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SPECIAL REVIEW

# Diel vertical migration of freshwater fishes – proximate triggers, ultimate causes and research perspectives

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## SUMMARY

1. Diel vertical migrations (DVM) are typical for many cold-water fish species such as Pacific salmons (*Oncorhynchus* spp.) and coregonids (*Coregonus* spp.) inhabiting deep lakes. A comprehensive recent overview of DVM in freshwater fish has not been available, however.
2. The main proximate trigger of DVM in freshwater fish is the diel change in light intensity, with declining illumination at dusk triggering the ascent and the increase at dawn triggering the descent. Additional proximate cues are hydrostatic pressure and water temperature, which may guide fish into particular water layers at night.
3. Ultimate causes of DVM encompass bioenergetics efficiency, feeding opportunities and predator avoidance. None of these factors alone can explain the DVM in all cases. Multi-factorial hypotheses, such as the 'antipredation window' combined with the thermal niche hypothesis, are more likely to explain DVM. It is suggested that planktivorous fish move within a layer sufficiently well illuminated to capture zooplankton, but too dark for predators to feed upon the migrating fish. In complete darkness, fish seek layers with a temperature that optimises bioenergetics efficiency. The strength of each factor may differ from lake to lake, and hence system-specific individual analyses are needed.
4. Mechanistic details that are still poorly explored are the costs of buoyancy regulation and migration, the critical light thresholds for feeding of planktivorous and piscivorous fish, and predator assessment by (and size-dependent predation risk of) the prey fish.
5. A comprehensive understanding of the adaptive value of DVM can be attained only if the behaviour of individual fish within migrating populations is explicitly taken into account. Size, condition and reproductive value differ between individuals, suggesting that migrating populations should split into migrants and non-migrants for whom the balance between mortality risk and growth rate can differ. There is increasing evidence for this type of partial DVM within populations.
6. Whereas patterns of DVM are well documented, the evolution of DVM is still only poorly understood. Because experimental approaches at realistic natural scales remain difficult, a combination of comprehensive data sets with modelling is likely to resolve the relative importance of different proximate and ultimate causes behind DVM in fish.

## Introduction

Diel vertical migration (DVM) is a behavioural pattern widely documented for pelagic phytoplankton, invertebrates and fish in both freshwater and marine ecosystems. The 'normal' variant of DVM consists of occurrence deep in the water column during day, an ascent towards the surface at dusk, residence in the upper part of the water column by night and a return to the deeper water at dawn. In a few fish populations, and often limited to few months of the year, the 'normal' pattern can switch into a 'reversed' DVM pattern with a descent at dusk and an

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ascent at dawn (Levy, 1990a; Hardiman, Johnson & Martinez, 2004), but I will not discuss this pattern in detail here. A number of reviews on patterns, triggers and evolutionary causes are available for zooplankton DVM (Hays, 2003; Pearre, 2003; Ringelberg & Van Gool, 2003) with the most recent attempting to integrate newer research results into a common framework (Williamson *et al.*, 2011). An overview on DVM in marine fish has been given by Neilson & Perry (1990). However, no recent review is available on studies targeting patterns and mechanisms of DVM in freshwater fish, or considered suggestions for potentially fruitful future research topics. The present review is intended to fill this gap. In a few cases, I also refer to studies of marine fish or occasionally to studies on DVM in zooplankton, where these support mechanistic insight or general conclusions.

I do not cover in detail the history of the study of DVM or the related discussion of its potential causes. Rather, I briefly summarise the main hypotheses on the triggers and causes of DVM and discuss them in the light of more recent research. Subsequently, I list some main research deficits which still hinder a detailed mechanistic understanding of DVM. Finally, I discuss how an appreciation of the behaviour of individual fish can help us understand DVM. Individuality here refers to systematic differences at two levels of organisation. First, there may be differences in migration patterns and causation in differing migrating populations ('between population' differences). Second, individuality can also be expected between members of the same population ('within population' differences), which I discuss in detail.

## Geographical and taxonomic overview

Research on DVM in freshwater fish originates from three main biogeographical areas. Several early studies were conducted in lakes of the Pacific Northwest of America, targeting migrating populations of Pacific salmon (*Oncorhynchus* spp.). A second geographical centre was in the North-American Laurentian Great Lakes in which coregonids (*Coregonus* spp.) and freshwater herrings (*Alosa* spp.) migrate vertically. Finally, research on DVM has been extensive on coregonids in Northern and Central Europe. Other fish genera occasionally included have been bullheads or sculpins (*Cottus* spp.), smelt (*Osmerus* spp.), sticklebacks (*Gasterosteus* spp.) and burbot (*Lota* spp.), although in these species DVM is not found in all ontogenetic stages. In fish species (or in particular ontogenetic stages) that perform DVM, there are two ecological traits in common: first, they are usually planktivorous, and second, they require cold or cool water (Magnuson, Crowder & Medvick, 1979) and hence live primarily in the pelagic zone of deep, thermally stratified lakes. These common features suggest that the thermal gradient in lakes, with a warm epilimnion (above the thermocline), a metalimnion (at the thermocline) and a cold hypolimnion (below the thermocline), is of fundamental importance (De Stasio, Golemgeski & Livingston, 2009) and may be a cause of DVM in freshwater fish. However, the thermal gradient of stratified lakes is correlated with other abiotic vertical gradients. Examples are hydrostatic pressure, illumination and turbidity, and oxygen and nutrient concentrations. These are in turn associated with, and often cause, biotic vertical gradients in the abundance of primary producers (phytoplankton), primary consumers (zooplankton) and secondary consumers (Mysidacea, Chaoboridae) (see Mehner, Hölker & Kasprzak, 2005), metazoans being the main prey of the migrating zooplanktivorous fish. The consequence of vertical gradients is that even the apparently structureless lakes (at least those that stratify) consist of a number of microhabitats that differ in environmental conditions. Migrations in which fish switch between these microhabitats can thus be classified as behavioural habitat choice. In this context, DVM has never been found in a completely homogeneous system, suggesting that environmental gradients are needed at least to trigger or cue vertical migration.

## Proximate causes of DVM

To understand the behaviour, it is useful to distinguish proximate and ultimate causes (for zooplankton DVM, see, for instance, Ringelberg & Van Gool, 2003). Proximate causes refer to sensory-motor and genetic developmental mechanisms guiding the fish. In contrast, ultimate causes refer to the selection that has led to the evolutionary development of the migration behaviour (Alcock, 2009).

The main proximate trigger of DVM in freshwater fishes is the diel cycle of illumination, which encompasses longer consistently bright (diurnal) or dark (nocturnal) periods separated by brief crepuscular periods (dusk, dawn) when light changes rapidly. There is broad consensus for several fish genera (*Oncorhynchus*, *Coregonus*, *Lota*, *Osmerus*) that the decline in illumination at dusk stimulates ascent, whereas the increasing illumination at dawn induces descent to the hypolimnion (Appenzeller & Leggett, 1995; Scheuerell & Schindler, 2003; Busch & Mehner, 2009; Probst & Eckmann, 2009). Further support for the triggering effect of light cycles has been gained by studies at high latitude in summer and on fish under ice (Steinhart & Wurtsbaugh, 1999; Jurvelius &

Marjomäki, 2008; Gjelland *et al.*, 2009; Kahilainen, Malinen & Lehtonen, 2009). In all these examples, migrations only occurred where there were diel phases of rapid changes in illumination, but stopped when the difference between day and night was low (as it is typical for Polar summer). Finally, daytime depths and migration amplitudes correlated with water transparency. In clear water, fish were located deeper and had to migrate further on a daily basis (Levy, 1990b), suggesting that light also determines the exact distribution of fish along the depth gradient by day.

