

Efficiency of fish feeding on plant-attached prey: Effects of inorganic turbidity and plant-mediated changes in the light environment

Abstract—We studied the effects of inorganic turbidity on the efficiency of perch (*Perca fluviatilis*) feeding on the cladoceran *Sida crystallina* attached to floating macrophyte leaves together with the effects of the floating leaves on the light environment. We expected feeding efficiency to decrease constantly along an increasing turbidity gradient without an enhancement in moderate turbidity values, as observed with planktivores feeding on free-swimming prey, because the inherent contrast between the prey and its background should not be affected by water quality when the prey is attached to a floating object. In the 2-h feeding experiments, the average feeding rate of perch at 0 NTU (nephelometric turbidity units) turbidity was 6.5 *S. crystallina* fish⁻¹, whereas the

feeding rates at 15 and 20 NTU were 1.1 and 0.4 *S. crystallina* fish⁻¹, respectively. At 30 NTU, no *S. crystallina* were captured. The results thus supported our hypothesis. Additionally, the low feeding rate of perch even in clear water suggested that the feeding conditions underneath floating macrophyte leaves were inherently unpropitious for perch because light environment underneath a floating leaf is dominated by harmful sidewelling light. The effects of macrophyte leaves on the spectral composition of light may also be unpropitious for fish feeding. Additionally, with motionless plant-attached prey fish cannot use their lateral line in prey detection or change to filter feeding when their visual field is reduced by increasing water turbidity.

The effects of inorganic turbidity on the feeding efficiency of planktivorous fish have been frequently studied. Feeding efficiency is usually reduced with increasing water turbidity (Vinyard and O'Brien 1976; Bruton 1985). This is because most planktivorous fish depend on their vision in prey detection, and increasing turbidity decreases their reactive distance (Vinyard and O'Brien 1976). However, the feeding efficiency of fish does not always decline constantly with increasing turbidity. Some studies have shown that moderate turbidity values (up to 20–30 NTU) may enhance the feeding success of planktivores foraging on transparent prey by providing contrast between the background and the prey (Boehlert and Morgan 1985; Utne-Palm 1999; Horrpila et al. 2004). Turbidities exceeding 30 NTU usually result in a reduced feeding efficiency compared with clear water (Vinyard and O'Brien 1976; Utne-Palm 1999).

Many freshwater zooplankton species are at least periodically attached to solid substrata, such as littoral macrophytes (Quade 1969). Factors governing the efficiency of fish feeding on plant-attached zooplankton have not been studied. Predictions cannot be made based on experiments with free-swimming prey, because there is a basic difference between planktonic and plant-attached feeding modes. When searching for planktonic prey, fish are scanning a three-dimensional volume of water, whereas in the case of attached prey they scan a two-dimensional surface. Thus, factors controlling the fish-induced mortality of cladocerans attached to the surfaces of the floating plant leaves are probably different compared with free-swimming species. This becomes evident when the factors affecting the prey detection by planktivorous fish are explored.

The effect of inorganic turbidity on fish feeding is both due to decreased light intensity and increased light scattering, the latter having more pronounced effects. Contrast between the prey and its background is more important than the absolute light level for the ability of a fish to detect its prey (Hemmings 1966). Light scattering from suspended inorganic particles is harmful, since it interferes with the background light level and reduces contrast. The visibility and contrast of an object are dependent on the properties of the object and the background and on the optical properties of the medium (Hemmings 1966; Eggers 1977). Contrast can be divided into inherent contrast and apparent contrast (Duntley 1962; Eggers 1977). The inherent contrast is determined by the properties of the background and the object:

$$C = (T - B)/B \quad (1)$$

where T is irradiance from the background and B is irradiance from the object (Lythgoe 1980). The apparent contrast is determined by the inherent contrast, properties of the medium (attenuation coefficient α), and the distance of the observer and the prey object (D ; Eggers 1977)

$$C_a = C \exp(-\alpha D) \quad (2)$$

For a prey swimming in the water, a change in water turbidity causes a change in the inherent contrast by affecting both T and B in Eq. 1 (Lythgoe 1980) and by increasing the attenuation coefficient (Eq. 2), thus causing an additional change in the apparent contrast. Increase in turbidity can lead to increase in the inherent contrast for transparent prey such as cladocerans and compensate the reduction in the visual field (Utne-Palm 1999; De Robertis et al. 2003). At high turbidities, the negative effects of turbidity on the apparent contrast overshadow the positive effects on inherent contrast and result in a reduced feeding efficiency.

