Influence of light on the swimming speed of coregonids in subarctic lakes

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Swimming speed of pelagic whitefish (*Coregonus lavaretus*) and vendace (*Coregonus albula*) was studied in two subarctic lakes at 69°N in northern Norway in June, August and September 2000. At this latitude, the light regime changes strongly during the summer months, from 24 hrs of daylight in June to 14 hrs in September. Swimming fish were monitored by a bottom mounted split-beam echosounder, and the hydroacoustic traces were analysed with software designed for fish track analysis. Fish tracks were smoothed using a locally weighted algorithm before estimating swimming speeds. The swimming speed was strongly influenced by light. Average swimming speed was highest in periods with low incident light or crepuscular light (16–18 cm s^{-1}) and lowest in darkness (8–10 cm s^{-1}). A positive relationship between fish size and swimming speed was observed during daylight, but not during periods of darkness.

Introduction

The light regime has a major influence on the behaviour of many aquatic organisms, including freshwater fish (Wootton 1998, Pavlov *et al*. 2000). Vertical and horizontal migration and shoaling correlated to the diel photoperiod are phenomena frequently observed among fish (Bohl 1980, Gliwicz & Jachner 1992, Comeau & Boisclair 1998, Ptak & Appenzeller 1998, Knudsen & Saegrov 2002), and fish are often characterised as diurnal, nocturnal or crepuscular depending on their daily activity pattern (Helfman 1981, 1993, Wootton 1998). The different behavioural characteristics are often assumed to be related to food search, predator avoidance,

physiological benefits, or combinations of these (Clark & Levy 1988, Wootton 1998, Metcalfe *et al*. 1999). In particular, swimming activity is frequently correlated with the time of the day (Trudel & Boisclair 1996, Briggs & Post 1997, Nøst & Langeland 1998, Jurvelius *et al*. 2000, Cech & Kubečka 2002). However, in other studies, no significant differences in swimming speed during the diel cycle have been found (Arrhenius *et al*. 2000, Torgersen & Kaartvedt 2001, Pedersen 2001). Many studies have addressed maximum swimming speed under laboratory conditions (Bernatchez & Dodson 1985, Feldman & Savitz 1999, Plaut 2001), whereas few authors have reported either maximum or normal fish swimming speed in the field. This is also the

case for coregonids in freshwater, although some work has been done in recent years (Anras *et al.* 1999, Jurvelius *et al.* 2000).

Studies of fish behaviour in the wild are often complicated by the properties of water. Different indirect methods like hydroacoustics, video recording, and biotelemetry have therefore been applied (Trudel & Boisclair 1996, Briggs & Post 1997, Aubin-Horth *et al.* 1999, Anras *et al.* 1999, Arrhenius *et al.* 2000). Hydroacoustics has the advantage of large sample volume, high resolution and independence of water transparency and light. Hence, hydroacoustics may provide detailed information about the location of fish in the waterbody at any time of the day and night, and also make it possible to explore how fast and in what direction individuals swim in the three dimensional pelagic habitat. When used stationary, a high signal-to-noise ratio is achieved and disturbance of the fish is eliminated. It is further possible to increase the precision of swimming speed estimates by incorporating smoothing of the swimming tracks from the hydroacoustic method (Mulligan & Chen 2000).

In the present study, fish tracks have been sampled using a bottom mounted echosounder and smoothing techniques in order to monitor, estimate and evaluate swimming behaviour of coregonid fish in the pelagic zone of a subarctic watercourse. Behavioural changes within the diel cycle might be due to endogenous circadian rhythms as well as responses to environmental conditions like light level (Thorpe 1978). At high latitudes, Muller (1978a, 1978b) has shown that circadian rhythms can be broken down in midsummer. By contrasting day and night samples along a subarctic summer season, starting with midnight sun in June and followed by the gradual development of dark nights towards August and September, we were able to study how swimming speed relates to changing light and circadian rhythms.

