Foraging, bioenergetic and predation constraints on diel vertical migration: field observations and modelling of reverse migration by young-of-the-year herring *Clupea harengus*

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Diel vertical migration (DVM) of young-of-the-year (YOY) herring *Clupea harengus* and one of their major predators, pikeperch *Sander lucioperca*, was examined using bottom-mounted hydroacoustics in Himmerfjärden, a brackish bay of the Baltic Sea, in summer. In contrast to previous studies on DVM of *C. harengus* aggregated across size and age classes, YOY *C. harengus* showed a reverse DVM trajectory, deeper at night and, on average, shallower during the day. This pattern was observed consistently on five acoustic sampling occasions in 3 years and was corroborated by two out of three trawl surveys. Large acoustic targets (target strength >-33 dB, probably piscivorous *S. lucioperca* >45 cm) showed a classic DVM trajectory, shallow at night and deeper during the day. Variability in YOY *C. harengus* vertical distribution peaked at dawn and dusk, and their vertical distribution at midday was distinctly bimodal. This reverse DVM pattern was consistent with bioenergetic model predictions for YOY *C. harengus* which have rapid gut evacuation rates and do not feed at night. Reverse DVM also resulted in low spatial overlap with predators.
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Key words: bioenergetics; optimal foraging theory; predation; risk-sensitive foraging.

INTRODUCTION

Many animals face strong selective pressure towards behaviours that maximize growth rate and minimize predation risk. Behavioural decisions frequently involve trade-offs when these two goals conflict (Werner & Gilliam, 1984). For pelagic fishes, diel vertical migration (DVM) is one behavioural method of balancing risk and growth (Clark & Levy, 1988). Predation risk, diet and energetic demands of individual fish are all strongly size-dependent (Byström *et al.*, 2006), suggesting that

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DVM behaviour should also vary with the size of an individual. Yet most studies of DVM in fishes (Hrabik *et al.*, 2006) have examined the behaviour of aggregated size classes, thus averaging over potentially important differences. A narrower focus on the behaviour of a single age class, young-of-the-year (YOY) of herring *Clupea harengus* L. reveals a different DVM pattern than that which has previously been described for this species.

It has long been observed that many pelagic fishes and their zooplankton prey undergo a classic DVM, characterized by a dusk ascent towards the surface and a dawn descent into darker conditions below the photic zone (Hutchinson, 1957). For planktivorous fishes, this pattern is consistent with tracking their zooplankton prey (Eshenroder & Burnham-Curtis, 1999) while avoiding the higher predation risk associated with high light intensity (Eggers, 1978). Under thermally stratified conditions, there is also a need to balance bioenergetic demands. Even in the absence of vertical differences in foraging opportunities, there may be a growth rate advantage to vertical migration if it allows an organism to spend time in more energetically favourable habitat where growth rates are higher for a given ration (Brett, 1971; Sims *et al.*, 2006). Where the vertical distribution of foraging opportunities is known and a bioenergetic model is available, it is possible to quantify the growth rate potential (GRP) associated with occupying different depths and temperatures at different times of day (Brandt *et al.*, 1992; Bevelhimer & Adams, 1993). Predation risk and the ratio of risk to GRP can also be calculated from light intensity at depth and from an empirical function relating light intensity to a predator's reaction distance (Mason & Patrick, 1993; Jensen *et al.*, 2006).

There have been numerous studies of the DVM patterns of *C. harengus*, with most reporting a classic DVM pattern for adult *C. harengus* or aggregated size and age classes of *C. harengus*. Some of the earliest hydroacoustic studies of fishes documented a classic DVM pattern for adult *C. harengus* off Norway (Runnstrom, 1941) and in the North Sea (Blaxter & Parrish, 1965) in the summer months. A similar classic DVM pattern was observed for *C. harengus* off Norway in winter (Huse & Korneliussen, 2000). From the Baltic Sea, Cardinale *et al.* (2003), Nilsson *et al.* (2003) and Orlowski (2005) all reported classic DVM for *C. harengus* and sprat *Sprattus sprattus* (L.). Larval *C. harengus* are weak swimmers and their vertical distribution is strongly influenced by turbulence (Heath *et al.*, 1988). Under calm conditions, however, they have been observed moving towards the surface (Munk *et al.*, 1989) or the bottom (Stephenson & Power, 1988) at dawn and dusk in a semidiel vertical migration. One of the few reports of a reverse DVM for a non-larval clupeid is for sardine *Sardina pilchardus* (Walbaum) schools off Portugal (Zwolinski *et al.*, 2007).

Reverse DVM has commonly been observed for zooplankton attempting to escape invertebrate predators (Ohman *et al.*, 1983), but reports of reverse DVM by fishes are relatively rare in scientific literature. Exceptions include basking shark *Cetorhinus maximus* (Gunnerus) feeding on reverse migrating zooplankton (Sims *et al.*, 2005) and young fishes of several species in San Francisco Estuary undergoing reverse DVM to facilitate horizontal tidal transport and retention (Bennett *et al.*, 2002). Stockwell & Johnson (1999) found three age classes of kokanee (land-locked sockeye) salmon *Oncorhyncus nerka* (Walbaum) switched from normal DVM in June to reverse DVM in August, suggesting that the relative importance of factors driving DVM may change seasonally.

Adult *C. harengus* are capable of filter feeding at night (Batty *et al.*, 1990); however, *in situ* observations of YOY *C. harengus* (Arrhenius & Hansson, 1994, 1999) indicate little or no nocturnal foraging by this age class. Swimming speed of YOY *C. harengus* also declines at night (Didrikas & Hansson, 2009). Furthermore, a bioenergetic model with no nocturnal feeding and a lower night-time activity multiplier provides a better fit to growth data for YOY *C. harengus* than do models which assume 24 h feeding (Van Tassell, 2002). If they are not actively foraging at night, then the traditional explanation for *C. harengus* DVM, that they track the distribution of their vertically migrating prey, cannot be valid for YOY *C. harengus*.

