Planktivore vertical migration and shoaling under a subarctic light regime

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Abstract: Visually foraging planktivorous fish are prey of visual predators, and their foraging behaviour may be affected by light levels both in terms of gain and risk. The large seasonal change in day length throughout a subarctic summer at 69° N was used to show the influence of light on diel vertical migration (DVM) and shoaling patterns in a planktivorous fish assemblage consisting two species (*Coregonus lavaretus* and *C. albula*). Under the midnight sun in June, night and day-time behaviour was similar with extensive shoaling and limited DVM. With increasingly darker nights towards autumn, the fish dispersed during the dark hours and showed more extensive DVM. Throughout the changing light regime of both the day and the season, the planktivores consistently chose depths with light levels compatible with visual foraging and reduced predation risk as revealed from reactive distance modelling of coregonids and their salmonid predators. The findings support the hypothesis that behavioural decisions are based on a trade-off between foraging rate and predation risk, and increased predator avoidance behaviour towards autumn suggested that this trade-off is state-dependent.

Keywords: Planktivory; piscivory; predator-prey; trade-off; state-dependence

Introduction

Light is important for visually oriented predators as darkness provides cover for their prey, and behavioural responses to changes in light intensity are often associated with predator-prey interactions (Blaxter 1975; Helfman 1993; Pitcher and Parrish 1993). The non-consumptive effects (non-lethal, e.g. reduced growth and birth rates) of a predator on its prey population may be as important as the consumptive effects (i.e. removal of individuals) in population regulation, and are often transmitted through dynamic traits such as behaviour of individuals in the prey population (Lima 1998*a*; Preisser et al. 2005; Pangle et al. 2007). The effect of modified traits may cascade to the resource populations of the prey (trait mediated indirect interactions, i.e. effects of a predator on a receiving species is mediated through a transmitter species, Dill et al. 2003; Werner and Peacor 2003). Knowledge of behavioural patterns is therefore crucial to understand community dynamics. In many fish species, behavioural traits such as diel vertical migration (DVM), shoaling, and swimming activity have been associated with predator-prey interactions and shown to be correlated to light intensity changes (Blaxter 1975; Helfman 1993; Pitcher and Parrish 1993).

Light intensity influences the visual acuity of prey and predator, affecting both predator efficiency and predator recognition in prey. The encounter rate and resulting feeding rate of a visual predator is a function of light intensity, prey availability, prey visibility, and activity levels of both predator and prey (Eggers 1977; Evans 1989). A predator increasing its foraging activity will simultaneously increase its predation risk, and there is therefore a trade-off between foraging gain and predation risk (Gilliam and Fraser 1987; Lima and Dill 1990). This trade-off may be state-dependent as animals that are either food-deprived or has a low reproductive value are expected to take higher risks than satiated animals or animals close to reproduction (Milinski 1993; Clark 1994; Damsgård and Dill 1998).

DVM-patterns observed for some planktivorous fish species support the trade-off hypothesis between foraging gain and predation risk (Clark and Levy 1988; Scheuerell and Schindler 2003; Hrabik et al. 2006). In aquatic environments, light intensity decreases with increasing depth and turbidity. During light hours, fish may reduce activity or migrate to deeper, darker and safer habitats to reduce predation risk. During darkness hours when predation risk from visually oriented predators is reduced, they may safely return to the surface waters where food is normally most abundant. Other hypotheses explaining DVM suggest that planktivorous fish track the DVM of their prey (Janssen and Brandt 1980; Eshenroder and Burnham-Curtis 1999), or that it is caused by bioenergetic benefits when there is a separation between the habitat optimal for foraging and the habitat optimal for growth (Brett 1971; Wurtsbaugh and Neverman 1988; Sims et al. 2006).

Predation risk have also influenced the evolution of shoaling (Pitcher and Parrish 1993). Improved predator detection, recognition, and avoidance is an important motivator to form shoals, although foraging gain may be reduced due to intra-shoal competition for food (Lima and Dill 1990; Magurran 1990; Pitcher and Parrish 1993). Shoaling reduces the probability of being preyed on, and the rapid, coordinated movement by shoals serves to protect individual members (Magurran 1990; Pitcher and Parrish 1993). Shoaling is recognized as an important anti-predator behaviour, and represents an alternative or supplementary defence strategy to DVM for pelagic fish.

Changes in activity patterns and vertical use of habitat typically occur during crepuscular periods (Blaxter 1975; Helfman 1993; Pitcher and Parrish 1993). In some planktivorous fish species, swimming activity has been observed to be highest in crepuscular light (Batty 1987; Iida and Mukai 1995; Gjelland et al. 2004). Periodic changes in behaviour may also be influenced by endogenous circadian rhythms as well as changes in light (Thorpe 1978), but these factors are often confounded since circadian rhythms typically have the same periodicity as the day-night cycle. At latitudes above the polar circle, however, the sun is above the horizon for 24 hrs a day during midsummer. Later in the season dark nights approach, and by autumnal equinox in September nights are as long as days. High latitude locations therefore provide excellent natural conditions for testing the light dependence of behavioural traits.

The objective of this study was to evaluate the effect of diel and seasonal changes in light intensity on DVM and shoaling patterns of planktivorous whitefish *Coregonus lavaretus* (L.) and vendace *Coregonus albula* (L.) combined in a subarctic lake in the Pasvik watercourse, northern Norway. These co-existing planktivores are predated on by piscivorous brown trout (*Salmo trutta* L.) (Kahilainen and Lehtonen 2002; Jensen et al. 2004, 2008). By contrasting day and night samples from June, August, and September, we investigated how behavioural traits relate to the changing light regime, i.e. both within the diel cycle and during the ice-free season. Specific hypotheses regarding the coregonid behaviour included: (1) DVM will be limited or absent in June under the midnight sun, but extensive after the onset of dark nights in August and September; (2) shoaling will be observed over 24 hrs in June, but only during daylight hours in August and September; (3) planktivorous fish choose depths with sufficient light for visual foraging, but with reduced predation risk; (4) the predator avoidance behaviour will be less pronounced in June after a long ice-covered winter, due to hunger and a long time span to the late autumn reproduction as compared to later months.

Methods

In order to evaluate DVM and shoaling patterns in planktivorous coregonids, we combined echosounding techniques with gillnetting for planktivores, planktivore diet analysis, and zooplankton sampling in a high latitude lake at periods of contrasting differences in the diel light cycle. Published literature on coregonid reactive distance and salmonid piscivore reactive distance in relation to light intensity were used to evaluate the influence of light level on the foraging opportunity and predation risk for the studied planktivores.

Study site and fish community

The pelagic fish community of the oligotrophic Lake Skrukkebukta was sampled around the 20th of June, August, and September 2000. Skrukkebukta has a surface area of 6.8 km^2, a mean depth of 14 m and a maximum depth of 38 m (Fig. 1a). It is part of the Pasvik watercourse, on the border between Russia and Norway at 69° N 30° E. The Pasvik watercourse originates in Lake Inari (1102 km^2, 118 m above sea level). The ice-free season in the watercourse lasts from the end of May or beginning of June to October – November.

The fish fauna of Pasvik is diverse for lakes at this high latitude, with 15 fish species recorded in the watercourse. Two morphs of whitefish have been described: a pelagic densely-rakered (DR) morph, which forages predominantly on zooplankton, and a larger benthic-dwelling sparsely-rakered (SR) morph, which forages on benthic prey (Amundsen et al. 2004; Østbye et al. 2006). DR whitefish and vendace are the dominant pelagic fish in the Pasvik watercourse (Bøhn and Amundsen 2001; Gjelland et al. 2007), with brown trout being the dominant pelagic predator (Bøhn et al. 2002; Jensen et al. 2004, 2008). The zooplankton community is dominated by small cladocerans, mainly *Daphnia* and *Bosmina* spp. (Bøhn and Amundsen 1998; Amundsen et al. 2008). As a consequence of spawning habitat loss of the brown trout after water regulation, at least 5000 brown trout (min. length 25 cm) are annually stocked in the watercourse in the beginning of June to compensate for the reduced natural recruitment. About 1000 of these fish are released into Skrukkebukta. The trout quickly turn to piscivory, feeding mainly on vendace and DR whitefish, and grow fast (Jensen et al. 2006*a*, 2008). Perch (*Perca fluviatilis* L.), pike (*Esox lucius* L.), and burbot (*Lota lota* L.) are important benthic piscivores associated with the littoral and profundal habitats of the lake (Bøhn et al. 2002). Some piscivorous waterfowl such as mergansers (*Mergus* spp.), loons (*Gavia* spp.), and terns (*Sterna* spp.) feed in Skrukkebukta. They are also visual foragers, but their impact on pelagic fish populations is not known.