Study area and fish community

Two lakes situated about 50 km apart in the Pasvik watercourse, northern Norway, were investigated: Ruskebukta in the upstream part and Skrukkebukta downstream (Fig. 1). Both lakes are located adjacent to the main path of the watercourse, and have negligible water flow. Ruskebukta (69°13´N, 29°14´E; 52 m above sea level) has an area of 5.3 km² and a maximum depth of 15 m. Skrukkebukta (69°33´N, 30°7´E; 21 m above sea level) has an area of 6.6 km² and a maximum depth of 37 m. The water chemistry of the two lakes is similar (Langeland 1993), and the ice-free season in the lakes and reservoirs lasts from May–June to October–November. Water temperatures in both lakes ranged between 9 and 14 °C. Stratification was observed only in Skrukkebukta in August. The Secchi-depth ranged from 2 to 6 m.

Altogether, 15 species of fish have been recorded in the Pasvik watercourse. Whitefish (*Coregonus lavaretus*) and vendace (*C. albula*) are the most abundant species in the pelagic zone (Amundsen *et al.* 1999, Bøhn & Amundsen 2001, Bøhn *et al.* 2002).

Methods

Hydroacoustic sampling was performed with a Simrad EY500 split-beam echosounder. A 70 kHz circular 11° transducer was used for bottom mounted up-looking recordings. The transducer was placed on the bottom at 15 m depths in both lakes, which corresponded to the maximum depth in Ruskebukta. Ping rate was 3.5–5 pings s⁻¹ with pulse duration of 0.2 milliseconds. Calibration was performed *in situ* using the Simrad Lobe calibration program. The target employed was a 38 mm copper sphere with target strength (TS) –39.5 dB. Data was logged around 06:00, 12:00, 18:00 and 24:00 h for a period of 30–60 minutes and stored on a portable computer. Hydroacoustic data was analysed with the Sonar5 post-processing program (H. Balk & T. Lindem, University of Oslo, Norway). Tracks from the up-looking surveys were sorted with the tracking feature of this software on the basis of the three-dimensional position of the successive echoes. Tracking criteria were set to maximum 15 cm change in range between successive echoes, maximum 1 missing echo and a minimum requirement of 15 echoes to form a track. Tracks were subsequently evaluated from the appearance on the echogram and the

stability of the target strength. Due to the general problems with the acoustic near-field (MacLennan & Simmonds 1992, Furusawa *et al.* 1999), minimum range was set to 3 m. Maximum range was 0.5 m below the water surface and the lower TS-threshold was set to –64 dB.

The June survey had sun throughout the diel cycle, the August survey took place just after the onset of nights darker than civil twilight (sun > 6° below the horizon, referred to as darkness), and the September survey, close to the autumn equinox, included many hours of darkness during the night (Fig. 2). Measures of light intensities as global irradiation (W m^{-2}, hourly averaged) were obtained from The Norwegian Crop Research Institute's research station at Svanhovd, situated between the two lakes. Global irradiation is made up of direct irradiation from the sun, reflected irradiation from the ground (albedo), and diffuse irradiation (scattered in the atmosphere). It comprises a broader spectrum of wavelengths than can be seen by the eye, and as a rule of thumb 40%–50% of this measure is within the range of visible light. Conversion from W m^{-2} to lux (used by e.g. Link & Edsall 1996, Koski & Johnson 2002) is very complicated due to the dependence on wavelength composition, and we did not attempt this transformation, as the relationship will be highly time, weather and water quality dependent.

