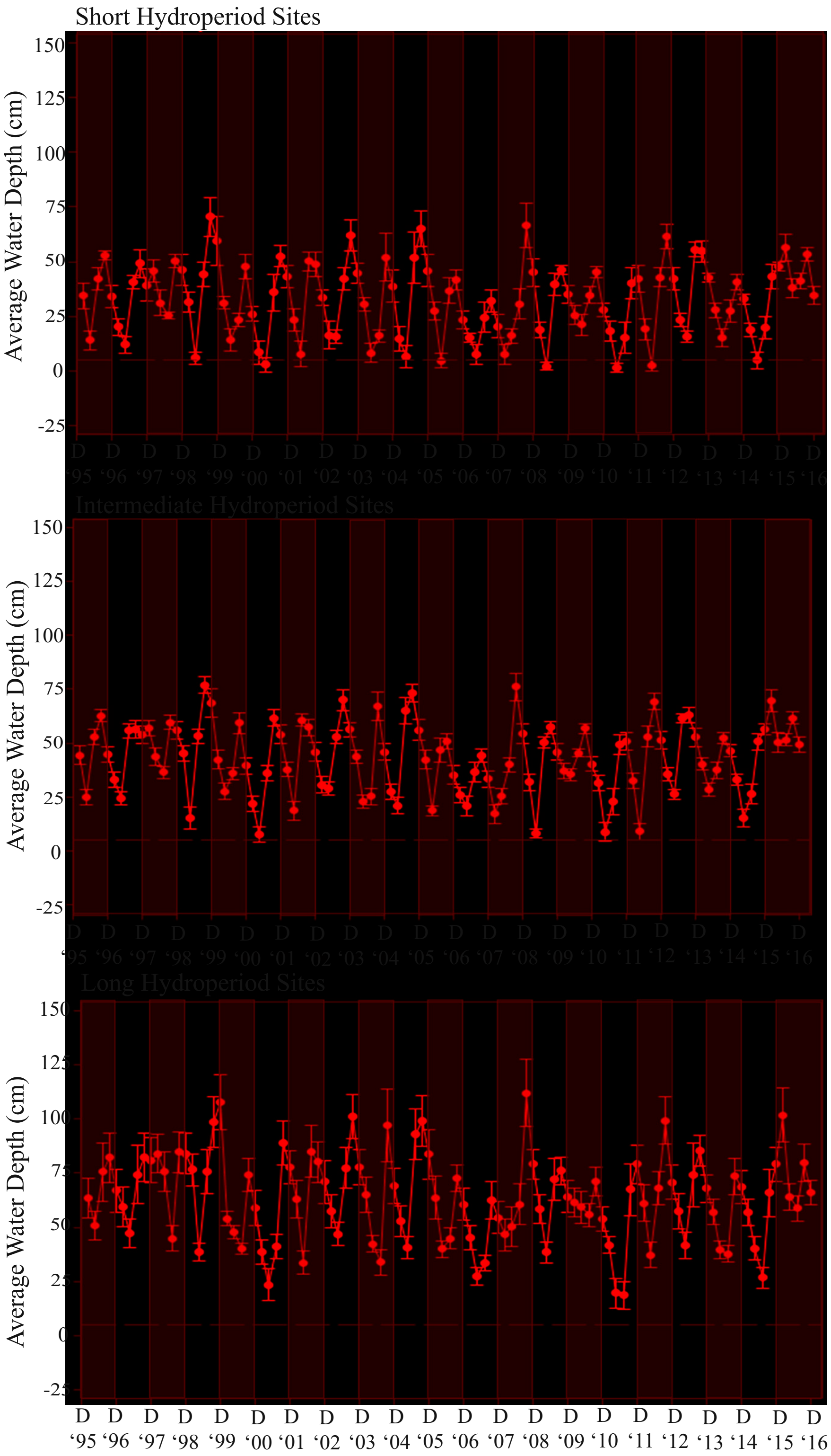

Fig. 2 Mean water depth with 95% confidence interval at each sample event averaged across all sites within the hydroperiod classification (Long, Intermediate, and Short hydroperiods). Values underneath the dashed reference line (5 cm) are considered too dry for fish species. Vertical bars enclose one year of samples (5 samples per year) from February to December (D)

Table 1 Assumptions made for the generalized linear models on the abundance-at-age data. Age and size at maturation is for females in species with sexual dimorphism

Topic	Assumption	Justification
Immigration/Emigration	Closed populations; No emigration or immigration across sites	Sites spatially isolated; located >15 km from each other
Population Structure	Populations exhibit age structured growth	Life tables reveal stable age structure of adults; Sample bias possible for smaller individuals
Population growth rate	Population is in stable equilibrium; neither increasing or decreasing in size	Tests on density dependence reveals intrinsic rate of growth~0
Size at birth/hatch	Eastern Mosquitofish (<7 mm) and Sailfin Molly (<9 mm) Golden Topminnow (<7 mm) and Bluefin Killifish (<6 mm) Least Killifish (<6 mm) Flagfish (<6 mm)	(Ala-Honkola et al. 2011; Beyger et al. 2012; Conrow and Zale 1985; Nordlie 2000)
Age/Size at Maturation	Eastern Mosquitofish (17 mm, ~84 days) Bluefin Killifish (18 mm, ~71 days) Sailfin Molly (18 mm, ~112 days) Least Killifish (10 mm, ~65 days) Golden Topminnow (22 mm, ~54 days) Flagfish (20 mm, ~164 days)	
Mortality	$Z = M$	Throw trap removal of species (fishing mortality F) is negligible

ordinary least-squares regression. We then calculated the number of individuals that were missing in our data by comparing the model predicted values to the observed abundance for each length class and converted it into a density (β) as follows:

$$\beta = \sum_{0}^{l} \frac{N_{est} - N_{obs}}{n} \tag{2}$$

where l is length class (in 1 mm increments), l_0 is the length at birth/hatch, N_{est} is the model predicted value, N_{obs} is the observed count per cohort, and n is the number of samples collected.

Estimating size-selectivity curves

Following the estimation of abundance per cohort, we then estimated size-selectivity of the sampling gear for each species. First, we estimated the probability of catching a fish based on its size by:

$$\hat{P}_{catch} = \frac{N_{obs}}{N_{est}} \tag{3}$$

where N_{obs} is the observed count per cohort and N_{est} is the model-predicted value. We then fit a nonlinear model using non-linear least squares (NLS) to our probability estimates using the size-selectivity equation:

$$P_{catch} = \frac{1}{1 + e^{-r(L - L50)}} \tag{4}$$

where r is a constant that controls the shape of the curve, L is fish standard length, and L_{50} is the length at which the probability of catch is 50% (Millar and Fryer 1999). Each model was run for a maximum of 1000 iterations against the response variable $\hat{P}_{catch}$ to best estimate model parameters r and L_{50}. Following model approximation, we tested the fit of these models by using the same methods as the age-structured models. Once all values of P_{catch} were calculated, we averaged the estimates for all sites and water-years by length class to generate the size-selectivity curve for each species. The final estimates of selectivity were multiplied by 0.63 to account for both the clearing (probability of removal if present, ~0.83) and capture efficiencies (probability of fish escaping before enclosure, ~0.20) derived from previous studies (Jordan et al. 1997). This produced size-selectivity curves that account for the size-selective nature of the throw trap and the clearing efficiency of the sampling methods.

Cohort analysis

Although we estimated spatial differences in neonate/larval abundance, we were ultimately interested in documenting temporal or seasonal patterns of juvenile density. We applied the generalized linear models to our time series to obtain an estimate of the instantaneous mortality rate (M) for every water-year, site, and species. Our estimates of mortality were then applied to a cohort analysis across 21 sites and 20 years for all species except the Sailfin Molly. We considered the data for Sailfin Molly to be too over-dispersed and the species was not abundant enough at each site to provide a robust cohort analysis. The same assumptions were made on population structure for each site (Table 1) and we conducted a backward projection cohort analysis to our catch-at-age data. Further, evidence suggests that our survey has no significant influence on population size (Wolski et al. 2004). This allowed us to set the catch equation of Pope's Approximation (Pope 1972) equal to zero and conducted a length-based cohort analysis based on the following equation:

$$N_{l,t} = N_{l+1,t+t}e^{M} \tag{5}$$

where $N_{l,\mathrm{t}}$ is the number of individuals of length l at time t, and $N_{l+1,\mathrm{t}+1}$ is the number of individuals surveyed of length $l+1$ at time $t+1$.

