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ARTICLE

Linking demographic transitions to population dynamics in a fluctuating environment

John V. Gatto, Jeffrey L. Kline, William F. Loftus, and Joel C. Trexler

Abstract: Recruitment has been linked to decreases in the ratio of age-specific mortality (M') to mass-specific growth (G'), and year-class strength may be predicted by the age when $M'/G' = 1$. Hydrological stress adversely affects these parameters for species inhabiting floodplains; however, the relationship between M' and G' in hydrologically variable environments is poorly understood. We evaluated age-specific mortality for six species from a 20-year time series and growth curves from otolith length-at-age data. We assessed the effect of hydrology on the transitional age (age $M'/G' = 1$) at 21 sites representing a hydrological gradient. Disturbance intensity influenced age-specific mortality but had no effect on mass-specific growth. The transitional age was inversely correlated with annual density, but weakly associated with population biomass. Hydrological disturbance shifted the transitional age to older ages, reducing recruitment overall. We demonstrated that the M'/G' transition was affected adversely by hydrological stress and can be applied to a diverse group of taxa. Growth, survivorship, and the transitional age should be evaluated to improve population modelling efforts used to predict the influence of future restoration actions.

Résumé : Le recrutement a été relié à des diminutions du rapport entre la mortalité selon l'âge (M') et la croissance selon la masse (G'), et la force de classes d'âge peut être prédite par l'âge quand $M'/G' = 1$. Bien que le stress hydrologique ait une incidence négative sur ces paramètres pour les espèces habitant dans les plaines inondables, la relation entre M' et G' dans des milieux variables du point de vue hydrologique n'est pas bien comprise. Nous avons évalué la mortalité selon l'âge pour six espèces à partir d'une série chronologique sur 20 ans et les courbes de croissance à partir de données de longueur selon l'âge tirées d'otolites. Nous avons évalué l'effet de l'hydrologie sur l'âge de transition (âge auquel $M'/G' = 1$) dans 21 sites définissant un gradient hydrologique. L'intensité des perturbations influence la mortalité selon l'âge, mais n'a aucun effet sur la croissance selon la masse. L'âge de transition est inversement corrélé à la densité annuelle, mais faiblement associé à la biomasse de la population. Les perturbations hydrologiques décalent l'âge de transition vers des âges plus avancés, réduisant globalement le recrutement. Nous démontrons que le stress hydrologique a un effet négatif sur la transition M'/G' et que cette dernière peut être appliquée à un groupe de taxons variés. La croissance, la survie et l'âge de transition devraient être évalués afin d'améliorer les efforts de modélisation démographique employés pour prédire l'influence de mesures de restauration futures. [Traduit par la Rédaction]

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Introduction

Biotic and abiotic controls of recruitment have long been the focus of efforts to understand and predict population dynamics of fish species (Hjort 1914, 1926). These controls may be density-independent (hydrology, temperature) or -dependent (disease, predation), with the magnitude of impact varied across life stages (Houde 1989). For example, environmental variability tends to control survival rates of the prerecruit stages and is more influential at earlier life stages than later ones (Fogarty et al. 1991). These processes have described recruitment variability by addressing their impacts on either growth or mortality, or both (Bergenius et al. 2002). Further work revealed a link among mortality, growth, and other physiological characteristics that describe a population's response to food availability (Beverton and Holt 1957, 1959). Faster growth has been associated with higher survival rates, leading to greater levels of recruitment (Beyer 1989; Ware 1975). These findings have led to an increased understanding in the relationship between mortality and growth, and stage-specific changes in this relationship are hypothesized to be an important indicator for recruitment levels (Houde 1997*a*).

Cushing (1975) identified three life stages associated with changes in the relationship of stage-specific mortality (M') and growth rate (G'). The M'/G' ratio is most variable at the larval and juvenile stages, with subtle changes in growth rate and mortality having large implications on recruitment (Houde 1987). Cohort biomass within a year class decreases when mortality is high relative to growth ($M'/G' > 1$) but increases when mortality is low relative to growth ($M'/G' < 1$). The size or age when $M'/G' = 1$ is inversely associated with recruitment and indicates a transitional stage that serves as an important indicator of recruitment success. Cohorts that achieve this transitional stage earlier (smaller sizes, younger ages) will experience higher recruitment, leading to larger year-

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class size (Houde 1997*a*). The timing of this transitional age or length may occur at any life stage, although it is most important in early life when recruitment levels are set. The relationship between M'/G' and recruitment variability has been modeled extensively, assuming density-dependent growth and mortality, and has been praised for its ability to incorporate both density-independent and -dependent processes (Anderson 1988). Understanding fluctuations in species' growth and mortality rates are important for predicting recruitment and future biomass relative to different hydrological conditions within anthropogenically impacted ecosystems (McClanahan et al. 2015).

Life-history strategies have important implications for population regulation and fisheries management (Winemiller 2005). Synchronization of reproductive strategy and migratory patterns with hydrology, and phenotypic plasticity to exploit pulses in primary production associated with flood dynamics, are adaptive characteristics of fishes specific to the hydrologic conditions of floodplain ecosystems (Bailly et al. 2008; Denver 1997). Hydrological modification has been shown to affect floodplain fishes negatively by changing the temporal inundation regime and disrupting movement patterns (King et al. 2003). Disturbance also reduces survival, growth, and abundance because of increased hydrological stress (VerWey et al. 2018). Reduced growth and survivorship, coupled with increased movement patterns following inundation, can disrupt the relationship between stage-specific growth and mortality and ultimately recruitment. The effects of hydrology on life history have been extensively evaluated (Mims and Olden 2012; Olden and Kennard 2010), but it remains unclear how hydrological stress influences the timing of the transitional size or age that has been linked to recruitment levels.

In this paper, we evaluate the influence of hydrological disturbance on stage-specific mortality, growth, and the M'/G' ratio and their relationship to fluctuations in population size and biomass. We used a combination of density-at-length data from a 20-year, multisite time series and age-at-length data based on otoliths extracted from fishes at localized sites to evaluate the influence of hydrological disturbance (hydrological stress) on the transitional size or age. Sites were characterized as three hydroperiod treatments based on hydrological variability (short, intermediate, long) to investigate how hydrological disturbance influences species-specific growth and mortality rates. We then used data derived from species' mortality and growth rates to determine whether disturbance disrupts the link between the timing of the transitional age (M'/G' = 1) and changes in density or biomass. Finally, we investigated whether disturbance intensity and (or) frequency influenced the onset of the transitional stage. Parameter estimates were compared among sites of varying hydrological disturbance to determine how hydrology influences demographic changes in mortality and growth rates. This permitted us to evaluate how subtle differences in either stage-specific mortality or growth influenced the transitional age or length (M'/G' = 1) and recruitment in a pulsed floodplain ecosystem.

