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EFFECTS OF RIVER HYDROLOGY AND PHYSICOCHEMISTRY ON ANCHOVY ABUNDANCE AND CYMOTHOID ISOPOD PARASITISM

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KEY WORDS

Estuaries
Anchovies
Isopods
Water Chemistry
River Flow
Preserved Collection Survey
Hillsborough River (Tampa Bay, Florida)
Alafia River (Tampa Bay, Florida)
Lironeca ovalis (Say, 1818) (Crustacea: Isopoda)
Bay Anchovy *Anchoa mitchilli* (Valenciennes, 1848) (Actinopterygii: Clupeiformes)

ABSTRACT

The flow regime of a river is an important driver of many ecosystem components. However, few studies explore how differences in flow rates and water chemistry can influence communities of parasites and their hosts. Here, we investigate the impact of dissolved oxygen, pH, salinity, water temperature, and river flow on the abundance and prevalence of cymothoid isopod parasitism (*Lironeca ovalis*) of the Bay Anchovy (*Anchoa mitchilli*) in the Alafia and Hillsborough rivers of Tampa Bay (Florida). We also explore seasonality by comparing monthly samples preserved throughout 2005–2007. Although both the Alafia and Hillsborough rivers had similar average water temperatures and salinity, and similar wet and dry season cycles, the upstream damming of the Hillsborough River had numerous negative effects on water flow rate, dissolved oxygen content, and acidity. This disruption in water quality corresponded with a lower abundance of anchovy hosts, fewer free-swimming cymothoids, and low prevalence of anchovy parasitism. Anchovies were much more abundant in the Alafia River, but flow negatively affected abundance—a negative effect that could be mitigated by positive changes in water temperature, salinity, and pH. Flow rates also negatively affected free-swimming cymothoid abundance; however, water flow was less important in predicting their parasitism of anchovies. In Alafia, fewer anchovies were parasitized when dissolved oxygen was high and water acidity was low, but more were parasitized during the wet season. These findings corroborate predictions that flow can moderate habitat stability and complexity which, in turn, can impact opportunities for parasitism of host communities.

Estuarine fish and their parasites are exposed to a large variety of hydrological, physical, and chemical conditions (Whitfield and Elliott, 2002), and these factors can affect the abundance of hosts available to parasitize as well as the prevalence and intensity of parasitism (Galli et al., 2001). For example, water acidity can affect parasite populations positively or negatively; where typically higher acidity correlates with higher prevalence, but prevalence can decrease when hosts are tolerant to the acidic water (Halmetoja et al., 2000). Low dissolved oxygen levels can also negatively affect the susceptibility of hosts (Coutant, 1985), and flow rates and freshwater influx can affect both host and parasite populations by altering surface water salinity (Brooks, 2005).

River damming can further alter these hydrological and chemical conditions by reducing freshwater flow and, by extension, oligohaline composition (salinity), temperature, and dissolved oxygen (Drinkwater and Frank, 1994; Friedl and Wüest, 2002), all of which are important to maintain habitat complexity and health (Bredenhand and Samways, 2009). Seasonality in salinity and water temperature can also moderate parasite abundance and prevalence in brackish water (Möller, 1978; Landsberg et al., 1998), and damming can further modify these cycles by altering oxygen and creating anoxic conditions or by disrupting regular thermal cycles (Friedl and Wüest, 2002).

Here, we explore the effects of river hydrology and water chemistry, as well as the impacts of damming and seasonality, on the abundance of bay anchovies (*Anchoa mitchilli*) and isopod parasitism between the Hillsborough and Alafia rivers—2 rivers that flow into Tampa Bay, Florida. Because seasonality is known to play a role in the river spawning of anchovies and parasite prevalence (Lindall et al., 1975; Leonardos and Trilles, 2003), we compared monthly samples from the 2 rivers throughout 2005–2008, with the goals to: (1) identify key seasonal trends in the abundance of *A. mitchilli*, (2) link these trends to the significant seasonal heterogeneity in river hydrology and chemistry, and finally (3) determine how changes in anchovy abundance and river attributes influence parasitism by cymothoid isopods (*Lironeca ovalis*; Landau et al., 1995; Leonardos and Trilles, 2003; Peebles, 2005). This isopod is a common gill ectoparasite of teleost schooling fish found throughout the eastern and Gulf coasts of the United States (Landau et al., 1995; Leonardos and Trilles, 2003; Jones et al., 2008). In particular, we compare river effects on two phases of its life-cycle: first among free-swimming juveniles that temporarily attach and feed on hosts (i.e., natatory-stage) and then as reproductive adults, which are attached to hosts permanently. Given that adult cymothoids have limited mobility and must tolerate the conditions experienced by hosts, it is possible that juveniles can respond differently to habitat change, as they can disperse if riverine conditions become unfavorable. Finally, in Tampa Bay damming is also known to interrupt freshwater flow, resulting in hypersaline environments that are too difficult for *A. mitchilli* to spawn or occupy (Peebles et al., 2007), and we explore these effects within the Hillsborough River, which has been dammed since 1944.

