



Journal of Fish Biology (2010) **76**, 1729–1741

doi:10.1111/j.1095-8649.2010.02612.x, available online at www.interscience.wiley.com

Effects of turbidity and prey density on the foraging success of age 0 year yellow perch *Perca flavescens*

C. G. WELLINGTON*, C. M. MAYER, J. M. BOSSENBROEK AND N. A. STROH

Department of Environmental Sciences and the Lake Erie Center, University of Toledo, 6200 Bayshore Road, Oregon, OH 43616, U.S.A.

(Received 4 January 2009, Accepted 3 February 2010)

Laboratory experiments were conducted to determine how larval and juvenile yellow perch *Perca flavescens* respond to changes in prey density when exposed to different levels and types of turbidity (phytoplanktonic or sedimentary). Across prey densities, consumption by *P. flavescens* tended to be less in phytoplanktonic turbidity compared with sedimentary turbidity. For larvae, this effect was dependent on turbidity level (consumption differed between turbidity types only at high turbidity), while for juveniles the difference with turbidity type was equal across turbidity levels. These results suggest that phytoplankton blooms are detrimental to the ability of late season age 0 year *P. flavescens* to forage and support the need to control factors leading to excessive phytoplankton growth in lakes.

© 2010 The Authors

Journal compilation © 2010 The Fisheries Society of the British Isles

Key words: eutrophication; functional response; recruitment; sedimentation.

INTRODUCTION

Yellow perch *Perca flavescens* (Mitchell) are ecologically and economically important throughout their range. They merge nearshore and pelagic food webs (Clapp & Dettmers, 2004), provide a key food source for larger sport fishes (Werner, 2004) and support both sport and commercial fisheries. *Perca flavescens* are in the top three species in the Great Lakes fishery (U.S. Census Bureau, 2001), and in some locations comprise 85% of the sport fish catch (Clapp & Dettmers, 2004). Recruitment of *P. flavescens*, like most freshwater fishes, often depends on visual foraging success during the age 0 year period (*i.e.* larval and juvenile stages) (Hairston *et al.*, 1982; Guthrie, 1986). Environmental factors that affect visual foraging, including turbidity level, turbidity type (*i.e.* sedimentary or phytoplanktonic) and prey density, are likely to co-vary spatially and temporally in lakes. Therefore, an understanding of the interactive effects of turbidity and prey density is crucial to predicting recruitment. Both turbidity and prey density can be influenced by human land use practices that affect sedimentation and overall productivity of phytoplankton and zooplankton, thus linking land-use management with fisheries ecology.

*Author to whom correspondence should be addressed. Tel.: +1 419 609 4120; fax: +1 419 609 4158; email: wellington.28@osu.edu

Turbidity tends to reduce light intensity and increase light scattering, which can decrease the visual field, or reaction distance, of *P. flavescens* (Richmond *et al.*, 2004). Field and laboratory evidences, however, suggest the effect of turbidity on foraging success may also depend on the turbidity type and life stage of the individual. In Oneida Lake, NY, U.S.A., for example, age 0 year *P. flavescens* growth rate increased with the introduction of zebra mussels *Dreissena polymorpha* with subsequent decline in phytoplanktonic turbidity (Mayer *et al.*, 2000). Also, in highly eutrophic European lakes, the biomass and growth rates of perch *Perca fluviatilis* L. declined along a productivity gradient, particularly in juveniles (Sandström & Karås, 2002; Radke, 2005). Conversely, in western Lake Erie, *P. flavescens* recruitment is positively correlated with Maumee River discharge, which is often sediment-rich (S. A. Ludsin, pers. comm.). In laboratory foraging studies, consumption is lower in phytoplanktonic than sedimentary turbidity (Radke, 2005; B. S. Elkington & C. M. Mayer, pers. comm.). Furthermore, consumption by larval and juvenile *P. flavescens* declines with increasing phytoplanktonic turbidity, but it does not decline for larvae in sedimentary turbidity (B. S. Elkington & C. M. Mayer, pers. comm.). These differing responses to turbidity type with life stage are important because events that drive turbidity may vary seasonally in lakes, exposing fishes to different intensities of sedimentary and phytoplanktonic turbidity at different life stages, thereby influencing foraging and recruitment.

Prey consumption is influenced not only by the visibility of prey but also by prey abundance. Consumption usually increases with prey density; for age 0 year *P. flavescens*, growth and survival are positively correlated with zooplankton density (Noble, 1975; Ludsin, 2000; Dettmers *et al.*, 2003; Clapp & Dettmers, 2004). The question follows: can high prey density compensate for factors such as turbidity type and level that may hinder prey detection and consumption? The question is important because of the tendency for turbidity and total phosphorus (implicitly prey density) to co-vary in many ecosystems (Grayson *et al.*, 1995). Because of the difficulty in interpreting correlational field data, manipulative experiments are needed to provide insight into the independent and interacting effects of factors affecting *P. flavescens* foraging ability.

The differing responses to turbidity type for different life stages of fishes may be due to physical attributes of both the turbidity type and age 0 year fishes. Phytoplankters often form large clumps and are pigmented, whereas sediment particles are usually small and lack photosynthetic pigments (Wotton, 1994; Kurmayer *et al.*, 2002). Smaller particles scatter more light, necessitating fewer particles to achieve the same turbidity level as formed with larger particles (Wotton, 1994). Smaller sediment particles also provide greater contrast with the typically larger prey items (Schael *et al.*, 1991). Phytoplankton aggregates, on the other hand, can be similarly sized to individual prey items (*i.e.* zooplankton). Additionally, the pigment in phytoplankton provides a higher absorption capacity, resulting in reduced light intensity, an unfavourable condition for visual foraging (Utne-Palm, 2002; Radke, 2005). Differences in response at different life stages could be due to changes in cone and rod-cell function in the fishes. Larval fishes have UV-sensitive cones that are believed to aid in detection of planktonic prey (Sandström, 1999). Also, a change in rod cell function results in a shorter visual field for larvae (<20 mm total length, L_T) than juveniles (>20 mm L_T) (Wahl *et al.*, 1993). Over a shorter distance, fewer

particles (phytoplankton or sediment) exist between a fish and its prey to interfere with detection, possibly reducing the effects of turbidity on larvae (Utne-Palm, 2002). Testing these explanations is important for understanding the mechanisms responsible for differing foraging responses in turbid conditions and the role of prey density in compensating for the effects of turbidity.

