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The relationship between ultraviolet and polarized light and growth rate in the early larval stages of turbot (*Scophtalmus maximus*), Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*) reared in intensive culture conditions

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Abstract

Even small changes in light intensity and spectral composition can have significant effects on the feeding rate, survivorship and growth of marine organisms. For fishes that can perceive them, ultraviolet-A radiation (320–400 nm, UVA) and polarized (POL) light purportedly increase the visibility of prey by enhancing target contrast. Consequently, the efficiency of prey location and ingestion (and, therefore, growth) should be higher in environments rich in UVA and/or POL light. We tested this hypothesis in growth rate experiments with larvae of Atlantic cod (*Gadus morhua*), turbot (*Scophthalmus maximus*) and Atlantic herring (*Clupea harengus*). Turbot larvae possess an UVA-sensitive retinal photoreceptor, while cod and herring larvae apparently do not. Cod, turbot and herring larvae were reared in intensive culture – for at least 18 to 35 d from first-feeding – in 45 l optically isolated matt-black tanks under four light conditions: UVA + POL; UVA + DIFFUSE; NOUVA + POL; NOUVA + DIFFUSE. All light environments were matched for photon flux. There were five replicates per light exposure treatment and larvae were sampled every 3 to 5 d for dry weight. There was no significant difference in growth for any of the larvae under any of the light treatment conditions. These results indicate that, for these species, neither UVA nor POL light significantly improves growth rate in typical intensive culture systems.

Keywords: Ultraviolet vision; Polarization vision; Fish larvae; Zooplanktivory

1. Introduction

Small changes in light intensity and "quality" (i.e. spectral characteristics) can have significant effects on the feeding rate, survivorship and growth of marine organisms (e.g. Downing and Litvak, 2001; Puvanendran and Brown, 2002; Peña et al., 2004). Despite this, the choice of light environment in indoor intensive culture systems has, with few exceptions, been little more than guesswork. For example, fluorescent tubes are commonly used as light sources in such culture systems (Brown et al., 2003). The spectral emission of these tubes is narrow-band and centred on wavelengths that result in them looking white to humans. To marine fishes, whose visual systems are often sensitive at wavelengths different from that of humans, these lights will not look white at all, and they will not appear as intense to them as they do to us; further, the total energy emitted from various fluorescent lamps may be the same while their spectral

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outputs can vary greatly. In addition, unless we know the details of their spectral sensitivity, we are unable to evaluate, a priori, if such lighting conditions might maximize their detection of food (see Browman, 2005).

Many fishes possess an independent retinal photoreceptor which is sensitive in the 340–400 nm range: the UVA (reviewed in Jacobs, 1992; Losey et al., 1999; Britt et al., 2001; Jordan et al., 2004). Although studied in far fewer fish species, polarization vision has been reported in salmonids and cyprinids (reviewed in Hawryshyn, 1992; Horváth and Varjú, 2004). Often, UVA and POL vision are coupled, as is the case for damselfish (Hawryshyn et al., 2003). Although there are several possible adaptive roles for UVA and POL vision in fishes, the one most relevant in the context of intensive culture systems is the possible contrast enhancement of small prey targets (discussed by Fineran and Nicol, 1978; Browman et al., 1994; Bowmaker and Kunz, 1987; Shashar et al., 1998; Loew and McFarland, 1990; Novales Flamarique et al., 1992; Loew et al., 1993; Britt et al., 2001). Since most zooplankton are small, transparent targets (Hamner, 1996; Johnsen and Widder, 1998), contrast enhancement can potentially lead to improved zooplanktivory by larval fishes which possess UVA and/or POL vision.

The limited number of studies on UVA-enhanced zooplanktivory are seemingly contradictory. In a laboratory experiment, UVA moderately increased prey location distances in juvenile rainbow trout (*Oncorhynchus mykiss*) (Browman et al., 1994). However, in a field experiment, there was no effect of UVA on the number of prey eaten by juveniles of the same species (Rocco et al., 2002). A third study found that UVA enhanced the feeding rates of cichlids (Jordan et al., 2004). While no studies have attempted to quantify how POL light affects feeding rates in fishes, it moderately increases prey location distances in juvenile rainbow trout (Novales Flamarique and Browman, 2001). Thus, if UVA and/or POL light enhance zooplantivory, they could potentially be used to increase the growth rates of fish larvae cultured in intensive systems.