In the case of cladocerans attached to the lower surfaces of floating plant leaves, there is no water between the background and the object, and the background light is independent of water quality. Hence, inherent contrast is less affected by water quality than in the case of free-swimming prey, and changes in apparent contrast should be mainly determined by the attenuation coefficient. It can be thus assumed that fish feeding on plant-attached cladocerans do not show an enhanced feeding efficiency at moderate turbidity levels. Their feeding efficiency should decline constantly with increasing water turbidity, probably following the increment of the attenuation coefficient, unless the fish are able to compensate the reduction in visibility by reducing their distance to the prey.

To study the effects of turbidity on the effectivity of fish feeding on plant-attached cladocerans, we performed a series of experiments with planktivorous perch (*Perca fluviatilis* L.) and the cladoceran *Sida crystallina* O. F. Müller attached to the floating leaves of the yellow water lily *Nuphar lutea* (L.). The rather large-sized *S. crystallina* is mostly attached to plants by a suction cup in its neck and forms high biomasses in the littoral zone of many lakes. Small planktivorous perch are common in the littoral zone of temperate lakes. For instance in Lake Hiidenvesi (southern Finland), small perch feed on *S. crystallina* (Pekcan-Hekim et al. 2005). It has been observed, however, that despite high biomass of *S. crystallina*, its share in the food of perch in Lake Hiidenvesi remains low. This may be attributed to the clay turbidity of the zone of floating-leaved macrophytes (10–30 NTU; Pekcan-Hekim et al. 2005). Perch was a suitable fish species for the experiments also because contrast is an important factor for prey detection of percids (Sandström 1999). Additionally, to clarify the feeding conditions underneath the floating plant leaves, we studied the effects of floating leaves on the light environment at various water turbidities. We studied the effects of floating leaves on the intensity, direction, and spectral composition of light, all factors that can affect the feeding efficiency of fish (Vinyard and O'Brien 1976; Helfman 1981; White et al. 2005).

Methods—Experimental design. In each feeding experiment, three small (7.0–9.3 cm) planktivorous perch were allowed to feed for 2 h on 75 individuals of plant-attached *S. crystallina* in a 10-liter experimental unit (water depth 20 cm). The perch were captured with a seine net and acclimated in the laboratory for 2 weeks. Water temperature in the experiments was set to 18°C to match the