Empirical patterns of YOY *C. harengus* DVM in a brackish bay of the Baltic Sea were investigated using a seabed-mounted acoustic transducer during five discrete summer sampling occasions in 3 years (2001, 2002 and 2004). Foraging and bioenergetic models were developed from field data and used to test alternative explanations for the observed DVM patterns. The potential role of predation risk by piscivorous pikeperch *Sander lucioperca* (L.) was evaluated through mapping of their DVM trajectories and the diel vertical distribution of their optimum light levels for feeding. The objectives were to: (1) describe the DVM pattern of YOY *C. harengus* and (2) evaluate this observed pattern relative to the foraging and growth rate benefits of alternative DVM trajectories and potential diel vertical patterns in predation risk.

MATERIALS AND METHODS

STUDY SITE

Data were collected in a coastal bay (Himmerfjärden; Fig. 1) of the north-western Baltic Sea Proper. This bay has been the site of numerous studies including research focused on nutrients (Tett *et al.*, 2003), food web analyses (Rudstam *et al.*, 1992; Hansson *et al.*, 1997a) and fisheries management (Hansson *et al.*, 1997b). The salinity in the bay is *c*. 6 at the surface and *c*. 0·5 higher at the bottom. These salinities are 0·5−1·0 lower than in offshore areas at this latitude of the Baltic Sea.

Zooplanktivorous fishes in the area are dominated by clupeids, primarily *C. harengus* but also *S. sprattus*. Abundances of pelagic fishes, derived from hydroacoustic surveys, show a 20-fold increase from mid-summer to August, a result of the reproduction of spring spawning *C. harengus* (Axenrot & Hansson, 2004). In addition to the clupeids, other species also occur in pelagic waters, *e.g.* smelt *Osmerus eperlanus* (L.) and sand goby *Pomatoschistus minutus* (Pallas), but in much lower abundance (Didrikas & Hansson, 2009). There are two species of pelagic piscivores in the area: *S. lucioperca* and brown trout *Salmo trutta* L. The population of *S. trutta* is relatively small and derives from reproduction in local streams. *Sander lucioperca* is the most abundant piscivore and has produced annual landings of 10 000−20 000 kg (Hansson *et al.*, 1997b). *Sander lucioperca* >15 cm total length (L_T) feed primarily on clupeids (Hansson *et al.*, 1997c). Cod *Gadus morhua* L. is the primary piscivorous fish in the open Baltic Sea, but it is uncommon in archipelagos and none were caught during this study.

Fish community composition has been studied with gillnet and trawl surveys many times since 1983, and provided the species composition picture described above. For example, in 2001, 25 m deep vertical gillnets were used to sample the entire water column, from bottom to surface (4, 6·25, 8, 10, 12, 15 and 18·75 mm bar mesh; Hansson, 1988). Pelagic trawling has been conducted on several occasions during the period 2002−2004, and catches were consistent with the fish assemblage composition described previously (Axenrot & Hansson, 2004; Didrikas & Hansson, 2009).
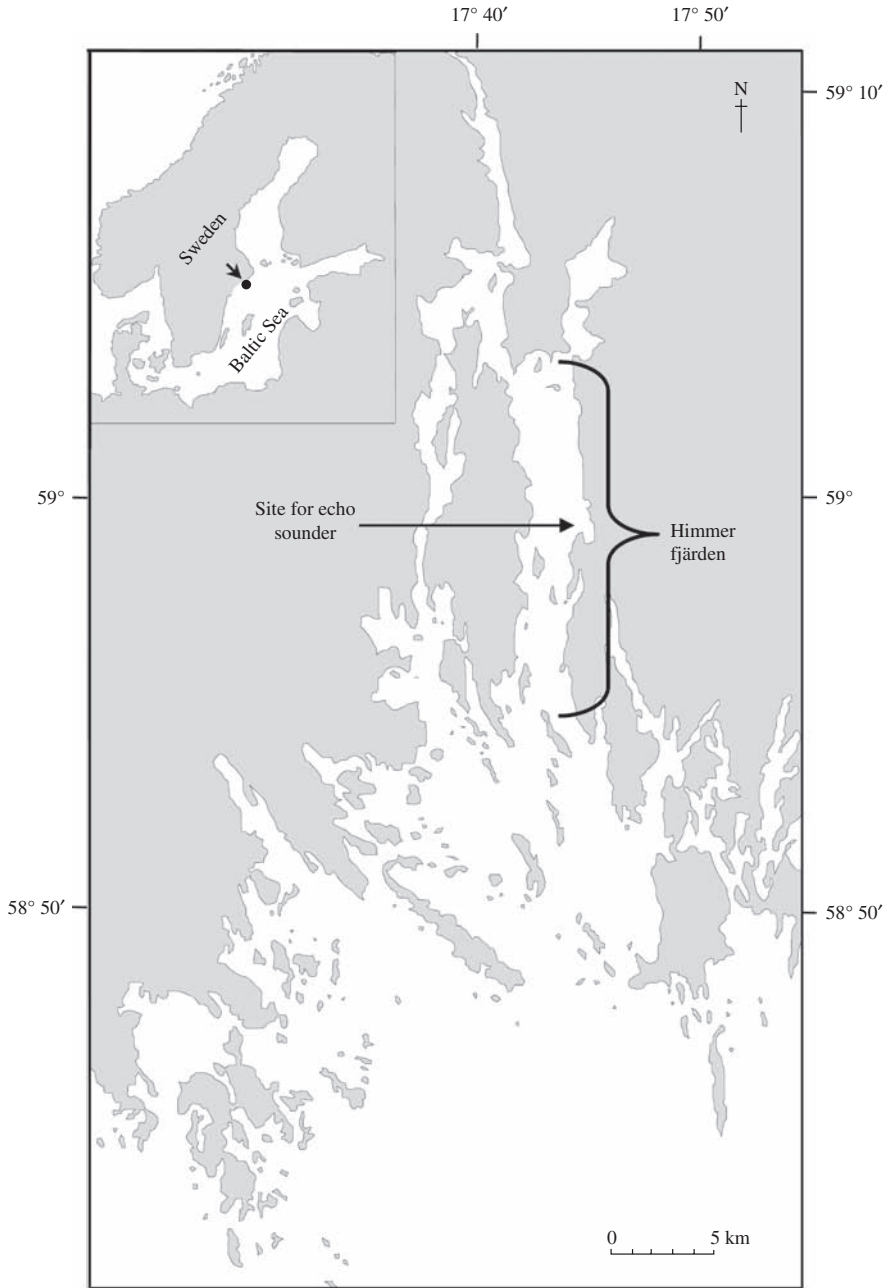
FIG. 1. The study site in Himmerfjärden, northern Baltic Sea proper.