A total of 547 tracks were accepted from the tracking analyses. As some of the fish had highly curvatured trajectories (Fig. 3), we chose a robust locally weighted regression (Cleveland 1979) to smooth all the tracks in each of the *x*, *y* and *z* directions with time. The smoothing window was set to the 15 closest points. The smoothing was implemented to minimize some of the bias resulting from measurement errors ('gitter') in the single echo detection, which will tend to overestimate swimming speed (Mulligan & Chen
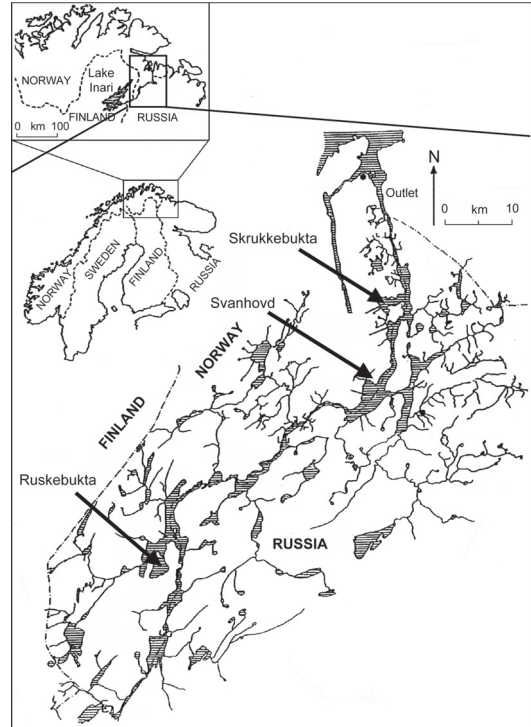

Fig. 1. Geographic location of the study sites in northern Fennoscandia. The global irradiation measurements were obtained from The Norwegian Crop Research Institute at Svanhovd.

2000). We then calculated the distance between the smoothed points using eq. 1, where x_i, y_i and z_i are the cartesian coordinates for each single echo detection given by the Sonar5-software:

$$d_i = \sqrt{\left(x_{i-1} - x_i\right)^2 + \left(y_{i-1} - y_i\right)^2 + \left(z_{i-1} - z_i\right)^2} \quad (1)$$

Further we calculated the velocity between each position (Eq. 2), and finally the mean swimming speed for each track (Eq. 3).

$$v_i = d_i/t, \quad\quad (2)$$

Fig. 2. Graphical presentation of solar heights (the sun's angle relative to the horizon) through the diel periods of the 20th to 21st of June, August and September at Svanhovd. The stippled lines indicate the horizon.
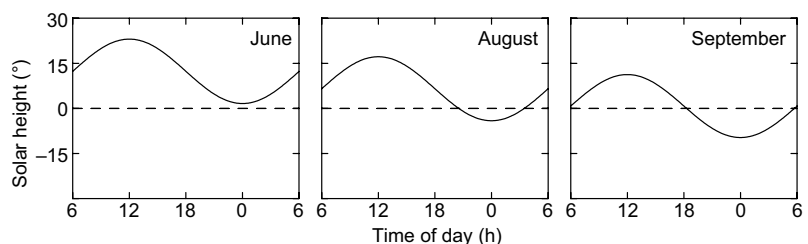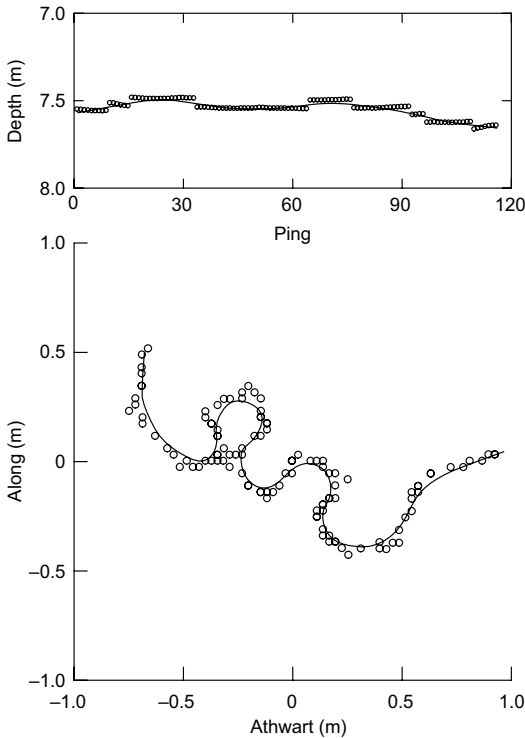
Fig. 3. Illustration of a fish track from Skrukkebukta in a September night. Circles show single echo detections, while the lines show the smoothed track. The upper pane shows smoothing in the depth, while the lower shows smoothing in the horizontal plane.