Reactive distance relative to light

The reactive distance can be defined as the distance at which an animal reacts to and initiates an attack on a prey (Holling 1959). In order to develop a reactive distance model of visual foraging in coregonid planktivores, we analyzed data on *Coregonus artedi* reactive distance in relation to prey size (Link 1998) and light intensity (Link and Edsall 1996). According to the inverse square law of spherical electromagnetic radiation, one might expect the light intensity scattered from a prey item to a predator to be inversely proportional to the distance between the predator and the prey. The amount of light scattered by the prey item may furthermore be a function of prey size. We found that there was a constant relationship C_s between prey size and reactive distance in the data of Link (1998), suggesting that the relationship between coregonid reactive distance D_c and prey size S is well described by the inverse square law (Eq. 1, Fig. 2a).

Eq. 1 $$C_S = S \cdot D_C^{-2}$$

The reactive distance in relation to light appeared to be log-linear, although there seemed to be maximum threshold at the highest light intensities (Fig. 2b, Link and Edsall 1996). Such a saturation intensity threshold (SIT) has also been observed for other fish species (e.g.Henderson and Northcote 1985; Mazur and Beauchamp 2003). We defined the 8.4 cm reactive distance observed at 1000 and 1500 lux as the maximum reactive distance reached at SIT, and used the rest of the data in a log-linear regression (Eq. 2, Fig 2b, a=0.0419 m, b=0.00839 m•lux^{-1}, r^2=0.85 for the full model including SIT).

Eq. 2 $$\begin{aligned} D_C(I \geq SIT) &= 0.084\text{m} \\ D_C(I < SIT) &= a + b \cdot \log(I) \end{aligned}$$

By solving the log-linear part of Eq. 2 for D_C = 8.4 cm, the saturation intensity threshold was estimated to 151 lux. If a constant M is introduced as a function of the constants a and b such that $M = \exp(a/b)$, the log-linear part of Eq. 2 can be rewritten (Eq. 3).

Eq. 3
$$b^{-1} = \log(M \cdot I) \cdot D_C^{-1}$$

The inverse square law applies to all light intensities, although the amount of light reflected from a prey required to stimulate an attack in a planktivore may depend on the background light intensity. Eq. 1 and Eq. 3 are now on a form that they can be combined if we take the square root of Eq. 1 and replace the constants C_S and b with another constant C (Eq. 4).

Eq. 4
$$C = S^{0.5} \cdot \log(M \cdot I) \cdot D_C^{-1}$$

According to Link (1998), the reactive distance experiments in relation to zooplankton size was performed at 40-200 lux. We estimated constant C (5.22 $m^{-0.5}$) by using the geometric mean (89 lux). This introduced a maximum bias of 8.5 % as compared to if all the experiments were done either at 40 or 200 lux. By rearrangement of Eq. 4, a model of coregonid reactive distance as a function of both light and prey size at light intensities below SIT is obtained (Eq. 5).

Eq. 5
$$D_C = S^{0.5} \log(M \cdot I) \cdot C^{-1}$$

We considered the visual foraging threshold I_T as the light level where the reactive distance produced by the reactive distance model would equal zero. Eq. 5 solved for I_T with $D_C = 0$ has the solution M^{-1}, giving an estimated visual foraging threshold at 0.0068 lux independently of prey size (Fig. 2b). The full coregonid reactive distance model as a function of light and prey size can now be given (Fig. 2d, Eq. 6, prey length and reactive distance in m).

Eq. 6
$$D_C(0.0068\text{ lux} < I < 151\text{ lux}) = 0.192S^{0.5} \cdot \log(148 \cdot I)$$
$$D_C(I \geq 151\text{ lux}) = 1.92S^{0.5}$$

This model produces reactive distance responses to light and prey size qualitatively consistent with the results seen in Vinyard and Obrien (1976) and Confer et al. (1978), with a smaller difference in reactive distance to various sizes of zooplankton at low light intensities than at high light intensities. To our knowledge, there is no publication on the light intensity threshold for coregonid visual foraging. Dembinski (1971) reported that vendace in Polish lakes were observed at depths with light intensities between 0.01 and 50 lux during the day. For comparison with Dembinski's data, we estimated the depths of the 0.01 and 50 lux light levels. The estimated depths of these light intensities are summarized in Table 1.

Research on piscivorous salmonids including lake trout (*Salvelinus namaycush*), cutthroat trout (*Oncorhynchus clarki*), and rainbow trout (*O. mykiss*) has revealed that these fish greatly increase reactive distances over the light range from 0.4 to 18 lux (Vogel and Beauchamp 1999; Mazur and Beauchamp 2003). The species-specific reactive distance may differ at a given light intensity, but the shape of the reactive distance to light relationship is remarkably similar and there is no further increase in the reactive distance above approximately 18 lux for any of the species. We assumed a similar relationship for brown trout. This assumption may be justified, since we were interested in the relative change in piscivorous reactive distance rather than the actual value of the reactive distance. The depths of the 0.4 and 18 lux light levels were therefore estimated to identify the depths of these predation risk thresholds, using the exponential light extinction function for light transmittance in water. For a relative comparison between planktivore coregonid reactive distance and piscivorous salmonid reactive distance, we used a derived reactive distance model from Vogel and Beauchamp (1999). The model presented by Vogel and Beauchamp includes turbidity dependence, however, at turbidities of 7.4 NTU (nephelometric turbidity units), the negative interaction term between light and turbidity would cause reactive distance to fall to zero if the model is extrapolated to 700 lux. Moreover, their data and those of Mazur and Beauchamp (2003) indicated a rather constant reactive distance in relation to light intensity above SIT. We therefore fitted a new maximum reactive distance $D_{T\max}$ model dependent on the turbidity Tb to the datapoints above 17 lux in Vogel and Beauchamp (1999) (Eq. 7, residual standard error 0.044, p<<0.001). Below $D_{T\max}$ we used Vogel and Beauchamps model (Eq. 7). The turbidity for Lake Skrukkebukta was not measured during this study, but according to Langeland et al. (1993) varied between 0.85 and 9.3 NTU in the beginning of September for 1990 and 1991, respectively. We used the mean 3.85 NTU of the values reported by Langeland (1993). Although the value of the reactive distance was highly dependent on the turbidity, the shape of the reactive distance model was little influenced by the turbidity. As our focus was on the relative change in piscivorous reactive distance rather than the actual value, our conclusions will not critically depend on the turbidity level.

Eq. 7
$$\begin{aligned} &D_{T\max} = \left(0.0154 + 0.0021\log(Tb)\right)^{-1}, \\ &D_T = 26.8 + 2.81I - 6.09\log(Tb) - 0.025I\log(Tb) \quad \text{for } D_T < D_{T\max} \end{aligned}$$

Light measurements

The light extinction coefficient k was estimated from light profiles sampled in 0.5 m intervals during June and August. No light profile for September was available, but as the

Secchi-depth was very similar to August, we estimated k for September from the relationship a between Secchi depth Z_{SD} and k in August (i.e. $k = a*Z_{SD}^{-1}$). Surface illumination (unit lux) was estimated using hourly averaged global irradiation data ($W•m^{-2}$) from Bioforsk Soil and Environment Division, Svanhovd research station, situated about 10 km from the study lake. Units were converted using 1 $W•m^{-2}$ = 120 lux (Lampert and Sommer 1997). The exact conversion between $W•m^{-2}$ and lux depends inter alia on weather and sun elevation. We verified that the converted daytime values from the global irradiation data and values produced by a illuminance model from Janiczek and DeYoung (1987) matched. For the August and September nights, when light level was too low for global irradiation measurements, the Janiczek and DeYoung (1987) model was used to estimate the surface illumination in lux.

Zooplankton sampling

Zooplankton samples were collected using a 30 l Schindler-Patalas trap with 65µm mesh size. Three replicates were taken at depths of 1, 3, 5, 7, 9, and 12 m during daytime at each sampling occasion, and at 1, 5 and 9 m depth at midnight in August and September. Samples were fixed with 4 % formalin. In the laboratory, all crustacean individuals in the daytime samples were counted and identified to species or genus, other prey taxa were identified to family level. Only cladocerans were counted in the night-time samples.

Gillnet sampling

Multi-meshed vertical gillnets (bar mesh sizes 8, 10, 12.5, 15, 18.5, 22, 26, and 35 mm from knot to knot in panels extending from the top to the bottom of the net) were used for catching fish. The nets were 12 m high and 16 m long, consisting of 2 m wide panels and marked at every second meter depth to allow for depth resolution of the catches. Two nets were set for 12 hours from the afternoon until the following morning, at the locations indicated in Fig. 1a. Gillnetting was conducted during four nights in June, and during two nights each in August and September. Species and length distributions were tabulated from each gillnet catch. Catch per unit effort (CPUE) for each 2 m depth interval was calculated as number of fish caught per 100 m^2 nets per night.