Methods

Study sites and species

We used a 20-year time series of population density estimates collected between 1996 and 2016 to explore the controls of recruitment in six common marsh fishes inhabiting the Everglades, Florida, USA (Trexler et al. 2003). Fishes were collected using a 1-m^2, 2-mm mesh throw trap following a standard protocol (Jordan et al. 1997; Loftus et al. 1990) at 21 monitoring sites (see online Supplementary Material, Fig. S1.1[1]). These sites were distributed in Shark River Slough (SRS), Taylor Slough (TSL), and Water Conservation Areas (WCA) 3A and 3B, accessed by airboat. Samples were collected in 5 months of each year (July, October, December, February, and April) to correspond with the south Florida hydrologic cycle (water year). Water year sampling occurs between July (early in south Florida wet season) and April of the following year (late in south Florida dry season), with water year designated to the year of the April sampling event. 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. Two sites, TSL MD and TSL TS, have five plots each and were divided to form two additional sites (TSL MDsh, TSL TSsh), with two plots each due to hydrological differences among plots. Sites located in WCA 3A and 3B yielded 75 samples per water year (3 plots × 5 throws × 5 sample events), sites in SRS and TSL yielded 105 samples per water year (3 plots × 7 throws per plot × 5 sample events), and sites at TSL MDsh and TSL TSsh yielded 70 samples per water year (2 plots × 7 throws per plot × 5 sample events); in dry years requiring helicopter access, five throws were taken per plot. The location of throws within each plot was determined using a random-number table. Plot sizes varied from 2100 m^2 (70 m × 30 m) to 10 000 m^2 (100 m × 100 m), depending on ambient vegetation and availability of sampleable habitat (Trexler et al. 2002, 2003). Plots were selected in spikerush-dominated slough habitats (peat and marl wet prairies; Gunderson and Loftus 1993), where vascular plant stem density varies within ranges evaluated by Jordan et al. (1997) to have consistent sampling efficiency for throw traps. After securing the trap, fishes and macroinvertebrates were removed following a standardized protocol of sweeps with a bar seine and dip nets (Jordan et al. 1997). Long-term monitoring at the 21 sites from July 1996 to April 2016 (20 water years) yielded over 20 000 community samples of over 400 000 fishes and invertebrates. There is no evidence of sampling impact at these study sites, possibly because randomization makes revisiting sampling points unlikely, and periodic marsh drying–regrowth overwhelms sampler effects on vegetation and soil (Wolski et al. 2004). From these samples, we report estimates of annual density (individuals·m^{-2}), size-specific mass of individuals of a species (g), and annual biomass (summed mass of all individuals of the same species in a year, g·m^{-2}).

To ensure adequate sample sizes for this study, we used only the six most common fish species: 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 life-span of these species is much less than 1 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 equivalent to the time between sequential samples. Thus, the 100 sequential samples in this study (20 years × 5 samples per year) represent between 34 and 51 generations for each species (Cashner 2020; Echelle and Echelle 2020; Ghedotti 2020).

Hydrological context

The 21 study sites were classified into three hydroperiod classes based on local hydrology: short (high hydrological stress), intermediate, and long hydroperiods (low hydrological stress). These classifications were developed using daily surface-water depth data extracted from the Everglades Depth Estimation Network (EDEN) and used to estimate several hydrological variables. EDEN uses water-surface models to interpolate measured water depths at monitored gauges to estimate daily water depth at our study sites (Liu et al. 2009; Telis 2006). Those data were used to calculate annual hydroperiod, a metric of disturbance intensity, which records the cumulative days that water was >5 cm within a water year. At 5 cm, only a slurry of organic matter remains, and fish generally suffocate in the low oxygen conditions and

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[1] Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2020-0101.

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organic matter blocking their gills (Loftus et al. 1990). Short-hydroperiod sites experienced <320 days inundated annually (five sites), intermediate-hydroperiod sites experienced 320–360 days inundated annually (10 sites), and long-hydroperiod sites experienced >360 days inundated annually (six sites). To describe temporal variability in annual hydroperiod within a site, the coefficient of variation (CV) was calculated for each site based on 20 years of data. We also quantified disturbance frequency or the number of drying events that occurred between 1996 and 2016. Sites classified as long hydroperiod experienced less than four drying events in 20 years, sites classified as intermediate hydroperiod experienced 4–12 drying events in 20 years, and sites classified as short hydroperiod experienced >12 drying events in 20 years. Mean hydroperiod, the CV of hydroperiod, and the number of drying events are highly correlated and accurately describe spatial–temporal variability in hydrology among sites. Further information on hydroperiod classifications and their respective hydrology can be found in Gatto and Trexler (2019).

Species-specific growth rates

We investigated the effect of hydrological disturbance on species-specific growth rates by collecting fishes at sites with varying levels of hydrological disturbance. Fishes were collected from two long-hydroperiod (WCA 04 and 05), two intermediate-hydroperiod (SRS 07 and WCA 02), and two short-hydroperiod sites (TSL MDsh and WCA 03) in each October from 2014 to 2016. An analysis of the length–frequency data within the time series determined that both juveniles and adults were present in October to collect the full range of sizes needed for a growth study. Furthermore, a previous study indicated that growth rates were different for *F. chrysotus* among sample periods, but no detectable differences were found for *G. holbrooki*, *H. formosa*, and *L. goodei* (Haake and Dean 1983). Historical age-at-length data (collected between 1996 and 2016) for *P. latipinna*, *J. floridae*, and *L. goodei* were also available for growth-curve analysis at sites SRS 50, SRS 37, WCA 08, WCA 04, and WCA 05.

To determine whether hydrological disturbance influenced species-specific growth rates, we estimated species-specific growth curves from age-at-length data determined from otolith ring counts for each site within hydroperiod treatments. Fish standard length (mm), wet mass (g), and sex (male, female, juvenile) were recorded prior to otolith extraction. Each pair of sagittal otoliths for 12 females and 12 juveniles ($n = 24$) was removed with forceps, then cleaned with a 20% bleach solution, rinsed with deionized water, and stored. Otoliths were cleaned of any remaining organic matter with 90% ethanol, dried, and embedded in Spurr low-viscosity embedding resin (10 g vinyl cyclohexene dioxide, 26 g nonenyl succinic anhydride, 6 g DER 736 (diglycidyl ether of polypropylene glycol), and 0.4 g dimethylaminoethanol; Spurr 1969). A Spurr-resin block was created by heating the resin overnight at 70 °C. Embedded otoliths were sanded and polished to create a thin section. One side of the otolith was sanded to the sagittal plane and attached to a microscope slide using Crystalbond adhesive. The remaining side was sanded and polished to create a thin cross-section, which exposed otolith growth rings. Otoliths were then etched using a 10% HCl solution prior to counting (Konnert 2002).

We considered three popular growth models to determine which model best fit our age-at-length data to evaluate species-specific growth rates: the von Bertalanffy (VBGM), Gompertz (GGM), and logistic (LGM) growth models (Kaufmann 1981). Multimodel inference (MMI) using Akaike information criterion (AIC) then determined which of the three candidate models best explained our data (Burnham and Anderson 2004). We used nonlinear least squares (NLS) with the Marquardt optimization method to estimate three parameters (L_∞, growth parameter K, and t_0). Length-specific growth rates were calculated using the differential equation for the best model ($\Delta\mathrm{AIC} = 0$). Length–mass relationships were calculated using ordinary least squares (OLS) regression based on log-transformed mass and length data. A generalized linear mixed model (GLMM) using the LaPlace estimation method was used to compare the log-transformed mass against the main effects of log-transformed length, region, sites within regions, and their interactions (region × length, site within regions × length) for each species. To account for temporal variability in length–mass relationships, we treated water years within a site as a random effect and used a Wald test for random effects.