$$v = \frac{\sum_{1}^{n} v_i}{n} \qquad (3)$$

v_i denotes the velocity between each position, t the time elapsed between each detection, n the number of calculated distances and v the average swimming speed of the track:

Swimming speed estimates were transformed using the natural logarithm to normalize the data, and the mean swimming speeds presented are the geometric means. No significant differences in swimming speed were found between the two lakes (*t*-test: $p > 0.05$), and in the further analysis fish tracks from both lakes have been pooled. All fish lengths were calculated from the relationship between target strength and fish length given for whitefish by Lindem and Sandlund (1984):

$$TS = 20\log_{10}(l) - 68 \qquad (4)$$

TS (target strength) is quoted in decibels (dB), and l is fish length in cm.

We measured fish in the ventral aspect, which is not expected to deviate much from the dorsal aspect (cf. Love 1977). Echograms from additional side-looking and down-looking hydroacoustic surveys showed strong light-dependent shoaling behaviour and vertical migration. This behaviour reduced the number of available tracks from the daylight surveys, especially in Skrukkebukta in August and September. During darkness, in contrast, the fish were randomly distributed and individual tracks could easily be recognised.

Gillnetting was done with two 16-m long and 12-m deep pelagic net-series with 8, 10, 12.5, 15, 18.5, 22, 26 and 35 mm mesh sizes in 2-m sections. Nets were set for 12 hours from the afternoon until the morning for two nights in each lake for each month. Species and length distribution were established from the gillnet catches. Whitefish and vendace constituted 95% of the fish caught in the pelagic zone. The June survey had a discrepancy in the size distribution between the hydroacoustic samples and the gillnet samples. The lower length of fish caught in the nets was approximately 7 cm while the lower limit for the hydroacoustics was set to 1.6 cm (–64 dB). The August and September surveys showed similar size distributions from the two methods. We believe that hydroacoustic targeted fish had the same species distribution as revealed in net catches, as we have no indication of other abundant species in the pelagic habitat (Bøhn *et al.* 2002).

Swimming speed is often denoted in body lengths per second, but calculating swimming speed in body lengths per second from hydroacoustic recordings introduces two problems. Firstly target strength has limited precision as a measure of individual fish length (MacLennan & Simmonds 1992). The combined variances of target strength and swimming speed will thus magnify the variance unrealistically in hydroacoustic studies. Secondly, neither optimal cruising speed nor optimal foraging speed is directly proportional to body length, but rather decrease relative to the body size throughout the life history (Ware 1978). Thus, we prefer to present swimming speed estimates in absolute terms (cm s^{-1}). However, due to the presence of many small targets in June, the mean swimming speed is presented for two different size-groups;

one consisting of small fish below –55 dB (1.6 to 4.5 cm) and one consisting of larger fish (ranging from 4.5 to 30 cm) (*see* Fig. 4).

Results

The diel activity pattern of the coregonid fish changed from June to August and September (Fig. 4). In June, under the condition of midnight sun, the swimming speed was higher around midnight than during the day. Later in the season, the fish showed a clear reduction in swimming speed at midnight hours (i.e. in darkness), as compared with that in both daylight and twilight conditions (Fig. 4). The variation in swimming speed also appeared to be lower at low light intensities. Swimming speed furthermore shifted from being independent to depend on fish length with increasing light (Fig. 5 and Table 1). This was tested for fish > 4.5 cm due to few smaller targets in seasons with darkness. Based on these observations we built an ANCOVA model with
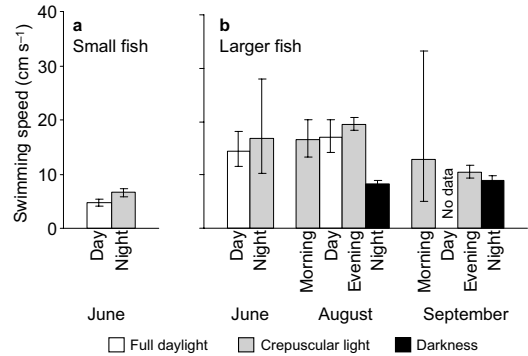