To account for the rapid life histories of our study species, we conducted our cohort analysis using a seasonal time cycle. Each year was analyzed individually using a six-season time step. The cohort analysis started in February and followed a cohort backward to April of the previous year. This timing was selected based on adult density in the time series and a 12/12 photoperiod corresponding to the onset of the reproductive cycle for these species. We assumed cohort duration to be one water year, permitting creation of a time step between February and April (T = 6) and assumed that all but one individual of the cohort died in that period ($\mathrm{N}_{\mathrm{a},6} = 1$). This satisfies the assumption of backward projection models describing mortality of all individuals within a cohort past a certain time. We then started our backward projection in February with

$$\mathrm{N}_{1,5} = e^{M} \tag{6}$$

where $\mathrm{N}_{1,5}$ is the number of individuals of length l in February (T = 5). To account for 60–90 days between sample periods, we used published age-at-length curves to account for growth between sample periods (Haake and Dean 1983). Our calculations of cohort abundance were projected backward in time to December (T = 4, 60 days), October (T = 3, 60 days), July (T = 2, 90 days), and ended in April (T = 1, 90 days).

Although we originally assumed that these study sites were closed systems, evidence suggests that these sites are not closed (Goss et al. 2013; Hoch et al. 2015). Furthermore, some level of reproduction and recruitment occur year-round for the study species in the Everglades (Haake and Dean 1983). We accounted for both immigration and continual reproduction by using a series of two condition statements in real time:

$$\text{If } \mathrm{N}_{l+1,t+1}e^{\mathrm{M}} > \mathrm{N}_{\mathrm{obs}} \text{ then } \mathrm{N}_{\mathrm{a,t}} = \mathrm{N}_{l+1,t+1}e^{\mathrm{M}} \tag{7}$$

$$\text{If } \mathrm{N}_{l+1,t+1}e^{\mathrm{M}} \le \mathrm{N}_{\mathrm{obs}} \text{ then } \mathrm{N}_{l,t} = \mathrm{N}_{\mathrm{obs}} \tag{8}$$

which compares our calculated values of $\mathrm{N}_{l,t}$ with the observed value in our time series. The larger of the two values was retained for any given length. Finally, we adjusted our estimates based on hydrology data collected from nearby monitoring gauges. Since our initial analysis was conducted independently of hydrology data, dry sites at the time of sampling were originally ignored. We corrected for this by setting all $\mathrm{N}_{\mathrm{a,t}} = 0$ when dry sample-periods were identified (depth < 5 cm, DSD = 0) for all three plots.

Seasonal and hydrological effects

We used a general linear model to examine how recruitment of juveniles for five species varied by season, year, hydrological region, and among sites within regions. The response variable was log-transformed density of recruits (number of fish per sample) estimated by our cohort analysis. Recruit density was calculated for the three plots combined ($n = 15–21$) and was log-transformed to meet the assumptions of normality and homoscedasticity for both the original and reconstructed time series. To determine the effect of hydrology on recruit density, we used hydrological variables derived from EDEN gauges. We calculated the number of days following a major drying event (DSD), a squared DSD term (DSD^2) and water depth at date of sampling. Our linear models used the main effects of season, water-year, site, species, DSD, DSD^2, and depth. To determine if there were changes in seasonality of recruitment between our original and reconstructed time series, we developed a separate series of linear models with the season of peak recruitment as the response variable. This tested the main effects of site, water-year, species, and density type (observed vs estimated).

We used multi-model inference (MMI) based on Information Theory (Akaike Information criterion) to evaluate the effects of hydrological drivers on recruitment (Burnham and Anderson 2004). We considered the variables DSD, DSD^2, depth, and the combination of these variables (with and without intercepts) as linear predictors of log-transformed recruit density. To determine the effect of annual variation of hydroperiod (a metric of annual disturbance intensity), we evaluated whether changes in annual hydroperiod would result in lower or higher maximum recruitment at each study site. Overall recruitment (total number of recruits throughout the year) was also evaluated to determine if changes in annual hydroperiod reflected changes in total recruitment. However, these models were not applied to long-hydroperiod sites because they lacked variability of the independent variables (>360 days annually). We then selected the best model ($\Delta AIC = 0$) and used an Analysis of Covariance (ANCOVA) to test the interaction between species and annual hydroperiod within a site on both annual recruitment and maximum recruit density as individual response variables. Although there were additional models that were equally valid ($\Delta AIC < 3$), we wanted to limit this analysis to a single model and considered the best model ($\Delta AIC = 0$) the most parsimonious explanation of recruitment for our ANCOVA models.

Results

Site descriptions and hydrological context

Hydroperiod ranged from 172 to 366 days at the 21 study sites (Table 2). We classified each site into one of three different disturbance regimes (short, intermediate, and long) based on the number of drying events (depth < 5 cm) each site experienced during the study (20 years). Long-hydroperiod sites experienced zero to three drying events over the 20 water years of the study, four to twelve for intermediate hydroperiods, and > 12 drying events in 20 years for short-hydroperiod sites. All six long-hydroperiod sites were located within WCA (sites 4–8). Three of these sites (WCA 4, 5, and 8) experienced zero or one drying event per plot over the duration of our study. Ten intermediate-hydroperiod and five short-hydroperiod sites were identified, primarily located within SRS and TSL. Both these regions included the most frequently disturbed sites in the study; WCA had only one short-hydroperiod site (WCA 3). Three sites located within SRS and TSL dried annually over the course of the study (TSL MDsh, SRS 37, and SRS 50).

Size-selective nature of throw traps

Observed adult density for each species closely matched model-predicted values and provided a good basis to back-calculate larval/neonate density. On average, our generalized linear models explained >63% of the variation observed for adult density. Model fit was weakest for the Bluefin Killifish (Mean $R^2 = 0.63 \pm 0.01$) and strongest for the Least Killifish (Mean $R^2 = 0.95 \pm 0.004$). We observed no significant lack-of-fit for >75% of all site, water year, and species combinations. Our analyses revealed that the number of larvae and juveniles (<7 mm to ~15 mm for all species) captured was low compared to model-predicted values (observed was <10% of predicted) across all sites and water years. Unlike juveniles, the model predictions for adults (individuals >18 mm SL except for Least Killifish) were well-matched to observed values (observed abundance was >80% of predicted) with little spatial-temporal variability in predictability. Therefore, selectivity was generally high (>80% theoretical selectivity) at size of maturation for five of the six species (Table 1) due to strong model fit of the estimated adult densities prior to accounting for clearing and enclosure efficiency for four of the six species (Fig. 3). These models achieved 100% theoretical selectivity for five of the six species (>20 mm SL for Eastern Mosquitofish, Bluefin Killifish, >25 mm SL for Flagfish, and > 30 mm SL for Sailfin Molly). Although the Least Killifish achieved 100% selectivity for mature individuals >14 mm SL, selectivity was generally low (<40%) for both juveniles and small

Table 2 Summary statistics of hydrological variables throughout the 20 years of the study by sites located in Shark River Slough, Taylor Slough, and Water Conservation Area at the date of sampling