HYDROACOUSTIC AND PHYSICAL SAMPLING

Fish densities and size distributions in 1 m layers were derived from a 70 kHz upward-facing hydroacoustic split-beam transducer (Simrad ES 70–11, Konsberg Maritime AS; www.simrad.com) mounted on a rack (Axenrot *et al.*, 2004) that was placed on the seabed at

a depth of *c*. 20 m. The transducer was connected, through a 100 m long cable, to the echo sounder (Simrad EY500), which was placed on the shore. The system was calibrated using a standard copper sphere provided by the echo sounder manufacturer and acoustic data were analysed with the Sonar5-Pro software (version 5.9.5; Balk & Lindem, 2002). Size distributions of fishes were derived from echoes from single fish, with minimum target strength set to −60 dB. Echoes were classified as coming from single fish if the length of an echo was in the range of 0·8–1·3 pulse length (pulse length 0·6 ms), maximum gain compensation of 3·0 dB and a maximum phase angle s.D. of 0·6. To further reduce the risk of misclassifying echoes from multiple fishes as derived from a single fish, multiple peak suppression was activated (medium). Hydroacoustic sampling was conducted on five separate occasions during three summers: 1–2 August and 16–17 August 2001; 29–31 July and 5–7 August 2002; 2–5 August 2004.

The rack on which the transducer was mounted was *c*. 1 m high with a near field of 1 m immediately in front of the transducer; thus there was an acoustic blind zone from the bottom to 2 m above the bottom. There was also a blind zone from the sea surface to 2 m depth, as many acoustic targets in this region are likely to be air bubbles produced by waves. Therefore, from the 20 m deep water column, acoustic recordings were taken from the depth interval 2–18 m.

Acoustic targets were divided into small fishes and large fishes [acoustic target strength (TS) for single fish −60 to −51 dB and >−33 dB, respectively], representing potential prey and predators. Clupeids dominate in the area and because the studies were conducted late in the summer, after the recruitment of YOY *C. harengus* to the pelagic fish assemblage (Axenrot & Hansson, 2004), the small fishes can be assumed to be primarily YOY *C. harengus* and are referred to as such. The target strength −60 to −51 dB corresponds to an L_T of 3·4–7·7 cm [$TS = 25·5 \log_{10} (L_T, \text{cm}) −73·6$, according to Didrikas & Hansson, 2004]. Fishes with a TS of >−33 dB are large and, based on the species composition of large fishes from physical sampling described above, most of these are *S. lucioperca* and are referred to as such. Assuming that *S. lucioperca* follows Love's (1977) standard equation for TS, −33 dB corresponds to L_T 45 cm at an acoustic frequency of 70 kHz [$TS = 19·4 \log_{10} (L_T, \text{cm}) −65·4$; Rudstam *et al.*, 2002].

Fish densities can vary greatly and occasional aggregations may have an overwhelming influence on arithmetic mean values. Therefore, the following procedure was followed for large and small fishes separately: (1) Densities were estimated for 1 m deep by 1 h long increments. (2) Total numbers were obtained by summing the 2–18 m depth range and the proportion of the total found in each 1 m layer was calculated. The average depth of the fish and the s.D. in vertical distribution were estimated. (3) When there was more than one observation for a time period (*e.g.* three observations from the period 0800–0900 hours during 2–5 August 2004 sampling period), measures of mean and s.D. in depth were derived as grand means of the average and s.D. calculated from the separate periods [step (2) above].

Physical samples from vertically stratified trawl surveys conducted at night were used to corroborate the hydroacoustic measurements. These surveys were conducted using a pelagic trawl (5 mm codend) with a 5 m vertical opening at three constant depths such that samples were obtained from three discrete 5 m depth intervals (Axenrot & Hansson, 2004). Tows lasted for *c*. 30 min at a speed of 2·5 knots (463 km h^{-1}). Surveys were conducted in Himmerfjärden on 26 August 2002, 27 August 2003 and 23 August 2004. All fishes caught were identified to species and measured (L_T) to the nearest mm. Catch per unit of effort (CPUE) was calculated by dividing the number of individuals caught by the duration of the tow.

Ambient light intensity was measured at the sea surface and at a water depth of 5 m. Surface light was measured using two different sensors, one for high and one for low light intensities (SKL 310/I for $10–146 \times 10^3$ lx and SKL 2630L/I for 10^{-4} to 10 lx, both from Skye Instruments Ltd; www.skyeinstruments.com). Underwater light was measured using a watertight sensor ($0·05–83 \times 10^3$ lx; SUD 033, International Light Technologies Inc.; www.intl-lighttech.com). Light intensity (L) at depth (x) was calculated using the Beer–Lambert equation (Hutchinson, 1957): $L_x = L_0 e^{-kx}$, where the extinction coefficient (k, m^{-1}) was calculated from light measurements at the surface and at 5 m depth: $k = −[\ln(L_5 L_0^{-1})] 5^{-1}$. The average *k* calculated in this manner was 0·66 m^{-1}. Water temperature and salinity vertical

TABLE I. Biological and physical variables used in the foraging and growth rate potential models. Additional bioenergetic variables can be found in Van Tassel (2002)

Variable	Value	Unit	Source
Biological variables			
YOY *Clupea harengus* mass	1	g	Assumption based on size of YOY *C. harengus* in July to August
YOY *C. harengus* swimming speed (v_j)	0·06–0·38	m s^{-1}	Didrikas & Hansson (2009)
Zooplankton length	1	mm	Assumption based on zooplankton found in YOY *C. harengus* diets
Zooplankton individual wet mass	0·015	mg	Hansson *et al.* (1990)
Zooplankton swimming speed (v_i)	1	mm s^{-1}	Assumption
Zooplankton areal density	600 000	n, m^{-2}	Hansson *et al.* (1990)
Physical variables			
Extinction coefficient (k)	0·66	m^{-1}	Calculated from light metres at the surface and at 5 m depth
Temperature (T)	9·6–19·7	°C	Measured
Light level at surface (I_0)	$0·008-6·5 \times 10^4$	lx	Measured
Bioenergetic variables			
YOY *C. harengus* energy density	3888	J g^{-1} wet mass	Arrhenius & Hansson (1996)
Zooplankton energy density	2813	J g^{-1} wet mass	Walve & Larsson (1999)

YOY, young-of-the-year; n, number of individuals.

profiles were measured at the study site with a conductivity–temperature–depth (CTD) probe (Sensordata AS; www.sensordata.no) once during each hydroacoustic survey.