MATERIALS AND METHODS

We explored the abundance of anchovies and their isopod parasites preserved in 1-L formalin-filled jars stored at the University of South Florida College of Marine Science (St. Petersburg, Florida). These samples originated from bi-monthly surveys of the Hillsborough and Alafia rivers in 2005, 2006, and 2007. Both rivers flow into Tampa Bay (Florida) and surveys were conducted ~3.5 km upstream from Tampa Bay (Hillsborough: 27°51′27.662″N, 82°21′59.788″W; Alafia: 28°1′13.08″N, 82°27′11.879″W); for Hillsborough River, the survey site is also ~13 km downstream from the Hillsborough River Dam. These rivers also differ in length (Hillsborough: 95 km, Alafia: 40 km) and watershed size (1,917 km^2 and 870 km^2, respectively). Each jar contained the entire contents of trawling samples using a 500-μm conical mesh net with 1-L plastic cod end jar. Trawls began approximately 2 hr after sunset and could last up to 4 hr. Bottom, mid-water, and surface depths were towed for 5 min, and net deployment occurred between both low and high slack. During towing, depth contour was held constant and estimated using the average cross-sectional depth of the sampling area in each river. Sample surveys were then preserved in 6–10% formalin. Additional details about these surveys are found in MacDonald et al. (2005).

In total, we analyzed 72 of these sample surveys (jars) from both Hillsborough and Alafia Rivers (e.g., 2 per month for 3 yr). For each jar, the number (abundance) of *A. mitchilli* and free-swimming *L. ovalis* were counted as well as the number of *A. mitchilli* with attached *L. ovalis* ectoparasites. Jars with no anchovies or isopods were counted as 0, and the prevalence of anchovy parasites was calculated as the proportion of anchovies with one or more attached *L. ovalis* in a jar. Due to physical disturbances during capture, as well as the preservation process itself (see Boyko and Williams, 2016), there is the possibility that some *L. ovalis* ectoparasites may have detached from hosts. Although detached cymothoids may leave a signature of infection (e.g., gill damage) useful to estimate the relative frequency of gill detachments (see Rameshkumar and Ravichandran, 2014), the small size of anchovies (~22 mm) prevented us from estimating this frequency without destructively sampling museum collections. Given this detachment possibility, we assume our surveys underestimate parasitism prevalence and overestimate free-swimming isopod abundance (e.g., we could not distinguish between free-swimming isopods captured during trawls and those that detached from hosts).

We explored predictors of anchovy abundance and parasitism with river water quality and hydrological data. Water quality predictors (i.e., dissolved oxygen, pH, salinity, and water temperature) were derived from monthly-averages of EP HIMP surveys (Hillsborough County, Environmental Protection Commission; http://www.epchc.org/) nearest to where anchovies were sampled (EP HIMP site ID: Hillsborough River4, and Alafia River4). Hydrological data on river flow (cubic feet per second [cf/s]) were monthly-averages from USGS surveys (USGS National Water Information system; https://waterdata.usgs.gov/nwis), and were also nearest to anchovy sampling sites (USGS NWIS site IDs: Hillsborough River at Rowlett PK DR Tampa Florida, and Alafia River near Gibsonton, Tampa, Florida).

Comparisons of water quality and hydrology among rivers were performed with linear mixed-effects models (LMM) using the *nlme* package (v0.8.3.3; Fournier et al., 2012) in R (v3.2.3; R Core Team, 2015). Abundance data of anchovies and free-swimming isopods were analyzed with negative binomial mixed-effects models (generalized linear mixed model; GLMM) using the *glmmADMB* package (v0.8.3.3; Fournier et al., 2012). All GLMM models assumed the "nbinom1" family of negative binomial distributions (e.g., variance proportional to the mean model; Fournier et al., 2012) and changes from default settings to help improve convergence that included a greater number of importance sampling steps (impSamp = 5,000) and evaluation steps (maxfn = 20,000). To account for the yearly and monthly variability among survey samples, both year and month were included as random-effects in our LMM and GLMM models. All river predictors (dissolved oxygen, pH, salinity, water temperature, flow) were continuous, but season was treated as a categorical predictor marking the wet and dry seasons of Tampa Bay (based on National Oceanic and Atmospheric Administration [NOAA] reports of monthly precipitation changes). We also tested for multicollinearity and dispersion of each predictor by estimating their variance inflation factor (VIF). Predictors were retained in models when VIF values did not exceed 3 (following Zuur et al., 2010) and VIFs were estimated using the *car* package (v3.0-0; Fox and Weisberg, 2019). The *lsmeans* package (v2.25-5; Lenth, 2016) was used to estimate least-square means (LS means). Finally, models exploring predictors of parasite prevalence were based on zero-inflated binomial (log link) GLMMs; inclusion of a zero-inflation parameter was necessary given that we could not distinguish unparasitized anchovies and parasitized-anchovies that lost isopod ectoparasites during sampling and preservation. These models were implemented using the *glmmTMB* package for R (v0.2.3; Brooks et al., 2017), assuming cbind (infected, uninfected anchovy number) as the response variable, and again assuming both year and month as random effects. Multicollinearity was tested with VIFs estimated from the *performance* R package (v0.2.0; Lüdecke, 2018) and, finally, LS means were estimated using the *emmeans* R package (v1.3.5; Lenth and Herve, 2018).

