

Differences in lens optical plasticity in two gadoid fishes meeting in the Arctic

Mikael Jönsson · Øystein Varpe · Tomasz Kozłowski ·
Jørgen Berge · Ronald H. H. Kröger

Received: 19 March 2014 / Revised: 27 July 2014 / Accepted: 9 September 2014 / Published online: 21 September 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract Arctic and boreal/temperate species are likely to be evolutionary adapted to different light regimes. Currently, the boreal/temperate Atlantic cod (*Gadus morhua*) is coexisting with the native polar cod (*Boreogadus saida*) in the Arctic waters around Svalbard, Norway. Here, we studied light/dark adaptative optical plasticity of their eye lenses by exposing fish to bright light during the polar night. Schlieren photography, high-definition laser scanning and ray tracing were used to determine the optical properties of excised crystalline lenses. Both species have multifocal lenses, an optical adaptation for improved color vision. In polar cod, the optical properties of the lens were independent of light exposure. In the more southern Atlantic cod, the optical properties of the lens changed within hours upon exposure to light, even after months of darkness. Such fast optical adjustment has previously only been shown in a tropical cichlid. During the polar night the Atlantic cod lens seems to be unregulated and dysfunctional since it had an unsuitable focal length and severe spherical aberration. We present a system, to our knowledge unique, for studying visual plasticity on different timescales in relation to

evolutionary history and present the first study on the polar cod visual system.

Keywords Experiment · Fish · Multifocal lens · Visual plasticity · Global warming

Abbreviations

BCD	Back center distance
BEP	Beam entrance position
LSA	Longitudinal spherical aberration
R	Lens radius
RIG	Refractive index gradient
RMM	Retinomotor movement

Introduction

Physiological plasticity helps animals to cope with variable environmental conditions by adjusting appropriate traits to current or predictable future conditions (Reed et al. 2010). However, the type and level of plasticity vary greatly between species. Some environmental conditions change in predictable cycles of different time scales, e.g. daily, lunar, or annual cycles. Animals exposed to short-term environmental cycles should be adapted to such variability, while animals accustomed to more stable conditions or slow cycles should be less flexible, i.e., have less plasticity or slower response times. Through the effects of global warming, more southern species have the opportunity to move northward into the Arctic due to increasing temperatures (Perry et al. 2005). However, light limitations on prey encounter rates can determine both spatial (Aksnes et al. 2004) and temporal (Varpe and Fiksen 2010) patterns of fish distributions, and it is hypothesized that the light regime (Fig. 1) in the Arctic will limit the success of

M. Jönsson (✉) · T. Kozłowski · R. H. H. Kröger
Lund Vision Group, Functional Zoology, Department of Biology,
Lund University, Sölvegatan 35, 223 62 Lund, Sweden
e-mail: mikael.jonsson@biol.lu.se

Ø. Varpe
Akvaplan-niva, Fram Centre, 9296 Tromsø, Norway

Ø. Varpe · J. Berge
The University Centre in Svalbard, P.O. Box 156,
9171 Longyearbyen, Norway

J. Berge
Faculty of Biosciences, Fisheries and Economy,
University of Tromsø, 9037 Tromsø, Norway

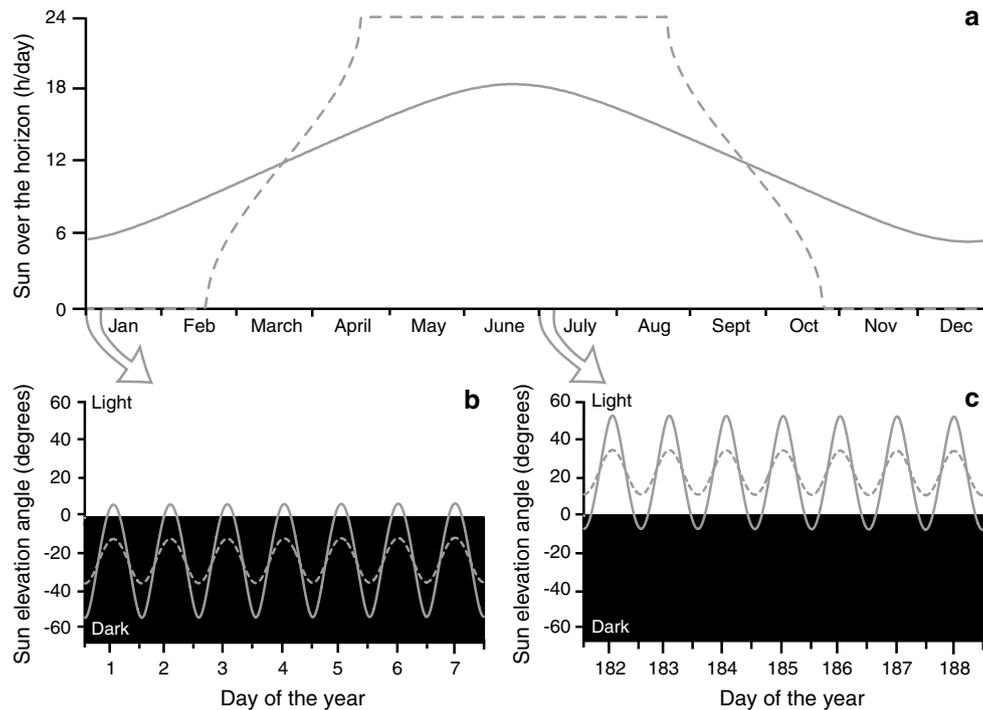


Fig. 1 Seasonal variation in light conditions in the Arctic, Longyearbyen on Svalbard at $78^{\circ}13'N$, $15^{\circ}38'E$ (dashed lines), and in the boreal zone, Oslo in Norway at $59^{\circ}55'N$, $10^{\circ}45'E$ (solid lines) plotted as the time the sun is above the horizon over the entire year (a)

and the elevation angle of the sun during the first week in January (b) and during the first week in July (c). Negative elevation angles indicate that the sun is below the horizon (black panels) and positive elevation angles indicate that it is above the horizon (white panels)

invaders as they are evolutionarily poorly adapted to the extreme light conditions (Kaaertvedt 2008). Arctic species, on the other hand, should be adapted to cope with stronger annual cycles in light levels rather than year round daily cycles. As maintaining plasticity is costly (DeWitt et al. 1998), visual foragers in the Arctic may benefit from having lower short-term plasticity, measured as their ability to adapt their eyes between light and dark periods, during the long and dark polar night compared to their boreal relatives that are adapted to continuous daily light cycles.

