

Water temperature, light intensity and zooplankton density and the feeding activity of juvenile brook charr (*Salvelinus fontinalis*)

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SUMMARY

1. The objective of this study was to evaluate the effects of zooplankton biomass (as a measure of density), fish biomass, light intensity and water temperature on the attack rate and swimming characteristics (i.e. swimming speed and angle of turn) of juvenile (1+) brook charr (*Salvelinus fontinalis*) in field enclosures. We used a portable underwater camera system in a series of pelagic enclosures to quantify the feeding behaviour of brook charr over a gradient of natural conditions.

2. In simple linear or non-linear regression models we found (i) that attack rate and angle of turn were positively related to water temperature, (ii) that attack rate and swimming speed were positively related to zooplankton biomass and light intensity and (iii) that attack rate was positively related to swimming speed. In multiple regression models, fish biomass, light intensity and variance of the angle of turn accounted for 87% of the variation in attack rate. Light intensity and water temperature accounted for 86% of the variation in swimming speed. Fish gut fullness and attack rate accounted for 83% of the variation in the variance of the angle of turn executed by fish.

3. The increase in the number of attacks as zooplankton biomass increases conforms to the general positive functional response observed in other fish species. Our results also support the hypothesis that swimming speed increases with prey biomass. We did not observe a plateau in attack rate as zooplankton biomass increased. As our experiments were performed under natural biotic and abiotic conditions, factors other than zooplankton biomass might affect or limit this response, such as water temperature and light intensity.

4. Because zooplankton biomass was correlated with water temperature and light intensity, it was not possible to evaluate the independent contribution of these factors on the attack rate and swimming characteristics (swimming speeds and angle of turn) of brook charr. However, this study highlighted the impact of these factors on the feeding behaviour of juvenile brook charr when feeding in the pelagic habitat under natural conditions, and their importance in future models of optimal foraging and fish habitat quality.

Keywords: attack rate, feeding activity, functional response, swimming characteristics, zooplanktivorous fish

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Introduction

Models that describe the foraging of zooplanktivorous fish usually consider encounter rate, attack rate, capture rate and handling time (Aksnes & Giske, 1993; Eggers, 1977; O'Brien, Evans & Browman, 1989).

These models make assumptions about how each variable varies in relation with biotic and abiotic factors. For zooplanktivorous fish, encounter rate is more important than attack rate, capture rate or handling time because zooplankton are relatively small, easily captured and swallowed whole (Gerking, 1994). Assuming that the capture success of zooplanktivorous fish is high (McMahon & Holanov, 1995; Biro, Ridway & McLaughlin, 1996), attack rate becomes a good index of capture rate and, thus, of foraging.

Attack rate on zooplankton by fish is highly variable, and hence there is variability in foraging (Confer & Blades, 1975; Vinyard & O'Brien, 1976). Foraging will obviously vary with prey density (Munk & Kiørboe, 1985; Batty, Blaxter & Richard, 1990). At high zooplankton density, attack rate increases and search time decreases. Attack rate will also vary with prey size and prey movement: as the prey size increases, search time decreases (Confer & Blades, 1975; Vinyard & O'Brien, 1976) while, as prey are more mobile, they increase their vulnerability (Howick & O'Brien, 1983). Miller *et al.* (1992) observed that the functional responses of alewife (*Alosa pseudoharengus* Lesueur), yellow perch (*Perca flavescens* Mitchill) and bloater (*Coregonus hoyi* Gill) to zooplankton density were best described by a Holling type II equation. The attack rates of these species increased with prey density until a plateau, which represents the capture rate limit. Batty *et al.* (1990) observed the same type of response with herring (*Clupea harengus* Linné) at a light intensity above 0.001 lx. Attack rates will also vary with some abiotic factors, such as light intensity and water temperature. As light intensity increases, attack rate increases because a larger volume of water is perceived by the fish (Vinyard & O'Brien, 1976; Henderson & Northcote, 1985; McMahon & Holanov, 1995). Colour also influences attack rate through contrast (Henderson & Northcote, 1985; Utne-Palm, 1999). Water turbidity will reduce attack rate (Benfield & Minello, 1996; Utne, 1997), not only by decreasing light intensity but also by scattering by suspended particles. Water temperature has an indirect influence on attack rate and feeding behaviour of fish through its influence on fish metabolism and energetic demands (Nicieza & Metcalfe, 1997; Biro, 1998). Weetmann, Atkinson & Chubb (1998) have shown that the feeding behaviour of a zooplanktivorous fish can be significantly affected by water temperature: attack rate,

swimming speed and schooling behaviour increased with water temperature until a specific limit was reached, related to the physiological constraints of each species.