Fig. 4. Mean geometric swimming speed with 95% confidence intervals (no correction for fish length). — **a**: Day and night samples for small fish (–64 to –55 dB) in June. — **b**: Larger fish (–55 to –38 dB) through the season and at different times of the day. Data from both lakes were pooled. White bars indicate noon samples, grey-shaded bars indicate twilight or sun close to the horizon, and black bars indicate darkness.

swimming speed as the response variable to the predictor variables light intensity, fish length, and the interaction term:
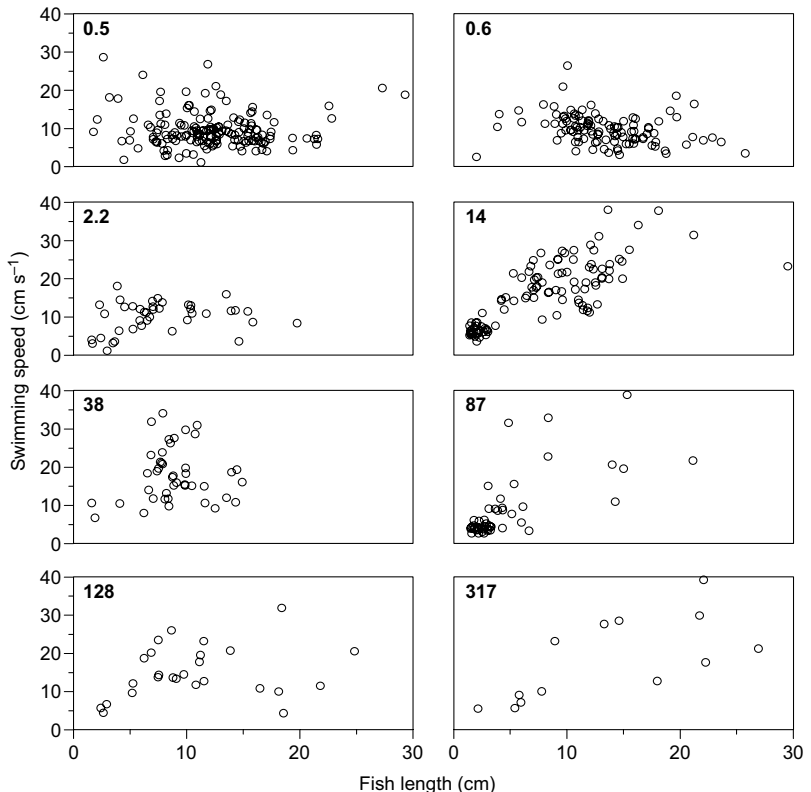

Fig. 5. Scatterplot of swimming speed to fish length for all data through the season, separated on different light intensities (numbers in boldface). The two lowest values, 0.5 and 0.6 W m^{-2} were classified as darkness in the field, whereas global irradiation values above 50 W m^{-2} were typical for situations with the sun high above the horizon. Fish length was derived from the relationship TS = 20log$_{10}$(*l*) – 68 (Lindem & Sandlund 1984).
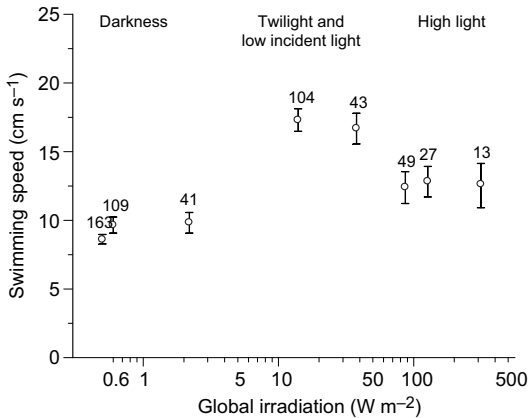
Fig. 6. Least square means with standard errors from the ANCOVA model (Table 2). Values are back-calculated from the logarithmic values used in the model. Light intensity is shown on a logarithmic scale, but was treated as a categorical variable in the model. Number of observations is indicated.