Currently, the Atlantic cod (*Gadus morhua*) is coexisting with its Arctic relative, the polar cod (*Boreogadus saida*) around Svalbard ($78^{\circ}N$, $15^{\circ}E$), Norway, offering a suitable system for analyzing the effects of evolutionary adaptation to different light cycles. As vision is one of the most important senses in most higher animals (Land and Nilsson 2012), it is crucial to adjust it to different light conditions (Wagner and Kröger 2005). In fish, light/dark adaptation may include adjustments in the lens (Schartau et al. 2009; Kröger 2013), mechanical restructuring of the retina called retinomotor movements, RMM (Douglas 1982; Burnside and Nagle 1983) and neural adaptation (Donner 1987). Most fishes, including the Atlantic cod (Anthony and Hawkins 1983), have a dual retina with both rod and cone photoreceptors (Nicol 1989). The highly sensitive rods are

used for vision in dim light, i.e., in the dark-adapted state, whereas in the light-adapted state the cones are used for color vision, mediated through the different absorption maxima of several classes of cone photoreceptors. In the Atlantic cod, at least two classes of cone photoreceptors are present, one long-wavelength-sensitive (red) cone and one short-wavelength-sensitive (blue) cone (Anthony and Hawkins 1983). In typical fish eyes, rods and cones do not share retinal space, but instead trade positions between the light and dark-adapted state through RMM (Douglas 1982; Burnside and Nagle 1983). RMM makes the dark-adapted fish retina functionally an all-rod retina, while the light-adapted retina is functionally an all-cone retina (Burnside and Nagle 1983). In the Atlantic cod, RMM occur both as pigment and photoreceptor migrations (Anthony and Hawkins 1983). Varying spectral properties of the retina complicate the creation of well-focused images.

In a typical fish eye, the crystalline lens is the only refractive element. It is rigid and spherical (ball-shaped) and not covered to any significant part by the iris, and the pupil is indifferent to light level (Walls 1942; Duke-Elder 1958). Lateral and oblique aberrations thus play minor roles, and optical performance is limited by longitudinal spherical and chromatic aberrations. Longitudinal spherical aberration (LSA) is compensated for by a radially

symmetric refractive index gradient (RIG) (Maxwell 1854; Campbell 1984; Kröger et al. 1994). Full compensation for LSA (monofocal lens) is optimal during the dark-adapted state, as fish vision is monochromatic, i.e., based on a single visual pigment, with a functionally all-rod retina. Creating an optimal image is more demanding in the light-adapted state, with several spectral classes of cone being operational. The main optical problem in creating well-focused images throughout the visual spectrum, which in light-adapted fish may span from ultraviolet to near-infrared (Bowmaker 2008), is the defocusing effect of longitudinal chromatic aberration. The problem is particularly severe in eyes of short depth of focus (large aperture and short focal length), such as most fish eyes (Kröger 2011, 2013). Longitudinal chromatic aberration is compensated for by fine adjustments of the RIG, where minute changes in refractive index may result in large changes in the optical properties of the lens (Gagnon et al. 2012; Kröger 2013). A light-adapted fish lens has an LSA-curve (focal length as a function of distance from the center of the lens at a specific wavelength) of complex shape, leading to several focal lengths for monochromatic light (multifocal lens). If polychromatic light enters the eye, each focal length creates a well-focused image for one spectral class of cone at the same distance from the lens (Kröger et al. 1999; Gagnon et al. 2012). The multifocality of the lens is species-specific, matching the color vision capabilities of the cone system and the visual needs of each species (Karpestam et al. 2007). The light/dark adaptive re-organizations of the fish retina (all-cone vs. all-rod) and lens (multifocal vs. monofocal) are completed within about an hour or less (Douglas 1982; Burnside and Nagle 1983; Schartau et al. 2009). We investigated whether light/dark adaptive changes in the lens occur in two gadoid species of different evolutionary histories that meet in the Arctic due to global warming.

Atlantic cod is a commercially important fish species that has been heavily harvested historically and suffered population collapses or severe stock reductions on both sides of the Atlantic (Hutchings and Myers 1994; Cook et al. 1997). The polar cod, on the other hand, has been harvested historically, but its current commercial value is limited. It is a common Arctic gadoid with a circumpolar distribution (Hop and Gjøsaeter 2013) and a completely unknown visual system. It may, however, be one of the most ecologically important fish species in the Arctic (Hop and Gjøsaeter 2013; Nahrgang et al. 2014) as it is an abundant food source for a variety of Arctic animals such as large marine mammals (Dahl et al. 2000; Labansen et al. 2007; Marcoux et al. 2012) and birds (Mehlum et al. 1996; Matley et al. 2012). Polar cod is rather small (40 cm total length, TL) compared to the Atlantic cod (1–2 m TL) but individuals of similar size co-occur and may therefore compete for resources (Varpe et al. in prep.). The larger

predatory Atlantic cod may also feed on the smaller polar cod, as has been observed previously when their ranges temporarily overlapped (Orlova et al. 2009). The abilities of the two species of adapting the visual system may affect both their competitive and predator–prey interactions.