Species-specific mortality

We evaluated spatial–temporal variation in species-specific mortality along a hydrological gradient using catch curves derived from density-at-length data within a 20-year time-series dataset. Age-specific mortality was estimated by classifying individuals into several distinct age classes. We accounted for the rapid life history of these species by generating both 10-day and 30-day cohorts. Preliminary analysis comparing these revealed that the 10-day cohort analysis was more robust, resulting in the species being divided into 31 different classes instead of 11 unique classes (Supplementary Material 2[1]). Age was back-calculated using the age-at-length data by rearranging each growth curve in terms of length. Following the methods of Gatto and Trexler (2019), we applied a generalized linear model to cohorts >30 days within the density-at-age data to linearize the discrete-time model:

$$(1) \qquad N_t = N_0^{-Mt}$$

where N_t is the population size of a 10-day cohort, N_0 is the initial population size, and M is the instantaneous mortality rate (individuals·10 days^{-1}). We fit a negative binomial error distribution because the response variable (cohort density) was estimated as integers (counts). To account for the annual life-span 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 (Gatto and Trexler 2019). To test the main effects of age class, region, sites within region, and their interactions (age class × region, age class × sites within region) on cohort density, we applied a GLMM using a negative binomial error distribution to our catch curves. Temporal variability was included as a random effect (water years within a site), and we applied a Wald test for random effects. A GLMM with a negative binomial error distribution was applied to model count data (Stroup 2015). These models were approximated using the LaPlace estimation method and applied only to sites and water years that were included in our growth study. For a description of a length-based approach to this analysis and all proceeding analyses, see Supplementary Material 3[1].

M'/G' ratio and the transitional size and age

The length–mass relationships and our estimates of M were used to investigate how hydrological disturbance influences demographic changes in the M'/G'. We evaluated stage-specific changes in the M'/G' by log-transforming the relationship between stage-specific survival and mass:

$$(2) \qquad \frac{N_s}{N_{s-1}} = \exp(-M_s) = \left(\frac{W_s}{W_{s-1}}\right)^{-M/G}$$

where N_s and N_{s-1} are cohort densities at two stages, and W_s and W_{s-1} are fish masses at two stages. Subsequent stages were defined as surviving from one 10-day cohort ($s - 1$) to the next (s), hereinafter referred to as age-specific. Our estimates of M were substituted for M_s, and both W_s and W_{s-1} were calculated from length–mass relationships for each species. Mass was calculated from the estimated length at the end of each 10-day cohort. The

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age-specific growth rate was calculated for each 10-day cohort by using the differential equation of the growth curves generated from the age-at-length data (Kaufmann 1981). Next, we calculated the age-specific mortality rates by multiplying the age-specific M'/G' by the age-specific growth rate. Because the M'/G' ratio declined as a power function of larval mass, we fit a nonlinear model to the M'/G' as a function of age class (Houde 1997*a*). We validated these models by regressing the model-predicted values against the observed values. Finally, the age of the transitional stage ($M'/G' = 1$) was calculated by setting $M'/G' = 1$ and solving the nonlinear model in terms of age.

Time-series analysis

We investigated how the timing of the transitional age related to changes in species density and biomass using a 20-year time-series data set. The previously described methods were used to calculate the age-specific M'/G' ratios for all sites and water years within the time series. For sites and water years outside the scope of our growth study, we used length–mass relationships from the literature to calculate the age-specific mass (Kushlan et al. 1986). Ages were calculated using our age-at-length data when available. We pooled our length-at-age data for each species and approximated a VBGM to substitute a growth curve for the remaining sites and water years. We found the use of a pooled growth curve for aging fish could accurately age individual fish based on their length because the use of 10-day cohorts was very robust.

Linear regression was then used to determine the relationship between the transitional age and annual density for each species. We considered annual biomass (cumulative biomass for all samples within a water year) and density (cumulative density for all samples within a water year) as response variables and the transitional age (age $M'/G' = 1$) for each water year as the independent variable. To account for unequal sample sizes, we calculated biomass density ($g \cdot m^{-2}$) and species density ($individuals \cdot m^{-2}$) based on the number of throw-trap samples collected that year. These variables were log-transformed and regressed using OLS for each species at each site. We next compared regional spatial scales (SRS, WCA, TSL) and local spatial scales (sites within regions) using a nested ANCOVA to test the interaction among sites with the transitional age for each species.

To determine the effect of hydrology on the transitional age, we investigated both disturbance intensity (site hydroperiod) and disturbance frequency (number of drying events). We regressed the transitional age against both annual hydroperiod and a squared term ($Hydroperiod^2$) for each species to determine whether annual variation in the timing of the transitional age was influenced by the number of days a site was inundated. The CV for hydroperiod, a metric of variability in disturbance intensity, was calculated using the annual hydroperiod for each site across the 20 years of the time series. This was regressed against the CV of transitional age using OLS to determine whether variability in the transitional age was driven by variability in disturbance intensity. Finally, a general linear model was applied to our data to examine how the transitional age (response variable) for each species was influenced by disturbance frequency (independent variable).

Results

Species-specific growth

Our analyses produced 79 different growth models for six species across eight different sites and six different years. MMI revealed that the VBGM best described our age-at-length data ($\Delta AIC = 0$) for most sites and water years (52%). Both the LGM and GGM performed equally well ($\Delta AIC < 3$) for several species (Supplementary Material 4[1]). Model-predicted values of length were highly correlated with observed values for *F. chrysotus* (mean $R^2 = 0.98 \pm 0.003$), *G. holbrooki* (mean $R^2 = 0.97 \pm 0.003$), *H. formosa* (mean $R^2 = 0.97 \pm 0.006$), *J. floridae* (mean $R^2 = 0.85 \pm 0.04$), *L. goodei* (mean $R^2 = 0.96 \pm 0.009$), and *P. latipinna* (mean $R^2 = 0.89 \pm 0.03$). We found no differences in L_∞, K, or t_0 among hydroperiods. Furthermore, estimates of L_∞ and t_0 were more variable than K (Table 1).

Table 1. Estimates of L_∞, K, and t_0 averaged across hydroperiods (mean ± SE) for each species.

		Hydroperiod		
Species	Estimate	Short	Intermediate	Long
F. chrysotus	L_∞	72.30 (10.45)	66.18 (9.44)	98.69 (15.64)
	K	−0.0088 (0.005)	−0.0089 (0.003)	−0.003 (0.001)
	t_0	6.38 (14.42)	24.36 (23.24)	−14.31 (2.95)
G. holbrooki	L_∞	35.06 (2.56)	35.26 (3.11)	32.92 (2.50)
	K	−0.018 (0.004)	−0.020 (0.007)	−0.019 (0.003)
	t_0	19.81 (12.00)	11.87 (13.16)	23.42 (10.55)
H. formosa	L_∞	21.44 (2.85)	23.75 (3.98)	24.49 (6.53)
	K	−0.015 (0.004)	−0.015 (0.007)	−0.019 (0.008)
	t_0	3.30 (18.93)	−15.91 (6.03)	2.03 (15.22)
J. floridae	L_∞	36.37 (4.74)	36.58	28.81 (0.39)
	K	−0.16 (0.004)	−0.013	−0.023 (0.002)
	t_0	144.9 (8.99)	148.8	132.5 (7.65)
L. goodei	L_∞	41.81 (8.76)	30.88 (1.49)	28.49 (1.12)
	K	−0.018 (0.005)	−0.018 (0.005)	−0.024 (0.005)
	t_0	17.33 (12.55)	13.62 (10.09)	26.43 (10.97)
P. latipinna	L_∞	38.77 (4.62)	47.62 (8.64)	41.44 (9.22)
	K	−0.026 (0.005)	−0.019 (0.007)	−0.016 (0.008)
	t_0	77.24 (15.62)	101.3 (31.27)	46.91 (37.25)

Note: Individual estimates for each site or water year can be found in Supplementary Material 4[1]. SE not available for all species due to lack of replication.

