Environ Biol Fish (2011) 92:125–139
DOI 10.1007/s10641-011-9822-2

Environmental correlates of the abundance and distribution of *Belonesox belizanus* in a novel environment

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Abstract Environmental factors, such as temperature, dissolved oxygen, salinity, and pH may influence the population dynamics of an introduced species by imposing limits to its distribution and abundance. In 1957, the non-indigenous pike killifish, *Belonesox belizanus* Kner, was released into a Miami-Dade County, Florida, canal, from which it has since spread across most of south Florida. The main goal of this study was to characterize patterns of covariation between *B. belizanus* density and temporal, spatial, and physicochemical variables, and attempt to identify which physicochemical variables may explain variation in densities of this species. Results of AIC_c model selection indicated that patterns of physicochemical variables such as pH, salinity, and temperature correlated with annual change in *B. belizanus* density, and that these physicochemical-density patterns were mesohabitat specific. For the southern most sites, the interaction between temperature and salinity provide the best model to explain *B. belizanus* density, whereas variability in pH provides the best model at northern sites. These patterns of covariance between density and specific physicochemical variables suggests that specific mesohabitat characteristics may play a role in mediating the physiological, behavioral, and/or ecological performance of this introduced species in Florida and elsewhere. Future studies will test hypotheses on the direct and indirect effects of these physicochemical variables within the context of specific mesohabitats on the behavior and physiology of *B. belizanus* in its novel environment in South Florida.

Keywords Introduction · Invasion ecology · Density · Florida

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Introduction

Global homogenization of biota has occurred through worldwide introduction and establishment of non-native species (Lodge et al. 1998; D'Antonio et al. 2001). While species colonize new areas naturally over geological time, the frequency of colonization and the distances traversed by species now exceed natural rates by several orders of magnitude (Lodge and Shrader-Frechette 2002). As introduction rates accelerate, population size of established non-native species increases, enhancing their ability to spread and invade new territories (Mooney and Cleland 2001). Managing the deleterious effects of introduced species has been a major goal of conservation biologists for several decades, but, ecological problems associated with invasive species are still not well understood. Contemporary studies have attempted to address questions about the mechanisms that underlie successful colonization by non-native species (Courtenay and Stauffer 1984; Taylor et al. 1984; D'Antonio et al. 2001; Sakai et al. 2001; Lockwood et al. 2007).

Individuals removed from their native population and introduced into a new environment are effectively released from conditions under which the parent population has evolved and from the control of biotic (e.g., species interactions, diseases, and parasites) and abiotic factors (e.g., climatic regime and stochastic weather events) that have determined the native distribution of the species (Taylor et al. 1984). Having been released from the ecological bottlenecks in their indigenous environment, introduced populations may be subjected to a suite of new challenges in their novel environment, which they must overcome in order to survive. Individuals of introduced species that have high genetic variability, wide physiological tolerance, and variable reproductive and feeding strategies have an increased chance of being released from the limiting effects of biotic and abiotic factors, and are able to invade novel environments (Wonham et al. 2000; D'Antonio et al. 2001; Lockwood et al. 2007). In addition, species that possess plastic traits (e.g., behavior and physiology) are believed to be more capable of adapting and, therefore, survive better in a novel environment than stereotypical, non-plastic species (Piersma and Drent 2003; Miner et al. 2005; Pigliucci 2005).

The ease with which some introduced freshwater fishes have become established in Florida aquatic ecosystems attests to their potential ability to bring about major changes in their novel environment (Courtenay et al. 1974). However, Trexler et al. (2000) showed that not all introduced fishes have flourished equally well in aquatic habitats of southern Florida. For example, within the family Cichlidae, *Cichlasoma urophthalmus* tend to dominate many different types of south Florida habitats; whereas *Cichlasoma bimaculatum* and *Oreochromis aureus* have not flourished well (Trexler et al. 2000). The amount of annual rainfall and minimum temperature may have played an important role in limiting the rate of spread and establishment of viable populations of introduced fish species, resulting in a perceived balance between native and introduced fish species in south Florida. Sporadic occurrence of natural disturbances such as droughts and hurricanes, may present opportunities for introduced species to overtake natives and radically alter the dynamics of aquatic communities in Florida (Trexler et al. 2000).

The pike killifish, *Belonesox belizanus* Kner, is an introduced species that became established in south Florida after its release in Miami-Dade County, Florida in November 1957 (Belshe 1961; Courtenay and Stauffer 1984). Its native distribution ranges from Rio Antigua, Mexico to northern Costa Rica (Belshe 1961; Miley 1978). For more than 20 years *B. belizanus* persisted as a small introduced population in several canals east of the Everglades National Park after its introduction (Loftus and Kushlan 1987; Courtenay 1997; Trexler et al. 2000). Since the 1980's, this initial introduction has expanded (Loftus and Kushlan 1987; Courtenay 1997; Trexler et al. 2000). Currently, *B. belizanus* has established one population in Hillsborough County, Florida (Fuller 2006), and a larger population throughout Miami-Dade, Collier, Broward, and Monroe counties, including Big Cypress National Preserve and Everglades National Park (Belshe 1961; Dunker 2003; Loftus et al. 2004; see also Fig. 1). Although *B. belizanus* occurs in many different habitats (e.g., canals, sloughs, ponds, mixed swamp forest; Loftus et al. 2004) within its invasive range in south Florida, *B. belizanus* has remained at relatively low, but variable densities (Loftus and Eklund 1994; Lorenz et al. 1997; Trexler et al. 2000; Dunker 2003). Throughout portions of its native range (Yucatan, Belize, and Honduras), *B. belizanus* have been observed in shallow water habitats and swamps similar to those found in south Florida (S. Taylor and W. Loftus, pers. obs., pers. comm.).

Despite the lower abundance of *B. belizanus* relative to other invasive fish species in south Florida, its occurrence in these habitats presents a major concern to the ecology of the south Florida aquatic ecosystem. *Belonesox belizanus* are voracious piscivores, such that it only takes a few individuals to decimate prey populations quickly, depriving native piscivores of their critical food resources (Belshe 1961;

