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Fish emigration from temporary wetlands during drought: the role of physiological tolerance

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With 4 figures and 2 tables

Abstract: Fish emigration patterns from four temporary wetlands exposed to drought were studied from May to August 2004 in the Brière Marsh, France. Two wetlands became totally dry, and two experienced severe water level decline and significant changes in physico-chemical characters. Irrespective of the degree of desiccation, emigration patterns of the six most commonly trapped species, representing 98.6 % of the total abundance (*Ameiurus melas, Anguilla anguilla, Scardinius erythrophthalmus, Lepomis gibbosus, Esox lucius* and *Gambusia holbrooki*), were similar among wetlands. Emigration timing was highly correlated with published physiological tolerance levels for these species, demonstrating a tight linkage between water quality and emigration patterns. Two non-native species (*A. melas* and *G. holbrooki*) showed the latest emigration from the temporary habitats, reflecting a high level of tolerance to drought conditions that may contribute to their success as wetland invaders.

Key words: fish movement, desiccation, tolerance, temporary waters, habitat selection.

Introduction

A fundamental issue in ecology is understanding patterns in animal movements and selective pressures underlying these patterns. This is of particular interest in harsh and spatially-varying environments (Chesson & Huntly 1997, Chesson 2000), where the degree to which organisms can select alternative habitats through movement influences their ability to avoid environmental stressors. In many aquatic systems, drought and flooding are natural features (Matthews 1998, Humphries & Baldwin 2003, Lytle & Poff 2004) that affect both the temporal and spatial variability of the environment. Indeed, except where humans regulate flow regimes with dams and diversions, almost all freshwater ecosystems are subject to fluctuations in water level (Matthews 1998). In many aquatic systems, there are elements of seasonal predictability to the flow regime; however, the onset, magnitude, and duration of flooding can vary from year to year such that organisms may require a high level of flexibility in their response (Lytle & Poff 2004). Flow regime generates temporary habitats (e. g., floodplains, backwaters) that are exploited by a wide range of organisms, including many fish species (see review in Williams 2006). These temporary waters serve as critical seasonal habitats for reproduction, juvenile development, growth, and refuges against predation depending on species life histories and flooding conditions (Snodgrass et al. 1996, Poizat & Crivelli 1997, Corti et al. 1999, Baber et al. 2002, Ostrand & Wilde 2002, King et al. 2003).

As water level declines in flooded areas, habitat quality can concurrently decline for a number of reasons including decreasing food availability (e. g., Capone & Kushlan 1991), increasing predation pressure

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(e. g., Kushlan 1976), and declining water quality (e. g., high temperature, low dissolved oxygen, high pH, Magoulick & Kobza 2003). Fish are occasionally trapped in desiccating pools resulting in high mortality costs (Lowe-McConnell 1964, 1975, Kushlan 1976, Capone & Kushlan 1991, Chapman & Kramer 1991, Poizat & Crivelli 1997); however, the majority of individuals emigrate from temporary habitats as waters fall (e. g., Poizat & Crivelli 1997, Magoulick & Kobza 2003). The degree to which fish can access and select alternative habitats through immigration to and emigration from temporary habitats influences the degree to which they can exploit the rich resources of flooding habitats, but also avoid environmental stressors such as high temperature, low dissolved oxygen, or low food availability. Emigration patterns vary among fish species (Poizat & Crivelli 1997) and are likely to be influenced by specific characteristics such as their physiological tolerance. For many fish species, physiological tolerance has been addressed through laboratory studies; however, the efficiency of these experimentally derived measures for predicting ecological processes in nature has been rarely addressed.

In this study, we quantified the timing and patterns of fish emigration from four temporary wetlands exposed to drought. We focused on interspecific variations in movement and related this to literature-derived physiological tolerance data to explore the potential role of physiological tolerance as a predictor of emigration patterns.

