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In shallow water ecosytems the abiotic environment is more important than prey abundance for foraging terns

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Abstract Shallow freshwater aquatic ecosystems are discrete feeding patches for fish eating birds. A unique feature of these ecosystems is that their physical conditions can change dramatically in a short period of time, particularly temperature, turbidity, and dissolved oxygen. Based on previous research we predicted that increasing turbidity will reduce the availability of fish to birds due to reduced visibility, while increasing temperature and decreasing dissolved oxygen will increase their availability through increases in activity and movement towards the more oxygenated surface areas, respectively. We also predicted that overall abundance of fish should increase feeding activity by terns. We measured these environmental variables, bird activity, and fish abundance from May to August from 2006 to 2008 in a marsh in southern Manitoba, Canada. Our results showed that only variation in dissolved oxygen levels affected feeding activity by terns. Since there was no relationship between bird and fish abundance either within or among years, these results suggest that it is the availability of prey (i.e. the upward movement of fish into the water column) and not their abundance per se that influences the number of avian predators present and hence the risk of predation to fish. These data demonstrate how the physical environment of aquatic ecosystems can impact terrestrial avian predators, and the link that exists between the physical environment and predator-prey interactions.

Keywords Predator-prey interactions · Dissolved oxygen · Avian predators · Interannual variation

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Introduction

Predators are a major ecological force. Through consumption of prey, they alter relative abundances, and change the size structure of prey populations (Crowder and Cooper 1982; Tonn and Magnuson 1982; Werner and Gilliam 1984; He and Kitchell 1990). To reduce the probability of being killed by predators, prey animals pursue antipredator strategies which include changes in morphology, physiology, life history traits and behaviour (see Mittelbach and Chesson 1987 for a review). Overall these strategies result in prey trading off growth rates against survivorship (Werner and Anholt 1996).

Within small freshwater ecosystems, it is usually assumed that the predators that impact the prey populations are resident within the system (Tonn and Magnuson 1982; Crowder and Cooper 1982; Werner et al. 1983; Turner and Mittelbach 1990; Eklöv and Persson 1996; Wanzenbock et al. 2006). Yet almost all such ecosystems have avian predators whose foraging range will include multiple freshwater ecosystems (e.g., Bluso-Demers et al. 2008) and will therefore be subject to temporal variation in this predation. Where these predators choose to forage can therefore result in significant and variable changes in the predator environment within individual ecosystems (Milinski and Heller 1978; Harvey and Stewart 1991; Allouche and Gaudin 2001; Collis et al. 2001; Hodgens et al. 2004; Steinmetz et al. 2008).

Avian piscivores are notoriously effective at locating fish when they become available and for most of these species, that means the fish must be near the surface to be detected (Ainley 1977). While local fish abundance will have a major influence on their availability, it can also be affected by variations in dissolved oxygen (DO), temperature, and turbidity. Levels of DO and temperature are normally linked by the physical properties of temperature dependent solubility of gasses in water, but within many freshwater aquatic ecosystems a high biomass of plant material can add significant variation to that relationship and significantly disrupt that linkage.

For many fish species, a common response to low DO is aquatic surface respiration – gulping air that allows some of the oxygen to be extracted within their swim bladder (Kramer 1987). This behaviour is known to increase their risk of capture by green heron, *Butorides striatus* (Kramer et al. 1983) and pied kingfisher, *Ceryle rudis* (Randle and Chapman 2004). Variation in turbidity is not known to alter the vertical distribution of fish, but increasing levels do decrease their detection by birds (Strod et al. 2008) and has been hypothesized to explain the distribution of plunge diving birds (Ainley 1977). The direct role of temperature in studies of aquatic predator-prey interactions has received limited attention (Krause and Godin 1995; Moore and Townsend 1998; Weetman et al. 1998, 1999; Anderson et al. 2001; Lass and Spaak 2003; Taylor and Collie 2003) but it is expected that fish will become more active with increasing temperatures (Atkinson 1994; Krause and Godin 1995). As well, with metabolic rates of fishes increasing with temperature (Clarke and Johnston 1999) there is an increase in the rate at which fish consume energy, likely resulting in an increased willingness to risk exposure to predators to gain access to food (Godin and Crossman 1994; Pink and Abrahams 2016).