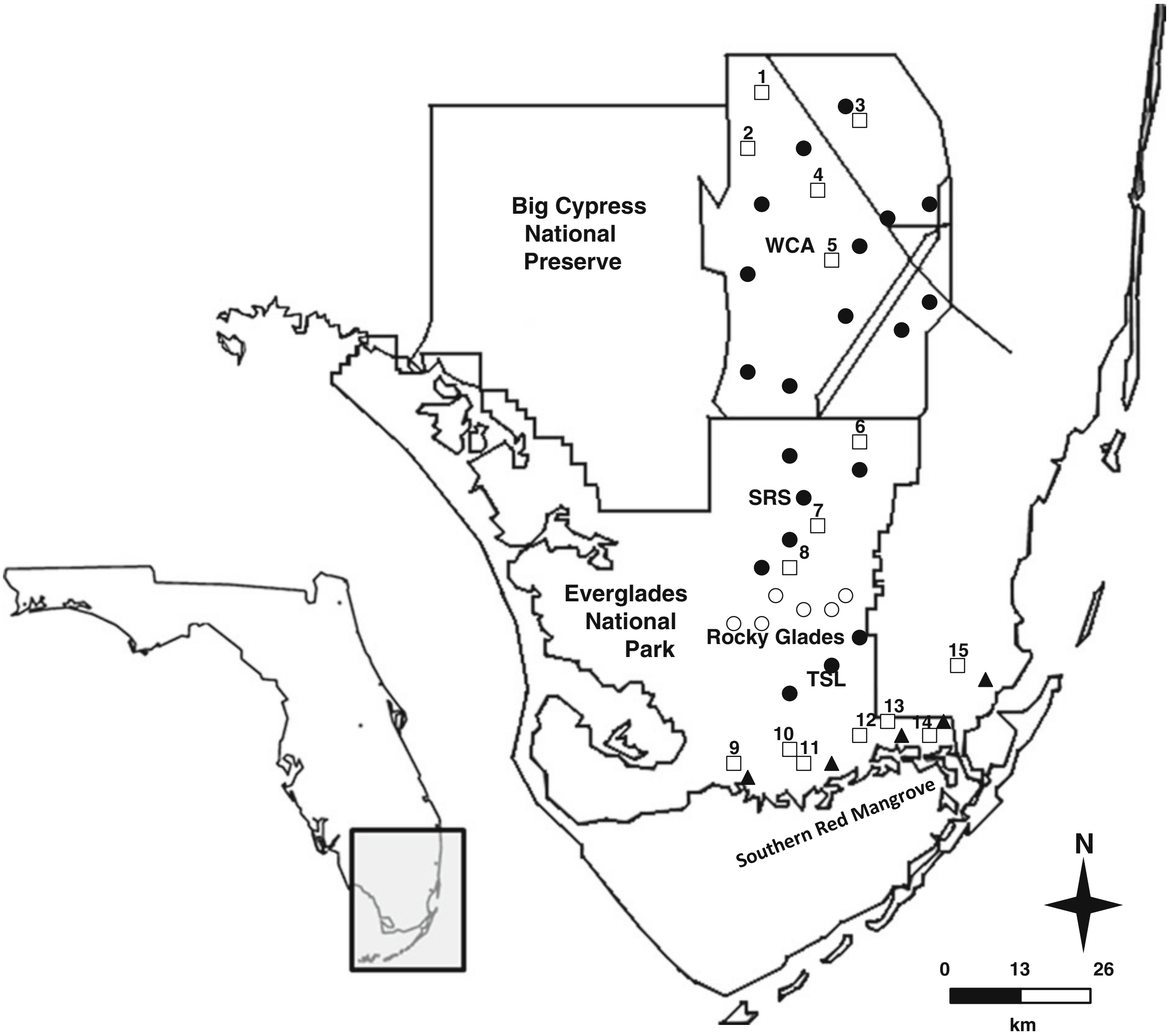

Fig. 1 Map of the study areas WCA, SRS, and TSL (*black circle*), Rocky Glades (*white circle*), and Southern Red Mangrove (*black triangle*); South Florida Water Management District physicochemical stations used in the study (*white square*). Numbers next to physicochemical stations were used to visualize which stations were paired with each dataset in the methods section (Table 1)

Lachner et al. 1970; Miley 1978). The negative impact of this introduced predator on the trophic dynamics of the Everglades National Park is especially enhanced when food resources become more limiting during the dry season as water levels remain low and large ponds are reduced to smaller mud pools (Loftus and Kushlan 1987; Trexler et al. 2005).

Considering the lack of published information regarding the range of distribution and abundance of *B. belizanus* in south Florida and the negative impact this introduced population imposes on the native ecosystem, this study is designed to explore how physicochemical variables such as temperature, dissolved oxygen, salinity, and pH relate to the abundance of this introduced species in South Florida. These physicochemical variables may not only directly affect the physiology of this species, but may also have an indirect effect on fish behavior, especially predator–prey interactions, which may regulate the abundance and distribution of *B. belizanus* in south Florida. Previous studies have shown that changes in predator–prey interactions reflected variation among species in their physiological tolerances to low oxygen either through its effects on the escape behavior of prey or swimming and feeding behaviors of the predator (Breitburg et al. 1997; Moore and Townsend 1998). Other studies have indicated that seasonal fluctuations in temperature can limit fish species densities either directly through its effects on physiology (Beitinger and Fitzpatrick 1979; Magnuson et al. 1979; Farkas et al. 2001) or indirectly through its effects on other environmental characters (i.e., DO or salinity) (Matthews and Berg 1997; Marshall and Elliott 1998). In light of the direct and indirect effects of the environment on a species, the goal of this study was to characterize patterns of covariation between *B. belizanus* density and temporal (months and years), spatial, and physicochemical variables and to determine which physicochemical variables may explain the variation in densities of this species. The information resulting from this analysis will contribute to our enhanced understanding of the factors that have allowed this introduced species to establish viable populations in Florida.

Methods

Fish abundance and distribution

We examined five datasets that documented the densities of *B. belizanus* in south Florida. These datasets differed in temporal scale, location, habitat type, and sampling techniques employed (Table 1, Fig. 1). Specific narratives on the differences of the datasets are given below.

Annual fish abundance data were taken from the Everglades Water Conservation Areas 3A and 3B (11 sites, WCA), Shark River Slough (6 sites, SRS), and Taylor Slough (3 sites, TSL) in the Everglades National Park from 1996 to 2005 (details of the sampling design are described in Trexler et al. 2000) (Fig. 1). Fishes were collected using 1-m^2 throw traps. Annual density (number of individuals per square meter) of *B. belizanus* for each site was calculated as the numbers of *B. belizanus* caught divided by the number of throw traps taken.

Annual fish abundances were taken from the Southern Red Mangrove fringe of Everglades National Park from 1993 to 2004 (details of the sampling design are described in Lorenz et al. 1997; 5 sites) (Fig. 1). Fishes were caught using permanently positioned drop nets (Lorenz et al. 1997). Annual *B. belizanus* density for each site was calculated as the number of *B. belizanus* caught, divided by the number of drop nets used in the sample, then divided by the area fished by the drop net (9 m^2).

Monthly fish abundances from the Rocky Glades region of Everglades National Park were from 2000 to 2004 (sampling design is described in Loftus et al. 2001; 6 sites) (Fig. 1). This region dried completely during the dry season and, as a result, only July through December data were available for this study. Fishes were caught using permanently positioned drift-fence arrays. Drift-fence arrays were used to describe directional animal dispersal and community successional patterns during the wet season, and were fished overnight for 24 h for each sampling event (Loftus et al. 2001). Because of the nature of drift-fence arrays, monthly *B. belizanus* density was calculated for each array in the form of catch per unit effort (CPUE, number of individuals per day) by dividing the number of *B. belizanus* caught by the number of days fished during that month.

Table 1 Description of unpublished *B. belizanus* databasets used in this current study. Datasets spanned different lengths of years, temporal scale (monthly or annually), location, habitat type, and sampling techniques. Physicochemical variables were measured at physicochemical stations and linked to density sites (corresponds to Fig. 1)

Location	Habitat type	Sampling gear	Years	Temporal scale	Fish caught	Physico-chemical stations	Researcher
Water Conservation Areas—(WCA)	Freshwater Marsh	Throw Trap	1996–2005	Annual	11	1–5	Trexler
Shark River Slough—(SRS)	Freshwater Slough	Throw Trap	1996–2005	Annual	83	6–8	Trexler
Taylor Slough—(TSL)	Freshwater Slough	Throw Trap	1996–2005	Annual	30	9, 10, & 12	Trexler
Rocky Glades	Shallow wetlands with solution holes	Drift fences/ Minnow traps	2000–2004	Annual/Monthly	993	7–10	Loftus
Southern Red Mangroves	Mangrove Swamp	Drop net/Rotenone	1993–2004	Annual	185	9–15	Lorenz

Physicochemical characteristics

Temperature, dissolved oxygen (DO), and pH data were acquired from the South Florida Water Management District's (SFWMD) corporate environmental database from monitoring stations closest to the fish collection sites described above (DBHYDRO; SFWMD 2006, Fig. 1, Table 1). Monthly averages of the physicochemical variables were used to calculate yearly averages. The nature of the physicochemical data was limited because variables were not measured at consistent times during the day or by the same researchers. There are diel shifts in these physicochemical variables that could not be accounted for in these analyses. For the Southern Red Mangrove sites, salinity and temperature were collected during fish sampling events, with the exception of one of the sites where temperature, salinity, and dissolved oxygen were acquired from SFWMD's database. For all other mangrove sites, dissolved-oxygen measurements were acquired from the SFWMD's database.