Methods

Study area

The study was carried out in the Grande Brière Mottière Marsh, a 7000-ha area (Loire River drainage, North West France, 47° 22′ N, 02° 11′ W) composed of a web of permanently flooded ditches. Surrounding areas are comprised of a heterogeneous patchwork of temporary wetlands (e.g., grazing grasslands, reed beds, hunting water ponds or dead-end ditches) that flood in winter and progressively dry out during spring and summer. We conducted a fish survey from spring to summer 2004 in four temporary wetlands (Sites A, B, C and D) that represented the range of habitats available in the marsh and were located in a 700-ha area that could be continuously monitored (Fig. 1). At the start of the survey, Site A was a 6.26-ha grassland with a mean water depth of 16.3 cm (± 4.7 S. D.) and 49.0 % (± 26.3 S. D.) vegetation cover composed of submerged Poaceae, sub-aquatic plants (e. g. *Ranunculus* sp.) and filamentous algae (*Enteromorpha* sp.). Site B was a 5.25-ha reed bed (*Phragmites* sp.) with a mean water depth of 22.2 cm (± 14.8 S. D.), a scattered reed cover (40.0 % ± 35.1 S. D.) and a substrate consisting mainly of peat and woody debris. Site C was a 2.13-ha water pond surrounded by reed on the banks. Mean water depth was 61.0 cm (± 12.6 S. D.), mean vegetation coverage along the banks was 33.2 % (± 23.5 S. D.), and the substrate was composed of mud and peat. Site D was a 0.34-ha dead end ditch with a mean water depth of 105.1 cm (± 40.0 S. D.). Banks were covered by scattered reed, and the substrate was composed of peat and mud.

All sites experienced a gradual change in physical and chemical conditions: Sites A and B dried out totally during the survey period, whereas Sites C and D were subjected to a decline in water level (Fig. 1). During the survey, water transparency (Secchi disk) decreased from 55.2 (± 15.2 S. D.) to 17.8 (± 4.9 S. D.) cm; water pH increased from 8.4 (± 0.1 S. D.) to 9.5 (± 0.2 S. D.); and conductivity increased from 648 (± 8.4 S. D.) to 1501 (± 10.9 S. D.) $\mu S \cdot cm^{-1}$ at Site D. Daily water temperature at Site D, calculated from maximal daily air temperature during the study period and the relationship between maximal daily air temperature and maximal daily water temperature obtained in 2005 (linear regression, $R^2 = 0.86$, $p < 0.001$), indicated a general increase in water temperature, with large daily fluctuations: 16.9 °C (May 31, 2004) to 32.7 °C (August 1, 2004, Fig. 1).

Fish sampling procedure

Fish were sampled using fyke nets (5 mm mesh) equipped with two wings (1.2 m high and 3 m long) and arranged in a V-shape directing the fish into the chamber (2 m long and 50 cm diameter). The nets blocked the whole water column. The survey commenced on May 28, 2004 for all of the four sites when water levels started to decrease continuously. Fyke nets were fished continuously (overnight) during the whole period (Fig. 1). During the periods of intense fish migration, nets were checked and fish catches processed daily, while during times of less activity visits were made every two or three days. We sampled fish emigrating from the four sites at the unique connection point between temporary flooded wetland and the adjacent habitat. Sites B, C and D were directly connected to the permanent ditch. Site A was connected to Site C that was still flooded when Site A totally dried out; it is likely that Site C was used as a first refuge by fish emigrating from Site A. Fish immigration into the wetland was permitted by the presence in each connection of an additional fyke net set in the opposite direction (Fig. 1). Immigrating fish represented only 26.9 % of the total catches; emigration was the dominant movement mode, and we therefore focused on emigration patterns during the dewatering period. Trapped fish were anesthetized using eugenol ($0.04 mL. L^{-1}$), identified, measured to the nearest mm and released approximately 10 m from the other side of the fyke net in which they were captured. Sites A and B were monitored until June 28 and June 18, 2004, respectively; and Sites C and D were monitored until August 3, 2004 (Fig. 1). Trapping was conducted until all fish had left each temporary wetland. Complete emigration from Sites C and D was confirmed by electrofishing the remaining water (mean water depth 33.8 cm (± 9.54 S. D.) and 84.8 cm (± 29.3 S. D.) in Sites C and D, respectively) at the end of the trapping sur-