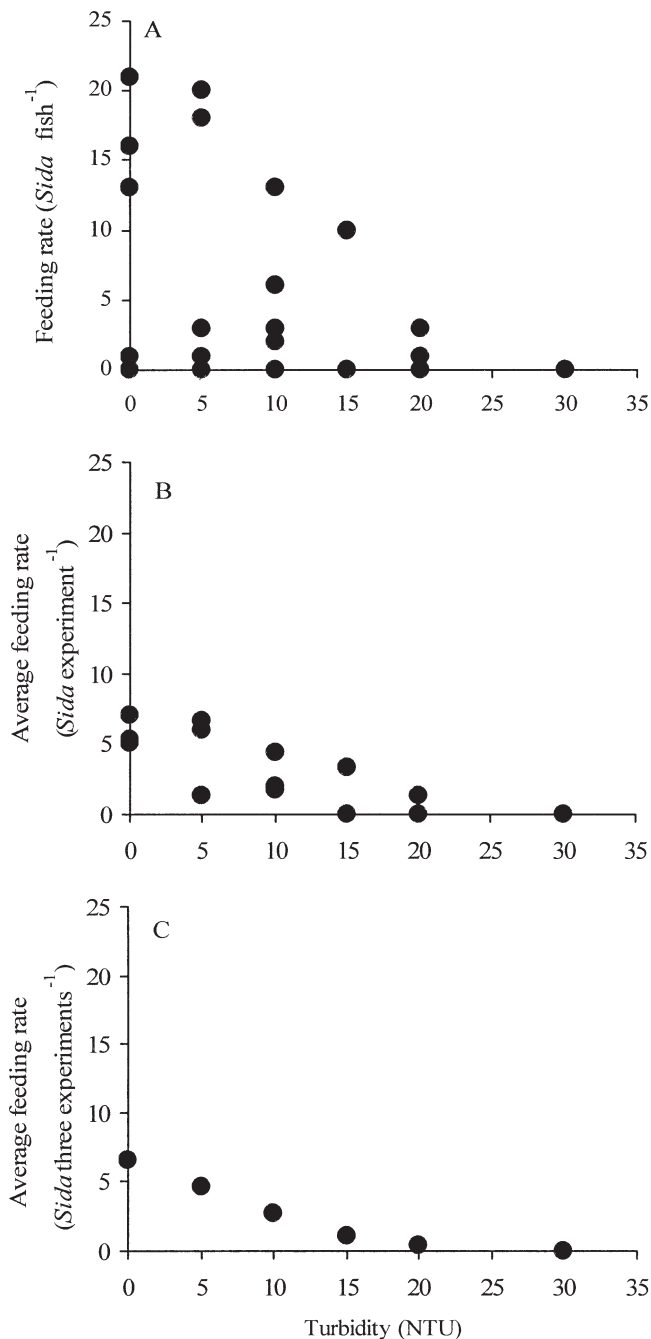


Fig. 1. The number of *Sida crystallina* eaten by perch at different water turbidities during the 2-h feeding experiments presented in three different ways: (A) feeding rate per individual fish; (B) average feeding rate per experiment (each circle represents three perch in the same experimental unit); (C) average feeding rate per three experiments (each circle represents three experiments, each of which included three perch).

experiments performed previously with perch and planktonic prey (Flik et al. 1997; Granqvist and Mattila 2004). The leaves of *Nuphar lutea* with attached *S. crystallina* were collected from the eutrophic Lake Hiidenvesi (southern Finland; for lake description see Horppila 2005), transported to the laboratory, and kept in buckets with air

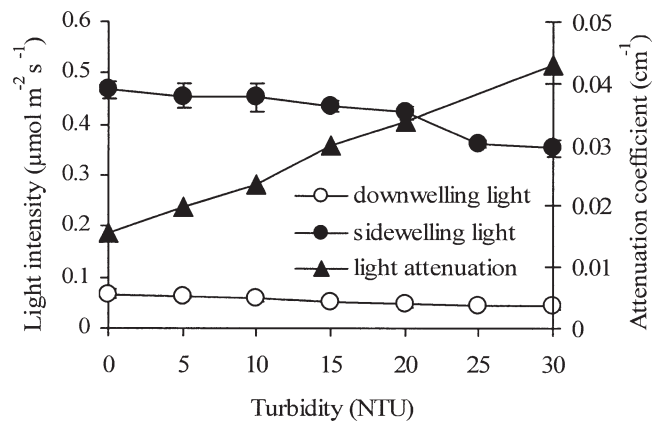


Fig. 2. The effect of water turbidity on the intensity of downwelling and sidewelling light ($\pm 95\%$ confidence limits) underneath a floating leaf of *Nuphar lutea* (left axis) and the light attenuation coefficient at different water turbidities (right axis).