The effects of turbidity level, turbidity type and prey density on larval and juvenile *P. flavescens* foraging were tested experimentally. Also, two potential mechanisms for the differing foraging responses to turbidity were examined: particle size and light intensity. It was hypothesized that (1) consumption would increase with prey density, but insufficiently to compensate for the effects of turbidity level and type. The rate of increase in consumption with prey density was expected to be lower in phytoplanktonic turbidity and high turbidity levels, with the exception of larvae foraging in sedimentary turbidity, for which no difference was anticipated with respect to turbidity level. (2) Consumption was expected to be negatively related to particle size and (3) light levels were expected to be lower in phytoplanktonic than sedimentary turbidity at the same turbidity level.

MATERIALS AND METHODS

A factorial experiment was conducted to quantify the effects of turbidity level, type and prey density on consumption by larval and juvenile *P. flavescens* during the summer of 2007. Treatments included: four levels of turbidity [<5 , 20, 50 and 100 nephelometric turbidity units (NTU)], two turbidity types (supplemented phytoplankton and lake sediment) and seven prey densities (5, 10, 30, 70, 100, 150 and 300 zooplankton l^{-1}). All treatment-level combinations were applied to both larval (mean \pm s.d. 19.1 ± 1.5 mm L_T) and juvenile (44.9 ± 5.4 mm L_T) *P. flavescens*. Fish were provided by Ohio State South Centers Aquaculture facility at Piketon, OH, U.S.A.

Turbidity levels were chosen to represent a naturally occurring range; levels >100 NTU have been observed, but only transiently in some turbid areas (Brown & Krygier, 1971; Bisson & Bilby, 1982). Four levels of turbidity were presumed sufficient to describe the linear relationship with consumption, suggested by preliminary data (B. S. Elkington & C. M. Mayer, pers. comm.). The sediment used to generate sedimentary turbidity was obtained from western Lake Erie and sieved (75 μ m mesh) to homogenize size and remove large particles that would quickly fall out of suspension. Phytoplankton cultures (obtained from the University of Toledo's Lake Erie Center pond) could not be maintained at turbidity levels $>c.$ 45 NTU. Therefore, to reach the desired levels of turbidity, phytoplankton was supplemented with homogenized spinach slurry. Preliminary trials showed no difference in consumption between trials with exclusively cultured phytoplankton and with supplemented phytoplankton at 15 NTU (t -test, d.f. = 4, $P > 0.05$). Seven levels of prey densities were chosen to be able to describe a curvilinear functional response.

Experiments with larvae were not replicated due to the high number of treatment levels ($4 \times 2 \times 7$, $n = 56$) and the short duration of the larval period (Balon, 1975). For juveniles, trials for some treatment combinations (20 and 100 NTU; supplemented phytoplankton and sediment; 10, 100 and 300 zooplankton l^{-1}) were conducted three times to gain data on variance, resulting in 24 additional trials ($2 \times 2 \times 3 \times 2$).

Experiments were conducted in microcosms (30 l aquaria) held on shelving racks under constant light and temperature conditions. Overhanging florescent lights provided a surface light level of 100 μ mol quanta $m^{-2} s^{-1}$. Trials were run at ambient water temperature, which did not vary $>3^\circ$ C among trials for a given life stage (larval, 18–21.5 $^\circ$ C; juvenile, 21–24 $^\circ$ C). Turbidity level was measured at the beginning and end of each trial using a YSI multi-variable probe (www.ysi.com) with a 6136 turbidity sensor attachment (range: 0–1000 NTU; resolution: 0.1 NTU; accuracy $\pm 5\%$ of reading or 2 NTU). Trials were discarded if turbidity level dropped >10 NTU.

All fish were starved 16–24 h before feeding trials to equalize hunger and allow gut contents to pass. Fish were acclimated to treatment aquaria with the appropriate turbidity conditions for 30 min before experimentation. Three fish were used in each aquarium to simulate the natural group foraging behaviour of *P. flavescens* (Juanes *et al.*, 2002). At the end of the acclimation period, zooplankton were added at the desired concentration and fish were allowed to forage for 1 h. Zooplankton came from a stock suspension obtained from the Lake Erie Center pond and passed through a 250 μm sieve to exclude most rotifers and nauplii, which *P. flavescens* >8 mm do not typically consume (Schael *et al.*, 1991; Ludsins, 2000).

At the end of each trial, the fish were euthanized under the University of Toledo Institutional Animal Care and Use Committee guidelines and immediately preserved in 70% ethanol. The L_T (nearest 0.1 mm) was measured and all consumed prey were enumerated, identified and measured according to body shape (Culver *et al.*, 1985) using a dissecting microscope and digitizing tablet viewed through a drawing tube.

MECHANISTIC STUDIES

The experimental procedure described above was also used to determine whether particle size is a plausible mechanism for the differing effects of phytoplanktonic and sedimentary turbidity on zooplankton consumption. Treatments included two size classes within a single particle type (sieved from a blended spinach slurry): small (63–500 μm) and large (>500 μm). Turbidity level and prey density were held constant at 10 NTU and 100 zooplankters l^{-1} , respectively. Each size class was replicated five times for both larval and juvenile *P. flavescens*.