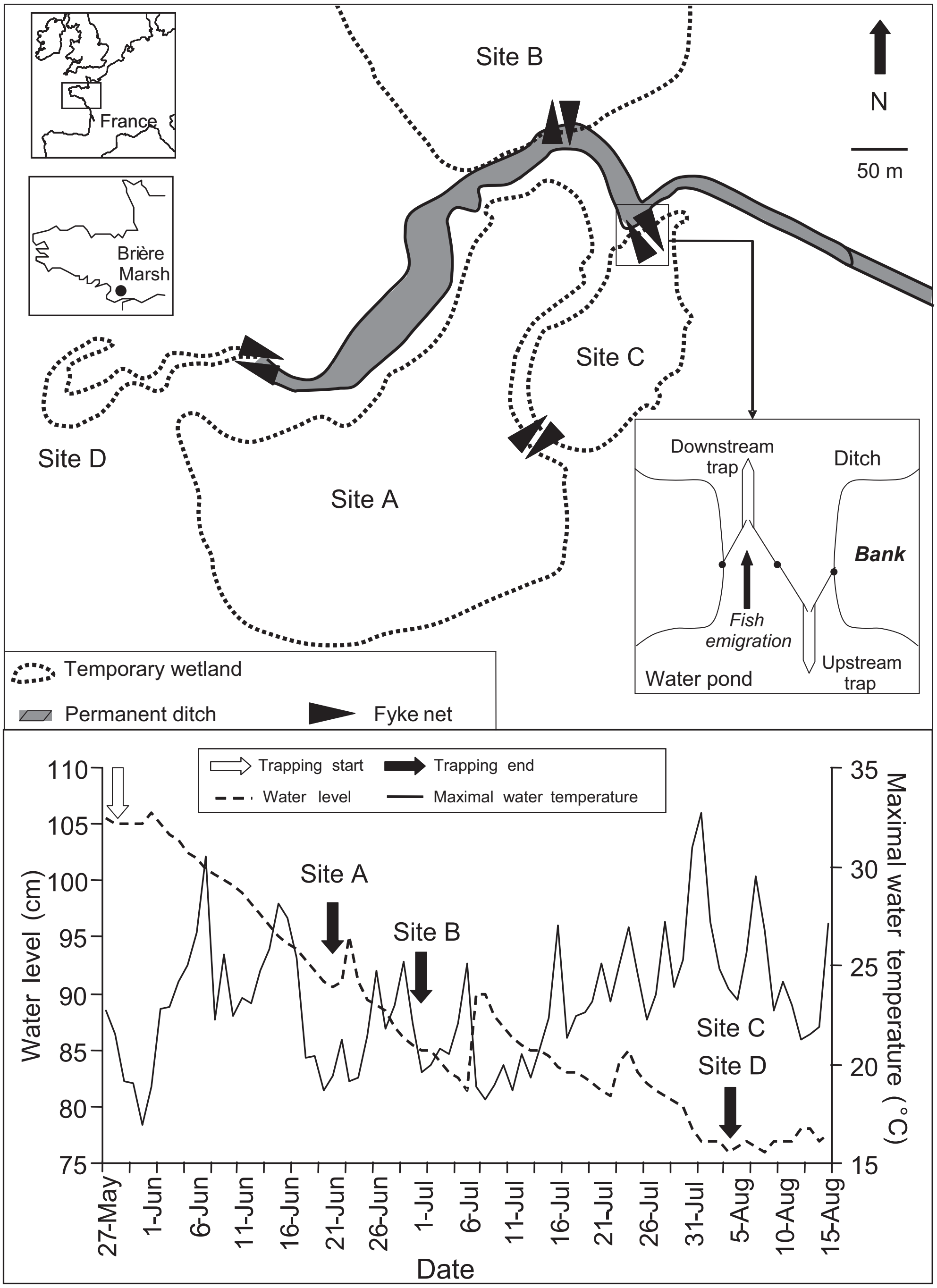

Fig. 1. Map of the study area, description of the trap setting, trapping period in the four temporary wetlands and water level and maximal water temperature at Site D (May to August 2004).

vey (August 4, 2004). No fish were caught in these two sites, whereas fish were recorded in the adjacent permanent ditch.

Data analyses

Trapping data

To facilitate comparisons between sites, trapping data were standardized to daily capture rates for each site and each species and expressed in catch per unit of effort (CPUE expressed in fish net^{-1} day^{-1}). Emigration start (ES) was calculated as the number of trapping days before the first individual was captured leaving a site, referenced to the beginning of the study. Emigration maximum (EMX) was calculated as the number of trapping days before the maximum CPUE value was reached. Emigration end (EE) was calculated as the number of trapping days before the last individual was captured. Two synthetic variables were then calculated to describe the timing of fish emigration from the temporary wetlands. First, emigration range (ER) was defined as the difference between ES and EE. Second, we calculated the emigration moment (EM) as the number of days of trapping required to catch 50 % of the total number of fish captured over the survey. These variables were calculated for each species and expressed relative to the trapping duration for each site.