The attack rate of zooplanktivorous fishes has been well studied under laboratory conditions (Luecke & O'Brien, 1981; Batty *et al.*, 1990; Utne-Palm, 1999; and cited studies). Most of these evaluated the attack rate or reaction distance with respect to a single biotic or abiotic factor. However, an evaluation of the influence of one or more biotic or abiotic factors on the attack rate of a zooplanktivorous fish under natural conditions has rarely been attempted.

The main objective of the present study was to evaluate the effects of zooplankton biomass (as a measure of density), fish biomass, light intensity and water temperature on the attack rate and swimming characteristics (i.e. swimming speed and angle of turn) of juvenile (1+) brook charr, *Salvelinus fontinalis* Mitchill, in field enclosures. Brook charr is a particulate feeder (Tremblay & Magnan, 1991; Magnan & FitzGerald, 1984) that can feed mostly on zooplankton (Bourke, Magnan & Rodriguez, 1999) and thus represents a good model to study the effects of biotic and abiotic factors on the feeding activity of a zooplanktivorous fish. A portable underwater camera system used in a series of pelagic enclosures allowed us to quantify the foraging behaviour and swimming characteristics of brook charr over a gradient of natural conditions.

Methods

Study site and experimental set-up

Lake Simpson, Mastigouche Reserve, 120 km north of Trois-Rivières, Québec, Canada (46°38'N, 73°15'W), is small and oligotrophic of area, 28.5 ha, mean depth, 3.3 m, conductivity, 12.5 $\mu\text{S cm}^{-1}$ and Secchi depth, 2.5 m (Magnan, 1988). The lake contains populations of brook charr and northern redbelly dace, *Phoxinus eos* Cope. Fourteen experiments were performed in six enclosures (3 m \times 4 m \times 2 m deep; 9.5 mm mesh size) anchored in the pelagic zone of the lake during the summers of 1995 and 1996. These enclosures allowed water and zooplankton to flow through freely and zooplankton were the only available food. Hatchery-reared brook charr (1+) from an F₂ generation were used. Seven days before each experiment, five juvenile

brook charr were deprived of food in a closed enclosure, free of zooplankton. Experimental fish were then acclimated to the experimental enclosure 3 day before each experiment, which consisted of (1) filming five brook charr inside the enclosure over a 12-h period to evaluate attack rate and swimming characteristics (i.e. swimming speed and angle of turn), (2) sampling zooplankton biomass inside the enclosure before the experiment and outside the enclosure during the experiment, (3) monitoring water temperature and light intensity and (4) capturing brook charr at the end of the experiment to collect their complete digestive tract content for an estimation of an index of daily ration.

Attack rate and swimming characteristics

Attack rates (AR) and swimming characteristics were estimated by filming five brook charr inside enclosures with a portable underwater camera system. For each experiment, six 1-h periods were filmed (starting at 6:30, 9:00, 12:00, 14:00, 16:00 and 18:30 hours). Each hour of filming was then analysed by counting the number of seconds that a fish could be seen swimming and feeding (both measured as number of fish seconds). Each attack by an individual on a zooplankter was recorded as having 1-s duration. Attack rate was expressed as the number of attacks on zooplankton (i.e. feeding bouts) divided by the total number of seconds where fish were seen swimming, times 60, which corresponds to the number of attacks per minute of swimming. Swimming characteristics were expressed as swimming speed (cm s^{-1}) and angle of turn (degrees s^{-1}) were estimated using the stereocinematographic method (Boisclair, 1992; Boisclair & Tang, 1993).