$$ \ln(\text{swimming speed}) = \text{constant} $$
$$ + (\text{light intensity}) + \ln(\text{fish length}) $$
$$ + (\text{light intensity}) \times \ln(\text{fish length}) $$

Light intensity was treated as a categorical variable due to the nonlinear response of swimming speed to light intensity (Figs. 4 and 5). The model was significant at $p < 0.001$ in all the terms (Table 2), and explained 47% of the variance in the ln-transformed data. The length-corrected back-calculated least-square means from the model are shown in Fig. 6, confirming the

observation that the highest swimming speeds occurred under intermediate light conditions.

Discussion

Circadian rhythms often brake down under the absence of dark nights, and whitefish are therefore likely to show an arrhythmic behavioural activity during the subarctic midsummer (Muller 1978a, 1978b). However, our results suggest that the pelagic coregonids in the Pasvik watercourse exhibited a rhythmic behaviour in June with a significantly higher swimming activity at night than at daytime. This is the opposite of what was observed in the later months, where the lowest swimming speed was found at night. In August and September, swimming speed in intermediate light intensities was two times higher than in darkness, with intermediate values in full daylight. Our results, thus, provide additional information to the experiments of Muller (1978a), where he showed whitefish swimming activity to be tightly coupled with the diel photoperiod. The sun is situated very low above the horizon at midnight in June (2.7°, global irradiation typically 10–20 W m^{-2}), resembling the situation of the twilight periods later in the summer or at other latitudes. Our August morning and evening surveys were performed in situations with low incident light and not true twilight. But due to the refraction properties of electromagnetic waves, most of the direct sunlight will be reflected

Table 1. Linear regressions between swimming speed and fish length: $\ln(\text{speed}) = a + b \times \ln(\text{length})$. Confidence intervals (CI) for the slope (b) are given.

Light	a	b	CI b low.	CI b up.	r^2	p
Below 2 W m^{-2}	2.32	−0.06	−0.24	0.11	0.00	0.47
Above 2 W m^{-2}	2.12	0.29	0.13	0.46	0.06	0.001

Table 2. Results from the ANCOVA model: $\ln(\text{swimming speed}) = \text{constant} + \text{light} + \ln(\text{fish length}) + \text{light} \times \ln(\text{fish length})$.

Source	Sum of squares	df	Mean square	F-ratio	P
Light	13.468	7	1.9	10.0	< 0.001
ln(fish length)	14.241	1	14.2	73.9	< 0.001
Light × ln(fish length)	920.712	7	3.0	15.3	< 0.001
Error	102.784	533	0.2		

from the water surface at low incident angles, giving prolonged twilight situations in the water column as compared with above surface. Including these periods with low incident light, there is a clear pattern of higher swimming speeds in all twilight periods throughout the season. This is in accordance with Helfman (1981, 1993), who found swimming speed in general to be highest at dusk in freshwater fish communities, and also that there were extended periods of twilight activities at high latitudes.