Physiological tolerance

We used literature-derived values as proxies of fish physiological tolerance. First, we used the physiological tolerance index (PTI) that represents the tolerance to changes in water quality (usually temperature, dissolved oxygen, turbidity and salinity) or to extreme conditions in water quality (Marchetti et al. 2004), following the classification of Halliwell et al. (1999) and with the addition of the extremely tolerant category from Marchetti et al. (2004), i. e. 1: intolerant, 2: moderately tolerant, 3: tolerant and 4: extremely tolerant. Second, we used the coefficient of water quality flexibility (WQF) after Verneaux (1981) with low values indicating a narrow range of acceptable water quality (see also Oberdorff et al. 2002). Third, because thermal tolerance is a well-documented parameter of physiological tolerance in fishes, we used the temperature upper avoidance (TUA) defined as the temperature at which fish spend less time in comparison to a control (detailed in Giattinna & Garton 1982) and that delimits the upper boundary of the zone of thermal preference (Coutant 1977). These three parameters were gathered from published sources for the six most abundant species captured during the trapping period (Table 1).

Table 1. Physiological tolerance index (PTI), coefficient of water quality flexibility (WQF) and temperature of upper avoidance (TUA in °C) of the six most commonly trapped species in wetlands of the Grande Brière Mottière Marsh, France, with bibliographical references.

Species	PTI	WQF	TUA (in °C)
European eel (*Anguilla anguilla*)	3[a]	–	29[c]
Pike (*Esox lucius*)	2[a]	5.5[b]	23[d]
Mosquitofish (*Gambusia holbrooki*)	4[a]	–	35[e]
Black bullhead (*Ameiurus melas*)	4[a]	6.5[b]	35[f]
Pumpkinseed (*Lepomis gibbosus*)	2[a]	5.5[b]	25[g]
Rudd (*Scardinius erythrophthalmus*)	3[a]	6[b]	28[h]

– denotes missing value. [a] Marchetti et al. (2004) adapted from Halliwell et al. (1999); [b] Verneaux (1981); [c] Sadler (1979); [d] Casselman (1978); [e] Cherry et al. (1976); [f] Beltz et al. (1974); [g] Evans (1977) and [h] Elliot (1981).

Results

Fish assemblage

In total, 6,321 fish belonging to 12 species were captured emigrating from the four temporary wetlands (185, 346, 552 and 5,238 from Sites A, B, C and D, respectively). The fish assemblage was dominated by six species that represented 98.6 % of the total number of fish captured. In order of decreasing abundance (based on mean relative abundance, Table 2), the six most sampled species were juvenile and adult black bullhead (*Ameiurus melas*, Rafinesque), subadult European eel (*Anguilla anguilla*, L.), juvenile and adult rudd (*Scardinius erythrophthalmus*, L), adult pumpkinseed (*Lepomis gibbosus*, L.), young-of-the-year pike (*Esox lucius*, L.), and juvenile and adult mosquitofish (*Gambusia holbrooki*, Baird & Girard). Species differed markedly in their relative abundance among the four sites, e. g., from 10.3 to 98.4 % for the black bullhead and from 30.3 to 1.4 % for the European eel (Table 2). The other species captured in the survey (representing 1.4 % of the total number) were roach (*Rutilus rutilus* L.), bream (*Abramis brama*, L.), prussian carp (*Carassius gibelio*, Bloch), tench (*Tinca tinca*, L.), common carp (*Cyprinus carpio*, L.), and pikeperch (*Sander lucioperca*, L.).

Table 2. Number, life stage, and relative abundance of the six most abundant species monitored emigrating from the four temporary wetlands (Sites A, B, C and D) in wetlands of the Grande Brière Mottière Marsh, France. Other fish species are listed in the text and represented 0.6, 1.1, 13.8 and 0.09 % of the total abundance in Sites A, B, C and D, respectively.

Species	N	Life stage	Relative abundance per site (%)			
			A	B	C	D
Black bullhead	5530	Juveniles & adults	10.3	10.7	57.6	98.4
European eel	320	Sub-adults	30.3	23.7	20.1	1.4
Rudd	204	Juveniles & adults	8.1	53.5	0.7	0.0
Pumpkinseed	78	Adults	8.6	6.9	6.2	0.1
Pike	59	Young-of-the-year	24.3	1.2	1.6	0.01
Mosquitofish	43	Juveniles & adults	17.8	2.9	0.0	0.0