Zooplankton biomass

Zooplankton biomass was estimated for every experiment. Vertical hauls were made using a 12-cm diameter Wisconsin plankton net (Wildlife Supply Company, Saginaw, MI, USA), with 80 μm mesh size at a depth of 1.7 m from the surface, for a total volume of 19.3 L. Samples were preserved in a 25% ethanol solution, filtered on preweighed (± 0.05 mg dry) 1 μm pore fibreglass filters, and dried at 60 °C for 6 h. Filters were then weighed (± 0.05 mg dry) for the estimation of zooplankton biomass (mg dry wt L^{-1}). For summer 1995, five zooplankton samples were

collected inside and five outside the enclosure at the beginning of each experiment (i.e. t_0). For summer 1996, five samples were taken inside the enclosure before the experiment and five others outside the enclosure before every hour of filming (i.e. t_0 – t_5). Zooplankton biomass was not estimated inside the enclosure after the beginning of an experiment to avoid disturbing or modifying the feeding behaviour of fish. An examination of the daily variation in zooplankton biomass outside the enclosure (available for 1996) showed that zooplankton biomass tended to decrease from the beginning (t_0) to the end (t_5) of experiments (i.e. from 6:00 to 19:00 hours) within 2 m of the surface. We thus built a regression model using the 1996 data to predict the mean daily zooplankton biomass (MDZB) outside the enclosure from the mean zooplankton biomass at t_0 ($\text{MZB}t_0$) inside the enclosure, where $\text{MDZB} = 0.974 \text{MZB}t_0 + 0.112$; $R^2 = 0.87$, $P < 0.006$. We then used this model to estimate the MDZB outside the enclosures in the 1995 experiments (Table 2).

Water temperature and light intensity

For each experiment, water temperature was measured at noon at a depth of 1 m with an electronic thermometer (YSI Instrument, dissolved oxygen meter model 57, ± 0.1 °C) (YSI Incorporated, Yellow Springs, OH, USA). Light intensity was estimated from the 1-h films (see section above) and was expressed on a grey scale from 0 to 256 units, with zero being equivalent to white and 256 to black. Measurements of light intensity were made on a diagonal line extending from the top corner to the opposite bottom of the images recorded. Each line consisted of 400 pixels, each having its grey unit (from 0 to 256). For each hour of filming, the variance of light intensity was estimated using three measurements: at the beginning, middle and the end of the hour. A daily variance of light intensity was then estimated using our six hourly estimates. As light is quickly diffused in the water column, a higher variance of light intensity between the surface and the bottom of the enclosure indicated a higher light intensity; as light intensity increases, the grey units of pixels near the surface decrease (i.e. towards white), but those at the bottom stay unaffected because of light adjustment by the cameras. Thus, the estimated variance of light intensity was used as index of the quantity of light inside our enclosures.

Index of fish daily ration

After each experiment, fish inside the enclosure were captured, measured (± 1 mm), weighed (± 0.01 g wet), and anaesthetised (MS-222) before their complete digestive tract content was sampled. The complete digestive tract content was dried at 60 °C for 24 h and weighed (± 0.05 mg dry) individually. The gut fullness of each fish was estimated as the dry weight of the entire contents of its digestive tract divided by its weight times 100 (Héroux & Magnan, 1996). The mean gut fullness was estimated for the five fish inside the enclosure. Héroux & Magnan (1996) and Héroux (1998) did not observe any significant periodicity in gut fullness of brook charr (1+) feeding on zooplankton in similar enclosures (eight samples over a 24-h period). Their estimates of gut fullness indices were comparable with ours (0.31 ± 0.13 g dry weight per 100 g wet fish weight). We expect therefore that our single daily estimate of the gut fullness adequately represents the daily mean fish gut fullness. Based on this, we estimated fish daily ration (g dry weight per 100 g wet fish weight day⁻¹) using the Eggers model (Eggers, 1977; Boisclair & Marchand, 1993; Héroux & Magnan, 1996). We used the evacuation rate (R ; h⁻¹) estimated in previous experiments conducted in the same lake for brook charr (1+) under similar environmental conditions and feeding on zooplankton ($R = -0.19 + 0.015$ water temperature, $R^2 = 0.82$, $P < 0.005$; Héroux & Magnan, 1996; Héroux, 1998). However, as our daily ration estimates are based on single rather than several samples of gut fullness over a 24-h period and our evacuation rates come from another study (Héroux & Magnan, 1996), we will consider these only as indices of fish daily ration (IFDR).