RESULTS

Flow and water chemistry of Alafia and Hillsborough rivers

Combining trends across years while accounting for monthly and yearly variability using GLMM, Alafia had a greater flow rate than did Hillsborough (Fig. 1; Alafia: LS mean = 357.54 cf/s, SE = 51.94; Hillsborough: LS mean = 85.96 cf/s, SE = 51.16; $t =$ –6.34, $P < 0.0001$), and more dissolved oxygen (Alafia: LS mean = 5.78 mg/L, SE = 0.47; Hillsborough: LS mean = 4.61 mg/L, SE =

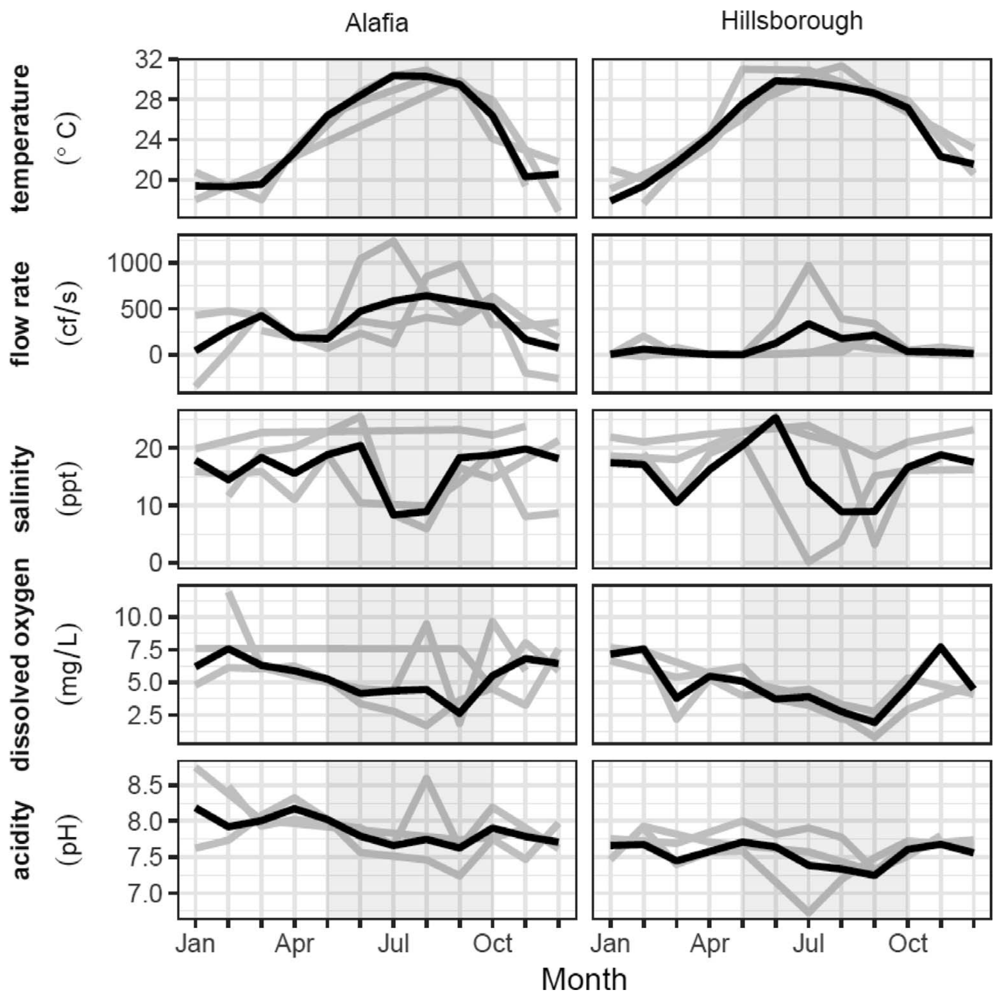

Figure 1. Monthly averages of hydrological and physicochemical measurements between Hillsborough and Alafia rivers for 2005, 2006, and 2007. Grey lines indicate individual year means, black lines are the pooled average across the 3 yr, and the shaded areas emphasize the wet season in Tampa Bay region (Florida). Tests for seasonal differences among rivers are found in Figure 2.

0.48; $t = -2.11$, $P = 0.0478$), but Hillsborough River tended to be less alkaline (Alafia: LS mean = 7.91 pH, SE = 0.095; Hillsborough: LS mean = 7.61 pH, SE = 0.095; $t = -3.67$, $P = 0.0021$). There were no differences in water temperature (Alafia: LS mean = 24.34 C, SE = 0.79; Hillsborough: LS mean = 25.06 C, SE = 0.79; $t = 1.66$, $P = 0.1153$) and salinity (Alafia: LS mean = 17.02 parts per thousand [ppt], SE = 2.56; Hillsborough: LS mean = 17.88 ppt, SE = 2.55; $t = 0.61$, $P = 0.5526$).

Modeling wet and dry seasons revealed significant seasonal heterogeneity in water characteristics and chemistry among rivers (Fig. 2). During the wet season, both Alafia and Hillsborough tended to be ~7 C warmer (RIVER: GLMM Wald's $\chi^2 = 4.8$, $P = 0.02872$; SEASON: Wald's $\chi^2 = 69.34$, $P < 0.0001$; RIVER × SEASON: Wald's $\chi^2 = 2.5$, $P = 0.1129$), had significantly greater flow rates (RIVER: Wald's $\chi^2 = 15.5$, $P < 0.0001$; SEASON: Wald's $\chi^2 = 8.5$, $P = 0.0035$; RIVER × SEASON: Wald's $\chi^2 = 1.5$, $P = 0.2272$), less dissolved oxygen (RIVER: Wald's $\chi^2 = 1.78$, $P = 0.1815$; SEASON: Wald's $\chi^2 = 7.013$, $P = 0.008093$; RIVER × SEASON: Wald's $\chi^2 = 0.039$, $P = 0.8432$), and were less alkaline (RIVER: Wald's $\chi^2 = 8.01$, $P < 0.0046$; SEASON: Wald's $\chi^2 = 3.4$, $P = 0.06458$; RIVER × SEASON: Wald's $\chi^2 = 0.0947$, $P = 0.75321$). Although seasonal differences could not be identified for salinity (RIVER: Wald's $\chi^2 = 0.44$, $P = 0.5065$; SEASON: Wald's $\chi^2 = 0.53$, $P = 0.4625$; RIVER × SEASON: Wald's $\chi^2 = 0.03$, $P = 0.8544$), trends suggest a drop during the mid to late wet season (Fig. 2).