Biological sampling

The fish were weighed to an accuracy of 1 gram, and fork length L_F measured to an accuracy of 1 mm. The relationship between target strength *TS* (the logarithmic domain of acoustic backscattering area, positively related to fish size) and fish length normally use total length L_T of the fish (Simmonds and MacLennan 2005). L_T was found by multiplying L_F with 1.08, a conversion factor found from subsamples of both coregonid species in the catches. The age of the coregonids was read from whole otoliths (Skurdal et al. 1985). Prey items in the coregonid stomachs were categorized as *Bosmina, Daphnia,* Cyclopoida, Calanoida, benthic invertebrates, insect pupae, or surface insects. The stomach fullness was subjectively determined on a scale from 0 (empty) to 100 % (full), and the contribution of each prey category to the total volume of the stomach content was likewise determined.

Acoustic sampling

To monitor and evaluate swimming behaviour of pelagic fish, sampling was performed using acoustics with a combination of mobile vertical (down-looking beam, oriented 90° from surface) and horizontal (side-looking beam, oriented approximately 5° from surface) techniques around midnight and mid-day (Fig. 1b). In addition, day-break recordings were made along 3 transects with the side-looking beam in August. The down-looking acoustics were used to quantify fish depth distributions, depth of shoals, and fish density estimation. The side-looking surveys covered approximately the upper 4 m of the water column (‘surface blind zone’ for down-looking acoustics) and were used in a qualitative way to judge if fish were present in surface waters, and if present, if fish were shoaling. The acoustic sampling was performed using a EY500 split-beam echosounder (Simrad, Horten, Norway) operating at 120 kHz (ping rate 5 pings•s^{-1} in June and 8-9 pings•s^{-1} in August and September, pulse duration 0.3 ms) with a 4x10° elliptic split-beam transducer mounted at 1 m depth on a rod attached to the boat. Volume backscattering strength (S_v) recording threshold was set to -70 dB re 1 m^{-1}. Beam pattern calibration was performed at the Simrad factory before the first and after the last survey. In the field, standard target tests were performed for each survey to ensure correct system operation. A 23 mm copper sphere with expected *TS* of -40.4 dB re 1 m^2 was used. The survey boat followed a zigzag transect design (Fig. 1a). After completion of the side-looking survey, the zig-zag route was reversed and the down-looking survey performed along the same transects. Only transects parts covering depths greater than 15 m were used, with a degree of coverage $c = 3$ (Aglen 1983) for each of the side- and down-looking surveys.

The acoustic data was analysed using the Sonar5 post-processing program (Balk and Lindem 2006). To avoid bias from the acoustic near-field (Simmonds and MacLennan 2005), the minimum range from the transducer was set to 3 m. Single echo detection (SED)-criteria were set at minimum echo length 0.8 (relative to transmitted pulse), maximum echo length 1.5, maximum gain compensation 4 dB, and maximum phase deviation 4 (electrical degrees). For the side-looking surveys, maximum range was set to 50 m. In the analyses of down-looking surveys, the maximum range was set to 0.5 m above bottom to avoid bottom-dwelling fish being included in the analyses. The metric area scattering coefficient, s_A [m^2•ha^{-1}] is a standardized measure of returned echo energy (MacLennan et al. 2002; Simmonds and MacLennan 2005). To evaluate vertical distributions, the echo energy was integrated over 2 m depth intervals. The resulting depth-specific s_A-values were averaged over all transects within the day- or night-time sampling occasion, weigthed by the number of pings in each transect.

Weighted variance $Var(\overline{s_A})$ for depth interval z was obtained using Eq. 8 (Shotton and Bazigos 1984),

Eq. 8 $$Var\left(\overline{s_{A(z)}}\right) = \sum_{i=1}^{n}\left[(s_{A(z,i)} - \overline{s_{A(z)}})^2 d_i\right] \cdot \left[(n-1)\sum_{i=1}^{n} d_i\right]^{-1},$$

where d is the number of pings in transect i and n is the number of transects. 95 % confidence limits $CL_{(z)}$ were obtained by Eq. 9, on the assumption of a poisson distribution (Jolly and Hampton 1990).

Eq. 9 $$CL_{(z)} = \overline{s_{A(z)}}\left[1 + Var\left(\overline{s_{A(z)}}\right) \cdot \overline{s_{A(z)}}^{-2}\right] \pm 2\sqrt{Var\left(\overline{s_{A(z)}}\right)}.$$

The zig-zag transect design may bias confidence intervals due to autocorrelation at the transect joints. However, since the transect parts closest to the joint were generally shallower than 15 m and therefore removed, this effect were reduced. The centre of gravity Cg (Helland et al. 2007) for the day and night distributions was calculated for each transect according to Eq. 10,

Eq. 10 $$Cg = \sum_{i=1}^{m} s_{A(i)} z_i \cdot s_A^{-1}$$

where $s_{A(i)}$ is mean scattering coefficient at depth interval i, s_A is scattering coefficient integrated over all m depth intervals and z_i is the mean depth of depth interval i. The Cg was subsequently tested for statistical difference between day and night and between months using two-way anova and Tukey HSD multicomparison test, and the model residuals inspected.

In order to estimate the density of pelagic coregonids, we used the acoustic survey from the September night when the fish distribution was well dispersed and therefore the best for acoustic density estimation and target strength measurements. Two different approaches were used to estimate fish densities, the first implied using the *Sv*/*TS*-scaling method provided in Sonar5 (Balk and Lindem 2006), which uses the observed *TS* for abundance estimation. The second method implied dividing the total scattering energy s_A by the average spherical scattering cross-section $\overline{\sigma_{sp}}$ of fish targets, where individual $\sigma_{sp} = 4\pi 10^{TS/10}$ and *TS* of individual fish was estimated from the fish catches. The variance and confidence intervals were computed as for the depth-specific s_A-values. We assumed that the volume densities in the upper 4 m equalled the average of the volume densities from 4-24 m, and therefore added 4/(24-4) = 20 % to the estimates from 4-24 m. The relationship between fish total length L_T (cm) and *TS* (dB) for coregonids has been described as $TS=19.72\log_{10}(L_T)-68.08$ (Lindem and Sandlund 1984, hereafter referred to as the Lindem-Sandlund equation) and $TS=25.5\log_{10}(L_T)-70.9$ (Mehner 2006, hereafter referred as the Mehner equation). A comparison between the observed *TS*-distribution and the catch-derived *TS*-distribution revealed an overestimation of *TS* by the use of the Mehner equation, leading again to a three-fold underestimate of fish density as compared to the S_v/*TS* scaling method (which is catch-independent). We therefore chose to present the density estimates based on the Lindem-Sandlund equation along with the estimates based on S_v/*TS* scaling.

Shoals were identified from the appearance of echotraces in the echograms, and the the upper and lower range of each shoal was recorded from the downlooking surveys. The length of the acoustic pulse (0.44 m) was subtracted from the lower range. Following the terminology of Pitcher and Parrish (1993), a group of fish that remains together for social reasons is called a shoal. This expression does not imply any specific structure or function of the group. Fish groups swimming in a synchronized and polarized manner are termed schools.

Schooling can be one of the behaviours of fish in shoals, but shoaling does not necessarily imply schooling (Pitcher and Parrish 1993). In this study, no information on the polarity and synchrony of groups of fish were available. Shoaling is therefore used as a description of the observed grouping behaviour.

Results

Reactive distance

The reactive distance relationship to light produced by the planktivore coregonid reactive distance model (Eq. 6) differed somewhat in shape from that of the piscivore salmonids reactive distance model (Eq. 7) (Fig. 2d). But the two models also share a similarity in that they reach a maximum reactive distance at light levels of 20-150 lux.. Coregonids obtain a relatively high reactive distance at light levels below approximately 2 lux, whereas the largest relative change in piscivore reactive distance occurs at approximately 2 -20 lux (Fig. 2d, Link & Edsall 1996; Vogel and Beauchamp 1999; Mazur and Beauchamp 2003). Thus, the planktivores may reach a substantial fraction of their highest reactive distance at light levels below the sharp increase in piscivore reactive distance. This may offer a foraging opportunity at light levels of low predation risk from salmonid piscivores also for the small but dietary important zooplankton *Bosmina longirostris*, *B. longispina*, and *Daphnia cristata* in our study lake (mean lengths in coregonid diet approx. 0.39, 0.55 and 0.70 mm, respectively, as given in Bøhn and Amundsen (1998)) (Fig 2d).