Characterization of fish density patterns

We used two temporal scales in the analyses. For SRS, WCA, TSL, and Southern Red Mangrove sampling sites, analyses were conducted on an annual scale. Both monthly and annual analyses were conducted using data from the Rocky Glades sampling sites. Monthly analyses of Rocky Glades data provided the resolution that allowed us to determine if seasonal changes in water quality associated with droughts or hurricanes correlated with *B. belizanus* density. SRS, TSL, and WCA datasets were combined for analyses because they overlapped in time period, sampling method, and researcher collecting the data.

Akaike's Information Criterion adjusted for small sample size (AIC_c) was used to assess the relative importance of competing candidate models for explaining *B. belizanus* density in the three different datasets (Burnham and Anderson 2002; Hazelton and Grossman 2009; Mickle et al. 2009). Separate AIC_c analyses were performed on each dataset because each differed on types of variables measured (i.e., Southern Red Mangrove dataset had no pH data; the Rocky Glades dataset had monthly and yearly record of all variables excluding salinity). Models were constructed based on expected interactions between physicochemical variables and possible temporal and spatial patterns (Tables 2, 3, and 4). Variables were either categorized as temporal (month and year), spatial (area—categorical), or physicochemical (dissolved oxygen, temperature, pH, and salinity). Within the temporal category only one model was developed (year) except for the Rocky Glades dataset where month was added as a variable in the temporal category resulting in three models produced (year, month, and a combination of the two, Table 2). Within the physicochemical category, 13 models were developed for all three datasets, incorporating the influence of each physicochemical variable alone and in combination with others. Nine additional models were developed for each dataset that combined the temporal and physicochemical variables. For the Rocky Glades dataset, nine models were further developed incorporating the monthly temporal scale. Eleven models were developed for the combined analysis of SRS, TSL, and WCA datasets to include the spatial component of that analysis (area, Table 4). Finally, for each dataset, a null model (intercept only) and a global model (incorporating all variables) were used in the AIC_c analyses. All models implicitly include an intercept term. Models with low ΔAIC_c and high Akaike weights (w_i) have the best combination of parsimony (fewer parameters) and fit (accuracy) for explaining *B. belizanus* density (Burnham and Anderson 2002). To evaluate each variable's relative importance in explaining the overall trends in fish density, individual variable weights were calculated using model weights (following Scheuerell et al. 2009). The AIC_c analyses were conducted using R statistical computing package (R Development Core Team 2009). To visualize the relationship between the variables and fish density, graphs were developed using the best models and their relationship to density for each dataset.

Results

Belonesox belizanus is widely dispersed in south Florida but is highly variable in their abundance (Fig. 2). For example, Trexler (unpublished data) collected only 11 *B. belizanus* over a ten-year period throughout WCA, whereas Loftus (unpublished data) collected 993 in the Rocky Glades over a five-year period (Table 1).

Table 2 Candidate models for the Rocky Glades dataset used in AIC$_c$ model selection for the density response variable. *K* indicates the number of model parameters. Variables used include month, year, dissolved oxygen (DO), pH, and water temperature (T). Interaction models include main effects

Model	Variables	*K*	Hypotheses—densities of *B. belizanus* are best explained by
Null	Intercept Only	2	None of the measured variables.
Temporal	Month	7	Differences in the intra-annual scale (monthly), differences at the inter-annual scale (yearly), or a combination of both.
	Year	6	
	Month + Year	10	
Physicochemical	DO	3	Sample differences in dissolved oxygen.
	pH	3	Sample differences in pH.
	T	3	Sample differences in temperature.
	DO + pH	4	A combination of dissolved oxygen and pH.
	DO + T	4	A combination of dissolved oxygen and temperature.
	T + pH	4	A combination of temperature and pH.
	DO + pH + T	5	A combination of dissolved oxygen, pH, and temperature.
	DO*pH	5	A combination of dissolved oxygen and pH and their interaction.
	DO*T	5	A combination of dissolved oxygen and temperature and their interaction.
	T*pH	5	A combination of temperature and pH and their interaction.
	DO + pH + T + pH *T	6	A combination of a physicochemical variable and an interaction between the other two.
	pH + DO + T + DO*T	6	
	T + DO + pH + DO*pH	6	
Temporal & Physciochemical	Month + DO	8	A combination of dissolved oxygen and monthly scale.
	Month + pH	8	A combination of pH and monthly scale.
	Month + T	8	A combination of temperature and monthly scale.
	Year + DO	7	A combination of dissolved oxygen and yearly scale.
	Year + pH	7	A combination of pH and yearly scale.
	Year + T	7	A combination of temperature and yearly scale.
	Month*DO	11	An interaction between the monthly scale and dissolved oxygen.
	Month*pH	11	An interaction between the monthly scale and pH.
	Month*T	11	An interaction between the monthly scale and temperature.
	Year*DO	11	An interaction between the yearly scale and dissolved oxygen.
	Year*pH	11	An interaction between the yearly scale and pH.
	Year*T	11	An interaction between the yearly scale and temperature.
	Month + DO + pH + DO*pH	10	A combination of a temporal variable and an interaction between two physciochemical variables.
	Month + DO + T + DO*T	10	
	Month + T + pH + T*pH	10	
	Year + DO + pH + DO*pH	9	
	Year + DO + T + DO*T	9	
	Year + T + pH + T*pH	9	
Global	All	13	Combination of all temporal and physicochemical variables.

Table 3 Candidate models for the Southern Red Mangrove dataset used in AIC_c model selection for the density response variable. *K* indicates the number of model parameters. Variables include year, dissolved oxygen (DO), salinity (S), and water temperature (T). Interaction models include main effects

Model	Variables	*K*	Hypotheses—densities of *B. belizanus* are best explained by
Null	Intercept Only	2	None of the measured variables.
Temporal	Year	13	Differences in the inter-annual scale (yearly).
Physicochemical	DO	3	Sample differences in dissolved oxygen.
	S	3	Sample differences in salinity.
	T	3	Sample differences in Temperature.
	DO + S	4	A combination of dissolved oxygen and salinity.
	DO + T	4	A combination of dissolved oxygen and temperature.
	T + S	4	A combination of temperature and salinity.
	DO + T + S	5	A combination of dissolved oxygen, temperature, and salinity.
	DO*S	5	An interaction between dissolved oxygen and salinity.
	DO*T	5	An interaction between dissolved oxygen and temperature.
	T*S	5	An interaction between temperature and salinity.
	DO + T + S + T*S	6	A combination of a physicochemical variable and an interaction between the other two.
	S + DO + T + DO*T	6	
	T + DO + S + DO *S	6	
Temporal & Physicochemical	Year + DO	14	A combination of dissolved oxygen and yearly scale.
	Year + S	14	A combination of salinity and yearly scale.
	Year + T	14	A combination of temperature and yearly scale.
	Year*DO	21	An interaction between yearly scale and dissolved oxygen.
	Year*S	21	An interaction between yearly scale and salinity.
	Year*T	21	An interaction between yearly scale and temperature.
	Year + DO + S + DO*S	15	A combination of the yearly scale and an interaction between two physciochemical variables.
	Year + DO + T + DO*T	15	
	Year + T + S + T*S	15	
Global	All	16	Combination of all temporal and physicochemical variables.