Shallow freshwater lakes in central North America are known to experience substantial variation in all these parameters through time (Abrahams et al. 2007) and support a range of avian predators. We sought to connect the variation in the physical characteristics of the aquatic environment with the range of aquatic environments available to avian predators. We did this by testing the hypothesis that habitat quality is primarily determined by availability of prey as mediated by changes in the aquatic physical environment and not the overall abundance of prey.

Material and methods

Research area

Research was conducted at the University of Manitoba's Field Station, Delta Marsh, Manitoba, Canada (98°23′W, 50°11′N) from May to August of 2006 to 2008. Data was obtained from a shallow (~1.5 m), turbid, slow moving body of water within Delta Marsh known as the Blind Channel. Delta Marsh is a 21,870-ha wetland located on the southern shore of Lake Manitoba. This is a relatively protected area, and many piscivorous fishes use it for spawning and feeding during the spring and summer months (Suthers and Gee 1986). Water levels in Blind Channel are primarily determined by seiches as a result of prevailing winds; increasing with northerly winds and decreasing with southerly winds. Winds can also affect the physical environment as seiches bring cooler, more oxygenated lake water into the channel. Over the course of the ice-free period Blind Channel experiences a wide range of turbidity, temperatures (peaking at around 28–30 °C) and dissolved oxygen levels (ranging from normoxia to extreme hypoxia) (Robb and Abrahams 2003).

To record DO, temperature and turbidity three YSI 6920 data sondes were placed at the bottom, middle, and surface of the water column in the center of the Blind Channel in the same location as our minnow traps. The sondes collected data every 30 min that was averaged to provide a daily value to correspond with measures of predator and prey abundances.

Measures of prey abundance

Forster's terns feed on small fish between 2 and 11 cm in total length approximately in proportion to their abundance (Fraser 1997). The abundance of these small fish (primarily fathead minnows, *Pimephales promelas*) was measured using ten minnow traps set just below the surface of the water. Five of these traps were deployed on the north side of the channel while the other five traps were set on the south side. This arrangement ensured that one side of the marsh with minnow traps would be relatively sheltered in high wind events. This was important as minnows were observed to aggregate in sheltered areas when winds were high and sampling only one side of the marsh would have resulted in inaccurate estimates of minnow abundance. All traps were set at permanent locations within the area that was surveyed for avian predators.

Minnow traps were checked every morning from May to August in all three study years. All captured fishes were identified to species and a count of the number of individuals of the species present was recorded. The number of fish captured among all traps at each location was averaged to provide a single measure of catch per unit effort (CPUE) that represented the abundance of fish during that 24 h period.

Measures of risk of avian predation

The most common avian predator in this system is the Forster's terns (*Sterna forsteri*), a plunge diver that generally takes fish in the top 30 cm of water. They capture one fish approximately once every three to six dives (Salt and Willard 1971), and so must dive often to feed on small fish. We also periodically observed belted kingfishers (*Megaceryle alcyon*) that feed primarily on small fish near the surface. The presence of these predators was monitored with three Panasonic CCTV WV-CP484 SDIII cameras with Pentax 3.5-8 mm F/1.4 CS auto iris lenses set up overlooking portions of the southern end of Blind Channel. This location was selected to avoid glare from either the setting or rising sun.

Cameras recorded to a March Networks mobile digital video recorder (MDVR) during daylight hours from May to August during all three years of the study. For each day, the daylight hours were broken down into 15 min sections within which two minutes were randomly chosen for viewing (the same two minutes of each camera were chosen for each day). From this subsample we determined the total number of avian predators present and divided that by the number of daylight hours to estimate the daily level of avian predation risk.