The goal of the research reported here was to determine if inclusion of UVA and/or POL light in intensive culture systems enhances growth rates during the early larval period in three species of marine fishes.

2. Materials and methods

2.1. Study species

Three marine species, all of which are commonly cultured under intensive conditions, were selected: turbot (*Scophtalmus maximus*), Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*). While turbot larvae possess UVA photoreceptors (Britt et al., 2001; Forsell et al., 2001), neither Atlantic cod nor herring appear to have them (Jon Vidar Helvik, personal communication; Forsell et al., 2001). Whether any of these species possess POL vision is unknown.

2.2. Procedures common to all experiments

The growth rate experiments reported herein were conducted at the Institute of Marine Research-Austevoll, Norway, during the summers of 1999, 2000 and 2001. The period immediately after first-feeding was targeted for study of the effects of light quality on growth.

Cylindrical black polyethylene tanks (45 l) were used to rear larvae. There were five replicate tanks for each of the four light exposure treatments. Each tank was optically isolated from its neighbours using matt-surface black plastic sheeting. Each five-replicate tank light exposure treatment was wrapped in matt-surface, completely opaque sail-cloth, so that it was optically isolated from the other treatments and from room lights.

Water in the system was recycled through a fluidized-bed bacterial sand filter and an ultraviolet sterilizer. To replace loss from evaporation, fresh water was added to the re-circulating systems at frequent intervals during the experiments. Water temperature (see below) was controlled using heat pumps. To prevent food items from being washed out of the rearing tanks, the central stand pipe drains were surrounded by filter material (250 μm mesh). Larvae were introduced into the tanks on Day 1, where Day 0 was defined as the day on which 50% of eggs had hatched. Larvae were fed twice daily (except for herring) at a prey density of 1 ml^{-1}.

On sampling days (see below), 12 larvae were collected from each rearing tank, rinsed with fresh water and placed into aluminium cups for dry weight measurement. Larvae were dried at 60 °C for 24 h (which was to constant weight), and weighed using a Mettler AE 200 microbalance (± 1 μg).

Four light exposure treatments were generated using naked (i.e. no cover glass) standard commercial 50 W tungsten halogen spot lamps and optical filters: 1 = a treatment control with no ultraviolet and non-polarized (NOUVA + DIFFUSE) light — produced using the naked lamps covered with 400 nm long-pass filters; 2 = no ultraviolet and polarized (NOUV + POL) — produced using UV-opaque polarizing sheet (Edmund Optics Cat. No. NT45-667, New Jersey, USA); 3 = ultraviolet-rich and polarized (UVA + POL) — produced

using the naked lamps covered with Polaroid HNP'B UV-transmissive polarizing sheet material; 4 = ultraviolet-rich and non-polarized (UVA + DIFFUSE) — produced using the naked lamps. Total photon flux (from 280–800 nm) was adjusted (using variable-voltage rheostats) so that it was the same (within 3%) for all four light exposure treatments 1.16 e+19, 1.16 e+19, 1.14 e+19, and 1.18 e+19 photons s^{-1} m^{-2}, for NOUVA + DIFFUSE, NOUVA + POL, UVA + DIFFUSE, AND UVA + POL, respectively (Fig. 1). Thus, the only difference between the exposure treatments was spectral and/or polarization content. The overall photon flux delivered to the four treatments was matched to crepuscular light intensities measured in surface waters (where the larvae of these species are found and at which they actively feed), next to the Austevoll Aquaculture Research Station, Storebö, Norway, under clear skies on May 28, 1999 (Novales Flamarique et al., 2000, see Fig. 3b). The downwelling spectral composition and intensity of the treatment groups was verified by direct measurement using an OL-754 scanning spectroradiometer (Optronic Laboratories, Orlando, Florida, USA). The optical characteristics of this instrument, and the protocols used for deployments and measurements, have been published elsewhere (Kuhn et al., 1999).