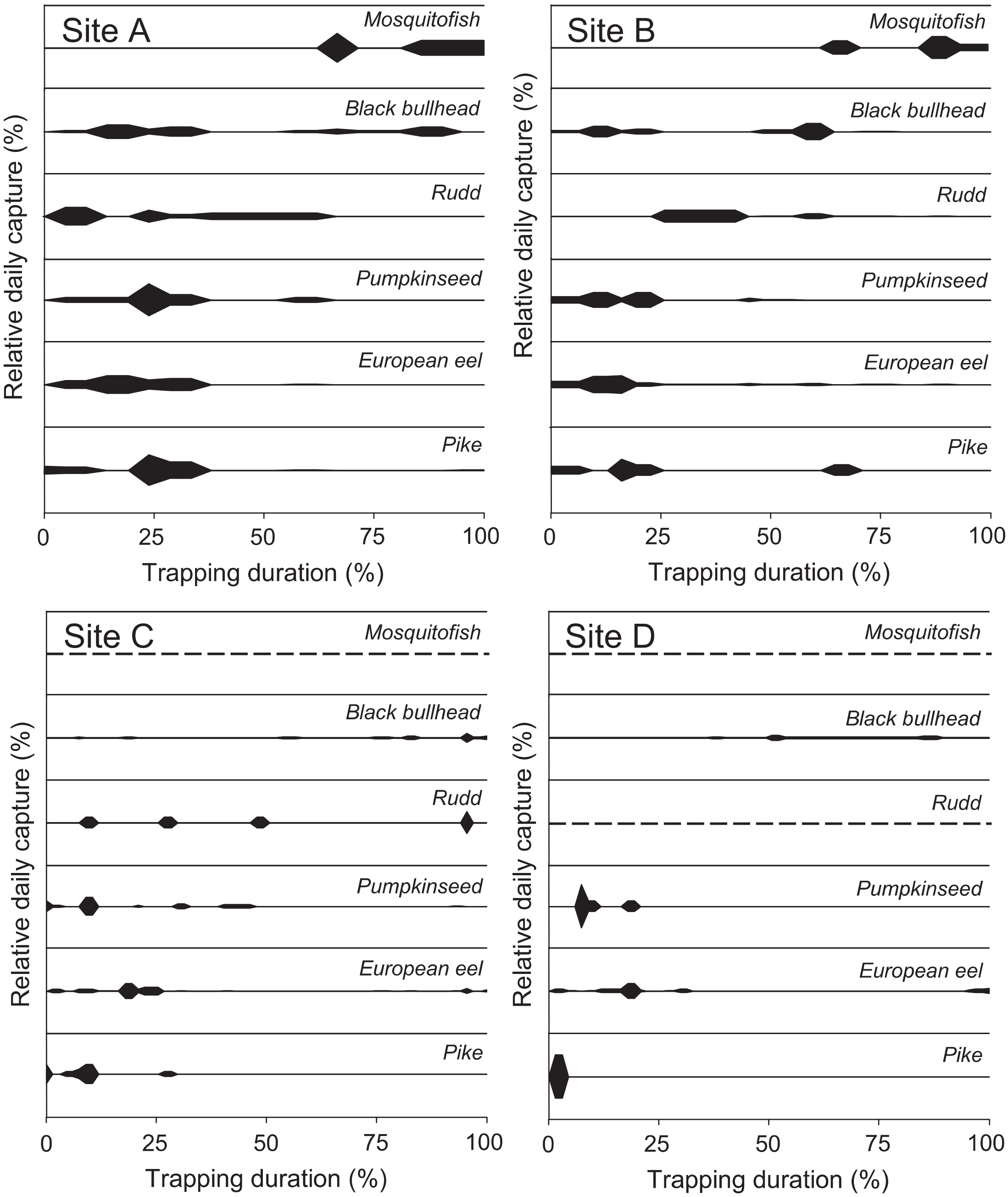

Fig. 2. Emigration patterns expressed relative to the trapping duration of the six studied fish species in the four temporary wetlands (Sites A, B, C and D). Shaded areas were constructed by joining daily catch values proportional to the total catch per site and per species. No mosquitofish were captured in Sites C and D and no rudd in Site D (dashed lines).

Fish emigration patterns among sites

Emigration patterns were analysed for the six most abundant species (i.e. mean abundance per site >5 %, Table 2). Fig. 2 illustrates daily catch proportional to the total catch of each species and relative to the trapping duration in the four sites (i.e. 22, 32, 32, and 68 days for Sites A, B, C, and D, respectively). Despite some variation at the start of the survey when Sites A and B are compared to Sites C and D, the interspecific patterning of emigration was surprisingly similar. Pike were the first to emigrate, and did so with the shortest emigration duration during the first third of the survey. European eel left temporary wetlands primarily during the first third of the survey but over a relatively long period. Pumpkinseed emigration was characterised by a short emigration duration that took place during the first half of the trapping