Gillnet catches and fish density

A total of 330 fish were caught in the pelagic gillnets. Of these, 10 SR whitefish and 1 pike was excluded from the further analyses. The remaining 97 % were planktivore coregonids; 28 % vendace and 69 % DR whitefish. DR whitefish dominated the catches in all months. The pelagic coregonid fish community consisted of small individuals with modal lengths of approximately 10 cm for both vendace and DR whitefish (Table 2). For the September night, when the fish were dispersed throughout the water column and young of the years (YOY) were included in the catches, comparison between the acoustically-derived *TS* distribution and the *TS* distributions estimated from catches had a relatively good agreement. The pelagic fish density in September was estimated to 1799 fish ha^{-1} (range 801 to 3197 for the 95 % lower and upper confidence intervals, respectively) by the *Sv*/*TS* scaling method. By the use of catch-derived *TS* estimates with the Lindem-Sandlund equation, the density was estimated to 1520 fish ha^{-1} (range 781 – 2503). The relatively good correspondence between density estimates obtained by the catch-independent method and the catch-dependent method in September, and also between the size distribution in catches and that observed with the echosounder, indicated that our September catches were representative for the pelagic community in this month, with the modification that the smallest fish were somewhat under-represented in the catches. The 20 % lower density estimate based on the catch-derived *TS* may thus be caused by an under-representation of YOY in the catches.

Zooplankton distribution and coregonid diet

The highest daytime zooplankton densities were found close to the surface in all sampling months. Around midnight, the vertical distributions of *Bosmina* and *Daphnia* were relatively even, whereas the depth distribution of both these species was skewed towards the surface during mid-day (Fig. 3). This indicated that there was a tendency towards reversed DVM in these two zooplankton species. The order of importance of the prey categories found in coregonid stomachs was *Bosmina*, chironomid pupae, *Daphnia*, surface insects, *Cyclops scutifer*, *Leptodorea kindti*, and with benthic prey items such as *Chydorus* and chironomid larvae as the least important of included prey items (Fig. 3). The coregonid stomach fullness was least in June, and increased towards September (Fig. 3).

Diel vertical migration and shoaling patterns

There was a consistent pattern of vertical migration, with day vertical fish distributions being deeper than midnight distributions in all months (Fig. 4). However, the difference in the centre of gravity D_{cg} between day and midnight depth distributions in June was only 1.2 m and not significant (Tukey test, P=0.77), as seen with the down-looking surveys (Fig. 4). The extent of the migration increased markedly from June towards August and September, with daytime fish distributions found at greater depths than in June. These differences were also statistically significant (Tukey test, D_{cg}=7.0 m and P<0.001 in August, D_{cg}=3.5 m and P=0.011 in September). By August, day and night distributions had little vertical overlap (Fig. 4). Day and night distributions partially overlapped in September, as most fish stayed deep in the water column during day, whereas fish dispersed and were widely distributed over the depths during night (Fig. 4 and 5). The overall effects of the time of the day (TOD) and season (month) and the interaction between these factors on the centre of gravity of the depth distributions were statistically significant (anova, r^2=0.84, P(TOD)<0.001, P((Month)<0.001, P(TOD x Month)=0.002). The water column was isothermal in June, whereas there was a well developed thermal stratification in August with a thermocline from 14 to 18 m (Fig. 4). By the September survey, surface temperatures had cooled and only a very weak thermocline at about 20 m depth was detected (Fig 4).

Water clarity increased from June to September, and the light therefore penetrated deeper in August and September. The difference between day and night vertical fish distributions were concordant to the depth differences of the light levels between day and night surveys in June, and the fish stayed at similar light levels during both night and day (Fig. 5). The increased depth of the day vertical fish distributions towards August and September was stronger than the increased light penetration (Fig. 4). Part of the coregonid distribution were above the 18 lux level in June. Virtually all of the acoustic energy (i.e. the fish) was returned from depths well below this light level in August and September (Fig. 4). In June, the peak of the density distribution overlapped with the 0.4 lux light level by day (12.2 m) and night (10.9 m). The distribution peaks were below the 0.4 lux light level in August and September (Fig. 4. In all surveys, the majority of the fish population (77-92 % of the echo distribution) was found above the 0.01 lux level, except during September night surveys when the light level was below 0.01 lux throughout the water column (Fig. 4 and 5).

Fish observed in the upper part of the vertical fish distribution were generally shoaling during daylight conditions, i.e. during both night and day in June and during days in August and September, whereas fish dispersed during August and September nights (Fig. 6). This pattern was seen both with the down-looking and side-looking surveys. Although there were relatively large variations in light levels for the uppermost shoals, the variation in the light levels at the deepest part of the deepest shoals was much less and centred around 0.1 lux (Fig. 5b). A sequence of side-looking echograms in August illustrates that after being dispersed at the low light levels around midnight, fish started shoaling before they migrated out of the epipelagic zone by day (Fig. 6).

Discussion

Our findings show that DVM behaviour in coregonids consistently varied with changes in the day-night light cycle. Deeper day-time than night-time distributions of the fish were observed in all months, and the range of the DVM increased with increasing differences in light levels between night and day from June to September. Through large seasonal changes in the light regime, the coregonid depth distribution was consistently observed between light intensities of approx. 0.01 and 20 lux when these light levels were available. This observation is likely to have an ecological significance, although we acknowledge that there may be species- and/or size specific differences within the depth distributions that we were unable to explore with our sampling scheme. Observations made with bottom-mounted up-looking echosoundings in the present sampling year (Gjelland et al. 2004) as well as long time series from the lake (Gjelland et al. 2007) ensures that we can be confident that young of the years (YOY) and both DR whitefish and vendace were present in the pelagic fish community in all three sampling months. The day and night distributions of fish had almost no depth overlap in August, indicating that DVM was performed by all year-classes of vendace and DR whitefish at least in this month. DVM has previously been reported for both species (e.g. Dembinski 1971; Kahilainen et al. 2004; Mehner et al. 2007). The pattern of a more extensive DVM as differences between day and night light levels increased supports the hypothesis that DVM is strongly influenced by the light level (Blaxter 1975). The preference of vendace for light levels above 0.01 lux reported by Dembinski (1971) adequately described the lower boundary for the planktivore coregonid depth distributions in our study. We also observed that shoal formation occurred in the upper parts of the depth distributions during daylight conditions. Changing light regimes was thus an important factor in controlling DVM and shoaling. However, several of the underlying risks and benefits related to these behaviours may be discussed.

The light range between approximately 0.01 lux to 150 lux appears to be of high ecological importance in pelagic communities dominated by planktivore coregonids and piscivore salmonids (Dembinski 1971, Link and Edsall 1996; Vogel and Beauchamp 1999, Fig. 2). Link and Edsall (1996) found that the reactive distance of *C. artedi* to *Limnocalanus macrurus* at the lowest tested light level (2 lux, 5.3 cm) was 63 % of the highest light level (1500 lux, 8.4 cm). According to the reactive distance function presented here, planktivorous coregonids may be able to initiate visual foraging at light levels about 0.007 lux. From this threshold and approximately two orders of magnitude of increasing light, the relative increase in piscivore reactive distance is negligible and the relative change in predation risk thus also small. At light levels above 20 lux the piscivores have reached their maximum reactive distance, and further increases in light intensity also offer little relative increase in the reactive distance of planktivore coregonids. Planktivore reactive distance is also influenced by the zooplankton prey size. Prey item sizes were not measured from the diet samples in the present study, but large zooplankton prey is rare in Skrukkebukta and many other *Coregonus* dominated lakes. Copepods and chironomid pupae may be 1-2 mm long, and *Daphnia cristata* may reach 1 mm length. The dominant coregonid prey in August and September was *Bosmina*. *B. longispina* and *B. longirstris* mean lengths in the coregonid diet has been measured to ca. 0.55 and 0.39 mm, respectively (Bøhn and Amundsen 1998). Even for these small prey items, the planktivore reactive distance is relatively high at the light levels when the sharp increase in piscivore reactive distance occurs. Link and Edsall (1996) showed that the coregonid reactive distance was substantial at 2 lux, the lowest light intensity used in their experiments. We made an extrapolation when we estimated a visual foraging threshold from the model derived from their data, and the precision of the threshold estimate may be difficult to evaluate without controlled experiments. There are, on the other hand, reasons to trust that the model produces reactive distance estimates that are real and reflect coregonid foraging behaviour. The reactive distance function is similar in shape to the reactive distance responses to light level and prey size in other planktivores (Vinyard and Obrien 1976; Confer et al. 1978), the size dependence of the model has a theoretical foundation in the inverse square law, and the model produce a visual foraging threshold that is close to the light levels at the lower end of the distribution of coregonids (Deminski 1971, this study). The fact that planktivore coregonids obviously must be able to feed on small zooplankton at low light intensities (0.01-1 lux), but that they seemed to avoid light levels below 0.01 lux (Deminski 1971, our observations) suggests a preference for a visual foraging mode with a visual threshold around this light level. The good correspondence between the estimated visual foraging threshold and the observed lower boundary of the fish distribution is therefore supporting the validity of the presented coregonid reactive distance model (Fig. 2d).