Statistical analyses

We determined whether the observed attack rate corresponded to successful prey captures by testing the existence of a significant linear relationship between our index of fish daily ration and attack rate. We assessed the correspondence between our index of light intensity and seasonal variations in light intensity (which decrease from 21 June to 21 December) by testing for the existence of a significant negative relationship between light intensity and the number of days separating an experiment from 21 June (summer solstice).

Multiple regression models were developed using attack rate (as a measure of feeding activity), swimming speed and angle of turn as dependent variables, and water temperature, light intensity, zooplankton biomass, fish biomass, fish gut fullness, index of fish daily ration as independent variables. Some of the dependent variables (e.g. attack rate) were also used as independent variables in some regression models because they can affect swimming speed and angle of turn (see Results). Collinearity between independent variables was estimated by examining the pairwise correlation coefficients. When collinearity occurred (significant correlations; $P < 0.05$), each collinear variable was used to build a separate model. Residual scatter plots, normal probability plots (Tabachnick & Fidell, 1983) and partial residual plots (Larsen & McCleary, 1972) were used to determine if assumptions of the multiple linear regression were satisfied (i.e. normality, linearity and homoscedasticity of residuals). When these conditions were not fulfilled, transformations were applied to the data (Montgomery & Peck, 1982). Zooplankton biomass was log-transformed and attack rate was arcsine-transformed to normalise the residuals and reduce their heteroscedasticity.

Results*Environmental factors and zooplankton biomass*

Water temperature ranged from 13.0 to 23.3 °C during the experiments and the variance of light intensity between 175.3 and 649.5 grey units (Table 1). We found a significant negative relationship between the variance of light intensity and the number of days separating the experiments from 21 June (Fig. 1; $r = -0.61$, $P < 0.02$), regardless of the daily variation in cloud and wind conditions. As expected, variance of light intensity was higher in June than in August and September (Fig. 1), reflecting the decrease in the angle of the sun from June to September. Our estimates of light intensity were therefore representative of the light intensity inside the enclosures. Mean daily zooplankton biomass (from t_0 to t_5) ranged between 0.067 and 0.194 mg wt dry L⁻¹ (Table 2) and was significantly correlated with water temperature ($r = 0.64$, $P < 0.01$) and light intensity ($r = 0.75$, $P < 0.001$). Light intensity was not correlated with water temperature ($P > 0.05$).

Table 1 Date (day of the year), water temperature (°C), variance of light intensity inside the enclosure (expressed in grey units; see text), index of fish daily ration (IFDR; g dry weight per 100 g wet fish weight day⁻¹), attack rate (no. of attacks per min of swimming), fish swimming speed (cm s⁻¹) and angle of turn (degrees s⁻¹) of experimental brook charr (1+) in pelagic enclosures

Experiment	Day of the year	Water temperature	Variance of light intensity	IFDR	Attack rate	swimming speed	Angle of turn
1995							
1	168	20.6	233.2	0.699	4.76	19.86	39.74
2	171	22.4	235.6	0.361	1.80	21.89	34.73
3	174	23.3	422.3	0.399	5.67	22.84	37.66
4	235	21.5	186.1	0.703	5.56	14.15	42.16
5	239	19.1	200.5	0.611	3.46	17.88	41.00
6	243	19.2	265.0	0.784	8.86	16.05	36.70
7	247	18.2	175.3	0.569	5.34	15.42	33.34
8	257	16.6	244.6	0.514	8.00	12.60	32.54
1996							
9	147	13.0	189.4	0.037	1.32	–	–
10	158	19.4	361.0	0.561	9.97	20.53	34.21
11	159	19.2	450.3	0.788	16.38	25.04	38.61
12	161	18.9	475.6	0.773	11.42	26.78	26.22
13	163	21.1	423.9	0.719	26.54	26.47	49.73
14	172	23.2	649.5	0.541	36.80	22.50	45.49