Table 2. Estimates of instantaneous mortality rates M ($individuals \cdot day^{-1}$) for each species (mean ± SE).

	Hydroperiod		
Species	Short	Intermediate	Long
F. chrysotus	0.025 (0.0003)	0.021 (0.0003)	0.023 (0.0004)
G. holbrooki	0.035 (0.0008)	0.037 (0.0008)	0.060 (0.0010)
H. formosa	0.025 (0.0005)	0.052 (0.0007)	0.059 (0.0013)
J. floridae	0.018 (0.0001)	0.012	0.009 (0.0010)
L. goodei	0.033 (0.0007)	0.035 (0.0006)	0.039 (0.0008)
P. latipinna	0.029 (0.0009)	0.032 (0.0002)	0.029 (0.0008)

Note: Values were averaged across each hydroperiod classification.

We compared 60 different length–mass relationships for four of the six species in this study. Individual mass was highly correlated with length for all species included in this analysis ($R^2 > 0.89$). GLMMs revealed a significant positive relationship between both individual mass and length for all species. Regional variability in these length–mass relationships was only found for *F. chrysotus* ($F_{[2,270]} = 3.27$, $p < 0.05$), and local-scale variability was detected for all species except *H. formosa* ($F_{[3,270]} = 1.35$, $p = 0.26$). We found significant interaction between log-transformed length and region for *L. goodei* ($F_{[2,408]} = 3.21$, $p < 0.05$). Our results also indicate that the slopes of these length–mass relationships were different among sites within regions for *F. chrysotus* ($F_{[3,270]} = 4.06$, $p < 0.01$) and *L. goodei* ($F_{[3,408]} = 6.76$, $p < 0.01$). Wald tests revealed significant random effects (water year within site) in our GLMMs for *G. holbrooki* ($Z = 2.30$, $p < 0.01$) and *L. goodei* ($Z = 2.57$, $p < 0.01$); however, the effects of temporal variability were small for both *G. holbrooki* (0.02 ± 0.008) and *L. goodei* (0.008 ± 0.003).

Species-specific mortality

Catch curves generated from the density-at-age data allowed us to estimate instantaneous mortality rates (M). We detected no

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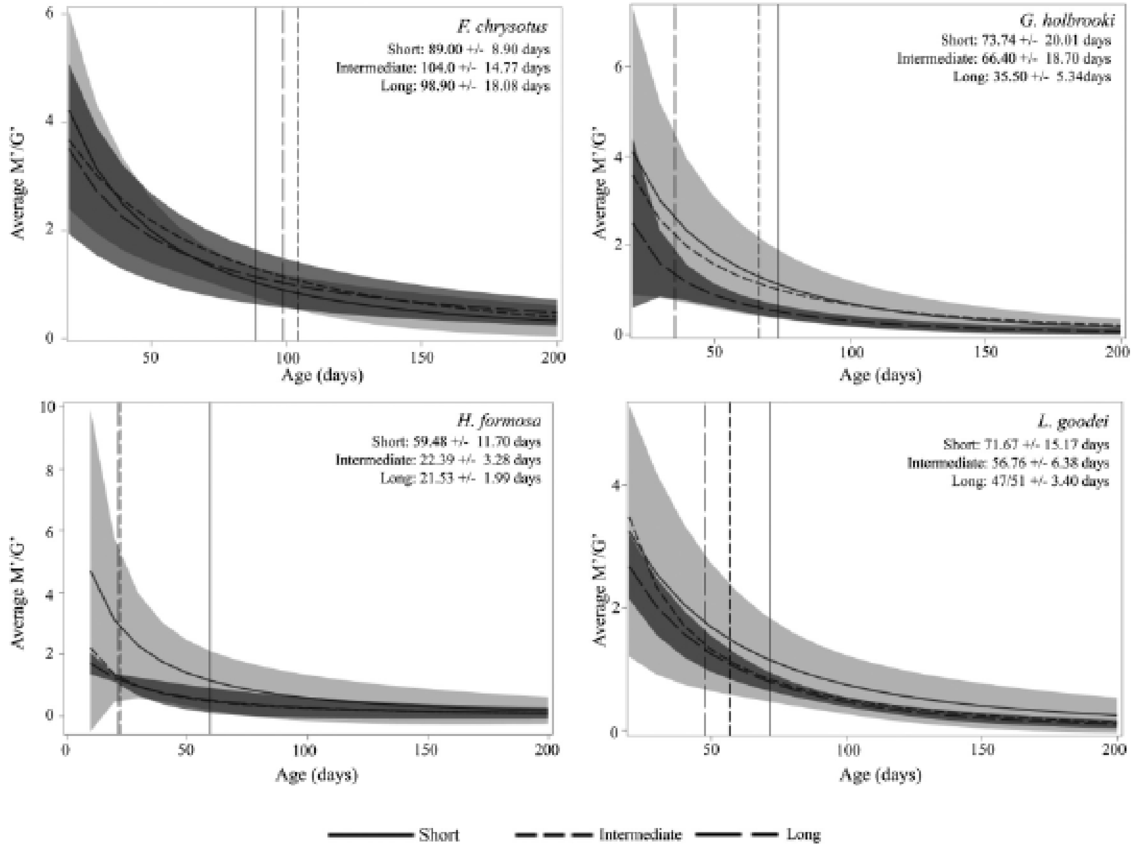
Fig. 1. Average M'/G' curves as a function of age (days) for short-, intermediate-, and long-hydroperiod sites. Estimates for *G. holbrooki* and *L. goodei* were based on two sites per hydroperiod from 2014 to 2016 ($n = 6$). Estimates for *F. chrysotus* and *H. formosa* were based on two sites per hydroperiod from 2014 to 2015 ($n = 4$). Shaded regions indicate 95% confidence intervals. Darkest areas indicate overlap in confidence intervals. Confidence intervals were excluded for intermediate-hydroperiod sites because overlap with both long- and short-hydroperiod curves obscured patterns. Vertical reference lines indicating the size at the transitional age were included for each hydroperiod type.



significant lack-of-fit for 93% of all models considered and found a significant negative relationship between density and age class for >85% of those models. Significant spatial variation was only observed at both local and regional scales for *G. holbrooki* and *H. formosa*, but there were differences among sites within regions for all species except *L. goodei* ($F_{[2,727]} = 1.68$, $p = 0.19$). We detected significant interaction between age class and site for both *H. formosa* ($F_{[3,378]} = 19.63$, $p < 0.01$) and *P. latipinna* ($F_{[2,283]} = 4.17$, $p < 0.01$), indicating spatial variation in the slopes of these curves. Furthermore, we found significant interaction between age class and regions for *G. holbrooki* ($F_{[2,570]} = 9.14$, $p < 0.01$) and *H. formosa* ($F_{[2,378]} = 14.74$, $p < 0.01$). We did not find temporal variability for *F. chrysotus* ($Z = 0.59$, $p = 0.28$) or *J. floridae*; however, we were unable to estimate a random effect for *J. floridae* because this species was only sampled for 1 year. Temporal variation was highest for *G. holbrooki* (0.58 ± 0.23) and weakest for *H. formosa* (0.20 ± 0.11). Estimates of M differed among hydroperiods for *G. holbrooki* ($F_{[2,15]} = 5.78$, $p < 0.05$) and *H. formosa* ($F_{[2,9]} = 6.95$, $p < 0.05$) and were highest at long-hydroperiod sites, indicating that disturbance intensity decreased mortality rates (Table 2; Supplementary Material 3, Table S3.1[1]).