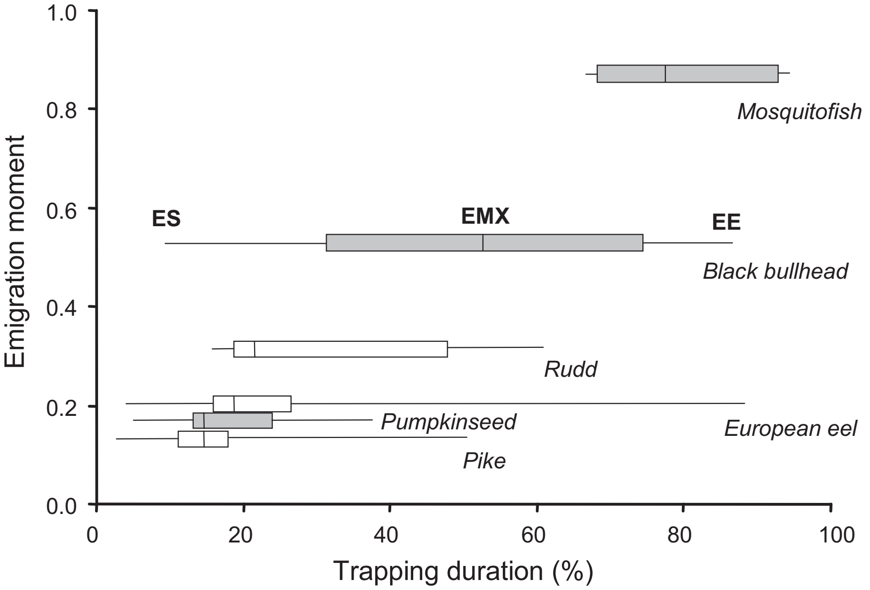

Fig. 3. Emigration range (emigration start ES and emigration end EE) and emigration moment (EM) expressed relative to the trapping duration of the six studied fish species in the four temporary wetlands. Each box plot is limited by the first and third quartile of captures and the vertical line represents the emigration maximum (EMX). Shaded boxes are used for non-native species and white boxes for native ones. See text for abbreviation definitions.

survey. Migration timing of rudd tended to occur during the first half of the survey. Black bullhead exhibited delayed emigration that occurred primarily during the second half of the survey, and mosquitofish emigrated the last and over a brief period.

Species emigration ranking

Trapping data of the four sites were pooled to quantitatively compare emigration among species. Fig. 3 illustrates emigration patterns using EM and ER (ES and EE). Pike tended to emigrate first (EM = 0.15) and relatively briefly (ER = 0.48), followed by pumpkinseed (EM = 0.16; ER = 0.32) and European eel (EM = 0.20) with the most extended range (ER = 0.84). The three other species emigrated later. Then, rudd left temporary wetlands (EM = 0.31) and their emigration was characterized by a relatively short range (ER = 0.45) whereas black bullhead emigrated later (EM = 0.53) and over a more extended time period (ER = 0.77). Mosquitofish was the last species to emigrate just before the complete drying out (EM = 0.87) and did so over a short period (ER = 0.28).

Physiological tolerance and emigration timing

Irrespective of the physiological descriptor (Table 1), the emigration moment (EM) was positively correlated with the physiological tolerance of the species (Fig. 4). Later emigrating species were characterized by a higher physiological tolerance (Pearson correlation, $R > 0.861$, $p < 0.028$, Fig. 4). Interestingly, two non-native species (black bullhead and mosquitofish) that had the highest physiological tolerance of the six species considered, emigrated the last (Fig. 4).

Discussion

Our results demonstrated that for the six most abundant fish species (1) emigration patterns differed among species, (2) interspecific patterning was similar among sites, and (3) there was a tight relationship between physiological tolerance and emigration timing. Matthews & Marsh-Matthews (2003) emphasized that little was known about the applicability of the results of laboratory tolerance studies to fish in the field under sustained drought conditions. This study suggests that literature data on fish species physiological tolerance from experimental studies are relevant to both understanding and predicting fish emigration from temporary wetlands during drought.