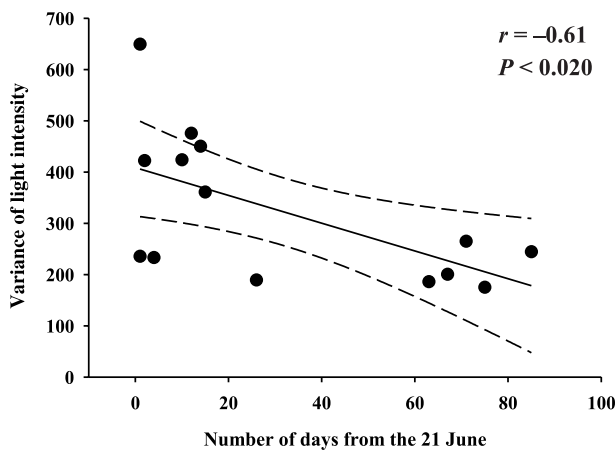


Fig. 1 Simple linear regression between variance of light intensity and the number of days separating each experiment from 21 June (summer solstice). Dotted lines represent the 95% confidence intervals.

Index of fish daily ration and feeding activity

Fish gut fullness ranged between 0.102 and 0.364 g dry weight per 100 g wet fish weight while our index of fish daily ration varied between 0.037 and 0.788 g dry weight per 100 g wet fish weight day⁻¹ (Table 1). Attack rate varied between 1.32 and 36.80 attacks per minute of swimming (Table 1). We found a significant (non-linear) positive relationship between the attack rate and the index of fish daily ration (Fig. 2; $R^2 = 0.60$, $P < 0.001$). As the attack rate increased, the index of

fish daily ration increased towards a plateau (Fig. 2). This suggests that most captures resulted in successful ingestion and that our estimate of attack rate represents prey capture. When a zooplankton prey is located by a fish, it has little chance to escape if attacked (McMahon & Holanov, 1995; Biro *et al.*, 1996). The asymptote could be related to the lower feeding efficiency of fish at higher attack rates (Fig. 2).

Effect of water temperature on attack rate and swimming characteristics

Mean fish gut fullness decreased significantly as water temperature increased (Fig. 3a; $R^2 = 0.63$, $P < 0.0007$), although three experiments at temperatures above 22 °C showed the highest mean zooplankton biomass (see Tables 1 and 2: Experiments 2, 3 and 14). A polynomial described the relationship between water temperature and the index of fish daily ration (Fig. 3b; $R^2 = 0.77$, $P < 0.0003$). This relationship was still significant when the experiment at 13.0 °C was excluded, which could have been considered as an outlier (i.e. $R^2 = 0.51$, $P < 0.02$). As 22 °C represents the upper avoidance temperature of brook charr (Cherry, Dickson & Cairns, 1977; Wismer & Christie, 1987), the results will be presented hereafter without the three experiments at temperature above 22 °C.

We observed a positive non-linear relationship between the attack rate and water temperature

Table 2 Mean zooplankton biomass (mg dry wt L⁻¹; SD in parentheses) inside and outside the enclosure before each experiment (t₀) and mean daily zooplankton biomass (mg dry wt L⁻¹, from t₀ to t₅)

Experiment	Day of the year	Mean zooplankton biomass inside the enclosure at t ₀	Mean zooplankton biomass outside enclosure at t ₀	Mean daily zooplankton biomass outside the enclosures (t ₀ -t ₅)
			1995	
1	168	0.0982 (0.033)	0.0670 (0.019)	0.0777*
2	171	0.1022 (0.010)	0.2143 (0.054)	0.1504*
3	174	0.1927 (0.109)	0.3348 (0.067)	0.1938*
4	235	0.0290 (0.016)	0.0930 (0.041)	0.0936*
5	239	0.0475 (0.026)	0.0659 (0.023)	0.0769*
6	243	0.0320 (0.024)	0.0512 (0.043)	0.0667*
7	247	0.1968 (0.112)	0.0890 (0.055)	0.0913*
8	257	0.0847 (0.036)	0.0782 (0.023)	0.0848*
			1996	
9	147	0.1225 (0.048)	0.0700 (0.039)	0.0896 (0.056)
10	158	0.0671 (0.048)	0.1291 (0.048)	0.0979 (0.034)
11	159	0.1015 (0.010)	0.2118 (0.064)	0.1242 (0.057)
12	161	0.1103 (0.021)	0.1890 (0.045)	0.1353 (0.044)
13	163	0.1418 (0.059)	0.1557 (0.026)	0.1559 (0.036)
14	172	0.1733 (0.058)	0.1926 (0.088)	0.1848 (0.066)

*Estimated from the significant relationship between mean zooplankton biomass at t₀ and the mean daily estimates outside the enclosures in 1996 (see text).