bubbling. Before each experiment, one leaf was wiped clean and settled in the experimental unit. *S. crystallina* (size 1–1.5 mm) were collected from leaves in the storage buckets with a pipette and moved into the experimental units. To ensure the attachment of *S. crystallina* to the leaf, they were released to the experimental unit with a pipette through three small holes cut into different parts of the floating leaf. The density of 75 individuals per leaf was chosen to match the density in Lake Hiidenvesi (Nurminen et al. 2005). Three replicate experiments were conducted at turbidity levels 0, 5, 10, 15, 20, and 30 NTU ($\pm 10\%$). Turbidity was created by adding small doses of clayish lake sediment and measured with a YSI-6820 sonde (YSI Corp.). Slight air bubbling was used to prevent the sedimentation of the suspended material. Numerous studies have shown that perch are highly active at crepuscular conditions (Craig 1977; Pekcan-Hekim et al. 1995). Hence, to simulate twilight conditions, the experimental chambers were lit from a 75° zenith angle with lamps that simulate daylight, and light intensity in the water surface was set to $0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ (measured with a LI-1400 datalogger equipped with an LI-192SA quantum sensor, LI-COR Biosciences). The experimental chambers were nontransparent. After each experiment, the stomach contents of perch were microscopically analyzed and the captured *S. crystallina* were counted. At each water turbidity, the light intensity underneath the floating leaf was measured (1 cm from the leaf surface). The light attenuation coefficient at each turbidity level was measured with light intensity measurements at 1 and 10 cm depths. Additionally, to estimate the quantity of sidewelling light, measurements were performed also with a spherical LI-193SA quantum sensor. The intensity of sidewelling light was estimated by deducting downwelling light (measured with LI-192SA) from the reading of the spherical sensor.

The effects of the floating leaves of *N. lutea* on the spectral composition of light at various water qualities were studied outdoors under natural light. A 50-liter bucket was filled with tap water with 0 NTU turbidity. Light intensity and spectral composition of light 1 cm below the surface

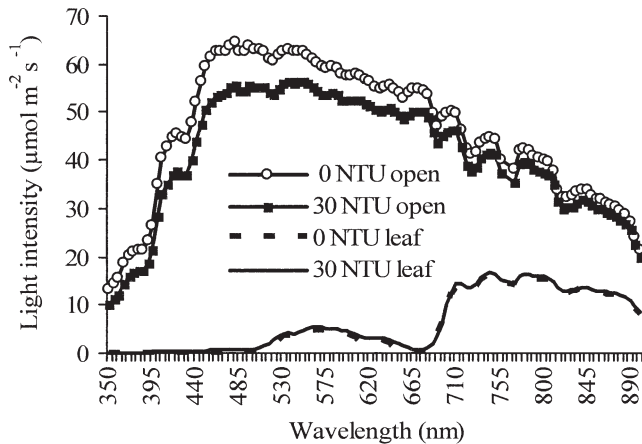


Fig. 3. The spectral composition of light underneath a floating leaf of *Nuphar lutea* and in the open water at 0 and 30 NTU water turbidity.

were measured with a multispectral RAMSES VIS-ACC radiometer (TriOS Optical Sensors). A floating leaf of *N. lutea* was placed on the water surface, and light intensity and spectral composition of light 1 cm below the leaf were measured. The measurements were repeated at turbidities 5, 10, 15, 20, and 30 NTU.

Statistical analyses: The effects of turbidity on the feeding rate of perch were tested with analysis of covariance (ANCOVA) by using the light intensity underneath the leaf as a covariate. The effects of turbidity on the maximum feeding rate of perch were analyzed with regression analysis. Additionally, the experiments at each turbidity level were pooled and the overall effects of turbidity on the feeding rate of perch were studied with regression analysis. The relationship of maximum and average feeding rates of perch to the light attenuation coefficient was studied by linear regression. The effects of turbidity on the ratio of downwelling and sidewelling light underneath the floating leaf were tested with analysis of variance (ANOVA). The statistical analyses were performed with the SAS statistical software, version 9.1 (SAS Institute).