Region	Site	Average Annual Minimum Depth (cm)	Average Annual Maximum Depth (cm)	Mean Hydroperiod (Days)	Number of Drying Events
SRS	06	26.29 (2.80)	73.84 (2.19)	356.77 (4.14)	3 (A), 3 (B), 8 (C)
SRS	07	19.24 (2.76)	62.61 (2.21)	348.73 (5.01)	11 (A), 11 (B), 12 (C)
SRS	08	16.30 (2.60)	61.32 (2.36)	331.22 (7.75)	13 (A), 11 (B), 13 (C)
SRS	23	15.00 (2.71)	59.66 (2.12)	322.60 (11.00)	7 (A), 11 (B), 7 (C)
SRS	37	9.54 (2.07)	54.25 (2.61)	316.68 (9.64)	17 (A), 18 (B), 16 (C)
SRS	50	7.29 (1.94)	54.04 (2.87)	299.50 (9.54)	17 (A), 17 (B), 17 (C)
TSL	CP	19.81 (2.72)	62.19 (1.53)	343.21 (7.75)	9 (A), 9 (B), 12 (C)
TSL	MD	20.76 (3.25)	62.49 (1.68)	344.81 (4.77)	13 (A), 13 (B), 13 (C)
TSL	MDsh	4.26 (1.79)	42.00 (1.61)	263.77 (10.14)	18 (B), 19 (E)
TSL	TS	16.98 (2.52)	54.10 (1.45)	341.32 (6.37)	13 (A), 13 (B), 13 (C)
TSL	TSsh	12.53 (2.46)	47.05 (1.51)	332.00 (6.83)	14 (D), 16 (E)
WCA	01	41.00 (2.34)	89.80 (3.55)	362.63 (1.73)	1 (A), 1 (B), 1 (C)
WCA	02	30.08 (3.13)	79.29 (3.31)	354.95 (4.94)	5 (A), 5 (B), 5 (C)
WCA	03	14.73 (2.70)	60.58 (3.19)	319.63 (10.10)	15 (A), 14 (B), 14 (C)
WCA	04	51.51 (2.71)	103.77 (3.81)	365	0 (A), 0 (B), 0 (C)
WCA	05	41.01 (3.13)	95.37 (3.99)	365	0 (A), 0 (B), 0 (C)
WCA	06	42.93 (4.11)	109.14 (4.59)	361.75 (2.59)	2 (A), 2 (B), 3 (C)
WCA	07	24.57 (2.74)	60.27 (2.24)	353.55 (5.82)	4 (A), 3 (B), 3 (C)
WCA	08	24.57 (2.35)	61.83 (2.36)	359.18 (4.30)	0 (A), 1 (B), 2 (C)
WCA	09	16.14 (2.59)	60.18 (3.40)	333.95 (8.41)	10 (A), 10 (B), 10 (C)
WCA	10	10.80 (2.20)	65.76 (4.13)	308.32 (12.00)	13 (A), 13 (B), 13 (C)

Under Number of Drying Events, parentheses indicate individual plots

adults at and above the size of maturation (<=11 mm SL). In contrast to the other species, capture efficiency was lowest for the Golden Topminnow and only achieved 95% selectivity (>80% for mature adults >22 mm SL).

Cohort analysis

Prior to cohort analysis to correct for size-biased sampling, our data did not reveal seasonal recruitment that was consistent among years for any species. However, after cohort analyses, peaks of recruitment were present on a consistent seasonal pattern at 15 of our 21 study sites and for four of the five species. This noticeable change in estimated recruitment was clearest at short-hydroperiod sites and occurred at all five short-hydroperiod sites. Unlike short-hydroperiod sites, accounting for under-sampling juveniles revealed seasonal recruitment for 70% and 50% of intermediate and long-hydroperiod sites respectively. Seasonal dynamics of recruitment seem most prominent at short hydroperiod sites and disappear as the environment becomes more stable. Long-hydroperiod sites experience annual peaks in recruitment; however, the timing of these peaks varied from year to year and failed to occur on a consistent seasonal basis.

On average, estimated recruitment was seven to 40-fold greater in our corrected data than in the raw data at times of highest recruitment; however, this difference was negligible at times of little to no recruitment. Though the mean relative difference was great, the absolute increases in recruit density attributable to corrections were often modest; large differences between the corrected and uncorrected data were most prevalent for Least Killifish. We attribute this to the small body size of both adults and juveniles, which resulted in larger under-sampling of both age classes. Further, higher mortality rates (steeper slope) were estimated for this species when compared to the other four analyzed (Table 3). Our cohort analysis added more recruits for

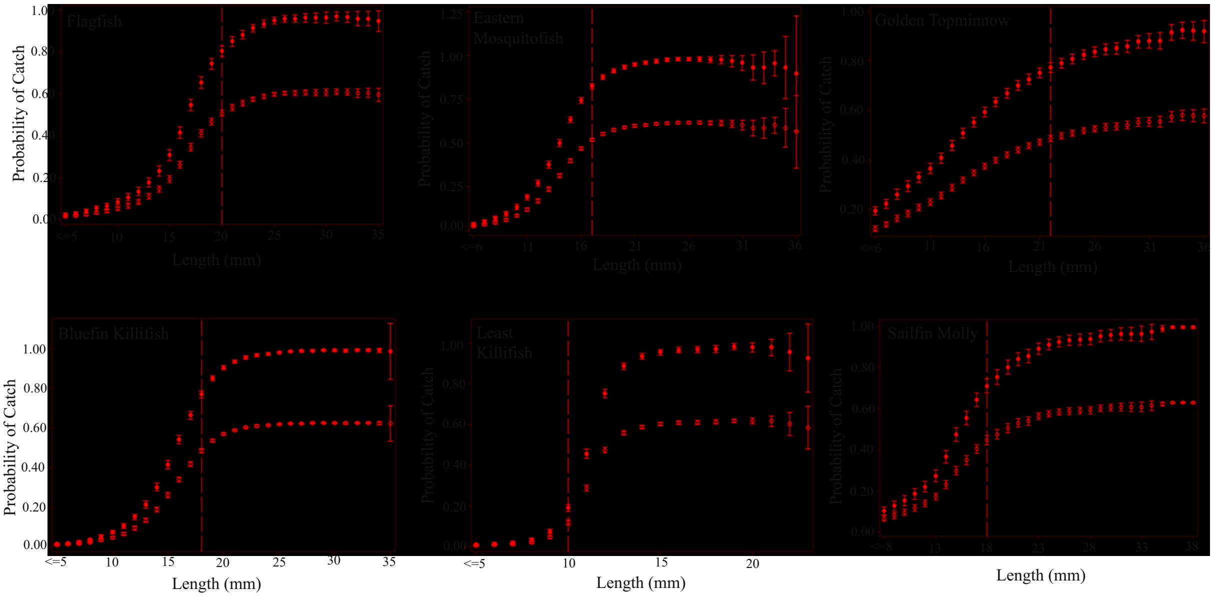

Fig. 3 The unadjusted (filled circles) and adjusted (open circles) size-selectivity curves for each study species in 1-mm increments. The dashed line indicates the size of maturation for that species

the Least Killifish since observed recruitment was significantly lower to support estimates of population size at N_{t+1} than for all other species.

Our analyses detected interspecific variation in the timing of recruitment along a hydrological gradient. We found that October through December were the primary months for peak recruitment of Bluefin Killifish, Eastern Mosquitofish, and Least Killifish (Fig. 4 a-c). In contrast, July through October had peak recruitment for Flagfish and December through February for Golden Topminnows (Fig. 4 d-e). Most seasonal shifts predicted by our models were directed toward a later sample period (e. g., July to October, October to December), with few changes to earlier sample periods (e. g., October to July). On average, peak recruitment occurred 1–3 months later in the water year than observed in the raw data, shifting the estimated time from the dry to wet season in some cases. Flagfish displayed the largest change in the timing of estimated recruitment, with peak recruitment approximately seven months later than observed in the raw data (in July rather than February). This shifts the Flagfish peak from early wet season to early dry season and was consistent across hydroperiods. Our analyses also revealed a three-month change from early in the dry season (February) to late in the dry season (April) at some sites for Flagfish. Dry-season recruitment was indicative for the Golden Topminnow in both our cohort analysis and our unadjusted data. Overall, the Least Killifish, Bluefin Killifish, Flagfish and Eastern Mosquitofish were recruiting during the peak of the wet season; whereas, the Golden Topminnow recruits during the transition period between the wet and dry seasons at intermediate and short hydroperiods.

Using the model-estimated density data, we found that hydrological differences among sites played an important role in fish recruitment. Recruitment varied among regions, sites within regions, seasons, years, and species ($F_{47,\ 10,499} = 158.49$; $p < 0.001$). Inter-season variation was primarily driven by fluctuations in water depth and proximity to a drying event at short and intermediate hydroperiod sites. Partial residual plots revealed that recruit abundance increased parabolically as a function of DSD and water depth at short and intermediate hydroperiod sites for all species (e.g., Bluefin Killifish, Fig. 5). MMI included DSD (>66% of sites on average) and DSD^2 (>63% of sites on average) as predictors of recruit density for both short and intermediate hydroperiod sites ($\Delta AIC < 3$). This suggests that recruitment at both short and intermediate hydroperiod sites increased rapidly following re-inundation of a habitat, but declined over time. Further, MMI included depth as an important predictor of recruitment for the majority of our models regardless of hydroperiod (>88% on average). This occurred most commonly for models that described recruitment at long-hydroperiod sites (>85% for all species at long

Table 3 Mean (± SE) slope parameter estimate over the 20-year time series by site and species

Estimated mean instantaneous mortality rates (*Z*)