Data analysis

For statistical analysis, 48 observations (one measure every 30 min) were averaged to provide a single daily measure. Based upon Durbin-Watson tests for autocorrelation, these data met the criteria for statistically independent observations within a time series. Due to technical issues, not all days had measures of DO and turbidity. There were also some gaps in the MDVR data due to fluctuations in recharging rates and periodic damage from high winds. To test for inter-annual variation in the abundance of terns, we included the Julian day as a covariate in an ANCOVA to account for seasonality effects.

We used parametric analyses on transformed data (Box – Cox transformations for environmental data and $\log_{10}(x + 1)$ for both minnow and tern observations) as the transformed data met assumptions for normality and homogeneity of variances necessary for parametric analysis. All analyses were conducted using STATISTICA software. Alpha levels were set at 0.05 for all analysis.

Results

Prey abundance as a predictor of predator abundance

The abundance of minnows differed significantly between years (ANOVA: $F_{(2, 97)} = 22.1, p < 0.0001$) as did the number of foraging birds (ANOVA: $F_{2,95} = 7.3$, $P < 0.00001$). Fish abundance in 2008 was significantly lower than in either 2006 or 2007, while the number of foraging birds in 2007 was significantly lower than that observed in 2006 and 2008 (Tukey HSD post hoc test).

Within the generalized regression model, which included year as a categorical predictor variable and minnow abundance as the continuous predictor variable, only year was a significant predictor of tern abundance (Table 1). Neither fish abundance nor Julian day variance explained the variation in bird abundance between years. Within years, summers that have high abundances

Table 1 Results of an ANCOVA with year as the predictor variable and $\log_{10}$ (mean number terns observed/h + 1) as the dependent variable

Predictor variable	F-value	*p*-value
Year	11.94	0.00002
Minnow CPUE	0.1106	0.7
Julian day	3.928	0.05

Average minnow CPUE (log transformed) and Julian day are the covariates (ANCOVA: Adjusted $R^2 = 0.248$, $F_{4,94} = 8.52$, $p = 0.000007$)

of fish do not necessarily have high abundances of birds (Fig. 1). On a smaller scale, a scatterplot of daily minnow CPUE and daily averages of the number of birds observed again indicate that there is no relationship between the two (Fig. 2). Overall, these data demonstrate that at small and large time scales, the abundance of minnows is not a good predictor of the abundance of foraging birds.

Environmental variables across years

Significant differences were observed in daily average measures of DO when compared between years (ANOVA; DO: $F_{(2,106)} = 8.937$, $p = 0.0003$); while no differences were found for temperature and turbidity (ANOVA: temperature: $F_{(2,109)} = 2.726$, $p = 0.07$; turbidity: $F_{(2,102)} = 0.1809$, $p = 0.8$). DO levels were significantly lower in 2006 and 2008 compared to 2007 (Fig. 3). The average DO level in 2006 was hypoxic (1.914 ± 0.15 mg/L, the lowest DO level recorded was 0.23 mg/L).

Dissolved oxygen, temperature and turbidity as predictors of predator abundance

In 2006 and 2008, only DO level was included in the forward stepwise regression as significant predictors of bird abundance (2006: $R^2 = 0.6328$, $F_{(1,\ 12)} = 20.68$, $p = 0.0007$; 2008: $R^2 = 0.1691$, $F_{(1,\ 40)} = 8.143$, $p = 0.007$); adding Julian day did not increase the variance explained (see overall model in Table 2). As DO levels decreased an increase in bird abundance was observed. In 2007, only day was included in the forward stepwise regression but the relationship was not significant between Julian day and bird abundance ($R^2 = 0.02330$, $F_{(1,\ 44)} = 1.265$, $p = 0.3$). Bird abundance was significantly greater during periods of extreme hypoxia compared to periods of normoxia in 2006 and 2008 (t-test; 2006: $t = -3.74$, $p = 0.003$, df = 12; 2007: $t = -0.161$, $p = 0.874$. df = 52; 2008: $t = -3.82$, $p = 0.00046$; Fig. 4).

Discussion

We observed the relative abundance of small fish, their physical environment, and the birds that feed upon them in order to understand the relative impact of the physical and biological environment on the abundance of avian predators. We found that DO levels best describe the abundance of avian predators in Delta Marsh. Neither the abundance of fish within the marsh, nor temperature and turbidity of the water had any significant impact upon the abundance of birds. Instead, we believe the behavioural and physiological response of the fish to hypoxia forces them to the surface where they are both detectable and accessible to birds.