However, light cannot be used for habitat and depth choice where it declines to zero during the night. In that case, other proximate cues may determine the exact vertical distribution of fish. It has been suggested that the changes in hydrostatic pressure set an upper limit to the range of possible vertical migrations (Eckmann, 1991), approximated by a maximum increase of 50% volume of the swimbladder during ascent (Fleischer & TeWinkel, 1998; TeWinkel & Fleischer, 1998). Alternative calculations and measurements suggested that these fish (*Coregonus* spp.) migrated within a depth range in which they can maintain vertical station (+50% to −30% buoyancy) (Clemens & Stevens, 2003, 2007). Recent research has confirmed that fish can use hydrostatic pressure for a precise determination of their depths (Holbrook & De Perera, 2011).

Vertical temperature gradients may similarly serve as a trigger guiding the fish to certain depths at night (Levy, 1990b). Thermoreception in fish is sensitive to small temperature gradients, and hence, fish may find layers with energetically optimum temperatures (Mehner *et al.*, 2010). However, the distinction between proximate and ultimate causes is difficult here because improving bioenergetics efficiency by switching between thermally differing layers is seen also as an evolutionary force which may have selected for DVM as a cyclic habitat-choice behaviour (see Ultimate causes of DVM below).

## Ultimate causes of DVM

Ultimate explanations for the evolution of DVM can be summarised into bioenergetics efficiency, feeding opportunities and predator avoidance. I discuss each of them individually first and deal with more integrative concepts subsequently. The avoidance of UV radiation is also receiving growing interest as an ultimate cause of zooplankton DVM (Leech *et al.*, 2009; Williamson *et al.*, 2011), in particular because UV-B entering the water has increased as a result of stratospheric ozone depletion (Karentz & Bosch, 2001). Although UV-B radiation can cause damage in early developmental stages of fish (Browman *et al.*, 2000), it has rarely been discussed as potential ultimate cause of fish DVM (but see Ylönen, Huuskonen & Karjalainen, 2004; Rechencq *et al.*, 2011). Another potential cause that is just beginning to be explored is parasitic infection. Infection by cestodes increased the proximity of three-spined sticklebacks (*Gasterosteus aculeatus* L.) to the surface of a lake during daytime, whereas most of uninfected fish performed DVM. The modified DVM patterns of infected fish thus increased the vulnerability to predation by birds, enabling the completion of the parasite's life cycle (Quinn *et al.*, 2012).

### *Bioenergetics efficiency*

A first ultimate explanation has emerged from physiological studies on salmonid metabolic rates and is termed the 'bioenergetics efficiency' hypothesis. It has been suggested that young sockeye salmon [*Oncorhynchus nerka* (Walbaum)] may save energy by staying in cold water, with a low metabolic rate, during the day, whereas they ascend into warmer surface water at night, even at the expense of increased metabolic costs, to feed on the zooplankton concentrated there (Brett, 1971). Evidence for this 'hunt warm-rest cool' strategy has recently been found from individually tagged dogfish [*Scyliorhinus canicula* (L.)]. These sharks could save about 4% of metabolic expenditure by migrating between layers of differing temperatures (Sims *et al.*, 2006). Although intriguing at the first sight, the bioenergetics hypothesis has some problems. If saving energy is the primary reason for the descent, fish could also reverse the DVM pattern by staying in the upper layers during the day and descending to the cold layers at night (Clark & Levy, 1988). This could even improve the feeding efficiency, if the migrating fish are visual feeders, because the fish would be located where zooplankton are dense during the hours of bright illumination.

Inconsistencies in the bioenergetics hypothesis become obvious also from comparison of growth of migrating and non-migrating early juveniles of kokanee salmon [*Oncorhynchus nerka* (Walbaum)] in a thermally stratified lake. Fish confined to the epilimnion attained a body mass in early autumn about twice as that of migrating fish (Johnston, 1990). Furthermore, DVM in coregonids was reported also from lakes, which did not thermally stratify at all (Sydänoja, Helminen & Sarvala, 1995) or was observed early in the year when the lake had not yet stratified and hence had no vertical temperature gradient (Stockwell & Johnson, 1999; Hardiman *et al.*, 2004; Mehner, Kasprzak & Hölker, 2007). In contrast to the bioenergetics efficiency hypothesis, no bioenergetics advantage can be expected by migration under such isothermal conditions.

Finally, the growth advantage of cyclic temperatures has not been demonstrated unequivocally in experiments where fish in all treatments were fed comparable rations. Biette & Geen (1980a) mimicked the diel temperature changes to which migrating young sockeye salmon are exposed (4.5–17.5 °C) and compared their growth with that of fish exposed to a range of constant temperatures. Salmon growth was the highest under cyclic temperature if the daily food ration was 5–7% of fish dry mass (dm) per day (Biette & Geen, 1980a). At constant high temperature, respiration rate was higher than at cyclic temperature, whereas at constant low temperature, defaecation and excretion rates exceeded those at cyclic temperatures (Biette & Geen, 1980b). However, at food rations >7% dm day$^{-1}$, salmon grew fastest at the constant high temperature, whereas fish held at the lowest temperature grew fastest at a daily ration of about 1% dm day$^{-1}$ (Biette & Geen, 1980a). In a similar way, juvenile sculpins (*Cottus extensus* Bailey & Bond) fed *ad libitum* grew faster if exposed to diel temperature fluctuations of between 5 and 15 °C than fish held at constant 5 °C (Neverman & Wurtsbaugh, 1994). However, sculpins held at a constant 15 °C grew fastest and at a rate comparable to that observed in the lake from which the fish originated (Neverman & Wurtsbaugh, 1994). Similarly, vendace [*Coregonus albula* (L.)] fed *ad libitum* grew faster when held at a constant 8 °C than fish that experienced fluctuations between 4.5 and 8 °C (Mehner *et al.*, 2011). Therefore, a bioenergetics advantage of cyclic temperature over constant high or low temperature seems to apply only under a narrow range of intermediate daily food rations. In contrast, at low or high food rations, the temperature regime mimicking DVM induced only suboptimal growth, and growth of fish held at constant temperature was always higher.

### *Feeding opportunities*

In some of the earlier studies on DVM in freshwater fish, it was proposed that migrating fish follow their preferred prey, which also exhibit cyclic habitat switches. By migrating, fish thus extended the time during which they can feed. For example, the extent and timing of DVM of adult alewives [*Alosa pseudoharengus* (Wilson)] in Lake Michigan coincided with the DVM of the dominant invertebrate prey, the opossum shrimp (*Mysis relicta* or *M. diluviana* according to most recent nomenclature) (Janssen & Brandt, 1980). Feeding opportunities for alewife were documented by the fact that shrimps dominated the gut contents during these months. Similarly, it was hypothesised that DVM of the bloater [*Coregonus hoyi* (Milner)] in Lake Michigan facilitated feeding on *M. relicta* (Eshenroder, Argyle & TeWinkel, 1998). However, the feeding opportunities hypothesis has been criticised for two reasons. First, DVM of fish was also observed in lakes in which zooplankton (the main prey) did not migrate but was consistently concentrated in the upper layers (Eggers, 1978; Clark & Levy, 1988; Mehner *et al.*, 2007). Second, DVM in zooplankton has been viewed primarily as a predator avoidance mechanism (Zaret & Suffern, 1976; Gliwicz, 1986; Lampert, 1993). If zooplanktivorous fish and zooplankton migrate together, the selective advantage of zooplankton DVM disappears (Eggers, 1978). In contrast, reciprocal DVM in planktivorous fishes and their zooplankton prey, as observed in British Columbia lakes (Levy, 1990a), should be the dominant pattern (see also Young & Yan, 2008).