Region	Site	Golden Topminnow	Eastern Mosquitofish	Flagfish	Least Killifish	Bluefin Killifish
SRS	06	0.12 (0.01)	0.37 (0.04)	0.27 (0.03)	0.74 (0.03)	0.33 (0.02)
SRS	07	0.11 (0.01)	0.27 (0.02)	0.24 (0.02)	0.67 (0.04)	0.29 (0.02)
SRS	08	0.11 (0.01)	0.31 (0.01)	0.30 (0.03)	0.62 (0.05)	0.30 (0.02)
SRS	23	0.14 (0.02)	0.31 (0.02)	0.33 (0.06)	0.60 (0.05)	0.34 (0.02)
SRS	37	0.09 (<0.01)	0.26 (0.02)	0.27 (0.02)	0.63 (0.02)	0.24 (0.02)
SRS	50	0.18 (0.03)	0.26 (0.02)	0.42 (0.06)	0.52 (0.05)	0.25 (0.03)
TSL	CP	0.14 (0.02)	0.19 (0.02)	0.42 (0.05)	0.52 (0.05)	0.28 (0.02)
TSL	MD	0.11 (0.01)	0.25 (0.02)	0.35 (0.02)	0.56 (0.05)	0.26 (0.02)
TSL	MDsh	0.10 (0.01)	0.26 (0.03)	0.21 (0.03)	0.48 (0.06)	0.25 (0.02)
TSL	TS	0.11 (0.01)	0.25 (0.02)	0.37 (0.05)	0.54 (0.06)	0.25 (0.02)
TSL	TSsh	0.04 (0.02)	0.22 (0.02)	0.36 (0.07)	0.56 (0.07)	0.21 (0.02)
WCA	01	0.15 (0.02)	0.32 (0.02)	0.34 (0.06)	0.70 (0.04)	0.34 (0.02)
WCA	02	0.12 (0.01)	0.31 (0.02)	0.29 (0.02)	0.73 (0.05)	0.33 (0.01)
WCA	03	0.09 (<0.01)	0.29 (0.04)	0.22 (0.02)	0.50 (0.05)	0.23 (0.01)
WCA	04	0.13 (0.01)	0.31 (0.02)	0.26 (0.06)	0.64 (0.05)	0.36 (0.02)
WCA	05	0.12 (0.01)	0.34 (0.01)	0.28 (0.04)	0.71 (0.03)	0.32 (0.01)
WCA	06	0.12 (0.01)	0.34 (0.02)	0.32 (0.04)	0.63 (0.03)	0.30 (0.02)
WCA	07	0.11 (0.01)	0.29 (0.01)	0.24 (0.03)	0.70 (0.03)	0.30 (0.01)
WCA	08	0.11 (0.01)	0.30 (0.01)	0.23 (0.03)	0.64 (0.03)	0.29 (0.02)
WCA	09	0.08 (0.01)	0.25 (0.02)	0.15 (0.02)	0.49 (0.04)	0.21 (0.01)
WCA	10	0.10 (0.01)	0.26 (0.01)	0.18 (0.02)	0.50 (0.03)	0.23 (0.02)

The slope for each Generalized Linear Model is equivalent to the instantaneous mortality rate (*Z*, individuals mm^{-1}). Estimates for each individual year were used in our VPA to estimate recruit abundance

hydroperiods). DSD and DSD^2 were less likely to explain recruitment variability at long-hydroperiod sites and were included in <57% of models, suggesting that depth acts as the primary hydrological driver of recruitment at long-hydroperiod sites (e. g., Least Killifish, Fig. 6).

Within a site, interannual variation in hydroperiod drove changes in both annual and maximum recruitment rates. Results from our ANCOVA suggest that the interaction between species and annual hydroperiod is different for each species; hydroperiod and maximum recruitment were either negatively correlated, positively correlated, or respond parabolically to hydroperiod (e.g., TSL MDsh, Fig. 7). Maximum recruitment rates for both the Eastern Mosquitofish and Flagfish displayed linear correlations with hydroperiod more frequently than any other species (9 of 16, 56.3% of models selected each) and were negatively correlated with hydroperiod for 33% of those models. Regardless of the relationship, annual hydroperiod significantly influenced maximum recruitment rates at all sites except four of the shortest hydroperiod sites (SRS 37; TSL CP, MDsh, TSsh). MMI revealed that quadratic models (Hydroperiod and Hydroperiod^2) best explained maximum recruitment at both intermediate and short-hydroperiod sites; however, parameter estimates for the squared term were not significantly different from zero for the majority of cases. Contrary to maximum recruitment rates, MMI revealed annual recruitment was positively correlated with hydroperiod for the majority of the cases (e.g., TSL MDsh, Fig. 8). The squared term, Hydroperiod^2, was not significantly different from zero in cases when the quadratic model was selected. Although each species reacted differently to changes in annual hydroperiod, each species responded differently across sites and no species-specific pattern was detected.

Recruit density was most variable, and often highest, at intermediate hydroperiod sites. We detected no

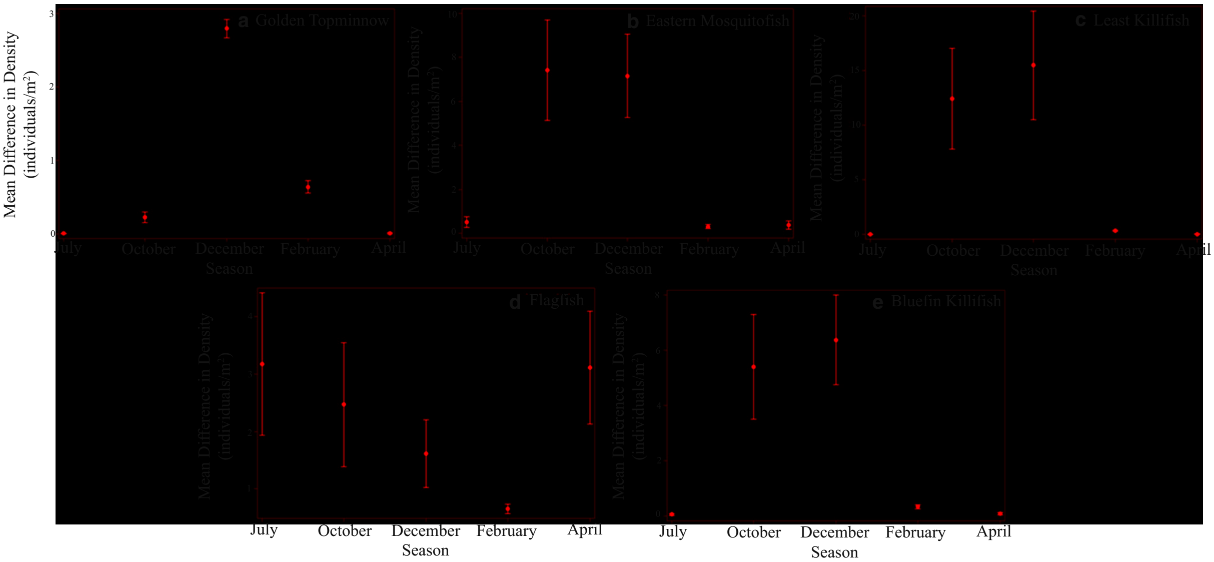

Fig. 4 An example of average differences in density between cohort analysis estimates and observed densities. Data for SRS Site 07 over the 20-year study for **a** Golden Topminnow, **b** Eastern Mosquitofish, **c** Least Killifish, **d** Flagfish, and **e** Bluefin Killifish. Estimates reveal seasonal changes in peak recruitment following cohort analysis

difference in maximum recruit density based on hydroperiod class for Golden Topminnows ($F_{2,\ 57} = 0.47$, $p =$ 0.63), Least Killifish ($F_{2,\ 57} = 2.16$, $p = 0.13$), and Flagfish ($F_{2,\ 57} = 1.72$, $p = 0.1875$). However, there were