Boisclair (1992) found a positive relationship between activity rate (metabolic costs associated with movements) and feeding rate for brook trout, *Salvelinus fontinalis*. Swimming speed has furthermore been shown to decrease with increasing level of stomach satiation for the cyprinid *Pseudorasbora parva* (Asaeda *et al.* 2001). These findings suggest that the swimming speed is positively correlated with feeding activity. Planktivorous coregonids are generally particulate feeders depending on vision to catch their prey (Janssen 1978, Dabrowski & Jewson 1984). Vendace larvae in lake Lentua (64°N, Finland) ceased feeding in the short dark nights of May (Huusko & Sutela 1998). Under the midnight sun, however, light is sufficient for feeding 24 hrs a day. Food concentrations in Ruskebukta and Skrukkebukta have been measured to approximately 50 and 70 mg m^{-3} dry mass of edible food for pelagic coregonids in June (Bøhn & Amundsen 2001), corresponding to about 1000–1500 J m^{-3}. Dabrowski *et al.* (1989) showed that the time spent foraging per day had to be kept high, possibly above 20 h, to keep a high daily growth rate of 4% at such low food concentrations. Furthermore, studies of coregonid otolith microstructure suggest that the longer photoperiod at high latitudes is associated with more extensive feeding (Huuskonen 1999). It therefore seems plausible that the coregonids in the subarctic Pasvik watercourse are active feeders throughout the 24-hr cycle during midsummer.

Koski and Johnson (2002) found in experiments planktivorous kokanee salmon (*Oncorhynchus nerka*) fingerlings to move slowly under low light intensity (0.1 lux), feeding on prey items that occasionally drifted by. In crepuscular light (15–30 lux), in contrast, the feeding behaviour changed to actively searching

for prey items at higher swimming speeds. This change was predicted from the change in reactive volume that followed from the change in visibility (Stockwell & Johnson 1997, Koski & Johnson 2002). These results may be comparable also with that for coregonids, as lake herring (*Coregonus artedii*) has been shown to feed most effectively at light intensities above 10 lux (Link & Edsall 1996). Interestingly, we found a low swimming speed (8–10 cm s^{-1}) with very low variation during the dark nights of August and September, values similar to those obtained for 15-cm herring (*Clupea harengus*) in darkness in laboratory studies (11 and 7 cm s^{-1} for feeding and non-feeding, respectively; Batty *et al.* 1986). This may indicate that there is a predominant "cruising speed" at which the planktivorous fish operate in darkness. As predatory danger is lower in darkness, it may be favourable for the planktivorous fish to cruise at low swimming speed in the epipelagic habitat even if reactive volume and feeding efficiency are very low. Fish feeding under sufficient light conditions will benefit from better visibility of prey and higher reactive volume (Link & Edsall 1996), and can maximise their feeding efficiency by increasing the swimming speed. Thereby they themselves can also shorten the time they are subjected to visual predators. Thus, the trade-off of feeding under favourable light conditions but at a higher predation risk should be reflected both in higher swimming speed and a lower proportion of tracks due to shoaling, as we indeed observed in our surveys. According to Asaeda *et al.* (2001), fish will reduce their swimming speed as stomach satiation is reached. If satiation is not reached at the same time for each individual, this would result in a pattern of high variation in swimming speeds in the population. The large variation in our swimming speed data for daylight and twilight samples may support this hypothesis, although anti-predator behaviour may be an alternative explanation for this pattern.

Anras *et al.* (1999) reported mean swimming speed for lake whitefish (*Coregonus clupeaformis*) telemetered in autumn. At the beginning of the period (October–November), they found a mean swimming speed of approx. 15 cm s^{-1} at 8 °C, thereafter decreasing as temperatures decreased and spawning approached.

Their results could be considered as minimum estimates of daily swimming speed, as they calculated swimming speed from the change in position over 100 second intervals. Swimming speed would be underestimated if the fish did not swim in straight trajectories. Curved swimming tracks have been reported by Cech and Kubečka (2002), and were also frequently seen within our tracks. Rudstam *et al.* (1984) reported routine swimming speed for bloater, *Coregonus hoyi*, with 15 cm bloater swimming at a mean speed of 18.6 cm s^{-1} in tanks around 09:00 in June. This is similar to our estimates for the same size group in crepuscular or stronger light, with values typically around 20 cm s^{-1} (Fig. 5). None of our tracks exceeded the critical swimming speed reported for the related *C. clupeaformis* (55–60 cm s^{-1}, 12.7 cm length) (Bernatchez & Dodson 1985).