To test whether light intensity explains the difference in foraging response with turbidity type, a light meter (LI-COR Integrating quantum radiometer/photometer; model LI-1885; www.biospherical.com) was used to gauge light levels 100 mm below the surface in turbid microcosms. All turbidity conditions used in the main factorial experiment (sedimentary and phytoplanktonic, <5, 20, 50 and 100 NTU) were compared. Treatments were replicated three times.

DATA ANALYSIS

All data were analysed using the general linear models (GLM) procedure of SAS 9.1 (SAS Institute Inc; www.sas.com) with an absolute or corrected (Kimball inequality) α level of 0.05. Treatment effects of turbidity level, turbidity type and prey density were described using average number of prey consumed per fish h^{-1} as the dependent variable (Kutner *et al.*, 2005). All factors were treated as fixed effects. Model specifics are provided below.

Linear regression was used to test for consumption and turbidity level and consumption and prey density relationships within each turbidity type and life stage. Additionally, consumption and prey density relationships were tested for each turbidity type divided into high and low turbidity levels for each life stage. ANCOVA for parallel slopes was used to determine the presence of an interaction between the treatment (turbidity level and type) and the covariate (turbidity level or prey density) within each life stage. If the slopes were parallel, ANCOVA was used to determine whether the linear intercepts differed. If the slopes were not parallel, an interaction could be inferred, and ANCOVA would not be appropriate for testing treatment differences. In the case of juveniles, because there was replication of some levels of each factor, a three-factor ANOVA was also employed to test for differences in the mean effects of treatments.

Additional analyses were conducted for testing whether particle size and light level could explain the differing foraging response to turbidity type. *t*-tests were used to determine whether there was a difference between prey consumption in small and large particle turbidity for each life stage. ANCOVA was used to determine whether increasing phytoplanktonic and sedimentary turbidity similarly reduced light intensity. Two-factor ANOVA was used to test for mean differences in light intensity between phytoplanktonic and sedimentary turbidity.

RESULTS

LARVAL *P. FLAVESCENS*

Consumption decreased with increasing phytoplanktonic turbidity level (linear regression, d.f. = 27, $P < 0.05$, $r^2 = 0.12$), but not with sedimentary turbidity level (linear regression, d.f. = 27, $P > 0.05$, $r^2 = 0.04$; Fig. 1). The slopes of the consumption–turbidity level relationships were not equal (ANCOVA test for parallel slopes, d.f. = 52, $P < 0.05$; Fig. 1), indicating that the effect of turbidity level on prey consumption differs between turbidity types.

Consumption increased with increasing prey density for both phytoplanktonic (linear regression, d.f. = 27, $P < 0.001$, $r^2 = 0.35$) and sedimentary turbidities [linear regression, d.f. = 27, $P < 0.001$, $r^2 = 0.41$; Fig. 2(a)]. The slopes of the consumption–prey density relationships were parallel [ANCOVA test for parallel slopes, d.f. = 52, $P > 0.05$; Fig. 2(a)], and the intercepts did not differ from each other [ANCOVA, d.f. = 53, $P > 0.05$; Fig. 2(a)]. This suggests increasing prey density affects prey consumption similarly in the presence of sedimentary and phytoplanktonic turbidity.

Because turbidity type interacted with turbidity level (Fig. 1), the effects of type were further divided into low (5 and 20 NTU) and high (50 and 100 NTU) turbidity levels. Consumption in all turbidity conditions tended to increase with increasing prey density [linear regression: phytoplankton high, d.f. = 13, $P < 0.01$, $r^2 = 0.46$; phytoplankton low, d.f. = 13, $P < 0.01$, $r^2 = 0.47$; sediment high, d.f. = 13, $P < 0.001$, $r^2 = 0.19$; sediment low, d.f. = 13, $P > 0.05$, $r^2 = 0.67$; Fig. 2(b)]. The slopes of these four consumption–prey density relationships were parallel [ANCOVA test for parallel slopes, d.f. = 49, $P > 0.05$; Fig. 2(b)], and the intercepts differed in

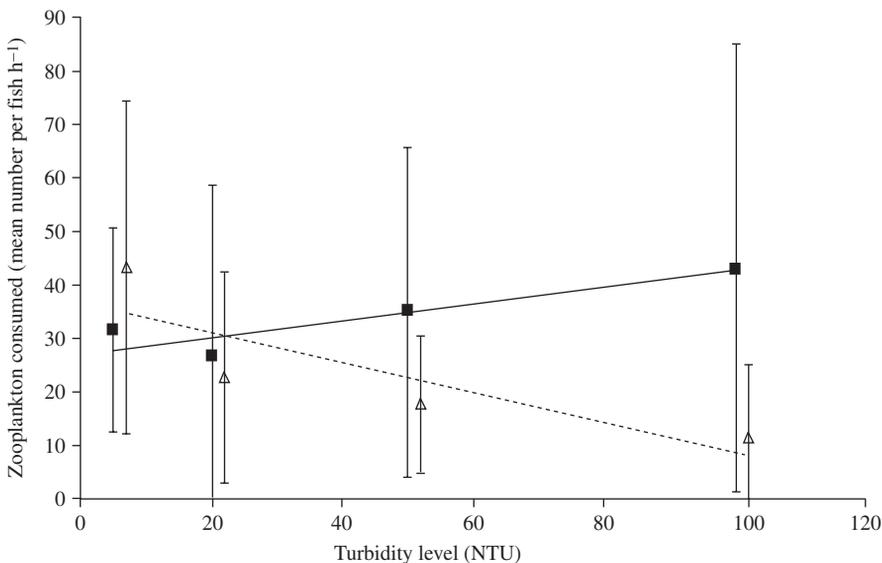


FIG. 1. Mean \pm s.d. zooplankton consumption by larval *Perca flavescens* compared with turbidity level and type (sedimentary ■ and phytoplanktonic △).