A positive relationship between reactive distance and foraging efficiency leads to a higher foraging efficiency in illuminated habitats, everything else being equal. Janssen's (1980) experiments showed that planktivorous *Coregonus artedi* is a selective, particulate feeder under illumination, but is also capable of less efficient non-selective gulp-feeding in darkness even at low prey densities. Our results support the hypothesis that increased foraging gain associated with increased light levels leads to a visual foraging mode preference in planktivorous coregonids. The relatively even coregonid distribution throughout the water column in the dark September night could be attributed merely to the lack of environmental cues for shaping the distribution. The observed pattern could however also be expected if planktivores were gulp feeding. In this foraging mode, one would predict highest foraging efficiency in habitats with the highest prey density (Janssen 1980), and foragers distributed according to an ideal free distribution. The night-time zooplankton distribution was relatively even during the period of autumn circulation, possibly resulting in the similarly even fish distribution.

The assumption that predation risk is significant in the planktivore fish community of Skrukkebukta is supported by our estimates of pelagic fish density and previous estimates of brown trout piscivory. Jensen et al. (2006*a*) estimated the annual brown trout consumption to 140 coregonids ha^{-1} at an average density of 0.6 trout ha^{-1}. The population of piscivorous brown trout was estimated to 1.6 times that of the annual brown trout stocking in the watercourse. As approx. 1000 trout of the annual stocking are released into Skrukkebukta, the brown trout predation in Skrukkebukta is likely to be 2-3 times the average of the watercourse. Thus, the brown trout consumption of coregonids in Skrukkebukta was probably in the range of 300 – 400 fish ha^{-1} year^{-1}. This represents about 20 % of the 1800 pelagic fish ha^{-1}

estimated in this study, or between 10 and 50 % taking the 95 % confidence limits into account. Knowing that on top of this comes the visual predation from waterfowls which may also be substantial (Steinmetz et al. 2003), we may conclude that the predation from visual predators in Skrukkebukta is significant. The small lengths of the pelagic coregonids also implies that they are vulnerable to predation throughout their whole life span (Bøhn et al. 2002; Jensen et al. 2004, Jensen et al. 2008). According to the cylinder foraging model (Eggers 1977), the encounter probability with a predator will be linearly related to predator density, whereas encounter probability will be related to predator reactive distance with a power of two. We therefore argue that the relative change in predator reactive distance with depth is much more important than predator depth-specific density for the predation risk of pelagic coregonids. Assuming that brown trout have a similar reactive distance to light relationship as other salmonid predators (e.g. *Salvelinus namaycush, Oncorhynchus clarki, O. mykiss*), brown trout reach maximum reactive distance at light levels above 18 lux (Vogel and Beauchamp 1999; Mazur and Beauchamp 2003). Since a large part of the coregonids in June and virtually all in August and September avoided light levels above 18 lux, we conclude that the coregonids consistently chose to reduce piscivore predation risk. The fact that the majority of the coregonids were found at depths of low piscivore foraging efficiency (i.e. below 0.4 lux) in August and September indicates a strong antipredator behaviour.

Predation risk can induce habitat shifts within size groups vulnerable to predation (Werner et al. 1983). According to the μ/g-rule (Werner and Gilliam 1984), animals with continuous growth up to a minimum reproductive size should choose behaviours that minimize mortality (μ) per unit increase in growth (g). This simple relationship has been extended to other animals in the μ/f-rule (Lima 1998*b*), were f denotes foraging rate (Gilliam and Fraser 1987; Clark and Levy 1988). The μ/f-rule emphasizes the trade-off between foraging and predator avoidance (e.g. Gilliam and Fraser 1987). In this study, zooplankton densities were highest in the upper water column during daytime, and a planktivore that were maximizing foraging gain should therefore have been expected to stay in upper waters instead of migrating to darker waters during daytime. On the other hand, such diel migration could be expected if the planktivores were following the μ/f-rule. The light level at which planktivorous fish can efficiently feed is lower than that of their predators and provides an anti-predation window at light levels sufficient for visual planktivorous foraging but with low predation risk. This combination minimizes the *μ/f*-ratio (Clark and Levy 1988). Observations of juvenile sockeye salmon in Alaskan lakes (Scheuerell and Schindler 2003), coregonids in Lake Superior (Hrabik et al. 2006; Jensen et al. 2006*b*), and coregonids in the present study all support the anti-predation window hypothesis.

Theoretical and empirical work has shown that food deprived or energetically stressed animals take larger predation risks than animals without such energy constraints. According to the asset protection principle (Clark 1994), individuals close to starvation should be more prone to experience high predation risk compared to animals in better condition. The optimal trade-off between foraging and predation risk is thus argued to be state dependent (Lima and Dill 1990; Milinski 1993; Lima 1998*b*), although field evidence is sparse. Damsgård and Dill (1998) showed that coho salmon (*Oncorhynchus kisutch*) in spring increased their risk-taking behaviour with resulting compensatory growth. In spring, after an ice-covered period of nearly 7 months in our study system, the energetic demands are likely high according to the need for compensatory growth. Combined with the low zooplankton abundance and the low stomach fullness of pelagic coregonids observed in June, this may have forced the coregonids to give a priority to food acquisition at the cost of higher predation risk, and resulting in a coregonid distribution at somewhat higher light levels than in later months. Animals should also lower their risk-taking in proportion to their reproductive value (Clark 1994). As reproductive value generally increases with age until first reproduction (Begon et al. 2006) and the reproductive value of maturing fish increases with increasing gonad development, one would expect the risk-taking behaviour to decrease towards autumn for both the immature and the mature coregonids in Skrukkebukta, which are autumn spawners. Both the hunger and age aspects of the asset protection principle are in accordance with the observation that a large part of the coregonid populations stayed at light levels above 0.4 and some even above 18 lux in June, whereas virtually all stayed at lower light levels later in the season. Interestingly, the μ/g principle discussed earlier is a special case of the asset protection principle, assuming a constant environment and a lack of temporal or age effects (Clark 1994).

Brett (1971) proposed with his bioenergetic hypothesis that DVM in planktivorous sockeye salmon depends on the spatial separation between optimal food densities and the optimal thermal habitat of the fish. Fish feeding in a warm, food-rich epilimnion would have higher growth efficiency by descending to colder water for digestion, which will increase their assimilation fraction and reduce their metabolic expenditure. Intuitively, this would result in fish foraging in the surface waters during the day, and then descending to deeper and colder water for digestion during the night when foraging opportunities in the surface waters are poor, i.e. a ‘reversed’ DVM (Stockwell and Johnson 1999). In all surveys, we observed DVM patterns that were opposite to this pattern. Moreover, the distribution patterns of the fish in June and September were very different, although the temperature regimes were similar. We therefore reject the hypothesis that temperature was driving the observed DVM-patterns in our study. A number of other authors have also reported coregonid DVM outside of summer stratification periods (Sydänoja et al. 1995; Jurvelius et al. 2000; Mehner et al. 2007; Jurvelius and Marjomäki 2008).

Given that many zooplankton taxa are capable of performing DVM (Wetzel 2001; Hays 2003), it is possible that DVM in fish reflects tracking of their prey (Janssen and Brandt 1980; Eshenroder and Burnham-Curtis 1999). The day- and night distributions of *Bosmina* and

Daphnia indicated a slight DVM in this two species, but in opposite direction to the migration of the coregonid fish. The observed pattern of coregonid DVM in Skrukkebukta could therefore not be attributed to tracking of prey DVM.

Light periodicity is a major synchronizer of the endogenous circadian clock (Boujard and Leatherland 1992), and it is possible that the observed DVM behaviour by coregonids may be initiated by endogenous rhythms. Mehner *et al.* (2007) suggested that coregonid DVM in Lake Stechlin is a genetically fixed behaviour inherited from adaptations in a different environment (e.g. stronger historical predation rate), rather than a behaviour adopted as to reduce the present-day predation risk. On the basis of our data, we cannot support this hypothesis as we demonstrate that there was an increase in the extent of the DVM through the season, compatible with increasing predator avoidance. Also, the findings of Hrabik et al. (2006) and Jensen et al. (2006*b*) support the hypothesis that ciscoes *Coregonus* spp. in Lake Superior alter their DVM pattern in response to variations in predation risk from lake trout. On the other hand, if the DVM behaviour was a fixed heritable trait, even a low predation rate could act to stabilize this trait, since a mutation in one individual leading to abandoning of DVM behaviour would lead to a large increase in the probability of this individual being among those few eaten by visual predators. As argued above, given that a visually oriented piscivore searches a cross-section as it swims, the predation risk for the prey fish will be proportional to the square of the reactive distance of the piscivore. This emphasizes the important role of light intensity in the predator-prey interaction when vision influences efficiency.