### *Predator avoidance*

The third, and most discussed, ultimate hypothesis of DVM is predator avoidance. It has been assumed that planktivorous fish avoid well-lit surface waters during the day, thus reducing mortality from visual predators. This hypothesis has been proposed, for example, for juvenile sockeye salmon (Eggers, 1978). It has been proposed that the distribution of fish in the water column, the timing and duration of their feeding, and their pattern of school formation and dispersal minimised their exposure to the main predator, northern squawfish [*Ptychocheilus oregonensis* (Richardson)]. Avoidance of predation by the deepwater form of lake trout [siscowet, *Salvelinus namaycush siscowet* (Walbaum)] might also explain DVM in deepwater coregonids [bloater; kiyi, *C. kiyi* (Koelz); lake herring, *C. artedi* Lesueur] in Lake Superior (Hrabik *et al.*, 2006; Jensen *et al.*, 2006). Although predation risk has been discussed as an important ultimate explanation in many other case studies on freshwater fish DVM (Scheuerell & Schindler, 2003; Hardiman *et al.*, 2004; Gjelland *et al.*, 2009; Kahilainen *et al.*, 2009), it has been noted that the often low densities of pelagic predators presumably impose only a slight direct predation risk and thus the selective value of DVM is not obvious (Narver, 1970; Mehner *et al.*, 2007; Jurvelius & Marjomäki, 2008).

Consequently, in isolation, none of the three ultimate explanations proposed convincingly explain all cases of DVM in freshwater fish (Clark & Levy, 1988). The foraging and bioenergetic hypotheses have been most successful at explaining DVM in predators (Bevelhimer &

Adams, 1993), where predation risk is not a consideration. Foraging and energetic approaches alone have failed to explain DVM in species feeding lower in the web, where predation may be an important source of mortality (Levy, 1990a,b; Stockwell & Johnson, 1999).

### *Multi-factor ultimate explanations*

A major step forward to understanding DVM from a multi-factorial perspective was taken by Clark & Levy (1988), who introduced the concept of the 'antipredation window'. They suggested that the visual range of fish predators and their fish prey differs substantially. Planktivorous fish (the prey) can feed at lower light intensity than their own predators (piscivorous fish) (Beauchamp *et al.*, 1999; Mazur & Beauchamp, 2003; Gjelland *et al.*, 2009) and hence may find a refuge under darker conditions. Therefore, prey fish actively seek layers characterised by this low illumination and continue feeding during the day but because of high light at the surface, these layers are relatively low in the water column. At dusk, this layer with the optimum illumination strength moves upwards and down again at dawn. Prey fish can move within this antipredation window and therefore feed along the zooplankton gradient while ascending and descending. In this way, prey fish minimise the ratio between predation risk (μ) and feeding gain or growth (g) (Gilliam & Fraser, 1987; Lima & Dill, 1990). Vertical migration within the antipredation window has been confirmed empirically by a study on juvenile sockeye salmon in several Alaskan lakes (Scheuerell & Schindler, 2003). It was demonstrated that prey fish were continuously located at illumination strengths sufficient to capture zooplankton, but too dark to be vulnerable to predators (adult sockeye), as indicated by the saturation irradiance threshold for the detection of prey by lake trout (Vogel & Beauchamp, 1999). Similarly, coregonids [vendace, and whitefish *Coregonus lavaretus* (L.)] in the Norwegian Lake Skrukkebukta occurred in layers too dark for predators to feed, but still sufficient for them to feed on zooplankton (Gjelland *et al.*, 2009). The consequence is, however, that migrating fish, while avoiding predators, adopt a feeding behaviour that results in less than the maximum possible growth rate (Clark & Levy, 1988). This suggests that predator avoidance is of high selective value even at low predator density. In turn, growth benefits to potentially stationary fish must be very high to take this elevated risk.

An interesting conceptual advance has recently been made in an experimental study of DVM in burbot [*Lota lota* (L.)] larvae (Donner & Eckmann, 2011). These authors tested the bioenergetics hypothesis of DVM by exposing the larvae to different constant and cyclic temperatures. However, in addition they measured temperature-dependent mortality rates of larvae in their treatments, thus evaluating the μ/g ratio of DVM behaviour directly. Specific growth rates of larvae fed *ad libitum* were maximised at the highest constant temperature, but larvae had also high mortality in these treatments. Therefore, the product of growth and survival in the experimental tanks was the highest for larvae exposed to cyclic temperatures mimicking regular DVM. The authors concluded that various ultimate factors interacted in selecting for DVM in larval burbot.

The antipredation window hypothesis predicts the location and migration of fish by day and during the crepuscular periods by taking into account predator avoidance and feeding opportunities of migrating fish. However, this hypothesis fails to predict the depth of occurrence in complete darkness during the night. Nocturnal depths of coregonids in Lake Stechlin (Germany) were not invariant, but seasonally variable, with the uppermost layers occupied in the middle of the summer (Helland *et al.*, 2007; Mehner *et al.*, 2007). Therefore, it has been proposed that fish optimise their bioenergetics efficiency at night by seeking layers with a temperature close to their final temperature preferendum (FTP) (Mehner *et al.*, 2010). In stratified lakes, the thermocline expands to deeper layers from early summer to autumn, and hence the nocturnal location of fish follows the vertical location of their preferred isothermal layers, with a progressive shift downwards with season (Busch & Mehner, 2009; Mehner *et al.*, 2010). A similar downward shift of nocturnal depth from summer to autumn has been observed in sockeye salmon (Levy, 1990b). The bioenergetic advantages of staying at a temperature close to FTP may be found in minimised costs for swimming (Ohlberger *et al.*, 2008c). Additionally, water layers warmer than those occupied during the day may speed up digestion during the non-feeding phase at night, thus facilitating higher feeding rates during the descent at dawn (Wurtsbaugh & Neverman, 1988; Neverman & Wurtsbaugh, 1994).