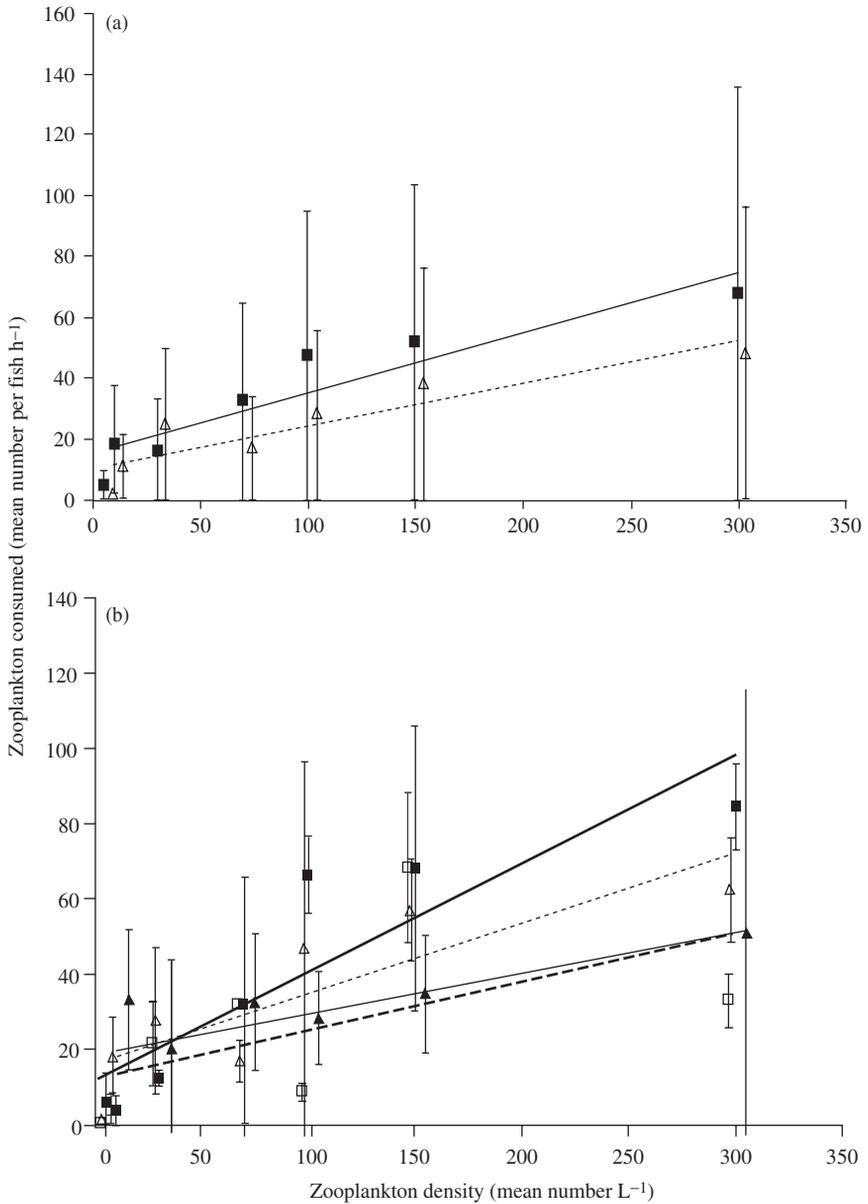


FIG. 2. Larval *Perca flavescens* consumption and prey density relationships. Consumption by (a) turbidity type (sedimentary ■ and phytoplanktonic △) and (b) turbidity level and type (low sedimentary ▲, high sedimentary ■, low phytoplanktonic △ and high phytoplanktonic □). Values are means \pm s.d.

terms of the interaction of turbidity type with turbidity level (ANCOVA, d.f. = 51, $P < 0.05$), thus reinforcing the differing effects of turbidity level on consumption for different turbidity types (*i.e.* that consumption is less in phytoplanktonic than sedimentary turbidity only at high turbidity levels).

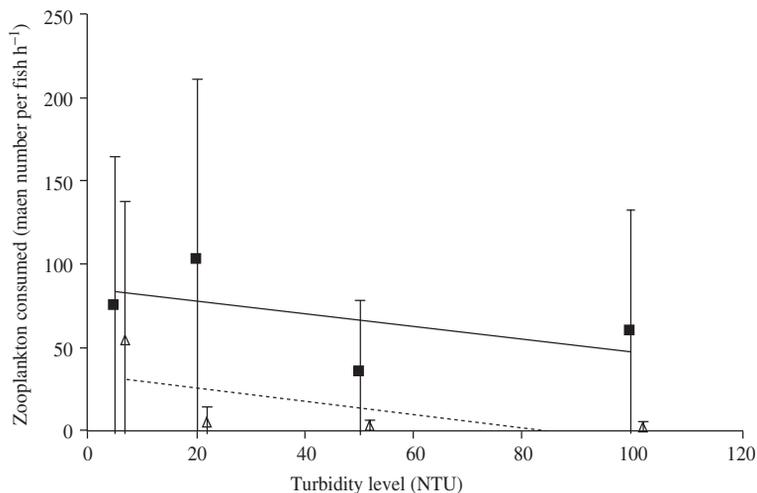


FIG. 3. Mean \pm S.D. zooplankton consumption by juvenile *Perca flavescens* compared with turbidity level and type (sedimentary ■ and phytoplanktonic △).

JUVENILE *P. FLAVESCENS*

Juvenile consumption marginally decreased with increasing phytoplanktonic turbidity level (linear regression, d.f. = 45, $P > 0.05$, $r^2 = 0.03$) but was not affected by increasing sedimentary turbidity level (linear regression, d.f. = 45, $P > 0.05$, $r^2 = 0.08$; Fig. 3). The slopes of the consumption–turbidity level relationships were parallel (ANCOVA test for parallel slopes, d.f. = 88, $P > 0.05$; Fig. 3), and the intercept for phytoplanktonic was less than for sedimentary (ANCOVA, d.f. = 89, $P < 0.001$; Fig. 3), indicating reduced consumption in phytoplanktonic turbidity.