Low levels of dissolved oxygen have been linked to both increases (Pihl et al. 1992) and decreases (Nestlerode and Diaz 1998) in predation risk when fish are the prey and invertebrates are the predator. In predator-prey systems that involve only fish, decreases in dissolved oxygen level result in an increase in predation risk under laboratory conditions (Wolf and Kramer 1987). In small scale experiments, hypoxic conditions resulted in greater consumption of prey by avian predators (Randle and Chapman 2004). In this study where both predators and prey were free to move about in the environment, hypoxia increased the number of

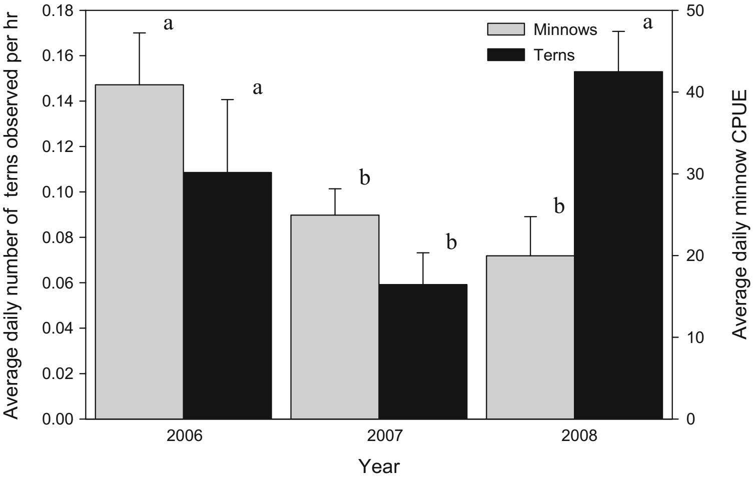

Fig. 1 Average minnow abundance (CPUE) and measures of tern abundance across the three sampling years. Error bars represent measures of standard error. When measures of minnow CPUE are compared across years 2008 is significantly different from both 2006 and 2007. A comparison of number of terns observed/h across years found 2007 to differ from both 2006 and 2008

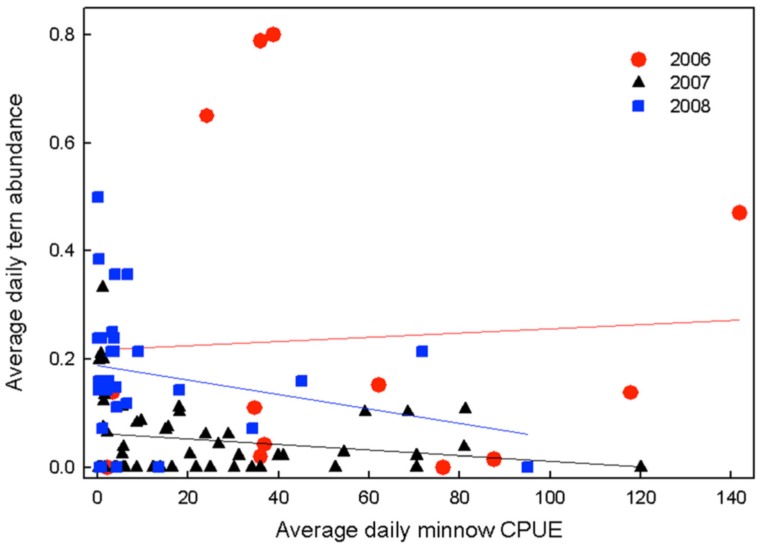

Fig. 2 Daily average measures of minnow CPUE and tern abundance across all three years. The red line represent the trendline for 2006 data, the black line represents the trendline for 2007 and the blue line represents the trendline for 2008 data. Significant differences occur between years with respect to average number of terns observed per hour, but there is no relationship between minnow CPUE and tern abundance

avian predators. As predation events require detection and encounters of the prey by the predators, increasing the numbers of predators will likely increase the predation risk of minnows.