FORAGING AND BIOENERGETIC MODELS

Time-specific and depth-specific estimates of foraging and growth rate potential were calculated to evaluate alternative hypotheses regarding the drivers of the observed DVM pattern of YOY *C. harengus*. The model framework and calculations are described by Jensen *et al.* (2006). Here, only a brief overview and the relevant variables for this application are provided (Table I).

Foraging rate potential (FRP) and growth rate potential (GRP) were calculated for 20 depth bins (1 m intervals) and 72 time bins (20 min intervals), representing a full 24 h cycle over the 20 m depth of the study site. FRP represents the number of encounters with prey predicted for a standard-size (1 g) YOY *C. harengus* within each depth–time bin. It is used here as a tool for comparing the relative foraging benefits found at different depths at different times of the day and is not meant to be an absolute estimate of consumption. FRP (F) is calculated for each depth–time bin from Gerritsen & Strickler's (1977) encounter rate model:

$$F = (\pi R^2 3^{-1})(3v_j^2 + v_i^2)d_i v_j^{-1} \tag{1}$$

Equation (1) provides depth-specific and time-specific estimates of prey (i, zooplankton) density (d_i), predator (j, YOY *C. harengus*) and prey swimming speeds (v_j and v_i, respectively) and predator reaction distance (R).

The prey field was based on published estimates of the night and day vertical distribution of zooplankton in Himmerfjärden during summer months (Hansson *et al.*, 1990). Prey densities were restricted to cladocerans and those copepod genera (*Temora*, *Eurytemora* and *Acartia*) which combined to constitute >90% of the diets of YOY *C. harengus* (Hansson *et al.*, 1990). Hansson *et al.* (1990) sampled zooplankton over three 10 m intervals at a station of 30 m depth. To apply these data to a 20 m station, the 0 to 10 m densities observed by Hansson *et al.* (1990) were used for the 1 to 10 m interval in the prey field, the 10 to 20 m densities for the 10 to 15 m prey field and the 20 to 30 m densities for the 15 to 20 m prey field. Daytime zooplankton density in the Baltic in the summer increases in an approximately linear fashion from the surface to the thermocline (located at 9 to 10 m during the present field studies) (E. Gorokhova, unpubl. obs.). Therefore, a linear trend was applied to zooplankton densities such that density increased from 0 individuals per m^2 at the surface to *c.* 44 000 individuals per m^2 in the 9 to 10 m bin. Thus, the average densities observed by Hansson *et al.* (1990) in the 0 to 10 m depth interval were preserved, while accounting for the observation that daytime zooplankton density increases with depth from the surface to the thermocline.

As reaction distance studies on YOY *C. harengus* are lacking, data from experiments on another pelagic planktivore, cisco *Coregonus artedi* LeSueur (Link & Edsall, 1996), were used. The predator (*C. artedi*, 205–240 mm L_T) and prey (*Limnocalanus macrurus*, 2·5 mm average length) used by Link & Edsall (1996) were larger than the average L_T of a YOY *C. harengus* in July to August (Arrhenius & Hannsson, 1996) and their zooplankton prey. The values of R reported by Link & Edsall (1996) were divided in half to approximate the reduced R for a smaller predator feeding on smaller prey before fitting a saturating function to their R and light intensity data: $R_{x,t} = 2·98 + 0·16 \ln(L_{x,t})$, where x and t are depth and time indices, respectively. The intercept (minimum R) was assumed to be zero as YOY *C. harengus* do not actively feed at night (Arrhenius & Hansson, 1994). This coarse estimate of the R function for YOY *C. harengus* is appropriate in this application because the goal is to compare relative FRP rather than absolute FRP by depth and time. It is therefore, the general shape of the R function that is more important than the absolute values.

Encounter rate and FRP are only equivalent if all encounters lead to ingestion. The probability of ingestion given an encounter event (or equivalently, the fraction of encountered prey that are ingested) was estimated by adjusting this probability until consumption by an individual YOY *C. harengus* following the average DVM trajectory matched daily consumption rate derived for YOY *C. harengus* in Himmerfjärden based on the growth rates given in Arrhenius & Hansson (1996) and the bioenergetics model of Van Tassell (2002). Using this method, the per cent of encountered prey that are ingested was estimated to be 0·25.

The FRP equation (1) also requires estimates of predator and prey swimming speeds. A swimming speed of one body length per second was assumed for a 1 mm zooplankton prey. For YOY *C. harengus*, an empirical relationship (Didrikas & Hansson, 2009) relating swimming speed to TS (*i.e.* body size; S in equation 2), *in situ* light intensity and *in situ* temperature was used:

$$\log_{10}(v_{x,t}) = -0·239 + 0·017(S) + 0·044 \log_{10}(L_{x,t}) + 0·028 T_x \qquad (2)$$

A bioenergetic model for YOY *C. harengus* (Van Tassell, 2002) was used to translate temperature and FRP by depth and time into relative GRP. This bioenergetic model is based on the Wisconsin model framework (Kitchell *et al.*, 1977), and it is similar to the approach used by Jensen *et al.* (2006). The major difference is that the YOY *C. harengus* bioenergetic model assumes no night-time feeding and reduced night-time activity costs.