We might expect use of temporary wetlands to reflect a trade-off between the benefits of temporary habitats and the costs of exploitation; and this trade-off is likely to vary among species. Temporary shallow habitats are known to provide good feeding and growth conditions for many fish (Neckles et al. 1990) and to provide protection against predators for juveniles and smaller species (Schlosser 1987). However, benefits might be counterbalanced by costs linked to physiological stress due to the reduction of both available habitat and water quality during drought (Magoulick & Kobza 2003, Matthews & Marsh-

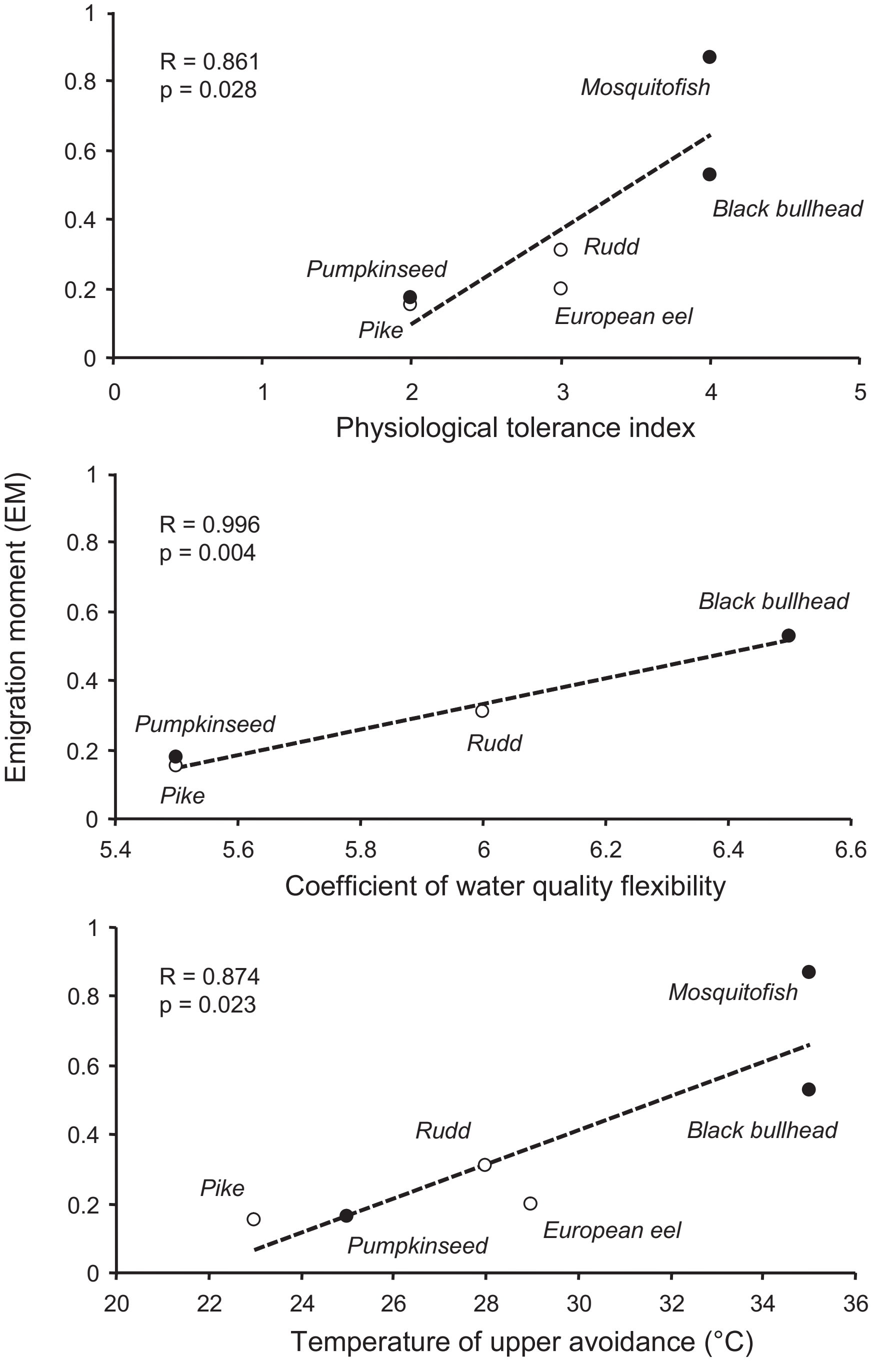

Fig. 4. Emigration patterns of fish species in the four temporary wetlands as a function of their physiological tolerance, i. e. the physiological tolerance index (PTI), the coefficient of water quality flexibility (WQF) and the temperature of upper avoidance (TUA in ˚C). Black symbols are used for non-native species and white symbols for native ones.