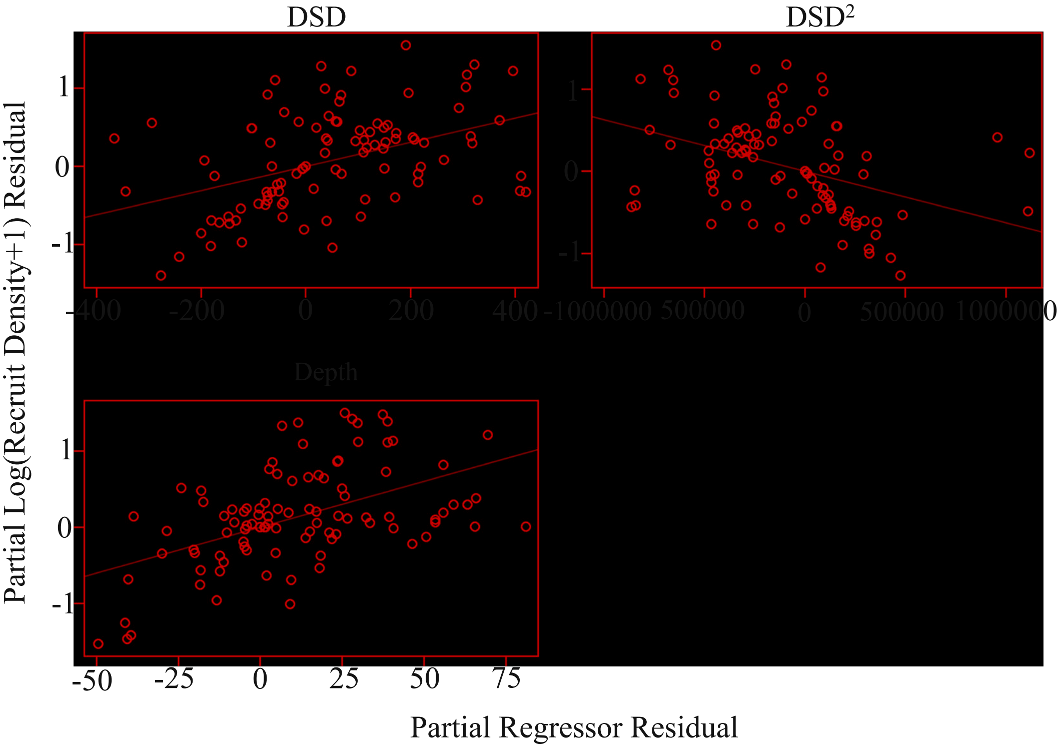

Fig. 5 Partial regression plots describing changes in Bluefin Killifish recruit density at WCA 10 (Intermediate Hydroperiod). The three-parameter quadratic model (no intercept) was selected based on AIC values. K = 3, AIC = −113.977, ΔAIC = 0, $R^2 = 0.72$

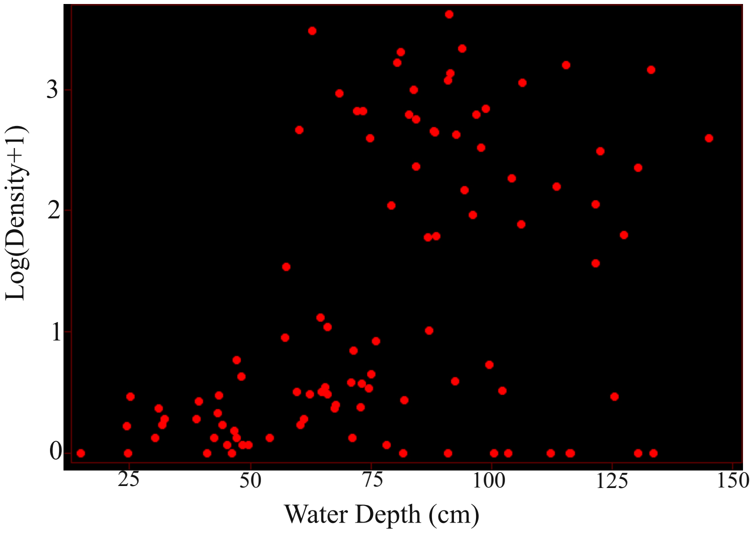

Fig. 6 Scatter plot describing how recruit abundance increases with increasing water depth for Least Killifish at WCA 06 (Long Hydroperiod) based on the linear model (no intercept) selected by AIC. K = 1, AIC = 13.81, ΔAIC = 0, $R^2 = 0.61$

noticeable differences in maximum recruitment for Eastern Mosquitofish ($F_{2,\ 57} = 6.94$, $p < 0.05$) and Bluefin Killifish ($F_{2,\ 57} = 17.71$, $p < 0.05$). On average, the density at maximum recruitment was greater at intermediate-hydroperiod sites when compared to short-hydroperiod sites for Flagfish (Mean Difference: +9.51 ± 5.58 recruits/m^2), Eastern Mosquitofish (Mean Difference: +7.74 ± 2.10 recruits/m^2), Bluefin Killifish (Mean Difference: +10.18 ± 1.44 recruits/m^2), and Least Killifish (Mean Difference: +9.78 ± 2.67 recruits/m^2), but this difference was negligible for the Golden Topminnow (−0.36 ± 0.32 recruits/m^2). We also observed increased recruitment at intermediate versus long-hydroperiod sites for Bluefin Killifish (+7.23 ± 1.40 recruits/m^2) and Least Killifish (+3.92 ± 3.04 recruits/m^2). However, the difference between long and intermediate hydroperiods was negligible for Golden Topminnows (−0.26 ± 0.42 recruits/m^2), Flagfish (+6.48 ± 6.72 recruits/m^2), and Eastern Mosquitofish (−0.09 ± 2.72 recruits/m^2). On average, intermediate- hydroperiod sites experienced higher recruitment annually compared to annual recruitment at short and long-hydroperiod sites.

Discussion

Our study has demonstrated that hydrology is a major abiotic control of fish recruitment in the Everglades, similar to other floodplain ecosystems (King et al. 2003; Agostinho et al. 2004; Balcombe et al. 2006). For six species examined, a site-by-site analysis of the hydrological drivers of recruitment revealed DSD to be a major driver of recruitment dynamics along a hydrological gradient. Our analyses also revealed that seasonal variation in recruitment was weakest for short-hydroperiod sites and driven by the number of days post-disturbance. Seasonal inundation creates optimal environmental conditions for reproduction and recruitment (Humphries et al. 1999; Agostinho et al. 2004; Balcombe et al. 2007). Other studies have demonstrated that inundation of the floodplain creates new habitats, refuge from piscivorous predatory fish, and newly available food sources generated from the pulses in primary production (Junk et al. 1989; Lake 2011; Bolland et al. 2015). Species at our sites exploit these features and may be dependent on adult dispersal into newly inundated habitats for reproduction because none are known to produce eggs tolerant of drying (Furness 2015). In contrast to shorter hydroperiods, annual variation in the seasonal timing of recruitment was greatest for long and intermediate-hydroperiod sites. Species located at these sites may respond to other environmental cues (e. g., temperature, photoperiod, light penetration), which may be less important drivers of recruitment in strongly pulsed habitats. Furthermore, depth was correlated with variation in estimated recruit density at long-hydroperiod sites. Pulsed ecosystems experience a wide range of water depths between seasons. Consequently, shallow-water stress (elevated temperature, risk of desiccation, risk of invertebrate predators) during the dry season may result in drastic changes in recruitment.