2.3. Procedures specific to the turbot experiment

Turbot eggs were acquired from Stolt Sea Farm A.S. and were maintained until hatching in 55 cm diameter, 40 cm deep, black matt fibreglass basins, at 17 °C. On Day 1, 1500 yolk sac larvae were transferred into each of the 20 rearing tanks, temperature was a continuous 18 °C. A water exchange rate of 100 ml min^{-1} was maintained in the rearing tanks until Day 6, when it was increased to 200 ml min^{-1}. Turbot larvae were fed on natural zooplankton (mainly copepod nauplii) from Day 2 to the end of the experiment. The harvesting procedure and provenance of zooplankton used has been described elsewhere (van der Meeren, 2003). Larvae were sampled for dry weight on Days 3, 6, 9 and 12.

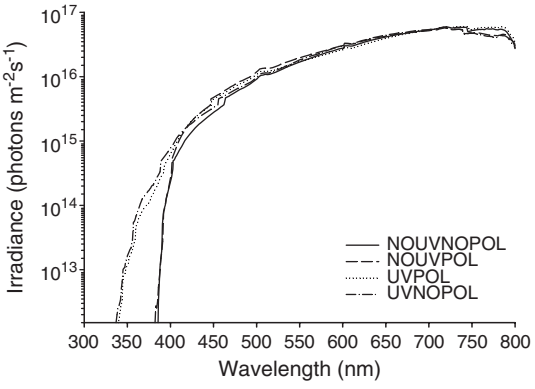

Fig. 1. Irradiance of the four light treatments used in all growth experiments. Total photon flux (280–800 nm) was adjusted, using variable-voltage rheostats, so that it was the same (within 3%) for all four light exposure treatments: 1.16 e+19, 1.16 e+19, 1.14 e+19, and 1.18 e+19 photons s^{-1} m^{-2}, for 1) NOUVA + DIFFUSE — NOUVNOPOL, 2) NOUVA + POL — NOUVPOL, 3) UVA + POL — UVPOL, and 4) UVA + DIFFUSE — UVNOPOL, respectively.

2.4. Procedures specific to the cod experiment

Cod eggs were obtained from broodstock at the Institute of Marine Research-Austevoll, Norway. Several females and males were maintained in 3 m diameter holding tanks at 10 °C and the eggs (from natural spawning events) were collected from the runoff in fine-mesh nets. Eggs were then incubated in the same type of fibreglass basins as used for turbot, but at 10 °C. On Day 1, yolk sac larvae were transferred in roughly equal numbers (approximately 4000) into each of the 20 experimental tanks at 10 °C. A water exchange rate of 100 ml min^{-1} was maintained in the rearing tanks until Day 21, when it was increased to 200 ml min^{-1}. Cod larvae were fed with rotifers (*Brachionus plicatilis*) from Day 3 to 21 and with a mixture of rotifers and *Artemia* nauplii until Day 27, after which they were fed on *Artemia* nauplii only. In connection with the change to larger food particles, the mesh size of the net surrounding the drain was increased to 500 μm on Day 21. Rotifers were cultured using 190 g of Rotimac (Bio-Marine California), plus 100 g of baker's yeast in 620 l culture tanks once a day. Decapsulated *Artemia* nauplii were cultured using DC DHA SELCO at 0.2 g ml^{-1} nauplii twice daily. The *Artemia* eggs and the DHA SELCO were obtained from INVE Aquaculture (Dendermonde, Belgium). *Artemia* were further enriched with a vitamin supplement of 0.0097 g per g of DHA SELCO. Larvae were sampled for dry weight on Days 5, 10, 15, 20, 25 and 29.

2.5. Procedures specific to the herring experiment

Fertilized herring eggs were obtained from broodstock at the Institute of Marine Research-Austevoll, Norway. Eggs (from natural spawning events) were collected and incubated in the same type of fibreglass basins as used for turbot, but at 6.5 °C. On Day 1, yolk sac larvae were transferred in roughly equal numbers (approximately 750) into each of the 20 rearing tanks at 10 °C. The initial flow rate was 100 ml min^{-1}, from Day 2 to the end of the experiment it was 170 ml min^{-1}.

At 3 dph rotifers were added to each tank, from Day 4–9 the larvae were fed rotifers twice a day, and from day 10 to 35 the larvae were fed 3 times a day. Larvae were sampled for dry weight on Days 4, 9, 14, 18, 23, 28, and 35.