Results—At 0 NTU, the maximum feeding rate was 21 *S. crystallina* fish⁻¹ (Fig. 1A). With increasing turbidity, the individual feeding rate decreased steeply, the maximum feeding rate at 20 NTU being three *S. crystallina* fish⁻¹. At 30 NTU, no *S. crystallina* were eaten. On the other hand, the maximum feeding rate per fish along the turbidity gradient closely followed a linear trend ($F_{1,4} = 76.056$, $p < 0.001$, $R^2 = 0.950$). The average feeding rate per experiment (Fig. 1B) showed a significant dependence on water turbidity (ANCOVA, $F_{5,11} = 24.12$, $p < 0.001$). The effect of light as a covariate on the feeding rate was insignificant ($F_{1,11} = 0.66$, $p = 0.4333$). At turbidities 0–10 NTU, *S. crystallina* were consumed in each experiment, but higher turbidities included experiments where no cladocerans were eaten. A very clear trend was observed when an average feeding efficiency for all perch at each turbidity level was calculated (Fig. 1C). On average 6.5 *S. crystallina* per fish were captured at 0 NTU, whereas the average feeding rates

at 15 and 20 NTU were 1.1 and 0.4 *S. crystallina* fish⁻¹, respectively (Fig. 1C). The decrease of the feeding rate along a turbidity gradient followed a parabolic function (nonlinear regression, $F_{2,3} = 405.89$, $R^2 = 0.9963$, $p = 0.0002$). Both maximum and average feeding rate of perch showed significant negative dependence on the light attenuation coefficient (linear regression, maximum feeding rate, $F_{1,4} = 72.52$, $R^2 = 0.948$, $p = 0.0010$; average feeding rate, $F_{1,4} = 25.96$, $R^2 = 0.866$, $p = 0.0070$).

The intensity of downwelling light underneath the floating leaf at 0 NTU was $0.067 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 2). With increasing turbidity, light intensity decreased linearly, being $0.043 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 30 NTU. Similarly, the light attenuation coefficient increased linearly with increasing turbidity, being 0.0156 cm^{-1} at 0 NTU and 0.043 cm^{-1} at 30 NTU (Fig. 2). The intensity of sidewelling light was on average eight times higher than the intensity of downwelling light (Fig. 2). The relationship between downwelling and sidewelling light was not affected by turbidity (ANOVA, $F_{6,14} = 1.37$, $p = 0.2933$).

Without the cover of a macrophyte leaf, light was dominated by wavelengths 450–600 nm (Fig. 3). The percentage distribution was not affected by water turbidities 0–30 NTU. Underneath the leaf, PAR light was dominated by wavelengths between 500 and 680 nm intensity, and other PAR (photosynthetically active radiation) wavelengths were very low. At all turbidity levels under the leaf, the highest intensities were measured at wavelengths $>700 \text{ nm}$ (Fig. 3).

Discussion—The results of the feeding experiments were coherent with the hypothesis that when fish are feeding on plant-attached prey, their feeding efficiency decreases constantly with increasing inorganic turbidity, with no enhancement at moderate turbidity values. As expected, the reduction in the feeding rate followed the increment of the attenuation coefficient. The results were different to those obtained with perch feeding on free-swimming prey. Granqvist and Mattila (2004) found no decline in the feeding efficiency of perch feeding on the mysid shrimp *Neomysis integer* when turbidity was increased from 1 to 30 NTU, and they suggested that the minor effects of turbidity were due to increased contrast. Our results thus supported the assumption that inherent contrast between plant-attached cladocerans and their background is not considerably affected by water quality variations.

Compared with studies performed with free-swimming planktonic prey, the overall effect of turbidity on the feeding efficiency of perch was very strong. At 10 NTU, the average feeding rate was $<50\%$ of that at 0 NTU, and at 20 NTU the feeding rate had dropped to 7% of that at 0 NTU. Such rapid relative changes in the feeding efficiency along a turbidity gradient have not been previously reported. In most studies, planktivorous fish, including perch, have been able to capture prey at low light and 30–40 NTU water turbidity (De Robertis et al. 2003; Granqvist and Mattila 2004; Horppila et al. 2004). It thus seems that some factor or factors make feeding on zooplankton attached to lower surfaces of floating plant leaves especially sensitive to the harmful effects of

turbidity. This could be due to (1) strong effects of turbidity on the reaction distance, (2) strong effects of reaction distance on the visual field, (3) low ability of fish to compensate for the increased turbidity by changing their behavior, or (4) inherently unpropitious feeding conditions underneath the leaf amplifying the harmful effects of turbidity.