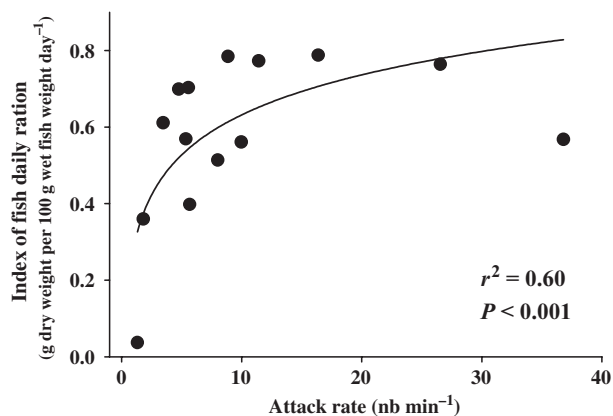


Fig. 2 Non-linear regression between the index of fish daily ration (g dry weight per 100 g wet fish weight day⁻¹) and attack rate (no. min⁻¹).

($R^2 = 0.39$, $P < 0.04$). Swimming speed was not significantly related to water temperature (Table 3). However, the angle of turn was positively related to water temperature (Table 3; $R^2 = 0.47$, $P < 0.02$).

Effect of zooplankton biomass and light intensity on attack rate and swimming characteristics

Attack rate was significantly related to zooplankton biomass, which explained 56% of the variation

(Table 3). Swimming speed was positively related to zooplankton biomass (Table 3; $R^2 = 0.63$, $P < 0.005$), but angle of turn was not (Table 3). We observed a significant positive relationship between attack rate and light intensity (Table 3; $R^2 = 0.66$, $P < 0.002$). Swimming speed was also significantly related to light intensity (Table 3; $R^2 = 0.80$, $P < 0.005$), but angle of turn was not (Table 3).

Relationships between attack rate and swimming characteristics

Swimming speed varied between 12.6 and 26.7 cm s⁻¹ with a mean of 20.2 ± 4.6 cm s⁻¹ (1.6 body length s⁻¹) while the angle of turn varied between 26.2 and 49.7 degrees, with a mean of 37.8 ± 6.0 degrees (Table 1). Attack rate was positively related to swimming speeds ($R^2 = 0.51$, $P < 0.02$), but was not significantly related to the angle of turn.

Multiple regressions predicting attack rate and swimming characteristics

Significant correlations were found between fish gut fullness, water temperature and zooplankton biomass, between zooplankton biomass, water temperature and light intensity, and between water temperature