Characterization of fish density patterns

In the Rocky Glades dataset, a 95% confidence set of models (calculated using Akaike weights; presented in terms of their relative importance) incorporated terms for pH, temperature (T), DO, and year had the most support from the data (Tables 5 and 6). Data substantially supported the model containing pH alone as being the best model explaining fish densities in the Rocky Glades sites (w_i=0.249). Linear regression indicated a very weak relationship between fish density and pH (R^2=0.121); with the highest density occurring within a pH range of 7.85–7.95 (Fig. 3). The second strongest model explaining fish density incorporated none of the variables (w_i=0.182) and had substantial support from the data with a very low ΔAIC_c (0.6; Table 5).

In the Southern Red Mangrove dataset, a 95% confidence set of models incorporating terms for salinity (S), temperature (T), an interaction between temperature and salinity (T*S), and DO and had the most support from the data (Tables 5 and 6). Data supported models depicting the interaction between temperature and salinity, salinity alone, and the model incorporating the additive effects as being the best models in explaining fish densities in the Southern Red Mangrove sites (T*S [w_i=0.263], S [w_i=0.213], and T+S [w_i=0.133]). Plotting the interaction between temperature and salinity along with the associated fish density as the relative size of the

Table 4 Candidate models for TSL, SRS, and WCA datasets used in AIC_c model selection for the density response variable. *K* indicates the number of model parameters. Variables include year, area, dissolved oxygen (DO), pH, and water temperature (T). Interaction models include main effects

Model	Variables	*K*	Hypotheses—densities of *B. belizanus* are best explained by
Null	Intercept Only	2	None of the measured variables.
Temporal	Year	11	Differences in the inter-annual scale (yearly).
Spatial	Area	4	Differences in area.
Temporal & Spatial	Year + Area	12	A combination of yearly and area variables.
Physicochemical	DO	3	Sample differences in dissolved oxygen.
	pH	3	Sample differences in pH.
	T	3	Sample differences in Temperature.
	DO + pH	4	A combination of dissolved oxygen and pH.
	DO + T	4	A combination of dissolved oxygen and temperature.
	T + pH	4	A combination of temperature and pH.
	DO + pH + T	5	A combination of dissolved oxygen, pH, and temperature.
	DO*pH	5	A combination of dissolved oxygen and pH and their interaction.
	DO*T	5	A combination of dissolved oxygen and temperature and their interaction.
	T*pH	5	A combination of temperature and pH and their interaction.
	DO + pH + T + pH*T	6	A combination of a physicochemical variable and an interaction between the other two.
	pH + DO + T + DO*T	6	
	T + DO + pH + DO*pH	6	
Temporal & Physicochemical	Year + DO	13	A combination of dissolved oxygen and yearly scale.
	Year + pH	13	A combination of pH and yearly scale.
	Year + T	13	A combination of temperature and yearly scale.
	Year*DO	21	A combination of dissolved oxygen and yearly scale and their interaction.
	Year*pH	21	A combination of pH and yearly scale and their interaction.
	Year*T	21	A combination of temperature and yearly scale and their interaction.
	Year + DO + pH + DO*pH	15	A combination of a temporal variable and an interaction between two physciochemical variables.
	Year + DO + T + DO*T	15	
	Year + T + pH + T*pH	15	
Spatial & Physicochemical	Area + DO	5	A combination of dissolved oxygen and area.
	Area + pH	5	A combination of pH and area.
	Area + T	5	A combination of temperature and area.
	Area*DO	6	A combination of dissolved oxygen and area and their interaction.
	Area*pH	6	A combination of pH and area and their interaction.
	Area*T	6	A combination of temperature and area and their interaction.
	Area + DO + pH + DO*pH	7	A combination of area and an interaction between two physciochemical variables.
	Area + DO + T + DO*T	7	
	Area + T + pH + T*pH	7	
Global	All	16	Combination of all temporal and physicochemical variables.

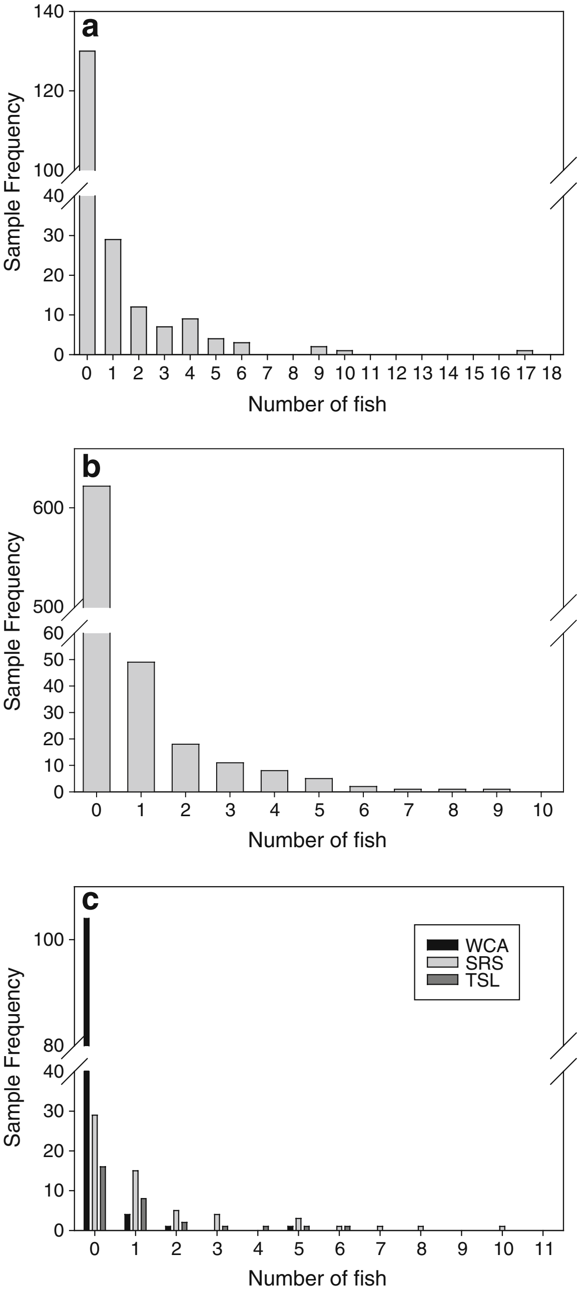

Fig. 2 Frequency distributions of the number of *B. belizanus* caught per sampling event in (**a**) Rocky Glades, (**b**) Southern Red Mangrove, and (**c**) WCA/SRS/TSL

symbol indicated that higher average fish densities occurred at low salinities and temperatures (Fig. 4).