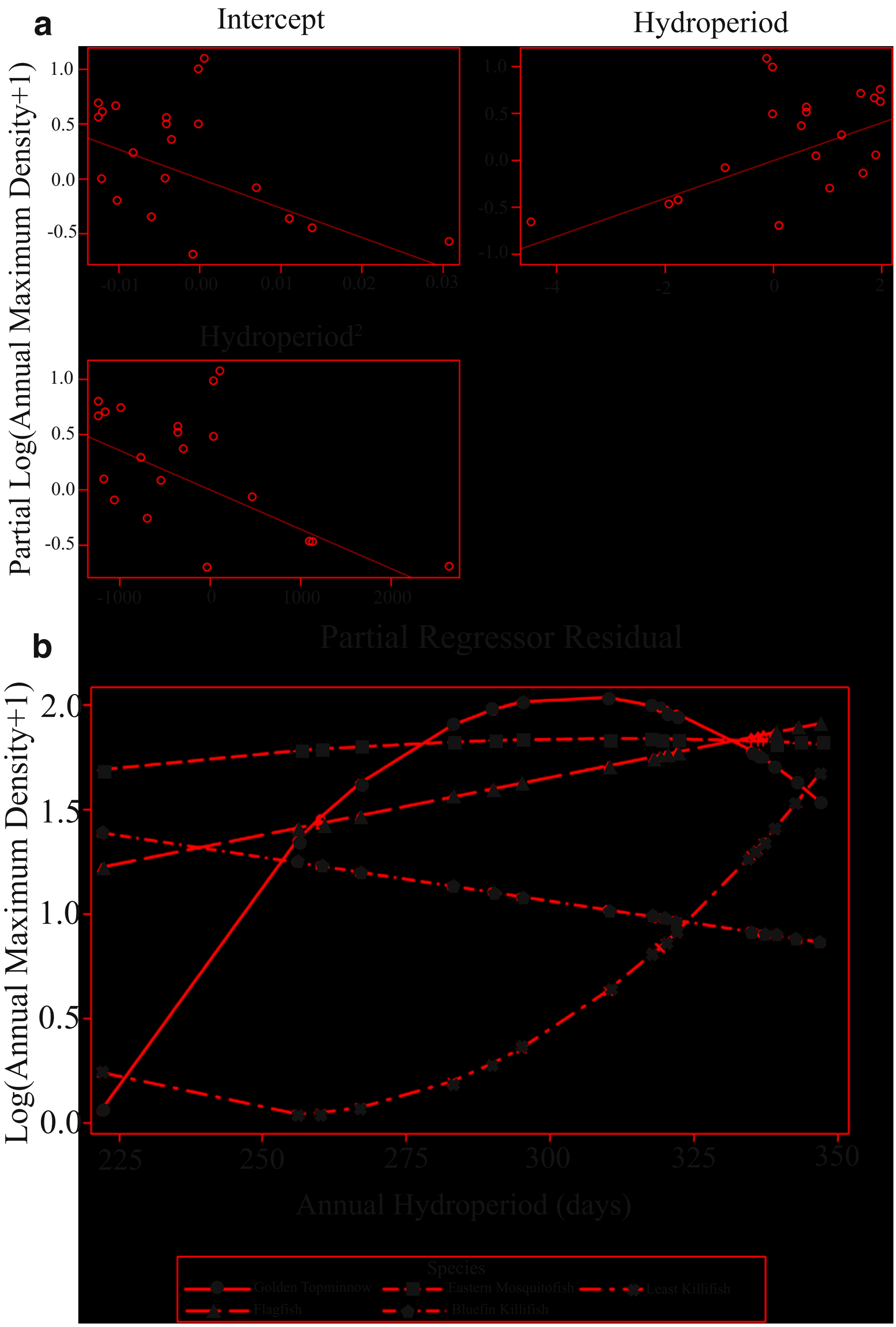

Fig. 7 **a** Partial regression plots describing annual variability in peak recruit density driven by site hydroperiod for Golden Topminnow at TSL MDsh (Short Hydroperiod). **b** Model predicted values of annual maximum recruitment versus the corresponding hydroperiod for each species

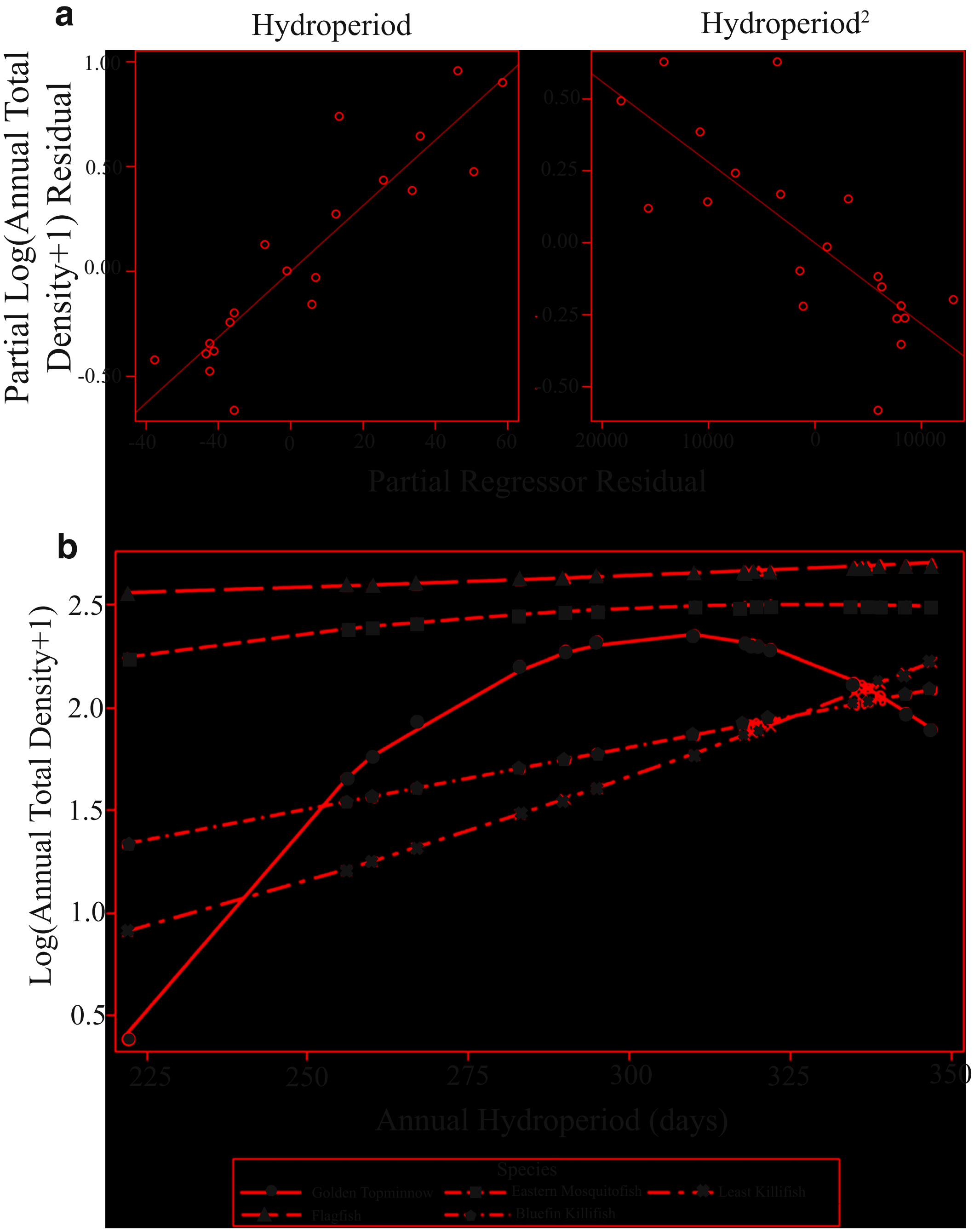

Fig. 8 **a** Partial regression plots describing annual variability in total annual recruit density driven by site hydroperiod for Flagfish at TSL MDsh (Short Hydroperiod). **b** Model predicted values of annual total recruitment versus the corresponding hydroperiod for each species

Hydrology induced immigration and emigration (Obaza et al. 2011; Goss et al. 2014) may have influenced the abundance-at-age data and resulting model-predicted values. Although such dispersal would violate one of our underlying assumptions (no dispersal), an analysis of model residuals suggested that both immigration and emigration did occur. These inferred movement rates were not equivalent (i.e., emigration ≠

immigration), which made accounting for individual movement difficult since no discernable pattern was observed. Our cohort analysis attempted to account for these movement patterns by retaining observed values that exceeded model predicted estimates (See Eqs. 7 and 8) to account for immigrants arriving between sample events. Although we assumed that missing cohorts were caused by sampling gear, these missing individuals may be emigrants that left to avoid stress associated with hydrological disturbance. We accounted for these individuals through our cohort analysis via the addition of missing individuals. Therefore, the assumptions made to the fitted models were robust, regardless of hydrologically induced movement.

Jordan et al. (1997) estimated the magnitude of two sources of sampling bias for a throw trap: clearing efficiency and escape probabilities. Although clearing efficiency and escape probabilities have been estimated at 83% and 20% respectively, these estimates do not account for the size-selective nature of mesh size. Our analyses calculated the size-selective nature of a 2-mm mesh and compared it to the other forms of bias associated with this gear. Size-selectivity seems to be the most variable form of gear limitation since it is both species and size-specific. Therefore, we suggest fitting catch curves to abundance-at-age data to describe size-selective bias in any sampling method (Schlechte et al. 2016). The combination of size-selectivity, recovery probabilities, and clearing efficiency can provide valuable information on how density estimates are influenced by sampling gear limitations.