The experiments and measurements were performed on a research vessel around Svalbard, Norway, during the polar night, a time of the year when very few studies have previously been performed due to the extreme climate and weather conditions. By experimentally exposing both fish species to either dark or day-light conditions and using schlieren photography, high-definition laser scanning and ray tracing to analyze the optical properties of their lenses, we addressed the question whether Atlantic and polar cod differ in short-term optical plasticity of the lens. Such measurements have previously only been performed in a laboratory setting on tropical fish used to stable circadian light/dark cycles (Schartau et al. 2009). It is unknown whether similar optical adjustments also occur in species adapted to the light regimes of temperate and Arctic zones. In the temperate zone, day length varies between summer and winter, i.e., there is a circa-annual cycle in addition to the circadian cycle. In the Arctic zone, the circa-annual cycle dominates, with little circadian variation in light level during summer and winter (Fig. 1), but with a transitional phase of circadian light cycles during spring and autumn. However, the absolute light level in the pelagic depends on several other factors such as sun elevation angle, ice and snow coverage, weather conditions, water transparency etc. As vision is dependent on the availability of light (Johnsen 2012) and as both vision (Niven and Laughlin 2008) and plasticity per se (DeWitt et al. 1998) are costly, it is likely that optical plasticity of the lens is affected by the slow light cycles in the Arctic. This is the first description of the completely unknown visual system of polar cod and our study is also an important step toward understanding whether Atlantic cod is a threat to polar cod through the effects of anthropogenic climate change. Our results may furthermore be of relevance for understanding the regulatory mechanisms that govern lens performance in vertebrates in general.

Methods

Experimental protocol

Experiments were carried out in January 2013 onboard the Research Vessel *Helmer Hanssen* from the University of Tromsø, Norway. To ensure a large enough catch, trawling for polar and Atlantic cod was done at three different locations around Svalbard; in Billefjorden (78°N 16°E) at 170 m depth, Kongsfjorden (79°N 12–13°E) at 300 m

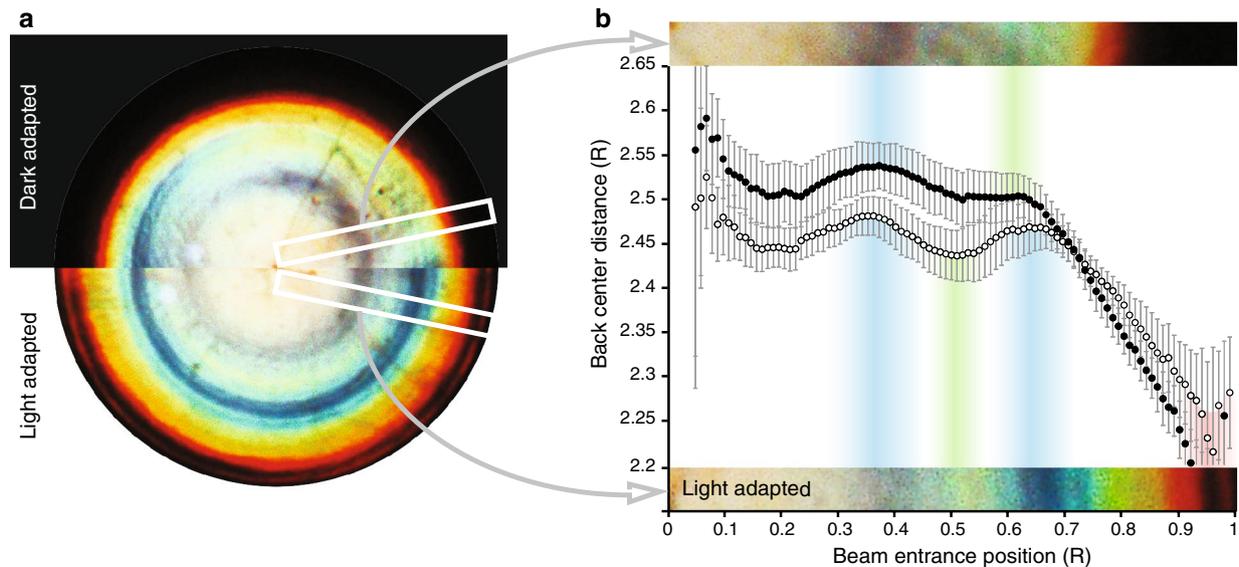


Fig. 2 Schlieren photograph (**a**) and LSA-curves from laser scanning (**b**) of dark (*closed circle*) and light-adapted (*open circle*) lenses from Atlantic cod (*Gadus morhua*) caught around Svalbard, Norway, during the polar night (January 2013). In panel **a**, the black field shows a dark-adapted lens and the white field a light-adapted lens. Lens size of the dark-adapted lens is normalized to the light-adapted lens so that both halves have the same size on the image. In panel **b**, all values are normalized to lens radius (R). Beam entrance position 0 is in

the center of the lens and 1 is at the surface. Back center distance is the distance from the center of the lens to where the exit beam intercepts the optical axis (*focus point*). Colored bands indicate relative wavelengths of focused light from specific lens zones (*plateaus in the graph*). Error bars denote 90 % confidence intervals of the mean, which indicate significant difference ($\alpha = 0.05$) if error bars are not overlapping

depth, and Rijpfjorden (80°N 18–19°E) at 210 m depth. To minimize exposure to light, fish were moved to dark tanks as fast as possible and remained there for several hours to make sure they were in good condition and had not been damaged by the trawl.