As stated above, the effects of turbidity on the contrast and reaction distance of fish searching for plant-attached prey in a given light intensity should not be stronger than for planktonic prey (although the reactive distance is shorter for stationary than for moving prey; Ware 1973). When exploring the effects of reaction distance on the visual field and the possibilities to compensate the reduced visibility by behavioral changes, the differences between three-dimensional and two-dimensional feeding modes must be considered. The maximal prey encounter rate by a fish searching for planktonic prey is given by (Aksnes and Giske 1993)

$$E = \pi(r \sin\theta)^2 vN \quad (3)$$

where r is the visual range of the fish, θ is the reactive field half angle, v is the swimming speed, and N is prey abundance. When fish are scanning for stationary prey on a two-dimensional surface, the width of the searched path (E_s) is given by (Ware 1973)

$$E_s = 2\sqrt{R_D^2 - P_D^2} \quad (4)$$

where R_D is the reaction distance and P_D is the distance of the predator from the surface. The number of possible encounters in a unit interval of time is given by the product of the path width, swimming speed, and prey density (Ware 1973). In planktivorous feeding (Eq. 3), with a given swimming speed and prey density and assuming a cylindrical visual field (Vinyard and O'Brien 1976), a 50% reduction in the visual range causes a fourfold reduction in the prey encounter rate. With plant-attached prey mode (Eq. 4), a 50% reduction in reaction distance causes only a 50% reduction in the search path width, providing that the fish approach the surface according to the decrease in reaction distance (i.e., compensate for the reduction in the third dimension). However, if the fish do not change their position with increasing turbidity, the visual field is more rapidly reduced. At the moment when R_D is reduced to be equal to P_D , the width of the visual field becomes zero. It thus seems that with plant-attached prey, it is especially important for the fish to respond to increased turbidity by changing their behavior. In our experiments, some behavioral response probably took place, since the individual feeding rates of some perch at 5 NTU were close to those obtained at 0 NTU, and the effect of turbidity on the maximum feeding rate was less strong than on the average feeding rate. At the highest turbidities, however, even behavioral changes obviously could not help in feeding.

Fairchild (1982) reported that largemouth bass (*Micropterus salmoides*) feeding on *S. crystallina* attached to

floating plant leaves made the final choice of attack from a 1-cm distance even when their reaction distance was 10 cm or more. This suggests that when fish are feeding on plant-attached prey the value of P_D is low even in clear water, limiting their possibilities to avoid a severe reduction in the visual field by approaching the scanned surface when turbidity increases. According to Richmond et al. (1977), reaction distance of perch for swimming cladocerans is 3.6 cm at light intensity that was present underneath the leaf at 0 NTU in our experiments. For stationary prey, the reaction distance is ~75% of that for motile prey (Ware 1973), and it can be thus assumed that at 0 NTU the reaction distance of perch was 2.5–3 cm. According to the equations by Vinyard and O'Brien (1976), a turbidity increment to 30 NTU reduces the reaction distance of fish to ~40% of that in 1 NTU. Hence, it is likely that the reaction distance of perch at 30 NTU was close to 1 cm, possibly going under the value of P_D and leading to the disappearance of the leaf surface from the sight of the fish.