2.6. Statistics

ANOVAs for each species and light treatment group indicated that the mean logged weight did not differ between replicates in 49 out of 68 comparisons (72%; for these cases: $4.05 > F > 0.32$, $P > 0.05$). For the remaining 19 cases, the application of the Least Significance Difference (LSD) test indicated that the difference was only because of either 1 replicate in 13 cases or 2 in 6 cases. Thus, the 5 replicates within each light treatment were combined for analysis of covariance (ANCOVAs); slopes of growth curves of the log weight–time regressions for light treatments were tested for each species separately.

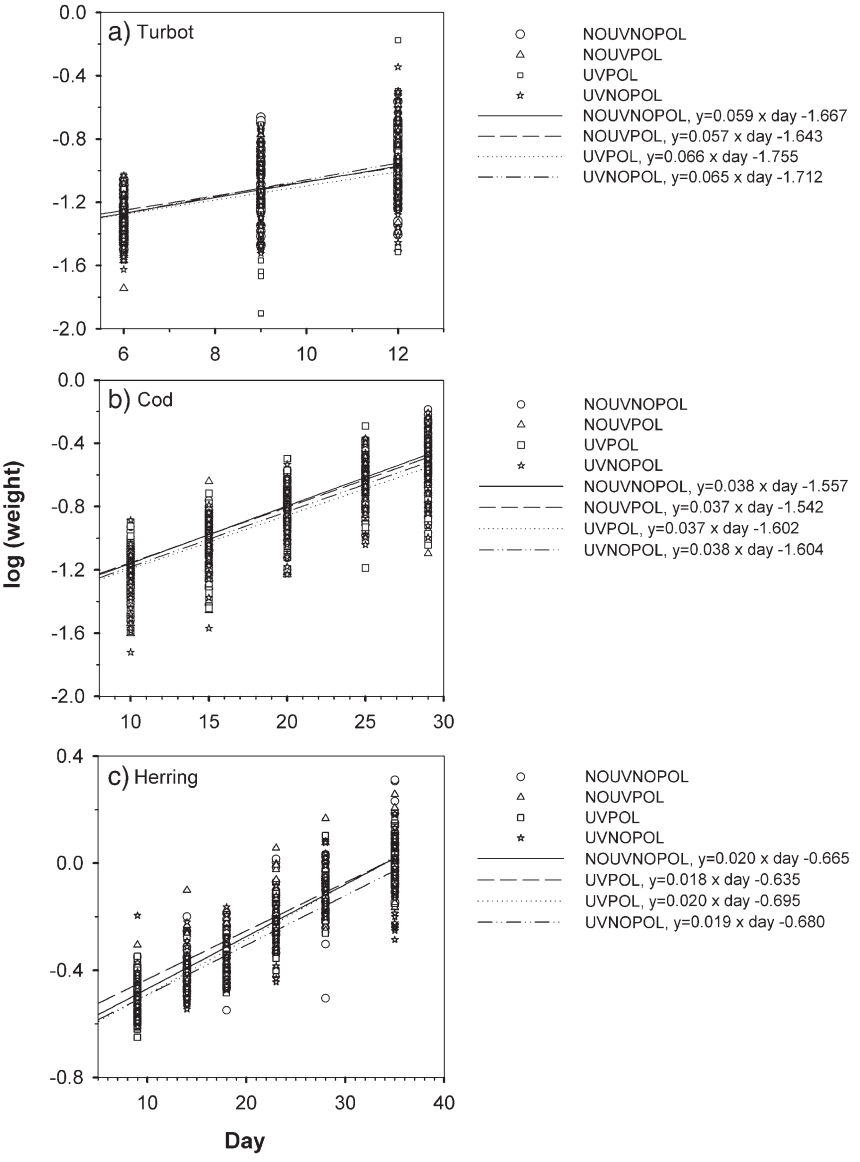

Fig. 2. Log weights of (a) turbot (*Scophtalmus maximus*), (b) Atlantic cod (*Gadus morhua*) and (c) Atlantic herring (*Clupea harengus*) larvae from each of the four light treatment groups 1) NOUVA + DIFFUSE — NOUVNOPOL, 2) NOUVA + POL — NOUVPOL, 3) UVA + POL — UVPOL, and 4) UVA + DIFFUSE — UVNOPOL, sampled over periods of 14, 30 and 35 days for turbot, cod and herring, respectively. Log weight–time