The transitional age, density, and biomass

Our time-series analysis revealed spatial–temporal trends in both mortality and growth for all species. The calculated M'/G' ratio for each age derived from eq. 2 was highly correlated with model-predicted values and declined exponentially as a function of age class (mean $R^2 = 0.97 \pm 0.04$ for all species). There was no evidence that the shape of these curves differed among hydroperiods for any species (Fig. 1; however, see Supplementary Material 3, Fig. S3.1[1]). These curves did reveal that the transitional age occurred earlier at long-hydroperiod sites compared with shorter-hydroperiod sites for the four species collected between 2014 and 2016.

Spatial–temporal differences in age-specific M'/G' were driven by larger differences in M' among hydroperiods than G'. On average, interannual variability in mortality was 1.57 to 2.41 times greater than growth, and this variability was lowest at short and long hydroperiods (Table 3). Analysis of age-specific M'/G' revealed that the transitional age occurred earlier for all species. On average, the transitional age occurred within 117.02 ± 3.44 days for *F. chrysotus*, 45.37 ± 0.86 days for *G. holbrooki*, 32.22 ± 1.39 days for *H. formosa*, 198.85 ± 7.40 days for *J. floridae*, 62.74 ± 1.53 days for *L. goodei*, and 190.51 ± 41.28 days for *P. latipinna*. We detected spatial–temporal differences in the onset of the transitional age at both regional and local spatial scales for *G. holbrooki*, *H. formosa*, and *L. goodei*. The transitional age was not different at regional spatial scales for *F. chrysotus* ($F_{[2,396]} = 0.60$, $p = 0.55$) and *P. latipinna* ($F_{[2,290]} = 0.37$, $p = 0.69$) or at local spatial scales for *J. floridae* ($F_{[18,346]} = 0.82$, $p = 0.67$). Temporal variation in the transitional age was also not found for *P. latipinna* ($F_{[20,290]} = 0.93$, $p = 0.55$).

Annual density decreased as the transitional age occurred later in life history for each species (Fig. 2; Supplementary Material 3, Fig. S3.2[1]). This revealed a negative correlation between the transitional age and annual density for 91.3% of all species–site

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Table 3. The coefficient of variation (CV) of age-specific mortality M' and growth G' for the early life stages (birth or hatch) of each species.

		Hydroperiod		
Species	Parameter	Short	Intermediate	Long
F. chrysotus	M'	61.30	46.90	41.31
	G'	24.37	32.10	18.33
	Ratio	2.52	1.46	2.25
G. holbrooki	M'	94.25	80.49	90.87
	G'	31.34	22.58	65.88
	Ratio	3.01	3.57	1.38
H. formosa	M'	74.31	130.29	65.15
	G'	39.05	67.48	56.77
	Ratio	1.90	1.93	1.15
L. goodei	M'	30.73	50.04	27.86
	G'	13.95	18.77	18.68
	Ratio	2.20	2.67	1.49
Hydroperiod mean	M'	65.15 (13.32)	76.93 (19.33)	56.30 (13.86)
	G'	27.18 (5.33)	35.23 (11.11)	39.91 (12.50)
	Ratio	2.41 (0.24)	2.41 (0.46)	1.57 (0.24)

Note: CV percentages were calculated at 20 days. The ratio of the CVs (M'/G') was also calculated. All species, sites, and years per hydroperiod classification were averaged together to calculate the mean CV at each hydroperiod classification (±SE). Sample size varies by hydroperiod classification per species ($n = 4$ to 6). Estimates not available for *P. latipinna* and *J. floridae*.

combinations. Of those models, 48.7% revealed a significant correlation between density and the transitional age (Supplementary Material 5[1]). This relationship was weakest for *P. latipinna* (mean R^2 = 0.08 ± 0.02) and strongest for *L. goodei* (mean R^2 = 0.37 ± 0.06). We detected spatial differences in this relationship at both regional and local spatial scales for *H. formosa*, *L. goodei*, and *P. latipinna*. No differences were found at regional spatial scales for *F. chrysotus* ($F_{[2,393]}$ = 1.96, p = 0.14) and *J. floridae* ($F_{[2,343]}$ = 0.11, p = 0.89) or at local spatial scales for *G. holbrooki* ($F_{[18,393]}$ = 5.25, p = 0.10). Significant interaction was detected for all species except *P. latipinna*, indicating that the slopes of these relationships differed at local spatial scales (sites within regions).

Annual differences in the transitional age poorly described changes in biomass for all species in the study. Although our analyses revealed a negative correlation between the transitional age and annual biomass for 61.9% of all species–site combinations, only 25.6% demonstrated a significant correlation between annual biomass and the transitional age. Biomass was weakly correlated with the transitional age, with the strength of this relationship highest for *L. goodei* (mean R^2 = 0.22 ± 0.05) and weakest for *G. holbrooki* (mean R^2 = 0.05 ± 0.01). Our ANCOVA revealed that the transitional age was not correlated with biomass for either *G. holbrooki*, *J. floridae*, or *P. latipinna*. This relationship only differed at regional and local spatial scales for *H. formosa* and *L. goodei*. Furthermore, we detected significant interaction between the transitional age and sites, indicating that the slopes of this relationship differed among sites for *H. formosa* ($F_{[20,362]}$ = 2.95, p < 0.01) and *L. goodei* ($F_{[20,381]}$ = 3.04, p < 0.01).

Hydrology and the transitional age

Time-series analysis revealed changes in species density and biomass across the hydrological gradient. Species density was highest at long-hydroperiod sites compared with intermediate- and short-hydroperiod sites for four of the six species (Fig. 3A; Supplementary Material 3, Fig. S3.3A[1]). Density was highest at intermediate-hydroperiod sites for both *J. floridae* and *F. chrysotus*. There were differences in annual biomass for all species except *J. floridae* (Fig. 3B; Supplementary Material 3, Fig. S3.3B[1]). Biomass increased for *F. chrysotus* when comparing short- and intermediate-hydroperiod sites but peaked at intermediate-hydroperiod sites. We found an increase in biomass from short- to long-hydroperiod sites, indicating that more stable sites maintain higher biomass. These trends were driven by changes in the timing of the transitional age for *G. holbrooki*, *H. formosa*, and *L. goodei* (Fig. 3C; Supplementary Material 3, Fig. S3.3C[1]). Populations that experienced the transitional age at earlier ages had higher recruitment, density, and biomass. This transitional age occurred later in life (older ages) at shorter hydroperiods and shifted to younger ages as sites became more stable (short to long hydroperiod). This was inversely correlated with density and biomass, as both increased as sites became more stable.