Anchovy abundance and isopod prevalence of Alafia and Hillsborough rivers

There were marked differences in anchovy and free-swimming isopod abundance between rivers (Fig. 3). Anchovies were 3 times more abundant in Alafia then in Hillsborough (Alafia: GLMM LS mean = 161.14, SE = 54.97; Hillsborough: GLMM LS mean = 47.09, SE = 27.86; Wald's $\chi^2 = 6.91$, $P = 0.0108$), and free-swimming isopods were nearly 10 times more abundant in Alafia (Alafia: GLMM LS mean = 14.61, SE = 10.29; Hillsborough: GLMM LS mean = 1.87, SE = 2.29; Wald's $\chi^2 = 6.27$, $P = 0.0123$).

Table I describes the overall, seasonal, and yearly variation of parasitism prevalence of isopod ectoparasitism of anchovies. In general, very few anchovies were parasitized, but anchovies from Alafia River tended to be more abundant and a have a greater likelihood of parasitism than anchovies sampled in Hillsborough.

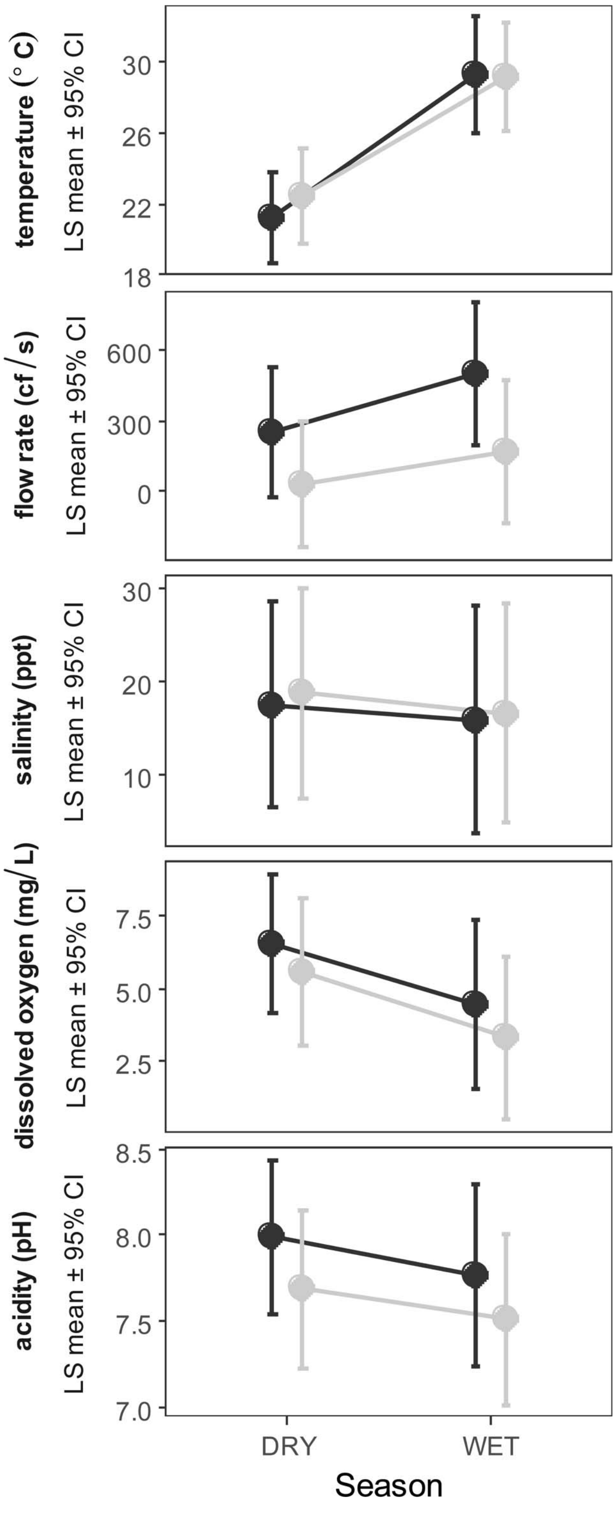

Figure 2. Comparison of least-square means (LS mean) of hydrological and physicochemical measurements taken during wet and dry seasons in the Hillsborough (grey bars) and Alafia (black bars) rivers. LS means were estimated from linear mixed-effects models (LMM) models on the pooled average across 3 yr (2005, 2006, and 2007) that included only season (wet and dry) as a fixed-effect and both year and month as random-effects.