A fish trying to hide from a potential predator in open water has two potential shelters: darkness, or shelter among conspecifics. The former action can lead to vertical migration, while the latter leads to shoaling. In the present study, the deepest shoal extended down to 0.04 lux. This is in accordance with Milne et al. (2005), who found shoal formation in

Coregonus artedi to occur at 0.04 lux. However, most shoals and shoal members were at light levels between 0.1 lux and 100 lux. Shoal formation at higher light levels supports our assumption that the predation risk from piscivorous brown trout significantly increased with light intensity in a similar manner as reported for American piscivore salmonids (Vogel and Beauchamp 1999; Mazur and Beauchamp 2003). No species should be considered an obligate shoaler, as shoaling is argued to be the result of an individuals' instantaneous decision of whether to join, stay, or leave a group (Pitcher and Parrish 1993), and as there may not be a distinct light intensity threshold for shoal formation (Ryer and Olla 1998). Foraging gain, predation risk and information transfer between shoal members are light dependent, and the prerequisites for the join-stay-leave decisions are thus dynamic with changing light conditions as the main trigger. Milne et al. (2005) found that *Coregonus artedi* increased the foraging gain during daylight condition, and also suggested that shoaling enhanced foraging gain. The observations of i) shoaling during upward migration (Knudsen and Gjelland 2004) and shoal formation preceding the downward migration; ii) shoal formation in the upper parts of the coregonid distribution; and iii) that coregonids generally avoided light levels corresponding to maximum predator efficiency, indicate that these coregonids try to extend their foraging periods in the surface waters, but are ultimately better off in somewhat darker parts of the water column due to a classical foraging gain to predation-risk trade-off.

In conclusion, the behavioural responses of the two coregonid species to the large changes in light conditions found at 69° N provided evidence for a strong link between the observed DVM and the diel patterns in light regime. The planktivore coregonids avoided light levels below the light threshold for visual foraging inferred from foraging experiments in other coregonids, suggesting a preference for a visual foraging mode. The planktivores also avoided light levels associated with high piscivore reactive distance, suggesting that the planktivore vertical distribution was influenced by piscivore predator efficiency. The observed DVM patterns are consistent with the antipredation window hypothesis both under conditions with continuous daylight and for conditions with alternating daylight-darkness. There was also a change in relative risk-taking behaviour from early to late summer, in accordance with state-dependence theory. Alternative hypotheses were found inferior as explanations accounting for the changing DVM-pattern during the investigated time period.

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Table 1. Secchi-depth Z_{Sd} (m, measured during mid-day), vertical extinction coefficient k (m^{-1}), and the estimated depths Z for the light levels 50, 18, 0.4 and 0.01 lux in the different surveys. Confer the text for estimation details. "--" means that all light levels were below the given level.

Survey	Z_{Sd}	k	$Z_{50 \text{ lux}}$	$Z_{18 \text{ lux}}$	$Z_{0.4 \text{ lux}}$	$Z_{0.01 \text{ lux}}$
June day	2.8	0.96	7.1	8.2	12.2	16.0
June night			5.9	7.0	10.9	14.8
August day	4.5	0.74	7.3	8.7	13.8	18.8
August night			--	--	3.8	8.8
September day	4.6	0.72	8.6	10.0	15.3	20.4
September night			--	--	--	--

Table 2. Summary description of the vendace and DR whitfish catches, with number of caught fish, minimum, median and maximum fork length (cm) and age (winters), and the percentage of mature fish.

		Length			Age			
	n	Min.	Median	Max.	Min.	Median	Max.	% mature
DR whitefish	225	7.1	10.2	29.0	0	3	10	29
Vendace	93	7.8	10.4	14.4	1	1	4	87

Figure captions

Fig. 1. (a) Bathymetric map of Lake Skrukkebukta with the five echosounder transects indicated by the thick white lines, and gillnetting/zooplankton sampling sites indicated by triangles. The colour of the depth polygons shifts for every 5 m depth. The geographical location of L. Skrukkebukta in Northern Europe is also indicated. (b) Illustration of the side-looking (horizontally directed beam) and down-looking (vertically directed beam) acoustic applications.

Fig. 2. (a) The relationship between prey size divided by reactive distance squared was constant over all prey sizes in the data of Link (1998), indicating that the inverse square law may apply. (b) Relationship between coregonid reactive distance (D_C) according to Eq. 2, triangles are the data points from Link and Edsall (1996). (c) D_C as a function of zooplankton size (Eq. 5), circles are the data points from Link (1998). (d) D_C in relation to light (Eq. 6) for various zooplankton sizes (solid=0.70 mm *Daphnia*, dash-dots=0.55 mm *Bosmina longispina*, dotted line=0.39 mm *B. longirostris*) compared to the reactive distance D_T (Eq. 7) of a piscivore salmonid (broken line, scale on the right side), adapted from the lake trout model of Vogel and Beauchamp (1999).

Fig. 3. (a-c) Catch per unit of effort (CPUE) of DR whitefish (light grey) and vendace (dark grey) in the gillnets from 0 to 12 m at the three sampling occations. (d-f) Bars indicate day-time depth distributions (± 1 SD) of *Bosmina* (*B*) and *Daphnia* (*D*) at the three sampling occations. o (± 1 SD, thick symbols) indicates the respective night-time depth distributions. Pies indicate the relative contribution of prey items in the coregonid diet; *B*=*Bosmina*, *D*=*Daphnia*, z=other zooplankton (predominantly *Cyclops* and *Leptodora*), p=chironomid

pupae, s=surface insects, t=benthic prey. Mean stomach fullness (SF) is given above the pies, with the number of analyzed stomachs in parenthesis.

Fig. 4. Vertical distribution of integrated echo energy s_A (lower x-axis) during day and night (solid lines), the weighted average over the five transects with down-looking echosounding shown in Fig. 1. Analyses were done in 2 m depth intervals for 4-24 m depth. Dotted lines show 95 % confidence intervals. Note the different x-scale between June and the other two months. Dash-dot lines show temperature profiles, scale on the upper x-axis.

Fig. 5. (a) Cumulative presentation of the distributions of average echo energy s_A from Fig. 4, here plotted against light level. — = day distributions, ···· = night distributions, o = June, Δ = August, □ = September. (b) Cumulative presentation of shoals seen in down-looking surveys, represented by their deepest end plotted against the light level at the relevant depth. The number of symbols in (b) equals the number of shoals.

Fig. 6. The sequence of echograms show examples of night (left) and day (right) recordings with side-looking acoustics in June (upper), August (middle), and September (lower). The echograms show acoustic registrations from 0 to 50 m range aside of the survey boat, for a distance of about 100 m. The side-looking acoustics sampled the upper 4 m of the water column. In August, additional recordings were made at daybreak (middle echogram)

Fig. 1

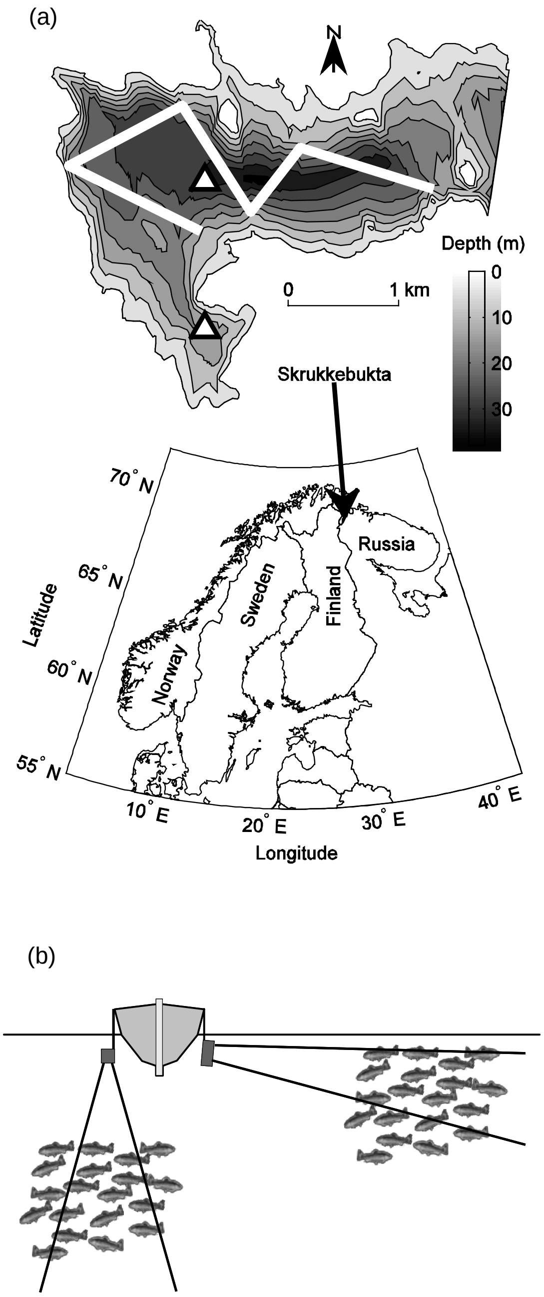

(a)
N
Depth (m)
0
10
20
30
0
1 km
Skrukkebukta
70° N
65° N
60° N
55° N
Latitude
Norway
Sweden
Finland
Russia
10° E
20° E
30° E
40° E
Longitude
(b)

Fig. 2.