Our analyses found some support for hydroperiod influencing the transitional age. Hydrological disturbance influenced transitional age for five of the six study species. Results indicated that disturbance intensity (annual hydroperiod and annual hydroperiod^2) was significantly correlated with the transitional age for *G. holbrooki*, *H. formosa*, *L. goodei*, and *P. latipinna*. Significant slopes for both hydroperiod^2 and hydroperiod were found for these four species, indicating a parabolic relationship between annual hydroperiod and the transitional age. Although we found a significant relationship for four species, these variables explained little variation in the models (R^2 < 0.04 for all species). The CV of the transitional age and hydrological variability within a site (CV hydroperiod) was not correlated for any species except *P. latipinna* (Supplementary Material 6[1]) but did show an increasing pattern. The number of drying events a site experienced (disturbance frequency) also increased the timing of the transitional age for all species except *F. chrysotus* (Fig. 4; Supplementary Material 3, Fig. S3.4[1]). These effects were greatest for *L. goodei* (~14.30 days at zero disturbances and increased to ~18.01 days at 20 disturbances) and *H. formosa* (~8.96 days at zero disturbances and increased to ~11.98 days at 20 disturbances). A full description of complementary results using a length-based approach can be found in Supplementary Material 3, Results[1].

Discussion

We documented landscape-scale patterns of life-history transitions indicated by age-specific values of M'/G' that were correlated with hydrological disturbance in all six species we studied. Our results revealed spatial–temporal differences in age-specific mortality at regional and local (sites within region) spatial scales, but little spatial–temporal variation in growth parameters (L_∞, K, t_0). Therefore, most variation in age-specific M'/G' among hydrological treatments was from impacts on survivorship rather than growth. The transitional stage (either age or length) leading to cohort biomass production ($M'/G' < 1$) occurred at earlier ages or smaller sizes for most species at long-hydroperiod sites compared with short-hydroperiod ones. For some species, we noted higher recruitment rates and biomass when this transitional stage occurred at earlier ages or smaller sizes. We also detected higher densities for all species except *J. floridae* and *F. chrysotus* at long-hydroperiod sites compared with shorter-hydroperiod ones, and those differences were reflected by the timing of the transitional age (younger to older, respectively). The transitional stage occurred at earlier ages and smaller sizes at long-hydroperiod sites, with short hydroperiod and presumably more stressful environments delaying the onset of biomass production and supporting less biomass and density for all species except *J. floridae* and *P. latipinna*. The transitional age occurred at older ages for these species at long hydroperiods. Moreover, the transitional age was weakly associated with changes in both density and biomass for these two species.

Quantifying stage-dependent mortality is crucial to predicting recruitment and understanding population dynamics of fish

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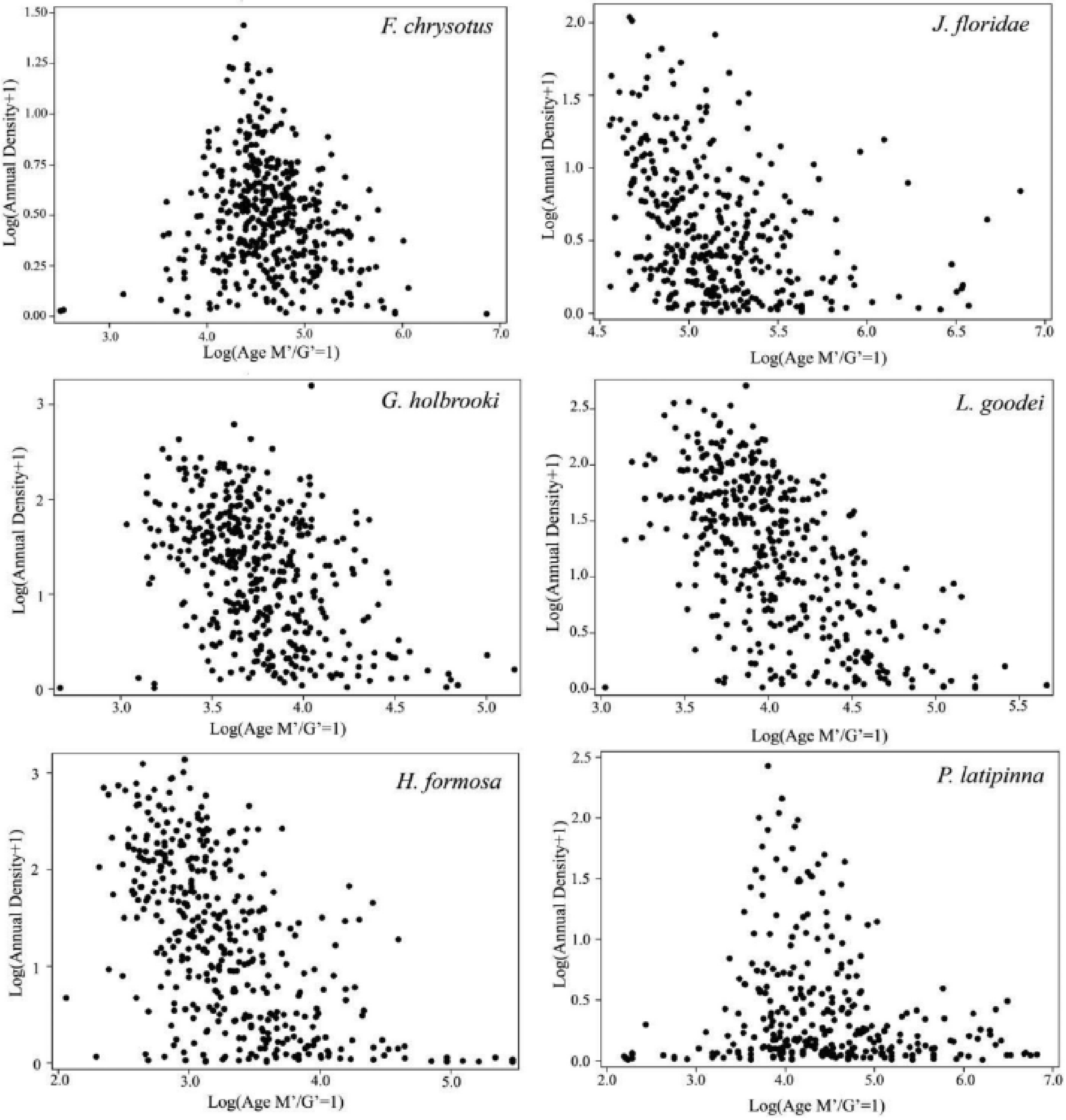
Fig. 2. Relationship between the log-transformed transitional age (days) and annual density for the pooled data of each species.



species (McMullen et al. 2017; Stige et al. 2019). We detected spatial–temporal trends in mortality that were correlated with hydrology. Although we expected to find higher mortality for populations at short hydroperiods due to hydrological stress, results here indicated that populations within longer hydroperiods (little to no hydrological stress) experienced higher mortality. These populations had higher density and biomass compared with shorter hydroperiods. Both compensation and density-dependent mortality can also act as stabilizing mechanisms, enhancing recruitment (Doherty 2002; Hixon and Webster 2002). This may explain why we observed higher mortality and higher recruitment at longer hydroperiods. Long-hydroperiod sites have more piscivorous fishes than shorter-hydroperiod sites (Chick et al. 2004; Parkos et al. 2011), which could contribute to this pattern. We found that the CV for mortality was higher than for growth, consistent with other studies documenting that mortality is more variable. Differences in CV suggest that mortality may contribute more to variability in recruitment than growth (Houde 1997*a*; Shoji and Tanaka 2007). However, populations at long-hydroperiod sites experienced higher mortality and higher recruitment, providing