This study measured CPUE of the minnows throughout all levels of DO and found no relationship between CPUE and number of foraging birds present. At low (hypoxic) DO levels, minnows compensate by using surface respiration and aggregate near the surface (Kevin Hedges, unpublished data). This behaviour will make the fish more available to their avian predators (Whitfield and Blaber 1978; Kramer et al. 1983) and should account for the results we observed.

Temperature, as well as dissolved oxygen, has been shown to influence predation risk in fish predator-prey interactions (Krause and Godin 1995) as well as invertebrate - anuran tadpole predator-prey interactions (Moore and Townsend 1998; Anderson et al. 2001). In this study however, no relationship was observed between temperature and abundance of predators. We did not observe any impact of aquatic temperature on avian foraging and believe this result is due to the combined effects of the shallow depth at which terns forage, and the generally turbid conditions within this system, the reason we believe that turbidity also did not impact our results. Changes in prey behaviour generated by temperature would only be evident when the fish were near the surface. This behaviour is associated with aquatic surface respiration that is generated by low DO and would therefore be accounted by that parameter in our analysis.

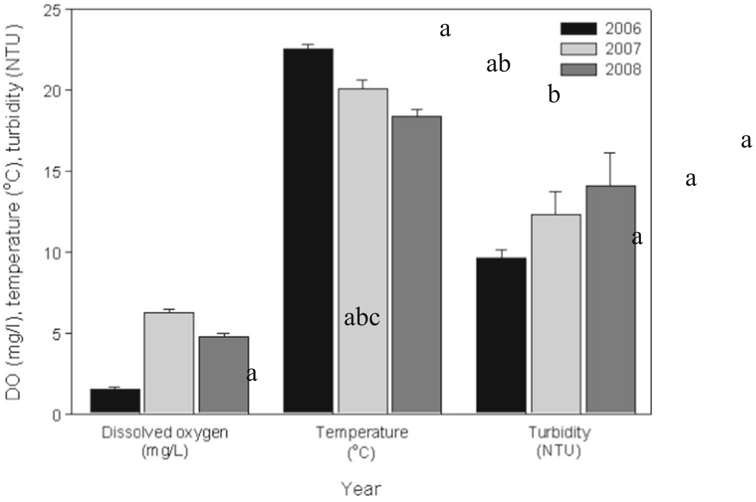

Fig. 3 Interannual variation in three measures of the abiotic aquatic environment: summer averages of dissolved oxygen (mg/L), temperature (°C) and turbidity (NTU). Error bars represent measures of standard error. There is a significant difference between each of the three years when DO values are compared while no differences exist in turbidity levels between years. When temperature is compared across the three years only 2006 and 2008 significantly differ

Table 2 Results of an ANCOVA with year as the predictor variable and $\log_{10}$ (tern abundance +1) as the dependent variable

Predictor variable	F-value	*p*-value
Year	10.09	0.00008
Dissolved oxygen	26.94	< 0.000001
Temperature	0.07519	0.8
Turbidity	2.196	0.1
Julian day	5.538	0.02

Measured environmental variables (dissolved oxygen, temperature and turbidity) and Julian day are the covariates (ANCOVA: Adjusted $R^2 = 0.3597$, $F_{(7,97)} = 9.121$, $p < 0.0001$). Significant differences exist in the tern abundance between years. Dissolved oxygen is the only covariate that significantly increases the variance explained by the model

In larger lakes, use of these shallow littoral zones by forage fish would make them available to plunge diving predators such as Forster's terns. In areas such as Delta Marsh, water bodies generally do not have gently sloping shorelines that may be occupied by small bodied fish. In these instances, there is the potential for the DO content of the water to have important effects on energy budgets for adult Forster's terns, as well the success of their fledglings. The main observation based on the results of this study is that it appears as if it is not the abundance of prey, but their availability to predators that is important. Under normoxic conditions, if prey are using deeper waters as a refuge from predation and are not physiologically stressed because DO levels are high, terns may have to increase their search area as these prey are not available in this location. Increased searching and travel distance to a new food patch increases the terns own energetic requirement for food. This could lead to a reduction in the amount of food provisioned to their fledglings, and a potential reduction in successful fledging. Future research examining the effects of dissolved oxygen levels on foraging success (not just presence) of terns, as well as its impact on the amount of food provisioned to young chicks would provide further insight into the consequences of a variable environment of the overall success of tern colonies.