Consumption increased with increasing prey density for both phytoplanktonic (linear regression, d.f. = 45, $P < 0.001$, $r^2 = 0.41$) and sedimentary turbidities [linear regression, d.f. = 45, $P < 0.05$, $r^2 = 0.09$; Fig. 4(a)]. The slopes of the consumption–prey density relationships were not parallel [ANCOVA test for parallel slopes, d.f. = 88, $P < 0.001$; Fig. 4(a)], which indicates that the effect of prey density on prey consumption differs between turbidity types. Furthermore, the results of a three-factor ANOVA using the replicated trials suggest mean consumption for sedimentary turbidity was higher than for phytoplanktonic turbidity (ANOVA, d.f. = 24, $P < 0.001$).

When the effects of turbidity type were divided into low and high turbidity levels, consumption always tended to increase with increasing prey density [linear regression: phytoplankton high, d.f. = 22, $P > 0.05$, $r^2 = 0.07$; phytoplankton low, d.f. = 22, $P < 0.05$, $r^2 = 0.18$; sedimentary high, d.f. = 22, $P > 0.05$, $r^2 = 0.15$; sedimentary low, d.f. = 22, $P < 0.001$, $r^2 = 0.74$; Fig. 4(b)], and differed both in terms of turbidity type (ANCOVA test for parallel slopes, d.f. = 86, $P < 0.001$) and turbidity level (ANCOVA test for parallel slopes, d.f. = 86, $P < 0.001$). The non-parallel slopes indicate that the effects of prey density on consumption differed depending on turbidity level and type. Prey density increased consumption less in high (compared with low) turbidity and in phytoplanktonic (compared with sedimentary) turbidity.

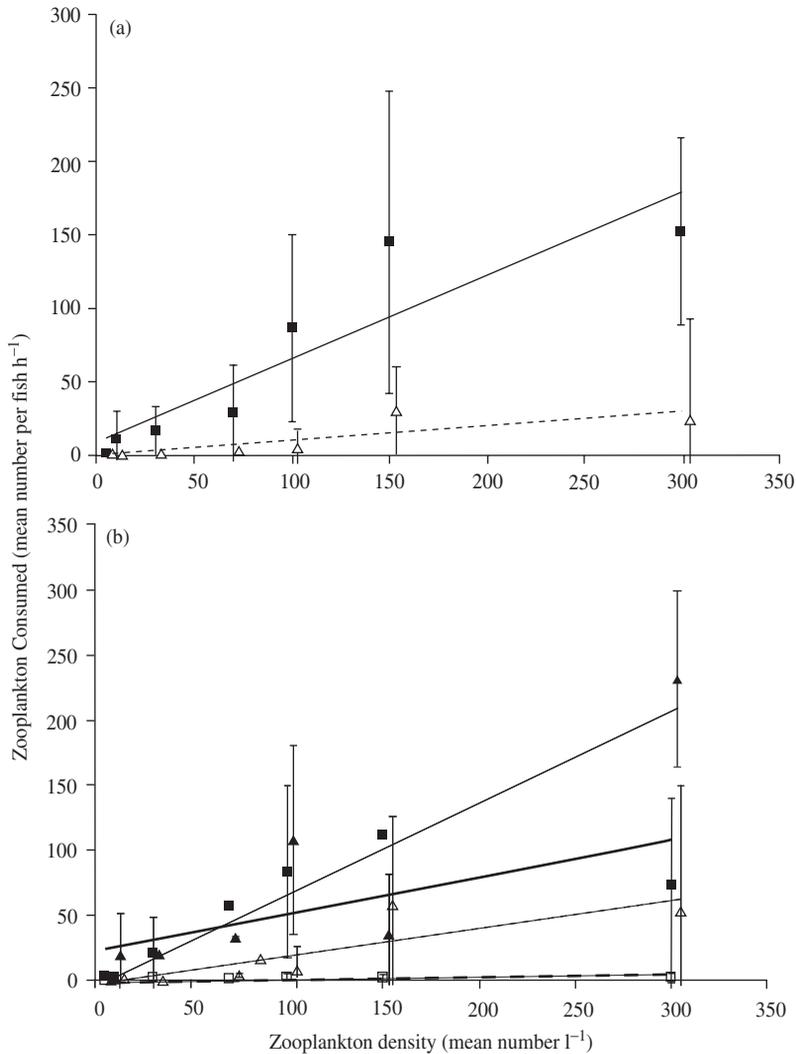


FIG. 4. Juvenile *Perca flavescens* consumption–prey density relationships. Consumption by (a) turbidity type (sedimentary ■ and phytoplanktonic △) and (b) turbidity level and type (low sedimentary ▲, high sedimentary ■, low phytoplanktonic ◻ and high phytoplanktonic ◻). Values are means \pm S.D.

MECHANISTIC STUDIES

Larval *P. flavescens* consumption was not affected by turbidity particle size (*t*-test, d.f. = 8, $P > 0.05$). Juvenile consumption, however, tended to be greater in large particle turbidity (phytoplankton size) than small particle turbidity (sediment size) (*t*-test, d.f. = 8, $P = 0.05$; Fig. 5).