Matthews 2003). Such trade-offs occur when a physiological, behavioural or ecological trait of an organism (e. g., wetland use in the present study) that confers advantage for performing one function (e. g., growth performance) simultaneously confers a disadvantage for performing another function (e. g., physiological maintenance) (Chase & Leibold 2003).

Our results suggest that the patterning of emigration is quite predictable and that habitat selection behaviour is involved. Habitat selection (interpreted as an evolutionary strategy, Morris 2003) might be useful in interpreting habitat use in spatially varying environments such as temporary wetlands. Habitat selection generally refers to the non-random use of space or habitat that results from the voluntary movement of organisms (Kramer et al. 1997). It has been argued that in seasonally flooding systems, habitat distributions reflect both habitat selection but also non-random movement (e. g., haphazard trapping in floodplain pools, or downstream flushing in high-gradient systems). In the low-gradient wetlands of the Grande Brière Mottière Marsh that we studied, fishes were clearly able to move from temporary to permanent waters, as evidenced by the absence of fish in the remaining water (Sites C and D) at the end of the survey and our observations of directed movement to and from the sites. Therefore, we assume that emigration among sites is voluntary to some degree, and therefore reflects an element of choice. If habitat selection is driving distribution in wetlands, we would expect each species to maximize its fitness by optimizing the time spent in temporary wetlands and to emigrate when use of the temporary wetlands does not benefit the fish in comparison to alternative habitats (e. g., permanent waters). This study suggests that the costs of staying in the temporary wetlands relate, at least in part, to the interaction between changing water quality conditions and the physiological tolerance of the inhabitants. The strong relationships observed between the species-specific emigration moments and physiological tolerance estimates suggest that tolerance indices are strong predictors of emigration patterns, and that environmental cues were effectively used by these species.

Physiological tolerance has been reported to influence freshwater fish assemblage composition and patterns of mortality in response to extreme conditions (e. g., Smale & Rabeni 1995, McKinsey & Chapman 1998, Ostrand & Wilde 2002). Kushlan (1974), in his study of a natural fish kill in the Big Cypress Swamp of Florida, classified fish species into three categories based on their survival. The mosquitofish fell into the most tolerant category, while centrarchids were eliminated rapidly supporting the results of our study. Physiological tolerance also has implications for persistence and impacts of non-native species (Kobza et al. 2004). In the wetlands of the Grande Brière Mottière Marsh, black bullhead and mosquitofish are non-native, well-established species. These two species were characterized by the highest emigration moments in our study that correlated with their high physiological tolerance. The capacity of mosquitofish and the black bullhead to exploit temporary wetlands may contribute to their widespread success as invasive species. Mosquitofish, because of their reputation as mosquito-control agents, have been stocked in many temperate and tropical areas throughout the world (Fuller et al. 1999), and they have been remarkably successful invaders with the greatest ecological impact of introduced poeciliid fishes (Courtenay & Meffe 1989, Fuller 1999). They inhabit a wide variety of habitats reflective of their broad physiological tolerance. For example, mosquitofish tolerate very high water temperatures (Otto 1973) and extremely low levels of dissolved oxygen (McKinsey & Chapman 1998). Successful exploitation of shallow hypoxic waters by mosquitofish has been attributed, in part, to their apparent proficiency at aquatic surface respiration (Lewis 1970, McKinsey & Chapman 1998). The black bullhead has been reported as a successful non-indigenous species (e. g. Wheeler 1978, Fuller et al. 1999). It may be favoured by its broad physiological tolerance range and its ability to perform aquatic surface respiration as reported by Sargent & Galat (2002). The way in which a species responds to resources, natural enemies, and the physical environment determines its ability to invade (Shea & Chesson 2002), and the role of high physiological tolerance in the success and extent of fish invaders has already been recognized (Marchetti et al. 2004).

In summary, this study provides evidence for strong patterning in emigration of fishes from temporary wetlands. Literature-derived physiological tolerance indices serve as good predictors of interspecific variation in emigration timing. However, it should be noted that residual variance in the relationships between tolerance levels and emigration timing suggest that other factors interact with physico-chemical stressors to influence emigration timing at the individual and species level. For example, species characteristics including body size and life history traits can affect patterns of movement and survival in seasonally flooding systems such as the Florida Everglades (Kushlan 1974, Trexler et al. 2001). Other biotic factors such as food availability and predation pressure are known to vary during the progressive drought of the temporary wetlands (Capone & Kushlan 1991) and may interact with physico-chemical stressors to affect population dynamics. Future studies that explore the interactive effects of abiotic and biotic stressors will be extremely useful in increasing our understanding of emigration patterns from temporary waters.

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