The feeding rate of perch was low even at 0 NTU, suggesting that feeding conditions underneath the leaves were inherently unpropitious. The low feeding rate could not be explained by light intensity. Flik et al. (1997) found that perch were able to consume 90% of the offered daphnids within 15 min at 18–20°C temperature at a light intensity of 0.777 lux, which corresponds to 0.014 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Similarly, Granqvist and Mattila (2004) and Richmond et al. (2004) have shown that perch are able to successfully forage on swimming prey at low light intensities. A decline in the prey density during the experiments could not explain the low feeding rate, because in all of the experiments >70% of *S. crystallina* remained uneaten. Instead, the generally low feeding rate was probably due to the following factors. First, motion of prey increases the effectivity of prey detection (Ware 1973), whereas plant-attached cladocerans are largely motionless. The lack of motion also prevents the fish from using their lateral line in prey detection. Second, planktivorous fish hunting swimming prey may compensate for the reduced visibility by changing from particulate to filter feeding (Lammens et al. 1987). When searching for plant-attached prey, such random feeding may not be possible. Third, the light direction underneath the leaves was unpropitious for prey detection. As usual underneath flowing objects, light was dominated by sidewelling light, which is very harmful for prey detection (Lythgoe 1980; Helfman 1981). Probably an important factor is also that underneath the leaves light intensity is lowest in the close proximity of the leaf and increases downward due to the effect of sidewelling light. Hence, fish searching for the attached cladocerans are in higher light intensity than their prey and have a raised contrast perception threshold, making it difficult for it to

Acknowledgments

The study was financed by the Academy of Finland (projects 50320 and 203107). Anne-Marie Hagman assisted with the spectral measurements and Kari Saulamo helped with the statistical analyses. We also thank the two anonymous reviewers for helpful comments.

detect a shaded target (Helfman 1981). Fourth, the spectral composition of light underneath the floating leaf was unprofitable for perch, which have sensitivity peaks at wavelengths 530–560 nm and 660–680 nm and low sensitivity for wavelengths >700 nm (Cameron 1982). The leaves of *N. lutea* strongly absorbed blue and red light, whereas green and yellow light penetrated the leaves more effectively. Wavelengths on the infrared region (>700 nm) were not strongly absorbed and consequently dominated the light environment underneath the leaves. Similar effects by other macrophyte species on light environment have been reported previously (Kirk 1994). No differences in the spectral composition of light at the different turbidities were found, which was expected, since suspended clay attenuates the different wavelengths relatively equally (Bristow et al. 1996).

In conclusion, the results suggested that when fish are feeding on zooplankton attached to floating macrophyte leaves, their feeding efficiency declines constantly along an increasing turbidity gradient. The effect of turbidity is very strong, since feeding efficiency on the motionless attached prey is inherently low and the light environment underneath the leaves is unpropitious for prey detection because of the effects of the leaves on the spectral composition, direction, and intensity of light.

Leena Nurminen and Jukka Horppila

Department of Biological and Environmental Sciences
University of Helsinki
Finland