Accordingly, the ultimate hypotheses introduced above do not operate independently, but in concert to explain the adaptive value of DVM in freshwater fish. Predator avoidance causes the fish to stay in deep layers by day. Feeding opportunities drive the migration within the antipredation window. Bioenergetics efficiency is enhanced when fish seek layers of optimum temperature at night. Therefore, DVM would reflect a three-way compromise between the three ultimate hypotheses on fish DVM (Levy, 1990b). Furthermore, the proximate

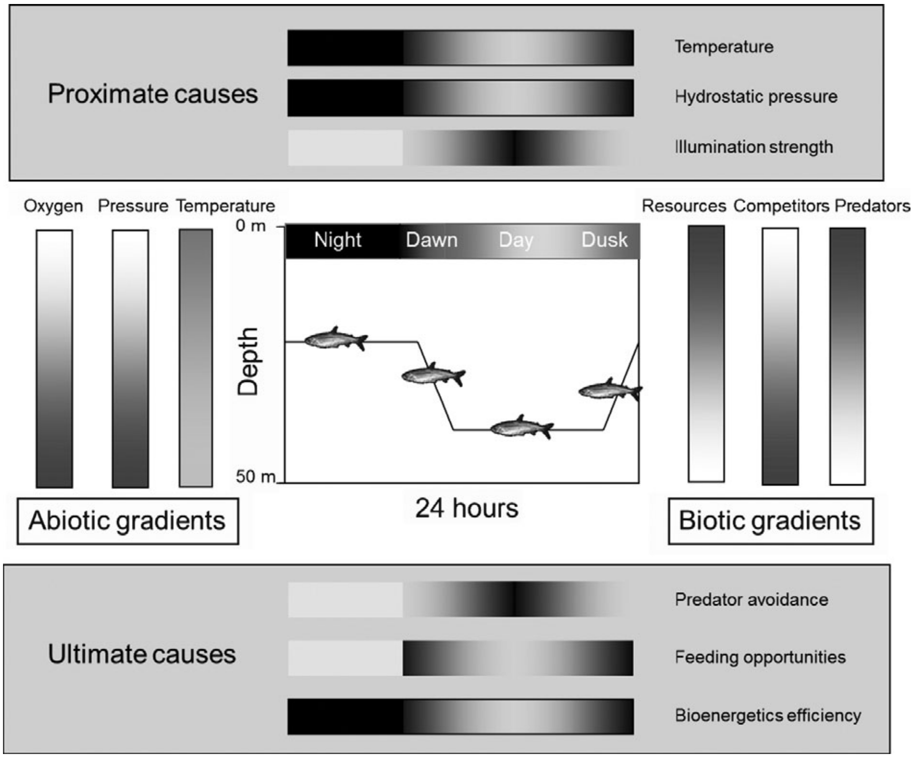

**Fig. 1** Conceptual overview of the vertical distribution of fish during Diel vertical migrations (DVM), vertical abiotic and biotic gradients, and effects of proximate and ultimate causes on fish during 24-h cycles. Dark fills mean strong effects.

triggers of migration, namely light, temperature and hydrostatic pressure, and oxygen concentration close to critical low thresholds, also may interact to guide the fish into particular depth layers, thus suggesting the DVM is caused by a complex interplay of various factors along several vertical gradients in stratified lakes (Fig. 1).

According to the strong temporal and spatial variability in the densities of prey and predatory fish, and the differing abiotic and biotic vertical gradients in lakes, a unified theory of DVM in freshwater fish is elusive (Stockwell & Johnson, 1999). Inevitably, each system needs to be analysed individually, and a specific combination of proximate and ultimate causes found in one lake may not apply to another lake (Fig. 1). However, what has so far been lacking is a comparative approach to DVM patterns across systems, for example, with respect to the vertical distribution by day or night, migration amplitudes, water transparency, and vertical gradients of zooplankton and predator density. The overview given above suggests that sufficient data have been gained from a range of systems inhabited by the same species or genus of migrating fish (e.g. *Oncorhynchus* or *Coregonus*). In such a comparative approach, valuable insight may come from combination of lakes in which local populations of the same species do or do not migrate vertically (see also Table 1).

## Research needs for a mechanistic understanding of DVM

Although the general patterns of DVM in freshwater fish are well described, there are several mechanistic details needed to complement understanding of DVM (see also Table 1). These deficits refer primarily to energetics of migrations and buoyancy (which are relevant to the bioenergetics hypothesis), to critical illumination strengths of planktivorous and piscivorous feeding (relating to the feeding opportunities and predator avoidance hypotheses), and to the assessment of predation risk by the prey (predator avoidance hypothesis). Furthermore, some ecological and physiological traits may differ between individuals within the same population, thus making it possible that migration trajectories and amplitudes are very plastic and variable within a population. Consequently, to further develop multi-factorial explanations, these individual differences have to be considered.

### *Energetics of migrations and buoyancy*

The energetics of the migration and buoyancy regulation in migrating fish remain largely unstudied. Because of the vertical gradient of hydrostatic pressure, the swimbladder

**Table 1** Overview of conceptual questions and hypotheses, which may be addressed in future research on Diel vertical migrations (DVM) of fish populations, and suggested approaches and related scientific disciplines with which collaboration would be useful

| Research questions | Hypothesis | Approach | Related disciplines |
|---|---|---|---|
| *Patterns of DVM* | | | |
| What determines daytime and night-time depths of migrating populations? | Daytime: critical illumination threshold, Night-time: thermal niches of populations | Across-system comparison | Lake physics |
| Is DVM always partial? | Migrating populations split into migrants and residents | Across-system comparison | Fish ecology |
| Do DVM patterns differ in coupled trophic levels? | In three trophic level food chains, DVM patterns differ between populations at adjacent trophic levels | Within-system comparison | Limnology |
| *Ultimate causes of DVM* | | | |
| What are the lower illumination thresholds for planktivorous and piscivorous fish feeding? | No feeding possible at complete darkness | Experimental | Sensory physiology |
| How much can migrating fish regulate their swimbladder volume, and what are the costs of this regulation? | Swimbladder regulation is limited, and costs are higher than so far assumed | Experimental | Physiology, Biophysics |
| How do prey fish assess predator type and density? | Chemical cues alone are not strong enough to induce DVM in prey fish | Experimental | Behavioural ecology |
| *DVM as an adaptive behavioural trait* | | | |
| Is DVM phenotypically plastic? | DVM patterns and amplitudes vary between seasons, years and lakes | Within- and across-population comparisons | Limnology |
| Is DVM an inducible defence? | DVM starts when critical predator densities are exceeded | Within- and across-system comparisons | Fish ecology |
| What are the fitness consequences of migrating *vs*. non-migrating tactics? | The fitness benefit of the dominant tactic is frequency-dependent | Within- and across-population comparisons | Fish ecology, Behavioural ecology |

of fishes will be compressed when fish descend and inflate during ascents. The gas bladder approximates Boyle's law (volume = pressure$^{-1}$) (Alexander, 1972). To remain neutrally buoyant over the entire depth range, fish have to keep the swimbladder volume constant by actively adding or removing gas. Very few studies have measured the speed by which fishes can regulate the bladder gas (Jones & Scholes, 1985; Arnold & Walker, 1992), but generally the speed seems to be too low (adaptation rates 0.3–2.5 m h$^{-1}$) to allow for full compensation of pressure changes during DVM. This is particularly problematic for physostomous fish, such as salmonids and coregonids, which have an open connection between the oesophagus and the gas bladder (*ductus pneumaticus*) but do not possess a special tissue (*rete mirabile*) that would allow a more rapid filling of the gas bladder (Clemens & Stevens, 2007). It was therefore assumed that coregonids are neutrally buoyant only at their night-time shallow position near the surface, but experience substantial swimbladder compression during the day when deeper in the water column (Fleischer & TeWinkel, 1998). In contrast, gas bubble release has been observed in ascending coregonids (Knudsen & Gjelland, 2004) that would suggest that fish can compensate for swimbladder inflation at the lower hydrostatic pressure in surface layers. Therefore, the exact depth of neutral buoyancy is still a matter of debate (Eshenroder & Burnham-Curtis, 2001; TeWinkel & Fleischer, 2001). However, it is undisputed that fish with compressed swimbladders have to produce additional lift to prevent sinking. Lift can be produced by swimming with the fins acting as hydrofoils, and the lift can be increased by additional tilt of fish relative to the horizontal orientation (Alexander, 1990; Strand, Jorgensen & Huse, 2005).