PREDATION RISK

No published studies of reaction distance as a function of light could be found for *S. lucioperca* or the congeneric walleye *Sander vitreus* (Mitchill). The eyes of *S. lucioperca*

and *S. vitreus* contain a reflective layer, tapetum lucidum, that improves vision under low light conditions (Ali *et al.*, 1977). Because of *S. lucioperca*'s specialized vision, it would be inappropriate to use reaction distance variables from other species.

Two different approaches were used to describe the depth-time distribution of predation risk for YOY *C. harengus*. The first approach was to map the observed depth–time distribution of *S. lucioperca* as a proxy for predation risk. As discussed by Jensen *et al.* (2006), this approach is appropriate for understanding the distribution of risk for an individual prey, but it implicitly assumes that predators have limited ability to track prey into other depth–time strata; *i.e.*, a depth and time with no observed predators is (perhaps incorrectly) seen as low risk. As an alternative, those depth and time cells thought to have optimal light intensities for foraging *S. lucioperca* were delineated. This zone of optimal light intensity (8–68 lx) is based on an analysis of laboratory and field experiments of *S. vitreus* light preferences (Lester *et al.*, 2004).

RESULTS

On all five sampling occasions, YOY *C. harengus* showed a clear inverse DVM (Fig. 2). YOY *C. harengus* moved from an average depth of 16–18 m at night to 10–12 m at mid-day. The average depth of YOY *C. harengus* generally remained below the thermocline, which ranged in depth from *c*. 8 to 10 m (Fig. 2). Variability in the depth distribution of YOY *C. harengus* typically peaked near dawn and dusk (Fig. 2); however, this pattern was less consistent than the DVM.

Summarizing the acoustic data into depth-time bins revealed distinctly different DVM patterns for YOY *C. harengus* and adult *S. lucioperca* (Fig. 3). YOY *C. harengus* again show clear evidence of an inverse DVM [Fig. 3(a)]. During the day, however, the depth distribution of YOY *C. harengus* appeared bimodal, with high densities in the 4 to 8 m depth range and from 14 m to the bottom. *Sander lucioperca* showed a classic DVM pattern, moving from depths of <5 m at night to the 14 to 17 m range during the day [Fig. 3(b)]. Here too, however, there was strong evidence of bimodality during the day, with high densities of *S. lucioperca* shallower than 5 m at mid-day. Except for this mid-day shallow aggregation, *S. lucioperca* followed a DVM trajectory that placed them slightly deeper than the 8 lx isolume.

On two of three occasions, the night-time trawl survey results show progressively higher CPUE of YOY *C. harengus* with increasing depth [Fig. 4(a), (b)], consistent with the acoustic observations. In 2004, however, YOY *C. harengus* CPUE was highest in the shallowest depth interval and decreased progressively with increasing depth [Fig. 4(c)]. Similarly, *S. lucioperca* CPUE was highest in the shallowest depth interval on two of three occasions [Fig. 4(a), (b)], consistent with the acoustic observations. Again, the pattern in 2004 was different, with highest *S. lucioperca* density at intermediate depth [Fig. 4(c)]. The CPUE of adult *C. harengus* and *S. sprattus* was consistently higher at deeper depths. The water column was thermally stratified on all three trawl survey dates [Fig. 4(d)]. The YOY *C. harengus* are thought to be less vulnerable to capture in the trawl than larger fishes (Axenrot & Hansson, 2004). Therefore, the trawl CPUE of YOY *C. harengus* probably underestimates their relative abundance. Ninety per cent of *S. sprattus* caught in the trawl survey were >10 cm L_T and thus unlikely to be included among the targets in the −60 to −51 dB TS interval.

By combining light intensity at depth with a reaction distance function (Fig. 5) and a zooplankton prey field [Fig. 6(a)], it was possible to estimate the depth–time
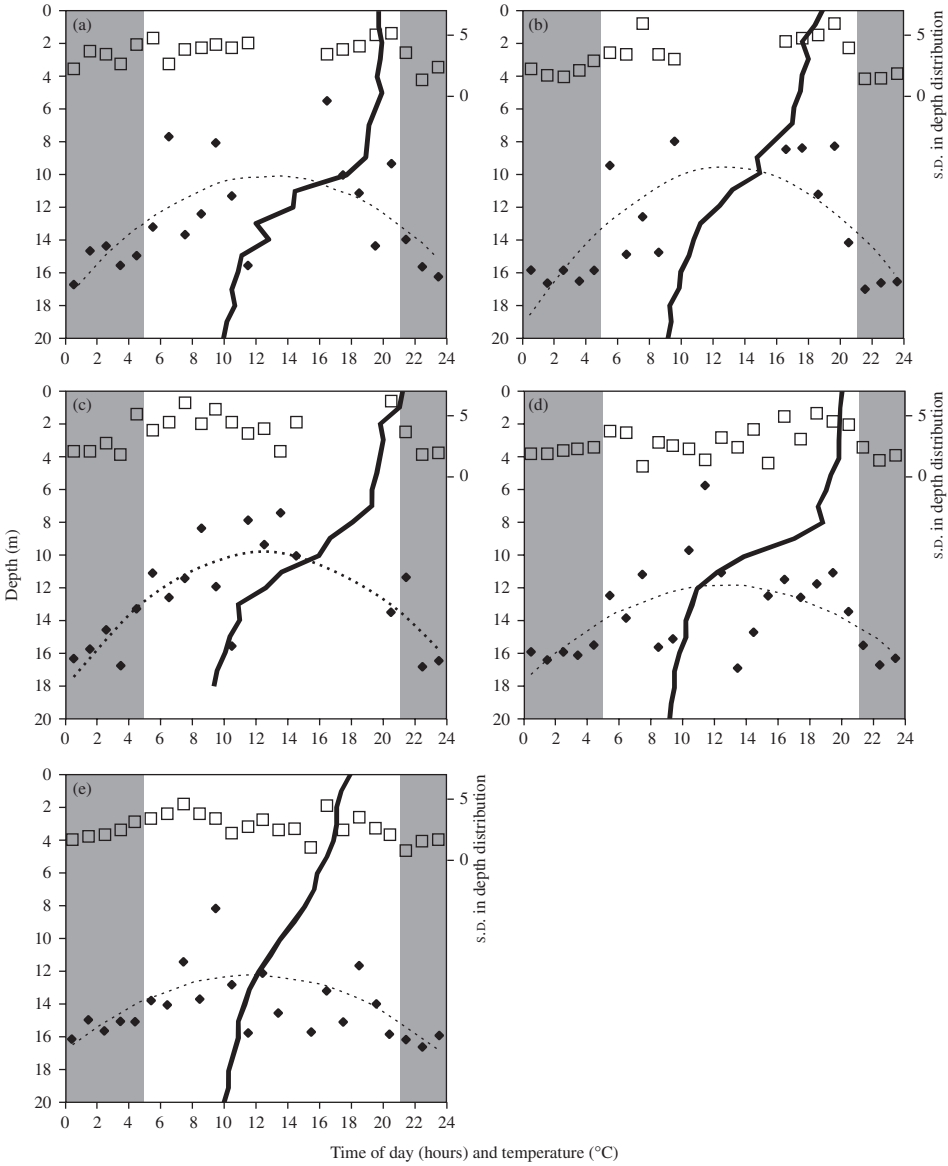
FIG. 2. Mean (◆) and s.d. (□) of the depth of young-of-the-year *Clupea harengus* by hour on five hydroacoustic sampling dates: (a) 1–2 August 2001, (b) 16–17 August 2001, (c) 29–31 July 2002, (d) 5–7 August 2002 and (e) 2–5 August 2004. (──, temperature profiles; ---, second-order polynomials fit to means and ■, night-time).