For each species, the catch was divided into a dark-adapted group (remained in the dark tanks) and an experimentally light-adapted group which was moved to white 50 L containers and exposed to bright halogen light (1,900 lux, 480 cd/m²) for 3–6 h prior to analysis. Fish from the two treatments were randomly selected, sacrificed by decapitation and pithing, their lenses excised and put in a modified H10-solution to keep cells viable during measurements (Schartau et al. 2010). The H10 composition was 120 mM NaCl, 2.50 mM KCl, 0.80 mM CaCl₂, 1 mM MgCl₂, 10 mM glucose and 3 mM HEPES. The pH was adjusted to 7.4 and osmolarity was adjusted by dilution to 310–320 mOsm using pre-made calibration curves (3300 Advanced Micro Osmometer, Advanced Instruments Inc.). Since lens cells are sensitive to high levels of oxygen, the solution was degassed prior to use by freezing and thawing. The lenses were suspended in the modified H10 both during Schlieren photography and laser scanning.

Schlieren photography

Lenses were suspended by their ligaments in an immersion chamber and rotated to a position where photographs could be taken along the optical axis of the lens. The schlieren photography setup is described in detail in Mallick and Kröger (2005) and consists of a point light source (3,200 K) directed toward a beam splitter that reflects the light into an immersion bath (modified H10) which contains the suspended fish lens. The light is focused by the lens on a diffuse reflector that reflects the light back through the lens and through the beam splitter. The fish lens focuses the light on a pinhole behind the beam splitter and only the light that passes the pinhole is registered by a camera (Sony Cybershot DSC-F828). By adjusting the distance between the lens and the diffuse reflector, different wavelengths of light are focused on the pinhole and an image of the lens containing a broad range of wavelengths, displayed as colored rings, is captured by the camera (Figs. 2a, 3a). Schlieren photography shows the degree of multifocality of a lens, but it is a relative measure indicating which zones are focusing longer and shorter wavelengths of light. The method does not provide quantitative data on light refraction and as the lens is hanging by its muscle while being

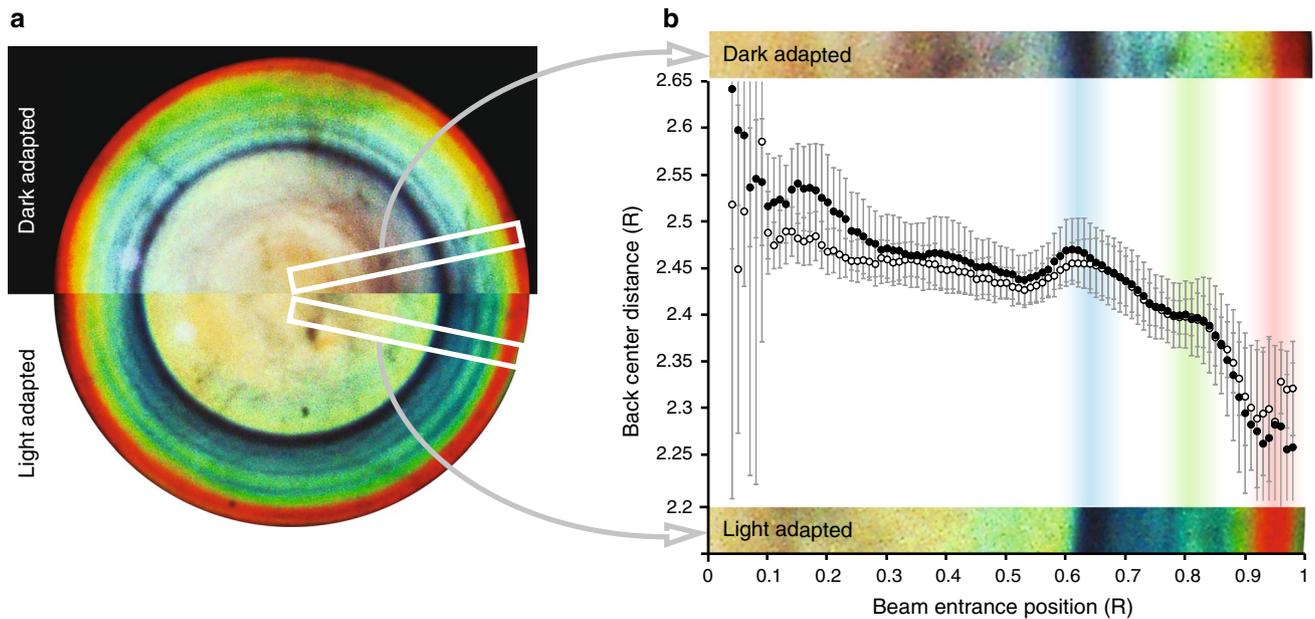


Fig. 3 Schlieren photograph (a) and LSA-curves from laser scanning (b) of dark (closed circle) and light-adapted (open circle) lenses from polar cod (*Boreogadus saida*) caught around Svalbard, Norway, during the polar night (January 2013). Presentation as in Fig. 2

photographed, it is affected by ship movements. Therefore, we also used laser scanning and ray-tracing analysis which gives quantitative data and where the lens is fixed and therefore not affected by ship movements.

Laser scanning

After schlieren photography was completed, the lens was moved to an immersion bath where 1 μL of a solution with 0.1 μm polystyrene beads (Sigma Aldrich) were added to every 10 mL of H10-medium to make the laser beam visible. The immersion bath had a black bottom with a lens holder on which the lens was placed so that the laser would pass the lens parallel to the optical axis. The laser-scanning setup is also described in detail in Malkki and Kröger (2005) and consists of a class 2 green laser (1 mW, 532 nm) with a focusing lens that focuses the laser beam in front of the lens holder in the immersion bath. The laser is attached to a linear motorized translator so that it can be moved smoothly from side to side. The laser beam enters the immersion bath and passes the lens which deflects the beam differently depending on where it enters the lens. The height of the beam is adjusted to pass through the center of the lens and the translator is used to scan through the entire lens twice. The scan is recorded from above (Sony Handycam HDR-CX730E) and the recordings are used for ray-tracing analysis using software custom-written in MATLAB R2013a. In the software, the user manually sets the first and last frame of the scan (when the laser passes through the lens as close as possible to the lens surface