Light intensity decreased with increasing turbidity level in both phytoplanktonic and sedimentary turbidities (linear regression: phytoplankton, d.f. = 4, $P < 0.001$, $r^2 = 0.77$; sedimentary, d.f. = 4, $P < 0.001$, $r^2 = 0.90$). The slopes of the relationships of light level with increasing turbidity for phytoplanktonic and sedimentary

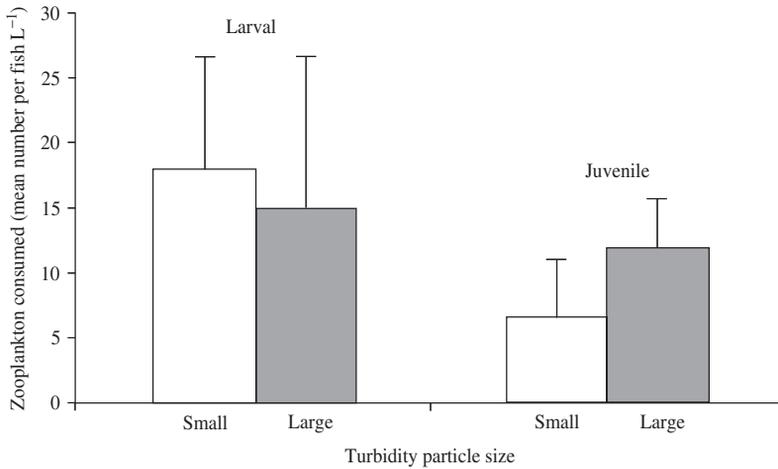


FIG. 5. Effects of turbidity particle size (small and large) on mean \pm S.D. zooplankton consumption by larval and juvenile *Perca flavescens*.

turbidities were different (ANCOVA test for parallel slopes, d.f. = 20, $P < 0.05$; Fig. 6), indicating a differing effect of turbidity type on light level. Also, the mean light intensity was lower in phytoplanktonic than sedimentary turbidity (ANOVA, d.f. = 16, $P < 0.001$).

DISCUSSION

Consistent with previous research, zooplankton consumption by age 0 year *P. flavescens* was reduced with increasing phytoplanktonic turbidity, but not with

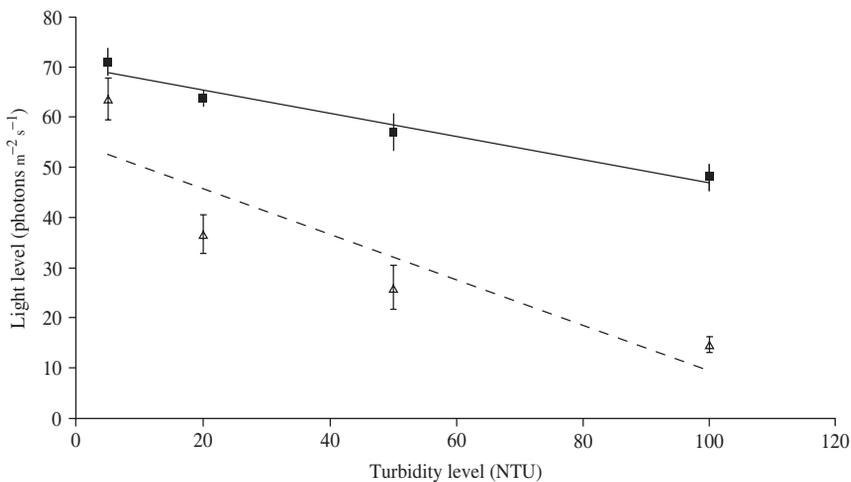


FIG. 6. Effects of turbidity level and type on sub-surface light levels. The change in light level differed between turbidity types (sedimentary ■ and phytoplanktonic △).

sedimentary turbidity (Granqvist & Mattila, 2004; Radke, 2005). As hypothesized, increased prey density was unable to compensate for the consumption-reducing effects of increased phytoplanktonic turbidity. This suggests that under eutrophic conditions, the visual interference of phytoplankton-generated turbidity outweighs the benefits of prey abundance for visually foraging fish. Consequently, *P. flavescens* foraging, growth and ultimately recruitment may be expected to decline with increasing cultural eutrophication, a trend already encountered with *P. flavescens* in areas of the Laurentian Great Lakes and *P. fluviatilis* in the Baltic Sea and lakes across Europe (Sandström & Karås, 2002; Radke, 2005).

Zooplankton consumption by larval and juvenile *P. flavescens* tended to decline with increasing phytoplanktonic turbidity, a trend consistent with previous foraging experiments (B. S. Elkington & C. M. Mayer, pers. comm.). For larval fish, consumption tended to be less in phytoplanktonic than sedimentary turbidity only at high turbidity levels. At low turbidity, phytoplankton might have slightly aided foraging through a mechanism such as increased colour contrast with prey. For juveniles, consumption was significantly lower in phytoplanktonic than sedimentary turbidity across all turbidity levels. The presence of turbidity type differences even at low turbidity levels is notable because these levels are often comparable with field conditions, where phytoplankton density is limited by self-shading and storm-driven sedimentary events are not permanently sustained (Brown & Krygier, 1971; Agusti *et al.*, 1987). The negative effects of low-level phytoplanktonic turbidity on juvenile *P. flavescens* are especially important in unstratified eutrophic areas where seasonal timing exposes juveniles more to phytoplanktonic turbidity (Moorhead *et al.*, 2008).

The absence of an effect of increasing sedimentary turbidity on consumption is consistent with studies of *P. fluviatilis* and larval *P. flavescens* (Granqvist & Mattila, 2004; Radke, 2005; B. S. Elkington & C. M. Mayer, pers. comm.). Juvenile *P. flavescens* have exhibited reduced consumption in sedimentary turbidity, and might have in this study had more replication been possible. The lack of consumption response does not preclude the possibility of subsidiary effects on foraging and recruitment. For example, equal consumption does not necessarily correlate with equal activity; there may be increased behavioural costs associated with foraging in turbid water due to more failed attacks (Granqvist & Mattila, 2004; Lunggren & Sandström, 2007). Conversely, there may be lower costs associated with feeding in turbidity due to reduced antipredator behaviour (Abrahams & Kattenfeld, 1997; Snickars *et al.*, 2004). Quantifying and separating these behavioural costs may be important to a more complete understanding of the role of sedimentary turbidity on *P. flavescens* recruitment.