Holding the vertical position by swimming is energetically costly, and these costs have to be considered in estimating the energetic balance of DVM. There is only one study available in which the additional oxygen requirement of fish at higher hydrostatic pressure was measured. Speers-Roesch, Lingwood & Stevens (2004) recorded about 20% higher oxygen uptake in fish exposed to an increase in pressure up to four atmospheres, similar to about 30 m depth. The increased energetic costs resulted from the enhanced swimming activity at the high pressure. Alternatively, fish could keep the volume of the swimbladder constant. Alexander (1972) estimated the costs of secreting gas into the swimbladder for descending fish to be substantial, but stated that there was much uncertainty about some of the data and that firm conclusions could not be reached. Modelling buoyancy regulation for cod (*Gadus morhua* L.) suggested that the regulation of swimbladder volume is energetically cheap but slow (Strand *et al*., 2005). In total, although it is often assumed that migration costs are low relative to the other components of a fish's bioenergetic budget, an exact quantification would be needed to compare the efficiency of several migration strategies. This is particularly relevant if the growth of fish performing DVM is only slightly higher than that of non-migrating fish (Busch, Johnson & Mehner, 2011). In these cases, even small amounts of additional energy needed to maintain depth or to regulate swimbladder volume would make DVM less efficient.

A mechanism by which fish may produce lift passively is by having a high whole-body fat content, as found in deepwater phenotypes of lake trout (Henderson & Anderson, 2002) or bloater (Eshenroder, Sideleva & Todd, 1999; Clemens & Stevens, 2003) in the Great Lakes. The deepwater phenotypes have a much greater lipid content than the others, making them more adept at maintaining buoyancy in deep waters (Clemens & Stevens, 2003). Recent experiments with vendace revealed, however, that the temperature the fish were exposed to had an effect on the body composition. Vendace held at cyclical temperatures over 6 weeks had lower lipid and higher water contents than fish held at either low (4.5 °C) or high (8.0 °C) temperature, despite being fed *ad libitum* with high energetic density rations (Mehner *et al*., 2011). It remains to be elucidated how the physiology and biochemistry of tissue growth in fish is influenced by cyclical temperatures, and whether certain characteristics of body composition are beneficial for fish exhibiting DVM.

Ontogenetic differences in thermal niches of fishes (Pörtner & Farrell, 2008), which should result in stage-specific migration trajectories, might also be important for bioenergetics. For example, juvenile coregonids have higher preferred temperature than adults (Tapaninen, Marjomäki & Keskinen, 1998; Ohlberger *et al*., 2008b; Clemens & Crawford, 2009). If migrating fish seek optimum temperatures at night, ontogenetic differences would suggest that juvenile vendace should be found in warmer water near the surface than adults. Individual, and in part size- or age-related, differences can be predicted also with respect to investment in reproduction. The reproductive value is low for immature juveniles, but high for mature individuals. Therefore, juveniles should accept greater risks to achieve higher food gains, whereas adults should decrease risk even at the cost of limited growth (Lima & Dill, 1990; Lima, 1998).

There is empirical evidence that the migration amplitude differs between ontogenetic stages of fish, as predicted from their differing thermal niches. Hamrin (1986) found that juvenile vendace ascended nearer to the surface than adult vendace at night. This pattern was confirmed by studies in Lake Stechlin, where similarly juvenile vendace occurred just below the thermocline at night, whereas adults were a few metres deeper (Mehner *et al*., 2010). The vertical segregation coincided with slightly differing thermal ranges occupied by the ontogenetic stages of vendace (Mehner *et al*., 2010). Similarly, migration amplitudes and intensities also differed between juvenile and adult bloater in the Great Lakes (Eshenroder *et al*., 1998). Further systematic comparisons of bioenergetics between juvenile and adult migrating fish would improve understanding of how energetic constraints contribute to the variability of DVM observed across many systems.

### *Illumination thresholds for feeding*

It has been suggested that planktivorous fish move within the antipredation window characterised by some minimum illumination strength required for their own feeding while minimising the risk of predation. However, there is no consensus on the amount of light needed for the efficient uptake of zooplankton. Whereas earlier studies presumed that fish continue feeding after ascent towards the surface at night (Brett, 1971; Janssen & Brandt, 1980), others reported a continuous decrease in stomach fullness after dusk, suggesting that fish stop feeding (Wurtsbaugh & Neverman, 1988; Neverman & Wurtsbaugh, 1994). Slow and unselective feeding in complete darkness has been demonstrated for coregonids, so non-visual feeding is evidently possible (Janssen, 1980; Mayr, 2002). The lower illumination threshold for feeding of vendace and Fontane cisco (*Coregonus fontanae* Schulz & Freyhof) inhabiting Lake Stechlin (Germany) was defined experimentally at about 0.01 ($10^{-2}$) lux, because fish were found feeding at low rates at 0.05 lux, but stopped at 0.005 lux (Ohlberger *et al*., 2008a). This threshold was confirmed by a comparison of several published light-dependent feeding rates of planktivorous fish (Gjelland *et al*., 2009). Brown trout (*Salmo trutta* L.) and Artic charr [*Salvelinus alpinus* (L.)] have been observed to feed on macroinvertebrates at somewhat lower light, down to 0.001 ($10^{-3}$) lux, but stopped feeding in complete darkness (Elliott, 2011). Feeding of smelt [*Osmerus eperlanus* (L.)] was substantially impaired below 0.1 $\mu$E m$^{-2}$ s$^{-1}$, equivalent to about 5.4 lux

(Horppila, Liljendahl-Nurminen & Malinen, 2004). In an elegant and technically sophisticated study, Boscarino *et al.* (2010) investigated the critical illumination threshold for alewife feeding on the opossum shrimp. They developed a new unit for illumination, referred to as alelux, to approximate the physiological mechanisms of the rod photoreceptors of the alewife. In experiments, alewives were observed feeding successfully at $10^{-7}$ alelux, but stopped feeding at $10^{-8}$ alelux. Conversion of alelux into lux is only an approximation, but $10^{-7}$ alelux would be equal to about $10^{-4.1}$ lux (Boscarino *et al.*, 2010), a threshold at least two orders of magnitude lower than that determined experimentally for coregonids (Ohlberger *et al.*, 2008a). However, even by applying this lower threshold, it was revealed in subsequent field studies that the alewife is not capable of feeding during the night at the new moon. All these results suggest that the lower illumination threshold for planktivory is strongly species-specific.