Coregonids of 1+ age in Pasvik are around 10 cm, and had swimming speeds in the same range as reported for 1+ yellow perch *Perca flavescens* (Aubin-Horth *et al.* 1999). On the other hand, our measurements of juvenile routine swimming speed (4.7 and 6.6 cm s^{-1}) are lower than compared with the means of 16 and 20 cm s^{-1} (non-smoothed data) observed for yellow perch fry (Arrhenius *et al.* 2000). This discrepancy is probably related to the increase in precision introduced by smoothing the tracks obtained with hydroacoustics, thereby diminishing the effects of the variance in target location. Our estimates are essentially the same as those reported on 0+ brook trout *Salvelinus fontinalis* (Boisclair 1992), and comparable to those obtained in experiments with 0+ Eurasian perch *Perca fluviatilis* (Persson & Greenberg 1990).

There is a general expectation that maximum sustained swimming speed (i.e. critical swimming speed) increases with body size (Beamish 1978, Kolok 1999, Plaut 2001), with critical swimming speed being proportional to the body length raised in a power between 0.5 and 1.1 (Magnuson 1970, Brett & Glass 1973). Optimal foraging speed for most pelagic planktivorous fish species should also follow such a relationship, with body length raised to the power of 0.4 (Ware 1978). Rudstam *et al.* (1984) estimated this exponent empirically to 0.8 for bloater (*C. hoyi*), whereas Cech and Kubečka (2002) report a positive relationship for several pelagic species without calculating the exponent. Our daytime data supports a positive relationship with an overall exponent of 0.3 (parameter *b* in Table 1) for fish > 4.5 cm, although the variation was high in daytime swimming speed.

Small fish typically have sustained swimming speeds > 3 body lengths s^{-1} (Videler 1993). Dabrowski *et al.* (1989) and Persson and Greenberg (1990) showed swimming speed to be highest at relatively low prey density, and Ware (1978) hypothesised foraging speeds to be between 0.4 and 1 times the critical swimming speed for planktivorous fish. For a 12-cm whitefish this would correspond to swimming speeds above 20 cm s^{-1} if critical swimming speed is comparable to that of *C. clupeaformis*. This was frequently observed in intermediate light or full daylight, whereas very few tracks in darkness exceeded 20 cm s^{-1}. Therefore, the positive relationship between the fish length and swimming speed at higher light intensities supports the suggestion that coregonid feeding activity is more strongly correlated with the light level than with circadian rhythms. Furthermore, Dabrowski *et al.* (1989) modelled juvenile coregonid growth and predicted optimum swimming speed for 3 cm juveniles to range from 4 to 12 cm s^{-1} depending on prey type. Our observed mean swimming speeds of 4.7 and 6.6 cm s^{-1} for fish below 4.5 cm (Fig. 4) fit well with these predictions. On the other hand, darkness samples showed low swimming speeds for larger fish, low variation and no relationship between swimming speed and fish size. Positive relationships between swimming speed and fish size have been used for correcting for encounter probabilities (e.g. Rudstam *et al.* 1984, Hansson & Rudstam 1995), but our results show that this should be done with care under darkness conditions.

Conclusion

In conclusion, the light regime seems to have a major impact on the swimming speed of whitefish and vendace in the Pasvik watercourse, and apparently breaks down the circadian rhythms of these coregonid fish species during the subarctic midsummer. Swimming speed was highest

at times with low incident or crepuscular light (2–50 W m^{-2}), and low in dark nights. In addition to feeding activity, anti-predator behaviour may be an important trigger for increased swimming speed at adequate light conditions. Vertical migration and shoaling support that predation during daylight conditions is an important factor determining the swimming patterns of these coregonid species. Implementation of positive relationships between swimming speed and body size in biological models should be done with caution, as our results showed such a relationship only in non-darkness periods.

Acknowledgements

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