There were no differences in anchovy abundance during the wet and dry seasons in Alafia (SEASON: GLMM Wald's $\chi^2 = 0.92$, $P = 0.3383$) or Hillsborough River (SEASON: GLMM Wald's $\chi^2 = 1.05$, $P = 0.3051$). When accounting for yearly and monthly variability, and for zero inflation, the rivers differed in prevalence (Wald's $\chi^2 = 25.85$, $P < 0.0001$; zero-inflation parameter $= -0.056$, SE $= 0.436$), where anchovies in Alafia were more parasitized than those in Hillsborough (Alafia prevalence: GLMM LS mean = 0.0271, LCI = 0.0122, UCI = 0.0592; z = –8.7, $P < 0.001$; Hillsborough prevalence: GLMM LS mean = 0.0034, LCI = 0.0011, UCI = 0.0106; z = –9.9, $P < 0.001$). There were rare cases in which individual anchovies had more than 1 isopod (n = 3).

Predictors of abundance and parasitism within rivers

Because there were differences in flow and water chemistry among Alafia and Hillsborough rivers (see "Flow and water chemistry of Alafia and Hillsborough rivers"), predictors of anchovy abundance and parasitism were analyzed separately for each river. Further, given that the abundance and parasitism of isopods was low (especially in Hillsborough River; Fig. 2), only the main-effects of flow and river characteristics (e.g., pH, dissolved oxygen), and not their interaction effects, were tested as predictors in Alafia River.

River flow had a negative effect on anchovy abundance in Alafia, but this negative effect could be heavily moderated by the strong positive effects of temperature, salinity, and pH (Table II). Further, increases in dissolved oxygen slightly exacerbated the negative effects of river flow, and the strong positive effects of temperature on abundance can be moderated by increases in pH. Finally, the positive effects of salinity on anchovy abundance were weakened by increased dissolved oxygen. Flow also negatively affected free-swimming isopod abundance, but the predicted effect was small (Table III); however, there were several predictors of parasite prevalence. Low dissolved oxygen and high acidity were associated with higher parasite prevalence (Table III) and, finally, the proportion of parasitized anchovies captured during the wet season was greater than the proportion infected during the dry season (Table III). Finally, when combining all isopods within samples (i.e., free-swimming + attached to hosts), we found that total isopod abundance was positively predicted by the number of anchovies, and that there were more isopods during the wet season, but that abundance was negatively affected by high temperatures (Table III).

Flow negatively affected the abundance of anchovies in the Hillsborough River, but only temperature and pH were found to moderate this negative effect (Table IV). Although temperature was not a significant predictor of anchovy abundance, there were crossover interactions with dissolved oxygen and salinity, indicating that the directionality in the effects of temperature on abundance will change depending on the amount of dissolved oxygen and salinity. There were too few parasitized anchovies to test predictors of parasitism abundance.

DISCUSSION

Our findings corroborate other studies that found river quality characteristics predict trends in parasite–host communities. Flow rate is a key predictor of organism abundance and estuarine health (Vega et al., 1998; Kimmerer, 2002), and we found that the