Critical illumination thresholds for piscivores are comparably scant. The foraging efficiency of visually oriented predatory fish is usually positively correlated with light intensity, but again has large interspecific variations (Confer *et al.*, 1978; Mazur & Beauchamp, 2003). In piscivorous salmonids, foraging efficiency and reactive distance are strongly based on the light-dependent visual detection of prey, whereby maximum reactive distances of 50–60 cm are obtained at daylight intensities of 15–20 lux (Vogel & Beauchamp, 1999; Mazur & Beauchamp, 2003). Below 0.4 lux, visual detection of prey is substantially impaired and reactive distances become very small. In contrast, reactive distances of planktivorous fish at this illumination are still in the range of 2 cm, even for very small zooplankton species, supporting the idea of the antipredation window (Gjelland *et al.*, 2009).

However, for two reasons, an exact definition of the minimum light requirements for planktivory and piscivory is critical for a mechanistic understanding of DVM. First, the intensity and duration of feeding during crepuscular and nocturnal periods are decisive for the food uptake of planktivorous fish, because zooplankton density available for fish is usually higher at night, thus potentially facilitating higher crepuscular and nocturnal feeding rates than by day (if critical illumination thresholds are lower than so far demonstrated experimentally). Second, it is generally assumed that piscivores stop feeding at night, making surface waters safe habitats for migrating prey. However, even slightly stronger illumination at night (by moon or light pollution) may induce enhanced nocturnal feeding activity of piscivores (e.g. Mazur & Beauchamp, 2006). Therefore, if DVM of prey fish is a response to predation risk, DVM patterns and amplitudes should be strongly variable between successive phases of the moon and might differ between urban and rural lakes. A systematic comparison of habitat use, together with empirical data on the illumination gradients over the diel cycle (Appenzeller & Leggett, 1995; Busch & Mehner, 2009), might elucidate whether observed DVM amplitudes correspond to the antipredation window, as predicted from critical illumination thresholds for feeding. More systematic experimental approaches on feeding intensity at low-light conditions, for example by using infrared illumination and cameras, may help quantifying the potential food uptake of fish by night.

### *Assessment and size dependence of predation risk*

A third mechanism that requests clarification is the way by which prey fish assess the location, type and density of their predators. If predator avoidance is a strong ultimate cause of DVM, perception of predator presence by the prey fish can be expected in lakes in which DVM occurs. In turn, if prey responded indiscriminately to occasional signs of danger by adopting permanent antipredator behaviour such as DVM, then they might incur considerable opportunity costs. Hence, prey fish should respond according to the perceived levels of risk (Kats & Dill, 1998; Ferrari, Sih & Chivers, 2009). Therefore, if DVM is considered as an inducible defence and a phenotypically plastic behaviour, migrations should stop when the costs of the defence (loss of growth) are no longer balanced by the reduced risk of mortality (the threat-sensitive predator avoidance hypothesis) (Helfman, 1989).

If it is assumed that prey fish move within the antipredation window, their visual range will be between 1 cm and about 1 m (Clark & Levy, 1988) and hence prey fish will rarely see predators. Analogous to zooplankton DVM (Loose, Von Elert & Dawidowicz, 1993), it is sometimes assumed that prey fish migrate in response to kairomones (chemical signals of danger) (Pohnert, Steinke & Tollrian, 2007) of predators, thus relying on a different sensory modality, as suggested by the sensory compensation model (Abjornsson *et al.*, 1997; Hartman & Abrahams, 2000). Fish pheromones (including kairomones) can be defined as an odour or mixture of odorous substances, released by the sender and evoking in the receiver adaptive, specific and species-specific response (Sorensen & Stacey, 2004). These chemical signals act as cues for a range of behaviour in fish, but most of them that have been chemically identified to date are associated with fish reproduction, while little is known about the chemical structure of pheromones involved in other types of fish behaviour (Burnard, Gozlan & Griffiths, 2008).

Exceptions are the alarm substances of fish which are released while predators feed upon prey and which induce fright reactions in conspecific prey (Chivers & Smith, 1998; Wisenden, 2000). Fish faeces accumulating on the lake bottom may be another source of chemical cues and have been shown to modify zooplankton diapause (Slusarczyk & Rygielska, 2004) or behaviour of conspecifics of Arctic char (Zhang, Brown & Hara, 2001). Furthermore, predator-naive salmon (*Salmo salar* L.) recognised a sympatric mammalian predator only if alarm cues were released from the diet of predators that originated from conspecifics (Roberts & de Leaniz, 2011).

Despite its logic, induction of DVM in freshwater fish *via* predator kairomones or cues released from skin or faeces, or modification of DVM patterns by alarm substances from conspecific prey, has not yet been demonstrated. There are several behavioural experiments and models which show unambiguously that fish respond with specific antipredator behaviour to single and multimodal predator cues (Hartman & Abrahams, 2000; Martin *et al.*, 2010). However, kairomones from predators alone rarely induced stronger predator avoidance reactions in prey fish as compared to behaviour in control treatments without predator cues (Mikheev, Wanzenböck & Pasternak, 2006; Ward & Mehner, 2010). A further difficulty is related to the density-dependence and temporal persistence of chemical cues. It is assumed (but not confirmed) that kairomone concentration increases with higher predator density. It remains to be quantified which minimum predator biomass per volume of water is needed to induce behavioural responses in prey via kairomones. Alarm substances will be released only if predators have killed or at least attacked the prey (Wisenden, 2000), thus requiring predator–prey encounters whose frequency is density- and activity-dependent. Therefore, the level of predation risk can vary over space and time because of seasonal changes in predator type and density or predator movements between microhabitats (Sih, Ziemba & Harding, 2000). According to the risk allocation hypothesis (Lima & Bednekoff, 1999), the degree of variation in this background risk should influence the cost-benefit ratio of DVM. If we assume that fish are able to perceive the type and size of predator, the spatial origin of risk and predator density (Botham *et al.*, 2008; Martin *et al.*, 2010), we have to expect that the antipredator function of DVM results in much more plastic and temporally and spatially variable migrations than described so far. If risky periods are infrequent, prey should be expected to exhibit high-intensity antipredator behaviour during the few risky periods, but should respond less intensely, but at a lower threshold concentration of alarm cues, if risky periods are frequent (Lima & Bednekoff, 1999; Brown *et al.*, 2006). Systematic comparison of such patterns, both temporally within a system and spatially across systems, is still completely missing in the exploration of DVM in freshwater fish. This gap is primarily attributable to missing information on predator density, distribution and activity over the diel cycle.

Another important deficit is the size-dependent quantification of predation risk for the individual prey fish. Fish predators are gape-limited (Hambright *et al.*, 1991; Mittelbach & Persson, 1998), and therefore, the individual predation risk should decline and approach zero if fish grow into a size refuge. In Scandinavian lakes where coregonids (vendace and several whitefish morphs) perform DVM, the individual predation risk from piscivorous perch drops below 25% in the pelagic area if fish become larger than 10 cm (Bøhn *et al.*, 2002). This suggests that vendace would reach a size refuge against perch predation during the second year of life. If piscivorous brown trout and pike (*Esox lucius* L.) are considered in addition to perch, the predation window encompasses on average 0-20 cm TL and may reach 25 cm maximum threshold in some lakes (Kahilainen & Lehtonen, 2003; Jensen *et al.*, 2008). Accordingly, all vendace, but not all whitefish, would presumably be subject to predation mortality. Therefore, those whitefish not exposed to predation risk should stop migrating and remain in the layer with the highest zooplankton density (because the metabolic cost of warm water can be balanced by high feeding rates in well-illuminated layers).