distribution of FRP [Fig. 6(b)] for YOY *C. harengus*. The prey field [Fig. 6(a)] showed high zooplankton densities in the 0 to 10 m range at night and below 8 m during the day. Foraging rate potential [Fig. 6(b)] peaked near the surface at night and was in the 6 to 9 m depth range at mid-day. Growth rate potential [Fig. 6(c)] was negative throughout the water column at night, consistent with the
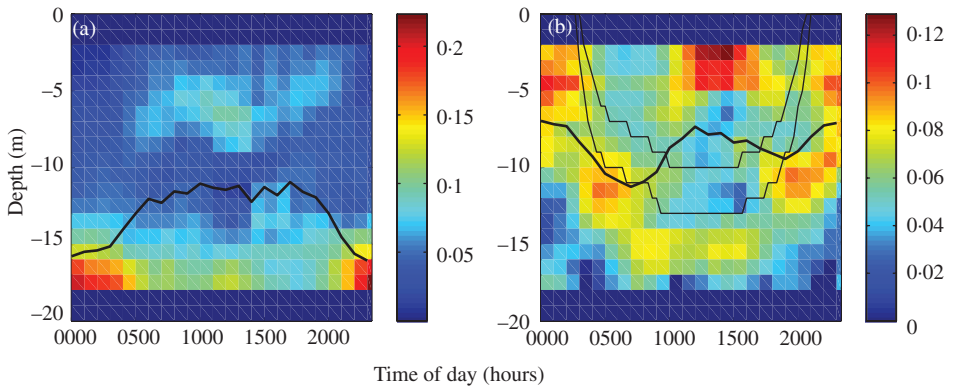
FIG. 3. Proportional densities (vertical colour bars) of (a) small acoustic targets (young-of-the-year *Clupea harengus*) and (b) large acoustic targets (*Sander lucioperca*) by depth and time of day after smoothing with a 3 h by 3 m moving average filter. ——, the weighted mean diel vertical migration trajectories; ——, in (b) show the upper and lower optical habitat based on studies of *Sander vitreus* by Lester *et al.* (2004).

assumed lack of nocturnal feeding by YOY *C. harengus*. Nocturnal energy and mass loss were minimized in colder water near the bottom at night [Fig. 6(c)]. Peaks in GRP occurred at the surface at early dawn and late dusk when zooplankton was assumed to be in its nocturnal vertical distribution. A growth-maximizing DVM trajectory [Fig. 6(c)] would place YOY *C. harengus* near the bottom at night and in the 6 to 9 m depth range during the day, with excursions to the surface at dawn and dusk.