In the TSL, SRS, and WCA datasets, a 95% confidence set of models incorporated terms for area, pH, temperature (T), and DO and had the most support from the data (Tables 5 and 6). Data substantially supported the models containing area and pH as being the best model explaining fish densities in TSL, SRS, and WCA sites (Area + pH [w_i=0.352] and Area + T [w_i=0.191]). Linear regression analyses indicated weak relationships between pH and fish densities across the different areas (Fig. 5; R^2_{TSL}=0.112, R^2_{SRS}=0.302, and R^2_{WCA}=0.228). For the intermediate and southern areas (SRS and TSL, respectively), higher fish densities occurred at the lower end of the pH ranges of those locations (pH between 7.30 and 7.55; Fig. 5). At the northern most area (WCA), higher fish densities occurred toward the higher end of the pH range, at approximately 7.32 (Fig. 5). There was a significant difference in pH between the three areas, with TSL sites having the largest increase and variability in pH (7.93 ± 0.066 units) compared with SRS (7.44 ± 0.029 units) and WCA sites ($7.24\pm2.41\times10^{-5}$ units) (ANOVA F=59.661, $P<0.001$). Frequency (counts) of *B. belizanus* collected show marked differences between WCA, TSL, and SRS areas (Fig. 2c). There was a significant difference among the three areas in average density of *B. belizanus,* with the greatest density occurring in the southern TSL sites ($9.76\times10^{-4}\pm2.153\times10^{-4}$ n m^{-2}), intermediate densities at SRS sites ($7.29\times10^{-4}\pm2.134\times10^{-4}$ n m^{-2}), and the lowest average density at the northern WCA sites ($5.22\times10^{-5}\pm2.409\times10^{-5}$ n m^{-2}) (ANOVA F=7.421, P=0.003).

Discussion

The ongoing introduction of species into novel environments provides an opportunity to study the processes that structure the distribution and abundance of species, their community associations, and their evolutionary relationships (Cassey et al. 2005). The average annual density of *B. belizanus* in south Florida has been persistently low during the past 52 years since its introduction (Lorenz et al. 1997; Dunker 2003). Among the physicochemical variables investigated, it is evident that specific habitat (site) variability plays an important role in potentially regulating *B. belizanus* densities in south Florida.

In those datasets that included pH as a physicochemical parameter, AIC_c analyses indicated that pH is very important in potentially explaining variation in the density of *B. belizanus* (Table 6). Environmental pH is known to affect the physiology and migratory

Table 5 ΔAIC$_c$ and AIC$_c$ weights (w_i) used to assess the relative performance of the candidate models for explaining densities of *B. belizanus*. Variables include temperature (T), dissolved oxygen (DO), and salinity (S)

Rocky Glades			Southern Red Mangrove			TSL, SRS, and WCA		
Model	ΔAIC$_c$	w_i	Model	ΔAIC$_c$	w_i	Model	ΔAIC$_c$	w_i
pH	0.0	0.249	T*S	0.0	0.263	Area + pH	0.0	0.352
Intercept Only	0.6	0.182	S	0.4	0.213	Area + T	1.2	0.191
T	1.1	0.143	T + S	1.4	0.133	Area	1.5	0.168
DO + pH	1.7	0.106	DO + S	2.8	0.065	Area*pH	3.0	0.078
T + pH	2.4	0.074	DO + T + S + T*S	3.2	0.054	Area*T	3.8	0.053
DO	3.2	0.050	DO*S	3.4	0.047	Area + DO	4.1	0.046
DO + T	3.9	0.035	DO + T	3.6	0.043	Area + DO + pH + DO*pH	5.2	0.027
Year	4.7	0.024	DO	3.9	0.037	Area + T + pH + T*pH	6.3	0.015
DO*pH	4.7	0.023	DO + T + S	4.1	0.035	Area*DO	6.7	0.012
DO + pH + T	4.9	0.022	T	4.2	0.032	Area + DO + T + DO*T	6.7	0.013
Year + pH	4.9	0.022	S + DO + T + DO*T	4.6	0.026	DO	6.8	0.012
DO*T	5.3	0.017	DO*T	4.7	0.025	DO + T	7.5	0.008
T*pH	5.5	0.016	Intercept Only	5.8	0.014	DO*T	8.2	0.006
Year + T	6.9	0.008	T + DO + S + DO *S	6.0	0.013	DO + pH	9.0	0.004
pH + DO + T + DO*T	7.6	0.006	Year + S	36.8	0.000	DO*pH	9.1	0.004
Month + T	7.8	0.005	Year	37.4	0.000	pH	9.4	0.003
DO + pH + T + pH *T	8.2	0.004	Year + DO	39.7	0.000	T	10.7	0.002
T + DO + pH + DO*pH	8.2	0.004	Year + T	42.4	0.000	DO + pH + T	10.7	0.002
Year + DO	8.5	0.004	Year + T + S + T*S	53.6	0.000	Intercept Only	10.9	0.001
Month + pH	9.7	0.002	Year + DO + S + DO*S	53.8	0.000	pH + DO + T + DO*T	11.6	0.001
Month	10.3	0.001	All	55.5	0.000	T + pH	11.9	0.000
Month + DO + T + DO*T	11.9	0.000	Year + DO + T + DO*T	56.2	0.000	T + DO + pH + DO*pH	12.3	0.000
Month + T + pH + T*pH	12.8	0.000	Year*DO	319.0	0.000	DO + pH + T + pH*T	12.4	0.000
Year + DO + pH + DO*pH	13.6	0.000	Year*S	330.2	0.000	T*pH	14.4	0.000
Month*T	13.7	0.000	Year*T	337.0	0.000	Year + Area	26.3	0.000
Year + DO + T + DO*T	13.7	0.000				Year + DO	37.7	0.000
Year + T + pH + T*pH	13.9	0.000				Year	37.9	0.000
Month + DO	14.2	0.000				Year + pH	39.0	0.000
Year*T	16.0	0.000				Year + T	40.0	0.000
Month + DO + pH + DO*pH	16.6	0.000				All	47.2	0.000
Month + Year	20.2	0.000				Year + DO + T + DO*T	53.8	0.000
Year*pH	20.4	0.000				Year + DO + pH + DO*pH	56.3	0.000
Month*pH	21.8	0.000				Year + T + pH + T*pH	57.9	0.000
Year*DO	22.7	0.000				Year*DO	320.8	0.000
All	27.6	0.000				Year*pH	324.8	0.000
Month*DO	30.5	0.000				Year*T	325.3	0.000

behavior of fishes. Changes in pH are known to directly affect ion uptake across gills and internal acid–base balance in fishes and ultimately affect survival rates (Laurent and Perry 1991; Baldigo and Lawrence 2001). Environmental pH may play an important role in regulating fish densities in south Florida habitats, especially where pH values are toward the lower end of the pH range measured (i.e., 7.30).

Table 6 Variable weights of components used in candidate models to explain variation in *B. belizanus* densities. Variable weights are summations based on models weights given in Table 5 and depict the relative importance of each component to each set of models

Variable	Rocky glades	Southern Red Mangrove	TSL, SRS, and WCA
Dissolved Oxygen (DO)	0.231	0.273	0.113
pH	0.489		0.403
Temperature (T)	0.301	0.336	0.232
Salinity (S)		0.539	
Year	0.058	0.000	0.000
Month	0.008		
Area			0.812
DO*pH	0.027		0.031
DO*T	0.023	0.051	0.007
DO*S		0.060	
T*pH	0.040		0.015
T*S		0.317	
Year*DO	0.000	0.000	0.000
Year*pH	0.000		0.000
Year*T	0.000	0.000	0.000
Year*S		0.000	
Month*DO	0.000		
Month*pH	0.000		
Month*T	0.000		
Area*DO			0.012
Area*pH			0.078
Area*T			0.053

Within the Rocky Glades dataset, one of the stronger models explaining fish density is one that excludes all of the physicochemical and temporal factors. This may have resulted because of the large seasonal variation in physicochemical parameters that occur in Rocky Glades sites. This large variation in environmental characteristics occurs during the transition between wet and dry seasons, and these results may be driven by the ephemeral nature of the aquatic microhabitats there (Loftus and Kushlan 1987; Trexler et al. 2005). This tremendous variability may have potentially masked any detectable relationship between physicochemical variables and *B. belizanus* density in the Rocky Glades.