References

- AKSNES, D. L., AND J. GISKE. 1993. A theoretical model of aquatic visual feeding. *Ecol. Modell.* **67**: 233–250.
- BOEHLERT, G. W., AND J. B. MORGAN. 1985. Turbidity enhances feeding abilities of larval pacific herring, *Clupea harengus pallasi*. *Hydrobiologia* **123**: 161–170.
- BRISTOW, B. T., R. C. SUMMERFELT, AND R. D. CLAYTON. 1996. Comparative performance of intensively cultured larval walleye in clear, turbid and coloured water. *Progr. Fish-Cult.* **58**: 1–10.
- BRUTON, M. N. 1985. The effects of suspendoids on fish. *Hydrobiologia* **125**: 221–241.
- CAMERON, D. E. 1982. The photopic spectral sensitivity of a dichromatic teleost fish (*Perca fluviatilis*). *Vision. Res.* **22**: 1341–1348.
- CRAIG, J. F. 1977. Seasonal changes in the day and night activity of adult perch, *Perca fluviatilis* L. *J. Fish Biol.* **11**: 161–166.
- DE ROBERTIS, A., C. H. RYER, A. VELOZA, AND R. D. BRODEUR. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Can. J. Fish. Aquat. Sci.* **60**: 1517–1526.
- DUNTLEY, S. Q. 1962. Underwater visibility, p. 452–455. *In* M. N. Hill [ed.], *The sea*, V. 1. Wiley.
- EGGERS, D. M. 1977. The nature of prey selection by planktivorous fish. *Ecology* **58**: 46–59.
- FAIRCHILD, G. W. 1982. Population response of plant-associated invertebrates to foraging by largemouth bass fry (*Micropterus salmoides*). *Hydrobiologia* **96**: 169–176.
- FLIK, B. J. G., D. K. AANEN, AND J. RINGELBERG. 1997. The extent of predation by juvenile perch during diel vertical migration of *Daphnia*. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* **49**: 51–58.
- GRANQVIST, M., AND J. MATTILA. 2004. The effects of turbidity and light intensity on the consumption of mysids by juvenile perch (*Perca fluviatilis* L.). *Hydrobiologia* **514**: 93–101.
- HELPMAN, G. S. 1981. The advantage to fishes of hovering in shade. *Copeia* **1981**: 392–400.
- HEMMINGS, C. C. 1966. Factors influencing the visibility of objects underwater, p. 359–374. *In* R. Bainbridge, G. C. Evans, and O. Rackham [eds.], *Light as an ecological factor*. Blackwell.
- HORPPILA, J. 2005. Project background and lake description. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* **59**: 1–11.
- , A. LILJENDAHL-NURMINEN, AND T. MALINEN. 2004. Effects of clay turbidity and light on the predator-prey interaction between smelts and chaoborids. *Can. J. Fish. Aquat. Sci.* **61**: 1862–1870.
- KIRK, J. T. O. 1994. *Light and photosynthesis in aquatic ecosystems*. Cambridge University Press.
- LAMMENS, E. H. R. R., J. GEURSEN, AND P. J. MACGILLAVRY. 1987. Diet shifts, feeding efficiency and coexistence of bream (*Abramis brama*) roach (*Rutilus rutilus*) and white bream (*Blicca bjoerkna*) in hypertrophic lakes. *Proc. V Congr. Europol. Ichtyol. Stockholm* **1985**: 153–162.
- LYTHGOE, J. N. 1980. Vision in fishes: Ecological adaptations, p. 431–466. *In* A. Ali [ed.], *Environmental physiology of fishes*. Plenum Press.
- NURMINEN, L., J. HORPPILA, A.-M. HAGMAN, J. NIEMISTÖ, AND Z. PEKCAN-HEKIM. 2005. Synthesis on the role of macrophytes in a clay-turbid lake—structuring and stabilizing functions affecting water quality. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* **59**: 105–123.
- PEKCAN-HEKIM, Z., J. HORPPILA, L. NURMINEN, AND J. NIEMISTÖ. 2005. Diel changes in habitat preference and diet of perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), and white bream (*Abramis bjoerkna*). *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* **59**: 173–187.
- QUADE, H. 1969. Cladoceran faunas associated with aquatic macrophytes in some lakes in Northwestern Minnesota. *Ecology* **50**: 170–179.
- RICHMOND, H. E., T. R. HRABIK, AND A. F. MENSINGER. 2004. Light intensity, prey detection, and foraging mechanisms of age 0 year yellow perch. *J. Fish Biol.* **65**: 195–205.
- SANDSTRÖM, A. 1999. Visual ecology of fish—a review with special reference to percids. *Fiskeriverket Rapport* **2**: 45–80.
- UTNE-PALM, A. C. 1999. The effect of prey mobility, prey contrast, turbidity and spectral composition on the reaction distance of *Gobiusculus flavescens* to its planktonic prey. *J. Fish Biol.* **54**: 1244–1258.
- VINYARD, G. L., AND J. O'BRIEN. 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *J. Fish. Res. Board Can.* **33**: 2845–2849.
- WARE, D. M. 1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Board Can.* **30**: 787–797.
- WHITE, E. M., S. C. CHURCH, L. J. WILLOUGHBY, S. J. HUDSON, AND J. C. PARTRIDGE. 2005. Spectral irradiance and foraging efficiency in the guppy, *Poecilia reticulata*. *Animal Behaviour* **69**: 519–527.

Received: 7 June 2005

Accepted: 24 November 2005

Amended: 28 December 2005