on both sides), the number of frames to be analyzed, and defines the edge of the lens. The software then selects evenly spaced sampling points based on the pre-defined number of sampling points needed (250 in this case) and detects entrance and exit laser beams. The average slope of the entrance beams is calculated and the entire data set is rotated so that the entrance beams are horizontal. The center beam is set to be the preliminary optical axis of the lens, which is fine-tuned at a later stage. The back center distance (BCD), i.e., the distance between the center of the lens and where the exit beam intercepts the optical axis, is measured and the corresponding beam entrance position (BEP) is registered. BEP is the lateral distance between the entrance beam and the optical axis. All measures are normalized to lens radius (R) and BCD is plotted against BEP to show the LSA-curve. Since correct determination of the optical axis is critical, its position is manually adjusted so that the LSA is symmetrical over the optical axis. The data from both halves of the lens are then averaged, producing a final LSA-curve going from BEP 0 to 1 R. The LSA-curve is plotted for 100 linearly spaced BEPs along R, linearly interpolated from the closest sampling points on either side of each of the 100 BEPs (Malkki and Kröger 2005).

Results

The schlieren photographs (Figs. 2a, 3a) depict lenses from both species, one half each dark and light adapted. The LSA-curves (Figs. 2b, 3b) show mean BCDs for the whole

dataset from each species [numbers of lenses (individuals in brackets): Atlantic cod $n_{\text{light}} = 13$ (9), $n_{\text{dark}} = 15$ (11), polar cod $n_{\text{light}} = 14$ (11), $n_{\text{dark}} = 15$ (11)]. The numbers of individuals were used to calculate confidence intervals.

Schlieren photography shows that the lenses of both Atlantic (Fig. 2a) and polar cod (Fig. 3a) are multifocal with several lens zones of different focal lengths, focusing different wavelengths of light on the pinhole. This is corroborated by the complex shapes of the LSA-curves obtained by laser scanning (Figs. 2b, 3b). Multifocality is preserved in both dark and light-adapted lenses. However, schlieren photographs of dark-adapted Atlantic cod lenses (Fig. 2a) show dark areas in the outer 0.25 R of the lens radius. This area focuses light beyond the detection limit of the camera sensor in the infra-red part of the spectrum. This is indicated by the LSA-curves showing decreasing BCDs toward the periphery of the lens (Fig. 2b). A lens zone of short focal length for green laser light focusses long wavelengths on the retina because of longitudinal chromatic aberration (increasing focal length with increasing wavelength). However, both schlieren photographs and laser scans also show a slightly increased focal length in the periphery, seen in the schlieren photographs as a red outer zone in light-adapted Atlantic cod (Fig. 2a) and a green outer zone in light-adapted polar cod (Fig. 3a) and as a rise in the LSA-curves for both species (Figs. 2b, 3b).

It is also evident from the schlieren photographs that the refractive index gradient of the lens changes if Atlantic cod is exposed to light (Fig. 2a). This is corroborated by the LSA-curves having the same general shape but on different levels, with dark-adapted fish having longer BCDs than light-adapted fish except for the periphery of the lens (Fig. 2b). In contrast, there is no change in the optical properties in response to light treatment in polar cod lenses, as indicated by both schlieren photographs (Fig. 3a) and LSA-curves (Fig. 3b).

Discussion

Here we show that two coexisting gadoid fish species both have multifocal lenses during the polar night. However, only one of them, the southern species Atlantic cod, adjusts its lens's RIG when experimentally exposed to daylight conditions. Atlantic cod is the first temperate/boreal fish species known to show fast adjustment of the lens's RIG, as it has previously only been demonstrated in the tropical cichlid *Aequidens pulcher* (Schartau et al. 2009). In contrast, the lens of the northern polar cod is indifferent to short experimental exposure to light during the polar night. However, it may still possess this ability during the brighter parts of the year or in the transitional periods of spring and autumn.

Multifocal lenses are regarded as necessary for sharp color vision if the fish retina is functionally all-cone during daylight conditions. If the demands of the retina change because of changes in opsin genes or opsin gene expression (evolutionary; e.g. Parry et al. 2005), an ontogenetic sequence of opsin gene expression (developmental; e.g. Evans and Fernald 1993), or complete switches between rod and cone vision (adaptive; e.g. Douglas 1982), the optical properties of the lens have to adjust for optimal vision (Kröger 2013). To cope with chromatic and spherical aberrations of their lenses, many animals adjust the lens's RIG (Pierscionek and Regini 2012; Kröger 2013). Fast changes between mono- and multichromatic retinal function brought about by RMM in fishes call for equally fast changes in lens RIG and thus optical properties. During the polar night, light levels are low with illumination coming from the moon, northern lights and bioluminescent organisms in the water column. Such dim conditions usually make the fish retina functionally all-rod, i.e., monochromatic with peak sensitivity at other wavelengths than during daylight conditions when several classes of cone may be used. The logical adaptation for optimal vision would therefore be a monofocal lens during the polar night, sacrificing color vision but instead maximizing the focusing ability to the sensitivity peak of the more sensitive rods. In accordance with this, the lens of *A. pulcher*, which is the only species previously evaluated for fast lens adjustments, has been shown to reduce its multifocality when experimentally deprived of light (Schartau et al. 2009). Surprisingly, our findings suggest that the polar cod lens is multifocal also during the polar night. This cannot be put into a functional context at the time being, because information on the photoreceptor and photopigment complements, as well as the presence or absence of RMM is lacking for polar cod.