Changes in recruitment can be masked by gear selectivity favoring large individuals (Frusher et al. 2003). These results indicate that under-estimates of population density are not uniform across the year and vary among species; when present, underestimated densities were greatest in times of high recruitment (primarily October through December in the data used) and least in times of limited reproduction (April through July in the data used). Although some of these changes were minor (e.g., Eastern Mosquitofish), our analyses did reveal some drastic changes for some species. For example, our analyses indicated that seasonal recruitment of Flagfish occurred during the late wet to early dry season (December to February). Our observed data indicated that this occurred predominantly in the early wet season (July), resulting in a 7–10 month difference between our observed and estimated values. This also indicates that this species recruits during a period that is more unpredictable and environmentally unfavorable (transition from wet to dry) in contrast to other species, which favor more stable environments (peak of wet season). This has large implications for management purposes, and the practical uses of cohort analyses can prevent errors in the estimation of seasonal recruitment. Furthermore, we were also able to estimate instantaneous mortality rates and apply these estimates to a cohort analysis specifically designed for annual species.

In contrast to other cohort analyses, which are conducted on an annual (year to year) time step, we used a seasonal time step because of the short life cycles of the species examined. This shift in temporal scale was both appropriate and necessary for a seasonally dynamic annual species. This approach allowed for estimation of temporal shifts in density by specifically targeting inter-season variation in catch data. Furthermore, species used in our analyses are born small, rapidly reach sexual maturity, and reproduce throughout much of the year (Haake and Dean 1983). These life history characteristics make typical use of annual cohort analyses both impractical and inaccurate. Our work illustrated how subtle differences in life history characteristics (e.g., growth, development) have large implications for larval mortality and recruitment (Houde 1989). These small differences in mortality may have contributed to high estimates and uncertainty for Least Killifish. This species grows rapidly and reaches sexual maturity at a small size (~10–12 mm in length) compared to the five other study species (~18–22 mm). Because of its small terminal size, Least Killifish were the most under-sampled of those considered (a larger portion of its life cycle was under-represented in collections) and provide a good example for the need to incorporate life history differences when conducting cohort analyses.

Uncertainties in the estimate of age-specific mortality (*M*) continue to be a major problem for cohort analyses (Lapointe et al. 1992; Maunder and Punt 2013). These concerns are often associated with guessing the relative contribution of natural and fishing mortality to total mortality. There is no fishing mortality in this study, but low population size may have caused unstable estimates of age structure in some populations for some years, violating one of the underlying assumptions of our models. This may have caused under- or overestimation of mortality needed for our backward projection models. We were unable to calculate daily or seasonal changes in mortality. Instead, we estimated annual changes in the instantaneous mortality rate (*M*) by fitting models to adult cohorts. Seasonal differences in mortality, which are likely present, may influence our results and future studies on seasonal sensitivity are needed. This would require an age-based model that follows a cohort month to month. Such an approach is beyond the scope of the present study. We believe that our study has addressed the major sources of error in cohort analyses, validating the use of our cohort analysis to predict larval and juvenile abundance in the Everglades.

We have provided a comprehensive survey of the size-selective nature of the 1-m^2, 2-mm mesh, throw trap. Our findings are consistent with previous studies that suggest capture probabilities vary across sizes and between species (Sistiaga et al. 2011). Differences in selectivity not only reflect organism morphology, but were also influenced by the size of maturation. Approximately, 63% efficiency (after correcting for clearing and enclosure efficiency) was achieved at or around the size of maturation for each species. Contrary to studies that use organism morphology to describe selectivity (Herrmann et al. 2012), minimum size at peak collection efficiency from our selectivity curves did not match sizes calculated from the morphometric analyses [Golden Topminnow: 11.09 mm (Morphometric) vs 18.00 mm (Selectivity); Eastern Mosquitofish: 14.56 mm (Morphometric) vs 17.00 mm (Selectivity); Flagfish: 7.91 mm (Morphometric) vs 20.00 mm (Selectivity); Bluefin Killifish: 9.75 mm (Morphometric) vs 18.00 mm (Selectivity); Least Killifish 10.20 mm (Morphometric) vs 12.00 mm (Selectivity)]. This suggests that morphometric data alone cannot accurately represent the size-selective nature of quantitative equipment. For our Everglades data collected using a 2-mm mesh throw trap, we determined that information collected on all species of fish examined <17 mm SL must be interpreted with caution. Juvenile individuals are best sampled using other quantitative methods that specifically target larval and early juvenile stages (Neal et al. 2012; Habtes et al. 2014). Furthermore, the efficiency of sampling gear can be improved by incorporating selectivity with clearing efficiency (Jordan et al. 1997) and recovery probabilities to fully understand the limitations of any sampling gear. Furthermore, these estimates can be used to back-calculate species density by dividing the observed density by the respective capture efficiency value (clearing efficiency X selectivity). The resulting estimates could be combined with a modified cohort analysis to improve future density estimates, detect seasonality of recruitment, and determine the abiotic controls of recruitment in pulsed ecosystems.

Acknowledgements We thank the many technicians, both past and present, who worked tirelessly in the field to collect the data used in this analysis. We are grateful to Dr. Yuying Zhang for introducing the concepts and equations needed to conduct the cohort analyses. Two anonymous reviewers provided helpful comments on a penultimate version of this paper that improved the final version. We also thank Jeff Kline, Everglades National Park, for making available data from sites 6, 23, and 50, and for his support of this project. This work was funded by a number of Cooperative Agreements between Everglades National Park and FIU (most recently by Critical Ecosystem Science Initiative Task Agreement P06AC00043). All animal use was approved by the FIU Institutional Animal Care and Use Committee (IACUC-16-34). This material was developed in collaboration with the Florida Coastal Everglades Long-Term Ecological Research program under National Science Foundation Grant No. DEB-1237517. This is contribution No. 895 from the Southeastern Environmental Research Center in the Institute of Water & Environment at Florida International University.

References

Aarts BG, Van Den Brink FW, Nienhuis PH (2004) Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: the transversal floodplain gradient. River Res Appl 20:3–23

Agostinho AA, Gomes LC, Veríssimo S, Okada EK (2004) Flood regime, dam regulation and fish in the upper Paraná River: effects on assemblage attributes, reproduction and recruitment. Rev Fish Biol Fish 14:11–19

Ala-Honkola O, Friman E, Lindstrom K (2011) Costs and benefits of polyandry in a placental poeciliid fish *Heterandria formosa* are in accordance with the parent–offspring conflict theory of placentation. J Evol Biol 24:2600–2610. https://doi.org/10.1111/j.1420-9101.2011.02383.x

Anderson JT (1988) A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J Northwest Atl Fish Sci 8:55–66

Arthington AH, Balcombe SR (2011) Extreme flow variability and the 'boom and bust'ecology of fish in arid-zone floodplain rivers: a case history with implications for environmental flows, conservation and management. Ecohydrology 4: 708–720

Balcombe SR, Arthington AH, Foster ND, Thoms MC, Wilson GG, Bunn SE (2006) Fish assemblages of an Australian dryland river: abundance, assemblage structure and recruitment patterns in the Warrego River, Murray–Darling Basin. Mar Freshw Res 57:619–633

Balcombe S, Bunn S, Arthington A, Fawcett J, McKenzie-Smith F, Wright A (2007) Fish larvae, growth and biomass relationships in an Australian arid zone river: links between floodplains and waterholes. Freshw Biol 52:2385–2398

Beyger L, Orrego R, Guchardi J, Holdway D (2012) The acute and chronic effects of endosulfan pulse-exposure on *Jordanella floridae* (Florida flagfish) over one complete life-cycle. Ecotoxicol Environ Saf 76:71–78. https://doi.org/10.1016/j.ecoenv.2011.09.015

Blackhart K, Stanton DG, Shimada A (2006) NOAA fisheries glossary. United States Department of Commerce, National Oceanic and Atmospheric Administration

Bolat Y, Demirci A, Mazlum Y (2010) Size selectivity of traps (Fyke-nets) of different mesh size on the narrow-clawed crayfish, Astacus Leptodactylus (Eschscholtz, 1823)(Decapoda, Astacidae) in Eschscholtz Lake, Turkey. Crustaceana 83:1349–1361. https://doi.org/10.1163/001121610x536969

Bolland J, Nunn A, Lucas M, Cowx I (2015) The habitat use of young-of-the-year fishes during and after floods of varying timing and magnitude in a constrained lowland river. Ecol Eng 75:434–440

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Methods Res 33:261–304

Cadrin SX, Vaughan DS (1997) Retrospective analysis of virtual population estimates for Atlantic menhaden stock assessment. Oceanogr Lit Rev 12:1553