Despite the tendency for consumption by age 0 year *P. flavescens* to increase with prey density, elevated prey density was insufficient to compensate for the effects of turbidity. Larval consumption was reduced in high phytoplanktonic turbidity, and juvenile consumption was less across all phytoplanktonic turbidity levels compared with sedimentary turbidity. Under such circumstances, a change in the type of functional response might be expected, *i.e.* the rate of change in consumption with prey density (Holling, 1959). Although rare for planktivorous fish larvae, switching from a type II to type III response has been noted for older fishes in unfavourable foraging conditions (Townsend & Risebrow, 1982). Functional response analysis reveals no difference in the response type between phytoplanktonic and sedimentary turbidity (Wellington, 2008). For juveniles, however, the absolute difference in consumption

did become more pronounced with increasing prey density. For example, at the lowest prey density (five zooplankters l^{-1}), consumption was about equal in phytoplanktonic and sedimentary turbidity. At 300 zooplankters l^{-1} , however, fish in phytoplanktonic turbidity only consumed the same amount as fish in sedimentary turbidity at 30 zooplankters l^{-1} [Fig. 4(a)]. These results reinforce the need to control land-use practices that affect high phytoplanktonic turbidity, even in areas where turbidity is correlated with prey density. In many lakes, phytoplankton growth is limited by phosphorus (Kalf, 2002); although legislation has successfully reduced point sources, non-point sources of soluble reactive phosphorus continue to rise in some lakes with agricultural catchments (Richards, 2008). Managers, therefore, will need to balance the demand for increasing agricultural production with environmental consequences, such as possible loss to fisheries.

Particle size did not provide a mechanistic reason for the differing foraging responses with turbidity type, as consumption was greater in large particle (phytoplankton size) turbidity. Differences in light intensity may provide a partial explanation. Light intensity was reduced more by phytoplanktonic than sedimentary turbidity. *Perca flavescens* are nocturnally inactive, and their reaction distance and consumption are reduced in low light (<10 lx) conditions (Granqvist & Mattila, 2004; Lungren & Sandström, 2007). Although light intensity in the trials did not drop below *c.* 13 μmol quanta $\text{m}^{-2} \text{s}^{-1}$ (*c.* 962 lx), the lower consumption in phytoplanktonic turbidity could partially be explained by reduced light (Thimijan & Heins, 1982). Bluegills *Lepomis macrochirus* Rafinesque, for example, experience decreased consumption when turbidity is combined with light levels <450 lx (Miner & Stein, 1993). Because lakes are not always exposed to full sunlight, understanding the interaction of turbidity and light levels is important and may help predict *P. flavescens* recruitment.

Overall, these results highlight the importance of turbidity level and type on the foraging success of age 0 year *P. flavescens* foraging in the laboratory. Moreover, it is shown that even increasing prey density cannot completely compensate for the negative effects of phytoplankton, especially at high turbidities and particularly for juveniles. Because recruitment is often dependent on strong visual foraging, the results also suggest that year-class strength could be influenced by the timing and extent of phytoplankton blooms. Thus, catchment management practices that reduce nutrients may benefit *P. flavescens* fisheries more than those aimed at reducing sedimentation, particularly when phytoplankton growth is nutrient limited. Additional research that could further inform these management decisions might examine the effects of phytoplankton type (green *v.* blue-green) on foraging success and the effects of turbidity that combines sediment and phytoplankton. Overall, this study provides important considerations for managers making decision about land-use practices that contribute to eutrophication in lakes.

This work was supported by the Great Lakes Fishery Commission and the National Science Foundation's Research Experience for Undergraduates Program (grant number EAR-0552552), which provided support for N.A.S. Fish were provided by The Ohio State University South Centers (J. Wallet). The authors also thank J. Reighard and B. Bodamer for their laboratory assistance. This is publication 2009-12 from the University of Toledo Lake Erie Center.