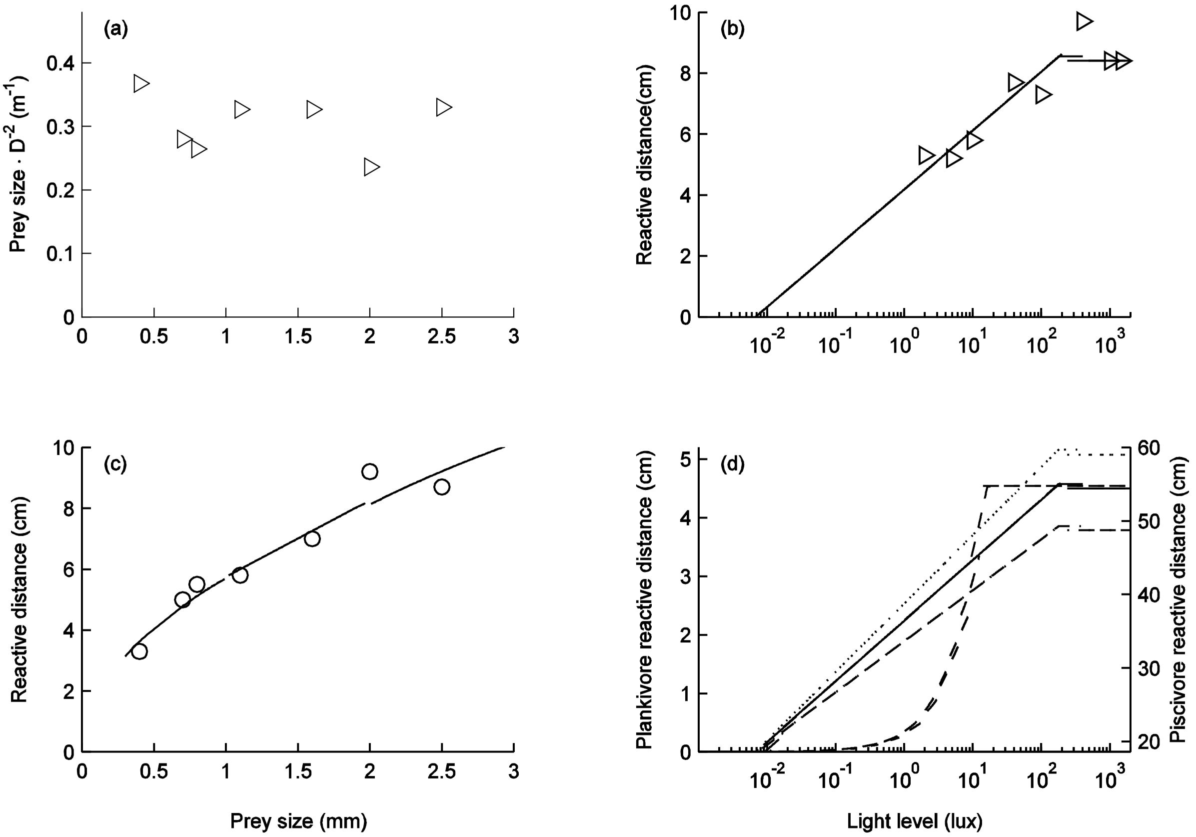

(a)
Prey size · D^{-2} (m^{-1})
0
0.1
0.2
0.3
0.4
0
0.5
1
1.5
2
2.5
3
(b)
Reactive distance(cm)
0
2
4
6
8
10
10^{-2}
10^{-1}
10^{0}
10^{1}
10^{2}
10^{3}
(c)
Reactive distance (cm)
0
2
4
6
8
10
0
0.5
1
1.5
2
2.5
3
Prey size (mm)
(d)
Plankivore reactive distance (cm)
0
1
2
3
4
5
Piscivore reactive distance (cm)
20
30
40
50
60
10^{-2}
10^{-1}
10^{0}
10^{1}
10^{2}
10^{3}
Light level (lux)

Fig. 3

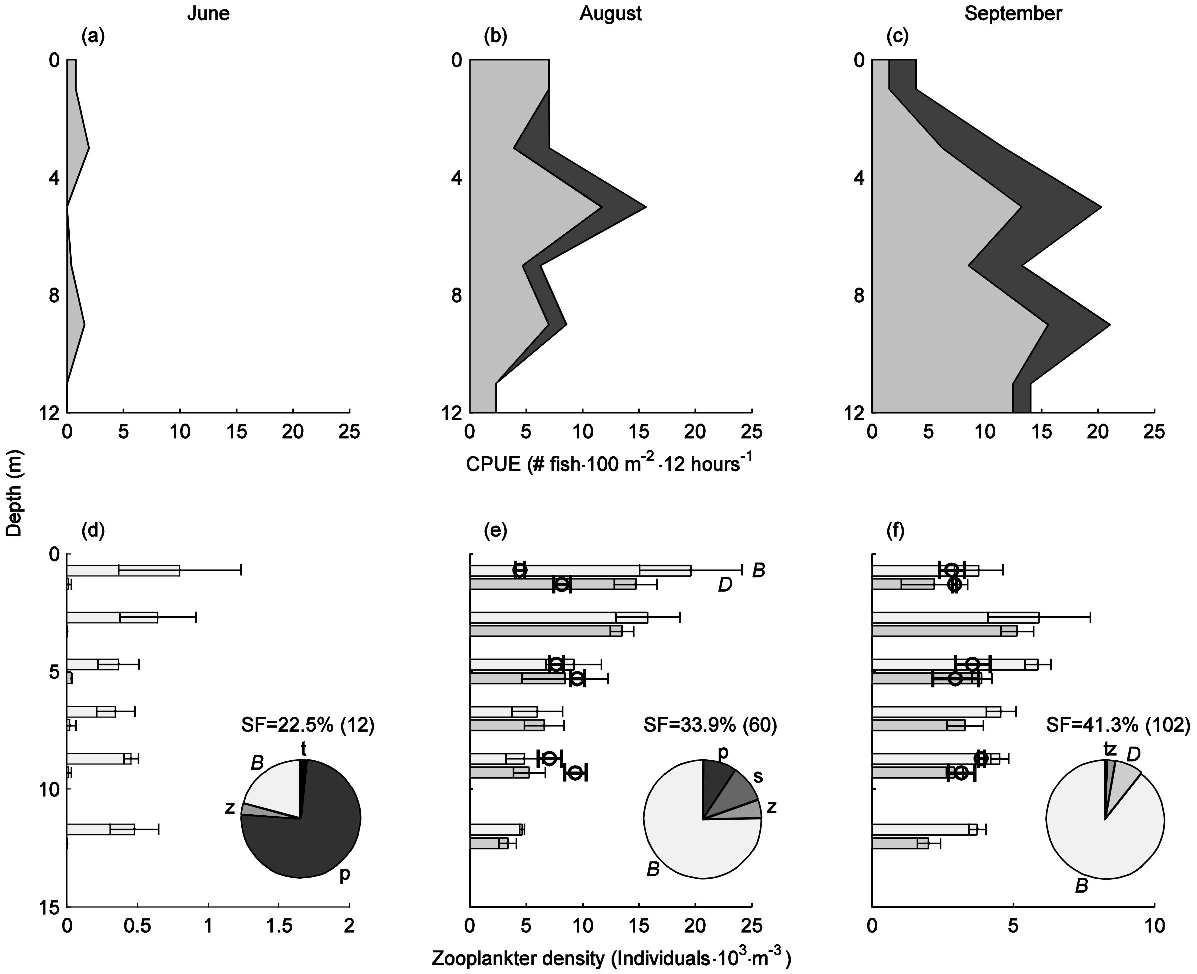

June
August
September
(a)
(b)
(c)
0
4
8
12
0 5 10 15 20 25
CPUE (# fish·100 m-2·12 hours-1
Depth (m)
(d)
(e)
(f)
0
5
10
15
0 0.5 1 1.5 2
0 5 10 15 20 25
0 5 10
B
D
SF=22.5% (12)
B
t
z
p
SF=33.9% (60)
p
s
z
B
SF=41.3% (102)
t z
D
B
Zooplankter density (Individuals·10³·m-3)

Fig. 4.