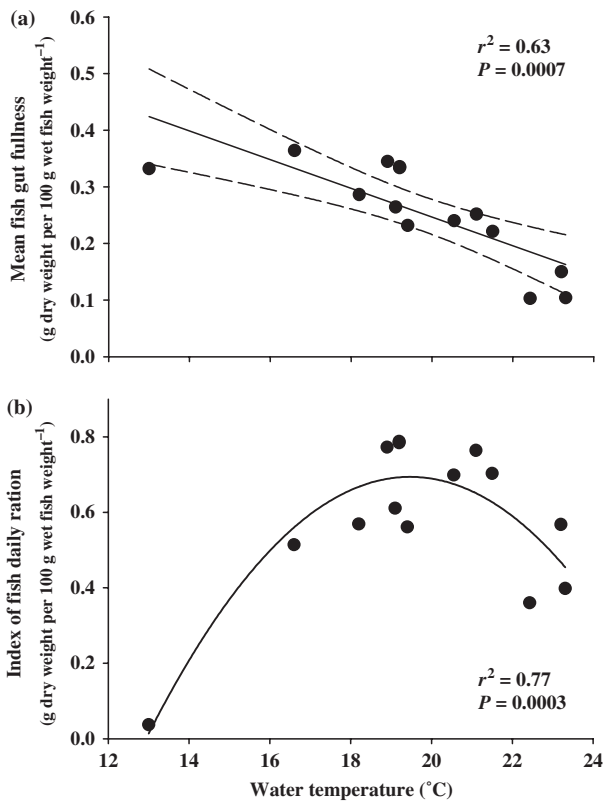


Fig. 3 (a) Linear regression between mean fish gut fullness (g dry weight per 100 g wet fish weight) and water temperature ($^{\circ}\text{C}$); (b) polynomial regression between the index of fish daily ration (g dry weight per 100 g wet fish weight day^{-1}) and water temperature ($^{\circ}\text{C}$). Dotted lines represent the 95% confidence intervals.

and the index of fish daily ration. These collinear variables were not considered simultaneously in regression analyses. The best predictors of attack rate

of brook charr in pelagic enclosures were fish biomass, light intensity and variance of the angle of turn, which explained 87% of the variation (Table 4). The best predictors of brook charr swimming speed in pelagic enclosures were water temperature and light intensity, which explained 86% of the variation (Table 4). No multiple regression model was found to explain the angle of turn of brook charr. However, the best predictors of the variance of the angle of turn were fish gut fullness and attack rate, which explained 83% of the variation (Table 4).

Discussion

Effect of water temperature on attack rate and fish daily ration

The overall temperature preference of brook charr is around $16\text{ }^{\circ}\text{C}$ (Coutant, 1977), its upper avoidance temperature near $22\text{ }^{\circ}\text{C}$, and its lethal temperature around $25\text{ }^{\circ}\text{C}$ (Cherry *et al.*, 1977; Wismer & Christie, 1987), depending on acclimation and (or) age. Changes in brook charr behaviour, such as loss of appetite, decreased activity or hyperventilation, are thus expected between 22 and $25\text{ }^{\circ}\text{C}$. At water temperature above $20\text{ }^{\circ}\text{C}$, individuals tend to aggregate in discrete cool areas and their feeding behaviour is affected by behavioural thermoregulation (Biro, 1998). Since no thermal refuge was available for brook charr in our study, a decrease in attack rate was probably the best behavioural response to increasing water temperature. As in others studies (Nicieza & Metcalfe, 1997; Biro, 1998; Weetman *et al.*,

Table 3 Simple regression models explaining the variation in attack rates (no. min^{-1}), swimming speeds (cm s^{-1}) and angle of turn (degrees s^{-1}) for experimental brook charr in pelagic enclosures

Dependant variable	Independent variable	Estimate	Prob. > F	R ²	Adj. R ²
Attack rate	Water temperature		n.s.		
	Zooplankton biomass	+1.05	0.008	0.56	0.51
	Light intensity	+0.001	0.002	0.66	0.62
Swimming speed	Water temperature		n.s.		
	Zooplankton biomass	+34.9	0.005	0.63	0.59
	Light intensity	+0.04	0.0005	0.80	0.77
	Attack rate	+25.4	0.02	0.51	0.45
Angle of turn	Water temperature	+3.08	0.02	0.47	0.41
	Zooplankton biomass		n.s.		
	Light intensity		n.s.		
	Attack rate		n.s.		

Table 4 Best predictive models of attack rates (no. min⁻¹), swimming speeds (cm s⁻¹) and variance of the angle of turn from the observed biotic and abiotic factors (i.e. fish biomass, fish gut fullness, index of fish daily ration, light intensity, water temperature, and zooplankton biomass). The estimates, the probability (*P*) associated with each independent factors, the standard error of the coefficients (SE), the *R*² associated with the model, the adjusted *R*², and the standard error of the estimate (*S*_{xy}) are also given

Dependent variable	Independent variables	Estimates	<i>P</i> > <i>t</i>	SE	<i>R</i> ²	Adj. <i>R</i> ²	<i>S</i> _{xy}
Attack rate	Intercept	+0.14			0.87	0.81	0.11
	Fish biomass	-0.01	0.07	0.007			
	Light intensity	+0.01	0.003	0.0002			
	Variance of the angle of turn	+0.0001	0.0001	0.00006			
Swimming speed	Intercept	-10.31			0.86	0.82	9.90
	Water temperature	+0.93	0.11	0.51			
	Light intensity	+0.04	0.0004	0.006			
Variance of the angle of turn	Intercept	+1843.5			0.83	0.78	329.2
	Fish gut fullness	-4797.3	0.002	1067.8			
	Attack rate	+1690.3	0.003	385.3			

1998), we observed a non-linear effect of water temperature on the index of fish daily ration in our experimental fish.