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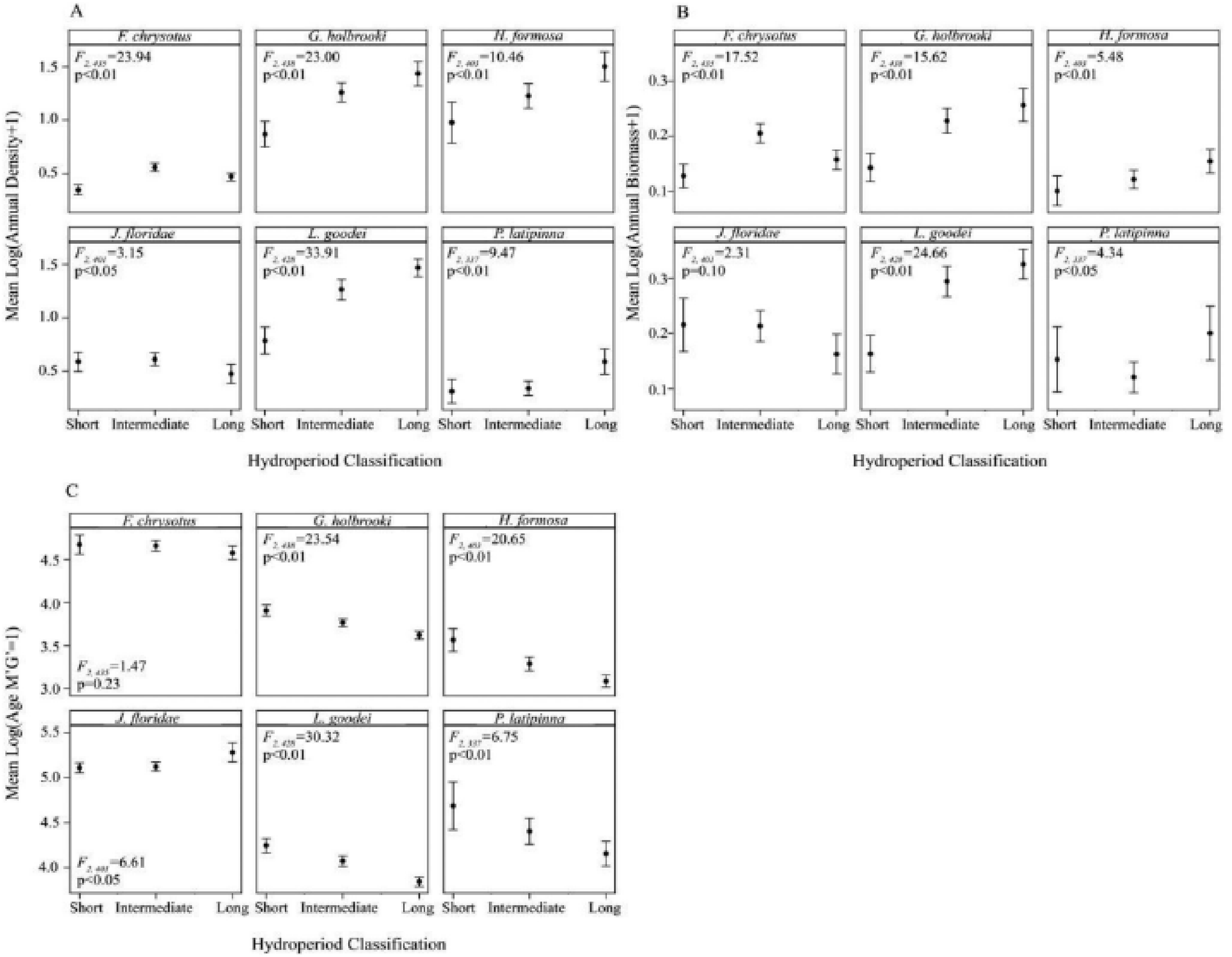

Fig. 3. Results from the general linear model (GLM) testing differences in species (A) annual density, (B) annual biomass, and (C) age $M'/G' = 1$ among hydroperiod classes.

some evidence that subtle changes in growth may yet play a role in recruitment dynamics for some species.

Population-level differences in somatic growth have been linked to population fluctuations in some species and may be more important than recruitment (Stawitz and Essington 2019). Although drought and disturbance can reduce fish growth rates and body condition in hydrologically pulsed ecosystems (Walters 2016), we found no differences in growth or on any of the estimated growth parameters among hydroperiod classes. Hydrological stress resulted in reduced density and biomass production for populations at short hydroperiods. Growth should be higher when exposed to lower density-dependent mortality via growth-selective predation and density-dependent growth (Takasuka et al. 2003, 2004). In this study system, Loftus et al. (1990) found evidence that slow growth at short hydroperiods is independent of density. Short-hydroperiod sites in the Everglades tend to be very oligotrophic and support low-quality basal food sources (Belicka et al. 2012; Trexler et al. 2015; Sanchez and Trexler 2016). Because subtle differences in either growth or mortality can contribute to large differences in recruitment (Houde 1987), small differences in growth below our ability to detect in these data could contribute to ecologically important recruitment variability for populations experiencing density-dependent mortality, possibly from predation, and is worthy of further study.

Timing of the transitional age has previously been linked to recruitment levels, with higher recruitment associated with cohorts experiencing this transitional stage at earlier sizes or younger ages (Houde 1997b). We found that the timing of the transitional age was inversely correlated with species density, but weakly correlated with species biomass. There was no evidence to suggest that site hydroperiod disrupted this relationship, with results largely species-specific. Density and the transitional age were highly correlated for less mobile, slowly recovering species (*H. formosa*, *L. goodei*) compared with more mobile, rapidly recovering species (*G. holbrooki*, *J. floridae*, *F. chrysotus*), which we believe results from differences in movement strategies associated with drying (Gatto and Trexler 2020; Hoch et al. 2015). Gatto and Trexler (2020) suggested that dispersal of more mobile species plays a greater role in recruitment in disturbed, spatially structured ecosystems than changes in growth and mortality. For less mobile species, trends in biomass and density at study sites were tightly linked with the transitional age and probably less influenced by dispersal. Differences in movement strategies may have a greater impact on fluctuation of biomass and density than the