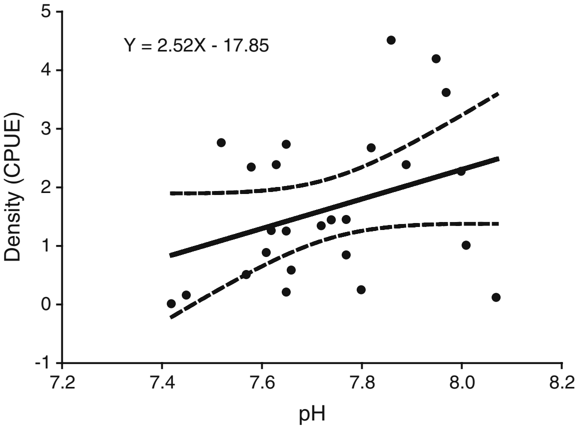

Fig. 3 Linear regression depicting the relationship between pH (the best model) and *B. belizanus* density for the Rocky Glades dataset, as determined by AIC_c analysis (Table 5). *Dashed lines* (− −) represent the 95% confidence intervals

Although considered a tropical freshwater fish species, *B. belizanus* is known to have moderate tolerance for variation in salinity (Belshe 1961). However, *B. belizanus* is more likely to be found in waters below 10 ppt and temperatures below 27°C (see Fig. 4). Interestingly, the majority of *B. belizanus* in the Southern Red Mangrove locations were collected during warmer months (25–27°C, June–September) in this study. As the summer progresses and temperatures rise, salinity in mangrove pools and microhabitats will rise accordingly and may indirectly affect *B. belizanus* densities through its direct affects on physiology. Investigating another tropical fish introduction to south Florida, Faunce and Lorenz

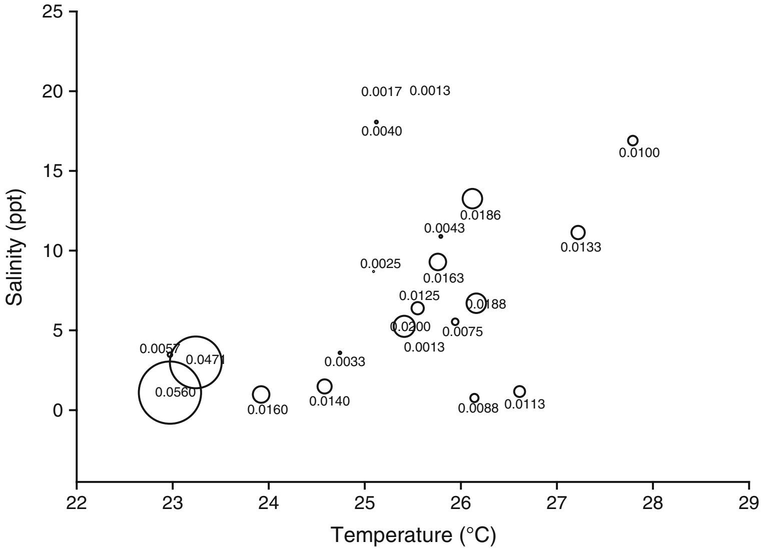

Fig. 4 Bubble graph depicting the relationship between *B. belizanus* density and the interaction between temperature and salinity (the best model) for the Southern Red Mangrove dataset. Relative size of the bubble represents fish densities. Bubbles and associated numbers are in density units of n m^{-2}

(2000) found that *Cichlasoma urophthalmus* reproduction was heavily influenced by water level, salinity, and, to a lesser extent, temperature. While not directly tested here, the affect of salinity on *B. belizanus* reproductive behavior may be a plausible reason that higher fish densities occurred in lower salinity water at Southern Red Mangrove sites.

Large fluctuations in physicochemical characteristics of freshwater systems in south Florida, which are largely driven by stochastic events, may be precarious for a non-native tropical fish species. As a result, fishes occur in very low densities, a scenario that may increase the probability of local extinction through chance events (Murdoch 1966). It is also likely that these chance events allow fish species other than *B. belizanus* to flourish in south Florida (e.g., *C. urophthalmus*; see Trexler et al. 2000). Investigating the TSL, SRS, and WCA sites the variability in mesohabitat physicochemical characteristics (especially pH) corresponded to a similar gradient in *B. belizanus* density; with the lowest densities found in WCA sites, (northern sites) while the most abundant sites were within TSL (southern). Environmental heterogeneity is important in structuring fish communities and may aid in explaining why a pattern emerges corresponding to larger densities at TSL compared with the other two areas, and hence the influence of the area term in the AIC$_c$ analyses. Green et al. (2006) conducted a five-year study comparing the community structure between two drainage systems (TSL and SRS) in the southern mangrove zone of Everglades National Park. These two drainage systems characterized a dichotomy in nutrient availability and tidal range. Taylor Slough is hydrologically isolated from the Gulf of Mexico, lacks recognizable tides, and is oligotrophic, whereas SRS drains into the Gulf of Mexico, has moderate diurnal tides, and is less oligotrophic. Green et al. (2006) observed lower standing crops, species richness, and density of fishes in SRS mangroves than in TSL mangroves. They concluded that the

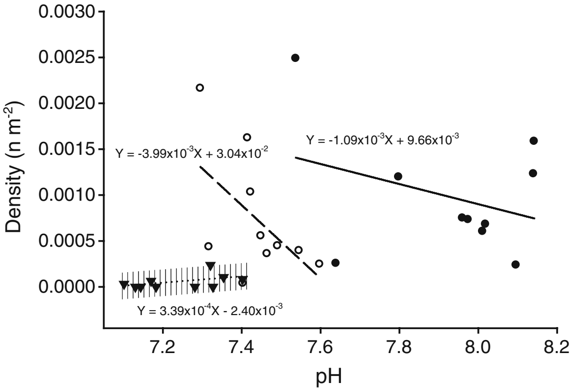

Fig. 5 Linear regressions depicting the relationship between pH (the best model) and *B. belizanus* density for TSL, SRS, and WCA datasets, as determined by AIC$_c$ analysis (Table 5). TSL data are represented by *closed circles* (*black circle*) and a *solid regression line*; SRS data are represented by *open circles* (*white circle*) and *a dashed regression line*; and WCA data are represented by *closed triangles* (*black triangle*) and a *dotted regression line*

time scale of water-level fluctuation shapes both the topography and hydrological linkage between habitats and may be of significant importance to fish-community structure. These spatial and temporal patterns may act as filters of the regional fish-species pool, while predation, fluctuating salinity, and low dissolved oxygen determine local community dynamics and act as proximate causes of spatial structure in estuarine fish communities. These findings highlight the importance of environmental fluctuation in community regulation, with fluctuations in physicochemical parameters serving as potential ecological bottlenecks in this seasonally affected marsh land. The current study indicates that similar environmental fluctuations may affect populations on an individual species-level.