Effect of zooplankton biomass on attack rate and swimming characteristics

An increase in attack rate or swimming speed was related to the increase in zooplankton biomass. This increase in the number of attacks as zooplankton biomass increases conforms to the general positive functional response observed in other fish species (Batty *et al.*, 1990; Miller *et al.*, 1992). Our results also support the hypothesis that swimming speed increases with prey biomass (Ware, 1975, 1978).

We did not observe a plateau in attack rate as zooplankton biomass increased. As our experiment was performed in an oligotrophic lake, it is possible that plankton biomass never reached the levels at which an asymptotic relationship would be seen. Also, as these experiments were done under natural biotic and abiotic conditions, factors other than zooplankton biomass might affect or limit this response (e.g. water temperature). Moreover, variation in our index of fish daily ration was not significantly related to zooplankton biomass, suggesting that the effect of water temperature might have been more important than zooplankton biomass under our semi-natural conditions. Light intensity might also limit feeding activity and attack rate in our experiments (see following section). We did not observe a maximum or a decline in swimming speeds

at high zooplankton biomass, as suggested by Ware (1975, 1978), probably for the same reasons that we did not observe a plateau in the attack rate.

Effect of light intensity on attack rate and swimming characteristics

Light intensity is considered an important factor controlling the feeding process of visual predators (Aksnes & Giske, 1993). In our study, light intensity explained about 60% of the variation in attack rate and about 80% of the variation in swimming speed. Such a response to light intensity has also been observed in previous studies (Henderson & Northcote, 1985; Benfield & Minello, 1996; Utne, 1997). As the light intensity increased, the water volume perceived by fish increased and the attack rate increased correspondingly. Increased contrast with a rise in light intensity could also be involved in the attack rate increase (Utne-Palm, 1999). Light intensity was positively correlated to zooplankton biomass, and thus it is difficult to separate the effects of these two factors. Swimming speed was positively related to light intensity, suggesting an increase in the reaction distance because of the larger volume of water sampled by fish. This supports the hypothesis that encounter rate and attack rate increase with increased swimming speed (Ware, 1975, 1978). The variance in swimming speed was significantly related to light intensity (*R*² = 0.42; *P* < 0.04), suggesting that light intensity could have played an equal or more important role than zooplankton biomass.

Attack rate and swimming characteristics

Swimming speed and angle of turn were positively related to the attack rate of brook charr in pelagic enclosures. As the angle of turn and its variance were positively related to the attack rate, and attack rate was itself positively related to zooplankton biomass, the angle of turn and its variance tended to increase with zooplankton biomass. This latter relationship supports the results of James & Findlay (1989) but contrasts with those of Sirois & Boisclair (1995) and Marchand & Boisclair (1998). This divergence from these two studies is probably because of the wider range of zooplankton biomass encountered in our study. Our results support the observations of Munk & Kjørboe (1985), who observed that swimming activity of herring was positively related to prey density, and those of James & Findlay (1989), who observed that the angle of turn of Cape anchovy (*Engraulis capensis* Gilchrist) was positively related to prey concentration when particulate feeding was involved.

This study allowed us to evaluate the effects of different biotic and abiotic factors, such as water temperature (+), light intensity (+), fish biomass (-) and zooplankton biomass (+), on the attack rate and swimming characteristics (i.e. swimming speed and angle of turn) of juvenile brook charr in pelagic enclosures. As zooplankton biomass was correlated to water temperature and light intensity, it was not possible to evaluate the relative contribution of these three factors on attack rate and swimming characteristics of brook charr. Other studies that manipulate these factors in the field will be necessary to understand better their independent effects. However, this study highlighted the roles of these factors on the feeding behaviour of juvenile brook charr when feeding in the pelagic habitat under natural conditions, and their importance in future models of optimal foraging and fish habitat quality.

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