References

- Abrahams, M. & Kattenfeld, M. (1997). The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behavioral Ecology and Sociobiology* **40**, 169–174.
- Agusti, S., Duarte, C. M. & Kalff, J. (1987). Algal cell size and the maximum density and biomass of phytoplankton. *Limnology and Oceanography* **32**, 983–986.
- Balon, E. K. (1975). Terminology of intervals in fish development. *Journal of the Fisheries Research Board of Canada* **32**, 1663–1670.
- Bisson, P. A. & Bilby, R. E. (1982). Avoidance of suspended sediment by juvenile coho salmon. *North American Journal of Fisheries Management* **4**, 371–374.
- Brown, G. W. & Krygier, J. T. (1971). Clear-cut logging and sediment production in the Oregon Coast Range. *Water Resources Research* **7**, 1189–1198.
- Clapp, D. & Dettmers, J. (2004). Yellow perch research and management in Lake Michigan: evaluating progress in a cooperative effort 1997–2001. *Fisheries Research* **29**, 11–19.
- Culver, D. A., Boucherle, M. M., Bean, D. J. & Fletcher, J. W. (1985). Biomass of freshwater crustacean zooplankton from length-weight regressions. *Canadian Journal of Fisheries and Aquatic Sciences* **4**, 1380–1390.
- Dettmers, J. M., Raffenberg, M. J. & Weis, M. K. (2003). Exploring zooplankton changes in southern Lake Michigan: implications for yellow perch recruitment. *Journal of Great Lakes Research* **29**, 355–364.
- Granqvist, M. & Mattila, J. (2004). The effects of turbidity and light intensity on the consumption of mysids by juvenile perch. *Hydrobiologia* **514**, 93–101.
- Grayson, R. B., Finlayson, B. L., Gippel, C. J. & Hart, B. T. (1995). The potential of field turbidity measurements for the computation of total phosphorus and total suspended solids loads. *Journal of Environmental Management* **47**, 257–267.
- Guthrie, D. M. (1986). Role of vision in fish behaviour. In *The Behaviour of Teleost Fishes* (Pitcher, T. J., ed.), pp. 75–113. London: Croom Helm.
- Hairston, N. G. Jr., Li, K. T. & Easter, S. S. Jr. (1982). Fish vision and detection of planktonic prey. *Science* **218**, 1240–1242.
- Holling, C. S. (1959). The components of predation as revealed by a study of small-mammal predation of the European Pine Sawfly. *Canadian Entomologist* **91**, 293–320.
- Juanes, F., Buckel, J. A. & Scharf, F. S. (2002). Feeding ecology of piscivorous fishes. In *Handbook of Fish Biology and Fisheries* (Hart, P. & Reynolds, J., eds), pp. 267–283. Oxford: Wiley-Blackwell.
- Kalff, J. (2002). Rivers and the export of materials from drainage basins and the atmospheres. In *Limnology* (Ryu, T. & Hakim, J., eds), p. 94. Upper Saddle River, NJ: Prentice-Hall.
- Kurmayer, R., Christiansen, G. & Chorus, I. (2002). The abundance of microcystin-producing genotypes correlates positively with colony size in *Microcystis* sp. and determines its microcystin net production in Lake Wannsee. *Applied and Environmental Microbiology* **69**, 787–795.
- Kutner, M. H., Nachtsheim, C. J., Neter, J. & Li, W. (2005). Multi-factor studies. In *Applied Linear Statistical Models*, 5th edn (Gordon, B., Hercher, R. T. & Stone, L., eds), pp. 812–879. New York, NY: McGraw-Hill.
- Ludsin, S. A. (2000). Exploration of spatiotemporal patterns in recruitment and community organization of Lake Erie fishes: a multiscale, mechanistic approach. Doctoral Thesis, The Ohio State University, Columbus, OH, USA.
- Lunggren, L. & Sandström, A. (2007). Influence of visual conditions on foraging and growth of juvenile fishes with dissimilar sensory physiology. *Journal of Fish Biology* **70**, 1319–1334.
- Mayer, C. M., VanDeValk, A. J., Forney, J. L., Rudstam, L. G. & Mills, E. L. (2000). Response of yellow perch (*Perca flavescens*) in Oneida Lake, New York, to the establishment of zebra mussels (*Dreissena polymorpha*). *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 742–754.
- Miner, J. G. & Stein, R. A. (1993). Interactive influence of turbidity and light on larval bluegill foraging. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 781–788.

- Moorhead, D., Bridgeman, T. & Morris, J. (2008). Changes in water quality of Maumee Bay 1928–2003. In *Checking the Pulse of Lake Erie* (Munawar, M. & Heath, R., eds), pp. 123–158. Philadelphia, PA: Taylor and Francis, Inc.
- Noble, R. L. (1975). Growth of yellow perch in relation to zooplankton populations. *Transactions of the American Fisheries Society* **104**, 731–741.
- Radke, R. (2005). Effects of phytoplankton-induced turbidity on predation success of piscivorous Eurasian perch. *Die Naturwissenschaften* **92**, 91–94.
- Richards, R. P. (2008). Trends in sediment and nutrients in major Lake Erie tributaries, 1975–2004. *Journal of Environmental Quality* **37**, 1894–1908.
- Richmond, H. E., Hrabik, T. R. & Mensinger, A. F. (2004). Light intensity, prey detection and foraging mechanisms of age 0 year yellow perch. *Journal of Fish Biology* **65**, 195–205.
- Sandström, A. (1999). Visual ecology of fish: a review with special reference to percids. *Fiskeriverket Rapport* **2**, 45–80.
- Sandström, A. & Karås, P. (2002). Effects of eutrophication on young-of-the-year freshwater fish communities in coastal areas of the Baltic. *Environmental Biology of Fishes* **63**, 89–101.
- Schael, D. M., Rudstam, L. G. & Post, J. R. (1991). Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatus*). *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 1919–1925.
- Snickars, M., Sandström, A. & Mattila, J. (2004). Anti-predator behaviour of 0+ year *Perca fluviatilis*: effect of vegetation density and turbidity. *Journal of Fish Biology* **65**, 1604–1613.
- Thimijan, R. W. & Heins, R. D. (1982). Photometric, radiometric, and quantum light units of measure: a review of procedures for interconversion. *HortScience* **18**, 818–822.
- Townsend, C. R. & Risebrow, A. J. (1982). The influence of light level on the functional response of a zooplanktonivorous fish. *Oecologia* **53**, 293–295.
- Utne-Palm, A. C. (2002). Visual feeding of fish in a turbid environment. *Marine and Freshwater Behavior and Physiology* **35**, 111–128.
- Wahl, C. M., Mills, E. L., Farland, W. N. & DeGesi, J. S. (1993). Ontogenetic changes in prey selection and visual acuity of the yellow perch. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 743–749.
- Wellington, C. G. (2008). Effects of turbidity and prey density on the foraging success of age-0 yellow perch. Master's Thesis, The University of Toledo, Toledo, OH, USA.
- Werner, R. G. (2004). *Freshwater Fishes of the Northeastern United States*. New York, NY: Syracuse University Press.
- Wotton, R. S. (1994). *The Biology of Particles in Aquatic Systems*, 2nd edn. Boca Raton, FL: CRC Press.

Electronic Reference

- U.S. Census Bureau (2001). *National Survey of Fishing, Hunting, and Wildlife-associated Recreation*. Available at <http://www.census.gov/prod/2003pubs/fhw01-us.pdf>