Why does abundance of *B. belizanus* remain low in its novel south Florida habitat? Environmental conditions in the tropics may be more stable than in temperate zones, allowing for increased diversity (Gaston 2000). Because *B. belizanus* is from tropical Central America, its ability to adapt to Florida's subtropical environment and seasonal fluctuations in temperature, dissolved oxygen, and salinity may be a formidable barrier to increasing its densities but not to its ability to establish viable populations (Davis 1988; Montague and Ley 1993; Marshall and Elliott 1998). This suggests that the conditions in south Florida may be sub-optimal, preventing population explosion of this tropical species. Yet, field collections in Yucatan and Belize, within the native range of *B. belizanus,* indicate that densities in these habitats are low as well (Zambrano et al. 2006; Trexler and Loftus, unpubl. data). This suggests that the low densities of *B. belizanus* in its introduced range in south Florida may be a conserved life history trait, and may not be altered by latitudinal variation in environmental features. The environmental characteristics in south Florida may be similar to those in the tropics because of the effects of the Gulf Stream and its proximity to Caribbean, although the interior Everglades and Big Cypress National Preserve are cooler than coastal mangroves during the winter season (Duever et al. 1994; McPherson and Halley 1997). Another factor potentially shaping the distribution and abundance of *B. belizanus* in south Florida is the environment's affect on predation. *Belonesox belizanus'* small size surrenders it to being an easy prey-resource for piscivorous fish and wading birds, especially during dry down events in south Florida habitats. For example, Frederick et al. (1999) investigated the exposure of Great egret nestlings (*Ardea albus*) to mercury in the Florida Everglades and documented that 32% of the diet by biomass was dominated by *B. belizanus* and introduced cichlids. This seasonal event leaves this fish susceptible to predation, perhaps having a major influence on its densities.

Although this study utilized the best possible data available on the abundance and distribution of *B. belizanus* and physicochemical variables within its distribution, the results of the analyses should be interpreted with caution. First, absence of *B. belizanus* in field collections during some years at specific sites (e.g., WCA) may have been caused by sampling-gear selectivity. Stationary methods of capture (e.g., minnow-traps and drop nets) may not work as efficiently as the throw trap or electroshocking methods to capture this species. It is highly likely that a more species-targeted collecting approach would have provided a better estimate of fish density. Second, physicochemical data were acquired from an independent source, removed from the actual *B. belizanus* sampling events and could not be rigorously linked to the exact sites and times where the fish were collected (except Southern Red Mangrove sites where physicochemical variables were measured along with fish collection). However, physicochemical variables were obtained from monitoring stations closest to the fish sampling sites. Moreover, for all of the physicochemical parameters in this study, diel shifts are known to occur and may have important implications in the structuring of fish populations (McCormick et al. 1997). Future studies would benefit from higher resolution measurements at actual fish-collection sites, taking into account diel fluctuations in fish counts and environmental parameters.

Although this study sought to define key physicochemical variables that potentially regulate *B. belizanus* density, the emerging pattern suggest that one physicochemical variable may not be as important as another unless it is placed within the framework of site specificity. Mesohabitat variability within the wetlands of south Florida may be enough to regulate the spread of this species. Another important environmental factor that may influence the population dynamics, which was not considered in this study is the hydrologic regime in south Florida (Trexler et al. 2005; Liston 2006; Rehage and Trexler 2006). The man-made waterways that connect most, if not all, natural aquatic systems in this region may provide a catalyst for the spread of this species by allowing it to overcome the ecological barriers of the expansion stage. This may explain its large distributional area even while its population density remains low in comparison to other non-native species. Thus, investigating the role played by fluctuating hydrological conditions associated with wet and dry periods in the population dynamics of *B. belizanus* in south Florida is a valuable area for future research (Trexler et al. 2005; Liston 2006).

Acknowledgements The authors would like to give a special thanks to Joel Trexler (FIU) and William Loftus (USGS) for the use of their datasets and their availability for consultation and insight throughout the development of this study. A special thank you is also extended to Robert M. Kobza (SFWMD) for his help in retrieving the environmental datasets used in this study. An overwhelming debt is owed to Jake Schaefer for his help in performing the AIC$_c$ analyses. Finally, the authors would like to thank J. Trexler, W. Loftus, R. Maliao, M. Wittenrich, the editor and two anonymous reviewers for their valuable comments on earlier drafts of this manuscript.

References

Baldigo BP, Lawrence GB (2001) Effects of stream acidification and habitat on fish populations of a North American river. Aquat Sci 63:196–222. doi:10.1007/PL00001352

Beitinger TL, Fitzpatrick LC (1979) Physiological and ecological correlates of preferred temperature in fish. Am Zool 19:319–329

Belshe JF (1961) Observations on an introduced tropical fish, *Belonesox belizanus*, in southern Florida. MS Thesis, University of Miami

Breitburg DL, Loher T, Pacey CA, Gerstein A (1997) Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. Ecol Monogr 67:489–507. doi:10.1890/0012-9615(1997)067[0489:VEOLDO]2.0.CO;2

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, pp 50–76

Cassey P, Blackburn TM, Duncan RP, Chown SL (2005) Concerning invasive species: reply to Brown and Sax. Austral Ecol 30:475–480. doi:10.1111/j.1442-9993.2005.01505.x

Courtenay WR Jr (1997) Nonindigenous fishes. In: Simberloff DS, Schmitz DC, Brown TC (eds) Strangers in paradise. Island, Washington, pp 109–122

Courtenay WR Jr, Stauffer JR Jr (eds) (1984) Distribution, biology and management of exotic fishes. Johns Hopkins University Press, Boston, p 430

Courtenay WR Jr, Sahlman HF, Miley WW, Herrema DJ (1974) Exotic fishes in fresh and brackish water of Florida. Biol Conserv 6:292–302

D'Antonio C, Meyerson LA, Denslow J (2001) Exotic species and conservation. In: Soulé ME, Orians GH (eds) Conservation biology: research priorities for the next decade. Island, Washington, pp 59–80

Davis TLO (1988) Temporal changes in the fish fauna entering a tidal swamp system in tropical Australia. Environ Biol Fish 21:161–172. doi:10.1007/EBF00004860

Duever MJ, Meeder JF, Needer LC, McCollom JM (1994) The climate of south Florida and its role in shaping the Everglades ecosystem. In: Davis SM, Ogden JC (eds) Everglades: the ecosystem and its restoration. St. Lucie, Delray Beach, pp 225–248

Dunker KJ (2003) Non-indigenous fishes in restored and natural wetlands on the Big Cypress Seminole Indian Reservation. MS Thesis, Florida Atlantic University

Farkas T, Fodor E, Kitajka K, Halver JE (2001) Response of fish membranes to environmental temperature. Aquat Res 32:645–655. doi:10.1046/j.1365-2109.2001.00600.x

Faunce CH, Lorenz JJ (2000) Reproductive biology of the introduced Mayan cichlid, *Cichlasoma urophthalmus*, within an estuarine mangrove habitat of Southern Florida. Environ Biol Fish 58:215–115. doi:10.1023/A:1007670526228

Frederick PC, Spalding MG, Sepulveda MS, Williams GE, Nico L, Robins R (1999) Exposure of Great Egret (*Ardea albus*) nestlings to mercury through diet in the Everglades ecosystem. Environ Toxicol Chem 18:1940–1947

Fuller P (2006) NAS-Nonindigenous Aquatic Species. U.S. Geological Survey. http://nas.er.usgs.gov/queries/FactSheet.aspx?SpeciesID=843. Accessed 20 September 2006