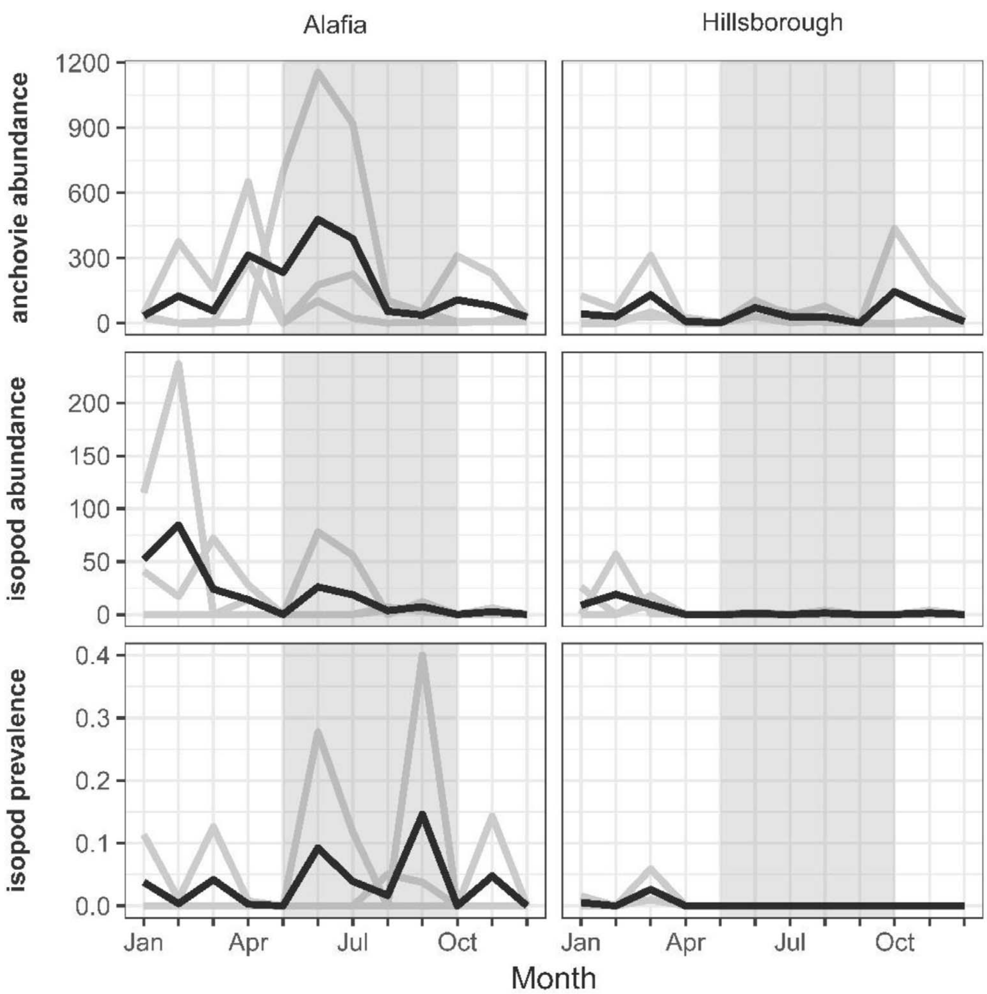

Figure 3. Monthly abundance of anchovies, free-swimming isopods, and prevalence of isopod parasitism of anchovies between Hillsborough and Alafia rivers in 2005, 2006, and 2007. Grey lines indicate individual year abundance, black lines are the pooled average across the 3 yr, and the shaded areas emphasize the wet season in Tampa Bay region (Florida).

Alafia River had on average 4 times the flow rate of Hillsborough. Correspondingly, Alafia also had a much higher abundance of both anchovies and isopods (Fig. 3)—despite having similar water temperatures and salinity as Hillsborough. The primary cause of this difference is an upstream dam on Hillsborough—which has maintained a freshwater reservoir since 1944. Here, instead of receiving freshwater inflow from a natural spring where the river begins, Hillsborough tends to receive a much higher level of saltwater intrusion from Tampa Bay and therefore experiences more variable (including negative) flow rates (Pillsbury and Byrne, 2007).

With less flow, there is a higher chance for anoxic conditions (Vega et al., 1998), and the dammed Hillsborough River did have significantly less dissolved oxygen than did Alafia (Fig. 1). Low dissolved oxygen levels can be stressful for aerobic organisms, and our findings corroborate Boesch et al. (2001) predictions that low oxygen levels will negatively affect anchovy–isopod interactions—given that few anchovies and isopods were collected in Hillsborough River. Our findings are also consistent with other studies that found low dissolved oxygen tended to negatively impact main or intermediate host abundance and therefore lowered infection rates (MacKenzie et al., 1995). However, it is also important to note that many other studies have found that low levels of dissolved oxygen can favor parasitism (Snieszko, 1974; Ahmad et al., 2016). In our particular case, the observed ranges of dissolved oxygen within Hillsborough, although lower than in Alafia, were still within reported tolerance ranges for anchovies in the Tampa bay (2.4–6.2 mg/L; Lindall et al., 1975). Similar to dissolved oxygen, salinity levels can also influence host and therefore parasite abundance (Copeland, 1966). For example, juvenile stage bay anchovies are capable of living at relatively low levels of salinity of <5 ppt whereas adult anchovies typically frequent higher-level salinities of around 10–30 ppt (Kimura et al., 2000; Peebles et al., 2007). However, we did not detect salinity effects in our study. Finally, the Hillsborough River was also less alkaline than the Alafia River, and previous studies have shown that estuarine systems with higher levels of alkalinity typically have higher infection rates (Overstreet, 1993). This could explain the greater abundances of anchovies and isopods in Alafia, as low alkalinity allows for high concentrations of metals that can have a negative impact on the hosts and their parasites (see Overstreet and Howse, 1977). Further, although Alafia was less acidic then

Table I. Prevalence of cymothoid isopod ectoparasitism of the Bay anchovy in Alafia and Hillsborough rivers between 2005 and 2007. Prevalence (P) and lower (L) and upper (U) 95% confidence intervals (CI) calculated following Wilson (1927) using the small-sample continuity correction described in Newcombe (1998), and n is the number (total abundance) of anchovies sampled.

River, season, and survey year	n	Prevalence		
		P	LCI	UCI
Overall (rivers combined)	7,496	0.0121	0.0098	0.0149
Dry season	3,531	0.0125	0.0092	0.0169
Wet season	3,965	0.0119	0.0089	0.0159
Overall Alafia	5,801	0.0141	0.0113	0.0176
Dry season	2,228	0.0157	0.0111	0.0220
Wet season	3,573	0.0132	0.0098	0.0177
2005	1,419	0.0261	0.0187	0.0392
2006	3,531	0.0113	0.0082	0.0155
2007	851	0.0059	0.0022	0.0145
Overall Hillsborough	1,965	0.0046	0.0023	0.009
Dry season	1303	0.0069	0.0034	0.0136
Wet season	392	0.0000	0.0000	0.0121
2005	652	0.0077	0.0028	0.0189
2006	120	0.0083	0.0004	0.0523
2007	923	0.0033	0.0009	0.0104

was Hillsborough, increases in acidity were also associated with higher parasite prevalence (Table III).

Low flow rates also negatively impact water temperature (Sinokrot and Gulliver, 2000; Caissie, 2006), which itself also strongly predicts organism abundance in estuarine habitats (Jonsson, 1991). Further, other studies have found that higher temperatures correlate with higher parasitism rates (Costello, 2006; Marcogliese, 2008; Key et al., 2011). We found that despite both Alafia and Hillsborough rivers having similar average temperatures (Fig. 1), temperature only predicted anchovy abundance in Alafia. Recorded temperatures within each river are well within known anchovy spawning ranges of 19–34 C (Leak and Houde, 1987; Zastrow et al., 1991). In other regions, such as the Chesapeake Bay, temperatures can reach as low as 3.4 C, and anchovies will not spawn at these temperatures, resulting in low abundances (Luo and Musick, 1991; Gamble, 1994).