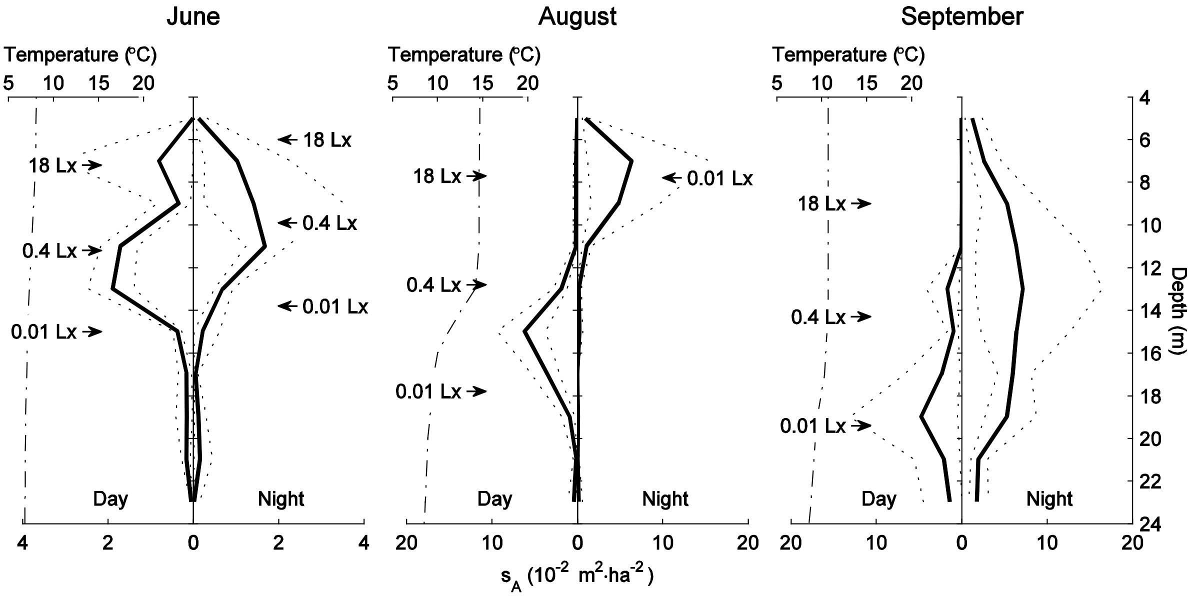

June
August
September
Temperature (°C)
5 10 15 20
18 Lx
0.4 Lx
0.01 Lx
Day
Night
Depth (m)
4 6 8 10 12 14 16 18 20 22 24
4 2 0 2 4
20 10 0 10 20
s_A (10^{-2} $m^2 \cdot ha^{-2}$)

Fig. 5

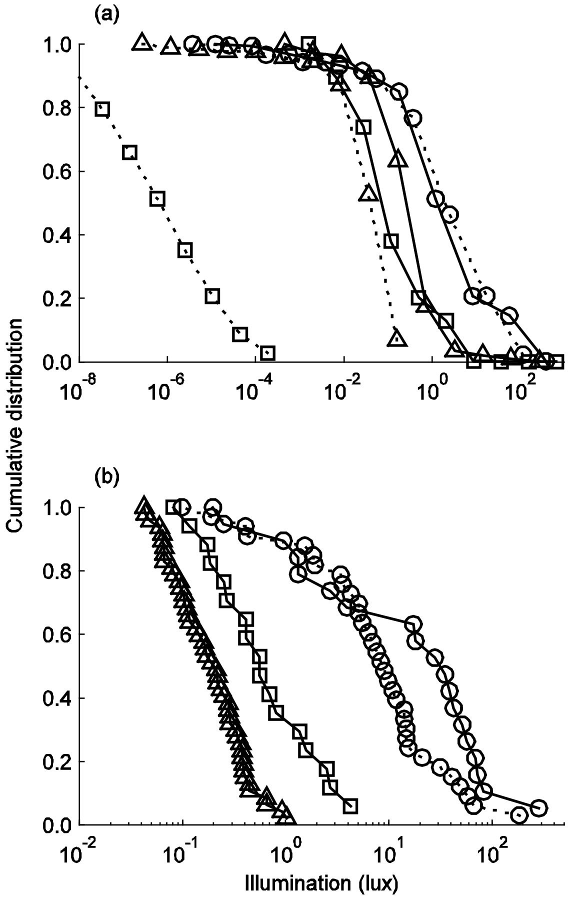
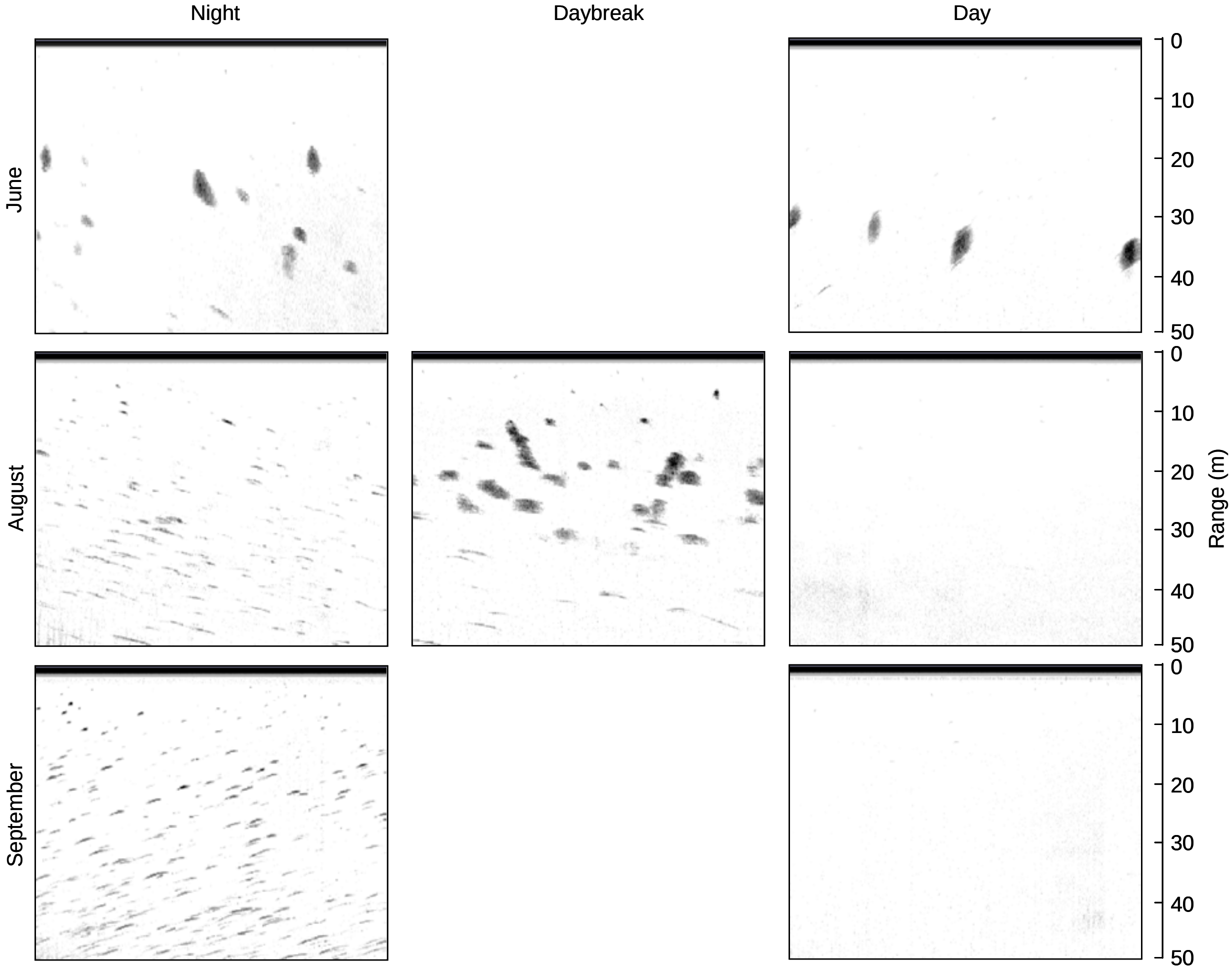

(a)
(b)
Cumulative distribution
Illumination (lux)
1.0
0.8
0.6
0.4
0.2
0.0
10^{-8}
10^{-6}
10^{-4}
10^{-2}
10^{0}
10^{2}
10^{-2}
10^{-1}
10^{0}
10^{1}
10^{2}

Fig. 6.


Night
Daybreak
Day
June
August
September
Range (m)
0
10
20
30
40
50