Results from schlieren photography and laser-scanning suggest that the dark-adapted Atlantic cod lenses were dysfunctional. The differences in BCD between the central and peripheral zones were too large to be useful for well-focused color vision. Dark zones on schlieren photographs are indicative for wavelengths beyond the sensitivity range of the camera being focused. Short BCDs in the dark part of the lens indicate that the focused wavelengths were in the infra-red part of the spectrum, which is heavily absorbed by water (Johnsen 2012). Furthermore, focal length of the central zone of the lens changed substantially by about 0.1 R. A spherical lens 4 mm in diameter with relative focal length of 2.5 R has a refractive power of 200 diopters. A change in focal length of 0.1 R corresponds to a change in refractive power of about 8 diopters. Considering the short depth of focus of fish lenses (Kröger et al. 1999; Kröger 2011, 2013), the central zone of the dark-adapted Atlantic cod lens cannot create a useful image if it does so in

light-adapted fish, which is the most likely scenario. We conclude that Atlantic cod appears to be severely visually impaired during the polar night and that the animals may rely on other senses for foraging. In accordance with this, rearing experiments with *A. pulcher* also resulted in poor optics in fish from dark and spectrally deprived treatments (Kröger et al. 2001). However, the dysfunctionality of the Atlantic cod lens is reversible, since we obtained results more typical for multifocal fish lenses from light-adapted animals. A remaining small dark zone in the very periphery of the lens (Fig. 2a) suggests that 3 h of light exposure may not be sufficient for full reversal of the effects of long-term light deprivation.

The adjustments of lens RIG in Atlantic cod upon exposure to light are probably limited to regions close to the edge of the lens (BEP 0.7–1 R) where the dark zones are on the schlieren photographs of dark-adapted lenses (Fig. 2a). As the RI in the outer zones decreases, BCDs increase (Fig. 2b), and the zones focus light of shorter wavelength compared to the dark-adapted lens. In the central part of the lens (BEP 0–0.7 R) the BCDs are reduced (Fig. 2b). This increasing refractive power of the central parts is likely to be due to the decrease in refractive index in the periphery and not to a change in refractive index in the center itself. The center of the lens can be understood as a lens embedded in a medium (the peripheral part of the lens) of a certain refractive index. When the RI in the lens periphery decreases during exposure to light, the central “lens” gets embedded in a medium of lower RI, which increases its refractive power (shorter BCD). The central parts furthermore consist of densely packed crystallin proteins (Kröger et al. 1994; Pierscionek and Regini 2012) that are unlikely to change in concentration. It is important to keep in mind that the actual changes in refractive index, i.e., in crystallin protein concentration, are minute even in the periphery and would barely be visible when plotted against BEP. In spherical and powerful gradient-index lenses, such as fish lenses, small changes in lens refractive index can lead to considerable changes in the shape of the LSA-curve [measurement: Kröger et al. (2001); modeling: Gagnon et al. (2012)].

Atlantic cod has been suggested to use chemical cues to a large extent when water turbidity reduces the efficiency of vision (Meager et al. 2005) and the species also has a keen auditory sense with directional capacities (Chapman and Johnston 1974; Hawkins and Sand 1977). These senses are independent of light and may be used for foraging by Atlantic cod during the polar night, possibly together with tactile prey search at close range. A recent polar night study in Svalbard waters showed that both polar and Atlantic cod, to some extent, fed during the polar night, but with low degrees of stomach fullness. Atlantic cod fed on benthic organisms to a greater extent than polar cod (Varpe et al. in prep) even if pelagic copepods were the most common

prey group for both fish species. This is indicating a partial dietary overlap between the species during the polar night (Varpe et al. in prep) and a more benthic foraging strategy fits well with poor visual capabilities of Atlantic cod during the polar night. For the polar cod, the senses used during foraging are largely unknown. Since the polar cod does not adjust its lens when exposed to simulated broadband daylight, it may be tuned to specific wavelengths of low intensity, for example from bioluminescence, during the polar night. There is a variety of bioluminescent planktonic organisms that are suitable prey for both cod species (Berge et al. 2012) assuming that they are visually capable to detect them.

The absence of lens RIG adjustment in polar cod indicates that it cannot adjust its lens to short-term changes in light conditions during the polar night, even if a minor increase in BCD (Fig. 3b) occurred in the periphery of the light-adapted lens, seen as a green band in the schlieren photograph (Figs. 3a, b). Even if the variations in light conditions in the Arctic are generally slow, recent work suggests that even small diurnal variations in illumination during winter may induce illumination-based vertical migrations in plankton and pelagic fish (Webster et al. 2013) with slight downward movements in fish during moonlight, indicating that they may try to equalize experienced light levels instead of adjusting their eyes to the varying conditions. However, due to the low light levels it is unlikely that the eyes of polar cod will light adapt during the polar night. The benefit would be minor while there would be a cost both for adjusting the lens and maintaining plasticity (DeWitt et al. 1998). The eyes of polar cod are well developed and dark/light adaptation of the lens may be important during spring and autumn, especially if they are competing with Atlantic cod which can almost instantly adjust the lens to changing light conditions. This leads to several important questions: (i) Does Atlantic cod have functional lenses in the Arctic spring and autumn and if so, is the long light deprivation during polar night the reason for the dysfunctional lens? (ii) Does polar cod change the lens RIG to light conditions during Arctic summer, i.e., becoming more multifocal, even though it is already multifocal during the polar night, and do they exhibit a diurnal adjustment pattern of the lens RIG during spring and autumn, in parallel with retinal restructuring by RMM? (iii) Do these two cod species compete for resources during any time of the year and how is the outcome of such competition dependent on the visual capabilities of the species? And finally, (iv) as polar cod is found further south along the Canadian coast, is the lack of a response to light in the Svalbard population a local adaptation or is the same adaptation present on the Canadian side? Also, does the more southern polar cod on the Canadian side have a similar response in lens RIG as Atlantic cod does around Svalbard?

Answering these questions would bring us closer to elucidating whether Atlantic cod poses a direct or indirect threat to the native polar cod in the high Arctic.