3. Results

ANCOVAs showed that in the case of cod and turbot there were not any significant differences in the growth curve slopes (Fig. 2) of the log weight–time regressions (for all cases: cod $F<0.57$ and $P>0.45$; turbot $F<0.80$ and $P>0.37$). In contrast, in the case of herring the slope differed significantly in two cases (UVA + POL > UVA + DIFFUSE, $F=7.22$, $P=0.007$; NOUVA + DIFFUSE > UVA + DIFFUSE, $F=4.99$, $P=0.02$) whereas the slopes did not differ significantly for the remaining combinations (for all cases: $F<1.98$, $P>0.16$).

4. Discussion

The growth rates of Atlantic cod and turbot larvae were not enhanced under either POL or UVA light. However, some light treatment-related changes in growth were observed in Atlantic herring. Herring larvae treated with UVA and POL light grew larger than those in the UVA only treatment group, and larvae that received no UV or POL light grew larger than those in the UV only treatment. Even if herring possessed a UVA photoreceptor (they do not), these findings are contradictory in the context of the proposed UVA and/or POL light enhanced growth. Although statistically significant, these between treatment differences in growth for herring larvae were slight (Fig. 2) and were, in any case, not related to light treatment in an easily interpretable manner.

There may exist specific UVA and POL lighting conditions under which prey contrast for a larval fish foraging on zooplankton in the sea would be maximized (see Johnsen, 2001, 2002, 2003). The lighting utilized in our experiment – a tungsten lamp and 100% linearly-polarized light striking a smooth water surface from 0° zenith all against the background of a black polyethylene tank – is certainly not representative of those conditions. Further, tungsten lamps emit significantly less irradiance in the 450 to 600 nm range than natural sunlight. However, these conditions are similar to those under which these larvae are typically reared in intensive systems. While we might have obtained a stronger effect had we used, for example, different light intensities and/or POL light incident angles, the conditions under which these experiments were conducted were the most relevant to use in testing whether or not UVA and/or POL light would enhance growth rates in today's intensive culture systems.

The culture conditions under which the contrast of food particles would be maximized are species and life stage specific. They are also strongly coupled to the optical characteristics of the food particle itself. Therefore, determining just what these conditions are, and recreating them on a commercial scale, will not be a simple task.

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References

Bowmaker, J.K., Kunz, Y.W., 1987. Ultraviolet receptors, tetrachromatic colour vision and retinal mosaics in the brown trout (*Salmo trutta*): age-dependent changes. Vis. Res. 27, 2101–2108.

Britt, L.L., Loew, E.R., McFarland, W.N., 2001. Visual pigments in the early life stages of Pacific northwest marine fishes. J. Exp. Biol. 204, 2581–2587.

Browman, H.I., 2005. Applications of sensory biology in marine ecology and aquaculture. Mar. Ecol., Progr. Ser. 287, 266–269.

Browman, H.I., Novales-Flamarique, I., Hawryshyn, C.W., 1994. Ultraviolet photoreception contributes to prey search behaviour in two species of zooplanktivorous fishes. J. Exp. Biol. 186, 187–198.

Brown, J.A., Minkhoff, G., Puvanendran, V., 2003. Larviculture of Atlantic cod (*Gadus morhua*): progress, protocols and problems. Aquacult 227 (1–4), 357–372.

Downing, G., Litvak, M.K., 2001. The effect of light intensity and spectrum on the incidence of first feeding by larval haddock. J. Fish Biol. 59, 1566–1578.

Fineran, B.A., Nicol, J.A.C., 1978. Studies on the photoreceptors of *Anchoa mitchilli* and *A. hepsetus* (Engraulidae) with particular reference to the cones. Proc. R. Soc. Lond. 283, 24–60.

Forsell, J., Ekström, P., Novales Flamarique, I., Holmqvist, B., 2001. Expression of pineal ultraviolet- and green-like opsins in the pineal organ and retina of teleosts. J. Exp. Biol. 204, 2517–2525.

Hamner, W.M., 1996. Predation, cover, and convergent evolution in epipelagic oceans. In: Lenz, P.H., Hartline, D.K., Purcell, J.E., Macmmillan, D.L. (Eds.), Zooplankton: Sensory Ecology and Physiology. Gordon and Breach, Sydney, pp. 17–35.