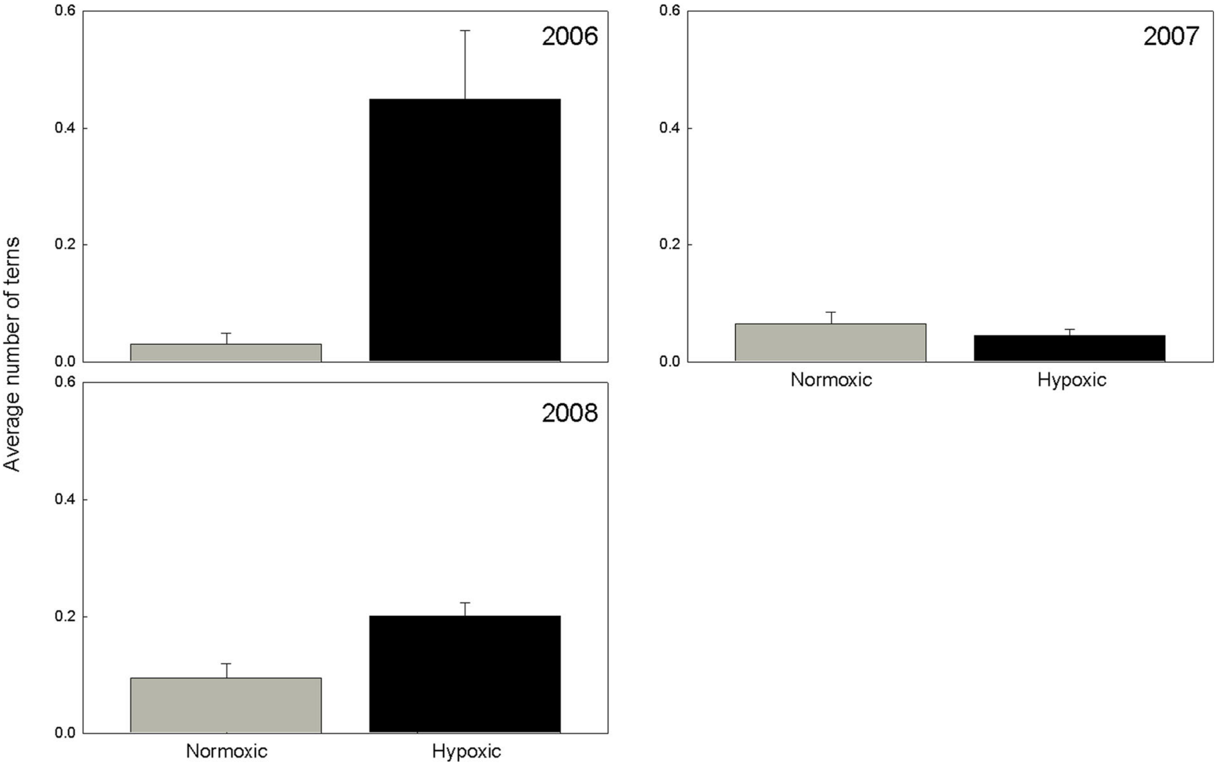

Fig. 4 A comparison of tern abundance, in each year of the study, on days when the water had high levels of dissolved oxygen to the number observed per hour during times of low dissolved oxygen levels; 2006 was a low DO level year, 2007 a high DO level year and 2008 a moderate DO level year. Error bars represent standard error

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Compliance with ethical standards

Ethics The research described in this manuscript was reviewed by the University of Manitoba's Animal Care Committee and determined to conform to the ethical requirements of the Canadian Council on Animal Care (Protocol Number F03–041/1/2/3).

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