In conclusion, we have shown experimentally that two related gadoid fish species have different short-term plasticity in lens optical properties during the polar night. The more southern Atlantic cod adjusts its lens to prevailing light conditions within hours, which has previously only been demonstrated in the tropical cichlid *A. pulcher*. This suggests that dynamic adjustments of lens RIG may be a general mechanism and of benefit across latitudes. However, there may be a latitudinal limit to where short-term plasticity is no longer beneficial, as polar cod does not react to short-term light treatment during the polar night. Our results also suggest that the Atlantic cod lens is dysfunctional during the polar night. We also present a system that is uniquely suited for studying visual plasticity on different timescales as a function of previous selection. This is the first description of the polar cod visual system and a first step toward understanding the visual competition between fish now coexisting in the Arctic as a secondary effect of global warming on marine ecosystems.

Acknowledgments We thank Anne Christine Utne-Palm for connecting Øystein Varpe with the Vision Group at Lund University. The work was supported by Grants to Øystein Varpe from the Fram Centre in Tromsø and to Ronald Kröger from Knut and Alice Wallenberg foundation, and is part of the Research Council of Norway funded projects CircA (project number 214271/F20) and Marine Night (project number 226417). Experiments followed local legislation and were approved by the regional ethics committee for animal research, Malmö/Lund Ethical Committee on Animal Experiments (Dnr: M141-13).

References

- Aksnes DL, Nejstgaard J, Soedberg E, Sornes T (2004) Optical control of fish and zooplankton populations. *Limnol Oceanogr* 49(1):233–238
- Anthony PD, Hawkins AD (1983) Spectral sensitivity of the cod *Gadus morhua* L. *Mar Behav Physiol* 10(2):145–165
- Berge J, Batnes AS, Johnsen G, Blackwell SM, Moline MA (2012) Bioluminescence in the high Arctic during the polar night. *Mar Biol* 159(1):231–237. doi:10.1007/s00227-011-1798-0
- Bowmaker JK (2008) Evolution of vertebrate visual pigments. *Vision Res* 48(20):2022–2041. doi:10.1016/j.visres.2008.03.025
- Burnside B, Nagle BW (1983) Retinomotor movements of photoreceptors and retinal pigment epithelium: mechanisms and regulation. *Prog Retin Eye Res* 2:67–109
- Campbell MCW (1984) Measurement of refractive-index in an intact crystalline lens. *Vision Res* 24 (5):409. doi:10.1016/0042-6989(84)90039-7
- Chapman CJ, Johnston ADF (1974) Some auditory discrimination experiments on marine fish. *J Exp Biol* 61(2):521–528
- Cook RM, Sinclair A, Stefansson G (1997) Potential collapse of North Sea cod stocks. *Nature* 385(6616):521–522. doi:10.1038/385521a0
- Dahl TM, Lydersen C, Kovacs KM, Falk-Petersen S, Sargent J, Gjertz I, Gulliksen B (2000) Fatty acid composition of the blubber in white whales (*Delphinapterus leucas*). *Polar Biol* 23(6):401–409. doi:10.1007/s003000050461
- DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends Ecol Evol* 13(2):77–81. doi:10.1016/S0169-5347(97)01274-3
- Donner K (1987) Adaptation-related changes in the spatial and temporal summation of frog retinal ganglion cells. *Acta Physiol Scand* 131(4):479–487. doi:10.1111/j.1748-1716.1987.tb08267.x
- Douglas RH (1982) The function of photomechanical movements in the retina of rainbow trout (*Salmo gairdneri*). *J Exp Biol* 96 (FEB):389–403
- Duke-Elder S (1958) The eye in evolution. In: Duke-Elder S (ed) System of ophthalmology, vol 1. Kilmington, London, pp 303–304
- Evans BI, Fernald RD (1993) Retinal transformation at metamorphosis in the winter flounder (*Pseudopleuronectes americanus*). *Visual Neurosci* 10(6):1055–1064
- Gagnon Y, Söderberg B, Kröger R (2012) Optical advantages and function of multifocal spherical fish lenses. *J Opt Soc Am A-Opt Image Sci Vis* 29(9):1786–1793
- Hawkins AD, Sand O (1977) Directional hearing in the median vertical plane by the cod. *J Comp Physiol* 122(1):1–8
- Hop H, Gjøsaeter H (2013) Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. *Mar Biol Res* 9(9):878–894. doi:10.1080/17451000.2013.775458
- Hutchings JA, Myers RA (1994) What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Can J Fish Aquat Sci* 51(9):2126–2146. doi:10.1139/f94-214
- Johnsen S (2012) The optics of life : a biologist's guide to light in nature. Princeton University Press, Princeton, NJ
- Kaartvedt S (2008) Photoperiod may constrain the effect of global warming in arctic marine systems. *J Plankton Res* 30(11):1203–1206. doi:10.1093/plankt/fbn075
- Karpestam B, Gustafsson J, Shashar N, Katzir G, Kroger RHH (2007) Multifocal lenses in coral reef fishes. *J Exp Biol* 210(16):2923–2931. doi:10.1242/jeb.002956
- Kröger RHH (2011) Physiological Optics in Fishes. In: Farrell AP (ed) Encyclopedia of fish physiology: From genome to environment, vol 1. Academic Press, San Diego, pp 102–109
- Kröger RHH (2013) Optical plasticity in fish lenses. *Prog Retin Eye Res* 34:78–88. doi:10.1016/j.preteyeres.2012.12.001
- Kröger RHH, Campbell MCW, Munger R, Fernald RD (1994) Refractive index distribution and spherical aberration in the crystalline lens of the African cichlid fish *Haplochromis burtoni*. *Vision Res* 34(14):1815–1822. doi:10.1016/0042-6989(94)90306-9
- Kröger RHH, Campbell MCW, Fernald RD, Wagner HJ (1999) Multifocal lenses compensate for chromatic defocus in vertebrate eyes. *J Comp Physiol A-Sens Neural Behav Physiol* 184(4):361–369. doi:10.1007/s003590050335
- Kröger RHH, Campbell MCW, Fernald RD (2001) The development of the crystalline lens is sensitive to visual input in the African cichlid fish *Haplochromis burtoni*. *Vision Res* 41(5):549–559. doi:10.1016/S0042-6989(00)00283-2
- Labansen AL, Lydersen C, Haug T, Kovacs KM (2007) Spring diet of ringed seals (*Phoca hispida*) from northwestern Spitsbergen Norway. *Ices J Mar Sci* 64(6):1246–1256. doi:10.1093/icesjms/fsm090
- Land MF, Nilsson D-E (2012) Animal eyes. Oxford University Press, Oxford
- Malkki PE, Kröger RHH (2005) Visualization of chromatic correction of fish lenses by multiple focal lengths. *J Opt A-Pure Appl Opt* 7(11):691–700. doi:10.1088/1464-4258/7/11/012