Coggins LG Jr, Pine WE III, Walters CJ, Martell SJ (2006) Age-structured mark–recapture analysis: a virtual-population-analysis-based model for analyzing age-structured capture–recapture data. N Am J Fish Manag 26:201–205

Conrow R, Zale AV (1985) Early life history stages of fishes of Orange Lake, Florida: an illustrated identification manual. Florida Cooperative Fish and Wildlife Research Unit, Technical Report 15. University of Florida, Gainesville

Frusher S, Hoenig J, Gardner C (2003) Have changes in selectivity masked recruitment declines in crustacean trap fisheries? Fish Res 65:467–474

Furness AI (2015) The evolution of an annual life cycle in killifish: adaptation to ephemeral aquatic environments through embryonic diapause. Biol Rev 91: 796–812. https://doi.org/10.1111/brv.12194

Gabr M, Fujimori Y, Shimizu S, Miura T (2007) Behaviour analysis of undersized fish escaping through square meshes and separating grids in simulated trawling experiment. Fish Res 85:112–121. https://doi.org/10.1016/j.fishres.2007.01.006

Godfrey PC, Arthington AH, Pearson RG, Karim F, Wallace J (2017) Fish larvae and recruitment patterns in floodplain lagoons of the Australian Wet Tropics. Mar Freshw Res 68: 964–979

Goss C, Loftus W, Trexler J (2013) Seasonal fish dispersal in ephemeral wetlands of the Florida Everglades. Wetlands:1–11. https://doi.org/10.1007/s13157-013-0375-3

Goss CW, Loftus WF, Trexler JC (2014) Seasonal fish dispersal in ephemeral wetlands of the Florida Everglades, Wetlands. 34(1):147–157

Haake PW, Dean JM (1983) Age and growth of four Everglades fishes using otolith techniques. National Park Service, South Florida Research Center, Everglades National Park,

Habtes S, Muller-Karger FE, Roffer MA, Lamkin JT, Muhling BA (2014) A comparison of sampling methods for larvae of medium and large epipelagic fish species during spring SEAMAP ichthyoplankton surveys in the Gulf of Mexico. Limnol Oceanogr: Methods 12:86–101

Herrmann B, Sistiaga MB, Nielsen KN, Larsen RB (2012) Understanding the size selectivity of redfish (Sebastes spp.) in North Atlantic trawl codends

Hoch JM, Sokol ER, Parker AD, Trexler JC (2015) Migration strategies vary in space, Time, and Among Species in the Small-fish Metacommunity of the Everglades. Copeia 2015: 157–169

Houde E (1989) Subtleties and episodes in the early life of fishes. J Fish Biol 35:29–38

Humphries P, King AJ, Koehn JD (1999) Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling river system, Austrelia. Environ Biol Fishes 56:129–151

Jordan F, Coyne S, Trexler JC (1997) Sampling fishes in vegetated habitats: effects of habitat structure on sampling characteristics of the 1-m(2) throw trap. Trans Am Fish Soc 126:1012–1020. https://doi.org/10.1577/1548-8659(1997)126<1012:sfivhe>2.3.co;2

Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences 106:110–127

Jurado-Molina J, Gatica C, Arancibia H, Neira S, Alarcón R (2016) A multispecies virtual population analysis for the Southern Chilean Demersal Fishery. Marine and Coastal Fisheries 8:350–360

Kaufman L, Ebersole J, Beets J, McIvor CC (1992) A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. Environ Biol Fish 34:109–118

Kibria G, Ahmed KKU (2005) Diversity of selective and nonselective fishing gear and their impact on inland fisheries in Bangladesh. NAGA 28:43–48

King A, Crook D (2002) Evaluation of a sweep net electrofishing method for the collection of small fish and shrimp in lotic freshwater environments. Hydrobiologia 472:223–233

King A, Humphries P, Lake P (2003) Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. Can J Fish Aquat Sci 60:773–786

Konnert TJ (2002) The effects of hydroperiod on the life history parameters of Poecilia latipinna and *Heterandria formosa* (Poechiliidae) in the Florida Everglades. Master's Thesis, Florida International University

Lake PS (2011) Drought and aquatic ecosystems: effects and responses. John Wiley & Sons, Hoboken

Lapointe MF, Peterman RM, Rothschild BJ (1992) Variable natural mortality rates inflate variance of recruitments estimated from virtual population analysis (VPA). Can J Fish Aquat Sci 49:2020–2027

Lassen H, Medley P (2001) Virtual population analysis: a practical manual for stock assessment. vol 400. Food & Agriculture Org.,

Liu Z, Volin JC, Dianne Owen V, Pearlstine LG, Allen JR, Mazzotti FJ, Higer AL (2009) Validation and ecosystem applications of the EDEN water-surface model for the Florida Everglades. Ecohydrology 2:182–194

Livingston PA, Jurado-Molina J (2000) A multispecies virtual population analysis of the eastern Bering Sea. ICES J Mar Sci 57:294–299

MacLennan DN (1992) Fishing gear selectivity: an overview. Fish Res 13:201–204

Maunder MN, Punt AE (2013) A review of integrated analysis in fisheries stock assessment. Fish Res 142:61–74

Millar RB, Fryer RJ (1999) Estimating the size-selection curves of towed gears, traps, nets and hooks. Rev Fish Biol Fish 9:89–116

Miller B, Kendall AW (2009) Early life history of marine fishes. University of California Press, Berkeley

Neal JW, Adelsberger CM, Lochmann SE (2012) A comparison of larval fish sampling methods for tropical streams. Marine and Coastal Fisheries 4:23–29

Nordlie FG (2000) Patterns of reproduction and development of selected resident teleosts of Florida salt marshes. Hydrobiologia 434:165–182. https://doi.org/10.1023/a:1004073125007

Obaza A, DeAngelis DL, Trexler JC (2011) Using data from an encounter sampler to model fish dispersal. J Fish Biol 78:495–513. https://doi.org/10.1111/j.1095-8649.2010.02867.x

Pope J (1972) An investigation of the accuracy of virtual population analysis using cohort analysis. ICNAF Research Bulletin 9:65–74

Porch CE, Turner SC, Powers JE (2001) Virtual population analyses of Atlantic bluefin tuna with alternative models of transatlantic migration: 1970-1997. Col Vol Sci Pap ICCAT 52:1022–1045

Reis EG, Pawson MG (1999) Fish morphology and estimating selectivity by gillnets. Fish Res 39:263–273. https://doi.org/10.1016/S0165-7836(98)00199-4

Rudstam LG, Magnuson JJ, Tonn WM (1984) Size selectivity of passive fishing gear: a correction for encounter probability applied to gill nets. Can J Fish Aquat Sci 41:1252–1255

Schlechte JW, Bodine KA, Daugherty DJ, Binion GR (2016) Size selectivity of multifilament gill nets for sampling Alligator Gar: modeling the effects on population metrics. N Am J Fish Manag 36:630–638

Sistiaga M, Herrmann B, Nielsen KN, Larsen RB (2011) Understanding limits to cod and haddock separation using size selectivity in a multispecies trawl fishery: an application of FISHSELECT. Can J Fish Aquat Sci 68:927

Telis PA (2006) The Everglades Depth Estimation Network (EDEN) for Support of Ecological and Biological Assessments: U.S. Geological Survey Fact Sheet 2006-3087, 4p

Trexler JC, Loftus WF, Jordan F, Chick JH, Kandl KL, McElroy TC, Bass O (2002) Ecological scale and its implications for freshwater fishes in the Florida Everglades the Everglades, Florida bay, and coral reefs of the Florida keys: an ecosystem Sourcebook CRC Press, Boca Raton:153-181

Trexler JC, Loftus WF, Chick JH (2003) Setting and monitoring restoration goals in the absence of historical data: the case of fishes in the Florida Everglades monitoring ecosystems: interdisciplinary approaches for evaluating ecoregional initiatives Island Press, Washington, DC:351-376

Winemiller KO (2004) Floodplain river food webs: generalizations and implications for fisheries management. In: Proceedings of the second international symposium on the management of large rivers for fisheries. Food and Agriculture Organization & Mekong River Commission, FAO Regional, pp 285–309

Wolski LF, Trexler JC, Nelson EB, Philippi T, Perry SA (2004) Assessing researcher impacts from a long-term sampling program of wetland communities in the Everglades National Park, Florida, USA Freshw Biol 49:1381–1390 https://doi.org/10.1111/j.1365-2427.2004.01256.x

Zeug S, Winemiller K (2008) Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. River Res Appl 24:90–102