DISCUSSION

A reverse DVM pattern was clearly apparent for YOY *C. harengus* on five separate sampling occasions over 3 years. A reverse DVM has not been previously reported for non-larval *C. harengus*, and is not evident for *S. lucioperca*, which appear to follow a classic DVM trajectory. A DVM pattern which places YOY *C. harengus* in cold water at night and in high prey density, high FRP depths during the day is consistent with growth maximization. High growth rates in juvenile fishes confer immediate survival benefits as they more quickly reach a size refuge from some predators, and larger individuals are more resilient to starvation (Sogard, 1997; Byström *et al.*, 2006). There was little acoustic evidence that YOY *C. harengus* exploit the high GRP apparent in near-surface waters at dawn and dusk. Cardinale *et al.* (2003) report stomach fullness data that indicate high crepuscular feeding activity in Baltic Sea *C. harengus*, and higher variability of YOY *C. harengus* depth distribution at dawn and dusk was observed in the current study. Munk *et al.* (1989) observed crepuscular ascents by larval *C. harengus* into near-surface waters under calm conditions. The high near-surface crepuscular GRP apparent in the present model results, however, may simply be an artefact of temporally coarse data on zooplankton depth distribution. That is, it is probable that the true depth distribution of zooplankton at dawn and dusk is intermediate to their night and day depth distribution.
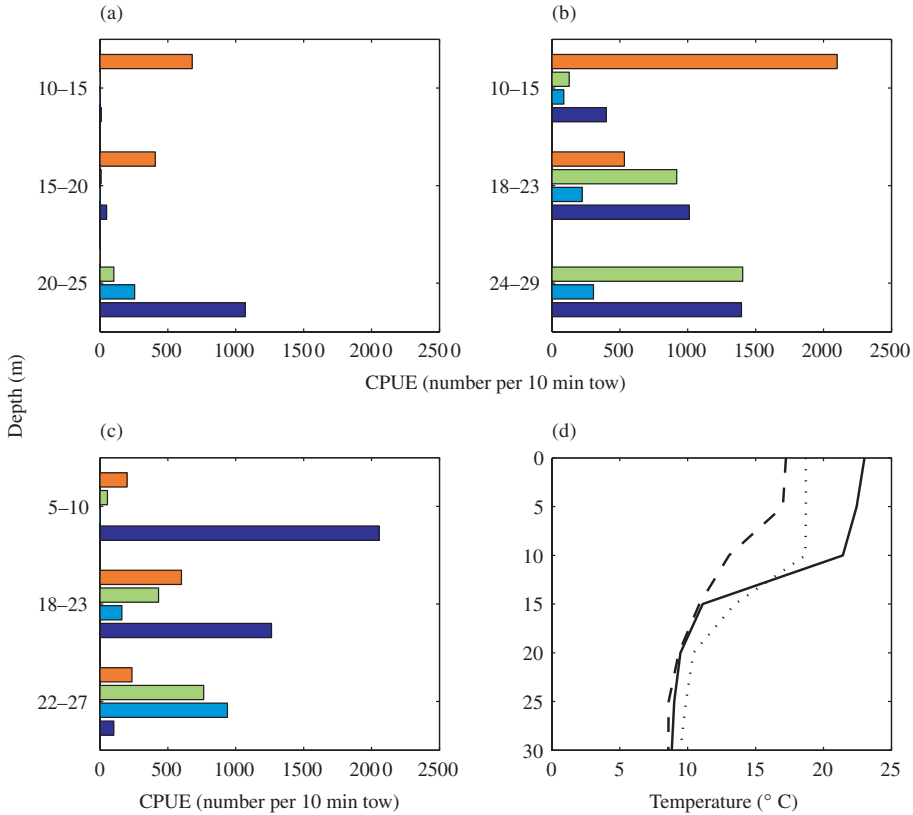
FIG. 4. Trawl catch per unit of effort (CPUE) for young-of-the-year *Clupea harengus* (■), adult *C. harengus* (■), *Sprattus sprattus* (■) and *Sander lucioperca* (■, × 100) on (a) 26 August 2002, (b) 27 August 2003 and (c) 23 August 2004. (d) Temperatures at depth (m) on the trawl survey dates (——, 2002; – –, 2003 and ...., 2004).

The reverse DVM pattern evident for YOY *C. harengus* is also consistent with minimizing overlap between predators and prey. At night, YOY *C. harengus* are near the bottom while *S. lucioperca* are near the surface. During the day, there is more overlap, but both peaks in YOY *C. harengus* fall in slightly greater depths than the corresponding peaks in *S. lucioperca*. Although the data are insufficient to test this hypothesis, it seems probable that the two peaks in YOY *C. harengus* densities during daytime represent distinct behavioural modes. The shallower peak coincides with the depth of maximum daytime GRP. The deep peak is located in lower, more bioenergetically favourable temperatures with low light intensity and is below the depth of maximum predator density. YOY *C. harengus* have limited stomach capacities, but high gut evacuation rates (Arrhenius & Hansson, 1994). Under these conditions, an optimally foraging YOY *C. harengus* might minimize its risk ratio (Werner & Gilliam, 1984) by moving rapidly between intense foraging activity at a depth of high GRP and seeking refuge at a depth with lower predation risk and more favourable temperatures. This hypothesis could be tested by depth-specific sampling of YOY *C. harengus* stomach fullness and digestive state.
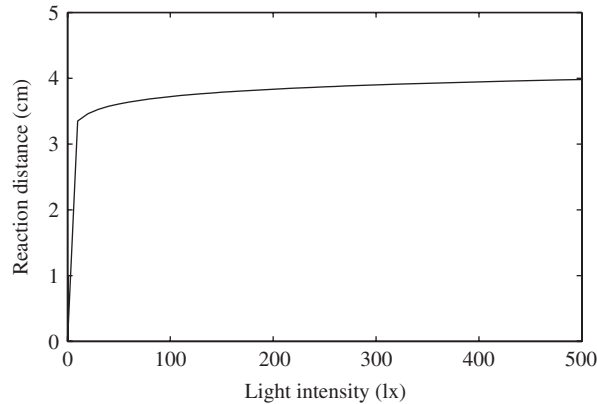
Fig. 5. Assumed reaction distance of young-of-the-year *Clupea harengus* as a function of light level.

Sander lucioperca consistently occurred outside the preferred 'optical habitat' of *S. vitreus* (Lester *et al*., 2004). There are several potential explanations. First, the large acoustic targets may not be *S. lucioperca*. This seems unlikely given the rarity of fishes this size other than *S. lucioperca* in Himmerfjärden (S. Hansson, unpubl. obs.). Second, *S. lucioperca* may simply have different light intensity preferences than *S. vitreus*. The bimodal daytime distribution of *S. lucioperca*, however, places them in both higher and lower light intensities than the 8 to 68 lx range identified as optimal for *S. vitreus*. Finally, there are few prey found within the 8 to 68 lx band. If the observed DVM patterns represent the equilibrium result of a game between predator and prey [as suggested by Iwasa (1982) for zooplankton], it makes sense that predator avoidance behaviour would force the predator to forage in conditions that are suboptimal. That is, prey should avoid conditions which offer the predator a maximum advantage.

If reverse DVM of YOY *C. harengus* is common and bioenergetically optimal, as it appears to be from the present results, why has it not been observed before or elsewhere? One possibility is that TS thresholds used in previous studies resulted in averaging over wide size ranges. Furthermore, the studies in the Baltic Sea by Cardinale *et al*. (2003), Nilsson *et al*. (2003) and Orlowski (2005) were all conducted in open sea areas where YOY *C. harengus* are less common than in the archipelago, as shown by the fish size distributions reported in these studies. It is widely agreed that DVM behaviour is related to some combination of factors involving foraging, bioenergetics and predation risk. All these factors are strongly size-dependent; therefore DVM behaviour should be expected to vary with size and ontogeny. In addition, the dominant predators and physical conditions differ substantially between the open Baltic Sea and Himmerfjärden.