It has to be noted critically that systematic analyses of predation windows and size refuges of prey fish are not available from most systems in which fish perform DVM. In addition to detailed information on diet composition of predators with respect to both prey species and sizes, information on density, activity and diel habitat use of the predatory species is also very scarce. Hydroacoustics, telemetry and stratified catches by active gear may fill this gap and would ultimately allow a comparison of DVM between lakes differing in density or composition of potential predators.

Overall, the predator avoidance hypothesis of DVM is built on a still relatively poor mechanistic understanding of real predation risk for, and risk assessment by, migrating prey. Stronger interdisciplinary approaches bridging research on the ecology of DVM and antipredator behaviour may be helpful.

## The adaptive value of DVM

By the focus on a cost-benefit analysis ($\mu/g$) of DVM, it is assumed that DVM maximises the fitness of migrating animals relative to non-migrants and that DVM is an adaptive behavioural trait. Adaptation can be defined as a hereditary trait of current benefit that has been shaped by natural selection in the past (Alcock, 2009). Most studies so far have focussed on the current benefit of the trait, for example by comparing the fitness of several migration strategies by cost-benefit analyses (see below). In contrast, evidence for natural selection shaping DVM behaviour and the hereditary nature of the trait is still lacking. There is increasing evidence that a significant proportion of the phenotypic variance in migratory traits of animals is genetic (Liedvogel, Åkesson & Bensch, 2011). Even a phenotypically plastic (and hence inducible) DVM behaviour could be a hereditary trait (Pigliucci, 2005). The trait would then be expressed in certain environments, but not in others, reflected by the concept of 'behavioural reaction norms' (Dingemanse *et al.*, 2010). It is highly likely that there is substantial heritability also for behavioural traits (Dingemanse & Reale, 2005; Brown, Burgess & Braithwaite, 2007; Bell & Aubin-Horth, 2010). Diel vertical migration would be a perfect application of the behavioural reaction norm because it can be assumed that migration is induced only under a certain set of environmental conditions under which a fitness benefit of migrants emerges. However, experimental approaches modifying the environmental conditions, or transplanting potentially migrating fish from one system into another one, have not yet been available. Therefore, in a strict sense, it has not yet been possible to show that DVM of freshwater fish is indeed adaptive, and all discussions on the evolutionary value of DVM are at risk of being 'just-so' stories (Gould & Lewontin, 1979). Consequently, more rigorous scientific approaches are needed to counter this criticism.

### *Current benefit of DVM*

The current benefit of the DVM has usually been deduced from the field conditions under which it was observed. Technically, it has remained challenging to show that the $\mu/g$ ratio for fish performing DVM is lower than the risk-benefit ratio of potentially non-migrating fish. By using an encounter rate and bioenergetics model, Jensen *et al.* (2006) calculated the cost-benefit ratio as predation risk over growth rate potential (GRP) (Brandt, Mason & Patrick, 1992) for predatory lake trout and their prey, the planktivorous deepwater ciscoes that feed upon opossum shrimp. The model suggested that lake trout maximised foraging and growth rates by tracking vertically migrating ciscoes. Two alternative DVM trajectories of ciscoes reflected a trade-off between growth and predation risk. The shallow trajectory (a daytime depth of 80 m) was characterised as a high risk–high gain strategy, to be expected at high lake trout densities. In contrast, the low risk–low growth strategy, which assumed descents of ciscoes down to 150 m, was predicted to occur at low predator densities (Jensen *et al.*, 2006). However, the migration trajectories of the larger-bodied cisco and the smaller-bodied kiyi were completely unrelated to densities of lake trout in Lake Superior over 2 years, so the theory was not confirmed (Stockwell *et al.*, 2010). Stockwell *et al.* (2010) concluded that light-based foraging theory, as summarised in the antipredation window, is probably not applicable to the DVM of ciscoes in the offshore demersal habitats of Lake Superior.

Several DVM scenarios were compared using a bioenergetics model for kokanee salmon (Bevelhimer & Adams, 1993). The model was applied only to large adult kokanee (>30 cm length) such that predation risk could be neglected in the analyses. The simulations demonstrated that vertical migrations can be energetically advantageous when kokanee and their prey are thermally segregated. The rule emerging from the model is to feed where the net energy intake is maximised and then reside when not feeding where energetic costs are minimised and food is digested to the point that next feeding is no longer limited by gut fullness (Bevelhimer & Adams, 1993). Therefore, the model could demonstrate a selective advantage of DVM when bioenergetics efficiency and feeding opportunity were taken into account simultaneously, but predation risk was assumed to be zero.

In a similar modelling approach using bioenergetics and illumination-dependent functional response curves, the feeding of small coregonids in Lake Stechlin was assumed to occur within the antipredation window (Busch *et al.*, 2011). Accordingly, coregonids had low feeding rates at low zooplankton density during day, but slightly increased feeding rates during the migration phases as long as light did not fall below the minimum threshold. Furthermore, these fish were modelled to stop feeding completely at night despite occurring in layers with high zooplankton density. However, the temperature at night approximated the final temperature preferendum of the coregonids, thus assuming that fish optimised their bioenergetic efficiency. The model could reliably predict growth rates of fish which had been empirically observed in Lake Stechlin (Busch *et al.*, 2011; Busch, Kirillin & Mehner, 2012), suggesting that the mechanistic detail employed here was appropriate to simulate the feeding and migration behaviour of fish in this lake. However, scenarios run by the model revealed that DVM was not the energetically optimum strategy. Whereas migrating fish would grow slightly faster than fish remaining permanently in the deep water, non-migrating fish remaining permanently near the surface would grow several times faster than migrants. The main reason for this differing performance is the high zooplankton feeding rate potentially achievable during full illumination near the surface (Busch *et al.*, 2011). Although not modelled, these results suggest that the predation risk high in the water column during the day must have been substantial to offset the potential gain from the high feeding rates. This assumption contrasts with the empirical observation that predator density is very low in the pelagic of Lake Stechlin (Mehner *et al.*, 2010).

The different outcome from these two technically similar approaches (Bevelhimer & Adams, 1993; Busch *et al.*, 2011) can be explained by the fact that coregonids in Lake Stechlin migrate only within a narrow thermal window between 3.5 °C (deep layers) and about 9–11 °C (shallow layers). In contrast, the thermal gradient in the North Carolina reservoir where kokanee performed DVM (Bevelhimer & Adams, 1993) was unusual because a thermocline was never expressed, and temperatures >15 °C often extended down to 18–20 m depth. Therefore, the permanent occurrence in the cooler surface layers of Lake Stechlin was energetically less costly for the coregonids than the permanent occurrence of kokanee in the warmer surface waters of the North Carolina reservoir. Consequently, DVM may be the superior strategy if the main waterbody is relatively warm, as in North Carolina, but may result in lower growth rates than stationary strategies if fish migrate only within relatively cold water, as in Lake Stechlin. These two studies again reveal that the behaviour of individual fish populations is shaped by the seasonally variable environmental gradients in their lakes (Stockwell & Johnson, 1999; Hardiman *et al.*, 2004), and hence the interplay of bioenergetics, feeding and predator avoidance may differ from system to system.