Trends in abundance, parasitism, and water quality characteristics were also dominated by seasonal shifts in the Alafia and Hillsborough rivers (Fig. 1). During the wet season, there is a significant increase in flow and temperature but also drops in salinity, dissolved oxygen, and acidity (Fig. 1). Throughout the wet season, both the Alafia and Hillsborough rivers experience extended rainfall (Kelly and Gore, 2008) and, due to this increased rainfall, there is increased freshwater input (Schmidt and Luther, 2002). This also explains the change in salinity that the Hillsborough River experiences during the wet season. The Hillsborough River increases in flow and alkalinity during the wet season. Alkalinity was found to be negatively correlated with higher flow, and because flow is greater during the wet season in both rivers, this corresponds with our observed decrease in alkalinity. Temperature also increased in both rivers during wet seasons—this corresponds with elevated ambient temperature during this period of the year. The increase in temperature also

Table II. Predictors of anchovy abundance in Alafia River between 2005 and 2007. Model results are based on a generalized linear mixed model (GLMM) with a negative binomial distribution fitted with year and month as random effects. The negative binomial dispersion parameter of this model was $\alpha = 1.001$ with SE = 0.000015. Significance of regression coefficients (*Coef.*) and their standard error (SE) were assessed with a z-test and are emphasized in bold, and tests of main effects were based on Wald's χ^2 tests. There was no evidence for multicollinearity among predictors: FLOW (VIF = 1.61), TEMPERATURE (VIF = 1.52), DISSOLVED OXYGEN (VIF = 1.03), SALINITY (VIF = 1.16), and PH (VIF = 1.05).

Predictor	GLMM regression coefficients		Wald's effect tests		
	Coef.	SE	χ^2	df	*P*
(Intercept)	−836.00	384.00			
FLOW	**−0.25**	**0.09**	**7.11**	**1**	**0.0077**
TEMPERATURE	**23.80**	**9.59**	**6.17**	**1**	**0.0130**
DISSOLVED OXYGEN	19.30	25.50	0.73	1	0.3917
SALINITY	**17.70**	**8.86**	**3.98**	**1**	**0.0460**
PH	**103.00**	**44.60**	**5.29**	**1**	**0.0214**
FLOW × TEMPERATURE	**−0.003**	**<0.01**	**19.95**	**1**	**<0.0001**
FLOW × DISSOLVED OXYGEN	**−0.01**	**<0.01**	**20.32**	**1**	**<0.0001**
FLOW × SALINITY	**−0.002**	**<0.01**	**6.23**	**1**	**0.0125**
FLOW × PH	**0.05**	**0.01**	**14.45**	**1**	**0.0001**
TEMPERATURE × DISSOLVED OXYGEN	0.30	0.29	1.04	1	0.3069
TEMPERATURE × SALINITY	−0.003	0.03	0.01	1	0.9212
TEMPERATURE × PH	**−3.10**	**1.18**	**6.86**	**1**	**0.0088**
DISSOLVED OXYGEN × SALINITY	**−0.22**	**0.09**	**5.02**	**1**	**0.0251**
DISSOLVED OXYGEN × PH	−2.43	2.16	1.26	1	0.2615
SALINITY × PH	−2.03	1.05	3.75	1	0.0528

impacts dissolved oxygen production, as the solubility of oxygen increases at higher temperatures; this prediction corresponds with our finding of less dissolved oxygen in both rivers during this season (Fig. 1; Abowei, 2010). Finally, the prevalence of isopod infection during both the wet and dry season were similar. However, the Hillsborough River had a lower level of infection during the wet season, presumably due to large amounts of rain causing higher levels of freshwater inflow over the Hillsborough River Dam (Chen et al., 2000); however, seasonal fluctuations in water regime can also affect organism abundances (Castillo-Rivera et al., 1994; McCullough, 1999; Ray et al., 2012).

Future research should examine river pollution and its effects on the trophic interactions between *A. mitchilli* and *L. ovalis*. Pollution in both fresh and saltwater systems can affect parasites (Poulin, 1992), but depending on the life cycle of the parasite, pollution levels can either positively or negatively impact parasite abundance (Overstreet and Howse, 1977). In our particular system, the parasitic isopod has a direct life cycle and, therefore, river quality will have a more direct effect on the physiology and ecology of the organism. Further, integrating anchovy size will also be key to explaining variability in parasitism among rivers, given the considerable variability in body length among anchovies (mean = 21.9 mm, SD = 2.75, min = 16.83, median = 21.67, max = 26.21, n = 30; B.N.M., unpubl. data), evidence for host size preference among cymothoid isopods (Marks et al., 1996), and that anchovy body size itself may be moderated by river quality

Table III. Predictors of free-swimming isopod abundance, prevalence of anchovy parasitism, and total abundance of cymothoid isopods (free-swimming + attached individuals) in Alafia River. Model results of abundance data are based on generalized linear mixed models (GLMMs) with a zero-inflated negative binomial distribution and results of prevalence based on a binomial zero-inflated GLMM. All models fitted sampling year and month as random effects. Significance of regression coefficients (*Coef.*) and their standard error (SE) were assessed with a *z*-test and are emphasized in bold, and tests of main effects were based on Wald's χ^2 tests.