Gaston KJ (2000) Global patterns in biodiversity. Nat 405:220–227. doi:10.1038/35012228

Green DPJ, Trexler JC, Lorenz JJ, McIvor CC, Philippi T (2006) Spatial patterns of fish communities along two estuarine gradients in Southern Florida. Hydrobiol 569:387–399. doi:10.1007/s10750-006-0144-x

Hazelton PD, Grossman GD (2009) The effects of turbidity and an invasive species on foraging success of rosyside dace (*Clinostomus funduloides*). Freshw Biol 54:1977–1989. doi:10.1111/j.1365-2427.2009.02248.x

Lachner EA, Robins CR, Courtenay WR Jr (1970) Exotic fishes and other aquatic organisms introduced into North America. Smithson Contrib Zool 59:1–29

Laurent P, Perry SF (1991) Environmental effects on fish gill morphology. Physiol Zool 64:4–25

Liston SE (2006) Interaction between nutrient availability and hydroperiod shape macroinvertebrate communities in Florida Everglades marshes. Hydrobiol 569:343–357. doi:10.1007/s10750-006-0141-0

Lockwood JL, Hoopes MF, Marchetti MP (2007) An introduction to invasion ecology. In: Lockwood JL, Hoopes MF, Marchetti MP (eds) Invasion ecology. Blackwell, Malden, pp 1–17

Lodge DM, Shrader-Frechette K (2002) Non-indigenous species: ecological explanation, environmental ethics, and public policy. Conserv Biol 17:31–37

Lodge DM, Stein RA, Brown KM, Covich AP, Brönmark C, Garvey JE, Klosiewski SP (1998) Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. Aust J Ecol 23:53–67. doi:10.1111/j.1442-9993.1998.tb00705.x

Loftus WF, Eklund AM (1994) Long-term dynamics of an Everglades fish community. In: Davis S, Ogden JC (eds) Everglades: the system and its restoration. St. Lucie, Delray Beach, pp 461–483

Loftus WF, Kushlan JA (1987) Freshwater fishes of Southern Florida. B Fla State Mus, Biol Sci 31:147–344

Loftus WF, Bruno MC, Cunningham KJ, Perry S, Trexler JC (2001) The ecological role of the Karst wetlands of Southern Florida in relation to system restoration. In: Kuniansky EL (ed) U.S. Geological Survey Karst Interest Group Proceedings, Water-Resources Investigations Report 01–4011, p 8

Loftus WF, Ellis G, Zokan M, Lorenz JJ (2004) Inventory of freshwater fish species within Big Cypress National Preserve: the basis for a long-term sampling program. Fact Sheet 2004–3131 (November 2004), U.S. Department of the Interior, U.S. Geological Survey

Lorenz JJ, McIvor CC, Powell GVN, Fredrick PC (1997) A drop net and removable walkway used to quantitatively sample fishes over wetland surfaces in the dwarf mangroves of the Southern Everglades. Wetl 17:346–359. doi:10.1007/BF03161424

Magnuson JJ, Crowder LB, Medvick PA (1979) Temperature as an ecological resource. Am Zool 19:331–343. doi:10.1093/icb/19.1.331

Marshall S, Elliott M (1998) Environmental influences on the fish assemblage of the Humber Estuary, U.K. Estuar Coast Shelf S 46:175–184. doi:10.1006/ecss.1997.0268

Matthews KR, Berg NH (1997) Rainbow trout responses to water temperature and dissolved oxygen stress in two Southern California stream pools. J Fish Biol 50:50–67. doi:10.1111/j.1095-8649.1997.tb01339.x

McCormick PV, Chimney MJ, Swift DR (1997) Diel oxygen profiles and water column community metabolism in the Florida Everglades, USA. Arch Hydrobiol 140:117–129

McPherson BF, Halley RB (1997) The south Florida environment: a region under stress. US Geol Surv Circ 1134

Mickle PF, Schaefer JF, Adams SB, Kreiser BR (2009) Habitat use of age 0 Alabama shad in the Pascagoula River drainage, USA. Ecol Freshw Fish 19:107–115. doi:10.111/j.1600-0633.2009.00395.x

Miley WW II (1978) Ecological impact of the Pike Killifish, *Beonesox belizanus* Kner, (Poeciliidae) in Southern Florida. MS Thesis, Florida Atlantic University

Miner BG, Sultan SE, Morgan SG, Padilla DK, Relyea RA (2005) Ecological consequences of phenotypic plasticity. Trends Ecol Evol 20:687–692. doi:10.1016/j.tree.2005.08.002

Montague CL, Ley JA (1993) A possible effect of salinity fluctuation on abundance of benthic vegetation and associated fauna in Northeastern Florida Bay. Estuar Coasts 16:703–717. doi:10.2307/1352429

Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. Proc Natl Acad Sci USA 98:5446–5451. doi:10.1073/pnas.091093398

Moore MK, Townsend VR Jr (1998) The interaction of temperature, dissolved oxygen and predation pressure in an aquatic predator-prey system. Oikos 81:329–336

Murdoch WW (1966) Population stability and life history phenomena. Am Nat 100(910):5–11

Piersma T, Drent J (2003) Phenotypic flexibility and the evolution of organismal design. Trends Ecol Evol 18:228–233. doi:10.1016/0962-8924(92)90014-E

Pigliucci M (2005) Evolution of phenotypic plasticity: where are we going now? Trends Ecol Evol 20:481–486. doi:10.1016/j.tree.2005.06.001

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rehage JS, Trexler JC (2006) Assessing the net effect of anthropogenic disturbance on aquatic communities in wetlands: community structure relative to distance from canals. Hydrobiol 569:359–373. doi:10.1007/s10750-006-0142-z

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With WA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annu Rev Ecol Syst 32:305–332. doi:10.1146/annurev.ecolsys.32.081501.114037

Scheuerell MD, Zabel RW, Sandford BP (2009) Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus spp*.). J Appl Ecol 46:983–990. doi:10.1111/j.1365-2664.2009.01693.x

SFWMD (2006) DBHYDRO (Environmental Data). South Florida Water Management District. http://www.sfwmd.gov/portal/page/portal/xweb%20environmental%20monitoring/dbhydro%20application. Accessed 20 September 2006

Taylor JN, Courtenay WR Jr, McCann JA (1984) Known impacts of exotic fishes in the Continental United States. In: Courtenay WR Jr, Stauffer JR Jr (eds) Distribution, biology, and management of exotic fishes. Johns Hopkins University Press, Baltimore, pp 322–373

Trexler JC, Loftus WF, Jordan F, Lorenz JJ, Chick JH, Kobza RM (2000) Empirical assessment of fish introductions in a subtropical wetland: an evaluation of contrasting views. Biol Invasions 2:265–277. doi:10.1023/A:1011488118444

Trexler JC, Loftus WF, Perry S (2005) Disturbance frequency and community structure in a 25 year intervention study. Oecologia 145:140–152. doi:10.1007/s00442-005-0094-4

Wonham MJ, Carlton JT, Ruiz GM, Smith LD (2000) Fish and ships: relating dispersal frequency to success in biological invasions. Mar Biol 136:1111–1121. doi:10.1007/s002270000303

Zambrano L, Vazquez-Dominguez E, Garcia-Bedoya D, Loftus WF, Trexler JC (2006) Fish community structure in freshwater karstic wetlands of the Yucatan Peninsula, Mexico. Ichthyol Explor Freshw 17:193–206