These modelling approaches demonstrate two shortcomings with respect to the cost-benefit analysis and hence the adaptive value of alternative migration strategies. First, quantification of potential growth rates and predation risks of fish can be difficult even in systems that are empirically well studied. A combination of hydroacoustics with trawling seems to be particularly promising in estimating density and diel depth distribution of predator and prey fish simultaneously (Yule *et al.*, 2007; Emmrich *et al.*, 2010). Second, fitness has not yet been measured comprehensively, but has been approximated usually only by growth rates and their ratios to predation risk. Reproductive success of migrating fish has neither been followed nor modelled. This deficit is presumably caused by the technical challenge of following individuals over their life time in large deep lakes. Further advances in telemetry methods could give insights into individual plasticity (for an application to sharks, see Sims *et al.*, 2006) and life-history consequences. Experiments in mesocosms that would allow the manipulation of zooplankton and predator densities have not yet been achievable, presumably owing to the sheer spatial dimension needed to create tanks deep enough to simulate light, temperature and pressure gradients similar to those observed in nature. Fine-meshed net cages (such as those used in aquaculture) extending from the lake surface down to the bottom across 30–40 m depth are an alternative, but currently there is no study available in which this enclosure type has been used to explore alternative migration strategies of fish.

### *The adaptive value at the individual level*

An interesting contribution from theoretical ecology is the development of individual-based models (IBMs) that use the same apparent unit as evolution, namely individuals (DeAngelis & Mooij, 2005). Therefore, IBMs may elucidate the consequences of individual behavioural plasticity. For example, individual-based neural network genetic algorithm (ING) has been used to simulate the life history of the marine fish Müller's pearlside [*Maurolicus muelleri* (Gmelin)] (Strand, Huse & Giske, 2002; Giske *et al.*, 2003). In addition, the model predicted DVM behaviour in good agreement with empirical observations. However, the strength of the individual approach became obvious from the differing predictions of DVM patterns for (i) juvenile and adult fish, (ii) individuals with differing stomach fullness (and hence differing satiation) and (iii) an asymmetry of timing between ascent and descent (Strand *et al.*, 2002). These modelled individual differences in migration speeds and trajectories were confirmed recently from empirical observations on coregonids in Lake Stechlin by applying stationary hydroacoustics at dusk and dawn over seven successive months. A higher migration speed and an earlier start of ascent and a slightly later start of descent were documented for small relative to large coregonids (Busch & Mehner, 2012). Fish starting earlier and swimming faster reach surface waters earlier and hence might feed at higher zooplankton densities during the crepuscular phase, despite a somewhat higher risk of leaving the antipredation window. According to bioenergetics models, individuals conducting such a high risk–high gain strategy may increase their growth rates by about 20% compared with individuals migrating 'with the crowd' (Busch & Mehner, 2012).

According to the traits by which individual fish within a population may differ (e.g. size, satiation, reproductive status), DVM can even be expected to become partial, with a split into migrant and non-migrant parts of the population. This would make the diel migrations conceptually similar to partial seasonal migrations, as known for fish or birds (Brodersen *et al.*, 2008). In this case, individually differing $\mu/g$ ratios and hence individually differing adaptive values may determine the 'decision' to migrate (Brodersen *et al.*, 2008). Examples of partial DVM in freshwater fish are still rare. The most comprehensive study analysed the frequency of non-migrant coregonids from 28 night-time hydroacoustic surveys in Lake Stechlin over 10 years (Mehner & Kasprzak, 2011). Across all surveys, the percentage of non-migrants varied between 7 and 33%, thus suggesting that DVM was partial on all occasions. A mechanistic understanding of the drivers of partial DVM in Lake Stechlin could not be achieved, because even correlations between the percentage of non-migrants and environmental conditions were weak (Mehner & Kasprzak, 2011). The results suggest, however, that feeding rates in diurnal habitats and the temperature in nocturnal habitats could influence the proportion of migrating fish. A somewhat higher energetic density (J (kg fresh mass)$^{-1}$) was found in migrating vendace relative to non-migrants, suggesting that DVM bears some costs that cannot be covered by individuals with lower body condition (Mehner & Kasprzak, 2011).

Similar observations of partial DVM from single surveys have been documented earlier (but not exactly quantified) for the coregonids in the Great Lakes (Fabrizio, Adams & Curtis, 1997; Eshenroder *et al.*, 1998; TeWinkel & Fleischer, 1999; Yule *et al.*, 2007), suggesting that partial DVM is more common than assumed hitherto. However, in all these studies, the non-migrant strategy was characterised by individuals residing permanently in deep water. Remaining near the surface was not observed, although the bioenergetics models indicated it results in better growth than remaining deep in the water column (Busch *et al.*, 2011). Evidence for a population split into surface non-migrants and migrating fish comes only from a single study on perch (*Perca fluviatilis* L.) larvae (Cech *et al.*, 2005).

Finally, it should be noted that the 'decision' to migrate may simultaneously be modified by the behaviour of the other population members. In that case, each individual is a player in a population game, and the resulting distribution may be a spatial evolutionary stable strategy (ESS) (Milinski, 1988). Theories related to the distribution of individuals across feeding patches can be subsumed under the Ideal Free Distribution (IFD) concept (Fretwell & Lucas, 1970), with its several variants which state that individuals should distribute between patches of differing resource quantities in a way that all get equal rewards (Tregenza, 1995; Tregenza & Thompson, 1998). The Ideal Free Distribution assumes that all individuals are 'ideal' in knowing where to maximise their expected gains, and 'free' to leave and enter the respective habitats. The theory has successfully been applied to zooplankton DVM both conceptually (Gabriel & Thomas, 1988) and experimentally (Lampert, McCauley & Manly, 2003; Lampert, 2005). However, its application to fish DVM is less straightforward because non-migrants and migrants feed in different patches primarily during the crepuscular migration phases. This antipredation window with sufficient illumination to feed is shorter for the non-migrants because the illumination window moves upwards after sunset and similarly reaches the non-migrants later after sunrise. Finally, individual fish are not totally free to leave a patch (to switch from the migrant to the non-migrant strategies), as has been found, for example, in zooplankton for which continued ascents and descents between the patches have been observed (Lampert, 2005). Taken together, feeding rates of resident fish are unlikely to be as high as those of migrants. Thus, although models are available (Hugie & Dill, 1994), social game theories may not be totally applicable to DVM of freshwater fish.

## Conclusions

Diel vertical migration in freshwater fish is well documented from a range of systems and species. The contribution of vertical gradients in light, temperature, pressure, zooplankton resources and fish predators to DVM is clearly substantiated in all empirical examples (Fig. 1). Owing to the variability of these gradients, the specific proximate and ultimate causes of DVM presumably differ from system to system. Therefore, it is suggested that, rather than merely adding more case studies, a systematic comparison of migration patterns and the underlying gradients across the systems should be performed. Furthermore, a number of potentially profitable research questions related to the ultimate causes of DVM are summarised in Table 1. Among others, the different ecological or physiological traits of fish individuals within a population may offer the most valuable insight into the evolution of DVM, if trait individuality also results in individually plastic migration patterns or trajectories. The methodological challenge here is to follow individuals and their migration trajectories over longer time periods, as has become possible for horizontal migrations of fish in small, shallow lakes (Brodersen *et al.*, 2008). Finally, it has become clear that research on DVM of freshwater fish will profit from a stronger interdisciplinary approach, for example in collaborations between behavioural, physiological and theoretical ecologists.

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