Predictor	GLMM regression coefficients		Wald's effect tests		
	Coef.	SE	χ^2	df	*P*
free-swimming isopod abundance*					
(Intercept)	13.28	9.68			
FLOW	**<−0.01**	**<0.01**	**4.84**	**1**	**0.0279**
TEMPERATURE	0.07	0.14	0.23	1	0.6343
DISSOLVED OXYGEN	<−0.01	0.18	<0.01	1	0.9932
SALINITY	−0.06	0.06	1.19	1	0.2746
PH	−1.41	1.16	1.48	1	0.2240
SEASON (wet)	0.49	1.21	0.17	1	0.6827
prevalence†					
(Intercept)	**5.75**	**0.02**			
FLOW	<0.01	<0.01	1.53	1	0.2167
TEMPERATURE	−0.04	0.06	0.41	1	0.5199
DISSOLVED OXYGEN	**−0.28**	**0.07**	**16.57**	**1**	**< 0.001**
SALINITY	0.07	0.11	0.35	1	0.5550
PH	**−1.21**	**0.42**	**8.26**	**1**	**0.0041**
SEASON (wet)	**1.58**	**0.54**	**8.39**	**1**	**0.0038**
total isopod abundance‡					
(Intercept)	3.14	6.86			
ANCHOVY ABUNDANCE	**<0.01**	**<0.01**	**5.37**	**1**	**0.0205**
FLOW	<−0.01	<0.01	2.45	1	0.1178
TEMPERATURE	**−0.42**	**0.11**	**13.92**	**1**	**0.0002**
DISSOLVED OXYGEN	−0.15	0.1	2.23	1	0.1351
SALINITY	−0.04	0.04	1.41	1	0.2358
PH	1.31	0.94	1.93	1	0.1644
SEASON (wet)	**3.46**	**1.35**	**6.61**	**1**	**0.0102**

* Negative binomial dispersion parameter: $\alpha = 1.78$ (SE = 0.90) and zero-inflation parameter: 0.57 (SE = 0.11). There was no evidence for multicollinearity among predictors: FLOW (VIF = 1.53), TEMPERATURE (VIF = 1.15), DISSOLVED OXYGEN (VIF = 1.26), SALINITY (VIF = 1.10), and PH (VIF = 1.20).

† Zero-inflation parameter: 0.59 (SE = 0.11). There was no evidence for multicollinearity among predictors: FLOW (VIF = 1.22), TEMPERATURE (VIF = 1.2), DISSOLVED OXYGEN (VIF = 1.46), SALINITY (VIF = 1.03), and PH (VIF = 1.41).

‡ Negative binomial dispersion parameter: $\alpha < 0.01$, and zero-inflation parameter: 0.46 (SE = 0.61). There was no evidence for multicollinearity among predictors: ANCHOVY ABUNDANCE (VIF = 2.37), FLOW (VIF = 2.25), TEMPERATURE (VIF = 2.22), DISSOLVED OXYGEN (VIF = 1.94), SALINITY (VIF = 1.22), and PH (VIF = 2.56).

Table IV. Predictors of anchovy abundance in Hillsborough River between 2005 and 2007. Model results are based on a generalized linear mixed model (GLMM) with a negative binomial distribution fitted with year and month as random effects. The negative binomial dispersion parameter of this model was $\alpha = 2.3958$ with SE = 0.8385. Significance of regression coefficients (*Coef.*) and their standard error (SE) were assessed with a *z*-test and are emphasized in bold, and tests of main effects were based on Wald's χ^2 tests. There was no evidence for multicollinearity among predictors: FLOW (VIF = 1.62), TEMPERATURE (VIF = 1.37), DISSOLVED OXYGEN (VIF = 1.17), SALINITY (VIF = 1.07), and PH (VIF = 1.23).

Predictor	GLMM regression coefficients		Wald's effect tests		
	Coef.	SE	χ^2	df	*P*
(Intercept)	296.56	398.15			
FLOW	**−5.05**	**1.56**	**10.46**	**1**	**0.0012**
TEMPERATURE	28.84	31.00	0.87	1	0.3522
DISSOLVED OXYGEN	−35.06	38.83	0.81	1	0.3667
SALINITY	−66.40	48.37	1.88	1	0.1698
PH	26.14	52.24	0.25	1	0.6168
FLOW × TEMPERATURE	**0.09**	**0.02**	**13.62**	**1**	**0.0002**
FLOW × DISSOLVED OXYGEN	0.07	0.06	1.64	1	0.2007
FLOW × SALINITY	<0.01	<0.01	0.19	1	0.6641
FLOW × PH	**0.28**	**0.10**	**8.68**	**1**	**0.0032**
TEMPERATURE × DISSOLVED OXYGEN	**0.85**	**0.25**	**11.37**	**1**	**0.0007**
TEMPERATURE × SALINITY	**0.51**	**0.10**	**24.26**	**1**	**<0.0001**
TEMPERATURE × PH	−5.90	4.17	2.00	1	0.1570
DISSOLVED OXYGEN × SALINITY	0.53	0.31	3.01	1	0.0826
DISSOLVED OXYGEN × PH	−0.39	5.03	0.01	1	0.9379
SALINITY × PH	6.62	5.99	1.22	1	0.2691

characteristics. Here, perhaps the combined effects of seasonal changes in water chemistry, flow, pollution, and host size would help further explain why we found a negative trend in isopod abundance in the more polluted Hillsborough River (Sandifer and Kerby, 1983).

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