Another explanation for the fact that previous studies have not seen reverse DVM may be avoidance behaviour related to ship noise. The vast majority of hydroacoustic studies use ship-based transducers. This has been true even for studies that explicitly focus on DVM (Cardinale *et al*., 2003; Nilsson *et al*., 2003; Orlowski, 2005; Hrabik *et al*., 2006). *Clupea harengus* are known to respond to ship noise, although both avoidance (swimming downwards and horizontally away from the vessel; Vabo *et al*., 2002; Hjellvik *et al*., 2008) and attraction (Røstad *et al*., 2006) to vessels have been
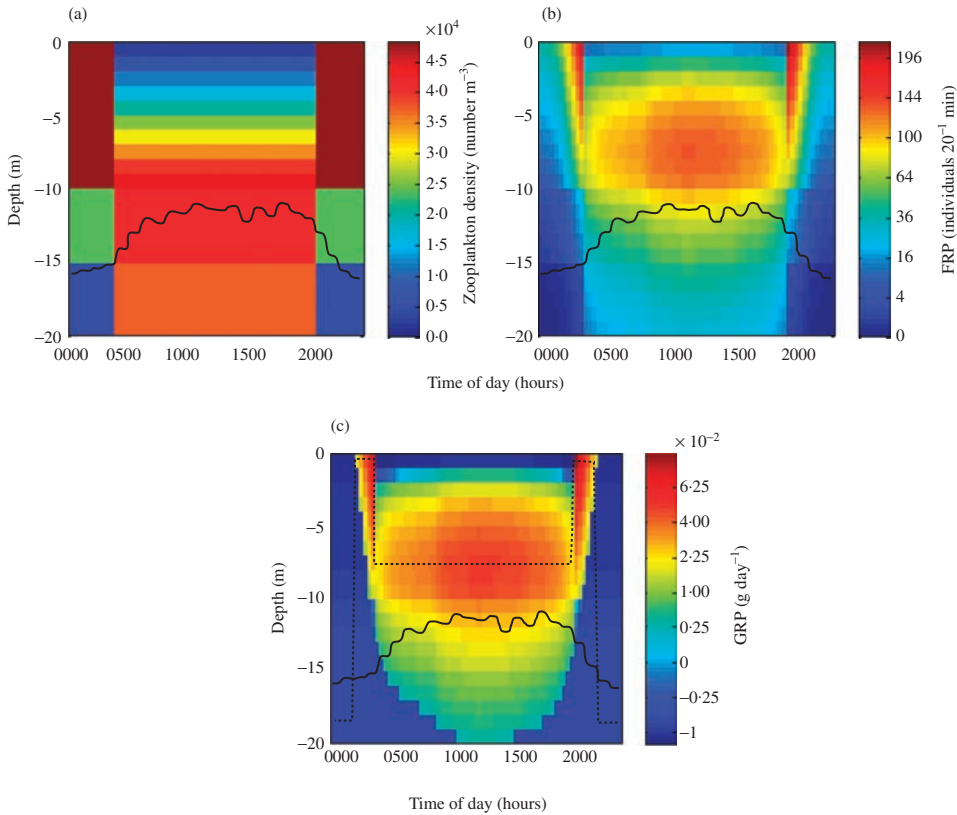
FIG. 6. (a) Zooplankton density, (b) foraging rate potential (FRP) and (c) growth rate potential (GRP) of young-of-the-year *Clupea harengus*. ——, mean diel vertical migration (DVM) trajectory. Colour mapping in (b) and (c) is on a square-root scale. ....., in (c) represents the maximum growth rate DVM trajectory.

documented. A stronger avoidance response during the daytime, when fishes are more active (Didrikas & Hansson, 2009) could lead to the appearance of a classic DVM pattern even if the day and night vertical distributions are the same.

The night-time trawl surveys corroborated the DVM patterns observed by the hydroacoustics on two occasions, but showed an opposite pattern on a third night. YOY *C. harengus* and *S. lucioperca* vertical distributions both differed from the norm on this occasion, indicating that physical conditions may have induced a change in DVM behaviour of both species. The source, however, is not apparent. The magnitude and depth of DVM in some coregonids has been shown to be strongly temperature-dependent (Mehner *et al.*, 2007; Busch & Mehner, 2009), and the present results suggest that temperature is an important factor for YOY *C. harengus* as well. The temperature profile in 2004, however, was not noticeably different, although the bottom temperature was *c*. 1° C warmer than in 2002 or 2003. Trawling occurred at least 2 h after sunset. Field notes indicate moderate to low cloud cover on all three trawl sampling occasions, with varying moon stage: three nights after the full moon in 2002, at the full moon in 2003 and half-moon in 2004. Moon set in 2004 occurred before trawling began, indicating that this was probably the darkest of

the three nights. In addition, *S. lucioperca* density in the shallowest depth stratum was lowest in 2004. This stratum was also shallower (5–10 m) in 2004 than in the previous 2 years (10–15 m). It is possible that the shallower distribution of YOY *C. harengus* on this night was a response to low light levels, lower predator density and presumably lower predation risk. The data, however, are insufficient to draw strong conclusions about the source of this difference in 2004.

The present results provide a more nuanced picture of *C. harengus* DVM and demonstrate the importance of body size in studies of fish behaviour, a consideration that has been too often absent in studies of fish DVM. Bottom-mounted hydroacoustics were used and the focus was on a narrow size range of acoustic targets. This use of behaviourally neutral sampling equipment and the focus on a size range dominated by a single cohort of *C. harengus* revealed a DVM pattern opposite to that observed in previous studies. Though this inverse DVM pattern is apparently new to the scientific literature on *C. harengus* behaviour, it is nonetheless consistent with foraging and bioenergetic model predictions and results in low spatial–temporal overlap between YOY *C. harengus* and their predators.

Future studies may reveal differences in DVM reflecting context-dependent alternative strategies for balancing foraging opportunity and predation risk. A diversity of studies on non-consumptive effects of predators (Peckarsky *et al.*, 2008) suggest that behavioural responses to predation risk may be equally or more important than the direct effects of consumption. Behavioural responses of zooplankton to predation risk and their proximal cues have been studied in some detail (von Elert & Pohnert, 2000; Van de Meutter *et al.*, 2004). Current understanding of the equivalent cues for fish behavioural responses expressed in DVM, however, remains limited.

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