Hawryshyn, C.W., 1992. Polarization vision in fish. Amer. Scient. 80, 164–185.

Hawryshyn, C.W., Moyer, H.D., Allison, W.T., Haimberger, T.J., McFarland, W.N., 2003. Multidimensional polarization sensitivity in damselfishes. J. Comp. Phys. A. 189, 213–220.

Horváth, G., Varjú, D., 2004. Polarized light in animal vision. Polarization Patterns in Nature. Springer, Berlin. 447 pp.

Jacobs, G.H., 1992. Ultraviolet vision in vertebrates. Amer. Zool. 32, 544–554.

Johnsen, S., 2001. Hidden in plain sight: the ecology and physiology of organismal transparency. Biol. Bull. 201, 301–318.

Johnsen, S., 2002. Cryptic and conspicuous coloration in the pelagic environment. Proc. R. Soc. Lond., B Biol. Sci. 269, 243–256.

Johnsen, S., 2003. Lifting the cloak of invisibility: the effects of changing optical conditions on pelagic crypsis. Integr. Comp. Biol. 43, 580–590.

Johnsen, S., Widder, E.A., 1998. Transparency and visibility of gelatinous zooplankton from the nothwestern Atlantic and Gulf of Mexico. Biol. Bull. 195, 337–348.

Jordan, R., Howe, D., Juanes, F., Stauffer Jr., J., Loew, E., 2004. Ultraviolet radiation enhances zooplantivory rate in ultraviolet sensitive cichlids. Afr. J. Ecol. 42, 228–231.

Kuhn, P., Browman, H.I., McArthur, B., St-Pierre, J.-F., 1999. Penetration of ultraviolet radiation in the waters of the estuary and Gulf of St. Lawrence. Limnol. Oceanogr. 44, 710–716.

Loew, E.R., McFarland, W.N., 1990. The underwater visual environment. In: Douglas, R.H., Djamgoz, M.B.A. (Eds.), The Visual System of Fish. Chapman and Hall, New York, pp. 1–43.

Loew, E.R., McFarland, W.N., Mills, E.L., Hunter, D., 1993. A chromatic action spectrum for planktonic predation by juvenile yellow perch, *Perca flavescens*. Can. J. Zool. 71, 384–386.

Losey, G.S., Cronin, T.W., Goldsmith, T.H., Hyde, D., Marshall, N.J., McFarland, W.N., 1999. The UV visual world of fishes: a review. J. Fish Biol. 54, 921–943.

Novales Flamarique, I., Browman, H.I., 2001. Foraging and prey-search behaviour of small juvenile rainbow trout (*Oncorhynchus mykiss*) under polarized light. J. Exp. Biol. 204, 2415–2422.

Novales Flamarique, I., Hendry, A., Hawryshyn, C.W., 1992. The photic environment of a salmonid nursery lake. J. Exp. Biol. 169, 121–141.

Novales Flamarique, I., Browman, H.I., Bélanger, M., Boxaspen, K., 2000. Ontogenetic changes in visual responses of the parasitic salmon louse, *Lepeoptheirus salmonis*. J. Exp. Biol. 203, 1649–1657.

Peña, R., Dumas, S., Saldivar-Lucio, R., Garcia, G., Trasviña, A., Hernández-Ceballos, D., 2004. The effect of light intensity on first feeding of the spotted sand bass *Paralabrax maculatofasciatus* (Steindachner) larvae. Aquac. Res. 35, 345–349.

Puvanendran, V., Brown, J.A., 2002. Foraging, growth and survival of Atlantic cod larvae reared in different light intensities and photoperiods. Aquaculture 214, 131–151.

Rocco, V., Barriga, J.P., Zagarese, H., Lozada, M., 2002. How much does ultraviolet radiation contribute to the feeding performance of rainbow trout, *Oncorhynchus mykiss*, juveniles under natural illumination? Environ. Biol. Fisches 63, 223–228.

Shashar, N., Hanlon, R.T., deM. Petz, A., 1998. Polarization vision helps detect transparent prey. Nature 393, 222–223.

van der Meeren, T., 2003. Analysis of biochemical components in copepods for evaluation of feed quality in juvenile production of marine fish. Fisken Og Havet 5.