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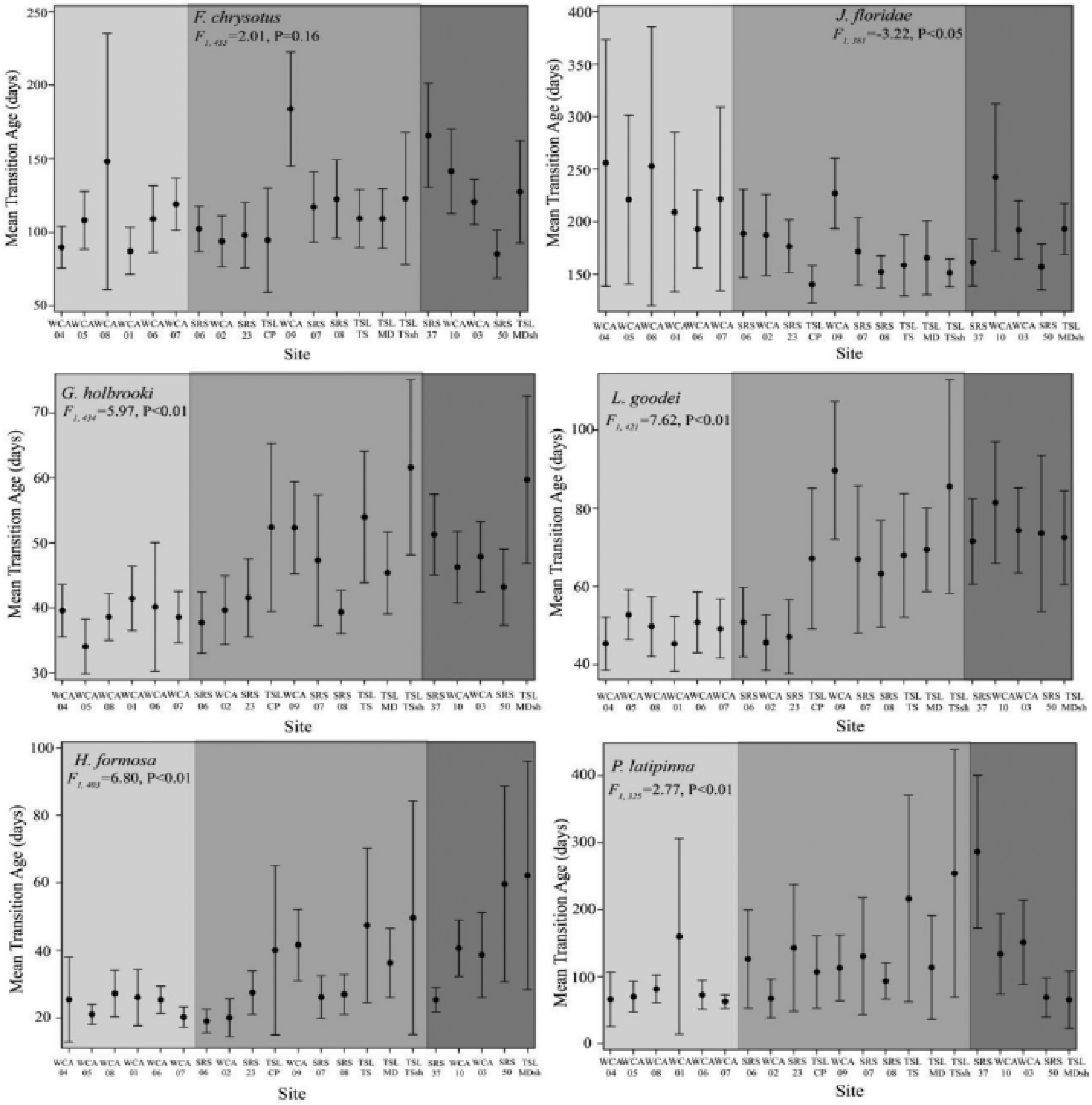
Fig. 4. Mean transitional age (age $M'/G' = 1$) at each site for each species. The transitional age was averaged across 20 years for each site. Sites are arranged from least disturbed (left) to most disturbed (right). Shaded bands indicate hydroperiod classification: long (light grey), intermediate (grey), and short (dark grey). WCA, Water Conservation Area; SRS, Shark River Slough; TSL, Taylor Slough.



factors acting on age-specific mortality and growth. Age-specific differences in movement may explain why the transitional age was more closely linked to changes in annual density than biomass in this study (Scharbert and Borcherding 2013). These results are consistent with findings that inundation of floodplains plays a major role in movement of juveniles and adults between permanent waterbodies and temporary wetlands (Balcombe et al. 2007; Yurek et al. 2016).

The frequency, intensity, and spatial extent of disturbances play major roles in altering species density and diversity (Huston and Huston 1994; Sousa 1984). These characteristics reduce density by removing individuals and relying on recolonization dynamics postdisturbance (McCabe and Gotelli 2000). Our results revealed higher recruitment, biomass, and density at long-hydroperiod sites. There was mixed evidence for hydroperiod treatments influencing demographic changes in M'/G'; however, the timing of the transitional stage did occur at smaller sizes or younger ages at more stable sites (longer hydroperiods). Disturbance frequency (number of drying events) resulted in the transitional age occurring later in life for *G. holbrooki*, *L. goodei*, and

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H. formosa. For some species, the M'/G' transition shifted from the juvenile life stage to postonset of sexual maturation (e.g., *H. formosa*). This resulted in a drastic shift in the transitional stage to size–ages postmaturation, which scaled to a large reduction in recruitment and possibly reproduction. Analyses also indicated a weak parabolic association with the timing of the transitional age and annual hydroperiod. Prolonged periods of drought during extreme drying events appear to shift the transitional age to an earlier age or smaller sizes. Pulses in primary and secondary production following inundation may temporarily enhance recruitment via increases in both growth and survival (Junk et al. 1989; King et al. 2003; Sommer et al. 2001).

Landscape changes and climate change are among the greatest threats to aquatic ecosystems (Mantyka-Pringle et al. 2014; Woodward et al. 2010). Deviations from historical hydrological conditions are the focus of restoration efforts in the Everglades (Davis and Ogden 1997) and management of aquatic systems generally (e.g., Poff et al. 1997). In the Everglades, restoration actions that lengthen the hydroperiod in overdried marshes would be expected to reduce hydrological stress, stabilize the effects of density-dependent mortality, and increase recruitment levels in part through an expected shift of the M'/G' transition to younger ages or smaller sizes (Trexler et al. 2005). Climate change scenarios that predict reduced hydroperiods in the future were modeled and generally predicted lower fish density (Catano et al. 2015). Climate change may also disrupt the relatively predictable seasonal hydrological regime, causing extreme events that would make the system very wet (longer hydroperiods, deeper water) or very dry (shorter hydroperiods, prolonged drought). This would alter the hydrologic conditions that are optimal for growth and survivorship and reduce recruitment (King et al. 2003). Decreased hydroperiods associated with climate change would also be expected to impact fish recruitment negatively by shifting the transitional age to older ages. Furthermore, saltwater intrusion is predicted to affect the southern reaches of TSL by shifting the present community to a more estuarine one (Catano et al. 2015). Our results suggest that this may benefit more salt-tolerant species, such as *P. latipinna*, which have been shown to grow faster in saltwater conditions (Trexler and Travis 1990). Enhanced growth, coupled with higher survivorship, would enhance recruitment for this species, but rising salinity levels may be detrimental to less-tolerant species (*L. goodei*, *F. chrysotus*; Lorenz and Serafy 2006). Tracking growth, survivorship, and shifts in the transitional age provides a measure to evaluate the interplay between future restoration actions and climate change on recruitment.

Recruitment has become a central focus for both maintaining sustainable fisheries and habitat restoration efforts (Oele et al. 2019; Zimmermann et al. 2019). This has led to extensive work on the importance of age-specific growth and mortality (Beyer 1989; Cushing 1975). These studies have linked the transitional age ($M'/G' = 1$) to higher recruitment and the transitional stage occurring at smaller sizes or earlier ages. In anthropogenically modified systems, hydrological stress negatively impacts both growth and survival of fishes (Walters 2016). We have expanded on previous work by evaluating the negative effects of hydrological stress on demographic changes in M'/G'. Although the focus of this study was on hydrological variability, a diversity of environmental factors can also impact fish stocks (Büntgen et al. 2015; Jenkins et al. 2010). Fisheries management and habitat-restoration efforts would benefit by focusing on linkage of environmental variability and demographic shifts in M' and G' and the transitional age for any species of concern.

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