- Marcoux M, McMeans BC, Fisk AT, Ferguson SH (2012) Composition and temporal variation in the diet of beluga whales, derived from stable isotopes. *Mar Ecol Prog Ser* 471:283–291. doi:[10.3354/meps10029](https://doi.org/10.3354/meps10029)
- Matley JK, Fisk AT, Dick TA (2012) Seabird predation on Arctic cod during summer in the Canadian Arctic. *Mar Ecol Prog Ser* 450:219–228. doi:[10.3354/meps09561](https://doi.org/10.3354/meps09561)
- Maxwell JC (1854) Solutions of problems. The Cambridge and Dublin Mathematical Journal 9:9–11
- Meager JJ, Solbakken T, Utne-Palm AC, Oen T (2005) Effects of turbidity on the reactive distance, search time, and foraging success of juvenile Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 62(9):1978–1984. doi:[10.1139/f05-104](https://doi.org/10.1139/f05-104)
- Mehlum F, Hunt GL, Klusek Z, Decker MB, Nordlund N (1996) The importance of prey aggregations to the distribution of Brunnich's guillemots in Storfjorden Svalbard. *Polar Biol* 16(8):537–547
- Nahrgang J, Varpe O, Korshunova E, Murzina S, Hallanger IG, Vieweg I, Berge J (2014) Gender Specific Reproductive Strategies of an Arctic Key Species (*Boreogadus saida*) and Implications of Climate Change. *PLoS One* 9 (5). doi:[10.1371/journal.pone.0098452](https://doi.org/10.1371/journal.pone.0098452)
- Nicol JAC (1989) The eyes of fishes. Oxford University Press, Oxford
- Niven JE, Laughlin SB (2008) Energy limitation as a selective pressure on the evolution of sensory systems. *J Exp Biol* 211(11):1792–1804. doi:[10.1242/jeb.017574](https://doi.org/10.1242/jeb.017574)
- Orlova EL, Dolgov AV, Rudneva GB, Oganin IA, Konstantinova LL (2009) Trophic relations of capelin *Mallotus villosus* and polar cod *Boreogadus saida* in the Barents Sea as a factor of impact on the ecosystem. *Deep-Sea Res Pt II* 56(21–22):2054–2067. doi:[10.1016/j.dsr2.2008.11.016](https://doi.org/10.1016/j.dsr2.2008.11.016)
- Parry JW, Carleton KL, Spady T, Carboo A, Hunt DM, Bowmaker JK (2005) Mix and match color vision: Tuning spectral sensitivity by differential opsin gene expression in Lake Malawi Cichlids. *Curr Biol* 15(19):1734–1739. doi:[10.1016/j.cub.2005.08.010](https://doi.org/10.1016/j.cub.2005.08.010)
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* 308(5730):1912–1915. doi:[10.1126/science.1111322](https://doi.org/10.1126/science.1111322)
- Pierscionek BK, Regini JW (2012) The gradient index lens of the eye: An opto-biological synchrony. *Prog Ret Eye Res* 31(4):332–349. doi:[10.1016/j.preteyeres.2012.03.001](https://doi.org/10.1016/j.preteyeres.2012.03.001)
- Reed TE, Waples RS, Schindler DE, Hard JJ, Kinnison MT (2010) Phenotypic plasticity and population viability: the importance of environmental predictability. *P Roy Soc Lond B Biol* 277(1699):3391–3400. doi:[10.1098/rspb.2010.0771](https://doi.org/10.1098/rspb.2010.0771)
- Schartau JM, Sjögreen B, Gagnon YL, Kröger RHH (2009) Optical Plasticity in the Crystalline Lenses of the Cichlid Fish *Aequidens pulcher*. *Curr Biol* 19(2):122–126. doi:[10.1016/j.cub.2008.11.062](https://doi.org/10.1016/j.cub.2008.11.062)
- Schartau JM, Kröger RHH, Sjögreen B (2010) Short-term culturing of teleost crystalline lenses combined with high-resolution optical measurements. *Cytotechnology* 62(2):167–174. doi:[10.1007/s10616-010-9268-y](https://doi.org/10.1007/s10616-010-9268-y)
- Varpe O, Fiksen O (2010) Seasonal plankton-fish interactions: light regime, prey phenology, and herring foraging. *Ecology* 91(2):311–318. doi:[10.1890/08-1817.1](https://doi.org/10.1890/08-1817.1)
- Wagner HJ, Kröger RHH (2005) Adaptive plasticity during the development of colour vision. *Prog Retin Eye Res* 24(4):521–536. doi:[10.1016/j.preteyeres.2005.01.002](https://doi.org/10.1016/j.preteyeres.2005.01.002)
- Walls GL (1942) The vertebrate eye and its adaptive radiation. McGraw-Hill, New York
- Webster CN, Varpe Ø, Falk-Petersen S, Berge J, Stübner E, Brierley AS (2013) Moonlit swimming: vertical distributions of macrozooplankton and nekton during the polar night. *Polar Biol*. doi:[10.1007/s00300-013-1422-5](https://doi.org/10.1007/s00300-013-1422-5)